Review

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The other ocean acidification problem: CO_2 as a resource among competitors for ecosystem dominance

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Predictions concerning the consequences of the oceanic uptake of increasing atmospheric carbon dioxide (CO_2) have been primarily occupied with the effects of ocean acidification on calcifying organisms, particularly those critical to the formation of habitats (e.g. coral reefs) or their maintenance (e.g. grazing echinoderms). This focus overlooks direct and indirect effects of CO_2 on non-calcareous taxa that play critical roles in ecosystem shifts (e.g. competitors). We present the model that future atmospheric [CO_2] may act as a resource for mat-forming algae, a diverse and widespread group known to reduce the resilience of kelp forests and coral reefs. We test this hypothesis by combining laboratory and field CO_2 experiments and data from 'natural' volcanic CO_2 vents. We show that mats have enhanced productivity in experiments and more expansive covers *in situ* under projected near-future CO_2 conditions both in temperate and tropical conditions. The benefits of CO_2 are likely to vary among species of producers, potentially leading to shifts in species dominance in a high CO_2 world. We explore how ocean acidification combines with other environmental changes across a number of scales, and raise awareness of CO_2 as a resource whose change in availability could have wide-ranging community consequences beyond its direct effects.

1. Introduction

Ecosystem collapses often go unanticipated because their drivers are unrecognized, have indirect effects or combine in unexpected ways to alter interactions between key species [1,2]. To redress this uncertainty, much work has been carried out to identify and quantify stressors and their cumulative effects by observing historical change (review on ecosystem collapses [3]), experimentally manipulating drivers (review of synergies [4]) and modelling their outcomes (alternate stable states [5]). By combining such lines of evidence, ecologists have demonstrated the tractability of identifying drivers of change [6] to develop frameworks for anticipating or managing change [7].

Ocean acidification, a result of rising carbon dioxide (CO_2) [8], is a particularly vexing stressor to assess as a potential driver of future ecosystem change [9]. This is because ocean acidification represents a series of changes in seawater chemistry, with each alteration representing a potential driver of change [10]. The diminishing availability of carbonate ion (CO_3^{2-}), and ensuing reduction in calcium carbonate ($CaCO_3$) saturation states are widely reported to reduce calcification in a wide range [11,12] of, but not all, calcifying organisms [13,14]. To date, much of the focus of ocean acidification research has been on the response of calcifiers, both algae and invertebrates, to the changing carbonate system, with a particular preoccupation on one property: the hydrogen ion concentration [H^+], which is frequently reported as pH owing to the relative

ease of its measurement. Initial insights were derived from manipulative experiments, particularly single-factor manipulations of CO_2 levels (i.e. pH) that assess change from a physiological and often single-species perspective. These assessments highlight the vulnerabilities of calcifying organisms (e.g. review [15]) and consider the potential extent of ecological change [16].

While there is recognition that ocean acidification may alter net primary production, via the increased solubility of biogenic calcareous structures and reduced survival of calcifying species that consume algae [11,17], it may also alter production directly, especially under elevated temperature [18]. Several reviews now recognize that ocean acidification can increase carbon fixation rates in some photosynthetic organisms (review [19,20]); however, the ecological implications of this increase are largely untested. Thus, CO_2 may not only act as a stressor but also act as a resource. CO_2 may not only limit primary productivity but also limit the growth rates of a population. Because such effects are variable among species, there is an enormous potential for shifts in species dominance, as some species gain a relative advantage from their response to elevated CO_2. Indeed, alteration of resource availability has a fundamental role in regulating the productivity of individuals, populations and, ultimately, communities [21].

2. Carbon dioxide as a carbon resource

CO_2 can act as a resource by increasing carbon fixation rates in some photosynthetic organisms. The degree to which this occurs is dependent on the carbon capture strategies and the degree to which carbon is limiting (review [20]). The relationship between aqueous CO_2, photosynthesis and growth is not simple, because not all photosynthesizing species require environmental CO_2 for their source of carbon (C). The majority of marine algae have carbon concentrating mechanisms (CCMs) that facilitate the active influx of CO_2 and/or bicarbonate ions (HCO_3^-) and elevate C concentrations at the site of C fixation (i.e. Rubisco), with few algae being CO_2-only users [22,23]. For these reasons, there has been uncertainty regarding whether algae with CCMs will benefit from CO_2 enrichment [24].

Despite the prevalence of CCMs, evidence suggests that many algae do respond positively to increasing CO_2 [12]. Indeed, the ability of some algae with CCMs to benefit from enriched CO_2 lends insights into the potential mechanisms for CO_2 effects. Species with CCMs can shift away from HCO_3^- towards aqueous CO_2 when CO_2 levels are high [25]. Thus, aqueous CO_2 may facilitate CCM C-acquisition or make it less energetically costly, and this capacity varies among species [26]. Such variation among species may be due to species-specific variation in CCMs themselves [27,28] or the ability of species to acquire other limiting resources (e.g. light or nutrients) [29].

As human activities modify environmental conditions, and therefore resource availability, some species of algae may be released from carbon limitations while others are not [30]. This mismatch has the potential to affect competitive abilities and alter community structure. Moreover, the effects of these shifts would be particularly profound if key functional groups, whose interactions structure entire communities, experience contrasting resource limitations.

Falkenberg *et al.* [31] reveal how variability in resource limitation may play a substantial role in 'kelp-to-turf'

phase-shifts. Kelps were shown to be limited by a single type of resource (e.g. only nutrients and not CO_2), whereas their alternate state (characterized by turf algae) was co-limited by both nutrients and CO_2. This difference in carbon limitation demonstrates the potential for elevated CO_2 to influence turf expansion [32], especially when amplified by human activities that also increase nutrient loads [33]. This response is characteristic of co-limitation by multiple resources [34]. Therefore, ocean acidification is unlikely to act alone, but instead acts in concert with other environmental conditions (e.g. nutrient pollution) and primary consumers (i.e. herbivores).

Indeed, there are a large number of resources that constrain the abundance of marine [35] and terrestrial plants [36] and determine the composition of space-holding species. Combinations of two or, sometimes, three of these limiting factors are often incorporated into models to account for the diversity and composition of plant communities (review [37]). Thus, interspecific variation in resource requirements is likely to affect relative species abundance in complex communities. Changes in any of these constraints could alter the probability of phase-shifts, particularly as many resources are undergoing large, rapid changes because of human activities [38].

Mat-forming algae (here defined as low-profile ground-covering macroalgal and turf communities) are fast-growing and can be effective competitors for space in kelp forests and on coral reefs. The hypothesis that phase-shifts towards mat-forming algae are likely to be more common under conditions of high [CO_2] is therefore of particular interest. If this model has validity, then enhanced CO_2 should cause mats to increase their extent and productivity in both temperate and tropical systems. Supporting evidence requires field observations of natural variation in [CO_2] to provide insights into ocean acidification effects at the ecosystem level (e.g. CO_2 seeps), and field and laboratory manipulations to establish the physiological reasons for such an effect [39]. Until now, such a combination of evidence has not been strongly pursued.

3. Ocean acidification as an indirect agent

While categorizing the potential effects of ocean acidification into direct negative effects (i.e. on calcifiers) and positive effects (i.e. on non-calcifying algae) provides a conceptual starting point, it is manifestly overly simplistic to forecast community persistence or change. While the detection of *direct* effects is readily achievable, it will not necessarily shed light on the drivers that will play predominant roles in shaping future communities relative to *indirect* effects [40]. Indirect effects yield not only 'unexpected results' but also some of the strongest ecological effects (i.e. phase-shifts) that have been regarded as 'catastrophes' on coral reefs [41] and 'collapses' of kelp forests [42]. They are often unanticipated, because the impact of one component (e.g. ocean acidification) on another (e.g. kelp decline) requires knowledge of a third species (e.g. kelp-competitors) or mediating factors (e.g. interactions among stressors), which are poorly understood (figure 1).

While the indirect climate effects on species interactions were initially surprising [43], we are starting to learn that they commonly lag behind the more intuitive and easily detectable direct effects, and can even reverse the direct effects of climate [16,44]. To date, most research on ocean acidification has focused on the direct environmental impacts on individual
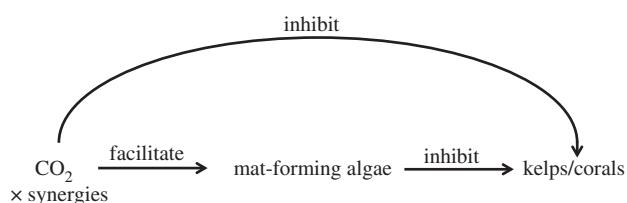
Figure 1. Diagram showing the indirect effect of enriched CO_2 on habitat-forming species (i.e. kelps and corals) via mat-forming algae. CO_2 facilitates the growth of mat-forming algae, which, in turn, inhibit the recruitment of kelps and corals. The indirect effects of CO_2 may rival the direct effects of CO_2, particularly where CO_2 combines with other stressors to accelerate the expansion of mats.

species of iconic status (e.g. corals), but the capacity for indirect effects to drive change may rival the known direct effects [40].

The indirect effects of ocean acidification may be especially important in communities where CO_2 can act as a resource and change competitive outcomes. Competitive ability is contingent on the relative availability of resources and the tolerance to environmental stress. Dominance may switch between subordinate species and their normally dominant competitors, or even change competitive interactions into facilitated interactions [45]. Studies of volcanic CO_2 vents reveal the potential for altered competitive balances between space-holders at projected near-future levels of CO_2 (750 ppm [46]). In particular, these studies reveal the potential for increased dominance of mat-forming macroalgae in low pH environments in temperate [47] and tropical zones [48].

Indirect effects that account for phase-shifts can be classified into two broad classes: those driven by strong consumer effects (i.e. trophic cascades) and those driven by strong producer effects (i.e. dominance of space; review [40]). The former class has attracted considerable attention in both tropical and temperate systems [49], but there is profound and widespread variation in its explanatory power (reviews of phase-shifts on coral reefs [50] and kelp forests [51]). While there is merit in understanding the future role of acidification on consumers and potential trophic cascades, there is also merit in examining the breadth of direct and indirect producer effects (figure 1). This review provides an alternative framework for forecasting community-level impacts of ocean acidification by focusing on producers' responses through the lens of phase-shifts in kelp forests and coral reefs. By 'kelp forests', we refer to canopies of brown seaweeds, including Laminariales and Fucales.

Our present understanding of the physiological effects of ocean acidification is primarily based on results obtained from closed experimental systems, particularly small laboratory experiments. Beyond physiological predictions, larger field mesocosm studies enable tests of direct and indirect effects that can modify the persistence of species and functional relationships. Together, such experimental knowledge can be compared against the pattern observed in natural systems. Such investigative frameworks have been established in the discipline of macroecology [52] in response to the persistent need to scale from small to larger experimental units and ultimately ecosystems [53]. For ocean acidification research, this challenge is particularly vexing, because the logistic constraints on manipulating large volumes of aqueous CO_2 place upper limits on tests of combinations of multiple stressors and species. Thus, there is considerable discussion on methods that integrate experimental research across laboratory, mesocosm and field systems to unravel the complexity of

functional relationships under future environmental conditions [9]. Nevertheless, the key question for ecosystems is not based on just the direct effects and fate of individual species, but on the stability and persistence of the system as a whole.

4. Mat-forming algae as competitive dominants

We focus on a group of fast-growing algae with quick rates of invasion and growth and wide physiological tolerance. We classify these relatively low-lying algae in a single term, 'mats' or 'mat-forming algae', to emphasize their similar physiological and ecological properties across the temperate and tropical communities. We propose that if we can identify similarities that occur between kelp forests of the temperate zone and coral reefs of the tropical zone, then we open a broader avenue of enquiry about the potential effects of environmental change via altered productivity.

Mats are characteristically small, with high surface-area-to-volume ratios and high demand for resources relative to surrounding kelps and corals. Physiologically, they require increased resource availability (e.g. nutrients [54]) to enable their normally ephemeral status to become competitively superior to perennial species of kelps and corals. The taxonomic identity potentially includes many tens to hundreds of species [55] from many lineages. Despite their taxonomic diversity, similarities in their biology have been found to be sufficiently large that authors have consistently referred to them as 'turf-forming algae' or 'turfs', 'epilithic algal matrix' or 'mats' [55]. These terms emphasize the carpet-like nature of these algae which we call 'mats'.

The 'coral–algal phase-shift' occurs as a function of reduced herbivory and water quality that independently, or in combination, enhances net production of algae [56]. Ephemeral algae that form dense carpet-like mats are a key mechanism that creates physically stressful conditions for corals [57,58]. On the Great Barrier Reef, 'mats' of algae (10–50 cm high) that bloom across large areas of coral reefs on coastal and inshore fringing reefs are known to overgrow established corals and prevent coral recruitment [58,59]. In the Caribbean, greater emphasis is placed on turf-forming algae comprising filaments of benthic algae and cyanobacteria (less than 1 cm height) that can also prevent settlement of coral planulae [60].

Kelps and corals form three-dimensional structures that are episodically disturbed and readily reassemble after natural disturbances. The loss of corals and kelps can occur when mats of algae colonize bare substrata after a disturbance, hence preventing recruitment by occupying purchases for attachment and smothering remnant corals. Many mat-forming species are normally subordinate to kelps and corals (e.g. ephemeral or early successional species), but increased resource availability enables their physiology and life history to become competitively superior [33,61].

The 'kelp–turf phase-shift' occurs on coasts associated with water pollution, because the altered water conditions favour a suite of turf-forming species, which due to their physiology (i.e. fast uptake of nutrients) and life history (ability to withstand high sediment loads) are well suited for polluted environments [33,62–64]. On Caribbean coral reefs, nutrient overloading also causes turfs to expand over extensive areas, leading to coral recruitment failure [65], similar to that observed in kelp forests [61].

Table 1. The total alkalinity (TA) and pCO_2 were increased, and pH decreased, in treatments where CO_2 was elevated. The effect on algae was similar among the methods (i.e. vents, versus field versus laboratory) and climes (i.e. temperate versus tropical). Measured: total alkalinity (TA) and pH; calculated, concentration (ppm) of pCO_2; calculated: effect-size (ES) of the treatments on algae. The magnitude of the effect-size (r) was calculated using Cohen's d for two independent groups (i.e. the difference between means divided by standard deviation (Cohen's d [68]).

	temperate				tropical			
	TA	pH	pCO_2	ES	TA	pH	pCO_2	ES
vents				0.70				0.82
elevated	2560	7.76	805		2302	7.83	748	
ambient	2563	8.01	305		2297	8.00	401	
field mesocosm				0.88				0.81
elevated	2357	7.91	647		2320	7.87	779	
ambient	2276	8.15	307		2320	8.10	416	
laboratory				0.82				0.73
elevated	2585	7.96	557		2260	7.84	828	
ambient	2263	8.14	300		2258	8.16	342	

5. Lines of evidence: carbon dioxide increases net productivity

(a) Comparison among methods: vents versus field mesocosms versus laboratory

Here, we compare the effects of CO_2 enrichment on mat-forming algae among several projects, combining findings from laboratory experiments and mesocosms with those of natural field studies. For field studies, we use observations of benthic communities around volcanic seeps that have been shaped by decades-long exposure to fine bubble streams of CO_2 seeping from the seabed, which cause local alterations in the seawater chemistry [47,48]. These seep sites complement and improve the interpretive value of laboratory experiments. While laboratory studies can be carefully controlled, the range of testable ecological interactions is quite limited. Conversely, field studies at CO_2 vents include interactions within acclimatized natural communities, but spatial and temporal variation in pH does not behave exactly the same as future ocean conditions [66]. The limitations of laboratory and field assessments suggest that combining both approaches will provide a more informed model.

Our comparisons focus on benthic communities exposed to similar elevations in CO_2 concentrations that are within the forecasted range of change by the end of this century [46,67]. Relative to ambient conditions ($8.0–8.1$ pH_T), two levels of projected future pH were compared in warm temperate (Mediterranean [47]) and tropical (Papua New Guinea [48]) regions (table 1). The future pH conditions were chosen to represent the projected near-future conditions anticipated for the end of the twenty-first century (pCO_2 approx. $580–1080$, depending on emission scenarios [69]). Near-future conditions were represented as $7.7–7.8$ pH_T (temperate) and $6.8–7.8$ pH_T (tropical). Experimental mesocosms in temperate [26] and tropical zones (i.e. the Coral Proto-Free Ocean Carbon Experiment [70]) are compared with the vents and their laboratory counterparts (figure 2).

Experimental and observational results are not directly comparable because they estimate responses from mats grown over different periods of time using different techniques. Laboratory experiments used similar techniques [18], but mesocosm experiments used floating docks in temperate conditions [26] and a Free Ocean Carbon Experiment in tropical conditions [70]. Observations at volcanic vents quantified the percentage cover of mats within space that would otherwise be suitable for recruitment (e.g. coral planualae settlement on space lacking live coral). At tropical vents, mats were quantified within 25×25 cm quadrats randomly assigned among reef without live coral. At temperate vents, mats were quantified after 3.5 months of development on uncolonized 15×15 cm volcanic rock tiles [47].

(b) General carbon dioxide effects on the net production of mats

Mats responded positively to conditions of ocean acidification among all studies reviewed here. Mats covered nearly 40% more space at temperate vents and 50% more space at tropical vents (figure 2a,b). In both cases, mats expanded their covers from a minority space holder (i.e. approx. 10–20% cover) to a majority space holder (i.e. approx. 60%), regardless of sources of loss.

The effect of enriched CO_2 in field mesocosms was to increase rates of growth (mg per day dry weight) by two to three times that of ambient conditions (figure 2c,d). In the laboratory, net productivity was substantially greater, probably owing to fewer sources of loss (e.g. herbivory), but the increased growth rate under enriched treatments was about twice that of ambient conditions (figure 2e,f). These consistently strong effects suggest that CO_2-induced increases in productivity may be quite general among a class of algae renowned for its taxonomic diversity, variation in morphology and life-history characteristics.

An unexpected and preliminary result is the similarity in magnitude of response between climes and experimental protocols (i.e. effect-sizes based on relative change in growth or percentage cover between ambient and elevated CO_2 conditions ranged from 0.70 to 0.88; table 1). We caution over interpretation of these similarities, because the responses
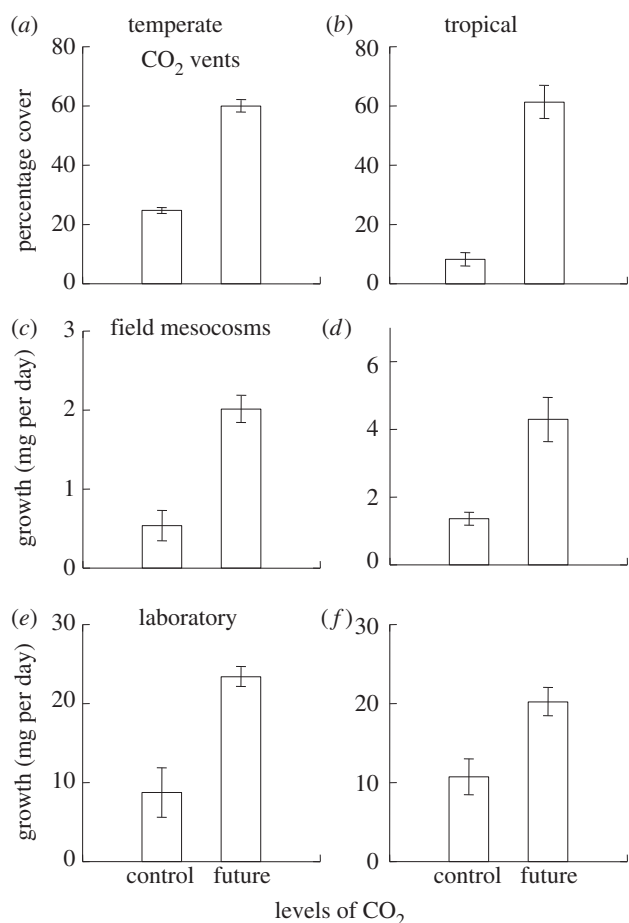
Figure 2. Elevated net productivity and cover of mat-forming algae under enriched CO_2 conditions. In the natural environment, the percentage cover of algal mats (standardized by available space, see §5c) is greater at CO_2 vents in temperate (a. Ischia, Mediterranean) and tropical seas (b. Papua New Guinea). Growth rates are greater under CO_2-enriched treatments within temperate (c) and tropical (d) field manipulations and temperate (e) and tropical (f) laboratory manipulations. 'Control' represents current CO_2 conditions (approx. 300–410 pCO_2) and 'future' represents end of this century conditions (approx. 550–830 pCO_2).

are derived from mats grown over different periods of time (electronic supplementary material, S1). In addition, the magnitude of CO_2-induced increases in productivity is likely to be contingent on the availability of nitrogen and light as well as species identity. Nevertheless, the consistency in direction of strong effects is clearly suggestive that mat-forming algae have the potential to respond positively to predicted levels of CO_2.

(c) Carbon dioxide effects on community composition

Mat-forming algae appeared to expand (i.e. higher percentage cover) under projected near-future conditions at CO_2 seeps, regardless of any differences in herbivory (figure 2). At the temperate vents, estimates of percentage cover of mats on the natural substrate were similar among ambient and low pH zones (mean percentage cover was 26% and 33%, respectively [47]). However, the differences among these zones were readily apparent in a study of succession, which monitored the development of rocky reef assemblages on uncolonized tiles of rock in each pH zone. During succession, calcareous taxa (primarily crustose coralline algae and barnacles) maintained similar percentage cover in both the

ambient and low pH zones for the early stages of succession (until approx. 3.5 months) but were overgrown by mat-forming algae (figure 2) in the low pH zone during the later stages [47]. At the tropical vents, overall abundance of non-calcareous macroalgae was twofold greater at the low pH than ambient zones (mean percentage cover of 3.33% and 1.60%, respectively [48]). When standardized by available space (hard substratum without live corals), however, the difference between these zones was more apparent, with mats of filamentous turf–algae being far more expansive under near-future conditions than at control sites (figure 2), whereas calcareous algae showed the opposite pattern [48].

In both tropical and temperate regions, shifts in the benthic communities surrounding the vents were consistent with proposed direct and indirect effects of ocean acidification on mat-forming algae. Mat-forming algae at temperate vents may limit the percentage cover of calcified taxa, which at the end of a year of development was 26% in the ambient pH zones and 17% in the low pH zones [47]. Hence, mat-forming algae appear to inhibit other taxa [47]. Among the tropical vents, at a pH below 7.7 (i.e. conditions beyond those expected for the end of the twenty-first century), no coral reef development was found, and the benthos was dominated by seagrasses, ephemeral macroalgae and volcanic sand, and a few individual colonies of robust coral species (massive *Porites* and *Favites pentagona*) [48].

(d) Herbivores

As anticipated, the densities of calcareous benthic grazers (e.g. sea urchins and gastropods) can be sparser in extremely low pH conditions [47,71,72]. However, in the projected near-future conditions presented in these analyses (figure 2), sea urchin densities are similar to control sites at tropical vents (K.E.F. 2013, unpublished data) and temperate vents [72,73]. In addition, the abundance of small mobile grazers (primarily gastropods) does not differ among the low pH and control sites at the temperate vents [74]. Differences in herbivorous fish populations are unknown at both these vents; however, herbivorous fish can easily access all areas of the temperate and tropical vents and did not appear to avoid areas of low pH ([74], K.E.F. 2013, personal observation). The increased probability that calcareous benthic grazers are sparser at low pH levels suggests that there is merit in understanding the conditions in which herbivory may be altered by enriched CO_2.

6. Discussion

(a) Ocean acidification and resource availability

Human-driven environmental changes are producing regional combinations of environmental conditions that may push many ecological systems outside the environmental envelope in which they evolved [75]. The relative abundance of sessile plants often reflects resource limitations, but many of these constraints are undergoing large, rapid changes capable of causing phase-shifts [76]. These new environmental conditions appear to favour species with fast rates of colonization, growth and short generation times that can competitively displace slower growing and longer-living space-holders when resource availability is increased [33,38,56].

The effects of CO_2 enrichment that we synthesized here were derived from substantially different species, regions

and experimental protocols (electronic supplementary material, S1). The consistency of positive effects on productivity alone suggests that previous reports of CO_2 effects on expansive covers of algae on temperate and tropical rocky coasts [71] and increasing dominance of mats over corals [30] may not represent an idiosyncratic set of case examples. Naturally, ephemeral mats may not only displace recovering kelp forests under elevated nutrients [33,61], but this loss may be strengthened by future CO_2 concentrations (i.e. nutrient $\times$ CO_2 synergy [77]). Similarly, mats may have variable effects on corals recovering from disturbance under current conditions [78], but CO_2 may strengthen their negative effects on corals via increased growth rates of mats [30] coupled with decreased growth rates of corals [79]. Together, these studies provide insights into ecological drivers that to date have attracted comparatively little attention, but represent potentially profound drivers of change to the competitive dominance of kelps and corals within their respective latitudes.

(b) Indirect effects on herbivores

The role of herbivores in the trends presented here is a current gap in understanding. The studies from the CO_2 seeps report that herbivores are present in end-of-century pH conditions, and at least some species are in similar abundance between the low pH and control sites. This suggests the increased dominance of mats in the projected near-future conditions is not predominantly due to the absence of calcareous grazers. However, decades of research have highlighted the importance of grazers in mediating competitive interactions between benthic space holders [80,81], and research is required to assess whether an increased supply of resources (e.g. CO_2) can change these ecosystems from predominant consumer control to predominant resource control (e.g. nutrients [82]).

There are several ways in which herbivores could contribute to or counter the trends reported here that deserve further attention. For example, changes in abundance or behaviour (resulting in reduced *per capita* herbivory) could contribute to the dominance of mat-forming algae. However, laboratory experiments reveal that gastropods reared on turfs grown in various CO_2 concentrations removed more algae per herbivore under elevated CO_2; this effect was driven by the indirect effect of CO_2 via changes to C : N ratios in the algae rather than the direct effect on the herbivore [83]. Thus, increased herbivory could compensate for increased growth by mats, although this was not apparent at the CO_2 seeps. Furthermore, some diatoms produce tissue with lower nutrient concentrations in response to elevated CO_2 [84]. If acidification were to similarly affect the nutrient status of benthic algae, individual herbivores would need to increase *per capita* rates of consumption to acquire sufficient energy for growth and development. Conversely, reduced nutrient content of algae could cause herbivores to grow more slowly and suffer higher mortality in the process, or even selectively graze certain species of algae. Elevated CO_2 can also affect the production of chemical herbivore deterrents in marine plants [85], which could further influence the interaction between herbivores and algae. Last, the effects of ocean acidification on herbivores are likely to be influenced by concurrent changes in temperature [86] that can affect population size and *per capita* rates of consumption [87]. While there is a multitude of potential interactions and indirect effects of acidification on herbivores that require further attention, the

results from CO_2 seeps suggest that an increased dominance of mat-forming algae is a likely emergent effect.

(c) Multiple stressors: ocean acidification as a non-additive stressor

Most ecological systems are exposed to multiple stressors. The projected rates of CO_2 absorption in the future [88] suggest that ocean acidification represents a relatively slow driver of future ecological change. However, the gradual trend in ocean acidification will be overlaid on additional stressors to marine ecosystems (e.g. temperature, fishing and nutrients) as well as short-term perturbations that occur at local to regional scales (e.g. storms, coral bleaching, coral disease and mass urchin mortalities). Many stressors combine in non-additive ways (i.e. synergies or antagonisms). Recent reviews reveal synergistic effects in about one-third of factorial experiments involving two stressor combinations [89], which increases to three-quarters when three stressors are considered [4]. Indeed, it is probably a simple function of sample size (n) that the frequency of synergistic and antagonistic effects will increase with an increase in number of stressors. Hence, the potential for acidification-related phase-shifts in response to gradual acidification is likely to increase with additional stressors [90].

Not surprisingly, the potential for non-additive effects between multiple stressors increases the probability of phase-shifts [56]. When combined with elevated nutrients, elevated CO_2 can release mats from co-limitation with nitrogen [31] to multiply the rate of expansion [77]. In addition, projected warming is likely to enhance mat productivity, because mats are not only better suited to the increasing availability of CO_2 [31], but these effects are also enhanced under warmer temperatures [18]. Whether additive or synergistic, such combinations of CO_2 with other stressors increase the probability of phase-shifts.

A tractable aspect of synergisms with local stressors is that local management may ameliorate the effects of CO_2 enrichment by reducing local stressors. For example, although CO_2 and eutrophication can yield multiplicative responses [77], a reduction of local stressors (e.g. nutrients) can negate this synergistic effect [26]. These results suggest that the management of local stressors (e.g. water pollution and overfishing) may have a greater contribution in determining the ecosystem effects of ocean acidification than current thinking allows. Such findings empower local managers because they show that reducing local stressors (e.g. nutrient pollution and overfishing) can reduce the effects of global stressors not under their governance (e.g. ocean acidification and temperature).

(d) Conclusion

Ocean acidification is often considered in terms of its direct negative effects on the growth and calcification of organisms with calcareous shells or skeletons. We argue that this focus overlooks the important role of ocean acidification as a resource, which can enhance the productivity of algae known to influence the status of kelp forests and coral reefs (i.e. mat-forming algae or mats). We have highlighted how ocean acidification can indirectly tip the competitive balance towards dominance by mats through mechanisms that generate new space (e.g. disturbance or storm events), which enables

colonization and persistence of mats rather than the original kelp or coral state.

Ocean acidification, therefore, has the capacity to act as a resource that shifts the status of subordinates into dominant competitors. Consequently, human activities that alter the availability of resources have important implications for the relative competitive abilities of major ecosystem components. We suggest that additional stressors will influence the effect of ocean acidification on producers, and that many cumulative impacts may reflect multiplicative rather than additive inter-actions. Contrary to conventional wisdom, we argue that if these synergies involve local stressors, then environmentally mediated ecosystem shifts may be greatly ameliorated by managing local stressors. Nevertheless, there are few assessments of whether management of local processes can weaken the feedbacks that reinforce altered state and enable the reversibility of phase-shifts. Importantly, we suggest that in the face of changing climate (e.g. ocean acidification and temperature), effective management of local stressors (e.g. water pollution and overfishing) may have a greater contribution in determining ecosystem states than currently anticipated. Thus, we highlight how ocean acidification has the potential to influence competitive abilities via changes in resource availability, with implications for the stability and persistence of the system as a whole.

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