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Moving ocean acidification research beyond a simple science: Investigating ecological change and their stabilizers

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ABSTRACT

The response of complex ecological communities to ocean acidification reflects interactions among species that propagate or dampen ecological change. Yet, most studies have been based on short-term experiments with limited numbers of interacting species. Both limitations tend to exaggerate measured effects and when combined with our predisposition for investigating change, we reduce insight into pathways of stability, acclimation and adaptation. Here, we review accepted and emerging insights into processes that drive ecological change (top-down and bottom-up) and the stabilizing processes by which ecological complexity may dampen change. With an emphasis on kelp forest examples, we show that boosted primary productivity from enriched CO_2 creates competitive imbalances that drive habitat change, but we also recognise intensifying herbivory on these habitats dampens this change. Foraging herbivores thrive on CO_2 enriched plants and over successive generations their populations expand. When we consider such population level responses, we open new questions regarding density-effects (e.g. competition, susceptibility to predation and disease), as well as the bottom-up benefits to predators. Nevertheless, research on predators has lagged behind because their wide-ranging behaviour typically imposes logistical difficulties for observational and experimental research. We know that ocean warming imposes elevated metabolic costs on their foraging whilst acidification hampers navigation of their larvae towards suitable habitat and impairs their hunting and avoidance of predators as adults. Connecting such top-down with bottom-up responses is fundamental for progress, and is also contingent on understanding the mechanisms that dampen change. These stabilizers have the potential to keep pace with abiotic change and thereby influence the drivers of acclimation and adaption. Certainly, we acknowledge that investigating change is often simpler and the associated bold messages appeal to citation impact. Yet, if we are to anticipate the ability of complex ecological communities to persist in changing environments, then understanding the shifting balance between the propagation of resource enrichment and its consumption across trophic levels is central to this challenge.

Contents

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1. Marine systems in future oceans

The absorption of rising levels of atmospheric CO_2 by the ocean modifies its chemistry (ocean acidification; Feely et al., 2004; Doney et al., 2012), altering ecological networks and their functions (Hoegh-Guldberg and Bruno, 2010; Nagelkerken and Connell, 2015). The current uncertainty about the direction and magnitude of species responses within their ecological networks (Gaylord et al., 2015) reflects the relative immaturity of the new discipline and inherent complexity of ecological networks. This 'web of life' is classically considered a network of organisms that are linked through the transfer of energy and nutrients, beginning with plants and their consumption by herbivores, and their consumption by predators and onwards up the chain. Within these ecological networks, change reflects a shifting balance between the propagation of resources (due to CO_2 enrichment) and its consumption; a chain of direct and indirect interactions that are strengthened or weakened by environmental change.

Early literature was heavy on negative reporting of ocean acidification that aligned with gloomy predictions for future marine ecosystems. Critically, research is moving on from these readily detectable direct effects on individual organisms to include tests of species interactions that underpin community dynamics (Nagelkerken and Connell, 2015). These interactions are not only recognised as drivers of abrupt community responses to environmental change (Walther, 2010), but also stabilizers against such change (Rosenblatt and Schmitz, 2014). Stabilizers involve processes that dampen the effects of disturbance (i.e. resistance, Connell and Ghedini, 2015) or hasten recovery (i.e. resilience, Scheffer et al., 2001). This distinction between mechanisms of resistance and resilience is useful when considering the stability of resource-consumer relationships under CO_2 enriched conditions. Unlike pulse disturbances that eventually relax (e.g. storms), CO_2 emissions act as a ramp disturbance that increase in intensity over time. Hence, understanding how communities might persist during ramp disturbances puts focus on mechanisms that resist community change (Nimmo et al., 2015). Here, we assess the propagation of bottom-up (resource) and top-down (consumption) responses in a high CO_2 world and highlight the stabilizing processes that resist the ramp disturbance of rising levels of CO_2.

1.1. Beyond direct negative effects: species interactions as drivers

With the recognition of ocean acidification (Feely et al., 2004) and altered carbonate chemistry (Caldeira and Wickett, 2003; Doney et al., 2009) came an avalanche of research on the vulnerability of calcifying organisms to decreasing pH. This literature documented the direct negative effects of ocean acidification on calcification and demography of marine taxa (Kroeker et al., 2010). Whilst negative effects of short-term exposure to ocean acidification are common, there is significant variation in the sensitivity of marine organisms depending on the taxonomic group, life history stages, presence of other species or co-occurring environmental changes (Kroeker et al., 2010, 2013a).

More recent research has revealed mechanisms that allow organisms to buffer the negative effects of reduced pH through physiological and metabolic adjustments (Georgiou et al., 2015; Stumpp et al., 2013; Leung et al., 2017). If physiological and metabolic plasticity is possible, then adjustability in energy and nutrient acquisition is also possible (i.e. transfer CO_2 resources), and such change in consumption could affect the broader network (Gaylord et al., 2015). Such thinking about environmental acclimation opened opportunities to explore ecological pathways through which organismal responses generate ecological dynamics that buffer change in community structure (Ghedini and Connell, 2016).

Whilst original progress was founded on tests of direct physiological effects on single species, there is now increasingly effort on incorporating the broader ecological network (Dupont and Portner, 2013; Russell et al., 2012). Carbon enrichment alters food webs by modifying predator-prey interactions (Munday et al., 2012), competitive interactions (Connell et al., 2013), population (Harvey et al., 2016) and community dynamics (Goldenberg et al., 2017). As increasing ecological complexity has been incorporated, it becomes clear that CO_2 enrichment drives change by acting both as a stressor and as a resource (Connell et al., 2013; Enochs et al., 2015; Kroeker et al., 2013b).

The resource-effects of CO_2 propagate from primary producers because algae (and plants) can benefit from increased availability of carbon for photosynthesis (Low-Décarie et al., 2014). The positive effects of CO_2 enrichment are not homogeneous, but can differ among species within a community according to specific physiological traits and nutrient limitations (Giordano et al., 2005; Hepburn et al., 2011). Whilst the majority of marine macroalgae have carbon concentrating mechanisms (CCMs) that actively uptake CO_2 or HCO_3^-, other algae use dissolved CO_2 (i.e. entering the cells by diffusion) as the carbon source for photosynthesis (Beardall et al., 1998; Raven et al., 2005). Hence, increases in the availability of dissolved carbon can shift competitive balance between algal taxa. Species that use CCMs are likely to show minor responses to elevated CO_2, but those that rely exclusively on CO_2 diffusion are anticipated to benefit from increases in CO_2 availability (Hepburn et al., 2011; Hurd et al., 2009). Recognising the unequal benefits of ocean acidification among species is key not only to identify shifts in competitive interactions (Diaz-Pulido et al., 2011; Fabricius et al., 2011; Falkenberg et al., 2013a), but also to scale the outcome of such changes to the level of communities (Kroeker et al., 2013b; Sunday et al., 2017).

1.2. Bottom-up effects: propagation of resource enrichment and imbalances

Recognising the propagation of CO_2 enrichment, from plants (Connell et al., 2013) to herbivores (Connell et al., 2017) and their predators (Goldenberg et al., 2017), provides a basis for assessing future community dynamics. An unresolved difficulty for the division of ecological processes between bottom-up effects or top-down effects is that they give the false impression that these processes act in isolation. Tests of boosted productivity open investigations into the shifting balance between productivity (bottom-up effects), its consumption (top-down effects), and within trophic-level change (competitive effects). Here, we discuss the unequal benefits of resource enrichment on competition, and also address the interplay between its propagation and consumption in Section 1.3 (below).

The unequal benefits of CO_2 enrichment can drive shifts in species dominance, causing subordinates to turn dominant (Connell et al., 2013). This potential for CO_2-driven change was first observed in laboratory (Connell and Russell, 2010; Falkenberg et al., 2013a) and then mesocosm experiments (Kline et al., 2012), as well as field-based observations at CO_2 vents (Fabricius et al., 2011; Nagelkerken et al., 2015). These studies revealed the indirect effects of CO_2 enrichment on two iconic and ecologically important marine systems, i.e. kelp forests and coral reefs (Connell et al., 2013). In both systems, CO_2 boost the growth of fast-growing, opportunistic, algal species (i.e. turf-forming algae; Connell et al., 2014), whose photosynthetic benefits appear to be derived from the absorption of CO_2 by diffusion (Falkenberg et al., 2013a; Hepburn et al., 2011). The unchecked expansion of turf algae on the reef can inhibit the recruitment of kelps and corals, over-time shifting these communities to turf-dominated states.

The competitive advantage of subordinate (e.g. turfs) over normally dominant species (e.g. kelps and corals) might be reinforced by co-occurring abiotic changes that strengthen bottom-up effects (warming, Connell and Russell, 2010; nutrient enrichment, Connell et al., 2008) or biotic changes that alter top-down dynamics (loss of herbivores, Hughes, 1994; range shifts, Bennett et al., 2015). Where such conditions persist, physiological responses (e.g. enhanced growth rates) can translate into population responses (e.g. increased abundance) that shift the structure of the community. Such shifts can pivot on a balance between primary productivity and its consumption, representing ecosystem collapses (see Section 1.3).

1.3. Top-down effects: shifts and balances of consumption

The shifting balance between the propagation of resource enrichment and its consumption across trophic levels is a fundamental dynamic of stability or collapse of food webs. Marine systems are renowned for some of the most striking effects of consumption on ecosystem collapses (e.g. Ling et al., 2015; Steneck et al., 2013). Whilst the effect of ocean acidification has received increasing attention with regard to herbivory (e.g. Connell et al., 2013), research on predation has lagged behind because of the logistic difficulty that wide ranging predators (e.g. fish) pose for observational (e.g. natural CO_2 seeps) and experimental research.

Consumers are sensitive to ocean acidification and warming through the imposition of elevated metabolic costs that increase the need for more intensive foraging (Kroeker et al., 2014; Pistevos et al., 2016). There is, however, uncertainty as to whether these physiological responses will strengthen top-down control so that observed increases in secondary production (Connell et al., 2017) are balanced by elevated rates of predation under warming (Nagelkerken and Connell, 2015). Behavioural responses to ocean acidification can diminish the sensorial and neurological abilities of herbivores to escape predators (Munday et al., 2009; Watson et al., 2014), of predators to hunt their prey (Dixson et al., 2014; Pistevos et al., 2016) and navigate to suitable habitats (Rossi et al., 2015, 2016). Potential feedbacks between shrinking habitats (i.e. loss of structural complexity) and the reduced capacity for dispersing individuals to find habitat and then forage to meet their metabolic requirements, let alone replenish their populations (Rossi et al., 2017), are yet to be explored.

The community consequences of altered predator-prey dynamics are potentially profound (Harvey et al., 2016) and tests of their effects on long-term population dynamics (Kroeker et al., 2014), and the strength of trophic linkages that structure communities (Binzer et al., 2012; Nagelkerken and Connell, 2015), are only beginning. It is quite possible that the indirect effects of CO_2 enrichment overwhelm its negative effects of on physiology of consumers (i.e. ocean acidification as a stressor) through its propagation as a resource to consumer populations (Connell et al., 2017). Indeed, the readily detectable effects of ocean acidification on impaired behaviour and physiology appear to be buffered by the complexity of indirect effects (Nagelkerken et al., 2015; Goldenberg et al., 2017) which represent some of the strongest effects identified in certain systems (Connell et al., 2011).

Herbivores form a critical linkage between top-down and bottom-up processes. Their population dynamics are not only influenced by predation pressure, but also by the direct physiological effects of abiotic change (e.g. on metabolic rates, O'Connor, 2009) and indirect effects via changes in food quality or abundance (Falkenberg et al., 2013b; Tylianakis et al., 2008). Ocean acidification can alone alter strength of herbivory by boosting primary production to sustain larger populations (Connell et al., 2017) and rates of population growth (Heldt et al., 2016), but also alter rates of per capita feeding via increased metabolic costs of reduced pH (Stumpp et al., 2013), changes in the palatability (Arnold et al., 2012) or nutrient content of food sources (Duarte et al., 2016).

Recognising change in the strength of herbivory is challenging because of the multitude of pathways that influence plant-herbivore interactions and their interaction with multiple drivers (Binzer et al., 2012; Burnell et al., 2013; Poore et al., 2013). Under some conditions, the strength of herbivory can increase disproportionately relative to productivity, resulting in catastrophic effects for productive communities that shift to less productive, simpler habitats, both in marine (Vergés et al., 2014) and terrestrial systems (Silliman et al., 2013). Whilst strong ecological responses to environmental change can underpin such shifts, their likelihood might be overestimated by predictions derived from simplified experiments. Notably, trophic responses to multiple drivers tend to be smaller in magnitude relative to those assessed in response to each driver in isolation (Rosenblatt and Schmitz, 2014). This finding is revealing: it suggests that the magnitude of ecological responses

might decline with increasing complexity of the system, where multiple trophic interactions and ecological processes downscale the strength of the perturbation (McCann et al., 1998; Leuzinger et al., 2011). It is a sign of maturity for a discipline to recognise the need to incorporate a higher degree of conceptual complexity of the breadth of responses in the systems of study.

2. The emergence of dynamics that stabilize food webs

The maturing of ecological theories tends to be characterised by exploration of limits to their explanatory power and the development of pluralistic approaches, findings and interpretations. A sign of the increasing maturity of research into ocean acidification has been a shift from the predominance of reporting of negative effects and ecological change to assessments of stabilizing mechanisms that buffer environmental change. The long-term consequences of ocean acidification might be dampened where organisms are able to adapt rapidly enough to keep pace with changing conditions (Kelly and Hofmann, 2013). Where transgenerational acclimation is unable to negate the effects of projected pH reductions, the persistence of ecological systems in their current state will be contingent on the potential for genetic adaption of their constituent species (Welch et al., 2014). In addition to the increasing attention on acclimation and adaptation, there is an emerging focus on the physiological (Georgiou et al., 2015) and ecological mechanisms (Ghedini and Connell, 2016) that, on shorter time-scales, actively buffer ecological responses to changing environments.

When studying ecological responses to abiotic change, the focus tends to be on detectable processes that underpin change, either at the level of individual organisms (e.g. changes in growth rates or calcification rates), populations (e.g. population growth rates, range shifts) or communities (e.g. changes in trophic interactions, species abundance, range shifts). In this active search for ecological change, processes that act in the opposite direction are less readily detected (Connell and Ghedini, 2015). Importantly, natural systems display an extraordinary ability to withstand variation in abiotic conditions, which can result in no change in community structure where communities resist disturbance (Sutherland, 1990). Such resistance builds upon compensatory mechanisms that buffer the effects of abiotic change at the level of individuals (Georgiou et al., 2015; Leung et al., 2017), populations (Reed et al., 2013) and communities (Graham and Mendelssohn, 2014; Isbell et al., 2015).

Compensatory dynamics have long been recognised as important mechanisms that stabilize communities (MacArthur et al., 1972; McNaughton, 1977). The study of compensatory dynamics has shown that fluctuations in the abundance of species in response to environmental change provide a buffer to community processes, such as productivity (Ernest and Brown, 2001; Hector et al., 2010). Such compensatory mechanism seems key to maintain community processes under periods of rapid environmental change (e.g. Hoover et al., 2014; Isbell et al., 2015). Changes in species densities are probably the most studied example of compensatory dynamic, but compensation can arise from a broad range of responses to abiotic change, including physiological (Georgiou et al., 2015), behavioural (Kondoh and Williams, 2001) or trophic responses (Ghedini et al., 2015; McSkimming et al., 2015; Ruesink and Srivastava, 2001) and changes in processes of competition within (Reed et al., 2013) or between species (Higgins et al., 2015; Lloret et al., 2012).

Changes in the strength of species interactions might be less readily detectable than fluctuations in species densities that can be visually observed. Nonetheless, trophic compensation might play an important stabilizing role by buffering community processes to environmental change before numerical responses of species take place (Ruesink and Srivastava, 2001). As an example, consumers can have stabilizing effects at a community-level where they counterbalance enhanced productivity stimulated by abiotic change (Ghedini et al., 2015). Increased herbivory in response to nutrient enrichment is one of the most studied and long-known examples of trophic control of productivity, where resource

enrichment simulates consumption on more productive communities providing a countering mechanism to the effects of eutrophication (McAllister et al., 1972; McSkimming et al., 2015; Sarnelle, 1992). Importantly, the compensatory effects of consumption are not limited to nutrient enrichment, but can extend to other abiotic changes that similarly enhance productivity, including ocean acidification, as we consider more in detail below.

2.1. Could the struggle for organismal homeostasis scale-up?

Ecosystems are structurally organised food webs within which energy and materials are transferred through trophic interactions (Enquist et al., 2003). Therefore, the study of changes in the use of energy by individual organisms offers a pathway to link fine-scale processes (i.e. individual responses) to broad-scale patterns (i.e. ecosystem-level responses) (Ernest et al., 2003).

Whilst processes that occur at the level of individual organisms cannot be directly scaled up to community responses, broad-scale patterns can be understood as emerging from the collective behaviours of assemblies of smaller units (Levin, 1992; Wootton, 2001). For example, the stabilizing effects of changes in consumption on enhanced productivity driven by resource-disturbance (e.g. carbon or nutrient enrichment) can be understood as the aggregate effects of individual consumer responses to these environmental changes. Here, a strengthening in *per capita* consumption can be underpinned by increased energetic costs in the new environmental conditions (e.g. increased costs of calcification due to ocean acidification; Leung et al., 2017; McSkimming et al.,

2015; Queirós et al., 2014) and changes in the palatability (loss of phenolic compounds; Arnold et al., 2012) or nutritional quality of food (changes in C:N ratios; Duarte et al., 2016). These behavioural responses allow individual consumers to adjust their energy intake to maintain homeostasis (Sokolova et al., 2012; Sousa et al., 2010) and maximize fitness in response to environmental variation (Kooijman, 2013). Simultaneously, the aggregate effects of these individual responses generate a dynamic that buffers enhanced productivity (Ghedini and Connell, 2016). Hence, physiological or behavioural responses, that work towards organismal homeostasis on an individual level, can collectively reduce the extent of ecological change at more complex levels of ecological organisation (e.g. populations, communities) (Lenton, 1998; Rapport et al., 1985). For instance, consumer responses can maintain food web stability by rapidly consuming and, thus, dampening the effects of the excess energy (boosted primary production) that enters the system as a consequence of human activities (CO_2, nutrients) (Rooney et al., 2006).

Stabilizing effects of trophic interactions might not only occur through instantaneous changes in *per capita* consumption (Ghedini et al., 2015), but also through enhanced population growth (Heldt et al., 2016) and size (Connell et al., 2017) (Fig. 1). Stabilizing responses *via* changes in population size emerge where *per capita* fitness increases under new environmental conditions (Heldt et al., 2016) and are more likely to be observed where research measures ecological responses over multiple generations. When we consider population responses, we also open new questions regarding density effects that are mediated by intra- and inter-specific competition, including
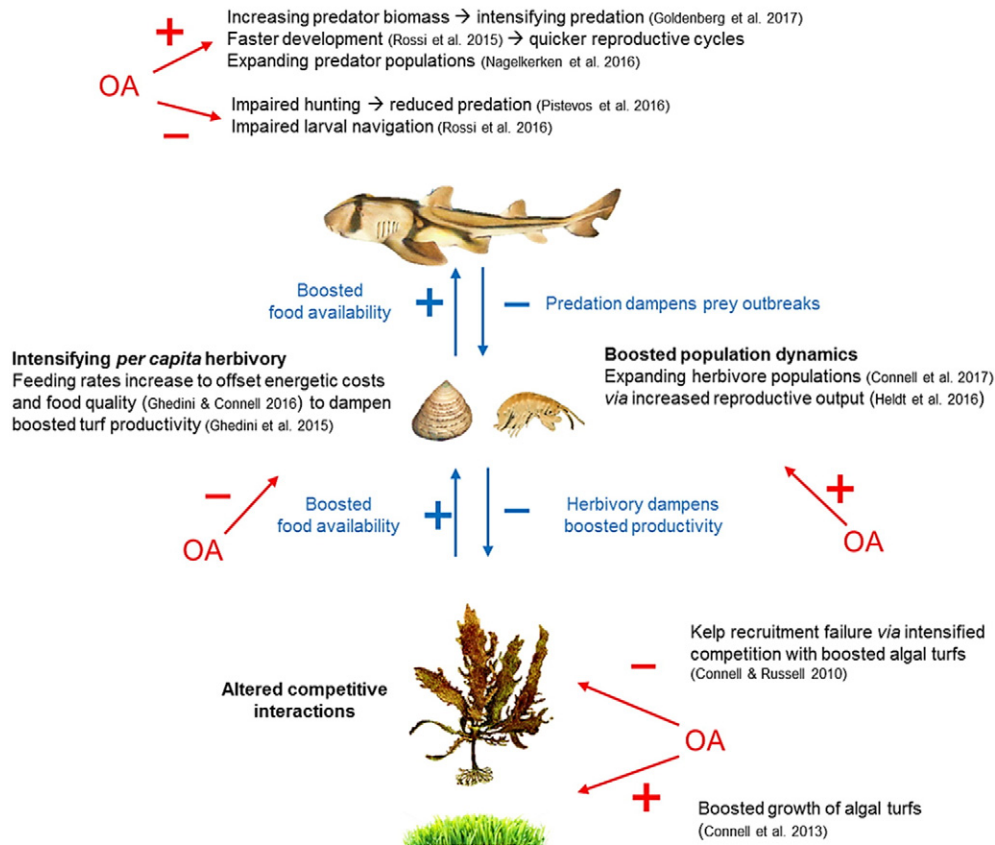
Fig. 1. Conceptual example from kelp forest research, showing bottom-up and top-down pathways through which ocean acidification (OA) stimulates ecological change (red arrows) that may be buffered by direct and indirect effects (blue arrows). Signs indicate positive (+) or negative (−) responses. Starting from the bottom of the figure (bottom-up), carbon enrichment enhances the competitive abilities of subordinate habitats (turf algae) over dominants (kelp); increasing potential shifts from kelp to turf-domination. Trophic compensation, *via* intensifying consumption, stabilizes against boosted production at lower trophic levels. The ensuing potential for population outbreaks of herbivores is suppressed by intensifying predation. Hence, ecosystem change reflects the shifting balance between the propagation of CO_2 enrichment and its consumption; a chain of direct and indirect feedbacks that are strengthened or weakened by ocean acidification.

susceptibility to predation and disease. Population size can influence individual fitness (Booth, 1995; DeLong et al., 2014), resource use (Svanbäck and Bolnick, 2007) and population growth (Sibly et al., 2005). But the role of population size in shaping consumer-resource interactions and community dynamics, including their eco-evolutionary trajectories, is only beginning to be explored.

2.2. Loss of resistance and manifestation of change

If organismal homeostasis forms a basis for the dynamics that counter change, it may also account for loss of community resistance as disturbance intensifies. Whilst organisms can adjust to varying environments (Leung et al., 2017; Reed et al., 2013), the pace of contemporary ecological change may overwhelm the capacity of organisms to maintain homeostasis to reduce their fitness and ecological role. Where organisms cannot adjust to environmental variation, the compensatory dynamics they support may be weakened. As temperature increases, consumer and producer responses can diverge (Lemoine and Burkepile, 2012), such that warming overwhelms the ability of consumers to counter the expansion of weedy species that drive phase-shifts (Mertens et al., 2015). Yet, increasing consumption under moderate warming (Kordas et al., 2011; O'Connor, 2009) can generate mechanisms that counterbalance increased productivity (Goldenberg et al., 2017). Similarly, consumers can buffer the negative effects of ocean acidification by increasing feeding (i.e. compensatory feeding; Duarte et al., 2016; Stumpp et al., 2013) to control enhanced productivity that is stimulated by the same conditions.

The controlling capacity of consumers might be eroded under declining survivorship and reproduction (Queirós et al., 2014). Hence, whilst adjustments in strength of trophic interactions during periods of abiotic change might stabilize community processes (e.g. increasing *per capita* feeding), accumulating disturbances might overwhelm these stabilizing mechanisms increasing ecological change (Rooney et al., 2006). The ensuing collapse of such compensatory dynamics could be sudden, leading to rapid loss of resistance in systems for which regime shifts appear abrupt.

The assessment of ecosystem and community responses to abiotic change usually focuses on processes that drive change, such as how intensifying top-down control may drive ecosystem shifts, and rarely considers mechanisms that prevent change (Connell et al., 2016; Nimmo et al., 2015). Importantly, changes in species interactions can stabilize community processes and structure, for example where changes at one trophic level buffer change at another (e.g. herbivory stabilizes boosted productivity). Whilst there is still much to understand about the importance and scales over which trophic interactions can act as stabilizing mechanisms (Gil et al., 2016), historical evidence of regime shifts suggests that trophic responses are an important mechanism of community stability (Hughes, 1994).

3. Final remarks

Research into ocean acidification is challenged by the assessment of the predominant direct and indirect pathways of ecological stability and change. If we can join the nexus between the changing forces of primary production (Connell et al., 2013; Kroeker et al., 2013b) and trophic structure by consumers (Roff et al., 2016; Goldenberg et al., 2017), we may be able to anticipate how altered trophic processes can propagate or counter ecological change. Indeed, natural communities are energetically connected webs of trophic and non-trophic interactions where the diversity of compensatory mechanisms that buffer community change is likely to be much greater than currently documented (Loreau and de Mazancourt, 2013). Much of the work on such stabilizing effects, as well as processes of acclimation and adaptation, represents considerable research investment. While such scholarship goes against current trends in publishing towards greater speed, efficiency

and citation impact, it is a critical perspective. Considerations of ecological change are necessary, but they are alone insufficient because stabilizing mechanisms are the basis on which ecological systems persist. Balancing our understanding of how trophic dynamics might stabilize against or propagate environmental change will signal increasing maturity regarding ecological research of ocean change.

Acknowledgements

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