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Ecological Leverage Points: Species Interactions Amplify the Physiological Effects of Global Environmental Change in the Ocean

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Abstract

Marine ecosystems are increasingly impacted by global environmental changes, including warming temperatures, deoxygenation, and ocean acidification. Marine scientists recognize intuitively that these environmental changes are translated into community changes via organismal physiology. However, physiology remains a black box in many ecological studies, and coexisting species in a community are often assumed to respond similarly to environmental stressors. Here, we emphasize how greater attention to physiology can improve our ability to predict the emergent effects of ocean change. In particular, understanding shifts in the intensity and outcome of species interactions such as competition and predation requires a sharpened focus on physiological variation among community members and the energetic demands and trophic mismatches generated by environmental changes. Our review also highlights how key species interactions that are sensitive to environmental change can operate as ecological leverage points through which small changes in abiotic conditions are amplified into large changes in marine ecosystems.

1. INTRODUCTION: RECONCILING VIEWS OF ENVIRONMENTAL STRESS IN AN ERA OF GLOBAL CHANGE

Environmental stress models have been influential in marine community ecology for decades (Connell 1975, Menge & Sutherland 1976). In these models, environmental stress is defined to include both physical stressors, such as large wave forces, and physiological stressors, such as high temperature or low salinity (Menge & Sutherland 1987). The strength of species interactions—including predation, competition, and facilitation—is hypothesized to vary predictably along environmental stress gradients that range from benign to harsh habitats (Menge & Sutherland 1987, Bertness & Callaway 1994, Bruno et al. 2003). Thus, stress is typically viewed as a property of the environment. Although environmental stress models have elucidated links among abiotic factors, species interactions, and community dynamics, these models tend to imply that all species within a trophic level are affected similarly by abiotic conditions. For example, ecologists have hypothesized that higher trophic levels may be more vulnerable to environmental stress than lower trophic levels (Menge & Sutherland 1987, Menge & Olson 1990, Voigt et al. 2003, Gilman et al. 2010), while often neglecting the importance of adaptation and physiological variation among species within trophic levels.

By contrast, physiologists typically define stress as a reduction in organismal performance or fitness caused by environmental changes (Schulte 2014). By viewing stress as a response of an organism rather than a characteristic of the environment, this definition inherently recognizes that not all species within a community are affected equally by a given environmental change. Indeed, the recognition that environmental change can affect species differentially is a central tenet of comparative physiology (Somero 2010, 2011; Somero et al. 2017). Although ecologists have long recognized that environmental change can alter the outcome of species interactions (e.g., Park 1954), this perspective has not been fully integrated into the study of marine communities and global change biology. In particular, as we discuss in greater detail in this review, marine ecologists seldom conceptualize a community as an assemblage of species that can span a broad range of physiological variation (but see Sagarin et al. 1999, Sanford 2002a, Harley et al. 2017).

We live in an era where the world's oceans are changing rapidly along multiple environmental axes. In this review, we draw on examples of the physiological and ecological responses to three primary processes associated with global environmental change: ocean warming, deoxygenation, and ocean acidification. Marine scientists are increasingly focused on these changing ocean conditions and recognize that environmental change is translated into community change via organismal physiology. However, in many ecological studies, physiology is assumed to be relatively interchangeable among community members (e.g., increasing temperatures and ocean acidification are viewed as universally stressful). From a physiological perspective, empirical studies suggest that climate change will differentially impact species within the same community, leading to winners and losers (Somero 2010). There is a growing appreciation that these same underlying physiological differences among community members often mediate changes in species interactions and community dynamics.

In this review, we highlight how a deeper understanding of physiological variation among community members can improve our understanding of the emergent ecological effects of global environmental change. We provide examples to demonstrate how attention to performance curves—in particular, asymmetries between species' performance curves—is critical to understanding the effects of global environmental change on organismal responses and species interactions. We then highlight how energetics provides both a framework for exploring the neglected effects of sublethal changes in the environment and a common currency for the combined physiological responses to warming, deoxygenation, and ocean acidification that directly affect species interactions. Finally, we describe how a focus on ecological leverage points—key species interactions that are sensitive to environmental change—can provide insight into the emergent effects of global change on communities and ecosystems.

2. DIRECT AND INDIRECT EFFECTS OF GLOBAL ENVIRONMENTAL CHANGE

As global environmental change progresses, many marine communities are undergoing shifts in species composition (e.g., Sagarin et al. 1999, Helmuth et al. 2006, Wootton et al. 2008, Sorte & Stachowicz 2011, Wernberg et al. 2013, Sanford et al. 2019). These changes can manifest as losses of poorly adapted species, novel additions of species (e.g., as species track changing environments and colonize new communities), and/or shifts in the relative abundances of species within a community. Changes in species abundances can be driven by the direct effects of environmental change on demographic rates (e.g., reproduction or mortality). However, changes in species abundances can also result indirectly from the influence of environmental change on the strength of species interactions (Sanford 1999, Kordas et al. 2011).

Two components can contribute to environmentally mediated shifts in the strength of species interactions. First, environmental change can alter per-capita interaction strength (i.e., the effect of a single individual on the density or population growth of another species). For example, changes in temperature, ocean pH, or dissolved oxygen can change the feeding rates of individual consumers (e.g., Sanford 2002b, Harvey & Moore 2017, Low & Micheli 2018). Second, the total impact of a species (or per-population interaction strength) is also influenced by changes in its population density. For example, predation intensity might increase if environmental changes increase the recruitment or abundance of a predator or the proportion of a predator population that is actively foraging (Sanford 1999, Kordas et al. 2011).

The potential for environmental change to drive a complex combination of direct and indirect effects is illustrated by recent changes in macroalgal communities in many marine ecosystems (Wernberg et al. 2013, Vergés et al. 2016, Teagle & Smale 2018, Rogers-Bennett & Catton 2019, Zacher et al. 2019). Increasing ocean temperatures can have direct effects that impede the growth of canopy-forming macroalgae in temperate regions (Harley et al. 2012, Muth et al. 2019). At the same time, macroalgal abundance in some marine communities can be impacted indirectly when increasing ocean temperatures alter species interactions, such as competition (Zacher et al. 2019) or herbivory (Vergés et al. 2014, Rogers-Bennett & Catton 2019). Increases in herbivory associated with warming can involve both per-capita and density effects (Franco et al. 2015). For example, in Panama, per-capita rates of consumption (i.e., bites per minute) by herbivorous parrotfish increased fourfold over an 8°C range of increasing temperature (Smith 2008). In addition, warming temperatures have facilitated poleward range expansions and increases in the population density of warm-adapted herbivores, including sea urchins and fish in some temperate regions, thus increasing the per-population effect of herbivores on macroalgal populations (Johnson et al. 2011, Vergés et al. 2014). Increasing temperature can also directly affect the demography and relative abundance of warm-adapted versus cool-adapted kelps, with cascading effects on facilitation and community composition (Wernberg et al. 2011, Teagle & Smale 2018).

3. LINKING ENVIRONMENTAL CHANGE TO ECOLOGICALLY RELEVANT PROCESSES THROUGH A PHYSIOLOGICAL LENS

Within this milieu of direct and indirect effects, comparative physiology can provide important insights into the variability of species responses to environmental change. Central to comparative

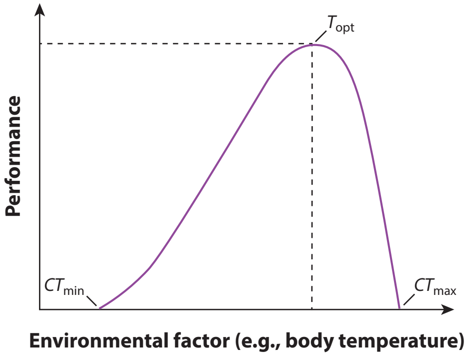

Figure 1

A generalized performance curve. Measures of organismal performance (rates of respiration, locomotion, growth, etc.) vary with an environmental factor, such as body temperature in this example for an ectothermic organism. Peak performance occurs at the organism's thermal optimum (T_{opt}). The critical thermal minimum (CT_{min}) and critical thermal maximum (CT_{max}) represent its lower and upper thermal limits, respectively.

physiology is the concept of the performance curve (Sinclair et al. 2016, Somero et al. 2017). Physiologists have long recognized that the relationship between an organism's environment and its performance is nonlinear (**Figure 1**). For many abiotic factors, there is a range of values over which the organism's performance is optimized, with declining performance under more extreme lower and upper values. Performance curves for a given environmental variable can be characterized by a number of parameters, including optimal conditions for peak performance and the critical upper and lower limits beyond which the organism cannot survive. Environmental conditions often select for adaptive variation in these physiological parameters both among and within species (Spicer & Gaston 1999, Kingsolver & Buckley 2017). For example, species that occupy habitats with warmer mean temperatures typically have higher optimal temperatures (T_{opt}) (Somero 2002, Somero et al. 2017). Similarly, organisms that reside in habitats with greater thermal variability often experience selection for broader thermal niches between their critical thermal minimum (CT_{min}) and critical thermal maximum (CT_{max}) (Compton et al. 2007, Sunday et al. 2011, Kingsolver & Buckley 2017). Within species, performance curves also often vary among life stages (Sinclair et al. 2016) and populations (Sanford & Kelly 2011). Collectively, these differences in performance curves, as well as differences between organisms' local and optimal environments, drive variability in species responses to environmental change.

A prevailing view among ecologists is that organisms within a community are well adapted to mean local environmental conditions (e.g., Hoegh-Guldberg & Bruno 2010). Although this may be true on average (A.R. Hughes et al. 2018), many organisms in nature spend substantial amounts of time under conditions that are outside of their optimal range. For example, Jurriaans & Hoogenboom (2019) examined the physiologies of two coexisting coral species at multiple sites in different regions of the Great Barrier Reef in Australia. Local temperatures frequently differed from conditions required for optimal coral performance, indicating that neither coral species was perfectly acclimatized or adapted to its environment. This is especially true for species inhabiting environments with considerable temporal variability, where they must contend with episodic fluctuations in temperature, dissolved oxygen concentrations, and pH (Bernhardt et al. 2018, Kroeker et al. 2020a).

Indeed, concerns have been raised that performance curves are almost always characterized under static environmental conditions (Dowd et al. 2015). This simplification neglects the reality that many marine ectotherms experience considerable environmental variability, including variability occurring over timescales much shorter than those projected for global environmental change. Importantly, when environmental conditions vary over time, performance averaged across this period does not equal performance measured at the mean condition. This outcome emerges from Jensen's inequality, a mathematical descriptor that highlights the effects of nonlinear averaging (Jensen 1906). Depending on the shape of the performance curve and where an organism lies along its curve, environmental variability can either increase or decrease performance compared with that predicted for static conditions, even when the mean does not change (Sinclair et al. 2016, Bernhardt et al. 2018). Given that both the mean and variance of many environmental drivers are shifting with climate change (Kroeker et al. 2020a), there is a strong need for additional work to understand the separate and interactive effects of these changes on organismal performance (Dowd et al. 2015).

Physiological variation in how species within a community respond to changes in the mean of variance of their environment is often associated with differing geographic or vertical distributions, evolutionary histories, phylogeny, and fitness of life history trade-offs (Somero 2002, 2005, 2010). For example, temperate marine communities often include a mix of species with different thermal performance curves that reflect variation in their biogeographic distributions [e.g., southern ranging, northern ranging, and cosmopolitan species (sensu Sagarin et al. 1999)]. Thus, coexisting species within a community may occupy different positions on their thermal performance curves, such that a given change in the temperature regime is detrimental to the performance of some community members while being beneficial for others (Harley et al. 2017). This, combined with the nonlinear shapes of performance curves, can lead to very different responses to global environmental change even among coexisting species that share similar ecological traits or are closely related taxonomically. Moreover, marine communities do not always have an even mix of warm-affinity and cool-affinity species. Rather, there may be systematic biases such that in some geographic regions, the majority of species are typically below their thermal optima, whereas in other regions, the majority of species are above their thermal optima (Stuart-Smith et al. 2015). Such biases may lead to geographic variation in the sensitivity of the broader marine communities to ocean warming.

Physiological variation among community members is not limited to thermal performance. A given change in pH can also have vastly different effects on even closely related taxa within a community. For example, three species of coralline algae from the coast of France showed strong differences in how elevated $p\mathrm{CO}_2$ (i.e., ocean acidification) influenced rates of calcification and other physiological processes (Noisette et al. 2013). Similarly, four coral species that co-occur in Papua New Guinea responded in markedly different ways to elevated $p\mathrm{CO}_2$ (Strahl et al. 2015). In particular, two species experienced a striking decline in calcification when exposed to high $p\mathrm{CO}_2$, whereas net calcification was unaffected in the other two species. Variability in response to ocean acidification is also likely to be especially pronounced among marine autotrophs, with responses largely tied to their inorganic carbon physiology (Koch et al. 2013). For example, naturally acidified volcanic vents are associated with a shift toward macroalgal species that are able to utilize the additional CO_2 directly or save energy by downregulating a carbon-concentrating mechanism (Cornwall et al. 2017).

4. CONSEQUENCES OF ASYMMETRIES IN PERFORMANCE CURVES FOR SPECIES INTERACTIONS

If interacting species have asymmetries between their performance curves, a given environmental change may affect the species differently and alter the strength or outcome of a species

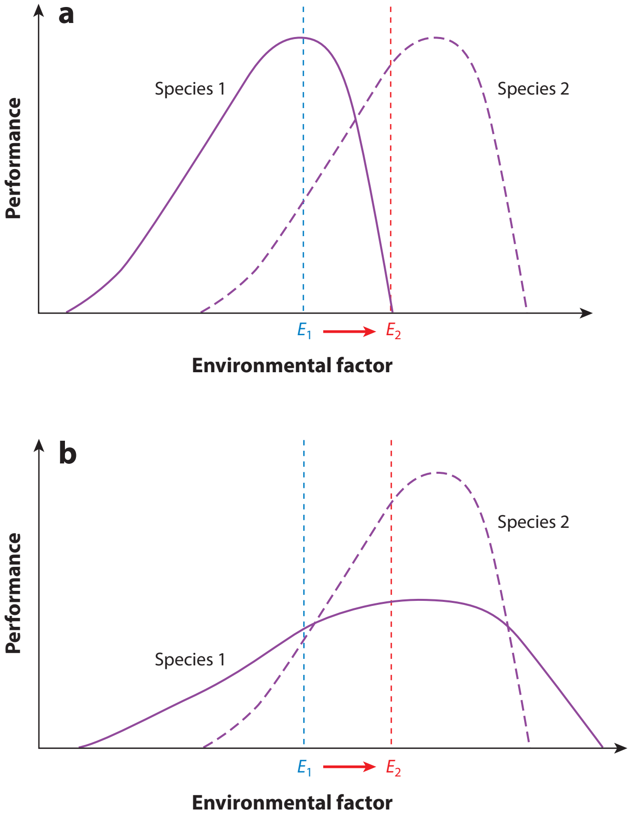

Figure 2

Asymmetries between performance curves. (*a*) Species 1 and 2 differ in their environmental optima. An increase in the environmental factor from E_1 (*blue dotted line*) to E_2 (*red dotted line*) leads to a decrease in performance for species 1 but an increase in performance for species 2. (*b*) Species 1 and 2 share the same environmental optima, but the shapes of their performance curves differ. An increase in the environmental factor from E_1 to E_2 leads to an increase in the performance of both species, but species 2 responds more strongly.

interaction. Performance curves can differ between species in several ways (Kordas et al. 2011, Dell et al. 2014). For example, curves can be partially overlapping such that two species have different optimal conditions for peak performance and different critical upper and lower limits (**Figure 2*a***). Alternatively, performance might peak at the same environmental value, but two curves might have different shapes, such that the rates or magnitudes of response to the same environmental change differ between two species (**Figure 2*b***). Such asymmetries between performance curves mean that environmental change could shift the balance between two competing species or might alter the interactions between a consumer and its resource or a parasite and its host (Byers 2021).

Given that coexisting species frequently differ in their physiological optima and tolerance ranges, global environmental change can alter competitive interactions and lead to shifts in relative dominance based on where species reside on their performance curves. Lord & Whitlatch (2015) documented how physiological variation in thermal performance mediated competitive

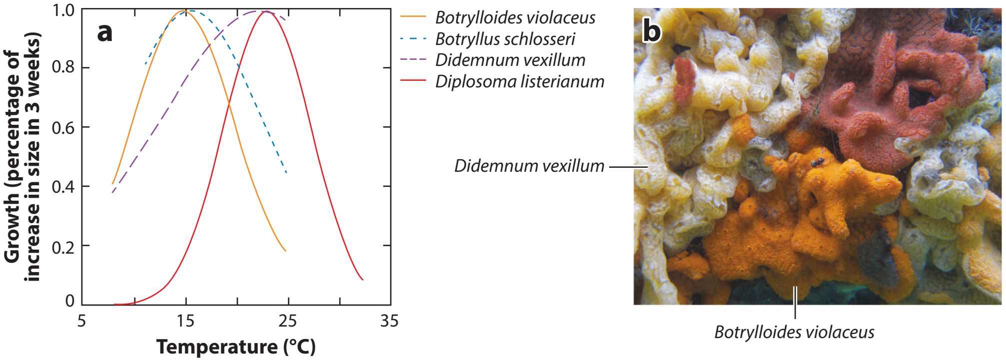

Figure 3

(*a*) Temperature-dependent growth in four species of compound tunicates. Coexisting species within marine fouling communities can occupy different portions of their thermal performance curves and thus respond differently to temperature increases. (*b*) Warm-adapted *Didemnum vexillum* (*off-white color*) overgrowing colonies of cool-adapted *Botrylloides violaceus* (*orange* and *rose colors*) in Connecticut, USA. Figure adapted with permission from Lord & Whitlatch (2015); copyright 2015 Ecological Society of America. Photo by Joshua Lord.

interactions among members of benthic fouling communities, including tunicates and encrusting bryozoans. In particular, the fouling communities studied included a mix of species with different biogeographic affinities. When temperatures were increased experimentally, species experienced slower growth if they were in the southern (warmer) portion of their geographic ranges but accelerated growth if they were in the northern (cooler) portion of their ranges (Lord & Whitlatch 2015). Since the thermal performance curves of these interacting species were offset (**Figure 3**) and reflected the different geographic ranges of these species, a temperature increase in a given geographic region increased the growth rates of some community members and depressed the growth of others. This led to increased overgrowth by the faster-growing species and altered competitive outcomes. Other studies suggest that increasing temperature may allow nonnative species to outcompete native species in fouling communities because the former are often introduced from warmer regions—again highlighting the importance of biogeographic and physiological context (Somero 2011, Sorte & Stachowicz 2011). Modeling approaches also suggest that climate change may alter the species composition of fouling communities as a result of the temperature dependence of growth and competitive interactions among a small group of key species (Sorte & White 2013).

Changes in other environmental factors may also play a similar role in mediating competition between species with differing physiologies. For example, declines in pH have been associated with a reversal in competitive dominance within an assemblage of crustose coralline algae in Washington State, USA (McCoy & Pfister 2014). In particular, when field experiments were repeated over time at a site with declining pH (Wootton et al. 2008), the formerly dominant alga (*Pseudolithophyllum muricatum*) that had won 100% of competitive bouts for space in the earlier trials (in the 1980s) won less than 25% of the bouts in the 2010s. Over this same 30-year period, the growing edge of *P. muricatum* became substantially thinner, impeding its ability to overgrow competitors (McCoy & Ragazzola 2014). Similarly, competitive interactions varied among benthic species along a spatial gradient of pH associated with volcanic CO_2 vents in the Mediterranean Sea (Kroeker et al. 2013b). Notably, calcareous species were overgrown by fleshy algae in areas of low pH, where the growth rates of the latter were increased. A similar pattern of competitive dominance with soft corals and fleshy macroalgae replacing hard corals and calcareous species has been documented near naturally acidified volcanic seeps in the western Pacific (Inoue et al. 2013, Enochs et al. 2015, Agostini et al. 2018), suggesting that altered competitive interactions and shifts in community composition may be a common response to ongoing declines in ocean pH (Wootton et al. 2008, Brown et al. 2018).

As with competitors for space, consumers within the same community may also respond quite differently to the same environmental change due to underlying physiological variation among species. A study of turban snails (*Tegula* spp.) found that the effects of increasing temperature on rates of snail herbivory were correlated with biogeographic affinity (Yee & Murray 2004). Although these species co-occur in southern California, warming temperatures to 23°C increased the feeding rate of the species with a geographic range that included lower latitudes (*Tegula aureotincta*) but decreased the feeding rate of the more northern, cool-adapted species (*Tegula brunnea*). Similarly, an increase in water temperature from ~12.5°C to 16.5°C led to a striking decrease in per-capita predation by the sunflower sea star (*Pycnopodia helianthoides*) but a 47% increase in predation by the ochre sea star (*Pisaster ochraceus*) (Gooding et al. 2009, Bonaviri et al. 2017). Although both species overlap in distribution in the shallow subtidal zone along the west coast of North America, *P. ochraceus* also ranges into the low- and mid-intertidal zone and thus is likely more temperature tolerant (Pincebourde et al. 2008, Bonaviri et al. 2017). The observation that consumers within the same community differ in their performance curves suggests that extreme events and longer-term shifts in ocean conditions may alter the relative impacts of some consumers within a community.

Moreover, a given consumer and resource might also differ from each other in their responses to environmental change (Kordas et al. 2011, Dell et al. 2014, Cheng et al. 2017, Gaylord et al. 2019). Dell et al. (2014) provided a framework for understanding how such asymmetries might alter the interaction between a consumer and resource under a scenario of environmental change. For example, interacting species can differ in how changes in temperature, pH, and dissolved oxygen influence metabolism rates, locomotion, and encounter rates, and these asymmetrical responses can increase the frequency of interactions between a consumer and its resource (Dell et al. 2014, Gaylord et al. 2019, Jellison & Gaylord 2019). Predator–prey interactions in the shallow subtidal zone of southeast Australia provide a good example of the ecological consequences of such asymmetries (Figueira et al. 2019). In this region, tropical and temperate fish species co-occur and are vulnerable to predation by temperate reef fish. Experiments demonstrated that as temperature increased to 25°C, the burst swimming speed of the tropical prey fish also increased. By contrast, the swimming speeds of both the temperate prey and the predator declined at 25°C. These asymmetrical responses to ocean warming resulted in tropical prey that were less vulnerable to predation relative to the temperate prey. This effect may facilitate the range expansion of tropical fish into this region if warming temperatures weaken the ability of resident temperate predators to control their populations (Figueira et al. 2019).

5. DEVIATIONS FROM THE OPTIMUM: ENERGETIC CONSEQUENCES AS A COMMON CURRENCY IN A MULTISTRESSOR WORLD

Variation in performance curves among species reflects underlying differences in physiological adaptation or acclimatization. While responses to environmental change may be influenced by acclimatization, these plastic physiological responses are constrained by trade-offs and evolutionary history (Somero et al. 2017). For example, differences in optimal temperatures (T_{opt}) can reflect selection for adaptive differences in protein structure and function associated with differing biogeographic and/or vertical distributions (Somero 2002, 2005). Similarly, variation among species in thermal tolerance (e.g., $CT_{\max}$) can arise from adaptive differences in cardiac function, the heat shock response, or other mechanisms (Somero 2010). Moreover, the most warm-adapted species (e.g., those from low latitudes or high intertidal habitats) are often those with the least ability to increase their thermal tolerance through acclimatization (Stillman 2003). These species with the least scope for acclimatization may be particularly sensitive to temperature increases associated with global environmental change (Stillman 2003, Somero 2010).

Performance curves also point to the central role of energetics in understanding physiological responses to environmental change (Somero 2002). When abiotic changes force species to spend more time under suboptimal conditions, these departures impose costs on the organism's energy budget. Although these sublethal effects are often neglected relative to environmental extremes and lethal limits, the energetic costs of seemingly minor environmental changes can have pervasive effects on fitness (Liao et al. 2021). At the simplest level, the surplus energy available for activity, growth, and reproduction is dependent on how much energy is assimilated from food (after subtracting energy lost to excretion) and how much is spent on routine maintenance (i.e., basal metabolism) and repair. In the most basic form, the energy budget of a heterotroph can be represented as follows:

$$\text{energy assimilated from food} + \text{reserves} - (\text{maintenance} + \text{repair}) = \text{activity} + \text{growth} \\ + \text{reproduction}.$$

Environmental changes that increase maintenance and repair costs by deviating from their optima will decrease energy available for activity, growth, and reproduction without some level of acclimatization or compensation (Somero 2002) (**Figure 4**). These energetic considerations can in turn strongly mediate species interactions. For example, increased metabolic costs can decrease energy allocated to growth or reproduction, with direct consequences for competition between species. Alternatively, organisms facing increased energetic costs may seek to compensate by increasing consumption rates, with consequences for trophic interactions.

While considering interspecific variation in physiological responses to a single environmental change is a logical starting point, the multivariate nature of global change adds substantial complexity. In marine ecosystems, the physiological responses to warming, deoxygenation, and acidification are likely to be extensive and varied both within and across species (Somero et al. 2016). Moreover, the response to any one of these factors is likely to be dependent on the levels of the others (Crain et al. 2008, Kroeker et al. 2013a, Boyd et al. 2015). Understanding even the emergent organismal effects, much less the community or ecosystem effects, in this multivariate, changing environment is extremely challenging (Kroeker et al. 2017). While there is an extensive body of knowledge regarding thermal performance curves, less is known about patterns of variation in O_2 performance curves, and even less is known about the performance curves associated with ocean acidification as most experiments have focused on one or two levels of each driver (Boyd et al. 2018). Moreover, the potential for interactions among multiple environmental drivers requires moving beyond single-driver performance curves to consider more complex response surfaces (Harley et al. 2017, Boyd et al. 2018).

Considering the effects of global change on organisms' energetic requirements may provide a common currency for accounting for the physiological response to multiple environmental changes (Sokolova 2013, Gilman 2017). Furthermore, the organismal response to alterations in energetic requirements can also be linked to changes at the community and ecosystem levels through species interactions.

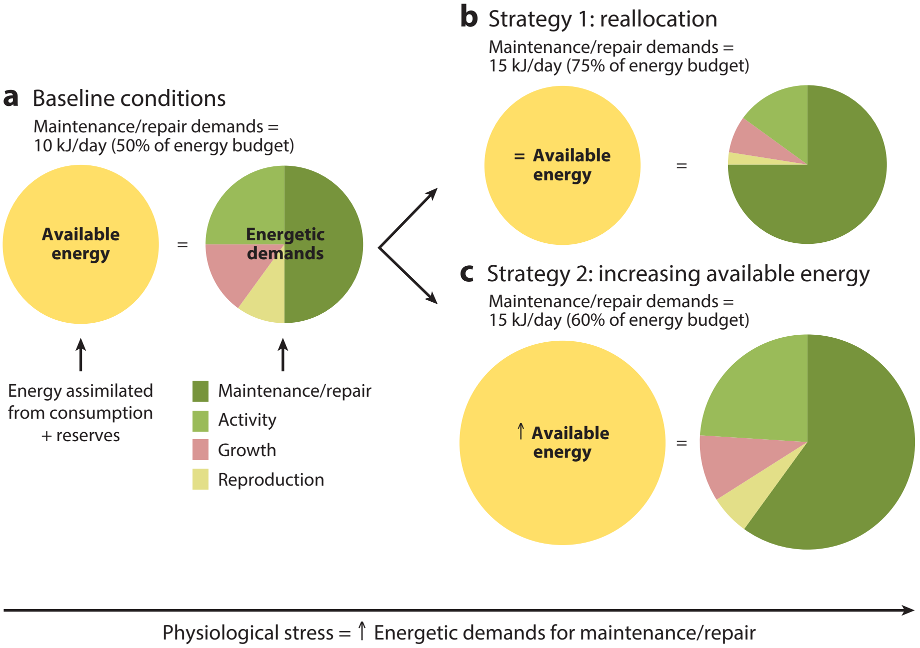

Figure 4

Conceptual diagram outlining two potential strategies for coping with physiological stress using a hypothetical energy budget for an iteroparous heterotroph. In all scenarios, the energy dedicated to maintenance/repair, activity, growth, and reproduction cannot exceed the available energy from consumption and reserves. (*a*) Under baseline conditions, the energetic demands for maintenance/repair are 10 kJ/day, or 50% of the hypothetical energy budget. (*b*) As physiological stress caused by global change increases the energetic demands for maintenance/repair to 15 kJ/day (75% of the energy budget), an organism must reallocate available energy away from activity, growth, or (most commonly) reproduction. (*c*) Alternatively, an organism may sometimes be able to meet the increased costs of maintenance/repair by increasing the available energy through greater consumption. Growth and reproduction may be maintained at baseline levels, whereas activity may increase to support greater consumption. In this scenario, maintenance/repair constitutes 60% of the total energy budget. The relative allocations to reproduction and growth are likely to differ among organisms with different life history strategies as well as among life stages.

6. THE ENERGETIC CONSEQUENCES OF GLOBAL CHANGE IN THE OCEAN

6.1. Ocean Warming

Decades of research on thermal physiology and the metabolic theory of ecology (Brown et al. 2004, Somero et al. 2017) have provided a strong foundation for understanding the energetic consequences of ocean warming. Biochemical reactions underlie all physiological responses, and each of these reactions is temperature dependent (Brown et al. 2004). Thus, each reaction and the accompanying higher-level processes have thermal performance curves. While an organism's thermal optima can (and often do) differ for different processes (Schulte et al. 2011), the shape is often unimodal (**Figure 5*a***). In this scenario, basal metabolic costs—the energetic requirements necessary for the maintenance and survival of the organism—increase with temperature to this optimum, before a sharp decline as temperatures become more physiologically stressful. By contrast, some marine organisms have thermal performance curves with a broad plateau or bimodal shape due to adaptive metabolic depression with increasing temperatures (Somero et al. 2017,

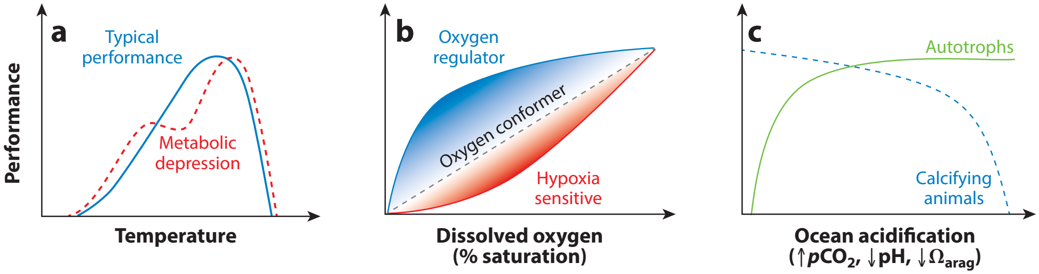

Figure 5

Generalized response curves for how performance (e.g., growth rate) varies with increasing temperature, dissolved oxygen concentrations, and ocean acidification. (*a*) Performance (e.g., heart rate) typically varies as a unimodal function of temperature (*blue curve*), although metabolic depression can result in a plateau as temperature increases (*red dashed curve*) (Liao et al. 2021). (*b*) The shapes of performance curves for dissolved oxygen differ among taxa that are oxygen regulators (*blue curve*), oxygen conformers (*gray dashed line*), and hypoxia sensitive (*red curve*). Different species can have performance curves that fall along the continuum among these strategies, as indicated by the shading between the curves. (*c*) The shapes of the performance curves for ocean acidification [i.e., increasing pCO_2, decreasing pH, and decreasing aragonite saturation state (Ω_{arag})] are poorly resolved for most taxa. For autotrophs, performance may increase with increasing pCO_2 (*green curve*) (Hutchins et al. 2013), whereas some calcifying animals, such as oyster larvae, experience decreasing growth with decreasing Ω_{arag} (*blue dashed curve*) (Waldbusser et al. 2015). Some evidence suggests unimodal performance curves for other animal taxa (Ries et al. 2009).

Liao et al. 2021) (**Figure 5*a***). In this scenario, marine organisms may be able to limit their energetic demands as temperatures increase, at least until more extreme temperatures are reached. Interspecific variation in the energetic costs of future warming will depend on the shape and steepness of the thermal performance curve (e.g., Q_{10} effects) and where an organism resides on the curve in their environment. The Q_{10} value is a metric used by physiologists to express how much the rate of a biological process changes with an increase in temperature of 10°C. Typically, Q_{10} values range from 2 to 3, but they can be much higher if a species is highly sensitive to a given temperature change (Somero et al. 2017). Analogous considerations apply to describing the effects of changes in oxygen, pH, and other environmental factors.

There are also energetic costs associated with exposure to more extreme temperatures, and marine organisms have numerous physiological mechanisms to cope with these stressful conditions (Hofmann & Todgham 2010, Somero et al. 2017). Most familiar to ecologists is probably the use of heat shock proteins (Hsps)—a class of molecular chaperones that are synthesized to broadly repair cell damage associated with thermal stress (Tomanek 2008). While this is only one of many mechanisms species may use to tolerate stressful temperatures (Somero 2002), the substantial research on acclimation and adaptation of the heat shock response (i.e., the induction of Hsp synthesis) highlights the potential energetic costs of these physiological responses. For example, snails (*Tegula* spp.) found higher in the rocky intertidal zone that are exposed to warmer temperatures have a higher induction temperature and a more robust Hsp response than their congeners found in the lower, cooler intertidal zones (Tomanek & Somero 1999). The close relationship between the environmental temperature organisms are exposed to and their heat shock responses suggests that species are fine tuning their responses because synthesizing these proteins is energetically costly (Somero 2002). The potential for wide interspecific variation in energy costs from the synthesis of stress-related proteins is also suggested by recent genomic studies that have shown considerable amplification of the numbers of genes encoding stress proteins, such as Hsp70, in species that regularly encounter extremely high temperatures (e.g., Zhang et al. 2016). Switching on several dozen genes to cope with thermal stress seems likely to afford a high level of protection to such species, but at a very high energy cost. Thus, both gradual warming and exposure to more extreme temperatures are likely to increase species' energetic costs in a future ocean (but see Liao et al. 2021 for discussion of adaptive metabolic depression).

6.2. Deoxygenation

As temperatures rise, marine organisms must also cope with reduced oxygen concentrations caused by lower oxygen solubility and decreased oxygen transport to the ocean's depths (Levin & Breitburg 2015, Breitburg et al. 2018). While the ecological effects of hypoxic events ($<$1.4 mL/L) associated with eutrophication have garnered considerable attention (Gray et al. 2002, Diaz & Rosenberg 2008), less is known about the sublethal effects of less extreme reductions in oxygen on species' energetic costs. Whereas the shapes of thermal performance curves are generally similar among species, the shapes of oxygen performance curves (e.g., oxygen consumption or metabolic rate as a function of environmental oxygen concentrations) can vary considerably among members of a community. Marine organisms can generally be divided into three groups—oxygen regulators, oxygen conformers, and those that are hypoxia sensitive (Prosser 1955, Leiva et al. 2018) (**Figure 5*b***)—although there is considerable variability and overlap among these categories (Mueller & Seymour 2011). Oxygen regulators (i.e., species that can maintain oxygen consumption rates across a range of oxygen levels in the environment) may compensate for reduced oxygen concentrations through several physiological mechanisms, including increasing ventilation rates and cardiac output, using respiratory molecules with a higher affinity for oxygen, or increasing the number of cells that circulate oxygen (Childress & Seibel 1998, Lefevre et al. 2017). In addition, some species may use anaerobic respiration for short periods of time (De Zwaan & Putzer 1985). Some of these mechanisms, including anaerobic metabolism, incur higher maintenance costs and require increased energy input or a reallocation of energy from reproduction, growth, or activity to maintenance. For oxygen conformers, on the other hand, oxygen consumption and metabolism generally scale with the oxygen available in the environment (Prosser 1955). For these species, energetic demands as well as overall performance will decrease with decreasing oxygen concentrations. Because of the differences in the shapes of the performance curves for regulators and conformers, temporal environmental variability in oxygen will have opposing effects on performance. Variability will decrease performance for oxygen regulators but will increase performance for conformers (compared with that predicted from the performance curve based on static conditions). For both regulators and conformers, there are hard constraints on the combinations of temperatures and dissolved oxygen concentrations that are viable for survival. When the oxygen supply in a habitat declines below the basal metabolic demand for maintenance, the organism is no longer able to persist in that environment (Deutsch et al. 2015). Finally, species that are sensitive to hypoxia show steep, nonlinear decreases in oxygen consumption and metabolic rates in response to even minor declines in environmental oxygen supply (**Figure 5*b***). For these species, energetic costs and performance are likely to decrease significantly with decreasing oxygen concentrations.

To date, there is a limited understanding of what drives variation among taxa along the continuum from oxygen regulators to oxygen conformers to hypoxia-sensitive species, and phylogenetic associations with these categories are not clear (Alexander & McMahon 2004). Whereas many teleost fish are considered oxygen regulators, the physiological responses among marine invertebrates are much more varied. Indeed, there can be variation in oxygen regulation among individuals of the same species, with smaller body sizes and a reduced body condition index associated with less oxygen regulation (e.g., Bayne 1971). Such intra- and interspecific variation in oxygen regulation may have important, but largely unexplored, consequences for species interactions and communities exposed to deoxygenation (Mislan et al. 2017).

6.3. Ocean Acidification

Although our understanding of the physiological responses to ocean acidification is more nascent than that of warming and deoxygenation, the energetic consequences of exposure to low pH and/or low carbonate saturation states are beginning to emerge. In particular, ocean acidification is thought to increase the costs of maintaining the intercellular acid–base balance necessary for physiological processes across a wide range of species (Pan et al. 2015, Frieder et al. 2018), as well as the costs of maintaining calcified structures (Cohen & Holcomb 2009, Melzner et al. 2011, McCulloch et al. 2012). In addition to the ion pumping necessary to maintain an intracellular acid–base balance, detailed physiological studies of oyster and sea urchin larvae have demonstrated that increased protein synthesis and turnover in response to acidification can also increase energetic costs (Pan et al. 2015, Frieder et al. 2018). By contrast, ocean acidification is likely to decrease the energetic costs for many autotrophs (Connell et al. 2013) by increasing the availability of the substrates used for photosynthesis or by decreasing the need for energetically costly carbon-concentrating mechanisms (Cornwall et al. 2017).

Despite these generalities, our understanding of ocean acidification response curves is limited. The few studies that have used regression designs for experimental exposure to acidification suggest that the functional responses of autotrophs may plateau at higher pCO_2 levels (Hutchins et al. 2013) (**Figure 5*c***), while the functional responses of heterotrophs may have a range of shapes or may even be linear within the range of pH/carbonate saturation states that organisms are likely to experience under near-future global change scenarios (Ries et al. 2009). Interspecific variation in response to ocean acidification may be related in part to species' ability to regulate extracellular and intracellular pH, as well as their mechanisms for calcification. All organisms regulate their internal acid–base balance to some degree through passive buffering (Seibel & Walsh 2003), but regulation (and associated energetic costs) is more common among fishes and species with more active lifestyles (Melzner et al. 2009). In addition, variability in the responses of calcifiers has been attributed to the degree to which species regulate pH/saturation state at the site of calcification (McCulloch et al. 2012). Variation in the responses among marine autotrophs is likely to depend on the degree of calcification, as well as the inorganic carbon physiology used for photosynthesis (Koch et al. 2013, Cornwall et al. 2017). Future research regarding the shapes of response curves for ocean acidification remains an important priority for understanding organismal variability in response.

6.4. Multidimensional Response Surfaces

Organisms' physiological and ecological responses to each of the environmental factors discussed above will likely depend on the background conditions and/or changes in other abiotic drivers (Crain et al. 2008, Boyd et al. 2015, Deutsch et al. 2015). While the number of manipulative experiments examining two or more variables has increased substantially in recent years to inform our understanding of interactions (e.g., Kroeker et al. 2013a), most of these studies have used factorial designs with a limited number of treatment levels for each variable—often focused on current versus end-of-century comparisons. To understand more nuanced differences in species responses to ongoing change or variability in environmental drivers within a community, it will be important to understand the shapes of multidimensional response surfaces. Quantifying complex response surfaces that describe organismal performance as a function of two or more environmental variables, however, is logistically challenging to do experimentally, and the results are often difficult to interpret (Boyd et al. 2018). Several approaches have been proposed to address these challenges that focus on identifying the most relevant levels of each variable and using a reduced or collapsed design (sensu Boyd et al. 2018) to assess experimentally. For example, when two or more environmental drivers covary (e.g., temperature, pH, and dissolved oxygen in upwelling ecosystems), studies can create response curves or surfaces that focus on the more limited combinations of conditions that organisms are likely to experience in nature (E.M. Donham, L.T. Strope, S.L. Hamilton & K.J. Kroeker, manuscript in review).

7. LINKING ENERGETICS TO SPECIES INTERACTIONS

As noted in Section 4, environmental changes often alter species interactions (e.g., competition and consumption), and some of these shifts are direct responses to changes in the energy budgets of the interacting species. In response to environmentally mediated increases in energetic demands, ectotherms may seek to increase their feeding rates, which has implications for the per-capita strengths of interactions between consumers and their resources (e.g., Sanford 2002b). Whether an organism increases its consumption rate or meets energetic shortfalls by reallocating energy from other processes (**Figure 4**) depends on several factors, including the physiological considerations discussed in Sections 5 and 6, as well as ecological considerations, such as whether resources/prey are readily available and whether there are trade-offs between increased foraging and predation risk. Changes in energetic demands that result in altered growth rates can also affect the per-capita strengths of competitive interactions, especially for sessile species, where growth is the primary determinant in the competition for space (Wootton et al. 2008, Kroeker et al. 2013a, McCoy & Pfister 2014). Finally, altered growth rates and energy reallocation from reproduction can affect demographic rates more broadly, with potential effects on population size and per-population trophic interaction strengths.

7.1. Warming and Consumption

To understand how environmentally mediated changes in energetics may affect the per-capita strengths of trophic interactions, an understanding of the direct effects on both the consumer and its resource(s) is necessary. For example, while warming may increase a predator's attack rate to meet increased energetic costs, warming might also affect the rate at which prey flee from the predator (Dell et al. 2011, 2014). Indeed, systematic variability in the thermal dependence of consumer or resource traits could ultimately determine the outcome of trophic interactions in a warmer ocean, even if warming increases a consumer's energetic demands. For example, a meta-analysis of the thermal dependence of ecological traits found that fleeing responses are more sensitive to temperature than attack rates, on average (Dell et al. 2011). Furthermore, warming may increase the per-capita impacts of herbivores on primary productivity because of the greater thermal sensitivity of respiration-limited metabolism versus photosynthesis-limited metabolism (O'Connor 2009). However, at the population level, the emergent effects of warming on herbivore–primary producer interactions will also be influenced by the temperature dependence of ecological processes that influence herbivore density (Gilbert et al. 2014).

7.2. Deoxygenation and Consumption

While some oxygen regulators may maintain consumption rates when exposed to moderate decreases in dissolved oxygen (Sobral & Widdows 1997, Desai & Prakash 2009), most studies have documented decreases in consumption rates in response to hypoxia, including in marine fishes (Chabot & Dutil 1999) and invertebrates (Le Moullac et al. 2007, Low & Micheli 2018). Decreasing consumption rates may be an adaptive response to intermittent or short-term hypoxia by limiting energy costly activities such as foraging and digestion (Thomas et al. 2019), although this strategy will inevitably impact growth negatively (Wu 2002). On the other hand, deoxygenation in the ocean is compressing the vertical zone that pelagic predators (e.g., tuna and billfishes) and their prey can occupy (Stramma et al. 2011, Mislan et al. 2017). This may increase encounter rates between predator and prey in the narrow surface mixed layer, leading to possible increases in consumption rates through this ecological mechanism (Prince & Goodyear 2006).

7.3. Ocean Acidification and Consumption

The effect of near-future experimental acidification on organisms' consumption rates is varied. While a synthesis of the literature found that exposure to experimental ocean acidification typically decreased consumption rates (Clements & Darrow 2018), examples of increased consumption rates exist (Saba et al. 2012, Kamya et al. 2017, Rodríguez et al. 2018). The heterogeneity in response to acidification may be due to species-specific factors (e.g., behavior) or condition-specific factors (e.g., $p\mathrm{CO}_2$ thresholds) (Frieder et al. 2018). Several field studies have suggested that higher food availability can offset the negative effects of acidification in natural settings (Thomsen et al. 2013, Kroeker et al. 2016, Doubleday et al. 2019), although it remains unclear whether these effects arose from increased consumption or higher-quality resources/prey. Exposure to elevated $p\mathrm{CO}_2$ in laboratory experiments and at volcanic vents has revealed a range of effects on the nutritional quality of macroalgae, including decreased C:N ratios (Falkenberg et al. 2013, Vizzini et al. 2017), such that the emergent effects on herbivore–producer interactions are still unclear (Poore et al. 2013). Analogous to effects of temperature and hypoxia on consumer–resource interactions, ocean acidification may also differentially impact predator and prey species through effects on locomotion, chemoreception, physical defenses, and behavioral responses (Ferrari et al. 2011, Kroeker et al. 2014, Jellison et al. 2016, Gaylord et al. 2019).

Although altered consumption rates may influence per-capita interaction strengths directly, the emergent effects at the community level ultimately depend on how these changes affect the growth, demographics, and relative abundances of the consumer and prey. For example, a higher thermal dependence of metabolic rates (as a proxy here for energetic costs) versus consumption rates suggests that warming can cause a decrease in consumer growth and fitness, even when organisms increase their consumption (Lemoine & Burkepile 2012, Iles 2014). Thus, although per-capita consumption rates might increase with warming, there can still be declines in growth rates, with implications for competitive interactions and population dynamics.

8. TROPHIC MISMATCHES ARISING FROM CHANGES IN PHENOLOGY AND ENERGETICS

Another important consideration regarding how altered energetics might influence species interactions and community structure is whether adequate resources are available to consumers in a changing ocean. Many consumers have evolved to take advantage of fluctuations or seasonal pulses in resources (Cushing 1969, 1990). By contrast, temporal misalignments in the relative abundances of consumers and their resources due to variability in their responses to environmental changes are referred to as phenological mismatches or trophic-level asynchrony. Such mismatches can be caused by differences in the cues and environmental drivers used by consumers and their resources, with some primary producers responding strongly to seasonal changes in light and many heterotrophs relying on temperature-based cues. For example, using a 44-year time series of pelagic phytoplankton production in the North Sea, Edwards & Richardson (2004) demonstrated a phenological mismatch between diatoms at the base of the food web and higher trophic levels. As the ocean has warmed, the peaks in abundance of most higher trophic levels have shifted earlier in the season, while the timing of peak abundance of diatoms shows much higher interannual variability and no change in the mean (Edwards & Richardson 2004). Similar phenological mismatches have also been documented in benthic communities. For example, a warming trend over a 30-year period in the Wadden Sea was associated with lower reproductive output and earlier spawning of the clam *Macoma balthica* but no change in the timing of the peak phytoplankton bloom that the clams rely on for food (Philippart et al. 2003). Moreover, the peak density of clam predators shifted earlier over the time series. Together, the mismatch in resources and the increase in predation pressure during a vulnerable life history stage led to a decline in *M. balthica* recruitment.

A global synthesis of observations demonstrates that mismatches may be more common in the ocean than on land and may be relatively substantial; the timing of spring and summer biological events in marine ecosystems has shifted 4.4 days earlier in the year, on average (Poloczanska et al. 2013). However, there is considerable variation among taxonomic and functional groups, with some taxa shifting much earlier than others. For example, peak abundances of invertebrate zooplankton and larval bony fish have shifted 11.6 and 11.2 days earlier on average, respectively, while phytoplankton blooms have only shifted 6.3 days earlier. This potential for trophic mismatches may serve as a one-two punch for consumer species that already have increased energetic demands associated with global change.

While more research has focused on how warming affects phenological events, increased energetic demands of consumers caused by warming or ocean acidification in periods or areas of naturally low resource availability can also cause trophic mismatches. For example, mussels (*Mytilus* spp.) in the Baltic Sea showed strong declines in growth and condition index when exposed to warming scenarios during the winter months. This was attributed to a strong effect of warm temperatures on the energetic demands of mussels (i.e., high Q_{10}), coupled with naturally low phytoplankton biomass during winter (Melzner et al. 2020). Interestingly, this effect on mussels was amplified at higher trophic levels. The growth of the sea star *Asterias rubens*, which feeds primarily on mussels, also declined significantly with winter warming. Because *A. rubens* did not increase its predation rate, the decline in sea star growth was strongly correlated with the lower condition index of the mussels in the experiment (Melzner et al. 2020). Importantly, this phenomenon is not limited to winter warming. Because colder water has higher CO_2 solubility, ocean acidification may be more pronounced during winter months in seasonally fluctuating environments, when primary producer biomass is often more limited by light or storms. In a study in subpolar kelp forests in Alaska, juvenile abalone (*Haliotis kamtschatkana*) experimentally exposed to future winter pH conditions lost body mass when they were fed the limited algal resources characteristic of winter months (Kroeker et al. 2020b). Together, these studies suggest that the effects of global change on species energetics can be exacerbated by seasonal mismatches in resource availability and quality.

9. ECOLOGICAL LEVERAGE POINTS

9.1. Linking Species Interactions to Community Change

The previous sections have highlighted how physiological variation and energetics can mediate the effects of environmental change on the intensity and outcome of species interactions. To what extent might these climate-driven changes in species interactions scale up to influence communities and ecosystems? A long history of theoretical and empirical studies in marine ecology indicates that not at all species interactions are equally important to the structure and dynamics of communities (Paine 1980). Rather, communities often include a subset of strong species interactions that have large effects on a community, nested among many weaker interactions (Paine 1992). For example, keystone species are strongly interacting species that have a large effect on communities, and one that is disproportionately large relative to their abundance (Power et al. 1996). Examples include sea otters, sea stars, sea urchins, and other species that exert a powerful influence on communities, often through predation or herbivory. On the other hand, foundation species are habitat-forming species such as corals, mussels, oysters, kelp, and seagrasses that also have a large total impact on communities through positive interactions with other community members (Sunday et al. 2017). Other species interactions with the potential to drive community-wide changes include parasitism and disease infections (especially when keystone and foundation species are impacted; Mouritsen & Poulin 2002) and mutualisms, such as those between symbiotic zooxanthellae and their coral hosts.

When these impactful species interactions are altered by environmental conditions, they may act as leverage points in the community that can magnify the effects of environmental change. Here, we define ecological leverage points (Sanford 1999) as key species interactions that are sensitive to abiotic change, such that relatively small changes in environmental conditions cause large changes at the community or ecosystem level. The leverage point concept has been applied in marine systems to understand how changes in temperature and pH might drive community-level changes via effects on predation, competition, or other key species interactions (Sanford 1999, Harley et al. 2006, Kroeker et al. 2013a, Sorte & White 2013). An analogous concept of the biotic multiplier has been proposed to describe top consumers that might amplify the effects of climate change, primarily in terrestrial ecosystems (Zarnetske et al. 2012, Urban et al. 2017). While both terms highlight similar pathways through which climate change might influence communities, the concept of ecological leverage points focuses attention on species interactions, rather than on species per se. This distinction recognizes that a given species may not have a universally high impact in all communities and contexts (Paine 1980, Power et al. 1996). In addition, in this review, we emphasize that a variety of species interactions can serve as ecological leverage points, including shifts in competitive dominance, intensification of predation/herbivory, increases in the frequency and severity of disease/parasite outbreaks, and disruption of facilitation/mutualism.

9.2. When and Where Are Leverage Points Likely to Occur?

As in physics and systems theory (Meadows 2008), the concept of an ecological leverage point emphasizes that a small amount of change force (in this case, change in an environmental driver) can translate into a large shift in system behavior (in this case, community structure and dynamics). Ecological leverage points thus require that a species interaction have a large community importance (sensu Power et al. 1996) and be sensitive to environmental change. Environmental sensitivity can occur in at least two forms. First, a species interaction may be environmentally sensitive if one or both species are living close to their physiological tolerance limits, such as those with a small thermal safety margin (Pinsky et al. 2019). For example, small increases in mean temperature can trigger loss of symbiotic zooxanthellae in coral hosts (i.e., coral bleaching), with widespread implications for the reef ecosystem (Baker et al. 2008). Alternatively, environmental conditions may be well within the tolerance range of the interacting species, but the rate of the species interaction may be affected strongly by a small environmental change (i.e., a high Q_{10} in a given region of a species' response curve). As one example of this latter phenomenon, the performance surfaces of a consumer and its resource may be strongly asymmetrical over a given range of environmental conditions, such that a small environmental change shifts the balance in the system from a resource surplus to a deficit (Harley et al. 2017).

Ecological leverage points have amplified the effects of climate change on the coral reef ecosystems of the Great Barrier Reef in Australia (**Figure 6**). Massive outbreaks of the crown-of-thorns sea star (*Acanthaster* spp.) periodically devastate coral reefs in the Indo-Pacific. Seasonal increases in water temperature (from ~24°C to 28–29°C) are associated with an approximate doubling of predation by *Acanthaster* cf. *solaris* on corals on the Great Barrier Reef (Keesing &

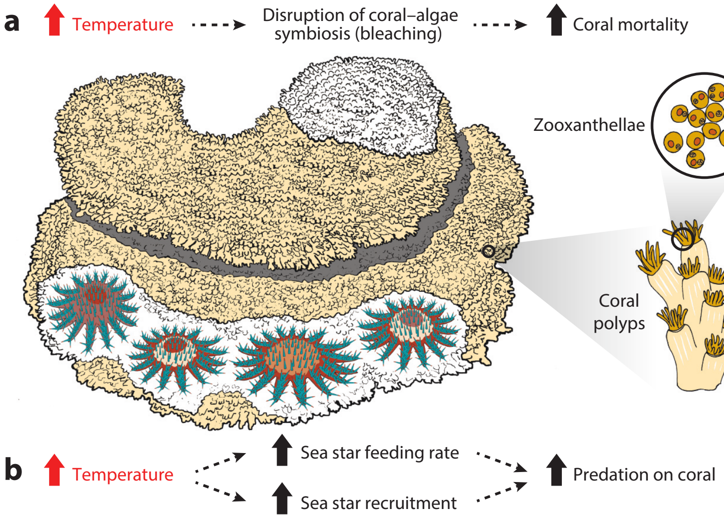

Figure 6

Ecological leverage points in coral reef ecosystems of the Great Barrier Reef, Australia. (*a*) Increases in ocean temperature can cause coral hosts (such as the table coral, *Acropora hyacinthus*) to lose their photosynthetic symbionts (*Symbiodinium* spp.), and this bleaching can contribute to widespread coral mortality. (*b*) Increases in mean ocean temperature may also contribute to increases in larval recruitment and population outbreaks of the crown-of-thorns sea star (*Acanthaster* spp.), as well as increases in per-capita feeding rates of sea stars on coral. Mass mortality of habitat-forming corals arising from these altered species interactions can transform coral reef ecosystems and threaten their long-term persistence.

Lucas 1992, Haszprunar et al. 2017). In Guam, where temperatures are typically 28–29°C, an *Acanthaster* cf. *solaris* outbreak killed 90% of corals inhabiting 38 km of coastline in less than two years (Birkeland & Lucas 1990). By contrast, in Hawaii, where water temperatures are often below 26°C, outbreaks of *Acanthaster* cf. *solaris* have historically spread slowly and have caused minimal damage to coral reefs (Birkeland & Lucas 1990, Kenyon & Aeby 2009). These observations suggest that the *Acanthaster*–coral interaction may function as an ecological leverage point on coral reefs, where relatively small increases in ocean temperature can contribute to large losses in coral cover. The metabolic rate of *Acanthaster* cf. *solaris* is strongly temperature dependent, with a high Q_{10} of 2–4 within the temperature range of 25–30°C (Birkeland & Lucas 1990). This suggests that the thermal sensitivity of this predator–prey interaction may be driven in part by the steep increase in energetic demand experienced by *Acanthaster* as temperatures exceed 25°C.

The influence of warming temperatures on the interaction between corals and their photosynthetic symbionts (*Symbiodinium* spp.) represents a second ecological leverage point in these coral reef ecosystems. Prolonged bleaching drives high levels of coral mortality, which can transform coral reef ecosystems through changes in species abundance and loss of habitat (T.P. Hughes et al. 2018). Many coral–algae symbioses occur close to their upper thermal limits, so sustained exposure to temperatures only 1–2°C above the average annual maxima is sufficient to cause coral bleaching and mortality (Baker et al. 2008). As a result of the major 2016 bleaching event, 30% of corals were killed on the Great Barrier Reef, which altered the structure and ecological functioning of large regions of this ecosystem (T.P. Hughes et al. 2018). While mortality during the early phases of the bleaching event resulted from the direct effects of warm water killing coral hosts, post-bleaching mortality of corals remained high into the austral winter and was likely a result of the disruption of the coral–algae symbiosis in affected hosts (Baker et al. 2008, T.P. Hughes et al. 2018).

These examples from the Great Barrier Reef illustrate how species interactions can amplify the effects of relatively small environmental changes. In addition to influencing communities through these indirect pathways, environmental change can alter demographic processes (such as reproduction or mortality), with direct consequences for populations. For example, a modest warming of 2°C increases the development and survival rates of *Acanthaster* larvae, likely contributing to population outbreaks of this keystone predator (Uthicke et al. 2015). After settlement, growth rates of juvenile *Acanthaster* also increase with increasing temperature and decreasing pH (Kamya et al. 2018). Similarly, as mentioned above, temperature increases can lead directly to mortality of corals, independent of the disruption of the coral–algae symbiosis. Thus, in many cases, community-level effects of climate change will arise through a combination of both indirect effects and reinforcing direct effects.

A variety of other ecological leverage points have been documented in marine ecosystems throughout the world (**Table 1**). These leverage points involve a broad range of species interactions, including competition, herbivory, predation, parasitism, disease, and mutualism. In most cases, the pathway through which these species interactions effect widespread changes in the community is through impacts on competitive dominants or habitat-forming foundation species, including kelps, corals, mussels, and others.

Most prior reviews of the potential for climate change to alter species interactions have focused on terrestrial and freshwater ecosystems and have neglected marine ecosystems (Tylianakis et al. 2008, Ockendon et al. 2014, Urban et al. 2017; but see Kordas et al. 2011). However, there are multiple reasons to expect that ecological leverage points might be particularly common and impactful in marine ecosystems. First, the spatial grain of environmental heterogeneity is often coarser in subtidal marine ecosystems than in terrestrial ecosystems. Ocean conditions (temperature, oxygen, and pH) can be relatively homogeneous over scales of hundreds of meters, and many benthic marine organisms are sessile or sedentary. Thus, subtidal marine organisms often have limited opportunities for behavioral regulation of the environmental conditions that they encounter, whereas mobile terrestrial organisms can exert behavioral control over the conditions that they experience by moving among nearby microhabitats with vastly different environments (Kearney et al. 2009, Sunday et al. 2011). Second, ectotherms in marine environments appear to be living closer to their upper thermal limits than those in terrestrial environments. This conclusion is supported by an analysis of thermal safety margins, defined as the difference between the upper thermal limit of a species ($CT_{\max}$) (**Figure 1**) and the 95th percentile of upper body temperatures the species experiences in the coolest microhabitat available (Pinsky et al. 2019). Marine ectotherms had smaller thermal safety margins than terrestrial ectotherms at all latitudes, and tropical marine ectotherms had the smallest safety margins overall. These considerations suggest that climate warming of a few degrees may often have a greater effect on the physiology of marine animals than on the physiology of their terrestrial counterparts. Lastly, trophic cascades tend to be stronger in marine systems than in terrestrial systems (Strong 1992, Shurin et al. 2002), suggesting that many marine food webs are shaped by a small number of strong species interactions. In particular, relative to terrestrial ecosystems, marine herbivores often exert stronger control over basal resources (Shurin et al. 2002). This suggests that interactions between marine herbivores and foundation species (e.g., sea urchin–kelp interactions) that are sensitive to environmental change might act as potent leverage points in many marine ecosystems (**Table 1**). Importantly, in some cases, the leverage exerted through herbivore–kelp interactions has been increased by the reduction of top predators in these ecosystems (Johnson et al. 2011, Rasher et al. 2020).

A growing body of research emphasizes that marine ecosystems can be characterized by tipping points, where a small increase in an environmental stressor might cross a threshold and lead to a sudden shift from one ecosystem state to another (Lubchenco & Petes 2010, Connell et al. 2017).

Table 1 Examples of ecological leverage points in marine ecosystems

Interacting species	Type of interaction	Environmental driver	Pathway to community change	Geographic region(s)	Reference(s)
Krill (*Euphausia superba*) and salps (*Salpa thompsoni*)	Competition (exploitation)	Increasing temperature, declining sea ice, and decreasing pH	Impact on krill-dependent predators (marine mammals and sea birds)	Antarctica	Loeb et al. 1997, Atkinson et al. 2004, Kawaguchi et al. 2013, Piñones & Fedorov 2016
Four species of colonial tunicates (pairwise interactions)	Competition (interference)	Increasing temperature	Impact on competitive dominants	Northeast Pacific	Sorte & Stachowicz 2011, Sorte & White 2013, Lord & Whitlatch 2015
California mussel (*Mytilus californianus*) and fleshy algae	Competition (interference)	Decreasing pH	Impact on competitive dominant	Northeast Pacific	Wootton et al. 2008, Gaylord et al. 2011
Calcareous species (barnacles, calcareous tubeworms, and coralline algae) and fleshy algae	Competition (interference)	Decreasing pH	Impact on competitive dominants	Mediterranean	Kroeker et al. 2013b
Corals (*Acropora* spp.) and white syndromes	Disease/parasitism	Increasing temperature	Impact on foundation species (corals)	Indo-Pacific	Bruno et al. 2007, Hobbs et al. 2015
Corals (*Acropora* spp.) and white-band disease	Disease/parasitism	Increasing temperature	Impact on foundation species (corals)	Caribbean	Randall & van Woesik 2015
Oysters (*Crassostrea virginica*) and parasites (*Perkinsus marinus* and *Haplosporidium nelsoni*)	Disease/parasitism	Increasing temperature and increasing salinity (drought)	Impact on foundation species (oysters)	United States, Atlantic, and Gulf of Mexico coasts	Soniat et al. 2008
Amphipods (*Corophium volutator*) and trematode parasites (*Maritrema subdolum*)	Disease/parasitism	Increasing temperature	Impact on ecosystem engineer (amphipods)	Wadden Sea, northwestern Europe	Mouritsen et al. 2005
Sea urchins (*Centrostephanus rodgersii*) and kelps (*Macrocystis pyrifera* and *Ecklonia radiata*)	Herbivory	Increasing temperature	Impact on foundation species (kelp)	Tasmania	Ling 2008, Johnson et al. 2011
Sea urchins (*Strongylocentrotus polyacanthus*) and coralline algae (*Clathromorphum nereostratum*)	Herbivory	Increasing temperature and decreasing pH	Impact on foundation species (coralline algae)	Aleutian archipelago, northeast Pacific	Rasher et al. 2020
Corals and zooxanthellae (*Symbiodinium* spp.)	Mutualism	Increasing temperature	Impact on foundation species (corals)	Australia	T.P. Hughes et al. 2018
Ochre sea star (*Pisaster ochraceus*) and mussels (*Mytilus* spp.)	Predation	Increasing temperature	Impact on foundation species (mussels)	Northeast Pacific	Sanford 1999, Pincebourde et al. 2008
Crown-of-thorns sea star (*Acanthaster* spp.) and corals	Predation	Increasing temperature	Impact on foundation species (corals)	Australia	Birkeland & Lucas 1990, Keesing & Lucas 1992, Uthicke et al. 2015
Crabs (*Cancer pagurus*) and sea urchins (*Strongylocentrotus droebachiensis*)	Predation	Increasing temperature	Impact on sea urchins leading to kelp recovery (trophic cascade)	Norway	Fagerli et al. 2014, Christie et al. 2019
Humans and pelagic tuna (*Thunnus* spp.)	Predation (fishing pressure)	Compression of vertical habitat by deoxygenation	Reduction of tuna populations, possibly reshaping the pelagic food web	Eastern tropical Atlantic, central North Pacific	Kitchell et al. 1999, Prince & Goodyear 2006, Stramma et al. 2011, Mislan et al. 2017

Such thresholds are particularly likely to be crossed during extreme events—for example, where the direct effects of marine heat waves lead to widespread mortality of foundation species like corals or kelps, which may have relatively small thermal safety margins (T.P. Hughes et al. 2018, Rogers-Bennett & Catton 2019). Nonlinear changes in species interactions, like those described in this review, can also contribute to such rapid shifts between ecosystem states (Monaco & Helmuth 2011, Harley et al. 2017). However, we emphasize that species interactions that operate as ecological leverage points need not result in abrupt ecosystem shifts, although that is one possible outcome. Rather, like the use of a lever in physics, a slow and steady application of change force (e.g., small increases in annual mean temperature or ocean acidification) can be amplified by key species interactions to generate large changes in community structure that may build over many years.

SUMMARY POINTS

1. Species within a community frequently differ in their physiological optima and environmental tolerances. Thus, ongoing changes in ocean temperature, dissolved oxygen, and pH can impact community members differently, leading to shifts in the strength and outcome of species interactions.
2. Global environmental change often causes species to spend increased time outside of the environmental ranges that are optimal for their physiological processes. Consideration of energy budgets offers a unifying framework for understanding both the pervasive effects of these sublethal changes in mean environmental conditions and the impacts of multiple stressors.
3. To cope with increased energetic demands imposed by ocean warming, deoxygenation, and ocean acidification, heterotrophs may reallocate energy away from growth and reproduction and/or increase rates of consumption. Both of these responses can have substantial consequences for species interactions, including altering growth rates and competitive outcomes and changing the intensity of herbivory or predation.
4. Key species interactions that are sensitive to environmental change can act as ecological leverage points, through which relatively small abiotic changes are amplified into large changes in natural communities. A range of considerations suggest that ecological leverage points may be more common in the ocean than on land.
5. Identifying ecological leverage points may allow marine scientists and managers to anticipate which ecosystems are especially vulnerable to accelerating global environmental changes. Further exploration of leverage points in marine communities will benefit from a continued integration of physiology and ecology.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Errata

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