Biological carbon pump affected by CO2 uptake in the Benguela Upwelling System

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Abstract

Eastern Boundary Upwelling Systems (EBUS) are well-known for their high productivity and fishery yields. However, being scarcely sampled and poorly represented in global models, their role as CO$_2$ sources and sinks to the atmosphere remains elusive. Here, we present a compilation of shipboard measurements over the past two decades, showing how the Benguela Upwelling System (BUS) in the southeast Atlantic Ocean acts as a CO$_2$ source in the north and CO$_2$ sink in the south. Surface warming of upwelled waters increases the partial pressure of CO$_2$ (pCO$_2$) and outgassing in both regions, but in the south, the biologically-mediated drawdown of CO$_2$ exceeds this warming effect. Here, the biological carbon pump owes its stronger impact on pCO$_2$ to higher shares of upwelling source waters carrying preformed nutrients supplied from the Southern Ocean. Their formation increases pCO$_2$ in surface waters and counteracts human-induced invasion of CO$_2$ in the Southern Ocean. However, their utilization in the BUS compensates for over 20% of the CO$_2$ loss occurring in the Atlantic sector of the Southern Ocean. This emphasizes the role of the BUS as key to improve our understanding of the ocean’s response to climate change and the future evolution of CO$_2$ in the atmosphere.

Main

Eastern Boundary Upwelling Systems (EBUS) are among the most productive regions in the ocean and contribute 11% to global new production, which refers to biomass largely produced on the basis of nutrients introduced via upwelling and vertical mixing from the deep dark ocean into surface waters$^{1-3}$. The associated assimilation of CO$_2$ through the generation of biomass and its transfer to the deep sea is an integral part of the biological carbon pump$^{4,5}$ which reduces atmospheric CO$_2$ concentrations through the storage of CO$_2$ as dissolved inorganic carbon (DIC) in the deep ocean$^5$. Even though it is widely assumed that the biological carbon pump responds to climate change, the magnitude and even the direction of change is still unknown$^6,7$. However, the amount of DIC kept by the biological carbon pump is assumed to be linearly related to the inventory of regenerated nutrients, which are released during the remineralization of biomass in the deep ocean$^8$. They stand in contrast to biologically unused so-called
preformed nutrients, whose formation represents a leakage through which the biological carbon pump
losses CO$_2$ and turned e.g. the Southern Ocean south of 44$^\circ$S into a natural CO$_2$ source to the
atmosphere$^{9,10}$. This leakage evolves when nutrients that upwell along with DIC at the Antarctic
Divergence$^{11}$ are not fully utilized by biological production due to light and iron limitation$^{12,13}$.
Nowadays, rising CO$_2$ concentrations in the atmosphere revert the air sea fluxes of CO$_2$ and converted the
Southern Ocean into a key site for anthropogenic CO$_2$ uptake with a current estimate of approximately
740 ± 290 Tg C year$^{-1}$.$^{14,15}$ Due to the counteracting effect of natural CO$_2$ released from the biological
carbon pump$^{12}$ of about 400 ± 180 Tg C year$^{-1}$.$^{14,15}$, this results in a CO$_2$ invasion of 380 ± 115 Tg C year$^{-1}$
between 1990 and 2009$^{15,17}$. However, approximately 34% (∼110 Tg C year$^{-1}$) of the natural CO$_2$ release
occurs within the Atlantic sector of the Southern Ocean between 44$^\circ$ and 58$^\circ$S$^{14,15}$ and the resulting
preformed nutrients are transported northwards and subducted beneath warmer and lighter subtropical
water masses$^{18-20}$. Loaded with preformed nutrients, these mode waters support primary productivity in
upwelling systems at lower latitudes and thus could potentially restore the CO$_2$ uptake efficiency of the
biological carbon pump. Although EBUS could act as regional CO$_2$ sinks through the utilization of
preformed nutrients and low sea water temperatures which increase the solubility of CO$_2$$^{21-23}$, global
models suggest that upwelling systems (in particular ones at lower latitudes) act as net CO$_2$ sources to the
atmosphere$^{24,25,26}$. This was also found to be the case in a modelling study of the Benguela Upwelling
System (BUS), which is located in the southeast Atlantic Ocean (Fig. 1) and considered the most
productive of all EBUS$^{27}$. The study however suffered from a model that poorly represented the BUS, and
an unclearly defined upwelling region$^{26}$. Other studies within the BUS hardly improve these conditions as
indicated by estimated CO$_2$ fluxes ranging from -5.1$^{25,24}$ Tg C year$^{-1}$ to 1.54 Tg C year$^{-1}$. It thus remains
elusive whether the BUS is a net CO$_2$ sink or CO$_2$ source to the atmosphere. Similar to the Southern
Ocean, the BUS also suffers from a sparsity of data and model outcomes$^{25,26}$ were constrained by pCO$_2$
data (partial pressure of CO$_2$) from the Surface Ocean CO$_2$ Atlas (SOCAT)$^{29}$. So far this data product
misses coverage particularly over the northern BUS shelf region, thus curtailing estimates of air-sea gas
exchange for the BUS (Fig. 1).
Here, we address this problem by presenting a compilation of shipboard pCO$_2$ data for the BUS from the extended SOCAT v2020 data base that includes data gathered from 14 cruises throughout the BUS from 2008 to 2019 (see Supplementary Table 1). This revised data set allows for a seasonal-based examination of regional air-sea fluxes of CO$_2$ across the BUS and underlying mechanisms affecting these fluxes, which indicate that the biological carbon pump in the BUS serves as a globally significant CO$_2$ sink.

Sea surface pCO$_2$ characteristics

In order to overcome the problem of unclearly defined upwelling regions that led to strong discrepancies in the definition of the BUSs offshore boundary, we specified the upwelling zone’s spatial extent by considering the average cross-shelf distribution of sea surface pCO$_2$ (Fig. 2a,b) for both the northern and southern subsystems (NBUS, SBUS). In general, upwelling systems exhibit highest pCO$_2$ in the nearshore region due to the upwelling of carbon-rich waters, and a decreasing trend offshore due to degassing and the biologically-mediated carbon uptake within the offshore-advecting upwelled water. By assuming that a decrease in pCO$_2$ variability marks a decreasing influence of upwelling on pCO$_2$, we determined the upwelling zone’s boundary as the distance from shore when the standard deviation (s.d.) decreases persistently by ~85% to below ±35.5 µatm in the NBUS and ±29.5 µatm in the SBUS.

In the NBUS, this results in an upwelling boundary at 340 km offshore, which lies within the range of other studies that considered an offshore extension from 300 to 800 km. In the SBUS, the decreasing variability in pCO$_2$ suggests a closer boundary at 200 km distance to shore. In comparison to the NBUS, the much lower intensity of upwelling observed in the SBUS may explain the discrepancy observed in the offshore extent of elevated pCO$_2$ values between the subsystems. Considering additionally the latitudinal extent of the SBUS (26°S to 34°S) and NBUS (16°S to 26°S) results in upwelling areas of 177,600 km$^2$ and 377,400 km$^2$, respectively.

To estimate the seasonal variability, pCO$_2$ data were averaged across the mean offshore extent and latitudes of the upwelling areas for the austral spring and summer (September-March), and austral autumn and winter seasons (April-August) (Fig. 2c). The resulting plot of pCO$_2$ variability with latitude indicates...
a seasonal influence in the northern region between ~17°S and ~21°S which diminishes towards the
south. The seasonality observed in the north corresponds to seasonal variations in upwelling intensities,
which for this region are strongest during the winter\textsuperscript{37}. However, when averaged across the whole NBUS,
the ~15% difference in seasonal means and high s.d. in pCO\textsubscript{2} between spring and summer (485.7 ±113
µatm), and autumn and winter (556.03 ±126 µatm), imply that the upwelling-related seasonality is only
weakly pronounced. In the SBUS, seasonal mean pCO\textsubscript{2}s of 378.15 ±65 µatm (spring, summer) and
381.91 ±36 µatm (autumn, winter) do not reflect the seasonality of upwelling intensities, which are
strongest during the summer\textsuperscript{38}. This could be attributed to a lower data coverage in SBUS as compared to
NBUS (Supplementary Fig. 1) or to the function of the SBUS as CO\textsubscript{2} source and sink as indicated by
pCO\textsubscript{2} concentrations above and below those in the atmosphere at the coast and further offshore (Fig. 2b).
Relative to the mean atmospheric pCO\textsubscript{2} of our reference year 2020 (~414 µatm), the seasonal as well as
annual mean pCO\textsubscript{2}s of 487.6 ±2.9 µatm for the NBUS and 379.2 ±1.74 µatm for the SBUS reveal the
opposing character of the two subsystems as a CO\textsubscript{2} source and sink, respectively.

Air-sea CO\textsubscript{2} flux estimates

In contrast to pCO\textsubscript{2}, the air-sea CO\textsubscript{2} fluxes reveal a pronounced seasonality in both systems as being more
than twice as high during upwelling than during non-upwelling seasons. The intensification of wind
during the upwelling season is considered the primary driver of this difference which, according to the
opposing signs, strengthens the CO\textsubscript{2} source and sink functions in the NBUS and SBUS, respectively
(Table 1).

Integrating the annual mean fluxes over the upwelling area results in a CO\textsubscript{2} emission of 14.98 Tg C year\textsuperscript{-1}
in the NBUS and a CO\textsubscript{2} uptake of -3.37 Tg C year\textsuperscript{-1} in the SBUS. These area-integrated CO\textsubscript{2} fluxes
correspond with those given in ref.\textsuperscript{31} for the NBUS (11.5 Tg C year\textsuperscript{-1}) and SBUS (-1.4 Tg C year\textsuperscript{-1}),
respectively, but are about 30% and 140% higher, mainly due to the use of a smaller area in the ref.\textsuperscript{31}
study. Similar to these data-based estimates, modelled carbon fluxes also indicate a CO\textsubscript{2} sink region in the
south and source region in the north\textsuperscript{26}, while modelled CO\textsubscript{2} fluxes from the entire BUS between 18\textdegree S to 28\textdegree S amount to 2.25 mol C m\textsuperscript{2} year\textsuperscript{-1} on average over the time period between 1982 and 2015. Comparing our measurements with modelled data by recalculating CO\textsubscript{2} fluxes for the same region with an offshore boundary at 800 km, results in a weaker annual CO\textsubscript{2} source into the atmosphere of 1.19 mol C m\textsuperscript{2} year\textsuperscript{-1}. This discrepancy seems to be caused mainly by a poleward misplacement of the outgassing cell in the applied model framework\textsuperscript{26}, which underestimates the CO\textsubscript{2} sink behavior of the SBUS.

Preformed nutrients as a driver of regional variability in sea surface pCO\textsubscript{2}

As seen for the Oregon upwelling system, the utilization of preformed nitrate (N\textsubscript{pref}), with concentrations of up to 12 \(\mu\)mol kg\textsuperscript{-1}, turned the upwelling area into a CO\textsubscript{2} sink\textsuperscript{21,23}, while the impact of N\textsubscript{pref} with concentrations of around zero \(\mu\)mol kg\textsuperscript{-1} were too low to support the sink functionality of the Peruvian upwelling system\textsuperscript{22}. In addition, the inaccessibility of phosphate (P) through lack of fixed nitrogen and the effect of surface warming on the CO\textsubscript{2} solubility denote further contributing factors turning the Peruvian upwelling system into a CO\textsubscript{2} source\textsuperscript{22}. Based on the biogeochemical analysis of water samples during our cruise to the BUS (see Methods section), South Atlantic Central Water (SACW), being the upwelling source water mass of the NBUS, exhibits preformed nutrient concentrations of 5.86 \(\pm\)0.36 \(\mu\)mol N\textsubscript{pref} kg\textsuperscript{-1} and 0.54 \(\pm\)0.01 \(\mu\)mol P\textsubscript{pref} kg\textsuperscript{-1}. In contrast, Eastern South Atlantic Central Water (ESACW) that dominates upwelling within the SBUS, holds higher preformed nutrient inventories of 8.61 \(\pm\)0.45 \(\mu\)mol kg\textsuperscript{-1} N\textsubscript{pref} and 0.75 \(\pm\)0.02 \(\mu\)mol P\textsubscript{pref} kg\textsuperscript{-1}.

In order to quantify the possible impact of preformed nutrients on the air-sea gas exchange, we calculated pCO\textsubscript{2} on the basis of upwelling source water mass characteristics as obtained from our data (see Methods section) and sea surface conditions (Table 2) by applying the CO2SYS program\textsuperscript{39,40}, which is commonly used for analysing the marine carbonate system\textsuperscript{39}. Three different scenarios were taken into account to demonstrate that the chosen source water mass characteristics comply with the obtained pCO\textsubscript{2} climatology.
In an initial step, we estimated pCO$_2$ of SACW and ESACW when being upwelled by using the respective in situ source water mass characteristics such as temperature (SWT), salinity (SWS), DIC and total alkalinity (TA) within isopycnal ranges of $\sigma_0$ 26.5 – 27.0 (Table 2). In a next step, we quantified the effect of biologically-mediated CO$_2$ uptake at the surface by assuming the complete consumption of all nutrients in the cold upwelled water. Considering a constant Redfield-C:P ratio of 117:1 $^{41}$, the impact of biology can be estimated by subtracting the amount of P-associated carbon (P$^*$117) from the source water’s initial DIC concentration. Additionally, we consider its associated effect on TA using a factor of ~0.12 $^{42}$. This results in pCO$_2$ decreasing below atmospheric concentrations, to levels of ~335 µatm in the NBUS and ~284 µatm in the SBUS. In a third step, the warming of upwelled water was considered by using SST instead of the in situ SWT of the source waters. This indicates a temperature increase of approximately 7°C and led to enhancements in pCO$_2$ by 102 µatm and 97 µatm in the NBUS and SBUS, respectively. The resulting pCO$_2$ of ~437 µatm (NBUS) and ~381 µatm (SBUS) resemble our estimated annual mean pCO$_2$ of the NBUS (487.6 ±2.9 µatm) and SBUS (379.2 ±1.74 µatm). This gives confidence in our outlined source water mass properties and the obtained CO$_2$ climatology, and suggests that deviations from the used classical Redfield-C:P ratio of 117:1, e.g., due to anoxic processes in bottom waters and surface sediments on the NBUS shelf, are of minor importance on the regional scale in the BBS$^{43-45}$. More importantly, it shows that, in contrast to the NBUS, the biologically-mediated drawdown of CO$_2$ overcompensates for the warming effect in SBUS, explaining the opposing CO$_2$ flux directions in the two subsystems. In comparison to SCAW, higher P$_{\text{pref}}$ concentrations of ESACW explain, in turn, the stronger biologically-mediated drawdown of CO$_2$ in the SBUS.

To further quantify this effect, we subdivided the biological impact by individually considering the decrease in pCO$_2$ through the use of regenerated versus preformed nutrients (Supplementary Fig. 2). Compared to a pCO$_2$ of ~437 (NBUS) and ~381 (SBUS) µatm after complete nutrient consumption, the utilization of regenerated nutrients merely results in a pCO$_2$ of ~650 and ~662 µatm in the NBUS and SBUS, respectively. This implies that the consumption of preformed nutrients reduces pCO$_2$ by about
32.8% (650 – 437 = 213 µatm) in the NBUS and 42.5% (662 – 381 = 281 µatm) in the SBUS, which resembles the mean share of $P_{\text{pref}}$ to the total P of 29% in the NBUS and 47% in SBUS (Table 2).

In addition, we assessed the contribution of $P_{\text{pref}}$ to the potential amount of $CO_2$ transfer into the ocean interior on the basis of new production rates from the BUS that were calculated e.g., by multiplying the volume of upwelling waters$^{1,46}$ with corresponding nutrient inventories of the source water masses$^{31}$. The resulting estimates for the NBUS ranged between 180 and 650 g C m$^{-2}$ year$^{-1}$, which, given our defined upwelling area of 377.400 km$^2$, amounts to 68 - 245 Tg C year$^{-1}$. With a mean share of $P_{\text{pref}}$ to the total P of ~29% in the NBUS (Table 2), the utilization of $P_{\text{pref}}$ results in a new production of around 19.7 - 71.1 Tg C year$^{-1}$. Considering the volume of upwelled waters in the SBUS$^{36}$ and corresponding nutrient inventories of ESACW (Table 2) which results in a new production of 0.279 Tg C year$^{-1}$, the contribution of $P_{\text{pref}}$ to new production from the SBUS is low. However, in comparison to the $CO_2$ release during the formation of $P_{\text{pref}}$ in the Atlantic sector of the Southern Ocean (110 Tg C year$^{-1}$), a new production driven by the utilization of $P_{\text{pref}}$ of 19.7 - 71.1 Tg C year$^{-1}$ implies that the biological carbon pump in the BUS countervails over 20% of the $CO_2$ loss in the subpolar South Atlantic region (Supplementary Fig. 3). This emphasizes the role of the BUS as a significant hub for restoring the $CO_2$ uptake efficiency of the biological carbon pump. Yet, its strength could be weakened with the predicted decrease in upwelling intensity in the NBUS$^{47,48}$. Whether the predicted enhancement in upwelling of the southern system$^{36,49}$ could however compensate for the lowered biological carbon pump efficiency of the NBUS, remains open for debate. Thus, in addition to the Southern Ocean, also a better understanding of the BUSs response to climate change is essential to predict the $CO_2$ uptake efficiency of the biological carbon pump and the future evolution of $CO_2$ in the atmosphere.

**Methods**

**Study region**

The Benguela Upwelling System (BUS) stretches across the north of Cape Frio from ~15°S to Cape Agulhas (~35°S), while being bound by warm waters of the Angola and Agulhas current to its northern
and southern ends, respectively\(^{38}\). Coastal upwelling is thereby controlled by south-easterly winds emanating from the interplay between the South Atlantic Anticyclone (SAA) and the continental low pressure trough, causing the emergence of distinct upwelling cells along the shoreline\(^{37}\). The strongest upwelling cell is located at Lüderitz (~26°S) and separates the northern (NBUS) from the southern (SBUS) upwelling region\(^{50}\). South Atlantic Central Water (SACW) is mainly formed in the Brazil-Malvinas confluence zone, where it is subducted beneath warmer subtropical water masses and transported eastward across the South Atlantic into the Cape basin\(^{51-53}\). Here it converges with the Agulhas water from the Indian Ocean to form ESACW that enters the SBUS from the south\(^{54-56}\). The majority of the SACW circumvents the SBUS along the Benguela Current and enters the BUS from the north via the Angola-Benguela Frontal Zone (ABFZ) as a poleward undercurrent, which, unlike ESACW, is nutrient-enriched and oxygen-depleted\(^{57}\). In addition, both SACW and ESACW comprise of subtropical mode waters which are characterized by preformed phosphate ($P_{\text{pref}}$) concentrations of ~0.6 $\mu$M, which in contrast to $P_{\text{pref}}$ of Southern Ocean waters (~1.6 $\mu$M)\(^{58}\) strongly correspond with the average $P_{\text{pref}}$ concentrations of the NBUS (~0.54 $\mu$M) and SBUS (~0.75 $\mu$M).

Upwelling intensities in both subsystems exhibit a seasonal pattern which is mainly driven by temporal shifts of the SAA. As the SAA moves north-westward, the NBUS experiences maximum upwelling intensities during austral winter (June-August), while leading to a dominating westerly wind regime which weakens upwelling in the SBUS. With the south-eastward displacement of the SAA, upwelling in the SBUS is mainly confined to the summer season (September-March)\(^{38,59,60}\). Additionally, the seasonality in upwelling is more pronounced in the SBUS as compared to the NBUS due to the perennial upwelling-favourable winds that reign in the northern region\(^{37}\). This is also reflected in primary productivity which in the SBUS is twice as large in the summer than winter\(^{61}\). Furthermore, studies have shown a decrease and intensification of upwelling in the NBUS and SBUS, respectively, over the past decade in response to global warming\(^{36,49}\) and a southward shift of the SAA\(^{47}\). The associated increase in sea water temperatures in the NBUS\(^{62}\) could potentially be related to the prominent decrease in
zooplankton size spectra in the BUS. Nevertheless, the productivity has remained consistently elevated, and still supports high fishery yields in both subsystems with sardine and horse mackerel as main target species in the SBUS and NBUS, respectively.

Sea surface pCO$_2$ data collection

For the analysis and quantification of air-sea gas exchanges within the BUS, continuous underway measurements were carried out as described in ref. study during 2008 and 2019 (Supplementary Table 1). Additional quality-controlled measurements on sea surface fCO$_2$ from the Surface Ocean CO$_2$ Atlas (SOCAT) v2020 were converted into pCO$_2$ and embedded into our analysis. All pCO$_2$ measurements were normalized to a reference year (2020) by using a mean yearly change rate in seawater pCO$_2$ of 1.5 µatm year$^{-1}$ and multiplying it with respective observations for both upwelling regions (NBUS, SBUS).

All normalized measurements were distributed on a 0.1° x 0.1° grid, with each value representing the average of all observations falling into the same grid cell. Overall, the extended data set on pCO$_2$ records used in this study covers the shelf and coastal areas along the continental margin off Namibia and South Africa, while spanning a timeframe from 1986 to 2020 with over 250 000 data points within the area from approximately 5°E to 18.7°E, and 16°S to 34.5°S.

Carbon flux calculation

Differences in the partial pressure of carbon between the sea surface (pCO$_{2,sw}$) and atmosphere (pCO$_{2,at}$) were used to determine carbon flux rates (FCO$_{2}$) using equation (1):

\[
FCO_2 = K_0 \times k \times (pCO_{2,sw} - pCO_{2,at})
\]

where $K_0$ is the solubility coefficient of CO$_2$ and $k$ represents gas transfer velocity of CO$_2$. The gas transfer velocity $k$ was calculated following equation (2):

\[
k = 0.251 \times u^2 \times \left(\frac{Sc}{660}\right)^{-0.5}
\]

$Sc$ is the Schmidt number of CO$_2$ in seawater, 660 represents $Sc$ at 20°C water temperature and $u$ refers to the wind speed (m/s) at 10 m above the sea surface. Additional data on sea surface temperature (SST)
(°C) and salinity (PSU) were thereby required for the determination of $S_c$ using the parameterization after Wanninkhof et al.\textsuperscript{70}. Data on wind speed, SST and salinity were based on shipboard measurements (Supplementary Table 1), which were distributed on a 0.1° x 0.1° grid and averaged over each grid cell. The flux calculation was performed using the average sea surface pCO$_2$, wind speed, SST and salinity of all grid cells within the defined NBUS and SBUS region. Seasonal flux estimates were calculated using gridded and averaged pCO$_2$, wind speed, SST and salinity data collected during spring and summer (September till March), and austral autumn and winter (April till August), respectively.

**Water column sampling and analysis**

The analysis of water mass characteristics and biogeochemical settings in the BUS was based on data gathered during *RV Meteor* cruise M153, which covered on- and offshore areas of both subsystems and hence allowed a direct comparison of both upwelling zones for one given timeframe. We collected CTD profiles of temperature, salinity and oxygen, and defined the upwelling SACW and ESACW source waters by using the definition provided by ref.\textsuperscript{71}. The analysis of dissolved inorganic nutrients (phosphate P, nitrate N) was carried out as outlined in ref.\textsuperscript{44,72}. Furthermore, the calculation of preformed and regenerated nutrients ($P, N_{pref}$ and $P, N_{reg}$ respectively) was performed following ref.\textsuperscript{58} by including the apparent oxygen utilization (AOU) as well as the oxidation ratios $R_{P,O_2} = 1/138$ (phosphate) and $R_{N,O_2} = 14/138$ (nitrate), using equation (3) and (4):

$$P, N_{reg} = R_{P,N,O_2} \times AOU$$  \hspace{1cm} (3)
$$P, N_{pref} = P, N - P, N_{reg}$$  \hspace{1cm} (4)

These oxidation ratios are based on our nutrient analysis, with a N:P-ratio of ~14:1, in line with ref. study\textsuperscript{31}. The analysis of dissolved inorganic carbon (DIC) was performed with a cavity ringdown spectrometer (Picarro G2201-I, 1510CFIDS2047_v1.0) attached to a Liaison A0301 and an AutoMate Prep device. For the analysis of total alkalinity (TA), samples were collected in 250 ml borosilicate bottles using silicone tubes (Tygon). The bottles were rinsed twice, filled from the bottom to avoid
bubbles and analysed on board using the VINDTA 2C system (Marianda, Kiel, Germany). The samples
were titrated with a fixed volume of hydrochloric acid (HCl) by equal increments of HCl (0.1 N HCl).
Both the Picarro and VINDTA 2C systems were calibrated using Certified Reference Material (CRM,
batch #177) provided by A. Dickson (Scripps Institution of Oceanography, La Jolla, CA, USA), while
affirming an accuracy of ±12 μmol kg⁻¹ and ±4.3 μmol kg⁻¹ for DIC and TA, respectively.

Statistical information

The uncertainty in average parameter calculations of pCO₂, CO₂ exchange coefficients and fluxes (Table
1) as well as biogeochemical characteristics of source waters (Table 2) is presented as the standard error
(s.e.), together with the number of values (n) used for the average calculation.

Data Availability

The underlying data of this study on pCO₂ and CO₂ flux coefficients were obtained from the Surface
Ocean CO₂ Atlas (SOCAT) v2020 (https://www.socat.info/index.php/data-access/) and from the Pangaea
data pool (access link to individual cruises provided in Emeis et al.31). Shipboard underway data of
German research vessels are further accessible via the German Oceanographic Data Centre (DOD) under
the Federal Maritime and Hydrographic Agency (https://www.bsh.de/EN/Home/home_node.html).
Average atmospheric concentrations of CO₂ were obtained from the Global Monitoring Laboratory
(GML) of the U.S. National Oceanographic and Atmospheric Administration (NOAA) Research
(https://www.esrl.noaa.gov/gmd/ccgg/trends/data.html).

Code Availability

The CO2SYS program for Python as applied in this study is freely available and documented under
https://pypi.org/project/PyCO2SYS/.

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**Author contributions**

TR and NL designed the study. The shipboard data collection and analysis in 2008 to 2014 was performed by TR, and in 2019 by TR and CS. CS led the writing of the manuscript. All authors discussed the results and contributed to the writing of the manuscript.

**Ethics declarations**

Competing interests

The authors declare no competing interests.

**Supplementary information**

Supplementary Figure 1-3
Supplementary Table 1

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Figures

Figure 1: Maps of pCO$_2$ measurements of research vessel cruises within the Benguela Upwelling System used in this study.

(a) Underlying cruise tracks of the 14 cruises (red) and those embedded in SOCAT v2020 (blue). (b) Recorded pCO$_2$ measurements (in µatm), normalized to the reference year 2020. (c) Normalized pCO$_2$ measurements (in µatm) interpolated on a 0.5° grid. Contour lines represent the atmospheric pCO$_2$ of the reference year 2020 based on Mauna Loa records (414 µatm). The interpolation was performed after the minimum curvature interpolation method$^{74}$ implemented in the Generic Mapping Tools (GMT).
Figure 2: Spatial and temporal variability of sea surface pCO₂.

a) Average cross-shelf distribution of all pCO₂ measurements (in µatm) of the northern part of the BUS (NBUS) with distance to the coast (in km). The grey line marks the offshore boundary of the upwelling zone. Values were normalized to the reference year 2020, and averaged over intervals of 10 km coastal distance.

b) As in a, except for the southern part (SBUS).

c) Average latitudinal pCO₂ concentrations across the NBUS and SBUS regions, for austral spring and summer (blue) and austral autumn and winter (red). The dashed grey line in each subplot represents the atmospheric pCO₂ of the reference year 2020 based on Mauna Loa records (414 µatm). The shaded areas in each subplot represent the standard deviation.
### Table 1: CO₂ exchange coefficients and flux rates for the northern and southern Benguela Upwelling System.

Annual and seasonal mean air-sea CO₂ gas exchange rates, with positive flux values indicating CO₂ outgassing. Each CO₂ exchange coefficient represents the average value calculated on the basis of shipboard data gathered during the 14 cruises and those embedded into SOCAT v2020, which we distributed on a 0.1°x0.1° grid. Uncertainties are given as the standard error. The corresponding *n* number of observations equals the number of grid cell values, each representing the average of all measurements falling into the same grid cell during the respective time period (Annual, September-March, April-August).

| Parameter                          | NBUS                              | SBUS                             |
|------------------------------------|-----------------------------------|----------------------------------|
|                                    | Annual   | Sep.-Mar. | Apr.-Aug. | Annual   | Sep.-Mar. | Apr.-Aug. |
| Sea Surface Temperature (°C)       | 17.66 ±0.07 | 18.01 ±0.07 | 15.99 ±0.07 | 17.31 ±0.06 | 17.69 ±0.07 | 15.62 ±0.07 |
|                                    | *n*=1549 | *n*=1348 | *n*=495    | *n*=1004 | *n*=855    | *n*=335    |
| Sea Surface Salinity (PSU)         | 35.25 ±0.01 | 35.24 ±0.01 | 35.24 ±0.01 | 34.88 ±0.03 | 34.85 ±0.03 | 34.99 ±0.02 |
|                                    | *n*=1549 | *n*=1348 | *n*=495    | *n*=979   | *n*=831    | *n*=332    |
| Wind Speed (m/s)                   | 7.96 ±0.08 | 7.85 ±0.10 | 7.94 ±0.11 | 7.95 ±0.12 | 8.14 ±0.13 | 5.62 ±0.32 |
|                                    | *n*=1543 | *n*=1348 | *n*=489    | *n*=697   | *n*=649    | *n*=75     |
| pCO₂,sw (µatm)                     | 487.55 ±2.9 | 475.42 ±3.07 | 556.03 ±5.67 | 379.15 ±1.74 | 378.15 ±2.24 | 381.91 ±1.99 |
|                                    | *n*=1535 | *n*=1326 | *n*=492    | *n*=1017 | *n*=894    | *n*=335    |
| Solubility coefficient of CO₂, *K₀* | 0.0345 ±0.0006 | 0.0342 ±0.0007 | 0.0363 ±0.0001 | 0.0350 ±0.0007 | 0.0346 ±0.0007 | 0.0367 ±0.0008 |
| Piston velocity, *k*               | 14.89 ±0.33 | 14.61 ±0.36 | 14.18 ±0.41 | 14.72 ±0.47 | 15.59 ±0.53 | 7.04 ±0.82 |
| Carbon Flux rate (mol C m⁻² yr⁻¹)  | 3.31 ±0.19 | 2.68 ±0.19 | 6.39 ±0.41 | -1.58 ±0.03 | -1.77 ±0.05 | -0.73 ±0.04 |
Table 2: Shipboard data on source water mass characteristics and sea surface conditions used for sea surface pCO₂ simulations with CO2SYS.

Properties of source water masses presented as average parameters within isopycnal ranges of σθ: 26.5 – 27.0 within the NBUS and SBUS, based on CTD casts and nutrient analysis during RV Meteor cruise M153. Sea surface temperature and salinity (<5 m water depth) are based on annual averages as estimated from shipboard data gathered during the 14 cruises, and those provided by SOCAT v2020. The effect on sea surface pCO₂ is estimated using CO2SYS with input parameters on total alkalinity (TA), dissolved inorganic carbon (DIC), source water and sea surface temperature (SWT, SST), salinity (SWS, SSS), total and preformed phosphate (Pₜₐ₉₉, Pₚ₉₉). Uncertainties are given as the standard error, with n number of observations used for average calculations.

|       | Source water mass (σθ: 26.5 – 27.0) | Sea surface (< 5 m depth) |
|-------|-------------------------------------|---------------------------|
|       | DIC⁻¹ | TA⁻¹ | Pₜₐ₉₉⁻¹ | Pₚ₉₉⁻¹ | Pₚ₉₉-% | SWT²   | SWS³   | SST² | SSS³ |
| NBUS  | 2314.23 | 2298.73 | 1.87 | 0.54 | 28.88 | 11.5 | 35.04 | 17.66 | 35.25 |
|       | ±6.9 | ±1.7 | ±0.03 | ±0.01 | ±0.1 | ±0.09 | ±0.01 | ±0.07 | ±0.01 |
|       | n=95 | n=97 | n=96 | n=96 | n=96 | n=267 | n=267 |
| SBUS  | 2246.17 | 2283.94 | 1.60 | 0.75 | 46.88 | 10.5 | 34.83 | 17.31 | 34.88 |
|       | ±6.2 | ±2.6 | ±0.05 | ±0.02 | ±0.2 | ±0.06 | ±0.01 | ±0.06 | ±0.03 |
|       | n=102 | n=101 | n=79 | n=79 | n=79 | n=265 | n=265 |

Units in *¹µmol kg⁻¹, *²°C, *³PSU.
Maps of pCO2 measurements of research vessel cruises within the Benguela Upwelling System used in this study. a Underlying cruise tracks of the 14 cruises (red) and those embedded in SOCAT v2020 29 (blue). b Recorded pCO2 measurements (in μatm), normalized to the reference year 2020. c Normalized pCO2 measurements (in μatm) interpolated on a 0.5° grid. Contour lines represent the atmospheric pCO2 of the reference year 2020 based on Mauna Loa records (414 μatm). The interpolation was performed after the minimum curvature interpolation method74 implemented in the Generic Mapping Tools (GMT).
Figure 2

Spatial and temporal variability of sea surface pCO2. a Average cross-shelf distribution of all pCO2 measurements (in μatm) of the northern part of the BUS (NBUS) with distance to the coast (in km). The grey line marks the offshore boundary of the upwelling zone. Values were normalized to the reference year 2020, and averaged over intervals of 10 km coastal distance. b As in a, except for the southern part (SBUS). c Average latitudinal pCO2 concentrations across the NBUS and SBUS regions, for austral spring and summer (blue) and austral autumn and winter (red). The dashed grey line in each subplot represents the atmospheric pCO2 of the reference year 2020 based on Mauna Loa records (414 μatm). The shaded areas in each subplot represent the standard deviation.

Supplementary Files

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