



Biological imprint dominates global mesoscale air-sea flux anomalies of carbon dioxide and oxygen

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Abstract.

Ocean mesoscale phenomena ("mesoscale eddies") are fundamental components in mediating air-sea heat and momentum fluxes through anomalies of sea surface temperatures and currents. Yet, their impacts on air-sea gas fluxes, such as carbon dioxide, CO₂, and oxygen, O₂, through changing solubility and biological cycling, remain underexplored. This study aims to diagnose global patterns of ocean mesoscale CO₂ and O₂ flux anomalies and their drivers. To this end, we use results from an ocean eddy-rich 0.1° GFDL climate model (CM2.6), namely a preindustrial control simulation and an idealized climate change simulation with a linear increase in atmospheric CO₂ until CO₂ doubling is reached. Mesoscale air-sea CO₂ and O₂ flux anomalies are isolated from large-scale signals by applying spatial filtering to monthly averaged model results.

We find that globally mesoscale variability explains approximately 6-7% of the variance in CO₂ and O₂ fluxes, with regional contributions exceeding 30%. We present an analytical framework to attribute air-sea CO₂ and O₂ flux anomalies to thermally-driven solubility effects versus biological imprints, based on the sign of the correlation between CO₂ and O₂ flux anomalies.

We find a clear regional imprint in the mechanisms by which mesoscale eddies influence CO₂ and O₂ fluxes. In subtropical and mid-latitude regions, CO₂ and O₂ flux anomalies are predominantly of the same sign, indicating that mesoscale eddies impact gas fluxes mainly through solubility changes. In tropical and high-latitude regions the effect of mesoscale eddies on CO₂ and O₂ flux is mostly of biological origin, as indicated by an opposite sign of CO₂ and O₂ flux anomalies, either caused by changes in biological productivity or upwelling of a respiration signal from the ocean interior. Although the regions with a biological imprint globally cover an area comparable to solubility-driven regions globally, the associated flux anomalies are larger in magnitude, causing the biological drivers to dominate the globally integrated absolute mesoscale anomalies, representing approximately two-thirds of the total signal, and account for 7-9% to global variance (compared to 5-7% for solubility-driven regions). Under CO₂ doubling, solubility-driven regions expand and fluxes intensify, increasing their relative contribution, though the large-scale patterns of drivers remain the same. The biological contribution remains dominant for O₂, while the relative importance of solubility-driven processes increases for both gases under warming. Our results highlight the spatial organization of mesoscale-driven air-sea gas fluxes into distinct regimes and demonstrate that, on a global scale, a biological imprint dominates the magnitude of mesoscale CO₂ and O₂ flux anomalies.



1 Introduction

Mesoscale ocean variability is increasingly recognized as an important component of the climate system, yet its role in regulating air-sea gas exchange remains poorly understood, in particular at global scale. The ocean has absorbed 27% of anthropogenic carbon dioxide (CO₂) emissions since 1850 (Friedlingstein et al., 2025), thereby mitigating atmospheric warming while driving ocean acidification (Orr et al., 2005). At the same time, ocean warming has reduced oxygen (O₂) solubility and strengthened upper-ocean stratification, limiting ventilation and contributing to the widespread decline of dissolved O₂ observed over the recent decades (Matear et al., 2000; Bopp et al., 2002; Keeling et al., 2010; Helm et al., 2011; Oschlies et al., 2018; Schmidt et al., 2017). Understanding how mesoscale ocean variability influences the physical and biological processes governing air-sea CO₂ and O₂ exchange is therefore essential for improving projections of the future marine carbon cycle and ocean biogeochemistry.

Air-sea fluxes of CO₂ and O₂ are determined by the air-sea differences in their partial pressures, which is continuously modified by interacting physical and biological processes within the surface ocean (Gu et al., 2023; Mongwe et al., 2018). Thermal changes alter gas solubility and, for CO₂, also modify seawater carbonate chemistry. Biological production consumes CO₂ while releasing O₂, whereas respiration has the opposite effect. Ocean circulation, vertical advection and mixing, further modify surface gas concentrations by transporting carbon, oxygen, and nutrients between the surface and ocean interior (e.g., Takahashi et al., 2002; Manizza et al., 2012; Rodgers et al., 2023; Oschlies et al., 2018).

Because these mechanisms leave distinct and often opposing signatures in CO₂ and O₂, the joint variability of both gases provides valuable information on the dominant processes controlling air-sea gas exchange. This complementary behavior has previously been exploited to separate physical and biological drivers of seasonal and interannual air-sea gas flux variability. Using model simulations, Resplandy et al. (2015) used a positive correlation/unidirectional behavior of seasonal and interannual variability of air-sea fluxes of CO₂ and O₂ to argue for the dominance of solubility-driven processes in driving the air-sea fluxes of gases in a region, reasoning that the solubility-driver affects either gas in the same direction. In contrast, if the correlation shows negative/counter-directional behavior, additional factors must be strongly influencing the system and cause a flip of the sign of the correlation. In particular, a systematic anticorrelation indicates a biological imprint on CO₂ and O₂ fluxes, as biological buildup of organic material coincides with an uptake of CO₂ and production of O₂, and vice versa for the opposing process of respiration of organic material. The coupled behavior of both gases therefore provides a process-based diagnostic that goes beyond analyzing either gas individually. While this concept has been successfully applied to large-scale variability, its applicability to the ocean mesoscale has not yet been explored systematically.

Mesoscale eddies and fronts are ubiquitous features of the global ocean circulation, containing most of the ocean's kinetic energy (Chelton et al., 2011b; Ferrari and Wunsch, 2009). By redistributing heat, nutrients, dissolved tracers, and momentum, they modify sea surface temperature, mixed-layer depth, vertical nutrient supply, biological productivity, and upper-ocean ventilation (e.g., Chelton et al., 2011a; Marshall and Speer, 2012; McGillicuddy Jr, 2016). Consequently, mesoscale variability generates pronounced anomalies in air-sea gas exchange across a wide range of spatial and temporal scales. Numerous observational studies have reported substantial CO₂ anomalies associated with individual eddies in regions such as the Southern



60 Ocean, the North Atlantic, or the eastern boundary upwelling systems (Pezzi et al., 2021; Ford et al., 2023; Jones et al., 2015). Likewise, eddies have been shown to influence oxygen distributions and ventilation, particularly in oxygen minimum zones (Czeschel et al., 2018; Schütte et al., 2026). The majority of studies to date have focused on larger-scale patterns of air-sea CO₂ and O₂ fluxes and their drivers, their climatological conditions and seasonal to interannual variability, utilizing in-situ cruise or Argo float data, satellite observations, or climate models (Claustre et al., 2020; Johnson et al., 2022; Friedlingstein et al., 2025; Ito et al., 2017; Hollitzer et al., 2024). In contrast, the role of smaller scale, transient ocean phenomena — such as ocean mesoscale eddies — in modulating air-sea gas exchange has only recently gained momentum (Guo and Timmermans, 2024; Li et al., 2025; Keppler et al., 2024) thanks to increasing amount of high-resolution observational platforms and mesoscale-rich ocean models. Despite these advances, a coherent process-based understanding of mesoscale air-sea gas exchange remains lacking. Existing studies consistently demonstrate that mesoscale eddies can generate large local anomalies in CO₂ fluxes, yet they also reveal substantial regional differences in both the magnitude and even the sign of these anomalies. This diversity suggests that different mechanisms dominate in different oceanic regimes, but these mechanisms have rarely been investigated explicitly. In particular, it remains unknown to what extent mesoscale air-sea gas flux anomalies are controlled by thermally driven solubility changes or by biologically mediated processes, how these drivers are distributed globally, and whether their relative importance changes under future climate warming. Addressing these questions requires global simulations that explicitly resolve ocean mesoscale variability coupled to biogeochemical processes. Eddy-rich climate models therefore provide a unique framework for investigating the mechanism linking mesoscale circulation to air-sea gas exchange.

Here, we investigate the global imprint of mesoscale ocean variability on air-sea CO₂ and O₂ fluxes using eddy-rich simulations of the Geophysical Fluid Dynamics Laboratory Climate Model version 2.6 (GFDL Climate Model 2.6) (Delworth et al., 2012; Griffies et al., 2015; Galbraith et al., 2015). Mesoscale anomalies are isolated through spatial filtering of monthly model output. Building upon the conceptual framework of (Resplandy et al., 2015), we use the joint behavior of CO₂ and O₂ flux anomalies to distinguish between thermally driven solubility effects and biologically mediated processes. This framework enables us to identify the dominant mechanisms controlling mesoscale gas exchange across the global ocean, quantify their contributions to regional and global variability, and assess how these mechanisms respond in an idealized CO₂ doubling experiment. To address this knowledge gap, the study is guided by three research questions:

85 1. How much of the variability in global air-sea CO₂ and O₂ fluxes is associated with ocean mesoscale variability? 2. Which mechanism dominates mesoscale gas flux anomalies, and how do these vary geographically? 3. How do these mesoscale drivers change under climate warming?

The manuscript is organized as follows. Section 2 describes the model simulations, the spatial filtering approach, and the framework used to diagnose mesoscale air-sea gas flux drivers. Section 3 presents the global distribution and magnitude of mesoscale CO₂ and O₂ flux anomalies, their variance contributions, and the resulting process-based classification of ocean regions. Section 4 discusses the dominant physical and biological mechanisms underlying the identified regimes and their implications for observations, Earth system models, and future climate change. The main conclusions are summarized in Section 5.



2 Methods

2.1 Climate model and experiments

We used for our analysis output from the Geophysical Fluid Dynamics Laboratory Climate Model version 2.6 (GFDL CM2.6). The ocean component of the climate model is the version five of the Modular Ocean Model (MOM5; Griffies et al., 2015) and with a nominal grid spacing of 0.1° is considered to be "mesoscale eddy-rich". It resolves ocean mesoscale variability in low and middle latitudes and partially resolving it in high latitudes and thus does not switch on mesoscale eddy advection or mixing parameterizations (Griffies and Hallberg, 2000; Griffies et al., 2015; Delworth et al., 2012). The model is run with volume-conserving Boussinesq kinematics and uses a Mercator grid that transitions to a bipolar Arctic projection north of 65°N . (Murray, 1996). The ocean model is run with a z^* geopotential vertical coordinate and 50 vertical levels, with approximately 10 m thickness of upper ocean layers to about 210 m at depth. The model uses a piecewise parabolic method for the advection scheme (Delworth et al., 2012), the nonlocal K-profile parameterization for vertical mixing (Large et al., 1994), and the submesoscale mixed layer eddy parameterization of Fox-Kemper et al. (2011). While the atmospheric model (GFDL Atmospheric Model 2.1, AM2.1), with approximately 50 km nominal resolution, is on a coarser spatial grid than the ocean model (GFDL Global Atmospheric Model Development Team et al., 2004; Delworth et al., 2012), air-sea fluxes are calculated on an exchange grid. The exchange grid is constructed by overlaying two grids, such that each exchange-grid cell corresponds uniquely to one parent cell in each of the original grids (Balaji et al., 2006). For air-sea fluxes, this involves atmospheric and ocean grid points and thus resolves air-sea flux variability forced by the ocean mesoscale. The model has been used extensively in previous studies to assess impacts of mesoscale eddies (e.g. Dufour et al., 2015; Pacheco et al., 2026), and it simulates large-scale fields of air-sea fluxes of O_2 and CO_2 consistent with observations (Fig. A1).

Ocean carbon and oxygen cycles are simulated in CM2.6 with a simplified version of the marine biogeochemical model component BLING (Biogeochemistry and Light Iron Nutrients and Gas), referred to as miniBLING (Galbraith et al., 2015). MiniBLING was developed to minimize the - as of today - added cost to these already computationally expensive ocean eddy-rich climate models, while keeping essential marine biogeochemical cycles relevant for large-scale carbon and oxygen dynamics. Despite its simplified structure with only three prognostic tracers (oxygen, O_2 , dissolved inorganic carbon, DIC, and a generic macronutrient), miniBLING has been shown to realistically reproduce the mean state and variability of air-sea CO_2 fluxes and large-scale biogeochemical distributions (e.g. Galbraith et al., 2015; Frenger et al., 2018; Yamamoto et al., 2018). miniBLING uses a simplified set of three prognostic tracers - dissolved inorganic carbon (DIC), oxygen (O_2), and Phosphate (PO_4). The number of prognostic tracers was minimized in miniBLING besides others by diagnosing alkalinity from a climatological alkalinity-salinity relationship, and replacing a dynamic iron cycle with a monthly iron climatology derived from a coarser resolution BLING simulation (see Galbraith et al., 2015, for details with respect to miniBLING and its simplifications). As part of CO_2 and O_2 cycling, two types of remineralization are distinguished: a rapid recycling pathway that is related to microbial loop dynamics (Oschlies and Schartau, 2005), and a slower rate that represents hydrolysis and mineralization of organic matter in sinking particles. We derive net community productivity, referred to as biological productivity in the following,



as the difference between phytoplankton uptake and both types of remineralization. Note that the transport of organic matter is not explicitly simulated in miniBLING.

We use results from two different CO₂-forcing experiments carried out with CM2.6, a preindustrial and a climate change simulation. The experiments were carried out by the Geophysical Fluid Dynamics Laboratory (GFDL) and have been evaluated in previous studies, serving various scientific questions, including about ocean heat, carbon or oxygen (e.g., Dufour et al., 2015; Frenger et al., 2018). The model simulations span 190 model years, where miniBLING was coupled to the ocean circulation component after an initial spin-up of the circulation of 48 years. Thereafter, the model is run in fully coupled physical–biogeochemical mode. The preindustrial experiment has atmospheric CO₂ concentrations of 285 ppm, hereafter referred to as "Control". The idealized climate change experiment branches off from Control in model year 120 and increases the CO₂ concentration by 1% per year until CO₂ doubling after 70 years, following standard protocol (Manabe and Stouffer, 1993). For both simulations, we analyse monthly mean output from the last decade of the simulations, that is, model years 181 – 190. The simulated large-scale background air-sea CO₂ and O₂ flux patterns are consistent with previous model assessments and observation-based estimates (Fig. A1), suggesting that the mesoscale anomalies are superimposed on a realistic large-scale state (Fay et al., 2021; Jin et al., 2025).

2.2 Attribution of air-sea CO₂ and O₂ flux anomalies to ocean mesoscale eddies

We apply a spatial filtering approach in order to isolate the imprint of mesoscale eddies on air-sea fluxes of CO₂ and O₂, assessing the imprint of mesoscale eddies as the difference between the original air-sea flux fields of CO₂ and O₂ and background flux fields (exemplarily see Fig. 1c). The background fields we obtain by spatially low-pass filtering monthly flux fields. We apply a median boxfilter (generic_filter, a function of the scipy.ndimage Python package; Virtanen et al., 2020) on the original monthly fields, similar to the approaches used in Wanninkhof et al. (2011); Moreton et al. (2021); Lu et al. (2022). Land points and sea-ice covered regions were set to missing values prior to the convolution and thus not considered for the computation of the median. Presence of sea-ice was defined as any sea-ice fraction larger than zero. The anomalies we then compute as the difference between the total and background fields contain imprints of coherent mesoscale eddies but also of other mesoscale phenomena, such as filaments. For the sake of simplicity, we here collectively refer to the imprint as "mesoscale eddies", noting that we mean mesoscale phenomena in general. Further, we distinguish in places anticyclonic versus cyclonic mesoscale eddies as commonly done in ocean mesoscale eddy research, based on positive versus negative sea surface height (SSH) anomalies.

We carry out correlation analyses as part of our analytical framework (see Section 2.3) to attribute drivers of mesoscale air-sea fluxes of CO₂ and O₂. We thereby rely on correlations between mesoscale CO₂ and O₂ flux anomalies (exemplarily see Fig. 1b) as well as correlations with anomalies of biological productivity.

As a model sanity check, we compare established expectations of physical air-sea interactions at the ocean mesoscale (Seo et al., 2023) with the modeled response. As expected, the model simulates ocean heat loss (i.e. cooling) associated with warm mesoscale sea surface temperature (SST) anomalies (Fig. B1), and ocean heat gain (i.e. warming) over cold anomalies. That is, the ocean SST anomalies are driving the air-sea heat flux exchange at the ocean mesoscale, with warm SST anomalies leading to an increased sensible and latent heat flux from the ocean into the atmosphere (note that the sign definition is such



that a positive heat flux is directed into the ocean), and vice versa for cold SST anomalies. The Pearson correlation between the mesoscale anomalies of SST and air-sea heat fluxes is consistently negative (Fig. B1), with global mean values of -0.82 and -0.80, respectively, thus largely in agreement with Byrne et al. (2015); Seo et al. (2023). Further, the spatial patterns of the correlations agree well with the ones found in the observational estimates, with highest correlations in the subtropics and somewhat lower correlations in tropical and mid to high latitudes (Fig. B1). The model also simulates subsequent effects on near-surface winds as apparent from a positive correlation of SST and wind stress (Fig. B2) (Small et al., 2008). The model thus captures physical air-sea interactions associated with ocean mesoscale eddies.

We test the robustness of our results against two methodological aspects: the size of the spatial filter and against changing the temporal resolution of the data. To separate mesoscale from large-scale features, we conduct a series of preliminary tests with various filter sizes, ultimately choosing a $3^\circ \times 3^\circ$ filter, which is smaller than typical filters such as those used in e.g. Wanninkhof et al. (2011), while being slightly coarser than the 2° threshold used by Guo and Timmermans (2024). The choice of a $3^\circ \times 3^\circ$ filter reflects a compromise to minimize the inclusion of boundary currents and larger-scale atmospheric-driven variability in the mesoscale imprint (by using a filter as small as possible; see Fig. B3 for the effect of increasing the filter size to $5^\circ \times 5^\circ$), while at the same time avoiding the inclusion of parts of the mesoscale imprint in the background field and thus muting the mesoscale signal (by using a filter as large as possible). As such the chosen filter size is not intended to represent a formal spatial correlation length but rather a pragmatic methodological scale to focus our air-sea flux analysis to variability closely associated with coherent mesoscale eddies and filaments (see also Fig. 1c-e). We note that using a smaller spatial filter tends to reduce the magnitude of the diagnosed mesoscale anomalies compared with larger filters, as smaller-scale features are progressively smoothed out. We also tested the robustness of our results to the temporal resolution of the original flux fields, namely monthly versus daily fields. Similarly to the smaller filter size we chose, the choice of a coarser temporal resolution (monthly) reduces the magnitude of the mesoscale induced air-sea flux anomalies (see Fig. B4). However, monthly fields were selected for the main analysis because a larger number of model years was available, allowing for a more robust statistical characterization of mesoscale variability. In summary, for the magnitude of the air-sea flux anomalies we expect to err low, given our choices of temporal frequency and filter size, and thus consider our results to be conservative estimates of air-sea flux anomalies of CO_2 and O_2 . Note that our choices do not affect the correlation analysis and related inferences with respect to driving mechanisms.

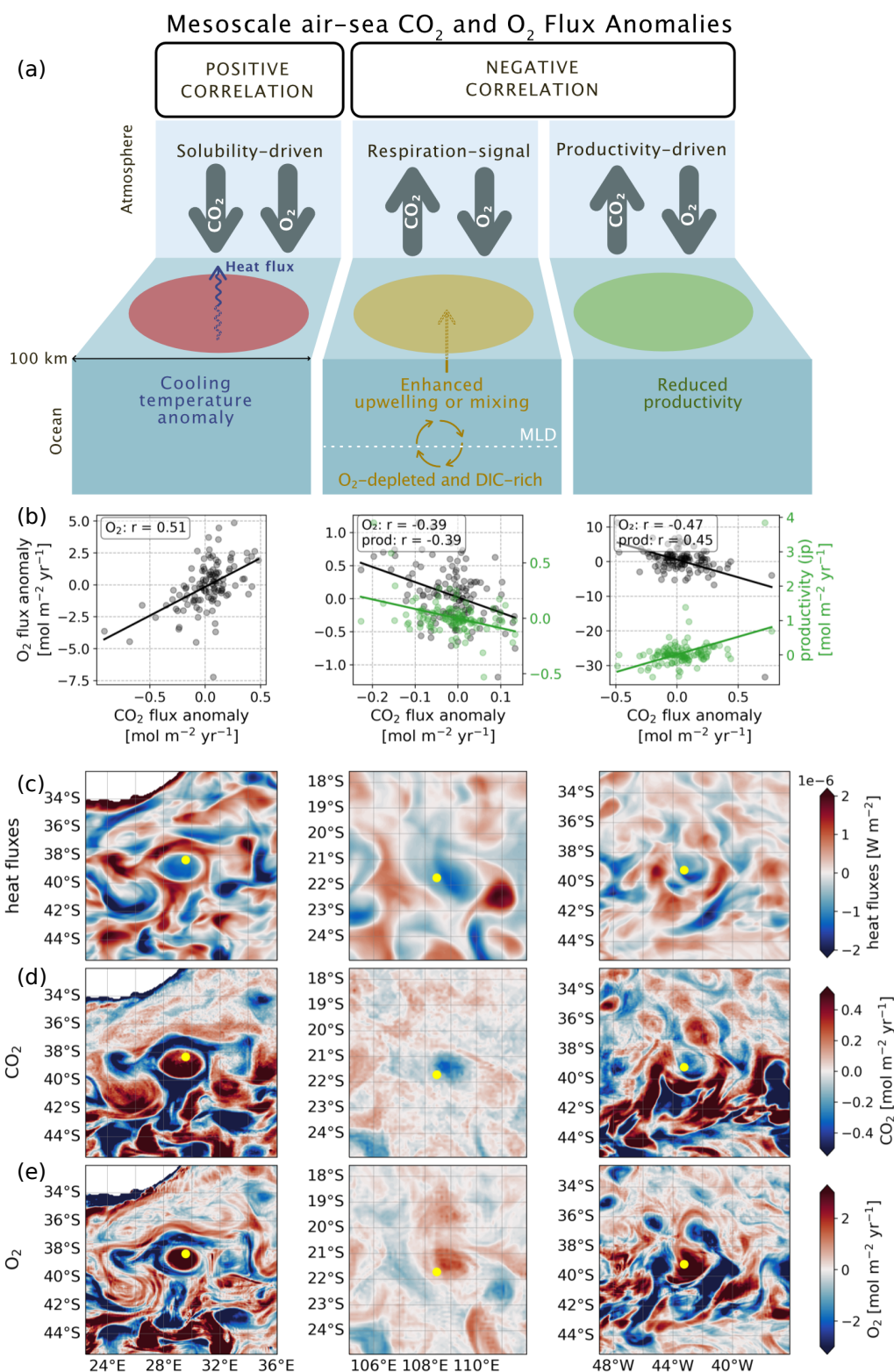




Figure 1. Schematic representation of the analytical framework we use to attribute drivers to mesoscale anomalies of air-sea fluxes of CO₂ and O₂ (see Section 2.3; adapted from Resplandy et al. (2015)). Depending on the sign of the correlation of mesoscale CO₂ and O₂ flux anomalies, the framework distinguishes between (a) "Solubility-driven", thermal effects (positive correlation of the two gases) due to sea surface temperature anomalies and a non-thermal biological imprint (negative correlation), associated with biological productivity or respiration; here exemplified for a positive (warm) sea surface temperature (SST) anomaly (left), a positive upward mixing or upwelling anomaly (middle), or a reduced biological productivity anomaly (right). "Heat flux" indicates sensible and latent heat fluxes, MLD mixed layer depth, and DIC dissolved inorganic carbon, and the gray wide arrows indicate the direction of the air-sea gas flux anomalies of CO₂ versus O₂ fluxes (outgassing versus ingassing). (b) scatter plots of CO₂ versus O₂ (black, corresponding to the left y-axes), and CO₂ versus biological productivity (green, corresponding to the right y-axes in the middle and right) of a single model grid box, marked with a yellow dot in panels (c-e). (c-e) sample snapshots of mesoscale eddy anomalies of air-sea heat (c), CO₂ (d), and O₂ fluxes (e). Note that positive fluxes are directed into the ocean (ocean warming, ingassing).

2.3 Analytical framework to attribute drivers to mesoscale CO₂ and O₂ flux anomalies

As outlined in the introduction, ocean mesoscale eddies can drive ingassing or outgassing of CO₂ and O₂ via different mechanisms (Fig. 1a). Inspired by Resplandy et al. (2015) who analyzed seasonal and interannual variability of air-sea fluxes of CO₂ and O₂, we make use of the fact that combining CO₂ and O₂ flux anomalies provides more information than considering gas flux anomalies individually, and thus a powerful way to attribute first-order drivers of flux anomalies.

In a first step, we assess the sign of the correlation of CO₂ and O₂ flux anomalies. If the correlation is positive (Fig. 1b, left panel), the solubility-driven effect is assumed to be dominant (Fig. 1a, left column). We use the canonical anticyclone as illustration, though these anomalies can occur with either polarity. For instance, anticyclonic eddies are typically associated with a positive SST anomaly (Fig. 1c, left column). Thus, they come with an initially reduced solubility of gases, including of CO₂ and O₂. The initially low solubility then entails a subsequent increase of solubility over the eddies' lifetimes as the initially warm SSTs are cooling down, that drives ingassing of both CO₂ and O₂, and increasing surface ocean gas concentrations. Temperature in a secondary effect for CO₂ also influences the dissociation of the dissolved inorganic carbon species in sea water (Wanninkhof et al., 2022). Though since this effect solely applies to CO₂ and it is solubility that similarly affects both CO₂ and O₂ and drives a positive correlation between the two gases, we refer to the temperature effect as "solubility-driven" in the following.

If the sign of the correlation of mesoscale air-sea CO₂ and O₂ flux anomalies is not positive but negative, we conclude the flux imprint stems from biological cycling of the gases in the ocean (Fig. 1a, middle and right columns). For instance, anticyclonic eddies canonically are thought to reduce biological production (Fig. 1a, right column), that is, reduced photosynthesis, through less vertical transport of nutrients from below. In the process of photosynthesis of organic matter production CO₂ is consumed and O₂ released, thus reducing sea water CO₂ and increasing O₂ concentrations, with potential subsequent uptake of CO₂ from the atmosphere and release of O₂. In an anticyclone with reduced biological productivity, this accordingly leads to release of CO₂ and uptake of O₂. At the same time, the enhanced winds over an anticyclone can "stir up", next to nutrients, also DIC-rich and oxygen-depleted waters (Fig. 1a, middle column). High DIC (and thus high CO₂ concentrations) and low O₂



concentrations are a signal of interior ocean waters stemming from accumulated remineralization of organic matter in the ocean interior, the reverse reaction of photosynthesis that frees CO₂ and nutrients but consumes O₂. If those waters reach the air-sea interface, they favor anomalous outgassing of CO₂ and ingassing of O₂, despite a potentially increased biological production. The same signal can also be observed in cyclones through an upward doming of isopycnals. We refer to this imprint
215 as the "respiration-signal".

Expanding on Resplandy et al. (2015), we further separate the biological imprint into the "productivity-driven" effect versus the "respiration" signal. Because the correlation between CO₂ and O₂ flux anomalies alone does not distinguish between these two drivers, we additionally use upper-ocean biological productivity (net community productivity; see Section 2.1; integrated over the upper 100 m) as an indicator (Fig. 1a, right column). We correlate the mesoscale air-sea CO₂ flux not only with O₂ but
220 also with biological productivity (Fig. 1b, middle and right panels). Depending on whether the correlation with the biological production anomaly is consistent - or inconsistent - with the gas flux anomalies expected from the productivity anomaly, we attribute the air-sea fluxes of CO₂ and O₂ to "productivity-driven" or to a "respiration-signal". For instance: if we find an anticyclonic eddy with outgassing of CO₂ and ingassing of O₂ together with an enhanced productivity anomaly we attribute the anticorrelation of the two gases to a modification of upwelling or upward mixing of interior ocean waters (Fig. 1c, middle
225 column). In contrast, if we find an outgassing of CO₂ and an ingassing of O₂ in combination with reduced productivity, we attribute the signal to biological productivity (Fig. 1c, right column).

Note that while the canonical notion is that anticyclonic eddies feature warm sea surface temperature anomalies, enhanced wind-mixing, and reduced productivity as depicted in our schematic, such anomalies can be of either sign for both cyclonic and anticyclonic eddies. The warm anticyclonic eddy in our schematic represents an illustrative example. Yet, due to, among others,
230 eddy-wind interactions (Dong et al., 2022; McGillicuddy et al., 2007) an anticyclonic eddy can show enhanced biological productivity. Also anticyclonic eddies may have cold SST anomalies, a common feature of subsurface intensified "mode water eddies" (Ni et al., 2021). For our framework it is not relevant if a cyclonic or anticyclonic eddy is causing a change of biological productivity or the upward transfer of a respired signal. Our goal here is to attribute the mesoscale air-sea fluxes to mesoscale ocean surface properties forced by mesoscale eddies, not to assess how eddies create those (near) surface anomalies of SST,
235 biological productivity, or upwelling and upward mixing.

We note further that all drivers due to mesoscale eddies impacting surface ocean properties may act simultaneously and can superimpose, thereby weakening or strengthening the observed correlations. In particular we expect the solubility-driver to be active most of the times, as the majority of mesoscale eddies carries a SST anomaly. Effects of mesoscale eddies on local winds (Seo et al., 2023) are implicitly accounted for to the extent they impact any of the processes depicted in (Fig. 1a),
240 such as higher wind speeds over anticyclonic eddies potentially enhancing upward mixing. A wind-effect of mesoscale eddies that we do not single out here are modifications of the gas transfer velocity, an effect found to be of second order importance (Wanninkhof et al., 2011; Salinas-Matus et al., 2025). In contrast to the solubility and biological drivers a modified gas transfer velocity does not change mixed layer gas concentrations but the time-scale of equilibration of mixed-layer concentrations with the overlying atmosphere, an effect thought to be important in sea-ice covered regions that we exclude from our analyses. In
245 summary, the aim of this study is to identify the first order, dominant driver of average ingassing or outgassing mesoscale



air-sea flux anomalies rather than strictly isolate individual effects or quantify relative contributions of all effects. Based on this analytical framework, this manuscript then examines the net flux anomalies, magnitude of flux anomalies, and variance contributions of mesoscale air-sea CO_2 and O_2 flux anomalies.

3 Results

250 3.1 Mesoscale induced anomalies of CO_2 and O_2 air-sea fluxes

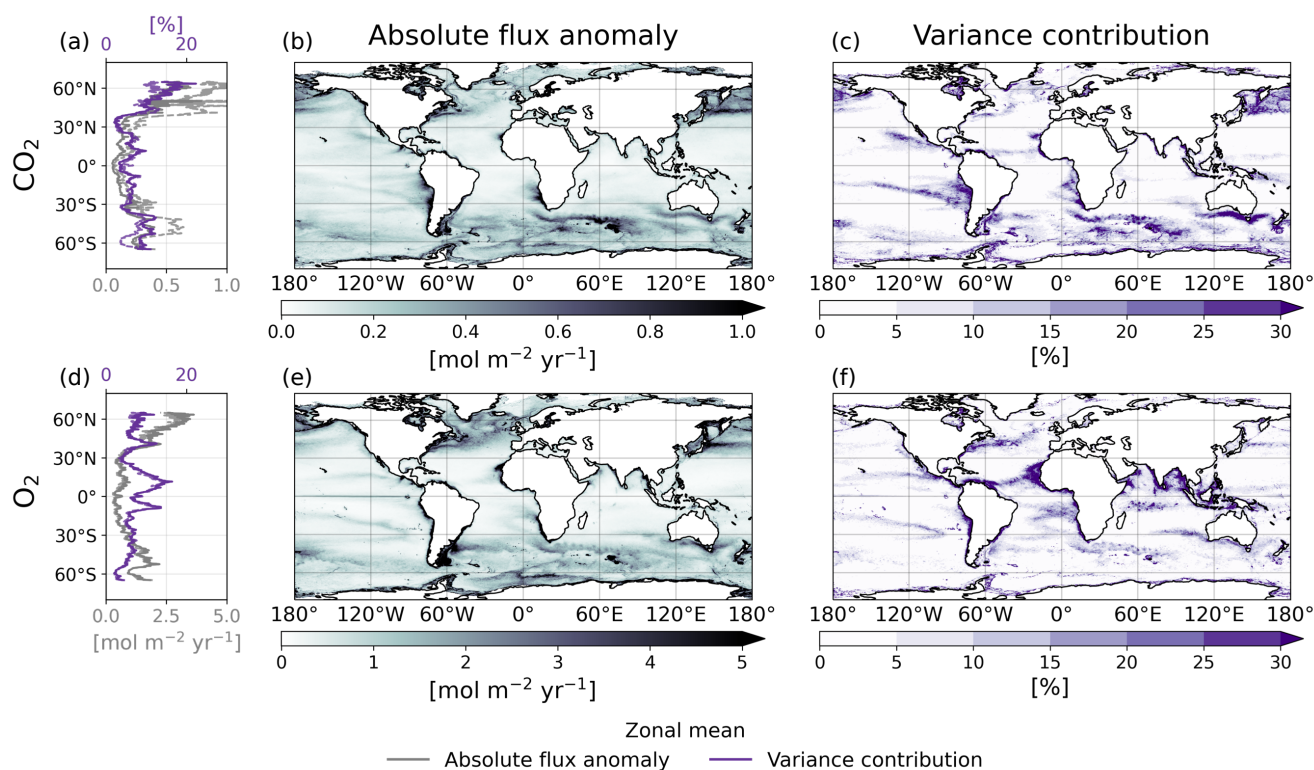


Figure 2. Magnitude of mesoscale flux anomalies and their contributions to total flux variance for (top) CO_2 and (bottom) O_2 . (b,e) show the magnitude of mesoscale flux anomalies, while (c,f) show the variance contribution of mesoscale variability, calculated as the ratio of mesoscale variance to total variance following Guo and Timmermans (2024). The magnitude of mesoscale flux anomalies is computed from the absolute flux anomalies prior to temporal averaging (that is positive and negative flux anomalies do not cancel in this case, in contrast to Fig. 3) Panels (a,d) show zonal mean values of the corresponding maps. Purple lines indicate the variance contribution (% , upper purple x-axis), while gray lines indicate the absolute flux anomaly magnitude ($\text{mol m}^{-2} \text{yr}^{-1}$, lower gray x-axis). Dashed lines denote the zonal mean values under CO_2 doubling. Since the changes under CO_2 doubling are very small for O_2 , the solid and dashed lines mostly overlap in (d).



Mesoscale variability makes a large contribution to air-sea CO₂ and O₂ flux variability in eddy-rich regions, both through large anomaly magnitudes and high contributions to the total flux variance. The magnitude of the mesoscale air-sea gas fluxes is highest in western and eastern boundary current regions and the Southern Ocean. These are regions known for high mesoscale eddy kinetic energy (see Pacheco et al., 2026, Fig. 1), such as the Gulf Stream and the Kuroshio Current western boundary current regions and the Antarctic Circumpolar Current in the Southern Ocean, or for their particularly long-lived eddies (eastern boundary current regions, e.g., Chelton et al., 2011b). The magnitude of the mesoscale air-sea flux anomalies is regionally as large as those of the total fluxes (Fig. 2a,d,b,e; A1a,d,b,e). This is consistent with previous studies that showed that regionally and temporally, the magnitude of the mesoscale flux anomalies can be large (Wanninkhof et al., 2011; Song et al., 2016), comparable to the background fluxes of CO₂ and O₂. This reflects also in the variance contributions where mesoscale flux anomalies account for more than 30% of the total variance in these regions for either gas (Fig. 2c,f). For CO₂, the mesoscale variance contribution is consistent with results by Guo and Timmermans (2024) (for O₂ we are not aware of any previous study). The variance contributions of CO₂ and O₂ regionally are not necessarily of the same size. In particular for the CO₂ flux it is larger in the Pacific and higher latitudes while for the O₂ flux it is larger in the Atlantic and Indian Oceans, showing up as a higher contribution in lower latitudes in the zonal average (Fig. 2a,d). The lower latitudes are emphasized for the variance contribution relative to the magnitudes of flux anomalies presumably as the background flux variance is smaller in these regions. In summary, the zonally averages of the magnitudes of the flux anomalies show similar large-scale patterns for the two gases, with overall large mesoscale anomaly magnitudes in the mid and high latitudes of regions with high eddy kinetic energy. Variance contributions to total variance for CO₂ and O₂, similarly is highest in mid to high latitudes for CO₂ but for O₂ it is highest in low latitudes, with 10 to 20%, but a global average of 6 - 7 %, for both CO₂ and O₂.

Next, we analyze mesoscale flux anomalies separately for anticyclonic and cyclonic eddies, a typical perspective in ocean mesoscale eddy literature (Chelton et al., 2007, 2011b). We determine polarity based on the sign of the SSH anomalies (see Section 2.3), with anticyclonic eddies defined based on an elevated SSH anomaly, and vice versa for cyclonic eddies. We then average the flux anomalies without taking the magnitude to obtain the average net flux anomalies. The net flux anomalies are highest in mid to high latitudes, with coherent zonal bands of net ingassing for anticyclonic eddies and outgassing for cyclonic eddies: global mean CO₂ and O₂ flux anomalies are 0.03 and 0.20 mol m⁻² yr⁻¹ for anticyclonic eddies, compared to -0.06 and -0.19 mol m⁻² yr⁻¹ for cyclonic eddies, respectively. While ingassing prevails for anticyclones, consistent with their typically positive SST anomaly and cooling heat fluxes, they show outgassing in some regions. Likewise also cyclonic eddies show ingassing in some regions. The occurrence of both outgassing and ingassing associated with anticyclones and cyclones is consistent with observational studies. Ship-based observations by Pezzi et al. (2021); Ford et al. (2023); Jones et al. (2015), for example, document cases where either cyclones or anticyclones lead to anomalous carbon ingassing or outgassing.

The net contribution of mesoscale eddies to air-sea gas exchange is small because opposing flux anomalies largely compensate each other. While clear banded structures of ingassing and outgassing emerge for anticyclonic and cyclonic eddies, respectively, the fluxes are substantially smaller than the average of the magnitudes of flux anomalies for both CO₂ and O₂ in Fig. 2b,e (note the different scales on the x-axes of the zonal means). Also, as discussed before, a notable net flux anomaly for anticyclonic and cyclonic eddies is largely constrained to mid and high latitudes, but muted in lower latitudes (different to



magnitudes of flux anomalies that are clearly larger than zero Fig. 3a,d). That the net flux anomalies are small and regionally average out is not surprising given that both polarities may show either ingassing or outgassing depending on what process is the dominant driver (Section 2.3). The regions that prevail with persistent ingassing or outgassing for anticyclonic and cyclonic eddies individually are regions where eddy kinetic energy and SST anomalies tend to be large and presumably persistently drive a solubility effect via cooling or warming. If we finally average over anticyclones and cyclones, thus all mesoscale eddies, we find that also the net effect of mesoscale eddies on fluxes mostly cancels out, resulting in near zero anomalies (Fig. 3a,d; gray line). Thus on a global scale we do not find a substantial net flux anomaly contribution to the total flux due to local flux modulations by ocean mesoscale eddies.

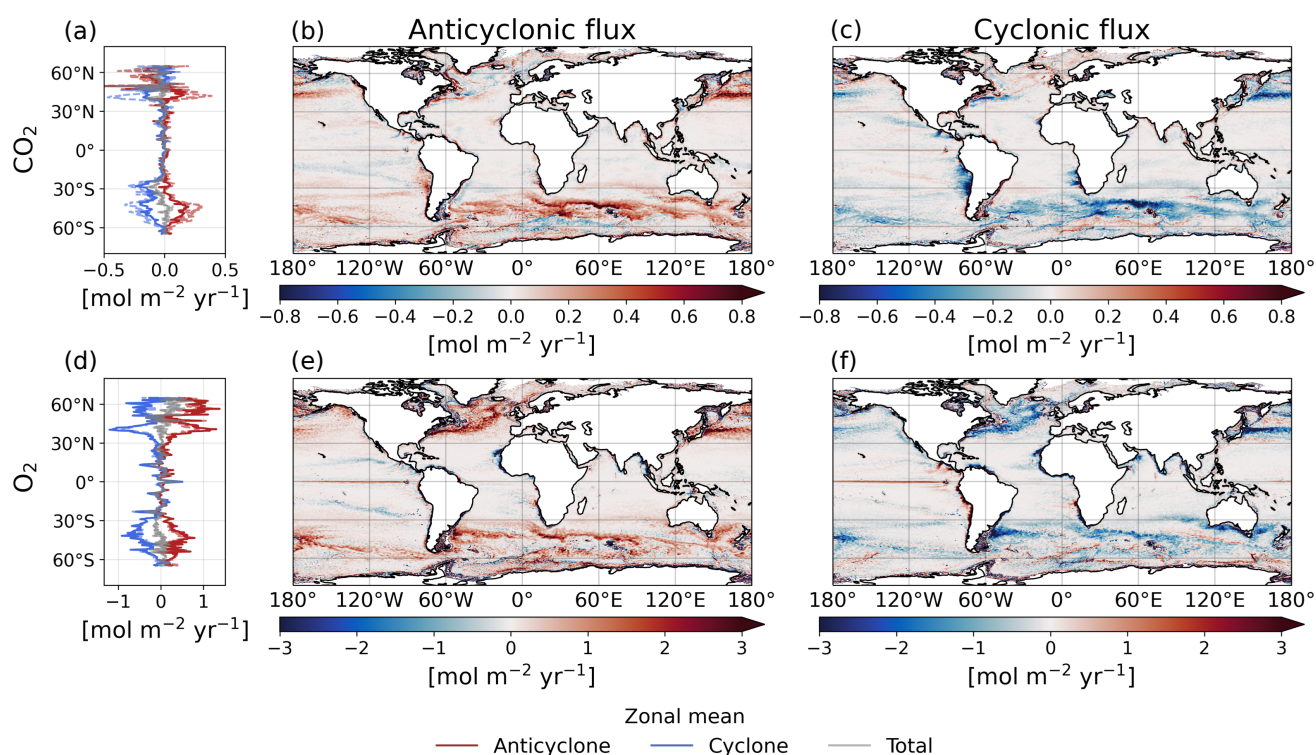


Figure 3. Net flux anomalies of mesoscale eddies separated by (b,e) anticyclones, (c,f) and cyclones, for (top) CO_2 and (bottom) O_2 . The polarity was determined by using the sign of the sea surface height (SSH) anomaly (see section 2.3). (a,d) Zonally averaged flux anomalies for anticyclones (red), cyclones (blue) and total mean anomalies (gray). Dashed lines correspond to the CO_2 doubling scenario. Since the changes under CO_2 doubling are very small for O_2 , the solid and dashed lines mostly overlap in (d). Note that positive fluxes are directed into the ocean (ingassing).



3.2 Drivers of mesoscale CO₂ and O₂ anomalies

295 We next analyze the drivers of mesoscale flux anomalies based on our analytical framework (Section 2.3). Based on Resplandy et al. (2015) and as laid out in Section 2.3 we use unidirectional versus counter-directional CO₂ and O₂ flux anomalies to distinguish between solubility-driven mesoscale air-sea gas flux anomalies and those driven by a biological imprint.

Correlation patterns between mesoscale CO₂ and O₂ flux anomalies identify the low- to midlatitude open ocean as a predominantly solubility-driven regime. The correlation between mesoscale CO₂ and O₂ flux anomalies shows a first-order zonal structure. This pattern differs markedly from the correlation of the total (large-scale + mesoscale) air-sea fluxes (Fig. C1), highlighting that the mechanisms governing mesoscale gas exchange are distinct from those dominating the large-scale signal. The contrast between mesoscale and total air-sea flux correlations underscores that mesoscale gas exchange cannot be inferred directly from the large-scale signal, an important consideration given that many Earth system models do not explicitly resolve mesoscale eddies. Regionally, the mesoscale correlation pattern identifies different driving mechanisms of the air-sea gas flux anomalies. In the subtropical gyres, extending into the mid-latitudes and parts of the tropics, the mesoscale flux anomalies show a positive correlation between CO₂ and O₂ (see Fig. C1 and blue regions in Fig. 4c), indicating that the solubility effect is the main driver there with a globally averaged Pearson correlation number in that region of +0.29 (and regionally more than +0.7, see Fig. C1, e.g. Agulhas region). These regions of a positive correlation of the air-sea fluxes of the two gases show also a positive correlation of the air-sea gas fluxes with heat fluxes, consistent with warming (of cold SST anomalies) driving outgassing, and cooling driving ingassing. The low-latitude oceans comprise a large part of the global ocean area, hence the solubility-driven regime accounts for slightly more than half of the global ocean surface.

In contrast, high latitudes, eastern ocean basins, and coastal regions show an anticorrelation of mesoscale CO₂ and O₂ fluxes, a signature of a biological imprint. The Southern Ocean, eastern boundary upwelling regions, western boundary currents, and their offshore extensions show a negative correlation of mesoscale CO₂ and O₂ fluxes. These regions feature an average Pearson correlation of -0.35 (and regionally much larger in magnitude), suggesting that effects of biological processes are driving the concentrations of CO₂ and O₂ in waters and subsequent mesoscale air-sea gas flux anomalies: either via photosynthesis in the surface ocean or via upwelling or mixing of interior ocean waters that carry the imprint of accumulated remineralization of organic matter (Fig. 4c, green and orange regions).

Although biologically driven regions occupy only about half of the global ocean, they contribute disproportionately to mesoscale air-sea gas flux variability. The area of these regions is comparable to the solubility-driven area (49% for productivity and respiration combined; Fig. 4d). Yet, the magnitude of the gas flux anomalies is systematically larger in the regions that show a biological imprint, making them contribute over-proportionally to global fluxes, with close to 60% for globally integrated fluxes (magnitude) for CO₂, and 70% for O₂ (Fig. 4e). In conclusion, fluxes associated with an anticorrelation of air sea CO₂ and O₂ fluxes dominate the global mesoscale air-sea gas flux anomaly magnitudes, highlighting an importance of a biological imprint. Also, for the contribution of mesoscale eddies to total air-sea flux variance the regions with the biological imprint show higher global values (between 7 and 10%) than solubility-driven regions 5 to 6 % (Fig. C2).



We next split up the biological imprint of mesoscale gas flux anomalies into the productivity- and respiration-dominated regimes. To attribute whether the biological imprint is due to biological uptake or accumulated respiration, we assess the consistency of gas flux anomalies with those expected from biological productivity alone (see Section 2.3; green regions in Fig. 4c). The North Atlantic, the Southern Ocean, and coastal eastern boundary upwelling regions show next to an anticorrelation of CO₂ and O₂ fluxes also a positive correlation of CO₂ flux anomalies with biological productivity. These regions of dominance of productivity-driven mesoscale air-sea flux anomalies in the surface ocean layer contribute with around 60% more than half to the total region that shows a dominance of the biological drivers in the mesoscale air-sea fluxes (anticorrelation of CO₂ and O₂, Fig. 4d). The average global mean fluxes are more similar between productivity- and respiration-driven regions than compared to solubility-driven regions (Fig. 4f) and the larger spatial extent of productivity-driven regions then makes them the larger contributor to the globally integrated mesoscale flux, particularly for O₂ (Fig. 4d,e). In contrast, in terms of variance contribution, respiration-dominated regions contribute disproportionately to total variance (Fig. C2). This is - in contrast to the productivity-driven regions - not due to larger flux anomalies but due to a weaker total/background variance in the region where respiration dominates as a driver.

3.3 Impact of CO₂ doubling on mesoscale air-sea CO₂ and O₂ fluxes

Under increasing atmospheric CO₂ and global warming, the area characterized by solubility-driven mesoscale flux anomalies expand. The solubility-driven areas increase to 60% while productivity- and respiration-driven areas are reducing to 27% and 13% respectively Fig. 4d). Key regions of a shift to a more solubility-driven regime include the North Atlantic, the Antarctic Circumpolar Current region, and the Southern Indian Ocean. (Fig. C3). Within the regions of biological imprint, the productivity-driver becomes more widespread Fig. 4d,e), in particular in eastern boundary upwelling extensions (Fig. C3).

Mesoscale air-sea flux anomaly magnitudes and contributions to total flux variance respond differently for CO₂ and O₂ across solubility-, productivity-, and respiration-driven regions. The magnitude of flux anomalies increases for CO₂ across all three driver regions, in contrast to O₂, where the magnitude of flux anomalies decreases (Fig. 4f). An exception is the respiration-driven regime, where O₂ flux anomaly magnitudes increase. However, because this regime occupies only a small fraction of the ocean area, it contributes little to the change in the globally averaged flux-anomaly magnitude (Fig. 4d,e,f). Consistently, zonally integrated absolute fluxes slightly decrease for O₂ but rise substantially for CO₂, particularly in solubility-driven regions (Fig. 4a,b). On the other hand, the contributions of mesoscale variance to the total flux variance globally remains largely unchanged for both gases (Fig. C2). For CO₂, however, regional changes are evident, with a reduced mesoscale contribution at high latitudes and a slight increase at low latitudes, although these changes are generally small (Fig. 2a).

4 Discussion

Biological imprints emerge as the primary contributor to global mesoscale air-sea flux variability of CO₂ and O₂. While the solubility-driven component is more prominent across large parts of the mid- to low-latitude ocean, biological control, including primary productivity and respiration imprints, is particularly pronounced in high- and polar-latitude regions as well as in Eastern

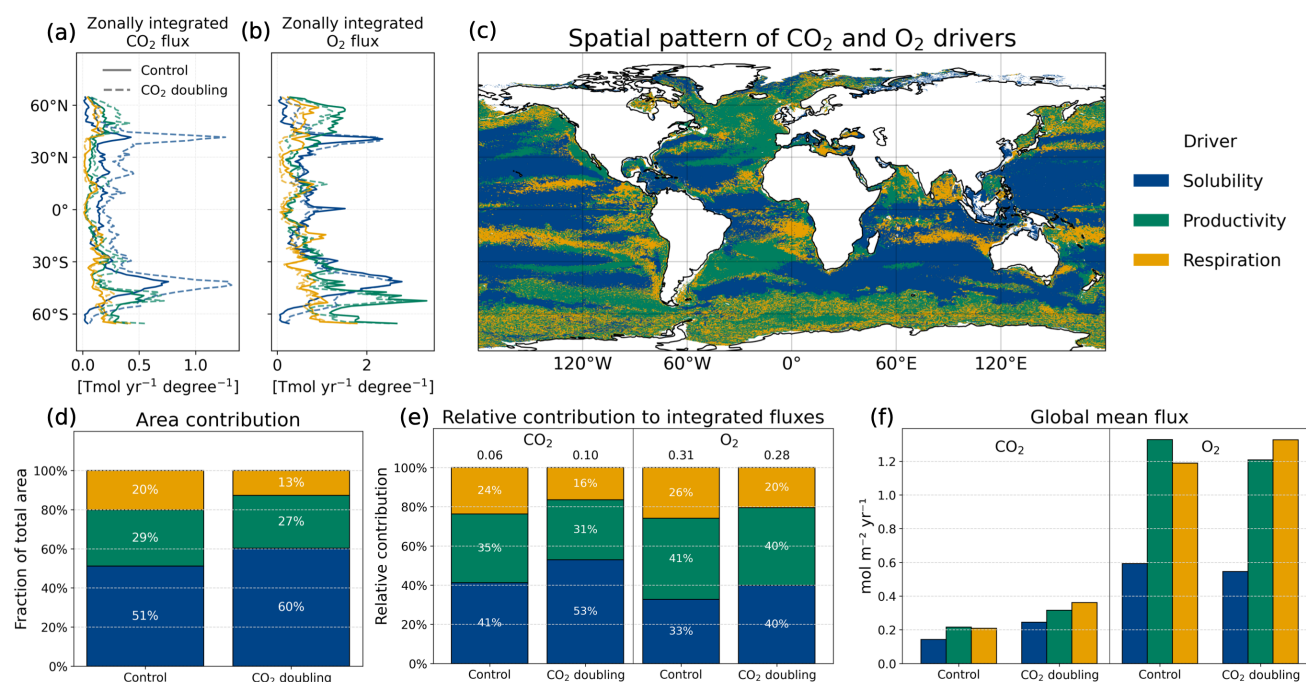


Figure 4. Dominant drivers of mesoscale air-sea CO₂ and O₂ flux anomalies; (a,b) Zonally integrated absolute mesoscale air-sea CO₂ and O₂ fluxes. Colors indicate the respective dominant driver of the integrated flux anomalies: solubility-driven (blue), non-thermal biological signatures due to productivity (green), and respiration (orange), as defined by the classification shown in Fig. 1. Dashed lines correspond to the CO₂ doubling climate change scenario. (c) Geographical distribution of dominant drivers of ocean mesoscale air-sea CO₂ and O₂ flux anomalies. (d) Areal contribution [%] of each driver to the total ocean area. (e) Contribution [%] of globally integrated absolute mesoscale fluxes to the total fluxes. The global flux is given in Pmol.yr⁻¹ above each column. (f) Global average of absolute mesoscale air-sea CO₂ and O₂ flux anomalies for each driver [mol m⁻² yr⁻¹].

Boundary Upwelling systems. These regions are also characterized by strong biological activity and upwelling, which likely interact to enhance the variability of air-sea CO₂ fluxes. These regions have disproportionately large flux anomalies, thereby increasing both the contribution of biological drivers to integrated mesoscale fluxes and their contribution to total variance. This suggests that biologically mediated mesoscale processes play a key role in shaping regional and global air-sea flux variability of the two gases. Accordingly, a larger fraction of the globally integrated absolute mesoscale air-sea gas flux can be attributed to biologically driven processes (Fig. 4e), despite solubility-driven effects dominating over a subtly larger area. These findings further imply that estimates of mesoscale air-sea CO₂ and O₂ fluxes based primarily on thermal controls may underestimate variability in biologically active regions.

Under CO₂ doubling the magnitude of mesoscale flux anomalies increases for CO₂ while there is little change for O₂. For carbon a major effect in the CO₂ doubling scenario is the increasing atmospheric CO₂ that, as it enters the ocean, causes acidification and shifts the equilibrium of sea water carbon chemistry (Doney et al., 2009). In particular, it enhances the sensitivity



370 of surface ocean carbon chemistry, leading to a stronger response of the air-sea CO₂ flux to environmental variability (Hauck and Völker, 2015). Consistently, we find a large increase in mesoscale-driven CO₂ flux variability, whereas O₂ variability generally shows smaller changes. Also, the sign of the response of O₂ flux anomalies is less clear across drivers. We attribute the increased magnitude of air-sea O₂ flux anomalies in the respiration-dominated region primarily to a change in area. This reflects a regime shift west of Australia, where a region characterized by weak flux anomalies transitions from respiration- to
375 solubility-driven control (Fig. 4d,f,C3). The otherwise subtle decrease of the mesoscale air-sea O₂ flux may be related to the reduced sensitivity of O₂ solubility to temperature at higher temperatures under global warming. In addition, mesoscale sea surface temperature anomalies show a small overall reduction (approximately 2%), which may further contribute to the decline. These thermal effects are less relevant for CO₂, where the acidification-driven increase in chemical sensitivity dominates the response. For CO₂, despite the increase in magnitude of flux anomalies, the mesoscale contribution to total variance remains
380 basically unchanged. Presumably this is due to a general enhanced CO₂ variability with a shifting carbon chemistry.

While mesoscale eddies can induce air-sea CO₂ and O₂ flux anomalies that are regionally comparable in magnitude to the mean flux, their globally integrated effect appears to be small. This is largely due to compensation between positive and negative anomalies, such that local enhancements and reductions in flux tend to cancel out. These results are consistent with results by Guo and Timmermans (2024); Wanninkhof et al. (2011) who only found a global net carbon uptake from mesoscale variability
385 of 0.72 MtC per year which is around four orders of magnitude smaller than the annual total ocean uptake of anthropogenic CO₂. Ford et al. (2023) suggested that, on a regional scale, anticyclones and cyclones are not perfectly symmetric in their flux anomaly magnitudes and can therefore act as a cumulative net CO₂ sink in the Southern Ocean, yet globally we do not observe such a consistent tendency. We conjecture that the net impact of mesoscale eddies on global ocean CO₂ uptake is dominated less by local modulation of fluxes and more by their influence on large-scale ocean circulation and stratification. In particular,
390 eddy-driven changes in overturning circulation, stratification, and isopycnal slopes are likely more important for setting the global carbon uptake. This is consistent with the understanding that the rate-limiting step for long-term CO₂ sequestration is not the air-sea gas transfer itself, but the transport of carbon into the ocean interior (Bopp et al., 2015; Frölicher et al., 2015).

We highlight that the solubility-driven effect identified here differs from how mesoscale air-sea gas flux variability due to SST anomalies tends to be interpreted. Phrasings in the literature tend to suggest enhanced outgassing with a positive SST
395 anomaly, therefore mesoscale gas flux anomalies are often expected to correlate positively with SST anomalies (Li et al., 2025; Ford et al., 2023; Pezzi et al., 2021). Rather than being primarily associated with SST anomalies, our results show a negative correlation of SST and gas flux. They align more closely with frameworks that link air-sea gas exchange to surface heat fluxes. In this view, heat loss over time enhances gas solubility and promotes ingassing of both CO₂ and O₂, while heat gain reduces solubility and drives outgassing (Wanninkhof et al., 2022). This interpretation is consistent with previous studies (Pezzi et al.,
400 2021), where solubility-driven flux variability is closely linked to heat flux rather than SST anomalies. Also, the role of heat fluxes in driving air-sea gas flux variability is consistent with large-scale and seasonal processes, where the tendency of SST anomalies (i.e., their change over time) rather than their absolute magnitude governs the response. For example, cooling of surface waters towards winter reduces pCO₂ and enhances CO₂ uptake. Similarly, poleward transport of warm waters into high latitudes, such as with western boundary currents, increases surface solubility as waters cool during their poleward journey,



enhancing CO₂ ingassing (Pedersen et al., 2025). At the mesoscale, in situations where solubility is the main driver, cold-core cyclonic eddies therefore tend to promote outgassing because they are warming, whereas warm-core anticyclones tend to promote ingassing since they are cooling.

In terms of the robustness of the categorization of drivers across geographical regions a caveat of the model framework used here is that the biogeochemical module miniBLING does not laterally advect, that is, transport organic carbon pools. It thus focuses productivity and export more directly over upwelling regions, an effect potentially relevant for the categorization in particular over eastern boundary upwelling regions that feature long-lived, far offshore propagating eddies (Lovecchio et al., 2022). Further ocean ecosystems are vastly simplified in the model, thus for instance a potential change of the productivity imprint with climate change due to a changing ecosystem composition will not be resolved. Future work could include a comparison with results from other mesoscale-rich biogeochemically coupled climate models to check the robustness of results across models (though climate change simulations that include ocean O₂ and carbon as prognostic tracers remain computationally expensive). Our study highlights the importance of considering eddies as transient features, whose effects on CO₂ fluxes depend critically on the temporal evolution of their properties rather than on their instantaneous conditions. Future studies could address this aspect rigorously by applying eddy detection and tracking algorithms to identify coherent mesoscale eddies and follow their evolution over time, thereby enabling a deeper understanding of processes by relating the temporal variability of mesoscale air–sea heat and gas fluxes, winds, and respiration signals.

Overall, we expect our estimates of the magnitude of mesoscale flux anomalies to represent a lower-bound estimate. The magnitude of the mesoscale flux anomalies in this study is sensitive to both the temporal resolution and the size of the box filter (see Fig. B4 and B3). Larger filter sizes yield stronger anomalies; however, we adopt a conservative approach by using a comparatively small 3°×3° box filter. Also, anomalies derived from monthly averaged fields are generally weaker than those from higher temporal resolution data, though exhibiting similar spatial patterns and producing nearly identical correlation structures. Finally, the apparent systematic underestimation of spatial gradients as compared to observations (see Fig. A1) might imply an underestimation of mesoscale anomalies (which typically relate to spatial gradients as they move properties laterally, for instance nutrients that fuel biological productivity). Taken together, our results likely underestimate the magnitude of mesoscale air–sea gas flux anomalies and their contribution to total variance (Section 2.3) while the general conclusions of this study we expect to be robust. Given the relative contributions of solubility- versus biologically driven regions, characterized by correlations and anticorrelations between CO₂ and O₂ fluxes, respectively, it would be interesting to test the findings in this study on different ocean biogeochemical models.

Local wind variability induced by mesoscale eddies represents another pathway through which eddies can affect air–sea gas fluxes. As discussed in Section 2.3, this indirect effect by mesoscale SST anomalies then feeds back on wind speeds and thus the transfer velocity, independent of solubility-, productivity-, or respiration-driven effects (Frenger et al., 2013; Park et al., 2006; White and Annis, 2003). Yet, we expect this effect to rather change the time scale of equilibration of the mixed layer with the atmosphere rather than mixed layer concentrations of oxygen or dissolved inorganic carbon, with little effect on time mean fluxes (see Section 2.3, as suggested in previous studies (Salinas-Matus et al., 2025; Wanninkhof et al., 2011). Other wind



effects, such as the modulation of vertical mixing, are implicitly captured within the productivity and respiration components
440 of our analysis framework.

5 Conclusions

In this study, we quantified the role of ocean mesoscale variability in shaping air–sea CO₂ and O₂ fluxes using a global climate model (GFDL CM2.6) with an eddy-rich ocean component (0.1° resolution) including a simple biogeochemical model miniB-LING. We find that mesoscale variability explains a substantial fraction of the air–sea CO₂ and O₂ flux variance (both 6–7%)
445 globally and regionally (more than 30%), both in the control and CO₂ doubling scenario. Despite the substantial contributions relative to background variability (Fig. 2c,f), and a regional importance of mesoscale flux perturbations by anticyclones versus cyclones (Fig. 3), our results suggest that the global net effect of mesoscale air–sea CO₂ and O₂ flux anomalies is limited due to compensation between positive and negative anomalies.

The dominant drivers of mesoscale air–sea flux anomalies vary regionally, and different drivers tend to be associated with
450 different magnitudes of flux anomalies. Area-wise, the solubility-driver dominates just over half of the ocean’s area (51%), mostly in the subtropics and mid-latitudes, where air–sea gas flux anomalies closely follow air–sea heat flux variability. Under CO₂ doubling, expanding subtropical gyres imply an increase of the area of the solubility-driven regions to 60% of the global ocean area. Yet, while solubility-driven processes dominate in terms of global area, biological processes dominate flux magnitudes and variance. Integrating absolute flux anomalies over the respective driver-regions solubility, productivity, and
455 respiration reveals that the biological drivers (productivity and respiration) account for roughly 60% of the mesoscale CO₂ flux anomalies, and for around 70% for O₂. This is because magnitudes of gas flux anomalies in the regions with a biological imprint are systematically stronger than for the solubility-driven regions. An exception is CO₂ for the CO₂ doubling scenario as described in the following.

The magnitude of flux anomalies increases under CO₂ doubling for CO₂, but not for O₂. This difference in the mesoscale-
460 driven variability between the two gases reflects the nonlinear nature of seawater carbon chemistry, which increases CO₂ sensitivity to perturbations as anthropogenic carbon accumulates. The higher magnitudes of flux anomalies under CO₂ doubling in combination with the increasing area of the solubility-driver pushes the contribution of absolute fluxes globally for CO₂ to just over half. The increase in magnitude of flux anomalies under CO₂ doubling highlights the importance of understanding air–sea flux variability in a changing climate, both for process understanding and for emerging applications such as monitoring,
465 reporting, and verification of marine carbon dioxide removal, where mesoscale variability may need to be explicitly considered.

The proposed categorization framework enables new opportunities to contextualize observations and evaluate models. Beyond providing insight into the role of mesoscale eddies in shaping surface carbon and oxygen anomalies, our analytical framework may also serve as a new approach for the interpretation of in-situ O₂ observations from BGC-Argo floats (Sharp et al., 2023; Ito et al., 2024) and the potential complementarity of surface underway CO₂ flux estimates from ships and Sail-
470 drone (e.g. Sutton et al., 2021; Nickford et al., 2020). In combination with observational estimates of nutrient, chlorophyll, and photosynthetically active radiation (PAR) available from BGC-Argo floats, this framework can help to disentangle biological



and solubility-driven signals within observed eddies. In return, characterizing observational based air-sea CO₂ and O₂ flux mesoscale and total variance, and emerging patterns with respect of driving mechanisms of heat fluxes versus biology can be used as a target for future high resolution global modeling.

475 *Code availability.* Python scripts to reproduce the analysis are available at: <https://doi.org/10.5281/zenodo.20845135> (Hocke, 2026a).

Data availability. The data of this study are available through GEOMAR at <https://hdl.handle.net/20.500.12085/7e54fc52-840d-4e82-a1b2-2b8bb82d3dea> (Hocke, 2026b)



Appendix A: Climatological air-sea fluxes of CO₂ and O₂ versus observational estimates

Simulated patterns of air-sea annual mean fluxes of CO₂ and O₂ are consistent with expectations based on the large-scale ocean overturning circulation. For CO₂, the range of variation is smaller in the observed than in the simulated mean flux estimates. Conversely, the magnitude of fluctuation is larger in the observed O₂ flux estimates than in the model solution. The zonally averaged flux of CO₂ in the model is characterized by strong ingassing highest in the midlatitudes (40-60°), with the highest values occurring regionally in the north Atlantic, where fluxes, along the Gulf stream and in the Labrador Sea, exceed 10 mol m⁻² yr⁻¹ in our control simulation (Fig. A1a,b). In contrast, equatorial regions, particularly in the (Eastern) Pacific Ocean, the Eastern Boundary Regions, as well as the Southern Ocean, show CO₂ outgassing associated with the upwelling of CO₂-rich deep waters, with maximum fluxes exceeding 5 mol m⁻² yr⁻¹. The pattern of mean O₂ fluxes differs from the mean CO₂ fluxes in that its zonal structure is more symmetric across hemispheres, and characterized by strong O₂ sinks at high latitudes, a weak sink at the equator, and a weak source in low- to mid-latitudes (Fig. A1d,e). The CO₂ outgassing in high latitudes, and tropical Pacific, and corresponding O₂ ingassing is indicative of upwelling of exchange with deep waters in the ocean interior, such as broad scale upwelling of circumpolar deep waters in the Southern Ocean and tropical upwelling, that carry a respiration signal. In contrast, regions of mean outgassing both gases in subtropical latitudes may indicate solubility as an important driver (Resplandy et al., 2015), with the relative importance of these drivers varying strongly across regions.

These patterns for CO₂ and O₂ compare favorably with previous studies and observation-based data products (Fay et al., 2021; Takahashi et al., 2002; Jin et al., 2025; Gruber et al., 2001). (Fig. A1c,f) Results by Resplandy et al. (2015), who analyzed six Earth System Models (ESMs) from the Coupled Model Intercomparison Project Phase 5 (CMIP 5) for CO₂, find similar patterns as well as magnitudes. Also observation-based reconstructions of air-sea CO₂ fluxes by Fay et al. (2021) (see Fig. A1), exhibit a very similar global structure. For O₂, the global observational constraints on O₂ air-sea fluxes remain more limited than for CO₂. A recent machine learning approach by Jin et al. (2025) provides new insights into global distribution patterns. The zonally averaged O₂ flux simulated here reproduces the general pattern of ingassing and outgassing reported in observational studies (Jin et al., 2025; Gruber et al., 2001), as well as the large-scale spatial distribution, although the flux magnitude is underestimated in the model, a bias it shares with other models (Resplandy et al., 2015; Li et al., 2022).

Reasons of disagreement of the model versus observations include not only model imperfection but also observational uncertainties. Sparse observations of air-sea gas fluxes can introduce substantial uncertainties into annual flux estimates, particularly due to strong seasonal cycles and interannual variability. A region of rather large differences for both gases is the Southern Ocean, where the models appear to underestimate the ingassing of O₂ and overestimate the outgassing of CO₂ and where the observational coverage is sparse. It remains to be unresolved if observational estimates underrepresent outgassing of CO₂ due to the lack of observations (Dong et al., 2024; Behncke et al., 2026). For O₂ Jin et al. (2025) actually report that their reconstruction overestimates O₂ ingassing in the high southern latitudes and outgassing in equatorial regions. Note though, that for O₂ that model-observational differences of air-sea fluxes are much less investigated compared to CO₂ (as there is large interest in the ocean as a sink for anthropogenic CO₂ emissions), quantitatively and if causes lie with observational estimates or models, an aspect for further research in the future. Note for CO₂ that the atmospheric CO₂ forcing matters a lot. The

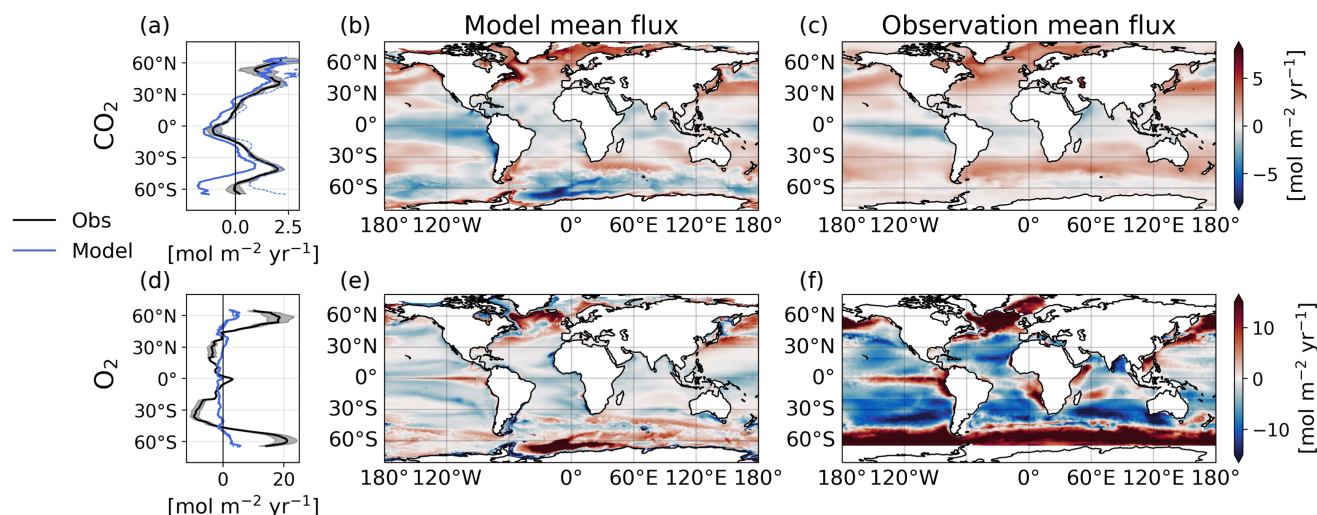


Figure A1. Annual mean air-sea fluxes [$\text{mol m}^{-2} \text{yr}^{-1}$] from the GFDL model (b,e) and observation-based products (c,f) for (top) CO_2 and (bottom) O_2 , with positive values indicating ingassing. Model results correspond to the preindustrial control simulation. Observation-based CO_2 fluxes are from Fay et al. (2021) (1990–2019) and O_2 fluxes from Jin et al. (2025) (2004–2024). (a,d) Zonally averaged fluxes for observations (black) and the model (blue); the dashed line denotes the CO_2 -forced simulation. Gray shading indicates the range across ensemble members and wind products. Positive values indicate oceanic ingassing.

zonally averaged O_2 flux changes only slightly in the CO_2 doubling scenario compared to CO_2 fluxes, consistent with the fact that while atmospheric CO_2 strongly increases due to anthropogenic CO_2 emissions, O_2 remains basically the same in the atmosphere (Keeling and Manning, 2014). For CO_2 the zonal mean of the CO_2 doubling simulation shows a clearly reduced
515 outgassing compared to the Control Fig. A1a, consistent with ingassing of anthropogenic carbon under increasing atmospheric CO_2 . The observations very roughly lie in between the Control and CO_2 doubling simulation, consistent with expectations that we are in a state between Control and CO_2 doubling.

Appendix B: Method diagnostics and validation

This section presents supplementary figures supporting the applied methodology, including the selection of datasets and filter
520 size, as well as comparisons with previous studies to validate the approach (e.g., Fig. B1 and Seo et al. (2023)).

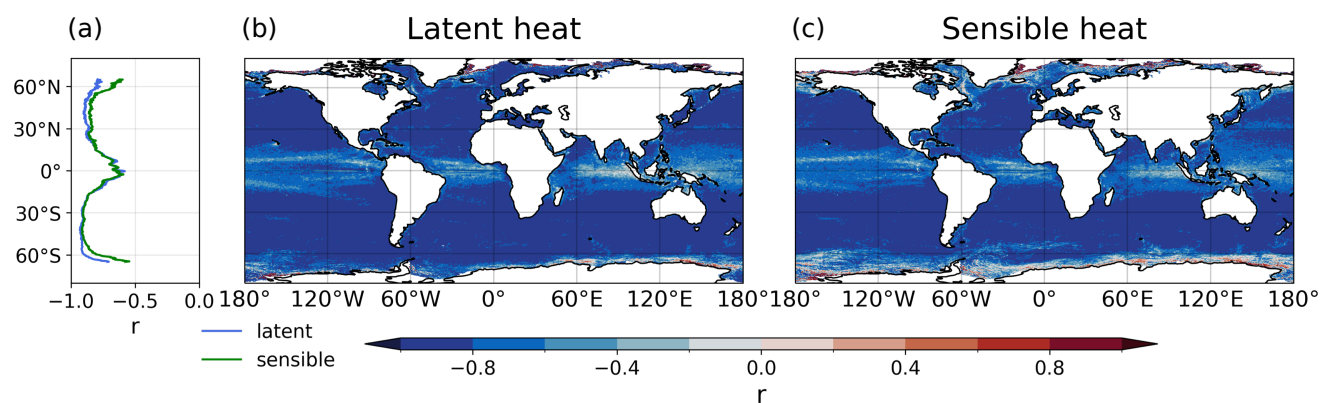


Figure B1. Pearson correlation r between (b) latent ((c) sensible) heat flux anomalies, and sea surface temperature anomalies. (a) Zonally averaged r for sensible (green) and latent (blue) heat fluxes.

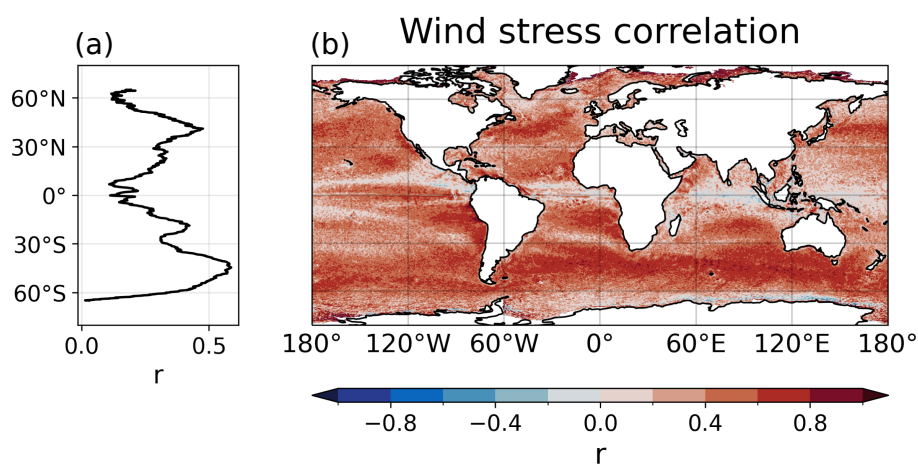


Figure B2. (b) Pearson correlation r between latent wind stress anomaly, and sea surface temperature anomalies. (a) Zonally averaged r .

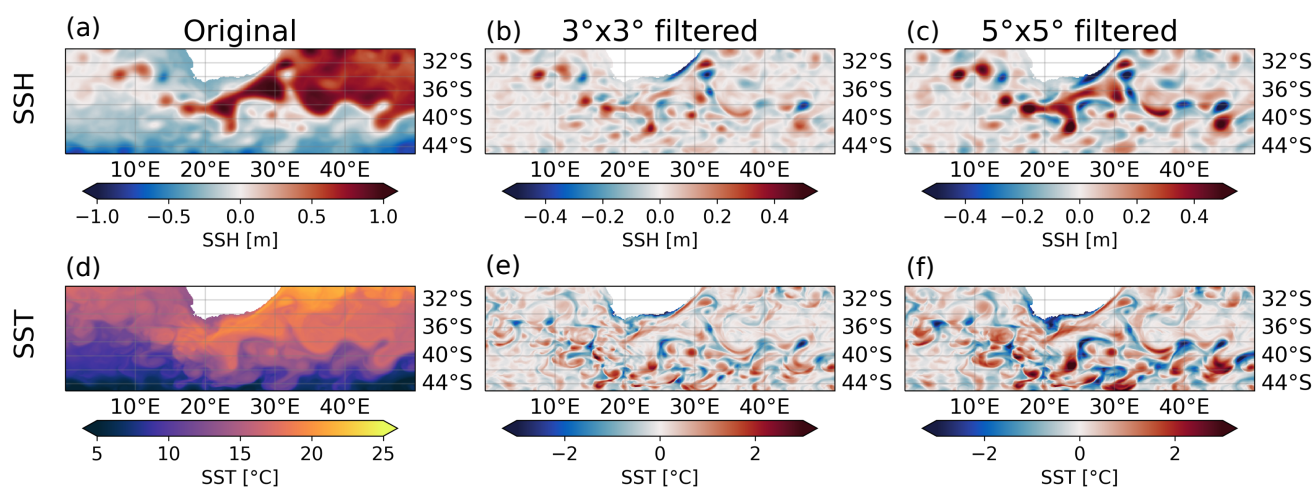


Figure B3. Exemplary snapshot of sea surface height (SSH [m], a-c) and sea surface temperature (SST [°C], d-f) in the Agulhas region. (a,d) shows the original fields. (b,e) display anomalies obtained by subtracting a 3°x3° median boxcar spatial filter and 5°x5° for c,f.

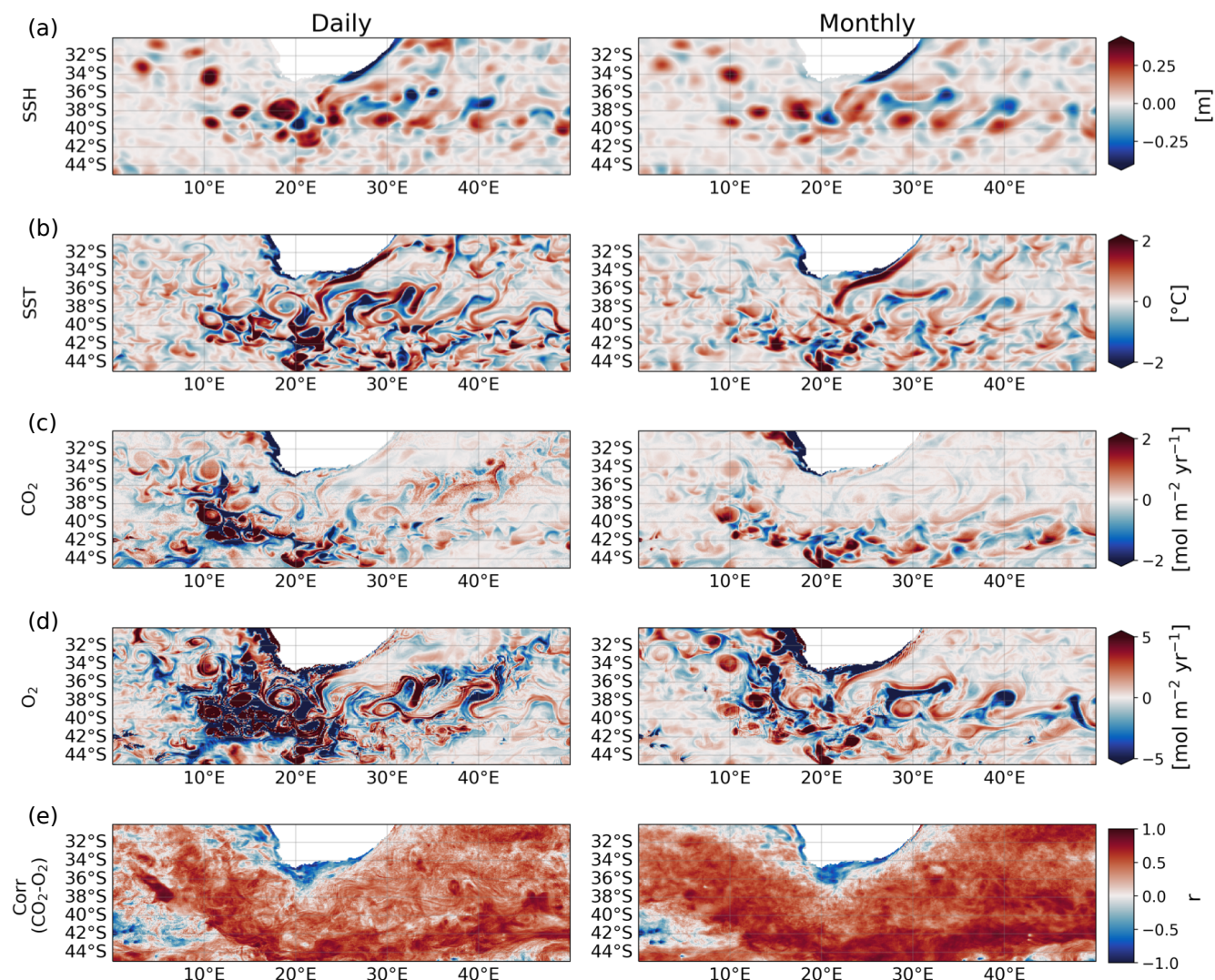


Figure B4. Exemplary snapshot (a-e) of (a) sea surface height (SSH [m]), (b) sea surface temperature (SST [°C]), (c) CO₂ and (d) O₂ flux [mol m⁻² yr⁻¹] anomalies (3°x3° Boxfilter) in the Agulhas region. The left column is calculated with daily data (snapshot of 1.1.181), the right column with monthly data (January 181). (e) shows the Pearson correlation r between CO₂ and O₂ flux anomalies of the respective datasets for model year 181 (daily) and model years 181-190 (monthly).

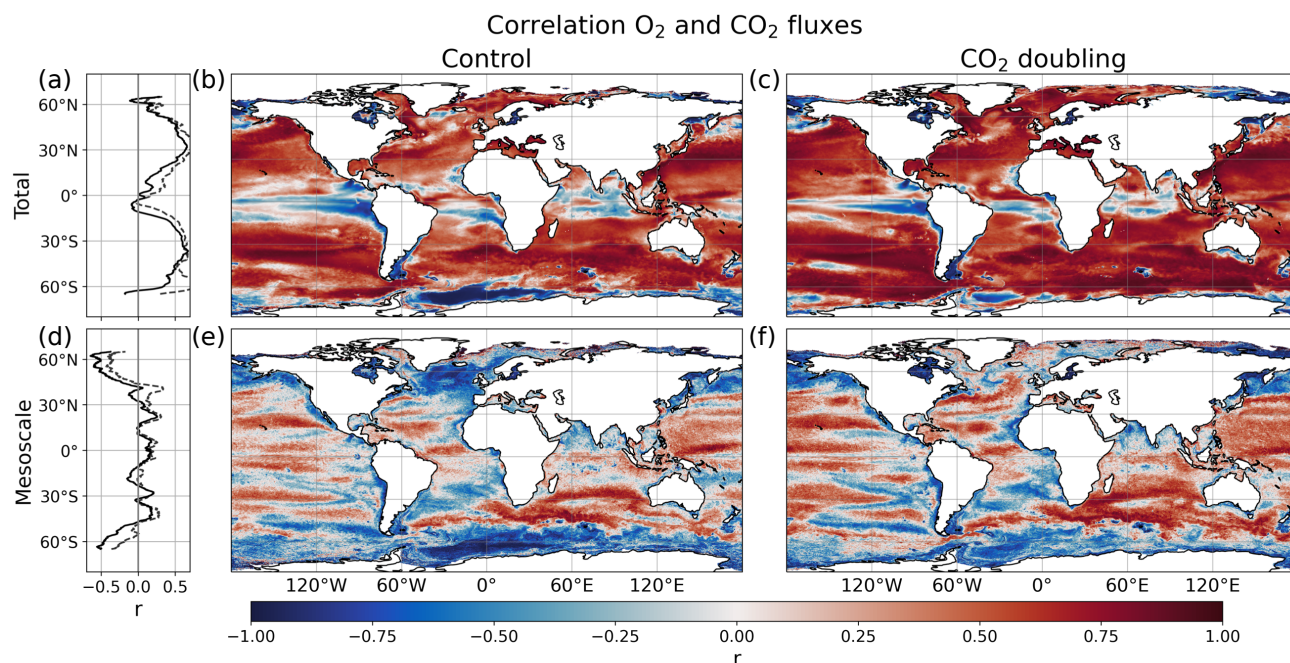


Figure C1. Correlation between air–sea oxygen and carbon dioxide fluxes. Zonal mean (a,d) and spatial distribution (b,c,e,f) of the Pearson correlation coefficient (r) between air–sea O₂ and CO₂ fluxes. Panels (b,e) show results for the control simulation, while panels (c,f) show results for the CO₂ doubling experiment. The upper row (a–c) represents the total correlation, and the lower row (d–f) represents the mesoscale contribution. The zonal mean correlations are shown for latitudes between 65°S and 65°N. Solid (dashed) lines in panels a and d represent the control (CO₂ doubling) experiment.

Appendix C: Correlation analysis and projected climate change effects

This section presents the categorization underlying global correlations introduced in the manuscript and their changes under CO₂ doubling. Figure C2 shows the global variance contributions of CO₂ and O₂ in the control and CO₂ doubling simulations, separated into solubility-, productivity-, and respiration-driven regions.

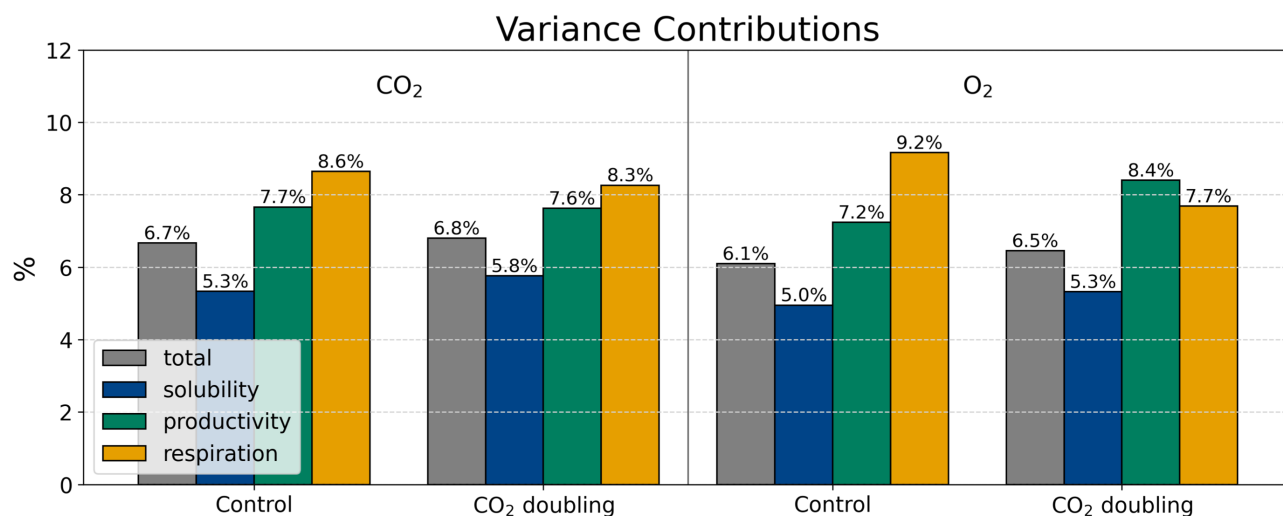


Figure C2. Variance contributions (mesoscale variance versus total variance in %) for CO₂ and O₂ in the control run (left) and in the CO₂ doubling scenario (right). The variance contribution is displayed for the whole area (gray), and the three driver categories solubility (blue), productivity (green) and respiration (yellow).

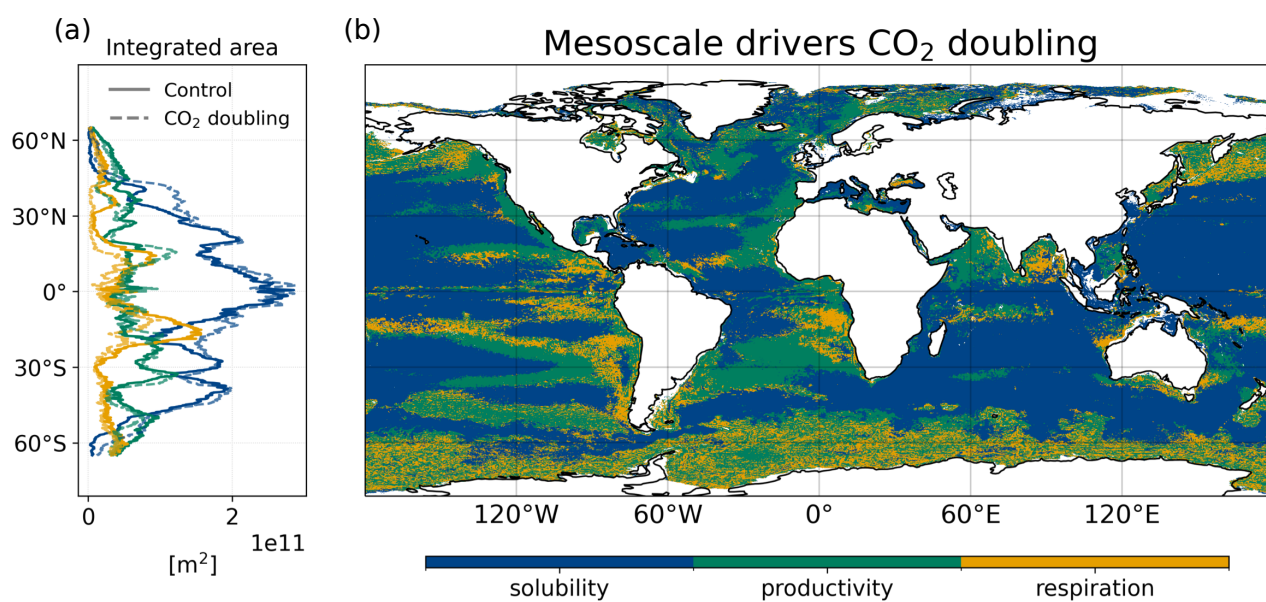


Figure C3. Spatial distribution of mesoscale drivers of CO₂ and O₂ flux anomalies in the CO₂ doubling climate change experiment.

(a) Zonally integrated area separated for each driver (solubility-, productivity- and respiration-driven). **(b)** As Fig. 4c.



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