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MINIREVIEW

EFFECTS OF CLIMATE CHANGE ON GLOBAL SEAWEED COMMUNITIES¹

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Seaweeds are ecologically important primary producers, competitors, and ecosystem engineers that play a central role in coastal habitats ranging from kelp forests to coral reefs. Although seaweeds are known to be vulnerable to physical and chemical changes in the marine environment, the impacts of ongoing and future anthropogenic climate change in seaweed-dominated ecosystems remain poorly understood. In this review, we describe the ways in which changes in the environment directly affect seaweeds in terms of their physiology, growth, reproduction, and survival. We consider the extent to which seaweed species may be able to respond to these changes via adaptation or migration. We also examine the extensive reshuffling of communities that is occurring as the ecological balance between competing species changes, and as top-down control by herbivores becomes stronger or weaker. Finally, we delve into some of the ecosystem-level responses to these changes, including changes in primary productivity, diversity, and resilience. Although there are several key areas in which ecological insight is lacking, we suggest that reasonable climate-related hypotheses can be developed and tested based on current information. By strategically prioritizing research in the areas of complex environmental variation, multiple stressor effects, evolutionary adaptation, and population, community, and ecosystem-level responses, we can rapidly build upon our current understanding of seaweed biology and climate change ecology to more effectively conserve and manage coastal ecosystems.

Key index words: adaptation; carbon dioxide; climate change; community structure; competition; ecophysiology; ecosystem function; herbivory; marine macroalgae; ocean acidification

Changes in global temperature and ocean chemistry associated with increasing greenhouse gas concentrations are forcing widespread shifts in biological systems. In response to warming, species ranges are shifting toward the poles, up mountainsides, and to deeper ocean depths (Parmesan and Yohe 2003, Perry et al. 2005). Factors including warming and ocean acidification are causing the reorganization of local communities as species are added or deleted and as interactions among species change in importance (Wootton et al. 2008, Harley 2011). Because greenhouse gas emission rates continue to accelerate, the climatically forced ecological changes that have been documented over the past half century will likely pale in comparison to changes in the coming decades.

Global change is, by definition, a global phenomenon, yet some biological systems have received more attention than others. Although a great deal of research has focused on systems like coral reefs and terrestrial forests (e.g., Hoegh-Guldberg et al. 2007, Aitken et al. 2008), considerably less attention has been devoted to seaweed-dominated ecosystems (Wernberg et al. 2012). Like corals and trees, seaweeds are key habitat structuring agents that harbor incredible biodiversity (Graham 2004, Christie et al. 2009). Seaweeds form the base of productive food webs that include economically valuable species (Graham 2004, Norderhaug et al. 2005) and extend well beyond the shallow waters in which seaweeds dwell (Harrold et al. 1998). Seaweeds are intimately linked to human cultural and economic systems via the provision of ecosystem goods and services ranging from food to medicine to storm protection (Rönnbäck et al. 2007).

Here, we describe how global climate change influences marine macroalgae and their associated ecosystems. We begin with the physical and chemical changes that are currently at work in the oceans, and how these changes may impact seaweed performance via changes in stress and resource availability. These direct linkages from environment to organism will

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drive species-level responses, including adaptation, migration, and extinction. We then consider how direct effects of climate change may modify interspecific interactions such as competition, herbivory, and disease, and broaden our focus to examine changes in whole ecosystem structure and function. Finally, we highlight key areas where our understanding is incomplete, and suggest productive avenues for future research.

ABIOTIC CHANGE IN COASTAL MARINE ENVIRONMENTS

Rising carbon dioxide concentrations in the atmosphere and in the oceans are driving a number of important physical and chemical changes. These include directional, global-scale trends like ocean acidification (the shift in ocean chemistry that includes reductions in pH and carbonate ion availability), warming, and sea-level rise, along with regionally specific increases or decreases in wave heights, upwelling, terrigenous nutrient runoff, and coastal salinity. As these abiotic trends are thoroughly reviewed elsewhere (e.g., Feely et al. 2004, IPCC 2007, Rabalais et al. 2009, Wang et al. 2010, Zacharioudaki et al. 2011), we pause here only to highlight two salient features of this suite of anthropogenically forced environmental change. First, the magnitude of change is remarkable. We have already exceeded the maximum CO₂ concentration experienced in the last 740,000 years (Augustin et al. 2004), and will soon exceed the range of CO₂ concentrations experienced in tens of millions of years (Pearson and Palmer 2000, IPCC 2007). Second, the rate of abiotic change is virtually unprecedented. The rise in CO₂ concentrations and global temperature since the industrial revolution are 100–1000 times faster than at any point in the past 420,000 years and are still accelerating (Hoegh-Guldberg et al. 2007). Corresponding rates of geochemical change in the oceans currently exceed anything recorded in the last 300 million years (Hönisch et al. 2012). Both the magnitude and the rate of environmental change pose serious challenges to marine species that must either tolerate or adapt to a new ocean.

INDIVIDUAL-LEVEL RESPONSES: GAPS IN THE ECOPHYSIOLOGICAL FRAMEWORK

Seaweed survival, growth, and reproduction are known to vary with numerous climatically sensitive environmental variables including temperature (e.g., Lüning and Neushul 1978), desiccation (Davison and Pearson 1996, Chu et al. 2012), salinity (e.g., Steen 2004a), wave heights (Seymour et al. 1989, Graham et al. 1997), nutrient supply via upwelling and run-off (Lobban and Harrison 1997), pH (Kuffner et al. 2008, Martin and Gattuso 2009, Diaz-Pulido et al. 2012), and carbon dioxide concentration itself (Kroeker et al. 2010). To date,

our understanding of the relationship between environmental change and the performance of individual seaweeds is based on a loose combination of mechanistic, physiological research, and phenomenological studies that correlate performance with environmental conditions. The seaweed physiological literature is extensive, but much of it predates our current understanding of future environmental scenarios, and it is not well linked to more ecologically oriented studies. Rather, climate change ecologists often make use of phenomenological studies to make broad-brush predictions for future change. Whether due to the lack of information or the lack of communication across disciplines, weak or missing mechanistic linkages between predicted future conditions and seaweed growth, reproduction, and survival are problematic. For example, climate change will result in novel patterns and combinations of stress, and a priori predictions regarding responses to simultaneous changes in the means and variance of multiple environmental stressors are difficult to make in the absence of a mechanistic understanding of sublethal and lethal stresses in seaweeds. (In this review, we use the term “stress” to denote disruptive stress sensu Davison and Pearson (1996); stressful conditions are those that adversely affect growth via damage and/or resource reallocation associated with damage prevention and repair). Below, we consider what is and what is not known about the two most broadly important aspects of environmental change, warming and ocean acidification, with a further emphasis on variable impacts across different algal life history stages. We then detail some of the ways in which an incomplete ecophysiological understanding impairs our ability to predict seaweed responses to complex environmental variation and multiple stressors.

Thermal ecophysiology. Temperature determines the performance of seaweeds, and indeed all organisms, at the fundamental levels of enzymatic processes and metabolic function (reviewed in Raven and Geider 1988, Lobban and Harrison 1997). Seaweeds have evolved biochemical and physiological adaptations, including variation in the identity and concentration of proteins and the properties of cell membranes, that enable them to optimize their performance with respect to the temperatures they encounter (Eggert 2012). Although seaweeds are generally well adapted to their thermal environment, they nevertheless experience temperatures in nature – particularly during periods of environmental change – that are sufficiently high or low to result in disruptive stress in the form of cellular and subcellular damage (reviewed in Davison and Pearson 1996, Eggert et al. 2012). Such damage and any reallocation of resources for protection and repair can slow growth, delay development, and lead to mortality (Davison and Pearson 1996). In response, seaweeds can produce heat shock proteins that repair or remove damaged proteins (e.g., Vayda

and Yuan 1994, Lewis et al. 2001). However, protein thermal physiology is not well understood in macroalgae (Eggert et al. 2012) and the upregulation of heat shock protein production is only one of many transcriptional changes that occur in seaweeds during periods of thermal stress (Collén et al. 2007, Kim et al. 2011). Relevant genomic, transcriptomic, and proteomic studies are only just beginning to scratch the surface and most links from gene expression to organismal performance are far from well established.

As a result of nonstressful conditions at intermediate temperatures and stress at the extremes, the relationship between temperature and most sub-cellular, tissue-level, or whole-organism processes is described by a hump-shaped thermal performance curve. From colder to warmer, these curves generally rise exponentially as rates of biochemical reactions increase, peak at some optimum temperature, and then fall rapidly as the biological components of the system become less efficient or damaged (Kordas et al. 2011, Eggert et al. 2012). When properly parameterized across the full-temperature tolerance range of a species, thermal performance curves have the potential to predict the physiological effects of any given warming or cooling scenario (barring any further acclimatization, adaptation, or context-dependent surprises; see below). The effect of a small increase in thallus temperature will be beneficial when the initial temperature is cooler than optimal and detrimental when it is warmer than optimal, and the precise change in performance can be predicted from the starting and ending temperature values along the curve. Unfortunately, the shapes of thermal performance curves and the positions of their optima are poorly described in most seaweeds. Although many physiological and ecological studies have linked seaweed performance to temperature, a substantial fraction of these studies do not investigate enough temperatures across a wide enough range to characterize the underlying, nonlinear relationship between the two. Furthermore, various physiological parameters within an organism differ in the shape and optimum temperature of their thermal performance curves, which limits our ability to use an easily measured parameter (e.g., photosynthesis) as a proxy for parameters that may be more ecologically relevant (e.g., growth and reproduction). Indeed, growth rates do tend to peak at lower temperatures than photosynthetic rates (Eggert et al. 2012), presumably because metabolic rates increase faster than photosynthetic rates at higher temperatures. Much remains to be learned regarding the thermal dependence of the key physiological processes that control growth, reproduction, and survival across the full range of temperatures experienced by an individual in its lifetime.

Ecophysiology of ocean acidification. Carbon dioxide concentrations in seaweed habitats are increasing

with anthropogenic emissions and, in some regions, with intensified upwelling of CO₂-enriched water (Feely et al. 2008). As with terrestrial plants (Long et al. 2004), it is tempting to predict that seaweeds will benefit from the increase in inorganic carbon concentration (Beardall et al. 1998). However, the situation in the sea is not so simple. CO₂-driven effects on photosynthesis and growth depend on the degree to which carbon is limiting, which in turn varies among habitat types and among taxa. Because CO₂ diffusion rates are much higher in air than in water, seaweeds that are exposed at low tide and those with floating canopies at the sea-air interface have greater access to CO₂ (Beardall et al. 1998). However, aerial exposure does not necessarily reduce the probability of carbon limitation, as exposure at low tide can dramatically reduce rates of carbon acquisition (Williams and Dethier 2005) and even emersed seaweeds can benefit from increasing atmospheric CO₂ concentrations (Gao et al. 1999, Zou and Gao 2002). Moreover, a strict focus on CO₂ in air or dissolved in water may be misleading as not all species require environmental CO₂ as a carbon source. Most green and brown algae (and many red algae) can also utilize bicarbonate (HCO₃⁻) by converting it to CO₂ intracellularly via CO₂ concentrating mechanisms (CCMs; see Raven et al. 2012 for review). Just as terrestrial C₃ plants are more likely to be CO₂-limited and therefore more likely to benefit from elevated CO₂ than C₄ plants (Long et al. 2004), seaweeds lacking CCMs are more likely to be carbon-limited and thus more likely to benefit from additional CO_{2(aq)}. For example, experimental addition of CO₂ greatly increased the growth rate of *Lomentaria articulata*, which cannot use bicarbonate (Kübler et al. 1999), but did not enhance photosynthetic rates of species with CCMs or of nonbicarbonate using species that were not carbon-limited (Cornwall et al. 2012). However, species with CCMs did shift away from bicarbonate and toward CO_{2(aq)} when CO₂ concentrations were high, which may benefit the seaweeds by reducing the energetic costs of using CCMs (Cornwall et al. 2012). Thus, although there may be variation among taxa based on carbon utilization strategy, noncalcifying seaweeds as a group will likely respond positively to increasing global CO₂ concentrations in general (see Kroeker et al. 2010).

In addition to providing carbon for photosynthesis, anthropogenic CO₂ emissions reduce seawater pH and the saturation state of calcium carbonate. As this increases the cost of calcification and the likelihood of dissolution, calcifying organisms are particularly sensitive to elevated CO₂ in seawater. Ocean acidification is consistently related to reduced growth rates in calcified macroalgae (Kroeker et al. 2010) and reductions in calcification rate at elevated pCO₂ have been demonstrated for crustose and articulated coralline red algae as well as calcified green *Halimeda* (Gao et al. 1993, Büdenbender

et al. 2011, Price et al. 2011). However, reduced calcification at higher pCO₂ did not emerge as a general pattern in a meta-analysis of multiple seaweed studies (Kroeker et al. 2010). This may be because the process of calcification, and likewise the effects of ocean acidification on calcification, varies among seaweeds (Price et al. 2011), and many species are able to create microclimates of chemistry favorable for calcification regardless of ambient conditions (Roleda et al. 2012a). It has therefore been suggested that the effects of ocean acidification on calcified species may be manifested as increased dissolution rather than reduced production of calcium carbonate (Roleda et al. 2012a). Reduced pH may have important consequences for noncalcifying taxa as well (Roleda et al. 2012b), although the cumulative effects of climatically realistic, CO₂-driven pH change on noncalcifying seaweeds remain poorly understood.

Stress and the completion of algal life cycles. Predicting true individual-level responses to climate change in seaweeds is challenging owing to the numerous life history stages and transitions upon which environmental change can act (Schiel and Foster 2006). Careful consideration of this complexity is important because thermal optima and tolerance limits can vary among life history stages within a species (e.g., Fain and Murray 1982), and climate effects at one life history stage may be magnified or offset by impacts (or lack thereof) at other life history stages (e.g., Ladah and Zertuche-González 2007).

To exemplify the degree to which we are ignorant of how climate change will impact seaweeds across all life history stages, we summarize what is known regarding the effects of warming and elevated CO₂ on one particularly well-studied species, the giant kelp, *Macrocystis pyrifera* (Fig. 1). Increased temperature is generally thought to have negative effects on

spore production (Buschmann et al. 2004), germination (Buschmann et al. 2004), recruitment (Deysher and Dean 1986a, Buschmann et al. 2004), and sporophyte growth (Rothäusler et al. 2009, 2011) and context-specific effects on gametogenesis depending on the source population and degree of warming (Lüning and Neushul 1978, Deysher and Dean 1986b, Muñoz et al. 2004). Warming has also been linked to mortality of spores, gametophytes, eggs, and sporophytes (Ladah and Zertuche-González 2007). Much less is known about the effects of increasing CO₂ concentrations. On the basis of current knowledge, we can expect positive effects on gametogenesis and variable effects (e.g., positive effect of increasing CO₂, but negative effect of decreasing pH) on germination (Roleda et al. 2012b). Studies assessing the potential for interactive temperature and CO₂ effects are uncommon (see below), and nonexistent for *M. pyrifera*. Thus, even for one of the best-studied seaweeds in the world, large knowledge gaps greatly hinder our ability to precisely predict future changes in population growth and persistence.

The importance of variability, rates of change, and environmental history. When predicting future ecological patterns – and when designing experiments to test those predictions – it is tempting to treat environmental change as a steady shift in mean conditions. However, environmental time series are complex (see Helmuth et al. 2006 for temperature examples and Wootton et al. 2008 for a pH example), and different aspects of an environmental signal, including extremes, range, and patterns of variability, will have different biological consequences. For example, seaweed reproduction may only occur if temperatures drop below some threshold for a sufficiently long period of time, whereas mortality may be more closely linked to high temperatures that exceed physiological tolerance (Breeman 1988, Wernberg et al. 2011b).

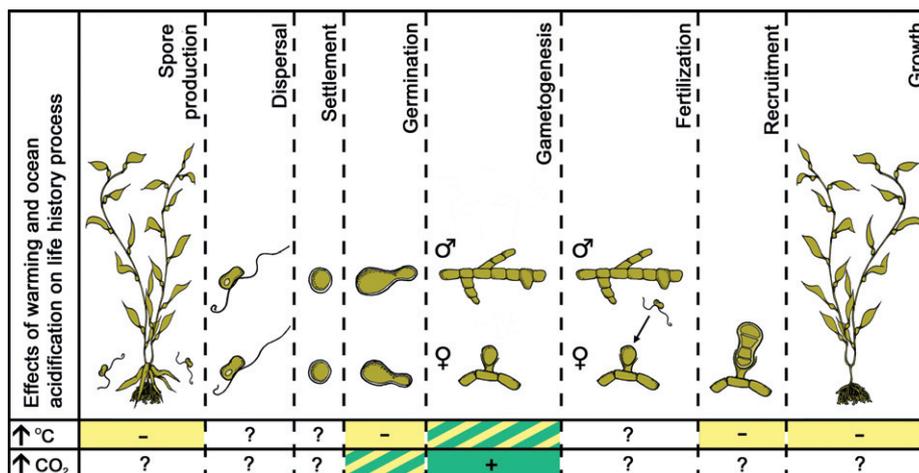


FIG. 1. Effects of increasing temperature and CO₂ on life history processes in *Macrocystis pyrifera*. Green boxes indicate experimental evidence of positive effects, yellow boxes indicate negative effects, hatched boxes indicate both positive and negative (i.e., context-specific) effects, and blank boxes represent unquantified responses owing to a lack of published information.

Mortality rates following short exposures to extreme temperatures or salinities can be similar to those found after longer exposures to less extreme conditions (Forrest and Blakemore 2006). In an experiment that manipulated the temporal variation of stress, higher variability muted negative impacts of stress on some seaweed taxa, but generated negative impacts in others (Benedetti-Cecchi et al. 2006). Although changes in variability can drive important biological changes in other systems (e.g., agricultural crops and forests; Southworth et al. 2000, Giesecke et al. 2010), studies on the effects of different magnitudes and temporal patterns of environmental variability, alone or in combination with changes in mean conditions, are exceedingly rare for seaweeds.

Additional aspects of environmental variability come into play when one considers that the physiological limits of individuals and populations are not constant (see below). The history of environmental variation is often a key predictor of future success, as an individual or population that has been exposed to stressful conditions in the past may be better able to cope with them in the future (Padilla-Gamino and Carpenter 2007a). Finally, rapid environmental changes are typically more detrimental than slow ones, as rapid change is more likely to outpace an organism's ability to acclimatize or a population's ability to adapt (O'Connor et al. 2012). We require a better understanding of the ecological consequences of the accelerating pace of change in the Earth's climate system to reduce the probability of ecological surprises.

Multiple stressors and nonadditive effects. All of the anthropogenically forced changes in the physical and chemical environment are occurring simultaneously, and in many cases, the impact of any particular stressor on the physiology and performance of marine macrophytes will depend upon the presence and magnitude of additional limiting or disruptive stressors. For example, the importance of – and limiting values of – various resources are environmentally dependent, with the degree of light limitation at low irradiance varying with temperature (e.g., Davison et al. 1991) and the enhancement of photosynthesis by elevated CO₂ varying with nutrient availability (Xu et al. 2010). The percent cover of algal turfs decreased with increasing CO₂ under ambient nutrients, but the reverse was true under elevated nutrients (Russell et al. 2009). There are also many interactions among disruptive stressors, including temperature, desiccation, pH, salinity, and ultraviolet radiation. For example, in tropical and warm-temperate crustose coralline algae, the negative effect of warmer temperatures on bleaching, growth rates, calcification rates, and survival were significantly greater under conditions of elevated CO₂/reduced pH (Anthony et al. 2008, Martin and Gattuso 2009, Diaz-Pulido et al. 2012). The magnitude and even the direction of UV effects depend upon temperature and CO₂ (Hoffman et al.

2003, Swanson and Fox 2007, Gao and Zheng 2010). Depending on the species and life history stage, desiccation has been shown to magnify or reduce the effects of high temperature (e.g., Hunt and Denny 2008, Chu et al. 2012). As of yet, it is difficult to predict when one stressor will increase or decrease the effect of another. There are also no known biases toward synergistic or antagonistic effects; in a meta-analysis of multi-stressor studies on *Fucus* spp., synergistic, additive, and antagonistic outcomes were all equally prevalent (Wahl et al. 2011). We desperately need to incorporate more ecophysiological research into a multi-stressor framework to improve our understanding of when, where, and why important context-dependent outcomes emerge.

POPULATION AND SPECIES-LEVEL RESPONSES: TOLERATE, ADAPT, MOVE, OR DIE

As described above, environmental change can elicit a wide array of responses in individual organisms. At the species level, responses to environmental forcing can be distilled down to a small set of basic alternatives: (i) persistence without acclimatization or adaptation (tolerance), (ii) persistence with acclimatization or adaptation, (iii) persistence enabled by migration to remain within some particular climatic niche and (iv) extinction. In this section, we devote our discussion to potential roles of acclimatization and adaptation in facilitating local persistence, to changes in seaweed distributional patterns, and to the potential for seaweed extirpations.

Scope for acclimatization and adaptation. There is a rich literature on seaweed acclimation (an individual-level response to experimental manipulation of the environment), acclimatization (an individual-level response to natural variation in the environment), and local adaptation (a population-level response to natural environmental variation) as a consequence of variation in temperature, salinity, light, and wave forces (Lüning 1990, Lobban and Harrison 1997, Eggert et al. 2012). Appropriately acclimated/acclimatized individuals or adapted populations may be better able to withstand coming environmental change. For example, warm-acclimated *Saccharina latissima* sporophytes required less light to achieve maximum photosynthetic rates and were more photosynthetically efficient at high temperatures (Davison et al. 1991), and warm-acclimated *Fucus vesiculosus* embryos were more likely to survive periods of thermal stress (Li and Brawley 2004). Although many species can acclimate to environmental changes, some algal populations or species may be less able to do so than others. For example, some tropical species and subpopulations appear to have limited scope for acclimation relative to their temperate counterparts, presumably due to reduced environmental variability in tropical habitats (Padilla-Gamino and Carpenter

2007a,b). Regardless, the use of appropriately acclimated/acclimatized individuals is a prerequisite for realistic climate change experiments; otherwise, short-term measurements may not reflect true long-term responses.

Unlike acclimation, relatively little is known about the degree to which evolutionary adaptation may “rescue” seaweed species in the face of environmental change. The existence of local ecotypes (e.g., Breeman 1988) clearly indicates that adaptation is possible, and there is evidence to suggest that seaweeds can evolve and even speciate fairly rapidly (in ~400 years in the case of *Fucus radicans*) when sufficient selective pressure is applied by the environment (Pereyra et al. 2009). However, the degree to which most multi-cellular marine species such as seaweeds, their competitors, and their consumers can adapt over climate change-relevant time scales (<100 years) is largely unknown (but see Sunday et al. 2011). Understanding the extent to which species will acclimatize or adapt to environmental change is crucial for predicting future ecological change.

Distributional shifts and the threat of extinction. Because environmental conditions directly and indirectly influence seaweed distributional patterns at a variety of scales (Breeman 1988), changes in the environment will result in changes in seaweed distributions. Some of the most readily detectable changes are at local (site) scales, where environmental change can result in shifts in the vertical distribution (often termed zonation) of intertidal and subtidal seaweeds. Sea-level rise will result in a general upward shift of benthic communities *en masse*, although the accompanying changes in the relative availability of appropriate substratum types and orientations at specific shore levels (e.g., on shores with wave cut platforms and cliffs) may drive changes in relative algal abundance (Vaselli et al. 2008). However, zonation patterns are determined by far more than just position relative to mean sea level. The upper limit of intertidal seaweeds is related to thermal and desiccation stress during low tide (e.g., Harley 2003), and long-term increases in air temperature have resulted in down-shore shifts in the upper limit of some species (Harley and Paine 2009). The depth range of subtidal kelps also depends critically on environmental factors such as temperature, water motion, and water transparency (Graham et al. 2007), and climate-related changes in these factors are predicted to reduce the depth range of kelp forests (Mélèder et al. 2010). When the upper and lower depth limits of a species are set by different agents (e.g., thermal stress, light availability, consumers; Harley 2003, Graham et al. 2007, Mélèder et al. 2010), climate change can result in certain species being squeezed out of the system entirely (Harley 2011).

Climate change will drive distributional shifts at larger, alongshore scales as well. Increased storm

frequency could restrict vulnerable species to protected shorelines, and changes in salinity may allow seaweeds to penetrate further into, or be forced further out of, estuarine embayments and lagoons. The most notable large-scale changes, however, are those occurring across latitudinal temperature gradients. Drastic population declines and even local extinctions have been documented at the warm (lower latitude) end of species’ biogeographic ranges during periods of warming (e.g., Serisawa et al. 2004). Range retraction at low latitudes can be offset by expansion into higher latitudes, as in western Europe where warm-water species have expanded northward (Lima et al. 2007). However, such expansions may not be a sustainable escape mechanism for species along coastlines with significant geomorphic barriers, such as the end of a continent. For example, poleward migration of seaweed species has been observed along the east and west coasts of Australia since 1940, but because there is no suitable habitat within the range of most species’ dispersal abilities further south, continued poleward retreat may result in numerous extinctions as species ‘fall off the map’ (Wernberg et al. 2011a). Indeed, extinctions have already been documented for several marine macroalgae, although the relative contribution of environmental change to these losses remains poorly understood (Brodie et al. 2009).

COMMUNITY-LEVEL RESPONSES: INTERSPECIFIC INTERACTIONS AND INDIRECT EFFECTS

Ecological change in coastal ecosystems reflects the combined influence of direct environmental impacts on individual species and indirect effects mediated by changes in interspecific interactions (Harley et al. 2006). We first describe some of the ways that competitive, trophic, and symbiotic relationships are likely to change in seaweed systems, and then discuss the consequences of these changes for entire ecosystems in the following section.

Competitive relationships. Seaweeds compete for nutrients, light, and space for attachment, and their relative success at acquiring these resources in the presence of other photo-autotrophs (or sessile invertebrates, in the case of space) depends upon both resource availability and environmental stress. The availability of several resources (e.g., CO₂, nitrate, ammonium) is changing due to human activities, and the effects of changing resource supply will depend on the magnitude and direction of these changes and the degree to which these resources limit algal growth and competitive ability. Increasing nitrogen loading tends to favor fast-growing species with high nitrogen requirements. In some cases, this may lead to competitive dominance by weedy taxa (Steen 2004b, Vermeij et al. 2010) and – should nutrients trigger a phytoplankton bloom – shading-out of benthic seaweeds by phytoplankton (Kavanaugh et al. 2009). In other cases, higher nitrogen

merely allows for the persistence of nitrogen-limited taxa and thus enhances algal diversity (Bracken and Nielsen 2004). Elevated $\text{CO}_2(\text{aq})$ will differentially affect seaweeds depending on their carbon capture strategy. The influence of elevated $\text{CO}_2(\text{aq})$ on seaweeds with carbon concentrating mechanisms, such as kelps, is highly light-dependent, and the overall effect of rising $\text{CO}_2(\text{aq})$ on kelp competitive ability remains unclear (Hepburn et al. 2011). On the other hand, for species that rely on aqueous CO_2 , like turf-forming rhodophytes in New Zealand, elevated $\text{CO}_2(\text{aq})$ should differentially favor their growth, which may in turn enhance their competitive ability (Hepburn et al. 2011).

Changes in the severity of environmental stressors (e.g., temperature, pH, salinity, wave forces) will also affect the outcome of competitive relationships. In some cases, environmental extremes remove otherwise dominant competitors, allowing subordinate species to persist (Sousa 1979) and facilitating the establishment of non-native taxa (Miller et al. 2011). Stress need not be lethal to influence the outcome of competitive interactions (Davison and Pearson 1996). For example, many important competitors for space are calcified taxa such as crustose coralline algae, corals, and mussels, and inhibition of growth by reduced pH likely contributes to increasing fleshy algal competitive dominance over these groups (Wootton et al. 2008, Diaz-Pulido et al. 2011, Hepburn et al. 2011). The effects of rising temperatures may increase or decrease competition, and even change competitive interactions into facilitative ones. Elevated temperature increased the competitive impacts of *Enteromorpha* on two species of *Fucus* (Steen 2004b). Conversely, the effects of intertidal *Ascophyllum nodosum* on understory barnacles, like the effects of subtidal *Ecklonia radiata* on *E. radiata* recruits, shifted from negative (competitive) to net positive (facilitative) at high temperatures (Leonard 2000, Wernberg et al. 2010).

Herbivory. Herbivores are key structuring agents in algal communities, influencing everything from the survival of individual seaweeds to total algal biomass and diversity (Lubchenco and Gaines 1981). The outcomes of pairwise plant-herbivore interactions depend on characteristics of both the alga and the herbivore, including the palatability of seaweeds, the per capita consumption rates of herbivores, and the individual and population growth rates and overall abundance of both. Abiotic factors associated with climate change are known to impact all of these attributes.

The amount of algal tissue that an herbivore can or will consume depends on the degree of morphological or chemical defense and on aspects of nutritional quality such as the C:N ratio (Duffy and Hay 1990, Van Alstyne et al. 2009). Elevated temperature reduced herbivore defenses in *F. vesiculosus* (Weinberger et al. 2011), and changes in nutrient availability have been shown to alter algal palatability

(e.g., Hemmi and Jormalainen 2002). Calcium carbonate in algal tissue is an important anti-herbivore defense (Hay et al. 1994) and ocean acidification may have dramatic impacts on the palatability of calcified seaweeds via reduced calcification or increased dissolution. Although elevated CO_2 would be expected to increase C:N ratios in noncalcified taxa, the effects of elevated CO_2 on seaweed palatability lags far behind our understanding of such effects in phytoplankton and terrestrial plants.

Climate change will also have direct effects on herbivores that will cascade down to primary producers. Several field studies suggest that warming sea surface temperatures are associated with increases in important herbivore populations and concomitant declines in certain algal species (Hart and Scheibling 1988, Ling 2008, Hernandez et al. 2010). Although warming may benefit some grazer populations, ocean acidification is likely to be generally detrimental to many invertebrate herbivores, particularly heavily calcified species such as sea urchins and molluscs (Dupont et al. 2010, Crim et al. 2011). Volcanic CO_2 vent systems provide a glimpse into this future; areas of reduced pH near CO_2 seeps are associated with reductions in urchin and shelled gastropod abundance, and the success of *Padina* spp. (despite a reduction of calcium carbonate in the thalli) and of highly palatable *Sargassum vulgare* near CO_2 vents has been attributed to the absence of urchin grazers (Porzio et al. 2011, Johnson et al. 2012). The impacts of ocean acidification on other herbivorous taxa, notably crustaceans and fish, appear to be relatively minor (Kroeker et al. 2010).

Although useful as a starting point, changes to algal and invertebrate performance or population size in isolation cannot fully predict changes in the importance of herbivory. Rather, the overall impact of herbivory depends upon the balance of production and consumption of algal tissue. Metabolic theory predicts that metabolic rate and scope for activity – which in ectothermic herbivores determine the demand for and ability to acquire food, respectively, – increase more quickly with temperature than algal photosynthetic rate and thus primary production (O'Connor 2009). As a result of these different temperature–performance relationships, experimental warming increased the relative importance of amphipod grazing and decreased algal biomass despite generally positive direct effects of warming on algal growth (O'Connor 2009). Such rate-dependent generalizations fall apart, however, when abiotic conditions become stressful, and stress differentially reduces the performance of one or more of the interacting species (Kordas et al. 2011). One trophic level or the other is often disproportionately susceptible to stress associated with extremes in temperature, salinity, and wave forces (Cubit 1984, Elfving and Tedengren 2002, Taylor and Schiel 2010), making seaweeds relatively safe or

relatively vulnerable to grazing at certain places and times. As the environment changes, the times and places that seaweeds are most, or least, impacted by herbivory will change as well (see e.g., Vinueza et al. 2006).

Epibionts, endophytes, and pathogens. Seaweeds live in constant association with a variety of microbes, fungi, animals, and other algae that live on or in their tissues. Of these relationships, the ecological role of epibionts is particularly well-studied, with effects on seaweed hosts ranging from reduced growth and reproduction to increased risk of mechanical breakage (e.g., Dantonio 1985). In kelp beds in eastern Canada, outbreaks of non-native epiphytic bryozoans are triggered by warming events, and these outbreaks have led to drastic reductions in the percent cover of habitat-forming *Saccharina longicruris* (Scheibling and Gagnon 2009, Saunders et al. 2010). In cases such as this, where bryozoan epibionts increase the risk of frond breakage (Krumhansl et al. 2011), any local increase in storminess may act synergistically with warming and infestations by epibionts.

In contrast to epibionts, the ecology of seaweed endophytes and diseases is poorly understood, particularly with regard to climate change (Eggert et al. 2010, Gachon et al. 2010). There is, however, mounting evidence that warming will negatively impact seaweeds by facilitating bacterial infections (Campbell et al. 2011, Case et al. 2011). Departures from optimal salinity and irradiance can also make seaweeds more susceptible to bacterial disease, as evidenced by experiments and observations on aquaculture species such as *Kappaphycus alvarezii* (Largo et al. 1995). Although evidence for primarily negative pathogen-mediated effects of environmental change is slowly accumulating, the generality and future magnitude of such negative effects remain essentially unknown.

SHIFTS IN COMMUNITY STRUCTURE AND ECOSYSTEM FUNCTION

Environmental change, coupled with shifts in species interactions and the shuffling of species distributions, will culminate in potentially far-reaching changes in community structure and ecosystem function (Harley et al. 2006). Because the responses of benthic assemblages are often highly idiosyncratic, generalizations and specific predictions are fraught with uncertainty. While the future states of marine ecosystems are far from certain, neither are they completely unforeseeable. Several predictions and testable hypotheses can be developed around our current understanding of seaweed-dominated, or potentially seaweed-dominated, ecosystems.

One system for which specific predictions have been made is the rocky intertidal zone in Britain, where the effects of climate change have been considered in great detail and where relevant long-term datasets exist (Hawkins et al. 2008, 2009).

Wave-protected and semi-exposed British shores are typically dominated by large fucoid algae, which are dominant competitors for primary space as well as ecosystem engineers that provide cool, moist microhabitats for associated species (e.g., Schonbeck and Norton 1980, Thompson et al. 1996). Rising air temperatures and increasing wave exposure will directly reduce fucoid canopies via lethal physiological and hydrodynamic stress (Hawkins et al. 2009). The appearance and/or increased abundance of warm-water herbivores is expected to further reduce algal cover (Mieszkowska et al. 2006, Hawkins et al. 2009). A more diverse grazer assemblage, coupled with the replacement of a structurally complex, cold-water barnacle species with a structurally simple, warm-water barnacle species, will reduce opportunities for fucoid size escapes from microscopic stages and thus inhibit the regrowth of the algal canopy (Hawkins et al. 2008). The net result is a decline in subcanopy habitat and a reduction in benthic primary productivity. These changes are predicted to reduce the abundance of many invertebrates that rely on cool moist microhabitats and decrease invertebrate production in the algal detritus food web of the strand line; both of these effects may negatively impact birds that forage on these invertebrate resources (Kendall et al. 2004).

Like intertidal fucoids, subtidal kelps provide habitat structure for numerous species, including many that are economically important (Graham 2004). Kelp forests in Australia, like fucoid communities in Britain, are experiencing range expansions and contractions of both seaweeds and important herbivores in association with warming temperatures (Ling 2008, Wernberg et al. 2011a). In this system, there is also evidence that ocean acidification will result in important shifts in community structure. Experimental increases of temperature and CO₂ increased the biomass of algal turfs (Connell and Russell 2010). Enhanced cover and biomass of turf-forming algae associated with elevated CO₂ occurred at the expense of coralline crusts, although the magnitude of this shift depended on nutrient and light levels (Russell et al. 2009, 2011). Increasing dominance of turfs in response to rising CO₂ may in turn inhibit kelp recruitment, which could cause or maintain phase shifts from kelps to turfs (Connell and Russell 2010). However, kelp canopy can, to some degree, inhibit the positive effects of elevated CO₂ on turfs, suggesting that intact kelp forests may be resistant, but not resilient, to phase shifts to turf-dominated communities (Falkenberg et al. 2012).

The degree to which results from southwestern Australia will generalize to other kelp systems, such as those under strong top-down control, is unclear. Limited information suggests that elevated CO₂ has variable but often positive effects on kelps like *Nereocystis luetkeana* and *M. pyrifera* (Thom 1996, Swanson and Fox 2007, Roleda et al. 2012b), but negative effects on crustose coralline algae (CCA; see above)

and important kelp consumers such as sea urchins (Dupont et al. 2010, Reuter et al. 2011). Because urchins benefit CCA by preventing overgrowth by other seaweeds, and CCA benefit urchins by providing settlement cues, models suggest that reductions in either taxa may result in a positive feedback loop (Baskett and Salomon 2010). In contrast to the negative effects of ocean acidification on herbivores, the effects of warming may be largely positive for herbivores (Hart and Scheibling 1988, Ling 2008, Hernandez et al. 2010). A long-term study of warming associated with power plant thermal effluent in central California has shown that a $\sim 3.5^{\circ}\text{C}$ increase in temperature results in increases in herbivore abundance, shifts from cold-water *N. luetkeana* to warmer water *M. pyrifera* canopies, and a replacement of understory kelps by foliose red algae (Schiel et al. 2004). A reasonable working hypothesis, therefore, is that kelps in the California Current system, particularly in the southern portions of their range, may respond positively to the direct and indirect effects of acidification, but negatively to the direct and indirect effects of warming (Fig. 2). The relative balance between these opposing forces, particularly in systems with complex trophic and competitive relationships, remains uncertain.

Tropical coral reefs are also quite sensitive to climate change (Fig. 3). In these systems, corals and CCA currently dominate in part because present-day conditions are relatively conducive to calcification and in part because herbivores benefit the slow-growing calcifiers – despite some negative impacts of bioerosion – by keeping fleshy macroalgae in check (Hoegh-Guldberg et al. 2007, O’Leary and McClanahan 2010). However, future changes in ocean climate are predicted to destabilize coral reef ecosystems, resulting in phase shifts from coral-dominated reefs to benthic systems dominated by fleshy macroalgae (Hoegh-Guldberg et al. 2007, Anthony et al. 2011, Diaz-Pulido et al. 2011). Fleshy macroalgae are positively affected by increased CO_2 (Kuffner et al. 2008, but see Jokiel et al. 2008), which along with elevated nutrients may increase their competitive ability. In contrast, reef-building corals appear to be in serious trouble due to the influence of climatic stressors; warming ocean waters are associated with mass coral bleaching events, increased pCO_2 decreases coral calcification and growth and increases dissolution, and storms cause physical damage to weakened reef structures (Hoegh-Guldberg et al. 2007). Other calcified habitat-forming reef organisms, such as CCA and the green alga *Halimeda* spp., are also expected to do poorly when pH and calcium carbonate saturation drop and temperatures rise (Kuffner et al. 2008, Price et al. 2011, Diaz-Pulido et al. 2012). Indeed, coralline algae are relatively rare or absent from both tropical and temperate sites with naturally occurring carbon dioxide seeps (Hall-Spencer et al. 2008, Fabricius et al. 2011, Porzio et al. 2011). CCA are particularly

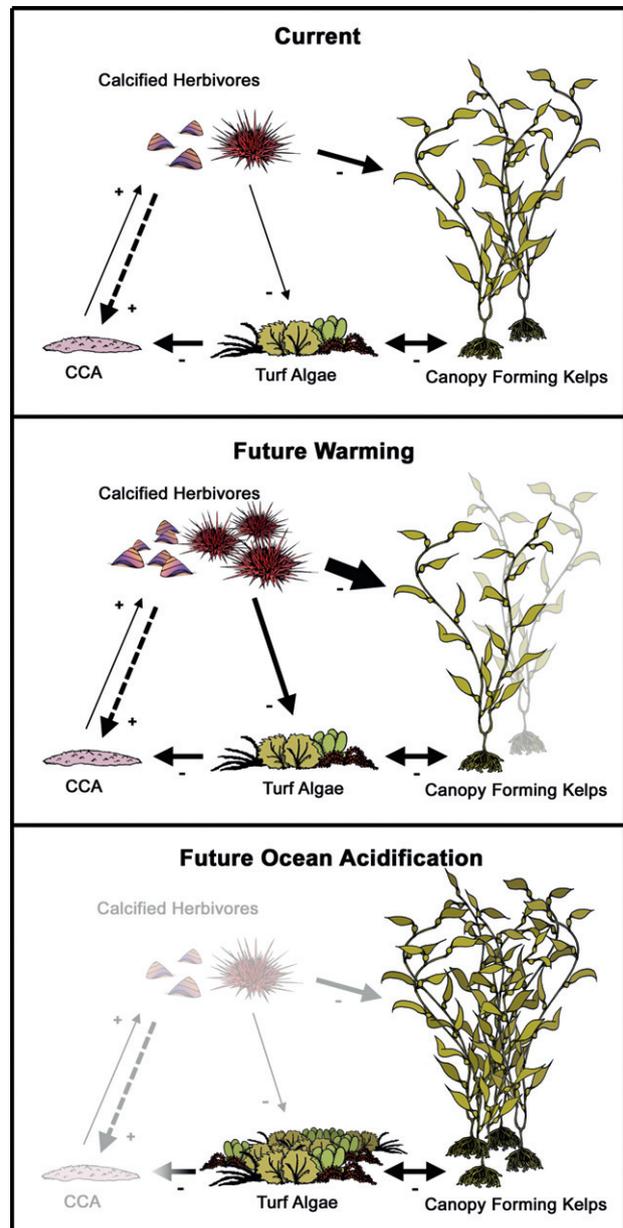


FIG. 2. Future ecological scenarios for temperate kelp forests. Solid and dashed arrows represent direct and indirect effects of one species on another, respectively (the flow of energy via trophic interactions is omitted for clarity). Faded icons represent functional groups that may still be present but play a strongly reduced ecological role. Relative to present-day conditions (upper panel), future warming (middle panel) will favor grazers and have direct and indirect negative impacts on canopy-forming kelps. Future increases in CO_2 (lower panel) will have strong negative effects on crustose coralline algae and positive effects on noncalcified seaweeds both directly via improved growth and indirectly via reduced consumption by calcified herbivores. The combined impacts of simultaneous warming and acidification in a more realistic climate change scenario remain poorly understood. See text for details.

important as they are the “cement” that helps hold coral reefs together and provide important settlement surfaces for coral larvae; the loss of these crusts is predicted to expedite phase shifts on

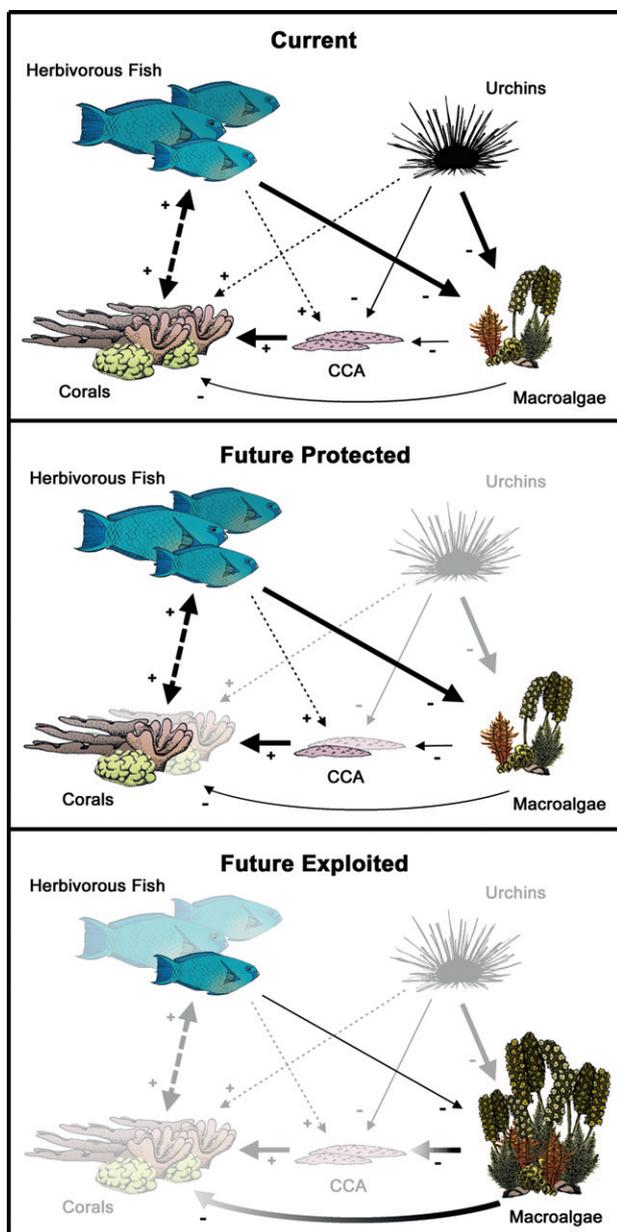


FIG. 3. Future ecological scenarios for tropical coral reefs. Arrows and shading as in Fig. 2. Relative to the present day (upper panel), the combination of warming and ocean acidification will reduce the dominance of calcified taxa such as crustose coralline algae and corals (middle and lower panels). However, the likelihood of fleshy macroalgae rising to dominance and out-competing the calcified taxa depends upon whether they are suppressed by herbivores (as may happen in a marine protected area, middle panel) or not (as may happen on a heavily fished reef, lower panel). See text for details.

tropical reefs (Diaz-Pulido et al. 2007). The key to triggering a phase shift from corals to fleshy macroalgae, however, may rest with the herbivores (Fig. 3). In areas where herbivore biomass can be maintained, the shift away from coral-dominated systems can be delayed, although perhaps not prevented indefinitely (Hughes et al. 2003, Hoegh-Guldberg et al. 2007,

Buddemeier et al. 2011). Should structurally complex corals be replaced with fleshy macroalgae, a considerable loss of biodiversity would result (Hoegh-Guldberg et al. 2007).

Ecosystem shifts, such as those described above, may occur rapidly once a system has been pushed beyond some threshold or tipping point (Scheffer et al. 2001). In some cases, the behavior of the system may not change over a wide range of progressive impairment (e.g., biomass removal or species loss), only to shift suddenly once a threshold is crossed (Speidel et al. 2001, Davies et al. 2011). Catastrophic phase shifts, as have been observed in kelp forests and on coral reefs, are facilitated by losses of resilience associated with changes in resource supply, food web structure, and disturbance frequency (Folke et al. 2004), all of which are altered by CO₂-induced environmental change. Catastrophic shifts are often difficult to anticipate, as relevant environmental thresholds may lie at or beyond the range of historical variation, but within the range of near-future environmental conditions. Should environmental conditions return to below-threshold values, recovery may proceed quickly, slowly, or not at all (Folke et al. 2004), and the recovery trajectory may differ considerably from the original perturbation trajectory (e.g., Baskett and Salomon 2010).

FUTURE DIRECTIONS: ADDRESSING THE BIG UNKNOWNNS

Although a great deal of progress has been made in recent years, there are still significant gaps in our understanding which hamper our ability to predict the outcomes of global change in seaweed-dominated systems. Some of the most important areas in which we lack a general or even basic understanding include (i) the importance of rates, timing, magnitude, and duration of environmental change, (ii) non-additive effects of multiple stressors, (iii) population-level implications of variable environmental impacts among life-history stages, (iv) the scope for population- or species-level adaptation to environmental change and (v) ecological responses at the level of communities and ecosystems, including tipping points and sudden phase shifts. With regard to uncertainties in the nature of environmental forcing, we require additional ecophysiological and ecomechanical studies – especially ones that move beyond single-factor ANOVA designs – and further development in the emerging field of ecological genomics to identify biological responses to key environmental drivers or combinations of drivers. Of particular use would be an ecophysiological framework from which the impacts of multiple stressors could be predicted a priori (Pörtner and Farrell 2008). Once understood, these drivers can be incorporated into demographic models to better describe and predict changes in population growth or decline. Although species-level research on seaweeds, at least with regard to climate change, lags

behind similar work in terrestrial environments (e.g., Aitken et al. 2008), there is no reason that phycologists could not model a research program based on the successes of terrestrial botanists, foresters, and agricultural scientists. As for community and ecosystem-level change, researchers can make rapid progress by focusing on ecological dominants (e.g., kelps) and strong interactors (e.g., sea urchins) as a starting point. Individual pieces of the ecological puzzle can then be interlinked with mathematical models and ground-truthed in areas where environmental conditions already approximate future projections (e.g., volcanic CO₂ vents and power plant thermal effluent plumes).

Seaweed beds, coral reefs, and other coastal ecosystems provide trillions of dollars of ecosystem goods and services every year (Costanza et al. 1997), and the degradation of these systems will have far-reaching consequences for human societies. Developing accurate predictions for the ecological effects of climate change in seaweed-dominated systems is therefore a high priority, as it will be invaluable for effective conservation and management. The climate change scenario leading from healthy coral reefs to degraded macroalgal beds is an excellent example of an ecological prediction that can be used to dictate management priorities. Although warming and ocean acidification are beyond our control in the near term, we can manage for coral reef resilience by conserving herbivore diversity and abundance and reducing nutrient loads (Hoegh-Guldberg et al. 2007). In some parts of the Caribbean, this strategy appears to work in practice; following high temperature and hurricane disturbances, coral recovery rates were higher in protected areas where algal cover was more effectively controlled by herbivores (Mumby and Harborne 2010). There is high yet largely untapped potential for similarly feasible local-scale management options in a wide variety of seaweed-dominated coastal ecosystems that are undergoing major ecological reorganization in response to anthropogenic change (e.g., Russell et al. 2009). Identifying the leverage points where conservation and management practices are most effective should continue to be a major focus of ecological research.

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