

## COVER SHEET FOR PROPOSAL TO THE NATIONAL SCIENCE FOUNDATION

PROGRAM ANNOUNCEMENT/SOLICITATION NO./DUE DATE <b>NSF 17-593</b> <b>03/02/18</b>		<input type="checkbox"/> Special Exception to Deadline Date Policy		FOR NSF USE ONLY <b>NSF PROPOSAL NUMBER</b>	
FOR CONSIDERATION BY NSF ORGANIZATION UNIT(S) (Indicate the most specific unit known, i.e. program, division, etc.) <b>DEB - Long-Term Ecological Research</b>					
DATE RECEIVED	NUMBER OF COPIES	DIVISION ASSIGNED	FUND CODE	DUNS# (Data Universal Numbering System)	FILE LOCATION
				<b>094878394</b>	
EMPLOYER IDENTIFICATION NUMBER (EIN) OR TAXPAYER IDENTIFICATION NUMBER (TIN) <b>956006145</b>		SHOW PREVIOUS AWARD NO. IF THIS IS <input checked="" type="checkbox"/> A RENEWAL <input type="checkbox"/> AN ACCOMPLISHMENT-BASED RENEWAL <b>1232779</b>		IS THIS PROPOSAL BEING SUBMITTED TO ANOTHER FEDERAL AGENCY? YES <input type="checkbox"/> NO <input checked="" type="checkbox"/> IF YES, LIST ACRONYM(S)	
NAME OF ORGANIZATION TO WHICH AWARD SHOULD BE MADE <b>University of California-Santa Barbara</b>		ADDRESS OF AWARDEE ORGANIZATION, INCLUDING 9 DIGIT ZIP CODE <b>Office of Research Rm 3227 Cheadle Hall Santa Barbara, CA 93106-2050</b>			
AWARDEE ORGANIZATION CODE (IF KNOWN) <b>0013201000</b>					
NAME OF PRIMARY PLACE OF PERF <b>University of California-Santa Barbara</b>		ADDRESS OF PRIMARY PLACE OF PERF, INCLUDING 9 DIGIT ZIP CODE <b>University of California-Santa Barbara CA 931066150 ,US.</b>			
IS AWARDEE ORGANIZATION (Check All That Apply)		<input type="checkbox"/> SMALL BUSINESS <input type="checkbox"/> FOR-PROFIT ORGANIZATION		<input type="checkbox"/> MINORITY BUSINESS <input type="checkbox"/> WOMAN-OWNED BUSINESS <input type="checkbox"/> IF THIS IS A PRELIMINARY PROPOSAL THEN CHECK HERE	
TITLE OF PROPOSED PROJECT <b>LTER: Environmental drivers and ecological consequences of kelp forest dynamics (SBV IV)</b>					
REQUESTED AMOUNT \$ <b>6,762,000</b>	PROPOSED DURATION (1-60 MONTHS) <b>72</b> months	REQUESTED STARTING DATE <b>12/01/18</b>	SHOW RELATED PRELIMINARY PROPOSAL NO. IF APPLICABLE		
THIS PROPOSAL INCLUDES ANY OF THE ITEMS LISTED BELOW <input type="checkbox"/> BEGINNING INVESTIGATOR <input type="checkbox"/> DISCLOSURE OF LOBBYING ACTIVITIES <input type="checkbox"/> PROPRIETARY & PRIVILEGED INFORMATION <input type="checkbox"/> HISTORIC PLACES <input type="checkbox"/> VERTEBRATE ANIMALS IACUC App. Date _____ PHS Animal Welfare Assurance Number _____ <input checked="" type="checkbox"/> TYPE OF PROPOSAL <b>Research</b>					
<input type="checkbox"/> HUMAN SUBJECTS Human Subjects Assurance Number _____ Exemption Subsection _____ or IRB App. Date _____ <input checked="" type="checkbox"/> INTERNATIONAL ACTIVITIES: COUNTRY/COUNTRIES INVOLVED <b>HK XX</b> <input checked="" type="checkbox"/> COLLABORATIVE STATUS <b>Not a collaborative proposal</b>					
PI/PD DEPARTMENT <b>Marine Science Institute</b>		PI/PD POSTAL ADDRESS <b>Santa Barbara, CA 93106 United States</b>			
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## PROJECT SUMMARY

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### Overview:

The Santa Barbara Coastal LTER (SBC LTER) is an interdisciplinary research and education program established in April 2000 with the goal of developing a predictive understanding of how environmental drivers interact with terrestrial and oceanic processes to alter material flows and influence the ecology of coastal ecosystems. SBC LTER's principal study domain is the semi-arid coast and nearshore waters of the Santa Barbara Channel in southern California, and its diverse and productive marine forests of giant kelp (*Macrocystis pyrifera*) serve as the focal study ecosystem. Analyses of our long-term data have identified many of the environmental drivers and ecological processes underlying the production and community dynamics of kelp forests. Still to be determined are 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. These and other unknowns form the basis of the overarching question that motivates our proposed research: How do natural and human drivers influence giant kelp dynamics and alter the long-term structure and function of kelp forest ecosystems??. The research proposed to address this question is integrated in a conceptual framework that focuses on the causes and ecological consequences of the dynamics of a relatively short-lived foundation species in a setting of long-term climate change and human use.

### Intellectual Merit:

The ecological effects of climate change are expected to be large, and long-term studies aimed at foundation species that define a community offer great potential for understanding the consequences of such effects on entire ecosystems. Short-lived foundation species serve as excellent models for examining ecological responses to environmental variation and climate change because, unlike populations of long-lived foundation species (e.g., trees, desert shrubs or corals), data collected over multiple generations are readily obtained. Research at the SBC LTER exemplifies the value of long-term data for understanding short-lived species as it focuses on coastal ecosystems dominated by the giant kelp *Macrocystis pyrifera*, a large, short-lived seaweed that provides the foundation for extremely productive and diverse marine forests that are highly valued in coastal temperate regions worldwide. The dynamic nature of giant kelp forests, characterized by frequent disturbance and rapid regeneration every few years, coupled with their high productivity and diverse food webs, make them ideal systems for investigating a plethora of ecological patterns and processes that requires many decades to centuries to address in other ecosystems. Such features underlie the broader ecological significance of an LTER site such as SBC, whose research on population dynamics, community properties and ecosystem processes has spanned multiple cycles of disturbance and recovery since it was established in 2000.

### Broader Impacts:

SBC LTER research provides the foundation for a diverse array of environmental education and outreach programs that include K-12 education and teacher professional development, undergraduate and graduate student training, and stakeholder engagement. Our K-12 schoolyard LTER program targets historically under-represented groups from underserved schools, while our undergraduate, graduate and postdoctoral training at UCSB (a Hispanic Serving Institution) emphasizes tiered mentorship in interdisciplinary research that enhances the educational experience of many students who historically have been under-represented in the sciences. The proposed research has direct applications to the policy and management of several topical issues for coastal regions. SBC LTER scientists have a demonstrated history of sharing their research results with resource managers, decision makers, stakeholders, and the general public to address these issues.

## SECTION 1 - RESULTS FROM PRIOR SUPPORT

LTER: Land/Ocean Interactions and the Dynamics of Kelp Forest Ecosystems (SBC III). Grant No. OCE-1232779, Funding (2012-2018) \$5,880,000 (plus supplements)

The Santa Barbara Coastal LTER (SBC) is an interdisciplinary research and education program established in April 2000 with the goal of advancing a predictive understanding of how oceanic and terrestrial processes alter material flows to influence the ecology of coastal ecosystems. It has focused on the semi-arid coast and nearshore waters of southern California where the movement and exchange of materials in the ocean and on land are highly seasonal and episodic. SBC's principal study domain is a 10,000 km<sup>2</sup> 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 border the Channel (Fig. 1). Diverse and productive marine forests of the giant kelp, *Macrocystis pyrifera*, serve as the focal ecosystem



**Figure 1.** (a) Map of the SBC study domain, (b) Satellite image showing the close proximity of giant kelp forests to the land-sea interface, (c) Submarine view of a giant kelp forest.

for our research. Kelp forests are prominent features on shallow subtidal reefs at the coastal margin in California and other temperate regions of the world and are highly valued for their ecosystem goods and services (Schiel and Foster 2015, Carr and Reed 2016).

### RESEARCH RESULTS AND DATA AVAILABILITY

The primary focus during our first 6-year funding cycle (SBC I, 2000-2006) was on *identifying and quantifying inputs to giant kelp forest communities from the ocean and land, and documenting patterns and sources of spatial and temporal variation in key elements of kelp forest structure and function*. We established a core group of long-term integrated measurements aimed at quantifying inorganic and organic subsidies to giant kelp forests in the Santa Barbara Channel and their effects on kelp forest community structure, productivity and dynamics. The novel datasets created from these measurements pertain to all five core research areas common to LTER sites, and are updated annually with extensive metadata in accordance with the LTER Network's Information Management Policy. All project data are available online through the data portal on SBC's website, linked to NSF's Environmental Data Initiative and discoverable

via DataOne. A more complete description of SBC's data and their accessibility can be found in Supplement 1- Electronically Accessible Datasets and Supplement 2- Data Management Plan.

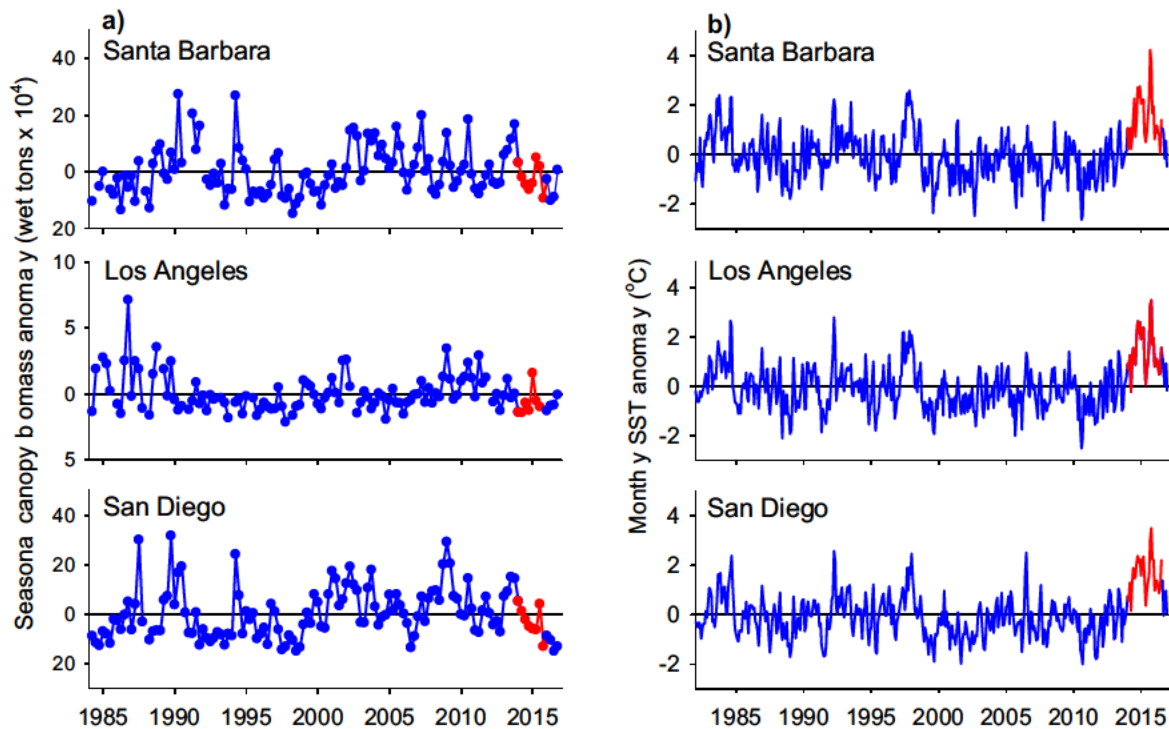
During SBC II (2006-2012) we sought to *determine how environmental drivers acting over different spatial and temporal scales interact to influence the community structure and ecological functions of giant kelp forests*. Our research approach focused on: (1) the influence of environmental drivers on exchange rates of nitrogen and carbon between giant kelp forests and adjacent marine and terrestrial habitats, (2) the direct and indirect effects of key environmental drivers on kelp forest community structure and function, and (3) the feedbacks between kelp forest structure and function.

Our analyses of time-series data and experiments from SBC I and II revealed significant temporal and spatial variability in giant kelp biomass and net primary production (NPP), which had cascading effects on the structure and diversity of the kelp forest food web. Results from SBC I and II also showed that the amount of inorganic nutrients, organic matter, and sediments exchanged between kelp forests and the adjoining land and sea varied significantly in response to natural and human-induced disturbances and to changes in climate and oceanic conditions. However, the full extent to which this variability in material exchange interacted with disturbance and climate to influence the ecology of giant kelp forests remained unresolved. Thus, the overarching question motivating the research of SBC III was: *How are the structure and function of kelp forests and their material exchange with adjacent terrestrial and marine ecosystems altered by disturbance and climate?* To answer this question, we focused our research around three central themes: (1) biotic and abiotic drivers of kelp forest structure and function, (2) material exchange at the land-ocean margin, and (3) movement and fluxes of inorganic and organic matter in the coastal ocean. Below we summarize our major results on these three themes with an emphasis on results that motivate the research proposed for SBC IV. The ten publications that are most significant in this regard are referenced in **bold** in throughout the Project Description, and in the References Cited. A complete database of SBC publications is updated annually and can be viewed on SBC's website.

### ***Theme 1. Biotic and abiotic drivers of kelp forest structure and function***

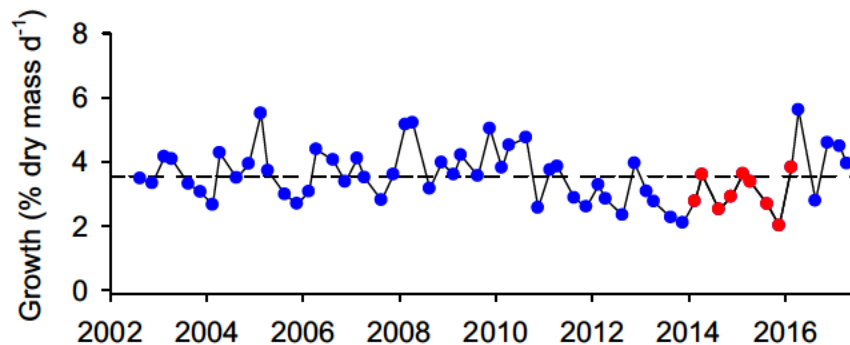
Kelps dominate shallow coastal reefs in cool temperate seas worldwide and are widely considered foundation species because their complex structure and high productivity provide habitat and food for a diverse array of organisms (Schiel and Foster 2006, Teagle et al. 2017). Consequently, factors that alter kelp abundance can have cascading effects on the myriad of species that depend on it. Using a combination of long-term data, experiments and models we investigated how climate variability and wave disturbance influence the structure and dynamics of kelp forest communities and the fate of kelp NPP.

Recent declines in kelp forests in both hemispheres have been attributed to ocean warming, and the Intergovernmental Panel on Climate Change predicted with high confidence that an increased frequency of sea temperature extremes will result in further declines (Wong et al. 2014). In 2014-2015 a large-scale warming event of unprecedented magnitude and duration not seen since the early 1900s, allowed us to test this prediction for giant kelp forests in southern California, and assess their purported value as a sentinel for detecting early signs of climate related impacts (Krumhansl et al. 2016). We observed the first signs of prolonged warming of bottom waters within kelp forests of the Santa Barbara Channel in late December 2013, and positive temperature anomalies persisted through December 2015 with daily deviations as high as +5.8 °C and monthly deviations averaging as much as +4.6 °C. Analyses of our long-term ecological data revealed that giant kelp and the majority of associated species did not decline in response to this extreme warming event and in fact remained within the ranges recorded in prior years (**Reed et al. 2016**). The exceptions were sea stars, and to a lesser extent, sea urchins, which suffered high mortality due to diseases linked to the warm water. We found that large seasonal and inter-annual fluctuations in giant kelp biomass characterized all of southern California, and negative kelp biomass anomalies during the warming of 2014-2015 were within the bounds



**Figure 2.** Regional trends in: (a) seasonal canopy anomalies of giant kelp biomass estimated from Landsat and (b) monthly sea surface temperature (SST) anomalies. Extreme warming of 2014-2015 shown in red.

observed during cooler years of the 32-year time series (Fig. 2). Perhaps most surprising was that kelp continued to grow at a rate  $> 2\%$  dry mass  $d^{-1}$  during the anomalous warming (Fig. 3) despite nitrate concentrations that were continuously below  $1 \mu M$  for periods lasting 50, 156 and



**Figure 3.** Daily growth rate of giant kelp as a percent of dry mass in the Mohawk kelp forest. Dashed horizontal line indicates the long-term mean = 3.75%. Warming event shown in red.

195 days (Reed et al. 2016). This is significant because  $1 \mu M NO_3$  has been shown to be the minimum concentration needed to sustain giant kelp growth (Gerard 1982a), and 21 days has been shown to be the maximum duration that growth in giant kelp can be sustained on internal nitrogen reserves (Gerard 1982b). These results are a major

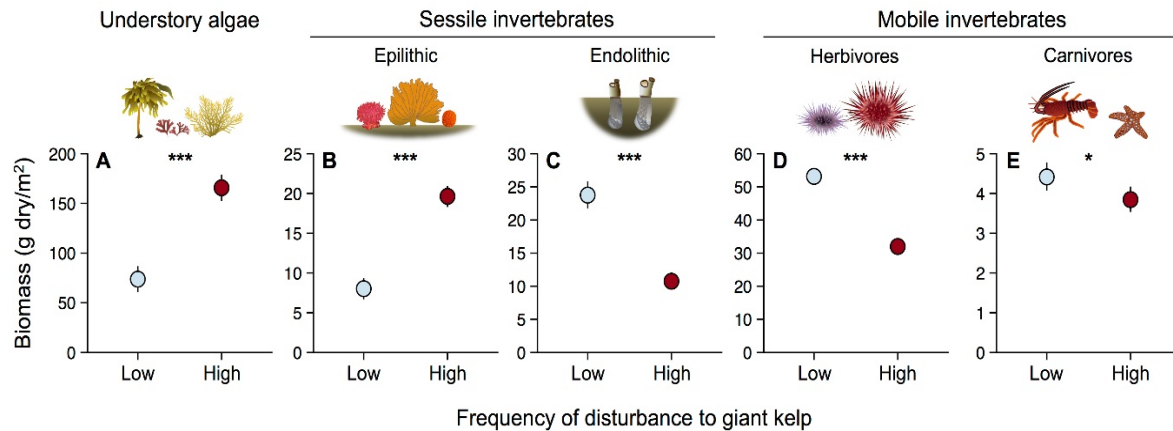
*impetus for continued research on sources and utilization of alternative forms of nitrogen recycled in the water column and on the seafloor, which will be explored in THEME 1c of SBC IV.*

Our ability to investigate local and regional dynamics of giant kelp and environmental drivers that underlie them has been greatly enhanced by our development of a novel long-term time series of kelp canopy biomass based on Landsat Thematic Mapper imagery calibrated to our monthly diver measurements of biomass collected in our long-term kelp NPP plots. We worked diligently during SBC III to inter-calibrate imagery from different Landsat missions (5, 7 and most recently 8) to produce a high frequency (1 to 2 times per month from 1984 present),



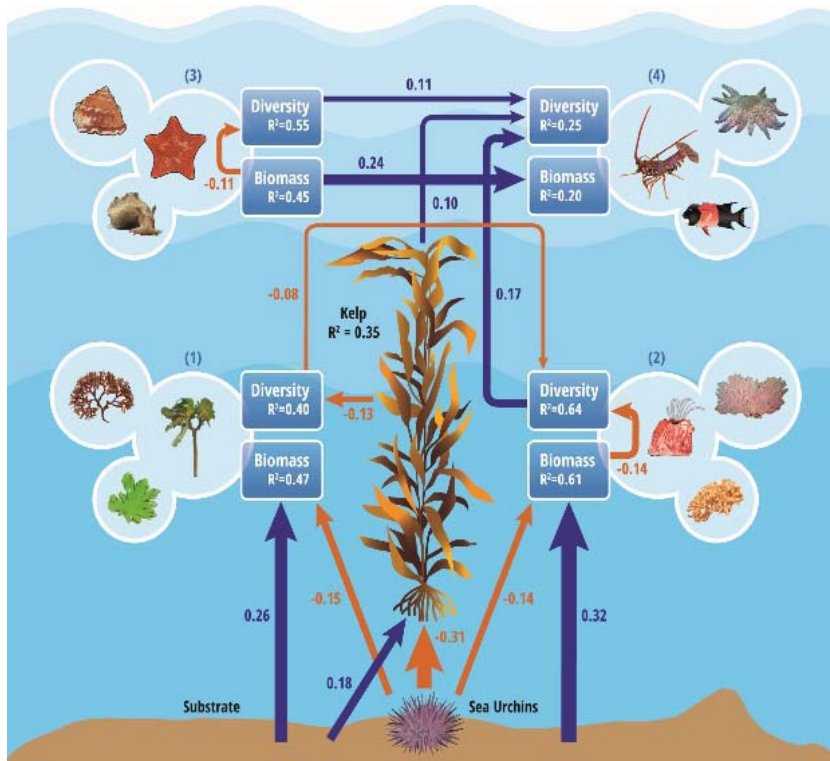
spatially extensive (1300 km extending from central California to Baja California, Mexico), and high resolution (30 m x 30 m) time series (Bell et al. 2017a). Using this time series we determined the importance of different environmental drivers in accounting for variability in the dynamics and persistence of giant kelp across a range of temporal and spatial scales (Cavanaugh et al. 2013, Bell et al. 2015, Young et al. 2016), and we assessed the degree to which variability in kelp and other environmental drivers account for different scales of spatial variability in the abundance of kelp forest biota (Lamy et al. 2018). The high temporal and spatial dynamics of kelp populations were a common theme in all of these studies, and wave disturbance emerged as a major source of this variation. This motivated new work to explore the extent to which local kelp populations function as a metapopulation system to promote recovery via spore dispersal from neighboring populations, challenging the widely held view that the persistence of local populations depends almost exclusively on self-replenishment. Establishing the boundaries of local populations is a necessary element of a metapopulation model, yet these delineations are often chosen arbitrarily. Hence, we used a hierarchical graph theory community detection approach that incorporated suitable habitat and population synchrony to classify each 30 m x 30 m Landsat pixel along the mainland coast in southern California into 249 spatially explicit local populations (Cavanaugh et al. 2014). By combining the Landsat time series with novel delineation methods and an innovative connectivity measure that we developed which incorporates oceanographic transport (Mitarai et al. 2009, Watson et al. 2010, Simons et al. 2013), we found that demographic connectivity via spore dispersal strongly predicted local population dynamics (Castorani et al. 2015). Our finding that well-connected populations had lower probabilities of extinction and higher probabilities of colonization that led to greater likelihoods of occupancy provided the first comprehensive evidence that southern California giant kelp populations function as a metapopulation system. Moreover, we discovered that fluctuations in population fecundity (i.e., the production of spores), rather than fluctuations in oceanographic transport, were the dominant driver of variation in connectivity via spore dispersal, and thus contribute substantially to metapopulation recovery and persistence (Castorani et al. 2017). *Still to be resolved is how environmental factors interact with dispersal to control the spatial dynamics and connectivity of giant kelp populations, which we propose to examine in THEME 3A of SBC IV.*

Disturbances often cause the disproportionate loss of habitat-forming foundation species, (Ellison et al. 2005). This is particularly true for giant kelp because its biomass extends throughout the water column and produces substantial drag that makes it disproportionately susceptible to being dislodged during large wave events (Dayton et al. 1992). During SBC II we initiated a large-scale (2000 m<sup>2</sup> plots), spatially replicated (4 sites), long-term (9 + years) disturbance experiment in which we manipulated the frequency of disturbance to giant kelp by mimicking annual loss from winter waves. By following the response of 205 reef taxa over time we discovered that repeated winter loss of giant kelp led to changes in community biomass and composition that were commensurate with how species use physical, trophic, and habitat resources affected by kelp (Castorani et al. *submitted*). The strongest response to annual disturbance of giant kelp was by benthic macroalgae and sessile invertebrates that rely on physical resources (light and space) mediated by giant kelp, and mobile invertebrate herbivores, particularly sea urchins, that rely on kelp for food (Fig. 4). Moreover, we found that resource availability and species interactions that shape the forest community were more significantly affected by repeated winter disturbance to giant kelp than by less frequent, but more severe disturbances. *We propose to test the predictions generated from the results of our long-term disturbance experiment in THEME 1A of SBC IV.*



**Figure 4.** Results from a 9-year disturbance experiment showing the effects of the frequency of disturbance to giant kelp on the aggregate biomass of the major community guilds.

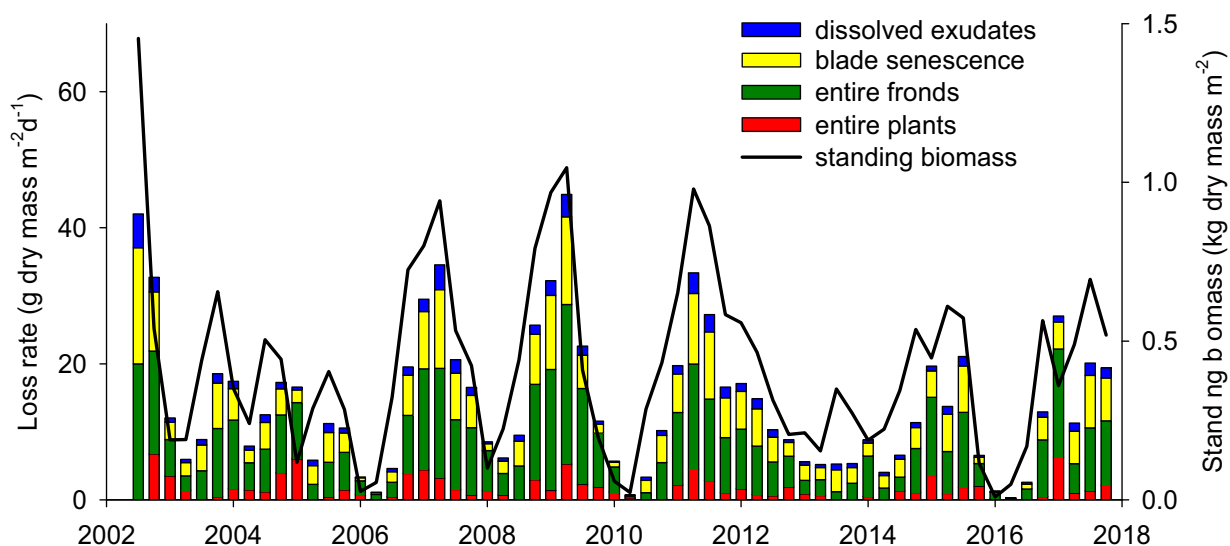
The perception of giant kelp as a key foundation species that many other species depend on dates back to Darwin's early observations (Darwin 1839). However, kelp's foundational role has yet to be quantified in a way that illuminates its effects on functional groups and species via the provision of food and habitat. To address this issue we applied structural equation modeling to our 15-year time series of reef community data to quantify the direct and indirect effects of giant kelp on reef community structure (Miller et al. 2018). We found that overall species richness and biomass of the community were positively associated with giant kelp biomass much like Darwin reported. However, we discovered that this association was largely driven by the dominant physical structure of giant kelp rather than its use as a food source by non-urchin consumers (Fig. 5), which is consistent with our previous results based on carbon stable isotope analyses (Miller et al. 2015). Kelp's dominant presence alters light, space and habitat to affect a



**Figure 5.** Piecewise SEM model of the effect of giant kelp biomass and sea urchin biomass on the biomass and diversity of four taxonomic functional groups, represented by the blue boxes: (1) understory macroalgae, (2) sessile invertebrates, (3) mobile grazers and (4) mobile predators. Arrows represent unidirectional relationships among variables. Blue arrows denote positive, and orange arrows negative, relationships. Arrows for non-significant paths ( $P \geq 0.05$ ) are not shown. The thicknesses of the significant paths reflect the magnitude of the standardized regression coefficients given alongside.  $R^2$  values inside boxes are conditional  $R^2$ . Data used in this analysis were collected annually in 39 plots from 2001-2016.

multitude of species interactions. *The specific mechanisms responsible for these indirect effects will be experimentally investigated in THEMES 1A and 1B of our proposed research.*

Giant kelp is one of the fastest growing multicellular autotrophs on Earth (Clendenning 1971), and the NPP of kelp forests rivals that of other highly productive ecosystems (Reed and Brzezinski 2009). We have been collecting monthly field measurements of kelp standing biomass and loss rates of whole plants and of fronds on surviving plants at three sites since 2000. Using these data, we developed an analytical model of kelp dynamics to estimate the specific growth rate and NPP of giant kelp for each season of each year (Rassweiler et al. 2008). During SBC III we expanded our investigations of kelp NPP to include the production and subsequent losses of dissolved organic carbon (DOC) and found that it accounted for 14% of total NPP, on average (Reed et al. 2015a). To better understand the processes governing the loss of fronds from living plants we followed the survivorship of individual fronds on tagged plants in our permanent plots and discovered that it was best explained by age-dependent mortality arising from programmed senescence rather than external environmental conditions (Rodriguez et al. 2013). This result challenged the widely held but untested assumption that declines in the surface canopy of kelp in summer results from low nutrients (Clendenning 1971, Jackson 1977, van Tüssenbroek 1993). By tracking individual blades on fronds at different locations in the forest we showed that their life span, size, thickness, nitrogen content, pigment content, and maximum photosynthetic rate varied across a light gradient in the forest in a manner consistent with the predictions of leaf life span theory developed for land plants (Rodriguez et al. 2016). Our recent findings on frond and blade senescence and DOC exudation enabled us to update our model of kelp NPP to more fully incorporate the broad suite of processes accounting for losses in standing biomass (Fig. 6). Doing so revealed that NPP of a persistent kelp stand averages  $\sim 5.5$  kg dry



**Figure 6.** Time series showing the loss rates of different components of the standing biomass of giant kelp in the Mohawk kelp forest.

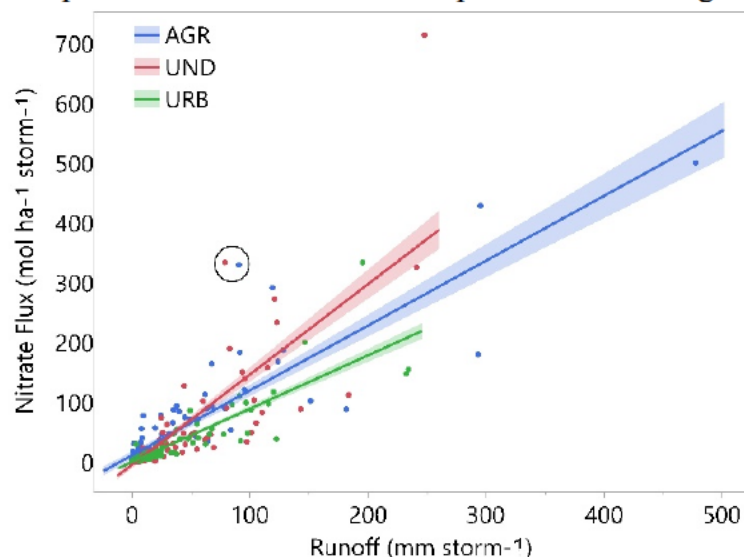
mass  $\text{m}^2 \text{y}^{-1}$ , and this high productivity results from the rapid growth ( $\sim 3.5\%$  per day) of a relatively small standing biomass ( $\sim 0.4$  kg dry mass  $\text{m}^2$  on average) that turns over  $\sim 12$  times annually (Rassweiler et al. *submitted*). Importantly, our revised model provides a more accurate basis for validating regional estimates of kelp NPP based on physiological condition obtained with remote sensing (Bell et al. 2017b) and for comparing kelp NPP with estimates of understory algal NPP (Harrer et al. 2013).



Results from laboratory and field incubation experiments specifically designed to study the fate of small detrital particles shed from kelp blades revealed that they represent < 0.2% of the particulate organic matter (POM) suspended in the nearshore water column (Yorke et al. 2013). The paucity of kelp particles in suspended POM is supported by our finding that phytoplankton biomass and production explained 62% of the variability in  $\delta^{13}\text{C}$  of suspended POM in the Mohawk kelp forest (Miller et al. 2013). This is consistent with the results of feeding experiments that showed the growth of kelp forest suspension feeders was unaffected by suspended kelp detritus (Yorke et al. *submitted*). In contrast, diet studies and stable isotope analyses show that living kelp and large pieces of kelp detritus are important sources of dietary carbon and nitrogen for invertebrate grazers in the kelp forest and the fish predators that feed on them (Page et al. 2013, Koenigs et al. 2015, Foster et al. 2015). Collectively, these results reaffirm the conclusion from our prior research (Page et al. 2008, Miller and Page 2012, Miller et al. 2015) that small kelp detrital particles do not represent a significant food source to reef suspension feeders, which instead rely on the production and delivery of phytoplankton as their primary diet. *In THEME 3C of SBC IV we propose to quantify the oceanographic processes that transport phytoplankton to kelp forests and their consumption by reef consumers.*

## Theme 2. Material exchanges at the land-ocean margin

Runoff from coastal catchments is the primary mechanism transporting materials from the land to the ocean in the SBC domain. Coastal catchments along the Santa Barbara Channel are characterized by large seasonal and inter-annual variations in rainfall, occasional fires and diverse land covers that include natural vegetation, and agricultural, suburban and urban development. Over the period from 2002 to 2016 annual rainfall varied from 18 to 122 cm, and included a prolonged drought and a few years with large amounts of rainfall. The episodic nature of stream discharge means that a few rain storms are responsible for transferring large pulses of sediment and nutrients into coastal ecosystems (Fig. 7). We used a 14-year time series of stream discharge, nutrient concentrations ( $\text{NO}_3^-$ ,  $\text{NH}_4^+$ , DON and  $\text{PO}_4^{3-}$ ) and total suspended solids (TSS) obtained by intensive sampling of 15 catchments during storms and regular sampling during baseflow, to calculate fluxes of these constituents and to develop statistical relationships between them and environmental conditions in the catchments (Aguilera and Melack, *submitted*). Annual fluxes for all forms of nitrogen were positively related to agricultural and impervious area. Fires followed by above average rainfall resulted in the highest ammonium and TSS fluxes. An analysis of the balance between wildfire N loss, plant and soil microbial N uptake and stream N export indicated that stream N export was 1500% higher than pre-fire export during the first



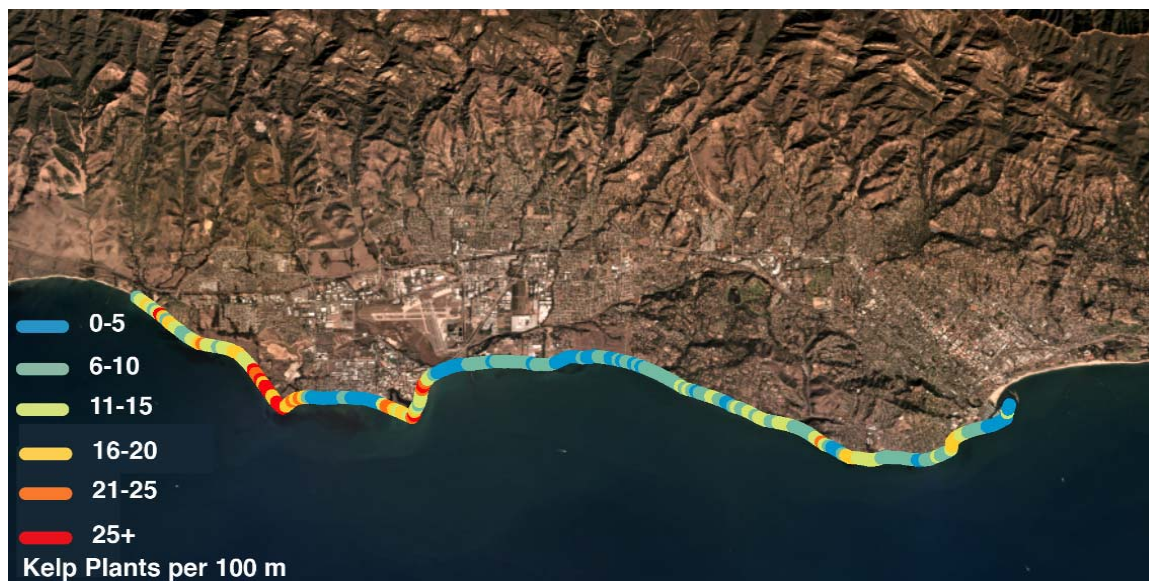
**Figure 7.** Relationship between nitrate storm fluxes and runoff. Regression lines are plotted for storms from 2002-2016 in three types of catchments based on predominant land cover: AGR, agricultural; UND, undeveloped; URB, urban/suburban. The shaded areas represent the confidence intervals for each regression line. The black circle highlights one of the storms during the onset of a wet year (WY 2005) when nitrate fluxes were similar in magnitude in an undeveloped site affected by fire and an agricultural site.

post-fire rain, but recovered within only three months to pre-fire levels (Goodridge et al. *submitted*).

Non-linear behavior of TSS and nutrients during storms was evident in the hysteresis in concentration-discharge (C-Q) relationships (Warrick et al. 2015, Aguilera and Melack 2018). High variance in TSS concentrations was common during high flow events, and different time-dependent hysteresis patterns were observed for similar discharge magnitudes. Hysteretic responses of nitrogen species were observed as dilution in urban sites and enrichment in undeveloped sites. The wide range of C-Q responses that occurred among sites and seasons reflected the variable hydrological and biogeochemical characteristics of catchments and storms. Nitrate had both transport-limited and supply-limited behavior, while DON concentration was typically greater at the end compared to the beginning of a storm.

Daily streamflow forecasts (2006-2100) for SBC watersheds using downscaled precipitation and temperature projections derived from 10 climate models for two emission scenarios were used to project ensemble precipitation and streamflow relative to historical conditions (1950-2005; Myers et al. 2017, Feng et al. *submitted*). These analyses predict increases in the magnitude and frequency of large storms combined with a shorter rainy season, which lead to increases in annual peak flows, and to nonlinear changes in the magnitude and variability of annual maximum discharges. These climate-driven changes will, in turn, increase the magnitude and variability of episodic fluxes of TSS and nutrients to the coastal ocean.

Material exchange in the coastal zone can also occur via the onshore transport of marine subsidies. One important form of exchange that we have identified is the deposition of drift kelp (wrack) on sandy beaches, which varies in time and space and can exceed 500 wet kg m shoreline<sup>-1</sup> y<sup>-1</sup> (Dugan et al. 2011, Leibowitz et al. 2016). The greatest losses of kelp plants and their subsequent deposition on beaches occur in fall and winter (Fig. 6) when wave disturbance is greatest. Sandy beaches, which by nature have low *in situ* NPP, depend on kelp subsidies to support a diverse food web. We have shown that kelp wrack on beaches is rapidly consumed by intertidal invertebrates, which are important prey for fishes and shorebirds (Dugan et al. 2003, Hubbard and Dugan 2003, Dugan and Hubbard 2016), as well as terrestrial insects, reptiles, birds and mammals (Hubbard and Dugan 2003, Spiller et al. 2010). Remineralization of kelp biomass adds nutrients to beach sands, and we found that the concentrations of dissolved inorganic



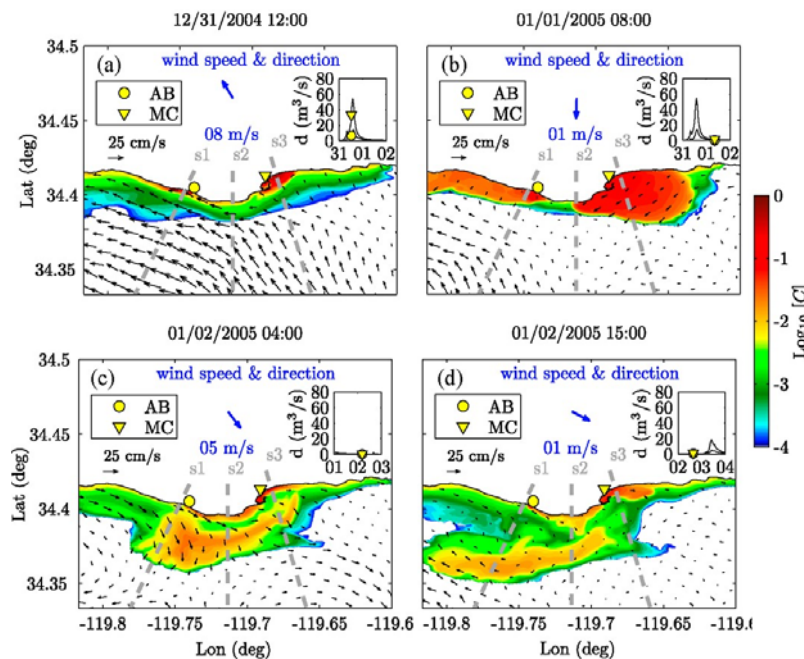
**Figure 8.** Spatial distribution of giant kelp plants stranded on beaches along a 25 km stretch of the Santa Barbara shoreline. Values are from monthly surveys and represent the mean number of plants per 100 m of shore. N = 20 months (August 2015-May 2017).

nitrogen (DIN) in beach porewater and the adjacent surf zone were positively related to the abundance of kelp wrack (Dugan et al. 2011). Estimates of the annual flux of nitrogen derived from kelp wrack from beaches into the nearshore ocean ranged from 1.8 to 9 moles N m<sup>-1</sup> shoreline for DIN and 2 moles N m<sup>-1</sup> shoreline for DON. Calculations based on porewater volume and residence time using the natural radioisotopic tracer <sup>222</sup>Rn indicate beach contributions to coastal DIN supply are quickly diluted, and elevated concentrations are limited to ~50 m from shore (**Goodridge and Melack 2014**), suggesting that this is not a significant source of recycled N to kelp forests.

We found that kelp deposition and retention on beaches are strongly influenced by coastal topography and beach width (Revell et al. 2011), and sea cliffs and seawalls often limit wrack deposition and wrack consumer abundance (Dugan et al. 2008, 2013). Our monthly surveys of newly stranded kelp plants showed them to be most abundant in the vicinity of headlands and least abundant on narrow stretches of beach where the tides interacted with sea cliffs or seawalls (Fig. 8). Wave disturbance alters the supply of kelp wrack and the ability of beaches to retain it (Revell et al. 2011), which in turn affects the diversity and abundance of beach invertebrates and birds (Hubbard and Dugan 2003, Hubbard et al. 2014, Schooler et al. 2017). *Determining the extent to which fluctuations in kelp wrack and the populations of consumers that rely on it are linked to the temporal and spatial dynamics of nearby kelp populations is a primary objective of the research proposed in THEME 3B of SBC IV.*

### **Theme 3. Movement and fluxes of inorganic and organic matter in the coastal ocean**

Characterizing the dispersion and dilution of freshwater runoff from land is crucial for understanding the importance of land-derived subsidies and other materials (e.g., nutrients, organic matter, sediments) to coastal ecosystems. In southern California runoff events are episodic and short-lived and the plumes are buoyant, making it challenging to measure their spatial and temporal evolution. Thus, we used ultra-high spatial resolution (100 m) Regional Ocean Modeling System (ROMS) simulations to characterize the dilution and dispersion of



**Figure 9.** Evolution of surface tracer concentrations (log base 10) from Arroyo Burro (AB) and Mission Creek (MC) during the first storm of Winter 2004-05. The black vectors show surface currents. The inset shows the hydrographs and corresponding instantaneous discharge rates from AB and MC. Wind speed and direction are shown in blue.

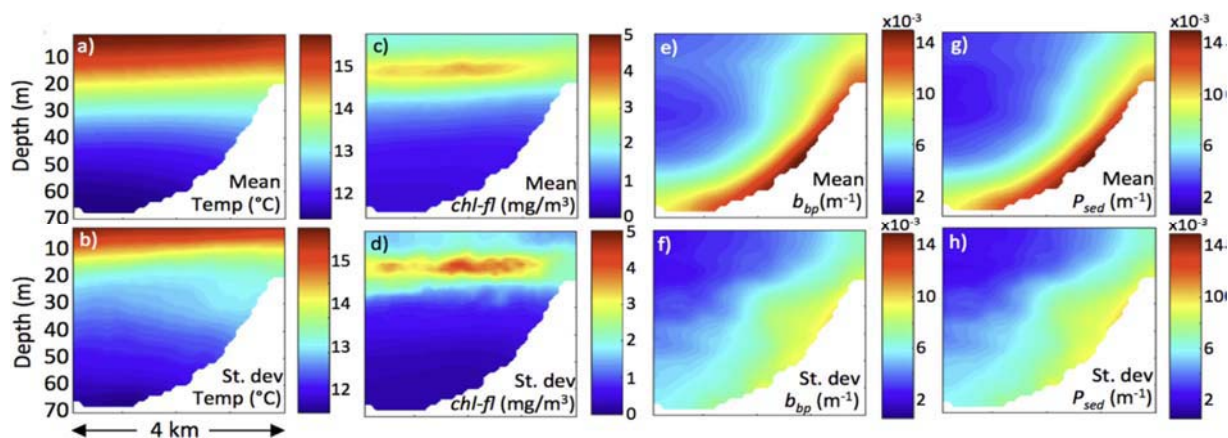
freshwater runoff into the Santa Barbara Channel. We focused our modeling efforts on two creeks that enter near the Mohawk kelp forest using discharge data collected during the two wettest winters between 2002-2009 (Romero et al. 2016). We found that plume evolution is tightly coupled to precipitation, freshwater discharge, wind forcing and submesoscale flow structures. During peak runoff, winds are typically onshore, causing downwelling and retention of freshwater close to shore leading to anisotropic dispersion as plumes spread 10 times faster along the coast than across the shelf (Fig. 9a). As the storm passes, the winds shift and the plume is advected offshore enhancing dilution (Fig. 9b-d). This pattern held



for all seven of the storms simulated. Plumes reach the bottom in the inner 1 km, but form layers a few meters thick at the surface offshore.

Using statistical probabilities derived from our measurements of concentrations and fluxes of nitrate, ammonium and DON during storms in multiple watersheds over several years with our model of plume dispersion and dilution, we are able to estimate the concentrations and duration of particular nutrients near kelp forests. For example, over a 12-year period an average of six storms per year with median runoff occurred, with median concentrations of nitrate ranging from 20  $\mu\text{M}$  in undeveloped watersheds to 50  $\mu\text{M}$  in suburban/urban watersheds to 150  $\mu\text{M}$  in moderately agricultural watersheds. Based on these values, our dilution model suggests that nitrate concentrations of 2, 5 or 15  $\mu\text{M}$ , as a function of land use, would persist in the vicinity of kelp forests for several days after each storm. Although significant, these pulses in nitrate occur during winter when DIN concentrations in coastal waters average between 3-7  $\mu\text{M}$ , which is above the threshold needed to support kelp growth (**Brzezinski et al. 2013**).

We have shown that wind-driven upwelling is weak and intermittent in the Santa Barbara Channel and that other oceanographic processes are important in transporting plankton, nutrients, and other subsidies to kelp forests (Washburn and McPhee-Shaw 2013). Using an autonomous ocean glider purchased with supplemental NSF funding, we examined cross-shelf exchanges of phytoplankton and suspended sediments on time scales of hours to weeks near the Mohawk kelp forest with 404 high-resolution cross-shelf sections of bio-optical properties collected on 92 days over a 15-month period (**Henderikx Freitas et al. 2016**). We observed rapid onshore transport of phytoplankton across the mid-shelf and inner-shelf, and a strong positive relationship between suspended sediment concentrations and surface wave height (Fig. 10). An analysis of optical

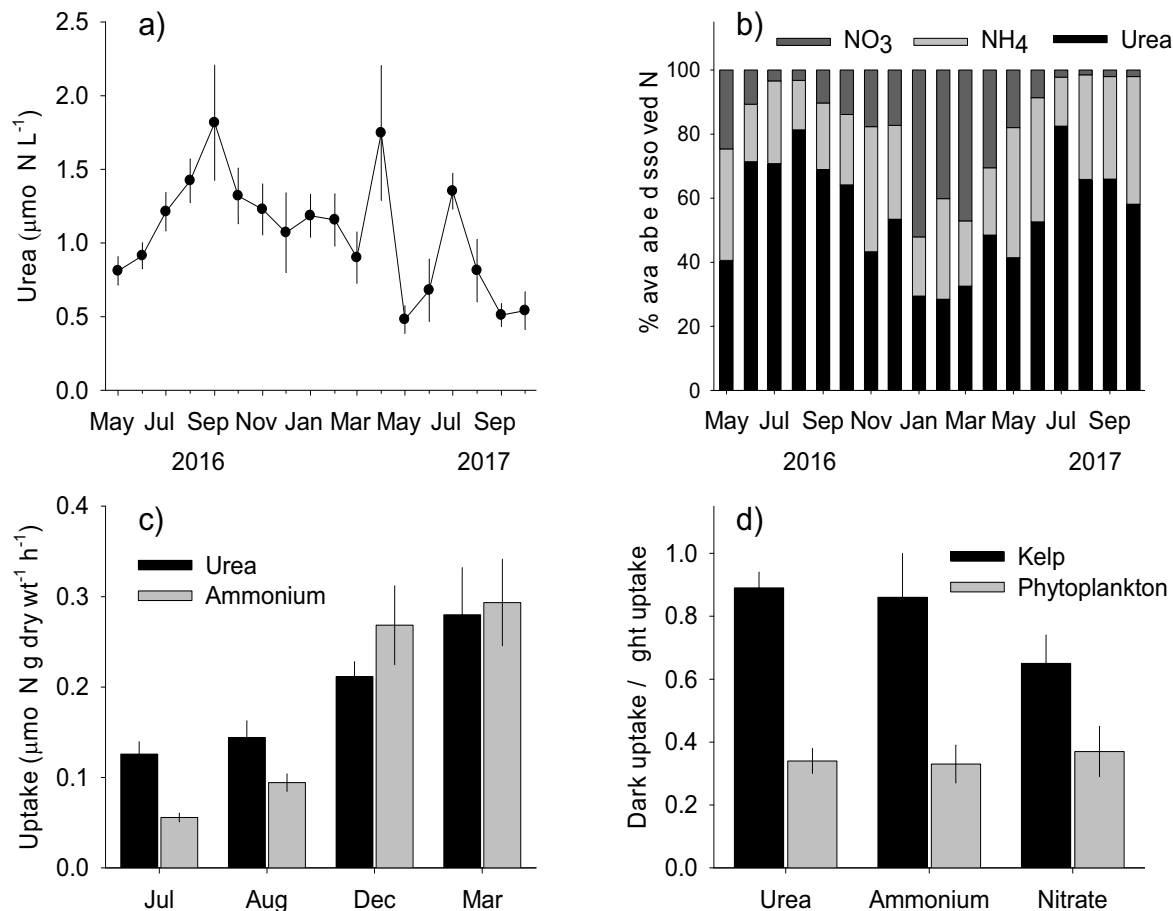


**Figure 10.** Section means and variability (standard deviations) of physical and bio-optical properties obtained using an autonomous ocean glider. Temperature (a and b), Chlorophyll fluorescence (c and d), Particle backscatter (e and f), and Suspended sediments (g and h). Means and standard deviations are taken over all

backscatter from 18 years of satellite imagery showed that this was a ubiquitous feature of the Santa Barbara Channel extending offshore to the 100 m isobath (Henderikx Freitas et al. 2017). *New research in SBC IV (THEME 3C) will use the glider to quantify variability in cross-shelf transport and the delivery of phytoplankton subsidies to kelp forest consumers.*

The limited capacity for giant kelp to store nitrogen, coupled with our observations of continued kelp growth during seasons and years with low nitrate availability (Fig. 3, **Brzezinski et al. 2013**, **Reed et al. 2016**), and our modeled estimates of N uptake by kelp that exceed available nitrate (Fram et al. 2008), have led us to search for alternative sources of N that sustain kelp year-round. To this end we expanded our monthly sampling of dissolved N to include urea, the simplest form of DON (Smith et al. *submitted*). We observed urea to be present in samples from all dates, depths and stations at concentrations ranging from 0.06 – 5.1  $\mu\text{M}$  (Fig. 11a). We found that urea on average accounted for ~45% of the dissolved N known to be used by kelp (i.e., nitrate, ammonium, urea) and as much as 80% during summer when nitrate accounts for

only ~5% of the available dissolved N (Fig. 11b). Unlike nitrate, concentrations of urea and ammonium were not correlated with temperature or other environmental variables associated with upwelled waters. Our *in situ* experiments provide the first direct evidence of urea uptake by kelp as a whole molecule and confirm uptake of urea and ammonium by kelp throughout the year (Fig. 11c), suggesting that they are important sources of N for kelp during extended periods of low nitrate availability. Results from additional laboratory experiments show that, unlike phytoplankton, the uptake of urea and ammonium by kelp is largely decoupled from irradiance, allowing 24-hour access to these sources of N (Fig. 11d).



**Figure 11.** (a) Mean (± SE) concentration of urea N in monthly samples collected at five kelp forest sites. (b) Percent of available dissolved N contributed by NO<sub>3</sub>, NH<sub>4</sub> and urea, (c) Mean (± SE) uptake rates of urea and ammonium by giant kelp blades during *in situ* incubations, and (d) Ratio of nitrogen uptake in the dark vs. light for urea, ammonium and nitrate.

Potential sources of nearshore urea and ammonium include microbial regeneration from organic matter in sediments, on the reef, and in the water column, as well as recycling by benthic and pelagic animals. Results to date show N concentrations of nearshore sediment porewater ranging from 5 to 25 μM for urea and 30 to 60 μM for ammonium, and temperature profiles within sediments indicate daily flushing of porewater to about 15 cm. Regeneration experiments using recirculating sediment bioreactors suggest that kelp forest sediments contribute up to 720 μM NH<sub>4</sub><sup>+</sup> m<sup>2</sup> d<sup>-1</sup>, which is sufficient to maintain the concentrations measured in the porewaters and to sustain a substantial flux to the near-bottom waters. Ongoing parallel studies that integrate excretion rates of consumers with time-series estimates of their standing biomass suggest that excretion by benthic kelp forest invertebrates contributes ~550 μM NH<sub>4</sub><sup>+</sup> m<sup>2</sup> d<sup>-1</sup> on average. Water column decomposition experiments using a <sup>15</sup>NH<sub>4</sub><sup>+</sup> pool dilution method revealed a



microbial remineralization flux of  $0.1 - 0.15 \mu\text{M NH}_4^+ \text{ h}^{-1}$ , which would consume ~40% of the DON pool on a daily basis. *Collectively, our novel findings of the availability and uptake of these previously understudied sources of N stimulate new research proposed for THEME 1C OF SBC IV on microbial regeneration of ammonium and urea and their utilization by kelp and phytoplankton.*

## **BROADER IMPACTS**

SBC investigators are very active in applying their knowledge of coastal ecosystems to inform and implement changes in local and regional policies. We serve as advisors and committee members for a number of local and national groups concerned with conservation and management of natural resources (see Biosketches). One of our more significant accomplishments was a recently completed study on climate change adaptation for use by local land use planners and decision-makers (Myers et al. 2017). Our objective was to identify potential vulnerabilities of coastal watershed, wetland and beach ecosystems to projected climate change impacts. The study relied extensively on SBC time-series data and modeling and was done in collaboration with climatologists from Scripps Institution of Oceanography, a coastal geomorphologist from the US Geological Survey and hydrologists from Northeastern University.

Outreach and education is a major activity for SBC. Funding for our Schoolyard LTER (SLTER) program targets K-12 students and teachers and is organized around a theme of watershed and marine ecology that incorporates SBC research. We recently published *The Golden Forest* (Blanchette and Dugan 2017) as a contribution to the LTER Children's Book Series. The book explores the SBC coastal ecosystem through the eyes of two 6<sup>th</sup> grade cousins and serves as a teaching tool for our SLTER program. By partnering with the REEF (UCSB's educational marine aquarium facility) we reached over 42,000 students and the general public during the first five years of SBC III. We also worked with over 800 Junior High School girls in collaboration with the American Association of University Women *Tech Trek*, a math and science summer program designed to develop interest and self-confidence in young women. Highlights from this program include a 90% increased interest in attending college and a 20% increase in test scores on curricula-based material. During this award period we partnered with the Santa Barbara Unified School District and middle schools in Ventura County to provide teacher professional development to ~30 teachers per year. This partnership includes the Ocean Science Sequence curriculum, developed by the Lawrence Hall of Science, which we "localized" using research findings from SBC publications and seminars by SBC researchers. Teachers reported a significant increase in their science content knowledge and presented this curriculum to over 2,000 local 6<sup>th</sup> graders during the past 3 years. Through these collective efforts we delivered the science and excitement of SBC research to over 70,000 K-12 and community members in Santa Barbara, Ventura, Los Angeles, and Kern counties, as well as visitors from Taiwan, India, Japan, South Korea and Europe. Title 1 schools that have a predominantly Latino/Latina student body make up ~70% of the schools participating in SBC's SLTER program.

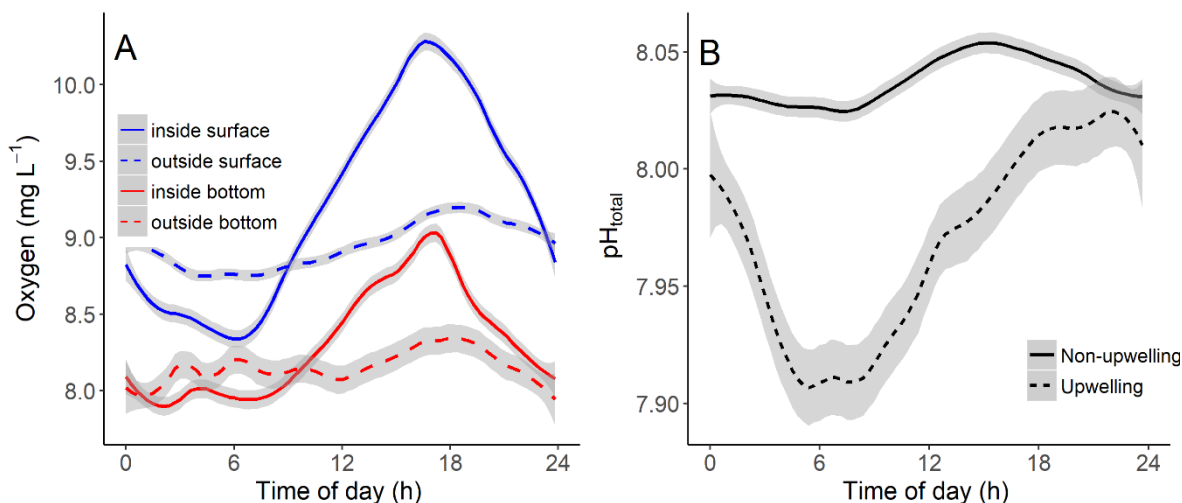
SBC made a substantial contribution to education and training at the university level; 15 postdoctoral fellows, 51 graduate students, 20 REU students and more than 300 undergraduate students participated in SBC research and education activities during the first five years of our current award. The active involvement of large numbers of undergraduate students in SBC research provides valuable undergraduate training, and also affords SBC's graduate students and postdocs significant opportunities for mentorship training. Graduate students and postdocs participate with investigators and research staff in a structured undergraduate training program that runs the entire academic year in which students actively participate in the collection, processing and analysis of SBC data. Many of these students develop their own independent research projects or choose to serve as docents at the REEF K-12 outreach program. As a Hispanic Serving Institution ~20% of UCSB's STEM majors are Hispanic. Research opportunities provided by SBC greatly enhance the educational experience of these students,

who historically have been under-represented in the sciences. Learning and mentoring from undergraduates with similar cultural backgrounds is proving effective for SBC, as we have had several alumni of our SLTER program enroll as undergraduates in STEM majors at UCSB and participate in SBC research and outreach programs.

With supplemental funding from an NSF Research Opportunity Award we have been providing research opportunities to students and science faculty from Santa Barbara City College (SBCC). SBCC students gain training and experience in scientific research, interact with UCSB scientists and graduate students, and participate in SBC's undergraduate training program. SBCC science faculty incorporate SBC research into their course curricula and conduct research with SBCC students with the help of SBC and UCSB infrastructure.

## RESULTS OF SUPPLEMENTAL SUPPORT

We received supplemental funding to purchase instruments to expand and improve our capacity to parameterize the carbonate system of nearshore coastal waters. These instruments are enabling us to collect time-series measurements of seawater carbonate chemistry (e.g., pH, total alkalinity, total CO<sub>2</sub>) and dissolved oxygen (DO), which are essential for determining the oceanographic and biological processes that underlie ocean acidification. Our efforts to date have focused on characterizing spatial and temporal variability in the physiochemical properties of seawater (Hofmann et al. 2013, Rivest et al. 2016) and assessing its biological consequences (Gaitán-Espitia et al. 2014, Kapsenberg et al. 2017). In early deployments of pH and DO sensors we observed diel patterns of co-variation of pH and DO concentrations that were distinctly different in vegetated (e.g., eelgrass meadows and kelp forests) and sandy unvegetated habitats (Kapsenberg and Hofmann 2016). These results spurred new deployments of DO and pH sensors within and outside of the kelp forest which showed strong vertical, horizontal and diel differences in DO (Fig. 12a). We observed that upwelling has a dominant signature on pH, but



**Figure 12.** Diel variation in (A) the concentration of dissolved oxygen and (B) pH. Dissolved oxygen data are from sensors placed near the bottom and surface inside and outside the Mohawk kelp forest; pH data were obtained from sensors placed near the bottom inside the Mohawk kelp forest. Data were collected over a 25-day period in spring 2015 that included a 5-day upwelling event. Lines represent mean values averaged over all days and shaded areas denote the 95% confidence interval.

that the presence of kelp can moderate these effects as photosynthesis progresses throughout the day (Fig. 12b). These new data highlight the variability of abiotic conditions in the kelp forest that are largely driven by the presence of the kelp itself. *We propose research in THEME 2 of SBC IV that aims to quantify how the dynamics of giant kelp affect sea water chemistry and organic matter cycling to modify the structure and function of the forest ecosystem.*

## **SECTION 2 – RESPONSES TO PREVIOUS REVIEWS**

The midterm review of SBC III was generally very favorable and NSF agreed with the review team that “SBC is a productive and well-functioning LTER”. Research in population dynamics and trophic structure was viewed as generating the most compelling advances in ecosystem ecology and as a strength of SBC going forward. The primary weakness highlighted by NSF was a perceived lack of clarity by the review team regarding the research focus of SBC (i.e., kelp forests vs. coastal ecosystems that include kelp forests), which raised concerns about the conceptual and practical integration of ocean and watershed research. Nutrient coupling between the watersheds and kelp forests was viewed as an unfinished task that needed to be completed, and the potential role of ocean acidification and carbonate chemistry in future studies needed to be resolved. Below we briefly describe how we are addressing these and other comments raised by NSF in our proposed research for SBC IV.

### **RESEARCH FOCUS**

The primary research focus of SBC continues to be long-term investigations of kelp forest ecosystems with the goal of advancing a predictive understanding of the processes that determine their structure and function under varying conditions of climate and human use. Like many ecosystems, the structure and function of kelp forests are influenced by the exchange of materials with neighboring ecosystems, and quantifying these exchanges and their ecological impacts is a major research objective of SBC. SBC’s initial proposal was funded in response to NSF’s desire to expand the LTER Network to include ecosystems at the land-ocean margin. Thus, documenting how climate variability, land use and fire alter the episodic delivery of terrestrial matter to kelp forests via runoff has been a key research element of SBC since its inception. A prolonged drought hampered progress in our assessment of the importance of pulsed delivery of terrestrially derived organic and inorganic material to kelp forests, and justification for continuing this research has been understandably scrutinized by past panels and NSF.

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 the Santa Barbara Channel and its fringing kelp forest ecosystems. 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. By dispersing and diluting these fluxes based on our measurements and modeling of coastal processes, we are now able to incorporate their contribution into our ongoing studies of nutrient supply to kelp forests in a changing climate by collecting data on precipitation and land cover change (e.g., due to fire) and running models of discharge and material fluxes. Therefore, in SBC IV we will no longer continue extensive sampling of runoff and its constituents in coastal watersheds, which will result in a major reduction of effort in our watershed research. By doing so, the five core research areas in SBC IV will be more clearly focused on kelp forests and their exchange of materials with adjacent beaches and coastal waters.

### **OCEAN ACIDIFICATION**

Results obtained from equipment purchased with supplemental funding have provided insight into the potential role of kelp forests as climate refuges from future ocean acidification and deoxygenation. We propose to build on these results in SBC IV by quantifying kelp-induced changes in carbonate chemistry and DO, and evaluating the role of kelp forests in affecting the ecological and evolutionary dynamics of reef species in a changing ocean (see *THEME 2*). To provide environmental context for this research we have added measurements of pH, DO, total alkalinity and  $p\text{CO}_2$  from sensors and discrete water samples to our long-term time series of seawater chemistry and physical properties.

## OTHER COMMENTS

SBC's past and proposed efforts to increase participant diversity are detailed in Broader Impacts of Section 1 (Prior Results) and in our Project Management Plan (Supplement 3). Plans for leadership transition and rotation of PIs are addressed in the Project Management Plan. The use of leveraged resources to pursue the long-term ecological questions that justify continued LTER support is described in Section 5 (Related Research Projects).

## SECTION 3 – INTELLECTUAL MERIT

Developing a predictive understanding of ecosystem responses to environmental change is a fundamental objective of ecological research and is central to effective resource management and conservation policy. Accomplishing this objective generally requires studying ecological patterns and processes over broad temporal and spatial scales to encompass the wide range of environmental variability inherent in most natural ecosystems (Lindenmayer and Likens 2009, Reed et al. 2015b, Hughes et al. 2017), and to account for the unprecedented rate and magnitude of environmental change caused by humans, including altered climate (Karieva and Fuller 2016). Indeed, this was a main reason for establishing the US LTER Network (Callahan 1984).

The ecological effects of climate change are expected to be large (Thomas et al. 2004, Pereira et al. 2010), and long-term studies aimed at dominant species that define a community offer great potential for understanding the consequences of such effects on entire ecosystems (Ellison et al. 2005). The foundations of many ecosystems are formed by long-lived species with life spans ranging from decades to centuries (Dayton 1972, Angelini et al. 2011, Osland et al. 2013). Populations of such species tend to react slowly to shifting environmental conditions, thus necessitating observations over long periods to detect responses to environmental change. In some systems, however, foundation species live only a few years, fluctuating widely in space and time in response to environmental variation (e.g., Dayton et al. 1992). Despite the more rapid changes, a long-term perspective is necessary in these systems to distinguish the effects of transient environmental variation from secular shifts caused by climate change and human actions. At the same time, short-lived foundation species offer excellent models for examining ecological responses to environmental variation and climate change because data collected over multiple generations are readily obtained. Research at SBC exemplifies the value of long-term data for understanding short-lived species as it focuses on coastal ecosystems dominated by the giant kelp *Macrocystis pyrifera*, a large, short-lived seaweed that provides the foundation for extremely productive and diverse marine forests that are highly valued in coastal temperate regions worldwide (Graham et al. 2007, Schiel and Foster 2015).

The major research objective of SBC is to develop a predictive understanding of how environmental factors determine the ecological structure and function of giant kelp forests under varying oceanic climate and human use. The dynamic nature of giant kelp forests, characterized by frequent disturbance and rapid regeneration every few years (Castorani et al. 2015, 2017), coupled with their high productivity (Reed and Brzezinski 2009, Rassweiler et al. *submitted*) and diverse food webs (Graham 2004, Byrnes et al. 2011, Miller et al. 2018) make them ideal systems for investigating a plethora of ecological patterns and processes that require decades to centuries to address in other ecosystems. Such features underlie the broader ecological significance of an LTER site such as SBC whose research on population dynamics, community properties and ecosystem processes has spanned multiple cycles of disturbance and recovery since it was established in 2000.

Analyses of our long-term data have identified many of the environmental drivers and ecological processes underlying the production and community dynamics of kelp forests. We have shown that many of giant kelp's foundational attributes are derived from its physical structure, which provides shelter for prey and foraging habitat for predators (Okamoto et al. 2012, 2016, Koenigs et al. 2015, Morton et al. 2016), directly alters seawater circulation and chemistry (Gaylord et al. 2007, Fram et al. 2008, Rodriguez et al. 2016, Rivest et al. 2016), and

directly and indirectly affects species interactions (Arkema et al. 2009, Byrnes et al. 2011, **Miller et al. 2018**). Still to be determined are the ecosystem consequences of disturbance and fishing that alter the area, abundance and size structure of giant kelp forests, the processes that sustain kelp growth during periods of low nitrate availability, the ecological and evolutionary consequences of kelp-induced changes in seawater flow and chemistry, and the degree to which environmental drivers influence forest persistence and trophic subsidies (both to and from kelp forests). 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?*”.

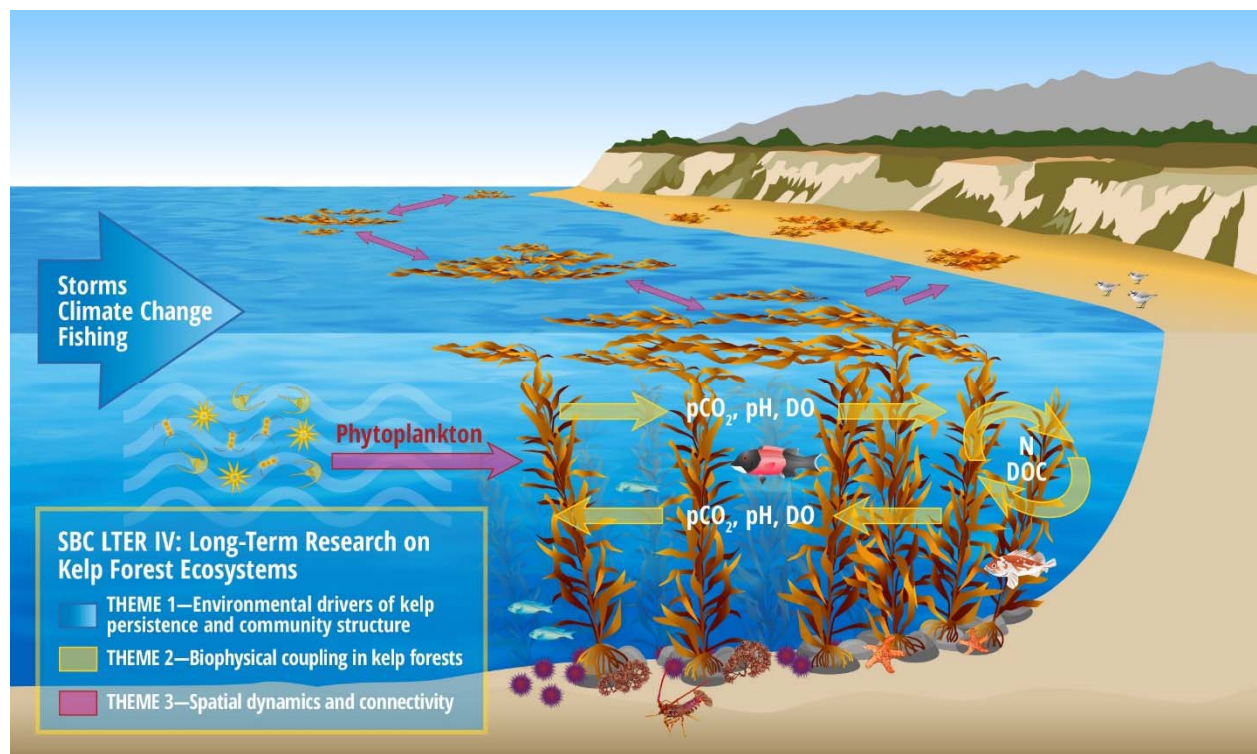
We address this overarching question by focusing our proposed research around three inter-related themes:

*THEME 1 - Environmental drivers of kelp persistence and community structure*

*THEME 2 - Dynamic biophysical coupling in kelp forest ecosystems*

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

These themes are linked in a conceptual framework (Fig. 13) by the causes and ecological consequences of the dynamics of a relatively short-lived foundation species in a setting of long-term climate change and human use (i.e., fishing and coastal development). Importantly, our proposed research will continue to be informed by our long-term datasets in the five core areas of LTER research (Table 1). Below we describe our proposed research in each of these themes.



**Figure 13.** 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.



SBC IV Research Theme	LTER Core Area	SBC dataset ID
<i>THEME 1A. Community and ecosystem consequences of climate variability, disturbance and pathways of recovery</i>	PP PD OM DP	36, 58, 74 28, 29, 30, 34, 74, 50 25 13, 28, 29, 30, 34, 35, 74
<i>THEME 1B. Ecological consequences of fishing</i>	PP PD DP	36, 58 15, 17, 18, 19, 74 28, 29, 30, 34, 35, 74, 77
<i>THEME 1c. Sources and utilization of recycled nitrogen</i>	PP IN	36, 112 10, 2005, 2007
<i>THEME 2A. Effects of kelp on physical and chemical fluxes</i>	PD IN	74, 112 10, 2005, 2007, 75, 6002, 6003
<i>THEME 2B. Effects of kelp on the processing and fate of dissolved organic matter</i>	PP OM IN	36, 112 36, 112 10, 2005, 2007
<i>THEME 2c. Ecological and evolutionary consequences of kelp-induced changes in seawater chemistry</i>	PD IN DP	112 10, 2005, 2007 35, 75, 6002, 6003
<i>THEME 3A. Demographic connectivity and metapopulation dynamics of giant kelp</i>	PD DP	74 35, 74
<i>THEME 3B. Trophic connectivity between kelp forests and beaches</i>	PD OM DP	51, 74, 91 40 35
<i>THEME 3c. Trophic connectivity between the coastal ocean and kelp forests</i>	PP PD	10, 2005, 2007 28, 34, 50

**Table 1.** List of research themes in SBC IV, the core LTER research areas addressed by each theme and the SBC long-term datasets (associated with each core area) that will be used in the research of each theme. Abbreviations for core research areas are PP = Primary production, PD = Population dynamics, OM = Organic matter, IN = Inorganic nutrients, DP = Disturbance patterns. Dataset IDs correspond to those listed in Supplement 1- Electronically Accessible Datasets.

## SECTION 4 - PROPOSED RESEARCH

### *THEME 1. Environmental drivers of kelp persistence and community structure*

Our previous findings highlight the capacity of giant kelp to persist in the face of severe nutrient and thermal stress associated with increased climate variability (Figs. 2 and 3). Yet, giant kelp forests do not persist indefinitely and are regularly disturbed by large waves that disproportionately remove kelp, and fishing which targets higher trophic levels. Changes in climate are expected to alter the frequency and severity of wave disturbance and fishing effort, which should influence kelp persistence and kelp forest community structure. The research proposed for *THEME 1* examines the consequences of changes in kelp persistence 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 enable kelp to persist during conditions of low nitrate availability.

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

**Rationale:** The results from our 9-year disturbance experiment conducted at four sites (Fig. 4) and analyses of a 16-year time series of temporal variability in kelp forest community structure at nine of our long-term study sites (Fig. 5) provide new expectations about how disturbance and climate variation indirectly structure reef communities by controlling the dynamics of giant kelp loss and recovery. Based on these results we predict that more frequently disturbed kelp forests will have a more abundant and diverse assemblage of understory macroalgae and epilithic sessile invertebrates, and lower biomass of omnivorous sea urchins that graze upon giant kelp detritus and of carnivorous invertebrates and fishes that use giant kelp for refuge or foraging habitat. In SBC IV, we propose to broadly test these predictions using complementary comparative and experimental approaches.

**Approach:** To test the generality of our predictions we will compare community structure of kelp forests in the Santa Barbara Channel with known disturbance histories in a new long-term study. We will use Landsat imagery to quantify the frequency of complete kelp canopy loss in winter (when kelp loss to wave disturbance is greatest; Reed et al. 2008, 2011, Bell et al. 2015) during the previous 10 years for all 232 island and mainland local kelp populations delineated in

the Santa Barbara Channel using methods that we developed in SBC III (**Cavanaugh et al. 2014**). To distinguish the effects of the frequency of wave disturbance from other more persistent sources of kelp loss (e.g., sea urchin grazing, sand burial), we will restrict our identification of local populations to those with a canopy during autumn (when kelp biomass is greatest; Reed et al. 2009) in each of the prior ten years. The forest community of algae, invertebrates and fishes in ten local populations selected across a gradient of time since last disturbance will be sampled by divers using the same methods employed in our long-term disturbance experiment. This process will be repeated annually in summer using different local populations each year until we have generated a sufficient sample size to robustly estimate the effects of disturbance frequency on the biomass, richness, evenness, and composition of kelp forest communities using mixed-effects models and multivariate analyses.

Recovery in many ecosystems can vary greatly in space and time, and the species composition and biomass of recovered communities can differ substantially, even following seemingly similar disturbances (Dethier 1984, Connell 1997, Chase 2007, 2010). We will experimentally examine rates, extent and pathways of recovery in kelp forest communities following disturbance in two ways. First, we will document variation in recovery by discontinuing the annual removal of giant kelp in our long-term disturbance experiment, and comparing community recovery and net primary production in plots where kelp had been experimentally removed on an annual basis for the previous nine years to those in control plots. Comparisons will be done using the same statistical methods used to examine the effects of annual kelp removal in the long-term disturbance experiment (Castorani et al. *submitted*).

Second, we will initiate a finer-scale experiment to determine the role of competition for space as a key process governing community recovery. We will examine the role 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 paired plots (1 m<sup>2</sup>) with and without understory algae removed will be nested within the larger kelp control and kelp removal plots to isolate the effects of giant kelp on competition between understory macroalgae and sessile invertebrates. Kelp and understory algae in the experimental plots will be removed quarterly, and community structure will be measured annually by divers. Results from structural equation models of our long-term community data (**Miller et al. 2018**) as well as information on diets (Byrnes et al. 2011) suggest that reef predators depend on sessile invertebrates as a food resource. To gain insight into how predators may affect the outcome of competition between sessile invertebrates and macroalgae, experimental sites will be selected to represent a gradient in the density of invertebrate and reef fish predators, including two marine reserves that have much higher predator abundance than other sites. To determine how legacy effects of disturbance alter pathways of benthic community recovery, we will manipulate macroalgae and sessile invertebrates in fully factorial combinations (+algae +invertebrates; +algae invertebrates; algae +invertebrates; algae invertebrates) in additional 1 m<sup>2</sup> quadrats nested within the circular kelp removal plots. In this case, manipulations of understory algae and invertebrates will be done only at the beginning of the experiment to evaluate effects over time on primary and secondary successional communities. Sampling to estimate rates and extent of community recovery will be done monthly for three months, quarterly during the remainder of the first year, and annually thereafter. Our null hypothesis is that all subplots will converge on the same community composition within the six-year award period. Our alternative hypothesis is that the starting conditions (i.e., the species present following selective removals) will alter the outcome of competition to drive persistent differences in community composition. Changes in community composition will be analyzed using multivariate statistics.

#### *THEME 1B. Ecological consequences of fishing*

**Rationale:** Unlike disturbances that directly remove giant kelp, human drivers such as fishing can influence kelp forest communities by reducing the abundance and size of targeted species with cascading consequences for unfished species that alter community structure and function

(Estes et al. 2011, Gilby and Stevens 2014, Caselle et al. 2018). A network of Marine Protected Areas (MPAs) established in 2012 throughout California provides us with an exceptional opportunity to experimentally investigate the effects of fishing on kelp forest structure and function by prohibiting fishing at two of our long-term kelp forest study sites where we had been collecting data for a decade prior to MPA establishment. This MPA network is set within a broader array of MPAs of varied ages and environmental contexts, which collectively cover 16% of California's nearshore habitats, offering an unparalleled opportunity for comparative work.

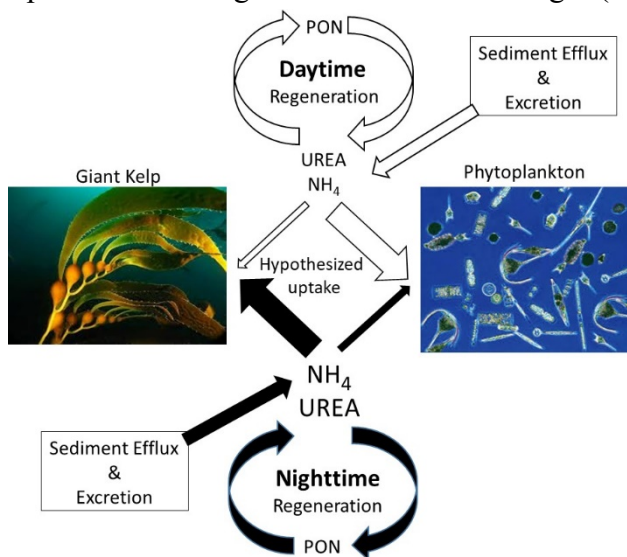
Approach: Studies of communities inside and outside MPAs can reveal not only the effects of fishing, but also how organism size mediates ecological processes. We have used MPAs to show that larger lobsters (an important kelp forest predator) in protected areas eat prey that are not attacked in fished areas, suggesting that food webs in most of California may not be representative of the trophic relationships that existed prior to widespread fishing (Berriman et al. 2015). We will follow up on this work with analyses of species-specific size structure data collected for kelp forest fishes (ongoing since 2000) and data on lobster sizes and fishing effort (initiated in 2012 in response to the designation of the MPAs). Communities in MPAs can take decades to recover their intact size and species structure, so we expect to track continued change within the MPAs throughout SBC IV and beyond. These analyses will be supplemented with data from long-term monitoring programs in the region (e.g., National Park Service, USGS, PISCO) that have collected abundance and size structure data as far back as 1984 inside and outside MPAs of varying age.

Our diver-collected time-series data on species abundance (N = 205 species) and community/ecosystem properties (e.g. biodiversity, food web complexity, NPP, organic matter accumulation) allow us to investigate the broad ecological effects of fishing in kelp forests at our long-term study sites. Logistical constraints, however, limit the area and number of plots that can be sampled by divers, and restrict our ability to capture complex spatial patterns in the recovery of kelp communities following the establishment of MPAs. In particular, gradients in species abundance typically form as fished species move across MPA boundaries, causing communities at the core of protected areas to differ from those near the edge (Halpern et al. 2009). For lobster we have shown that such "spillover" effects dissipate with distance from a MPA (Kay et al. 2012). Because of the rarity of spatially continuous data on marine benthic systems, previous work on this topic has been forced to interpolate across discrete sampling points with consequent limitations on the ability to resolve the spatial details of spillover. We will use our Landsat time series of kelp canopy biomass to investigate the shape of these spillover effects with a resolution that is unprecedented in marine communities. Although giant kelp itself is not harvested, its abundance may be strongly linked to fishing through the cascading effects of fishing on lower trophic levels (Behrens and Lafferty 2004). Thus, expansion of kelp habitat in the vicinity of MPAs following MPA establishment could indicate spatial patterns of change in the rest of the kelp forest community. The large spatial extent and high temporal resolution of the Landsat kelp data combined with diver-collected time-series data of kelp forest biota from SBC and other long-term programs in the region enable us to test how such trophic effects vary among kelp forests throughout California that have different suites of predators.

#### *THEME 1C. Sources and utilization of recycled nitrogen*

Rationale: Our prior results show that urea is present throughout the year and is a major form of dissolved N used by kelp and nearshore phytoplankton in addition to nitrate and regenerated ammonium (Fig. 11a-c). These novel findings likely account for the persistence and sustained growth of giant kelp observed during seasons and years of low nitrate availability (Figs. 2 and 3; **Brzezinski et al. 2013, Reed et al. 2016**). These results, along with our finding that the uptake of urea and ammonium by kelp is decoupled from irradiance while their uptake by phytoplankton is strongly light dependent (Fig. 11d), lead us to hypothesize that the diel light cycle mediates the partitioning of the regenerated N supply between kelp and phytoplankton. The higher surface area to volume ratios of phytoplankton give them an N uptake advantage over kelp during

daylight (Duarte 1995), and we hypothesize that phytoplankton uptake causes recycled N concentrations to be at a minimum during the day. At night N regeneration continues, but lower phytoplankton demand results in higher concentrations of urea and ammonium, enhancing kelp uptake (Fig. 14). This hypothesis is supported by observed diel fluctuations in ammonium near kelp forests with higher concentrations at night (Brzezinski et al. 2013).



**Figure 14.** Hypothesized mechanisms influencing the supply of urea and  $\text{NH}_4^+$  to giant kelp. Sources of recycled N include water column regeneration, sediment efflux, and excretion by reef consumers. White and black arrows depict daytime and nighttime processes, respectively. The larger font for urea and  $\text{NH}_4^+$  in nighttime versus daytime denote higher concentrations at night due to decreased phytoplankton demand. Daytime uptake of regenerated N by phytoplankton minimizes kelp access to these resources during the day while continued kelp uptake at night, when phytoplankton uptake is inhibited by darkness, provides a temporal refuge favoring greater uptake of regenerated N by kelp at night.

**Approach:** To test our hypothesis we will: (1) quantify the kinetics of regenerated N use by giant kelp and phytoplankton in light and dark in the laboratory, (2) quantify rates of N regeneration in the water column and in sediments, and (3) conduct field experiments to compare rates of kelp and phytoplankton urea and ammonium use during the day and night. These studies will be conducted across seasons as we predict N regeneration rates in the water column will vary with the structure of planktonic communities (Mulholland and Lomas 2008) and associated shifts in remineralization processes.

The kinetics of N acquisition by kelp and whole plankton communities will be evaluated across seasons by determining uptake rates of nitrate, ammonium and urea as a function of substrate availability and irradiance using a laboratory incubation system that allows N utilization to be studied under controlled conditions (Smith et al. *submitted*). These data will define the relative affinity of kelp and phytoplankton for urea, ammonium and nitrate and reveal how their N uptake systems are influenced by light and temperature, providing a framework for interpreting utilization rates *in situ* and parameterizing mechanistic models (see below).

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 measures 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 methods will be used to quantify microbial urea and ammonium regeneration (Slawyk et al. 1990).

The hypothesized diel oscillation in recycled N supply to kelp from plankton dynamics on the shelf is modified locally within the forest through excretion of recycled N by reef consumers (Fig. 14). Ongoing work on urea and ammonium regeneration by zooplankton, kelp epiphytes and benthic invertebrates within the forest will allow us to compare the relative magnitude of this local supply of recycled N with that advected into the forest as a result of diel dynamics on the shelf. Similarly, ongoing research on sediment efflux and regeneration rates of urea and ammonium in sediments using flow-through sediment bioreactors will quantify the magnitude of benthic sources.

The partitioning of recycled N between kelp and phytoplankton will be assessed seasonally, concurrent with measurements of water properties (temperature, salinity, flow), water column regeneration of urea and ammonium, and benthic ammonium efflux. We will focus on urea and ammonium use by the kelp canopy in comparison to near-surface phytoplankton. Diel fluctuations in urea and ammonium concentration and rates of urea and ammonium use by kelp and phytoplankton will be assessed at peak daytime irradiance and at night by *in situ* measurement of  $^{15}\text{N}$ -urea,  $^{15}\text{N}$ -ammonium and  $^{15}\text{N}$ -nitrate uptake by blades and the planktonic community enclosed in polyethylene bags as per the methods of Smith et al. (*submitted*). Measurements will be made in the canopy and at depth where shading by the canopy may inhibit phytoplankton uptake during the day.

Numerical modeling will be used to couple the experimental results on N uptake and regeneration to our ongoing time series in order to examine the partitioning of recycled N between kelp and phytoplankton at spatial and temporal scales not amenable to empirical studies. Model construction will use data on the response of kelp and whole phytoplankton communities to nutrients and light in the laboratory to predict *in situ* uptake rates by kelp and phytoplankton from the nutrient concentrations and light levels measured in the field studies. Predicted uptake rates will then be tested against the observed rates of uptake by phytoplankton and kelp during the N-partitioning field experiments. By using seasonally resolved data we will be able to extend the analysis to investigate whether considering water temperature and phytoplankton community composition improve the model's predictive power. The refined model will allow us to use our existing and ongoing time series of phytoplankton and kelp biomass, nutrients, light and ocean physical properties to reconstruct the partitioning of recycled N across years at our long-term study sites.

## ***THEME 2. Dynamic biophysical coupling in kelp forest ecosystems***

Our prior results show that the physical structure of giant kelp alters water flow within the forest (Gaylord et al. 2007, Fram et al. 2008). Kelp's high productivity and metabolism also alter the chemical properties of seawater (Frieder et al. 2012, Kapsenberg and Hofmann 2016, **Rivest et al. 2016**, Kowec et al. 2017) and its organic constituents (**Reed et al. 2015a**). How this biophysical coupling changes with oceanographic conditions and the size and density of the forest to affect the kelp forest community remains largely unknown. Here we propose research aimed at quantifying: (1) the biophysical effects of kelp on water residence time and chemistry (*THEME 2A*), (2) how these effects interact with microbial communities to influence the processing and fate of dissolved organic matter (*THEME 2B*), and (3) the consequences of kelp-induced changes in seawater conditions on physiology, behavior and eco-evolutionary dynamics of kelp forest inhabitants (*THEME 2C*).

### ***THEME 2A. Effects of kelp on physical and chemical fluxes***

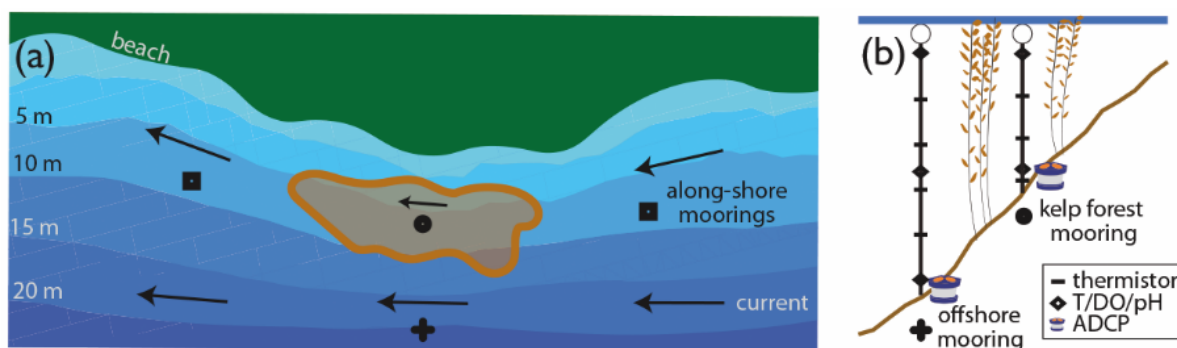
***Rationale:*** As alongshore flows impinge upon a kelp forest, a portion of the flow (10-60%) enters the forest and is slowed substantially, while the remainder is deflected around the forest perimeter in a region of accelerated flow (Gaylord et al. 2007, Rosman et al. 2007). As a result of this deflection only a fraction of material transported to the forest (e.g., plankton, larvae, nutrients) actually enters it. The slower flows within the kelp forest result in increased water residence time. Consequently, there is increased time for chemical reactions, material processing and larval settlement, and only a fraction of material produced within or entering the forest (e.g., organic matter, larvae, recycled nutrients) is exported. A mechanistic understanding of how forest size and kelp density modulate the water entering a forest and its residence time within the forest is essential for quantifying how kelp forests modify their physicochemical environment. However, the full extent to which water column chemistry (e.g., pH, DO,  $p\text{CO}_2$ , nutrients) is altered within a forest or varies with kelp forest area, architecture, season or climatic state (e.g., ENSO) is unknown. Moreover, we do not know how variation in residence time affects the microbial processing and export of kelp production or the capacity of kelp forest organisms to



acclimate and adapt to changes in carbonate chemistry. The long-term context of SBC research provides an opportunity to fill knowledge gaps linking physical, chemical, and biological processes in kelp forests, enabling us to develop a more quantitative and predictive understanding of their dynamics.

**Approach:** We propose to augment our long-term kelp forest sites at Mohawk (MK) and Arroyo Quemado (AQ) with additional physical and chemical sensors to quantify the residence time and carbonate chemistry of water within the kelp forest for the duration of SBC IV. 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 examine how residence time varies with kelp forest architecture and alongshore current speed.

We will estimate residence times through the MK and AQ kelp forests by evaluating the temporal lag of temperature changes inside versus outside the forests. We expect temperature changes (due to advection of temperature gradients) within a forest to be slightly attenuated relative to changes outside the forest because of retention of water in wake structures within the forest. One way to model the retention times would be to assume that mixing will produce a first-order decay process  $dT/dt = -kT$  similar to a continuously stirred tank reactor where  $k$  is a rate coefficient (with units of 1/time). Values of  $k$  will be estimated through regression of observed temperature changes. Other approaches such as cross-correlation analyses of temperature records and measured horizontal currents within the forest will also be used. To that end, moored instrumentation will be deployed to measure along-shore, across-shore and vertical gradients in currents, temperature, pH and DO (Fig. 15). The across-shelf positioning of acoustic Doppler



**Figure 15.** Schematic representation (not to scale) of enhanced instrumentation at Mohawk and Arroyo Quemado reefs. Panel (a) shows moorings inside (circle), outside (plus), and along-coast (squares) relative to the reef. Each mooring consists of a thermistor string, as shown in panel (b). The kelp forest and offshore mooring include pH/DO sensors (shown as diamonds) and bottom-mounted ADCPs.

current profilers (ADCPs) will allow for direct measurements of vertical changes in flows inside and outside the kelp forests (Fig. 15b). As in our earlier work (Gaylord et al. 2007), we will clear kelp near ADCPs positioned inside the forests to ensure their functioning. The top to-bottom thermistor strings moored offshore and in the forests (Fig. 15b) will allow horizontal gradients to be calculated throughout the water column to quantify across-shelf baroclinic transport processes while the array of along-shore thermistor strings (Fig. 15a) will be used in the cross-correlation analysis. The thermistor strings located inside the kelp forest and immediately offshore will be equipped with pH and DO sensors positioned near the surface and bottom to quantify kelp-induced changes in water column chemistry (Fig. 15b), and will be used to inform experiments in *THEME 2C*. Surveys by divers and autonomous aerial and underwater vehicles will be used to document changes in kelp forest area and density.

The high sampling frequency of all sensors will allow us to evaluate changes on short timescales (minutes), while the between-site difference in proximity to Point Conception allows longer time scale analysis of synoptic oceanographic conditions, with AQ typically being colder

due to more frequent exposure to upwelled water than MK. Furthermore, data obtained from the instrument arrays will be augmented periodically with water samples for measurement of  $p\text{CO}_2$ , nutrients and sensor calibration, and glider surveys for synoptic measurements of cross-shelf transport (*THEME 3C*). Data will be collected over the duration of SBC IV and will capture a wide range of oceanographic conditions and kelp forest states that will be used to construct a statistical model for predicting kelp forest residence time as a function of ambient oceanographic conditions (e.g., current velocities, temperature, water column stratification), kelp forest area, and kelp population density and size structure. We will test the generality of this statistical model by periodically collecting similar data at other kelp forest sites.

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

**Rationale:** Giant kelp is a large source of C-rich dissolved organic matter (DOM) that accounts for ~14% of total kelp NPP (**Reed et al. 2015a**). This material is available to microbial communities that play an important role in recycling nutrients and may make refractory organic matter available to the rest of the kelp forest food web. Our analyses show that kelp-derived DOM is enriched in fucose, galactose and mannose, and we found that kelp exudates fueled free-living heterotrophic bacterioplankton growth in laboratory cultures. We also found that, while a substantial portion (~8-30%) of kelp-derived DOC is labile and remineralized within a few days, nearly two-thirds of it resisted degradation over four weeks (Carlson, unpublished data). This time scale suggests DOM export from kelp forests to the surrounding coastal ocean is likely to be significant, which is consistent with our previous finding of a plume of DOC emanating offshore from the Mohawk kelp forest (Halewood et al. 2012). The net effect is that a portion of the DIC taken up to support kelp NPP is released as exported DOC. Quantifying remineralization rates of kelp-derived DOM and its accumulation along a spatial gradient from within the forest to the waters offshore of it will provide an estimate of DOM export and the amount of kelp DOM available to kelp forest food webs via the microbial loop. Kelp blades themselves host a diverse microbiome of epiphytic bacteria (Vollmers et al. 2017), and the microbial community on kelp blades may influence the flux and composition of DOM in kelp forests by remineralizing kelp exudates and by promoting blade senescence. The dynamics of this process will depend not only on kelp as the source of DOM and a reservoir of microbial diversity, but on the effect of the forest as a whole on water residence time.

**Approach:** To evaluate the role of microbial communities in the remineralization and trophic transfer of kelp-derived DOM, we propose to measure temporal and spatial gradients in recycled nitrogen (ammonium and urea, *THEME 1C*), DOM (quality, quantity and bioavailability), and bacteria (biomass, production and community structure) on kelp and in the water column as DOM and recycled N are exported from within to outside of the kelp forest. This work will be done at MK and AQ where we will measure water residence times (*THEME 2A*) and where we have monthly estimates of kelp biomass and kelp DOC production since 2002 (Rassweiler et al. *submitted*). We will characterize the composition of the microbial community monthly in the water column and on the surface of kelp blades at different stages of blade growth and senescence. Microbes living on kelp blades will be collected from biofilms swabbed from the surface of replicate blades, filtered to remove larger host cells, and stored in RNA*later* stabilizing solution for subsequent molecular analysis.

We will determine microbial community composition by extracting prokaryotic DNA and RNA from biofilms and water column samples and sequencing in multiplex using the Illumina HiSeq to generate 16S rRNA gene amplicon sequences, metagenomes and metatranscriptomes (*sensu* Vollmer et al. 2017, Ji et al. 2017). Relationships between microbial community structure and function will be assessed by determining whether key remineralization functions (e.g., carbohydrate-active enzymes, respiration and fermentation pathways, N fixation) identified by transcriptome sequences are linked to microbial community composition. Microbial community composition and functional gene expression will be examined in relation to environmental

factors such as blade age and condition, distance away from the kelp forest, and the residence time of water in the kelp forest.

Bulk DOM, DOM bioavailability, bacterial biomass and production (Halewood et al. 2012) will be measured seasonally within the kelp forest and along a cross-shelf transect at distances of 10 m, 100 m, 500 m and 1000 m from the offshore edge of the kelp forest. DNA and RNA will be collected for 16S rRNA and metagenomic analysis to assess spatial gradients in phylogenetic and functional microbial diversity (Wear et al. 2015). Microbial remineralization experiments (Carlson et al. 2004, Wear et al. 2015) will be conducted seasonally on DOM released directly from kelp (Reed et al. 2015a), 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. These data will be combined with time-series data of kelp standing biomass, kelp DOC production, and water flow velocity and residence time to estimate the export potential of kelp-derived DOM for different environmental conditions.

#### *THEME 2C. Ecological and evolutionary consequences of kelp-induced changes in seawater chemistry*

**Rationale:** Giant kelp forests act as massive photosynthetic bioreactors, and our preliminary data show that kelp alters the pH and DO concentration of seawater in their vicinity (Fig. 12). Such biologically driven changes in seawater properties enable kelp forests to dampen the episodic impacts of low pH associated with upwelling and deoxygenation that co-occurs with high  $p\text{CO}_2$ /low pH water, and allow them to serve as local refuges from deoxygenation and acidification (Frieder et al. 2012, Kowec et al. 2017). 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  $p\text{CO}_2$ /low pH seawater is predicted to intensify under future climate scenarios (Gruber et al. 2015, Chan et al. 2017), which could alter the eco-evolutionary dynamics (*sensu* Lallensack 2018) of kelp forest biota. We propose to evaluate 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,  $p\text{CO}_2$ , pH and  $\text{CaCO}_3$  saturation state ( $\Omega$ ). Research in *THEME 2C* will focus on three areas: (1) an assessment of macroalgal and sessile invertebrate recruitment and community-level calcification inside and outside the kelp forest, (2) an *in situ* test of transgenerational effects and the role of epigenetic mechanisms using purple sea urchins (*Strongylocentrotus purpuratus*), a dominant kelp forest herbivore (Pearse 2006), as a model study organism, and (3) a test of how variable  $p\text{CO}_2$ /pH and DO alter sea urchin feeding and metabolism within and outside of kelp forests.

**Approach:** To assess the role of the kelp forest as a refuge from future acidification and as a buffer to the influences of upwelling, we will first investigate the potential for calcification in the benthic community across a gradient in kelp's influence on seawater as it moves through the forest from outside into the interior. We will determine whether the abundance and growth rate of calcifying macroalgae and sessile invertebrates are related to kelp-induced variability in benthic pH by deploying standardized Calcification Accretion Units (CAUs) designed to quantify relative abundances of recruiting benthic organisms and net community  $\text{CaCO}_3$  deposition rates (Vargas-Angel et al. 2015). CAUs will be deployed within and outside of the MK and AQ kelp forests, co-located with sensors measuring pH and DO (*THEME 2A*). Population and community metrics of CAUs placed within and outside of the forest will be analyzed as a function of chemical (DO,  $p\text{CO}_2$ , pH,  $\Omega$ ), physical (temperature, residence time), and biological (kelp population density and size structure) properties of their surrounding environment using linear mixed models and multivariate analyses.

Second, we will examine the effects of kelp-induced changes in pH/ $p\text{CO}_2$  on transgenerational plasticity in purple sea urchins. We recently discovered that female sea urchins conditioned in the lab under variable conditions of  $p\text{CO}_2$ /pH and temperature typical of SBC kelp forests produced offspring that were more tolerant of high  $p\text{CO}_2$  (Wong et al. 2018). Epigenetic processes acting over the 5-month conditioning period altered phenotypic traits of

progeny such as the transcriptome, suggesting that females “prime” their offspring to encounter future low pH environments. Motivated by these results, we propose to investigate whether this process occurs in nature by testing whether kelp-induced changes in the environment influence the provisioning of offspring by sea urchins via a transgenerational mechanism (Marshall 2008). To do this we will cage adult purple sea urchins within and outside of the kelp forests at MK and AQ from late summer to early winter when adults are performing gametogenesis. Cages will be co-located with pH sensors in order to capture the differential in abiotic exposures during gametogenesis. Caged urchins will be fed weekly to normalize feeding opportunity between the experimental groups. Upon collection from the field, urchins will be spawned and larvae raised in culture (using a North Carolina II design – see Kelly et al 2013) to early pluteus stage under conditions that reflect low and high  $p\text{CO}_2$  conditions in the kelp forest. Measured response variables used to assess the performance of the progeny will include Image J-based morphometrics of eggs and all stages, total protein and lipid, dual assessment of gene expression (using Tag-Seq) and levels of DNA methylation (using methylation-sensitive next-generation sequencing) across the genome in order to explore how maternal transgenerational effects in embryos occur *in situ* in populations inside and outside the kelp forest.

Because urchin grazing is a key driver of kelp forest community structure, we propose to investigate how kelp-induced changes in seawater properties influence the metabolism and feeding of adult sea urchins. Variable conditions of  $p\text{CO}_2$ /pH, DO and temperature exact physiological costs on metazoans that are often expressed as impaired oxygen uptake and reduced aerobic performance (Evans et al. 2013). Like other metazoans, sea urchins are likely to respond to such changes by varying their activity level and feeding rate. We will test this hypothesis in the laboratory using an experimental setup similar to the one we used to examine sea urchin reproduction and feeding (Foster et al. 2015, Wong et al. 2018). Individual mass-specific rates of oxygen uptake and feeding of purple sea urchins will be measured as a function of  $p\text{CO}_2$ /pH, DO and temperature, which will be varied to mimic the diel and seasonal patterns that we measure within and outside the kelp forests at MK and AQ. Experiments will be conducted seasonally to capture potential differences attributable to reproductive condition. Metabolic rate will be measured as the rate of oxygen consumption using intermittent flow-through respirometry for individual urchins acclimated to the various treatments. If the results from these experiments indicate urchin feeding and metabolism are affected by variable conditions of  $p\text{CO}_2$ /pH, DO and temperature that mimic our kelp forest sites, then we will expand these experiments to the MK and AQ kelp forests using an experimental design similar to that used for the transgenerational experiment.

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

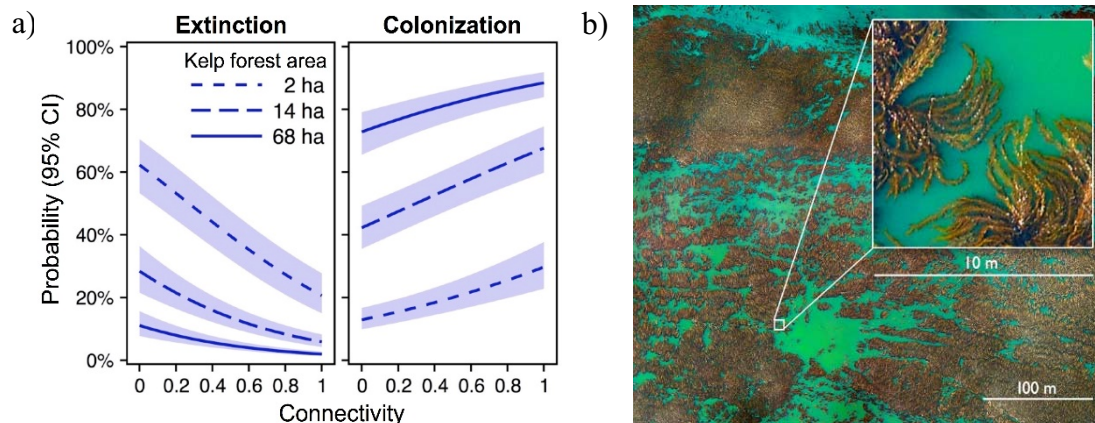
Kelp forests are spatially patchy and are demographically connected to each other via the exchange of individuals and trophically connected to other ecosystems via the movement of organic matter. How demographic connectivity among local kelp populations varies with environmental drivers to affect the stability of the larger kelp metapopulation is poorly understood, as is the degree to which synchronous fluctuations in organic matter delivered to and from kelp forests affect the dynamics of the consumer populations that feed on this material. The research proposed in *THEME 3* will contribute to filling these knowledge gaps.

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

**Rationale:** Kelp forests in California and other regions of the world are largely restricted to shallow coastal reefs whose distribution is patchy. We have shown that the rapid recolonization and recovery of kelp populations following local extinction depend on connectivity with neighboring extant populations via the dispersal of planktonic spores (Reed et al. 1988, 2004, Gaylord et al. 2006, Alberto et. 2011), which in turn allows local kelp populations to function as a metapopulation that promotes regional persistence (Reed et al. 2006, **Castorani et al. 2015**, 2017). However, high rates of dispersal can also synchronize local population dynamics, thereby

reducing metapopulation stability at the regional scale and increasing the risk that all local populations will go extinct simultaneously (Harrison and Quinn 1989, Heino et al. 1997, Palmqvist and Lundberg 1998). We have found that giant kelp population synchrony (i.e., the tendency of local populations to fluctuate together in time) is high at small distances, but decreases rapidly with distance to ~500 m and then more slowly to ~200 km (Cavanaugh et al. 2013). The effect of dispersal in enhancing or diminishing metapopulation persistence is further complicated by spatial heterogeneity in the environment, which can influence population synchrony (Moran 1953) and cause local extinctions (Pulliam 1988, Griffen and Drake 2009). We have quantified the environmental factors that control fluctuations in kelp abundance (e.g., wave disturbances, nutrients, grazing; Reed et al. 2011, Bell et al. 2015), but how environmental drivers *interact* with dispersal to control kelp metapopulations is not well understood.

**Approach:** We propose to test how environmental factors and demographic connectivity via spore dispersal interact to control multiple components of kelp metapopulation dynamics. First, we will examine the combined effects of environmental factors and connectivity on extinction and recolonization dynamics. Our previous work demonstrated that connectivity is more important in reducing extinction risk and enhancing recolonization for small kelp forests than for large ones (Fig. 16a). Hence, we will explore these small-scale patterns in greater detail at our



**Figure 16.** (a) Effects of demographic connectivity and kelp forest size on the probabilities of extinction and colonization of local kelp populations between consecutive six-month periods. (b) Orthomosaic of the Carpinteria kelp forest obtained using a DJI Phantom UAV equipped with a digital camera. Flight altitude was 100 m, which resulted in a pixel resolution of 4.5 cm.

long-term kelp forest sites using monthly unmanned aerial vehicle (UAV) flights to characterize canopy dynamics on sub-meter scales (Fig. 16b). Using this new high spatial resolution time series, we will identify small-scale extinction events and relate local patterns of recolonization to connectivity and environmental factors. If connectivity is the dominant driver of recolonization, then portions of the forest that are most connected to neighboring populations should be the first to recolonize. Alternatively, patterns of recolonization may track gradients in depth, substrate, or other measured environmental factors, or depend on the interaction between connectivity and environmental conditions. This analysis will also enable us to test methodologies we have developed to define local populations of giant kelp based on the relationship between synchrony and distance (Cavanaugh et al. 2014). While this prior work assumed that synchrony-distance relationships were universal for all of southern California, the proposed UAV sampling will enable us to comprehensively assess geographic variation in fine-scale synchrony, and local mechanisms of recolonization.

While connectivity among local populations may have a positive effect on local population persistence, it may also increase spatial synchrony in dynamics among local populations and therefore reduce metapopulation stability. Thus, in SBC IV we will characterize spatial and



temporal variability in patterns of synchrony using the Landsat kelp time series to help us understand how synchrony is related to metapopulation persistence. Spatial variation in population synchrony will be analyzed using neighborhoods of varying size. The strength of population synchrony can also vary in time, and recent developments in wavelet analysis (Walter et al. 2017) will be used to examine the time scales, temporal variability, and secular trends in the strength of synchrony among populations. We will use matrix regression to quantify the drivers of spatial synchrony in kelp biomass dynamics by comparing synchrony in kelp biomass dynamics between local populations to synchrony in environmental variables (e.g., SST, wave height) and connectivity. We will quantify connectivity among all populations by applying our demographic connectivity model (Castorani et al. 2017) to water parcel dispersal estimates from newly created ROMS solutions (R. Simons, pers. comm. 2017).

### *THEME 3B. Trophic connectivity between kelp forests and beaches*

**Rationale:** We have shown that kelp forests export large amounts of biomass to sandy beaches, which contributes substantially to sustaining their diverse food webs (Dugan et al. 2003, 2011, Schooler et al. 2017). Kelp forest NPP is delivered to beaches via two routes: large pulses of whole plants following storms, and a more continuous supply of blades and fronds driven by year-round senescence (Rodriguez et al. 2013, 2016). Beach morphology (e.g., slope, width) influences the retention of wrack on the shore and can decouple wrack delivery from accumulation. We have shown that kelp plants cast ashore are spatially patchy and accumulate near headlands (Fig. 8), but we have yet to quantify the accumulation of smaller blades and fronds, which likely represent a more predictable food source for beach consumers. Consequently, the extent to which the biomass of different wrack forms and the populations of consumers that rely on them are linked to the dynamics of proximate kelp populations is unknown. We propose to: (1) determine the extent to which spatial and temporal variability in beach kelp wrack abundance and form (i.e., plants, fronds, blades) are synchronous with biomass fluctuations in nearby kelp forests, and (2) examine how the timing, amount and form of wrack subsidy influence the community structure and ecosystem function of beaches.

**Approach:** We will evaluate temporal and spatial scales of connectivity between kelp forests and beach ecosystems via the delivery of kelp subsidies to beaches using time series (monthly) and event-based (large storms) measurements of wrack abundance and composition (i.e., entire plants, fronds or blades) and beach morphology (slope, width) at our long-term beach study sites. To evaluate connectivity and synchrony between beaches and kelp forests, patterns of wrack deposition will be compared with canopy biomass fluctuations in proximate kelp forests. Canopy biomass will be estimated from our Landsat kelp data. We have shown that the physiological condition of kelp as measured by its Chl:C ratio is a good predictor of canopy biomass growth, and that Chl:C can be estimated from SST and PAR (Bell 2016, Bell et al. 2017b). Thus, to generate continuous kelp loss data and predict frond losses from the canopy we will model kelp demographics using data on sea surface temperature (SST), PAR, and frond density, initiation and senescence rates collected in our long-term NPP plots. Modeled physiological condition and changes in frond density and initiation will be validated using diver surveys, field measurements of Chl:C, and high-resolution UAV imagery.

Abundance, biomass, and diversity of beach consumers and wildlife (invertebrates, reptiles, birds and mammals) will be measured in surveys with frequency depending on mobility and life history (birds, reptiles, and mammals: monthly-seasonal, invertebrates: biannual). These data will be linked to time-series data of wrack composition and abundance to determine how kelp forest disturbance and senescence cycles influence the structure and function of beach ecosystems. We will use field experiments that manipulate the abundance of kelp wrack to determine how beach consumers and ecosystem functions (e.g., sand respiration, secondary production) respond to future changes in wrack subsidies. Consumption rates and preferences for different wrack types by species of talitrid amphipods, the dominant beach primary consumers,

will be determined in laboratory experiments to evaluate how changing wrack type and species composition influence consumer assemblages and food webs on sandy beaches.

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

**Rationale:** Suspension feeders account for most consumer biomass in SBC kelp forests (Reed et al. 2016), and our prior results indicate that they rely on the allochthonous production of phytoplankton as their primary source of dietary carbon (Page et al. 2008, Miller and Page 2012, Miller et al. 2013, 2015). In SBC II we showed that the high phytoplankton production along the mainland coast in the eastern Santa Barbara Channel is associated with strong, but intermittent cross-shelf gradients in biological and biogeochemical properties (Goodman et al. 2012, Halewood et al. 2012). Results obtained from ocean glider missions during SBC III showed rapid changes in concentrations of phytoplankton and suspended sediments across the shelf (Henderikx Freitas et al. 2016). We also demonstrated that a glider acting as a virtual (i.e., quasi stationary) mooring, when supplemented with ADCP data, can determine cross-shelf fluxes of important water column constituents (Henderikx Freitas 2016 and recent work). We propose new research in SBC IV aimed at measuring the delivery of phytoplankton to kelp forests and the response of sessile reef suspension feeders to this delivery.

**Approach:** We will deploy SBC's Teledyne Webb G2 glider as a virtual mooring to quantify cross-shelf fluxes of suspended particles, chlorophyll and DO concentrations offshore of the MK and AQ kelp forests. The major advantages of the glider are that coincident scalar and velocity measurements (Ellis 2016) and flux determinations are obtained at higher vertical resolution (~1 m) than could be afforded by a fixed mooring, and measurements are made with a single suite of sensors. The resulting cross-shelf flux measurements will quantify the onshore delivery of phytoplankton to kelp forests and reef suspension feeders. These observations will be contextualized at larger spatial scales through analysis of available satellite data for suspended particle concentrations, Chl and SST at both moderate- (~1 km, Henderikx Freitas et al. 2017) and high spatial resolutions (30 m; Landsat 8; Franz et al. 2015). Surface current patterns obtained from the regional HF radar network will identify larger-scale flow patterns producing cross-shore transport of phytoplankton, suspended particles and DO (Bassin et al. 2005).

We will build on our prior work on the trophic importance of phytoplankton subsidies to kelp forest consumers (Page et al. 2008, Miller et al. 2013) by investigating the response of suspension-feeding invertebrates to the supply and taxonomic composition of phytoplankton. The abundance and size of kelp forest invertebrates are monitored seasonally in fixed plots at MK and AQ, where monthly water samples of chemical and biological properties and continuous *in situ* fluorometer records of phytoplankton biomass are collected. These two kelp forests will also serve as the focal sites for our investigations on the biophysical coupling between kelp and material fluxes in and out of kelp forests (see *THEME 2* above). A subset of individuals of common species representing different phyla (bivalves, ascidians, sponges, bryozoans) in these plots will be marked and photographed. Image analysis software developed in collaboration with the Santa Barbara Channel Marine Biodiversity Observation Network (SBC MBON) will be used to measure total abundance and size of marked individuals over time to estimate individual and population growth. Selective feeding by sessile invertebrates in response to variation in phytoplankton community composition and abundance will be measured in short-term seasonal efforts over multiple years. During four-day periods each season, daily water samples for chlorophyll, POC, and phytoplankton community composition will be collected at the surface, midwater and bottom (total water column depth ~10m) within and immediately offshore of the kelp forest, augmented by near-continuous chlorophyll measurements by the *in situ* fluorometers moored in the midwater at the offshore forest edge. Phytoplankton species composition and abundance will be enumerated using an inverted microscope after settling in an Utermohl chamber. On days 2 and 4 of each sampling period, suspension feeders will also be sampled for gut contents to evaluate feeding selectivity as compared with available phytoplankton assemblages in the previous 48 hours. To supplement microscopy, we will analyze water and gut

content samples using metabarcoding techniques by extracting for DNA, sequencing in multiplex using the Illumina MiSeq to generate 18S rRNA gene amplicon sequences, and assigning taxonomy using pipelines developed by the SBC MBON.

## CONCEPTUAL INTEGRATION AND SYNTHESIS

The ecological consequences of the dynamics of a relatively short-lived foundation species in a setting of long-term climate change underlie the conceptual foundation of SBC research. Our proposed research builds substantially upon our prior results to advance a predictive understanding of how disturbance, climate variation and human actions alter the structure and function of kelp forest ecosystems, and to identify the mechanisms that underlie these processes. Kelp forests are connected to each other and to the coastal ocean and intertidal beaches via material exchange (Fig. 13). Predicting the causes and consequences of kelp forest responses to environmental change requires integrated studies of a wide range of physical, chemical and biological processes occurring on the seafloor and in the water column within and outside of the kelp forest and on adjacent beaches. Thus, integration across the research themes of SBC IV is a natural and necessary requirement for advancing a predictive understanding of how kelp forests respond to environmental change now and into the future.

Our research is organized spatially in a dynamic setting of changing climate and oceanography from the scale of a local kelp forest community and the ecological interactions and ecosystem processes occurring within it (*THEMES 1* and *2*) to a much larger landscape of interacting kelp forests and adjacent waters and beaches (*THEME 3*). Synthesis of our findings across different spatial and temporal scales is achieved through statistical, analytical and numerical models that combine long-term ecological and environmental time-series data with relationships, mechanisms and processes obtained from shorter-term, but more intensive studies. We successfully used this approach in SBC III to examine environmental drivers of long-term fluctuations in species biomass (**Reed et al. 2016**) and the ecological interactions that drive them (**Miller et al. 2018**), the role of disturbance, ocean circulation and connectivity in structuring kelp population dynamics (Bell et al. 2015, **Castorani et al. 2015, 2017**), patterns and drivers of macroalgal NPP (Harrer et al. 2013, **Rodriguez et al. 2013**, Rassweiler et al. *submitted*), and material fluxes from land and their dilution in the coastal ocean (Romero et al. 2016, Aguilera and Melack 2018, *submitted*, Feng et al. *submitted*). We will continue using this approach in SBC IV. For example, the results that we obtain from detailed studies of N uptake and regeneration (*THEME 1C*) will be combined with ongoing time series of nutrients, irradiance, and biomass of kelp and phytoplankton in a numerical model that will allow us to examine nutrient partitioning between kelp and phytoplankton over a wide range of kelp forest sizes and oceanographic conditions. This work will draw from the statistical model that we develop for predicting residence time and kelp-induced changes in seawater chemistry (*THEME 2A*), which will enable us to examine these processes over a much longer time frame at kelp forests where we have long-term data. Similarly, results generated from our long-term disturbance experiment (Castorani et al. *submitted*) and shorter-term behavioral studies of predatory lobster will be coupled with our long-term time series of kelp canopy biomass derived from Landsat imagery (which was validated using long-term kelp data collected by divers) to test the generality of our predictions of community response to disturbance (*THEME 1A*) and fishing (*THEME 1B*) across broader spatial and temporal scales.

Integration and synthesis of our research with the broader ecological community occur via our participation in LTER network activities and in non-LTER research networks. SBC researchers are active participants in the current LTER Network Synthesis Working Groups addressing ‘Metacommunity stability’ and ‘Population and community synchrony’, and SBC long-term data figure prominently in both of these working groups. As the only kelp forest site in the LTER Network, the synthesis of our work within the discipline of kelp forest ecology is achieved by collaborations with other projects (see Section 5 - Related Research Projects) and by our participation in the Kelp Ecosystem Ecology Network (KEEN), which was founded by

former SBC postdoc Jarrett Byrnes. KEEN includes 79 members from >20 bioregions and six continents who use standardized sampling and experimental methods (based on those developed by SBC LTER) to create unified open access datasets for assessing past, and predicting future, changes in kelp forests worldwide (e.g., Ling et al. 2015, Krumhansl et al. 2016). The kelp clearing experiment that we propose for *THEME 1A* follows the standard KEEN protocol, and we intend to integrate the results obtained from it into a broader synthesis by KEEN scientists.

## **SECTION 5 – RELATED RESEARCH PROJECTS**

The research platform provided by our project extends well beyond that supported by core LTER funding. During the first five years of our current award, SBC investigators have successfully leveraged SBC data and research infrastructure to attract funding from 14 agencies for 42 new projects totaling nearly \$25 M. The projects described below are particularly relevant to the research that we propose in SBC IV.

The SBC MBON (PI: Miller, Co-PIs: Carlson, Iglesias-Rodriguez, Rassweiler, Reed and Siegel) is jointly funded by NASA, BOEM, and NOAA and is one of three marine prototypes in the US established to integrate new information with existing data to improve understanding of marine health and biodiversity. The SBC MBON collaborates closely with SBC LTER on a number of topics and utilizes many of our long-term datasets in their analyses. For example, we are partnering with the SBC MBON to integrate SBC LTER's kelp forest community data with those collected by other monitoring and research programs to facilitate synthesis efforts on regional patterns and drivers of metapopulation and metacommunity synchrony (*THEMES 1A* and *3A*). The SBC MBON developed a novel automated system for identifying benthic invertebrates from photos using cutting-edge convolutional neural networks (deep learning), which we will use in our proposed studies of selective feeding of phytoplankton by reef suspension feeders (*THEME 3C*). Next-generation genomic sequencing of phytoplankton and microbes of the SB Channel has been developed by the SBC MBON, which is essential for evaluating the phylogenetic and functional diversity of phytoplankton and microbes proposed for *THEMES 2B* and *3C*. Our proposed research on all three of these topics will benefit greatly from collaborations with postdocs supported by the SBC MBON.

A group of SBC investigators (PI: Siegel, Co-PIs: Bell, Cavanaugh, Nidzieko, Miller and Reed) recently received funding from ARPA-E in the Department of Energy to develop a scalable monitoring system for large-scale farming of giant kelp for biofuel production. This collaborative project builds on SBC's long-term investigations of kelp NPP and physiological condition, and seeks to develop methods for remotely monitoring giant kelp biomass, physiological condition, productivity, and macromolecular composition using newly developed sensors mounted to autonomous aerial (UAVs) and unmanned underwater (UUVs) vehicles and automated image analysis software developed in collaboration with the SBC MBON. SBC's long-term study sites will be used for testing the sensors and analysis software developed using ARPA-E funds, and this equipment and technology have been incorporated into the research planned for *THEMES 2A*, *3A* and *3B*.

Ongoing collaborations with additional projects funded by NSF and other agencies that leverage SBC funding provide valuable insight and contextual data on topics related to the research proposed in SBC IV including: coastal oceanography of the SB Channel, population and ecosystem connectivity, dynamics of kelp and beach ecosystems, ocean remote sensing, a site REU for global change biology, and education outreach.

## **SECTION 6 – BROADER IMPACTS: OUTREACH AND EDUCATION**

SBC's Education and Outreach includes programs that range from K-12 education, to teacher professional development, undergraduate and graduate student training, and stakeholder engagement. SBC students, postdoctoral scientists, and investigators are actively engaged in all

facets of our education and outreach efforts. Below we describe the primary activities of each area and plans for future development and implementation.

## **SCHOOLYARD LTER**

Our Schoolyard LTER (SLTER) efforts during SBC IV will focus on two foundational programmatic elements: (1) environmental education programs for middle school students and (2) professional development for ocean science literacy. SBC's SLTER program is co-led by Outreach Coordinator Simon and SBC Researcher Dugan with substantial involvement by SBC students, staff and investigators. The combination of Simon (who serves as Director of UCSB's Marine Outreach) and Dugan (who serves as SBC's Project Coordinator) ensures tight coupling between SBC research and a broad range of outreach activities.

**Environmental Education:** Our annual summer environmental education program employs SBC research themes to engage students in learning about the coastal marine environment. Our program is offered in collaboration with the American Association of University Women's summer *Tech Trek* program, which brings 150 middle school girls to UCSB each summer for a residential math/science program designed to develop interest, excitement and self-confidence in young women entering the eighth grade. Our SLTER program has developed a series of lessons for *Tech Trek* on how press and pulse disturbances impact ocean systems and their influence on kelp forest dynamics. Over the past three years, we have expanded the program's ocean exploration theme in partnership with the Ocean Education Trust and Dr. Bob Ballard. Via *NautilusLive!* we engage students in real-time interactions with scientists while the RV Nautilus is at sea exploring the Santa Barbara Channel using their ROV and seafloor mapping technologies. This effort will inform the development of new educational materials and programming that will be implemented at the REEF, UCSB's educational marine aquarium facility.

**Ocean Science Sequence:** This exciting partnership began in 2014 as an outcome of our previous NSF funded cross-site study on environmental literacy in K-12 education in collaboration with the BES, KBS, and SGS SLTER programs. Our program emphasizes the importance and value of "place" by aligning global phenomena with local impacts as studied through the lens of the SBC LTER. We work with the entire Santa Barbara Unified School District (SBUSD) 6th Grade (12 schools/24 teachers/~750 students / year), as well as middle schools in Ventura County (3 schools/6 teachers/~600 students/ year) using curricula on climate and ocean processes that we developed with the Lawrence Hall of Science to improve literacy about climate change. To do so we work with teachers in professional development workshops and in their classrooms to improve student understanding of key environmental concepts, including ocean circulation, weather, and potential influences on biodiversity. We will continue to use SBC research and field sites as the basis of our activities and focus on ecological concepts highlighted in our newly published SLTER book *The Golden Forest* (Blanchette and Dugan 2017).

As a result of our SLTER program and partnership with SBUSD, the Santa Barbara County Office of Education asked that we aid them in implementation of this teacher development model in all schools in the County. We plan to honor this request in SBC IV by continuing to develop and align our educational materials with the Next Generation Science Standards (NGSS) for middle school science and the guidelines for California's Environmental Education Initiative.

## **UNDERGRADUATE EDUCATION**

SBC's undergraduate education program includes research and science education experiences through mentoring by graduate students, postdocs, research staff and investigators. Undergraduate students who participate in our interdisciplinary research program are exposed to a variety of hands-on research and training in kelp forest and beach ecology, coastal oceanography, watershed science, and data management and analysis. Students from this pool and elsewhere are selected to participate in our Research Experience for Undergraduates (REU)



program and in several other mentorship programs sponsored by the University of California. REU students work closely with SBC researchers on a wide range of topics and most choose to pursue an advanced degree following their undergraduate education.

We will continue to provide opportunities for undergraduate students to engage in our SLTER programs through docent and internship positions. Our training program provides a foundation of pedagogical and content knowledge that allows student docents to effectively communicate and teach marine science generally and SBC research in particular. This foundation has been instrumental in motivating several of our docents to pursue careers in both formal and informal science education. In SBC IV we will focus on enhanced training in metacognition by engaging undergraduate students in reflective exercises for evaluating their own learning styles and depth of content knowledge through their experience in communicating science to K-12 students.

### **POST GRADUATE EDUCATION**

Graduate students and postdoctoral scientists from a range of disciplines will be actively involved in all aspects of the research proposed for SBC IV. Our graduate student training is coordinated with several graduate programs at UCSB, most notably the Interdepartmental Graduate Program in Marine Science, the Bren School of Environmental Science and Management, and the Departments of Ecology, Evolution and Marine Biology, Geography and Earth Science. We will continue to work with these programs to promote opportunities for interdisciplinary graduate research that examines the response of coastal ecosystems to natural and human-induced alterations in the environment. This will enable valuable cross-training on environmental issues pertaining to coastal ecosystems, provide a common language for communicating scientific information on these issues, and contribute to the creation of a diverse scientific community of students and postdoctoral scientists that fosters respect and appreciation for other disciplines. SBC investigators will continue to teach an annual 10-week course for graduate and advanced undergraduate students that focuses on major research themes of the SBC LTER. Broader exposure to LTER science is achieved by a student-organized California LTER Graduate Student Symposium held annually with CCE and MCR. This well-attended symposium has been popular with our graduate students as an informal venue to share their work and ideas with students from other LTER sites. Additionally, SBC consistently supplements LTER Network funding to enable all of its graduate students to participate in LTER Network All Scientists Meetings, which further enhances their training, education and career development.

### **APPLICATION TO POLICY AND MANAGEMENT**

The research proposed for SBC IV has direct applications to the policy and management of several topical issues for coastal regions. For example, SBC research on marine protected areas is providing long-term perspectives pertaining to the effects of fishing and marine conservation on kelp forest ecosystems that will inform future management decisions, while our long-term data on the abundances of invasive species are being used to inform federal agencies (NOAA, BOEM) about the factors affecting the extent and ecological consequences of their spread. In addition, results from SBC research on kelp forests continue to be incorporated into the evaluation of a state-mandated mitigation project aimed at compensating for the loss of marine resources caused by the operation of a coastal nuclear power plant. Similarly, SBC's research and long-term data on sandy beach ecosystems are routinely used to inform local and state coastal management practices such as coastal armoring, beach grooming and beach sand replenishment. These data formed a major component of a climate change vulnerability assessment of the region's coastal ecosystems that SBC investigators prepared in collaboration with local land use planners for the cities of Santa Barbara County (Myers et al. 2017).

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(The 10 most significant publications from SBC III that motivate the research proposed for SBC IV are in **bold**)

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## **FACILITIES, EQUIPMENT & OTHER RESOURCES**

### **FACILITIES**

#### ***Laboratory***

SBC Principal and Associate Investigators have laboratory space in the Marine Science Institute (MSI), Department of Ecology, Evolution and Marine Biology (DEEMB), Department of Geography, Department of Geology, Earth Resources Institute, Environmental Studies Program and the Bren School of Environmental Science and Management at UCSB that is sufficient for the project's needs. In addition, over 900 ft<sup>2</sup> of laboratory space in UCSB's Marine Science Building has been assigned specifically for SBC LTER use. We also have access to common laboratory space in the Marine Science Institute (MSI) Building, Bren Hall and in DEEMB's marine biotechnology building, including environmentally controlled temperature rooms and rooms supplied with running seawater. MSI's Analytical Laboratory is a professionally managed shared-use instrumentation and chemical analysis facility that is well equipped to perform the chemical analyses anticipated for this project. Major capabilities of the Analytical Lab include elemental analysis of inorganic and organic substances, stable isotope ratio determination of biological materials, and automated determination of nutrients in natural waters.

#### ***Clinical***

Not required for this project

#### ***Animal***

Not required for this project

#### ***Computer***

Each of the investigators in this project maintains computing capabilities commensurate with their specific research activities. Data management for the project has the advantage of utilizing the computing capabilities of the Marine Science Institute (MSI). MSI has a 1000 Mb/s connection to the UCSB campus backbone, which provides shared access to a 622 Mb/s CALREN-2 connection providing access to the Internet. MSI supports the research servers, which are all presently running CentOS release 6.9 (64-bit). The main data server provides network file sharing (Samba and NFS) and runs Git for revision control systems, as well as SAS, Matlab, GSLIB, Python, R and PERL for scientific applications. Currently, we have 11.5 TB of storage (expandable) available. The second server runs the Apache web server, and the Tomcat java servlet engine and a third is the primary database server, running PostgreSQL, MySQL and the personnel database (LDAP). MSI's server room is cooled by dual chillers that are connected to the campus chilled water loop. Back-up for electrical outages is provided by an emergency generator for the building. Distributed server backups (via Amanda) are coordinated with MSI. Backup and archiving occur at several levels and time frames. Daily backups, managed with BackupPC software, occur on site with independent hardware, with weekly full backups of all systems archived to tape and to network connected infrastructure located off site.

The Earth Research Institute (ERI) provides computational support for the processing of satellite imagery and ROMS ocean circulation modeling. It consists of a network of more than 100 UNIX servers, workstations, and clusters. Two Linux clusters are available for SBC research. One is used for conducting ROMS simulations and offline particle tracking and has 16 Quad-Core 2.6 GHz AMD CPU's with 64 Gb of RAM and 7.3 Tb of disk. Another cluster is used for high performance MATLAB post-processing and analysis of satellite imagery, and has 16 Quad-Core 2 GHz AMD 8350 CPU's, with 16 GB of RAM and 5.5 TB of disk. The size of the ROMS outputs are very large (often 2-3 TB per three-month simulation) and we have a 42 TB data server (with backup) for SBC ROMS output and satellite data sets that is integrated with the Linux clusters at ERI. We also have access to a 1008 CPU MPI cluster for campus researchers that was funded on a NSF Major Research Infrastructure grant.

SBC LTER IV is proposing work involving imagery of the seafloor and kelp canopies. To manage and analyze this imagery we are collaborating with the UCSB Center for Bio-Image Informatics, led by B.S. Manjunath. Manjunath is leading LIMPID (Large-scale Image Processing Infrastructure Development), a new project supported by the NSF Office of Advanced Cyberinfrastructure. Encompassing databases, image analysis and scientific disciplines including marine science, LIMPID is based on BisQue, an established cloud-based image informatics platform that makes it easy to share, distribute and collaborate with large image datasets. BisQue is now a core service of CyVerse and provides a flexible metadata model based on linked semi-structured document resources. A core feature is that resources retain their provenance; when data or code are created or modified, it is marked by the analysis or session of the action.

### ***Office***

All SBC Principal and Associate Investigators have adequate office space to meet their needs and those of the postdocs and graduate students associated with this project. All offices are equipped with phone and internet services.

### ***Other***

Special facilities are not required at our field sites, which are all located close to campus.

## **MAJOR EQUIPMENT**

Most chemical analyses will be done using instrumentation in MSI's Analytical Laboratory. Major equipment items in the MSI Analytical Lab include: a microprocessor-controlled gas chromatograph (GC) with various detectors, including flame ionization and photo-ionization; two automated organic elemental analyzers for CHN analyses; an isotope ratio mass spectrometer interfaced with a CHN sample introduction system; and an automated 5-channel wet-chemical analyzer (FIA) for nutrients.

Equipment purchased with previous LTER funding include: an ISUS V3 chemical free nitrate analyzer, 6 Wetlabs Eco-DFLSB fluorometers, 2 pumped in situ fluorometers, 1 Wetlabs Eco-triplet rhodamine, chlorophyll and CDOM fluorometer, 6 Wetlabs ECO-VSFSB volume scattering function meters and 6 Seabird Electronics SBE37SM CTD's, 40 Brancker TR-1050 self-contained temperature loggers, 6 Optode self-contained oxygen sensors, 5 Honeywell Durafet pH sensors with temperature probes, 1 high Resolution TCO<sub>2</sub>/ pCO<sub>2</sub> system, 8 ISCO automated stream samplers, a LiCOR CO<sub>2</sub> analyzer and soil respiration chamber for measuring metabolism in beach sands, 1 Teledyne Webb Slocum Autonomous Glider system, 5 acoustic Doppler current profilers, one 22 ft. research boat and trailer equipped for SCUBA and water sampling operations, one mini-rosette with CTD and winch for nearshore oceanographic sampling, a Ford Expedition and a Ford 350 pickup truck equipped for towing the 22 ft. research boat, and one Toyota pick-up truck for travel to local field sites.

The laboratories of several investigators are equipped with additional instrumentation that will be used to do the proposed work including: a Turner 10AU fluorometer for phytoplankton chlorophyll determination (Brzezinski), and 2 SeapHOx Ocean CT(D)-pH-DO sensors (Hofmann). Additional oceanographic instrumentation available to this project include two acoustic Doppler velocimeters, 18 acoustic Doppler current profilers (Washburn and MacIntyre), 12 high-frequency radar units (Coastal Ocean Dynamics Applications Radars, CODAR) for measuring surface currents (Washburn) and two DJI Phantom UAVs equipped with digital cameras (Cavanaugh and Bell). In partnership with MCR LTER, SBC investigators (Carlson, Iglesias-Rodriguez, Hofmann) also maintain instrument systems for precise measurement of seawater carbonate system parameters including total alkalinity, TCO<sub>2</sub>, and DO for time series measurements and field instrument calibration. These instruments include a computer-controlled Automated Total Alkalinity Titration System (fabricated by Dr. Andrew Dickson's Laboratory at UCSD), a high precision, high speed, low volume TCO<sub>2</sub> analyzer

system (Marianda Inc.'s Automated Infra-Red Inorganic Carbon Analyzer), a high precision Brinkman Dossimat O<sub>2</sub> Winkler Titration system, and a muffle furnace for treating HgCl<sub>2</sub> exposed bottles.

## **OTHER RESOURCES**

UCSB has the facilities and trained technical staff typical of large research universities. Resources that will be of most value to this project include: machine, electronic, and carpentry shops for constructing apparatuses for the laboratory and field, a large capacity seawater system, a fleet of small vessels that are maintained by a certified boat mechanic, and a research diving program that includes ~ 130 scuba tanks, and a compressor and technician to fill them. Use of university equipment and consultant and technician services are available to us, generally on a recharge basis.

UCSB is highly supportive of the SBC LTER and provides additional resources (e.g., support for graduate students, analytical costs, transportation services) when available.

## SUPPLEMENT 4. POSTDOCTORAL MENTORING PLAN

A central educational activity of the SBC LTER's Senior Personnel is the mentoring of Postdoctoral Scholars, providing them with strong interdisciplinary skills in marine science and ecology. Given today's demands on postdocs as they enter the job market, it is ever more important to prepare them to do team-based research. Most newly minted PhDs have just finished an independent research project (their dissertation), and must accustom themselves to working in a collaborative setting. If the PhD is about learning to conduct research, the postdoctoral phase is the time to learn how to direct the research of others, to hone leadership skills, and to recognize that collaboration is an important key to success.

Given this rapid demand for a new set of academic skills, the SBC LTER provides an ideal setting in which to train postdoctoral scientists. Mentoring these early career scientists in the next step of their careers is a core objective of our project. Broadly, our mentoring philosophy for postdocs is to encourage the development of strong interdisciplinary skills, to provide them with ready access to knowledge to build their disciplinary backgrounds, and to provide a stimulating intellectual atmosphere amidst the practical experience that is needed for a successful transition to academic or other professional careers.

More specifically, our Postdoctoral Mentoring Plan has four objectives: (1) development of a research project and enhanced professional skills, (2) training in interdisciplinary marine and environmental science, (3) skill building in a collaborative, team-based research program, and (4) hands-on mentoring of junior scientists, including the development of an effective communication style and the awareness of diversity including experience in training undergraduate students who are from groups that are often under-represented within STEM.

- (1) *Professional skills*: Objective 1 will be achieved by active mentoring through the research process of designing, executing, analyzing and publishing results in peer-reviewed literature and presentations at scientific meetings. Training in grant proposal writing is also an active area of postdoctoral mentoring.
- (2) *Interdisciplinarity*: SBC post docs typically work on inter-disciplinary research projects with multiple investigators that have different areas of expertise. Thus, Objective 2 will be realized by fostering interactions with a diverse group of scientists who bring a range of skills and perspectives to bear on the questions posed by our research program.
- (3) *Team-based research*: Immersion in collaborative team-based research will be accomplished through the development of a close working association with SBC investigators and their collaborators. This association includes individual discussions and small group meetings as well as participation in broader synthetic activities and collaborations at larger conferences (e.g., LTER synthesis working groups, LTER All Scientists Meetings, ESA and the Ocean Sciences meeting) all of which increase opportunities for intellectual exchange, growth and networking.
- (4) *Mentoring*: SBC postdocs will be introduced to effective mentoring skills in a workshop led by co-PI Hofmann, who has extensive experience in this area. The workshop will include activities such as participating in the UCSB chapter of the Society for Advancement of Chicanos/Hispanics and Native Americans in Science annual outreach event, and mentoring undergraduate and graduate students at UCSB, a Hispanic Serving Institution within the UC system.

In addition to the specific training associated with SBC research, Postdoctoral Scholars will be mentored through the job application and interview process by SBC investigators. This includes guidance in developing a competitive application that includes statements of research and teaching, preparation for a compelling job seminar, and advice in negotiations. In addition, UCSB's Graduate Division offers additional resources for training of postdoctoral scholars, including affiliate membership in the National Postdoctoral Society, access to resources from the UC Council of Postdoctoral Scholars, and online research training courses offered through UCSB's contract with the Collaborative Institutional Training Initiative (CITI).



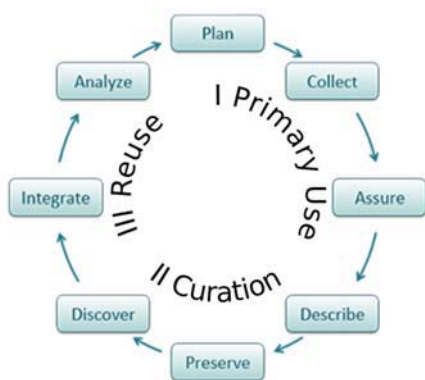
## SUPPLEMENT 2. DATA MANAGEMENT PLAN

The principal mission of SBC LTER's Information Management System (SBC IMS) is to ensure the availability of the Project's data and other products to a broad research community. Our primary objective is to facilitate diverse research and outreach goals by focusing on ease of data access, organization, integrity, and long-term preservation over the complete data life cycle. Since its inception, SBC has used cross-platform Internet Standards that are compatible with other LTER Network needs to simplify our data presentation and delivery. Importantly, the SBC IMS meets all data guidelines and requirements established by NSF and the LTER Network. Moreover, its design enables SBC to adapt to changes in these guidelines and requirements that occur as emerging technologies and information needs continue to evolve. As the project matures during SBC IV, we will continue to streamline the SBC IMS and converge on standard practices that facilitate and improve data integration within and beyond the LTER Network.

## POLICIES

SBC has adopted the LTER General Use Agreement and the Network's "Type I-II" designations for its data. Nearly all 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 sooner. We also employ a "Type 0 (zero)" designation for data acquired from outside parties that are typically already in the public domain and occasionally republished (e.g., USGS stream discharge, CDIP wave data). Our practice for the few Type II datasets we manage (e.g., from a student thesis before completion) is to describe data in our public catalog, but to set distribution information for the data tables to "offline", and instruct interested parties to contact us. After a short embargo period, these Type II datasets become "Type I". To ensure that researchers contribute their data to the SBC IMS, all participation in SBC-funded research is contingent upon data being published in a timely manner. All datasets include a statement of intellectual rights (SIR). In 2017, in accordance with the practices adopted by the LTER Network, SBC revised its SIR to a CC-BY 4.0 - Attribution, a license that allows data users to adapt, transform or redistribute data for any purpose, if appropriate credit to the project is given. For data that SBC LTER does not own (e.g., Type 0, above), original licensing applies.

## OPERATION, INFRASTRUCTURE AND RESOURCES



**Figure S2.1.** DataONE data life cycle, adapted to show three major phases addressed by the SBC IMS. Credit: DataONE project.

The SBC IMS is integrated with all stages of the data life cycle to promote reuse (Fig. S2.1). The basic three-phase data life-cycle begins with the primary user (Phase I), and involves data planning and collection, followed by quality control and assurance. In the second phase (curation) data are described and preserved for further discovery, where they can be reused (Phase III) and integrated into synthetic analyses, which typically restarts the cycle.

Different aspects of the SBC IMS are engaged during different phases of the data life cycle (Table S2.1). Phase I steps (planning > collection > assurance) are essential for primary research use, and aspects of the IMS that are important in this phase are local servers and user accounts for the project's researchers and students, plus mechanisms for

maintaining their work in progress. Curation steps (Phase II) that describe and preserve formal datasets are critical elements of the data cycle that require considerable expertise in metadata construction and informatics combined with close communication with project scientists. SBC LTER recognizes that the value of long-term data extends beyond its use in any individual

research project, and takes particular care to describe data for easy discovery, integration and further use in Phase III (Reuse).

**Table S2.1.** Description of three major Phases of the data management lifecycle (Fig. S2.1), showing how the requirements of each phase are managed within the SBC LTER. \*IMS tools are cumulative; e.g., Phase III also employs tools used for Phases I & II.

	<b>I - Primary Use</b>	<b>II - Curation</b>	<b>III - Reuse</b>
Life cycle Steps	Plan > Collect > Assure	Describe > Preserve	Discover > Integrate > Analyze
Facilitates	Local, site-based research	Data archive	Secondary use and further synthesis
Requires	User accounts for researchers; file and processing servers; sharing mechanisms for researchers; backup	Metadata database and code base for export; understanding of best practices and QC; repository access	Enhanced, consistent metadata; time-series datasets constructed with reuse in mind; customized project data catalog
Supplied by	MSI/UCSB, with IMS team as representative or mediator, informed by researcher needs	IMS team, in consultation with project scientists; EDI repository	IMS team, in consultation with project scientists and the broader data management community
Tools used by SBC IMS*	LINUX, SAN, SMB, ext4, rsync, LDAP	PostgreSQL, EML, SVN, GitHub, Metabase, Perl, R, EDI tools for data package QC	Controlled vocabularies; term dictionaries; web technologies (e.g., XML, XSLT, JavaScript, CSS)

**Phase I – Primary Use** (Plan > Collect > Assure): SBC leverages the UCSB Marine Science Institute (MSI) and the UCSB campus network infrastructure for server systems, and IMS staff have the knowledge and system privileges to effectively facilitate SBC research activities. Our server systems have been stable for many years, which enables scientists to remain familiar with the file system structure, and an orientation is provided for new users. Every research group has dedicated directories for “working” and “final” data products that are accessible after login. Data are placed immediately into the “working” directories. All SBC personnel are provided with login access that allows them to view any data file in the working and final directories, but write-access is limited to those responsible for data collection and maintenance. Off-site backups (in another building on the UCSB campus) provide for disaster recovery, and individual files can be restored as needed from daily on-site backups.

The primary responsibility for data quality lies with the individual research groups and laboratories, as it is essential for the most basic use. The primary information manager provides oversight so that flag-fields are internally consistent and can be accommodated in metadata. Only fully processed data that have undergone appropriate quality control and quality assurance are placed in the “final” data areas. The information manager also advises on conventions for handling sampling sites and taxonomy, and guidance for file organization.

**Phase II – Curation** (Describe > Archive): SBC IMS is co-located with the Moorea Coral Reef LTER (MCR LTER), and the Santa Barbara Channel Marine Biodiversity Observation Network (SBC MBON). The IMS of the three projects are closely linked and share many tools,

and in some cases personnel, which provides coverage during absences. The three projects have jointly planned all IMS improvements since 2014 (since 2009 with MCR LTER).

The variety of SBC's data and processing pathways requires multiple strategies for building formal data packages (i.e., data plus metadata). All datasets have metadata stored in our relational database, Metabase2, adapted in 2011 from another LTER site (Georgia Coastal Ecosystems). About half our data packages are generated by data logging instruments whose repetitive formats are created using scripts that modify standardized EML templates. Scripts are produced in the same languages as the data owners use for processing, which accommodates the different skill sets of SBC's scientists and allows them to assist IMS staff in the publication of their datasets.

Nearly all SBC data are published as ASCII tables, which are most appropriate for long-term archival purposes. Other formats we regularly handle are KML (e.g., for site descriptions and reference datasets like perimeters of recent fires), and native binary formats such as GIS or KML for spatial analysis products from recent work in fire-affected watersheds, and netCDF for gridded kelp biomass from Landsat.

Completed data packages are archived in the repository of the Environmental Data Initiative (EDI), which was founded in 2016, as a re-visioning of the original LTER Network Information System (NIS) to serve the data archiving needs of a larger community of ecosystem-based researchers. SBC LTER's transition from the LTER NIS to EDI has been seamless, largely due to our close association with M. O'Brien, a Co-PI on the EDI project. O'Brien served as SBC's information manager for 12 years, is currently housed in SBC IMS space at UCSB and continues to mentor SBC's IMS staff. Data contributions to EDI are mirrored at DataONE.

**Phase III – Re-use** (Discover > Integrate > Analyze): Effective discovery and reuse depends on data that are not simply 'available,' but also that can be understood. The SBC IMS addresses this need in a variety of ways. For ongoing time-series, SBC's practice is to compile data into a single multi-year product, which enhances the convenience for data users interested in assessing long-term patterns. Changes in methodology are unavoidable in the case of some long-term time series. SBC records any such changes to methods protocol documents and dataset metadata, and formats are standardized. Many data repositories do not routinely support the concept of a dataset that is a "time-series" for which revisions are expected. However, support for revisions is fundamental to the EDI system, an essential feature for LTER sites.

Designing datasets for ongoing collections or new installations requires considerable planning and discussion. For example, SBC received funds for instrumentation to examine pH dynamics in near shore waters, and formal data collection with SeaFET sensors began in 2012. Data processing and dataset design were integrated with the SBC IMS from the start. Our personnel assembled a working group of scientists and data managers to advise on high-level considerations such as vocabularies, and guidelines for measurement descriptions, using both LTER-centric venues (e.g., All Scientist Meeting), and other similar projects (e.g., European Project on Ocean Acidification, EPOCA). We developed three design patterns (i.e., templates) for: (a) passive *in situ* instrument observations, (b) short-term process studies, and (c) laboratory-processed benchmark seawater samples. This data processing and management scheme and the data template for this new instrument are described in detail in **Rivest et al. 2016** (with time series data packages archived with EDI). We are using a similar process for other instruments recently obtained for other carbonate system constituents.

The SBC website has many customized features to assist in discovery of SBC research, sampling and data. We use the LTER research project schema to describe our major research themes, and to cross reference thematic papers and datasets. Our local data catalog is based on EML datasets (identical to those in EDI), with an additional customized layer to group data packages into collections. Our website will undergo significant upgrades during SBC IV, to maintain security and accessibility, to streamline the data catalog using the PASTA API (see **Milestones and Deliverables**), and to highlight new data collections during SBC IV. SBC

continues to be closely involved in community efforts to enhance consistent data quality and presentation. With the release of EML 2.2 during SBC IV, we expect to be able to annotate SBC measurement descriptions with formal descriptions from community dictionaries such as the Darwin Core Vocabulary, or ontologies, which will streamline discovery and improve understanding. SBC plans to take advantage of these improvements as they arise (see *Milestones and Deliverables*).

**Personnel and Governance:** Margaret O'Brien led the IMS at SBC LTER for 12 years. Since taking on responsibilities with EDI in 2016, she has been transitioning many tasks to Li Kui (hired in 2016) who is currently responsible for about 80% of Phase II tasks. This transition strategy has helped to more fully integrate data management with other project activities, and will be completed within year 1 of SBC IV (see *Deliverables and Milestones*, below). The process of defining data manager roles and skill sets is germane to other LTER sites, and the templates SBC LTER has developed for its own planning have been shared with other LTER sites.

SBC's IMS is documented at several levels: (1) as a general, internal Information Management Plan which is updated annually, (2) as an IM Guide (Wiki), whose intended audience is the IM staff and assistants, and (3) as schematics, guides and other supporting documentation of individual system components. The IM Plan is available on the Information Management page of the SBC website; the IM Guide and project documentation are housed with code and schemas, as appropriate for their specific uses.

Communication between SBC scientists and Information Management is fostered by the SBC IMS Advisory Committee (IMSAC), which includes Kui, the PI and four Co-PIs. The IMSAC establishes priorities for IMS activities and increases the scope of researcher involvement.

### ***DATASETS PLANNED FOR SBC IV***

SBC LTER has generated approximately 200 data packages since its inception in April 2000, with approximately half being long-term time-series. All of SBC's data packages (listed in Supplement 1- SBC Data Inventory) have extensive EML metadata and can be accessed from multiple sources (e.g., EDI, DataONE and BCO-DMO). Several datasets routinely collected during SBC I-III will be discontinued, most notably the 16-year time-series of stream discharge and chemistry, which will be archived for future use in hydrological models of runoff to calculate nutrient and TSS loadings to coastal waters (see Project Description). Hence, we anticipate that 40-50 existing data packages for ongoing time series will continue to be updated in SBC IV as per current practices.

During SBC IV, existing time-series will be redesigned or expanded to accommodate new project initiatives. For example, the new data collected as part of *THEME 1A* (Kelp Persistence and Community Structure) will be structured similar to those of the long-term data for the kelp forest community, and the expanded sensor data targeted for Arroyo Quemado and Mohawk Reefs (*THEME 2*, Biophysical Coupling) will be similarly structured after our long-term CTD, ADCP and SeaFET data. Data packages for some short-term process studies will be modeled after existing packages (e.g., the CTDs collected by glider for *THEME 3C* are structurally similar to profiled and moored CTDs). Image data collected by drones (*THEME 3A, 3B*) will be processed and structured similar to the kelp biomass data derived from Landsat. New data packages will be required for several studies, most notably nitrogen kinetics (*THEME 1C*), species abundance measured by photographic imagery (*THEME 3C*), and molecular data (*THEMES 2B, 2C*). In these cases, we will engage the larger community, including LTER sites and ecosystem data managers for examples, formats, guidelines and lessons learned. We anticipate that 10-20 new data packages will be created for targeted SBC IV studies.

### ***Milestones and Deliverables***

IMS improvements planned for SBC IV will focus on streamlining tasks and convergence on standard practices that facilitate and improve data integration (Table S2.2). Deliverables are presented generally in the order they will be addressed, although exact timing will depend on resources, and will be integrated with overall project planning.

**Table S2.2.** Major IMS improvements planned for SBC IV.

Deliverable	Description
SBC LTER Website update	Modernize security, accessibility, languages and design. Eliminate duplication of metadata in data catalog by using EDI web services. Web content to be supplied by Metabase2, instead of legacy systems.
Matlab-based data package curation is transitioned from IMS staff to laboratories	Currently, research staff processing oceanographic sensor data using Matlab, with the publication of these data packages performed by IMS staff using Matlab scripts. We will transition the data package construction step from the IMS personnel to research staff.
Publications database update	Streamline and simplify for non-IMS personnel and for anticipated changes to NSF reporting practices.
Dataset measurement metadata linked to formal vocabularies	EML 2.1 (current version) allows only ad hoc metadata, whereas EML 2.2 will allow data to be annotated with external vocabulary terms. Adoption of external vocabularies for datasets will be gradual, starting midway through SBC IV. Some concomitant adaptation of Metabase will also occur to support this enhanced metadata.



## **SUPPLEMENT 3. PROJECT MANAGEMENT PLAN**

### **GOVERNANCE**

SBC is governed by an Executive Committee chaired by the lead PI (Reed) and includes the four Co-PIs (Hoffman, Miller, Siegel, Stier) and three Associate Investigators. The PI and Co-PIs will serve on the Executive Committee for the entire six-year funding period. The Associate Investigators on the Executive Committee are rotating positions filled by individuals with lead roles in 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, administrative policies and staffing are discussed at scheduled meetings that are open to all project participants. Decisions relating to funding and personnel are made by the Executive Committee and are usually by consensus. The Lead PI chairs these meetings and sets their agendas with consultation 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 effective in instilling a culture of shared ownership, enthusiasm and pride for the project among its participants.

### **PROJECT MANAGEMENT**

The SBC LTER is administered by the Marine Science Institute (MSI) at UC Santa Barbara. Day-to-day management of the project is overseen by the PI with assistance from a part-time Project Coordinator. Management actions include: (1) coordinating the activities of different research groups to maximize efficiency and integration, (2) overseeing information management and education/outreach and their integration with research (3) working with MSI staff on the project's administrative services (e.g., budgets, personnel, procurement, travel) to maximize efficiency and ensure compliance with campus policies, (4) scheduling and planning project meetings and events, (5) preparation of project-related reports and proposals, (6) responding to inquiries and requests from the LTER Network and non-LTER entities, and (7) serving as the site representative at meetings and functions on and off campus.

Two full time and four part-time research staff are employed to maintain our long-term measurements and experiments. Graduate and undergraduate students employed on the project assist in these activities. An Information Manager (Kui) and an Education/Outreach Coordinator (Simon) round out the project staff. Coordination between research and information management is facilitated by an Information Management System Advisory Committee (IMSAC) consisting of the Information Manager (Kui), the PI and Co-PIs. The primary objective of IMSAC is to facilitate SBC's collaborative and synthetic research efforts and improve the quality of resultant synthetic products and datasets.

As in previous SBC awards, the allocation of funds will be structured around the primary research themes (Section 4- Proposed Research) with an investigator assigned to lead each sub-theme (Table S3.1). A separate allotment of funds will be set aside to cover the costs of project management, core long-term measurements, IM, REU internships and Outreach. The coordination of research and the exchange of information and ideas among project participants are facilitated because 22 of the 25 investigators on our proposal are located at UCSB and one other is within driving distance (see Biographical Sketches). Informal and scheduled meetings involving investigators, postdoctoral scientists, students and staff to discuss project-related business occur on a daily basis. The sharing of data, documents, and other project related products is made easy through our central data server to which all participants (UCSB and non-UCSB) have access (see Supplement 2 - Data Management Plan). We hold an annual meeting for all SBC participants and other interested parties to insure coordination across the SBC program, enhance interdisciplinary discussions and plan for upcoming events such as midterm reviews, renewal proposals and opportunities for research and synthesis activities, both within and outside

the LTER Network. This event is well attended and serves as an excellent venue for information exchange and team building.

### **DIVERSIFICATION AND INTEGRATION WITH NON-LTER SCIENTISTS**

The diverse nature of SBC's study habitats and research themes has attracted a diverse group of scientists (in terms of area of expertise and career level) to work at our site. SBC does not have a formal agreement with a federal agency or non-governmental organization that facilitates collaborations and provides research support. Instead, we rely upon the long-term nature of 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 nearly \$25 million from 14 different funding sources for 42 collaborative research projects during the first five years of SBC III.

Integration of non-LTER scientists into SBC research is achieved by developing consortia with non-LTER investigators and organizations to examine issues relevant to consortia members. For example, we are collaborating with the Ocean Margin Ecosystem Group for Acidification Studies (OMEGAS), the California Current Acidification Network (C-CAN), and the Southern California Coastal Ocean Observing System (SCCOOS) to measure parameters of the carbonate system of the coastal ocean. This is part of an effort to understand the consequences of ocean acidification for near-shore marine communities of the California Current Large Marine Ecosystem. Another example of such integration with non-LTER entities is the recent consortium that we formed with scientists from the Bureau of Ocean Energy Management, US Geological Survey, National Park Service, NASA and NOAA to combine and synthesize long-term datasets from multiple sources to develop an improved understanding of regional dynamics of kelp forest ecosystems and the environmental factors that most influence them (Proposed Research *THEME 1A*), and our collaboration with kelp ecologists throughout the world via our participation in the Kelp Ecosystem Ecology Network (see Proposed Research- Synthesis and Integration).

The SBC is actively engaged in efforts to increase diversity in bio- and geo-sciences. Efforts to increase the participation of under-represented groups in STEM are achieved through our ongoing outreach efforts (see Sections 1 and 6) and by our participation in a new event at UCSB called GEMS Preview Day. The purpose of the event is to introduce prospective graduate students to the natural sciences early in their undergraduate careers (GEMS stands for Geography, Earth Science and Marine Science, which are the academic units at UCSB that participate in the program). In addition, SBC faculty are involved in outreach via symposia at annual meetings of the UCSB chapter for the Society for Advancement of Chicanos/Hispanics and Native Americans in Science, through leadership and mentoring in the UCLEADS program, and by recruitment of graduate students through an NSF *Bridges to the Doctorate* program.

### **PLANNING FOR THE FUTURE**

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, which provide a useful mechanism that aids in leadership transition, as planned for SBC IV. Reed, who has been the lead PI of the SBC LTER since its inception, will transition to being a Co-PI during the first two years of the new award and Co-PI Miller, who has been an active participant in the project since 2006, will take over as the lead PI. Miller is a mid-career marine ecologist with broad training in oceanography and ecology. His research focuses on processes occurring at population, community and ecosystem levels of organization using traditional field methods and emerging technologies (e.g., molecular biology, image recognition and machine learning). He currently serves as the lead PI of the Santa Barbara Coastal Marine Biodiversity Observation Network (a highly interdisciplinary program that collaborates closely with SBC LTER), and has

demonstrated the leadership skills, expertise and scientific breadth to lead SBC LTER in the foreseeable future. As a Co-PI Reed will remain actively engaged in SBC LTER research and will mentor Miller in his new leadership role. D. Siegel (physical oceanography and remote sensing), G. Hoffman (molecular physiology, global change biology) and A. Stier (population and community ecology) will serve as Co-PIs. Siegel served in this capacity in SBC II and III, while Hoffman participated in SBC II and III as an Associate Investigator. Stier is a new Assistant Professor in the Department of Ecology, Evolution and Marine Biology with research interests that are highly complementary to the project. Collectively, the five investigators on the cover page possess diverse and complementary scientific expertise, and are at varying levels of career development that will provide SBC with experienced leadership in the foreseeable future.

Planning for a long-term project like an LTER also 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. Nine of the 24 Investigators listed on this proposal were added to the project during our current award cycle and all are early to mid-career scientists who offer a potential for a long-term commitment to the project.

**Table S3.1.** Participation of SBC Investigators in the research themes proposed for SBC IV. The lead investigator of each subtheme is shown in **bold**. Additional information on the expertise of each investigator can be found in their Biographical Sketch.

***Theme 1 - Environmental drivers of kelp persistence and community structure***

- *THEME 1A - Community and ecosystem consequences of climate variability, disturbance and pathways of recovery*  
**Stier**, Bell, Castorani, Cavanaugh, Miller, Rassweiler, Reed
- *THEME 1B - Ecological consequences of fishing*  
**Rassweiler**, Cavanaugh, Eliason, Lenihan, Miller, Reed, Stier
- *THEME 1C - Sources and utilization of recycled nitrogen*  
**Brzezinski**, Burkepile, Eliason, Melack, Miller, Moeller, Reed, Santoro, Smith

***Theme 2 - Dynamic biophysical coupling in kelp forest ecosystems***

- *THEME 2A - Effects of kelp on physical and chemical fluxes*  
**Nidzieko**, Carlson, Hofmann, MacIntyre, Siegel, Washburn
- *THEME 2B - Effects of kelp on the processing and fate of dissolved organic matter*  
**Carlson**, Brzezinski, Miller, Moeller, Nidzieko, Reed, Santoro, Washburn, Wilbanks
- *THEME 2C - Ecological and evolutionary consequences of kelp-induced changes in seawater chemistry*  
**Hofmann**, Carlson, Eliason, Miller, Nidzieko, Stier, Washburn

***Theme 3 - Spatial dynamics and connectivity of kelp forests and adjacent ecosystems***

- *THEME 3A - Demographic connectivity and metapopulation dynamics of giant kelp*  
**Cavanaugh**, Bell, Castorani, Reed, Siegel
- *THEME 3B - Trophic connectivity between kelp forests and beaches*  
**Dugan**, Cavanaugh, Melack, Miller, Ohlmann, Page
- *THEME 3C - Trophic connectivity between the coastal ocean and kelp forests*  
**Miller**, Brzezinski, Iglesias-Rodriguez, Moeller, Nidzieko, Page, Siegel, Washburn