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REVIEW

Biogeochemistry of greenhouse gases in coastal upwelling systems: Processes and sensitivity to global change

Zouhair Lachkar[1,*], Marcela Cornejo-D'Ottone[2], Arvind Singh[3], Javier Arístegui[4], Boris Dewitte[5,6,7,8], Sarah Fawcett[9,10], Veronique Garçon[11], Elisa Lovecchio[12], Veronica Molina[13,14], and P. N. M. Vinayachandran[15]

Major coastal upwelling systems are among the most productive marine ecosystems in the world. They contribute disproportionately to the cycling of carbon and nutrients in the ocean and influence marine biogeochemistry beyond their productive regions. Characterized by intense microbial respiration (both aerobic and anaerobic), major coastal upwelling systems are also hotspots for the production and outgassing of potent greenhouse gases (GHG) such as CO_2, N_2O, and CH_4. Quantifying and understanding these roles in the context of a changing climate is therefore a subject of great interest. Here we provide a short synthesis of the current knowledge of the contributions of major coastal upwelling systems to the cycling of GHG. Despite variations within and among different systems, low-latitude coastal upwelling systems typically act as a net carbon source to the atmosphere, while those at higher latitudes function as weak sinks or remain neutral regarding atmospheric CO_2. These systems also significantly contribute to oceanic N_2O and CH_4 emissions, although the extent of their contribution to the latter remains poorly constrained. We also overview recent and future changes to upwelling systems in the context of a warmer climate and discuss uncertainties and implications for GHG production. Although rapid coastal warming is anticipated in all major coastal upwelling systems, the future changes in upwelling-favorable winds and their implications within the context of increased stratification are uncertain. Finally, we examine the major challenges that impede our ability to accurately predict how major coastal upwelling systems will respond to future climate change, and present recommendations for future research to better capture ongoing changes and disentangle natural and forced variability.

Keywords: Coastal upwelling system, Greenhouse gases, Biogeochemical cycles, Oxygen minimum zone, Climate change

1. Introduction

Major coastal upwelling systems occupy less than 2% of global ocean area but contribute disproportionately to global primary production (>10%) and fish catch (>20%; Bakun, 1990; Chavez and Toggweiler, 1995; Pauly and Christensen, 1995; Barber et al., 2001; Carr and Kearns,

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[1] Arabian Center for Climate and Environmental Sciences, New York University Abu Dhabi, Abu Dhabi, United Arab Emirates
[2] Pontificia Universidad Católica de Valparaíso, Valparaíso, Chile
[3] Physical Research Laboratory, Ahmedabad, Gujarat, India
[4] Instituto de Oceanografía y Cambio Global, IOCAG, Universidad de Las Palmas de Gran Canaria, ULPGC, Las Palmas, Spain
[5] Centro de Estudios Avanzados en Zonas Áridas, Coquimbo, Chile
[6] Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Catolica del Norte, Coquimbo, Chile
[7] Núcleo Milenio de Ecología y Manejo Sustentable de Islas Oceánicas (ESMOI), Universidad Catolica del Norte, Coquimbo, Chile
[8] CECI, Université de Toulouse, CERFACS/CNRS, Toulouse, France
[9] Department of Oceanography, University of Cape Town, Cape Town, South Africa
[10] Marine and Antarctic Research Centre for Innovation and Sustainability (MARIS), University of Cape Town, Cape Town, South Africa
[11] Laboratoire d'Etudes en Géophysique et Océanographie Spatiales (LEGOS), Toulouse, France
[12] National Oceanography Centre, Southampton, United Kingdom
[13] Universidad de Playa Ancha and HUB Ambiental UPLA, Valparaíso, Chile
[14] Center for Oceanographic Research COPAS COASTAL, Universidad de Concepción, Concepción, Chile
[15] Indian Institute of Science, Bangalore, Karnataka, India

* Corresponding author:
Email: zouhair.lachkar@nyu.edu

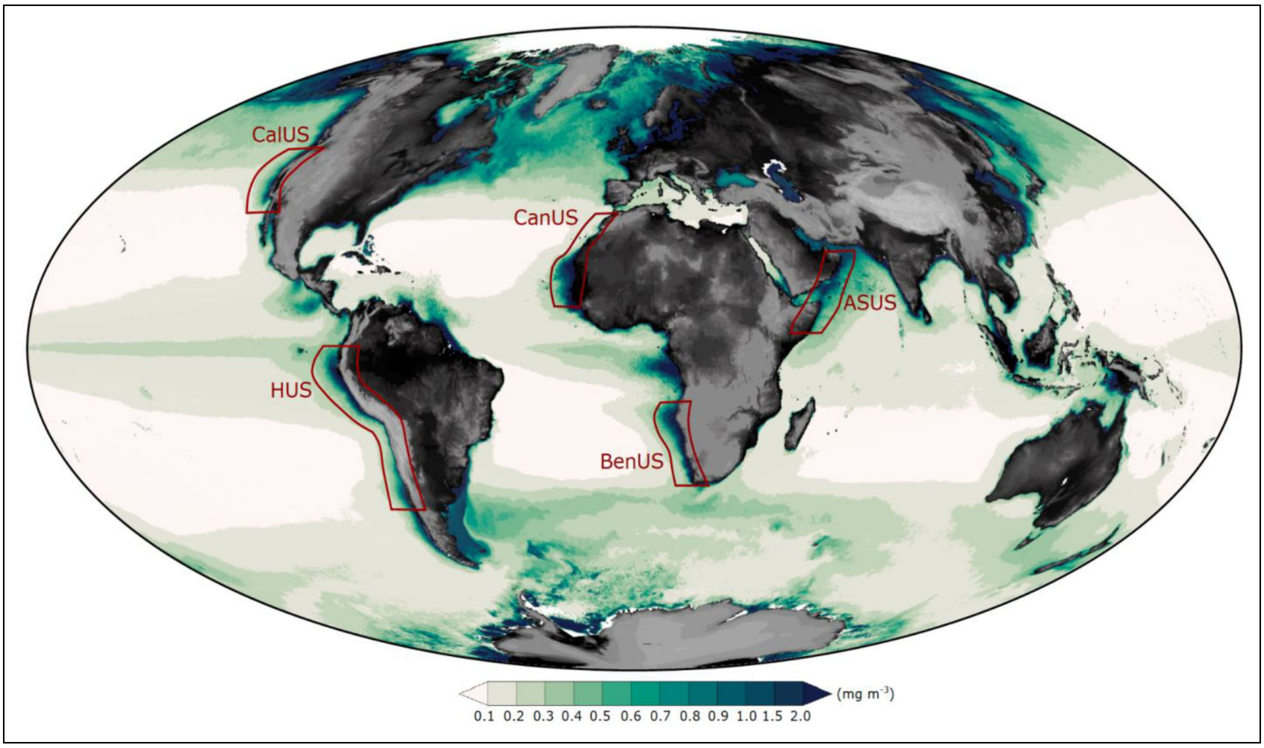

Figure 1. Global sea surface chlorophyll-*a* distribution. Annual-mean surface chlorophyll-*a* concentration (in mg m^{-3}) derived from SeaWiFS satellite data for 1997–2007. Red-contoured areas indicate the locations of major coastal upwelling systems, namely the California upwelling system (CalUS), the Humboldt upwelling system (HUS), the Canary upwelling system (CanUS), the Benguela upwelling system (BenUS), and the Arabian Sea upwelling system (ASUS).

2003; Chavez and Messié, 2009). Located at the eastern boundaries of the Pacific and Atlantic oceans and along the western boundary of the northern Indian Ocean, these systems are distinguished by distinctive wind patterns that transport surface waters offshore. In response, nutrient-rich deeper waters upwell into the sunlit layer, fueling primary productivity and thus favoring the uptake of CO_2 (Gregor and Monteiro, 2013; Turi et al., 2014). However, upwelling systems can also act as sources of CO_2 (due to the high CO_2 content of the upwelled water leading to its diffusion into the atmosphere) and other greenhouse gases (GHG; nitrous oxide, N_2O, and methane, CH_4) to the atmosphere, particularly in the nearshore region during the upwelling season (Paulmier et al., 2011; Gregor and Monteiro, 2013; Lachkar and Gruber, 2013; Turi et al., 2014; Morgan et al., 2019; Resplandy et al., 2024).

There are five major coastal upwelling systems in the ocean: the Benguela and Canary upwelling systems (BenUS and CanUS) in the Atlantic Ocean, the Humboldt and California upwelling systems (HUS and CalUS) in the Pacific Ocean, and the monsoon-driven Arabian Sea upwelling system (ASUS) in the Indian Ocean (**Figure 1**). Other coastal upwelling systems that are less prominent or are not connected to major boundary current systems also exist in the three basins (e.g., East–South China seas, South Australia, west coast of India, Java–Sumatra coasts, and the Gulf of Mexico) but are not included in this review, nor are large-scale open ocean upwelling systems such as around the equator and in the Southern Ocean. The Pacific systems that we consider have narrow continental shelves (weak iron supply from the shelf) and are distinguished by high nutrient and low oxygen levels (Mackas et al., 2006; Messié and Chavez, 2015). They are also highly variable due to the efficient connection with equatorial variability that propagates energy at a wide range of frequencies to the eastern subtropical boundaries via ocean-atmospheric teleconnections (e.g., the El Niño-Southern Oscillation, the Madden-Julian Oscillation). The Atlantic upwelling systems have wider continental shelves (hence more iron supply from the shelf), contain younger deep-water masses, and are not as strongly influenced by tropical-extratropical teleconnections (Mackas et al., 2006). Due to its unique geography, the northern Indian Ocean (bounded by the Eurasian landmass at relatively low latitudes) hosts the only major western boundary upwelling system in the world. Unlike in the Pacific and the Atlantic oceans, the differential heating and cooling of the Eurasian landmass and Indian Ocean waters give rise to seasonally reversing monsoonal winds that result in a vigorous upwelling along the coasts of Somalia and Oman driven by poleward summer monsoon winds (Morrison et al., 1999; Wiggert et al., 2005; Lévy et al., 2007; Resplandy et al., 2012). The high biological productivity that characterizes the surface waters of all five major upwelling systems results in intense organic matter respiration at depth that contributes, together with the sluggish ventilation, to the formation of large perennial

Figure 2. Overview of physical and biogeochemical processes in major coastal upwelling systems. Upwelling-favorable winds cause upwelling of nutrient-rich waters along the coast, fueling productivity in the sunlit layer. While biological carbon fixation can promote CO_2 uptake from the atmosphere, the upwelling of deep, carbon-rich waters can lead to CO_2 outgassing, especially in nearshore areas. Intense aerobic respiration results in the build-up of inorganic carbon and the depletion of oxygen at subsurface, resulting in the formation of a perennial oxygen minimum zone (OMZ) within the poorly ventilated subsurface layer, notable for its high carbon concentrations. Anaerobic respiration such as denitrification (predominantly occurring in the suboxic core of the OMZ) and methanogenesis (primarily occurring in anoxic sediments) generate potent greenhouse gases (GHG), namely N_2O and CH_4, respectively. N_2O is also generated as a by-product of nitrification in the oxycline. The release of GHG into the atmosphere is modulated by solubility gradients driven by surface temperature, as well as by the presence of mesoscale and submesoscale eddies and filaments. Furthermore, the atmospheric deposition of nutrients, such as iron (through mineral dust deposition), can also stimulate productivity and consequently, influence the emissions of GHG into the atmosphere.

subsurface oxygen minimum zones (OMZs). However, unlike in the four eastern boundary upwelling systems where the regions of maximum oxygen deficiency are co-located with the upwelling zones along the eastern boundaries of the Atlantic and the Pacific oceans, the Arabian Sea OMZ (the world's thickest) is shifted eastward from the region of upwelling in the western Arabian Sea (Morrisson et al., 1999; McCreary et al., 2013; Rixen et al., 2020; Vinayachandran et al., 2021). Beyond the differences observed among the various systems, substantial spatial heterogeneity is also evident within each major coastal upwelling system. This diversity includes variations in dynamics, seasonality, and the sources of upwelling waters between their northern and southern subregions (Lévy et al., 2007; Arístegui et al., 2009; Chavez and Messié, 2009; Pitcher et al., 2021).

Major coastal upwelling systems are widely recognized as crucial sites for the cycling of GHG (**Figure 2**). The accumulation of CO_2 produced by respiration in OMZ waters results in the formation of dissolved inorganic carbon concentration maxima known as carbon maximum zones (Paulmier et al., 2011). Because of the potential upwelling of these CO_2-rich waters to the surface, major upwelling systems can act as a net source of CO_2 to the atmosphere despite the high rates of carbon fixation induced by biological productivity at the surface (Paulmier et al., 2011; Lachkar and Gruber, 2013; Turi et al., 2014; de Verneil et al., 2022; Curbelo-Hernández et al., 2023). In the anoxic/suboxic core of the most intense OMZs (e.g., in the eastern tropical Pacific Ocean and the Arabian Sea), the degradation of organic matter typically uses alternate electron acceptors such as nitrate (denitrification), CO_2 (methanogenesis), or sulfate (sulfate reduction; Naqvi et al., 2010). Such forms of anaerobic respiration can lead to the accumulation of potent GHG in the OMZs such as N_2O and CH_4 that are released as by-products of respiration (Elkins et al., 1978; Codispoti and Christensen, 1985). As a result, major upwelling systems can be significant hotspots for the production of GHG (Capone and Hutchins, 2013). Yet, the emissions of these climate active gases into the atmosphere associated with these upwelling systems are still highly uncertain (Weber et al., 2019; Yang et al., 2020).

Some of these facets (upwelling of cold, nutrient- and carbon-rich, low pH and low oxygen waters that stimulate high productivity) have spurred oceanographers to make major coastal upwelling systems the most studied oceanic regions (e.g., Arístegui et al., 2009; Hutchings et al., 2009; McClatchie, 2014; Grados et al., 2018; Chevallier et al., 2021; Bograd et al., 2023). Yet, despite decades of progress in deciphering the functioning and variability of these systems, significant gaps remain in our understanding of their contribution to large-scale cycling of GHG. Additionally, their vulnerability and response to future climate change is still debated, as predictions of changes in upwelling-favorable winds are highly complex and remain tainted with important uncertainties (Vecchi et al., 2006; Rykaczewski et al., 2015; Sandeep and Ajayamohan, 2015; Wang et al., 2015; Bograd et al., 2023; Chang et al., 2023). Furthermore, the fate of major OMZs under future climate change also remains unclear, as model projections consistently reveal profound discrepancies in their projected evolution of dissolved oxygen in the tropical thermocline (Bopp et al., 2017; Oschlies et al., 2018; Long et al., 2019; Busecke et al., 2022). Other factors that are likely to affect these ecosystems and the intensity of their associated OMZs include enhanced deposition of iron and anthropogenic nitrogen from the atmosphere (Naqvi et al., 2000; Galloway et al., 2004; Duce et al., 2008; Jickells et al., 2017; Guieu et al., 2019; Suntharalingam et al., 2019; Moffett and Landry, 2020) and an increased riverine supply of nutrients (eutrophication) (Smith, 2003). These nutrient inputs will likely enhance local productivity and coastal hypoxia (Diaz and Rosenberg, 2008) and hence affect the production and potential emissions of critical GHG to the atmosphere. However, aerosol deposition can also stimulate bacterial abundance and metabolism, fueling heterotrophic activity and reducing net carbon fixation (Pérez-Barranco et al., 2022).

As several excellent and extensive reviews of eastern boundary upwelling systems (EBUS) can be found in the literature (e.g., Mackas et al., 2006; Chavez and Messié, 2009; Garcia-Reyes et al., 2015; Bograd et al., 2023), in this study we provide an overview of the role of major coastal upwelling systems in influencing the surface ocean-lower atmosphere biogeochemistry in the context of a changing climate. More specifically, in Section 2, we consider the impacts of major upwelling systems on the cycling of GHG. In Section 3, we review the recent and future potential changes in major upwelling systems and discuss their implications for GHG cycling, and the uncertainties around them. Finally, in Section 4, we discuss and summarize key challenges and list recommendations for future research.

2. Major coastal upwelling systems as hotspots for GHG cycling

2.1. Role of microbial processes

Major upwelling systems are areas of intense biogeochemical cycling, where biological processes interact with the unique physico-chemical conditions promoting enhanced recycling of carbon, nitrogen, and sulfur by a rich, diverse, and active microbial community. These microbial communities are characterized by contrasting metabolisms, in terms of their carbon sources (heterotrophic versus chemolithoautotrophic) and oxygen requirements (aerobic versus anaerobic), associated with the high reducing power that is available in these ecosystems (Capone and Hutchins, 2013). In fact, aerobic respiration contributes not only to organic matter degradation and CO_2 production but also to the microbial loop, with bacterial/archaeal production reaching up to 780 mg C m^{-2} d^{-1} in the BenUS and up to extremely high values of 8740 mg C m^{-2} d^{-1} in the HUS (Troncoso et al., 2003; Cuevas et al., 2004; Levipan et al., 2007). Moreover, aerobic respiration consumes oxygen, favoring its depletion in the water and generating steep oxyclines and hypoxic, suboxic, and anoxic conditions in the subsurface waters of upwelling zones (Capone and Hutchins, 2013). In turn, oxygen deficient conditions enhance microaerophilic chemolithoautotrophic communities, such as ammonia and nitrite oxidizers that aerobically oxidize NH_4^+ to NO_3^-, producing N_2O as a byproduct (Santoro et al., 2011; Löscher et al., 2012). In fact, nitrite oxidation has been found to occur at nanomolar oxygen concentrations in the oxygen deficient waters of the upwelling area off Concepcion (Bristow et al., 2016) and was reported to contribute significantly to oxygen consumption in the OMZ of the Eastern Tropical North Pacific, reaching up to 69% of the respiration rates (Beman et al., 2021). In particular, major upwelling systems support a rich nitrifying assemblage that varies along with the upwelling dynamics (Fernández and Farías, 2012; Rocke et al., 2020; Molina et al., 2021). Microbial ecology studies, based on "omic" analyzes in different major upwelling systems, have revealed that the nitrifying assemblages are comprised of key functional microbial groups, such as ammonia-oxidizing archaea and the nitrite-oxidizing bacteria affiliated with *Nitrosopumilus* and *Nitrospina* as part of the diversity of microbes found in OMZs (e.g., Murillo et al., 2014; Bertagnolli and Stewart 2018; Reji et al., 2019). Past studies in the CanUS and the HUS indicate that microbial ammonia oxidation leading to N_2O production is predominantly performed by archaea over bacteria, with the highest N_2O production rates at low O_2 concentrations (e.g., Löscher et al., 2012).

Oxygen deficiency triggers anaerobic respiration of organic matter with different electron acceptors such as NO_3^- and NO_2^- by denitrifiers and SO_4^{2-} by sulfate reducers, resulting in the production of NH_4^+ and H_2S, respectively. These latter chemical species represent substrates for keystone chemolithoautotrophic denitrifying microbes in upwelling systems with OMZs, namely anaerobic ammonium oxidizers (anammox) and sulfide-oxidizers (Murillo et al., 2014; Samkamaleson et al., 2021). Despite the sulfate-rich conditions of seawater, CH_4 production by methanogens has been reported in upwelling systems, a process shown to be enhanced during the upwelling period (Levipan et al., 2007). On the other hand, CH_4 oxidation could also occur aerobically or anaerobically by different methanotrophs that could use dimethylsulfide, among other metabolites, in upwelling areas (Flores-Leiva et al., 2013). Peculiar microbial bacteria able to oxidize CH_4 with nitrite as an electron acceptor have been detected in OMZs connected to major upwelling systems. This NO_2^--dependent anaerobic CH_4 oxidation pathway, known as n-damo, is accomplished by NC10 oxygenic bacteria (Padilla et al., 2016). Thus, the different microbial communities inhabiting OMZs have metabolisms that link different biogeochemical cycles, impacting GHG reservoirs and budgets. Whether overall these microbial processes enhance or mitigate air-sea fluxes is still to be elucidated.

2.2. Distribution and variability of GHG emissions

While major coastal upwelling systems make a small contribution to global air-sea carbon fluxes, they exhibit high CO_2 flux densities as well as a high spatio-temporal variability (Gregor and Monteiro, 2013; Turi et al., 2014; Brady et al., 2019; de Verneil et al., 2022; Curbelo-Hernández et al., 2023). For instance, the annual sea-to-air CO_2 flux was estimated to be around 5.6 mol C m^{-2} yr^{-1} in the northern HUS, and up to 6 mol C m^{-2} yr^{-1} in the ASUS during summertime and 9.1 mol C m^{-2} yr^{-1} off Cape Blanc in the central CanUS during wintertime (Mogollón and Calil, 2018; de Verneil et al., 2022; Curbelo-Hernández et al., 2023; see **Table 1** and **Table 2** for a summary of recent CO_2 and other GHG emission estimates in major coastal upwelling systems). Intense and sustained upwelling, which transports CO_2-enriched waters to the surface, along with the presence of warm waters, causes low-latitude upwelling systems such as the ASUS, the HUS, the central CanUS, and northern BenUS to act as net carbon sources to the atmosphere (Mogollón and Calil, 2018; Brady et al., 2019; Siddiqui et al., 2023). In contrast, higher-latitude upwelling systems (e.g., the southern BenUS, northern CalUS, and northern CanUS) that are characterized by colder temperatures and a weaker or shorter upwelling season act as weak carbon sinks or are neutral with regard to atmospheric CO_2 (Gregor and Monteiro, 2013; Fiechter et al., 2014; Turi et al., 2014; Curbelo-Hernández et al., 2023; Siddiqui et al., 2023). These net fluxes can, however, mask strong contrasts between the outgassing-dominated nearshore areas and the offshore regions dominated by biologically mediated atmospheric carbon uptake (Gregor and Monteiro, 2013; Lachkar and Gruber, 2013; Turi et al., 2014).

Previous estimates suggested N_2O emissions associated with coastal upwelling systems to be approximately 0.2 Tg N yr^{-1}, representing around 5% of the total oceanic N_2O source (Nevison et al., 2004). A more recent reconstruction of N_2O air-sea fluxes indicates that coastal upwelling systems play a larger role, contributing nearly 22% (0.91 ± 0.07 Tg N yr^{-1}) of oceanic N_2O emissions (Yang et al., 2020). In northern and central Chile and off Peru, where an intense and shallow OMZ develops, high N_2O concentrations are observed. Yang et al. (2020) estimated that the HUS contributes 0.23 ± 0.06 Tg N yr^{-1} (**Table 2**). Similarly, the shallow and intense OMZ associated with the ASUS is estimated to cause N_2O emissions to the atmosphere in the range of 0.10–0.56 Tg N yr^{-1} (Suntharalingam et al., 2019; Yang et al., 2020). The average N_2O emissions from the BenUS have been estimated to range between around 0.03 Tg N yr^{-1} (Arévalo-Martínez et al., 2019; Ganesan et al., 2020) and 0.1 Tg N yr^{-1} (Yang et al., 2020). Finally, the CalUS and CanUS, combined, contribute less than 0.05 Tg N yr^{-1} (Kock et al., 2012; Ganesan et al., 2020; Yang et al., 2020). These contributions come with strong seasonal and interannual fluctuations, with high (low) rates during upwelling (non-upwelling) periods (Cornejo et al., 2006; Molina et al., 2021). Once in the atmosphere, air masses can transport the N_2O excess to remote regions. For instance, the N_2O outgassed from the South Pacific OMZ can reach the Samoa region in the middle of the South Pacific, with concentrations around 0.4 ppb higher than in the remainder of the South Pacific (Babbin et al., 2020). During El Niño events, on the other hand, the oxygenation of surface waters, the decrease in productivity, and the deepening of the thermocline (Graco et al., 2017) modify the pelagic (Molina et al., 2020; Srain et al., 2020) and benthic (Neira et al., 2001) microbial communities of coastal areas. These changes reduce GHG accumulation and air-sea exchange (Molina et al., 2021). Thus, the interannual variability associated with the El Nino/Southern Oscillation (ENSO) alters the origin of upwelling waters, oceanic N_2O production rates, and the contribution of N_2O to the atmosphere, which is also observed in the atmospheric transport to remote areas (Babbin et al., 2020).

The CH_4 concentration in major coastal upwelling systems is similarly highly heterogeneous. For instance, in the HUS, the surface layer off Peru was reported to be up to 20% supersaturated (Kelley and Jeffrey, 2002), while the supersaturation off northern Chile reaches up to 1000% (24.4 nM; Farías et al., 2021). Yoshikawa et al. (2014) showed considerably lower CH_4 concentrations eastward along a 17°S transect (1.67–2.40 nM), with a slight supersaturation resulting in CH_4 fluxes to the atmosphere (up to 4.8 µmol m^{-2} d^{-1}). Although CH_4 supersaturation at the surface and throughout the water column is usually attributed to in situ production, the rates of sedimentary anaerobic oxidation of CH_4 in the surface layers of the organic-rich sediments in the upwelling zone of south-central Chile (up to 10.7 nmol cm^{-3} d^{-1} at 10 cm depth) and the flux to the water column (33.3 mmol m^{-2} d^{-1}) (Treude et al., 2005) suggest that sediments could contribute to the

Table 1. Recent estimates of CO_2 emissions in major coastal upwelling systems

Major Coastal Upwelling System	Flux Estimate[a] Flux Density (mol m^{-2} yr^{-1})	Flux Estimate[a] Area-Integrated Fluxes (Tg yr^{-1})	Method Used	References
Arabian Sea				
Oman (coast to 300 km offshore)	+2.7	+11.4	Model simulations	de Verneil et al. (2022)
Somalia	+3.2	+32.9	Model simulations	de Verneil et al. (2022)
Benguela				
Southern, 30–35°S, coast to 500 m isobath	−1.4 ± 0.6	−1.8 ± 0.8	Measurements of DIC and TA	Gregor and Monteiro (2013)
Southern, 26–34°S, coast to 200 km offshore	−1.38	−2.94	Measurements of DIC and TA	Gregor and Monteiro (2013)
Northern, 16–28°S, coast to 340 km offshore	+3.45	+15.64	Shipboard pCO_2 measurements	Siddiqui et al. (2023)
Northern, 18–28°S, coast to 800 km offshore	+2.25 ± 0.77	+25.97 ± 8.88	Model simulations	Brady et al. (2019)
California				
Coast to 800 km offshore	−0.05 ± 0.20	−0.9 ± 3.6	Model simulations	Turi et al. (2014)
Coast to 100 km offshore	+0.78	+1.6 ± 3.6	Model simulations	Turi et al. (2014)
Coast to 800 km offshore	−0.27 ± 0.71	−2.74 ± 7.2	Model simulations	Brady et al. (2019)
Canary				
Madeira, Canary, and Cape Verde archipelagos (winter)	−1.61	−2.79	Measurements of DIC, pH, and TA	Curbelo-Hernández et al. (2023)
Cape Blanc (winter)	+7.3 to +9.1	NA	Measurements of DIC, pH, and TA	Curbelo-Hernández et al. (2023)
Central Canary, coast to 800 km offshore	+1.23 ± 0.23	+14.05 ± 2.63	Model simulations	Brady et al. (2019)
Humboldt				
Coast to 300 km offshore	+5.6 ± 2.9	28 ± 15	Model simulations	Mogollón and Calil (2018)
Coast to 800 km offshore	+3.16 ± 0.83	+36.63 ± 9.62	Model simulations	Brady et al. (2019)

DIC = dissolved inorganic carbon; TA = total alkalinity; NA = not available.

[a] Positive flux means outgasing from sea to air; negative flux means gas moving into the sea (sourced from the atmosphere).

concentrations observed in the water column. In the upwelling area off Mauritania (CanUS), CH_4 concentrations were reported to range between 2.1 nM and 5.5 nM (Conrad and Seiler, 1988; Kock et al., 2008; Forster et al., 2009), with saturation values ranging from near equilibrium to 200% supersaturation and the highest concentrations and supersaturation observed near the coast (Kock et al., 2008). These authors suggested that enhanced CH_4 concentrations were probably caused by methanogenesis in anoxic microniches of sinking organic particles and/or by methanogenesis in the shelf sediments. The CH_4 emissions to the atmosphere (averaging upwelling and non-upwelling seasons) ranged from 0.77 mmol m^{-2} d^{-1} to 1.59 mmol m^{-2} d^{-1}, making the Mauritanian upwelling region a hotspot of CH_4 emissions (Kock et al., 2008).

2.3. Large-scale influence of upwelling systems on GHG cycling

The influence of upwelling systems on the cycling of GHG extends well beyond their productive nearshore regions, reaching far into the adjacent open ocean. This large-scale influence is mediated by the lateral cross-shore exchange of tracers such as organic carbon compounds, nutrients, oxygen and microbial communities; this transport smooths the cross-shore biogeochemical gradients at the boundary of upwelling systems and shapes the offshore biological activity (Gruber et al., 2011; Letscher et al., 2016). Both mean and mesoscale processes contribute to this coastal-open ocean biogeochemical coupling (Renault et al., 2016a), with an impact that extends up to thousands of kilometers off the upwelling coast (Combes et al., 2013; Nagai et al., 2015; Lovecchio et al., 2018).

Table 2. Recent estimates of N_2O and CH_4 emissions in major coastal upwelling systems

GHG[a]	Major Coastal Upwelling System	Flux Estimate[a]: Flux Density (mol m^{-2} yr^{-1})	Flux Estimate[a]: Area-Integrated Fluxes (Tg yr^{-1})	Method Used	References
N_2O	**Arabian Sea**				
	Entire sea	NA	0.1–0.56	Model simulations	Suntharalingam et al. (2019)
	Entire sea	0.004–0.005	0.21–0.26	Observation-based climatology	Yang et al. (2020)
	Coast to 200 km offshore	0.006–0.007	0.12–0.14	Observation-based climatology	Yang et al. (2020)
	Benguela				
	Coast to 150 km offshore	0.0078	0.026–0.031	Atmospheric measurements and inverse modeling	Ganeshan et al. (2020)
	Coast to 150 km offshore	0.01	0.026	Onboard measurements	Arévalo-Martínez et al. (2019)
	Coast to 200 km offshore	0.0047–0.0052	0.09–0.1	Observation-based climatology	Yang et al. (2020)
	Southern, coast to 50 km offshore	−0.0006–0.0063	0.004 ± 0.002	Onboard measurements and model	Mashifane et al. (2022)
	California				
	Coast to 150 km offshore	0.005	0.018–0.02	Atmospheric measurements and inverse modeling	Ganeshan et al. (2020)
	Coast to 200 km offshore	0.0017–0.0020	0.019–0.023	Observation-based climatology	Yang et al. (2020)
	Canary				
	Coast to 150 km offshore	0.006	0.01	Atmospheric measurements and inverse modeling	Ganeshan et al. (2020)
	Coast to 200 km offshore	0.004–0.005	0.020–0.024	Observation-based climatology	Yang et al. (2020)
	Humboldt				
	5–16°S, 75–86°W	0.01–0.046	0.2–0.9	Onboard measurements	Arévalo-Martínez et al. (2015)
	Coast to 200 km offshore	0.012–0.021	0.17–0.29	Observation-based climatology	Yang et al. (2020)
CH_4	**Benguela**				
	Northern (Walvis Bay during upwelling)	0.151 ± 0.199	0.04 ± 0.03	Atmospheric inversions	Morgan et al. (2019)
	Northern	<0.05	<0.17	Onboard measurements	Emeis et al. (2018)
	Canary				
	Offshore Mauritania	0.0002–0.0003	0.001–0.002	On board measurements	Kock et al. (2008)
	Humboldt				
	Central Chile	0.003 ± 0.001	0.001–0.004	Fixed time-series station	Farias et al. (2021)

GHG = greenhouse gases; NA = not available.

[a] Fluxes correspond to outgasing of GHG from sea to air.

Numerous studies have attempted to quantify the impact of these cross-shore fluxes on the cycling of carbon. According to models, more than 1/3 of the organic carbon produced in the nearshore CanUS and CalUS leaves the shelf to be remineralized offshore; such lateral transport supports a fully three-dimensional biological pump at the edge of upwelling regions, resulting in a lateral decoupling between regions of production and regions of remineralization (Lovecchio et al., 2017; Frischknecht et al., 2018). This lateral decoupling is confirmed by observations, which show that the lateral advection of slow sinking ("suspended") particulate organic carbon (POC) from the NW African coast fuels high levels of mesopelagic respiration in the open waters adjacent to the CanUS (Alonso-González et al., 2009; Fernández-Castro et al., 2016). Coastal organic carbon and upwelled nutrients "leak" into the open ocean at the highest rates in regions of high mesoscale activity, reducing primary production and organic carbon export in the nearshore and increasing them in open waters (Lachkar and Gruber, 2011; Santana-Falcón et al., 2020; Hailegeorgis et al., 2021). Filaments in the Peru upwelling system have been observed to export and subduct upwelled nutrients, possibly also injecting coastal organic carbon into the subsurface offshore waters (Hauschildt et al., 2021). Satellite data indicate that cyclonic eddies formed in the nearshore CalUS transport coastal organic carbon up to 1000 km offshore, delivering 20.9 ± 11 Gg C yr^{-1} to the upper 100 m of the open North Pacific (Amos et al., 2019). In the CanUS, a model study showed that narrow filaments relocate offshore up to 80% of the coastal organic carbon at the shelf break, while eddies trap it and propagate it for hundreds of kilometers thanks to several cycles of organic matter recycling and new production in the eddy cores (Lovecchio et al., 2018; Lovecchio et al., 2022). Providing a lower-end estimate, a modeling study by Santana-Falcón et al. (2020) showed that filament transport in the CanUS can export up to 23% of non-refractory organic carbon within 100 km of the shore, with strong seasonal variability (up to 6-fold) and maximum offshore transport during the peak upwelling season. Convergence regions between coastal currents are also efficient at collecting and laterally exporting upwelled nutrients and organic carbon, fueling vertical export fluxes that exceed local production and, hence, supporting a net-heterotrophic water column offshore (Auger et al., 2016; Lovecchio et al., 2017). Globally, upwelling systems are also one of the most important sources of dissolved organic carbon (DOC), the largest organic carbon pool in the ocean (Hansell and Orellana, 2021). In the CanUS, DOC is conveyed offshore by filaments and subsequently accumulates in the oligotrophic North Atlantic Gyre (Álvarez-Salgado et al., 2007; Burgoa et al., 2020). Overall, organic carbon leaking offshore from the productive region of upwelling systems constitutes a source of nutrients for the water column and to benthos of oligotrophic open ocean waters and can be exported to deeper depths, resulting in longer carbon sequestration times.

The large-scale oxygen cycle is also shaped by the lateral coupling between upwelling systems and open waters, with an impact on the cycling of N_2O, CH_4, and CO_2. Low oxygen concentrations that build up on the upwelling shelves can propagate offshore, especially via mesoscale eddy transport. In the Peruvian upwelling system, coastal-generated subsurface anticyclonic eddies with core oxygen concentrations below 1 μmol kg^{-1} and an associated nitrogen deficit have been observed up to 900 km from the coast; such eddies trap oxygen-deficient equatorial water transported along the upwelling shelf by the Peru-Chile undercurrent and transport it to the open Pacific, lowering its oxygen concentrations and favoring denitrification and N_2O inventories (Hormazabal et al., 2013; Cornejo D'Ottone et al., 2016; Thomsen et al., 2016). In the Mauritanian upwelling system, data have shown that westward-propagating cyclones and mode-water anticyclones formed off the coast can host oxygen minima of 10 μmol kg^{-1} and <2 μmol kg^{-1}, respectively, both significantly lower than the typical 40 μmol kg^{-1} found in the open North Atlantic OMZ (Karstensen et al., 2015; Schütte et al., 2016). Computed downward fluxes of POC in the core of the eddies indicate that they largely exceed the fluxes in the surrounding oligotrophic waters (Fiedler et al., 2016). Local remineralization plays a key role in the build-up of low oxygen concentrations in these eddies, whose integrated effect may lower O_2 in the North Atlantic OMZ by 7 μmol kg^{-1} between 50 m and 150 m depth and may trigger nitrogen loss that would otherwise not occur (Löscher et al., 2015; Schütte et al., 2016; Karstensen et al., 2017). Microbial communities associated with low-oxygen upwelling environments can also be laterally advected out of upwelling regions. Data suggest that subsurface eddies formed along the sulfidic shelves of upwelling systems, such as off Peru, export sulfide-oxidizing denitrifying bacteria to sulfide-poor offshore OMZ waters, thereby coupling the microbial communities of the coastal and open ocean waters (Callbeck et al., 2018). Such subsurface eddies form in all four eastern boundary upwelling systems from their shelf undercurrents and propagate offshore for several months, with a small portion of them (<5%) traveling for more than 1000 km (Frenger et al., 2018).

3. Recent and future changes

The emissions of GHG in the major coastal upwelling systems considered here are sensitive to variations in upwelling intensity and changes in the physical and biogeochemical environment caused by ongoing global anthropogenic change. For instance, changes in upwelling intensity can alter the supply of inorganic carbon to the ocean surface, with the potential to impact upwelling-driven CO_2 outgassing. Changes in upwelling intensity can also alter biological productivity, potentially affecting both surface CO_2 uptake and GHG production at depth through changes in aerobic and anaerobic respiration. Beyond local changes in upwelling, major global ocean perturbations such as ocean acidification and deoxygenation can also alter the production and emission of GHG in these major coastal upwelling systems. Indeed, by increasing the volume of suboxic or anoxic waters or by changing their depth, ocean deoxygenation can affect the production and the potential release of potent GHG such as N_2O and CH_4 to the atmosphere. Additionally, ocean acidification can impact the production and emissions of GHG by affecting important processes such as nitrification or methanogenesis (Hopkins et al., 2020). Next, we provide an overview of recent and potential future changes in physical and biogeochemical conditions in the major coastal upwelling systems and their implications for GHG emissions.

3.1. Recent trends in physical and biogeochemical conditions

Major upwelling systems are strongly sensitive to variations in upwelling-favorable winds on a multitude of scales ranging from synoptic to seasonal, interannual and longer (Chavez and Messié, 2009; García-Reyes et al., 2015; Abrahams et al., 2021; Bograd et al., 2023). Bakun (1990) hypothesized an increase in coastal upwelling intensity in response to an enhanced land-ocean pressure gradient under a warmer climate. This paradigm has been challenged by subsequent studies. Besides its lack of physical validation (e.g., along-shore winds in coastal jet regions are not entirely in geostrophic balance), the wind data used in Bakun (1990) were biased due to changes in the size (height) of the merchant ships in the 1960s (Tokinaga and Xie, 2011). Using corrected winds yields no trend in upwelling favorable winds in the Peru upwelling system (see figure 1 of Belmadani et al., 2014). An alternative hypothesis posits an increase (decrease) in upwelling intensity in poleward (equatorward) portions of major upwelling systems as a result of the projected poleward expansion of the Hadley circulation under a warmer climate (e.g., Lu et al., 2007; Rykaczewski et al., 2015; Sandeep and Ajayamohan, 2015). As these changes are likely to profoundly affect the upwelling ecosystems and alter production of GHG (Lachkar and Gruber, 2013; Lachkar et al., 2018), multiple investigations of recent upwelling changes have been carried out based on available observations and model simulations. While several studies suggest important increases in upwelling-favorable winds in the poleward portions of major eastern and western boundary upwelling systems, consistent with a poleward shift of the Hadley circulation (e.g., García-Reyes and Largier, 2010; Sandeep and Ajayamohan, 2015; Varela et al., 2015; Aguirre et al., 2019), other studies reveal trends that are indiscernible or spatially inconsistent (Barton and Roy, 2013; Casabella et al., 2014; Tim et al., 2015; Gómez-Letona et al., 2017; Abrahams et al., 2021) or highly sensitive to data sources and analysis periods (Nararyan et al., 2010; Sydeman et al., 2014; Taboada et al., 2019; Bograd et al., 2023). Furthermore, previous studies suggest no clear data-based support for the Bakun (1990) hypothesis of upwelling intensification (Tim et al., 2015; Tim et al., 2016). Other studies have highlighted the role of changes in the properties of upwelling source waters in driving important changes in physical and biogeochemical conditions in upwelling systems (Rykaczewski and Checkley, 2008; Rykaczewski and Dunne, 2010; Varela et al., 2016).

Irrespective of trends in upwelling intensity, multiple studies have documented weaker warming rates in coastal upwelling systems relative to adjacent open oceans over recent decades, thus highlighting their role in buffering ocean warming (Varela et al., 2016; Gomez-Letona et al., 2017; Varela et al., 2018; Seabra et al., 2019; Siemer et al., 2021). Contrasting with a robust role in mitigating warming, a lack of consensus characterizes historical trends in productivity in coastal upwelling systems. Indeed, while early works based on short satellite data time-series suggest an increase in net primary production (NPP) in several eastern and western boundary upwelling systems (e.g., Goes et al., 2005; Demarq, 2009; Kahru et al., 2009), more recent studies with longer time-series have reported inconsistent trends or even a decline in productivity in most major upwelling systems (e.g., Roxy et al., 2016; Gómez-Letona et al., 2017; Lamont et al., 2019; Weidberg et al., 2020). For instance, carbon-based satellite productivity models show decreasing trends in NPP in the CanUS, in contrast to chlorophyll-based NPP models, noting that the carbon-based models yield unrealistically low NPP estimates in upwelling waters (Gómez-Letona et al., 2017; Siemer et al., 2021).

Upwelling systems are naturally prone to low O_2 and low pH because of the upwelling of deep, O_2-depleted, carbon-rich water to the surface layer (Gruber, 2011). Ocean deoxygenation and ocean acidification—driven by anthropogenic activity—have the potential to increase the occurrence of coastal hypoxia and water-column calcium carbonate undersaturation in several major coastal upwelling systems (Gruber, 2011; Capone and Hutchins, 2013). For instance, rapid progression of ocean acidification accompanied by a shoaling of undersaturated water with respect to the calcium carbonate mineral, aragonite, has been reported in the CalUS in several near-shore locations (Feely et al., 2008). Similarly, oxygen content has been decreasing at a rate of 0.09–0.34 μmol kg^{-1} yr^{-1} in the tropical thermocline for the past five decades (Stramma et al., 2008), with profound but poorly understood implications for adjacent upwelling systems (Bograd et al., 2008; Chan et al., 2008; Piontkovski and Al Oufi, 2015; Espinoza-Morriberon et al., 2021; Lachkar et al., 2021). These changes have the potential to affect key biogeochemical transformations in upwelling systems, by increasing the volume of the oceans with suitable conditions for GHG production (Bakun and Weeks, 2004).

3.2. Future impacts of climate change on upwelling systems

The fate of upwelling systems in a warming world is an important question considering that upwelling regimes regulate the productivity of critical fisheries and marine ecosystems. This issue has been debated intensively since the pioneering study by Bakun (1990). Nevertheless, climate change projections from state-of-the-art global climate models indicate a rapid warming trend in all major upwelling systems, which is associated with a flattening of the mean thermocline and increased vertical stratification, two processes that hinder the mechanical effect of the alongshore wind stress (by reducing upwelling) and need to be compensated by a substantial increase in upwelling-favorable winds to maintain efficient nutrient supply to the euphotic layer. On the other hand, along-shore wind projections remain uncertain in tropical upwelling systems. Indeed, only the poleward regions of major coastal upwelling systems exhibit a significant positive trend in the winds associated with the strengthening and poleward displacement of the subtropical atmospheric pressure systems (Rykaczewski et al., 2015; Wang et al., 2015). Difficulties in inferring physical drivers (i.e., whether local or remote) of the long-term evolution of upwelling systems are related to the spatial scales of variability involved in both oceanic and atmospheric processes relevant for upwelling dynamics. In particular, atmospheric fluxes from atmospheric reanalyzes and coupled models exhibit significant biases in a narrow (100 km) coastal fringe where the observed alongshore wind reduces sharply (Astudillo et al., 2017). This on-shoreward reduction in the upwelling-favorable winds is referred to as the "wind drop-off" (Capet et al., 2004). The "shape" of the wind drop-off constrains key aspects of the circulation in a high-resolution modeling framework. A broader wind drop-off weakens the vertical shear of the alongshore current below the thermocline, flattens the isopycnal tilt, and tends to reduce eddy kinetic energy, resulting in an increase in NPP (Capet et al., 2004; Renault et al., 2016b). It is also influential on mixed-layer temperature through modulating the heat flux contribution to the heat budget (Astudillo et al., 2019). High-resolution model experiments under climate change scenarios have evidenced the key role of the non-linear coastal upwelling dynamics and associated eddy-induced circulation (Capet et al., 2008; Gruber et al., 2011) for understanding long-term trends in upwelling systems, in terms of circulation (Echevin et al., 2012; Chang et al., 2023; among others), biogeochemistry (Lachkar et al., 2016; Renault et al., 2016a; Pozo Buil et al., 2021), and trophic levels (Brochier et al., 2013). The time of emergence of the trends derived from these more realistic modeling frameworks remains to be established considering the role of natural variability (e.g., ENSO, and the Interdecadal Pacific Oscillation, IPO) and the sensitivity to the details of the downscaling methods (Echevin et al., 2020; Pozo Buil et al., 2021; Vallivattathillam et al., 2023). For instance, the observed contemporary cooling trend off Peru has been suggested to result from changes in equatorial oceanic circulation associated with the more frequent occurrence of Central Pacific El Niño events since the 2000s rather than to changes in the winds (Dewitte et al., 2012).

In response to climate warming, the ocean lost 2% of its O_2 between 1960 and 2010 (Ito et al., 2017; Schmidtko et al., 2017) and is expected to lose a further 3%–4% of its O_2 inventory by 2100 under the high-emission scenario (Bopp et al., 2013; Breitburg et al., 2018; Kwiatkowski et al., 2020). This deoxygenation has been associated with an expansion of OMZs (Stramma et al., 2008; Stramma et al., 2010; Breitburg et al., 2018) that could increase the production of N_2O. However, enhanced stratification and increasing atmospheric N_2O concentrations from human emissions may also induce a decrease in the N_2O flux to the atmosphere (Martinez-Rey et al., 2015; Bange et al., 2024). Additionally, the anticipated decrease in the export of organic matter and its remineralization in the low- to mid-latitude ocean is expected to reduce N_2O production via nitrification and denitrification processes (Bange et al., 2024). Landolfi et al. (2017) have suggested that by 2100, under the RCP8.5 scenario, total N_2O production in the ocean may have declined by 5% and N_2O emissions may be reduced by 24% relative to the preindustrial condition due to a decrease in organic matter export and anthropogenically driven changes in ocean circulation and atmospheric N_2O concentration. As yet unclear is whether N_2O production from nitrification increases exponentially or linearly with decreasing oxygen and whether a threshold oxygen concentration exists below which net N_2O production switches to N_2O consumption. Furthermore, the correlation between N_2O and oxygen varies with the microorganisms present and nutrient concentrations (Voss et al., 2013). Land-sea-atmosphere interactions in major upwelling systems modulate warming-induced ocean deoxygenation. For instance, the effect of nutrients delivered to the surface ocean by atmospheric deposition may be to stimulate primary production and CO_2 uptake but also to release N_2O, which could exacerbate warming, offset the increased biological CO_2 uptake, and thus accelerate deoxygenation (Garçon et al., 2019a). Furthermore, Earth system models show inconsistent future trends in the evolution of OMZs (**Figure 3**; see also Kwiatkowski et al., 2020) although future global deoxygenation is robust across the models (Bopp et al., 2017). This lack of consistent trends in the future OMZ predictions is because the thermal (solubility) and nonthermal (ventilation and remineralization) effects oppose each other in the tropical thermocline where major upwelling OMZs are located (Bopp et al., 2017; Long et al., 2019; Lachkar et al., 2023). Indeed, although O_2 solubility is projected to decrease in the future, models also project a potential decrease in apparent oxygen utilization in the tropical thermocline, mostly driven by stronger ventilation at the thermocline depth (Bopp et al., 2017).

Overall, the future impact of climate change on upwelling systems remains uncertain and is likely to depend on the magnitude of global warming. While a rapid coastal warming is expected in all major upwelling systems even in the most optimistic scenario, unclear is whether coastal winds will increase or decrease in tropical upwelling systems and whether or not the increase in upwelling-favorable winds in the mid-latitude EBUS (Rykaczewski et al., 2015) could offset the effect of enhanced coastal stratification on upwelled nutrient supply. More efforts are needed to reduce biases in global coupled models and in comparing downscaling methods in a regional modeling framework. Improvement in our predictive capability at climatic timescales in these regions also requires a better understanding of mechanisms associated with remote and local forcings, as basin-scale climate modes (e.g., ENSO, IPO, and Atlantic Multidecadal Oscillation) and their teleconnections will also undergo changes (e.g., Cai et al., 2018; Yeh et al., 2018), with regional impacts that are not straightforward (e.g., Hu and Fedorov, 2018). Finally, our understanding of the impact of current global anthropogenic perturbations, such as warming, acidification, and deoxygenation, on the production and emissions of GHG is, at best, in its infancy (as discussed by Bange et al., 2024).

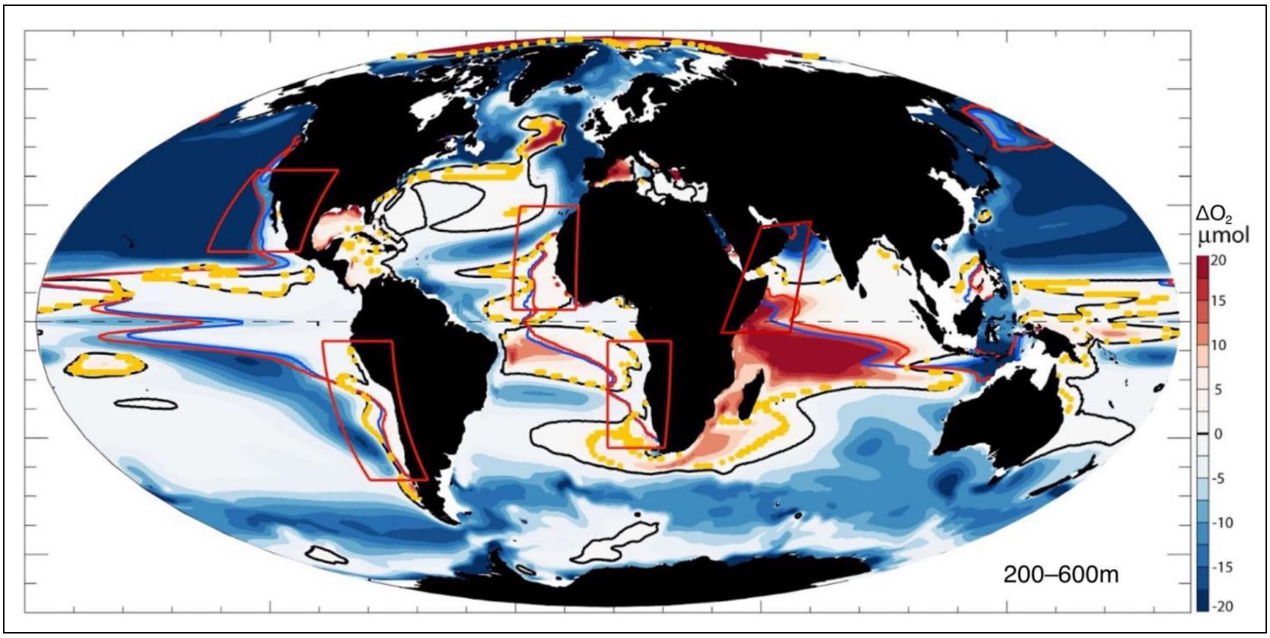

Figure 3. Projected future O_2 changes in the thermocline. Effect of climate change on oxygen concentration (in µmol kg^{-1}) in the depth range of 200–600 m in the CESM (community Earth system model) Large Ensemble (Kay et al., 2015) using 34 members: difference in mean conditions between the present (1950–2005, "historical" scenario) and the future (2050–2100, RCP8.5 scenario) for dissolved oxygen (positive values indicate an increase of O_2 in the future). The blue and red contour lines show the isolines of 20 µmol kg^{-1} for the present and future climates, respectively. The orange dots (stippling) correspond to the locations where the change in oxygen concentration is not significant at the 99% level according to a Wilcoxon rank sum test.

4. Outlook

4.1. Summary and challenges

Due to their high socioeconomic importance, upwelling systems are among the most observed of all ocean regions (e.g., Arístegui et al., 2009; Hutchings et al., 2009; McClatchie, 2014; Grados et al., 2018; Chevallier et al., 2021). However, there is still significant uncertainty regarding the ongoing and future impacts of climate change in these systems (Bograd et al., 2023). This uncertainty arises in part because upwelling systems are highly variable spatially and temporally, due to both local and remote atmospheric and oceanic forcings that occur on (sub)seasonal to decadal (and longer) timescales, as well as to the topographic complexities of their respective coastlines (Mackas et al., 2006). In addition, the length and resolution of the observational datasets currently available for the major upwelling systems are not comparable. For example, monitoring of the CalUS under the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has been ongoing since 1949 (indeed, CalCOFI is the longest continuous coastal monitoring program in the world; Bograd et al., 2003; McClatchie, 2014), while monitoring has been less routine in the CanUS (Todd et al., 2019) where efforts have instead focused on process studies (e.g., Parrilla et al., 2002; Barton and Arístegui, 2004). Our understanding of the functioning of upwelling systems may thus be biased toward the better observed systems. For instance, from a meta-analysis of the literature, Sydeman et al. (2014) reported that upwelling-favorable winds have intensified in all the major EBUS except the CanUS, yet the extracted trends are highly dependent on the length and resolution of the datasets used, as well as latitude and season.

While there are clearly commonalities in the behavior of the major upwelling systems (e.g., García-Reyes et al., 2015; Bograd et al., 2023), there are also significant differences in their location, structure, and drivers that will likely yield divergent responses to climate change. For instance, the BenUS and CanUS are broadly characterized by wider continental shelves and fed by younger waters, the HUS and CalUS are located on narrower continental shelves and are strongly influenced by the major Pacific OMZs (Mackas et al., 2006) and ENSO (Dewitte et al. 2012; Frischknecht et al. 2015), and the ASUS is highly sensitive to monsoon variability. Additionally, different datasets suggest different trends, both across upwelling systems and within the same system. The choice of reanalysis product has been shown to influence the derived trends in alongshore wind stress and upwelling intensity, with different products even yielding contrasting results for the same upwelling system (Narayan et al., 2010; Taboada et al., 2019). For instance, a decline in the nearshore temperature of the BenUS, along with an increase in the cross-shelf temperature gradient, has been attributed to increased upwelling intensity (Santos et al., 2012), yet the ocean-land pressure gradient appears unchanged (Tim et al., 2015). There may also be regional (i.e., latitudinal) variations in the response of a particular upwelling system to change. For example, the poleward migration of the atmospheric high-pressure systems (Lu et al., 2007) will likely intensify upwelling-favorable winds at the poleward latitudes of upwelling systems but weaken them toward the equator (Rykaczewski et al., 2015; Sandeep and Ajayamohan, 2015; Wang et al., 2015).

A further challenge in predicting climate-driven changes to upwelling systems is extracting robust long-term trends from the overlapping signals of multiple scales of variability. The dominant mode of variability arises due to the seasonally varying equatorward (poleward in the case of the ASUS) wind stress that facilitates offshore Ekman transport and coastal upwelling. However, upwelling duration, intensity, and frequency vary considerably across and within the different systems. For example, the southern BenUS experiences pulsed upwelling (i.e., upwelling events of 3–10 days) during the summer upwelling season (Nelson and Hutchings, 1983; Burger et al., 2020; Pitcher et al., 2021), while the northern BenUS is characterized by regions of intense year-round upwelling (e.g., at Lüderitz; Hutchings et al., 2009). Additionally, upwelling intensity is controlled by wind-driven Ekman transport, cross-shore geostrophic transport, and indirectly by eddy-induced offshore heat transport. Ongoing and future changes in geostrophic transport have to-date not been well-studied even though they may oppose the changes in Ekman transport (Oerder et al., 2015; Ding et al., 2021). The different upwelling systems experience varying degrees of sub-seasonal variability that can lead to stochastic events that are difficult to predict. For example, the southern BenUS is characterized by predictable remineralization-driven seasonal hypoxia (Monteiro and van der Plas, 2006; Pitcher et al., 2014; Flynn et al., 2020), punctuated by unpredictable episodes of severe hypoxia or even anoxia (Monteiro et al., 2011) that can be so severe as to cause mass fish kills. If such events cannot be predicted today, then anticipating their future frequency and severity (and that of similarly stochastic events such as marine heatwaves) is challenging.

How conditions within and among the major upwelling systems are changing and will continue to change is a function of both local and remote processes (Bograd et al., 2023), with projections of their trends dependent on our understanding and ability to predict changes in these processes. For instance, climate-driven changes occurring remotely may alter the properties (e.g., nutrient and oxygen concentrations) of water masses that upwell onto the upwelling system shelf (Rykaczewski and Dunne, 2010; Pitcher et al., 2021), while warming influences in situ stratification and thus the depth from which source waters upwell (Jacox and Edwards, 2011) and the magnitude of the nutrient supply to the surface layer. Similarly, a slowing of equatorial circulation may reduce upwelling system ventilation, leading to nearshore deoxygenation (Echevin et al., 2020), while anthropogenic nutrient loading at the coast may directly cause regional eutrophication and deoxygenation (Kessouri et al., 2021). The numerous coincidentally changing processes will likely also interact to strengthen or diminish one another, making it difficult to disentangle the dominant driver(s) of future change. For example, increased upwelling intensity might be expected to deliver more nutrients to phytoplankton, enhancing productivity and carbon export and subsequently, bottom-water oxygen utilization. Coincidentally, enhanced upwelling will decrease the residence time of both surface and bottom waters, potentially decreasing phytoplankton productivity, carbon export, and on-shelf oxygen consumption (Jacox et al., 2016; Flynn et al., 2020). An additional example is the combination of upwelling changes with large scale anthropogenic perturbations such as ocean deoxygenation and acidification that can drive contrasting responses in different upwelling systems. For instance, regional simulations of the CalUS and CanUS yield opposite trends in ocean acidification in a scenario of enhanced upwelling-favorable winds (Lachkar, 2014).

The regional complexity (both common and unique) of the various upwelling systems, along with the differences in the datasets and reanalysis products available for them, pose a challenge for climate models tasked with projecting the magnitude and direction of future change. Moreover, the trends that such models project have been shown to be influenced by model resolution, parameterization, large-scale circulation, and boundary conditions (e.g., Bograd et al., 2008; Echevin et al., 2020; Pozo Buil et al., 2021; Bograd et al., 2023). Additionally, while many existing modeling studies have relied on the CMIP5 ensemble of climate models, outputs from the CMIP6 models, with updated physics and biogeochemistry and some with improved resolution, are now available (Bograd et al., 2023). This ensemble may yield new and/or different insights into the future state of upwelling systems. Given the lack of consensus as to how upwelling systems have already changed in response to climate change, such insights are imperative for understanding the future health of these important ecosystems and our ability to manage them.

4.2. Recommendations for future research

To address some of the challenges described in the previous section, we make the following few broad recommendations for future research.

1) Enable and improve the detectability of long-term changes in major upwelling systems.

This objective requires an improvement in the length and resolution of key observational datasets, especially in the less studied systems such as the CanUS, ASUS, and HUS. To this end, suitable observational strategies involving regular monitoring of key physical and biogeochemical variables (following the example of successful programs such as CalCOFI) need to be devised. This effort can be achieved through the deployment of fixed oceanographic moorings that ensure continuous local monitoring of these systems or through targeted field campaigns and the deployment of robotic underwater gliders and profiling floats (Argo; Jayne et al., 2017) to cover larger areas. Building on the Framework for Ocean Observing, Garçon et al. (2019b), for instance, provided a first readiness level assessment for ocean observing of the oxycline in the major coastal upwelling systems. This assessment was to determine current ocean observing design and future needs in these regions. Fisheries and ecosystem management appear to be a societal requirement for all regions, but maturity levels of observational elements and data management and information products differ substantially between regions. Data need to be consolidated to derive regional budgets of key variables such as nutrients and GHG. This recommendation aligns with that of the recent report from the TPOS 2020 program (see Chapter 5 of Kessler et al., 2019) calling for an enhanced observational network in the far eastern Pacific.

Understanding the natural spatial and temporal variability for the less well sampled GHG, such as N_2O and CH_4, can be enhanced by expanding the existing datasets and improving their quality. Data harmonization efforts that involve the implementation and standardization of analytical and quality-control procedures are needed to improve the accuracy of datasets and their interoperability. This recommendation aligns with the recent assessment by Wilson et al. (2020).

Understanding and separating the different scales of variability in the various upwelling systems is essential to extract robust climate-change driven trends from the overlapping signals of natural variability. To this end, the use of large-ensemble model simulations to disentangle natural and forced variability is strongly advised. Particular care should be given to the choice of resolution and to generalizing this effort to all major upwelling systems.

2) Assess the vulnerability of major upwelling systems to climate change.

Contrast major upwelling systems in the context of a changing climate while aiming at improving understanding of the factors that control their sensitivity to global change and explain their differences. For instance, the future evolution of major OMZs varies among different upwelling systems for reasons that remain unclear. Achieving clarity requires that groups working on different systems share expertise, build collaborations and design comparative studies that involve coordinated observational and modeling strategies to answer similar questions across systems.

Multiple efforts have been dedicated to comparing and understanding similarities and differences among eastern boundary upwelling systems (e.g., Chavez and Messié, 2009; Demarq, 2009; Lachkar and Gruber, 2012). We recommend that these efforts be broadened to include other major upwelling systems such as the ASUS that share many commonalities with EBUS (both in terms of drivers and sensitivity to climate change). Including ASUS is particularly relevant given the significance of this system as a host of a major OMZ and a hotspot of GHG cycling.

Coordinate and design appropriate strategies for downscaling global climate simulations for upwelling systems. Efforts in this direction have been undertaken in a few systems (e.g., Machu et al., 2015; Howard et al., 2020; Pozo Buil et al., 2021; Vallivattathillam et al., 2023). A more coordinated effort is required for a broader understanding.

More process studies based on both model and field experiments are needed to disentangle the role of local versus remote forcing in driving changes in different upwelling systems and to understand how concurrent perturbations (e.g., wind changes vs upper ocean warming) can counteract each other or lead to unexpected changes in upwelling systems.

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Author contributions

All authors contributed to the writing of the manuscript and approved it for publication.

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