



Under Pressure: Climate Change, Upwelling, and Eastern Boundary Upwelling Ecosystems

Marisol García-Reyes^{1*}, William J. Sydeman¹, David S. Schoeman²,
Ryan R. Rykaczewski³, Bryan A. Black⁴, Albertus J. Smit⁵ and Steven J. Bograd⁶

¹ Farallon Institute for Advanced Ecosystem Research, Petaluma, CA, USA, ² School of Science and Engineering, University of the Sunshine Coast, Maroochydore, QLD, Australia, ³ Department of Biological Sciences and Marine Science Program, University of South Carolina, Columbia, SC, USA, ⁴ Marine Science Institute, University of Texas at Austin, Port Aransas, TX, USA, ⁵ Department for Biodiversity and Conservation Biology, University of the Western Cape, Bellville, South Africa, ⁶ Environmental Research Division, National Oceanic and Atmospheric Administration Southwest Fisheries Science Center, Monterey, CA, USA

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*Correspondence:

Marisol García-Reyes
marisolgr@faralloninstitute.org

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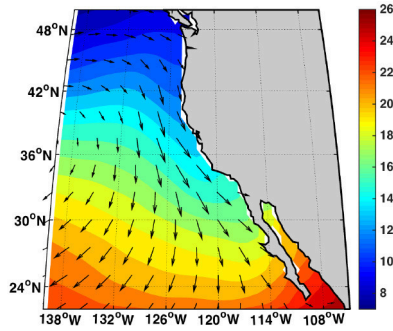
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The IPCC AR5 provided an overview of the likely effects of climate change on Eastern Boundary Upwelling Systems (EBUS), stimulating increased interest in research examining the issue. We use these recent studies to develop a new synthesis describing climate change impacts on EBUS. We find that model and observational data suggest coastal upwelling-favorable winds in poleward portions of EBUS have intensified and will continue to do so in the future. Although evidence is weak in data that are presently available, future projections show that this pattern might be driven by changes in the positioning of the oceanic high-pressure systems rather than by deepening of the continental low-pressure systems, as previously proposed. There is low confidence regarding the future effects of climate change on coastal temperatures and biogeochemistry due to uncertainty in the countervailing responses to increasing upwelling and coastal warming, the latter of which could increase thermal stratification and render upwelling less effective in lifting nutrient-rich deep waters into the photic zone. Although predictions of ecosystem responses are uncertain, EBUS experience considerable natural variability and may be inherently resilient. However, multi-trophic level, end-to-end (i.e., “winds to whales”) studies are needed to resolve the resilience of EBUS to climate change, especially their response to long-term trends or extremes that exceed pre-industrial ranges.

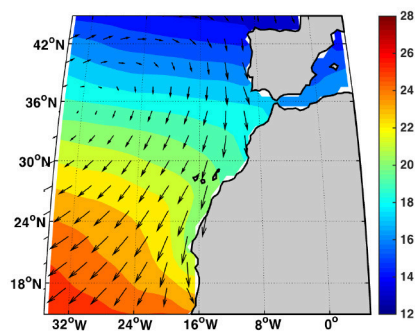
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INTRODUCTION

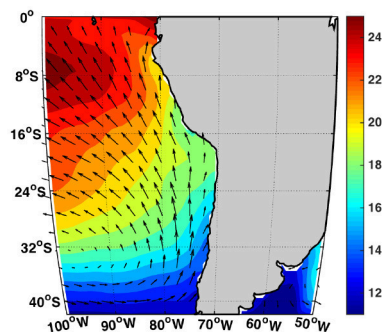
Eastern Boundary Upwelling Systems (EBUS) are biologically productive marine regions covering <1% of the ocean area, but providing up to 20% of the world’s capture fisheries (Pauly and Christensen, 1995). These systems, embedded in the California, Humboldt, Canary/Iberian, and Benguela Currents (Table 1), provide ecosystem, economic, and recreational services to about 80 million people living along their coasts and in their immediate hinterlands. The high levels of productivity in the EBUS result from large-scale atmospheric pressure systems that favor along-shore, equatorward winds, which in combination with the Coriolis effect, advect surface water

TABLE 1 | Eastern Boundary Upwelling Systems (EBUS).**California**

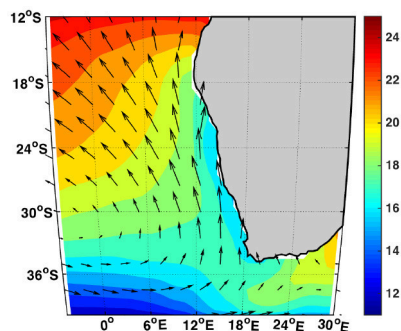
The California Current spans from central Baja California, Mexico, to central British Columbia, Canada. Upwelling is more intense in central/northern California and highly seasonal off Oregon and Washington. This system experiences significant natural variability from such sources as the El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation with important ecosystem consequences.

**Iberian/Canary**

The Iberian/Canary Current extends from the Iberian peninsula to West Africa, and is divided by the Gulf of Cadiz at the entrance to the Mediterranean Sea. The most intense and persistent upwelling is found off Northwest Africa. The Iberian section is heavily influenced by the North Atlantic Oscillation.

**Humboldt**

The Humboldt Current is the largest of the four EBUS, extending from the tip of the South American continent to the equator, where it connects with the equatorial current. Environmental and biological variability are heavily influenced by ENSO.

**Benguela**

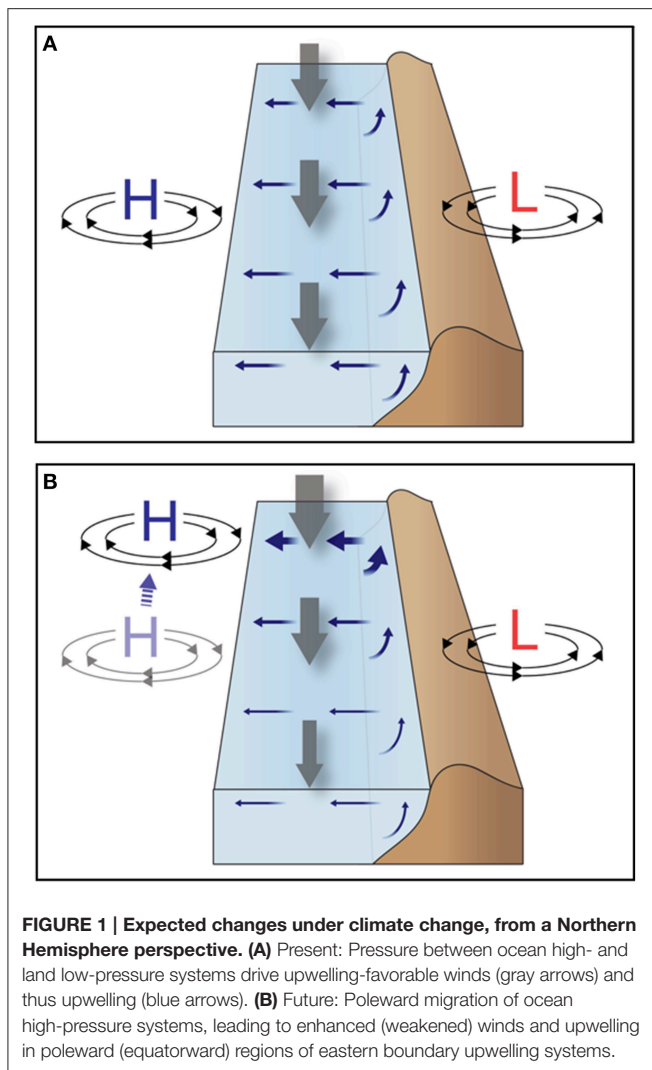
The Benguela Current extends from the southeast tip of Africa to Angola. Upwelling is strongest and most persistent off Namibia in the Lüderitz region. Interannual variability in the physical and biological conditions relate to Benguela Niños and Pacific ENSO. In the south it is largely influenced by the variability in the Agulhas Current.

Maps show long-term means (1960–2014) of sea surface temperature (SST, °C) and wind speed (m/s) and direction for summer months (June (December) in the northern (southern) hemisphere) around EBUS. SST is from the HadISST1 dataset (Rayner et al., 2003), and wind data are from the NCEP/NCAR reanalysis (Kalnay et al., 1996), which is generally congruent in mean wind velocity patterns with those from other sources (Kent et al., 2013).

offshore (Figure 1). Due to mass conservation, this advection causes deeper, cold, nutrient-rich waters with high CO₂ concentrations, low pH, and low oxygen concentrations to be upwelled from depth into the coastal photic zone (Huyer, 1983)

where they fuel primary production in the form of phytoplankton blooms.

In embayments and other wind-protected inshore areas and in places where local circulation patterns may favor retention



of local water masses, primary production can be intense and sustained (Graham and Largier, 1997). These “upwelling shadows” are sites of the highest chlorophyll concentrations in EBUS (Vander Woude et al., 2006), contrasting with lower productivity in areas with strong advection; this variability may influence zooplankton and higher trophic levels (Santora et al., 2011). Overall, the “bottom-up” drivers of nutrient enrichment, advection and retention, coupled with the transfer of carbon and energy up the food web make EBUS “hotspots” of productivity and upper-trophic-level biodiversity (Aristegui et al., 2009; Block et al., 2011), providing substantial economic value to coastal communities.

Because the mechanisms underpinning upwelling originate from large-scale atmospheric-oceanographic coupling, the amplitude and timing of upwelling-favorable winds are sensitive to climate variability (Montecinos et al., 2003; Macias et al., 2012), and are *highly likely* to be affected by global warming (Barros et al., 2014; Bakun et al., 2015). In particular, it is predicted that global warming will impact atmospheric pressure gradients and hence the coastal winds that cause upwelling

(Bakun, 1990; Bakun et al., 2015). Recent observations (Sydeman et al., 2014a) generally support this notion, and global model projections suggest intensification of regional coastal winds during the twenty-first century (Rykaczewski et al., 2015; Wang et al., 2015).

Understanding how these winds will change is of vital importance. For example, weaker upwelling may limit nutrient enrichment of the photic zone with potentially negative impacts on primary production (Chhak and Di Lorenzo, 2007). By contrast, stronger upwelling may increase nutrient input, but at the same time increase offshore transport (Cury and Roy, 1989; Botsford et al., 2006; Bakun et al., 2010, 2015). Other impacts include increased turbulence with increased winds (Cury and Roy, 1989; Yáñez et al., 2001) and changes in chemical mechanisms, e.g., ocean acidification and deoxygenation (Gruber, 2011; Doney et al., 2012), that may affect productivity.

Management of fisheries and other marine resources in EBUS could be improved by better understanding how nutrient enrichment and primary production are related to upwelling processes, and how they are likely to change in the future. While there have been a number of studies on this topic (Diffenbaugh et al., 2004; Di Lorenzo et al., 2005; Auad et al., 2006; Bakun et al., 2015), the Intergovernmental Panel on Climate Change 5th Assessment Report (IPCC AR5) has concluded that there is low confidence in projections regarding upwelling (Stocker et al., 2013; Barros et al., 2014). In part, this is a result of the substantial spatial heterogeneity in physical characteristics within EBUS, which emphasizes the role of local processes and resultant local biotic effects (Nelson and Hutchings, 1983; Dorman and Winant, 1995; Barton et al., 2013; Bakun et al., 2015). However, the low confidence in predictions regarding the ecological future of EBUS is driven more heavily by uncertainty surrounding the potentially counteracting effects of intensifying winds on the one hand, and increasing thermal stratification on the other. The former might lead to enhanced nutrient influx, while the latter could limit it (Di Lorenzo et al., 2005).

Even though the underlying complexity of upwelling-ecosystem relationships presents a challenge to forecasting, knowledge of EBUS is deep, as these systems have been extensively studied for nearly a century (Peña and Bograd, 2007), and there is a vast body of literature examining climatic impacts on upwelling as well as upwelling impacts on ecosystems. Given this context, and a spate of studies published while the IPCC AR5 was being prepared, we provide here a new synthesis of current research focused on the present and future impacts of climate change on coastal upwelling. We emphasize here the drivers of upwelling-favorable winds, the factors influencing nutrient enrichment, and potential changes in biogeochemistry.

PRESSURE, WIND, AND UPWELLING IN A WARMING WORLD

In EBUS, cross-shore atmospheric pressure gradients lead to alongshore, equatorward winds that drive coastal upwelling. Recognizing this, A. Bakun proposed that increasing global concentrations of greenhouse gasses would enhance

warm-season upwelling (Bakun, 1990). The proposed mechanism was simple: air over land would warm more rapidly than air over the ocean, and resultant deepening of the continental thermal low-pressure systems (CTLPS) should increase the cross-shore pressure gradients that drive upwelling-favorable winds.

Trends in Upwelling-Favorable Winds

Several studies have focused on assessing trends in upwelling-favorable winds, and they found mixed results. The failure to reach consensus revolves largely around two related phenomena: (1) the small amplitude of unidirectional wind trends relative to amplitudes of seasonal, interannual, and decadal wind variability, and (2) the short duration of most observational time series relative to decadal variability. Further complications include (i) disparate data sets examined, (ii) inconsistencies in data treatment, including analyses of warm season vs. annual means as well as variable observation periods or quality and density of data, and (iii) changes in measurement techniques or models used to interpolate or reanalyze data (Cardone et al., 1990; Josey et al., 2002). Based on these differences, the IPCC AR5 (Stocker et al., 2013) concluded *low confidence* in common trends in upwelling-favorable winds.

A recent meta-analysis of published studies (Sydeman et al., 2014a), each with more than 20 years of observational or model-derived data, however, finds a more coherent pattern of intensifying upwelling-favorable winds in the Humboldt and the California Systems during the warm season. In the Benguela System, only annual data are available, but there, too, alongshore winds are intensifying. By contrast, in the Canary System, wind trends are equivocal, and even appear to be weakening in the Iberian region. Importantly, there is stronger agreement that significant trends of upwelling intensification are evident at higher latitude for all EBUS. Among studies excluded from the meta-analysis, either because they did not meet the strict selection criteria or because they were published after the analysis was completed, most (Di Lorenzo et al., 2005; Alves and Miranda, 2013; Barton et al., 2013; Bylhouwer et al., 2013; Stocker et al., 2013; Cropper et al., 2014; deCastro et al., 2014; Jacox et al., 2014; Sydeman et al., 2014b; Varela et al., 2015) show results consistent with the findings of Sydeman et al. (2014a). Those containing seemingly contradictory results (Demarcq, 2009; Dewitte et al., 2012) add uncertainty, but do not refute the findings of the meta-analysis, as they focus on local regions, use short time series and do not add uncertainty. Despite the fact that the meta-analysis by Sydeman et al. generally supports Bakun's proposition, we still cannot attribute coastal wind intensification in EBUS to global warming because we cannot discount the role of multi-decadal climate variability in the observed trends (Chhak and Di Lorenzo, 2007; Narayan et al., 2010; Pérez et al., 2010; Macias et al., 2012; Santos et al., 2012; Cropper et al., 2014; Jacox et al., 2014), nor is it a test of the Bakun hypothesis mechanism.

A gap in our understanding arises because the vast majority of studies focus on measures of central tendency (means or medians) in wind magnitude. Even though ecologically consequential changes in variance and phenology (timing of upwelling) have been observed in EBUS, studies examining

trends in variance and timing remain rare. Such work is hindered by the complexities of the systems; the only generality that can be made is that upwelling-favorable winds tend to be most intense during the warm months of the year (Huyer, 1983; Nelson and Hutchings, 1983). Beyond this, however, the timing, intensity, and persistence of upwelling-favorable winds are remarkably variable within and among EBUS (Chavez and Messié, 2009). Of all EBUS, the most information on this subject is available from the California Current. In the central-northern portion of this system, upwelling winds primarily occur during the warm months of the year, while the seasonal range of pressure gradients in the southern portion of the system is reduced, and upwelling can occur there year-round. This pattern, however, is not static. Over recent decades, the timing of upwelling has trended toward later and shorter upwelling seasons in the northern portion of the California System and longer upwelling seasons in the southern portion (Bograd et al., 2009; García-Reyes and Largier, 2010). In contrast, a modeling study on wind stress curl (Difffenbaugh et al., 2004) found increased (decreased) upwelling in the late season in the northern (southern) California System.

Resolving these issues is important because variation in the timing of upwelling strongly influences ecosystem productivity. Years with early upwelling tend to be more productive at the upper trophic levels than those with later onset of upwelling (Black et al., 2011; García-Reyes et al., 2013b). Adding complexity to the picture, increases in the variability (extremes) of upwelling-favorable winds in the California Current have been observed since the late 1940s (Macias et al., 2012; García-Reyes et al., 2014), a finding consistent with increased upwelling-favorable winds during the warm months (Sydeman et al., 2014a). Less variability has been observed in the strength of upwelling winds through the year in the central Benguela and Canary Currents (Shannon and Nelson, 1996; Varela et al., 2015), though this conclusion might be influenced by a lack of studies. Clearly, further research is needed in all EBUS on changes in the timing and variability of upwelling given the influence these phenomena have on their ecosystems (Black et al., 2011; García-Reyes et al., 2014).

Wind projections from coupled atmosphere-ocean general circulation models (AOGCM) assembled for the IPCC AR5 have limited agreement that upwelling-favorable winds will intensify in response to climate change. Projections for the Humboldt (Garreaud and Falvey, 2009; Goubanova et al., 2011; Echevin et al., 2012; Belmadani et al., 2014; Rykaczewski et al., 2015; Wang et al., 2015), Benguela (Jury and Courtney, 1995; Rykaczewski et al., 2015; Wang et al., 2015), and Iberian Systems suggest future intensification of upwelling winds (Miranda et al., 2013; Casabella et al., 2014; Lopes et al., 2014; Rykaczewski et al., 2015; Wang et al., 2015). In contrast, the California System projections show non-significant or decreasing trends (Mote and Salathé, 2010; Rykaczewski et al., 2015; Wang et al., 2015). Furthermore, recent publications on wind trends based on global models reveal consistency in the spatial heterogeneity found by the meta-analysis, with increasing (decreasing) upwelling-favorable winds for poleward (equatorward) regions of EBUS (Rykaczewski et al., 2015; Wang et al., 2015). Note that these projections agree with observational records only in the Humboldt and Benguela Systems, though observational records corroborate that

intensification trends are most likely in poleward regions of EBUS (Sydeman et al., 2014a).

The variability in trends derived from global-scale models may be due either to their relatively coarse resolution, which precludes adequate representation of smaller-scale coastal processes, including upwelling (Miranda et al., 2013; Casabella et al., 2014), or to their failure to adequately incorporate processes relevant to upwelling, e.g., cloud cover, inversion-layer height (Winant et al., 1988), or land-ocean pressure gradients. Downscaling global models to the coastal domain of EBUS is required to address some of these issues. Promising results from this type of approach have been obtained in the Humboldt System (Garreaud and Falvey, 2009; Belmadani et al., 2014).

Drivers of Wind Intensification

While Bakun's proposition of wind enhancement with global warming appears to be generally supported, the mechanism of change [intensification of CTLPS relative to the Ocean High-Pressure System (OHPS)] may require revision. Wang et al. (2015) suggest support for this mechanism in their analyses of AOGCM outputs, but they did not examine the intensification of the CTLPS and consequent steepening of the cross-shore pressure gradient, key elements of the Bakun hypothesis. A more comprehensive analysis (Rykaczewski et al., 2015) of AOGCM output demonstrates that Bakun's mechanism breaks down at this crucial step: no deepening of the CTLPS occurs with increasing temperatures, except in the Canary Current System.

Changes in the structure of CTLPS seem intuitive under climate change. Nevertheless, the latitudinal differences in upwelling-favorable wind trends found in models (Rykaczewski et al., 2015; Wang et al., 2015) and in observations from recent decades (Sydeman et al., 2014a), in conjunction with evidence that winds in the EBUS are driven mainly by the magnitude and position of the OHPS (García-Reyes et al., 2013a; Schroeder et al., 2013), suggest that wind trends might be more sensitive to the poleward migration of the OHPS rather than changes in the CTLPS (**Figure 1**; Falvey and Garreaud, 2009; Belmadani et al., 2014; Bakun et al., 2015; Rykaczewski et al., 2015). Indeed, Rykaczewski et al. show that, in an ensemble of AOGCMs, the location of maximum upwelling along the EBUS coasts is correlated with the central latitude of the OHPS. Moreover, most AOGCMs show poleward expansion of the OHPS in the future (Diffenbaugh, 2005; Lu et al., 2007; Garreaud and Falvey, 2009; Echevin et al., 2012; Belmadani et al., 2014) caused by poleward expansion of the Hadley Cells in both hemispheres (Lu et al., 2007; Seager et al., 2010), and intensification of the OHPS in the northern hemisphere (Li et al., 2012). While one study using reanalysis data shows no evidence of trends in the position of mid-latitude atmospheric pressure centers over the past decades (Stocker et al., 2013), the prominent natural variability in the position of these systems over decadal time scales might mask potential trends (Bograd et al., 2009; Gutiérrez et al., 2011; Santos et al., 2012; Stocker et al., 2013). Understanding and predicting the intensity and position of OHPS is of great importance to the ecology of EBUS (Schroeder et al., 2013, 2014), making this area ripe for future analyses.

WATER TEMPERATURES AND THE COUNTERACTING ROLES OF UPWELLING AND STRATIFICATION

Global ocean temperatures have increased during the twentieth century and are expected to continue rising (probably at an accelerating rate) with climate change (Stocker et al., 2013). It is well known that coastal sea surface temperatures (SST) in EBUS are distinctively cooler than offshore regions at similar latitudes due to the nearshore upwelling of cold, nutrient-rich water. Moreover, global trends in SST may be counteracted by upwelling intensification in the poleward domains of the EBUS. Therefore, trends in coastal temperature in EBUS are expected to differ substantially from regional and global patterns of temperature change; indeed upwelling systems are viewed more generally as a source of significant bias in the global patterns of temperature change.

There is substantial but conflicting evidence on SST trends in EBUS (Mendelsohn and Schwing, 2002; Arístegui et al., 2009; Belkin, 2009; Demarcq, 2009; Lebassi et al., 2009; García-Reyes and Largier, 2010; Rouault et al., 2010; Gutiérrez et al., 2011; Seo et al., 2012; Barton et al., 2013; Barros et al., 2014; Sydeman et al., 2014b; Salvanes et al., 2015). Agreement among studies is low for two reasons: (1) the varying spatio-temporal resolutions of SST data capture different aspects of upwelling processes, and (2) trends are obscured by the interannual to multi-decadal variability that result from regional/local ocean and atmospheric processes. Different SST datasets also suggest different trends within and among EBUS, depending on resolution and other intrinsic factors (Belkin, 2009; Demarcq, 2009). In general, the coarse resolution of most SST datasets makes it difficult to separate nearshore upwelling-related temperatures (which could be decreasing due to upwelling intensification) from regional and eastern boundary current temperatures (which are likely to be increasing). Also, these data cannot resolve smaller-scale advection or retention areas within EBUS, which could potentially have contrasting trends. Where high-resolution data have been analyzed, for example Lima and Wetthey's (2012) analysis of daily AVHRR data at 0.25° resolution, recent cooling trends are obvious for coastal areas in all but the Canary EBUS, especially at high latitudes and in summer months. There is, however, agreement among studies that coastal and offshore temperature trends differ. These studies exhibit decreasing or slowly increasing trends in nearshore SST, compared with increasing trends offshore in the Benguela (Rouault et al., 2010; Santos et al., 2012; Salvanes et al., 2015) and California systems (Mote and Salathé, 2010), a pattern consistent with observed increased upwelling-favorable winds (Sydeman et al., 2014a). When studying EBUS as units, given their spatial complexity, climate-change associated trends may be obscured by the counteracting effects of offshore warming and inshore cooling.

In general, regional ocean climate oscillations like the El Niño-Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) for the California and Humboldt Current Systems, the Northern Atlantic Oscillation for the Canary/Iberian Current System, and Benguela Niño for the Benguela Current System

(Minobe and Mantua, 1999; Lluch-Cota et al., 2001; Mendelssohn et al., 2003; Montecinos et al., 2003; Richter et al., 2010; Seo et al., 2012), impose considerable variability on temperatures and complicate attempts to assess long-term trends (Demarcq, 2009). Indeed, many of the observed trends in recent decades might be associated with these oscillations (Santos et al., 2012; Barton et al., 2013). Though predictions are controversial, some of these climate oscillations are expected to increase in amplitude or variance with climate change (Timmermann et al., 1999; Kuzmina et al., 2005; Sydeman et al., 2013; Cai et al., 2015), which would further mask monotonic trends.

AOGCM ensembles (Hoegh-Guldberg et al., 2014) show that modest rates of warming (0.22–0.93°C between 2010 and 2039) are expected within the four EBUS in the near-term, but the reliability of such projections is questionable, as AOGCMs do not represent upwelling adequately. In simulations of historical periods, large discrepancies between observed and predicted EBUS coast SST fields are found (Stock et al., 2011; Cambon et al., 2013), which could translate into biases in projected changes. However, coastal upwelling generally occurs within 50 km of the shore and these projected temperature changes might be more representative of the offshore portions of EBUS less influenced by upwelling. As with studies on wind fields, dynamic downscaling of AOGCMs might help in the resolution of these questions regarding future trends in coastal temperatures.

Warming of the ocean surface will, in time, propagate down through the water column and increase thermal stratification (Gruber, 2011). In upwelling systems, strong stratification limits the depth from which water is upwelled, and therefore the amount of nutrients brought to the euphotic zone (Chhak and Di Lorenzo, 2007; Jacox and Edwards, 2011; Jacox et al., 2015). Without alternative inputs from sources like rivers, the interplay between the intensity of upwelling winds and stratification determines the amount of nutrients entrained in the systems and thus strongly mediate biological productivity (McGowan et al., 1998; Di Lorenzo et al., 2005). On a global scale, stratification of the water-column between 0 and 200 m has increased by an estimated 4% during the period 1971 to 2010 as a result of climate change (Stocker et al., 2013). In the EBUS, however, stratification studies are sparse, as are associated observational data. In the central California Current EBUS, Palacios et al. (2004) estimated that stratification has increased since the 1950s in coastal and offshore areas. However, this change may reflect interdecadal variability (Bograd and Lynn, 2003; Chhak and Di Lorenzo, 2007), and its impacts on the nutrient input and consequent biological productivity have not been assessed except by theoretical modeling (Brochier et al., 2013; Schroeder et al., 2014). In other systems, similar studies are lacking due to the paucity of observational data on water-column temperature. At resolutions that capture the upwelling process, negative trends in nearshore SST seem to be consistent with increasing trends in upwelling-favorable winds (García-Reyes and Largier, 2010; Rouault et al., 2010; Lima and Wetthey, 2012; Santos et al., 2012; Seo et al., 2012; deCastro et al., 2014). While not a measure of stratification, negative temperature trends suggest that the threshold at which stratification limits the nutrient content of

upwelled water has not yet been reached, at least in some regions of the EBUS.

There is limited research on the future of stratification in EBUS under climate change, once again because AOGCMs fail to resolve upwelling adequately. Nevertheless, a modeling study by Brochier et al. (2013), based on downscaling of an AOGCM (Echevin et al., 2012), found that stratification might increase in the Humboldt Current under global climate change. In conjunction with negligible change in winds, their models showed limited nutrient input into the euphotic zone, which would negatively affect biological productivity. Ultimately, the ecological impacts of ocean warming and stratification might be ameliorated by increased upwelling-favorable winds combined with the innate resiliency of systems adapted to considerable intraseasonal to decadal temperature variability (Hare and Mantua, 2000; Santos et al., 2005). However, climate change impacts could still be important (Gruber, 2011), especially in regions where rising temperatures and decreasing upwelling co-occur.

UPWELLING, STRATIFICATION AND BIOGEOCHEMISTRY

Variability in the biogeochemical properties of upwelled waters will influence the ecology and productivity of EBUS. The deep waters brought toward the surface by upwelling are typically rich in nutrients and dissolved CO₂, a consequence of the relatively long period where they have been isolated at depth from the euphotic zone and air-sea gas exchange (Feely et al., 2008). Below the euphotic zone, heterotrophic processes remineralize organic matter, consuming oxygen, and releasing CO₂ in the process (Capone and Hutchins, 2013). Variability in the rate of upwelling associated with changes in local wind forcing, ventilation processes, or the source-water pathways that supply the EBUS have the potential to influence oxygen, nutrient, and CO₂ concentrations in upwelled waters at the surface (Rytkaczewski and Dunne, 2010).

Efforts to explore variability in source-water properties have been more intense in the California Current System than in any other EBUS. Here, decreased pH of shelf waters has been associated with strong upwelling at interannual scales (Feely et al., 2008), though longer-term data are generally not available. Over longer periods, decadal-scale changes in ventilation and source-water properties have likely resulted in decreased oxygen concentrations and shoaling of the oxygen minimum layer in the California (Bograd et al., 2008; McClatchie et al., 2010) and Benguela Systems (Monteiro et al., 2008; Salvanes et al., 2015). Such changes, however, have also been associated with known modes of decadal variability in ocean-atmosphere processes (Deutsch et al., 2005; Chhak and Di Lorenzo, 2007).

Over centennial time scales, increased ocean stratification associated with surface warming may further reduce the ventilation of deep-water masses. As these water masses continue to be forced to the surface by the upwelling process, future decreases in oxygen concentration and pH and increases in

nutrient concentration are expected (Ryckaczewski and Dunne, 2010). While EBUS biotic systems might be resilient to changes in acidity and oxygen given their adaptations to naturally variable conditions (Capone and Hutchins, 2013), persistent changes in pH or oxygen may have important repercussions, such as displacement of suitable habitat (Hamukuaya et al., 1998; Grantham et al., 2004).

SYNTHESIS

There is robust observational evidence that upwelling-favorable winds have intensified in recent decades in some EBUS. Climate models also demonstrate, with high confidence, increasing (decreasing) trends in upwelling-favorable winds in the poleward (equatorward) regions of the EBUS. Recent decadal-scale trends in winds are consistent with predictions of the Bakun hypothesis of increasing upwelling with climate change. However, the mechanisms responsible for changes in winds are likely to be different. An alternative mechanism is that OHPS have migrated poleward and will continue to do so (**Figure 1**), as supported by a high level of agreement among different generations of global models. Reconciliation of this mechanism with a general lack of trends in strength and position of mid-latitude pressure systems in previous decades, which is almost certainly due to large degree of decadal-scale variability, will require further investigation.

There is low confidence regarding the future effects of climate change on coastal temperatures and biogeochemistry in the EBUS. This is partially due to the complexity of integrating global (climate change) and local (coastal upwelling) processes, but also due to the resolution, availability, and period of available data combined with the large degree of interannual to decadal

variability in temperatures and biogeochemical properties. Most global climate models do not have the resolution to represent the upwelling process adequately; therefore the changes in physical and biogeochemical properties projected for the EBUS by the current generation of models are unlikely to be as accurate as those for other portions of the world's oceans. Downscaling of climate models shows promise in correcting this bias by including higher-resolution representation of winds and more accurately modeling relevant atmospheric and oceanic processes such as land- and ocean-air interactions, cloud formation, and oceanic mesoscale processes.

Owing to their inherent natural variability, it might be expected that EBUS will prove more resilient to climate change than other ocean ecosystems, but evidence of this resiliency is based more on these systems' abilities to recover from short-term climate extremes. Much of our understanding of ecosystem responses to extremes stems from observations associated with ENSO (as well as PDO) in the California Current (Peterson and Schwing, 2003; Blamey et al., 2012; Sydeman et al., 2013; Black et al., 2014). How EBUS will respond to long-term changes in the mean magnitude of upwelling winds, stratification, and the biogeochemistry of source waters remains uncertain, as do interactive effects with natural interannual extremes, which could also change in behavior under climate change.

This lack of clear expectations for EBUS ecosystem properties is worrying because these regions are biologically rich, and thus highly relevant to society in terms of economics, conservation, and biodiversity. Given the uncertainties in present and future trends in the intensity and seasonality of upwelling, the paucity of studies on stratification, and the resultant effects on source-water characteristics, confidence in predicting biological

TABLE 2 | Observed and projected climate-change impacts on Eastern Boundary Upwelling Systems (EBUS).

	Observed	Expected	Uncertainty
Upwelling-favorable winds <i>High confidence</i>	Intensification of upwelling-favorable winds (except Canary/Iberian System) during warm months. Increased variability and trends in phenology.	Increasing (decreasing) trends in upwelling winds in poleward (equatorward) regions of the EBUS.	The influence of large-scale decadal variability.
Large-scale drivers of upwelling-favorable winds <i>Medium confidence</i>	No evidence of multi-decadal trends in strength or position of pressure systems.	Models suggest poleward migration of ocean high-pressure systems, but little to no change in intensity of the thermal continental low-pressure cells.	
Coastal temperature and stratification <i>Low confidence</i>	Complex integration of global (climate change) and local (coastal upwelling) processes. Differences in global and EBUS SST trends are observed.	Complex integration of global (climate change) and local (coastal upwelling) processes. Ocean warming and stratification might be ameliorated by increased upwelling.	Trends are sensitive to location (nearshore vs. offshore), resolution, period and dataset considered, as well as to decadal variability.
Biogeochemistry <i>Low confidence</i>	Decreased pH and oxygen concentration.	Decreased pH and oxygen concentration, and increased nutrient concentration.	Uncertainty due to short period of data availability.

These assessments are based on variable periods and datasets (see text and references). Confidence, based on amount of evidence and agreement among evidence, is noted in italics.

impacts remains low. This synthesis (Table 2) highlights the need for comprehensive “winds to whales” studies that investigate consequences of present and future changes on various components of the upwelling process as well as the need to improve coupling between ecological and physical models.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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