Community Responses to Climate-Related Variability and Disease

THE CRITICAL IMPORTANCE OF LONG-TERM RESEARCH

By Bruce A. Menge, Jennifer E. Caselle, John A. Barth, Carol A. Blanchette, Mark H. Carr, Francis Chan, Sarah Gravem, Tarik C. Gouhier, Jane Lubchenco, Margaret A. McManus, Kristen Milligan, Mark Novak, Peter T. Raimondi, Libe Washburn, and J. Wilson White

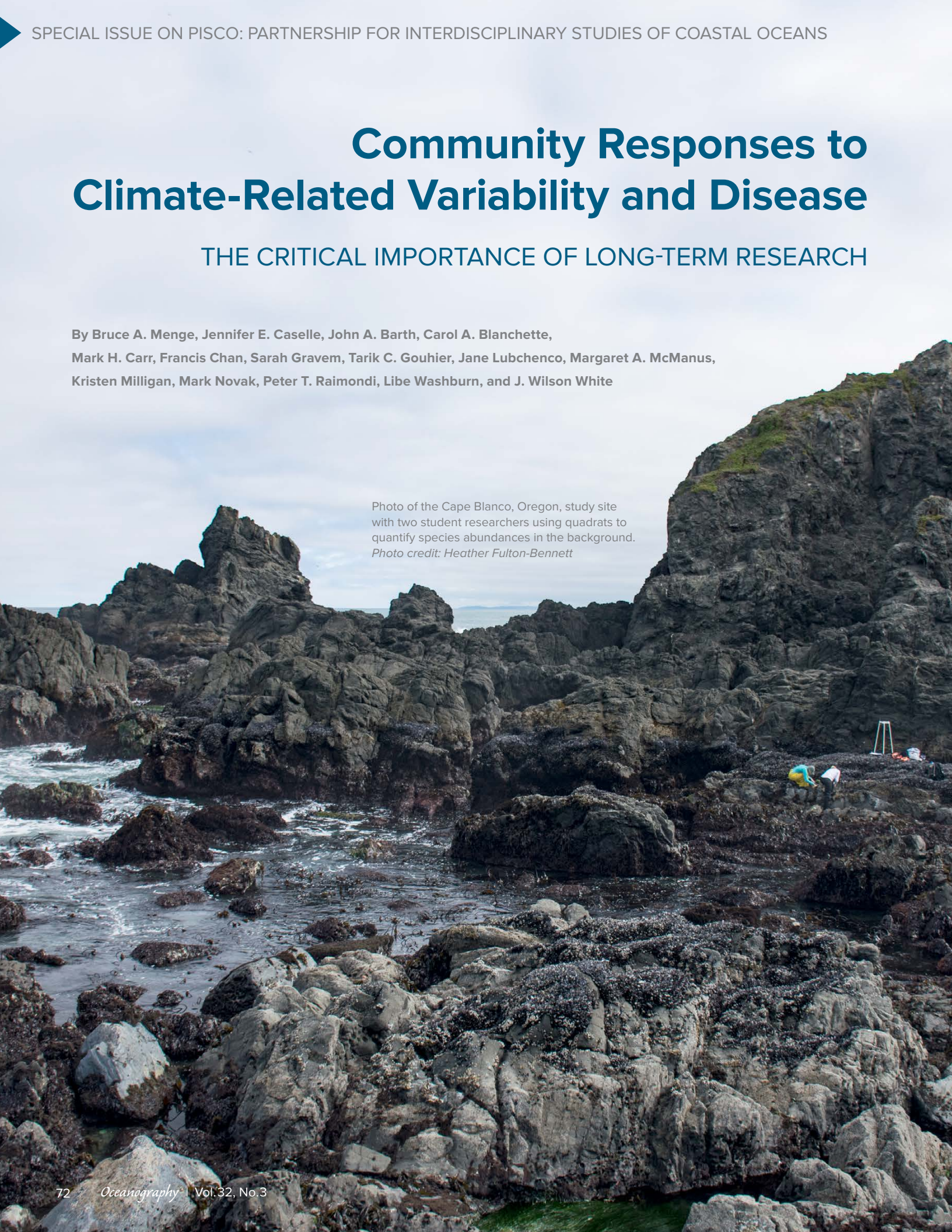

Photo of the Cape Blanco, Oregon, study site with two student researchers using quadrats to quantify species abundances in the background. *Photo credit: Heather Fulton-Bennett*

ABSTRACT. A major goal of the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) has been to understand the impacts of climate change and variability on the coastal ecosystems of the inner shelf of the California Current Large Marine System in particular, and other marine and even nonmarine systems more generally. Insights can result from determination of impacts of climatic perturbations such as the El Niño-Southern Oscillation, the North Pacific Gyre Oscillation, and the Pacific Decadal Oscillation, as well as impacts of climate-related surprises on populations, communities, and ecosystems. To gain insight into warming impacts at organismal levels, we also investigated mechanistic suborganismal (physiological, molecular) responses to thermal conditions. Warmer water was connected to changes in ecological subsidies, growth of dominant space occupiers (mussels and barnacles), and heightened physiological stress impacts. Fortuitously, PISCO researchers were ideally positioned to document ecosystem vulnerability and resilience to an unprecedented ecological surprise—coast-wide collapse of keystone predator (sea star) populations—and to investigate its consequences. As these examples suggest, long-term sampling is critically important for helping society anticipate and adapt to present and future disruptions caused by global change.

INTRODUCTION

Global change (GC) due to increasing CO_2 and other greenhouse gases is perhaps the overarching challenge of our time (IPCC, 2014). GC is manifested in the atmosphere and ocean; increasing ocean stratification, deoxygenation, and acidification; and disruption of ecological systems, among other things. Understanding ecological responses to GC requires long-term biological and environmental data sets (Poloczanska et al., 2008; Brown et al., 2011). In the late 1990s, such data sets were rare, so a major long-term goal of the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) was targeting GC ecological impacts. However, natural climatic variability such as the El Niño-Southern Oscillation (ENSO), the North Pacific Gyre Oscillation (NPGO), and the Pacific Decadal Oscillation (PDO) complicates efforts to identify anthropogenic GC effects (Francis and Hare, 1994; Di Lorenzo et al., 2008; Brown et al., 2011). Moreover, GC also alters ENSO frequency and intensity (Cai et al., 2018; Ham, 2018) and possibly also NPGO and PDO (e.g., Zhang and Delworth, 2016). These natural patterns and GC have a common feature—they directly or indirectly alter thermal regimes, with alternating warmer- and colder-than-average water and air temperatures. Thus, investigating ecological responses to the shorter-term climatic variability, ideally coupled with mechanistic physiological research, may provide insight into likely coastal ecosystem responses to GC.

Rocky intertidal and subtidal ecosystems are ideal model systems for investigation of impacts of GC. They are dominated by organisms with research-favorable traits, including relatively short generation times, sessile or sluggish mobility, mostly small size, ease of observation, and, in the intertidal, amenability to experimentation. Benthic habitats in the California Current Large Marine System (CCLME) have been relatively intensely investigated, enabling pursuit of timely research questions.

Below, we summarize responses of key CCLME processes to climatic modes like ENSO, NPGO, and PDO, examine research into how intertidal organisms deal with physiological stress, and summarize the 2013 sea star wasting event and its consequences.

CLIMATIC VARIABILITY AND INNER SHELF ECOSYSTEMS

Upwelling—the wind-driven injection of deep, cold, salty, nutrient- and CO_2-rich, and O_2-poor water from depth to coastal ecosystems (Huyer, 1983)—is the dominant feature of Eastern Boundary Upwelling Systems (EBUS; Chavez and Messié, 2009; Checkley and Barth, 2009) such as the CCLME. How sensitive is benthic community structure to climatic variability relative to thermal, nutrient, and chemical changes occurring during upwelling? This issue is complex: upwelling, storm surge, and temperatures are all reflections of climate, including natural multi-year patterns and anthropogenic-driven components. For example, as verified by recent evidence (Garcia-Reyes and Largier, 2012; Iles et al., 2012), upwelling intensity increases with GC (Bakun, 1990). Analyses of model climate projections suggest that upwelling will last longer and be more intense by 2100 in most EBUS under business-as-usual scenarios (Wang et al., 2015). Increasing wave heights consistent with climate change predictions have also been documented (Ruggiero et al., 2010). Such complications challenge efforts to sort GC-driven from naturally occurring variation.

Globally, mussels and barnacles are dominant components of temperate rocky intertidal communities (Lewis, 1964; Stephenson and Stephenson, 1972). Mussels in particular are critically important elements in these systems, dominating space on the shore, harboring enormously diverse biota (Lafferty and Suchanek, 2016), and supporting abundant and functionally important apex predators (Paine, 1974, 1994; Robles et al., 2009). Hence, understanding links between oceanic conditions and sessile invertebrate performance is critical in forecasting potential future climate-related changes.

Impact of Natural Climate Variation on Ecological Subsidies

As summarized in Menge et al. (2019, in this issue), ecological subsidies (inputs of nutrients, propagules, and particulate food from pelagic environments) vary with coastal oceanic conditions. To explore the dependence of ecological subsidies on climatic variation, we built on data sets collected in the period from 1989 to 1998, prior to PISCO's beginning in 1999. Compared to the 1990s, in the 2000s phytoplankton and mussel recruit subsidies increased by orders of magni-

tude (Menge et al., 2009). Further, phytoplankton and mussel recruitment phenologies shifted to earlier and later in the year, respectively. These changes correlated with the 10- to 15-year NPGO (e.g., Figure 1). Mussel recruitment also increased with phytoplankton abundance, suggesting an important bottom-up effect on the supply of mussels to rocky shores. Remarkably, these relatively local supply-side measures were sensitive to long-term, ocean basin-scale climatic fluctuation (Figure 2), suggesting likely future alterations of local-scale inputs with changing climate (Menge et al., 2009).

Using a longer (1989–2009) data set, we found that upwelling and multiple climate modes (ENSO, NPGO, PDO) influenced barnacle (*Balanus glandula* and *Chthamalus dalli*) and mussel (*Mytilus* spp.) recruitment (Menge et al., 2011). However, recruitment of all species varied most strongly with the NPGO and upwelling (Figure 3). Overall, large-scale climate and upwelling variability explained 37%–40% of recruitment variance across the central to southern Oregon coast.

In 2005, coastal upwelling onset was delayed by ~1 month, and was weak early and strong late in the season (Barth et al., 2007). Consequently, coastal waters were warmer, had low nutrient levels, low levels of primary production, and low barnacle and mussel recruitment. Whether these "intraseasonal oscillations" influence the northern CCLME more under GC remains to be seen, but the predicted northward movement of the atmospheric jet stream under GC influences their prevalence in this region (Meehl et al., 2007).

Impact of Natural Climate Variability on Secondary Production

To determine the responses of intertidal organisms to oceanic processes during their benthic, adult stages, Sanford and Menge (2001) investigated barnacle growth rates of two abundant intertidal species, *B. glandula* and *C. dalli*, in relation to upwelling-driven differences in phytoplankton and zooplankton abundances and thermal conditions. They found that these factors jointly explained differences in barnacle growth. Increased growth in response to phytoplankton blooms was observed, but also occurred post-blooms, when zooplankton abundances (e.g., crustacean larvae) and temperatures were relatively high (Sanford and Menge, 2001), suggesting these barnacles were omnivorous.

Mussel growth in relation to environmental variation was similarly context-dependent (Blanchette et al., 2007; Menge et al., 2008). Around Point Conception, California, intertidal mussel growth increased southward with temperature (Figures 4 and 5). Further, in contrast to intertidal mussels (faster growth south of Point Conception), mooring mussels grew equally fast around the Point (Figure 5). Blanchette et al. (2007) suggested that similar growth rates of submerged mussels were likely a reflection of opposing gradients in temperature (warmer southward) and food (higher northward).

In Oregon, mussel growth varied with both short-term ENSO- and long-term PDO-influenced temperature and food abundance (Menge et al., 2008; Figure 6). In the 1990s, mussel growth rates were slower at less productive sites than they were at more productive sites, but in the 2000s, growth rates increased at the less productive sites to levels seen at the more productive sites. Mussel growth at less productive sites was slower during cool phases of ENSO and PDO and faster during warm phases, but did not vary among the more productive sites. Both temperature (variance explained = 32%) and phytoplankton (variance explained = 12.5%) were climate-driven proximate factors underlying mussel growth rate differences.

Mechanistic Insight into Organismal Responses to Climate Change: Large-Scale Eco-physiological Approaches

Anthropogenic GC increases traditional stresses on marine organisms and also creates new ones (Somero, 2012). Such stresses have population, community, and ecosystem consequences, so understanding biological system responses is an essential aspect of climate change research (Poloczanska et al., 2008; Doney, 2010; Somero, 2012).

The mussel *M. californianus* spans a broad vertical range on relatively wave-exposed shores along most of the North American west coast. Hence, it exhibits increasing thermal stress with increasing height on the shore (Gracey et al., 2008; Petes et al., 2008a,b). Further, it is exposed to a broad wave-exposure range, from wave-beaten headlands to gently wave-swept coves, so thermal stress increases as wave splash decreases (Dahlhoff et al., 2002). In response to increased stress (higher on the shore, in more protected

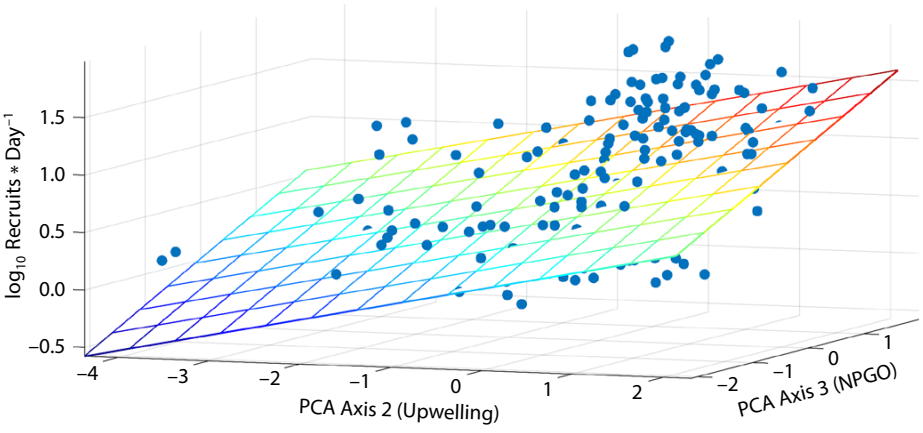

FIGURE 1. Multiple linear regression describing *Mytilus* spp. recruitment in relation to upwelling on PCA axis 2 (loading = 0.96) and North Pacific Gyre Oscillation (NPGO) on PCA axis 3 (loading = 0.82) (adjusted $R^2 = 0.300$, $p < 2.2 \times 10^{-16}$). PCA = Principal Component Analysis. *From Menge et al. (2011)*

shore areas), several researchers documented increases in mussel physiological responses. Specific responses were observed in heat shock proteins and ubiquitin (Halpin et al., 2002, 2004), heart rate (Braby and Somero, 2006), carotenoid concentration (Petes et al., 2008a), and gene expression (stress response genes; Gracey et al., 2008; Place et al., 2011).

Integration of physiological and ecological approaches has led to valuable insights into the physiological responses of key species such as mussels, whelks, and sea stars to joint influences of thermal stress and food abundance. For instance, among-site differences in growth of mussels (*M. californianus)* observed in Oregon (Menge et al., 2008) were based on differences in metabolic enzymes (citrate synthase and malate dehydrogenase) and protein synthetic capacity (RNA:DNA ratios; Dahlhoff and Menge, 1996). This difference was highly plastic: the physiology of reciprocally transplanted mussels quickly converged with that of resident mussels (Dahlhoff and Menge, 1996). More recent research on gene expression (using microarrays) has shown that metabolic genes are up-regulated in *M. californianus* with increasing food (Gracey et al., 2008; Place et al., 2012; Somero 2012).

These examples suggest that mussel physiology appears exquisitely attuned to variable living conditions. Despite highly plastic physiological stress responses, however, GC, especially if it is rapid, can have severe impacts on the distribution and abundance of mussels. For example, Jones et al. (2009, 2010) documented a

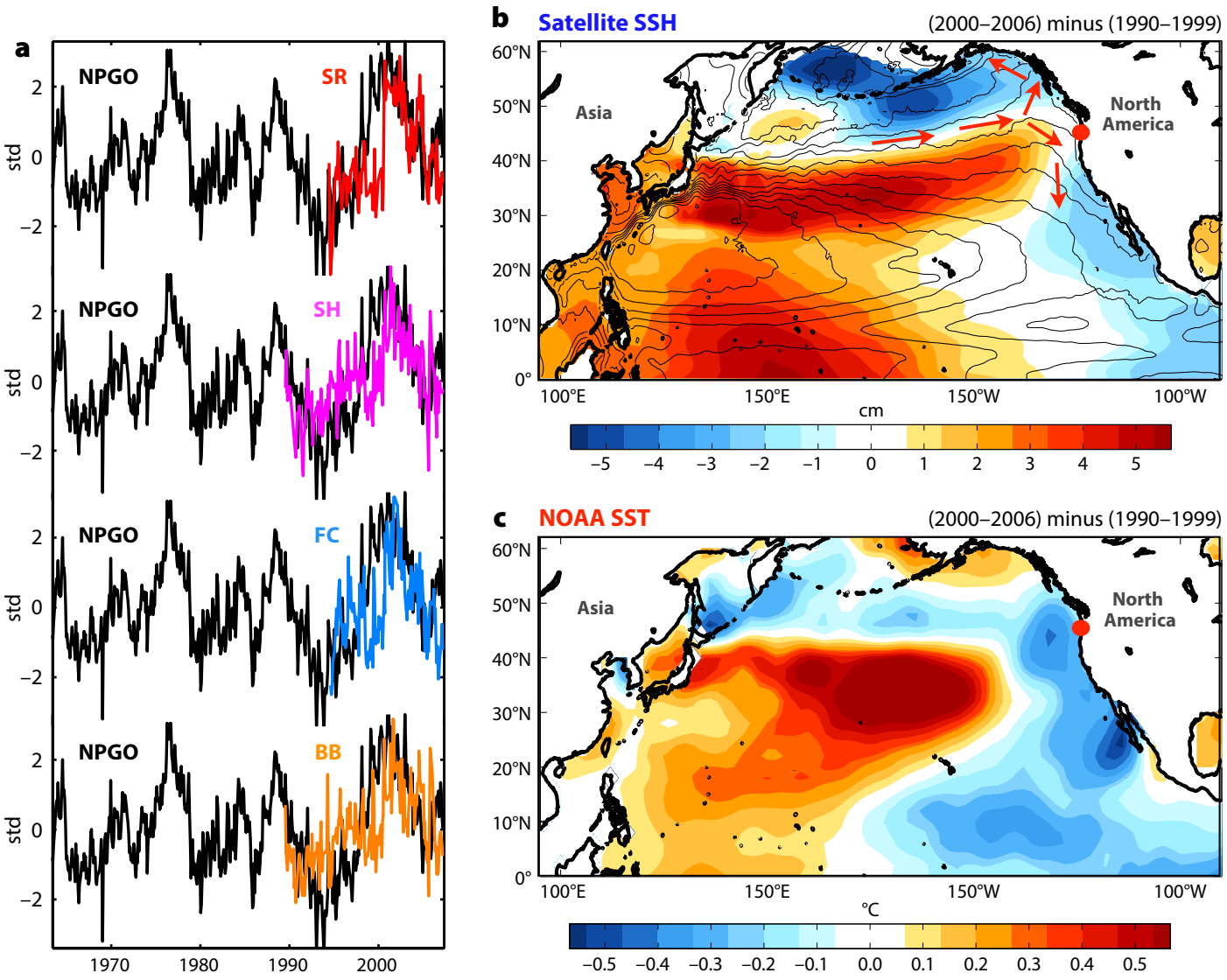

FIGURE 2. (a) Time series of normalized mussel recruitment at four locations (Seal Rock: 44.50°N, 124.08°W; Strawberry Hill: 44.25°N, 124.115°W; Fogarty Creek: 44.84°N, 123.97°W; and Boiler Bay: 44.83°N, 124.06°W) compared to the North Pacific Gyre Oscillation (NPGO) index. The time series are normalized by their standard deviation (std; the y-axis scale numbers indicate the actual standard deviations of the NPGO index, by which the index is standardized). (b) Difference in satellite sea surface height (SSH) between the periods 2000–2006 and 1990–1999 (shaded colors) and mean SSH (black contours). The strong dipole of SSH in the Northeast Pacific indicates an intensification of the North Pacific Current and its branches along the eastern boundary (red arrows), which is consistent with the positive phase of the NPGO. (c) Same as (b) for the NOAA sea surface temperatures (SST). *From Menge et al. (2009)*

warming-related sharp contraction northward of the mussel *M. edulis* along the US mid-Atlantic coast. Similarly, Sorte et al. (2017) demonstrated a >60% decrease in mussel abundance along the New England coast over the past 30+ years.

Such results indicate that the consequences of oceanic variability can be seen even at the level of gene expression and thus will likely be sensitive to GC.

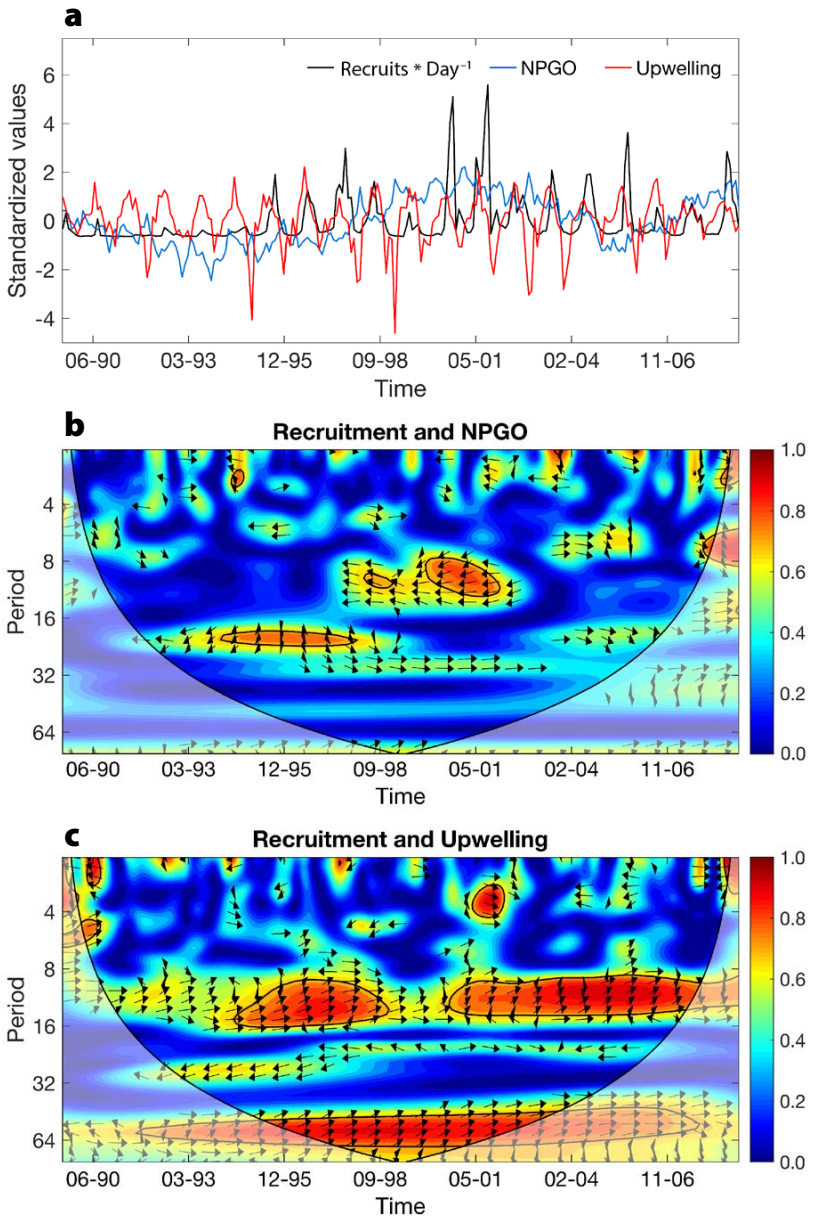

FIGURE 3. (a) Standardized time series and pairwise wavelet coherence of *Mytilus* spp. recruitment, (b) NPGO, and (c) upwelling from 1989 to 2008 (month-year on x-axis). Period (y-axis) is in months, so for the NPGO, red blobs indicate correlations of mussel recruitment at periods of, for example, ~12 months (05-01) and ~24 months (12-95). Wavelet coherence describes the amount of correlation (color bar; 0 = blue, no correlation; 1 = dark red, complete correlation) in the fluctuations of two time series, in this case the NPGO and mussel recruitment. Black arrows indicate the phase angle between the fluctuations of the two time series. Arrows pointing to the left indicate anti-phase (inverse) fluctuations, whereas arrows pointing to the right indicate in-phase (positive) fluctuations. Black contour lines indicate regions in which the observed wavelet coherence values are statistically significantly ($\alpha = 0.05$) based on Monte Carlo randomizations applied to 1,000 pairs of surrogate time series whose first order autoregressive coefficients match those of the original time series. Translucent areas represent the "cone-of-influence" where edge effects can influence the analysis. *From Menge et al. (2011)*

Are consumers affected similarly? The consumer-stress model of environmental stress theory (Menge and Olson, 1990; Menge et al., 2002; Siddon and Witman, 2003) suggests that consumers are more stress-susceptible than their prey (i.e., there is a mobility-stress tolerance trade-off). Although consumer mobility enables survival by allowing movement to low-stress microhabitats, reduced activity leads to reduced consumption in more stressful environments. In contrast, sessile prey are fixed in place and must tolerate conditions or die, so would be expected to evolve greater stress tolerance.

Similar to the findings for mussels, both mobile predatory whelks and sessile barnacle prey showed greater metabolic activity, increased growth capacity, and enhanced production of stress proteins with increases in stress and food at scales ranging from meters to tens of kilometers (Dahlhoff et al., 2001, 2002). In contrast, sea stars (*P. ochraceus*) showed minimal physiological response to thermal stress (Dahlhoff et al., 2002; Monaco et al., 2016), but as predicted by theory, died when experimentally forced to live without access to shelter higher than normal on the shore (Petes et al., 2008b). Consistent with this result, other researchers have shown that *P. ochraceus* activity is sensitive to temperature, both cold and hot (Pincebourde et al., 2008, 2009, 2012; Sanford, 1999), and modifies its activity to minimize exposure to thermal extremes (Szathmary et al., 2009; Monaco et al., 2016).

Thus, research testing physiological responses to stress can provide critically important information useful in predicting responses of marine organisms to GC. Can they modify their physiology or behavior to adjust to the changing conditions? Because change is occurring relatively quickly, can they alter gene expression or genetically adapt quickly enough to persist (e.g., Somero, 2012)? The US east coast mussel example (Jones et al., 2009, 2010) is sobering, but temperature change there has been faster than at most places on Earth (Pershing et al., 2015).

Further, thermal and wave size variation in coastal habitats is more extreme in the northwest Atlantic than in the northeastern Pacific (Menge and Sutherland, 1976). However, another stress, ocean acidification, is globally most severe in the northeast Pacific, posing an additional threat and complicating efforts to predict future ecosystem states based simply on thermal changes (Chan et al., 2017; see also Chan et al., 2019, in this issue).

Long-Term Data Sets Enable Detection and Interpretation of Ecological Surprises

In addition to their utility and importance for evaluating ecosystem responses to climate change, long-term data sets provide a critical context for understanding sudden, dramatic changes in species' abundance. For example, in fall 2013, observers in British Columbia and southern California reported startling, massive die-offs of sea stars (Hewson et al., 2014; Stokstad, 2014). By spring 2014, this event had reached epizootic proportions, afflicting all 20+ species of sea star along the entire North American west coast (Hewson et al., 2014; Eisenlord et al., 2016; Montecino-Latorre et al., 2016; Harvell et al., 2019).

This was not the first sea star mass mortality event (Dungan et al., 1982; Menge, 1983; Eckert et al., 2000; Blanchette et al., 2005; Bates et al., 2009). However, it was unprecedented in two aspects: the spatial extent of the event was exceptionally large (thousands of kilometers of coastline), and it afflicted *all* sea star species, not just one. With collaborators in British Columbia, Washington, and Baja California, PISCO researchers immediately began (1) documenting the impact of the wasting disease on coastal sea star populations, (2) investigating sea star resilience to such massive losses, and (3) assessing impacts on intertidal and subtidal communities.

Combining contemporary surveys with prior time series (back to 2000 or earlier) showed that abundances of the sea star *P. ochraceus* decreased by 60% to 90% or more compared to long-term averages (Menge et al., 2016; Miner et al., 2018). This led to an immediate, sharp decline in the rate of predation on mussels (Menge et al., 2016). However, mussel response was more spatially variable and slower than expected (unpublished data from authors Gravem and Menge). Perhaps the most striking response was a dramatic but also spatially variable increase in sea star recruitment in spring 2015 (Menge et al., 2016; Miner et al., 2018; Moritsch and Raimondi, 2018). It led to increased sea star abundance, often to levels higher than before wasting, but because most of the stars were small, biomass recovery was slow (Menge et al., 2016; Moritsch and Raimondi, 2018). As of summer 2019, predation rate at most sites was still less than pre-2013. However, as expected, mussel abundance in the primarily macrophyte-dominated low intertidal has increased, displacing macrophytes at increasing numbers of sites (unpublished data from authors Gravem and Menge). At present, sea stars are losing the battle to mussels, but slowly enough that sea star populations may be able to recover sufficiently to prevent an alternative mussel-dominated low intertidal state.

In contrast, coastal populations of the subtidal sea star *Pycnopodia helianthoides* have been nearly extirpated with as yet no sign of recovery (Harvell et al., 2019). From shallow, kelp bed depths to 1,280 m water depth, this large sunflower star declined by 80% to 100% from Alaska through California, a ~3,000 km distance. Although the sunflower star is a diet generalist (Mauzey et al., 1968; Duggins, 1983), sea urchins are a primary prey. Prior small-scale experiments indicated that *P. helianthoides* predation could have cascading effects on kelp through predation on urchins, but the spatial generality of this effect was unclear (Duggins, 1983). However, community consequences of sea star wasting suggest *P. helianthoides* was indeed a keystone predator in kelp beds. The collapse of shallow-water populations evidently

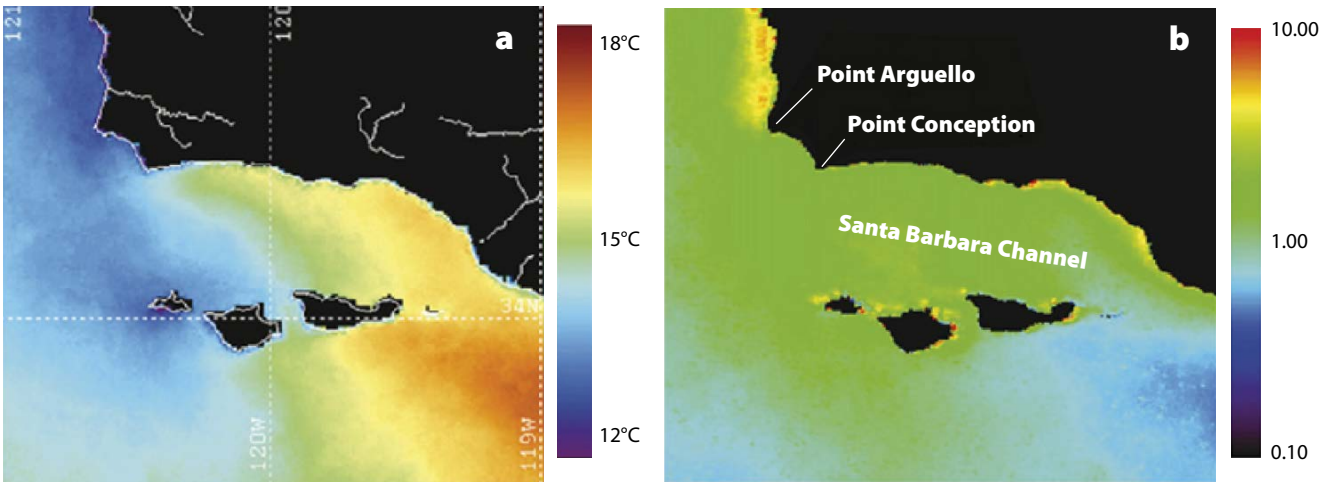

FIGURE 4. Representative seasonal composite satellite images of (a) sea surface temperature, and (b) chlorophyll-*a* (in mg m^{-3}, from SeaWIFS) from summer 2000. Note the sharp discontinuity in temperature around Point Conception and the high concentration of offshore chlorophyll-*a* north of Point Arguello relative to the Santa Barbara Channel. *Images created by Mark Otero, ICESS, UCSB. From Blanchette et al. (2007)*

triggered sea urchin outbreaks in several locations, with subsequent reductions in kelp abundance through an indirect trophic cascade effect (Schultz et al., 2016; Burt et al., 2018). Unlike the *P. ochraceus* example, however, *P. helianthoides* loss apparently was not followed by a recruitment event of sunflower stars (Harvell et al., 2019). Although sea otters are also major predators of sea urchins (Estes and Palmisano, 1974; Estes and Duggins, 1995; Burt et al., 2018), otters are absent south of Cape Flattery, Washington, to the San Francisco Bay Area of California, and no other subtidal predator in this region seems capable of controlling sea urchin populations. This system is presently in a highly dynamic state, so the longer-term consequences of these changes will only be revealed with time, but it is clear that kelp domination is threatened.

DISCUSSION

The impacts of variation in ENSO and PDO on marine pelagic ecosystems are well known (e.g., selected citations from an extensive literature include Barber and Chavez, 1983; Francis and Hare, 1994, Mantua et al., 1997; Chavez et al., 2003; Peterson and Schwing, 2003), as are, increasingly, effects of NPGO (Di Lorenzo et al., 2008; Chenillat et al., 2012; Sydeman et al., 2013). Coral reefs and kelp beds also suffer extensive damage during warming events (e.g., El Niño and marine heatwaves; Glynn, 1988; Wernberg et al., 2016; Hughes, et al. 2018). Effects on temperate marine benthic ecosystems, however, are mixed. For example, in his decades-long research on the Washington intertidal system, Paine (1986) found little detectable effect of the 1982–1983 El Niño. Navarrete et al. (2002) found little to no effect of the 1997–1998 El Niño on invertebrate recruitment in Chile. In contrast, kelp (*Macrocystis pyrifera*) beds were found to be highly sensitive to El Niño (Dayton and Tegner, 1984; Dayton et al., 1999), as was algal composition in the Galápagos (Vinueza et al., 2006, 2014), and barnacle recruitment was elevated in California during the 1997–1998 El Niño (Connolly and Roughgarden, 1999).

During PISCO's existence, benthic processes such as recruitment and growth appeared responsive to climatic variation as expressed in ENSO, NPGO, and PDO. In these and all cases cited above, these responses seem likely to be primarily either positive or negative to thermal changes. Mussel and barnacle growth were faster under warmer conditions, and mussel and barnacle recruitment was increased by cool-water-associated increases in phytoplankton abundance. Further, these responses appear to be detectable at physiological and molecular levels, suggesting an approach that will facilitate prediction of future species' responses to global change. Remarkably, these hard-bottom biological systems also respond to basin- to subregional-scale climatic variation across a wide range of spatial, temporal, and organismal scales, even down to the molecular level (see also Palumbi et al., 2019, in this issue).

Until recently, a hallmark of northeastern Pacific coastal ecosystems was consistency in local to large-scale patterns of abundance, distribution, diversity, and biogeography (Paine, 1986, 1994; Dayton et al., 1992). Although seasonal and short-term variability resulting from, for example, ENSO cycles was often dramatic, the system seemed resilient to such perturbations, typically recovering within a few months to years (Dayton et al., 1992). With global change, however, these systems appear to have entered a new phase characterized by greater variation in pattern and process, biogeographic shifts (see Sanford et al., 2019; Raimondi et al., 2019, in this issue), and often dramatic changes in the abundance of key species. Consequences of these changes are

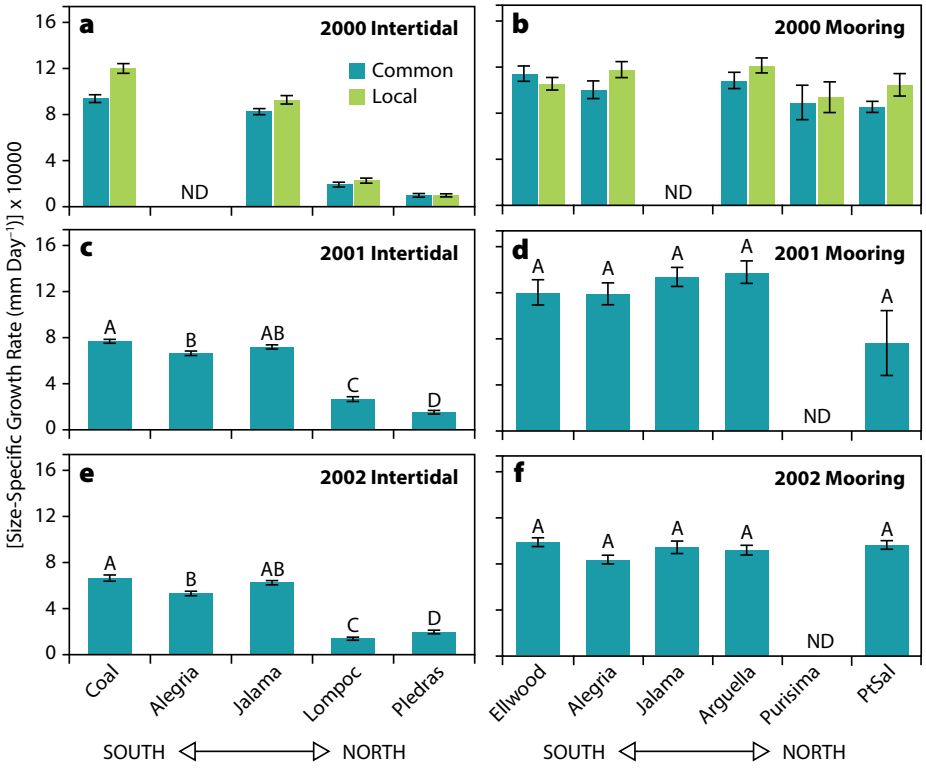

FIGURE 5. Size specific growth rates (mm/day × 10,000) for mussels from mussel growth experiments in 2000 (a and b), 2001 (c and d), and 2002 (e and f) from intertidal sites (a, c, and e) and mooring sites (b, d, and f). In (a) and (b), we were interested in comparing growth of mussels from a single, common source (dark green bars; site near Santa Cruz, California) to that of mussels from the specific site of the experiment (light green bars). In panels (c–f), we used only mussels collected from the single common intertidal source, so all bars are dark green. Intertidal and mooring sites are arranged from the southernmost site on the left to the northernmost site on the right. ND = no data for some sites/years. Data are site means ±1 standard error of the mean. Means with different letters (A, B, C, D) above the bar are different at α = 0.05 based on Tukey-Kramer multiple comparisons. *From Blanchette et al. (2007)*

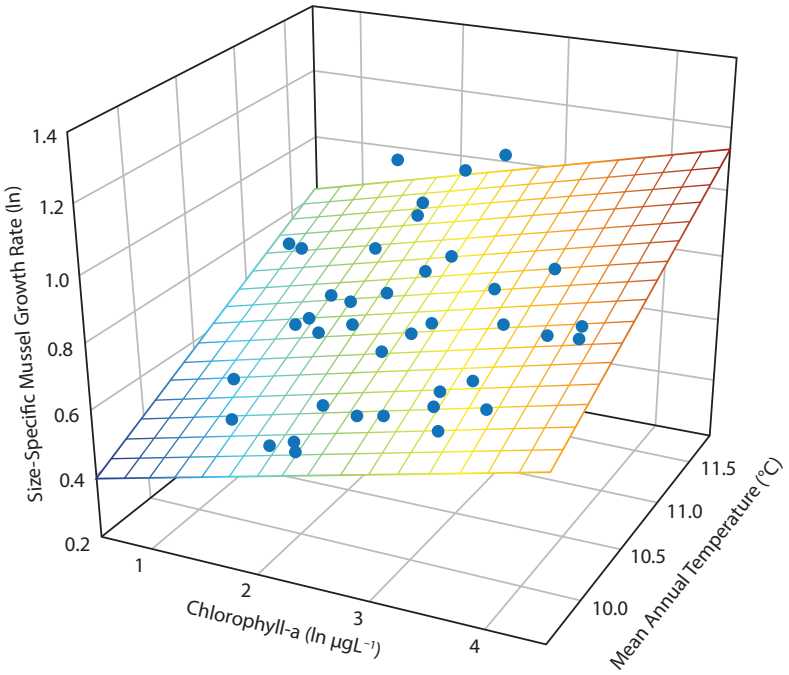

FIGURE 6. Influence of food availability (proxied by chlorophyll-*a*) and temperature (mean annual growing season, June through the following May) on growth of *Mytilus californianus*. Statistics are from a multiple least squares regression test. Regression is mussel growth = −2.53 + (0.081 × (chl-*a*) + (0.293 × temperature); F = 14.2, p <0.001, adj R^2 = 0.44, n = 39. *From Menge et al. (2008)*

sometimes large and sometimes subtle or slow to occur (e.g., sea star wasting consequences exhibit both). PISCO data streams have been crucial in discovering, monitoring, and analyzing changes, and identifying coastal "hot" and "cold" spots, defined as areas that are more or less productive, respond to or rebound from change quickly or slowly, or are exposed to more or fewer extreme environmental variations (e.g., Guichard et al., 2003; Menge et al., 2004; Helmuth et al., 2006; Krumhansl et al., 2016; Chan et al., 2017). An era of unprecedented and difficult-to-predict change in coastal ecosystems is dawning, and with others (e.g., Poloczanska et al., 2008; Brown et al., 2011) we believe strongly that maintaining and evolving long-term, coupled research and monitoring programs is one of the most powerful tools available to deal with such challenges.

REFERENCES

Bakun, A. 1990. Global climate change and the intensification of coastal upwelling. *Science* 247:198–201, https://doi.org/10.1126/science.247.4939.198.

Barber, R.T., and F.P. Chavez. 1983. Biological consequences of El Niño. *Science* 222:1203–1210, https://doi.org/10.1126/science.222.4629.1203.

Barth, J.A., B.A. Menge, J. Lubchenco, F. Chan, J.M. Bane, A.R. Kirincich, M.A. McManus, K.J. Nielsen, S.D. Pierce, and L. Washburn. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. *Proceedings of the National Academy of Sciences of the United States of America* 104:3,719–3,724, https://doi.org/10.1073/pnas.0700462104.

Bates, A.E., B.J. Hilton, and C.D.G. Harley. 2009. Effects of temperature, season, and locality on wasting disease in the keystone predatory sea star *Pisaster ochraceus*. *Diseases of Aquatic Organisms* 86:245–251, https://doi.org/10.3354/dao02125.

Blanchette, C.A., D.V. Richards, J.M. Engle, B.R. Broitman, and S.D. Gaines. 2005. Regime shifts, community change, and population booms of keystone predators at the Channel Islands. *Proceedings of the California Islands Symposium* 6:435–441.

Blanchette, C.A., B.S.T. Helmuth, and S.D. Gaines. 2007. Spatial patterns of growth in the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. *Journal of Experimental Marine Biology and Ecology* 340:126–148, https://doi.org/10.1016/j.jembe.2006.09.022.

Braby, C.E., and G.N. Somero. 2006. Following the heart: Temperature and salinity effects on heart rate in native and invasive species of blue mussels (genus *Mytilus*). *Journal of Experimental Biology* 209:2,554–2,566, https://doi.org/10.1242/jeb.02259.

Brown, C.J., D.S. Schoeman, W.J. Sydeman, K. Brander, L.B. Buckley, M. Burrows, C.M. Duarte, P.J. Moore, J.M. Pandolfi, E. Poloczanska, and others. 2011. Quantitative approaches in climate change ecology. *Global Change Biology* 17:3,697–3,713, https://doi.org/10.1111/j.1365-2486.2011.02531.x.

Burt, J.M., M.T. Tinker, D.K. Okamoto, K.W. Demes, K. Holmes, and A.K. Salomon. 2018. Sudden collapse of a mesopredator reveals its complementary role in mediating rocky reef regime shifts. *Proceedings of the Royal Society B* 285:20180553, https://doi.org/10.1098/rspb.2018.0553.

Cai, W., G. Wang, B. Dewitte, L. Wu, A. Santoso, K. Takahashi, Y. Yang, A. Carreric, and M.J. McPhaden. 2018. Increased variability of eastern Pacific El Niño under greenhouse warming. *Nature* 564:201–206, https://doi.org/10.1038/s41586-018-0776-9.

Chan, F., J.A. Barth, C.A. Blanchette, R.H. Byrne, F.P. Chavez, O.M. Cheriton, R.A. Feely, G.E. Friederich, B. Gaylord, T.C. Gouhier, and others. 2017. Persistent spatial structuring of coastal ocean acidification in the California Current System. *Scientific Reports* 7:2526, https://doi.org/10.1038/s41598-017-02777-y.

Chan, F., J.A. Barth, K.J. Kroeker, J. Lubchenco, and B.A. Menge. 2019. The dynamics and impact of ocean acidification and hypoxia: Insights from sustained investigations in the Northern California Current Large Marine Ecosystem. *Oceanography* 32(3):62–71, https://doi.org/10.5670/oceanog.2019.312.

Chavez, F.P, J. Ryan, S.E. Lluch-Cota, and M. Niquen. 2003. From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science* 299:217–221, https://doi.org/10.1126/science.1075880.

Chavez, F.P., and M. Messié. 2009. A comparison of Eastern Boundary Upwelling Ecosystems. *Progress in Oceanography* 83:80–96, https://doi.org/10.1016/j.pocean.2009.07.032.

Checkley, D.M.J., and J.A. Barth. 2009. Patterns and processes in the California Current System. *Progress in Oceanography* 83:49–64, https://doi.org/10.1016/j.pocean.2009.07.028.

Chenillat, F., P. Riviere, X. Capet, E. Di Lorenzo, and B. Blanke. 2012. North Pacific Gyre Oscillation modulates seasonal timing and ecosystem functioning in the California Current upwelling system. *Geophysical Research Letters* 39(1), https://doi.org/10.1029/2011GL049966.

Connolly, S.R., and J. Roughgarden. 1999. Increased recruitment of northeast Pacific barnacles during the 1997 El Niño. *Limnology and Oceanography* 44:466–469, https://doi.org/10.4319/lo.1999.44.2.0466.

Dahlhoff, E.P., and B.A. Menge. 1996. Influence of phytoplankton concentration and wave exposure on the ecophysiology of *Mytilus californianus*. *Marine Ecology Progress Series* 144:97–107, https://doi.org/10.3354/meps144097.

Dahlhoff, E.P., B.A. Buckley, and B.A. Menge. 2001. Physiology of the rocky intertidal predator *Nucella ostrina* along an environmental stress gradient. *Ecology* 82:2,816–2,829, https://doi.org/10.2307/2679963.

Dahlhoff, E.P., J.H. Stillman, and B.A. Menge. 2002. Physiological community ecology: Variation in metabolic activity of ecologically important rocky intertidal invertebrates along environmental gradients. *Integrative and Comparative Biology* 42:862–871, https://doi.org/10.1093/icb/42.4.862.

Dayton, P.K., and M.J. Tegner. 1984. Catastrophic storms, El Niño, and patch stability in a southern California kelp forest community. *Science* 224:283–285, https://doi.org/10.1126/science.224.4646.283.

Dayton, P.K., M.J. Tegner, P.E. Parnell, and P.B. Edwards. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecological Monographs* 62:421–445, https://doi.org/10.2307/2937118.

Dayton, P.K., M.J. Tegner, P.B. Edwards, and K.L. Riser. 1999. Temporal and spatial scales of kelp demography: The role of oceanographic climate. *Ecological Monographs* 69:219–250, https://doi.org/10.1890/0012-9615(1999)069[0219:TASSOK]2.0.CO;2.

Di Lorenzo, E., N. Schneider, K.M. Cobb, K. Chhak, P.J.S. Franks, A.J. Miller, J.C. McWilliams, S.J. Bograd, H. Arango, E. Curchister, and others. 2008. North Pacific Gyre Oscillation links ocean

climate and ecosystem change. *Geophysical Research Letters* 35(8), https://doi.org/10.1029/2007GL032838.

Doney, S.C. 2010. The growing human footprint on coastal and open-ocean biogeochemistry. *Science* 328:1,512–1,516, https://doi.org/10.1126/science.1185198.

Duggins, D.O. 1983. Starfish predation and the creation of mosaic patterns in a kelp-dominated community. *Ecology* 64:1,610–1,619, https://doi.org/10.2307/1937514.

Dungan, M.L., T.E. Miller, and D.A. Thomson. 1982. Catastrophic decline of a top carnivore in the Gulf of California rocky intertidal zone. *Science* 216:989–991, https://doi.org/10.1126/science.216.4549.989.

Eckert, G.L., J.M. Engle, and D.J. Kushner. 2000. Sea star disease and population declines at the Channel Islands. Pp. 390–393 in *Proceedings of the Fifth California Islands Symposium*. H.W. Chaney, K.L. Mitchell, and D.R. Browne, eds, Santa Barbara Museum of Natural History, Santa Barbara, CA.

Eisenlord, M.E., M.L. Groner, R.M. Yoshioka, J. Elliott, J. Maynard, S. Fradkin, M. Turner, K. Pyne, N. Rivlin, R. van Hooidonk, and others. 2016. Ochre star mortality during the 2014 wasting disease epizootic: Role of population size structure and temperature. *Philosophical Transactions of the Royal Society B* 371:20150212, https://doi.org/10.1098/rstb.2015.0212.

Estes, J.A., and J.F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. *Science* 185:1,058–1,060, https://doi.org/10.1126/science.185.4156.1058.

Estes, J.A., and D.O. Duggins. 1995. Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. *Ecological Monographs* 65:75–100, https://doi.org/10.2307/2937159.

Francis, R.C., and S.R. Hare. 1994. Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: A case for historical science. *Fisheries Oceanography* 3:279–291, https://doi.org/10.1111/j.1365-2419.1994.tb00105.x.

García-Reyes, M., and J. L. Largier. 2012. Seasonality of coastal upwelling off central and northern California: New insights, including temporal and spatial variability. *Journal of Geophysical Research* 117(C3), https://doi.org/10.1029/2011JC007629.

Glynn, P.W. 1988. El Niño-Southern Oscillation 1982–83: Nearshore population, community and ecosystem responses. *Annual Review of Ecology and Systematics* 19:309–345, https://doi.org/10.1146/annurev.es.19.110188.001521.

Gracey, A.Y., M.L. Chaney, J.P. Boomhower, W.R. Tyburczy, K. Connor, and G.N. Somero. 2008. Rhythms of gene expression in a fluctuating intertidal environment. *Current Biology* 18:1,501–1,507, https://doi.org/10.1016/j.cub.2008.08.049.

Guichard, F., P. Halpin, G.W. Allison, J. Lubchenco, and B.A. Menge. 2003. Mussel disturbance dynamics: Signatures of oceanographic forcing from local interactions. *The American Naturalist* 161:889–904, https://doi.org/10.1086/375300.

Halpin, P., C. Sorte, G.E. Hofmann, and B.A. Menge. 2002. Patterns of variation in levels of Hsp70 in natural rocky shore populations from microscales to mesoscales. *Integrative and Comparative Biology* 42:815–824, https://doi.org/10.1093/icb/42.4.815.

Halpin, P.M., B.A. Menge, and G.E. Hofmann. 2004. Experimental demonstration of plasticity in the heat shock response of the intertidal mussel *Mytilus californianus*. *Marine Ecology Progress Series* 276:137–145, https://doi.org/10.3354/meps276137.

Ham, Y.G. 2018. El Niño events set to intensify. *Nature* 564:192–193, https://doi.org/10.1038/d41586-018-07638-w.

Harvell, C.D., D. Montecino-Latorre, J.M. Caldwell, J.M. Burt, K. Bosley, A.A. Keller, S.F. Heron, A.K. Salomon, L. Lee, O. Pontier, and others. 2019. Disease epidemic and a marine heat wave are associated with the continental-scale collapse of a pivotal predator (*Pycnopodia helianthoides*). *Science Advances* 5(1):eaau7042, https://doi.org/10.1126/sciadv.aau7042.

Helmuth, B., B.R. Broitman, C.A. Blanchette, S. Gilman, P. Halpin, C.D.G. Harley, M.J. O'Donnell, G.E. Hofmann, B.A. Menge, and D. Strickland. 2006. Mosaic patterns of thermal stress in the rocky intertidal zone: Implications for climate change. *Ecological Monographs* 74:461–479, https://doi.org/10.1890/0012-9615(2006)076[0461:MPOTSI]2.0.CO;2.

Hewson, I., J.B. Button, B.M. Gudenkauf, B. Miner, A.L. Newton, J.K. Gaydos, J. Wynnne, C. Groves, G. Hendler, M. Murray, and others. 2014. Densovirus associated with sea star wasting disease and mass mortality. *Proceedings of the National Academy of Sciences of the United States of America* 111:17,278–17,283, https://doi.org/10.1073/pnas.1416625111.

Hughes, T.P., J.T. Kerry, A.H. Baird, S.R. Connolly, A. Dietzel, C.M. Eakin, S.F. Heron, A.S. Hoey, M.O. Hoogenboom, G. Liu, and others. 2018. Global warming transforms coral reef assemblages. *Nature* 556:492–496, https://doi.org/10.1038/s41586-018-0041-2.

Huyer, A. 1983. Coastal upwelling in the California Current system. *Progress in Oceanography* 12:259–284, https://doi.org/10.1016/0079-6611(83)90010-1.

Iles, A.C., T.C. Gouhier, B.A. Menge, J.S. Stewart, A.J. Haupt, and M.C. Lynch. 2012. Climate-driven trends and ecological implications of event-scale upwelling in the California Current System. *Global Change Biology* 18:783–796, https://doi.org/10.1111/j.1365-2486.2011.02567.x.

IPCC (Intergovernmental Panel on Climate Change). 2014. Summary for policymakers. Pp. 1–32 in *Climate Change 2014: Impacts, Adaptation, and Vulnerability: Part A. Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* C.B. Field, V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, and others, eds, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jones, S.J., N. Mieszkowska, and D.S. Wethey. 2009. Linking thermal tolerances and biogeography: *Mytilus edulis* (L.) at its southern limit on the East Coast of the United States. *Biological Bulletin* 217:73–85, https://doi.org/10.1086/BBLv217n1p73.

Jones, S.J., F.P. Lima, and D.S. Wethey. 2010. Rising environmental temperatures and biogeography: Poleward range contraction of the blue mussel, *Mytilus edulis* L., in the western Atlantic. *Journal of Biogeography* 37:2,243–2,259, https://doi.org/10.1111/j.1365-2699.2010.02386.x.

Krumhansl, K.A., D.K. Okamoto, A. Rassweiler, M. Novak, J.J. Bolton, K.C. Cavanaugh, S.D. Connell, C.R. Johnson, B. Konar, S.D. Ling, and others. 2016. Global patterns of kelp forest change over the past half-century. *Proceedings of the National Academy of Sciences of the United States of America* 113:13,785–13,790, https://doi.org/10.1073/pnas.1606102113.

Lafferty, K.D., and T.H. Suchanek. 2016. Revisiting Paine's 1966 sea star removal experiment, the most-cited empirical article in the *American Naturalist*. *The American Naturalist* 188:365–378, https://doi.org/10.1086/688045.

Lewis, J.R. 1964. *The Ecology of Rocky Shores,* 1st ed. The English Universities Press Ltd., London, UK.

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1,069–1,079, https://doi.org/10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2.

Mauzey, K.P., C. Birkeland, and P.K. Dayton. 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. *Ecology* 49:603–619, https://doi.org/10.2307/1935526.

Meehl, G. A., T.F. Stocker, W.D. Collins, P. Friedlingstein, A.T. Gaye, J.M. Gregory, A. Kitch, R. Knutti, J.M. Murphy, A. Noda, and others. 2007. Global climate projections. Pp. 747–845 in *Climate Change 2007: The Physical Science Basis.* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and J.L. Miller, eds, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Menge, B.A., and J.P. Sutherland. 1976. Species diversity gradients: Synthesis of the roles of predation, competition, and temporal heterogeneity. *The American Naturalist* 110:351–369, https://doi.org/10.1086/283073.

Menge, B.A. 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia* 58:141–155, https://doi.org/10.1007/BF00399210.

Menge, B.A., and A.M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution* 5:52–57, https://doi.org/10.1016/0169-5347(90)90048-I.

Menge, B.A., A.M. Olson, and E.P. Dahlhoff. 2002. Environmental stress, bottom-up effects, and community dynamics: Integrating molecular-physiological and ecological approaches. *Integrative and Comparative Biology* 42:892–908, https://doi.org/10.1093/icb/42.4.892.

Menge, B.A., C.A. Blanchette, P. Raimondi, T.L. Freidenburg, S.D. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M.M. Foley, and J. Pamplin. 2004. Species interaction strength: Testing model predictions along an upwelling gradient. *Ecological Monographs* 74:663–684, https://doi.org/10.1890/03-4060.

Menge, B.A., F. Chan, and J. Lubchenco. 2008. Response of a rocky intertidal ecosystem engineer and community dominant to climate change. *Ecology Letters* 11:151–162, https://doi.org/10.1111/j.1461-0248.2007.01135.x.

Menge, B.A., F. Chan, K.J. Nielsen, E. Di Lorenzo, and J. Lubchenco. 2009. Climatic variation alters supply-side ecology: Impact of climate patterns on phytoplankton and mussel recruitment. *Ecological Monographs* 79:379–395, https://doi.org/10.1890/08-2086.1.

Menge, B.A., T.C. Gouhier, T.L. Freidenburg, and J. Lubchenco. 2011. Linking long-term, large-scale climatic and environmental variability to patterns of marine invertebrate recruitment: Toward explaining "unexplained' variation. *Journal of Experimental Marine Biology and Ecology* 400:236–249, https://doi.org/10.1016/j.jembe.2011.02.003.

Menge, B.A., E.B. Cerny-Chipman, A. Johnson, J.M. Sullivan, S.A. Gravem, and F. Chan. 2016. Sea star wasting disease in the keystone predator *Pisaster ochraceus* in Oregon: Insights into differential population impacts, recovery, predation rate, and temperature effects from long-term research. *PLOS ONE* 11:e0153994, https://doi.org/10.1371/journal.pone.0153994.

Menge, B.A., J.E. Caselle, K. Milligan, S.A. Gravem, T.C. Gouhier, J.W. White, J.A. Barth, C.A. Blanchette, M.H. Carr, F. Chan, and others. 2019. Integrating coastal oceanic and benthic ecological approaches for understanding large-scale meta-ecosystem dynamics. *Oceanography* 32(3):38–49, https://doi.org/10.5670/oceanog.2019.309.

Miner, C.M., J.L. Burnaford, R.F. Ambrose, L. Antrim, H. Bohlmann, C.A. Blanchette, J.M. Engle, S.C. Fradkin, R. Gaddam, C.D.G. Harley, and others. 2018. Large-scale impacts of sea star wasting disease (SSWD) on intertidal sea stars and implications for recovery. *PLOS ONE* 13:e0192870, https://doi.org/10.1371/journal.pone.0192870.

Monaco, C.J., D.S. Wethey, and B. Helmuth. 2016. Thermal sensitivity and the role of behavior in driving an intertidal predator-prey interaction. *Ecological Monographs* 86:429–447, https://doi.org/10.1002/ecm.1230.
Montecino-Latorre, D., M.E. Eisenlord, M. Turner, R. Yoshioka, C.D. Harvell, C.V. Pattengill-Semmens, J.D. Nichols, and J.K. Gaydos. 2016. Devastating transboundary impacts of sea star wasting disease on subtidal asteroids. *PLOS ONE* 11:e0163190, https://doi.org/10.1371/journal.pone.0163190.
Moritsch, M.M., and P.T. Raimondi. 2018. Reduction and recovery of keystone predation pressure after disease-related mass mortality. *Ecology and Evolution* 8(8):3,952–3,964, https://doi.org/10.1002/ece3.3953.
Navarrete, S.A., B.R. Broitman, E.A. Wieters, G.R. Finke, R.M. Venegas, and A. Sotomayor. 2002. Recruitment of intertidal invertebrates in the southeast Pacific: Inter-annual variability and the 1997–1998 El Niño. *Limnology and Oceanography* 47:791–802, https://doi.org/10.4319/lo.2002.47.3.0791.
Paine, R.T. 1974. Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berlin)* 15:93–120, https://doi.org/10.1007/BF00345739.
Paine, R.T. 1986. Benthic community-water column coupling during the 1982–83 El Niño. Are community changes at high latitudes attributable to cause or coincidence? *Limnology and Oceanography* 31:351–360, https://doi.org/10.4319/lo.1986.31.2.0351.
Paine, R.T. 1994. *Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective*. Ecology Institute, Oldendorf/Luhe, Germany, 152 pp.
Palumbi, S.R., T.G. Evans, M.H. Pespeni, and G.N. Somero. 2019. Present and future adaptation of marine species assemblages: DNA-based insights into climate change from studies of physiology, genomics, and evolution. *Oceanography* 32(3):82–93, https://doi.org/10.5670/oceanog.2019.314.
Pershing, A.J., M.A. Alexander, C.M. Hernandez, L.A. Kerr, A. Le Bris, K.E. Mills, J.A. Nye, N.R. Record, H.A. Scannell, J.D. Scott, and others. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350:809–812, https://doi.org/10.1126/science.aac9819.
Peterson, W.T., and F.B. Schwing. 2003. A new climate regime in northeast Pacific ecosystems. *Geophysical Research Letters* 30(17), https://doi.org/10.1029/2003GL017528.
Petes, L.E., B.A. Menge, and A.L. Harris. 2008a. Intertidal mussels exhibit energetic trade-offs between reproduction and stress resistance. *Ecological Monographs* 78:387–402, https://doi.org/10.1890/07-0605.1.
Petes, L.E., Mouchka, M.E., R.H. Milston-Clements, T.S. Momoda, and B.A. Menge. 2008b. Effects of environmental stress on intertidal mussels and their sea star predators. *Oecologia* 156:1,432–1,939, https://doi.org/10.1007/s00442-008-1018-x.
Pincebourde, S., E. Sanford, and B.S.T. Helmuth. 2008. Body temperature during low tide alters the feeding performance of a top intertidal predator. *Limnology and Oceanography* 53:1,562–1,573, https://doi.org/10.4319/lo.2008.53.4.1562.
Pincebourde, S., E. Sanford, and B. Helmuth. 2009. An intertidal sea star adjusts thermal inertia to avoid extreme body temperature. *The American Naturalist* 174:890–897, https://doi.org/10.1086/648065.
Pincebourde, S., E. Sanford, J. Casas, and B. Helmuth. 2012. Temporal coincidence of environmental stress events modulates predation rates. *Ecology Letters* 15:680–688, https://doi.org/10.1111/j.1461-0248.2012.01785.x.
Place, S.P., B.A. Menge, and G.E. Hofmann. 2011. Transcriptome profiles link environmental variation and physiological response of *Mytilus californianus* between Pacific tides. *Functional Ecology* 26:144–155, https://doi.org/10.1111/j.1365-2435.2011.01924.x.
Poloczanska, E.S., S.J. Hawkins, A.J. Southward, and M.T. Burrows. 2008. Modeling the response of populations of competing species to climate change. *Ecology* 89:3,138–3,149, https://doi.org/10.1890/07-1169.1.
Raimondi, P.T., C. Melissa Miner, B.A. Menge, C.A. Blanchette, and D.P. Lohse. 2019. Quantitative biogeography: Large-scale, long-term change in the rocky intertidal region of the California Current Large Marine Ecosystem. *Oceanography* 32(3):26–37, https://doi.org/10.5670/oceanog.2019.308.
Robles, C.D., R.A. Desharnais, C. Garza, M.J. Donahue, and C.A. Martinez. 2009. Complex equilibria in the maintenance of boundaries: Experiments with mussel beds. *Ecology* 90:985–995, https://doi.org/10.1890/08-0919.1.
Ruggiero, P., P.D. Komar, and J.C. Allan. 2010. Increasing wave heights and extreme value projections: The wave climate of the US Pacific Northwest. *Coastal Engineering* 57:539–552, https://doi.org/10.1016/j.coastaleng.2009.12.005.
Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283:2,095–2,097, https://doi.org/10.1126/science.283.5410.2095.
Sanford, E., and B.A. Menge. 2001. Spatial and temporal variation in barnacle growth in a coastal upwelling system. *Marine Ecology Progress Series* 209:143–157, https://doi.org/10.3354/meps209143.
Sanford, E., J.L. Sones, M. García-Reyes, J.H.R. Goddard, and J.L. Largier. 2019. Widespread shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves. *Scientific Reports* 9:4216, https://doi.org/10.1038/s41598-019-40784-3.
Schultz, J.A., R.N. Cloutier, and I.M. Cote. 2016. Evidence for a trophic cascade on rocky reefs following sea star mass mortality in British Columbia. *PeerJ* 4:e1980, https://doi.org/10.7717/peerj.1980.
Siddon, C.E., and J.D. Witman. 2003. Influence of chronic, low-level hydrodynamic forces on subtidal community structure. *Marine Ecology Progress Series* 261:99–110, https://doi.org/10.3354/meps261099.
Somero, G.N. 2012. The physiology of global change: Linking patterns and mechanisms. *Annual Review of Marine Science* 4:39–61, https://doi.org/10.1146/annurev-marine-120710-100935.
Sorte, C.J.B., V.E. Davidson, M.C. Franklin, K.M. Benes, M.M. Doellman, R.J. Etter, R.E. Hannigan, J. Lubchenco, and B.A. Menge. 2017. Long-term declines in an intertidal foundation species parallel shifts in community composition. *Global Change Biology* 23:341–352, https://doi.org/10.1111/gcb.13425.
Stephenson, T.A., and A. Stephenson. 1972. *Life Between Tidemarks on Rocky Shores*. W.H. Freeman and Co., San Francisco, CA, 425 pp.
Stokstad, E. 2014. Death of the stars. *Science* 344:464–467, https://doi.org/10.1126/science.344.6183.464.
Sydeman, W.J., J.A. Santora, S.A. Thompson, B. Marinovic, and E.D. Lorenzo. 2013. Increasing variance in North Pacific climate relates to unprecedented ecosystem variability off California. *Global Change Biology* 19:1,662–1,675, https://doi.org/10.1111/gcb.12165.
Szathmary, P.L., B.S.T. Helmuth, and D.S. Wethey. 2009. Climate change in the rocky intertidal zone: Predicting and measuring the body temperature of a keystone predator. *Marine Ecology Progress Series* 374:43–56, https://doi.org/10.3354/meps07682.
Vinueza, L.R., G.M. Branch, M.L. Branch, and R.H. Bustamante. 2006. Top-down herbivory and bottom-up El Niño effects on Galápagos rocky-shore communities. *Ecological Monographs* 76:111–131, https://doi.org/10.1890/04-1957.
Vinueza, L.R., B.A. Menge, D. Ruiz, and D.M. Palacios. 2014. Oceanographic and climatic variation drive top-down/bottom-up coupling in the Galápagos rocky intertidal meta-ecosystem. *Ecological Monographs* 84:411–434, https://doi.org/10.1890/13-0169.1.
Wang, D., T.C. Gouhier, B.A. Menge, and A.R. Ganguly. 2015. Intensification and spatial homogenization of coastal upwelling under climate change. *Nature* 518:390–394, https://doi.org/10.1038/nature14235.
Wernberg, T., S. Bennett, R.C. Babcock, T. de Bettignies, K. Cure, M. Depczynski, F. Dufois, J. Fromont, C.J. Fulton, R.K. Hovey, and others. 2016. Climate-driven regime shift of a temperate marine ecosystem. *Science* 353:169–172, https://doi.org/10.1126/science.aad8745.
Zhang, L., and T.L. Delworth. 2016. Simulated responses of the Pacific Decadal Oscillation to climate change. *Journal of Climate* 29:5,999–6,018, https://doi.org/10.1175/JCLI-D-15-0690.1.

ACKNOWLEDGMENTS

We thank the many research assistants, graduate students, postdoctoral scholars, and undergraduate interns who have contributed to our continually expanding understanding of CCLME dynamics. Research support was provided by the David and Lucile Packard, Gordon and Betty Moore, and Andrew W. Mellon Foundations, and the National Science Foundation. This is PISCO publication number 497.

AUTHORS

- Article lead authors are **Bruce A. Menge** (mengeb@oregonstate.edu), Department of Integrative Biology, Oregon State University, Corvallis, OR, USA, and **Jennifer E. Caselle**, Marine Science Institute, University of California, Santa Barbara, CA, USA.
- Contributors from Oregon State University are **John A. Barth** (College of Earth, Ocean, and Atmospheric Sciences), **Francis Chan**, **Sarah Gravem**, **Jane Lubchenco**, **Kristen Milligan**, and **Mark Novak** (Department of Integrative Biology), and **J. Wilson White** (Coastal Oregon Marine Experiment Station and Fisheries and Wildlife).
- Contributors from the University of California, Santa Barbara, are **Carol A. Blanchette** (Marine Science Institute) and **Libe Washburn** (Department of Geography).
- Contributors from the University of California, Santa Cruz, Department of Ecology and Evolutionary Biology are **Mark H. Carr** and **Peter T. Raimondi**.
- Contributor from the University of Hawai'i at Mānoa, Department of Oceanography is **Margaret A. McManus**.
- Contributor from Northeastern University Marine Science Center is **Tarik C. Gouhier**.

ARTICLE CITATION

Menge, B.A., J.E. Caselle, J.A. Barth, C.A. Blanchette, M.H. Carr, F. Chan, S. Gravem, T.C. Gouhier, J. Lubchenco, M.A. McManus, K. Milligan, M. Novak, P.T. Raimondi, L. Washburn, and J.W. White. 2019. Community responses to climate-related variability and disease: The critical importance of long-term research. *Oceanography* 32(3):72–81, https://doi.org/10.5670/oceanog.2019.313.

COPYRIGHT & USAGE