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- (2) for other NSF grants when more than \$25,000 has been budgeted in the proposal for repair, alteration or improvement (construction) of a building or facility.

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The AOR shall require that the language of this certification be included in any award documents for all subawards at all tiers.

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Overview

The California Current Ecosystem (CCE) LTER program addresses two over-arching questions: **What are the mechanisms leading to ecological transitions in a coastal pelagic ecosystem? What is the interplay between changing ocean climate, community structure, and ecosystem dynamics?** The study region is the southern sector of the California Current System (CCS), a major upwelling biome where the 73-year California Cooperative Oceanic Fisheries Investigations (CalCOFI) time series program provides essential information characterizing natural climate variability and progressive changes. CCE spans a biogeographic boundary region, hence is an early sentinel of climate change; shows low-frequency variations correlated with much of the North Pacific; exhibits a broad gradient of ocean conditions over a short geographic distance; and has mature physical-biogeochemical models. Phase III support of CCE has led to extensive new findings: elucidation of “conditional top-down” dynamics leading to environmentally contingent variation between bottom-up and top-down ecosystem control; ecological and biogeochemical impacts of cross-shore filaments, and their climate sensitivities; a predictive framework for the biotic impacts of El Niño Southern Oscillation (ENSO) events; physical drivers and ecological importance of extratropical marine heatwaves that are now a dominant form of ecosystem disturbance; changing nutrient stoichiometry at the base of the food web; and elucidation of molecular-level ecophysiological responses of phytoplankton to Fe-stress. This renewal proposal builds on our previous analyses of the mechanisms underlying abrupt ecological transitions with three new, inter-related program foci: (1) investigation of marine heatwaves and resultant multiple stressors on organisms and communities, (2) elucidation of ecological stoichiometry and the response of multiple trophic levels to altered elemental ratios of source nutrients, and (3) expanded analysis of top-down pressures mediated by a diverse suite of organisms. Multi-scale measurements of the five core LTER variables and their responses to ocean changes (warming, increased stratification, acidification, deoxygenation, and altered nutrient stoichiometry) in the NE Pacific will be sustained.

Intellectual Merit

CCE-LTER studies are making excellent progress towards diagnosing mechanisms of ecosystem change in a major upwelling ecosystem and developing a quantitative framework for forecasting future changes. In Phase IV we will build on previous work to investigate the impacts of multiple stressors on organismal ecophysiology and community shifts. Sustained long-term, spatially-resolved time-series at multiple spatial scales will continue to evaluate community shifts at multiple temporal scales, with new measurements allowing interrogation of communities at finer taxonomic levels. Planned process studies featuring Lagrangian-design *in situ* multi-factorial experiments (temperature, macronutrients, micronutrients, light, grazing) combined with advanced genomic and transcriptomic analyses will complement the timeseries measurements, inform next-generation biogeochemical models and test hypotheses related to ecological stoichiometry and marine heatwaves. A suite of imaging techniques (spanning organisms from μm to cm), molecular and morphological methods, and active and passive acoustic approaches (zooplankton to marine mammals) will be used to quantify vertical structure and co-occurrence of organisms across trophic levels and test top-down ecosystem control hypotheses.

Broader Impacts

Coupled phytoplankton-to-fish models, developed in concert with multi-trophic level measurements, will be used to develop the foundation for forecasting the effects of climate perturbations (El Niños, marine heatwaves, ocean warming) on key living resources including fishes, invertebrates, marine mammals, and seabirds. The study region is also important for CO_2 exchange and carbon sequestration, as well as human recreation, navigation, and the livelihoods of millions of U.S. residents. The site encompasses both existing and proposed National Marine Sanctuaries and constitutes the major spawning habitat for most of the epipelagic fish biomass in the CCS. This research will involve extensive training of graduate students, undergraduate REUs, and will create teacher opportunities. Public programs and outreach efforts reaching thousands of people will be expanded in collaboration with the Birch Aquarium at Scripps, to increase public awareness and understanding of climate effects on the ocean, to connect the public to ocean research, and to expand the pipeline of ocean science careers. We will also partner with local indigenous communities through the UC San Diego Intertribal Resource Center and the Native American Student Alliance.

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1. Brief Historical Development of CCE, Conceptual Framework, & New Directions for Phase IV

The California Current Ecosystem (CCE) Long-Term Ecological Research (LTER) site is a coastal upwelling biome and the site of a 73-year (ongoing) spatially resolved ocean timeseries (CalCOFI) that has demonstrated physical forcing on multiple spatiotemporal scales with concomitant impacts on ocean biota. The CCE includes a biogeographic boundary region that serves as an early sentinel of climate change; is representative of productive coastal upwelling biomes found along the eastern boundaries of all major ocean basins; exhibits a large gradient of ocean conditions (encompassing much of the range of ocean productivity found in the world ocean) over small geographic distances; and shows low-frequency changes that are correlated with changes in much of the NE Pacific. **CCE research is motivated by the observation of dramatic shifts in zooplankton (Fig. 1) and forage fish assemblages associated with changes in climatic modes and uncertainty in the mechanisms underlying these changes.**

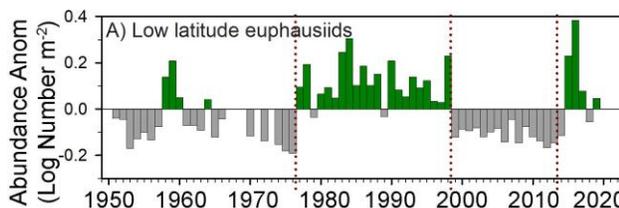


Fig. 1 – Ecological transitions illustrated by changes in the abundance of low-latitude krill in the CCE region. Red dashed lines show transitions in the Pacific Decadal Oscillation climate mode (Ohman, unpub.)

In CCE **Phase I** (2004-2010) our conceptual view was that abrupt changes in ecosystem state are explained by nonlinear responses of pelagic populations to linear changes in physical forcing (Hsieh et al. 2005). Our early view favored the perspective of stable states or ‘regimes’ (i.e., resilient ecosystem states with feedback mechanisms that resist reversion to prior states, Fig. 2, Model III). Phase I also introduced

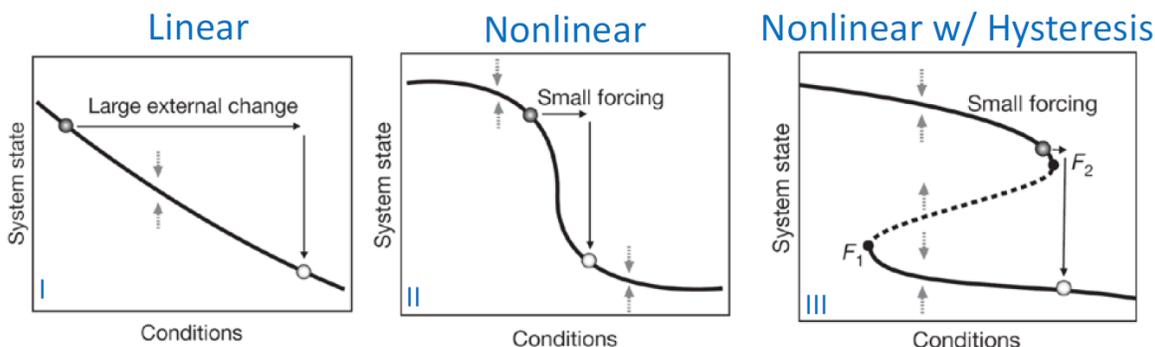


Fig. 2 – Conceptual models for trajectories of ecosystem change, from Scheffer et al. (2009). Model I (Linear), Model II (Nonlinear with threshold), Model III (Nonlinear with threshold and hysteresis).

our 4 hypothesized mechanisms of ecosystem change (Fig. 3) and our *space-for-time* exchange process studies (Hopkinson and Barbeau 2008; King and Barbeau 2007; Landry et al. 2009; Rykaczewski and Checkley 2008; Stukel et al. 2011a). Other studies documented long-term changes in the physical and chemical environment (Bograd et al. 2009; Chhak and Di Lorenzo 2007; Kim and Miller 2007).

In CCE **Phase II** (2010-2016) our role in a synthetic cross-LTER paper (Bestelmeyer et al. 2011) revealed a lack of evidence for preferred ecosystem modes or 'regimes'. Instead, ecological transitions in the CCE are characterized by strong linear coupling of biological processes to low-frequency climate forcing with temporal integrations associated with multiple trophic levels leading to apparent ecosystem state changes (Di Lorenzo and Ohman 2013). Furthermore, such transitions are reversible, hence inconsistent with Figure 2, Model III. Phase II introduced a new focus on ecological disturbance regimes associated with mesoscale fronts (e.g., de Verneil 2015; Kahru et al. 2012a; Landry et al. 2012; Li et al. 2012; Ohman et al. 2012; Powell and Ohman 2015a). We also continued to document biotic responses (e.g., changing nutrient availability and altered population distributions from phytoplankton to fish) to long-term changes (e.g., Bograd et al. 2015; Goericke and Ohman 2015; Netburn and Koslow 2015). Modeling advances included size-structured models (Fuchs and Franks 2010; Poulin and Franks 2010; Taniguchi et al. 2014), 'emergent-properties'-type models (Goebel et al. 2013; 2014), data-assimilating physically-coupled models (Song et al. 2012), and food-web models (Stukel et al. 2012).

Phase III (2016-2022) continued our focus on the mechanisms underlying ecosystem transitions and expanded our focus on variability in mesoscale (i.e., 10s of km) physical forcing. We demonstrated the impact of mesoscale fronts (regions where two water masses meet) and filaments (narrow jets of coastal water flowing offshore) on vertical and lateral transport of organic matter (Kelly 2020; Stephens et al. 2018; Stukel et al. 2017), nutrients (Zaba et al. 2020a), and organisms (Chenillat et al. 2016; Krause et al. 2020) and showed spatiotemporal decoupling of new and export production (Kahru et al. 2020; Kelly et al. 2018; Kranz et al. 2020). Satellite remote sensing syntheses revealed temporal variability in mesoscale fronts and filaments tied to large-scale physical forcing (Chabert et al. 2021; Kahru et al. 2018). Phase III also focused on analyses of the strong 2015-2016 El Niño and of the increasingly frequent extreme marine heatwaves in the North Pacific (Kahru et al. 2018; Lilly and Ohman 2018; Morrow et al. 2018), incorporation of 'omics' methods to investigate microbial populations and their activities (Coale et al. 2019; Gutierrez-Rodriguez et al. 2019; Hogle et al. 2018; Kolody et al. 2019; Valencia et al. 2021), increased use of *in situ* imaging for investigating fragile taxa (Biard et al. 2018; Biard and Ohman 2020; Ohman et al. 2019; Stukel et al. 2018a; Whitmore and Ohman 2021), and a greater focus on forecasting ecological responses to interannual variability in physical forcing (Cordero-Quirós et al. 2019).

This **Phase IV** renewal proposal retains a focus on the mechanisms underlying ecosystem transitions or abrupt ecological changes in our pelagic upwelling ecosystem, while continuing measurements of the core variables central to all LTER sites: **disturbance regimes, inorganic nutrients, primary production, organic matter, and population studies**, all of which are closely integrated into our studies of mechanisms underlying ecosystem changes (and highlighted in **green** throughout this proposal). We will use three inter-related program elements (**time-series observations, experimental process cruises, modeling**) to explicitly test core hypotheses that underpin CCE research, as well as **new hypotheses** related to **marine heat waves, ecological stoichiometry, and top-down ecosystem regulation**. Our ultimate goal is to develop a quantitative framework for forecasting future ecological transitions. Two additional program elements (**information management, and education, outreach and capacity building**) will be used to disseminate the information to stakeholders and the broader public.

The overarching questions we will address in the CCE program remain:

What are the mechanisms leading to ecological transitions in a coastal pelagic ecosystem? What is the interplay between changing ocean climate, community structure, and ecosystem dynamics?

We have identified four principal mechanisms that could lead to the observed ecosystem shifts (e.g., Di Lorenzo and Ohman 2013; Lindegren et al. 2016; Ohman et al. 2013) in the CCE pelagic ecosystem:

- **1) Along-shore transport** – Temporal variations in north-south transport introduce organisms of different geographic origins into the CCE study region.
- **2) In situ food web changes**– Changes in species composition, trophic connections, and pathways of energy flow occur in response to changes in water-column vertical stratification. Stratification

modifies the rate of supply of limiting nutrients (macronutrients or trace metals) for phytoplankton production. Altered **nutrient supply** leads to altered rates of **primary production** and/or compositional changes in the phytoplankton, which propagate through the food web (i.e., bottom-up forcing).

- **3) Cross-shore transport**– Temporal changes in the rates of cross-shore transport, via mean flow, coastal filaments, or propagation of mesoscale eddies, determine the probability of **retention/loss of nutrients** and organisms in the nearshore coastal zone.
- **4) Top-down pressure** – Altered abundances (or dietary shifts) of predators or grazers lead to selective mortality and altered abundances and composition of the planktonic food web.

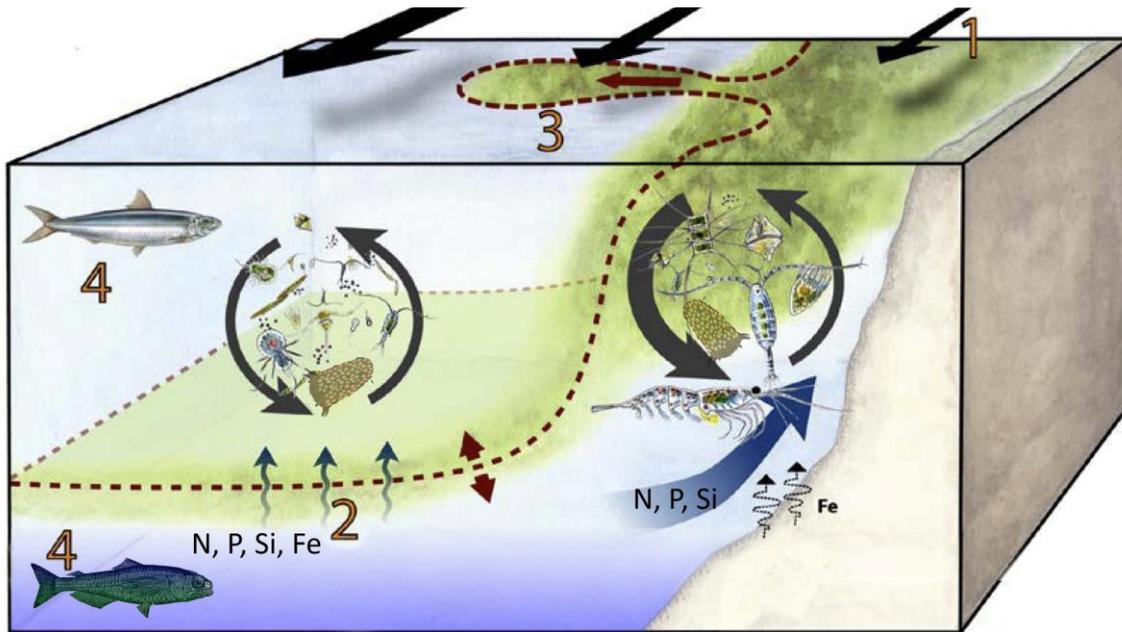


Fig. 3 – Conceptual framework illustrating hypothesized mechanisms leading to ecological transitions in the CCE region. **1) Along-shore transport, 2) In situ food-web changes, 3) Cross-shore transport, 4) Top-down pressure.** These mechanisms of ecosystem change respond to climatic and other forcing at multiple temporal scales including ENSO, the Pacific Decadal Oscillation, and marine heatwaves. The diagram also illustrates spatial variations in CCE food webs associated with strong coastal boundary upwelling (large blue arrow) and weaker wind stress curl upwelling offshore (small blue arrows).

Our conceptual framework is illustrated in Fig. 3, which depicts spatial differences in ecosystem structure across the CCE region, and also encapsulates these four primary mechanisms underlying ecosystem temporal change that are the focus of CCE. The CCE conceptual framework should be considered in combination with the conceptual models underlying ecosystem change in Fig. 2.

We will continue to evaluate these 4 mechanisms in CCE IV, building on knowledge gained during previous funding cycles and adding several **major new or expanded research directions**. (1) Alongshore advection (transport) anomalies will be quantified by calculation of volume transports from glider, shipboard hydrography, and satellite altimetry time series and by ensemble models of regional circulation. (2) *In situ* food web changes will be analyzed through a combination of our experimental process cruises (space-for-time exchange with **added multi-factorial manipulative experiments**), **new retrospective time-series measurements of elemental stoichiometry**, and coupled biogeochemical models. (3) Changes in cross-shore transport and loss/retention of organisms will be analyzed via ocean glider and satellite remote sensing time series, ocean circulation models, and results from recent filament-focused process cruises (Phase III). (4) Altered top-down pressure, **proposed as an intensive focus in CCE IV**, will be assessed using **new in situ measurements on our process cruises, a new suite of modeling approaches**, and analysis of predator-prey abundance relationships in existing time-series. We also plan a **new research focus to investigate how recent marine heat waves may alter the relationships between our 4 core mechanisms** (e.g., by modifying relationships between nutrient

supply and cross-shore transport or between along-shore transport and predator abundances).

2. Results from Prior LTER Support – Ecological Transitions in the California Current Ecosystem: CCE-LTER Phase III, OCE-1637632. \$6,762,000 + supplements, 8/1/16 – 7/31/2022

The over-arching questions driving CCE research noted above have motivated our site since Phase I. However, each phase of CCE has included a focus on specific topics. In Phase III these expanded foci were: cross-shore fluxes and their sensitivity to climate forcing (Fig. 3, mechanism #3), prediction of the biotic effects of ENSO (El Niño-Southern Oscillation), and increased use of -omics tools to investigate microbial communities. In this section, we report selected results from Phase III research. In Phase III, CCE has produced 155 publications (121 journal articles, 8 conference proceedings and reports, 21 PhD theses, 4 masters theses, and 1 magazine article; see the CCE LTER website for a complete listing).

Ten significant publications from Phase III funding

Persistent Fe-limitation in subsurface chlorophyll maxima. Hogle et al. (2018, *PNAS*) utilized experimental Fe-addition experiments, biogeochemical proxies from previous CCE research, and metatranscriptomic analyses to show that ubiquitous subsurface chlorophyll maxima in the CCE are consistently Fe-limited or Fe- and light-colimited (Fig. 4). From proxies derived from CalCOFI measurements, they also show a multi-decadal increase in the size of the subsurface Fe-limited domain in the CCE.

Ecological and biogeochemical impact of cross-shore filaments.

Chabert et al. (2021, *J. Geophys. Res. Oceans*) used satellite altimetry, wind products, and CCE process cruise measurements to understand cross-shore flows and particle export associated with coastal upwelling filaments. They found that cross-shore organic matter flux can reconcile spatial imbalances of new production and export in the CCE region and show how transport associated with mesoscale features is linked to interannual variability in climate forcing.

Productivity in coastal filaments. Kranz et al. (2020, *J. Geophys. Res. Oceans*) conducted a comprehensive comparison of production metrics during Lagrangian experiments (following a moving frame of reference) on the CCE-P1604 and CCE-P1706 cruises (net and gross primary production, nitrate uptake, phytoplankton growth rates, net community production (NCP), sinking organic matter flux). NCP and nitrate uptake exceeded sinking particle flux in the coastal regions of a filament but were lower than sinking particle flux in the offshore terminus of the filament as a result of cross-shore transport.

Biogeochemical impact of mesoscale fronts. Stukel et al. (2017, *PNAS*) found that a combination of dense, Si-enriched, Fe-depleted diatoms with substantial zooplankton aggregations at a deep-water front led to extremely high vertical export of sinking particles. They showed that subduction of sinking particles contributes a substantial additional downward flux of organic matter into the deep ocean.

Interannual variability in microbial communities. James et al. (in press, *Nat. Comm.*) initiated a spatially resolved time series (2014-2020 and ongoing) of microbial community composition using 16S and 18S ribosomal DNA sequencing to target prokaryotes and protists, respectively. They found that nitracline depth (i.e., the depth at which nitrate concentrations increase rapidly) was a robust predictor of microbial community structure and diversity in the CCE and documented distinct ecological shifts between a warm phase (2014 – 2016 marine heatwave and El Niño) and a subsequent cool period. Retrospective

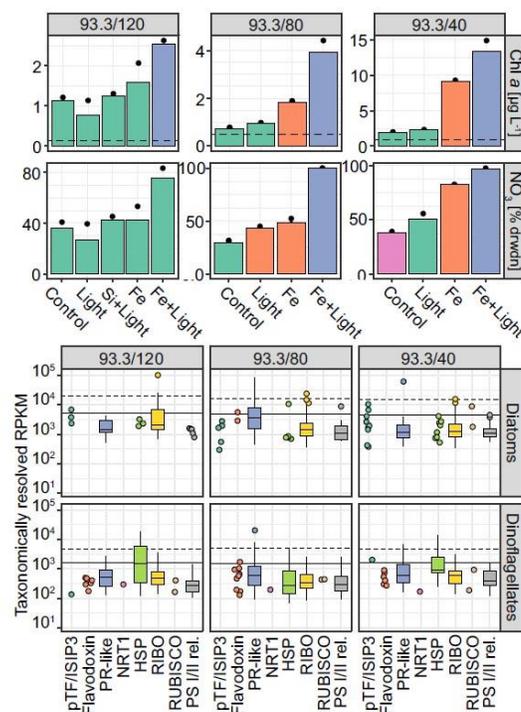


Fig. 4 – Multi-factorial Fe-limitation experiments and metatranscriptomics results from Hogle et al. (2018) at 3 CalCOFI stations. Top panels show bulk responses (chl increases and nitrate drawdown) to treatments. Bottom panels show taxon-specific transcription-level responses as quantified by comparing relative transcript abundances from known iron-stress genes and genes related to essential cellular processes.

analyses (to 2006) and ongoing future sampling will develop this into a core CCE ecological time series.

El Niño impacts on euphausiids. Lilly & Ohman (2021, *Prog. Ocean.*) utilized ~70 years of CalCOFI/CCE zooplankton time series data to understand the effects of two major types of El Niño on spatial displacements of euphausiids (krill). The study spans 7 El Niños and the marine heatwave of 2014-15 to elucidate the CCE **disturbance regime**. The authors found differential effects of Eastern Pacific and Central Pacific El Niños on euphausiid habitat usage in the CCE region related to the biogeographic habitats of the animals and provide a framework for predicting future impacts of different types of El Niño.

Conditional Top-Down ecosystem dynamics. Lindegren et al. (2018, *Global Change Biol.*) analyzed ~60 years of CCE, CalCOFI, and related **population data** to search for evidence of changing methods of pelagic ecosystem regulation during different climate states. Their nonlinear threshold models uncovered a particularly interesting novel pattern (that we term “Conditional Top-Down” forcing), where top-down predator control is expressed only during periods of weak upwelling, low nutrient concentrations, and low primary production (Fig. 5).

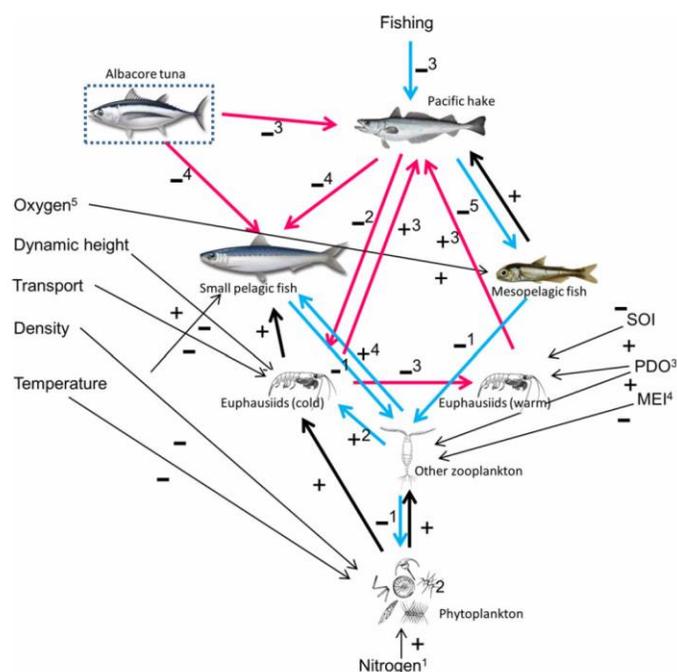


Fig. 5 - Simplified food-web model showing threshold dependent interactions between taxa and external covariates that are above (blue) or below (red) an estimated threshold along with non-threshold-dependent interactions (black). Lindegren et al. (2018)

Phenology of blue whale migrations. Szesciorka et al (2020, *Scientific Reports*) documented a decadal-scale trend in the timing of arrival of blue whales in their CCE feeding grounds. This earlier arrival is linked to warming waters and a time-lagged response to the biomass of euphausiids, the blue whales' exclusive prey in this region. The result has implications for conservation strategies, as the blue whales are exposed to increased anthropogenic threats at their feeding grounds.

Physical drivers of Marine Heatwaves (MHW). The 2019 MHW generated widespread concern for sensitive marine ecosystems along the west coast of North America. Amaya et al. (2020, *Nat. Comm.*) showed that this MHW primarily resulted from a prolonged weakening of the North Pacific High-Pressure System, which reduced surface winds and decreased evaporative cooling and wind-driven upper ocean mixing. Warmer ocean conditions then reinforce the MHW through a positive low-cloud feedback.

Variability in water mass contributions to upwelled nutrients. Bograd et al. (2019, *Geophys. Res. Lett.*) analyzed historical hydrographic data to quantify the variability of water mass contributions to the CCE region from the Subarctic, Subtropical, and Eastern Tropical Pacific. This analysis established that each of the major source waters has its own combination of temperature, salinity, **nutrient**, and O_2 signatures that can be identified and quantified. This paper underscores the influence of remote source waters and the importance for CCE of oceanic changes occurring far afield in the larger Pacific Ocean.

Results from Phase III Filament and Cross-shore Flux Studies

A major focus of CCE Phase III was the role of cross-shore fluxes as a mechanism leading to ecosystem shifts. The potential importance of this mechanism was suggested by prior California Current research, including demonstrated variability in cross-shore fluxes (Combes et al. 2013; Davis and Di Lorenzo 2015), preliminary evidence for an imbalance between production and export in coastal regions (Stukel et al. 2011a), and the **presence of coastal euphausiid species** in offshore ribbons of water (Brinton 1981). Our proposal was also guided by recent high-resolution modeling results showing high cross-shore carbon

and nutrient transport mediated by meso- and submesoscale jets and filaments (Nagai et al. 2015). Consequently, we initiated a multi-disciplinary program to utilize modeling approaches, satellite remote sensing, time-series analysis, and targeted process studies to investigate cross-shore fluxes of nutrients, organic matter, and organisms, and the transformations that occur during transport.

We conducted three 32-day process cruises (P1706, P1908, and P2107 in Jun 2017, Aug 2019, and Jul-Aug 2021, respectively) that included a series of coordinated activities: radiator surveys mapping the larger study region while towing an undulating profiling instrument (SeaSoar) and conducting surface measurements of biogeochemical and ecological properties (Fig. 6); smaller scale ‘transects’ across mesoscale features of interest that allowed two-dimensional mapping of ecological standing stocks and rates (Fig. 7); and three- to four-day quasi-Lagrangian experiments. These cruises also featured use of multiple autonomous sampling platforms (Spray gliders, *Zooglider*, and Carbon Flux Explorers) to enable broader spatial sampling and greater replication of measurements from hydrography to biogeochemistry and zooplankton community dynamics (Bourne et al. 2021; Whitmore and Ohman 2021; Zaba et al. 2020a). The cruises covered a range of conditions including a strong filament that remained coherent for >30 days (P1706), a weaker filament with more narrow offshore flows that dissipated after ~2 weeks (P1908), and a period with weak winds and no distinct filaments (P2107). Comparison of conditions during these three cruises with satellite remote sensing, CalCOFI data, and timeseries derived from autonomous gliders and moorings will allow us to constrain the roles of these mesoscale filaments in offshore fluxes.

Preliminary results have yielded substantial insight into the ecology of these features: The California Undercurrent (CUC) was the primary source for nutrients upwelled into these filaments, and filament water sourced from the CUC had higher chlorophyll than other regions of the filament (Zaba et al. 2020a). High nutrients in the coastal source region of the filament stimulated exceptionally high phytoplankton biomass, net primary production (NPP), and nitrate uptake (Kranz et al. 2020). During offshore advection, phytoplankton become Fe-limited and then N-limited, leading to substantial decreases in NPP. Multi-factorial experiments assessing both bulk phytoplankton responses and transcription-level acclimation identified molecular pathways enabling resistance to acidification for Fe-stressed phytoplankton (Lampe et al. submitted). O₂ utilization by heterotrophs (zooplankton and bacteria) exceeded NPP in much of the filament, leading to net heterotrophy (Kranz et al. 2020; Wang et al. 2020). Net production of dissolved and particulate matter in the coastal region of the filament supported excess bacterial and zooplankton utilization in the offshore region of the filament (Rivera et al. in review) with these regions linked by current speeds of up to 0.78 m s⁻¹ (Zaba et al. 2020a). Despite the decrease in NPP along the filaments, carbon export was much higher in all regions of the filaments than typically occurs in the region and the offshore terminus of these filaments had higher fluxes of sinking particles than coastal regions (Kelly 2020; Stukel and Barbeau 2020). Export from the euphotic zone of the filament was typically comprised of sinking fecal pellets, which were replaced at deeper depths by large aggregates (Bourne et al. 2021). Using satellite-remote sensing to diagnose surface

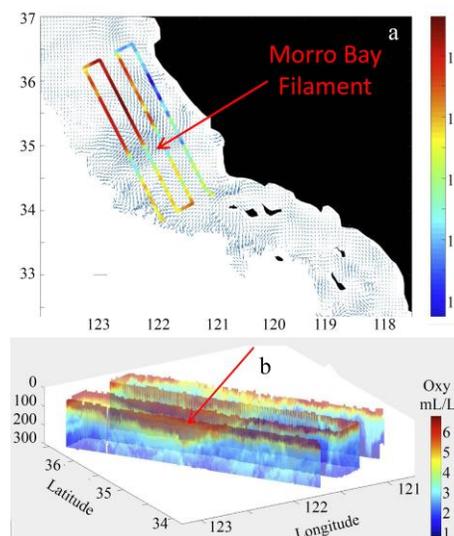


Fig. 6 – Results from first P1706 radiator survey. (a) Ship-track sea surface temperature superimposed on CODAR surface currents. (b) Oxygen sections along radiator tracks. Filament axis is shown with red arrows.

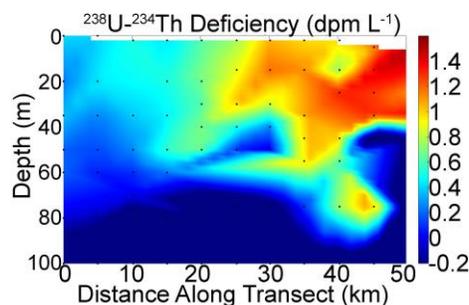


Fig. 7 – ²³⁸U-²³⁴Th disequilibrium (proxy for sinking particulate organic carbon) section on a cross-shore transect during P1706. Left side is offshore; right is near coast and shows high carbon export on the coastal side of the filament

currents and water parcel age and matching those results to locations of CCE LTER process cruises, Chabert et al. (2021) showed that cross-shore flows lead to higher offshore phytoplankton concentrations and that the balance between sinking particle export and new production was positively correlated with advective age of a water parcel (Fig. 8). Chabert et al. (2021) further determined that over a 26-year timeseries the offshore extent of older advected waters was driven by mesoscale variability that covaried with large-scale ENSO forcing. These results highlight the potential roles of climate-driven shifts in cross-shore transport as drivers of lower trophic level ecological transitions, while reinforcing our view that ecological transitions in the CCE are primarily linear responses to such drivers (i.e., Fig. 2, Model I).

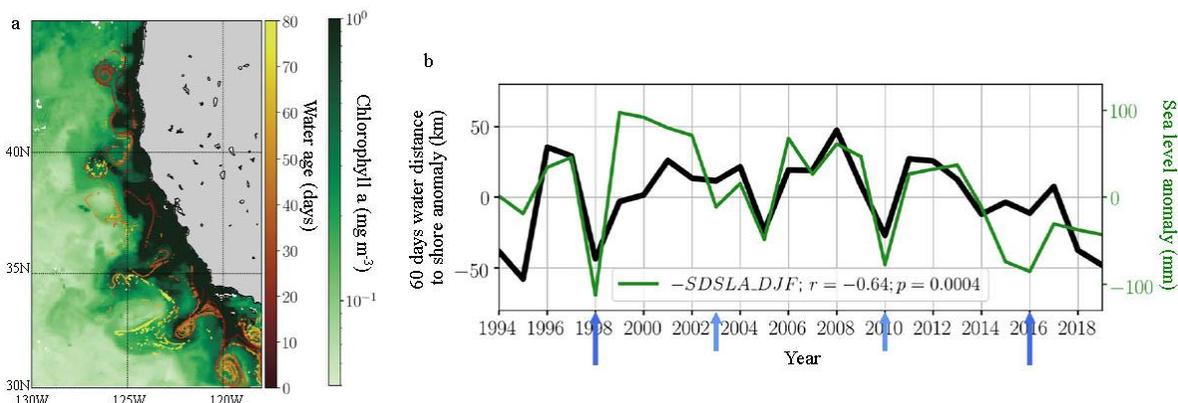


Fig. 8 – (a) Water parcel age (brown) vs. chlorophyll concentration (green). (b) Correlation of San Diego sea level anomaly (southern California ENSO index) with average distance from shore of 60-day old upwelled water (Chabert et al. 2021). Blue arrows indicate El Niño events.

Results from Phase III Ecological Forecasting Studies

El Niño Southern Oscillation (ENSO) is recognized as one of the potentially predictable drivers of California Current System (CCS) variability and its ecological conditions and represents the dominant element of the CCE 'Disturbance Regime.' Changes in the physical state and biogeochemical variables of the CCS arise from the local and remote sources of variability imprinted by ENSO. Dynamical and statistical ENSO forecasts are now routinely made in climate centers around the world. In the U.S., these are oriented toward forecasting precipitation and temperature over land. Yet the response of the CCS to potentially predictable ENSO forcing has only begun to be explored.

In response to this need, CCE scientists hosted a workshop at SIO in 2016, jointly supported by US CLIVAR and NOAA, entitled Forecasting ENSO Impacts on Marine Ecosystems of the US West Coast. This workshop drew a cross-section of 51 physical and biological scientists from across the U.S. The reports from that workshop (Di Lorenzo and Miller 2017; Di Lorenzo et al. 2019) identify key physical processes and biological ecosystem indicators that are amenable to operational forecasts.

Subsequently, CCE scientists published a collection of 5 papers in Deep-Sea Research I that summarize some of the responses to ENSO forcing measured across trophic levels in the CCE region (introduction by Ohman 2018). We also initiated physical-biological modeling studies to identify some of the limitations to, and the uncertainties in, the potentially predictable impacts of ENSO on the CCE. Cordero-Quirós et al. (2019) found clear responses of nutrients, phytoplankton, and zooplankton to ENSO events in the CCS within a frequently used global modeling framework (CESM-POP2-BEC), although the coarse resolution of that model did not allow realistic development of fronts and eddies in the CCS, which both play important roles in establishing the ecosystem. Also, the simplified ecological model (BEC), with only a single zooplankton category, limited the capacity of the model ecology to separate ENSO response among phytoplankton size classes. Next, Cordero-Quirós et al. (2021) showed that the ENSO variability in a high-resolution, "eddy-scale" CCS model (ROMS-NEMURO) is more realistic due to its proper representation of upwelling fronts and eddies. The model revealed trophic level interactions during ENSO events in which the larger components (diatoms, euphausiids, copepods) were suppressed in the coastal upwelling zones during El Niño, while the smaller components (flagellates, ciliates) were enhanced.

Three other significant contributions pertaining to El Niño impacts include Lilly and Ohman's (2018) analysis of **temporal changes in the zooplankton community** from 70 years of CalCOFI samples encompassing 7 El Niño events. They identified, for the first time, a tendency toward different community changes **in response to Eastern Pacific (EP) and Central Pacific (CP) Niño events**. Lilly and Ohman (2021) subsequently found differences in the impacts of CP and EP El Niños on spatial habitat usage (habitat compression or expansion) of 10 species of euphausiids. These results were then used to forecast the expected future spatial displacements of euphausiids in the year 2100. In a related study, Lilly et al. (2019) used high frequency measurements from the CCE1 and CCE2 moorings to document the fundamentally different effects of the marine heatwave of 2014-15 (surface-expressed) and the El Niño of 2015-16 (surface and subsurface influences) in the CCE region. This analysis underscores the importance of understanding differences in climate forcing underlying different types of 'heatwave' events.

These studies have provided an excellent foundation for the further refinement of dynamical ecosystem forecast models of ENSO on the CCE.

Results from Phase III Metagenomics and Metatranscriptomics Studies

At its inception, CCE focused on **population dynamics of metazoan zooplankton** (especially krill and copepods), with phytoplankton and bacteria dynamics investigated at relatively coarse taxonomic resolution through epifluorescence microscopy, HPLC pigment analyses and flow cytometry. However, in Phase III, we made a substantial investment in emerging metagenomics and metatranscriptomics ("-omics") methodologies, which now allow us unprecedented ability to investigate **prokaryotic and protistan population dynamics** and functional interactions, as well as **metazooplankton diversity patterns**.

A new timeseries of prokaryotic and protistan community composition and diversity (using 16S and 18S sequencing) was initiated in 2014, with samples collected from ~25 stations spanning the coastal-offshore and north-south gradients on quarterly CalCOFI cruises (James et al. in press). This timeseries augments existing HPLC-based pigment and microscopy timeseries, allowing unparalleled ground truthing of next-generation sequencing approaches. The first 6 years of this timeseries demonstrate that nitracline depth is a better predictor of community shifts than other environmental parameters (e.g., temperature, salinity, nutrient and chlorophyll concentrations). It also shows that diatoms are the most sensitive indicators of ecosystem changes occurring during shifts into marine heatwave (MHW) and El Niño conditions.

"-Omics" approaches have also been used for more targeted studies to enhance process-level investigations of multiple microbial taxa from viruses to phytoplankton. Kolody et al. (2019) used a robotic environmental sampling device to investigate diel transcriptional patterns of Fe-limited phototrophs and discovered viruses capable of infecting the majority of abundant taxa and synchronizing their transcriptional activity with that of their hosts. Kranzler et al. (2019) used metatranscriptomic analysis of cell-associated diatom viruses to investigate early, active, and lytic stages of viral infection and found that diatom Si limitation facilitates viral infection and subsequent mortality. Coale et al. (2019) used *Phaeodactylum tricornutum* as a model diatom for reverse genetic experiments and identified a novel siderophore acquisition pathway for obtaining Fe. They subsequently showed that associated genes were present in diverse diatom lineages suggesting that symbiotic relationships with siderophore-producing bacteria are widespread. Hogle et al. (2018) modified Fe and light conditions in experimental incubations with subsurface chlorophyll maximum (SCM) communities while sampling the metatranscriptome to identify Fe-stress-associated genes. They identified persistent Fe limitation at the SCM from transcriptomic analyses of CalCOFI samples. Diner et al. (2021) developed a monthly timeseries of pathogenic *Vibrio* species at five coastal sites and found associations between these bacteria and both diatom and copepod lineages. Stephens et al. (2019) used NO₃ isotopes and 16S rRNA gene sequencing and detection of *amoA* transcripts to demonstrate the importance of euphotic zone nitrification during stratified periods. Our studies have also uncovered the important contributions of gammaproteobacteria, dinoflagellates, diatoms, and radiolarians to sinking particles; active growth of dinoflagellates and marine stramenopiles on sinking particles; greater similarity with mixed layer communities for sinking protists relative to sinking prokaryotes; the over-representation of grazer-resistant taxa on sinking particles; and the importance of grazing pathways in structuring the biota found associated with sinking particles (Gutierrez-Rodriguez et al. 2019; Valencia et al. 2022; Valencia et al. 2021). CCE metabarcoding studies using 18S and COI markers have revealed the capability for deep resolution of zooplankton community structure (Matthews et al. 2021). These process-level investigations will be key to linking timeseries-

derived changes in gene expression and rRNA gene sequences to ***in situ* food web changes (Fig. 3, CCE principal mechanism of ecosystem change #2).**

****See Section 7 (pg. 33) for Results of Prior Broader Impacts, Supplemental Support, Data Availability.****

3. Proposed Research

Context of the California Current System (CCS) and Ecosystem (CCE)

The California Current is the eastern limb of the large clockwise circulation of the subtropical gyre of the North Pacific Ocean and carries cool, relatively fresh water southward from the Subarctic Pacific (Fig. 9). The California Current System off central and southern California includes: 1) this offshore southward flow, along with 2) a persistent but variable subsurface California Undercurrent that transports tropical water northward, and 3) the Inshore Countercurrent, a surface northward-flowing feature that continues north of Pt. Conception (Hickey 1993; Lynn and Simpson 1987). The Undercurrent, which has a mean depth of ~250 m and originates in a region of denitrification leading to climate-linked variability in nutrient stoichiometry, may play a particularly important role as it **transports nutrient-rich water** and tropical species northward, promotes retention of vertically migrating taxa in the CCE, and serves as a major source of upwelled water that in turn intersects with coastal filaments

(Johnson and Checkley 2004; Zaba et al. 2020a). These large-scale currents interact with coastal upwelling locations and intense mesoscale eddies, fronts, and filaments to generate a mosaic of water parcels with varying biogeochemical properties and ecological communities in our study region (Chenillat et al. 2018; Kahru et al. 2012a; Landry et al. 2012; Nagai et al. 2015; Strub and James 2000).

Broad cross-shore **patterns in nutrient delivery**, and hence ecosystem structure, are driven by both coastal and wind-stress curl upwelling. The North Pacific High pressure system yields winds from the north (particularly in summer) that drive near-surface waters offshore by Ekman transport, bringing cool, nutrient-rich water into the euphotic zone near the coast (Bakun 1975; Jacox et al. 2018). Offshore of the coastal margin, weaker and more diffuse upwelling is associated with wind-stress curl (i.e., induced by an onshore-to-offshore gradient in the intensity of alongshore winds). These general patterns intersect with temporally varying winds and topographic features (e.g., the upwelling center at Point Conception) to create strong spatiotemporal variability in upwelling rates. Over long timescales, coastal upwelling is expected to increase as a result of global warming and concomitant increases in land-sea temperature gradients (Bakun 1990; Rykaczewski and Dunne 2010; Sydeman et al. 2014). On interannual timescales, coastal upwelling is strongly modulated by the El Niño-Southern Oscillation, Pacific Decadal Oscillation, and North Pacific Gyre Oscillation forming an important part of the CCE **disturbance regime** (Chenillat et al. 2012; Chhak and Di Lorenzo 2007; Di Lorenzo et al. 2008; Jacox et al. 2015). Recent extratropical MHWs have also depressed upwelling, but with distinctly different mechanistic features (Amaya et al. 2020; Bond et al. 2015; Di Lorenzo and Mantua 2016). Modified upwelling rates interact with different sources of upwelled water to change the **concentrations and ratios (N:P:Si:Fe) of nutrients** entering the euphotic zone (Bograd et al. 2015; King and Barbeau 2011; Messie and Chavez 2015; Rykaczewski and Dunne 2010). These processes have, for instance, driven a **long-term decrease in N:P and Si:N ratios** within the Southern California Bight (Bograd et al. 2015), while differing proportions of wind-stress curl and coastal upwelling likely alter Fe:N ratios, with commensurate impacts on ecosystem services including carbon sequestration (Brzezinski et al. 2015; Stukel and Barbeau 2020).

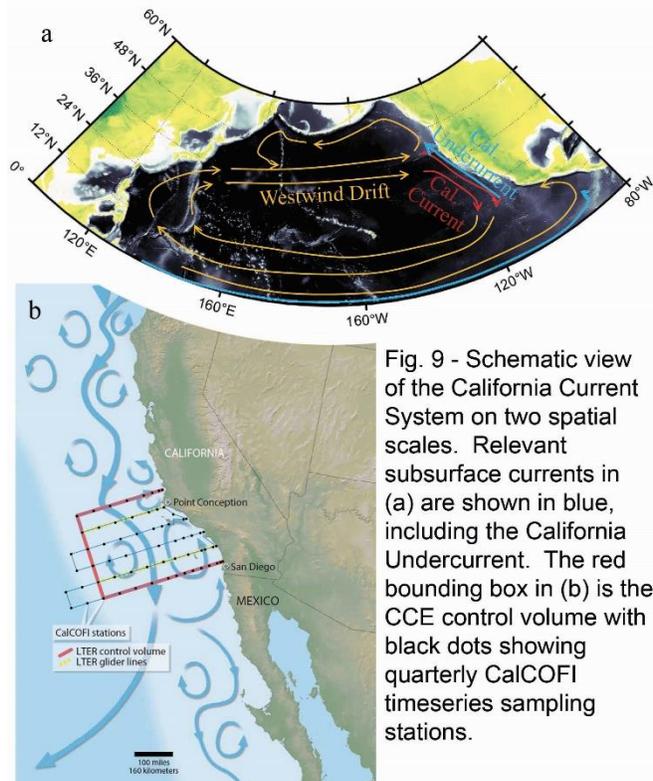


Fig. 9 - Schematic view of the California Current System on two spatial scales. Relevant subsurface currents in (a) are shown in blue, including the California Undercurrent. The red bounding box in (b) is the CCE control volume with black dots showing quarterly CalCOFI timeseries sampling stations.

In the coastal upwelling domain, cold nutrient-rich water (including Fe from sediments) is drawn into the euphotic zone stimulating strong blooms of larger phytoplankton (diatoms and dinoflagellates). These blooms in turn support elevated concentrations of large consumers, including planktonic copepods and euphausiids. The coastal upwelling domain is characterized by a shallow euphotic zone and nitracline and a productive food web where phytoplankton growth exceeds grazing and net community production is typically positive (Kranz et al. 2020; Landry et al. 2009), promoting rapid biomass accumulation and both lateral and vertical export (Chabert et al. 2021; Kelly et al. 2018; Nagai et al. 2015). Ekman transport and mesoscale features advect a large portion of this nutrient-, organic matter-, and plankton-enriched water into the offshore wind-stress curl domain (Amos et al. 2019; Stephens et al. 2018). In this region, wind-stress curl transports water from the deeper nitracline up to the base of the euphotic zone. Nutrient fluxes in this region are smaller per unit area compared to coastal upwelling, but substantial in the aggregate because they occur over a much larger area. The combination of low-Fe upwelled waters in this domain and Fe drawdown during offshore Ekman transport leads to chronic Fe limitation in transition regions between the coastal upwelling and wind-stress curl domains (Hogle et al. 2018; King and Barbeau 2007; King and Barbeau 2011). *Fe-limitation and lower nutrient flux* select for smaller primary producers (e.g., mixotrophic flagellates and cyanobacteria) that compete more effectively for scarce nutrients (Goericke 2011a; Taylor et al. 2015). These small primary producers are regulated by small protistan zooplankton, leading to tighter coupling of growth and grazing and high nutrient recycling. The offshore region is characterized by strong density stratification (which is likely to increase as a result of climate change) and a deep maximum in chlorophyll *a* (and microbial biomass) at the base of the euphotic zone, where diminishing light meets the top of the nitracline. Upstream modifications to subsurface water masses, changes in the source water masses for upwelling, and variable ratios of coastal versus wind-stress curl upwelling all intersect to drive *long-term changes in the nutrient ratios* of upwelled water fueling ecosystem production (Bograd et al. 2015).

Modified biogeochemical properties, changing phytoplankton communities, and altered physical environments (including advection) drive *long-term changes in metazoan zooplankton communities*. Some taxa (e.g., low-latitude and mid-latitude euphausiids) show predictable responses to local mixed-layer temperatures or to large-scale physical forcing (Fig. 10). However, other taxa (e.g., salps and pyrosomes, Fig. 17), respond to unknown combinations of drivers yet exert substantial impacts on the ecosystem (Lavaniegos and Ohman 2003; Miller et al. 2019). These diverse zooplankton play important roles in top-down pressure on primary producers (Landry et al. 2009), as food for diverse fish species (Rykaczewski 2019), and in sequestering CO₂ in the deep ocean (Stukel et al. 2013).

The CCE region is a major spawning center for epipelagic fishes (e.g., Pacific sardine, northern anchovy, Pacific hake, and jack mackerel), many of which migrate extensive distances to spawn here in preference to upwelling centers elsewhere in the California Current System (Saunders and McFarlane 1997; Smith and Moser 2003). The preference for this habitat has been hypothesized to relate to the more retentive ocean circulation (Bailey 1981; Parrish et al. 1981). Large historical variations in landings of these fish have been attributed to the interaction of natural ecosystem variations and human fishing decisions (Hsieh et al. 2005; Jacobson et al. 2001; Rykaczewski and Checkley 2008). The CCE region is also an

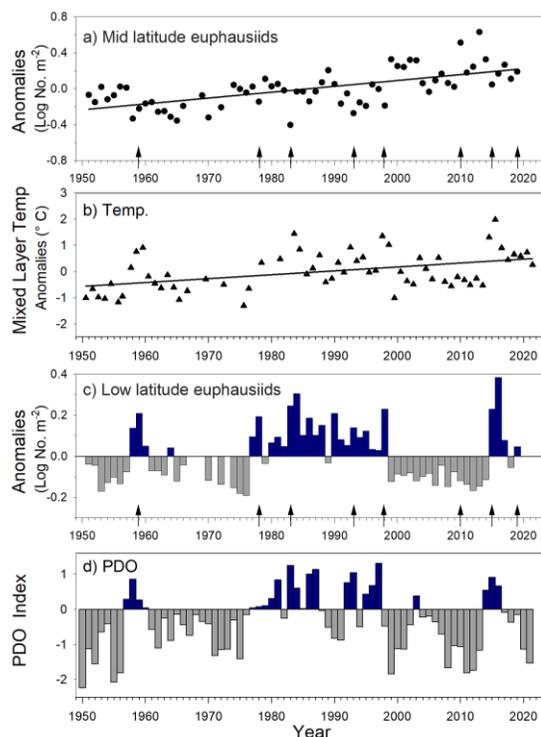


Fig. 10 – The abundance of mid-latitude euphausiid species (a) is strongly correlated with local mixed-layer temperature (b), while the low-latitude euphausiids (c) are better explained by large-scale forcing associated with the Pacific Decadal Oscillation (c). Arrows indicate El Niño years. Ohman, unpub.

important spawning habitat for mesopelagic (deep ocean) fishes, and CCE research has shown that the biomass of these fishes (myctophids, gonostomatids, etc.) is comparable to or greater than that of coastal epipelagic (fishes (Davison et al. 2015; Koslow et al. 2014; Netburn and Koslow 2018). Mesopelagic food web analyses and bioenergetic constraints suggest that these mesopelagic fishes may exert substantial predation pressure on vertically migrating zooplankton taxa (Davison et al. 2013; Kelly et al. 2019).

Although early research in the CCE suggested the possibility of alternate stable states in the ecosystem (Hsieh and Ohman 2006; McGowan et al. 2003), recent studies have not found evidence for positive feedbacks that would be necessary to stabilize alternate states. Rather, it seems that rapid transitions in zooplankton communities reflect linear tracking of altered circulation and *in situ* food web changes (Fig. 2, Model I), with temporal lags related to the life spans of the organisms (Di Lorenzo and Ohman 2013; Lilly and Ohman 2018). While substantial recent research in other ecological programs has sought to identify precursors of abrupt change (i.e., "tipping points", Carpenter et al. 2011; Dakos et al. 2015; Nazarimehr et al. 2020), the coarse temporal resolution of our longest population time series (quarterly zooplankton sampling) complicates this approach for CCE. However, we hope that recent high temporal resolution time-series based on autonomous platforms (satellites, moorings, and gliders) in the CCE region will allow us to diagnose such precursors in the future. Furthermore, the adoption of high-spatial resolution flow-through sampling (i.e., Imaging Flow Cytobot, Underwater Vision Profiler, explained in detail later) will allow us to utilize spatial statistics to investigate early warning indicators (Buelo et al. 2018; Majumder et al. 2019). Another important question that CCE will address in Phase IV is whether ecological transitions forced by extratropical MHWs (which have become a **dominant form of disturbance** in the past decade) behave similarly to those driven by ENSO variations. It is not clear whether extratropical MHWs will exhibit the same linear tracking responses that we have detected during ENSO variations.

Approaches to address four hypothesized mechanisms underlying ecosystem transitions

1) Along-shore transport: The importance of anomalous alongshore advection in driving ecosystem changes (e.g., dominance of mid- vs. low-latitude euphausiid assemblages, sudden emergence of pyrosome swarms) will continue to be addressed using a combination of observational and modeling approaches. *In situ* shipboard and autonomous *Spray* glider data will be combined with satellite altimetry to estimate geostrophic flows and diagnose north-south volume transports. These observations will also be incorporated into data-assimilative physical models (Edwards et al. 2015; Song et al. 2016; Zaba et al. 2020b) and correlation of alongshore velocity anomalies with indices of relative abundance of representative taxa will be tested. **As a novel part of this proposal**, we will also address the ways in which modified subsurface transport alters nutrient stoichiometry leading to synergistic effects with *in situ* food web changes (see Ecological Stoichiometry section below).

2) *In situ* food web changes: We will continue to utilize a *space-for-time exchange* approach (i.e., exploiting natural variability across the CCE region as an analog of how food web structures and rate processes will respond to temporal changes in environmental forcing) while also **adding new *in situ* multi-factorial experiments** to investigate responses of organisms at multiple trophic levels to modified temperature (e.g. **marine heatwaves**) and **nutrient stoichiometry**. Our experimental process cruises will target regions of different nitracline depths, phytoplankton floristics, and water-column structure (i.e., including coastal upwelling, wind-stress curl upwelling, and stably stratified domains). Our *space-for-time exchange* approach has recently been tested using results from process studies during the 2014-2015 MHW and 2015-2016 El Niño (Morrow et al. 2018). Modeling syntheses and time-series measurements (with **new retrospective elemental analyses planned**) will enable us to extrapolate results from multi-factorial experiments on our process cruises over broader spatiotemporal scales.

3) Cross-shore transport: This hypothesis was a major focus of CCE Phase III process studies; thus, continued analysis of these results will remain a priority in Phase IV. Anomalous cross-shore transport will be diagnosed by a combination of geostrophic flows from satellite altimetry plus ageostrophic flows (Chabert et al. 2021), data-assimilative models developed to specifically simulate circulation during our process cruises (Miller et al. 2015; Stukel et al. 2018c), and longer data-assimilative hind-cast products to infer spatiotemporal variability in cross-shore transport (Edwards et al. 2015). Alongshore transport will be partitioned into Ekman flow, eddy transport, and narrow coastal filaments and compared to distributions of taxa and biogeochemical properties measured on CalCOFI cruises.

4) Top-down pressure: This hypothesis **will be a major focus of CCE Phase IV** process cruise studies,

modeling approaches, and time-series analyses (see Variability in Top-down Pressure section below).

While we cannot currently reject any of our 4 major mechanisms (Fig. 3), evidence points to mechanisms #1 and #2 as the strongest causes of ecological transitions in the CCE. We hope that a heightened focus on mechanism #4 in CCE Phase IV and synthesis of field studies focused on mechanism #3 conducted during Phase III will determine whether these hypothesized mechanisms should ultimately be rejected, considered less important drivers, or are equally important causes of ecological transitions.

CCE Phase IV New Research Focus: Marine heatwaves (MHWs)

In the past decade, the CCE has experienced several long-duration marine heatwaves (Fig. 11, 12) that have the potential to fundamentally alter the relationships among the 4 alternative mechanisms underlying ecosystem transitions. We define MHWs as occurring when sea surface temperatures are >1.3 standard deviations above the detrended mean but note that this definition includes MHWs caused by different mechanisms, including ENSO events and extratropical MHWs (eMHWs, note that we use *MHW* as an inclusive term for multiple types of marine heatwaves and *eMHW* only for those with extratropical origins). eMHWs in 2014-2015 and 2019-2020 are associated with some of the highest surface temperature anomalies in the 70+ year CalCOFI time-series. eMHWs can persist for more than a year, have spatial extents covering thousands of square kilometers, lead to substantially increased stratification and depressed upwelling rates, and have a myriad of effects on biota at all trophic levels. These eMHWs are also “pulses” of warming that in some ways simulate future conditions (especially in the offshore domain) expected as a result of the “press” of anthropogenic climate change. **In CCE Phase IV, we propose a concerted effort to: 1) utilize continued time-series measurements to quantify the extent and magnitude of MHWs and their effects on biota, 2) use physical circulation models coupled to new biogeochemical models to mechanistically investigate the direct effects of MHWs on biota through altered temperature, circulation, and nutrient supply, and 3) conduct novel manipulative, multi-factorial experiments *in situ* to develop a process-level understanding of physiological responses to temperature and nutrient changes.**

Marine heatwaves in the CCE. Historically, El Niño-Southern Oscillation (ENSO) has been the dominant source of interannual variability in the CCE disturbance regime. However, eMHWs with distinctly different physical forcing mechanisms have had profound impacts on the system, with particularly strong eMHWs forming throughout the region in 2014-2015 and 2019-2020 (Fig. 12) (Di Lorenzo and Mantua 2016; Thompson 2019; Weber et al. 2021). While El Niños usually are associated with enhanced poleward transport of subtropical taxa into the ecosystem (Lilly and Ohman 2021; Lynn and Bograd 2002), some recent MHWs have originated in the extratropical North Pacific and are driven less by advection than by reduced energy transfer from the ocean to the atmosphere (Amaya et al. 2020; Bond et al. 2015). This leads to enhanced surface expression of warming and substantially reduced nutrient input into the surface layer, although the subsurface expression of recent eMHWs may be weaker than strong El Niños (Leising et al. 2015; Zaba and Rudnick 2016). The mechanistic link to sea-air energy dissipation also suggests that predicted long-term decreases in the thickness of the surface mixed layer may drive a long-term strengthening of eMHWs (Amaya et al. 2021). Definitions of MHWs are varied in the literature

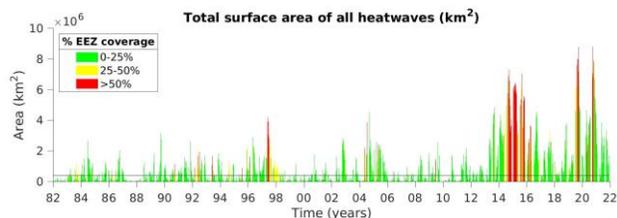


Fig. 11 – Total area and percentage of CCS experiencing a MHW from 1982 – 2021. A. Leising, unpub.

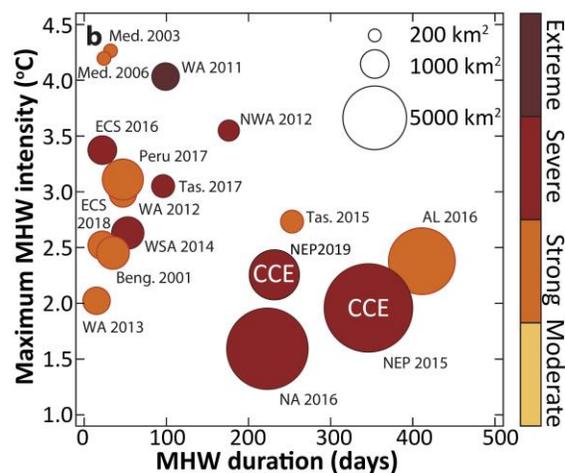


Fig. 12 – Comparison of northeast Pacific (NEP) eMHWs to other global MHWs (modified from Oliver et al. 2021). Color indicates severity of impacts.

(Hobday et al. 2016; Oliver et al. 2021), but the ecological impacts of recent MHWs have been profound in the CCE (see below) and globally (Cheung and Frölicher 2020; Jacox et al. 2020; Smale et al. 2019). MHWs are also having quantifiable socioeconomic costs (Smith et al. 2021) and are expected to become more frequent, intense, and have longer durations in the future as a result of increased baseline temperatures (Frölicher et al. 2018; Oliver et al. 2019).

Recent eMHWs are associated with decreased chlorophyll concentrations and **net primary production** (Kahru et al. 2018; Kelly et al. 2018; Morrow et al. 2018). They have also led to a shift towards smaller phytoplankton, a compression of the upwelling-influenced coastal domain, and unprecedented harmful algal blooms in the northern California Current (McCabe et al. 2016; McClatchie et al. 2016; Santora et al. 2020). These lower trophic level changes are likely related more to **reduced nutrient injection** than to a direct impact of temperature on organisms, because of the strong relationship between nutrient availability and phytoplankton biomass and community structure (James et al. in press and Fig. 13c, Fig. 14). Indeed, nitrate and chlorophyll concentrations at the CCE2 mooring location remained consistently low for the longest period in our time-series, 10-m depth nitrate concentrations were depressed across the CCE, and the nitracline deepened during the 2014-2015 eMHW (Lilly et al. 2019; McClatchie et al. 2016). However, temperature can also directly impact autotrophy-heterotrophy balances with respiration and heterotrophic processes typically increasing faster with warming than photosynthesis (Kvale et al. 2015; López-Urrutia et al. 2006; Marsh Jr et al. 1986; Rose and Caron 2007; Yang et al. 2018).

The 2014-2015 eMHW induced **substantial shifts in mesozooplankton and ichthyoplankton communities** that were qualitatively similar to shifts towards subtropical species as experienced during El Niño events (Lilly and Ohman 2018; Thompson et al. 2022). However, mechanisms driving population changes may differ between eMHWs and El Niños. Specifically, increases in subtropical zooplankton species in the CCE domain during El Niños are typically driven by anomalous poleward advection (Fig. 3, Mechanism #1), which was not pronounced during the 2014-2015 eMHW (Lilly and Ohman 2021). However, this eMHW allowed reproduction within the CCE domain of some subtropical species (e.g., *Euphausia eximia*) that rarely reproduce in the region even during El Niño events (Lilly and Ohman 2021). This could potentially lead to non-linear ecosystem responses (Fig. 2, Models II or III) to eMHWs in contrast to linear forcing that seems to prevail as a result of ENSO events. In contrast, temperate euphausiid species seem to respond to *in situ* food web changes (e.g., bottom-up forcing related to reduced upwelling and phytoplankton production; Fig. 3, Mechanism #2) leading to shoreward range contraction within the domain through similar mechanisms during both El Niños and eMHWs (Lilly and Ohman 2021; Robertson and Bjorkstedt 2020).

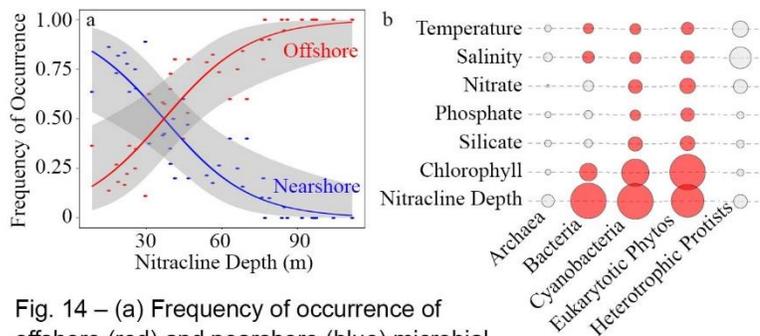


Fig. 14 – (a) Frequency of occurrence of offshore (red) and nearshore (blue) microbial communities in CCE as a function of nitracline depth. (b) Explanatory power of environmental variables with respect to abundance of different microbial groups. Size is proportional to explanatory power, red is significant. Modified from James et al. in review.

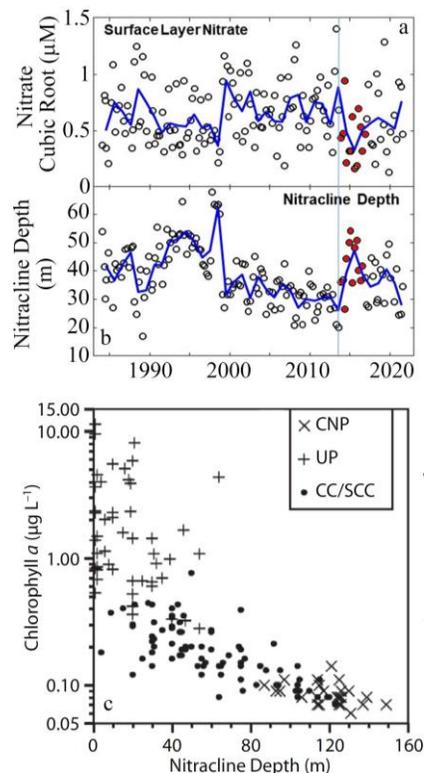


Fig. 13 – Response of average 10-m nitrate concentration (a) and nitracline depth (b) to the 2015-2016 MHW (updated from McClatchie et al. 2016) and the relationship between nitracline depth and Chlorophyll a (c, Ohman et al. 2013). Red symbols are from 2014-2015 eMHW.

Other subtropical taxa were also very abundant during the 2014-15 eMHW and subsequent El Niño (Cavole et al. 2016; Cimino et al. 2021; McClatchie et al. 2016), while the pyrosome *Pyrosoma atlanticum*, reached abundances not seen in the region since the 1960s (Lavaniegos and Ohman 2003; Miller et al. 2019).

Impacts of the MHWs were also seen at higher trophic levels, with ranges shifting north and reduced abundances of sardine, jack mackerel, and anchovy eggs in the CCE during the 2014-15 eMHW (Leising et al. 2015; McClatchie et al. 2016) although anchovy abundances have rebounded recently despite continued anomalously warm conditions and a typical preference of anchovy for cool periods (Muhling et al. 2020; Thompson 2019; Weber et al. 2021). The compression of the upwelling-influenced coastal habitat in 2014-15 led to unprecedented numbers of whale entanglements, as whales sought prey (anchovy) inshore and overlapped with crab fishing gear (Santora et al. 2020). In the Farallon Islands, seabird breeding success was depressed during the eMHW and novel species migrated into the region, while baleen whale abundances were lower in the CCE region during the 2014-15 eMHW and spatially restricted to the coastal domain (McClatchie et al. 2016).

Expected future impacts. The ability to diagnose the impact of future MHWs on biota is difficult because these phenomena have subjected taxa to conditions outside their historical ranges, thus making prior correlative relationships unpredictable (Muhling et al. 2020). We anticipate that MHWs will, like climate change, lead to **shift and shuffle of plankton communities** as species' ranges change at different rates in response to warming and **altered nutrient supply** and create phenological mismatches between predators and prey (Asch 2015; Asch et al. 2019; Barton et al. 2016). The seasonal timing of the MHWs can be particularly important for taxa with annual spawning periods (Shanks et al. 2020) and may also affect the persistence of the MHWs through feedbacks with seasonal mixed layers (Amaya et al. 2021). Primary drivers may also be spatially variable with the dominant bottom-up forcing (e.g., temperature or nutrient supply) depending on the nutrient status of the ecosystem (Hayashida et al. 2020).

The mechanistic impact of MHWs on populations depends in part on organism growth rates. For forage fish and top predators with longer generation times, the recent MHWs acted as strong **disturbances** to the system which altered their habitat directly (altered temperature and stratification) and through decreased prey availability (Morgan et al. 2019). For microbial populations with generation times on the order of days, MHWs are better viewed as a modification to the **disturbance regime**; i.e., an individual upwelling or vertical mixing event is a disturbance to the community and a MHW decreases the frequency of these disturbances (Flöder and Sommer 1999; Holbrook et al. 2020). The impact of MHWs on different organisms thus likely depends on the duration relative to their lifetimes, with bacteria and phytoplankton responding through community shifts while higher trophic levels respond either through migration or physiological adaptation with potential lagged responses to MHWs driven by changes in recruitment. Results from forests and coral reefs suggest that longer duration forcing events increase the probability of crossing an ecosystem tipping point (van der Bolt et al. 2018). Additionally, the rate of temperature increase may be potentially as important for taxa as the absolute magnitude of temperature anomalies because it constrains options for adaptation or migration. Although there is evidence that environmental variation is filtered through marine food webs to produce successively lower frequency variability at higher trophic levels (Barton et al. 2020; Di Lorenzo and Ohman 2013), we do not yet have a comprehensive understanding of how MHWs in particular influence population dynamics for a broad range of organisms with contrasting generation lengths, traits, and life history strategies.

Increased temperatures are also expected to modify biogeochemical properties of the ecosystem. We anticipate increased C:P ratios for phytoplankton under warmer, more oligotrophic conditions as a result of both physiological adaptations and community shifts (Moreno and Martiny 2018). Increased stratification and warmer temperatures are also likely to lead to decreased oxygen saturation, particularly in the mesopelagic (deep ocean) zone where an oxygen minimum zone already exists (Bograd et al. 2008; Weber et al. 2021). These impacts in the mesopelagic are likely to intersect with decreased sinking carbon supply to mesopelagic and benthic communities (Kelly et al. 2018) and hence the response of taxa to MHWs may depend on their ability to migrate (laterally and vertically) in the water column, potentially increasing their vulnerability to visual predators (Jacox et al. 2020; Koslow et al. 2011).

Hypotheses

- **eMHWs lead to spatial compression of coastal upwelling habitat and associated biota.** We will

use retrospective analyses of satellite time series (to diagnose spatial extent of eMHWs and impacts on phytoplankton) and CalCOFI and autonomous glider time series (to diagnose habitat usage by higher trophic levels). New ensemble model runs, combined with empirical-dynamical machine-learning will allow us to diagnose the mechanisms contributing to MHWs formation, investigate teleconnections that amplify MHWs, and predict the future intensity, frequency, duration, and spatial extent of MHWs.

• **Nutrient or food supply is of primary importance for lower trophic levels (phytoplankton, herbivorous zooplankton), which are only sensitive to expected temperature changes in the CCE when nutrients are replete.** Process cruises will serve as a platform for advanced multi-factorial analyses of organismal and community responses to altered temperature and nutrients through deckboard and novel *in situ* manipulative experiments. These will be combined with cutting edge transcriptional and physiological assays to address plasticity/tolerance of different taxa. While these experiments will allow us to manipulate conditions to simulate MHWs during “normal” periods, we anticipate that the frequency of MHWs will allow us to sample within a MHW during at least one of three planned process cruises. Retrospective time-series analyses will be used to diagnose relationships between abundances of different taxa and environmental drivers and to validate ecosystem models.

• **eMHW disturbances are more likely to lead to ecological transitions through *in situ* food web changes (rather than changes in advection as is common during ENSO events), and hence may lead to non-linear biotic responses to forcing (Fig. 2, Models II or III).** Our multi-faceted time-series (quarterly CalCOFI cruises, moorings spanning biogeochemistry to top predators, continuous autonomous glider surveys, satellite remote sensing, and pier-based coastal sampling) will continue to be crucial to observing and diagnosing the magnitude and ecological impact of MHWs. The long-term, spatially resolved CalCOFI time-series will be particularly useful (when combined with high-resolution mooring and satellite time-series) because it will allow us to assess biotic impacts of warming across time scales from short term intense warming events (e.g., days to weeks) to eMHWs, ENSO cycles, and long-term warming. Data assimilating model runs, coupled to new biogeochemical models will be used to quantify altered temperature and nutrient supply during past and near-future MHWs and impacts on biota.

CCE Phase IV New Research Focus: Ecological Stoichiometry

The elemental stoichiometry of nutrients supporting an ecosystem has the potential to structure marine and terrestrial food webs (Hessen et al. 2013; Sterner and Elser 2017; Welti et al. 2017). Limiting nutrients vary for different primary producers (Boyd et al. 2010; Lomas et al. 2004; Quigg et al. 2003), while the variability in elemental stoichiometry (i.e., ratios of different elements) of primary producers affects food quality and hence the relative success of and competition between herbivorous taxa (Cross et al. 2003; DeMott and Gulati 1999; Frost et al. 2006; Hall 2004). These consumers can, in turn, modify nutrient limitation patterns for autotrophs (Daufresne and Loreau 2001; Hillebrand et al. 2009), while the nutritional quality of autotrophs can affect decomposition, the rate of recycling within the ecosystem, and the amount of carbon storage within the ecosystem (Cebrian 1999; Hessen et al. 2004). Shifting nutrient stoichiometry can also control the competitive or mutualistic relationships between phytoplankton and bacteria (Danger et al. 2007). At the community level, elemental stoichiometry can vary as a result of cellular plasticity (e.g., reduction of metalloenzyme inventories or substitution of trace metals, Morel et al. 2020; Saito et al. 2011) or by replacement of populations with different elemental requirements. C:N:P ratios may also vary systematically with community growth rates (Elser et al. 2003). Stoichiometric plasticity is, however, typically much more substantial for primary producers than consumers (Sterner and Elser 2017). Shifts in autotroph stoichiometry can thus limit herbivore growth and alter the biogeochemical roles (e.g., as nutrient recyclers) of consumers (Andersen et al. 2004; Urabe et al. 2002). Organismal elemental balances affect such diverse processes as: photophysiology, sinking rates, expressions of mixotrophic behavior, organic matter exudation, symbiotic relationships, and viral infection rates (Armstrong et al. 2002; Behrenfeld and Milligan 2013; Brzezinski et al. 2015; Kranzler et al. 2019; Lagaria et al. 2011; Stukel et al. 2011b; Tuo et al. 2014) while altering prey selectivity patterns including switches from carnivory to omnivory (Denno and Fagan 2003). Furthermore, in the CCE, nutrient stoichiometry is a better predictor of ecosystem services (carbon export) than net primary production is (Stukel and Barbeau 2020).

In the CCE, the primary, potentially limiting elements for phytoplankton are nitrogen (available in the form of nitrate, nitrite, ammonium, urea, and dissolved organic nitrogen), phosphorus (available as phosphate

and in organic forms), iron (made bioavailable by a wide variety of Fe-binding ligands), and silicon (required by diatoms). Heterotrophic organisms can be limited by many of these elements, as well as organic carbon. The relative importance of these limiting nutrients varies in some predictable ways across the CCE productivity gradient (i.e., nutrient-replete in recently upwelled waters, followed by Fe-limited in transition regions, and N-limited in offshore areas, King and Barbeau 2011; Stukel and Barbeau 2020), although nutrient limitation patterns also vary with depth (Hogle et al. 2018), are redistributed and mixed by mesoscale circulation features (Stukel et al. 2017; Zaba et al. 2020a), and are modified by the physiological adaptations and activity of organisms spanning multiple trophic levels. CCE research has also demonstrated distinct processes altering water column stoichiometric balances on interannual timescales: deoxygenation is leading to increased rates of water column denitrification both locally and in the Eastern Tropical Pacific (upstream of the California Undercurrent) and hence reduced N:P ratios in the CCE (Goericke et al. 2015; White et al. 2019); Fe-limitation has increased in the region, potentially as a result of increased upwelling (Hogle et al. 2018); and modified source waters for upwelling have led to decadal scale changes in N:P and Si:N ratios (Bograd et al. 2015). Variable N:P and Si:N ratios in the California Undercurrent are particularly important, due to the current's role as source water for coastal upwelling (Bograd et al. 2015; Zaba et al. 2020a), and highlight the sensitivity of the CCE to tropical forcing. Notably initial analysis of these data showed a **long-term decline in N:P and Si:N ratios** (Bograd et al. 2015), although continued time-series sampling suggests more complex interannual variability (Fig. 15 a,b). These processes highlight the importance of **modified along-shore and cross-shelf transport (mechanisms #1 and #3)** in changing elemental ratios in the CCE.

Modified elemental stoichiometry intersects in complex ways with other changes in the ecosystem. For instance, recent MHWs have led to direct impacts of warmer temperatures, but also increased stratification and nutrient limitation; conditions strongly linked to increased C:N and C:P ratios (Lee et al. 2021; Martiny et al. 2013; Yvon-Durocher et al. 2015). Increased wildfire incidence produces aerosolized ash, which could become a substantial source of limiting elements to surface communities (Hamilton et al. 2021; Kramer et al. 2020; Wagner et al. 2021). The relative importance of wind-stress curl and coastal upwelling also varies on seasonal and interannual timescales (Pickett and Paduan 2003; Rykaczewski and Checkley 2008) and coastal upwelling likely supplies more Fe-rich waters due to interactions with the benthic boundary layer along the narrow shelf. Changing nitracline, phosphocline, and ferricline depths may also differentially affect stoichiometric ratios in the surface mixed layer and deep chlorophyll maximum, with commensurate impacts on food quality for zooplankton. Increased abundances of pyrosomes (colonial pelagic tunicates that filter feed at a high predator:prey size ratio) in the CCE during the most recent decade (Miller et al. 2019) likely modify nutrient recycling patterns, because these gelatinous herbivores can feed much more efficiently on picophytoplankton (the smallest autotrophs, which tend to have high C:P ratios). Altered zooplankton communities also likely intersect with bottom-up limitation of phytoplankton through the diel vertical migration patterns exhibited by many CCE taxa (Ohman and Romagnan 2016; Stukel et al. 2013); vertical migrators export material with very low C:N and N:P ratios from the euphotic zone, relative to sinking particles (Hannides et al. 2009). Modified prey quality may further affect the efficacy with which consumers regulate prey biomass leading to multiple impacts throughout the ecosystem and **altering top-down relationships (mechanism #4)**.

Hypotheses

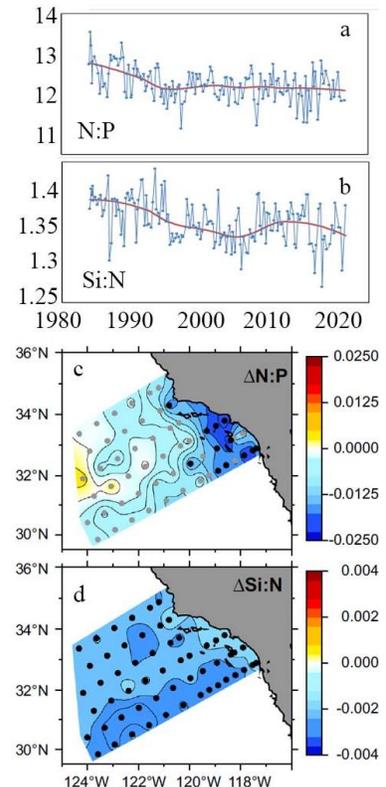


Fig. 15 – Timeseries of nitrate:phosphate (a) and silicic acid:nitrate (b) at station 93.3 at the $\sigma_{\theta}=26.5 \text{ kg m}^{-3}$ isopycnal (representative of California Undercurrent water that gets upwelled in the CCE) (updated from Bograd et al. 2015). (c and d) show linear trends in nitrate:phosphate (c) and silicic acid:nitrate (d) ratios (y^{-1}) from 1984-2012 at the $\sigma_{\theta}=26.5 \text{ kg m}^{-3}$ isopycnal (Bograd et al. 2015).

- **The ecosystem will become more N limited, but community C:P ratios will increase during MHWs and stratified conditions as a result of a shift in community composition.** We will test these two hypotheses using **new retrospective time-series analyses of seston and zooplankton C:N:P ratios** of archived samples from quarterly, spatially-resolved CalCOFI cruises (GF/F filters for seston; preserved net tows for zooplankton) from 2006 – present (continuing in future) in concert with phytoplankton population time-series measurements. We will also conduct **novel multi-factorial manipulative *in situ* experiments** (modifying temperature, N, P, and Fe) in different nutrient regimes (e.g., replete, Fe-limited, N-limited) to explicitly test nutrient limitation patterns, while measuring NPP, taxon-specific phytoplankton growth rates, nutrient uptake rates, protistan grazing rates, transcriptional changes, Fe-ligand availability, and taxon-specific stoichiometry using a sorting flow cytometer combined with an MS-ICP-MS (Fig. 16). Trace element concentration measurements in deep source waters for upwelling will be made on process cruises to determine baselines for micronutrient:macronutrient ratios for testing alternate hypotheses.
- **Metazoan zooplankton exhibit less variable C:N:P stoichiometry than protistan prey and have lower fitness when C:P and C:N ratios at the base of the food web are high.** We will test these hypotheses using **time-series analysis of seston and zooplankton C:N:P ratios** (see above). We will also conduct new **at-sea experiments with key zooplankton taxa (e.g., *Calanus pacificus*, *Euphausia pacifica*, and *Pyrosoma atlanticum*) to assess the stoichiometry (C:N:P:Fe) of their egesta and excreta** relative to their prey and to quantify their egg production rates (crustaceans only) to assess fitness relative to prey quality. **We will introduce the use of down-scaled multi-taxa plankton functional group models (e.g., SPECTRA, COBALT) in the CCE** to enable high physical resolution/high biological resolution models that contain multiple limiting nutrients to allow explicit hypothesis testing guided by experimental results.

New in CCE Phase IV: In situ multi-factorial experiments.

Environmental changes fundamentally drive physiological responses of individual organisms, which then affect growth rates (and for some taxa migration) leading to community succession and ecosystem transitions. **The resultant community shifts are clearly evident in our time-series data (e.g., Figs 10 and 17).** Biennial process cruises are a core component of CCE LTER, designed to investigate mechanistically the processes driving ecosystem change. **In Phase IV, we will focus on investigating the importance of multiple stressors on CCE biota using a multi-factorial experimental design (targeting physiological responses) coupled with a “space-for-time” sampling approach (investigating community shifts).** A core strategy of our process cruises is the use of a quasi-Lagrangian sampling plan (Landry et al. 2009; Stukel et al. 2015). Using *in situ* arrays tethered to satellite-tracked surface drifters and subsurface drogues designed to track the mixed layer, we will follow water parcels for 5 – 7 days. This allows repeated sampling of a single water parcel including rate measurements from phytoplankton and bacteria to metazoans using multiple complementary methods (Kranz et al. 2020; Morrow et al. 2018; Rivera et al. in review). It also allows us to relate measured rates to *in situ* net rates of change of

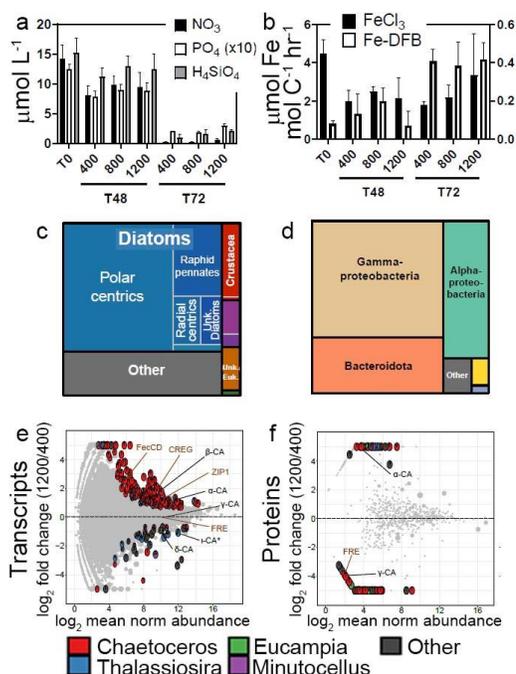


Fig. 16 – Example of some of the measurements that will be made during multi-factorial experiments (a) Nutrient concentrations at T0, T=48 h, and T = 72h. (b) Inorganic and organic Fe uptake rates. (c) Eukaryote community composition. (d) Prokaryote community composition. (e) Relative increase in transcript abundance of different genes for specific centric diatom taxa in incubations at $p\text{CO}_2 = 1200$ relative to $p\text{CO}_2 = 400$. (f) Relative change in protein concentration for specific centric diatom taxa in incubations at $p\text{CO}_2 = 1200$ relative to $p\text{CO}_2 = 400$. Results are from experiments assessing phytoplankton responses to modified CO_2 on CCE-P1908 Cruise (Lampe et al., submitted)

communities in the water column (Landry et al. 2009) for process-level understanding of community change.

A novel advance planned for CCE Phase IV is the introduction of *in situ* multi-factorial experiments conducted in paired clear acrylic tanks suspended from our *in situ* arrays at a single depth in either the mixed layer or at the deep chlorophyll maximum ('Process Cruise' section and Fig. 21). One of each pair of acrylic tanks will include two digital thermometers (one inside/one outside) linked to a heating element programmed to maintain a temperature +2°C relative to ambient (the other incubator will be at ambient temperature). Each tank will contain a suite of experiments with altered nitrate, phosphate, Fe, and protistan zooplankton abundances, and combinations of the above to enable multi-factorial experiments involving temperature, nutrient stoichiometry, and top-down grazer control. These experiments will be incubated for 1 – 5 days following which rate measurements (e.g., **net primary production, nitrate uptake and drawdown**, taxon-specific phytoplankton growth and protistan grazing rates) will be combined with quantification of **changes in microbial populations** (16S/18S sequencing) and transcriptomics patterns (see, e.g. Hogle et al. 2018). These manipulations will be conducted during 5 Lagrangian experiments in water parcels with distinctly different ecological communities and biogeochemical characteristics (i.e., spanning the gradient from newly upwelled nutrient-rich water to stratified oligotrophic conditions) on each of 3 process cruises. Cruises will target different seasons to maximize the ecological variability assayed by these experiments. A crucial goal of this sampling plan is to distinguish between changes observed in the ecosystem (e.g., on CalCOFI time-series cruises) that result from organismal plasticity and acclimation to local conditions versus selection of better suited organisms and changes in community structure. The utilization of transcriptomics measurements in concert with these multi-factorial experiments and process rate characterization of community responses will be crucial for informing modeling efforts and interpreting -omics results from CalCOFI time-series measurements.

CCE Phase IV Expanded Research Focus: Variability in Top-down Pressure in the CCE

Variability in top-down pressure is one of the four main mechanisms that we have proposed to drive **long-term change in populations** (from microbes to fish) in the CCE (Fig. 3). Research in the CCE region has addressed predation by epipelagic predators such as forage fish, seabirds, and blue whales on copepod and euphausiid populations (Koslow 1981; Nickels et al. 2018; 2019; Ohman and Hsieh 2008; Rose et al. 2015; Santora et al. 2017), while demonstrating distinct temporal variability in these predator assemblages linked to broader oceanic drivers (Rykaczewski and Checkley 2008; Sydeman et al. 2015). At lower trophic levels, we have shown that protists are the dominant herbivores in the region, although spatiotemporal variability in mesozooplankton (especially euphausiid) biomass can also exert top-down control on phytoplankton communities (Landry et al. 2009). CCE research has also suggested that bottom-up drivers typically dominate the system, although modified wasp-waist and top-down processes may be important during oligotrophic periods (Lindegren et al. 2018). Nevertheless, key questions remain related to the relative importance of top-down pressure on populations at different trophic levels and spatiotemporal variability in top-down and bottom-up drivers of the ecosystem. **In CCE Phase IV, we propose a concerted process-study and modeling effort that will leverage our existing time-series and data collected on future cruises to quantify top-down pressure across multiple trophic levels.**

Conditional top-down ecosystem control – **Bottom-up** (i.e., resource supply drives positive correlations between successive trophic levels), **top-down** (i.e., changes in higher trophic level consumers drive negative correlations between successive trophic levels), and **wasp-waist** (i.e., internal dynamics of intermediate trophic levels such as forage fish drive top-down impacts on lower trophic levels and bottom-up impacts on higher trophic levels) dynamics have all been hypothesized to control aquatic ecosystems (Boyce et al. 2015; Cury et al. 2000; Power 1992; Worm and Myers 2003). The relative importance of these controlling mechanisms likely vary in time and space (Hunt et al. 2002; Lindegren et al. 2018; Lynam et al. 2017). Several studies have suggested a dominant role for bottom-up dynamics in the Northeast Pacific (Chavez et al. 2003; Sydeman et al. 2009; Ware and Thomson 2005), although some Eastern Boundary Current upwelling regions exhibit evidence of wasp-waist dynamics (Bakun 2006; Cury et al. 2000; Rice 1995). Lindegren et al. (2018) synthesized hydrographic, climatic, biogeochemical, and multi-trophic level (phytoplankton to predatory fish, seabirds, and cetaceans) time-series data for the CCE from 1951 – 2010 and used a generalized additive model with threshold effects to investigate temporal variability in food web dynamics (Fig. 5). Their analysis suggests that the CCE is broadly regulated by bottom-up processes (upwelling and nutrient availability), although threshold-dependent top-down effects

(e.g., between mesozooplankton and phytoplankton) can be important for intermediate trophic levels during periods of low nutrient availability (e.g., during El Niño events). We refer to this process as “**conditional top-down**” ecosystem dynamics and consider it related to, but distinct from, evidence of temporal variability in top-down and bottom-up control found in other ecosystems (e.g., Hunt et al. 2002; Koltz et al. 2018; Menge et al. 2003; Whalen et al. 2013), while also noting that it distinctly differs from early predictions that top-down control would dominate at intermediate or high productivity levels (Fretwell 1987; Oksanen et al. 1981).

While this analysis yields intriguing insight into the system, it comes with distinct caveats associated with its coarse taxonomic resolution and focus on fish and euphausiids. Of particular importance for CCE are questions related to whether or not these patterns will hold if the analysis is expanded to include protistan grazers (dominant herbivores in the CCE, Landry et al. 2009) and a more diverse zooplankton community (including gelatinous filter feeders that have recently become dominant grazers in the system, Fig. 17). Furthermore, it is important to ascertain whether the patterns elucidated from the Lindegren et al. (2018) dataset (pre-2010) still apply in an ocean subject to increasingly frequent MHWs that may have substantially altered functional relationships in the system (e.g., emergence of anchovies during warm conditions; population booms of *Pyrosoma atlanticum* after 50 years of low abundance). The changes experienced in the system since 2010, combined with experimental and modeling studies, provide an excellent dataset for testing conditional top-down control of the ecosystem and ascertaining whether top-down control will become more dominant in a future (potentially more stratified) ocean, with concomitant impacts on the likelihood of linear versus non-linear ecosystem transitions (Fig. 2).

Predation on metazoan zooplankton – Metazoan zooplankton (particularly euphausiid species) are sentinels of change in the CCE (Fig. 10). In addition to bottom-up drivers and along- and cross-shore transport, **a modified predator landscape can potentially drive changes in these populations**. Historical records suggested alternation between sardine- and anchovy-dominated ecosystem states, with varying top-down pressure on individual species, but a consistently important overall predatory impact on zooplankton populations (Lluch-Belda et al. 1989). However, in the early-to-mid 2010s, sardine and anchovy abundances simultaneously dropped, potentially releasing copepods from predation pressure (Hill et al. 2017; Sydeman et al. 2020; Thayer et al. 2017). Subsequently and surprisingly, MHWs have been associated with an increased abundance of anchovies, which are usually favored during cool conditions in the CCE (Muhling et al. 2020; Thompson 2019; Weber et al. 2021). The processes that promote anchovy dominance in these warm waters and the top-down impact of modified epipelagic fish abundance on zooplankton communities are unknown.

In addition to forage fish (e.g., sardines and anchovies), metazoan zooplankton have a diverse suite of predators with distinctly different functional impacts on zooplankton communities. Mesopelagic (deepwater) predators, such as myctophids and siphonophores, that feed on vertically-migrating taxa with daytime residence depths of 200 – 500 m (Ohman and Romagnan 2016; Powell and Ohman 2015a; Stukel et al. 2013) have been shown to have substantial predation impacts in the CCE (Choy et al. 2017; Davison et al. 2013; Kelly et al. 2019; Koslow et al. 2014; Robison et al. 2020). Zooplankton vertical migration behavior is believed to be an adaptive response to minimize predation by visual epipelagic

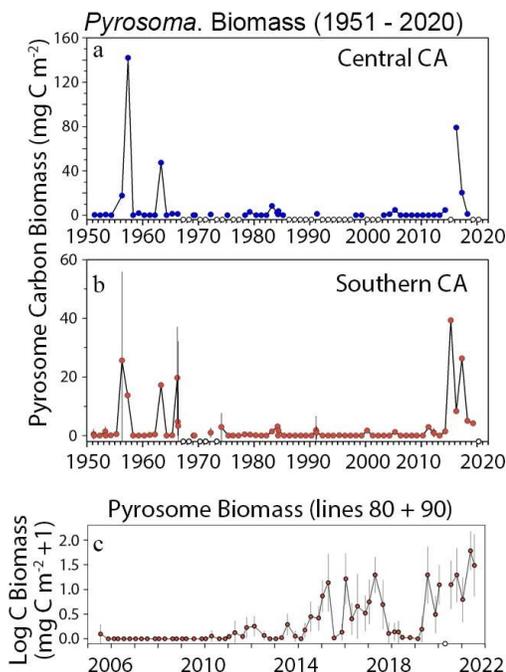


Fig. 17 - Pyrosome biomass in the Central California Current (a) and Southern California Current (b) measured in bongo tows with 505- μ m mesh over the past 70 years. Pyrosome biomass in the Southern California Current from 202- μ m PRPOOS net from 2006 – present (c). M. Ohman, unpub.

predators during the daytime (Gastauer et al. 2021; Ohman 1990; Ohman and Romagnan 2016) but it exposes vertically migrating taxa to extensive populations of mesopelagic predators (Davison et al. 2015; Netburn and Koslow 2018; Robison et al. 2020). The demonstrated high biomasses of these deep-water predators and the temporally varying abundances of epipelagic predators, suggest that foraging by these distinct classes of predators could drive top-down changes in zooplankton populations.

Baleen whales also consume substantial zooplankton biomass in the CCE, although their trophic roles may shift during different climatic regimes (Barlow et al. 2008; Fleming et al. 2016). They may also be exerting increased top-down pressure in recent years as a result of modified phenology leading to increased residence time in the CCE (Szesciorka et al. 2020). These whales appear to be selective for specific zooplankton taxa (e.g., *Thysanoessa spinifera*) with predation impacts concentrated around bathymetric features (Nickels et al. 2018; 2019). Similarly, temporally variable seabird populations may be highly selective for feeding on zooplankton and forage fish that aggregate near the surface. Seabirds are likely only minor predators in most years but can exert substantial mortality when prey populations are low (Saraux et al. 2021). Many other predators with distinctly different feeding ecologies (passive ambush predators (some cnidarians and ctenophores), active ambush predators (chaetognaths and some carnivorous copepods), filter feeders (whales, sardines), and cruise-feeding predators (several epipelagic fish)) likely intersect with zooplankton populations in distinct ways. We will use a trait-based ecology approach (e.g., Barton et al. 2013) to investigate the top-down impacts of these distinct functional groups.

Grazing and viral impacts on phytoplankton and microbes – CCE research showed that protistan grazing is the primary source of mortality for phytoplankton, although mesozooplankton grazing can be locally dominant, particularly within euphausiid swarms (Landry et al. 2009). During such periods of high mesozooplankton grazing, total grazing can substantially exceed growth causing strongly negative net phytoplankton rates of change (Landry et al. 2009). Food-web calculations suggest, however, that suspension-feeding mesozooplankton derive a substantial amount of their food from heterotrophic protists, a supposition supported by reasonably high heterotrophic:autotrophic ratios for nano- and microplanktonic protists (Stukel et al. 2011a; Taylor et al. 2015). This highlights the importance of intra-guild predation in the ecosystem, a process that may dampen top-down interactions and stabilize trophic dynamics. However, these bulk phytoplankton analyses obscure many more specific grazer-prey relationships. E.g., egg production rates (EPR) of *Calanus pacificus* seem to respond to total phytoplankton concentration, while EPR of *Eucalanus californicus* (also a suspension-feeding calanoid) correlates only with >20- μ m phytoplankton (Nickels and Ohman 2018). Both are likely exhibiting much more complex relationships with a diverse prey field and responding to diverse physico-chemical cues.

The above analyses of metazoan grazing have focused, primarily, on crustacean grazers. However, salps (comparatively large, filter-feeding, gelatinous taxa) are also periodically dominant grazers in the system (Lavaniegos and Ohman 2003; Smith et al. 2014), while the pyrosome *Pyrosoma atlanticum* has increased substantially in abundance since the eMHW of 2014-2015 (Fig. 17)(Sakuma et al. 2016). The latter deserves special attention, as it has recently become one of the biomass dominants in the California Current System from Southern California to Oregon (Miller et al. 2019). While some investigators have suggested that the outbreak in Oregon may have been an unprecedented response to warming (Morgan et al. 2019; O'Loughlin et al. 2020), *P. atlanticum* was also abundant in the California Current in the 1950s and 1960s (Lavaniegos and Ohman 2003), although its current persistence at high levels may be unprecedented (Miller et al. 2019). Either way, it is likely the largest perturbation in mesozooplankton communities during the CCE LTER era (2004 – present). These taxa have the ability to be dominant grazers (potentially removing >22% of phytoplankton standing stock per day) and are likely non-selective filter feeders that feed at a low trophic level, but may have higher retention efficiencies for larger protists (Drits et al. 1992; O'Loughlin et al. 2020; Schram et al. 2020). It is not clear what has caused the increased pyrosome abundance or whether that has altered top-down relationships in the system.

CCE research has also investigated the impact of viruses on microbial communities, finding that viruses may be responsible for ~40% of the mortality impact on phytoplankton that protists mediate (Pasulka et al. 2015). Furthermore, there is evidence that direct and indirect interactions between grazers and viruses may be significant enough to impact the dynamics of natural populations and regulate phytoplankton community diversity (Pasulka et al. 2015). Preliminary evidence suggests that protistan grazing has little impact on prey diversity, but that viral lysis increases microbial diversity (Fig 18, Schwenck et al., unpub.). Furthermore, viral lysis has indirect stimulatory impacts on phytoplankton growth likely mediated through

increased bacterial diversity. Further research is needed to fully understand the roles of viruses within these communities. The relative contributions of protistan grazers, metazoan suspension- and filter-feeders, and viruses to phytoplankton mortality also likely have different impacts on microbial diversity – a process that will receive greater attention in CCE Phase IV.

Hypotheses

- **Bottom-up dynamics dominate the CCE food web, with top-down processes becoming increasingly important during periods of low nutrient input (e.g., El Niños and eMHWs).** We will use generalized additive models as a tool for retrospective time-series analyses to analyze trophic relationships in greater taxonomic depth and over longer temporal ranges (e.g., Lindegren et al. 2018). *In situ* imaging platforms (e.g., UVP6, Zooglider, and newly introduced ISIS) and multi-frequency acoustic methods (EK-80) will be used to quantify abundances of epi- and mesopelagic predator abundances (e.g., Biard and Ohman 2020; Davison et al. 2015; Ohman et al. 2019). These will be coupled with prey encounter rate calculations to quantify predatory impact from predator abundance (e.g., Robison et al. 2020), vertical life tables to estimate mortality rates for copepod populations from time-series data, and mass-balance constrained ecosystem models (e.g., Kelly et al. 2019; Stukel et al. 2021) to assimilate available measurements and quantify grazing and predation by different groups. Novel **mechanistic forward models with Bayesian ensemble parameter estimation** will be used to investigate predation on mesozooplankton in the epi- and mesopelagic (e.g., Stukel et al. submitted).
- **Non-selective filter feeders (e.g., pyrosomes) and taxa that can switch between feeding on different trophic levels (e.g., anchovies) promote intraguild predation thus decreasing top-down control of the ecosystem, while protistan grazing and viral lysis promote greater microbial diversity than grazing by filter-feeding and suspension-feeding metazoans.** Viral and protistan grazing dilution experiments and metazoan gut content analyses, **newly combined with next-gen sequencing techniques** to quantify top-down control of microbial communities at the population level (e.g., Pasulka et al. 2015) will test this hypothesis. **Novel end-to-end coupled biogeochemical/food web models will be used to investigate temporal variability in trophic dynamics (Petrik et al. 2019).**

Core LTER Research Areas

In the course of our hypothesis-oriented research in the CCE-LTER site, we will continue to address core measurements held in common among all LTER sites. Many of these measurements are made in collaboration with CalCOFI during quarterly survey cruises (Fig. 19).

Primary production – Rates and patterns of primary production will be measured by ^{14}C uptake incubations on 4 cruises/year in collaboration with CalCOFI (Fig. 19, 1984 - present). In addition to *in situ* measurements, we have parameterized algorithms to estimate primary productivity from satellite remote sensing for this region (Kahru et al. 2015; Kahru et al. 2009). In Phase IV, our investigations of controls of primary production will include **multi-factorial experiments** quantifying the effects of irradiance, N, Si, Fe, CO_2 , and temperature on phytoplankton specific growth rates and ecophysiological responses. The roles of grazing pressure by nano-, micro-, and

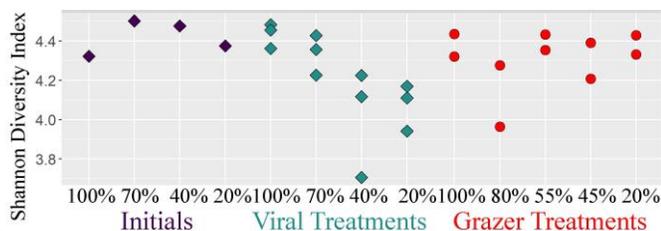


Fig. 18 – Results of protistan grazing and viral lysis treatments on microbial diversity (Schwenck et al., unpub.). % refers to percent unfiltered seawater in experimental treatment

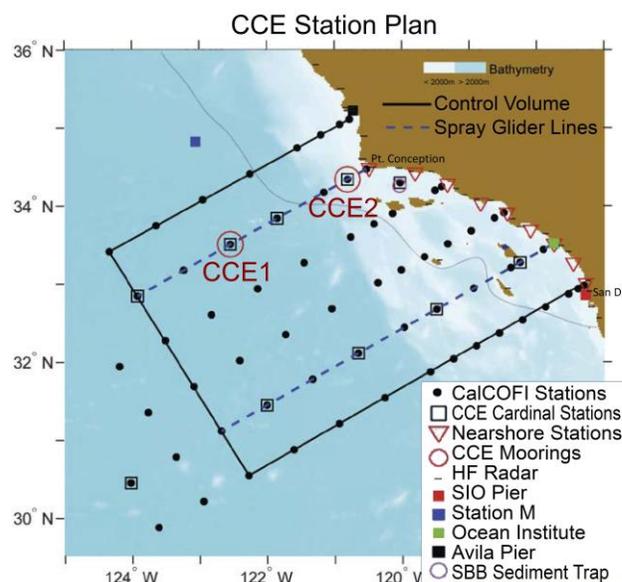


Fig. 19 – CCE time-series sampling plan.

mesozooplankton are also addressed on process cruises (Landry et al. 2009; Morrow et al. 2018).

Population dynamics and trophic structure – We focus on organisms representing different trophic levels as well as “sentinel species,” many of which provide excellent indications of ecosystem changes in the CCS. These organisms will be sampled or sighted (seabirds) on quarterly CalCOFI cruises, characterizing spatial and temporal variability, or observed acoustically at CCE moorings (marine mammals). Populations include: **Bacteria** – heterotrophic prokaryotes by flow cytometry (Taylor et al. 2015), populations by rRNA DNA barcoding (Valencia et al. 2022); **Phytoplankton** – *Prochlorococcus*, *Synechococcus*, and picoeukaryotes by flow cytometry and underway laser fluorometry (Chekalyuk et al. 2012; Taylor et al. 2015), phytoplankton pigments by HPLC (Goericke 2011b), eukaryotes by rRNA DNA barcoding and **underway imaging flow cytobot** (Hogle et al. 2018; James et al. in press); **Particle-feeding zooplankton** – selected species of copepods, salps, doliolids, and pyrosomes (microscopy, Lavaniegos and Ohman 2007); **Omnivorous zooplankton** – selected euphausiid species (microscopy); **Carnivorous zooplankton** – selected hydromedusae and siphonophores (microscopy); **Zooplankton functional groups and size classes** by Zooscan (Gorsky et al. 2010; Ohman and Romagnan 2016); **Zooplanktivorous fish** – Pacific sardine, northern anchovy, and jack mackerel (Southwest Fisheries Science Center); Seabirds – Sooty Shearwater, Cassin’s Auklet, Rhinoceros Auklet, Cook’s Petrel, and Black-vented Shearwater (at-sea observers, Sydeman et al. 2015).

Organic matter accumulation – We measure the rate of organic matter export from the euphotic zone on sinking particles using sediment traps and ^{234}Th : ^{238}U methods on our CCE process cruises (Stukel and Barbeau 2020; Stukel et al. 2019a) and have used these data to develop algorithms for estimating carbon flux time series from satellite remote sensing (Kahru et al. 2020; Kelly et al. 2018). We also quantify microbial communities in association with these sinking particles (Gutierrez-Rodriguez et al. 2019; Valencia et al. 2021) and both characterize the lateral fluxes of and quantify the chemical nature of non-sinking organic matter (Stephens et al. 2018). CCE associate, K. Smith (MBARI) quantifies organic matter deposition on the seafloor (3800 m depth) at the Station M benthic time-series station.

Inorganic nutrients and movements through the ecosystem – Changes in concentrations and fluxes of nutrients are addressed in our time-series, experimental, and modeling studies. Time-series observations on the quarterly augmented CalCOFI cruises address long-term changes in nutrient stoichiometry and source-sink dynamics (Bograd et al. 2015; White et al. 2019) as well as spatial controls of nutrient concentrations (NO_3 , NO_2 , NH_4 , $\text{Si}(\text{OH})_4$, PO_4), nutricline depths, nutrient input into the euphotic zone via upwelling and horizontal transport, and trace element limitation. Experimental process studies address nutrient fluxes from Thorpe-scale overturn analyses (Li et al. 2012) and trace metal (especially Fe) availability and utilization (Brzezinski et al. 2015; King et al. 2012). The CCE1 and CCE2 multi-disciplinary moorings further provide high temporal resolution measurements of NO_3+NO_2 covariance with physical processes in time series that have existed for 12 years. Horizontal gradients in nutrient concentrations, combined with volume transports from circulation models, permit us to calculate nutrient fluxes into and through our study site, to constrain the major sources and sinks of nutrients.

Patterns and frequency of disturbances – CCE taxa respond to disturbances on many timescales ranging from individual upwelling events (for microbial communities, responding on daily timescales) to El Niños and eMHWs (for krill and fish, responding to interannual forcing). Hence, we characterize disturbances across multiple scales using (1) the CCE1 and CCE2 moorings in the Southern California region (Figs. 19 and 20) together with *Spray* ocean gliders and continuous measurements from the Scripps pier, (2) high-frequency temperature and Chl *a* measurements from our Education, Outreach, and Capacity Building partners, the Ocean Institute (Dana Point, CA), California Polytechnic State University Poly (San Luis Obispo, CA) and from the Scripps pier, (3) satellite remote sensing of sea surface temperature and ocean color, (4) quarterly shipboard measurements of hydrographic, meteorological, biogeochemical, plankton, and ichthyoplankton characteristics, and (5) analyses of paleoceanographic proxies to characterize longer term (~2,000 year) variability from the varved sediment record of the Santa Barbara Basin (Field et al. 2006; Osborne et al. 2020).

Components of the CCE-LTER program

A core principle of CCE science is that intensive process-oriented experimental studies can be synthesized with modeling approaches to quantify functional relationships within the system, which can then be related to longer-term *in situ* and remotely sensed time-series measurements (Fig. 20). These

time-series measurements in turn serve as validation tools for improving models and for extrapolating the results of (spatiotemporally restricted) experimental studies and conducting retrospective analyses into past changes in the system. The CCE-LTER program is comprised of five components: **Experimental process studies, Time-series studies, Modeling, Information Management (IM), and Education, Outreach, and Capacity Building (EOCB)**. We briefly describe the first three here; IM and EOCB are described in their own sections below.

Experimental Process Studies – Three

CCE process cruises are planned for Phase IV, each of 31-day duration (fall 2023, summer 2025, and spring 2027). Each cruise will involve 32-34 graduate students, undergrads, scientists, and technicians, spanning diverse disciplines (plankton ecology, experimental physiology, bioacoustics, metagenomics and transcriptomics, seabird and mammal ecology, trace metal and organic geochemistry, biogeochemical fluxes, physical oceanography, and others). Cruises will be centered around five 5–7-day quasi-Lagrangian “cycles” of repeated activity while following satellite-tracked drogues in water chosen to represent regional spatial variability (Fig. 21, Landry et al. 2009; Stukel et al. 2015). This design allows extended time in coherent water parcels for detailed experimental work spanning biogeochemistry to higher trophic levels. Important components of the cruises include (1) daily depth-stratified (6 depths) *in situ* experiments to quantify **primary production**, phytoplankton growth rates, **nutrient limitation**, and zooplankton grazing rates (King et al. 2012; Kranz et al. 2020; Morrow et al. 2018); (2) novel multi-factorial ‘warming manipulations’ conducted *in situ* in the mixed layer or deep chlorophyll maximum to investigate microbial responses to modified temperature, nutrient stoichiometry, irradiance, and CO₂ using novel acrylic incubators deployed at depth with digital temperature sensors coupled with heating elements to maintain temperatures +2°C relative to ambient; (3) multi-factorial experiments conducted in deckboard incubators to enable diel sampling; and (4) new investigation of multiple aspects of higher trophic level ecology: zooplankton grazing rates, egg production rates, and vertical migration (Morrow et al. 2018; Nickels and Ohman 2018; Ohman and Romagnan 2016); abundances of fish and large gelatinous organisms (Davison et al. 2013; Lara-Lopez et al. 2012); investigation of mesopelagic communities (Biard and Ohman 2020; Netburn and Koslow 2018; Stukel et al. 2019b; Valencia et al. 2022); and quantification of biogeochemical fluxes (Bundy et al. 2016; Stephens et al. 2019; Stukel and Barbeau 2020). Phase IV process cruises will also rely heavily on cutting edge imaging and

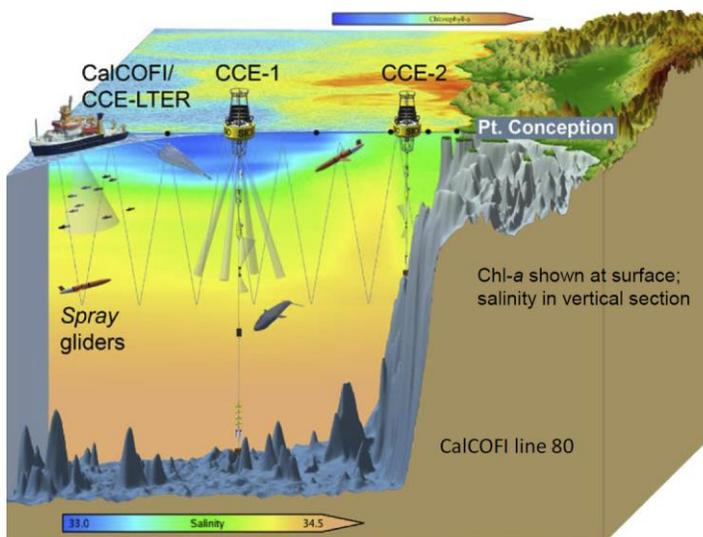


Fig. 20 – Integration of shipboard with autonomous measurements and 4D ocean modeling in the CCE region (Ohman et al. 2013).

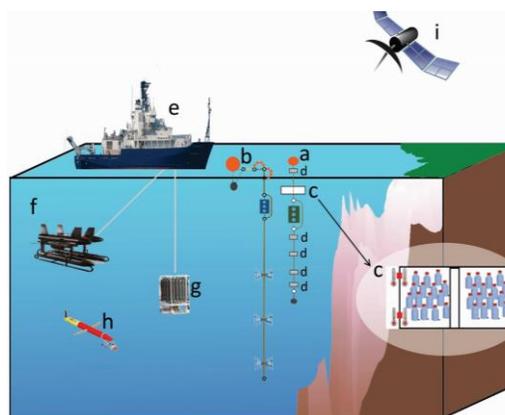


Fig. 21 – Overview of process cruises centered around quasi-Lagrangian experiments conducted near experimental (a) and sediment trap (b) free-drifting arrays. Experimental array includes a chamber for multi-factorial experiments (c and shown in greater detail in callout) and attachment points for 5 additional sets of *in situ* experiments (d) at other depths spanning the euphotic zone. Cruises will also feature a suite of imaging and acoustic devices that are either on the ship in flow-through configuration (e), towed (f), CTD rosette-mounted (g), or autonomous (h), along with traditional nets and sampling apparatuses. Cruise sampling will be guided by satellite remote sensing (i).

acoustic approaches to complement traditional sampling methods. We will use an Imaging FlowCytobot to image 10 – 200 μm protists (Kahru et al. 2021; Olson and Sosik 2007), an Underwater Vision Profiler to quantify 200 μm – 1 mm taxa (UVP6, Biard and Ohman 2020; Picheral et al. 2010), and an *In Situ* Ichthyoplankton Imaging System to quantify >1-mm metazoans (ISIIS, Cowen et al. 2013). We will also deploy the autonomous *Zooglider* near our Lagrangian drifters to investigate undisturbed zooplankton using built-in imaging and acoustic capabilities (Gastauer et al. 2021; Ohman et al. 2019; Whitmore and Ohman 2021) and use a ship-mounted multi-frequency acoustic system to quantify abundances and vertical distributions of zooplankton and nekton (EK80, Whitmore et al. 2019). These combined approaches will yield unprecedented ability to investigate depth-resolved trophic relationships from protists to fish to better constrain top-down pressure in the CCE. Additional details of multi-factorial experiments are in the ‘Multi-factorial experiments’ section above.

Time-Series Observations – We use diverse approaches to observe the state of the ecosystem and its changes over time and space. Most core LTER measurements are carried out in cooperation with the CalCOFI program using ships as sampling platforms (see core LTER Research Areas section above and CalCOFI section below). Other platforms, such as satellites, ocean gliders, instrumented moorings, a deep-sea benthic observatory at Sta. M (K. Smith), and shore/coastal stations acquire data at higher temporal and spatial frequencies to complement the shipboard sampling (Figs. 19 and 20 and separate section below on “Related Research Projects”). Our measurements can be characterized as (1) discrete in time (quarterly CalCOFI augmented sampling), or (2) semi-continuous (CCE1 and CCE2 moorings, *Spray* gliders along CalCOFI lines 80 and 90, satellite remote sensing, benthic fluxes, and nearshore observations). This approach allows us to observe at least some system variables at virtually all relevant temporal and spatial scales. A novel addition to our timeseries in CCE Phase IV is an increased focus on optical imaging using an imaging flow cytobot for underway sampling of protists (Olson and Sosik 2007) and a UVP6 for vertical profiles of mesozooplankton (Picheral et al. 2010) on quarterly CalCOFI cruises. These instruments will also provide timeseries that are directly comparable to similar measurements made by Northeast U.S. Shelf (NES) and Northern Gulf of Alaska (NGA) LTERs, respectively.

Satellite remote sensing of ocean color, sea surface temperature (SST), and sea surface height are important components of our time series, providing synoptic measurements of the CCE study region (CCE associate M. Kahru). The CalCOFI (and CCE-augmented CalCOFI) timeseries have been important testbeds for developing chlorophyll and net primary productivity algorithms for decades (Kahru and Mitchell 1999; Kostadinov et al. 2009; O'Reilly et al. 1998; Smith and Wilson 1981) and will be crucial in developing algorithms for ocean properties from next-generation satellites (e.g., PACE, Werdell et al. 2019). Merged, multi-satellite 1- and 4-km datasets of bio-optical variables including Chl *a* concentration and primary production are optimized for our region and updated and posted ~weekly (Kahru et al. 2015; Kahru et al. 2012b). Satellite remote sensing measurements contribute to our inferred trends in the LTER core variable of primary production rates (Kahru et al. 2009) and to our estimation of cross-shore fluxes (Fig. 3, Mechanism #3) (Chabert et al. 2021). Recent advances include satellite detection of dinoflagellate blooms (Kahru et al. 2021), quantification of variability of sinking particle flux and its temporal lags relative to net primary productivity (Kahru et al. 2020; Kelly et al. 2018; Smith et al. 2018), the importance of filaments to cross-shore transport (Chabert et al. 2021), light-mediated zooplankton behavior (Ohman and Romagnan 2016), and investigation of marine heatwaves and El Niños (Kahru et al. 2018).

Modeling – CCE modeling follows the principle that ecological advances proceed most rapidly when models are treated as hypotheses that are well matched to observational and experimental systems (i.e., model what you measure). We use a broad range of approaches including ocean and atmosphere circulation models, coupled ecosystem models of varying levels of spatial and biological resolution, ocean and ecosystem inverse models, and Lagrangian transport models.

Ocean and atmospheric circulation: With a physically forced, often bottom-up-driven ecosystem, CCE prioritizes accurate modeling of the atmosphere-ocean system. The main physical circulation model is the Regional Ocean Modeling System (ROMS) with multiple configurations for the CCS. The primary model domain for analysis of decadal and inter-decadal variability spans the central and eastern North Pacific 180°-110°W, 20°-62°N to incorporate basin-scale teleconnections and modified source waters and permit dynamical analysis of transitions between the CCS and neighboring regions. With ~5-km resolution this ROMS configuration also simulates realistic mesoscale dynamics and biological responses to eddies, fronts, and filaments (Chenillat et al. 2018; Chenillat et al. 2015; Cordero-Quiros et al. 2021).

Empirical-dynamical modeling: To complement the ROMS simulations and further explore the role of large-scale Pacific dynamics on the CCE ecosystem processes, we will use a novel ensemble of simulations with a Linear Inverse Model (LIM). The LIM is able to effectively capture the dynamics and evolutions of eMHWs (Xu et al. 2021) (**MHW focus**) and diagnose the relative impacts of tropical (e.g., ENSO) vs. extra-tropical teleconnections and drivers on the CCE (Zhao et al. 2021).

Passive tracers: To investigate changes in ocean transport associated with anomalous extreme conditions since 2010, we will use a 10-member ensemble of a coupled ocean-atmosphere regional climate simulation using ROMS coupled with the Weather Research and Forecasting Model. These model simulations (funded by another NSF project related to CCE) are seeded with passive tracers to now allow us to resolve and track upwelling processes and source waters for upwelling (**ecological stoichiometry focus**) and cross-shelf transport (**mechanism #3 underlying ecosystem transitions**).

Data assimilation: CCE pursues a wide range of different data-assimilation (DA) approaches to ensure accurate simulation of ocean circulation and ecosystem response. Multi-decadal DA using ROMS 4DVARS is used to assess ocean responses to climate variability including ENSO phases and MHWs (e.g., Edwards et al. 2015; Jacox et al. 2015). Shorter (30- to 90-day) dynamically-consistent sea-state estimates are used to interpret process cruise measurements within the context of four-dimensional ocean currents (Miller et al. 2015; Stukel et al. 2018c) and calculate annual and interannual variability in volume transport and heat budgets associated with El Niño and MHW events (Zaba et al. 2018; 2020b). In Phase IV, these DA models will be used to diagnose circulation differences between eMHWs and El Niño events and subsequent impacts on biota (**MHW focus**) and to quantify modified along-shore (**mechanism #1**) and cross-shore transport (**mechanism #3**). Unique to Phase IV, we will also use DA to constrain ecological parameterizations within biogeochemical models using a mechanistic Bayesian approach to assimilate rate and standing stock measurements (Stukel et al. submitted) and to constrain estimates of predation-mediated mortality in the epi- and mesopelagic (**top-down focus/mechanism #4**).

Biogeochemical and lower trophic level models: Previous CCE biogeochemical modeling focused on use of a moderate-complexity plankton functional group model (NEMURO) run within high-resolution circulation models to quantify the impact of mesoscale fronts and eddies on CCE biota (Chenillat et al. 2016; Li et al. 2012) and demonstrate the importance of accurate zooplankton simulation (Chenillat et al. 2021). However, the low biogeochemical resolution of NEMURO (which lacks P or Fe and has only two phytoplankton taxa and no heterotrophic bacteria) makes it insufficient for modeling biotic responses to changing elemental ratios (**ecological stoichiometry focus**) or simulating changes in photosynthesis-respiration balances as a result of **MHWs**. Consequently, in Phase IV we will use an ecological model with greater taxonomic resolution, (COBALT, Stock et al. 2020). COBALT, developed as a community model by the Geophysical Fluid Dynamics Lab contains heterotrophic bacteria, three phytoplankton groups, and three zooplankton groups (all with variable N:P:Fe ratios, **ecological stoichiometry theme**). GFDL COBALT has been run in a global, comparatively-low-resolution configuration. Because CCE research has shown the importance of high-resolution, mesoscale-resolving models for simulating our domain (Cordero-Quirós et al. 2019), we will use the global COBALT runs as boundary conditions for high-resolution California Current COBALT runs. The increased biological resolution provided by COBALT will be coupled to the incorporation of higher taxonomic resolution sampling in our timeseries using IFCB and UVP imaging approaches for protists and small mesozooplankton, respectively. This will allow us to assess impacts of *in situ* community changes on ecosystem dynamics (**mechanism #2**).

Phytoplankton-to-fish: To investigate the coupled climate-physics-biogeochemistry-ecosystem dynamics, we will use a high-resolution biogeochemical model for the CCE coupled to the novel FEISTY model (Petrik et al. 2019). This coupled system can examine the impacts of extreme events on marine organisms (**MHW focus**), changes in the plankton community composition on export and energy for higher trophic levels, and top-down predation pressure on plankton dynamics in a temporally varying ocean (**top-down focus/mechanism #4**). While the FEISTY model currently is one-way coupled to lower trophic levels, ongoing work is focused on two-way coupling to more accurately simulate the interplay of bottom-up and top-down controls on the ecosystem with CCE timeseries data used as a benchmark for assessing model accuracy. In a complementary approach, we will use inverse foodweb model approaches to assimilate new process cruise datasets (standing stocks and rates spanning nutrients to nekton) into mass-balance constrained phytoplankton-to-fish models (Kelly et al. 2019; Stukel et al. 2018b) to provide powerful data constraints on ecosystem carbon and nitrogen flows and predation by

different taxa (**top-down focus/mechanism #4**).

4. Regional, Cross-Site, and Collaborative Studies

Linkages to other LTER sites - CCE has a physical connection to Santa Barbara Coastal (SBC) LTER, as CCE includes sources of ocean forcing that influence their kelp forest site and SBC Associate Investigator M. Brzezinski is a collaborator with CCE (e.g., Brzezinski et al. 2015). CCE also has natural links to the three other pelagic LTERs (Palmer (PAL), Northern Gulf of Alaska (NGA), and Northeast U.S. Shelf (NES)) and has begun formal group meetings between these LTERs to discuss shared themes and ensure inter-comparability of data. CCE co-PI M. Stukel also participates in PAL cruises to maintain a carbon export time-series, while recent CCE graduate student T. Kelly is currently a post-doc at NGA. CCE scientists have also contributed to several cross-site synthesis studies. Most recently these collaborations include: Rastetter et al. (2021) highlighted the importance of long-term time series for discerning time lags in ecosystem responses; Harms et al. (2021) investigated long-term changes in organic matter fluxes in terrestrial, freshwater, wetland and marine ecosystems; Ducklow et al. (in review) synthesized results of marine LTERs in relation to climate variability and change. We are also pursuing cross-site analyses of impacts of MHWs and ENSO influences and look forward to expanding interactions with others in the LTER network.

Linkages to other networks and collaborative studies

CCE is active within the Southern California Coastal Ocean Observing System (SCOOS). SCOOS is a network of shore-based oceanographic sampling sites maintaining timeseries from the Mexican border to Point Conception, with the goal of providing scientific data needed to inform decision-making in coastal Southern California. CCE co-PIs and Associates also participate in a suite of measurements made at the Scripps pier and at the Cal Poly Pier through SCOOS. In a collaboration with the Santa Barbara Channel Marine Biodiversity Observation Network, Kahru et al. (2021) used satellite remote sensing to monitor the evolution of a coastal dinoflagellate bloom.

Members of CCE collaborate actively with others in the PICES community (the North Pacific Marine Sciences Organization). CCE participants have ongoing cooperative work with colleagues who work on other Eastern Boundary Current upwelling ecosystems off Mexico, Peru, and Chile. Recent joint work on stable isotope analysis has been done with a colleague in Brazil. Numerous collaborations in physical oceanographic modeling have been established with colleagues in Spain, Canada, and South Africa. Biophysical modeling, underwater imaging, Lagrangian structure analysis, biophysical modeling, and analysis of biotic effects of ocean frontal systems are ongoing with multiple people in France. We work actively on Trait-based Approaches in Ecology with a group in Denmark. We have participated in a broad international effort compiling marine particle size distributions from underwater imaging. We are part of an international publication advocating for quantitative observations of planktonic ecosystems. We regularly include colleagues from other countries in CCE Process cruises, most recently including scientists or graduate students from Ghana, The Netherlands, and France.

5. Related Research Projects

CalCOFI – The *California Cooperative Oceanic Fisheries Investigations* (CalCOFI) program provides 73 years of invaluable context measurements for CCE. CalCOFI is a consortium of NOAA Fisheries, the California Department of Fish and Wildlife, and the University of California (via Scripps), and is supported by NOAA. Our partnership with CalCOFI is fundamental to CCE, because this is the platform from which we sample most of our LTER core variables (primary production, nutrients, population studies, organic matter recycling), as well as their hydrographic context. There are 4 CalCOFI cruises per year, each covering a pattern of 66 stations in the CCE region (Fig. 19). In addition, two of those cruises sample 38 additional stations in the Central California region in winter and spring (the time of peak spawning of key clupeid fishes). A comprehensive suite of hydrographic and meteorological variables is measured at each station, to a high technical standard. CalCOFI supports sample processing, quality control, and digital posting of: CTD profiles, dissolved nutrients, O₂, Chl *a*, primary production, photosynthetically active radiation, Secchi depth, meteorological variables, and others. Zooplankton and ichthyoplankton have been sampled since 1949 and all samples are archived in the SIO Pelagic Invertebrate Collection and the Southwest Fisheries Science Center Ichthyoplankton collection. Total CO₂, alkalinity, and pH

measurements are made by the A. Dickson and/or T. Martz labs with separate funding.

With NSF support for CCE, we will extend CalCOFI cruises by 2 days each to take additional measurements and samples for “CCE-Augmented CalCOFI” and to ensure that offshore endmember stations are sampled. CCE augmentations include sampling for flow cytometry for heterotrophic and autotrophic picoplankton; phytoplankton community structure via taxon-specific pigments (HPLC) and rRNA DNA; metagenomic analyses of bacterial and protistan communities; particulate organic carbon, nitrogen, and phosphorus (**POP is new in CCE phase IV, but time-series will be retroactively developed from frozen samples**); zooplankton C:N:P (**also new to phase IV**); total organic carbon; finer mesh (202- μm) zooplankton samples for analysis by digital ZooScan (Gorsky et al. 2010; Ohman and Romagnan 2016); underway sampling of pCO_2 and pH; underway Advanced Laser Fluorometry characterization of phytoplankton pigments and variable fluorescence (Chekalyuk et al. 2012); underway phytoplankton sampling with **imaging flow cytobot** (IFCB, new in Phase IV, Olson and Sosik 2007); and mesozooplankton imaging with **vertically profiling UVP6** (also new in Phase IV, Picheral et al. 2010). CCE also supports costs for seabird observers on two CalCOFI cruises each year.

California Underwater Glider Network (CUGN) – The CUGN uses *Spray* gliders (Rudnick 2016; Rudnick et al. 2004; Sherman et al. 2001) for continuous observations along CalCOFI lines 80 (off Point Conception) and 90 (off Dana Point) in our study region. The CUGN started in 2005 and has been continuous on these lines since 2009 (Davis et al. 2008; Johnston and Rudnick 2015). *Spray* samples from 0-500 m, telemetering data ashore at each surfacing on 3-hr intervals. The present measurements are temperature, salinity, pressure, Doppler currents, acoustic backscatter (1 MHz), oxygen, and Chl-*a* fluorescence. The *Spray* gliders allow high spatial and continuous temporal resolution measurements that are important for characterizing ENSO variability in the system and responses to MHWs (Todd et al. 2011; Zaba and Rudnick 2016). CCE has also exploited their ability to detect zooplankton biomass to investigate responses of zooplankton to ocean fronts (Powell and Ohman 2015a; b). We also deploy additional gliders during CCE process cruises to aid in characterization of water parcels and for characterization of cross-shore fluxes (Zaba et al. 2020a). The CUGN is led by Daniel Rudnick (SIO), a CCE associate, and is supported by NOAA. Nearly real-time CUGN data and graphical displays are publicly available online.

CCE Interdisciplinary Moorings – CCE’s interdisciplinary mooring program has two deep-water moorings that sample the core of the California Current (CCE1, 4000 m depth) and the coastal upwelling region off Pt. Conception (CCE2, 770 m depth). These have been in place since Nov. 2008 and Jan. 2010, respectively, and are replaced annually with funding from NOAA (PIs Uwe Send & Mark Ohman; NSF supplies partial ship support through CCE). Data are telemetered in real time and posted publicly. Measurements include pCO_2 in the upper ocean and atmosphere, meteorological variables, temperature and salinity, dissolved O_2 , pH, aragonite saturation state by proxy (Alin et al. 2012), Doppler currents, nitrate + nitrite, Chl *a* fluorescence, turbidity, wavelength-specific light attenuation, and 190 kHz acoustic backscatter. The moorings are co-located with CalCOFI stations 80.80 and 80.55, respectively, allowing shipboard validation measurements four times per year and overlap with CUGN *Spray* glider measurements on line 80. High-frequency mooring measurements help us characterize the onset and decline of ENSO events and MHWs (Lilly et al. 2019), resolve upwelling events and the time variability of nutrient utilization and are used in our

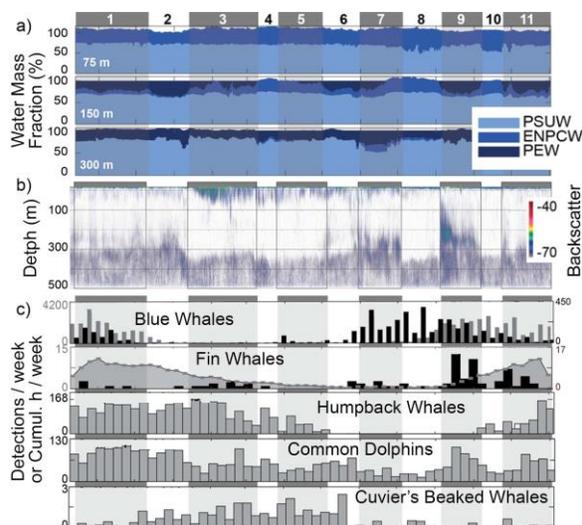


Fig. 22 – Occurrence of select cetacean top predators (c) in relation to epi- and mesopelagic prey (b) and water mass fraction (a) at the CCE1 mooring site. Blue, fin whale and common dolphin foraging were strongly related to high mesopelagic biomass during higher presence of the California Undercurrent. In contrast, the bathypelagic squid predator Cuvier’s beaked whale was foraging during higher influence of northern waters (Baumann-Pickering, unpub.)

studies of ocean acidification (Martz et al. 2014). Since 2006, the CCE2 mooring has been associated with a passive acoustic monitoring station for detecting odontocete echolocation signals, vocalizations of mysticetes, and the soundscape more generally (Hildebrand et al. 2021; Krumpel et al. 2021). These were developed using U.S. Navy, IOOS, and private foundation support and will now be deployed with NSF funding via CCE. These instruments provide high-frequency measurements of top predators in the system, to help quantify **variability in top-down forcing** (Fig. 22).

Deep-water sediment trap and abyssal benthic timeseries – Although not “essential” to CCE science, the Station M timeseries (led by K. Smith, CCE Associate) and Santa Barbara Basin Sediment Trap timeseries (led by R. Thunnell and C. Benitez-Nelson) provide 32- and 28-year timeseries, respectively, of carbon export flux to the deep ocean with ~2-week temporal resolution. The Station M timeseries also includes a suite of records of the abundance, diversity, and activity of benthic taxa, sediment community O₂ consumption, and other variables. In coordination with CCE and CalCOFI measurements, Station M has become one of the premiere benthic-pelagic coupling timeseries in the world ocean, documenting diverse phenomena including: the impact of specific pelagic zooplankton taxa (salps) on sediment community oxygen consumption (Smith et al. 2014); a substantial increase in the importance of episodic pulses of sinking particles for benthic communities (Smith et al. 2018); and the importance of a single diatom species for such episodic pulses (Preston et al. 2019). The Santa Barbara Basin timeseries allows analysis of long-term changes in denitrification and deoxygenation (Davis et al. 2019), impacts of ocean acidification on calcium-carbonate modulated export fluxes (Thunell et al. 2007), impacts of changing Si:N ratios on opal fluxes (Anderson et al. 2008), and changes in the occurrence of toxic diatoms (Umhau et al. 2018) and is complementary to paleo-reconstructions done from Santa Barbara Basin sediments by CCE, extending 1700 years (Brandon et al. 2019; Field et al. 2006).

6. Response to Midterm review

The review team was highly laudatory about CCE’s accomplishments and organization but identified the “primary vulnerability facing CCE” as a difficulty in elucidating (at the site review) 1) the ways in which CCE’s long-term data collections serve to address the site’s underlying questions about ecological transitions, and 2) how results from CCE contribute to understanding ecological process and theory. The review team noted that “there are many areas of ecology where CCE is making substantial contributions and discoveries, for example, in top down vs. bottom up drivers of community structure, ecological succession and trophic cascades, the role of competition in shaping communities, supply-side ecology, larval transport processes, the microbial loop, and carbon export to the deep ocean”, but found that the review team “had to infer connections between the data and the ecological processes of interest.” They concluded that this was “fundamentally a concern about how results are communicated, rather than problems with the research occurring at the site” and noted that “communication challenges were in part due to the ecological expertise of several committee members and NSF personnel compared to the oceanographic emphasis of the site.”

We believe that results from our unparalleled timeseries offer considerable insight into ecological processes in terrestrial, coastal, aquatic, and benthic, as well as pelagic ecosystems. We have thus taken care in this proposal and in recent publications to highlight important ecological themes emerging from the CCE timeseries. For instance: Lindegren et al. (2018) identified a new “conditional top-down” ecosystem control framework; Szesciorka et al. (2020) demonstrated long-term changes in phenology of blue whale migrations; Smith et al. (2018) identified long-term changes in benthic-pelagic coupling that may serve as a modification to the benthic disturbance regime; Kranzler et al. (2019), Kolody et al. (2019), and Diner et al. (2021) all investigated parasite-host relationships; Coale et al. (2019) elucidated novel diatom-bacteria symbioses; and Stukel et al. (2019b) and Whitmore and Ohman (2021) used a trait-based approach to quantify how zooplankton with different feeding strategies modify ecosystem function.

We also believe that our incomplete communication of some ecological connections stemmed, in part, from our focus in CCE Phases II and III on the importance of sub/mesoscale circulation as a disturbance regime (CCE II) and cross-shore transport mechanism (CCE III). Modified circulation has the potential to restructure population connectivity patterns and bottom-up forcing in pelagic ocean ecosystems in unique ways that differ substantially from terrestrial ecosystems. We failed to communicate these concepts effectively to terrestrial and freshwater aquatic ecologists. We believe that we are addressing this communication issue in part by more clearly elucidating **three new or expanded research foci for CCE**

IV that not only relate directly to the two overarching questions and four mechanistic hypotheses that drive our site research, but also allow us to test broadly relevant ecological theories:

- **Marine heatwaves:** Recent MHWs in 2014-2015 and 2019-2020 have caused extreme changes to the CCE and broader North Pacific. These events may be altering the **disturbance regime** in our system with uniquely different ecosystem impacts from ENSO, while also serving as analogues for similar disturbances and resilience in other biomes. Research in this area will focus on mechanisms of succession, physiological adaptation, and seasonal dependencies, while testing our hypothesis that populations show linear-tracking (Fig. 2, Model I) of physical forcing during abrupt ecological transitions.
- **Ecological stoichiometry:** Changing **nutrient stoichiometry** (identified through timeseries data and mediated in part by changes in along-shore and cross-shore transport) may be altering bottom-up processes in the CCE. Our research on this theme is guided by the rich theoretical framework of ecological stoichiometry theory (e.g., Sterner and Elser 2017; Van de Waal et al. 2018).
- **Variability in top-down forcing:** Recent technological and modeling advances will allow us to address top-down processes in much greater detail. Our research will be guided, in part, by the “conditional top-down” theory of Lindegren et al. (2018) stemming from 67-years of **population timeseries** data in the CCE. This focus builds on extensive ecological research elucidating bottom-up and top-down control mechanisms across many ecosystems (e.g., Costamagna and Landis 2006; Hunt et al. 2002; Menge et al. 1997; Munsterman et al. 2021; Rosenblatt and Schmitz 2016; Scheffer et al. 2008).

A second critique was that CCE was not sufficiently utilizing our “time series to increase replication and for retrospective analyses” and that we should “increase the generalizability of (our) work by retrospectively matching satellite information with the time-series sampling through CalCOFI.” We believe that this critique reflects a shortcoming in our communication, rather than a lack of research bridging the scales of our Process studies and time-series analyses. We consider the primary goal of our Process cruises to be elucidation of quantitative and mechanistic relationships that will allow us to interpret and model our timeseries data. This synthetic approach is exemplified in several recent studies:

- In a study directly linking process cruise measurements to 26 years of satellite remote sensing, Chabert et al. (2021) utilized satellite altimetry to determine water mass ages of the sampling locations on 8 of our experimental process cruises to show that water mass age was an excellent predictor of the balance between new and export production actually measured at sea and demonstrate correlation of the offshore extent of young waters with **ENSO climate forcing**.
- Stukel et al. (2017) used hydrographic data from *in situ* characterization of a mesoscale front to force a data-assimilating regional circulation model of the feature. By combining the model with extensive process cruise measurements spanning nutrients to zooplankton and our autonomous glider time series they show that the fronts are regions of substantially enhanced **downward organic matter flux**.
- Hogle et al. (2018) utilized Fe addition experiments and metatranscriptomic analyses of phytoplankton taxa to show that subsurface chlorophyll maxima are consistently Fe-limited and conducted a retrospective analysis of CalCOFI time-series data based on biogeochemical proxies determined from previous CCE research to find a multi-decadal increase in the size of the subsurface Fe-limited domain.

We plan to address this criticism further in Phase IV by using satellite data to diagnose mesoscale features such as fronts, eddies, and filaments (e.g., Kahru et al. 2018) and matching these features to CCE sampling locations (on CalCOFI timeseries cruises and CCE process cruises) to quantify the impact of these features on biological communities from phytoplankton to fish. We will also use satellite observations to classify CalCOFI sampling stations relative to MHW dynamics (is the station experiencing a MHW? of what magnitude, duration, and spatial extent?) for assessing biotic responses to MHWs.

7. Results of Prior Broader Impacts, Supplemental Support, and Information Management

CCE-LTER’s Education, Outreach and Capacity Building (EOCB) program provides opportunities for local and national audiences to engage with the scientific practices utilized and data generated by the site. The multi-dimensional EOCB program at CCE engages the public and K-12 audiences through a partnership with Birch Aquarium at Scripps (BAS), the public outreach center for Scripps Institution of Oceanography (SIO); a collaboration with the Ocean Institute, a nonprofit educational center in Dana Point, CA; Research Experiences for Teachers (RET); and a Research Opportunity Award (ROA). CCE research and findings are incorporated into undergraduate and graduate classes and the site hosts a Research Experience for Undergraduates (REU) program each summer. The site also engages the public broadly

through presentations by CCE students, PhD's, and staff, media appearances on topical ocean issues and access to site information including glider, mooring, and remote sensing data and imagery.

CCE's collaboration with BAS has continued during Phase III. The current EOCB coordinator is Cari Paulenich who also serves as Program Manager of Public Engagement at BAS. C. Paulenich coordinates CCE outreach efforts, working with site PIs (M. Ohman, K. Barbeau), site personnel, and students to support the education and outreach efforts of the site. The relationship between CCE and BAS allows the site to leverage the reach and science interpretation strengths of the aquarium. BAS served approximately 450,000 guests per year until 2020, and has continued to provide programming and services to guests throughout the pandemic.

Through efforts at BAS, CCE graduate students shared their work around plankton ecology with the general public at Full Moon Pier Walks (over 1930 guests) and at SEA Days events (over 1800 guests). Graduate students and researchers also participated in Exploring Ocean STEM Career Nights for middle and high school students (420 students), serving on panels and facilitating hands-on stations featuring their work and discussions of their career pathway. CCE graduate students and EOCB staff partnered with a high school teacher in San Diego to develop a multi-series of lessons focused around El Niño in the California Current, allowing authentic exploration of CCE data. CCE-LTER hosted Teacher Professional Workshops from Spring 2017-2019, entraining a total of 47 teachers from Southern California in content and research methodologies used by the site and the teachers received NGSS-aligned curriculum to implement in their classrooms and share with their educator networks. Teachers who participated in the workshops continued to engage with the site, including participating in virtual programming opportunities during the pandemic. When the site was unable to host the workshop due to COVID-19 restrictions, the EOCB coordinator continued to support teachers online as they implemented curriculum in their classroom.

CCE-LTER hosts multiple REU students each summer, with two participants funded by NSF REU funds and additional participants supported with institutional funds. Students are recruited from the Southern California region with a focus on students from groups underrepresented in STEM. The REU students are partnered with a host lab and receive guidance from a dedicated mentor throughout their experience. During their time with CCE, the REU students may participate in shipboard research, data analysis, modeling, etc. The pandemic necessitated a move to a virtual format to allow for students to remain connected with the site while ensuring safety.

CCE-LTER continues to partner with the Ocean Institute, a private ocean education facility in Dana Point, California focused on ocean science and maritime history. They offer two programs that feature connections to CCE research and the students who participate in their hands-on programming are taught to collect samples and data that are shared with CCE scientists. The site continues to collect data for the Ocean Institute Chl-a time series through their weekend public experiences.

Education and outreach efforts extend beyond Southern California. At Cal Poly in San Luis Obispo California, undergraduate students are trained in data collection methods to assist with time series on the Cal Poly pier. At Florida State University, researchers and graduate students developed and taught an online "inter-session" course for high school students at the Illinois Math and Science Academy. This course featured lectures followed by group projects using oceanographic datasets related to modules about marine primary production and the biological carbon pump. For each module, one of the datasets was drawn from CCE core datasets.

Category	Grad. Students	Post-docs	REU	UGrad Other	Technical Staff	Cruise Volunteer	Teacher RET	High School Courses	UGrad Course	Grad Course
SIO/ UCSD	53	8	28	17	17	8	1	1	5	11
Other Institutions	13	1	2	7	4	40	1	1	1	3
Total	66	9	30	24	21	48	2	2	6	14

Supplemental Support - Research Opportunity Award (ROA) – The aim of this award was to measure diel phytoplankton growth and grazing mortality rates in the CCE region, providing a research experience

for Dr. Darcy Taniguchi, an assistant professor at California State University San Marcos (CSUSM), a Minority-Serving, Primarily Undergraduate Institution, and for REU student Anissa Garcia, a female Hispanic American. Ms. Garcia completed four diel experiments on the CCE P2107 Cruise. Preliminary results indicate greater day-night variability in the nearshore and offshore regions, with smaller diel differences in between. These results will be shared by Ms. Garcia at the 2022 Ocean Sciences Meeting. The Taniguchi lab is also working to identify the dominant protistan groups at each sampled station. These data and the experimental methods used to measure phytoplankton growth and grazing mortality are being incorporated into outreach materials, including with BAS and in high school lesson plans.

Supplemental Support - Research Experience for Teachers (RET) - CCE-LTER received a RET supplement in Spring 2020; however, due to the pandemic, the program was initiated in Summer 2021. Rosina Garcia, a STEM middle and high school teacher from the San Diego Unified school district is our RET. San Diego Unified school district is the second largest public school district in California and serves approximately 120,000 students from more than 15 ethnic groups. CCE has introduced Ms. Garcia to the site and its research. CCE Graduate students will work with her in Winter 2022 to develop a series of lessons for piloting in her classroom that can then be distributed broadly, ensuring authentic data lessons. In summer 2022, we will engage Ms. Garcia with scientists and REU students directly so she can take those experiences back to her classroom. We anticipate collaborating with Ms. Garcia and her classroom well beyond the RET.

Equipment Supplement - After conducting a cross-site discussion to assess the most pressing needs for permanent equipment that would permit CCE scientists to complete their commitments during Phase III studies and beyond, we identified five pieces of permanent equipment of highest priority: 1) an Underwater Vision Profiler 6–HF, for *in situ* imaging of planktonic organisms and marine snow, obviating the need to borrow a UVP5 from colleagues, as we have done in the past; 2) a non-metallic sheave block and wire rope for Trace Metal Biogeochemistry, to replace the present assembly that has reached end-of-life; 3) a Suntest XLS+ irradiation lamp with controlled wavelength outputs to conduct organic matter photooxidation experiments at sea; 4) a Jasco FP 4025 Fluorescence detector, to quantify ammonium *in situ*; and 5) a Stirling Ultracold -80 freezer to hold important CCE samples taken for a variety of studies. All items of equipment have been ordered and have either been delivered or will be shortly.

Data Availability

Information Management (IM) continues to play a vital role in CCE-LTER research, education, and public outreach activities. In March 2021, CCE-IM transitioned to a new Information Manager, Marina Frants, a PhD oceanographer and professional data analyst. As of January 2022, there are 95 datasets (totaling 128 data tables and related metadata) in Datazoo, the central CCE data repository. All of these datasets are also publicly available in the Environmental Data Initiative (EDI) repository and BCO-DMO (see attached supplementary document). In addition to Datazoo, CCE-LTER maintains several specialized websites indexed in Datazoo that provide visualization tools and download ability for specific data sets including several zooplankton databases (Zooplankton Database (ZooDB), Brinton and Townsend Euphausiid Database (BTEDB), Zooscan Database (ZooscanDB)) and towed profiling vehicle databases (Moving Vessel Profiler and SeaSoar data). Further information is given in the Data Management Plan below. In the past two years, Datazoo has recorded >4800 site access events from >1200 unique users (see Data Management Plan). Dr. Frants is a member of the CCE-LTER Executive Committee and works in close collaboration with project researchers and staff. In Phase IV, we will continue to maintain high IM standards while expanding the range of available data products. Additional details are in the *Datasets* and *Data Management Plan* supplementary documents.

8. Broader Impacts

We will increase the reach of the CCE-LTER site over the next six years through activities and programs that address the research foci of the site while continuing to build upon our programming success with Birch Aquarium at Scripps (BAS), the public outreach center for SIO, and with our outreach partner, the Ocean Institute. EOCB efforts will also take place at our partner institutions, encouraging an audience outside our immediate research area to learn about the work conducted by CCE.

The CCE-LTER site will support a new program in development at BAS, in partnership with the San

Diego Unified School District. This experiential program will engage K-12 students in authentic experiences both onboard a ship and along the San Diego Bay waterfront, connecting students with careers in blue tech and the research domain. As the second largest public school district in the state of California, San Diego Unified serves more than 121,000 students from 15 ethnic groups who speak over 60 languages and dialects. This new program will take place in a location central to the entire district, allowing greater access for students from communities underrepresented in STEM, including those who have traditionally faced barriers in traveling to the UC San Diego campus in La Jolla, CA. Graduate students and researchers with the CCE site will serve as content and technical consultants during the development phase of the project (Years 1 and 2), while refining their own science translation skills as they work with BAS educators to support curriculum for K-12 audiences. As the curriculum will allow K-12 students to get on the water and take measurements that are representative of the work CCE does, consultation and experiences with seagoing scientists is key to make the experiences as authentic as possible. Station themes may include: plankton identification and ecology, ocean food webs and carbon transport, and impacts of changing ocean conditions, like marine heatwaves and ocean acidification, on ocean ecosystems. Additionally, the site will provide professional development for the educators at BAS, expanding their understanding of site research processes and preparing them for disseminating the experiences with students. This will include detailed descriptions of research cruise activities, exploration of authentic data, and training on various content areas. As the program moves forward, CCE site members will engage with participating teachers and students to strengthen the connection between research conducted at the site and the local community (Years 3-6). This may include graduate students and researchers participating directly in programs as a scientist-expert aboard the vessel. The opportunity for graduate students and researchers to participate directly with the students will allow them to refine their science communication skills and develop hands-on components that they can take to other outreach opportunities.

To support the continuation of the STEM pipeline, members of the CCE site will also engage with K-12 students during non-school time, including in summer camps, through lab tours, career chats, and facilitation of hands-on interactive science activities. These programs will provide students access to more in-depth engagement with the scientific enterprise and facilitate exploration of individual interests in ocean science. With the loss of learning due to the pandemic and the challenges associated with maintaining hands-on activities in a remote setting, interest and support for out-of-school experiences has grown. During sessions facilitated by BAS and taking place on the Scripps Institution of Oceanography campus, middle school students will connect their experiences in the water to site research and the individuals who collect it. We will encourage all levels of CCE personnel to participate, and work to ensure that the K-12 students see themselves reflected in the site participants.

The opportunity to engage with scientists, on a personal and local level, is more important than ever. We will continue to participate in public events aimed at learners of all ages, encouraging scientists to use sound interpretive practices to make the research accessible to all. These events include Sunset Pier Walks (BAS) during which the general public is invited to explore a working research pier while engaging with CCE research and the opportunity to learn about the Chlorophyll-Temperature Time Series via boat tours at the Ocean Institute. Graduate students and researchers will continue to provide outreach to local groups and media around relevant ocean science topics.

We will continue to support the REU program with program funds and continue to leverage institutional resources to support this program. Through targeted outreach to regional community colleges and Hispanic-Serving Institutions, we will seek to recruit students from groups traditionally underrepresented in STEM. We will encourage this next generation of scientists to engage in Education and Outreach opportunities and REU students will meet with members of the CCE site to learn about the multitude of pathways available to them, including the role of education and outreach, in scientific research.

CCE seeks to engage with the local indigenous community and recognizes the importance of native knowledge in scientific endeavors. We aim to develop a working partnership with the UC San Diego Intertribal Resource Center and the Native American Student Alliance to facilitate sharing of knowledge and resources. CCE also intends to participate in events at BAS celebrating the local Kumeyaay community and conduct outreach efforts to audiences such as the Kumeyaay Community College to share site research efforts and experiences while also hoping to broaden participation in site activities.

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