SANTA BARBARA COASTAL LONG TERM ECOLOGICAL RESEARCH PROGRAM

MIDTERM REVIEW BRIEFING DOCUMENT

PREPARED FOR THE NATIONAL SCIENCE FOUNDATION SITE REVIEW TEAM

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PROJECT OVERVIEW

The Santa Barbara Coastal LTER (SBC LTER) is an interdisciplinary research and education program established in April 2000 to investigate the relative importance of land and ocean processes in structuring coastal ecosystems. Its principal study domain is a 10,000 km^2 area that includes the Santa Barbara Channel (located in the northern portion of the Southern California Bight) and the steep coastal watersheds, small estuaries and sandy beaches that adjoin it (**Fig 1**). The focal ecosystem of SBC is giant kelp (*Macrocystis pyrifera*) forests, a diverse and highly productive marine ecosystem that occurs on shallow rocky reefs at the interface of the land-sea margin in the Santa Barbara Channel and other temperate regions throughout the world. Giant kelp forests are ecologically important to the areas in which they occur, and they also provide highly valued provisioning, cultural and regulating services.

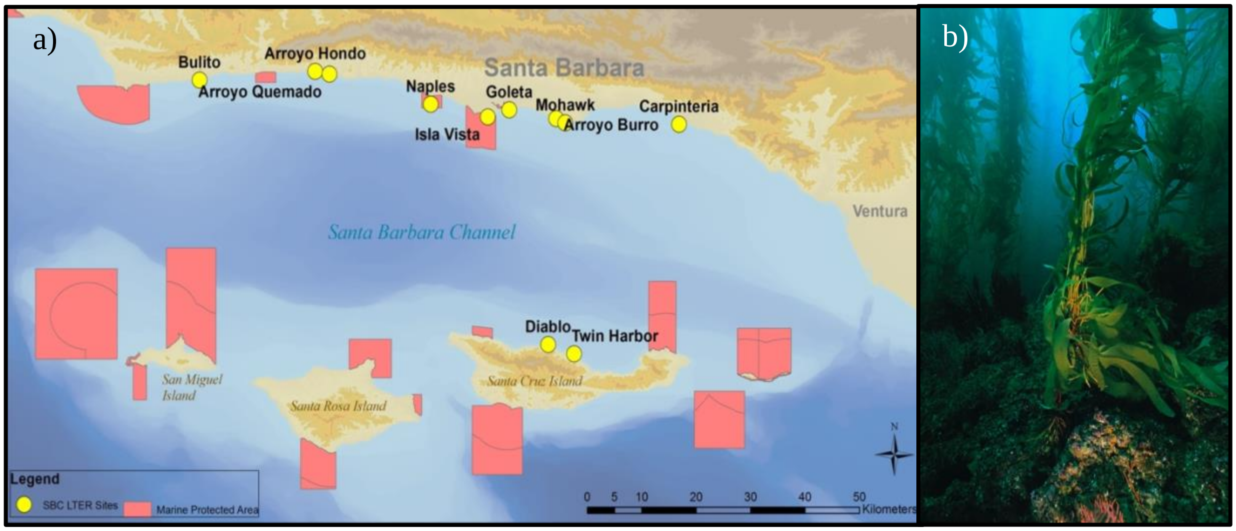

Figure 1. (a) Map of the SBC study domain, showing long-term kelp forest sites and marine protected areas (MPAs) (b) Submarine view of a giant kelp forest.

Project research encompasses all five core areas common to LTER sites. During our first 6-year funding cycle (SBC I) we focused on identifying and quantifying inputs to giant kelp forest communities from land and sea and documenting patterns and sources of spatial and temporal variation in key elements of kelp forest structure and function. We established core long-term measurements to quantify inorganic and organic subsidies to giant kelp forests and their effects on kelp forest community structure, productivity and dynamics. During SBC II we sought to determine how environmental drivers acting over different spatial and temporal scales interact to influence the community structure and ecological functions of giant kelp forests. SBC III explored the roles of disturbance and climate on material exchanges and forest dynamics using long-term measurements, manipulative experiments, and integrated synthesis using models.

Analyses of our long-term data have identified many of the environmental drivers and ecological processes underlying the dynamics of kelp forests. However key unanswered questions about the ecosystem consequences of wave disturbance and fishing that alter the area and architecture of giant kelp forests, the processes that sustain kelp growth during warm, low nitrate conditions, the ecological and evolutionary consequences of kelp-induced changes in pH and dissolved oxygen, and the degree to which climate variability influences forest persistence and trophic subsidies to and from kelp forests remain. These and other unknowns form the basis of the overarching question that motivates our proposed research in SBC IV: *How do natural and human drivers influence giant kelp dynamics and alter the long-term structure and function of kelp forest ecosystems?* Our research is organized around three general themes to address this question: (1) Environmental drivers of kelp persistence and community structure, (2) Biophysical coupling in kelp forest, and (3) Spatial dynamics and connectivity. Our conceptual framework links these themes in a framework focused on the causes and ecological consequences of the dynamics of a relatively short-lived foundation species, giant kelp, in a setting of long-term climate change and human use (**Fig 2**).

Because SBC is the only temperate reef site in the US LTER Network and the only kelp forest site in the International LTER Network, broader scale long-term synthesis is achieved by partnering with other entities to extend the spatial scale of our data sets and analyses and by collaborations with non-LTER scientists.

During the three-year period of this review 37 Investigators, 8 postdoctoral fellows, 38 graduate students, 9 REU students and 196 additional undergraduate students participated in SBC sponsored research, resulting in 75 peer-reviewed publications, 7 dissertations/theses and >

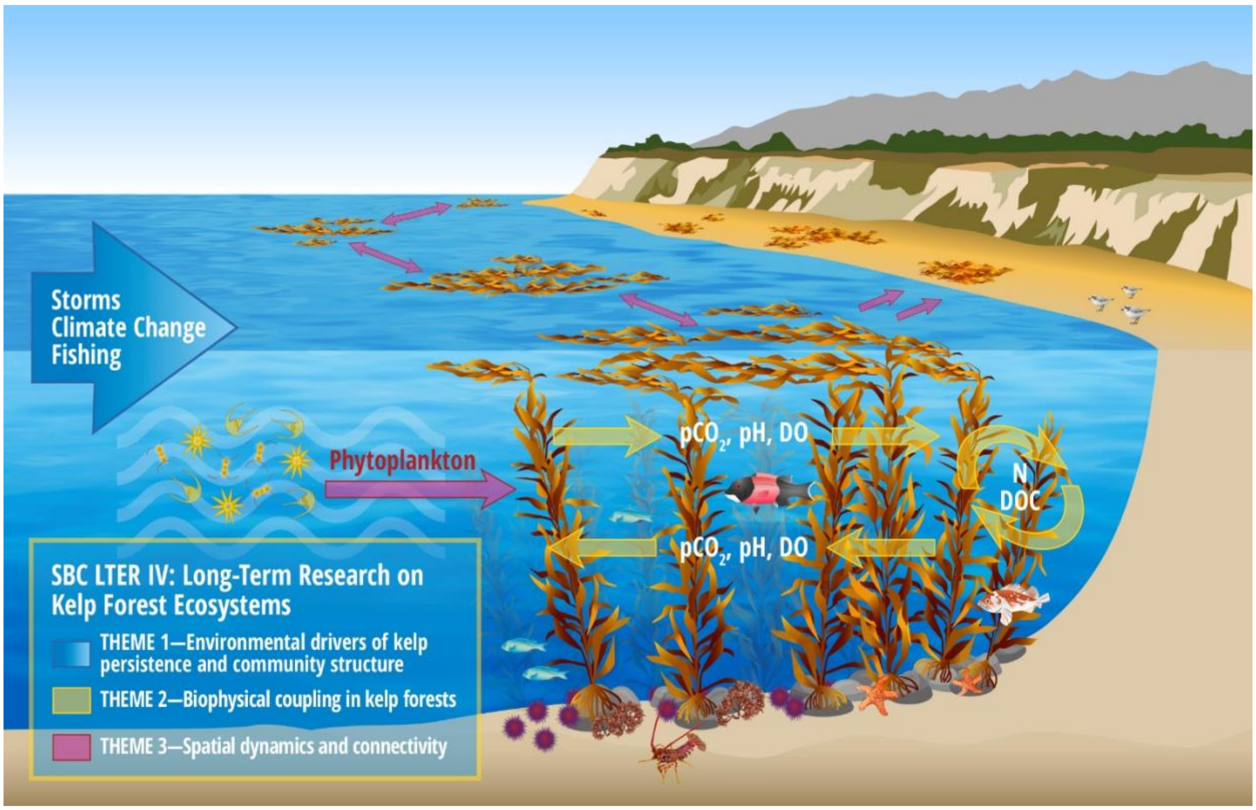

Figure 2. Conceptual framework for SBC IV illustrating the three major research themes that integrate across populations, communities and ecosystems to address the overarching question *"How do natural and human drivers influence giant kelp dynamics and alter the long-term structure and function of kelp forest ecosystems?"* Arrows are color coded by research theme.

$11 million in collaborative research funding from 15 different sources. A multifaceted outreach program serves to deliver SBC research findings to K-12 education, resource managers, policy makers and the general public to enhance broader benefits to society.

SITE BASED RESEARCH

Below we summarize our core data collection and major research activities in the three general thematic areas upon which our current award, SBC IV, is structured.

CORE DATA COLLECTION

We collect data on a core group of long-term integrated measurements aimed at quantifying climate, disturbance and inorganic and organic subsidies to and from giant kelp forests and their effects on kelp forest community structure, productivity and dynamics. These data and accompanying metadata are easily accessed from the SBC data catalog, which facilitates browsing by (1) Habitat, (2) Measurement type, and (3) LTER Core research area (all 5 areas are covered). A web link to our research sites provides an interactive map that allows the viewer to easily obtain information on the locations and frequency of data collection and the year data sets were initiated. During SBC IV, we broadened our geographic coverage of ocean instrument data via collaboration with other programs (PISCO, NPS); pH sensors and bottom temperature loggers now include two additional mainland and 21 additional Channel Islands sites.

THEMED RESEARCH

THEME 1. Environmental drivers of kelp persistence and community structure

Our previous findings highlight the capacity of giant kelp to persist through periods of increased climate variability. Yet, giant kelp forests are subject to warming and nutrient stress that can cause severe declines, and are regularly disturbed by storms and fishing. Changes in climate are expected to alter the frequency and severity of wave disturbance and fishing effort, and cause more persistent and severe warming and accompanying low nitrate conditions. The research in *THEME 1* examines patterns, causes and consequences of kelp persistence and loss on the structure and function of the kelp forest community, the drivers of kelp forest recovery following disturbance, the ecological consequences of fishing, and the sources and utilization of different forms of nitrogen that may enable kelp to persist during conditions of low nitrate availability.

THEME 1A. *Community and ecosystem consequences of climate variability, disturbance and pathways of recovery*

In 2014–2016 the west coast of North America experienced a marine heatwave unprecedented in the historical record. We used our Landsat time series to examine spatial patterns in the response of kelp to this heatwave from its southern range limit in Baja throughout southern California. The impacts were most severe in Baja, while the Santa Barbara Channel region where SBC is located exhibited high levels of resistance and resilience, despite large positive temperature anomalies. Giant kelp loss throughout the region was more sensitive to exceedance of an absolute temperature threshold than to relative changes (Cavanaugh et al. 2019). Such fluctuations in kelp have community-level consequences: analyses of our long-term kelp forest community data showed that community stability was positively and indirectly related to giant kelp stability due to kelp's direct positive association with species richness, via increased species stability and species asynchrony (Lamy et al. 2020). Ecological theory posits that both species and spatial insurance, whereby organism abundance varies asynchronously by species or in space, respectively, reduce metacommunity variation over time, yet these mechanisms are rarely examined in natural systems. Using our long-term data, we partitioned these mechanisms and found that species insurance was the strongest stabilizing force in kelp forests (Lamy et al 2019).

After discontinuing the annual removal of giant kelp in our long-term disturbance experiment, conducted over 9 years at four sites, we are continuing to collect data on community recovery and net primary production (NPP) in kelp removal and control plots. Recovery in these plots has proceeded for 3-4 years depending on site. In the meantime, further analysis of the long term experiment revealed that understory macroalgae partly compensated for canopy NPP losses and increasing habitat quality magnified this effect. Disturbance-driven increases in understory NPP were still rising after 5–10 years of disturbance, demonstrating the value of long-term experimentation for understanding ecosystem responses to changing disturbance regimes (Castorani et al. 2021). Sea urchin grazing was one element of kelp habitat quality, and heavy urchin grazing can transform kelp forests to deforested barrens. Using a long-term urchin recruitment dataset across southern California collected by a research consortium led by SBC LTER, we showed that large-scale patterns of recruitment, and therefore urchin abundance and grazing, are strongly influenced by climate (Okamoto et al. 2020). At smaller scales, we used mesocosm foraging trials and our long-term data on sea urchin biomass to construct a 21-year time series of estimated urchin grazing rates which we combined with long-term measurements of kelp frond loss to predict when grazing exceeds the supply of kelp detritus. Sites where grazing was higher than detrital supply averaged 50 times less kelp than sites where detrital supply exceeded predicted grazing rates (Rennick et al. in review), providing insight into when and where urchins are likely to force state transitions in kelp forests. On the organismal scale, a first description of the gut microbiome of red and purple urchins showed different microbiomes in forested vs barren habitats and suggests that microbes may enable urchin persistence under low-food conditions, facilitating hysteresis between these states (Miller et al. 2021).

An undergraduate (now graduate) student, Raine Detmer (Moeller lab), developed and analyzed a model of the effects of variable storm regimes on giant kelp population dynamics and of the cascading effects on kelp-mediated competition between benthic organisms. Simulations of severe storm regimes resulted in a greater abundance of understory macroalgae and a lower abundance of sessile invertebrates than did milder regimes. The model's predictions were consistent with empirical data from our 20-yr time series of community dynamics, suggesting that interannual variability in disturbance that affects giant kelp abundance can have strong consequences for benthic community structure (Detmer et al. 2021).

We initiated a finer-scale long-term experiment to quantify the role of competition for space as a key process governing community structure and recovery in kelp forests. The experiment is designed to measure the effects of giant kelp in mediating competition between sessile invertebrates and understory macroalgae at 10 kelp forest sites using paired circular plots (8 m radius) of two treatments: kelp removal and control. Smaller plots (0.5 m^2) with and without understory algae removed are nested within the larger kelp control and kelp removal plots. This experiment was delayed by the COVID-19 pandemic, but in now completely deployed.

THEME 1B. Ecological consequences of fishing

Human drivers such as fishing can influence targeted species with cascading consequences for community structure and function. Marine Protected Areas (MPAs) established in 2012 prohibited fishing at two of our long-term study sites and is set within a broader network of MPAs of varied ages covering 16% of California's nearshore habitats.

In 2012 we initiated a new time series on lobster abundance, size and fishing effort in response to the designation of the MPAs. We combined these data with landings data from the CA Dept of Fish and Wildlife (CDFW) to show that an increase in spiny lobster within the MPAs has benefited the commercial lobster fishery outside of the MPAs through spillover, an often asserted but seldom documented phenomenon. Despite a 35% reduction in fishing area, increases in lobster populations inside the two newly established MPAs increased total catch by 225% after only 6 years, benefiting the fishery overall (Lenihan et al. 2021). This study was coauthored by a CDFW biologist who promoted the results to her agency, an example of SBC LTER's growing connection with local and regional resource managers.

We are also using data from other long-term monitoring programs in the region to address questions about effects of fishing on kelp forests. Trophic cascades are often hypothesized to be major drivers of kelp forest community structure, with fishing reducing predation on sea urchins that then overgraze kelp to form barrens. To test this idea, we examined the effect of older MPAs established in 2002 on the two abundant species of urchins in our region: the heavily fished red urchin *Mesocentrotus franciscanus*, and the virtually unfished purple urchin *Strongylocentrotus purpuratus*, using data collected since 1984 by the National Park Service in the Channel Islands. We hypothesized that urchin populations inside MPAs would be depressed by higher predation, benefiting kelp. Instead, our analyses revealed that after 15 years of protection from fishing, purple urchin populations and kelp abundance were unaffected by reserves, while red urchin biomass significantly increased (Malakhoff and Miller 2021). These results revealed the overwhelming direct effect of protecting fished species in marine reserves over indirect effects that are often predicted, but seldom clearly documented. Indirect effects due to marine reserves may eventually occur in our local kelp forests, but very effective predators, large reserves or extended time periods may be needed to induce them. The direct effects in themselves are significant for management of fished species, and have ecological consequences; our work showed that compared to MPA reefs, fished reefs were supplied with less nitrogenous animal waste that may sustain macroalgae during low-nutrient periods (Peters et al. 2019, see below).

THEME 1C. Sources and utilization of recycled nitrogen

Our prior results show that urea and ammonium are present throughout the year in coastal waters and are major forms of locally regenerated dissolved N used by kelp and nearshore phytoplankton that may account for the persistence and sustained growth of giant kelp observed during periods of low nitrate availability. These results, along with our finding that the uptake of urea and ammonium by kelp is decoupled from irradiance, led us to hypothesize that the diel light cycle mediates the partitioning of regenerated N between kelp and phytoplankton.

To test our hypothesis we quantified the kinetics of regenerated N use by giant kelp and phytoplankton in light and dark in the laboratory (Smith et al. 2021). Urea uptake by giant kelp decreased 3–12% in darkness (relative to in light) compared to a 66–85% decline for phytoplankton. Similar differences were observed for ammonium and nitrate, suggesting that light intensity and photoperiod influence the availability of N to kelp and phytoplankton. Kelp's capacity to acquire N during both day and night may help offset its low uptake rates relative to phytoplankton, increasing its ability to compete for N during periods of low N availability.

In additional field and laboratory work, we tested whether the benthos is a potentially significant source of locally regenerated N to kelp forests. Flow-through bioreactor incubations showed that the top 2 cm of sediment can supply 0.05 to 0.90 mmol NH_4^+ m^{-2} day^{-1}. *In situ* measurements of temperature fluxes in sediment porewater adjacent to SBC study reefs indicated that porewater flushes to a depth of 15 cm every two hours; the mean porewater NH_4^+ concentration was 40 µM. Diel water sampling demonstrated that giant kelp forests may be exposed to NH_4^+ concentrations greater than 1µM for 4-8 hours per day. These measured reservoirs and exchange rates of NH_4^+ suggest that marine sediment provides a significant source of nitrogen to the water column helping to offset nitrogen demand by giant kelp during periods of summer stratification and low nitrate supply (Lowman et al., in prep).

Kelp forest consumers that excrete ammonium and urea are another possible source of N for reef macroalgae, and protection from fishing increased the magnitude of this source (Peters et al. 2019). In further work, we found that increased disturbance to giant kelp in long-term kelp removal plots reduced fish biomass and the amount of excreted ammonium relative to control plots. The amount of NH_4^+ excreted by consumers in control plots was sufficient to support ~ 45% of the N demand of understory macroalgae and ~ 10% of the demand of all macroalgae including kelp, suggesting that consumer excretion, in addition to sediment fluxes, helps sustain macroalgal growth during stratified periods (Peters et al., in prep).

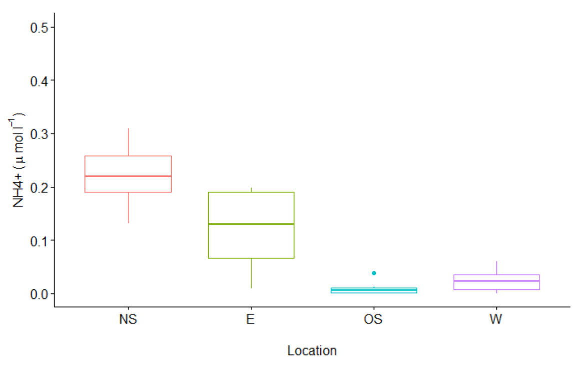

Figure 2. Ammonium (NH_4^+) concentrations were higher downstream of Mohawk kelp forest, suggesting high N remineralization rates on the reef. Sites OS (offshore) and W are located up-current from Mohawk Reef, while NS and E are located down-current. Triplicate measurements were taken every four hours over a ~12h period in August 2021. Pairwise comparisons were all significant except OSxW.

We predict N regeneration rates in the water column will vary with the structure of planktonic communities and associated shifts in remineralization processes. In the coming months we will begin testing this prediction by quantifying seasonal rates of N regeneration in the water column (this research was delayed by COVID). Water column regeneration rates will be determined at the three kelp forests where kelp NPP and oceanographic properties are measured as part of our long-term studies. Monthly measurements of concentrations of urea, ammonium, nitrate, POC, PON and phytoplankton chlorophyll *a* will be augmented with rate measurements of urea and ammonium regeneration in spring, summer and fall, with particular emphasis on the stratified summer periods when the relative contribution of recycled N to kelp N demand should be highest. Isotope pool dilution will be used to quantify microbial urea and ammonium regeneration. SBC graduate student Natalie Dornan (Santoro lab) will be leading this research. In summer 2021, a preliminary experiment showed export of regenerated N (NH_4^+) from the Mohawk kelp forest (**Fig. 2**), suggesting high N regeneration rates that exceed macroalgal uptake. This work links with Theme 2, as water residence time will be a key element in understanding fluxes of regenerated N in kelp forests.

THEME 2. Dynamic biophysical coupling in kelp forest ecosystems

Our prior results showed that the physical structure of giant kelp alters water flow within the forest (Gaylord et al. 2007, Fram et al. 2008), and kelp's high productivity and metabolism alter seawater chemistry (Reed et al. 2015, Hoshijima and Hofmann 2019). How this biophysical coupling changes with oceanographic conditions and the size and density of the forest is largely unknown. Research in this theme aims to quantify: (1) the biophysical effects of kelp on water residence time and chemistry (*THEME 2A*), (2) how these effects interact with microbial communities to influence processing and fate of dissolved organic matter (*THEME 2B*), and (3) the consequences of kelp-induced changes in seawater on kelp forest inhabitants (*THEME 2C*).

Theme 2a. Effects of kelp on physical and chemical fluxes

In prior work we showed that flow is attenuated inside kelp forests due to drag and increased around the forest edge due to diversion around the exterior. Research in this subtheme aims to understand how forest size and kelp density modulate the residence time of water, essential for quantifying how giant kelp forests modify their physicochemical environment.

To address this aim, we have augmented our long-term kelp forest sites at Mohawk (MK) and Arroyo Quemado (AQ) with additional physical and chemical sensors to quantify spatial and temporal scales of variation in seawater properties (i.e., temperature, salinity, and DO) inside, outside and offshore of the kelp forest as it varies naturally through time in its footprint area and kelp density. MK and AQ are well suited for this purpose because many SBC core measurements are made at these sites. Moreover, the difference in size between these two kelp forests (AQ is ~5 times larger than MK) coupled with high seasonal and inter-annual variability in kelp abundance will allow us to develop predictive models of how residence time varies with forest architecture and alongshore current speed. Some reviewers of our proposal expressed concern over our reliance on two forests for this work. We carefully considered including three forests as suggested, but ultimately decided that the strain in resources and technician workload of a third site would come at the cost of the quality of measurements across the program. Moreover, we are confident that the dynamic fluctuations in kelp coupled with the difference in size and oceanographic setting of AQ and MK will provide a wide range of biological and physical conditions from which to build predictive models of how kelp forest size and density alter water residence times to influence changes in seawater chemistry. We discuss this further below in the responses to program comments.

We are working to develop residence time estimates that are a function of stratification, kelp forest area, and kelp density. Examples of this are shown in **Fig. 3**. The arrival of a warm front is shown in each column; the panels on the left are from the spring when kelp density is high and the right panels are from the fall when kelp density is low. The sharp temperature increase observed outside the forest in the top panels is muted and delayed in the interior of the forest, as shown in the lower panels. The delay inside the forest is elevated in the spring when kelp density is higher.

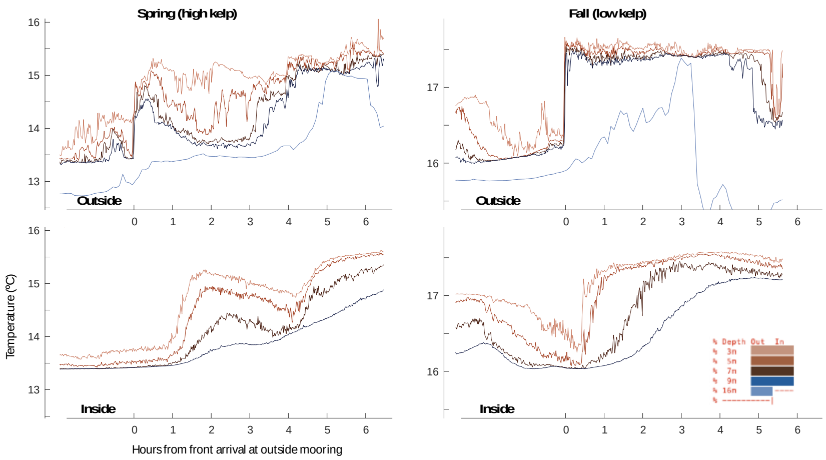

Figure 3. Example of delayed temperature signals that will be used to estimate site-specific residence time. The left panels are from spring, the right panels are from the fall. Upper panels are from the outside of the kelp forest, lower panels are from the kelp forest interior. Lighter colors are higher in the water column.

We are using the inside-outside paired instrumentation at MK and AQ to better resolve details of the flow through the kelp canopy. For example, on July 29, 2021, we conducted several hours of in situ surveys around and offshore of a portion of Mohawk Reef. A REMUS 600 AUV ran 675 m-long cross-shore transects to within 50 m of the kelp forest while an instrumented surfboard was paddled around the kelp forest and RGB drone imagery was collected hourly. We observed gradual warming of the kelp forest surface water through the morning. When detrended, a reversal of the local temperature gradient was evident and several processes were revealed (**Fig 4**). The surface transects show how rapidly scalar gradients can evolve along the inner shelf. There was always a temperature gradient across this kelp forest, a distance of only 60 m but as strong as any other local feature on the inner shelf. Significant gradients can be formed at the kelp forest scale in as little as a couple hours, indicating that our field-intensive studies are warranted and likely to

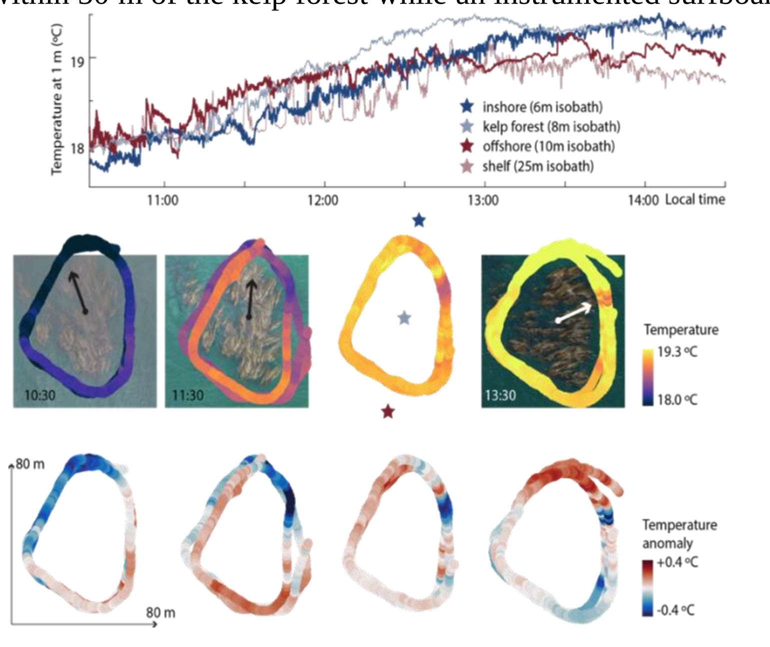

Figure 4. Preliminary data showing cross-shelf gradients in the vicinity of a kelp forest and the creation of additional features as the flow interacts with the kelp canopy. We hypothesize that scalar variability is created at O (1 m) by kelp canopy and that scalar features at the scale of the kelp forest of O(100 m) are created at locations where flows impinge upon the kelp forest.

observe significant features. Finally, filaments of cool water exiting through gaps in the kelp forest suggest the structure of the kelp canopy is an important determinant of residence time; a proposal to study these features has been submitted to NSF.

THEME 2B. Effects of kelp on the processing and fate of dissolved organic matter

Our prior work demonstrated that giant kelp is a large source of C-rich dissolved organic matter (DOM) accounting for ~14% of total kelp NPP (Reed et al. 2015). More recently, we discovered that kelp-derived DOM is enriched in fucose, galactose and mannose, and fueled free-living heterotrophic bacterioplankton growth in laboratory cultures. A portion of this DOM is labile and available to microbial communities and can play an important role in recycling nutrients within and around the forest, while nearly 25% of kelp-derived DOC resisted degradation over four weeks (**Fig 5**). Quantifying remineralization rates of kelp-derived DOM and its accumulation along a spatial gradient across the forest to the waters outside will provide an estimate of kelp DOM export vs. that available to kelp forest food webs via the microbial loop. Microbial remineralization experiments are being conducted seasonally on kelp DOM and on DOM that accumulates in the surface waters within the kelp forest and up to 1000 m offshore to determine degradation rates and bioavailability. We have begun using a new high-throughput system for measuring microbial respiration that has made these experiments much more tractable.

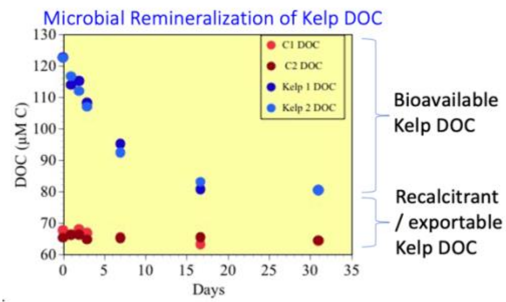

Figure 5. Microbial remineralization experiment in which kelp-derived DOC and unamended control were incubated with SBC bacterioplankton. ~ 75% of kelp derived DOC was remineralized over two weeks; 25% was recalcitrant to rapid degradation and exportable from the local ecosystem.

To begin resolving spatial gradients in dissolved organic compounds, bacterioplankton communities and associated microbial activity as water moves through a kelp forest, graduate student Chance English (Carlson lab) conducted cross-canopy sampling at the AQ kelp forest in February 2021 (**Fig 6**). Results to date show that DOC concentrations, bacterial abundance and bacterial respiration were significantly higher inside the kelp forest, suggesting that kelp DOM is recycled rapidly within the forest, enhancing bacterial growth and fueling the microbial loop. Results from an in situ microbial remineralization experiment at AQ demonstrated that bacteria inoculum from inside the canopy grew and respired organic matter faster than that from outside the forest. Further, bacteria sourced from inside the canopy maintain elevated respiration rates when grown with DOC sourced from outside the kelp canopy. The microbial assemblages in close proximity to kelp and associated DOM production may alter the bacterial community to one capable of turning over DOC at a higher rate regardless of its source. Future work will include the monitoring of initial microbial assemblages using 16s rRNA gene metabarcoding to identify and track microbial communities along transects and in experiments.

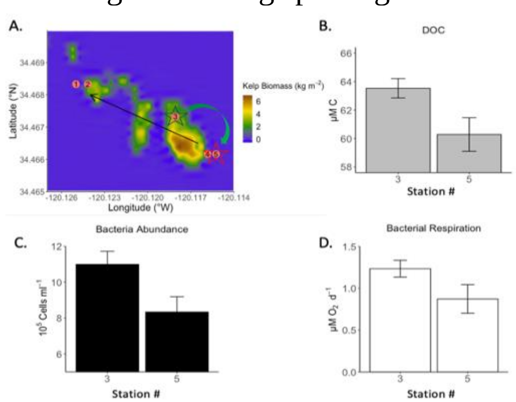

Figure 6. Transect stations from outside through Arroyo Quemado kelp canopy in Feb. 2021 (A). Comparison of DOC (B), bacterial abundance (C) and bacterial respiration (D) for inside (Stn. #3) and outside (Stn. #5) of the kelp canopy. Black arrow represents prevailing water flow. Stars represent stations where source water for remineralization experiment was collected.

The microbial community living on kelp itself may use kelp DOM and influence kelp physiology and condition. We found major differences in the microbiome of healthy kelp blades and senescing blades fouled with epifauna; microbial communities on senescent blades were enriched with potentially pathogenic members of *Shewanella* and *Flavobacteriaceae* (James et al. 2020). In marine microbial communities, assembly order can shape the rate of organic matter processing, especially when pioneer taxa unlock substrates for subsequent arrivals. To address such phenomena graduate students Sevan Esaian and An Bui (Wilbanks and Moeller labs) are investigating community assembly of the kelp microbiome. Their results suggest that microbial communities on deeper blades assemble over time, while those on surface blades track ambient conditions (**Fig. 7**). In-progress analysis is identifying taxa that drive these shifts.

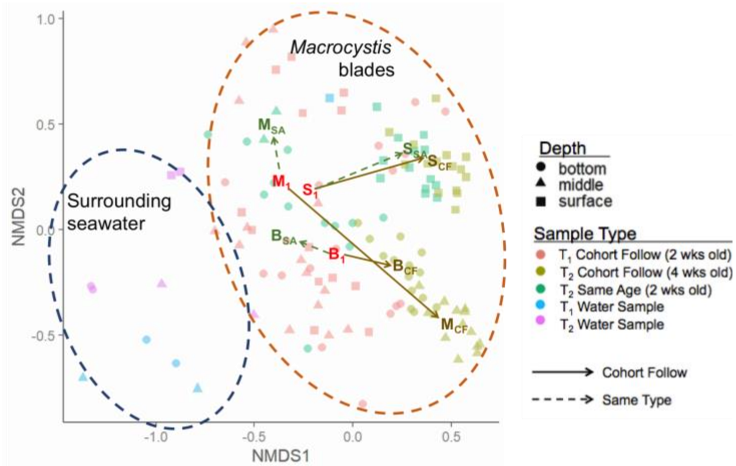

Figure 7. Shifts in kelp blade microbiome as a function of depth and age visualized using NMDS. Blade communities (orange circle) are distinct from those of the surrounding seawater (blue circle). Communities differ by depth initially (red points), and shift over time. Notably, while surface blades (marked S) shift in similar directions in community space over time regardless of whether they are aging or newly maturing blades, blades in midwater or near the benthos show evidence of community assembly.

THEME 2C. Eco-evolutionary consequences of kelp-induced changes in seawater chemistry

The massive and dense biomass of giant kelp forests has the potential to significantly alter water chemistry via photosynthesis and respiration. Such biologically driven changes in seawater properties may enable kelp forests to dampen the episodic impacts of low pH associated with high pCO_2/low pH water, and allow them to serve as local refuges from deoxygenation and acidification. Understanding the role of kelp in buffering the impacts of these biogeochemical changes in the coastal ocean is important because the influx of upwelled, nutrient-rich, but high pCO_2/low pH seawater is predicted to intensify under future climate scenarios.

To this end we are investigating the potential for giant kelp to influence the eco-evolutionary dynamics of kelp forest metazoans by examining the consequences of kelp forests as modifiers of seawater properties including DO, pCO_2, and pH, using calcifying sea urchins as model species. In laboratory experiments, we found that elevated pCO_2 conditions predicted for coastal environments in the future adversely impacted the early development of the red sea urchin *M. franciscanus* while moderate warming improved growth and thermal tolerance (Wong and Hofmann 2020). Further investigation revealed between-treatment differential expression of genes related to cellular stress response, transmembrane transport, metabolic processes, and regulation of gene expression. Temperature contributed significantly to expression variance, while the transcriptomic response to pCO_2 was relatively muted (Wong and Hofmann 2021). In the purple urchin, *S. purpuratus*, we explored intra- and intergenerational plasticity by examining relationships between changes in DNA methylation, transcription, and embryo spicule length in treatments that represented upwelling (~1200 µatm pCO_2, 13°C) and non-upwelling conditions (~500 µatm pCO_2, 17°C). We found plasticity in DNA methylation and gene expression in response to different maternal environments, indicating that different forms of environmentally induced plasticity occur across different time scales and that DNA methylation may be uncoupled from transcriptional responses to the environment (Strader et al. 2020).

Motivated by these laboratory results, we investigated whether this process occurs in nature by testing whether kelp-induced changes in the environment influence the provisioning of offspring by sea urchins via parental effects. To do this, we caged and fed adult purple sea urchins within and outside of the kelp forests at MK and AQ from late summer to early winter when adults undergo gametogenesis in 2018 and 2019 (2020 experiments were aborted due to COVID). Cages were co-located with pH sensors in order to capture differential abiotic exposures during gametogenesis. After 6 months of exposure to these different conditions, urchins were spawned and larvae raised in culture using a crossing design where progeny were raised at the conditions their parents experienced and the reciprocal adult condition, to explore how maternal transgenerational effects in embryos occur *in situ* in populations inside and outside the kelp forest. Ongoing analyses of the larval development from these experiments by Ph.D. candidate Logan Kozal provide evidence that maternal condition influences the performance of the progeny. For example, larvae from mothers conditioned outside the kelp forest exhibited higher thermal tolerance that those conditioned within the forest, likely reflecting the higher variability in temperature there (Kozal et al. in prep). In addition, larvae spawned from mothers conditioned inside kelp forests in both 2018 and 2019 exhibited longer spicules per unit body size, regardless of developmental treatment (**Fig. 8**). These findings reproducibly demonstrate that *in situ* environmental variation in the SBC can alter larval biocalcification via transgenerational plasticity. We are now preparing to assess gene expression and DNA methylation in the progeny; to do so, Ph.D. student Sam Bogan (Hofmann lab) developed a bioinformatic pipeline to model urchin gene expression as a function of DNA methylation in *S. purpuratus*; this has been publicly shared on Github (Bogan and Strader 2021).

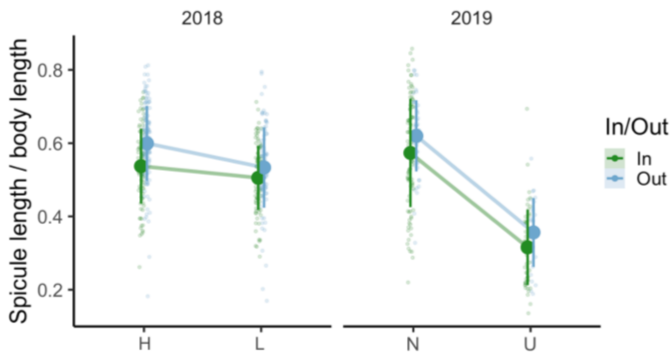

Figure 8. Larval calcification is affected by maternal conditioning to *in situ* environments in and out of giant kelp forests. Spicule lengths (µm) / body length (µm) ± SD in larval *S. purpuratus* are plotted according to maternal treatment (color), developmental treatment (x-axes), and study year (panels). L = low pCO_2 H = high pCO_2, N = non-upwelling, and U = upwelling.

THEME 3. Spatial dynamics and connectivity of kelp forests and adjacent ecosystems

Kelp forests are spatially patchy and are demographically connected to each other via the exchange of individuals and trophically connected to other ecosystems via the movement of organic matter. Research in this theme focuses on how demographic connectivity among local kelp populations affects the stability of kelp metapopulations, and how organic matter delivered to and from kelp forests affects the dynamics of consumer populations.

THEME 3A. Demographic connectivity and metapopulation dynamics of giant kelp

Kelp forests in California and other regions of the world occupy shallow coastal reefs whose distribution is patchy, and how environmental drivers interact with dispersal to control kelp metapopulations is not well understood. The Landsat time series of giant kelp canopy has been invaluable for investigating spatiotemporal patterns in kelp to improve this understanding; the processing of Landsat satellite imagery to kelp canopy biomass and area products has now been completely automated (Bell et al. 2020a), ensuring the continuity of this time series. New work is investigating the finer-scale patterns and drivers of resistance and resilience of giant kelp populations throughout the region. Using hyperspectral aerial imagery collected by NASA's AVIRIS sensor to examine the physiological condition of the kelp canopy in the Santa Barbara Channel, we found that the condition of the kelp canopy is related to the availability of seawater nitrate on a regional scale (1 km) but local patterns (20 m) are related to kelp senescence and demography (**Fig. 9**, Bell & Siegel *in revision*).

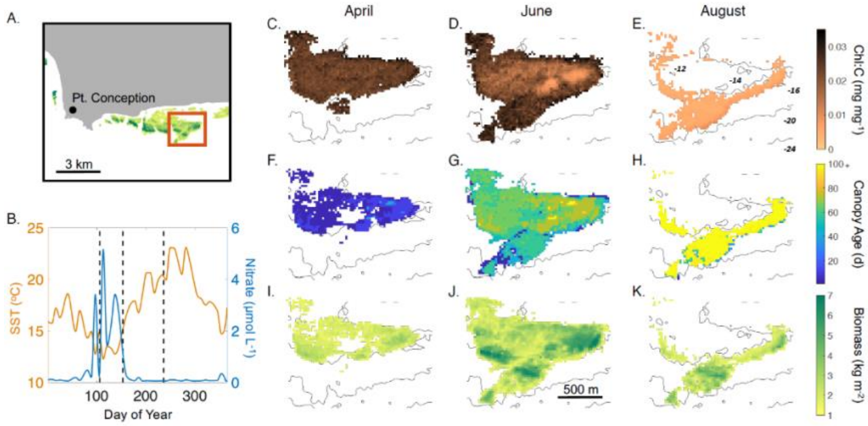

Figure 9. (A) Western SBC with large kelp forest highlighted in red box. (B) Time series of sea surface temperature (orange line) and seawater nitrate concentration (blue line) near the kelp forest with hyperspectral image dates in 2015 shown as the dashed black lines. (C - E) Chl:C (AVIRIS, 18m pixels), (F - H) canopy age and (I - K) canopy biomass density (Landsat, 30m pixels) for the kelp forest across the three dates.

To characterize canopy dynamics on sub-meter scales, identify small-scale extinction events and relate local patterns of recolonization to connectivity and environmental factors, we have initiated high-resolution monitoring of select kelp forests along the Santa Barbara coastline using small unoccupied aerial systems (sUAS; quadcopter drones) and developed an automated method for processing these data (Cavanaugh et al. 2021). sUAS provide the capability for mapping kelp canopy dynamics on scales that align more closely with in situ monitoring (cm to 10s of m), and differentiating species of canopy forming kelps. We have also been investigating the use of a sUAS mounted hyperspectral imager and 10-band multispectral imager to measure canopy biomass and physiological condition of SBC kelp forests (Bell et al. 2020b). Starting in February 2021, we began monthly time series of 10-band sUAS flights at the MK and AQ kelp forests to examine the dynamics of canopy biomass and physiological condition (**Fig. 10**). In the next three years, we will examine the relationship between local scale declines in physiological condition driven by frond senescence and how these spatial dynamics are related to canopy loss. Additionally, we will examine forest scale dynamics in physiological condition associated with upwelling processes and how these changes are related to primary production and the expansion of giant kelp into previously unoccupied areas. This effort will be aided and expanded on by a recent NSF award to SBC Investigators Castorani, Bell and

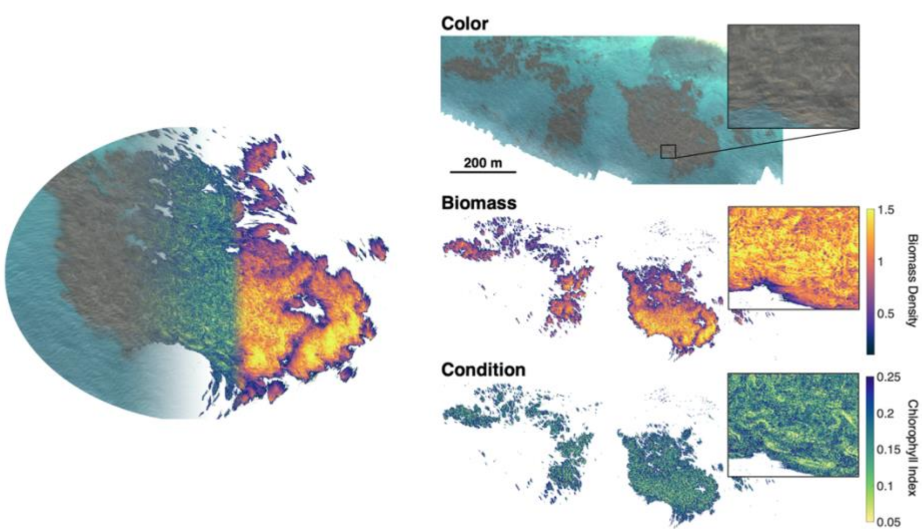

Figure 10. (A) Color orthomosiac and canopy biomass and condition from the Arroyo Quemado kelp forest on March 17, 2021 using the MicaSense 10-band multispectral sensor. The ability to capture all spectral band images simultaneously allows for the co-registration of all image products in space.

Cavanaugh to investigate the patterns and causes of synchrony in giant kelp forests and consequences for coastal ecosystem structure and function.

THEME 3B. Trophic connectivity between kelp forests and beaches

We have shown that kelp forests export large amounts of biomass to sandy beaches (Dugan et al 2011) which contributes substantially to sustaining their diverse food webs (Schooler et al 2017). Nutrient regeneration and organic matter processing of kelp wrack by consumers, particularly talitrid amphipods, and microbial degradation are key ecosystem functions on beaches. In mesocosm experiments, talitrids enhanced porewater concentrations of ammonium and nitrate that may be used by microbes or exported offshore by up to 198 μM day^{-1} (Lowman et al. 2019).

Species diversity and resource partitioning by beach detritivores may affect ecosystem function. Consumption rates of four talitrid species on five macrophyte species indicated that these consumers do not partition wrack resources, suggesting they are functionally redundant (Michaud et al. 2019). Additional experiments manipulating richness of six detritivore species showed no effect on kelp consumption; instead, species identity and body size drove variation in consumption rates (Emery et al. 2021). These results show that beach detritivore species are not functionally redundant and that the disproportionate loss of larger talitrid species by coastal urbanization (Schooler et al. 2019) heavily impacts ecosystem function. Such impacts on beaches are growing worldwide, exemplified by new synthesis on impacts of coastal armoring on beach fauna in collaboration with SBC's colleagues from Chile (Jaramillo et al. 2021).

Sandy beaches are highly vulnerable to anthropogenic and climate impacts that reduce beach habitat area from the sea (sea level rise, storms) and land (coastal armoring, development). Using SBC's long-term beach data, we collaborated with USGS scientists to develop predictive relationships between the presence and extent of beach habitat zones and modeled projections of total water level (TWL) and beach profiles. These results were used as part of a multidisciplinary coastal vulnerability assessment for local government in Santa Barbara (Myers et al. 2019).

To evaluate connectivity and synchrony between beaches and kelp forests, we are collecting detailed data on the abundance of kelp wrack at our five study beaches, quantifying smaller blades and fronds as well as whole plants. We are also developing methods to use drone imagery to get a more spatially comprehensive and rapid estimate of wrack abundance collected in tandem with the kelp forest imagery in Theme 2a and used to assess the level of synchrony between kelp standing biomass and kelp wrack abundance and flux, and the subsequent connectivity between subtidal kelp forests and intertidal beaches.

THEME 3C. Trophic connectivity between the coastal ocean and kelp forests

Suspension feeders account for most consumer biomass in SBC kelp forests, and our prior results indicate that they rely on the allochthonous production of phytoplankton (Miller et al. 2015). Understanding variability in phytoplankton production and community structure is therefore important for understanding dynamics of kelp forest food webs. We created a 22-year monthly time series of the relative abundance of five distinct phytoplankton groups in the SBC by combining phytoplankton pigment data with bio-optical models (Catlett et al. 2021). Our observations indicated that nanophytoplankton groups respond most rapidly to seasonal upwelling, followed by diatoms and picophytoplankton as the water column stratifies in the summer. On decadal time scales, dinoflagellate blooms are associated with the warm phase of the North Pacific Gyre Oscillation. These results suggest that surface ocean advection plays a substantial role in driving SBC's phytoplankton composition.

In spring 2021 we began a focused research campaign to better understand the linkage between phytoplankton and reef suspension feeders. Over 2-week periods each season, we are collecting concurrent field measurements at MK and AQ, along with measurements offshore, using SBC's Teledyne Webb G2 glider to quantify cross-shelf fluxes of phytoplankton to kelp forests that will be contextualized at larger spatial scales using satellite data. On the reefs, we are investigating the response of suspension-feeding invertebrates to the supply and taxonomic composition of phytoplankton. Three days per week during each two-week period each season, water samples for chlorophyll, POC, and phytoplankton community composition are being collected in the kelp forest, augmented by near-continuous chlorophyll measurements by moored fluorometers. On a subset of the same days, suspension feeders are also sampled for gut contents to evaluate feeding selectivity as compared with available phytoplankton assemblages. To supplement microscope counts of phytoplankton, we will analyze water and gut content samples using DNA metabarcoding techniques (Catlett et al. in prep). This campaign will begin to define whether kelp forest food webs rely on specific groups of phytoplankton more than others and the physical drivers and transport processes that deliver these crucial trophic resources to the reef.

RESPONSES TO CONCERNS RAISED IN PROGRAM COMMENTS OF SBC III PROPOSAL

LTERs are expected to fill a unique niche at NSF in pursuing ecological questions that require collection and synthesis of long term data. Developing these questions in the context of a strong and compelling conceptual framework is critical. In part, SBC hangs its hat on the idea that community dynamics may differ in systems with short-lived foundations species. Several reviewers and the Panel noted that, while this may be a reasonable if not compelling framework, the proposal did not address what has been learned about this conjecture from prior studies or how dynamics appear to differ from systems with longer-lived foundation systems.

To clarify, we posit that giant kelp is a dynamic, relatively short-lived foundation species (FS), and that this allows us to investigate how FS affect community structure. Because many FS, such as corals and trees, are long-lived, obtaining sufficient data to examine the drivers and effects of their fluctuations would take centuries or longer. In the past three years, we have endeavored to more explicitly make this connection. For example, Lamy et al. (2020) is the first study we know of to show that dampened temporal fluctuations in the biomass of a FS enhances species richness to increase the stability of the communities it supports, a basic premise of the FS concept.

Some new studies have been added in the present cycle, some well justified and following on prior finding but also some that were not well developed. In particular, the studies focused on ecological and evolutionary consequences of kelp-induced changes in seawater chemistry raised some concerns. It was not clear to some reviewers why some aspects of this theme required long-term studies or how some of the studies related to the overall conceptual framework of the SBC LTER. While NSF is supportive of evolutionary work being conducted at LTER sites, where appropriate, the case needs to be made to reviewers in the context of the LTER solicitations.

Over the years, SBC has been able to increase our level of data collection in the ocean acidification arena, mainly due to NSF supplements earmarked for pH sensors. We see the eco-evolutionary work being carried out in Theme 2 of our research program as a way to explore and predict species- and community-level consequences of measured changes in these parameters over long time periods. Like many of our research components, these are not intended to be long-term at this point, but to represent a focused research campaign.

There was a general concern that that sampling only two kelp beds would prove inadequate to address some of the questions outlined. This seems to be a fundamental concern that the LTER should discuss going forward.

In an all-hands research planning workshop held in early 2019, we had a lively discussion on reviewer, panel, and program comments on our proposal, including this one. In the end we decided that given our human and instrumentation resources, combined with the scientific questions at hand, we should continue to focus Theme 2 research at the Mohawk (MK) and Arroyo Quemado (AQ) kelp forests. The main reasons for this were (1) the difference in size between these two kelp forests (AQ is ~5x larger than MK) coupled with high seasonal and inter-annual variability in kelp abundance will allow us to examine how residence time varies with kelp forest architecture and alongshore current speed despite the fact that we have only two sites augmented with instruments; and (2) the instruments in question, particularly the Acoustic Doppler Current Profilers (ADCPs), pumped Conductivity Temperature Depth loggers, and SeaFet/SeaPhox ocean pH sensors, are expensive. Our fleet of these assets is aging and requires maintenance; any problem without backup instruments to swap into moorings results in data gaps. A recent BIO-OCE equipment supplement will ease these concerns, but adding an additional site would still be a stretch. In addition, each site represents a significant workload for our research staff already tasked with maintaining the core LTER datasets. When the COVID-19 shutdown hit UCSB, we got a critical infrastructure exception for safely maintaining our instruments, but were relieved that we had not pushed our capacity by adding a third site.

The work on population conductivity (sic) *would greatly benefit from engaging a population ecologist.*

On this point some reviewers were confused about our goals in Theme 3a, on kelp demography and connectivity, suggesting that we should be doing population genetics. In SBC II and III we compiled a significant body of work on population genetics and connectivity of giant kelp across southern California and metapopulation dynamics taking into account patch colonization and extinction, propagule dispersal, and source/sink connectivity (e.g. Reed et al. 2006, Alberto et al. 2011, Cavanaugh et al. 2013, Johannson et al. 2015, Castorani et al. 2015, 2017). In SBC IV our focus is on how connectivity influences the recovery and resilience of kelp forests on shorter timescales, a question that we are addressing using patterns of kelp abundance combined with distance and oceanographic current models rather than genetics. To that end, we have several investigators with expertise in population modeling, notably Holly Moeller (UCSB), Kyle Cavanaugh (UCLA), and Tom Bell (WHOI).

A surprising number of reviewers reacted to the reduction of studies in adjacent watershed and their potential impact on dynamics on the kelp bed systems. NSF is fully aware of the reason for this re-distribution of effort and we think it was a sound decision based on prior reviews. Nevertheless, some reviewers were not convinced by the rational for this change as developed in the proposal. The working group would not recommend reversing directions, but a clearer explanation for decision might be needed. It also appears to us that this effort was not abandoned, just reduced in scope.

As alluded to, SBC received clear direction from NSF and prior reviews that guided us to deemphasize the terrestrial component of our research. The Program is correct, however, in that this effort has not been abandoned, and we should have made that clearer. The patterns and statistical relationships generated by our 16 years of study in coastal watersheds provide a solid basis for understanding the timing and magnitude of nutrient and TSS fluxes to coastal waters of Santa Barbara Channel and its fringing kelp forest ecosystems (Feng et al. 2019, Feng and Beighley 2020). Combining statistical relationships of fluxes from different land cover types with our hydrological models of runoff driven by measurements of rainfall allows us to calculate nutrient and TSS loadings to coastal waters by storm, season, year and land cover type. Rainfall data required to drive the hydrological model are available from Santa Barbara County and from a few additional SBC gauges that we continue to maintain (though COVID caused a gap in this).

Information management seems to be adequate, but we urge the LTER to look at some suggestions provided by the panel.
This was productively discussed in the research workshops mentioned above. We note that all SBC core datasets are updated annually, a point of reviewer confusion.

The management is solid, the transition plans have been well planned, and the site seems to be *operating well. However, the transition to the new directions was slow and there may need to do some tuning of resource allocations and focus going forward. SBC may need to develop more efficient processes for prioritizing work and resources at the LTER that best supports the work within the conceptual framework of the site.*

In SBC IV we have endeavored to be more nimble in this regard although everything was upended by COVID. Nevertheless, we have now begun a new long-term experiment and a significant research campaign on phytoplankton subsidies to kelp forests.

INFORMATION MANAGEMENT

The data managed by the SBC Information Management System (IMS) are diverse, and include contributions from many scientific disciplines in the major ecosystems of our coastal area: watersheds, beaches, kelp forests, and coastal oceans. The system supports products from all SBC's research approaches (e.g., long-term time-series, experiments and measurement-intensive process studies, synthesis, and modeling), plus legacy studies and exogenous reference data. As the project matured during SBC IV the IMS adapted to new research themes. Several existing data packages were modified to accommodate higher frequency data (e.g. light, temperature, pH, oxygen), and new ongoing data packages were designed. Additionally, several scientific collaborators take advantage of SBC's well-established data management policies and practices, publishing their related data through our system, and SBC provides expertise and consultation for collaborators as they develop data management plans. With increasing frequency, the IMS is asked to post data specifically to accompany a paper or to meet other publication requirements.

POLICIES

SBC has adopted and posted the 2017 LTER Network's Data Policies. All SBC metadata conform to LTER best practices for content such as keywords, personnel, geo-location, methods and data accessibility. The vast majority of SBC data are Type I, i.e., publicly available within 1-2 years of collection or laboratory analysis, although some ongoing electronic data are available much sooner. Type II data (e.g., from a student thesis) is generally held back until the paper is published. Type I and Type II data are released under CC-BY 4.0 - Attribution. We also employ a "Type 0" designation for data acquired from outside parties that is occasionally republished with the original licensing (e.g. KML files of fire perimeters in the watersheds).

INTEGRATION WITH SITE RESEARCH

The SBC IMS has well-developed definitions of data types and processes for their maintenance (see IM Plan). Time-series datasets are formalized via planning and discussion among scientists and IM staff, have established workflows that encompass the entire data life cycle, and are compiled into a single product to facilitate temporal analyses. During regular updates, any methodological changes are documented and formats adapted, ensuring that interpretations are valid. The primary information manager is also closely involved in data processing.

OPERATION, INFRASTRUCTURE AND RESOURCES

SBC IMS leverages the Marine Science Institute (MSI) and the UCSB campus infrastructure for servers, user accounts and backups. The organization of the file server remains stable so that users are familiar with its structure, and new users are given an orientation. All research groups have dedicated directories for "final" data products that are intended to be shared or published. All SBC users may view any data file, but write-access is limited to those responsible for collection and maintenance. With this system, working data are backed up, available quickly, and easily located and monitored by the IMS personnel.

Li Kui replaced Margaret O'Brien as SBC's lead Information Manager in 2019. Kui is responsible for planning all SBC data packages, and creating and maintaining production workflows. O'Brien has a mentoring and advisory role, and is liaison to EDI. SBC participates actively in Network-wide and EDI-supported data projects, in addition to collaboration with the Moorea Coral Reef LTER IMS, a site co-located at MSI. As a result, IMS improvements are planned with broad input and with leveraging or future redistribution in mind.

Recent IM accomplishments and progress

- 2019: SBC LTER Website update: The site was modernized to meet security requirements and to improve accessibility. Content is now supplied by our metadata database; all code is client-side. Design was carried out by the SBC IM team and undergraduate programmers.
- 2019: Bibliography: Coincident with website upgrades, and anticipating changes to reporting protocols, we streamlined and simplified storage of bibliographic material.
- 2017-2018: LTER-Core-Metabase: After 4 years of using Metabase2, and to better fit the skillset of the new primary data manager (Kui), we streamlined our metadata database. This work led to the "LTER-Core-Metabase" project, a collaboration among five LTER sites.
- 2018-2020: Excel-to-EML: IM Li Kui created a simple metadata management system called "Excel-to-EML" that has been adapted by several research groups.
- 2019-2021: Data processing for the ongoing time-series datasets was transitioned to the IM team. The primary accomplishments included: a) logbooks documenting instrument deployment/retrieval and survey records; b) automated initial data QC by cross-checking logbook with sensor outputs; c) R or Matlab scripts for QA/QC and formatting for each ongoing dataset, and d) created scripts to push data into the publication pipeline.

CROSS-SITE AND BROADER SCALE SYNTHETIC RESEARCH

LTER Network cross site projects

Former SBC post doc and present Associate Investigator Thomas Lamy, now faculty at the French National Research Institute, participated in a cross-site working group to synthesize the general relationships between metacommunity parameters and stability across a diverse range of ecosystems. Several products resulted: Wang et al (2019) developed a partitioning framework of variability and synchrony measures. Lamy et al. (2019) used this new approach on SBC data to show that species insurance can stabilize community biomass. Further work found that spatial asynchrony stabilized metacommunity biomass of SBC macroalgae (Lamy et al. 2021). Record et al. (2021) described how LTER data could inform metacommunity theory and applications.

Former SBC postdoc Max Castorani, now faculty at UVA and an investigator with VCR LTER, participated in a working group using LTER data from several sites including SBC to understand drivers of ecosystem stability. A paper is in press (Walter et al. 2021) concluding that stability is more strongly related to richness synchrony than to species richness itself.

SBC Investigators Reed, Miller and Lamy participated in an iLTER synthesis including sites in the Arctic, Mediterranean, Baltic and North Seas, that revealed quasi-synchronous biological shifts in marine ecosystems coincident with a climatic regime shift (Kroencke et al. 2019).

SBC Co-PI Reed is leading a synthesis (*BioScience* in revision) on the long-term effects of climate change on coastal ecosystems including five other sites (FCE, GCE, MCR, PIE, VCR).

SBC Investigators Reed, Miller, Castorani and Rassweiler participated in a cross-site synthesis effort to show the importance of long-term data collection and experiments for addressing ecological questions with implications for policy (Iwaniek et al. 2021).

Margaret O'Brien, SBC's former lead Information manager and current IM advisor, is a co-PI helping to lead the EMERGENT synthesis working group, which is advancing efforts to harmonize molecular information for microbial taxa, streamlining their use in syntheses with related ecosystem level data and spurring future microbial ecology research at LTER sites.

Non-LTER cross-site and broader scale research

SBC Investigators Dugan, Page, and Melack participated in a Coastal Vulnerability Assessment of the Santa Barbara area that relied on SBC LTER data to synthesize projected changes in climate, coastal erosion and flooding, watershed runoff and impacts to sandy beaches and coastal salt marshes (Meyer et al. 2019). The group identified potential climate change-related tipping points for coastal systems and found that tipping points for beaches and wetlands could be reached with just 0.25 m or less of SLR (~ 2050), with > 50% subsequent habitat loss that would degrade overall biodiversity and ecosystem function (Barnard et al. 2021).

SBC Investigator Cavanaugh expanded the capabilities of our kelp Landsat dataset to the entire globe by partnering with Zooinverse to develop a web-based citizen science project (Floating Forests) that uses the efforts of volunteers to analyze Landsat imagery of giant kelp from across the world. More than 2 million classifications of > 500,000 images by nearly 6,000 volunteers have been completed to date.

CONTRIBUTIONS TO THE LTER NETWORK

SBC investigators contribute to the governance, research mission and information management of the LTER Network by serving on a variety of Network-wide committees. PI Miller is a member of the Science Council. Co-PI Dan Reed serves on the Publications Committee. Co-PI Gretchen Hofmann is a member of the Diversity, Equity, and Inclusion Committee. Education and Outreach Coordinator Scott Simon is a member of the Education and Outreach Committee. IM Li Kui and IM advisor Margaret O'Brien both serve on the Information Management Committee. O'Brien took a key role in developing the structure for a new LTER Network Data Center, and is a co-PI of the resulting Environmental Data Initiative (EDI).

OUTREACH, EDUCATION, TRAINING, BENEFITS TO SOCIETY

OUTREACH AND K-12 EDUCATION

SBC partners with UCSB's Research Experience & Education Facility (REEF), a teaching aquarium and marine ecology educational facility for UCSB and K-12 schools and colleges in Santa Barbara and Ventura counties. SBC's Schoolyard LTER (sLTER) program is organized around a theme of kelp forest ecology and is developed around and delivered through the REEF's *Oceans-to-Classrooms* curricula. We focus on long-term connections with underserved, low-achieving schools that include year-round on- and off-campus programs. SBC sLTER curriculum is rich in STEM content, and meets California State Science Standards, Common Core Standards and the Next Generation Science Standards as well as NOAA's Climate and Ocean Literacy Principles. Our programs reached >31,000 students in grades K-12 in the past 3 years, including visits by schools from numerous southern and central California counties as well as a group of students from Taiwan. During the pandemic we rapidly developed new remote content and utilized live distance learning strategies to deliver SBC-sLTER content beginning in Spring 2020. This included the creation of the *VirtualREEF* YouTube channel, and development of infrastructure needed to deliver live content from the REEF Aquarium. As of fall 2020, *VirtualREEF* had >3000 views, and we shared the science and marine life of the SBC with 48 different schools and groups including students in Chicago, Costa Rica and Colombia. We continue to develop and adapt marine science lesson plans that engage students with learning about the local environment by incorporating ongoing SBC research and working with project data with the goal of building skills in science through activities that move from structured or guided investigation to open-ended inquiry and experimentation. In the past three years SBC collaborated with three partnership programs to deliver its sLTER content: 1) the American Association of University Women's Tech Trek Program, an on-campus summer residential science and math program designed to develop interest, excitement and self-confidence in young women entering the 8th grade 2) Santa Barbara County Education Office (SBCEO), and 3) UCSB's Gevirtz Graduate School of Education and the Harding University Partnership School (HUPS) with whom we collaborated on a Fourth/Fifth Grade published anthology, "Dive Deep into Writing," which included poetry, fiction, and non-fiction writings.

We remain committed to equipping educators with the tools they need to teach ocean and environmental science, foster science literacy, and cultivate the next generation of ocean stewards. We continue to use our SBC LTER Schoolyard Series book, The Golden Forest, to broaden our K-12 outreach efforts. Our book highlights connections between giant kelp forest and sandy beach ecosystems and has been provided to hundreds of K-8 teachers as part of our partnership with the SBCEO to enhance science content knowledge. Other programmatic outreach efforts include: (1) developing SBC's Subtidal Field Guide and (2) annually hosting a booth at the Santa Barbara Earth Day Festival, which attracts >30,000 people, to raise public awareness about LTER research. This popular booth features a model of a kelp forest in which SBC students and staff act as 'dive buddies' for children who tour the forest and collect data on kelp forest species using underwater dive slates, and a kelp holdfast dissection activity. In 2019, the virtual kelp forest was featured at World Oceans Day, hosted at the SBMNH Sea Center for ~2,800 visitors. SBC participated in the virtual Earth Day festival in 2021.

TRAINING AND PROFESSIONAL DEVELOPMENT

SBC LTER contributes substantially to undergraduate involvement in research at UCSB. During the past three years 8 postdoctoral fellows, 38 graduate students, 9 REU students and 194 additional undergraduate students participated in SBC research. Each year 20-30 undergraduate students receive academic credit to participate in an SBC research training program that runs the entire academic year (this program involved fewer students in 2020 due to COVID). Students in the program actively participate in the collection, processing and analysis of core data and many develop their own independent research projects. REU students work closely with SBC researchers on a wide range of topics and many choose to pursue an advanced degree following their undergraduate education. Opportunities for training in public education and student mentoring arise from SBC's partnership with the REEF, which is also designed to provide UCSB undergraduates majoring in Aquatic Biology with training in communicating their knowledge of marine ecology in an educational format. SBC investigators, graduate students, post docs and research staff actively participate in this aspect of undergraduate training, which engaged 30-69 undergraduate interns annually for the REEF during the past three years. In a collaboration with SBC graduate student Xochitl Clare, we hosted two *REEFlections* annual symposia that provided an opportunity for undergraduates who work both at the REEF and in a research lab to communicate their work and mentorship experiences to the UCSB and public community.

SBC graduate student and postdoctoral training are coordinated with several graduate programs on the UCSB campus to promote opportunities for interdisciplinary training in ecology, physiology, geology, geography, hydrology, oceanography, and coastal policy. This enables valuable cross-training on environmental issues pertaining to coastal ecosystems, provides a common language for communicating scientific information on these issues, and contributes to the creation of a diverse scientific community of students and postdocs that fosters respect and appreciation for other disciplines. Graduate seminars hosted by SBC faculty, the SBC Annual All Scientist Meeting and SBC workshops on key research themes served to engage SBC graduate students in the culture and diverse research offered by SBC. A student-organized cross-site LTER graduate student symposium with Moorea Coral Reef and California Current Ecosystem LTERs and the triannual LTER Network's All Scientist Meeting serve to expose SBC graduate students to the research and career opportunities offered throughout the Network.

BROADER BENEFITS TO SOCIETY

We are committed to sharing our research results with resource managers, decision makers, stakeholders, and the general public who are interested in applying our findings to policy issues concerning natural resources, coastal management, and land use. To this end SBC researchers actively use their expertise and data to inform these entities to the betterment of society. Below are some examples of the broader benefits of SBC research in three years of SBC IV.

- SBC LTER data and studies are showing the effects of marine reserves on ecosystems and fishing. New work showing spillover bolsters the case for marine reserves as management tools and may help improve the design of future reserves and networks.

- SBC LTER expertise and data on patterns and drivers of kelp productivity is informing the possibility of kelp farming for biofuels off the coast of CA. DOE is funding several projects on this topic; one is using SBC LTER data to develop a model for kelp farm siting.
- SBC investigators and students responded to the Refugio State Beach oil spill in 2015 and worked with agencies on impacts and restoration. SBC LTER data was used to document natural communities at impacted sites to calculate the NRDA settlement finalized in 2020.
- SBC investigators Dugan, Melack, Page and Reed worked with USGS and Scripps Institution of Oceanography researchers to provide local city and county officials with a vulnerability assessment of coastal ecosystems to climate change.
- SBC investigators and students are collaborating with the Bureau of Ocean Energy Management (BOEM), to assess factors affecting the spread and ecological impact of the invasive bryozoan *Watersipora subtorquata*, which is rapidly increasing at SBC.
- SBC investigators Rassweiler, Reed and Okamoto worked with NPS and BOEM biologists to quantify the how well BACI analyses of ecological monitoring data detected anthropogenic impacts in kelp forests (Rassweiler et al. 2021).
- SBC investigators serve as science advisers for public and non-governmental agencies tasked with managing coastal resources.

PROJECT MANAGEMENT

GOVERNANCE

SBC is directed by an Executive Committee chaired by lead PI Miller and includes Co-PIs Hofmann, Reed, Siegel and Stier, Project Coordinator (PC) and Associate Investigator Dugan, and 3-4 Associate Investigators. The PI, Co-PIs and PC serve on the Executive Committee for the entire six-year funding period. The Associate Investigators on the Executive Committee (currently Santoro, Carlson, Nidzieko and Brzezinski) are rotating positions that are generally filled by individuals with lead roles in short-term (2-3 year) studies that are ongoing at the time of their appointment. Since its inception SBC has incorporated a philosophy of shared governance in which strategic planning pertaining to the project's research direction, resource allocation, and administrative policies are discussed at scheduled meetings that are open to all investigators, post docs, graduate students, and staff. Lead PI Miller chairs these meetings and sets their agendas with input from the Executive Committee. The meetings serve to keep participants informed of the project's broad range of activities, which aids in coordination and integration of the different project components. This management style has been very effective in instilling a culture of shared ownership, enthusiasm and pride for the project among participants.

PROJECT MANAGEMENT AND INSTITUTIONAL SUPPORT

Day to day management of the project is overseen by PI Miller with assistance from a part time Project Coordinator (Associate Investigator Dugan). Two fulltime and several part time research staff are employed to maintain SBC's long-term measurements and experiments. Graduate and undergraduate students employed on the project assist in these activities. Technician Clint Nelson leads diving and boating safety for the project and is heavily involved in UCSB's Diving Safety Program, helping to train new scientific divers. Information Manager Kui and Outreach Coordinator Simon round out the project staff. Coordination between research and information management is facilitated by an Information Management Advisory Committee [currently Kui, O'Brien, Washburn, and Reed (chair)]. The allocation of funds is structured around the primary research themes with a lead investigator assigned to each sub theme. We allocate funds to shorter-term (2-4 year) research campaigns to gain insight into processes underlying the patterns observed in our long-term observations and experiments. Separate funds are set aside for project management, long-term measurements, IM and Education/Outreach.

SBC's research and education programs greatly benefit from an off-campus overhead rate on its core NSF funding and generous in-kind support from UCSB's Office of Research, the Division of Mathematical Life and Physical Sciences, the Bren School of Environmental Science and Management and the Graduate Division. Administrative support is provided by UCSB's Marine Science Institute (MSI), which offers SBC participants efficient and friendly service in contracts and grants, personnel, budgets, purchasing, and travel, and expert analytical chemistry services via MSI's Analytical Laboratory. Research facilities on campus extensively used by SBC researchers also include a flow-through seawater system, small boat and diving operations, and computational resources provided by MSI and the Earth Research Institute.

The coordination of research and the exchange of information and ideas among project participants are facilitated because the majority of project participants are located at UCSB. Informal and scheduled meetings involving investigators, postdoctoral scientists, students and staff to discuss project related business occur on a daily basis (pre-COVID). The sharing of data, documents, and other project related products is made easy through our central data server to which all participants have access. Science meetings designed to update participants on the status of ongoing research are held approximately monthly during the academic year and an annual one-day retreat for all SBC participants and other interested parties helps to ensure coordination across the SBC program and to enhance interdisciplinary discussions. Unfortunately, these meetings were curtailed in the past 1.5 years by COVID, although we did host a discussion series that covered all research subthemes as well as education and outreach on Zoom in Spring 2021.

DIVERSITY

Efforts to increase the participation of under-represented groups are achieved through our ongoing Schoolyard program, which targets middle school students in traditionally underserved, low-achieving schools (see Section VII. Outreach, education, training and benefits to society). We also link with campus programs devoted to increasing educational opportunities for low-income students and groups underrepresented in higher education. Since 2001, the number of domestic Underrepresented Minority (URM) undergraduate students at UCSB has increased by 89%, and in fall 2014 UCSB was recognized as a Hispanic Serving Institution (HSI) for achieving 25% Latino undergraduate enrollment. It is the first HIS in the prestigious Association of American Universities, an association of 62 leading research universities in the United States and Canada. Women and URM students, post docs and faculty participating in SBC have access to professional development training and mentoring in team science leadership, management, and proposal writing. This year, the Marine Science Institute and The Ocean Fund are starting an annual scholarship program for underrepresented students interested in scientific diving, with the goal of supporting them through the prerequisites of open water certification and practice dives; as the most active local scientific diving program at UCSB, SBC LTER has committed to incorporating these students into our field program to build their experience level.

PLANNING FOR THE FUTURE

Planning for a long-term project like an LTER requires a strategy for replacing expertise in research areas vacated by scientists that have left the project and for adding expertise in areas of new research initiatives. The addition of new Associate Investigators is accomplished either by active recruitment to fill a specific research need, or via invitation to collaborating scientists who are interested in becoming formally associated with the project. In both cases the addition of new investigators is determined by consensus of the Executive Committee with input from Associate Investigators. Fourteen of the 24 Associate Investigators on SBC IV were added during SBC III; all are early to mid-career scientists who offer potential for long-term involvement.

Miller assumed the lead PI role at the start of SBC IV; former lead PI Reed remains a Co-PI and member of the executive Committee. There are no plans for a leadership transition during this award cycle. In the unanticipated event that PI Miller is no longer able to perform the duties required of a lead PI, then this role will be assumed by one of the four Co-PIs as determined by the Executive Committee. All four Co-PIs have considerable leadership experience and all are willing and capable of leading SBC if called upon.

The UCSB campus lies in the center of the physical study domain of SBC LTER and the long-term continuity of our project relies on recruiting UCSB researchers into leadership positions. The structure of our Executive Committee fosters the participation and mentoring of early to mid-career Associate Investigators in project governance and management and aids in leadership transition. During the latter half of SBC III, several new faculty were recruited at UCSB, resulting in the addition of four early-career Associate Investigators as well as an early-career Co-PI, Adrian Stier, greatly aiding plans for SBC's future leadership. Of future interest to SBC is an upcoming search for a new Director of the Marine Science Institute; the former Director, Mark Brzezinski, is an Associate Investigator of SBC and the current Interim Director is SBC Co-PI Gretchen Hofmann. SBC investigators are actively involved in this recruitment.

COLLABORATIONS WITH FORMAL AND INFORMAL PARTNERS

The diverse nature of SBC's study habitats and research themes has attracted an interdisciplinary group of scientists to work at our site. Unlike several other LTER sites, SBC does not have a formal agreement with a federal agency or NGO that facilitates collaborations and provides research support. Instead, we rely upon the long-term LTER support and the temporally and spatially comprehensive data that it generates to serve as a platform for attracting collaborations with other extramurally funded projects. We have been very successful in this regard, generating $11.5 million from 10 different funding sources in collaborative research projects during the first three years of SBC IV. Some of SBC's prominent collaborations in the past three years include:

Plumes & Blooms (PnB) is a long-term study of ocean color variability of the Santa Barbara Channel led by SBC Co-PI Siegel. The project is a collaboration with the Channel Islands National Marine Sanctuary and has been funded by NASA since 1996. Seasonal oceanographic cruises provide in situ data that are used to validate NASA satellite data products and develop novel means of assessing phytoplankton community structure for upcoming NASA satellite missions (e.g. Plankton, Aerosol, Cloud and marine Ecosystems mission, PACE). SBC LTER and PnB share data and expertise, particularly contributing to SBC-IV Theme 3C.

The Southern California Bight Marine Biodiversity Observation Network (MBON) is a demonstration program aimed at assessing marine biodiversity and factors that influence it. The project is funded by NASA, BOEM and NOAA, led by Miller and includes 7 other SBC investigators as Co-PIs. SBC is an MBON data contributor and the overlap of investigators on both projects makes for a strong partnership that is allowing SBC to explore more datasets and methodologies, such as environmental DNA (Lamy et al. 2021).

San Onofre Nuclear Generating Station (SONGS) Mitigation Monitoring program is a cooperative program with the CA Coastal Commission evaluating the success of restoration of 150 acres of upland to tidal wetland and the construction of an artificial reef supporting 373 acres of kelp forest habitat. This long-term project is led by SBC investigators Page and Reed; informal exchange of data, expertise and results have been ongoing since SBC's inception.

Southern California Coastal Ocean Observing System (SCCOOS) is one of eleven regional observing systems that deliver ocean observations to serve safety, the economy, and the environment. SBC investigators participate, with Washburn chairing the SCCOS executive committee. SBC partners with SCOOS to maintain an HR radar array in the Santa Barbara Channel and a real-time oceanographic instrument array on Stearns Wharf in Santa Barbara.

Regional Ecosystem Services Observation Network (RESON) is a Research Collaboration Network funded in late 2020 by NSF's Coastline and People (CoPe) program. Led by SBC investigators Miller, Nidzieko ,and Eliason, RESON aims to design a network to monitor coastal ecosystems in California, taking advantage of technological advances in sensors systems as well as human networks. RESON includes participants from CCE LTER, NOAA and the Chumash Tribe, strengthening our connections to regional researchers, stakeholders and Tribal Nations.