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Climate Change Impacts on Eastern Boundary Upwelling Systems

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Abstract

The world's eastern boundary upwelling systems (EBUSs) contribute disproportionately to global ocean productivity and provide critical ecosystem services to human society. The impact of climate change on EBUSs and the ecosystems they support is thus a subject of considerable interest. Here, we review hypotheses of climate-driven change in the physics, biogeochemistry, and ecology of EBUSs; describe observed changes over recent decades; and present projected changes over the twenty-first century. Similarities in historical and projected change among EBUSs include a trend toward upwelling intensification in poleward regions, mitigated warming in near-coastal regions where upwelling intensifies, and enhanced water-column stratification and a shoaling mixed layer. However, there remains significant uncertainty in how EBUSs will evolve with climate change, particularly in how the sometimes competing changes in upwelling intensity, source-water chemistry, and stratification will affect productivity and ecosystem structure. We summarize the commonalities and differences in historical and projected change in EBUSs and conclude with an assessment of key remaining uncertainties and questions. Future studies will need to address these questions to better understand, project, and adapt to climate-driven changes in EBUSs.

> The California Sardine Equals Any in the World
>
> Fishing Industry Holds High Place in State's Resources
>
> —*Long Beach Daily Telegram*, July 26, 1917

> Swan Song of Coastal Sardine
>
> The year 1951 marks the disappearance of the sardine from the coastal waters of California.
>
> —*Los Angeles Times*, June 18, 1951

PROLOGUE

The city of Monterey, California, is famous for the cultural and economic influence of a robust and lucrative sardine fishery. Sardine canneries dotted the Monterey coast—Cannery Row—during the first few decades of the twentieth century and dominated the local economy (**Figure 1**). During the 1936–1937 fishing season, the total sardine landings of 791,334 tons represented the largest one-season landing of any single species of fish on the West Coast (Ueber & MacCall 1992), and there were "enough 10-inch sardine in these landings that together, if laid end to end, [they] would reach from the earth to the moon and back" (Reinstedt 1978, as quoted in Ueber & MacCall 1992,

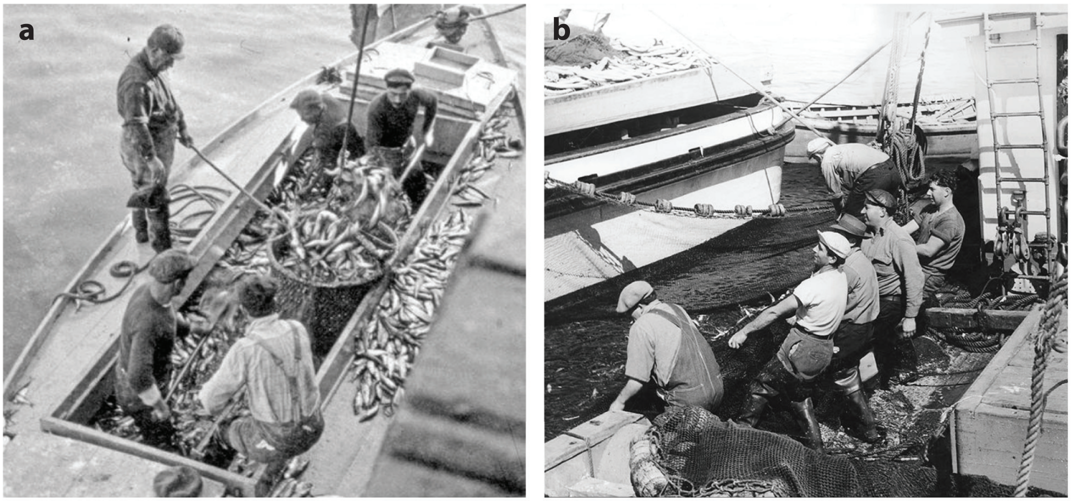


Figure 1

Historical photographs of the sardine fishery in Monterey, California, in (*a*) the 1920s and (*b*) 1939. Photographs provided by the California History Room at the Monterey Public Library (City of Monterey 2022).

p. 35). This early-twentieth-century era of "pax-sardinia" in California waters (Ueber & MacCall 1992, p. 35) immortalized the Monterey waterfront and its Cannery Row, which Steinbeck (1945, p. 1) famously described as "a poem, a stink, a grating noise, a quality of light, a tone, a habit, a nostalgia, a dream." From the 1900s through the 1940s, sardines were caught by the billions by up to 500 fishing vessels, canned and reduced in 16 canneries (peaking in 1945) on Cannery Row, and shipped to and consumed by people across the globe from the "sardine capital of the world" (SAH 2022).

This era didn't last. Through a combination of pressures from overfishing, management conflicts, and climate (Ueber & MacCall 1992), the magnificent California sardine fishery collapsed. By 1966, the biomass of the California sardine stock was just 4,000 tons, 0.1% of its peak biomass (Parrish 2000). As one fisherman noted in 1968, in the last year of this era of sardine fishing, "we caught them all in one night" (Ueber & MacCall 1992, p. 35). The last working Monterey cannery closed in 1973. Today, Monterey's Cannery Row is a popular destination for tourists, anchored by the Monterey Bay Aquarium, which seeks to "inspire conservation of the ocean" (Monterey Bay Aquar. 2022) at the location of the original Hovden Cannery.

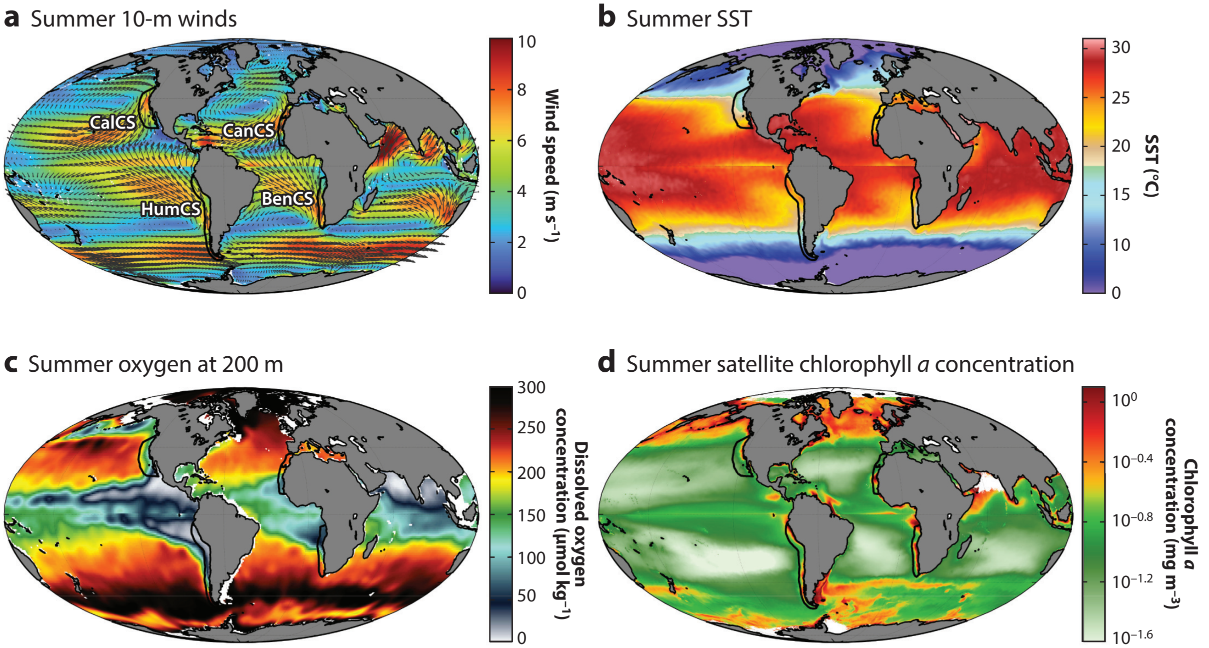
INTRODUCTION

The Physical, Ecological, and Socioeconomic Importance of the Eastern Boundary Upwelling Systems

The story of the Monterey sardine fishery underscores the importance of healthy and resilient marine ecosystems to the vitality of our coastal communities. It also stresses the need to understand the drivers of ecosystem change and the importance of using that scientific information to manage our living marine resources. In fact, the social and economic impacts of the sardine collapse motivated the state of California to invest in monitoring and studying the coastal ecosystem. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) began in 1949 with an initial aim to explore the causes of the sardine collapse (Bograd et al. 2003). Still active after 73 years, CalCOFI is the longest continuous and ongoing coastal ocean monitoring program in the world, conducting regular ship surveys of the physical, chemical, and biological conditions of the California Current System (CalCS).

The CalCS is one of four global eastern boundary upwelling systems (EBUSs) (**Figure 2**). Comprising only a small area of the global ocean, EBUSs provide a disproportionately large contribution to overall ocean productivity and up to 20% of global fish catch (Pauly & Christensen 1995, IPCC 2014). As these systems are among the most important marine regions to human society, they are also among the most observed and studied. The long time series provided by CalCOFI and comparable programs in the other global EBUSs—the Humboldt Current System (HumCS) (e.g., Grados et al. 2018, Chevallier et al. 2021), the Canary Current System (CanCS) (Arístegui et al. 2009), and the Benguela Current System (BenCS) (Hutchings et al. 2009a,b)—have permitted the study of the physical dynamics, ecosystem function, marine resources, and community impacts within the EBUSs and have led to an improved understanding and appreciation of the impacts of climate variability and change on these ecosystems and their living marine resources.

Climate change is impacting global ocean ecosystems (Bindoff et al. 2019), including the four major EBUSs. While ocean observing systems operating in the EBUSs have produced a wealth of knowledge, there is still uncertainty about how climate change will impact these systems and the human communities that depend on them. How will the EBUSs respond to persistent ocean warming and to shifts in the amplitude and timing of wind-driven coastal upwelling? How will changes in the physical and chemical properties of EBUS water masses influence changes in



a Summer 10-m winds

b Summer SST

c Summer oxygen at 200 m

d Summer satellite chlorophyll *a* concentration

Figure 2

Maps showing global means in several key properties during the warm season (June through August in the Northern Hemisphere and January through March in the Southern Hemisphere). The locations of the four EBUSs are shown by black outlines in each panel. (*a*) 10-m wind speed (*colors*) and vectors from the ERA5 atmospheric reanalysis (1979–2021) (Hersbach et al. 2020). (*b*) SST from the 2018 World Ocean Atlas (observations from the 1981–2010 period) (Boyer et al. 2018). (*c*) Dissolved oxygen concentrations at 200-m depth from the 2018 World Ocean Atlas (observations from the 1955–2010 period). (*d*) Concentration of ocean chlorophyll *a* estimated from multiple satellite ocean-color sensors over the 1998–2017 period (Garnesson et al. 2019). Abbreviations: BenCS, Benguela Current System; CalCS, California Current System; CanCS, Canary Current System; EBUS, eastern boundary upwelling system; ERA5, European Centre for Medium-Range Weather Forecasts Reanalysis 5; HumCS, Humboldt Current System; SST, sea surface temperature.

ecosystem productivity, community structure, and species distributions? How will our coastal communities respond to what are likely to be substantial and potentially unexpected changes in our coastal ecosystems? Can we anticipate and prepare for the world's next sardine story?

Commonalities and Differences Among the Eastern Boundary Upwelling Systems

There are many physical and biological attributes common to all of the EBUSs, including seasonally varying equatorward wind stress driving offshore Ekman transport and coastal upwelling; cross-shore variations in the magnitude of alongshore wind stress driving offshore upwelling; significant alongshore advection, including a poleward undercurrent; impingement by vast oxygen minimum layers, resulting in persistent natural hypoxia and vertical compression of viable habitat (Helly & Levin 2004); water masses characterized by high subsurface nutrient content but low dissolved oxygen content, with their ecological impacts governed by the strength of the water-column stratification; and high temporal variability, driven by both local and remote atmospheric and oceanic forcing on scales ranging from seasonal to decadal and longer (e.g., regime shifts and secular trends) (see tables 1–5 in Mackas et al. 2006). The upwelling of nutrient-rich water supports high primary production, which in turn supports high biomass of zooplankton, fish, marine mammals, and birds (Watermeyer et al. 2020). Regional circulation modulated by the upwelling cycle supports the retention and aggregation of plankton (including fish eggs and larvae), greatly impacting recruitment, productivity, and community structure (Agostini & Bakun 2002). Given their common physical drivers and ecosystem attributes, comparative EBUS studies have been especially insightful in determining the mechanisms by which climate change alters marine ecosystems (for reviews, see Hutchings et al. 1995, Carr & Kearns 2003, Mackas et al. 2006, Chavez & Messié 2009, Checkley & Barth 2009, Demarcq 2009, Fréon et al. 2009, Strub et al. 2013, Lluch-Cota et al. 2014, Sydeman et al. 2014, Wang et al. 2014, Bakun et al. 2015, García-Reyes et al. 2015, Rykaczewski et al. 2015, Kämpf & Chapman 2016).

These commonalities imply potentially similar responses in each system to global climate change highlighted by warming surface waters, enhanced stratification, and declining subsurface oxygen content (see, e.g., Bakun et al. 2015). However, there are important differences in both the physical structure and forcing of EBUSs that could drive divergent responses to climate change. Principal among these are the geographical differences between the Atlantic and Pacific (see, e.g., table 1 in Mackas et al. 2006). The Pacific systems are at the eastern boundaries of a broad subtropical basin, have generally narrow continental shelves (except in the Southern California Bight), and are characterized by older subpycnocline waters, with high nutrient and low oxygen levels. In addition, the Pacific systems are profoundly impacted by the El Niño–Southern Oscillation (ENSO) cycle, with equatorial Pacific conditions impacting the eastern subtropical boundaries through both oceanic and atmospheric teleconnections (Dewitte et al. 2012, Garçon et al. 2019). By contrast, the Atlantic systems lie within a relatively narrow subtropical basin, have relatively broader continental shelves, contain younger deep-water masses, and are not impacted as strongly by tropical–extratropical teleconnections (Mackas et al. 2006). In addition, the latitudinal ranges of the systems vary greatly (**Figure 2**), leading to a stronger influence of the Arctic Ocean in the Atlantic (CanCS) but a stronger influence of the Southern Ocean in the Pacific (HumCS). There are also strong region-specific differences within each system, driven in part by topographic complexity along the coasts that produces spatial hot spots of enhanced coastal upwelling and productivity (Mackas et al. 2006). The extent to which climate models capture these differences and project different trajectories for EBUS physics and biology is an important topic of this review and is presented in the section titled Projected Changes in the Eastern Boundary Upwelling Systems.

HYPOTHESES AND MECHANISMS OF CHANGE

Atmospheric Drivers and Upwelling Intensity

The persistent alongshore winds that stimulate coastal upwelling in EBUSs arise from the strong cross-shore atmospheric pressure gradient that exists between the dominant high-pressure (anticyclonic) systems present over the eastern portions of subtropical ocean basins and the low-pressure (cyclonic) systems present over the adjacent land masses (García-Reyes et al. 2015). Summer intensification of the continental low-pressure systems, driven in part by the seasonal warming of the underlying continent, contributes to the climatological cycle of the upwelling-favorable winds. This understanding of the upwelling process motivated Bakun (1990) to propose that an increased warming of the air mass over the continent in comparison to the ocean—as is expected with anthropogenic warming—will result in an increase in upwelling-favorable winds and the supply of cool, nutrient-rich waters to the ecosystems. In contrast to Bakun's (1990) suggestion of widespread intensification of upwelling winds, more recent work has emphasized the poleward migration of high-pressure systems as a potential consequence of the expansion of Hadley circulation in response to anthropogenic climate change (Lu et al. 2007). Rykaczewski et al. (2015) hypothesized that this migration of the oceanic high-pressure systems will exert a dominant influence on long-term changes in the intensity, location, and seasonality of upwelling-favorable winds, with a general intensification of those winds in the poleward portions of the EBUSs and a weakening of winds in the equatorward portions during the upwelling season.

Other hypotheses are more comprehensive in consideration of atmospheric and oceanic processes influencing upwelling. Upwelling intensity (i.e., the total volume of upwelled water) is influenced primarily by two components: wind-driven Ekman transport and cross-shore geostrophic transport. The Ekman transport can be further divided into contributions from coastal divergence (i.e., offshore Ekman transport) driven by alongshore winds at the coastal boundary and contributions from vertical velocities (i.e., Ekman suction or pumping) driven by wind-stress curl, which may extend farther offshore. In addition to changes in the intensity of coastal wind stress, changes in the intensity or location of atmospheric pressure systems could affect upwelling driven by wind-stress curl, altering the spatial extent of upwelling and the properties of the upwelled waters (Pickett & Paduan 2003, Rykaczewski & Checkley 2008, Jacox et al. 2014). Cross-shore geostrophic transport can also modulate upwelling at the coastal boundary; although it has received relatively little attention, this process has been identified as an important contributor to both mean upwelling intensity and its future evolution (Marchesiello & Estrade 2010, Oerder et al. 2015, Jacox et al. 2018, Ding et al. 2021).

Vertical Structure and Source Waters

While change in upwelling associated with atmospheric forcing has been the focus of countless research efforts in recent decades, potential physical and biogeochemical changes in the water column offer additional mechanisms to explore when considering EBUS responses to anthropogenic climate change. Hypotheses concerning water-column changes can be categorized into mechanisms that are associated with conditions within the EBUSs themselves and processes that are remote to the EBUSs. For instance, changes in the local stratification can alter the mixed-layer depth and the depth from which upwelling waters are drawn, with stronger stratification leading to shallower source depths and reduced nutrient supply (Lentz & Chapman 2004, Jacox & Edwards 2011). Remote processes can affect the biogeochemical properties of EBUSs by altering the properties of water masses that are eventually upwelled. EBUSs are fed by water masses of subarctic, subtropical, and equatorial origin, and the biogeochemical properties of these water masses are sensitive to variation in water-mass formation and ventilation resulting from long-term climate change. These changes can have consequences for the nutrient, oxygen, and inorganic carbon concentrations of waters upwelling in EBUSs (Rykaczewski & Dunne 2010, Pitcher et al. 2021).

Long-term changes in the frequency or intensity of basin-scale ocean–atmosphere phenomena, or in the strength of their teleconnections to EBUSs, represent another remote-forcing mechanism through which climate change can influence EBUS properties. Under present-day conditions, the remote processes associated with ENSO, the Benguela Niño, or other modes of natural variability (Bonino et al. 2019) can affect the winds (Jacox et al. 2015), mean circulation (Montes et al. 2011), eddy activity (Conejero et al. 2020), water-mass composition (Bograd et al. 2019), and biogeochemical properties of EBUSs (Garçon et al. 2019). Changes in these patterns of variability can also impact EBUS source waters, their properties, or the riverine input to coastal waters (Dunn et al. 2018).

Primary Production

As noted above, several plausible hypotheses have been offered to describe the physical and chemical response of EBUSs to climate change. In terms of their impacts on primary and secondary production, these mechanisms may reinforce or oppose each other. Enhanced nutrients in source waters would support increased productivity, increased stratification (and consequently reduced nutrient supply) would tend to limit productivity, and increased upwelling could enhance productivity to a point but limit productivity if it is too strong (Jacox et al. 2016). There is no clear consensus on which mechanism(s) will be the most prominent driver of future productivity changes, with various retrospective and forward-looking studies suggesting dominant roles for wind (Auad et al. 2006), stratification (Roemmich & McGowan 1995), and source-water nutrient concentrations (Rykaczewski & Dunne 2010).

Ecosystem Structure and Function

EBUSs support a diversity of mid-trophic-level species that serve as a backbone for translating primary productivity into ecosystem diversity. The HumCS and BenCS have been described as wasp-waist, where small pelagic species may exert both bottom-up control on upper trophic levels and top-down control on primary producers (Cury et al. 2000). By contrast, diversity in mid-trophic-level species in the CalCS may transfer more control to bottom-up processes (Madigan et al. 2012). Variability in upwelling—particularly when paired with other anthropogenic stressors, such as fishing pressure—can act synergistically to have cascading effects in EBUSs (Essington et al. 2015). Climate change impacts and resultant changes in local oceanographic features can mediate the competition among fisheries and top predators for forage fish, requiring increased understanding of not only trophic transfer (Cury et al. 2011, Young et al. 2015) but also spatial patterns of aggregation (Santora et al. 2021). Increasing physical variability has been hypothesized to translate to increased ecosystem variability as well (Sydeman et al. 2013), portending future change in marine ecosystems. For EBUSs, however, we hypothesize that the dominant driver of climate-driven changes in ecosystem structure and function will be the regional and phenological trends in physics and biogeochemistry (Barange et al. 2018), with implications for changing vertical and horizontal species distributions (often deeper and poleward, respectively) due to optimal habitat changes (Cheung et al. 2013, Blamey et al. 2015).

HISTORICAL CHANGES IN THE PHYSICS AND BIOGEOCHEMISTRY OF THE EASTERN BOUNDARY UPWELLING SYSTEMS

The Bakun (1990) hypothesis has motivated many studies scouring the historical record for evidence of upwelling intensification in EBUSs. These studies have used a variety of data sources, including in situ and remotely sensed ocean observations, historical reanalysis products, and sea surface temperature (SST) proxies derived from sediment cores. Both regional and cross-EBUS observational studies have described varying upwelling trends, depending on the data set analyzed and variable explored.

Regional Observations

In the CanCS, several studies have reported a weakening or no significant trend in upwelling intensity off the Iberian Peninsula (Lemos & Pires 2004, Barton et al. 2013, Bode et al. 2019) and off northwest Africa (Gómez-Gesteira et al. 2008, Barton et al. 2013), while others have reported an upwelling intensification trend off northwest Africa (Cropper et al. 2014, Benazzouz et al. 2015). In the BenCS, Santos et al. (2012a,b) attributed a nearshore cooling trend (and stronger cross-shore SST gradient) off Namibia and South Africa to increased upwelling intensity, although Tim et al. (2015, 2016) did not find a trend in the ocean–land pressure gradient that would have been consistent with the Bakun (1990) hypothesis. Regionally varying rates of change in upwelling intensity have also been reported in the Pacific systems. García-Reyes & Largier (2010) and Foreman et al. (2011) reported increases of 10–25% in upwelling-favorable wind speeds from historical in situ buoy observations in the northern CalCS. Aguirre et al. (2019) similarly found an increase in upwelling-favorable wind stress in the southern HumCS, in accordance with a poleward shift in the Southeast Pacific Anticyclone. Other studies have expanded the timescale of observation through SST proxies derived from sediment core data. Both McGregor et al. (2007), using a 2,500-year record near Cape Ghir off Morocco, and Gutiérrez et al. (2011), using a 150-year record off Peru, found significant twentieth-century SST declines that they noted were consistent with upwelling intensification.

Complementing these observational studies, output from atmospheric and ocean models over the historical period have also described EBUS trends. Casabella et al. (2014) did not find a significant historical trend in upwelling at the northern end of the CanCS, while Tim et al. (2016) found that changes in radiative forcing over the period 1850–2005 did not result in discernible upwelling trends in any EBUSs.

Observations Across the Eastern Boundary Upwelling Systems

Inconsistent results among data sources are especially evident in cross-EBUS historical comparisons. Narayan et al. (2010) found contrasting historical trends in alongshore wind stress off northwest Africa from the National Centers for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) reanalysis (Kalnay et al. 1996) and the Comprehensive Ocean–Atmosphere Data Set (COADS) but consistent trends toward intensification in the other systems from both data sets (see table 1 in Narayan et al. 2010). Pardo et al. (2011) compared trends in SST and offshore Ekman transport derived from the NCEP/NCAR reanalysis over 1970–2009, finding a weakening trend in upwelling intensity in the CanCS, an increasing trend in the BenCS, a small weakening trend in the HumCS, and no discernible trend in the CalCS. Taboada et al. (2019) found contrasting trends in upwelling intensity in each EBUS depending on the reanalysis product used and noted a need to adjust these products for large-scale biases, especially in coastal regions. Abrahams et al. (2021) reported upwelling intensification throughout the HumCS but varying trends in upwelling intensity, frequency of events, and duration in the other EBUSs.

Sydeman et al. (2014) performed a meta-analysis on 22 published studies (and 187 nonindependent time series) from all four EBUSs and found intensification trends in three of the four systems. However, the trends were highly dependent on the length and period of the time series, time of year (stronger in the warm season), latitude (stronger positive trends at higher latitudes), and data type (stronger for direct observations versus modeling). García-Reyes et al. (2015) found weak evidence of upwelling intensification in the higher latitudes of the EBUSs and noted the consistency of these observations with the anticipated poleward shift in the subtropical high-pressure systems (Li et al. 2013, Aguirre et al. 2019). Using a single high-resolution (0.3°) wind product (the Climate Forecast System Reanalysis), Varela et al. (2015) investigated EBUS upwelling trends over a common period, 1982–2010, and found weak, nonsignificant increasing trends in the coastal regions of the CanCS and BenCS and statistically significant increasing (decreasing) trends in the northern (southern) portions of the CalCS and HumCS (see summary of other studies in tables 1 and 2 in Varela et al. 2015). A later study by Varela et al. (2018) found that 92% of coastal upwelling regions showed a mitigated warming (SST) trend at the coast relative to offshore, suggesting that coastal upwelling (whether intensifying or not) may serve as a buffer to large-scale global warming. Seabra et al. (2019) found a similar mitigation of long-term warming in the CalCS coastal region and a cooling in the HumCS, based on the National Oceanic and Atmospheric Administration

(NOAA) Daily Optimum Interpolation SST data set over the period 1982–2018. Overall, coastal regions in the EBUSs had approximately half the warming rate of coastal regions outside EBUSs, with the effect most prevalent in the Pacific.

It is clear from a review of prior studies that there is no consensus on how climate variability and change have impacted the EBUSs over recent decades, nor is there broad historical support for the Bakun (1990) hypothesis of upwelling intensification. While there is some consistency in derived trends in upwelling intensity (and associated SST trends) across EBUS studies, both observational and modeling, the results were highly dependent on the data source or model used, the variable considered (either direct or indirect measures of upwelling intensity), and the time period and season evaluated.

PROJECTED CHANGES IN THE EASTERN BOUNDARY UPWELLING SYSTEMS

Atmospheric Drivers and Upwelling Intensity

Global modeling studies have projected consistent changes in the dominant subtropical atmospheric pressure systems that drive coastal upwelling in the EBUSs, notably their general strengthening and poleward displacement (Wang et al. 2014, Rykaczewski et al. 2015, Tim et al. 2016). Correspondingly, these studies have projected upwelling intensification in the poleward regions of the EBUSs and a weak or decreasing trend in the equatorial regions, though with important differences that reflect model resolution and forcing. In the CanCS, a majority of climate models project a poleward displacement of the Azores High (Rykaczewski et al. 2015, Sousa et al. 2017a, Sylla et al. 2019, Varela et al. 2022), resulting in stronger and weaker upwelling-favorable winds off the Iberian Peninsula and northwest Africa, respectively (Miranda et al. 2013; Lopes et al. 2014; Rykaczewski et al. 2015; Cordeiro Pires et al. 2016; Sousa et al. 2017a,b; Sylla et al. 2019; Mignot et al. 2020; Varela et al. 2022). Weakening upwelling intensity is especially prevalent during summer off northwest Africa, while the intensification in the northern CanCS corresponds with more frequent high-intensity upwelling events and an extension of the upwelling season (Miranda et al. 2013, Rykaczewski et al. 2015, Tim et al. 2016). A similar pattern is seen in the BenCS projections; the projected poleward displacement of the South Atlantic High drives latitudinal changes in alongshore winds, yielding upwelling intensification and weakening at the poleward and equatorward ends of the BenCS, respectively (Rykaczewski et al. 2015, Aguirre et al. 2019, Rixen et al. 2021).

Projections of changes in the Pacific subtropical highs follow a similar pattern to those in the Atlantic systems (Gillett & Fyfe 2013, Rykaczewski et al. 2015, Aguirre et al. 2019). The projected poleward displacement of the North Pacific High (Rykaczewski et al. 2015, Arellano & Rivas 2019) drives increases in upwelling-favorable winds in the central and northern CalCS (Snyder et al. 2003, Li et al. 2014, Rykaczewski et al. 2015, Brady et al. 2017, Xiu et al. 2018, Arellano & Rivas 2019, Howard et al. 2020, Pozo Buil et al. 2021) but weakening at the southern end (Wang et al. 2014, Rykaczewski et al. 2015, Tim et al. 2016, Brady et al. 2017, Howard et al. 2020). Snyder et al. (2003) also projected a strengthened wind-stress curl within the CalCS, which can impact plankton community structure and trophic interactions (Rykaczewski & Checkley 2008). Similarly, in the HumCS, a projected strengthening and poleward displacement of the South Pacific High (Belmadani et al. 2014, Rykaczewski et al. 2015, Chamorro et al. 2021) leads to increased and decreased alongshore winds in the HumCS off Chile and Peru, respectively (Goubanova et al. 2011, Belmadani et al. 2014, Wang et al. 2014, Oerder et al. 2015, Rykaczewski et al. 2015, Tim et al. 2016, Oyarzún & Brierley 2019, Chamorro et al. 2021). Oerder et al. (2015) noted a reduction in nearshore wind-stress curl off Peru, contributing to a decline in upwelling intensity in this part of the HumCS.

Importantly, a key element of the Bakun (1990) hypothesis—that stronger land–sea pressure gradients driven by differential warming trends would result in upwelling intensification—is not supported by most climate models (e.g., Rykaczewski et al. 2015). While differential land–sea warming trends are ubiquitous among models, it is the latitudinal shifts in the subtropical high-pressure systems that have the greater influence on the changing location and magnitude of upwelling winds as simulated by global models (Rykaczewski et al. 2015). And while the trends in upwelling intensification are generally consistent among EBUSs (see table 1 in Rykaczewski et al. 2015), Tim et al. (2016) noted that these trends are generally significant only for simulations with high greenhouse gas concentrations [e.g., the Representative Concentration Pathway 8.5 (RCP8.5) scenario], in which consistent trends are seen in all ensemble members. Of all the EBUSs, there was greatest uncertainty in the magnitude, and even sign, of the upwelling trends in the CalCS (Wang et al. 2014, Rykaczewski et al. 2015, Tim et al. 2016).

The projected spatially explicit changes in upwelling intensification in each EBUS are accompanied by important phenological changes. In the poleward regions of the EBUSs, where intensification is broadly projected, there is also a projected trend toward longer upwelling seasons (Rykaczewski et al. 2015, Tim et al. 2016). Brady et al. (2017) reported stronger projected upwelling in spring but weaker in summer in the CalCS, leading to reduced total seasonal upwelling, with these trends emerging only in the latter half of the twenty-first century under a high-emissions scenario. Snyder et al. (2003) projected a later spring transition to upwelling conditions in the CalCS from a regional climate model, while the ensemble of global models assessed by Rykaczewski et al. (2015) projected an earlier spring transition and lengthening of the upwelling season, with this pattern consistent among all EBUSs. While trends in upwelling intensification will have important implications for biological productivity, changes in seasonal timing may drive important changes in trophic interactions in the EBUSs (Bograd et al. 2009).

Future changes in cross-shore geostrophic transport have received relatively little attention, though several regional studies have shown its influence on projected upwelling trends in the HumCS and CalCS (Oerder et al. 2015, Ding et al. 2021). Often, projected changes in geostrophic transport oppose changes in Ekman transport, thereby mitigating the wind-driven upwelling changes (Oerder et al. 2015, Ding et al. 2021), though in some cases changes in geostrophic transport are projected to reinforce wind-driven increases or declines in upwelling (Ding et al. 2021).

Surface Warming and Vertical Structure

As with the rest of the global ocean, the EBUSs are projected to experience significant surface warming through the twenty-first century, with SST expected to increase by approximately 1.5–3.5°C by 2100 in a high-emissions scenario (RCP8.5) and approximately 1–2°C in a low-emissions scenario (RCP4.5) (**Figures 3** and **4**). Upwelling intensification in the poleward regions of the EBUSs may mitigate the coastal near-surface warming trend and increase cross-shore SST gradients, as noted for the northern CalCS (Li et al. 2014) and northern CanCS (Lopes et al. 2014, Cordeiro Pires et al. 2016, Sousa et al. 2017a, Varela et al. 2022). Conversely, weaker cross-shore SST gradients may result from declining upwelling intensity in the northern HumCS and off northwest Africa (Sousa et al. 2017a, Chamorro et al. 2021, Varela et al. 2022). These projections are consistent with the mitigated near-shore warming trends observed in the recent historical record (Seabra et al. 2019), particularly for the Pacific systems. The projected near-surface warming also drives a shoaling mixed-layer depth in the EBUSs, though with significant model spread

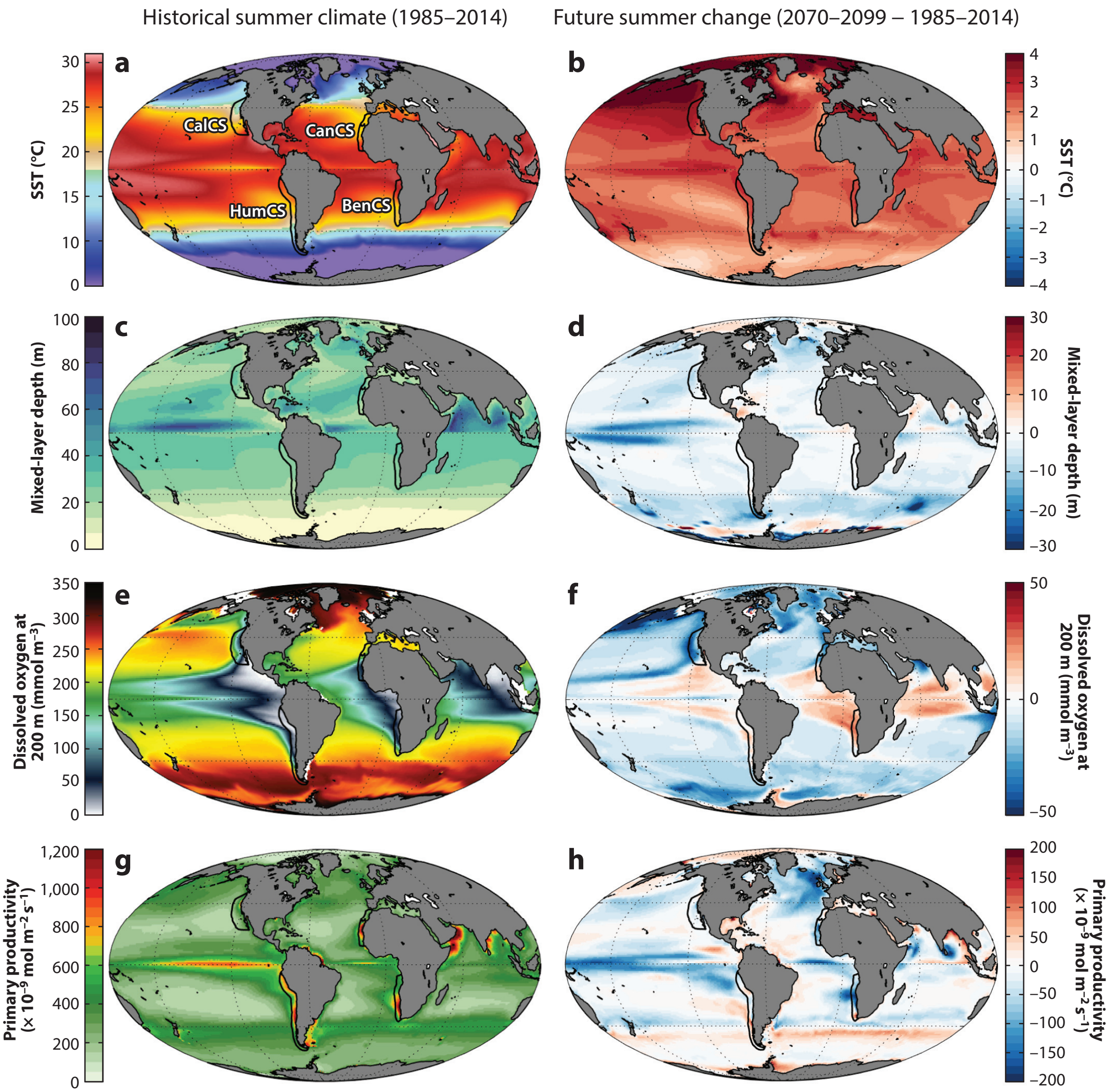
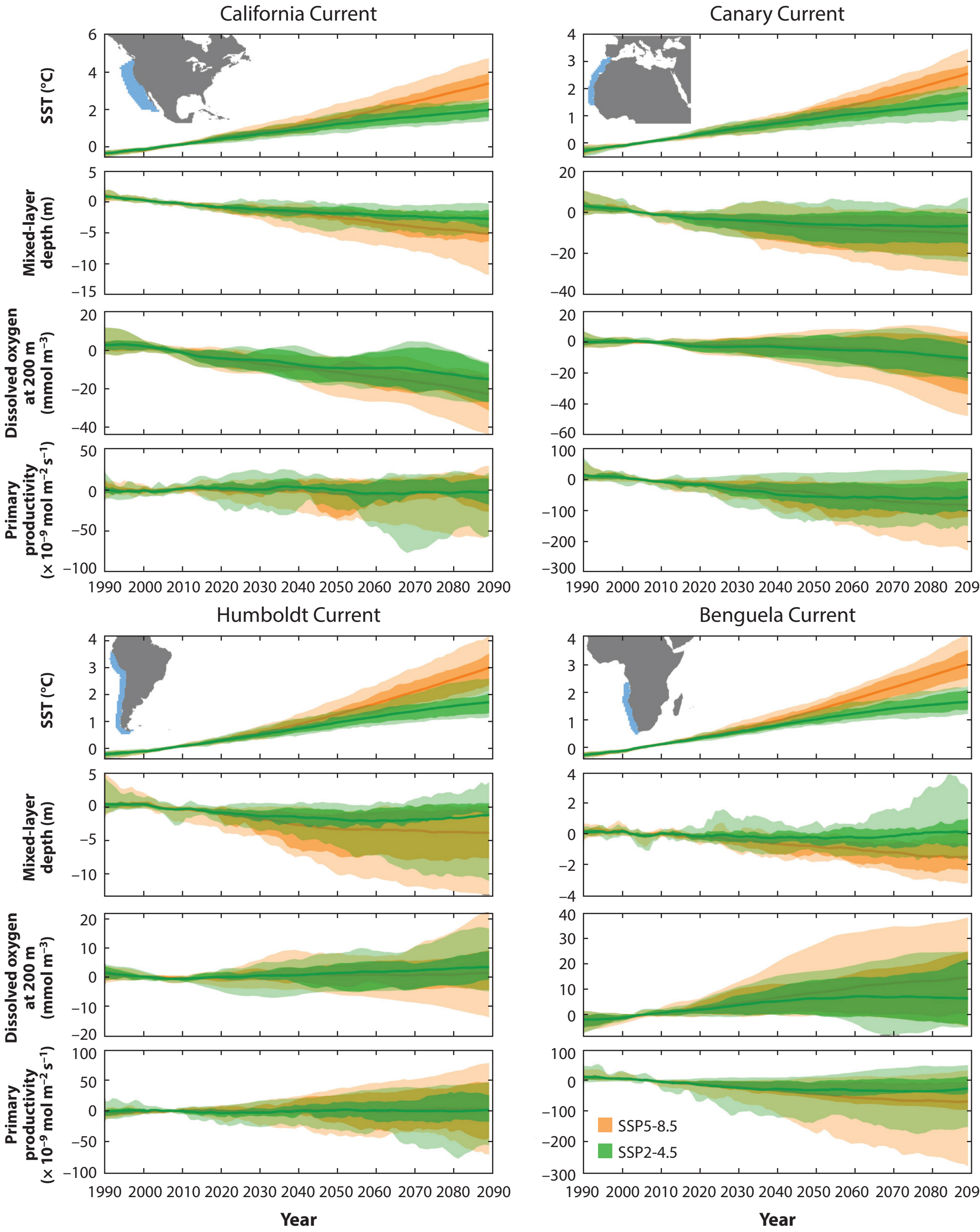


Figure 3

Maps showing the ensemble mean climate during the summer period from the CMIP6 historical experiment for 1985–2014 (*left*) and the ensemble mean future changes from the CMIP6 SSP5-8.5 experiment (2070–2099 relative to 1985–2014; *right*) for (*a*,*b*) SST, (*c*,*d*) mixed-layer depth, (*e*,*f*) dissolved oxygen at 200-m depth, and (*g*,*h*) primary productivity. Summer is defined as July through September in the Northern Hemisphere and January through March in the Southern Hemisphere. Data are from the NOAA Climate Change Web Portal (**https://psl.noaa.gov/ipcc/cmip6**) and the Earth System Grid Federation portal (**https://esgf-node.llnl.gov**). Abbreviations: CMIP, Coupled Model Intercomparison Project; NOAA, National Oceanic and Atmospheric Administration; SSP, Shared Socioeconomic Pathway; SST, sea surface temperature.



(*Caption appears on following page*)

Figure 4 (*Figure appears on preceding page*)

Projected twenty-first-century change in several key properties of the four EBUSs: SST, mixed-layer depth, dissolved oxygen at 200-m depth, and vertically integrated primary productivity. The time series show change relative to the 1991–2020 mean, averaged over the large marine ecosystems associated with each EBUS (*blue regions on inset maps*). Projections are taken from the CMIP6 ensemble under the SSP5-8.5 and SSP2-4.5 scenarios, and a 20-year smoothing was applied. For each scenario, solid lines mark the ensemble mean, and dark and light shading indicate the 25th–75th and 10th–90th percentiles, respectively. Data are from the NOAA Climate Change Web Portal (**https://psl.noaa.gov/ipcc/cmip6**) and the Earth System Grid Federation portal (**https://esgf-node.llnl.gov**). Note that the time series are averaged over the EBUS regions, although the northern and southern portions of each EBUS often have contrasting trends. Abbreviations: CMIP, Coupled Model Intercomparison Project; EBUS, eastern boundary upwelling system; NOAA, National Oceanic and Atmospheric Administration; SSP, Shared Socioeconomic Pathway; SST, sea surface temperature.

(**Figure 4**) and significant increases in water-column stratification in the coastal regions of the CalCS (Xiu et al. 2018, Howard et al. 2020, Pozo Buil et al. 2021), HumCS (Oerder et al. 2015, Oyarzún & Brierley 2019, Echevin et al. 2020), and BenCS (Cordeiro Pires et al. 2016, Sousa et al. 2020).

Source Waters, Dissolved Oxygen, and Acidification

Climate change is expected to have significant impacts on the biogeochemistry of EBUSs. In the Pacific EBUSs, modeling studies project decreases in pH and associated increases in the volume of water undersaturated with respect to $CaCO_3$, implying increasingly corrosive conditions for calcifying organisms. The near-surface waters of the northern and central CalCS are expected to depart their present range of pH variability by the 2040s, becoming corrosive with respect to aragonite and causing near-permanent undersaturation of the productive layer (Hauri et al. 2013). Analogously, the nearshore waters off Peru are projected to become undersaturated with respect to aragonite in the next few decades irrespective of the future emissions scenario, and to become permanently undersaturated with respect to calcite in approximately 60% of the euphotic zone by 2090 under a high-emissions scenario (Franco et al. 2018). The complex nature of the biophysical interactions that drive pH trends in the EBUSs is such that analogous changes in the atmospheric forcing can result in opposite ocean acidification trends in different systems. For example, the CanCS and CalCS show, respectively, increasing and decreasing pH as a result of projected upwelling intensification, which can dampen or enhance acidification due to rising atmospheric CO_2 (Lachkar 2014). This is likely due to the different contributions of physical and biological drivers of acidification in the two systems, that is, the increase in the advection of undersaturated water versus changes in the ratio of production and remineralization, with the first mechanism dominating in the CalCS and the second in the CanCS.

Projected declines of global ocean oxygen concentrations are also set to affect the EBUSs, especially those that are more tightly coupled to oxygen minimum zones. Climate projections show deoxygenation trends in some upwelling systems and increases in others (**Figure 3**), though changes in oxygen are not well constrained (Garçon et al. 2019). In analogy to acidification, complex biophysical interactions regulate oxygen concentrations in the EBUSs, meaning that projected oxygen trends can vary even within subregions of the same upwelling system under the same forcing scenario (Bograd et al. 2008, Rixen et al. 2021). Furthermore, these projected trends are sensitive to model resolution and parameterization, large-scale biases in circulation, and oxygen-minimum-zone representation (Echevin et al. 2020, Pozo Buil et al. 2021). For example, in an ensemble of high-resolution downscaled projections, two members showed an overall ∼30–40% increased subsurface nitrate and an ∼50-m-shallower hypoxic boundary layer along the California coast. However, an opposite response, featuring a decrease of subsurface nitrate (∼20%) and a deepening of the hypoxic boundary layer by ∼30 m along the entire coast, was found in one member of the ensemble (Pozo Buil et al. 2021).

Acidification, deoxygenation, and changes in macronutrient concentrations in the EBUSs are driven by interactions with the wider ocean basins as well as with the local atmosphere, coastline, and human activities (Garçon et al. 2019). These forcings can counteract or reinforce each other; for example, the effect of decreased source-water oxygen is twice as large as the effect of increased local remineralization of organic matter in driving the expansion of future hypoxic areas in the CalCS (Dussin et al. 2019), and the projected slowdown of the equatorial circulation reduces the ventilation of the HumCS, inducing a future nearshore deoxygenation trend (Echevin et al. 2020). At small scales, variability in coastal upwelling, advection, and biological activity generates patterns of ocean acidification and hypoxia that are spatially heterogeneous both in their mean and in their trends (Cheresh & Fiechter 2020). This patchiness is further exacerbated by human activities on urban and agricultural land, resulting in the discharge of organic material and nutrients that fuel eutrophication, deoxygenation, and acidification in the EBUSs (Kessouri et al. 2021).

Primary Production and Organic Carbon Cycling

Earth system models exhibit a large spread in future projections of primary productivity in all EBUSs (**Figure 4**). When these projections are averaged over the entirety of each system, the multimodel mean trends tend to be toward lower productivity, consistent with the stratification-induced decreases in euphotic-zone nutrient supply and export production that are projected for much of the subtropical oceans (Fu et al. 2016, Sousa et al. 2020). However, there is limited consensus among models on the sign of productivity change in each system; for models in which increased upwelling and/or enhanced source-water nitrate overwhelm increased stratification, future productivity can increase (Rykaczewski & Dunne 2010, Xiu et al. 2018). Furthermore, the sign of productivity trends can vary within individual EBUSs, often with increased productivity in the poleward portions and decreased productivity in the equatorward portions (**Figures 3** and **4**). While these findings hold for different emissions scenarios, the magnitude of change and the degree of uncertainty (i.e., the magnitude of model spread) increase under higher-emissions scenarios (**Figure 4**). Similarly, downscaled regional models project productivity trends that are in most cases qualitatively consistent with their parent climate models but can differ substantially in magnitude and in some cases even have opposite sign (Echevin et al. 2020, Howard et al. 2020, Pozo Buil et al. 2021).

Uncertainties in the future of productivity, combined with uncertainties in ecosystem shifts induced by changes in temperature, acidity, and oxygenation, imply crucial uncertainties in the future of organic carbon export and sequestration in EBUS regions. This uncertainty further extends to the adjacent open basins, which receive and export significant amounts of coastally produced carbon (Bonino et al. 2021), highlighting how understanding the future of EBUSs is key to refining projections of the organic carbon cycle on larger scales.

Ecosystem Structure and Function

Understanding how marine animals will be affected by future trends in environmental conditions is an important challenge. Distributional shifts are among the most anticipated ecological responses to global warming (e.g., Hazen et al. 2013, Pinsky et al. 2018), with many species expected to shift their ranges poleward or deeper, altering community structure and trophic interactions. Changes in forage fish populations and distributions in the EBUSs have the potential to drive ecosystem response and reorganization from higher-trophic-level predators to fisheries themselves (Pikitch et al. 2014, Checkley et al. 2017). In the CalCS, northward shifts in sardine distribution under climate change may reduce fish catch in some regions while increasing it in others (Fiechter et al. 2021, Smith et al. 2021), while also altering predator reliance on individual species (Petatán-Ramírez et al. 2019). On the other hand, projected increases in upwelling may mitigate warming trends (Seabra et al. 2019, Varela et al. 2022), providing areas of climate refugia for EBUS fauna (Hu & Guillemin 2016, Lourenço et al. 2016, Barceló et al. 2018).

Deoxygenation trends can also have broad-reaching ecological impacts. For example, determining how changes in oxygen concentrations will affect EBUS structure and function requires both constraining future oxygen trends (Garçon et al. 2019) and understanding how organisms respond to different oxygen thresholds over the long and short terms (Chan et al. 2008, Vaquer-Sunyer & Duarte 2008). Even intermittent occurrence of hypoxia can result in sublethal levels of habitat degradation, meaning a decline in juvenile fish growth rate, restriction of the habitable zone and therefore habitat crowding, and ecological crunches or bottlenecks (Eby et al. 2005).

Modeling work is underway to explore the potential ecosystem effects of climate change in the EBUSs. In a BenCS example, Lockerbie & Shannon (2019) imposed a twofold increase in primary production over 10 years as a plausible future scenario for the southern BenCS, based on observed seasonal and annual variability in productivity and upwelling (Lamont et al. 2014, 2018). They found that the ecosystem may be able to support increased fishing on prey species under such conditions (Shannon et al. 2020). Using a different modeling platform (Atlantis), Ortega-Cisneros et al. (2018) evaluated the effects of climate change based on projections of temperature and vertical and horizontal water mixing in the southern BenCS, finding warming to have the strongest (and most negative) impacts on modeled species, with large pelagic fish and demersal fish being most affected by the cumulative effects of fishing and warming. In a first prototype spatial projection of the southern BenCS using the Ecospace platform, total catch was lower under the high-emissions scenario [Shared Socioeconomic Pathway 5-8.5 (SSP5-8.5)] than under the low-emissions scenario (SSP1-2.6), with demersal fish contributing a larger portion of the total catch, anchovy and sardine stocks falling to lower levels, and the abundance of the endangered African penguin also being correspondingly lower (L.J. Shannon, unpublished results).

These examples demonstrate the diversity and uncertainty around future projections of climate change in EBUSs and the need to pay careful attention to defining responses of functional groups or species to climate variables if we are to improve ecosystem projections and better inform EBUS users, such as the fishing or ecotourism sectors. Trait-based vulnerability assessments are useful in identifying species that are likely to be most sensitive to climate change in EBUSs and would warrant more detailed research and careful monitoring (e.g., Ortega-Cisneros et al. 2018). Improved ecosystem projections will provide invaluable information for environmental planning related to regulating ecosystem services, such as nutrient cycling or climate regulation, which interact with provisioning services such as fisheries.

SUMMARY OF CLIMATE CHANGE IN THE EASTERN BOUNDARY UPWELLING SYSTEMS

Common Changes Across the Eastern Boundary Upwelling Systems

While there is considerable uncertainty in how EBUSs will evolve with climate change, there are a number of robust changes in their physics, biogeochemistry, and ecology that are consistent among the current family of global and regional climate models (see the sidebar titled Climate Change Projections in the Eastern Boundary Upwelling Systems). These changes include a poleward shift of the dominant subtropical high-pressure systems that drive upwelling dynamics; a subsequent intensification of upwelling in the poleward regions of the EBUSs, along with generally weaker trends or trends of uncertain sign in the equatorward regions; a secular warming

CLIMATE CHANGE PROJECTIONS IN THE EASTERN BOUNDARY UPWELLING SYSTEMS

Temperature

- Coastal warming modulated by upwelling trends
- Stronger cross-shore SST gradient
- Enhanced stratification

Wind

- Poleward displacement of subtropical highs
- Stronger alongshore wind stress in poleward regions; weaker to no trend in equatorial regions
- Stronger offshore wind-stress curl

Upwelling

- Upwelling intensification (weakening or no trend) in poleward (equatorward) regions
- Later spring transition (northern CalCS)
- Longer upwelling season in poleward regions (HumCS, CanCS, and BenCS)

Nutrients

- Permanent aragonite undersaturation by 2050 (CalCS) or 2100 (HumCS)
- Deoxygenation and higher nutrient content (CalCS and HumCS)

Productivity

- Increased offshore transport of phytoplankton (CanCS and BenCS)
- Nonlinear productivity response to upwelling intensification (CalCS)
- Uncertain directional change in productivity

trend that enhances water-column stratification and reduces mixed-layer depth, which may act to counteract enhanced upwelling in driving productivity trends; a mitigated warming in near-coastal regions where upwelling intensifies, leading to stronger cross-shore SST gradients; a continuing deoxygenation trend accompanied by increasing ocean acidification, with impacts largest in the Pacific systems on which the naturally occurring oxygen minimum zone impinges; and potentially large but uncertain changes in productivity, species distributions, and trophic interactions.

Competing Influences on Upwelling Systems: California Current Case Study

To illustrate and quantify the projected trends in EBUSs and their complex upwelling dynamics, we take the CalCS as a case study (**Figure 5**). Trends in the key processes and conditions driving the efficacy of coastal upwelling in the CalCS demonstrate that factors such as wind forcing, water-column structure, and remotely driven nutrient content may sometimes compete and that changes in these factors may differ regionally. Enhanced coastal wind stress in the northern CalCS (north of ~40°N) leads to increases in Ekman transport and vertical velocity at the base of

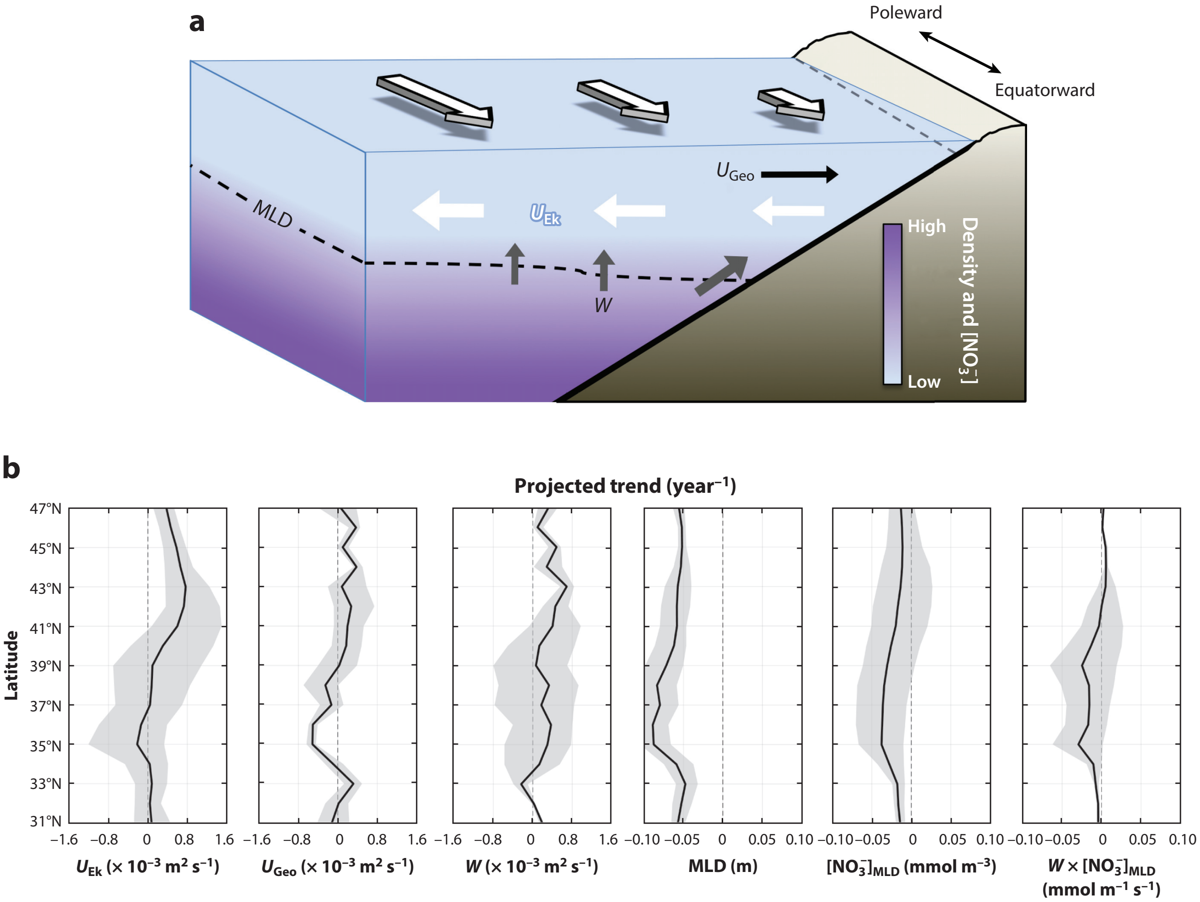


Figure 5

Factors influencing the magnitude of upwelling and upwelled nutrient supply. (*a*) Schematic representation of a section of coast in an EBUS. Equatorward winds (*arrows above the ocean surface*) drive offshore Ekman transport, while cyclonic wind-stress curl (wind stress decreasing closer to the coast) drives divergence in Ekman transport and consequently Ekman suction (curl-driven upwelling). Cross-shore geostrophic transport (U_{Geo}) is driven by the alongshore pressure gradient associated with a north–south gradient in sea surface height. Net vertical transport (W) through the base of the mixed layer is the sum of U_{Ek} and U_{Geo}. Vertical nitrate flux through the base of the mixed layer is calculated as the product of vertical transport (W) and the nitrate concentration at the base of the mixed layer ([$NO_3{}^-$]$_{MLD}$). (*b*) Future changes in each component of the schematic as quantified for the California Current System, based on the ensemble of downscaled regional projections described by Pozo Buil et al. (2021). Projected trends are linear trends over the 1980–2100 period under the RCP8.5 scenario. Gray shading indicates the spread of the three ensemble members (forced by GFDL-ESM2M, IPSL-CM5A-MR, and HadGEM2-ES), and black lines mark the ensemble means. Sign conventions are consistent with the schematic; positive U_{Ek} and negative U_{Geo} are upwelling favorable. Upwelling metrics are calculated as was done by Jacox et al. (2018); U_{Ek} is Ekman transport integrated over one-degree latitude bins, from the coast to 75 km offshore, capturing both the coastal divergence and curl-driven components; and U_{Geo} is integrated over the depth of the mixed layer (typically tens of meters) for the same one-degree latitude bins. All transport components are expressed as volume transport per meter of coastline (m^2 s^{-1}). Abbreviations: EBUS, eastern boundary upwelling system; GFDL-ESM2M, Geophysical Fluid Dynamics Laboratory ESM2M; HadGEM2-ES, Hadley Centre Global Environment Model version 2 Earth-System configuration; IPSL-CM5A-MR, Institut Pierre Simon Laplace Climate Model 5A Medium Resolution; MLD, mixed-layer depth; RCP, Representative Concentration Pathway. Panel *a* adapted from Jacox et al. (2018).

the mixed layer, which is projected to shoal system-wide. Combined with a weakly negative trend in nutrient concentration at the base of the mixed layer, the ensemble mean nitrate flux [i.e., the Biologically Effective Upwelling and Transport Index (BEUTI); see Jacox et al. 2018] is projected to have a weak negative or no trend. These projections are relatively robust across the downscaled Earth system models for the northern CalCS. In the southern CalCS, there is on average a weak positive trend in Ekman transport and vertical velocity combined with a lower nutrient content that renders upwelling less biologically effective (i.e., a declining nitrate flux into the euphotic zone), though there is also a lack of agreement among models. Overall, the downscaled Earth system models show a tendency for declining primary productivity (Pozo Buil et al. 2021) (**Figure 5**) driven by these interacting factors, although there are significant model spread and uncertainty in these projections.

Implications for Ecosystem Services

The ocean accounts for a notable part of nature's contributions to people (NCP) (Brauman et al. 2020). Perhaps the most obvious component, especially in EBUSs, is the role of the ocean in helping to meet the increasing demand for food to sustain the increasing world population. The annual per capita consumption of fish has more than doubled since 1960 (Barange et al. 2018), corresponding to an increase of 3.2% per annum in fish production for human consumption (UN 2016). The aquaculture sector has largely offset the resulting decline in the biomass of assessed fish stocks in the wild (11% decline from 1977 to 2009; Worm et al. 2009). Further declines in wild-caught fish are predicted in the future, depending on region, as a result of global warming (Cheung et al. 2013). This will further increase the demand for fish production by means of aquaculture. A worrying aspect of this is that 70% of farmed finfish rely on artificial feeding (UN 2016, chapter 12), much of which is currently dependent on fishmeal and oil derived from small pelagic reduction fisheries in EBUSs (Shannon & Waller 2021). Thus, climate-ready fisheries management will be even more important in the EBUSs if the global demand for fish as both food and feed continues to increase.

Interactions among different NCPs are only starting to be explored in the EBUSs. Marshall et al. (2017) used ecosystem models to explore the effects of ocean acidification on provisioning ecosystem services (fisheries) in the CalCS, for example. It remains for regulating and provisioning NCPs to be more explicitly examined in EBUSs, and this should be a priority for future research.

KEY QUESTIONS AND REMAINING UNCERTAINTIES

Significant advances in climate modeling over the past two decades have provided robust predictions of climate-driven changes in EBUS dynamics, as summarized above. An important caveat is that much of the existing literature—and therefore this review—has relied primarily on the Coupled Model Intercomparison Project 5 (CMIP5) ensemble of climate models, while output from CMIP6 models is now available and being more frequently presented in the literature. While CMIP6 models have higher spatial resolution and revised model physics and biogeochemistry, comparisons of CMIP5 and CMIP6 show similar projected trends in EBUS properties (e.g., alongshore winds, mixed-layer depth, and source-water properties).

Even with continuing model improvements, there remain a number of significant uncertainties and unanswered questions in the field of EBUS studies (see the sidebar titled Questions for the Future). Future studies will need to address these questions to better understand, project, and adapt to climate-driven changes in the EBUSs.

QUESTIONS FOR THE FUTURE

Upwelling Intensity and Phenology

- Will better resolution of atmospheric processes alter our expectations for future changes in upwelling?
- What are the times of emergence for poleward migration of the subtropical highs and changes in upwelling intensity?
- How will the cross-shore structure of wind stress change?
- What is the direction of change in upwelling intensity in the equatorward EBUS regions?
- How will the timing and duration of the upwelling season change?
- How will changes in upwelling intensity and timing modulate upper-ocean warming and stratification?

Climate Modes and Extreme Events

- How will changes in the large-scale climate modes (e.g., the intensity, timing, and frequency of ENSO and the Benguela El Niño, and their teleconnections) alter upwelling processes in the EBUSs?
- How will the properties and pathways of source waters to the EBUSs change? How will these changes impact the properties of upwelled waters?
- How will the frequency and severity of extreme events (e.g., marine heatwaves, hypoxia, and acidification) that affect EBUSs change?

Ecosystem Productivity, Structure, and Function

- How will the relative contributions of upwelling intensification, increasing stratification, and changing source-water properties impact nutrient supply and productivity?
- Will phenological changes in upwelling dynamics lead to predator–prey mismatches?
- What are the implications of the export and sequestration of organic carbon within EBUSs?
- Will changes in biogeochemical properties (deoxygenation, acidification, and nutrient supply), combined with changing upwelling dynamics, lead to more frequent attainment of critical biological thresholds?
- How will community structure, species distributions, and trophic interactions change?

Marine Ecosystem Services

- What are the most vulnerable ecosystem components to climate change in the EBUSs?
- How can ecosystem-based management and marine policy adapt to the projected ecological changes in the EBUSs?

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