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### Key Points:

- Eddies contribute substantially to low  $[O_2]$  extreme events near Eastern Boundary Upwelling System regions
- Low  $[O_2]$  extreme events occur more frequently in eddies versus non-eddy locations
- Cyclonic eddies tend to contain lower oxygen concentrations than anticyclonic eddies

### Supporting Information:

Supporting Information may be found in the online version of this article.

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## Quantifying the Contribution of Ocean Mesoscale Eddies to Low Oxygen Extreme Events

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**Abstract** Ocean mesoscale eddies have been identified as drivers of localized extremely low dissolved oxygen concentration ( $[O_2]$ ) conditions in the subsurface. We employ a global physical-biogeochemical ocean model at eddy-permitting resolution to conduct a census of open-ocean eddies near Eastern Boundary Upwelling Systems adjacent to tropical Oxygen Minimum Zones (OMZs). We track cyclonic and anticyclonic eddies with a surface signature over the period 1992–2018 and isolate their subsurface oxygen characteristics. We identify strongly deoxygenating eddies and quantify their contribution to low  $[O_2]$  extreme events. Our results show that model simulated low  $[O_2]$  extreme event frequency is 2–7 times higher in eddies versus non-eddy locations, with regionally more than half of low  $[O_2]$  extreme events outside of the permanent OMZs being associated with eddies. Our study highlights the need for further work to investigate the drivers, characteristics and potential ecosystem impacts of low  $[O_2]$  extreme events.

**Plain Language Summary** Over the recent past the oxygen content of the global ocean has been declining, with consequences for marine ecosystems. Ocean eddies (rotating currents of water on the order  $\approx 100$  km diameter) have been identified as vehicles of extremely low oxygen concentrations but are understudied in the context of biogeochemical extreme events in the ocean. This investigation is the first of its kind to use a four-dimensional data set (time, latitude, longitude, depth) to create a regional scale census of eddies and their oxygen conditions across the period 1992–2018 as they travel offshore from typically low oxygen waters of the near-coastal Atlantic and Pacific, carrying and modifying low oxygen signals into otherwise more oxygenated ocean regions. We track eddies associated with low oxygen conditions and assess how much they contribute to low oxygen extreme events. In some places eddies contribute to more than half of the simulated low oxygen extreme events, signaling the need to further explore the role that eddies play in marine extreme events.

## 1. Introduction

Over the last 50 years, the global inventory of oceanic dissolved oxygen has declined by  $\approx 2\%$  (Schmidtko et al., 2017) and further ocean deoxygenation is projected this century in response to continued anthropogenic ocean warming (e.g., Kwiatkowski et al., 2020). Alongside changes in the mean state, the ocean is also experiencing increases in the frequency of extreme events, including marine heatwaves (Frölicher et al., 2018) and biogeochemical extremes (e.g., Gruber et al., 2021). Results from the Geophysical Fluid Dynamics Laboratory Earth System Model suggest that the number of simulated low oxygen extreme days per year has increased five-fold globally since the pre-industrial era (Gruber et al., 2021), with such events likely to co-occur with acidity extremes (Burger et al., 2020). Identifying the physical and biogeochemical processes which bring about low oxygen extremes in the ocean is particularly important for understanding ecosystem impacts, as oxygen-depleted waters are known to affect marine life and biogeochemical cycling (e.g., Codispoti, 2010; Vaquer-Sunyer & Duarte, 2008).

Cyclonic (CE) and anticyclonic (ACE) eddies influence the spatiotemporal distribution of biogeochemical properties in the ocean via a number of physical-biogeochemical mechanisms (McGillicuddy, 2016). Potential mechanisms include lateral transport processes, such as “eddy trapping”, where the strong rotation of an eddy is capable of isolating water masses within the eddy structure (Chelton, Schlax, et al., 2011). Low dissolved oxygen concentration ( $[O_2]$ ) source waters in tropical Oxygen Minimum Zone (OMZ) regions may then be trapped by eddies forming in these locations before propagating westward (Schütte, Karstensen, et al., 2016). In addition to transport of low  $[O_2]$  waters, eddies may also impact  $O_2$  consumption at depth by affecting the export of organic

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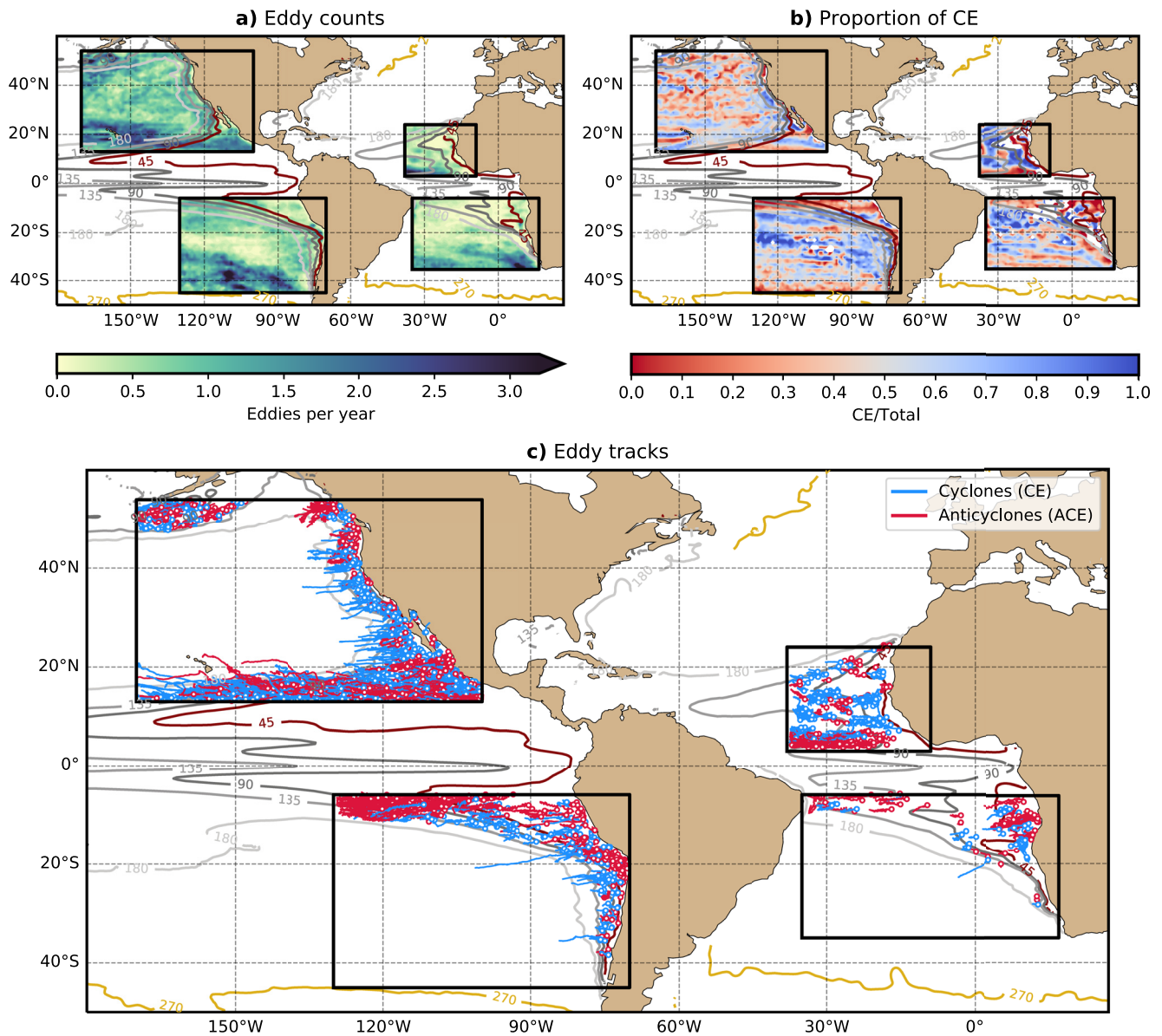
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matter from the productive sunlit near-surface ocean. Chelton, Gaube, et al. (2011) and Gaube et al. (2014) show mesoscale variability in near-surface chlorophyll to be associated with the movement of westward propagating eddies. Such covariation occurs due to lateral transport and local modulation of environmental conditions and ecosystems (see Lévy, 2008; McGillicuddy, 2016 and references therein). Potential modulation of export of organic matter will then change subsurface organic matter remineralization, and influence  $O_2$  consumption at depth.

Eastern Boundary Upwelling Systems (EBUS) are characterized by high biological productivity and energetic ocean currents, which produce large numbers of eddies (Mahadevan, 2014). Eddies originating in EBUS locations tend to be long-lived, which allows them to propagate far offshore and into the subtropical gyres (Chelton, Schlax, et al., 2011; Lovecchio et al., 2018). Therefore, this may allow eddies originating in these regions to transport biogeochemical signals across large distances and  $[O_2]$  gradients, as well as allow  $O_2$  depletion via biological consumption to accumulate, provided eddies are well isolated. Low  $[O_2]$  conditions in eddies, particularly CEs, are well documented in observational studies of the Atlantic (Karstensen et al., 2015; Löscher et al., 2015; Schütte, Karstensen, et al., 2016) and Pacific EBUS regions (Arévalo-Martínez et al., 2016; Czeschel et al., 2018; Stramma et al., 2013). The influence of subsurface anticyclonic “puddies” (poleward undercurrent eddies) on the redistribution of low  $[O_2]$  conditions from EBUS into the subtropical gyres has been described by Frenger et al. (2018). These long-lived subsurface eddies can develop extremely low  $[O_2]$  conditions ( $<1\text{--}10\text{ mmol m}^{-3}$ ), as observed in “dead zone” eddies of the eastern tropical North Atlantic (Karstensen et al., 2015; Schütte, Karstensen, et al., 2016) and in the Pacific near Hawaii (Lukas & Santiago-Mandujano, 2001). The low  $[O_2]$  conditions associated with EBUS eddies have been shown to impact ecosystems (Christiansen et al., 2018; Hauss et al., 2016) and marine  $N_2O$  production (Grundle et al., 2017). In summary, eddies in EBUS have been observed to feature low  $[O_2]$  values, with implications for ocean biogeochemistry. Here, we provide a first model-based assessment of the influence of eddies that are detectable at the ocean surface in and around Atlantic and Pacific EBUS regions on  $[O_2]$  and occurrence of low  $[O_2]$  extreme events.

## 2. Methodology and Data

Numerical models provide fully spatiotemporally resolved fields to study eddy dynamics and associated biogeochemical properties. Here, we employ a publicly available hindcast global physical-biogeochemical ocean model without data-assimilation at “eddy-permitting” resolution ( $0.25^\circ$  horizontal spacing, 75 vertical layers) over the period 1992–2018. As detailed in Perruche et al. (2019), the physical ocean model simulation (FREEGLORYS2V4; NEMOv3.1, Madec, 2008) provides daily ocean dynamical forcing for the biogeochemical simulation (FREEBIORYS2V4; PISCES-v2, Aumont et al., 2015) with atmospheric forcing derived from ERA-interim reanalysis (Dee et al., 2011). The biogeochemical model represents P, N, Fe and Si nutrients, living compartments (two phytoplankton, two zooplankton), and non-living compartments (semi-labile dissolved organic matter, small sinking particles, large sinking particles) (Aumont et al., 2015), and is included as the ocean biogeochemical component in CMIP6-class Earth System Models (e.g., Séférian et al., 2020). Though eddy-resolving simulations ( $1/12^\circ$ ) are considered preferable to investigate the mesoscale (e.g., Moreton et al., 2020), eddy-permitting configurations represent a compromise between spatial resolution to represent the eddies' spatial scales, and the need for sufficient computational resource to run multiyear simulations and to save results at daily frequency. Daily frequency outputs are required to resolve the temporal scale of mesoscale eddies as they propagate offshore from EBUS regions. Multidecadal simulations are also required to produce a sufficiently large sample to analyze concurrences of mesoscale eddies and extreme events which are, by definition, rare. We evaluate the skill of the eddy permitting FREEGLORYS2V4 model by comparison of model-derived eddy characteristics with eddy characteristics based on satellite altimetry estimates of sea level anomalies distributed by Copernicus Marine Environment Monitoring Service, formerly Archiving, Validation and Interpretation of Satellite Oceanographic data (AVISO) (Pujol & Mertz, 2020). We find that the physical model is able to adequately reproduce eddy lifetime and amplitude behaviors. As expected given that the eddy-permitting model resolves only the larger fraction of the mesoscale, there is a model bias in terms of radius and area (Figure S1 in Supporting Information S1). FREEBIORYS2V4 also adequately reproduces observed climatological OMZ extent at  $\approx 200\text{ m}$  depth when compared to World Ocean Atlas 2018 (WOA18; Garcia et al., 2019) (Figure S2 in Supporting Information S1). Atlantic  $[O_2]$  is lower than WOA observations in the coastal zone ( $\approx 25\text{ mmol m}^{-3}$ ) and higher in the open ocean ( $\approx 15\text{ mmol m}^{-3}$ ), indicating a bias in the offshore  $[O_2]$  gradient.



**Figure 1.** (a) Total counts of model-derived eddy centroids (CEs and ACEs) per year in  $1^\circ \times 1^\circ$  bins, (b) proportion of CEs relative to total eddy counts (blue indicates a higher proportion of CEs and red a higher proportion of ACEs), which exceed a 1 week lifetime, across the simulation period 1992–2018, in  $1^\circ \times 1^\circ$  bins. (c) Tracks of long-lived model-derived CEs (blue) and ACEs (red) that exceed a 4 week lifetime and originate in low oxygen waters ( $<200 \text{ mmol m}^{-3}$  depth averaged over  $\approx 50\text{--}200 \text{ m}$ ), across 1992–2018, representing a subset of the longer-lived eddies analyzed in Section 3. Initial detection points of eddies are indicated by white dots. In all panels, focus regions are marked by black boxes and background contours show climatological  $[\text{O}_2]$  at  $\approx 200 \text{ m}$  depth ( $\text{mmol m}^{-3}$ ), with red and yellow marking the  $45 \text{ mmol m}^{-3}$  and  $270 \text{ mmol m}^{-3}$  contours, respectively.

We produce an eddy- $[\text{O}_2]$  census over the full 1992–2018 model simulation period. We identify mesoscale eddies from their surface signature [Sea Surface Height (SSH)] by employing a tracking algorithm based on the Oliver et al. (2015) implementation of the Chelton, Schlax, et al. (2011) satellite observation eddy tracking algorithm. For further tracking algorithm details see Text S1 in Supporting Information S1. Tracking is performed in four focus regions adjacent to OMZs and around EBUS of the North-Eastern Atlantic (NEA), South-Eastern Atlantic (SEA), North-Eastern Pacific (NEP), and South-Eastern Pacific (SEP) (see Figure 1). The modeled large-scale pattern of eddy counts and proportion of cyclones is similar to equivalent observational estimates in the literature (Figures 1a and 1b; Chaigneau et al., 2009; Chelton, Schlax, et al., 2011). We constrain the data set to eddies which exceed a 1 week lifetime, to avoid the influence of spurious phenomena in the tracking algorithm, and to focus the analysis on eddies with sufficient longevity to influence subsurface biogeochemistry via transport

processes or modulation of export. Long-lived eddy pathways (Figure 1c) broadly coincide with zones of mean westward flow (Figure S3 in Supporting Information S1).

To isolate the  $[O_2]$  signal associated with tracked eddies, we extract the  $[O_2]$  field beneath the eddy centroid from surface to 300 m depth, the depth range over which previous observations indicate  $[O_2]$  to be substantially influenced by eddies (Schütte, Karstensen, et al., 2016). To explore the balance of physical and biogeochemical processes occurring within eddies, the  $[O_2]$  signal is decomposed into Apparent Oxygen Utilisation (AOU) and oxygen saturation ( $O_{2sat}$ ) components. Deviation of  $[O_2]$  from  $O_{2sat}$  provides an estimate of biological oxygen debt in the subsurface ocean due to biological consumption modulated by interior ocean transport and mixing, where

$$AOU = O_{2sat} - [O_2], \quad (1)$$

and  $O_{2sat}$  is calculated from model temperature and salinity fields and according to the solubility constants as presented in Weiss (1970). Anomalies for key variables, including  $[O_2]$ , AOU and  $O_{2sat}$ , are produced relative to the non-eddy background field. The non-eddy background is estimated by spatiotemporally filtering fields to remove the mesoscale; using a rolling monthly window and  $15^\circ$  longitude,  $5^\circ$  latitude spatial cut-off wavelengths, following Schütte, Brandt, et al. (2016). We present depth profiles of oxygen properties associated with tracked eddies in Section 3.

In Section 4, we assess low  $[O_2]$  extreme events. We define extreme events as instances of depth minimum  $[O_2]$  ( $[O_2]_{min}$ ) beneath the eddy centroid, across 0–300 m depth, that fall below the first percentile of climatological  $[O_2]_{min}$  for the same location over the full simulation period 1992–2018. Our local fixed percentile-based extremes method follows an approach developed for marine heatwaves (Frölicher et al., 2018) and is consistent with a recent assessment of ocean biogeochemical extremes (Gruber et al., 2021). We also define metrics to characterize low  $[O_2]$  extreme events in eddies. Similar to those employed by Oliver et al. (2019) for marine heatwaves, these are:

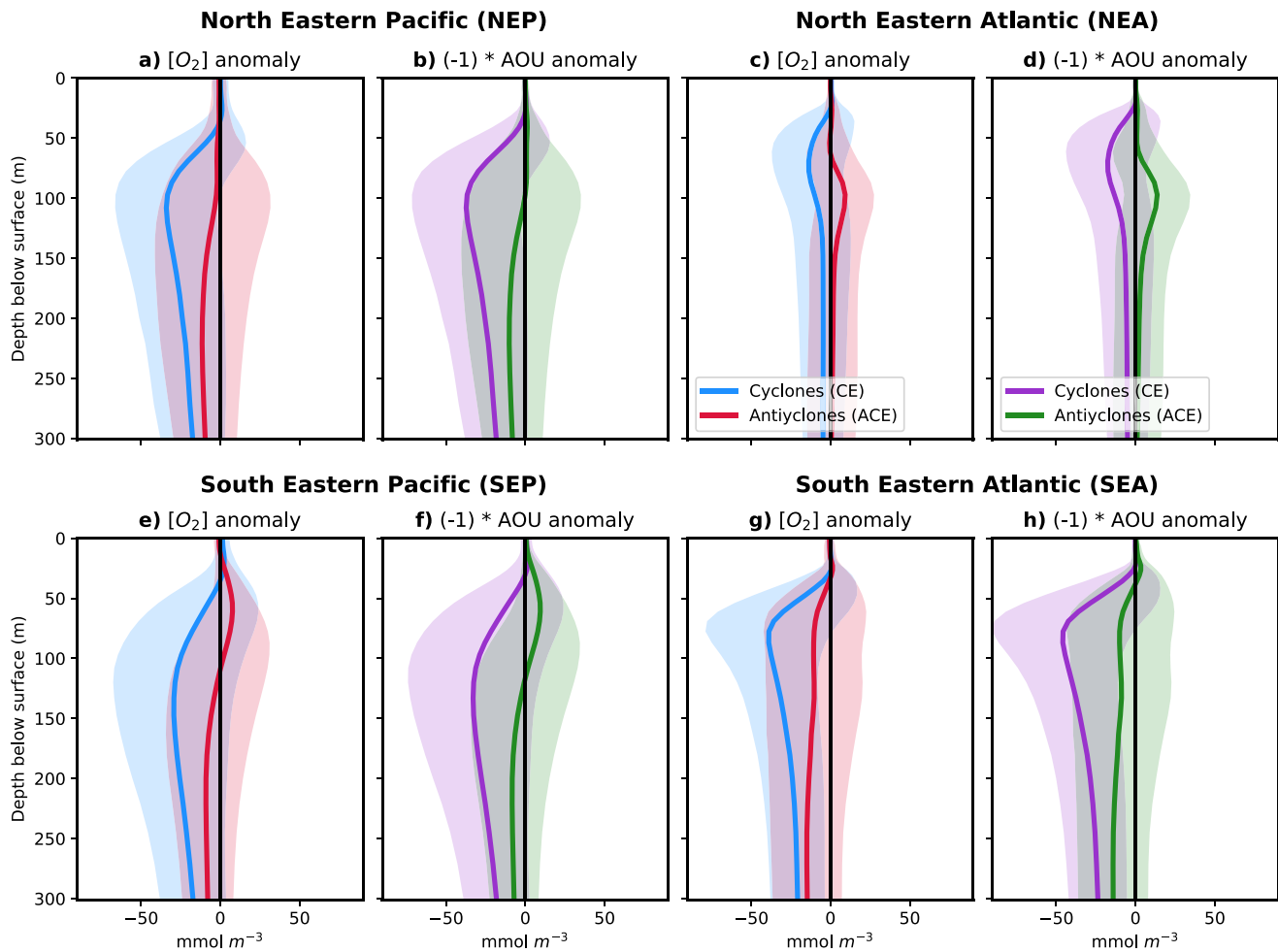
1. Frequency—the fraction of CE, ACE, and non-eddy conditions in a location which simultaneously experience low  $[O_2]$  extreme events, relative to the total number of CEs, ACEs, and non-eddies, respectively [%].
2. Intensity—the average  $[O_2]$  within CE, ACE, and non-eddy  $[O_2]$  extreme events, with the intensity of each event defined as the minimum across 0–300 m depth beneath the eddy centroid [ $mmol\ m^{-3}$ ].

In addition, we assess the contribution of eddies to low  $[O_2]$  extreme events by quantifying the number of contiguous eddy low  $[O_2]$  extreme events in each grid cell relative to the total number of contiguous low  $[O_2]$  extreme events. A contiguous event is defined as consecutive days of low  $[O_2]$  extreme conditions and taken to be eddy-induced if more than half of its duration coincides with an eddy. Eddies are assumed to impact an area corresponding approximately to the average eddy diameter, which is taken as five grid boxes.

In Section 4, we consider only low  $[O_2]$  extreme events identified outside of the natural OMZs, as  $[O_2]$  is permanently low inside OMZs. A value of  $45\ mmol\ m^{-3}$  is used to identify model OMZ locations (Karstensen et al., 2008), where any grid cell with a climatological  $[O_2]$  value below this threshold at any depth level is removed.

### 3. Eddy Oxygen Depth Profiles

To evaluate modeled profiles of eddies propagating from low  $[O_2]$  EBUS waters westward to the more oxygenated open ocean (e.g., Schütte, Karstensen, et al., 2016), we capture composite  $[O_2]$  anomaly profiles as a function of depth beneath the centroids of CEs and ACEs down to 300 m (Figure 2). The modulation of subsurface  $[O_2]$  by eddies is clear, with anomalies most pronounced beneath the mixed layer at  $\approx 50$ –200 m depth. CEs are shown to be more  $[O_2]$  depleted relative to the non-eddy background field across all regions. SEA CEs exhibit the largest negative  $[O_2]$  anomalies of up to  $\approx -80\ mmol\ m^{-3}$  at 80 m. Negative  $[O_2]$  anomalies associated with ACEs are consistently less intense than CEs, and ACE responses are statistically indistinguishable from zero. Furthermore, ACEs show positive mean  $[O_2]$  anomalies over part of the water column, though with considerable variability around the mean values.



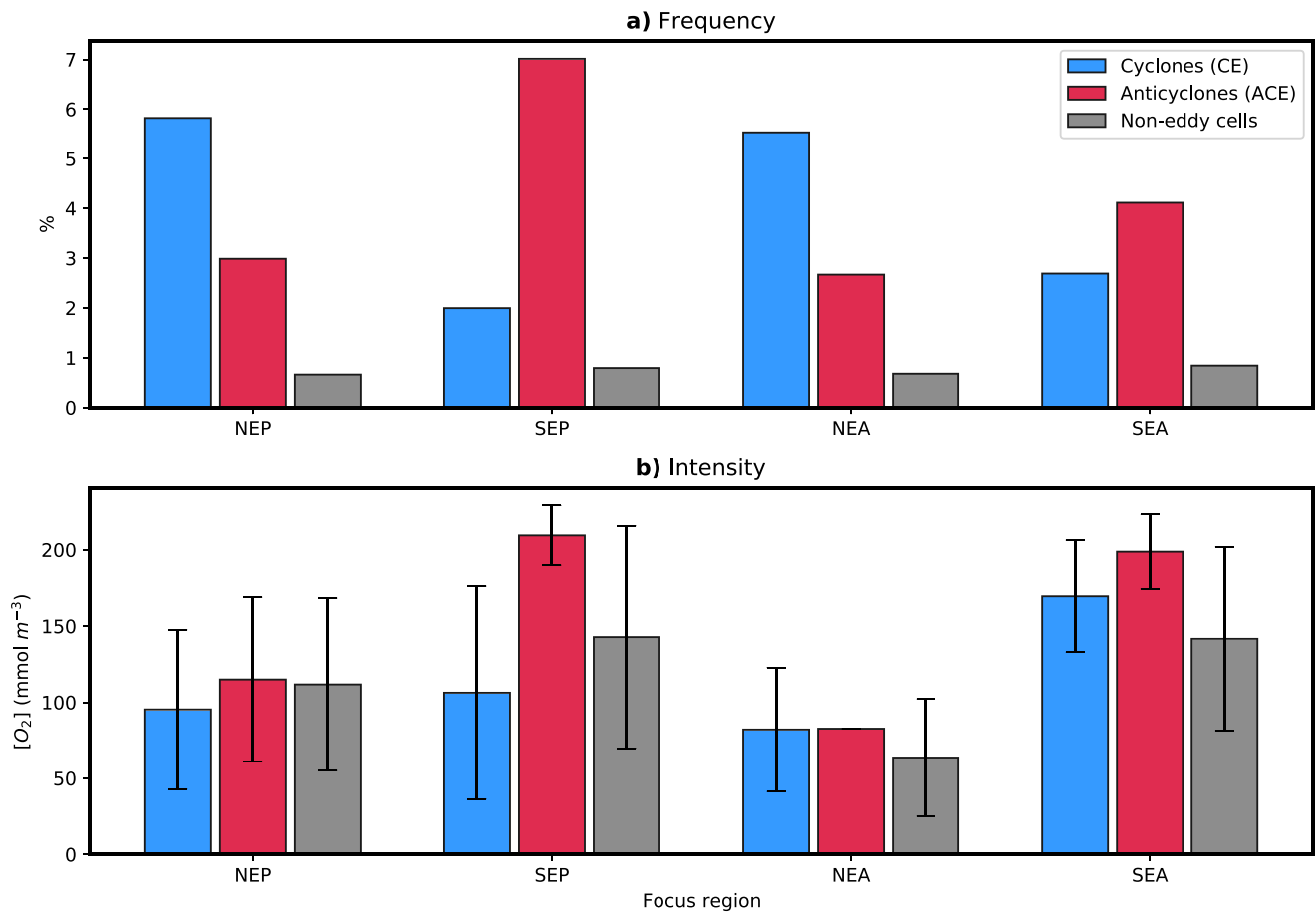
**Figure 2.** Composite  $[O_2]$  (blue for centroids (CEs), red for ACEs;  $\text{mmol m}^{-3}$ ) and  $(-1) \times \text{Apparent Oxygen Utilisation}$  (purple for CE, green for ACE;  $\text{mmol m}^{-3}$ ) anomaly depth profiles beneath centroids of CE and ACEs which originate in low  $[O_2]$  waters [ $<200 \text{ mmol m}^{-3}$  averaged over 50–200 m depth, as in Frenger et al. (2018)], tracked over the period 1992–2018. Anomalies expressed relative to a non-eddy background field. Solid lines are mean values of all eddies at each model depth. Shading represents  $\pm 1$  standard deviation.

We decompose the eddy composite  $[O_2]$  signal into AOU (Figure 2) and  $O_2\text{sat}$  (Figure S4 in Supporting Information S1) components and find that negative  $[O_2]$  anomalies are dominated by increased AOU, indicating that the  $[O_2]$  signal is mostly due to enhanced consumption in waters trapped within eddies. Enhanced  $O_2$  utilisation in CE via AOU is partially offset by simultaneous increases in  $O_2\text{sat}$  due to increased solubility of  $O_2$  in cold-core CE. For example, in the SEA, CE exhibit an AOU anomaly of  $\approx 45 \text{ mmol m}^{-3}$  at  $\approx 100 \text{ m}$  depth, counteracted by  $\approx 7 \text{ mmol m}^{-3}$  mean  $O_2\text{sat}$  anomaly at the same depth (net  $[O_2]$  anomaly  $\approx -38 \text{ mmol m}^{-3}$ ). Consistent with overall  $[O_2]$  anomalies, ACEs show either less intense AOU anomalies and/or anomalies of varying sign over depth, and there is lower confidence in the dominant sign of the anomaly. CE feature larger anomalies than ACEs which is consistent with CE of a more coastal origin tending to trap lower  $[O_2]$  waters.

#### 4. Eddy Oxygen Extremes

Considering the potential importance of eddies in driving extremely low  $[O_2]$  conditions in and around EBUS regions (e.g., Frenger et al., 2018; Schütte, Karstensen, et al., 2016), we present low  $[O_2]$  extremes associated with CE and ACE outside of the permanent OMZs (as defined in Section 2). Figure 3 shows the frequency and intensity of low  $[O_2]$  extreme event metrics associated with CE and ACE in each focus region. We find that the frequency of low  $[O_2]$  extreme events is consistently higher in eddies compared to non-eddy locations (Figure 3a). For instance, in the NEP and NEA, the frequency of CE low  $[O_2]$  extreme events is highest,

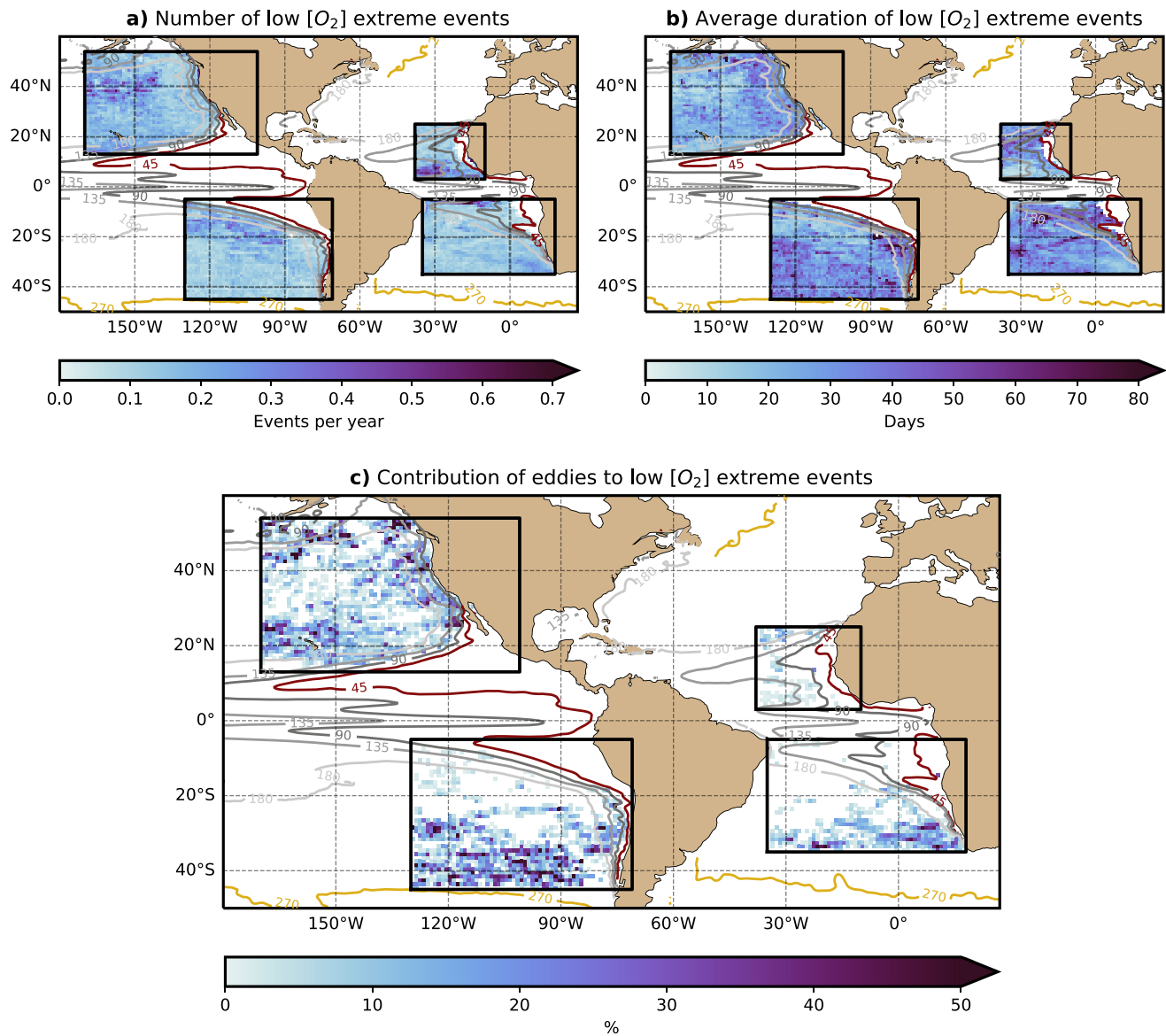




**Figure 3.** (a) Frequency (percentage of total CEs/ACEs/non-eddies which experience low [O<sub>2</sub>] extreme events) and (b) mean intensity (minimum [O<sub>2</sub>] concentration [mmol m<sup>-3</sup>] within CE/ACE/non-eddy low [O<sub>2</sub>] extreme events across 0–300 m depth beneath the eddy centroid) of low [O<sub>2</sub>] extreme events (<first percentile). CE (blue bars), ACE (red bars) and non-eddy low [O<sub>2</sub>] extreme events (gray bars) in focus regions, across the period 1992–2018. Error bars indicate variability in each regional metric ( $\pm 1$  standard deviation). Only eddies outside of permanent OMZs are included.

between 5% and 6% of total CEs in both regions, compared to  $\approx 3\%$  in ACEs, and  $<1\%$  in non-eddying locations. In the SEP and SEA, ACE low [O<sub>2</sub>] extreme event frequency exceeds that of CE events (e.g., in the SEP:  $\approx 7\%$  of ACEs,  $\approx 2\%$  of CEs, and  $<1\%$  of non-eddy locations). While conditions are more frequently extreme inside eddies relative to non-eddying locations, these events are not necessarily more intense, that is, lower in [O<sub>2</sub>] (Figure 3b). There is a tendency for SEP CE low [O<sub>2</sub>] extreme events to exhibit greater intensity (i.e., lowest minimum [O<sub>2</sub>]) beneath eddy centroids relative to ACEs ( $\approx 106$  mmol m<sup>-3</sup> for CE low [O<sub>2</sub>] extreme events, compared to  $\approx 209$  mmol m<sup>-3</sup> in ACEs), though with substantial variability around mean values. The high frequencies of low [O<sub>2</sub>] extreme events in ACEs in the SEP and SEA mentioned previously are associated with lower intensities compared to CE or non-eddy events.

Finally, we present the spatial pattern of the contribution of eddies to the total number of [O<sub>2</sub>] extreme events. On average, we find less than one contiguous low [O<sub>2</sub>] extreme event per year per  $1^\circ \times 1^\circ$  bin in the EBUS focus regions (Figure 4a), with an average duration of events of the order of weeks to months (Figure 4b). The percentage contribution of eddies to the total number of contiguous low [O<sub>2</sub>] extreme events (as defined in Section 2), across  $1^\circ \times 1^\circ$  bins in each focus region, is substantial. In some areas, eddies coincide with over 50% of contiguous low [O<sub>2</sub>] extreme events, particularly in Pacific EBUS regions and the subtropical gyres (Figure 4c). Meanwhile, the contribution of eddies to contiguous low [O<sub>2</sub>] extreme events in Atlantic regions is generally smaller, consistent with generally fewer occurrences (Figure 1a), though with higher contributions in the southernmost areas of the SEA.



**Figure 4.** (a) Number of contiguous low  $[O_2]$  extreme events (<first percentile) per year, (b) average duration of low  $[O_2]$  extreme events, (c) percentage contribution of eddies (CEs and ACEs) to contiguous low  $[O_2]$  extreme events in focus regions outside permanent Oxygen Minimum Zones (red contour), across the simulation period 1992–2018, in  $1^\circ \times 1^\circ$  bins. Contours show climatological  $[O_2]$  concentrations (mmol  $m^{-3}$ ), with red and yellow marking 45 mmol  $m^{-3}$  and 270 mmol  $m^{-3}$  contours, respectively.

## 5. Discussion and Conclusions

Mesoscale ocean eddies, especially cyclones (CEs), are shown to significantly influence subsurface dissolved oxygen concentration ( $[O_2]$ ) globally in and around Eastern Boundary Upwelling System (EBUS) regions. With the advantage of a daily spatiotemporally resolved model data set, we find strong negative  $[O_2]$  and positive Apparent Oxygen Utilisation (AOU) anomalies in CEs beneath the mixed layer (Figure 2). The low  $[O_2]$  and high AOU conditions may arise due to the trapping of source waters of eddies originating in Oxygen Minimum Zones (OMZs), or due to consumption of oxygen within eddies as they propagate offshore, or a combination of both (e.g., Frenger et al., 2018). Observational studies of eddy- $[O_2]$  modulation in the North-Eastern Atlantic (NEA) find isolation of water masses within eddy boundaries, in addition to elevated productivity, as likely drivers of low  $[O_2]$  conditions (1–10 mmol  $m^{-3}$ ) beneath the mixed layer in CEs and anticyclonic mode-water eddies (e.g., Karstensen et al., 2015; Schütte, Karstensen, et al., 2016). Global climate modes may also influence eddy

behavior and characteristics via changes to vertical mixing and the oxycline. For example, eddy  $O_2$  fluxes may be impacted by El Niño events, as noted in the South Eastern Pacific (SEP) by Espinoza-Morriberón et al. (2019).

Concerning  $O_2$  consumption within eddies, Gaube et al. (2014) show through altimetry observations that EBUS regions are generally dominated by areas of negative correlation between SSH and near-surface chlorophyll (CHL) anomaly, with surface depressing CEs related to positive CHL anomalies (an indicator of biological productivity). The Gaube et al. (2014) results are therefore consistent with the findings of our investigation where CEs are associated with positive AOU anomalies across EBUS regions (Figure 2). Elevated levels of production and export of organic material particularly in CEs is supported by a modeling study carried out for the Northern Canary Upwelling System (Lovecchio et al., 2022). Our findings are also consistent with Biogeochemical-Argo float observations of eddies in the North Pacific Subtropical Gyre, where positive AOU anomalies are observed in CEs, and attributed to enhanced remineralization of sinking particles (Xiu & Chai, 2020).

In this study, we quantify, for the first time, how oxygen conditions inside eddies contribute to low  $[O_2]$  extreme events. We provide evidence that extremely low  $[O_2]$  conditions occur more frequently within CEs and/or anti-cyclones (ACEs) relative to non-eddy conditions (Figure 3). Elzahaby and Schaeffer (2019) show the marked influence of warm-core ACEs on the incidence of marine heatwave events, in the eddy-rich Tasman Sea, with considerable imprints on temperature at depth. This draws parallels to our investigation, where we identify significant impacts of eddies on subsurface  $[O_2]$  extremes in eddy-rich focus regions.

We present strong evidence that eddies preconditioned in coastal waters contribute substantially (regionally >50%) to the number of low  $[O_2]$  extreme events outside of permanent OMZs, particularly across large areas of the Pacific (Figure 4). Considering the average impact area of the eddies, outside of permanent OMZs a location is impacted by eddies on average 12 times per year, translating to an exposure of only 3% of the temporal extent of the simulation period, and thus an order of magnitude lower than their contribution to local extreme events. This indicates that eddies disproportionately amplify extremely low  $[O_2]$  conditions. The processes responsible for the other >50% of low  $[O_2]$  events in the EBUS focus regions are beyond the scope of this study but may include waves, jets and filaments associated with the equatorial current system, or large-scale heaving of deeper ocean layers with low  $[O_2]$  waters. A similar analysis of extreme events carried out using a tenth percentile threshold for low  $[O_2]$  events (not shown), as opposed to the first percentile, yielded generally lower eddy percentage contributions in all focus regions, implying that eddies amplify more strongly the most extreme low  $[O_2]$  events.

There are several reasons why we expect our results to be a conservative estimate of the contribution of eddies to low  $[O_2]$  extreme events. First, as shown in the physical model validation (Figure S1 in Supporting Information S1), the eddy-permitting resolution ( $\approx 0.25^\circ$ ) fails to resolve eddies at the lower boundary of the mesoscale (below  $\approx 75$  km radius). Second, the methodology employed here, where eddies are identified by their SSH signature, means we do not consider subsurface eddies that lack a surface impact (e.g., Frenger et al., 2018), though subsurface eddies are expected to account for a distinctly lower fraction of overall eddy counts (Schütte, Karstensen, et al., 2016). Third, the eddy tracking algorithm used here (based on Chelton, Schlax, et al., 2011) is widely used in other investigations, however it does appear to underestimate eddy counts, particularly low-amplitude eddies (Faghmous et al., 2015). The eddy count underestimation is also noted in comparison to other methods such as Mason et al. (2014) (not shown). With these considerations in mind, it may be that we underestimate the contribution of eddies to the occurrence of low  $[O_2]$  extremes.

Localized intensely low  $[O_2]$  conditions in eddies impact marine life and biogeochemistry (Christiansen et al., 2018; Grundle et al., 2017; Hauss et al., 2016). While organisms may tolerate oxygen depleted conditions in areas with consistently low  $[O_2]$ , even in permanent OMZ regions zooplankton abundance has been shown to be highly sensitive to small ( $\approx 3 \mu M$ ) changes in oxygen at submesoscales (Wishner et al., 2018). Here, we show that, outside of the OMZs, eddies can contribute substantially to periodic low  $[O_2]$  conditions relative to local variability. However, relative thresholds, as commonly applied in extreme event detection (e.g., Frölicher et al., 2018), will be most consequential for marine life where critical physiological thresholds are also crossed (e.g., Sampaio et al., 2021). Further, as noted by Gruber et al. (2021), the exposure timescales for extreme biogeochemical conditions associated with eddies will vary depending on whether organisms (1) are retained within an eddy's structure [for example, pelagic plankton (Condie & Condie, 2016)] or (2) encounter an eddy only at a fixed location (e.g., benthic and sessile communities). Exposure timescales for current-following (or Lagrangian) extreme events would correspond with eddy lifetimes (here, up to months), whereas a fixed-in-space (or Eulerian)



extreme would expose ecosystems only during the period of extreme conditions at a given location as an eddy is passing by ( $\approx$ days to weeks). Accordingly, the cumulative intensity of a low  $[O_2]$  extreme event is higher if lower trophic level ecosystems are transported within an eddy. Ecosystem responses to marine extreme events may be different for acute versus chronic exposure to stressors, with high cumulative intensity marine heatwaves having been shown experimentally to increase Southern Ocean diatom mortality (Samuels et al., 2021). By contrast, high cumulative intensity marine low  $[O_2]$  extreme events associated with offshore-moving eddies may serve as niches with enhanced survival and reproduction of certain low- $[O_2]$ -tolerant zooplankton species (Christiansen et al., 2018; Hauss et al., 2016). Future lines of research might involve the investigation of the influence of eddies on absolute  $[O_2]$  concentration thresholds known to be important for marine life and biogeochemistry (i.e., hypoxic and suboxic thresholds).

## Data Availability Statement

FREEBIORYS2V4 ocean biogeochemistry hindcast data is available at the Copernicus Marine Environment Monitoring Service (CMEMS) (<https://doi.org/10.48670/moi-00019>), and the accompanying FREEGLORYS2V4 ocean physical hindcast data was made available from Mercator Ocean on request. The satellite observational Sea Surface Height product is available at CMEMS (<https://doi.org/10.48670/moi-00148>). The WOA18 observed oxygen data is available at NOAA National Centers for Environmental Information (<https://www.ncei.noaa.gov/data/oceans/woa/WOA18/DATA/oxygen/>). Eddy tracking code by Eric Oliver is described in Oliver et al. (2015). Additional Supporting Information available here: <https://zenodo.org/record/6826997#.Ys7JN3bMKz7>.

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