Physical oceanographic mechanisms associated with recent ecological responses in the California Current Ecosystem

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Abstract. The California Current System (CCS) is an upwelling eastern boundary ocean current that supports a productive ecosystem through a multitude of physical processes. The fundamental aspects of the ocean circulation are highlighted here and connected to their roles in driving and modulating various components of the California Current Ecosystem (CCE) in the context of pulse and press disturbances. Recent short-term climate events (pulses), such as marine heat waves, that generated highly anomalous responses in the ecology are identified and explained in terms of physical process drivers. The long-term vulnerability of the ecosystem to long-term climate changes (presses) is also discussed. The need for ecologists to collaborate with physical scientists to unravel the press vs. pulse impacts on the CCE through sustained physical-ecological observations and high-resolution modeling is emphasized.

1. Introduction

The California Current System (CCS[1]) flows equatorward along the western coast of North America, spanning a broad eastern swath of the North Pacific subtropical gyre (Hickey 1998, Checkley and Barth 2009). As one of the four major eastern boundary upwelling systems (EBUS), including the Peru-Humboldt, Benguela, and Canary current systems, it is characterized by seasonal upwelling, cool sea surface temperatures (SST), and high biological productivity (Chavez and Messié 2009). Though covering a relatively small region of the global ocean, the intense upwelling and other frontal-scale processes associated with it provide nutrients for biological activity in the productive California Current Ecosystem (CCE[1]).

The vigorous physical oceanographic and climate variability of the CCS exerts a profound influence on biological dynamics (e.g., Ohman et al. 2013). Wind-driven upwelling along the coast and offshore draws cold, nutrient-rich waters from depth into the sunlit surface layers, stimulating phytoplankton growth and cascading through food webs to support zooplankton,

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[1] In this discussion, we use the term California Current System (CCS) to refer to the physical components of the circulation and the term California Current Ecosystem (CCE) to refer to the ecological components.

forage and top predator fish, seabirds, and marine mammals. This nutrient supply is highly variable and governed by a rich tapestry of physical processes that vary over a multitude of time scales. In a purely ecological context, Bender et al. (1984) describe pulse disturbances as short-term alterations of species numbers followed by a return to the preexisting conditions, whereas the press disturbances are sustained changes to species densities. Here we consider a generalized version of this definition, in which a pulse disturbance is one in which the disturbance agent (herein we mostly consider changes to ocean physics, although other biotic and chemical disturbance agents exist in the CCS, see Stukel et al. 2025) is short-lived relative to the relevant life spans of the community or population of interest. Conversely, a pulse disturbance is one in which the disturbance agent acts continuously over a period of time that is long relative to organismal life spans. Thus from an ecological perspective, these physical forcings provide pulse and press disturbances depending on the time scale of the forcing and ecological response time (e.g., Ducklow et al. 2022). For example, since phytoplankton life spans are order of days to weeks while Pacific hake have a life span of ~15 years, an El Niño event (typical duration of one year) would be considered a pulse disturbance when studying Pacific hake populations, but a press disturbance (or alternately a change in the disturbance regime) when investigating phytoplankton responses (Fig. 1).

Physical circulation also fundamentally shapes ecological communities through two additional mechanisms: modified alongshore currents and modified cross-shore currents. The former impacts the advection of different biological communities into regions of the CCS and can be particularly important in the southern CCS (e.g., the Southern California Bight) which is a biogeographic boundary region. The latter is closely linked to bottom-up nutrient supply (upwelling favorable winds drive both nutrient input and offshore currents) that characterizes the central and northern CCS seasonally, although it is distinct as an ecological mechanism in that it relates to passive transport of biogeochemical properties and ecological communities (Fig. 2).

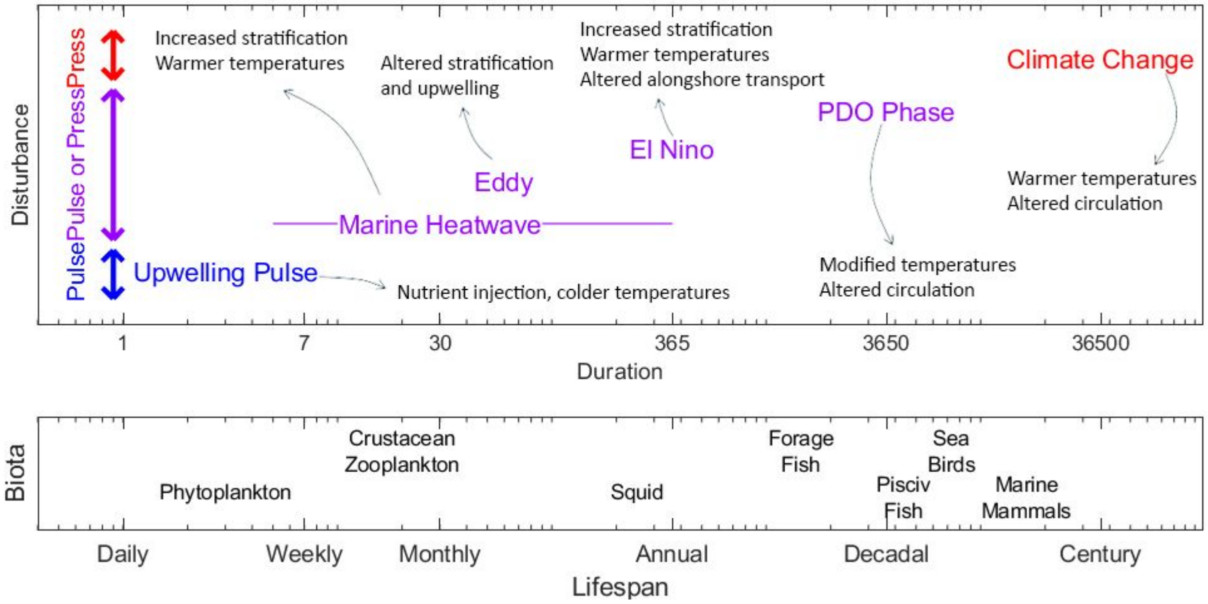

Figure 1. Disturbance time scales in the CCS. Upper panel shows different physical disturbances and their typical durations (x axis), as well as their categorization as "press" or "pulse" disturbances. Most disturbances can be categorized as either press or pulse depending on the life span and response time of the population or community of interest. Typical biotic life spans are shown in the lower pane.

Recent ecological responses to physical disturbance have led to significant socioeconomic consequences for human-ocean interactions. For example, in 2015 an unprecedented bloom of *Pseudo-nitzschia* occurred along the U.S. West Coast, which was driven partly by extremely warm ocean temperatures. This bloom resulted in record high concentrations of the toxin domoic acid in the water column that precipitated the closure of several shellfish industries, including the economically vital Dungeness crab fishing industry that lost nearly 100 million USD within the

CCE (Moore et al. 2019, Smith et al. 2021). Additionally, the warm ocean in 2015 contributed to kelp losses that led that year to closures of the commercial red sea urchin industry valued at over 3 million USD (Smith et al., 2021). Advancing our mechanistic understanding of the physical drivers and their ecological impacts is critical for improving climate and ecosystem forecasts, and for informing the development of effective adaptation and mitigation strategies.

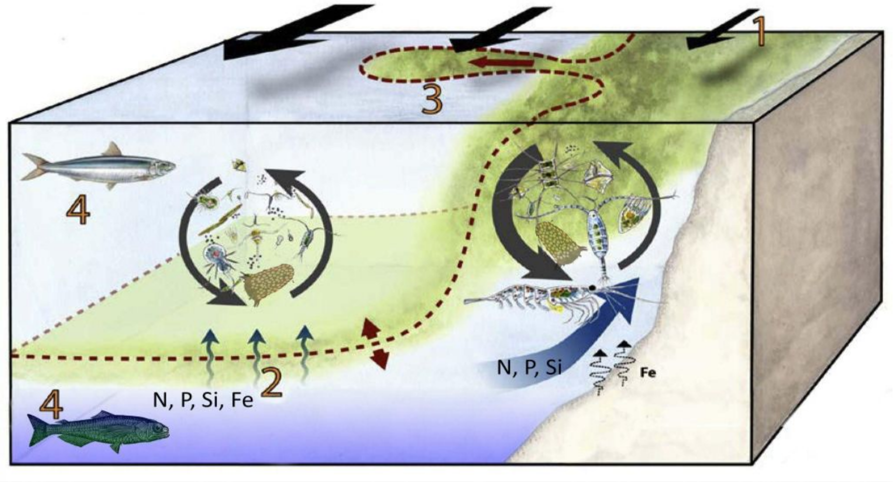

Figure 2. Conceptual diagram of the California Current Ecosystem basic ecological state and its processes illustrating hypothesized mechanisms leading to ecosystem transitions in the CCS region. 1) Along-shore transport, 2) Altered stratification and nutrient supply, 3) Cross-shore transport, 4) Top-down pressure. 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 wavy blue arrows). These and other processes and their ecological impacts will be elucidated in the following sections. Source: CCE-LTER.

The CCS provides an interesting natural laboratory for investigating how marine ecosystems respond to physical forcing (e.g., Miller et al. 1999). Its strong alongshore gradients, frequent perturbations, and wealth of long-term datasets (e.g., CalCOFI [California Cooperative Oceanic

Fisheries Investigations; Bograd et al. 2003], CODE [Coastal Ocean Dynamics Experiment; Beardesley and Lentz 1987], U.S. GLOBEC [U.S. Global Ocean Ecosystem Dynamics; Di Lorenzo et al. 2015], CCE-LTER [California Current Ecosystem - Long Term Ecological Research; Ohman et al. 2013], the Newport Hydrographic Line [Peterson et al. 2002], the Trinidad Head Line [Robertson and Bjorkstedt, 2020], among many others) make it uniquely valuable for detecting and interpreting physically forced signals in ocean biology. Additionally, extensive numerical modeling experiments have provided fundamental insights into the processes governing physical and ecological interactions (e.g., Gruber et al. 2006, Franks et al. 2013, Goebel et al. 2013, Fiechter et al. 2018). They also help quantify the level of predictability of the various components of the ecosystem (Di Lorenzo and Miller 2017).

Here we explain the basic physical environment of the CCS, its relation to ecology, and the myriad disturbance pulses and presses that have affected its ecology. We will highlight how key recent physical events have disturbed the system and note how long-term changes due to global warming are becoming increasingly evident. Finally, we will examine aspects of predictability in the physical system that might be exploited in an ecological response framework for societal benefit.

2. California Current System

Seasonal Behavior

The CCS forms the eastern edge of the North Pacific subtropical gyre, which is driven by large-scale wind fields. Its seasonal wind dynamics are largely controlled by the position and strength of the North Pacific High, a semi-permanent high-pressure system centered in the northeastern

Pacific. During spring and summer (April through September), the North Pacific High intensifies and shifts to a northward position that generates persistent equatorward winds along the western coast of North America (Figure 3, cf. Monteiro et al. 2011). These winds drive increased offshore Ekman transport and thus the coastal upwelling season. The period from late spring through early summer typically marks the peak of nutrient input and biological productivity (e.g., Jacox et al. 2018). Offshore near surface transport results in a lowered sea surface near the coast and an onshore pressure gradient force. Beneath the surface Ekman layer, this pressure gradient force can be in near geostrophic balance with predominantly alongshore motion, but this balance breaks down in the frictional bottom boundary layer, resulting in near-bottom onshore transport that ultimately upwells (Allen et al. 1995). In models, this reversal in cross-shore transport between the surface and depth provides a retention mechanism by helping vertically migrating zooplankton remain in the nearshore region. (Batchelder et al. 2002)

In fall and winter, the North Pacific High weakens and retreats southward, reducing the strength of equatorward winds and allowing for occasional reversals. These periods are dominated by storm activity, onshore winds, low upwelling and reduced primary productivity. Reduced alongshore winds also allow development in winter of a northward, nearshore current called the Davidson Current (Hickey, 1979), which is important in larval transport processes (e.g., Strub et al. 2024).

Beneath the equatorward flowing surface currents, the California Undercurrent occurs as a poleward-flowing subsurface current along the western continental slope of North America (Hickey 1979, Collins et al 2003). It transports salty, nutrient-rich water from the equatorial Pacific into the CCS subsurface region (e.g., Auad et al. 2011), playing a key role in maintaining the productivity of the eastern boundary current system. The undercurrent's flow is influenced by wind patterns and alongshore oceanic pressure gradients, and it connects with the coastal Davidson Current in winter (e.g., Strub and James 2002, Zaba et al. 2018). A thorough analysis of the California Undercurrent drivers and momentum balance is provided by Chen et al. (2021). The Undercurrent may also play a role in retention of vertically migrating zooplankton (Strub et al. 2024). Models have clarified how transport in the frictional bottom boundary layer, under influence of the poleward undercurrent (or its shallower, coastal manifestation), drives downslope offshore transport which often removes material from the shelf, where it may otherwise be entrained by mid-water upwelling (Siedelecki et al. 2012, Damien et al. 2023a, Pham et al., 2024).

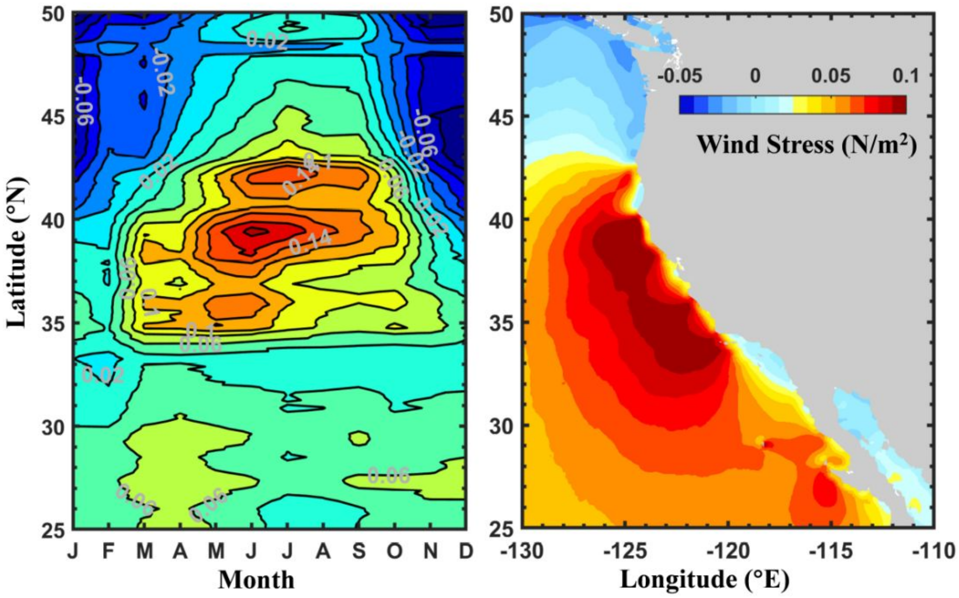

Figure 3. (Left) Seasonal cycle of alongshore wind stress (N/m2, positive equatorward), averaged over 3 degrees adjacent to the coast. (Right) Spatial map of the annual mean alongshore wind stress over the California Current region. Values are in N/m2, positive equatorward. Data are from QuikScat satellite product (podaac.jpl.nasa.gov) over 1999-2009.

Spring Transition

One of the most ecologically significant seasonal shifts in the CCS is the spring transition, the relatively abrupt change from the downwelling-favorable winter regime to the upwelling-favorable summer regime. This transition typically occurs between March and May and varies interannually in both timing and intensity (e.g., Bograd et al. 2009, Jorgensen et al. 2024). See Holt and Mantua (2009) for discussions of quantitative metrics of the spring transition in the CCE.

The timing of the spring transition has profound consequences for the ecosystem. An early transition can lead to an extended upwelling season, more time for phytoplankton accumulation, and better alignment with the reproductive cycles of zooplankton and fish larvae. Conversely, a late transition can result in a truncated bloom period or a mismatch between food availability and consumer demand.

Upwelling Characteristics

Coastal upwelling drives a rapid injection of nutrients into the euphotic zone that is experienced by phytoplankton communities as a pulse disturbance (Stukel et al. this issue). This upwelling triggers phytoplankton blooms, typically dominated by diatoms, within days of upwelling onset (e.g., Ware and Thompson 2005). The strength and duration of upwelling pulses determine the intensity of primary production. Strong, sustained upwelling supports large phytoplankton biomass, while brief or weak events may lead to incomplete bloom development or rapid nutrient depletion. The timing of upwelling also matters; mismatches between nutrient supply and light availability (e.g., during early spring or under heavy fog) can limit photosynthesis even when nutrients are abundant. Zooplankton populations, especially copepods and euphausiids, respond with a lag of several days to weeks, followed by forage fish such as anchovies and sardines, and eventually predators like salmon, whales, and seabirds (Sydeman et al. 2020, Stukel et al. this issue). This cascading response reflects the bottom-up control exerted by coastal upwelling (e.g., King et al. 2011, Lindegren et al. 2018).

Upwelling driven by wind-stress curl, also contributes to enhanced upper-ocean nutrient supply in the CCS (Rykaczewski and Checkley 2008). This process occurs in the nearshore environment, for example in the lee of capes, but also over a larger offshore area than the narrow coastal upwelling region; as a result, it contributes significantly to the total amount of upwelled water depending on location, season, and event. While some estimates of the area-averaged curl-driven upwelling volume transport are comparable to the coastal upwelling, its nutrient content is generally lower due to a shallower source-depth from which curl driven upwelling draws (Jacox and Edwards 2012). Curl-driven upwelling in the open ocean is associated with the oligotrophic offshore regions of the CCS where community-level primary production is weaker and the smaller phytoplankton thrive (e.g. Venrick, 2009, Goebel et al. 2013). The consistently weaker intensity, but larger spatial extent of wind-stress curl upwelling relative to coastal upwelling, affords interesting future opportunities for testing hypotheses about how characteristics of the upwelling regime shape biotic responses.

Upwelling is not a steady-state phenomenon and exhibits strong short-term variability driven primarily by atmospheric conditions. Wind pulses and relaxations cause alternating cycles of upwelling and downwelling. During relaxation events, warm surface water can move back toward the coast, stratifying the water column and suppressing nutrient flux. These oscillations, often on timescales of 3–10 days, affect bloom dynamics and food web stability. Intermittent upwelling may create more favorable conditions for larval fish by balancing nutrient input with retention, while strong, continuous upwelling can cause offshore export of planktonic stages (Peterson and Schwing 2003). The ecosystem impacts of this variability are profound. It is often seen that early-onset and moderate, pulsed upwelling during spring supports higher fish recruitment, whereas delayed but steady upwelling can reduce survival due to reduced food supply for larvae and intense continuous upwelling can reduce survival due to advection of larvae away from the shelf.

Concise measures of the time variability and spatial structure of upwelling events have been developed to help interpret the local and regional ecological response. The Bakun Index (Bakun 1973) was conceived as a quick and easy way to estimate the volume transport due to the coastal upwelling component along the coast from the cross-shore, sea level atmospheric pressure gradient (which provides the geostrophic component of the alongshore wind). It is based on simple Ekman theory to quantify the offshore transport of the surface layer of the ocean, which is efficiently replaced by subsurface nutrient rich waters. However, it is inadequate to accurately estimate actual upwelling along the US west coast (Seo et al. 2012, Rykaczewski et al. 2015). The simple approach does not account for alongshore variations in sea level due to such things as variations in alongshore wind and Rossby wave activity adjacent to the coast (Marchesiello and Estrade 2010) or to offshore Ekman pumping-derived upwelling. In recent years, new local upwelling indices that account for the geostrophic cross-shore transport associated with these alongshore sea level variations have been developed, combining observations with models to better estimate total volume of upwelling (Jacox et al. 2018): the Coastal Upwelling Transport Index (CUTI), and total nitrate brought into the photic zone, the Biologically Effective

Upwelling Transport Index (BEUTI). CUTI is a quantified estimate of vertical transport into (or out of) the surface mixed layer, calculated from surface wind stress, sea surface height, and mixed layer depth, which are all derived from a regional ocean data-assimilative reanalysis product, for 1 degree latitude bins extending 75km offshore. BEUTI is a quantified estimate of nitrate flux into (or out of) the surface mixed layer, calculated by multiplying vertical transport at the base of the mixed layer by nitrate concentration at the base of the mixed layer (i.e., $\text{BEUTI} = \text{CUTI} * [\text{NO}_3^-]_{\text{MLD}}$) using the same ocean reanalysis and same grid. Fig. 4a shows a 40-year record of these indices at one point, 34N, along the California coast, illustrating how subsurface nitrate concentration varies with time thereby altering the vertical flux. Fig. 4b shows the anomalies of BEUTI, indicating a trend towards higher values (more nitrate available) in the 2000's and later, except for lower values in the mid-2010's due to marine heat waves, as discussed below.

Alongshore variations in these indices (Jacox et al. 2018) each highlight an important feature of the CCS that the total upwelling field is not uniform along the coast or in the pelagic ocean. Bathymetric features and coastline geometry introduce spatial heterogeneity. Prominent upwelling centers include Cape Mendocino (northern California), Point Arena (central California), Point Conception (southern California), and the Oregon shelf. Enhanced upwelling in these regions may occur in part via topographic wind intensification, whereby the orientation of the coast and local wind stress combine to amplify Ekman transport. Additionally, the shelf width and bottom slope influence how efficiently deep water can rise to the surface (Lentz and Chapman 2004) as well as the relative balance of macro- and micronutrients (e.g., iron) in the upwelled waters. Alongshore changes in shelf width can drive local upwelling at transitions (Pringle 2002). In addition to variability in upwelling velocities, variability in source depth of upwelling significantly alters nutrient supply through changes in upwelled water nutrient concentration (e.g., Frischknecht et al. 2018).

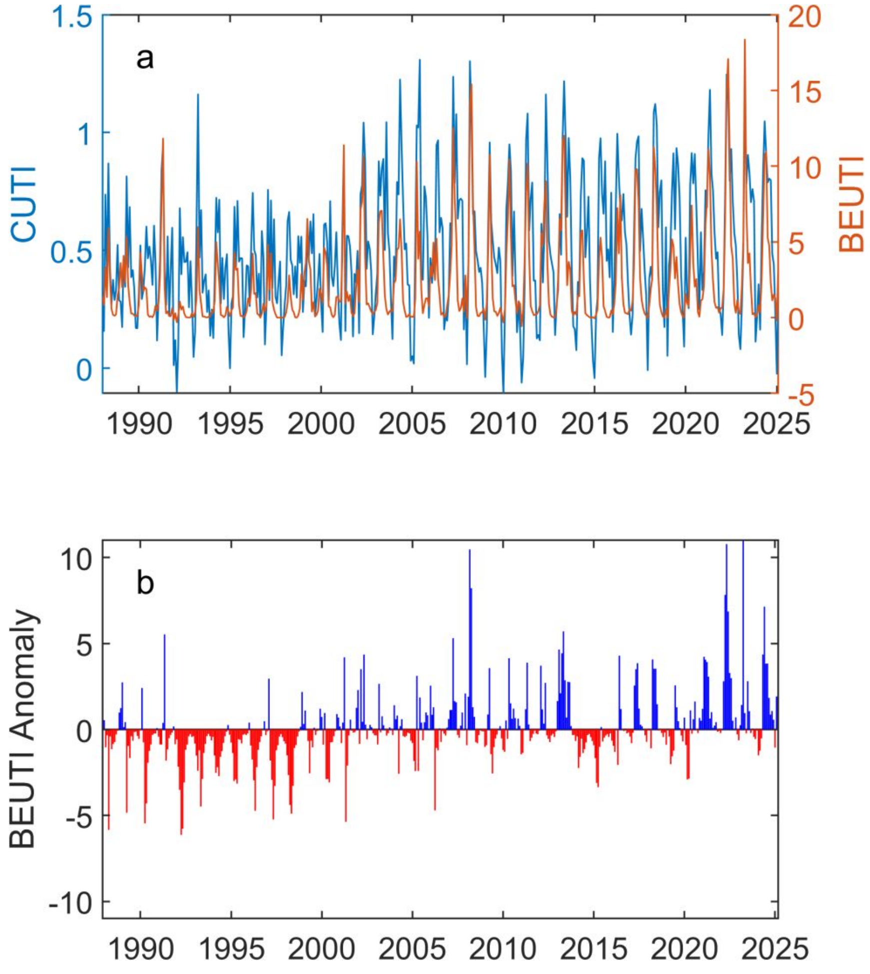

Figure 4. Coastal upwelling and bottom-up ecosystem control. a) The Coastal Upwelling Transport Index (CUTI, left axis and blue line) is an estimate of the monthly volume of upwelled water integrated from the coast to 75 km offshore at 34°N (units of $m^2 s^{-1}$). The Biological Effective Upwelling Transport Index (BEUTI, right axis and red line) is derived from CUTI and nitrate concentrations and provides an estimate of the amount of nitrate upwelled (units of mmol N $m^{-1} s^{-1}$). From Jacox et al. (2018). b) Monthly anomaly of BEUTI. Data plotted from https://mjacox.com/upwelling-indices/.

Not all regions affected by upwelling-favorable winds are zones of nutrient enhancement. In the lee of headlands or within bays, upwelling shadows can form areas where stratified water is retained due to reduced mixing and weak advection. These zones often act as retention areas for planktonic organisms, larvae, and eggs, increasing biological residence time and potentially enhancing local recruitment (Graham and Largier 1997, Fiechter et al. 2018). Examples of this include Monterey Bay and Bodega Bay, which exhibit distinct physical regimes compared to adjacent upwelling jets. These retention zones are critically important for larval survival, as they provide stable conditions with high food availability and reduced offshore transport.

Jets, Filaments, and Fronts

Seasonal winds not only drive upwelling but also generate strong alongshore coastal jets, typically 10–50 km wide, that accelerate equatorward and are in geostrophic balance with the upwelled isopycnals (Hickey 1998). These jets are key mechanisms for transporting water, nutrients, and organisms along the shelf and slope, though they are also often baroclinically unstable. Instabilities can grow from small meanders to large, detached filaments and eddies, redistributing biomass across the shelf-break. Encounters with headlands or changes in bathymetry can enhance this eddy-generating behavior.

These filaments can stretch for hundreds of kilometers and may carry coastal phytoplankton and zooplankton into oligotrophic offshore waters, effectively linking nearshore productivity with pelagic ecosystems. Such offshore flow and the lagged response of plankton communities can drive krill spatial and temporal patterns (Messié and Chavez 2017, Messié et al. 2022). In addition, wind-driven jets and filaments create fronts and eddies that enhance biological aggregation, often serving as foraging hotspots for higher trophic level predators (Woodson and

Litvin 2015, Abrahms et al. 2018). Importantly, these fronts can be relatively long-lived (>month duration) and hence can support extensive higher trophic level production. However, water flow along these fronts is often rapid and hence phytoplankton and protistan communities typically experience these fronts as pulse disturbances, with often enhanced nutrient fluxes, before they are rapidly advected away from the feature.

Mesoscale Eddies

Instabilities in the CCS also support the formation of mesoscale and submesoscale eddies (e.g., Capet et al. 2008, Kurian et al. 2011). These evolving sinuous features, typically ranging from 1-200 km in disturbance scale and lasting days to months, introduce lateral transport mechanisms that profoundly influence the distribution of heat, nutrients, plankton, and other tracers across the shelf and into the open ocean (e.g., Gruber et al. 2006, 2011, Chenillat et al. 2018, Amos et al. 2019, Ueno et al. 2023). Eddy activity can also contribute to the offshore flattening of isopycnals, thereby modifying mean coastal upwelling (Gruber et al. 2011).

Mesoscale eddies form primarily through baroclinic and barotropic instabilities of the CCS (e.g., Moore et al. 2009). When the flows become unstable, energy is transferred from current shear or stratification into growing and propagating eddy features that often exhibit wave-like properties (e.g., Kelly et al., 1998). These eddies can also be generated when coastal jets interact with bathymetric features, such as capes and banks, resulting in semi-stationary features (e.g., Centurioni et al. 2008) or through instabilities in offshore filaments and upwelling fronts (e.g., Nagai et al. 2015). Studies often focus on statistics of two primary types of mesoscale eddies, cyclonic (counterclockwise rotation in the northern hemisphere) and anticyclonic (clockwise rotation). Cyclonic eddies are typically associated with uplift of isopycnals and vertical nutrient input to more well-lit waters, while anticyclonic eddies have a depressed thermocline, trapping relatively low-nutrient, warm water in their cores. Both types can persist for weeks to months and travel hundreds of kilometers generally westward (Stegmann and Schwing 2007), often carrying distinct physical properties and biological communities with them (Chenillat et al. 2016). In addition, subsurface or subthermocline eddies have been suggested to be important in transferring properties of the undercurrent waters offshore, generating long-lasting, isolated pockets of anomalous waters (Pelland et al. 2013, Molemaker et al. 2015, Frenger et al. 2018, McCoy et al. 2020).

One of the most important functions of mesoscale eddies in the CCS is their role in lateral transport. Eddies formed near the coast, especially at upwelling centers like Point Arena and Cape Mendocino, can detach and move offshore, carrying cold, nutrient-rich water into oligotrophic zones (e.g., Combes et al. 2013). This eddy-mediated export affects nutrient budgets and productivity far from the immediate zone of upwelling, while redistributing coastal plankton communities (Abdalah et al. 2022, Chenillat et al. 2016). It also contributes to offshore phytoplankton blooms, as trapped nutrients continue to support biological activity within the eddy core. These structures act like floating oases in nutrient-poor offshore waters, often attracting zooplankton and higher trophic levels (e.g., Logerwell et al. 2001, Yen et al. 2006). Conversely, anticyclonic eddies formed offshore can advect warm, stratified water onto the shelf, altering local temperature structure and suppressing upwelling. These warm anomalies can displace resident species, modify larval transport pathways, and reduce productivity by inhibiting nutrient flux (e.g., Nagai et al. 2015, Chenillat et al. 2016).

Eddies not only move water laterally but also induce vertical motion due to their dynamical characteristics, especially around the fronts that occur at their edges. Cyclonic eddies enhance upward vertical transport, promoting nutrient injection into the euphotic zone and prolonging phytoplankton blooms (Chenillat et al. 2015). Anticyclonic eddies can drive downwelling, trapping surface-derived organic material and redistributing it to depth (Chenillat et al. 2015). These vertical motions affect biological processes such as primary production, carbon export, and oxygen consumption (McGillicuddy et al. 2007). These eddy-mediated vertical transport mechanisms are crucial for understanding nutrient dynamics in the CCS, particularly during periods when wind-driven upwelling is weak or absent. In this context, mesoscale eddies provide a unique pathway for nutrient delivery that can sustain productivity and alter food web structure.

Eddies can also trap and retain biological communities, functioning as coherent ecological harbors. Once a parcel of water, along with its planktonic and microbial inhabitants, becomes entrained in an eddy, it may remain largely isolated from surrounding waters for extended periods (e.g., Kessouri et al. 2022). This physical coherence can enhance ecological interactions, such as predator-prey coupling and microbial recycling. For example, plankton surveys have shown distinct community composition within eddy cores compared to surrounding waters (Abdala et al. 2022). In some cases, larvae of commercially important fish species are retained within eddies, potentially improving survival due to increased food availability and protection from dispersal (e.g., Logerwell et al., 2001). By trapping plankton communities for extended periods, eddies also offer unique opportunities for studying ecological succession in plankton.

Another critical effect of mesoscale eddies is their role in subduction, the process by which surface or near-surface water is advected by tilted horizontal currents into the deeper ocean. This occurs primarily along eddy peripheries and frontal zones, where strong convergence drives water downward (Gruber et al. 2011, Nagai et al. 2015). Subduction transports organic material, including phytoplankton, detritus, and dissolved carbon, from the biologically active surface into the ocean interior. This mechanism contributes to the biological carbon pump, sequestering carbon from the atmosphere and influencing long-term climate regulation. In the CCS, subduction events associated with mesoscale features have been implicated in both carbon export and oxygen depletion (Stukel et al. 2017). Eddy-transport activity can contribute to subduction, thereby suppressing primary production (the "eddy quenching" effect) in the nearshore regions and enhancing it offshore (Gruber et al. 2011). When organic-rich waters are subducted into intermediate depths, microbial respiration can consume oxygen, contributing to the intensification of the oxygen minimum zone (OMZ) in the deeper waters of the CCS (e.g., Stramma et al. 2010).

Modeling results clearly indicate that mesoscale and submesoscale processes, sometimes in competing ways, largely control the offshore transport, and organize the spatial patterns of, coastal biogeochemical and ecological properties across the CCS (e.g., Gruber et al. 2011, Lachkar and Gruber 2011, Woodson and Litvin 2015, Nagai et al 2015, Renault et al. 2016, Lévy et al. 2018, Kessouri et al. 2020, Guiet et al. 2020, Renault et al. 2021, Deutsch et al. 2021, Damien et al. 2023a,b). These processes also lead to spatial decoupling of phytoplankton production and organic carbon export into the deep sea by the biological carbon pump (Plattner et al., 2005, Amos et al. 2019, Chabert et al. 2021, Messié et al. 2025), thus linking coastal upwelling to offshore midwater and benthic communities (Ruhl et al. 2020, Messié et al. 2023).

Surface Mixed-Layer Depth and Thermocline

The depth of turbulent mixing (mixed-layer depth, MLD) in the upper ocean controls significant aspects of the ecological response to physical oceanographic forcing. The MLD regulates the balance between local vertical nutrient transport from depth, where it is darker and less susceptible to fostering phytoplankton growth, and exposure to sunlight near the surface, where growth tends to be nutrient-limited except during active nutrient-enhancement (vertical mixing) events. The MLD is controlled by numerous processes, including wind mixing, evaporation, precipitation, heating and cooling by the atmosphere, and lateral transport leading to convergent or divergent ML currents (e.g., Amaya et al., 2021). MLD evolution occurs over time scales of hours (solar heating, land and sea breezes, rainfall events) to days (wind-driven upwelling events, eddy instabilities, synoptic storms) to weeks (ocean eddy evolution, seasonal atmospheric forcing) to decades (climate variations and global warming processes). The MLD undergoes seasonal variations and is generally deeper in winter than in summer. As a result, temperature and salinity anomalies created in winter can remain below the shallow MLD in summer and return to the surface in the following fall/winter when the mixed layer deepens again (Alexander and Deser 1995, Alexander et al. 1999). The ecological responses to these MLD changes are intimately intertwined with the processes previously mentioned in the section.

The wind-driven mixing that can generate rapid variations in mixed-layer depth at the surface also helps structure the upper ocean over the course of the seasons into a warm surface layer that lies above a cooler, weakly mixed, well-stratified deep ocean. The strong temperature gradient that separates the two oceanic “layers” is called the (seasonal) thermocline, which varies from being shallower near the coast to being deeper offshore in the CCS. At the depths of the thermocline (80-200m), the temperature variations are strongly correlated with nitrate in the sense that cold waters are more nutrient-rich than warm surface waters, which are rapidly depleted of nitrate in the photic zone by phytoplankton. Variability in nitrate supply can be estimated using the depth of the nitracline (NCDx, defined as the depth at which nitrate concentrations first exceed 1 μmol L^{-1}, but extended to negative values if surface nitrate exceeds 1 μmol L^{-1}, following Forsch et al., this issue) as a proxy. NCDx has a strong bottom-up control on the ecosystem, and shows distinct variability at multiple time scales (Fig. 5a). The nitracline depth is correlated with multiple metrics indicative of the base of the ecosystem including surface chlorophyll concentration (Fig. 5b) and the relative contribution of coastal and offshore taxa to the microbial community (Collier & Palenik 2003, James et al. 2022).

Source Waters of Upwelling

A more subtle aspect of upwelling in EBUS is the type of water that is upwelled. Depending on the wind forcing, strength of upper ocean mixing and stratification, and nearshore bathymetry, different depths of the ocean can be plumbed by vertical mixing during upwelling events (Lentz and Chapman 2004, Jacox and Edwards 2011). Upwelled waters in the CCS can originate from depths of 100–300 meters, often from within or just above the OMZ. These waters are typically cold, rich in nitrate, phosphate, silicate, and (in areas with a relatively wide shelf) trace metals like iron, which are all key nutrients for phytoplankton growth. The deeper the upwelling, the more nutrients, which are sequestered at depth in the aphotic zones, can be lifted into the photic zone near the ocean surface. Additionally, the vertical structure of nutrients can change over time due to altered local remineralization processes as well as changes in the distant sources of waters that are advected laterally into the CCS (Bograd et al. 2015, Pozo Buil and Di Lorenzo 2017).

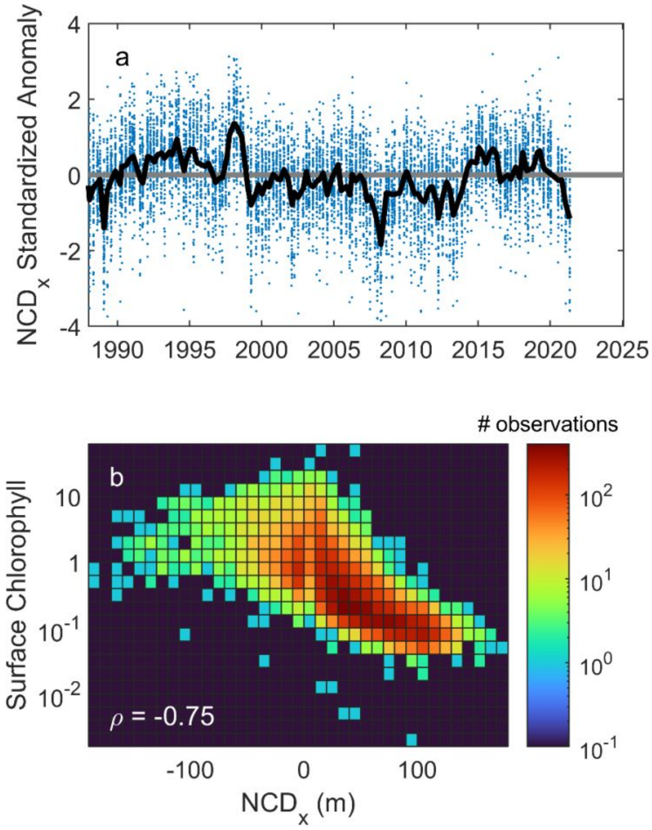

Figure 5. a) Standardized anomaly (anomaly divided by the standard deviation of the time-series) of the nitracline depth extended (NCD$_x$, see Forsch et al., this issue, for detailed definition) averaged over the southern California Current Ecosystem (approximately San Diego to just north of Point Conception and coast to ~500 km from shore). Nitracline depth has been shown to be a strong proxy for nitrate supply and hence bottom-up forcing in the ecosystem. Black line is the regional mean in the CalCOFI grid. Blue dots are individual sampling locations. Grey line is zero. b) Bivariate histogram of surface chlorophyll a (mg m^{-3}; a proxy for phytoplankton biomass) and NCD$_x$ (m). Color represents the number of observations within a specific surface chlorophyll and NCDx bin. The Pearson correlation between NCD$_x$ and $\log_{10}$(surface chlorophyll a) is -0.75 ($p \ll 10^{-6}$).

These distant source waters can be of tropical, midlatitude, or high latitude origin, depending on the location and depth (Thomson and Krassovski 2010, Bograd et al. 2019). Hence, distant changes in the North Pacific Ocean can exert a remote influence on ecological response in the CCS, and long-term variability in the biogeochemistry of the source water masses can impact the productivity of future upwelling events in the CCS (Rykaczewski and Dunne 2010). Changes in the source waters for upwelling have also been implicated in increased subsurface nitrate and phosphate concentrations, as well as a decline in the N:P ratio of deepwater nutrients (Bograd et al. 2015), which could potentially impact phytoplankton communities.

Hypoxia

Upwelling in the CCS naturally brings subsurface water to the surface. These deeper waters are enriched in nutrients, but also depleted in oxygen, due to the respiration from bacterial decomposition of sinking organic matter at depth. When these waters are upwelled, they can expose coastal ecosystems to oxygen levels below critical thresholds, which are called hypoxic events (e.g., Damien et al. 2024). These are the most frequent and severe off central and northern California (Hofman et al. 2011), along the Oregon shelf (Peterson et al. 2013), and in nearshore bays where water residence time is longer than in the unsheltered open ocean. When these events are linked with strong, sustained upwelling and minimal wind relaxation, they can increase surface production and consequent export to the bottom areas of the shelf where oxygen is already low, driving additional organic matter decomposition and causing anoxic events. These can drive massive mortality events in bottom dwelling species (e.g., Siedlecki et al 2015).

Low oxygen can effectively compress the habitable volume of the water column, an effect that can be exacerbated by warmer temperatures that decrease the amount of oxygen that water can hold and increase metabolic oxygen demand (Deutsch et al. 2015, Iglesias and Fiechter 2025). This leads to compound disturbances, in which organisms are responding to multiple interacting stressors. Species that are tolerant of only narrow ranges of these parameters must either acclimate, adapt, migrate, or perish (e.g., Cornett et al. 2024, Earhart et al. 2022). This leads to vertical compression, with species forced into thin bands of suitable water, or horizontal displacement, often moving into deeper or offshore waters (e.g. Liu et al. 2023). Anchovy habitat in the CCS has, for instance, been predicted to decrease sharply by 2100, potentially leading to local extirpation in the southern CCS (Howard et al. 2020a). Pelagic predators like salmon and hake, as well as demersal fish such as rockfish and flatfish, may alter their behavior, foraging success, and metabolic efficiency in response to these stressors (e.g., McClatchie 2025, Koslow et al. 2019). Habitat compression can also increase trophic overlap, intensifying competition and predation (e.g., Bertrand et al. 2011). Altered environmental conditions due to co-occurring stressors (e.g., oxygen, pH, temperature) may be moving species out of their normal environmental windows and decreasing predictability of ecological responses to external forcing (Muhling et al. 2020).

Coincident with increasing hypoxia is a decrease in pH levels driven by anthropogenic CO_2 emissions (Wolfe et al. 2023). In subsurface waters of the CCE, CO_2 is supersaturated (and hence pH is low) as a result of remineralization of exported organic matter. Upwelling events thus bring relatively acidic water to the surface, with potential consequences for many organisms, but especially those with calcium carbonate shells, such as pteropods (Bednarsek et al. 2014, 2019, 2022).

3. Key Recent Climate Events

The basic processes that control upwelling and transport, and their impact on the marine ecosystem in the CCS are modulated in many interesting ways by climate variations (e.g., Miller et al. 2015). Short-term climate forcing events act as disturbance pulses on higher trophic levels (and fished stocks) of the CCS, although they would more accurately be considered press disturbances or modifications to the disturbance regime with respect to phytoplankton and most zooplankton. In the following sections, we discuss several classes of these key climate events that profoundly affect the CCE. We focus on the more recent events, which have been more extensively sampled in nature, especially ecologically and biogeochemically, compared to historical events.

El Niño/Southern Oscillation (ENSO)

ENSO, which is a coupled ocean-atmosphere dynamical climate oscillation of the tropical Pacific, has a strong remote impact on the CCS and its ecosystem through what are termed teleconnections. ENSO alters the CCS remotely through a combination of atmospheric (regional wind changes affecting upwelling, transport, evaporation, and heating) and oceanic (coastally trapped waves propagating into the CCS from lower latitudes and affecting transport, thermocline depth, and temperature) pathways emanating from the tropics as stationary wave-like disturbances (e.g., Frischknecht et al. 2015). The largest El Niño events since 1980 occurred in 1982-83, 1997-98 and 2015-2016, but their structure and evolution varied both in the tropics and the CCS (e.g. Frischknecht et al 2017, Lilly and Ohman 2021).

The altered physical states of the CCS due to ENSO often have a strong influence on ecology (Fig. 6a). In general, El Niño tends to bring warmer ocean conditions, anomalous northward ocean current transport (Fig. 7cd), a deepened thermocline, suppressed vertical mixing, and reduced equatorward winds and upwelling, while La Niña often cools the ocean, lifts the thermocline, enhances vertical mixing and southward transport (Fig. 7cd), and is associated with stronger upwelling through enhanced winds. During El Niño, depressed isopycnals can push down the oxygen minimum zone, resulting in higher oxygen concentrations at shallower depths in locations with hypoxia.

Associated with these events are broad-scale changes in productivity, lower during El Niño and higher in the case of La Niña, that cascade up the food web and alter migration patterns and reproductive success of fish, birds, and marine mammals. El Niño typically expands the oligotrophic region of the offshore ocean and contracts the productive coastal zones, leading to fewer diatoms and more small phytoplankton (Venrick 2012, Kahru and Mitchell 2002). El Niño is also frequently associated with a shift from large, cold-water copepods to smaller, warm-water species with lower lipid content, a reduction in euphausiid abundance leading to food shortages for seabirds and fish, poleward shifts in the distribution of species, expanded ranges of subtropical-associated species into the CCS such as subtropical fish, sardines, pelagic tunas and seabirds (e.g., Lluch-Belda et al. 2005, Song et al. 2012, Lonhart et al. 2019, Lin et al. 2025, Russell et al. 2025), and declines in recruitment and survival of cold-water species like salmon and anchovy (Hooff and Peterson 2006). La Niña usually brings reverse conditions. These biotic responses can result from both changes in in situ growth of taxa within the CCS and due to altered alongshore and offshore advection patterns affecting zooplankton (Lilly et al. 2022, Strub et al., 2024) as seen in Figure 7.

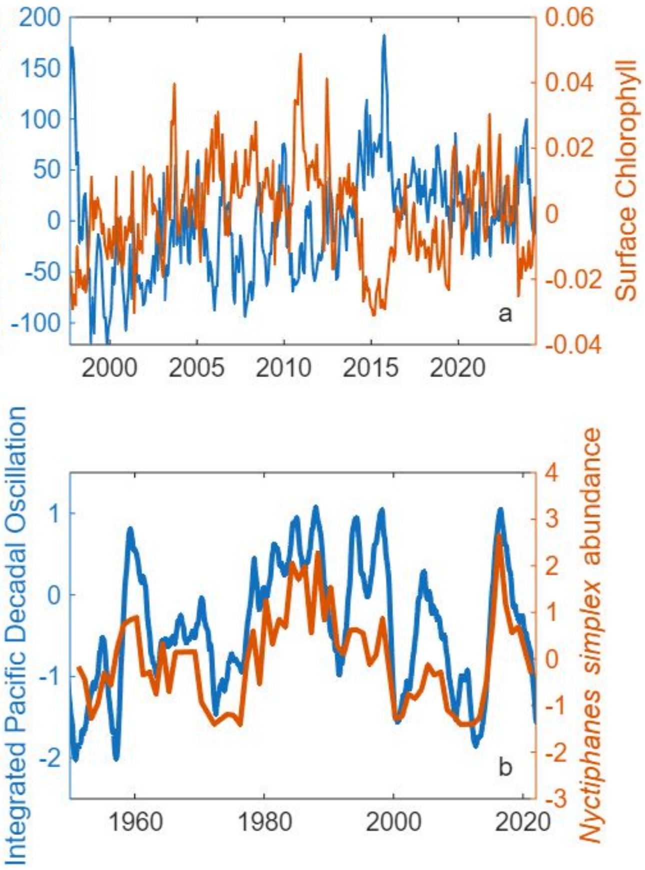

Figure 6. Biotic responses to physical forcing. a) Time-series of San Diego sea level detrended anomaly (used as an index of El Nino-Southern Oscillation (ENSO) influence in the CCE region) and average surface chlorophyll a monthly anomaly in the southern CalCOFI region. Surface chlorophyll is derived from a multi-satellite merger product (Kahru et al. 2015). Note the inverse correlation between ENSO and chlorophyll, especially during the particularly strong El Ninos in 1997-1998 and 2015-2016. b) Time-series of *Nyctiphanes simplex* (a warm-water euphausiid species) and the Pacific Decadal Oscillation Index (which was temporally integrated over the 2-year life span of *Nyctiphanes simplex* following Di Lorenzo and Ohman 2013). For additional details on the *Nyctiphanes simplex* time series see Ohman (this issue).

ENSO events usually reach their maximum intensity in winter, while CCE productivity is highest in late spring. The warm or cold conditions that are established in winter thus provide a preconditioned winter ocean state that can influence the spring CCE through its altered stratification and thermal impacts on physiology, growth, spawning, and migration. ENSO events also can often trigger trophic mismatches, the temporal decoupling between the availability of prey and the needs of predators. For example, seabird chick mortality can spike when peak zooplankton biomass occurs too early or late relative to hatching (e.g. Piatt et al. 2020).

On seasonal time scales, ENSO has a predictable physical component. It thus provides a physical basis for our greatest opportunity for creating an ecological forecasting system in the CCE (Di Lorenzo and Miller 2017, Cordero-Quirós et al. 2022, Chen et al. 2024). Note, however, that different “flavors” of ENSO (e.g., Eastern Pacific vs. Central Pacific maximum tropical amplitude) can add additional complexity to the ecological response, as highlighted by Lilly and Ohman (2021), further challenging the prospects of CCE predictions. Additionally, due to ENSO’s interaction with other chaotic components of the climate system, its influence on the CCS should be viewed as a distribution of possible outcomes rather than a recurrent one-to-one response (e.g., Fiedler and Mantua 2017, Cordero-Quirós et al. 2019, 2022).

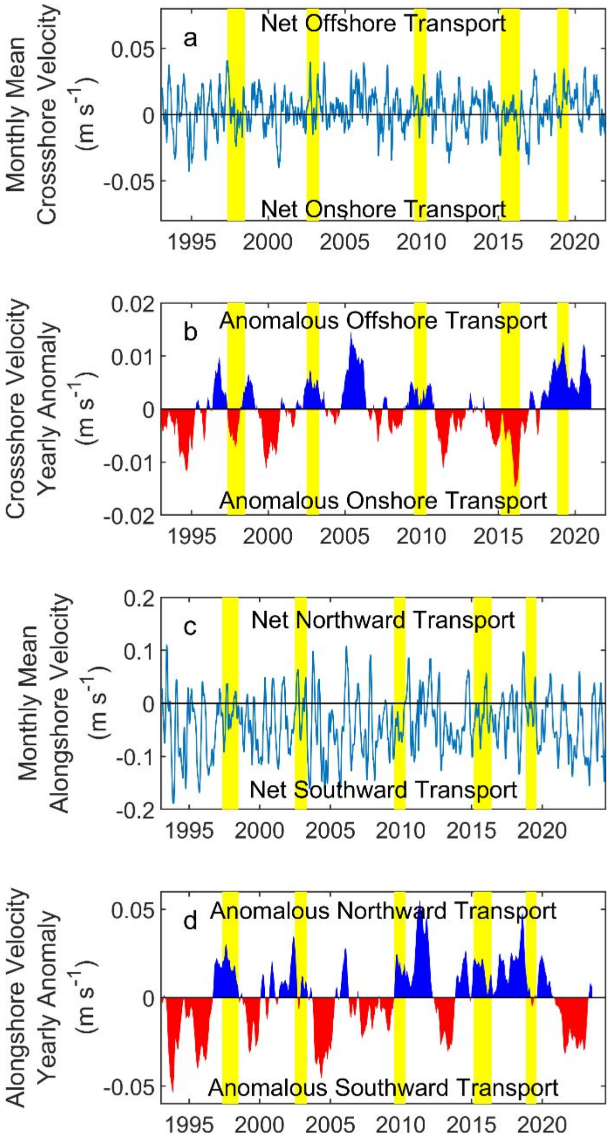

Figure. 7. Time series of cross-shore and alongshore currents from the GLORYS model outputs. Alongshore is calculated across line 93.3 of CalCOFI (extending southwestward from San Diego). Cross-shore is calculated across the 60 stations from line 93.3 to 76.7 (San Diego to north of Point Conception). All are averaged over the upper 50 m. Note the strong northward transport variations associated with El Niño events in 1997-98, 2002-03, 2009-10, 2015-16 and 2018-19 (vertical yellow bars). La Niña events in 1995-96, 1998-99, 2007-09, and 2021-23 are associated with anomalous southward flow. Anomalies are relative to the monthly climatology.

PDO, NPGO, and PMM

Several climate pattern indices are associated with anomalous forcing of the CCS and the CCE. The Pacific Decadal Oscillation (PDO; Mantua et al. 1997, Newman et al. 2016), which can be thought of as the primary (dominant) pattern of North Pacific SST, has a large-scale coherent structure that extends along the U.S. West coast and has the opposite sign in the middle of the subtropical gyre. It is primarily driven by changes in the Aleutian Low, which can be stochastic or associated with ENSO teleconnections and by coupled atmosphere-ocean processes in the North Pacific (Newman et al. 2016). The North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al. 2008) can be regarded as the second most dominant pattern of North Pacific SST and is forced by anomalies of the North Pacific High (Ceballos et al. 2009). Associated with both SST patterns are changes in upper-ocean circulation and transport. The main influence of PDO on the CCE is through the large-scale coherency of SST, which organizes patterns of ecological response over thousands of kilometers along the North American West Coast (Fig. 6b), potentially leading to large-scale synchrony in biotic responses (e.g., Miller and Schneider 2000, McGowan et al. 2003). The NPGO in contrast drives significant changes in circulation and offshore upwelling that affect the CCE (Di Lorenzo et al. 2009). These two climate patterns each exhibit timescales of years-to-decades and, because of their construction, are out-of-phase temporally with each other.

The response of the CCE to PDO can be thought of as a longer time scale version of ENSO and with a similar ecological effect (e.g., Miller et al 2004). NPGO, in contrast, has a direct link with salinity variations that serve as a proxy for nutrients because of the high salinity in the nutrient-rich undercurrent. They both exhibit coherency with upwelling intensity, which is regionally dependent (Macias et al. 2012).

Persistent changes in the physical climate state, such as a prolonged PDO or NPGO phase, can result in ecological transitions, where the structure and function of the ecosystem reorganize into a new state that can persist for long periods (Bestelmeyer et al. 2011). These shifts can involve replacement of anchovy-dominated periods by sardine-dominated periods and vice versa (Chavez et al. 2003; but see the cautionary evidence of Lindegren et al. 2013 and Siple et al. 2020), long-term changes in zooplankton community structure, altered recruitment patterns of groundfish and salmonids, and reorganizations of pelagic predator foraging behavior. These regimes can potentially be nonlinear and thereby difficult to reverse, highlighting the potential hysteresis of ecosystem responses to physical forcing. However, the CCE so far has not shown evidence of hysteresis (Bestelmeyer et al. 2011). Instead, it exhibits either linear or nonlinear ecological responses to long-term changes in the physics, with the ecological response times damped by the lifetimes of the organisms (Di Lorenzo and Ohman 2013, Messié et al. 2023).

The Pacific Meridional Mode (PMM) is related to the NPGO and to ENSO. PMM represents the low-latitude subtropical component of the NPGO and is also linked to forcing by the North Pacific High (Amaya 2019). It also is connected to the central tropical Pacific ENSO variations as the precursor pattern to ENSO through a unique wind-evaporation-SST (WES) feedback. In the warm phase, the NPO weakens the trade winds, reducing evaporative cooling and generating a positive SST “footprint”, which then drives winds that reinforce the southwest portion of the warmest SST anomalies, while damping them to the northeast, resulting in southwestward propagation. Its strongest signature is in the southern CCS off the coast of Baja California. In summer, the PMM can feedback on the subtropical atmosphere, impacting the strength of upwelling favorable winds in the central and south CCS (~30˚N-40˚N) and driving a predictable signal in the seasonal evolution of wind-driven Ekman transport (Amaya et al. 2024).

Marine Heatwaves

In recent decades, a series of intense warm ocean temperature extremes—known as marine heatwaves (MHWs)—have strongly impacted the CCE (e.g., Gomes et al. 2024). As a result, a great deal of attention has been directed towards identifying these extreme events as they become more common and occur with higher intensity and larger spatial scale relative to a fixed past baseline (Amaya et al. 2023a).

The notorious “Blob”, which began in late 2013, and peaked in 2014-15, drew the greatest amount of concern because of how large and persistent it was (Bond et al. 2015). It commenced in the southern Gulf of Alaska (Blob pattern, winter 2013-14) and then developed components along the U.S. West Coast associated with PDO structures (the Arc pattern, autumn 2014) and the PMM (Baja pattern, winter 2015), with large coastal anomalies (Koehlinger et al. 2023). Different persistent anomalous atmospheric forcing patterns were implicated in driving these MHW (Amaya et al. 2016), including SST features associated with El Niño, but they are often referred to together as “The Blob”. These SST patterns each occurred during winter seasons with a deep MLD that persisted into the spring and summer months, profoundly affecting the CCE.

Among the strong impacts of the Blob were massive bird and marine mammal mortality events, widespread harmful algal blooms (HABs), and fishery disruptions (Cavole et al. 2016, McCabe et al. 2016). While low trophic levels were influenced by altered nitracline depth as seen in Fig. 5a (Landry et al. 2024), most high trophic levels deaths were linked to starvation, as warm water suppressed upwelling, decreased primary production (Fig. 5b, 6a), reduced prey energy density, and pushed forage fish deeper or farther offshore, beyond reach for surface-feeding birds and marine mammals.

Another MHW, dubbed Blob 2.0, occurred in the summer of 2019 (Amaya et al. 2019). It also was driven by persistent atmospheric anomalies (reduced wind), but because it occurred in the summer, after the ecosystem had already experienced its most productive season that year, it did not exert as strong a control on the CCE. While these "Blob" MHWs have received substantial recent attention, they exist within a continuum of MHWs of differing magnitude and duration, with distinct characteristics of each MHW affecting the biotic response (Chen et al. 2024).

While MHWs are generally associated with a reduction in primary production in the upper layer of the ocean, the vertical structure of ecological response has received less attention. CalCOFI observations reveal that chlorophyll decreases in the surface layer (above the subsurface chlorophyll maximum), while unexpectedly increasing in the subsurface layer (Li et al. 2025). The reduction of surface layer chlorophyll is primarily attributed to suppressed nutrients upwelled to the upper ocean, while the enhancement of subsurface chlorophyll arises from the combination of enhanced lateral nutrient flux from the west, reduced upward vertical nutrient export into the subsurface layer, and improved light availability driven by reduced cloud cover and the redistribution of phytoplankton in the water.

Bottom temperature extremes or "bottom MHWs" occurring along the seafloor of continental shelves have also been documented (Amaya et al. 2023b, Alexander et al. 2025). Bottom MHWs can occur independently of surface MHWs in regions where the mixed layer does not routinely reach the sea floor. They can also be more intense and longer lasting than surface MHWs, especially in regions with a sharp thermocline like Baja and the Gulf of California. Overall, bottom MHWs may play a direct role in influencing demersal and benthic species such as groundfish (e.g. McClatchie et al., 2010) and squid (e.g., Zeidberg et al 2012).

Delayed Spring Transition

A high-profile physical and ecological event in the northern CCS was the delayed upwelling event in the spring of 2005 (Schwing et al. 2006, Barth et al. 2007). Weak spring winds caused an extended delay in the onset of upwelling conditions, with the 2005 spring transition occurring in mid-May, over a month later than normal. A further delay in the “biological spring transition” (i.e., provision of nutrient-rich waters to the surface), produced negative anomalies in phytoplankton biomass that lasted through June (Kosro et al. 2006, Jacox et al. 2016). While the ocean anomalies were not particularly high amplitude and the cumulative upwelling and primary production had recovered by the fall season, the spring delay had a profound effect on the local ecosystem, which relies on phenological timing to successfully reproduce. The delay postponed krill development (Mackas et al. 2006) and forced large numbers of auklets to abandon nests along central California (Sydeman et al. 2006a). This climate event was also associated with very low California Chinook salmon runs in subsequent years. This is a classic case of “trophic mismatch,” where physical-biological decoupling led to reproductive failures. Changes in the timing (phenology) of CCE coastal upwelling have also been linked to ENSO variations (Bograd et al. 2009). Long-term warming of surface waters may also be leading to phenological changes in fish larvae (Asch et al. 2015), with unknown implications for future recruitment.

4. Long-Term Climate Changes

Temperature Changes

Global warming continues to exert a strong press on marine ecosystems, including the CCE. The trends in SST are not as evident in the CCS as in some other regions, as its strong interannual and decadal variability (section 3) leads to relatively long times of emergence for secular trends (e.g., Henson et al. 2017). But long-term temperature records at the Scripps Pier (Rasmussen et al. 2020) and at other locations along the U.S. West Coast document a clear, significant warming trend, and global climate models project continued warming under future climate scenarios (e.g., Bograd et al. 2023). For species sensitive to temperature and upper ocean stratification, the long-term influence of warming SST on the CCE may result in ecological responses similar to those seen during El Niño and warm PDO events. However, these warm disturbances may not serve as good models for long-term warming if the rate of warming is important, or if other environmental variables do not track changes in temperature. For example, El Niño tends to bring warmer waters and weaker upwelling to the CCS, while in the future some areas may see warmer waters with stronger upwelling. Additionally, coarse resolution global climate models, which are typically used for climate projections, are unable to properly resolve mesoscale eddy interactions with upwelling processes in the CCS, leading to unrealistic representations of ecological response (e.g., Cordero-Quirós et al. 2019) so that high-resolution regional downscalings are essential for assessing ecological impacts (Howard et al. 2020b, Siedlecki et al. 2021, Pozo Buil et al. 2021, Sunday et al. 2022).

Wind-Stress Changes

The classic perspective of global warming impacts on EBUS includes the Bakun Hypothesis, in which local thermodynamic arguments suggest that regional upwelling winds in the EBUS may increase due to increased land-sea temperature contrast (Bakun 1990). However, only weak signatures of that process have emerged in observations and in global climate models (e.g., Schmidt et al. 2020). A more robust feature of climate model projections of the impact of global warming are poleward shifts in the locations of upwelling favorable winds in the EBUS (Bakun et al., 2016). These types of shifts have been observed in the historical record (Sydeman et al. 2014) and noticed in global climate model analyses (Rykaczewski et al. 2015), producing increased upwelling in the poleward portion of the CCE and reduced or unchanged upwelling strength in the equatorward part. These changes would tend to favor reduced productivity in the southern parts of the CCE and enhanced production in the northern end, though the ultimate impact on productivity is also mediated by changes in the chemistry of upwelling source waters. A recent analysis of a 73-year time series of ocean optical clarity has already identified a declining trend in offshore productivity in the southern CCS paired with an increasing trend in the coastal upwelling domain (Kahru et al. 2023). These changes are thought to relate to increased stratification (decreased nutrient supply) offshore and increased wind stress (increased nutrient supply) along the coast, consistent with the Bakun Hypothesis in that region. However, note that Tokinaga and Xie (2010) demonstrated that the ship-based wind data used by Bakun (1990) were biased due to long-term changes in the height of merchant vessels. As a result, the trends reported by Bakun (1990) for EBUS regions such as Peru do not hold when the data are corrected (e.g., Belmadani et al., 2014).

Source Water Changes

Surprisingly, high-resolution regional modeling suggests that it is not wind and upwelling changes that necessarily translate to consistent predictions of productivity or ecosystem changes. Instead, there is an emerging consensus that it is the subsurface nitrate distributions that are the first-order factor in driving modeled coastal ecological changes through stratification changes and remote chemical properties (Howard et al. 2020b, Pozo Buil et al. 2021, Siedlecki et al. 2021, Jacox et al. 2024).

For example, another interesting aspect of basin-scale adjustment to global warming is through the way that source waters of upwelling may change. One global earth system model has shown that due to remote changes in productivity in the North Pacific, the nutrient content of upwelling water in the CCS may actually increase (Rykaczewski and Dunne 2010). Locally, the chemistry of upwelled waters can also be modified by changes in stratification and mixed layer depth. Future changes in the former effect (remote changes in source waters) are much less certain than changes in the latter (increased stratification / decreased mixed layer depth). But across models and regions the predominant controlling effect on projections of productivity and associated phytoplankton biomass is the subsurface nitrate concentration and not simply upwelling strength (Jacox et al. 2024).

Mesoscale Eddy Changes

Climate model projections can also reveal changes in mesoscale eddy statistics. Global warming scenarios have revealed that eddy activity might increase throughout the CCS toward the end of the century (Cordero-Quirós et al. 2022b, Wang et al. 2025). This result appears to be due to changes in the baroclinic energy conversion due to increasing stratification. Since eddy features tend to aggregate nutrients and other key biogenic material such as larvae, changes in eddy kinetic energy associated with these features can profoundly affect the ecological state. For example, some studies show that areas in the ocean where eddy kinetic energy is higher tend to facilitate the transfer of energy within the trophic chain, thus providing foraging 'hot-spots' for higher trophic predators (Santora et al. 2017, Fiechter et al. 2020) while other work suggests that mesoscale eddy heterogeneity across the CCS can hinder the ability of small pelagic fish to return to productive coastal waters (Guiet et al. 2020). Additionally, the "eddy quenching" effect on primary production (Gruner et al. 2011) in the nearshore regions of the CCS may be altered by the changing stability properties of the CCS currents under global warming.

Acidification

Increased atmospheric carbon dioxide from fossil fuel emissions is absorbed by the ocean, leading to a buildup of dissolved inorganic carbon (DIC) and shifting the ocean's carbonate system." As surface waters absorb more CO_2, chemical equilibria shift, forming carbonic acid and reducing both pH and carbonate ion concentration. This reduces the saturation state for calcium carbonate minerals (aragonite and calcite), making it more difficult for organisms like calcifying plankton (pteropods and foraminifera), bivalves, and corals to build and maintain shells.

The long-term changes in the CCE due to acidification (Gruber et al. 2012, Turi et al. 2016, Wolfe et. 2023) have started to become clear in some pH-sensitive species (Bednarsek et al. 2014, Bednarsek and Ohman, 2015), but its effects on the overall productivity of the system are not clear, especially when considering multiple stressors (e.g., Deutsch et al 2020, Gruber et al. 2021).

Deoxygenation

Decadal-scale reductions in dissolved oxygen were identified below the thermocline in the CalCOFI dataset in the Southern California Bight by Bograd et al. (2008). The reason for that decrease is not clear, but it may be due to reduced vertical mixing because of increasing stratification in the CCS (McGowan et al. 2003, Kim and Miller 2007) or to changes in the oxygen content in the source of these deep waters that are advected in from the south (e.g., Deutsch et al., 2011) or from the west (e.g., Pozo Buil and Di Lorenzo 2017). The impact of this type of oxygen depletion on coastal benthic and demersal species is of great interest (e.g., McClatchie et al. 2010, Andersson et al. 2015, Kekuewa et al. 2022, Feely et al. 2024).

5. Predictability

Ocean and ecological forecasts are increasingly seen as critical to effective stewardship of marine ecosystems like the CCS (e.g., Tommasi et al. 2017). Our ability to make these forecasts is dependent on predictability in the physical state and its connection to marine species. Some physical mechanisms, and consequently some ocean variables, are more predictable than others. For example, substantial predictability in the CCS comes from persistence – if conditions are anomalous then they are likely to remain anomalous through a characteristic decorrelation timescale (e.g., Hervieux et al. 2019). The ocean evolves much more slowly than the atmosphere, so ocean temperature is more persistent (e.g., several months) than, say, wind stress forcing and wind-driven upwelling (e.g., Jacox et al. 2019).

In addition to persistence, remote forcing from the tropics, via ENSO-related atmospheric and oceanic teleconnections, provides a window for forecasting that can extend to longer timescales, especially for forecasts of winter/spring conditions. Significant ENSO-related forecast skill in the CCS has been found for ocean surface and bottom temperatures, marine heatwaves, stratification, sea surface height, and even aspects of upwelling intensity and phenology (Siedlecki et al. 2016, Jacox et al. 2022, 2023, Amaya et al. 2024). When ENSO is in a neutral state, CCS ocean conditions are typically harder to predict. Some recent studies though have shown that other climate modes like the PMM may enhance the predictability of the CCS independent of ENSO (Cluett et al. 2024, Amaya et al. 2024).

In contrast to shorter-term predictions, long-term climate projections (e.g., Howard et al. 2020b, Siedlecki et al. 2021, Pozo Buil et al. 2021) do not offer outlooks for specific years. But, they can project statistics of changes in the system, such as shifts in the mean and variability of oceanographic conditions, and they can offer a range of potential futures with some characterization of the uncertainty in those projections. For some variables, it may take decades for the signals to rise above the noise, while for others the long-term trends have already emerged. For example, Hameau et al. (2019) suggests the times of emergence for anthropogenic warming and deoxygenation in the California Current region were decades ago, Turk et al. (2019) estimates the carbon dioxide fugacity time of emergence to be 20 years or less in the CCE, while Brady et al. (2017) predict an upwelling time of emergence between 2040 and 2100 depending on CCE region. These projections can aid communities, industry, and policy makers in developing plans for adaptation (e.g., Smith et al. 2023; also see https://resilientca.org/topics/ocean-and-coast/#adaptation-strategies).

6. Sustainability and Timescales of Change

The marine ecosystem in the CCS exhibits both resilience and fragility (e.g. Leising et al. 2025). Many species have evolved to tolerate broad ranges of environmental variability, particularly in response to seasonal upwelling and interannual forcing associated with El Nino, marine heat waves and climate modes like PDO and NPGO. However, this adaptive capacity is being tested by the combination of recent climate-driven extremes and long-term changes in climate, including acidification and deoxygenation exacerbated by warming ocean temperatures (e.g. Sunday et al. 2022).

A firm understanding of the mechanisms by which physical oceanographic changes drive a marine ecosystem response is essential to developing a framework for long-range prediction (e.g., Sydeman et al. 2006b, Di Lorenzo and Miller 2017). Observations in the CCE are some of the densest in space and time available in the ocean, rendering it as an ideal place to develop such frameworks by providing a baseline for this understanding. Modeling studies, while limited in their ability to represent trophic niches, provide enhanced understanding of the possible mechanisms involved and allow us to understand the potential response of the ecosystem to future changes in oceanographic conditions. Much work has been done to understand physical variability (including extremes) and long-term change in the CCS. There is a growing recognition of the need to better understand interactions between the two, as well as their individual and combined impacts on the ecosystem.

As we have seen in this discussion, the time scales of change are extremely important in a pulse vs. press context. Are we in a changing disturbance regime? What are the possible outcomes for the ecological baselines? How will this affect our economy and sustainability? For example, the PDO has long been seen as a valuable proxy for various ecological changes in the CCS. But as basin-wide warming becomes more prominent, the role of the PDO has become muddied (Cluett et al. 2025). Were ecological changes related to the oscillatory nature and dynamics (e.g., upwelling changes) associated with the PDO? Or were they simply related to ocean temperature, for which PDO was a good proxy prior to the emergence of warming trends?

We have also learned that how we define baselines matters, and that description of extreme events heavily depends on this (Amaya et al. 2023a). The CCE has been through ‘regime shifts’ in the past (e.g., Miller and Schneider 2000, Hare and Mantua 2000, McGowan et al. 2003), and there are some gaps to be filled in order to understand whether extremes are now happening at a quicker rate. Ocean warming leads to changes in the physical environment that affect habitat and distribution of species from different levels in the trophic chain. While some species show resilience and adaptability, it is still challenging to identify thresholds for long-term change. Modeling tools offer a 'sneak peek' into plausible ocean scenarios in the future, while present ocean observations are key to building understanding of the ecosystem response to current climate events. Improving modeling capability and accuracy, paired with optimization of observing systems, is crucial to support science-informed decision making. Finally, we must recognize that model capability and optimal observing systems are insufficient without understanding, and thereby having testable hypotheses about the underlying mechanisms linking physical and biological processes in the ocean.

7. Conclusions

It is imperative that ecologists collaborate with physical scientists to unravel the press vs. pulse impacts on the California Current Ecosystem. The CCS is complicated with tremendous spatial heterogeneity. There is a strong dichotomy between the nearshore highly productive region and the offshore oligotrophic ocean, with commensurate differences in controlling physical environmental variables. The northern CCS is much more biologically productive than the southern CCS, and both regions have different characteristic climate patterns and oceanic processes that link physics with ecology. The mechanistic impacts of future long-term warming will vary for different organisms, since some will respond directly to temperature change, while others will respond to reduced nutrient supply and others to altered lateral advection.

Revisiting the classic PDO/ENSO/NPGO correlations with ecological responses in a more mechanistic way is one way forward to understanding what really matters to the ecosystem. What are the dominant physical processes (e.g., Fig. 2) associated with these nominal temperature correlations with ecological variables? Is the total change or the rate of change in a physical variable more important to ecology? Are thermal controls on physiology more important than their impact on stratification and consequent impact on nutrient fluxes and primary production? Is ocean current transport, which often correlates with temperature, and its impact on ecology more associated with large-scale wind forcing or local current instability processes?

The combined impacts of multiple stressors on the ecosystem must also be assessed more rigorously (e.g., Gruber et al. 2021, Sunday et al. 2022). Impacts of temperature, deoxygenation, pH, and nutrient concentrations of source waters will likely merge to deliver unanticipated impacts on the marine ecosystem, especially when considering phenological and spatial shifts among various species under long-term press disturbances (e.g. Glibert et al. 2022). Disentangling the integrated ecosystem-level impact of individual species responses to these multiple stressors acting at different timescales will be challenging and require coordinated physical and ecological monitoring. Such monitoring should be incorporated into the development of more advanced ecosystem models linking physics through plankton to higher trophic levels at relevant spatial scales of ecosystem change (Blanchard et al. 2024).

Short-term and long-range predictions of the ecological states will depend on our ability both to forecast the physical environmental changes and to wield a mechanistic understanding of which aspects of the changing physical environment can drive observed changes in ecological communities. Sustained long-term observations of the physical-biogeochemical-ecological system (Capotondi et al. 2019) combined with high-resolution modeling studies are crucial to unraveling these intricate interactions. And these types of practical forecasts (Jacox et al. 2020) can aid resource managers and policy makers in sustaining an economically valuable and socially beneficial California Current Ecosystem along our West Coast.

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Data availability

Data used in this study are available on the CCE LTER DataZoo website:

https://oceaninformatics.ucsd.edu/datazoo/catalogs/ccelter/datasets and also deposited at the Environmental Data Initiative: https://edirepository.org/. The CCE LTER data on the

Environmental Data Initiative is easily searchable through the CCE LTER landing page at: https://ccelter.ucsd.edu/data/. The CUTI and BEAUTI upwelling indices are available at https://mjacox.com/upwelling-indices/.

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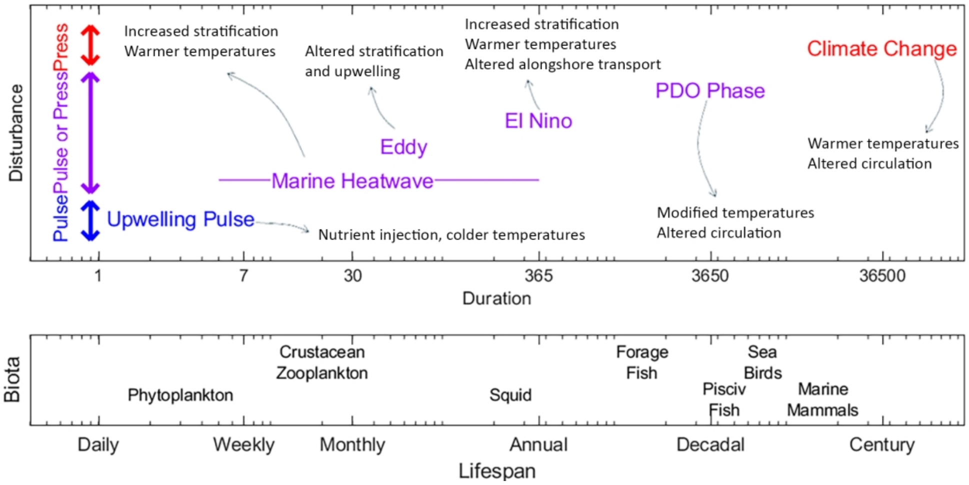

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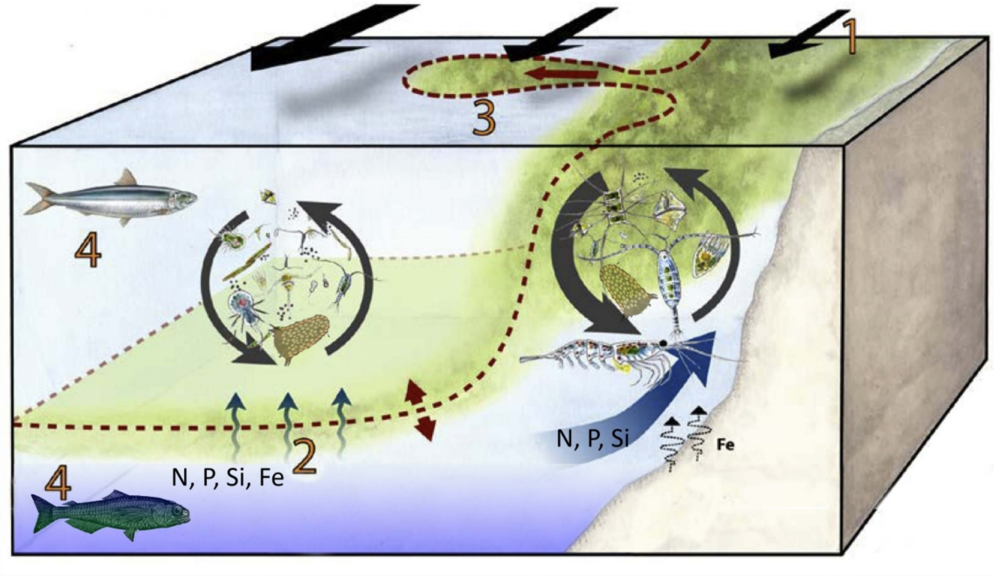

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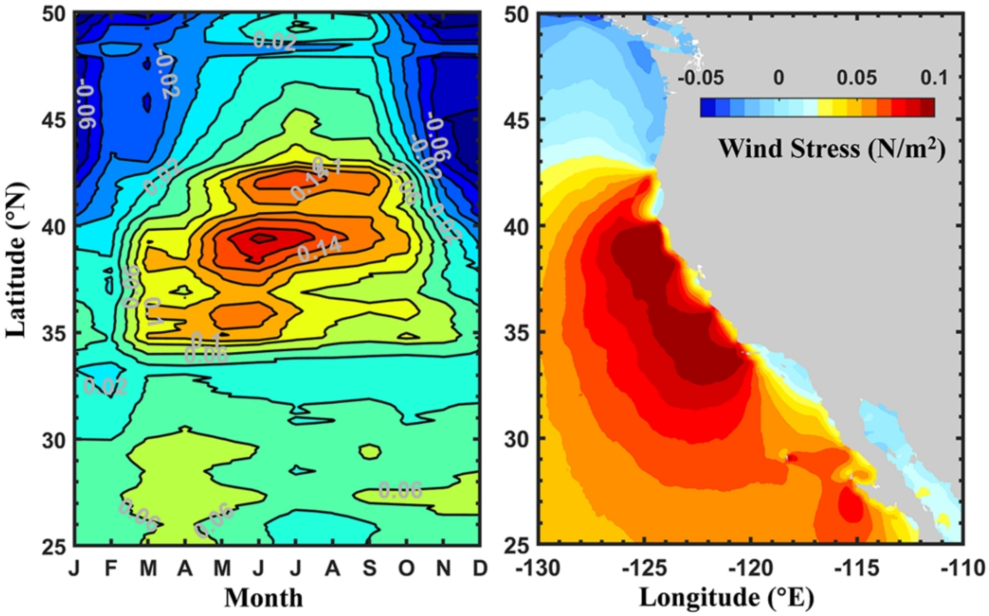

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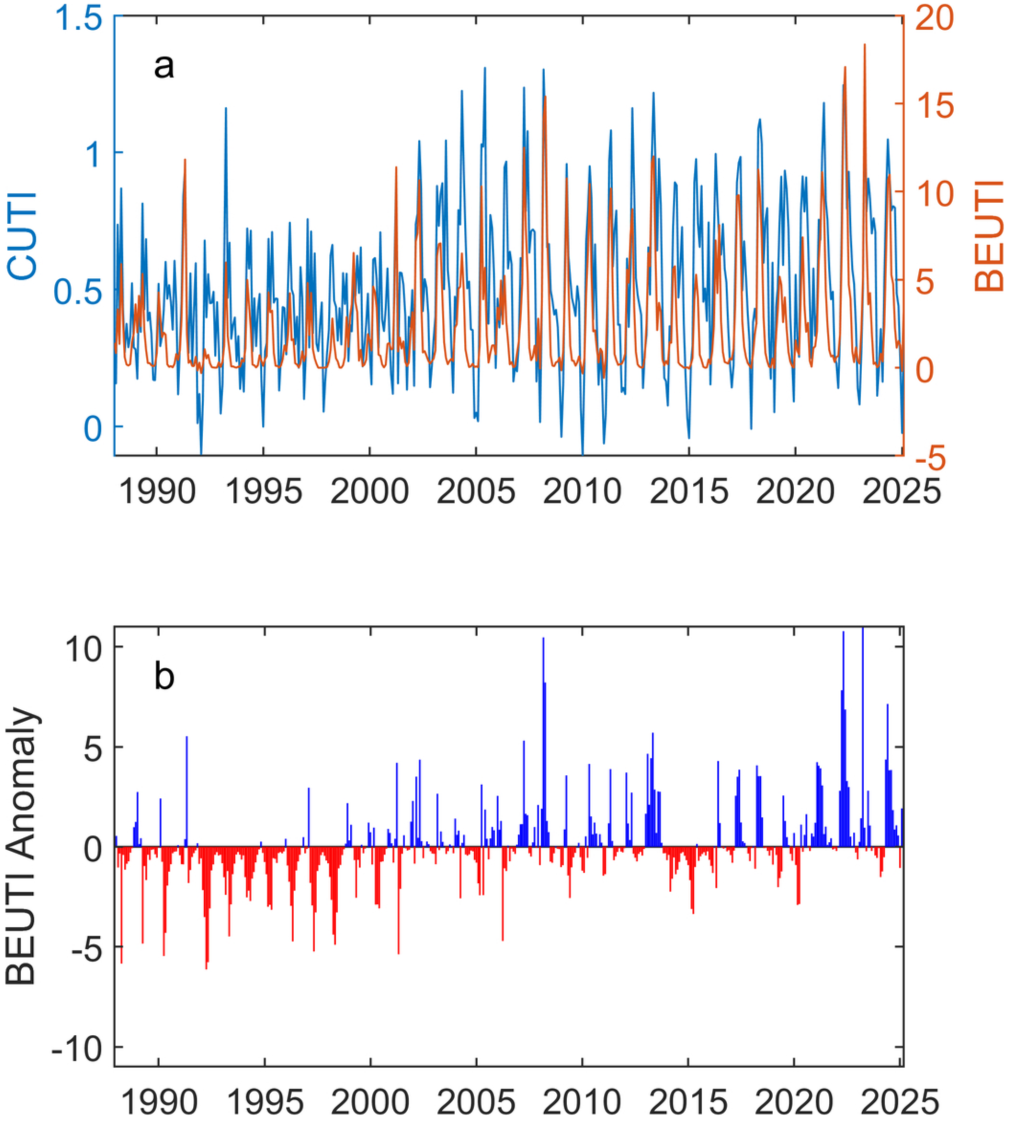

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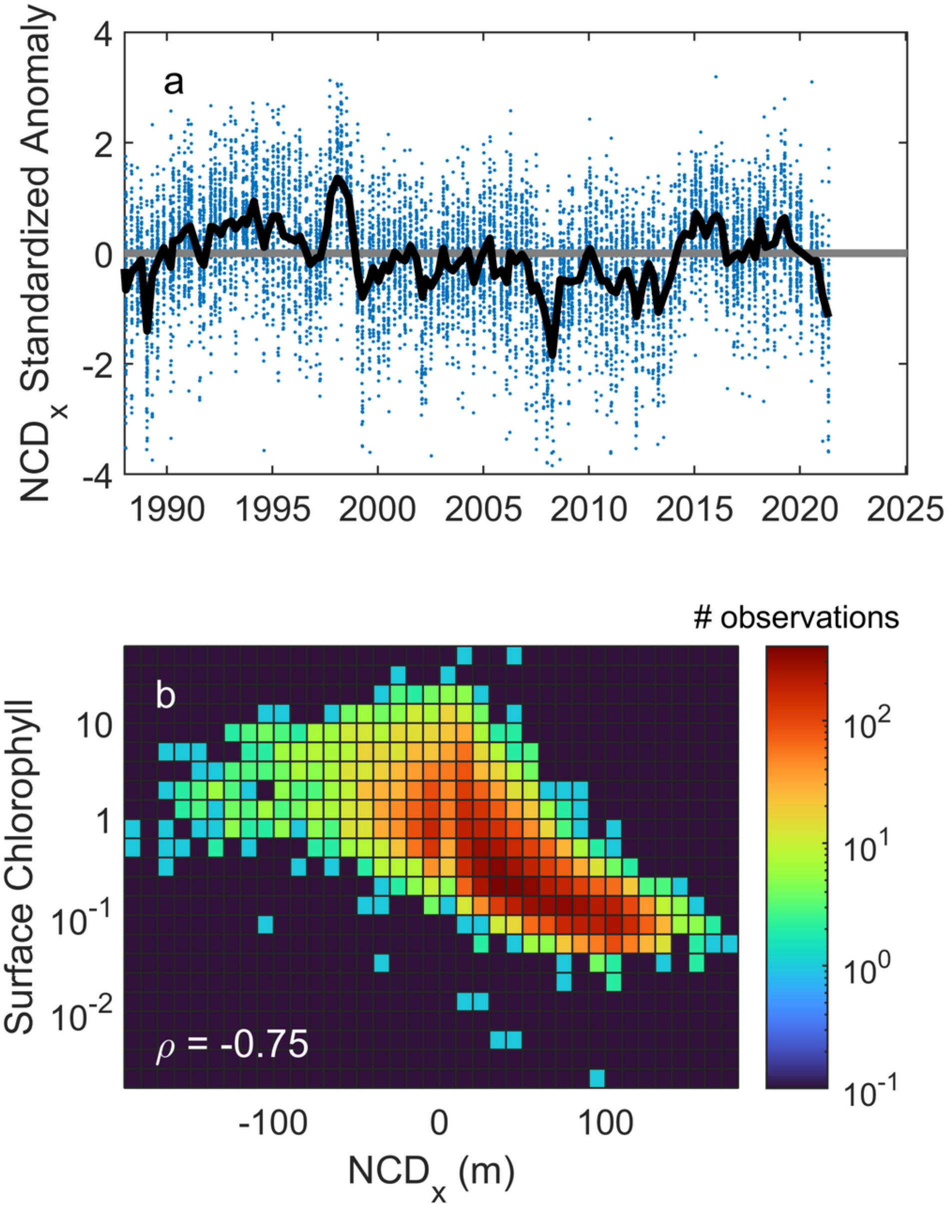

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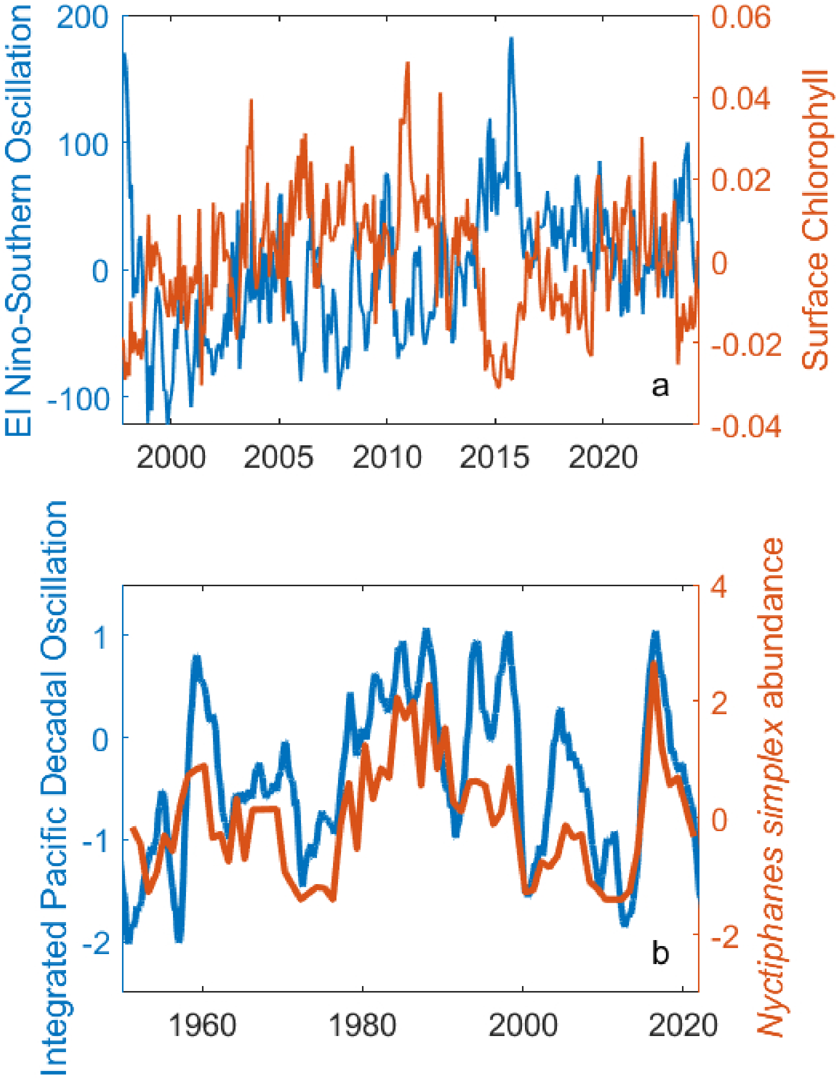

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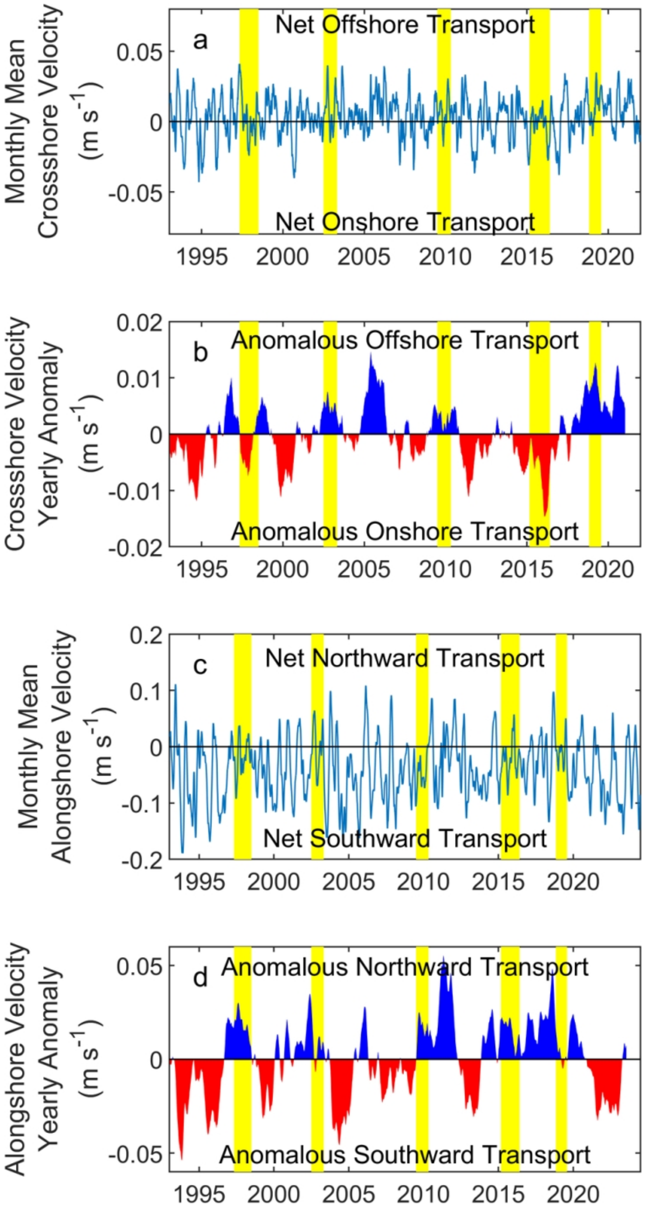

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