Anticipated Effects of Climate Change on Coastal Upwelling Ecosystems

Article *in* Current Climate Change Reports · June 2015

DOI: 10.1007/s40641-015-0008-4

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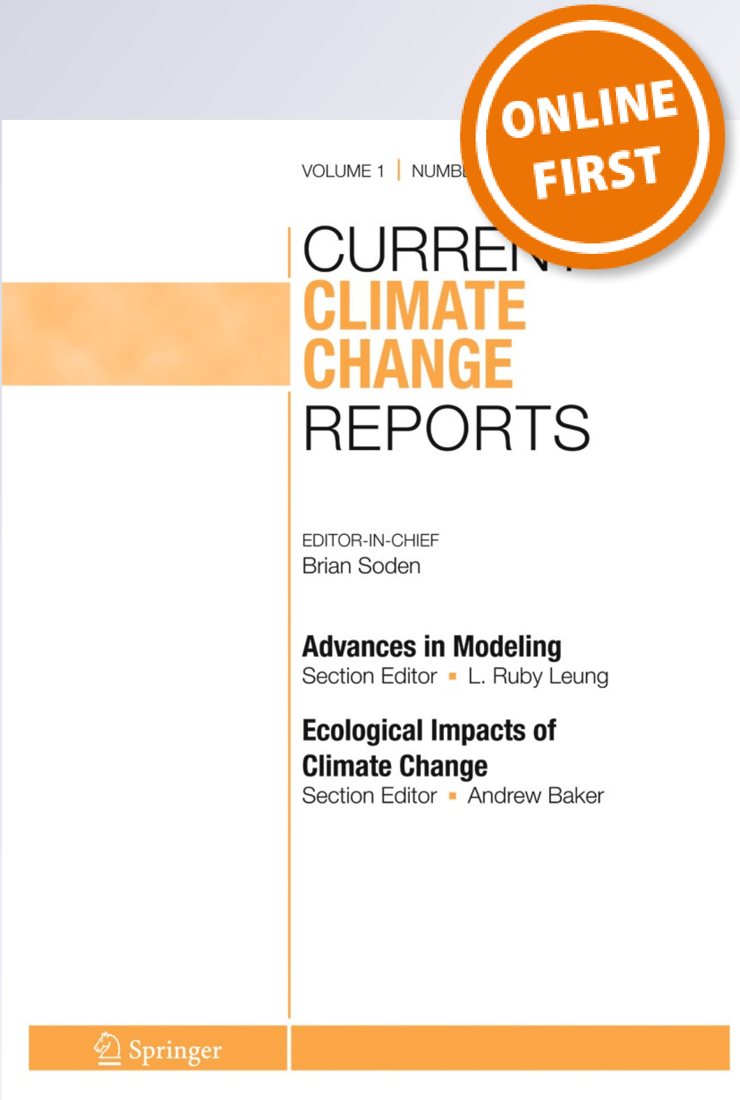
Current Climate Change Reports

e-ISSN 2198-6061

Curr Clim Change Rep
DOI 10.1007/s40641-015-0008-4



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ECOLOGICAL IMPACTS OF CLIMATE CHANGE (A BAKER, SECTION EDITOR)

Anticipated Effects of Climate Change on Coastal Upwelling Ecosystems

A. Bakun · B. A. Black · S. J. Bograd · M. García-Reyes · A. J. Miller · R. R. Rykaczewski · W. J. Sydeman

Abstract Ecosystem productivity in coastal ocean upwelling systems is threatened by climate change. Increases in spring and summer upwelling intensity, and associated increases in the rate of offshore advection, are expected. While this could counter effects of habitat warming, it could also lead to more frequent hypoxic events and lower densities of suitable-sized food particles for fish larvae. With upwelling intensification, ocean acidity will rise, affecting organisms with carbonate structures. Regardless of changes in upwelling, near-surface stratification, turbulent diffusion rates, source water origins, and perhaps thermocline depths associated with large-scale climate episodes (ENSO) maybe affected. Major impacts on pelagic fish resources appear unlikely unless couples with overfishing, although changes toward more subtropical community composition are likely. Marine mammals and seabirds that are tied to sparsely distributed nesting or resting grounds could experience difficulties in obtaining prey resources, or adaptively respond by moving to more favorable biogeographic provinces.

Keywords Climate change · Eastern boundary upwelling systems · Ecosystem effects · Ocean acidity · Hypoxia · Upwelling efficacy

This article is part of the Topical Collection on *Ecological Impacts of Climate Change*

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Introduction

Major coastal upwelling zones exist along the edges of the eastern boundary currents of the Pacific and Atlantic Oceans (Fig. 1a). These *eastern boundary upwelling systems* (EBUS) are among the most productive of the world's marine ecosystems [1, 2]. In EBUS, alongshore winds interact with the earth's rotation to force surface waters offshore, thereby pumping (i.e., "upwelling") nutrient-rich deeper waters into the illuminated surface layers in the coastal zone [3, 4] where they are available for photosynthesis. The resulting phytoplankton blooms nourish a vigorously productive zooplankton community as well as massive resident populations of small pelagic fish (sardines, anchovies, etc.) that are extremely important to the world's fisheries. These small pelagic fish species often comprise a substantial portion of the total animal biomass in EBUS, and fluctuations in their abundance have both top-down and bottom-up effects [5], serving as a key

Published online: 07 March 2015

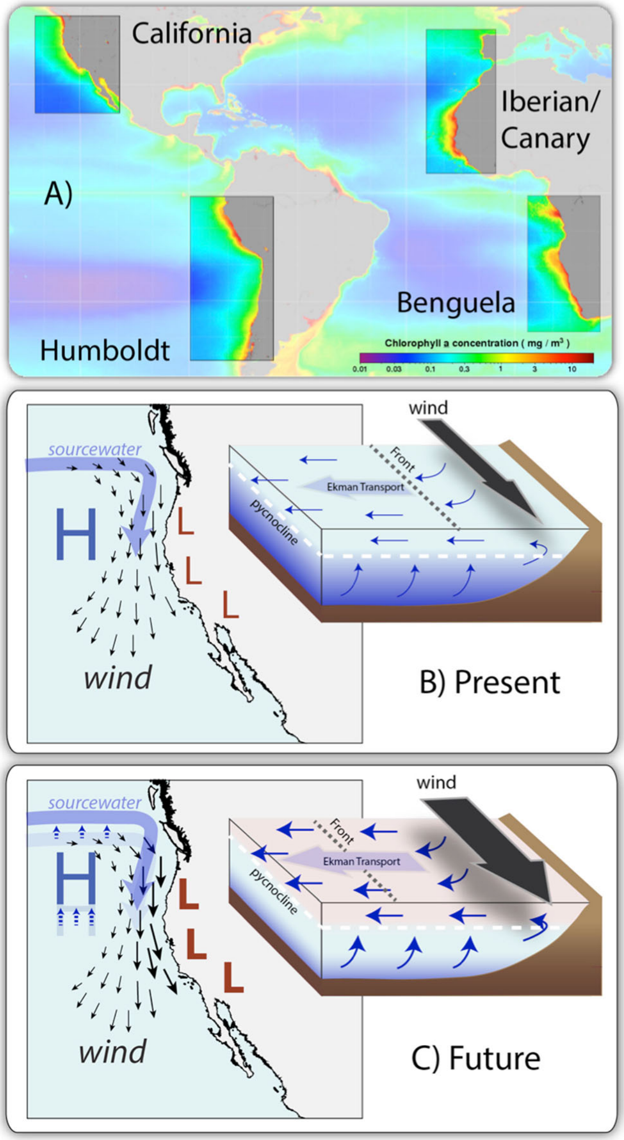

Fig. 1 Summary illustration of anticipated climate change impacts on EBUS. **a** Global chlorophyll-a annual average concentrations and the locations of major coastal upwelling zones. **b** Present state of coastal upwelling zones with the California Current as an example. **c** Potential future state of coastal upwelling zones with the California Current as an example. Anticipated changes include the poleward migration of the Oceanic High and source waters. Continental thermal lows are anticipated to deepen, which will intensify upwelling-favorable (equatorward) winds. Changes in the water column include greater stratification, greater rates of upwelling, and greater offshore transport as well as the offshore migration of the upwelling front

trophic control for large populations of higher trophic-level seabirds, marine mammals, and a variety of commercially important fish. Accordingly, there is much current interest and concern about potential effects of climate change on the ecological functioning, resource productivity, and environmental health of EBUS. Here, we present a vision of potential impacts of climate change on upwelling-ecosystem processes and outline prominent mechanisms that could potentially produce major biological impacts.

For this brief review, we focus on the four principal EBUS [4] of the world, as these appear to present major similarities in essential physical dynamics and ecosystem structures and functions. These are the *Benguela Current* off southwestern Africa, the *Canary Current* off northwestern Africa including its northern extension off the Iberian Peninsula of southwestern Europe, the *Peru-Humboldt Current* off western South America, and the *California Current* off the western continental USA and northwestern Mexico (Fig. 1a). Our objectives are modest. In moving beyond the realms of invariant physical and chemical laws into the nonlinearly linked, multi-leveled world of complex-adaptive marine biological ecosystems, confident prediction becomes ever more elusive. However, our abilities to employ some degree of intelligent management toward the preservation of the resources, services, and cultural/esthetic values relative to global change seems sufficiently important to warrant putting faith in informed speculation. As Mark Twain famously commented, "History does not repeat itself, but it does rhyme." Charles Darwin advised that "without speculation there can be no original or true observation." Accordingly, our hope is to provide a useful conceptual template against which observed ecosystem changes may be arranged as they become apparent, thereby aiding efforts in identifying significant changes and societal impacts.

Predicted Physical Changes

Like many marine ecosystems, EBUS are expected to experience a sequence of alterations associated with heating near the earth's surface, as well as from changes in ocean carbonate chemistry due to the continuing buildup of greenhouse gasses in the earth's atmosphere. The latest assessment of general circulation models (GCMs) forced by increasing greenhouse gas concentrations clearly show warming in the lower troposphere with impacts on surface land and ocean temperatures [6]. Beyond the direct consequences of increasing global ocean temperatures (e.g., increased ocean stratification, altered pathways of subduction, etc.), local-to-regional responses in EBUS temperature fields are likely to show extensive spatial variations due to changing wind distributions and consequential impacts on coastal and offshore upwelling. As one example, GCM predictions indicate that the Hadley Cells that influence the distribution of the pressure systems that force upwelling-favorable winds will be altered in both latitudinal extent and intensity (Fig. 1b, c). The Hadley Cells are predicted to expand poleward in both hemispheres, and observational evidence indicates this has already begun to occur [7, 8]. These changes to the Hadley Cells suggest that the regional EBUS may expand poleward in both hemispheres. Due to the asymmetric response of surface temperatures in the northern (more land) and southern (less land) mid-latitude oceans, combined with tropical warming, the Northern Hemisphere Hadley Cell is predicted to decrease in intensity while that of the Southern Hemisphere will increase in intensity [9]. It is still unclear how these future shifts in the Hadley Cell might impact the ocean high-pressure systems [6], which are major drivers of upwelling winds and appear to be largely responsible for their variability [10]. In addition to these dynamical changes in the Hadley Cells, local thermodynamic arguments suggest that regional upwelling winds in the EBUS may increase due to increased land-sea temperature contrast as suggested by Bakun [11], often referred to as the Bakun Hypothesis (BH). The BH suggests that under global warming, continental temperatures will rise faster during the local heating seasons than will temperatures in the nearby ocean, thereby steepening the cross-shore pressure gradients that drive upwelling-favorable winds (Fig. 1b, c). This idea was originally supported by emerging interregional patterns of observed sea-surface wind stress, and has been periodically tested against time series of observed data in all four regional EBUS [12, 13]. Most recently, using the amassed literature that has tested the BH, Sydeman et al. [14] conducted a meta-analysis that confirms the emergence of a general pattern of increasing reports of positive trends in upwelling-favorable wind intensity in a majority of upwelling regions (California, Benguela, and Humboldt) during past decades during which the concentrations of greenhouse gasses have continued to increase. This pattern of increased upwelling-favorable wind intensity could be due to other climate-related mechanisms, such as natural multi-decadal climate variability, but the likelihood of significant greenhouse gas-related interactions cannot be dismissed. Attempts to test the operation of the BH mechanism using large grid-scale climate models have had mixed results [15–17], although simulations done with finer spatial resolution climate models of the California system offer evidence that representation of the BH dynamics may be dependent on model resolution [18, 19]. Additional regional downscaling of different large grid-scale climate models is needed to obtain ensembles of spatially explicit projections of wind attributes in these systems that could improve consensus. Finally, predictions of physical change are complicated by basin-scale modes of climate variability at interannual to decadal scales that strongly impact upwelling intensity and ocean conditions. The Pacific EBUS are particularly impacted by the El Niño Southern Oscillation (ENSO), with effects on upwelling and across trophic levels in association with strong El Niño and La Niña events. To a smaller scale, the Atlantic is affected by ENSO-like variability (e.g., the Benguela Niño; [20]). In the Canary/Iberian EBUS, variation in the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO) impact these ecosystems [21]. The current generation of GCMs has no consensus on whether the statistics of ENSO, Pacific Decadal Oscillation (PDO), NAO, or AMO events will be altered in the future, so any likely changes to their intensity, spatial extent, frequency, and impacts on upwelling within EBUS remain unclear [6, 22].

Biophysical Responses

Changes to the physical environment of EBUS can directly affect the physiology (e.g., metabolism and respiration) of marine life with impacts on growth, reproductive capacity, and behavior. As metabolic rates increase with temperature, fish growth may be enhanced with ocean warming, but warming may also have direct negative impacts on the production of phytoplankton and zooplankton. For many fish species, the greatest risk from climate change may operate during larval and/or juvenile stages, when survival and recruitment are strongly dependent on having sufficient planktonic food resources at the right time and place [23–27]. If changes to physiological functions are substantial, variation in species' abundances can translate into changes in productivity, phenology, and community composition, hence interspecific relationships and ecosystem functions [28]. Some of the most critical impacts may include changes to habitat characteristics upon which fish and other upper trophic level species depend. Indeed, the effects of climate change operating through habitat or food web variation is thought to be already significant for many species of commercially valuable fish and wildlife [29–33].

Enhanced Coastal Upwelling

Intensified upwelling-favorable winds [11] would lead to an increased upwelling rate, greater turbulence in the upper ocean, and swifter offshore transport of surface waters. With low to moderately strong upwelling, upwelled nutrients would support a robust phytoplankton community (Fig. 2), which would in turn sustain flourishing zooplankton and upper trophic level communities. While enhanced upwelling may lead to enhanced nutrient enrichment, the increased intensity of upwelling-favorable winds could lead to less phytoplankton production within the primary upwelling zone due to deeper wind-driven mixing of the water column and increased light limitation. In addition, changes in species composition of phytoplankton and zooplankton communities are a likely result that in turn may impact successively higher levels of the trophic web.

Enhanced Offshore Transport

With strongly enhanced upwelling, the rate of offshore transport of surface waters would increase, potentially leading to problematic consequences. Phytoplankton and zooplankton would be transported more rapidly toward convergent

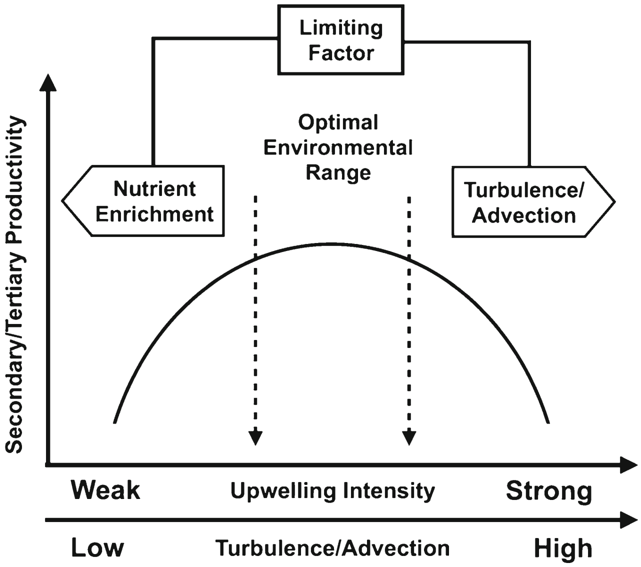

Fig. 2 The "optimal environmental window" shows highest levels of productivity at moderate upwelling intensity. When upwelling is strong, biota can be advected offshore, while at low upwelling intensity nutrients in the upper water column can be limiting to productivity. Adapted from reference [86]

offshore frontal systems, which themselves may be forced further offshore (Figs. 1b, c and 2) [3, 34, 35]. Under this scenario, positively buoyant planktonic organisms or other organisms able to maintain a preferred depth (e.g., euphausiid crustaceans and large-bodied copepods) could become progressively concentrated as the waters in which they are entrained converge horizontally and are thereby driven downward. The resulting concentrated food resource could attract planktivorous seabirds (e.g., auklets and shearwaters), small pelagic fishes and other nekton, marine mammals (e.g., balaenopterid whales), and their predators. Furthermore, the marked difference in ontogeny, generation times, and swimming capabilities between phytoplankton and zooplankton may result in a spatial mismatch between herbivorous zooplankton and their phytoplankton forage, and/or flushing of any weakly mobile organisms from favorable habitats associated with the near-coastal upwelling zone [36]. If the planktonic grazers that otherwise would exert control on phytoplankton growth are displaced, and the nutrient supply remains high, rapidly reproducing phytoplankton may become more abundant. Consequently, the total amount and offshore extent of new primary production might increase.

Changes in Ocean Vertical Structure

Upper ocean warming could increase water column stratification [37–39], potentially counteracting the effects of intensifying upwelling-favorable winds by reducing the efficacy of coastal upwelling to deliver nutrients to the euphotic zone. This mechanism was modeled by Chhak and Di Lorenzo [40] who showed shallow, presumably nutrient-poor, source waters are associated with weaker winds and enhanced stratification during warm conditions in EBUS. Enhanced stratification in the southern part of the California Current has been implicated in the observed long-term decline in zooplankton biomass [38, 41], although this decline has been attributed primarily to a change in the abundance of pelagic tunicates [42, 43]. Some modeling studies [e.g., 44] also suggest that the increase in upwelling-favorable winds could effectively counteract enhanced thermal stratification. The interplay among stratification, the depth and origin of upwelled waters, and the strength of upwelling winds are unresolved questions pertaining to understanding nutrient fluxes and productivity in EBUS.

Remote Stratification/Ventilation and Source Waters Changes

Biogeochemical properties of waters entering upwelling zones can have significant influence on local biological processes. Variability in source waters may be classified into two categories: 1) changes in the properties of surface waters that are supplied to the poleward regions of the predominant equatorward-flowing eastern boundary currents and 2) changes in properties of deep and remote source waters that are eventually upwelled from below the pycnocline. Surface waters of the poleward limbs of the subtropical gyres (e.g., the North Pacific Current), which are driven by the surface winds and are expected to shift poleward under global warming (see section 2), supply a substantial portion of the surface waters in EBUS (Fig. 1b, c). Over interannual to decadal time scales, increased zooplankton biomass [45–47] and variability in the productivity and abundance of zooplankton, fishes, and higher predators of the California Current have been attributed to the meridional position of the North Pacific Current [48–50]. Given a general meridional gradient in surface nutrient, phytoplankton, and zooplankton concentrations (with greater concentrations found at more poleward locations), poleward displacement of zonal currents with global warming may supply the poleward endpoints of EBUS with more nutrients and larger plankton populations advected into the poleward regions of EBUS.

Regarding the second mechanism, water masses upwelled by coastal winds are rich in nutrients in part because of the relatively long time period during which these water masses were below the euphotic zone. Model experiments tracing the history of these waters in the North Pacific indicate that they are subducted from the surface layer at locations well offshore of the EBUS and may remain at depth for decades prior to being upwelled, in the meantime accumulating remineralized nutrients and carbon dioxide while oxygen is being consumed by respiration [51]. The general expectation of increased vertical stratification and decreased mixing in the source regions, particularly during winter cooling seasons, may further limit the ventilation of these water masses under global warming.

As a result, deep waters supplied in the future by upwelling may be characterized by increased macronutrient concentrations, reduced pH, and decreased oxygen concentrations. While nutrient content may enhance productivity, reduced oxygen and pH could negatively impact ecosystem functions (see next section). Potential feedbacks between local biological production and biogeochemical properties of source waters should be considered in new regional climate models.

Hypoxia, Dead Zones, and Acidification

As a result of enhanced stratification and reduced ventilation, next generation GCMs predict a decline in dissolved oxygen with high certainty [37, 52, 53]; large-scale ocean circulation could advect these modified deep waters into EBUS [54]. A reduction in mid-depth dissolved oxygen content results in a shoaling of the oxygen minimum zones to depths from which upwelled waters are derived. A long-term trend toward declining oxygen content in the southern California Current has been observed, with the hypoxic boundary (defined as the depth at which dissolved oxygen is 60 uM/kg) shoaling by up to 80 m over the period 1984–2006 in the Southern California Bight [55, 56]. Benthic organisms found in regions where a low oxygen layer intersects the continental margin could be directly impacted [57], while pelagic species could find their viable habitats significantly compressed [55, 56, 58–60].

Increasing occurrences of hypoxia are expected due to enhanced coastal productivity and subsequent increases in respiration, combined with generally lower levels of dissolved oxygen at depth on the inner continental shelf [61, 62]. In the northern California Current, hydrographic observations have revealed a recent increase in the frequency and severity of hypoxic events, and even occasional water column anoxia, on the inner continental shelf [61, 62]. The biological impacts of these events can be catastrophic, with widespread mortality of macroscopic benthic organisms, resulting in periodic dead zones such as those observed on the Oregon continental shelf [61]. Other species, such as Humboldt squid, which have migrated north into the California Current in recent years [63], may be able to take advantage of low-oxygen environments.

In anoxic zones, methane (CH_4) bubbles formed at depth as a by-product of anoxic respiration can collect poisonous hydrogen sulfide gas (H_2S), and carry it upward to the oxygenated ocean layers and atmosphere in massive submarine eruptions. Such events, some extending over more than 20, 000 km^2 of ocean surface [64–68], have been repeatedly observed near the coast of Namibia, resulting in widespread mortality of marine life and corrosive, foul-smelling emissions over land. The importance of this phenomenon in EBUS beyond the Benguela system has not been examined, though the entire northern sector of the Arabian Sea, an upwelling region, has been identified as a major zone of methane emissions [69–71].

Another consequence of rising atmospheric CO_2 concentrations is the reduction in oceanic pH via the dissolution of CO_2 into seawater. This process will lead to more acidic waters which will make it increasingly difficult for important lower trophic level marine organisms, such as oysters and pteropods, to precipitate calcium carbonate ($CaCO_3$) to form shells and exoskeletons [72–74]. Impacts on calcareous plankton may reduce prey availability for fish while failures in bivalve reproduction could substantially alter intertidal and benthic habitat. Seasonal upwelling of low-pH ("corrosive") waters has been observed in the California Current [74–76], but GCMs may fail to accurately project ocean acidification due to their lack of detail in fine-scale atmosphere-ocean dynamics related to upwelling; future projections as to the growth of acidification in EBUS remain uncertain.

Trophic Interactions, Match-Mismatch, and Phenological Responses

Changes in the timing and amplitude of coastal upwelling, i.e., phenological changes, can have profound impacts on the EBUS [e.g., 41]. This was particularly evident in 2005 in the California Current, when a significant delay in the spring transition [77, 78] appears to have led to ecosystem changes affecting primary production [79], to zooplankton [80], to fish, birds, and mammals [81–83]. These ecosystem disruptions may be associated with mismatches between physical forcing and the productivity and life cycles of predator and prey [23, 84]. Related to the concept of spring transition, upwelling winds in the California Current occur in distinct winter and summer seasonal "modes," each with unique atmospheric drivers [10] and differential impacts on biological processes, as documented in rockfish (*Sebastes* spp.) growth and seabird reproductive success [85]. Changes to the timing of these modes and transitions may be biologically relevant and need to be more thoroughly studied using coupled climate models. New comparative research on seasonal modes of upwelling and ecosystem consequences between the California and Benguela systems is now underway.

Upper Trophic Responses

Commercially Important Fish Populations

Mid trophic level biomass in upwelling systems is generally dominated by extremely large populations of one to several species of small pelagic planktivorous "forage" fish (anchovies, sardines, etc.). The relationship between upwelling and productivity in these species is thought to be dome-shaped (Fig. 2) [86]. When upwelling is weak, limited nutrient input restricts primary and secondary productivity. Yet when upwelling is too strong, turbulence and offshore advection could decrease fish production due to disruption of feeding strata [87, 88] and/or excessive offshore transport of planktonic larvae and prey away from favorable coastal habitats [86, 89]. Moderate upwelling is thought to result in maximum production of this key small pelagic fish component, a concept that is known as the *optimal environmental window hypothesis* [86]. Similarly, the best fish production may occur when the timing or spatial distribution of prey is well-matched to the ecological needs of the (fish) predators; this is known as the *match-mismatch hypothesis* [23] and has been applied to cod stocks in the North Sea [90] as well as salmon and seabirds in California [82, 91]. Based on a regional climate model, upwelling-favorable wind stress curl off northern California is hypothesized to shift to later in the year in response to an increase in CO_2 concentrations [19]. This may have negative impacts on the survival of larvae spawned during fixed periods earlier in the year. For example, it is thought that many rockfish in southern and central California release young in the winter to avoid the turbulent and advective periods later in the year when upwelling is at its peak. If the timing of upwelling changes, a temporal mismatch between fish larvae and their food may reduce survival. In another example, delayed transition to upwelling is hypothesized to have resulted in a temporal mismatch between arrival of coho salmon smolts at sea and food production from upwelling [92]. Finally, another hypothetical response may be that climate change and overfishing might jointly promote explosive population growth of less mobile and anoxia-tolerant planktivorous jellyfish [93–96].

Seabirds and Marine Mammals

Seabirds and marine mammals are abundant and diverse in EBUS. These species garner tremendous public support for marine ecosystem conservation and interest in relation to climate change impacts. It is difficult to confidently forecast exactly how climate change will affect productivity, survivorship, or populations of upper trophic level marine organisms. However, changes in these species may be amplified in comparison to changes in lower trophic levels [97, 98], and therefore, they serve as excellent indicators (high signal-to-noise ratio) of climate-ecosystem shifts [82]. Clearly, changes in temperature or ocean chemistry (oxygen concentrations or pH) are unlikely to directly affect physiological functions of upper trophic level species, so most climate change impacts on them are likely to operate indirectly via shifts in habitat characteristics or food web quality [32]. Changes in habitat qualities are highly likely to result in range shifts and redistributions [99], though a recent meta-analysis demonstrated that redistributions have been well documented only for fish [33]. Among seabirds, recent reductions in productivity (breeding success) and populations have been related to climate change in the California [14, 100] and Humboldt [101] systems via changes in anchovy and juvenile rockfish (*Sebastes* spp.) food resources. Redistributions of seabird populations have been documented in the Benguela system, related to changes in anchovy and sardine prey resources there [102]. Of particular concern for seabirds is that they require nesting sites on opportune, appropriately configured islands. Similarly, seals and other pinnipeds may require protected beaches where they can safely "haul out" to rest and to bear and care for pups. If climate change results in prey species moving away from the available protected nesting and rearing sites, the seabirds and marine mammal populations may no longer be viable components of the regional ecosystems. However, the ongoing and potential effects of climate change on EBUS-associated marine mammals have been less intensively studied than in the case of seabirds. In one example, Salvadeo et al. [103] related a redistribution of Pacific white-sided dolphins in the Gulf of California to ocean warming. Despite high levels of conservation concern, the impacts of climate change on seabirds and mammals remain relatively under-studied.

Ecosystem Variability

EBUS are known to be highly variable across a wide spectrum of spatial and temporal scales, in both the forcing and response of the system. In some cases, a climate event can force large, temporary changes in overall productivity or community composition; these effects were seen during the large 1997-98 El Niño event [104] and the delayed upwelling in 2005 [78] in the California Current. In other cases, climate-driven regime shifts can alter the overall community structure of the system, changing, for example, a sardine-dominated forage base to one dominated instead by anchovies [105]. EBUS can therefore be characterized as both resilient (quick recovery from disturbances) and robust (maintenance of ecosystem function and relatively high productivity) to natural climate variability, maintaining an abundance of species of high commercial and conservation value. However, the scale of future responses to anthropogenic climate change may be beyond the historical scales of variability [106], making forecasting the response of EBUS to climate change difficult.

Summary

Figure 1 highlights some of the potential climate-driven changes in EBUS. In summary:

1. A possible tendency for increased coastal upwelling intensity as climate change proceeds could partially buffer coastal upwelling ecosystems from the increases in

temperature and decreases in nutrient supply that may impact other types of regional-scale ocean ecosystems.

2. There are many possible biological impacts in EBUS including,

    - Spatial or temporal (phenological) mismatch between production and consumption,
    - Changes in composition or intensity of primary productivity, with direct trophic linkages to and subsequent changes in community composition of heterotrophs,
    - Redistribution of populations through habitat changes, and
    - Geochemical impacts on biology via noxious gas, acidification, and lack of oxygen.

3. The high intrinsic variability in EBUS suggests that they may be resilient to the changes we have discussed here in the absence of over-exploitation or additional major anthropogenic impacts (e.g., pollution).
4. Exceptions to this conclusion may occur as a result of shifts toward increasing dominance by zooplanktivores (jellyfish, etc.) [93–95].
5. An increasing incidence of hypoxia or anoxic events is likely to lead to the increased occurrence of dead zones, noxious gas emissions, and vertical compression of suitable habitats.
6. There appears to be potential for highly visible mortalities and population declines as megafauna (seabirds, pinnipeds, etc.) adjust to changes in prey distributions relative to suitable nursery locations. Other more versatile components that may be less tied to predator-free shore zones might successfully exploit opportune ecological "loopholes" that develop.
7. EBUS are highly resilient and robust, yet the impacts of climate change could be profound and difficult to forecast as they begin to exceed recent millennial ranges of precedent variability.

Acknowledgments We thank S.A. Thompson for editing, formatting, and referencing this paper. AJM thanks NSF for funding under grants OCE-1026607, OCE-0960770 and OCE-1419306. BAB, WJS, MGR, RRR and SJB thank NSF for funding under grant OCE- 1434732.

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