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TAKING THE PULSE OF MARINE ECOSYSTEMS

The Importance of Coupling Long-Term Physical and Biological Observations in the Context of Global Change Biology

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ABSTRACT. Research programs that co-locate environmental sensors with "biology" can enable the linking of environmental data with changes in biological or ecological processes. The coastal and marine Long Term Ecological Research (LTER) programs use this strategy, measuring parameters such as air and sea temperature, wave and storm energy, and seawater chemistry along with biological responses to them. This investment in technology has proven to be valuable and a major scientific asset for understanding how climate change, and environmental change in general, might alter marine populations and communities. Such a strategy can also aid in studies of global change biology of critical species, helping to place laboratory experiments and predictions of response in a broader environmental context. This coupling of long-term physical and biological observations has already detected fingerprints of change in sites such as the Palmer LTER situated on the western Antarctic Peninsula. In addition, new autonomous pH sensors recently deployed at two marine LTERs—Santa Barbara Coastal and Moorea Coral Reef—are generating long-term data sets that highlight the responses of their marine communities to rapidly changing ocean conditions.

INTRODUCTION

Forecasting the consequences of climate change is a central research priority for the scientific community (e.g., Sutherland et al., 2006; Walther, 2010; Dawson et al., 2011; Buckley and Kingsolver, 2012; Ibáñez et al., 2013). In marine ecosystems, investigators have explored issues specific to coral reef decline (Hoegh-Guldberg et al., 2007; Frieler et al., 2013), the combined impacts of ocean acidification and ocean warming on marine organisms (Boyd, 2011; Harvey et al., 2013), and projected consequences to fisheries (Cheung et al., 2009, 2012). At the same time, policymakers have focused on the impacts of climate change on marine resources that are important to economies (e.g., IPCC, 2007b; Kelly et al., 2011; Rau et al., 2012; Melillo et al., 2013). At the heart of all these efforts is the need to understand the adaptive capacity and vulnerability of organisms in the face of rapid environmental change (Williams et al., 2008; Dawson et al., 2011).

Given this critical scientific and policy effort, knowledge of the physical environment is central to studying the forces that will change the distribution of marine organisms, challenge their physiological tolerances, and alter species interactions, ultimately reshaping marine ecosystems. With this in mind, we highlight some long-term physical and biological data sets that have been collected at US coastal marine Long Term Ecological Research (LTER) sites that are now, and will be in the future, essential tools for beginning to understand the consequences of environmental change in the context of global change biology.

MEASURING ENVIRONMENTAL CHANGE

With long-term monitoring as a key component of their mission, the LTER sites are uniquely poised to capture environmental changes on time scales of years to decades that are relevant to ecosystem-level observations. Here, we highlight examples from the coastal marine LTER sites that frame the argument that documenting and understanding the nature of changes in the physical environment, in addition to monitoring biological and ecological attributes, is critical to our ability to predict responses of species and ecosystems to global change. Below, we focus on three key environmental parameters that are now being measured at several LTER sites and are likely to be drivers of ecological changes in these ecosystems in the near future: (1) air and sea temperature, (2) wave and storm energy, and (3) seawater chemistry.

Air and Sea Temperature

Temperature is well known to affect organisms and populations in a climate change context (Parmesan, 2006), with range shifts tending to be dominant responses of populations to temperature change. For marine ecosystems, using long-term data sets to link physiological and organismal responses to temperature is especially important as most ectothermic marine species are already operating at or near their thermal limits (Sunday et al., 2012). One example of foundational temperature data is from the Palmer (PAL) LTER site on the western Antarctic Peninsula (WAP). Air temperatures over Antarctica (Chapman and Walsh, 2007) and seawater temperatures in the Southern Ocean have warmed (Gille, 2002). This region of the Southern Ocean has one of the fastest warming rates on Earth, with a 3°C increase in annual mean air temperature and a 6°C rise in mean winter temperature over the last six decades (Vaughan et al., 2003). This rapid increase in temperature is linked to a decline in sea ice extent. Recorded since 1990, PAL LTER data have captured a dramatic decline in sea ice in the WAP region (Stammerjohn et al., 2008), with associated consequences for WAP marine ecosystems (Steinberg et al., 2012; see also further discussion in Ducklow et al., 2013, in this issue).

Wave and Storm Energy

Most climate change models show that the future will be characterized by increases in the frequency and possibly the severity of many forms of large abiotic disturbances across the globe (Easterling et al., 2000; Meehl et al., 2000; Hemer et al., 2013). Over the last 60 years in the eastern Pacific, the frequency of large waves driven by winter storms has increased (Graham and Diaz, 2001; Bromirski et al., 2003; Ruggiero et al., 2010). This increase in physical disturbance could have detrimental effects on coastal ecosystems dominated by the giant kelp *Macrocystis pyrifera*, a foundational species that provides habitat and energy to fuel a highly complex and productive food web (Dayton, 1985; Graham, 2004; Reed and Brzezinski, 2009). Large waves associated with winter storms often tear out giant kelp (Figure 1), reducing their abundance and likely changing the structure of the associated kelp forest food web as well as light, hydrodynamics, and the three-dimensional structure of the habitat (Graham et al., 2007). Periodic disturbances are a natural component of almost every ecosystem, and many ecological models predict that the mortalities caused by occasional disturbances can be vital for maintaining biological diversity as well as renewing essential nutrients. For example, elevated resources resulting from the loss of giant kelp have been shown to enhance the diversity and production of understory algae (Reed and Foster, 1984; Arkema et al., 2009; Miller et al., 2011). However, models also predict a decrease in species diversity when the frequency or severity of disturbances becomes too great (Connell, 1978).

Long-term research at the Santa Barbara Coastal (SBC) LTER site has demonstrated the overwhelming importance of wave disturbance as a dominant structuring force in kelp forest ecosystems (Cavanaugh et al., 2011; Reed et al., 2011). SBC LTER researchers examined the relative importance of nutrient availability (bottom-up), grazing pressure (top-down), and storm waves (disturbance) in controlling the abundance and productivity of giant kelp offshore central and southern California. Central California kelp forests exist in a region of high wave exposure and high nutrients, but low urchin grazer abundance, relative to southern California forests. While both bottom-up and top-down theories predict that central California kelp biomass and production should be greater than that of southern California due to increased productivity and reduced grazing pressure, SBC LTER scientists predict that the intense wave disturbances on the central coast could overwhelm the bottom-up and top-down forces (Reed et al., 2011). Indeed, SBC LTER researchers found that biomass and production of giant kelp were generally lower in central California (Figure 2).

In addition to the direct effects of wave disturbance on kelp biomass and

Figure 1. Piles of giant kelp line the sandy beaches of Southern California following a large wave event. *Photo credit: Shane Anderson*

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productivity, SBC LTER researchers have also shown that the effects of wave disturbance on giant kelp cascade through the kelp forest food web. Results of experimental kelp removals and model simulations suggest a sequence of change in food web structure following multiple consecutive years of large storms (Byrnes et al., 2011). A single storm hitting a relatively undisturbed kelp forest appears to increase complexity, while concentrating most species at the resource and primary consumer trophic levels. Higher trophic levels do not disappear after initial kelp loss, but rather diversity within these higher trophic levels declines. As storms continue year after year, food webs begin to collapse, and the richness of species, whether grouped by trophic level or functional attributes, declines. Thus, an increase in the frequency of large storms (as widely predicted by climate change models) is likely to lead not only to decreases in giant kelp primary productivity, but also to decreases in the diversity and complexity of kelp forest food webs.

The idea that changing climate conditions may lead to larger, more frequent, and intense storms has received increasing support in recent years in the wake of several large hurricanes and "superstorms" in the United States (e.g., Katrina and Sandy). Storm intensity continues to be measured at the Virginia Coast Reserve (VCR) LTER, contributing to a time series starting in the 1880s. These data reveal a pattern of increasing storm intensity over the last century in this barrier island region of the US East Coast (Figure 3). Researchers at VCR LTER have also shown that infrequent but extreme events such as major storms have a significant effect on the state of the dynamic barrier island coastline and should be considered in long-term projections of how future increases in storm intensity will alter the structure of the shoreline ecosystem (Fenster and Hayden, 2007).

Seawater Chemistry

Driven by increasing atmospheric CO_2 levels, ocean acidification has emerged as the most recent threat to healthy ocean ecosystems (Hoegh-Guldberg et al., 2007; Fabry et al., 2008; Doney et al., 2009). A few long-term data sets on carbonate chemistry have captured surface ocean acidification. Three low-latitude, open-ocean pH monitoring programs—Hawaii Ocean Time-series (http://hahana.soest.hawaii.edu/hot), Bermuda-Atlantic Time-series Study (http://bats.bios.edu), and the European Station for Time Series in the Ocean, Canary Islands (http://estoc.plocan.eu)—have measured an average decline of 0.002 pH units per year (Bates, 2007; Dore et al., 2009; González-Dávila et al., 2010). Additionally, time-series data describing shifts in carbonate chemistry in coastal regions have appeared in the last five years (Wootton et al., 2008; Provoost et al., 2010; Waldbusser et al., 2011; Wootton and Pfister, 2012). These data sets, along with projections of future acidification (Caldeira and Wickett, 2003; IPCC, 2007a), sparked a global research effort to understand the biological implications of future ocean conditions. Over the past decade, laboratory acidification experiments have highlighted largely negative and complex species-specific effects in response to reduced pH/elevated pCO_2 (Fabry et al., 2008; Doney et al., 2009; Kroeker et al., 2010, 2013; Harvey et al., 2013). Despite this growing knowledge base, the lack of information on environmentally relevant pH conditions for these study species clouds the predictive interpretation of laboratory-based biological experimental results.

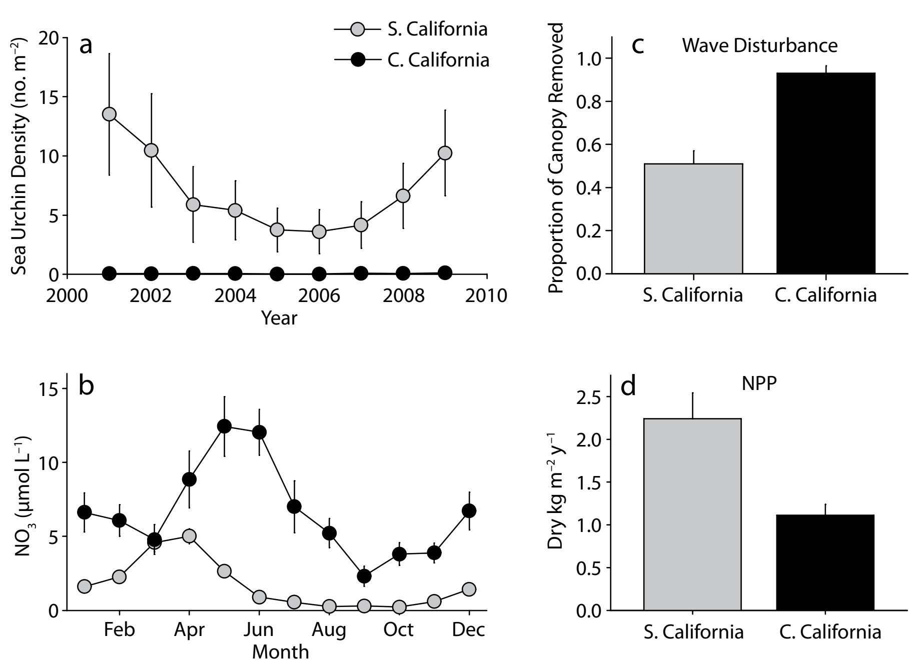

Figure 2. Wave disturbance in Southern California affects the abundance of giant kelp. Despite lower sea urchin densities (a) and higher nitrate loads (b) in Central (black) vs. Southern California (gray), kelp forest density (c) and net primary productivity (d) are limited by wave disturbance. *Figure reproduced with permission from the Santa Barbara Coastal LTER*

Although the long-term data sets of open-ocean carbonate chemistry have been essential to our understanding of global changes in oceanic pH, these data do not directly inform ocean acidification processes in coastal or nearshore marine ecosystems, habitats that provide many services to humans (Ruckelshaus et al., 2013) and are the locations of most of the world's fisheries. Additionally, projections of future ocean pH conditions from the Intergovernmental Panel on Climate Change and others are based on global emission scenarios and large-scale ocean processes that lack resolution necessary to predict changes on regional and local scales (see Wootton and Pfister, 2012). Long-term data sets of carbonate chemistry parameters in shallow, coastal ecosystems are essential for predicting biological responses to ocean acidification. Ultimately, the biological impacts of ocean acidification in nearshore benthic marine communities will depend on (1) the degree of acclimatization/adaptation to local pH regimes and (2) the rate and magnitude of pH changes in these regions in the future.

New LTER Technology: SeaFET, An Autonomous pH Sensor

New autonomous pH sensors called SeaFETs (Martz et al., 2010) are currently measuring ocean conditions at two LTER sites—SBC and Moorea Coral Reef (MCR). Data from these instruments are not only providing environmentally relevant information on local pH conditions, but also advancing the way we think about pH variability. SeaFET deployments in nearshore regions around the globe have revealed remarkable differences in pH variability across ecosystems (Hofmann et al., 2011; Frieder and Levin, 2012; Price et al., 2012; recent work of Francis Chan, Oregon State University, and colleagues), dispelling the notion of ocean acidification as a homogenous, global environmental stressor. The LTER SeaFET deployments highlight the importance of quantifying pH both spatially and temporally as a holistic approach to ocean acidification research emphasizing the need to co-locate pH sensors with biological experiments and ecological monitoring sites (Price et al., 2012; Hofmann et al., 2013).

Specifically, LTER SeaFET deployments have revealed striking differences in the patterns of variability in pH dynamics across a variety of spatial scales (Figure 4). The SBC LTER is located in the Santa Barbara Channel region of Southern California. Here, complex bathymetry and oceanographic processes as well as a coastline perforated with kelp forests contribute to large temporal and spatial fluctuations in pH in the nearshore environment. For example, over two months, pH at a mainland site fluctuated between 7.603 and 8.232 (mean pH: 7.934), while pH at Anacapa Island ranged from 7.847 to 8.075 (mean pH: 7.953). Although separated by only 54 km, these sites share similar species compositions and mean pH values, yet they differ dramatically in the temporal pattern of pH variability. Within the MCR LTER, located in the center of the tropical Pacific Ocean, spatial patterns of pH variability are maintained across relatively small spatial scales (~ 1 km). Here, the range of variability in pH differs between an exposed fore reef site and a fringing reef site 1 km shoreward across a lagoon (Figure 4). During the three-week deployment, pH at the fore reef and fringing reef ranged from 8.062–8.116 (mean pH: 8.088) and 8.042–8.226 (mean pH: 8.130), respectively. These data provide a glimpse of the variability in environmental conditions across a range of temporal and spatial scales that organisms are currently experiencing, and they provide an important context for interpreting the responses of organisms to experimental ocean acidification

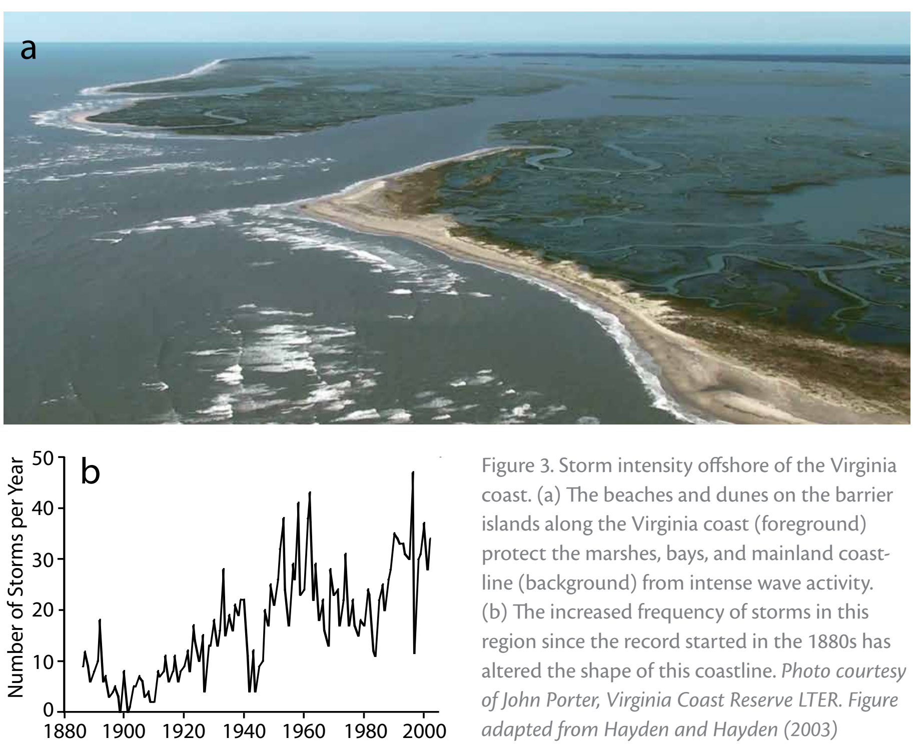

Figure 3. Storm intensity offshore of the Virginia coast. (a) The beaches and dunes on the barrier islands along the Virginia coast (foreground) protect the marshes, bays, and mainland coastline (background) from intense wave activity. (b) The increased frequency of storms in this region since the record started in the 1880s has altered the shape of this coastline. *Photo courtesy of John Porter, Virginia Coast Reserve LTER. Figure adapted from Hayden and Hayden (2003)*

conditions in laboratory experiments.

Understanding the natural pH variability to which breeding populations are locally adapted or acclimatized is critical in order to predict species' performance under future ocean acidification scenarios. Several SeaFET networks have successfully linked natural pH variability to performance and ecosystem processes (Price et al., 2012; Hofmann et al., 2013; Padilla-Gamiño et al., 2013). For example, in the remote tropical Pacific, reefs that spent more hours at low pH showed slower net calcium carbonate accretion rates and a greater abundance of fleshy colonizers (Price et al., 2012). The LTER framework of established, well-characterized sites provides a unique opportunity to explore biophysical coupling between site-specific "pH-seascapes" (Hofmann et al., 2011) and tolerance of local populations to future ocean acidification. Differences in pH variability across these small spatial scales may foster a diversity of pH-related phenotypes among breeding populations, increasing the potential for resilience of species at regional scales. In this light, data from SeaFETs in LTERs may contribute to studies of acclimatization and adaptation potential of marine species to future ocean acidification (Kelly and Hofmann, 2012). Biological studies complementary to ongoing SeaFET deployments at LTER sites will serve to ground our understanding of the effects of ocean acidification under natural environmental conditions while informing effects of changing ocean conditions on marine ecosystems.

LONG-TERM STUDIES AND GLOBAL CHANGE BIOLOGY

The importance of LTER-based long-term data sets is amplified when placed in the context of global change biology, an integrative field that focuses on predicting the response of species and biological communities to human-induced changes such as climate change, eutrophication, or ocean acidification. Some of the first synthetic reports noted species range shifts as fingerprints of climate change (Parmesan and Yohe, 2003; Root et al., 2003; Parmesan, 2006). Recently, researchers have called for moving "beyond prediction" to concrete action in management and conservation efforts (e.g., Williams et al., 2008; Dawson et al., 2011; Pettorelli, 2012; Ibáñez et al., 2013). As these discussions advance, it is clear that species' sensitivities to abiotic conditions and their adaptive capacities are ideally framed with knowledge of the physical environment and the degree of natural variability that has acted as a selective force in the past.

In this light, LTER data sets will support a range of activities in experimental biology and ecology that focus on addressing the responses of species, populations, and ecosystems. Ecologically relevant data help parameterize laboratory and mesocosm experiments. Here, there has been a growing appreciation that knowing a species' physiological plasticity of important traits is a central element in determining adaptive capacity in the face of abiotic change such as temperature, physical disturbance, and pH (Visser, 2008; Helmuth, 2009; Dawson et al., 2011; Buckley and Kingsolver, 2012; Chown, 2012; Ibáñez et al., 2013). In addition to physiological plasticity, rapid evolution and adaptation is another type of response to climate change and may also play an important role in species' future tolerances (e.g., Bradshaw and Holzapfel, 2006). LTER data sets will certainly play a role in studies of this nature

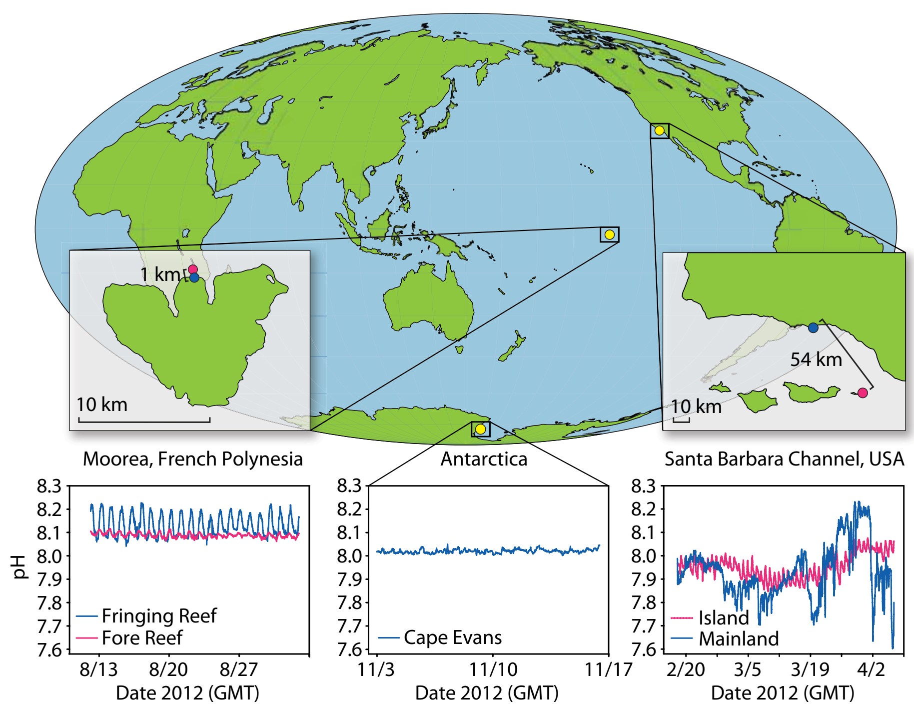

Figure 4. Dynamics of pH at 5–15 m water depth in three different ocean regions. Data panels from different ecosystems are plotted on the same vertical range of pH (total hydrogen ion scale). Map insets show sites and relative distance for Long Term Ecological Research (LTER) data series that highlight differences in pH dynamics on regional and local scales. *SeaFET pH time series used with permission from the Moorea Coral Reef and Santa Barbara Coastal LTERs. pH time series from Antarctica provided by Gretchen Hofmann*

both in terms of describing the rate of change of environmental conditions and in supporting hypotheses-based testing of how genetic responses might contribute to species' responses to abiotic change in marine ecosystems (see Gienapp et al., 2008; Kelly and Hofmann, 2012; O'Connor et al., 2012; Kelly et al., 2013).

Finally, LTER data sets support the study of how environmental change will alter ecosystem structure and function via impacts on species interactions. Studies of this essential research area are lagging as compared to studies of species range shifts (e.g., Harley et al., 2006; Walther, 2010). Changes in present-day interactions will have far-reaching consequences for community composition and function (Lurgi et al., 2012). Key predator-prey interactions can be sensitive to temperature (Sanford, 1999), and relatively small changes in seawater pH can alter competitive interactions (Kroeker et al., 2013) as well as larval settlement behavior (Doropoulos et al., 2012). Understanding how climate change will affect not only individual species but also interactions among species will be critical to forecasting the community and ecosystem-level impacts of changing climate conditions.

CONCLUSION

The network of coastal LTER sites is positioned to meet one of the grand challenges in the Anthropocene: documenting and forecasting the impact of global change on marine ecosystems. Collectively, the LTERs highlighted here are gathering data sets for coastal and pelagic ecosystems that host high biodiversity and support critical ecosystem services. The future of these LTER efforts will continue to frame questions central to global change biology and support ecological and organismal studies in these key ecosystems, as evidenced by the emerging data sets on carbonate chemistry that will support research in ocean acidification (Edmunds et al., 2013, in this issue). One of the inherent complexities in predicting the outcome of environmental change-related impacts is the difficulty of layering projected changes on existing natural environmental variability. This research area will continue to be active within the LTER community, where LTER-based long-term ecological studies are critical for providing key insights in ecology and environmental change, and will continue to be a valuable source of information to inform future research.

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