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Simulating potential impacts of bottom trawling on the biological carbon pump: a case study in the Benguela Upwelling System

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Bottom-trawl fishery is known to cause major disturbances to marine sediments as the dragging of trawl gears across the seabed fosters sediment resuspension, which can lead to organic particle remineralization and release of benthic CO₂ and nutrients into bottom waters. However, its effects on carbon cycling and biological productivity, especially in highly productive regions like the Benguela Upwelling System (BUS), are less well studied. Here, we simulated carbon (C) and nutrient pathways from the trawled coastal seabed to overlying water masses that are being upwelled into the sunlit surface within the BUS, using shipboard data on sea surface and water column characteristics and published benthic CO₂ emission estimates from bottom-trawled sediments. The latter reports 4.35 and 0.64 Tg C year $^{-1}$ to be released from the seabed into upwelling source waters after bottom trawling in the northern (NBUS) and southern (SBUS) subsystems, respectively. Based on these values, we estimated a corresponding nitrate (N) input of 1.39 and 0.47 µmol kg⁻¹ year⁻¹, enhancing source water nitrate concentrations by ~5% and ~2%. Trawl-induced nitrate input into the sunlit surface could support a new production of 3.14 and 0.47 Tg C year⁻¹ in the NBUS and SBUS, respectively, recapturing only 2/3 of CO₂ released after bottom trawling into biomass, mainly due to differences in stoichiometric C:N ratios between the sediment (~9) and surface biomass (Redfield, 6.6). The remaining benthic CO2 can thereby lead to an increase in surface CO2 concentration and its partial pressure (pCO₂), impeding CO₂ uptake of the biological carbon pump in the BUS by 1.3 Tg C year⁻¹, of which 1 Tg C year⁻¹ is emitted to the atmosphere across the northern subsystem. Our results demonstrate the extent to which bottom trawling may affect the CO₂ storage potential of coastal sediments on a basin-wide level, highlighting the need to better resolve small-scale sediment characteristics and C:N ratios to refine trawl-induced benthic carbon and nutrient effluxes within the BUS.

KEYWORDS

Benguela coastal upwelling system, bottom trawling effects, biological carbon pump, carbon and nutrient cycling, CO_2 emissions

1 Introduction

The burial of carbon as organic matter in ocean sediments forms an integral part in the global carbon cycle by removing carbon from its three main reservoirs: the ocean, the atmosphere and the terrestrial biosphere (Siegenthaler and Sarmiento, 1993; Avelar et al., 2017; Rixen, 2023). The underlying mechanism refers to the assimilation of CO₂ through the generation of biomass by plants on land and by phytoplankton in the ocean and its transfer into marine sediments. In the ocean, the fixation of CO₂ into biomass in the sunlit surface ocean and its transport across the water column and into sediments is commonly termed as the biological carbon pump (Volk and Hoffert, 1985; Boyd et al., 2019). Hereby, coastal upwelling ecosystems, especially along the eastern margins of the Pacific and Atlantic basins, play a crucial role for the sediment carbon storage. They belong to one of the most productive regions in the ocean, contributing 11% to global new production, which refers to biomass largely produced based on upwelled nutrients (Eppley and Peterson, 1979; Chavez and Toggweiler, 1995; Messié et al., 2009), while supporting high amounts of carbon being transferred and stored in the ocean and sediments. Due to their outstanding biological productivity, these upwelling systems are particularly vulnerable to anthropogenic pressures like fisheries (Sala et al., 2021). Hereby, bottom trawling fisheries are being regarded as the greatest source of physical disturbance to the seafloor (Amoroso et al., 2018; O'Hara et al., 2021), with the potential to alter carbon-rich sea sediments and their capacity to store atmospheric CO₂ (De Borger et al., 2021; Epstein et al., 2022). However, the impact of bottom trawling on biogeochemical cycling and release of carbon into the water column and atmosphere is still subject to intense discussion (Palanques et al., 2014; Pusceddu et al., 2014; Hale et al., 2017; Paradis et al., 2019; Tiano et al., 2019).

The ocean's carbon storage received broad recognition and became part of nationwide climate change mitigation strategies through the concept of 'Blue Carbon' (BC) (Hilmi et al., 2021; Christianson et al., 2022). BC was promoted in 2009 and intended to facilitate carbon quantification and to provide guidance for sustainable resource management and conservation of carbon stored by marine ecosystems within the coastal and open ocean (Nellemann et al., 2009). Although coastal ecosystems like mangroves, seagrasses and saltmarshes are currently assigned to BC (Pendleton et al., 2012), biomass carbon storages within the water column and sediment across the continental shelf, slope and deep ocean remain unconsidered, despite their relevance in mitigating greenhouse gas (GHG) emissions (Howard et al., 2017; Luisetti et al., 2019). The inclusion of sediments, especially those located in productive upwelling ecosystems into the BC framework should therefore be perceived as a key interest to sustain and manage carbon storages and to foster climate change mitigation strategies. As a precondition, various criteria have to be met before establishing marine ecosystems as BC, such as whether they can be managed to facilitate climate change mitigation or are currently affected by anthropogenic disturbances, with the impact being observable and quantifiable (Lovelock and Duarte, 2019). However, a lack of data to elaborate carbon emissions and sequestration capacities, human impacts and the effectiveness of management strategies to reduce GHG emissions in coastal sediments are all key criteria that currently prevent these coastal habitats from being assigned to the BC concept, albeit of rising scientific concerns on the quantity and vulnerability of sediment carbon storages to anthropogenic activities (Avelar et al., 2017; Atwood et al., 2020; Sala et al., 2021).

Hence, the goal of our study is to further incentivize the integration of sediments in the BC discourse by elucidating the impact of human interventions through bottom trawl fisheries on the sedimentary carbon storage and its potential role in driving atmospheric CO₂ emissions in one of the most productive coastal upwelling systems, namely the Benguela Upwelling System (BUS). We thereby focus on the effects of bottom trawling on the resuspension of particulate matter at the seafloor (Oberle et al., 2016; Breimann et al., 2021) that has further been linked to increased oxygen consumption and organic matter remineralization which, in turn, can cause high amounts of nutrients and dissolved inorganic carbon (DIC) to be released into the water column (Almroth-Rosell et al., 2012; Bradshaw et al., 2021; Breimann et al., 2021) (Figure 1). By combining sea surface measurements with water column profiles of the upwelling source waters from the past two decades across the BUS, we simulated the impact of bottom trawling on the water column and sea surface partial pressure of CO_2 (pCO₂) using CO2SYS simulations (Lewis and Wallace, 1998; Humphreys et al., 2020) and recently published global benthic CO₂ emission estimates from bottom trawling activities (Sala et al., 2021). Hereby, CO₂ emissions of bottom trawling are defined as the labile fraction of carbon released into the bottom water as aqueous CO2 (DIC). This DIC stems from the remineralization process of resuspended sediment after the occurrence of bottom trawling, and is referred to as the benthic CO_2 efflux. By estimating the effect of the benthic CO_2 efflux on the biological productivity, we additionally shed light on the role of carbon to nutrient ratios in mitigating CO₂ emissions from bottom trawling activities.

2 Study site

The region under study is the Benguela Upwelling System (BUS), which is located along the west coast of southern Africa and stretches from the Angola Benguela Frontal Zone at around 17°S to the southwestern tip of South Africa at approximately 34°S (Kämpf and Chapman, 2016). Due to the offshore wind-driven advection of water masses, this region is dominated by coastal upwelling, a process known to uplift cold, CO2- and nutrient-rich water masses from the deep ocean into the surface region. With multiple upwelling cells along the shoreline, the Lüderitz Cell at around 26°S is the strongest one separating the BUS into a northern (NBUS) and southern part (SBUS) (Hutchings et al., 2009), which cover areas of 377,400 and 177,600 km², respectively (Siddiqui et al., 2023). Both subsystems are influenced by two distinct source water masses dominating the bottom shelf region, namely South Atlantic Central Water (SACW) in the NBUS, and Eastern South Atlantic Central Water (ESACW) in the SBUS (McCartney, 1977; Gordon et al., 1992; Shillington et al., 2006). Near the coast, upwelling of CO2- and nutrient-rich waters leads to an



initial rise in the sea surface partial pressure of CO_2 (pCO₂) above that of the atmosphere and outgassing of CO₂ at the air-sea interface, which is further amplified by the warming of upwelling waters and ultimate reduction of the CO2 solubility in seawater. In turn, the availability of nutrients creates a favorable environment for primary producers to fix CO₂ into biomass, which could also be displayed e.g., by enhanced satellite chlorophyll concentrations in close proximity to the coast (Weeks et al., 2006; Demarcq et al., 2007; Lamont et al., 2019), leading to a continual decrease in pCO₂ within the offshore-advecting upwelling waters. In the SBUS, the biologically-mediated CO₂ uptake offsets the increase of CO2 due to surface warming of upwelling waters, causing this region to act as an atmospheric CO2 sink, while in the NBUS, the impact of surface warming on the pCO2 exceeds the effect of the biological carbon pump and promotes CO2 outgassing (Siddiqui et al., 2023). The biologically-mediated CO₂ uptake is strongly affected by the upwelling source water's nutrient concentration, which comprise of (a) biologically-unused, so-called preformed nutrients, (b) regenerated nutrients originating from remineralization of organic matter within the water column, and (c) those nutrients released by the remineralization of organic matter in sediments across the sedimentwater interface via diffusional processes (Neumann et al., 2016).

The biological productiveness of the BUS promotes the sinking and subsequent remineralization of organic matter (OM) previously formed at the sea surface. Biogeochemical oxygen consumption linked to organic matter remineralization causes low dissolved oxygen concentrations, leading to the development of an Oxygen Minimum Zone (OMZ) in both the NBUS and SBUS. In the latter case, the OMZ is mostly controlled by the seasonality in biological productivity (Pitcher et al., 2014; Lamont et al., 2015), while in the NBUS, the OMZ is mainly governed by the seasonality in the poleward advection of poorly oxygenated SACW, leading to a greater expansion of the OMZ across the Namibian shelf and continental slope (Monteiro et al., 2006; Mohrholz et al., 2008). The high biological productivity and low bottom oxygen in the water column foster the accumulation of OM at the seafloor. In the NBUS, this has led to the formation of a mud belt region of mainly diatomaceous ooze (Emeis et al., 2004) in shallow depths across the 100 – 200 m isobath from where OM is further transported laterally and deposited across the upper to central slope off Namibia (Monteiro et al., 2005; Inthorn et al., 2006; van der Plas et al., 2007) (Figure 2A).

Meanwhile, at the base of the marine food chain, primary producers further support a vast richness in marine species that are relevant for the fishing industry, with the hake directed bottomtrawl fishery being the most economically valuable one in both Namibia and South Africa (Mwafila, 2017). Bottom trawling activities in the BUS mainly occur along the outer continental shelf and upper slope region within water depths between 200 and 1000 m (Figure 2B). The inner shelf (<200 m) remains largely unaffected as a result of trawl restrictions within the Namibian Exclusive Economic Zone (EEZ). These restrictions were previously passed for the protection of juvenile fish, as well as due to fishing legislations within Marine Protected Areas (MPAs) that are located within the shallow coastal zone, with the MPAs' spatial extent making up less than 2% of the Namibian EEZ (Finke et al., 2020). In the BUS, trawling gears are dragged across unconsolidated sediments that can mainly be classified as terrigenous, biogenic and authigenic (Rogers and Rau, 2010). Surficial sediments from the north are further characterized by relict, nitrogen-poor particulate organic matter, which originated from the inner-shelf zone from where it was redistributed under low oxygen conditions across the bottom shelf to offshore depocenters off Namibia (Monteiro et al., 2005; Inthorn et al., 2006; Bruni et al., 2022).



FIGURE 2

Map showing (A) published carbon storage within the first meter of sediment (Mg C km⁻²) (Atwood et al., 2020) and (B) the benthic CO₂ emission estimates from bottom trawling activities (Mg CO₂ year⁻¹) (Sala et al., 2021) within the Benguela Upwelling System's northern (NBUS) and southern (SBUS) part.

3 Material and methods

3.1 Modelling concept

We elucidate the impact of bottom trawling on the biological carbon pump by focusing on changes in the water column, sea surface pCO₂ and new production that could arise from the additional release of CO₂ into the bottom water after the remineralization of resuspended sediments. It was shown that the release of sedimentary carbon through bottom trawling may extend up to 10 m or more above the seafloor (Churchill, 1989) and lead to resuspended sediments being remineralized and further advected laterally and vertically across the water column (Pusceddu et al., 2014; De Borger et al., 2021; Morys et al., 2021). Additional experimental model results from a study in the Eastern Mediterranean indicated bottom trawl-induced plumes of sediment along the outer continental shelf and upper slope promoted the supply of remineralized benthic nutrients into the euphotic zone during coastal upwelling, increasing annual net primary productivity by 15% (Dounas et al., 2007). Thus, we assumed the released sedimentary carbon as reported by (Sala et al., 2021) to be fed into the upwelling source waters that are overlaying the bottom shelf region, and subsequently, to be upwelled together with the source waters into the surface region within the individual subsystems. We also took into account the release of nutrients during the remineralization process of resuspended organic matter and their transfer into the upwelling source water masses. The extent to which source water mass concentrations of carbon and nutrients are raised by bottom trawling is hereby controlled by the volume of upwelling waters which the benthic nutrients and carbon are dispersed into. To

address the effect of bottom trawling on the air-sea gas exchange, we simulated sea surface pCO₂ using the CO2SYS routine with source water masses' DIC, Total Alkalinity (TA) and nutrient concentrations, as well as source water temperature and salinity (SWT, SWS) as input parameters (Table 1). We assumed upwelled nutrients and carbon of the source water masses to be consumed at the surface following the Redfield C:N ratio of 106:16 (Rixen et al., 2023), and ultimately to be transformed into organic matter and exported into deeper water layers below the euphotic zone. With this, we follow the bottom-up principle which has been previously applied within the BUS to outline new production rates and carbon export fluxes on the basis of upwelling source water mass inventories (Eppley and Peterson, 1979; Messié et al., 2009; Waldron et al., 2009). With a constant Redfield-ratio of 106:16 (C:N), the impact of biology was estimated by subtracting the amount of nitrate-associated carbon from the source water's initial DIC concentration, and adding the associated release of total alkalinity (TA) to the original source water TA. Additionally, we considered the surface warming effect of the upwelling source waters to account for the decrease in the CO₂ solubility of seawater and its impact on pCO₂ by using the locally measured sea surface temperatures and salinities (SST, SSS) instead of those of the source water masses. In order to quantify the effect of bottom trawling on the sink and source functionalities of the BUS, we translated the increase in pCO₂ into equivalent changes in CO₂ fluxes. Therefore, we used the offshore increase in pCO2 through bottom trawling to add to the basin-scale average pCO2 as estimated from ordinary kriging interpolations (see section 3.5) for calculating the annual CO₂ fluxes within both subsystems. Lastly, we shed light on changes in new production rates on the basis of nutrients and carbon that were released after bottom trawling and upwelled into the surface region, and by taking

Parameter	Value (\pm standard error)		
	NBUS	SBUS	Unit
Benthic CO ₂ efflux*1	4.35 3.62*10 ¹¹	0.64 5.33*10 ¹⁰	Tg C year ⁻¹ mol C year ⁻¹
Dissolved Inorganic Carbon, DIC*2	2237.97 ± 18.48	2193.86 ± 22.91	µmol kg ⁻¹
Total Alkalinity, TA*2	2303.90 ± 1.35	2297.49 ± 3.89	µmol kg ⁻¹
Nitrate, N*2	26.49 ± 1.04	21.06 ± 0.20	µmol kg ⁻¹
Source Water Temperature, SWT*2	11.58 ± 0.13	10.33 ± 0.09	°C
Source Water Salinity, SWS*2	35.05 ± 0.02	34.83 ± 0.01	PSU
Volume of upwelled water*3,4	0.9	0.4	Sverdrup, 1*10 ⁶ m ³ s ⁻¹
Sea Surface Temperature, SST*3	17.63 ± 1.97	17.34 ± 1.27	°C
Sea Surface Salinity, SSS*2	35.26 ± 0.39	35.04 ± 0.52	PSU
Wind Speed*2	7.88 ± 2.98	7.99 ± 2.09	m/s
Annual mean sea surface partial pressure of CO ₂ , pCO ₂ *2	492.30 ± 115,82	383.90 ± 53.73	μatm
Solubility coefficient of CO ₂ , K ₀ *2	0.0346 ± 0.0021	0.0349 ± 0.0013	/
Piston velocity, pv *2 upper/lower boundary	14.58 29.1/5.36	14.88 24.46/7.86	1
Carbon Flux rate *2 upper/lower boundary	3.45 16.14/-0.65	-1.38 1.68/-2.11	mol C m ⁻² yr ⁻¹

TABLE 1 Parameters used for simulating impacts of bottom trawling, including the benthic CO₂ efflux, average hydrographic conditions of source water masses, CO₂ exchange coefficients and flux rates for the northern and southern Benguela Upwelling System.

*1 Sala et al. (2021), *2 Siddiqui et al. (2023), *3 Bordbar et al. (2021), *4 Muller et al. (2014).

note of the efficiency at which these nutrients and carbon are being recaptured into biomass. A schematic overview of the bottom-up approach is given in Supplementary Figure 1.

3.2 Surface sediment characteristics

We used undisturbed sediment core samples that were collected on board RV *Africana* (AFR258), *Meteor* (M48/2, M76/2, M103/1) and *Maria S. Merian* (MSM17/3) (see Table 2) with a multicorer (Oktopus Kiel) to outline the stoichiometric carbon to nutrient ratios within the top sediment layer. The sampler was equipped with acrylic tubes of 10 cm diameter and 60 cm length, and was used to retrieve sediment cores that were sliced in 1cm intervals, kept frozen under -20°C and freeze-dried in the home laboratory, and analyzed for concentrations of total nitrogen and organic carbon with an Elemental Analyzer (Carlo Erba NA 1500).

3.3 Benthic CO₂ efflux

We used published global benthic CO_2 efflux estimates of bottom trawling and dredging fishing practices (Sala et al., 2021). The benthic CO_2 efflux was derived from the amount of carbon stored within the top layer of the sediment as based on recently published global carbon stocks (Atwood et al., 2020), and the labile fraction of carbon that is

TABLE 2 Average stoichiometric carbon to nutrient ratios of multicore samples collected during various cruises to the northern Benguela Upwelling System.

Cruise	Number of stations	Water depth range (m)	Sediment depth range (cm)	C _{org} : N _{tot} (molar)
AFR258 02.12.2009 - 16.12.2009	5	48-300	0 - 15.0	8.80
M48-2 05.08.2000 - 23.08.2000	23	34-1906	0 - 0.5	9.85
M76-2 17.05.2008 - 04.06.2008	9	64-234	0 - 41.5	8.77
M103-1* 27.12.2013 - 18.01.2014	37	34-2126	0 - 9.0	8.99
MSM17-3 20.01.2011 - 07.03.2011	45	23-4825	0 (surface)	9.38
average				9.16

*Lahajnar (2015).

remineralized and released at the sediment-water interface after the occurrence of bottom trawling. The latter is inferred from the sediment type and trawl activity as estimated from automatic identification systems (AIS) data that was used for tracking the fishing trawlers' distance, speed, and the applied gear type with its corresponding penetration depth. The sediment type was thereby used as a proxy for the labile carbon fraction due to its impact on organic matter preservation and remineralization. For each sediment type (coarse, sandy, fine and biogenic), the proportion of labile organic carbon was assigned using literature values, amounting e.g., to 0.04 for sandy sediments and to 0.7 for muds, silts or biogenic sediments. The CO_2 efflux was then modelled using an average first-order reaction constant *k* for the degradation process as a function of oceanic region (Atlantic = 1.00).

Hereby, several studies outlined the underlying first-order reaction constant k as applied by Sala et al. (2021) to be overestimated, since it based on a reactivity value for highly reactive, fresh organic carbon that has recently been transferred to the sediment surface, and applied to a bulk of less reactive compounds within deeper sediment layers.

To shed light on the applicability of *k* by Sala et al. (2021) for the BUS, we took into account the degradation index (DI) inferred from amino acids of sediment samples collected during cruise MSM17/3. According to Dauwe et al. (1999), the DI derived from amino acids of particulate matter samples can be directly linked to the degradation rate, allowing to assess the quality of organic matter and first-order reaction constants. We estimated an average DI of 0.12 (standard deviation ± 0.1) for surface sediment samples collected at water depths between 200 - 1000 m (in line with the bottom trawled area), with 0.36 as the highest value. Given the linear correlation between DI and k, these values imply the reactivity constant k to fall within a spectrum of 0.1 - 1 (Dauwe et al., 1999), where k=1 is used by Sala et al. (2021) to infer the benthic CO₂ efflux of the BUS. Hereby, higher values are indicative for well-preserved, fresh organic matter and lower values implying less well-preserved organic matter and faster degradation process.

3.4 Physical and biogeochemical water column characteristics

We used data on upwelling source water mass compositions within the NBUS and SBUS taken from Siddiqui et al. (2023). This dataset is based on water samples collected with multiple CTD/ Rosette systems during various cruises to the BUS which we listed in Supplementary Table 1, including data from the Global Ocean Data Analysis Project version 2.2020 (GLODAPv2_2020). Water samples were analyzed for temperature, salinity, oxygen, DIC, total alkalinity (TA) and nutrients (phosphate P, nitrate N) following the methods described in Emeis et al. (2018) and Flohr et al. (2014). The upwelling waters, SACW and ESACW, were defined using potential temperatures (theta, θ) and definitions by Mohrholz et al. (2014) following Equations 1, 2, respectively:

$$SACW: \theta = 8.56 * Salinity - 289.08 \tag{1}$$

$$ESACW: \theta = 9.44 * Salinity - 319.03$$
(2)

Additional samples for suspended matter were retrieved with the multiple CTD/Rosette system during Meteor cruise M153, Sonne cruise SO283 and SO285. The filtration volume of sea water on precombusted (450°C) and tarred glass fibre filters (WHATMAN GF/F, ~0.7 μ m, 47 mm diameter) varied between 5 and 30 L. The filtration was stopped when filters were satisfactorily covered. After filtration, the samples were rinsed with deionised water to remove sea salt and subsequently dried in the ship's dry oven at 40 °C for 48 hours prior to analysis of total nitrogen and organic carbon.

3.5 Air-sea interface conditions

The analysis and quantification of air-sea CO_2 fluxes was based on data taken from Siddiqui et al. (2023), comprising of continuous underway measurements collected between 2008 and 2019 according to methods described in Emeis et al. (2018), and additional qualitycontrolled measurements from the Surface Ocean CO_2 Atlas (SOCAT) v2020 (Bakker et al., 2016). Data on the sea surface CO_2 partial pressure (pCO₂) were normalized to the reference year 2020 (Takahashi et al., 2009, 2014) and spatially interpolated on a 0.1° x 0.1° grid using ordinary kriging performed with the R automap package (Hiemstra et al., 2009). Annual variogram models applied during the ordinary kriging procedure, together with autocorrelation length scales that were used to correct for spatial autocorrelation following Landschützer et al. (2014), can be found in Siddiqui et al. (2023).

Carbon flux rates (FCO₂) were determined using the partial pressure at the sea surface $(pCO_{2,sw})$ and of the atmosphere $(pCO_{2,at})$ following Equation 3:

$$FCO_2 = K_0 * k * (pCO_{2,sw} - pCO_{2,at})$$
(3)

with K_0 as the solubility coefficient of CO₂ (Weiss, 1974) and k as the gas transfer velocity of CO₂ (Wanninkhof, 2014), calculated using Equation 4:

$$k = 0.251 * u^2 * \left(\frac{Sc}{660}\right)^{-0.5}$$
(4)

with *Sc* as the Schmidt number of CO_2 in seawater, 660 as *Sc* at 20° C water temperature, and *u* referring to wind speed (m s⁻¹) at 10 m above sea surface. *Sc* was determined using shipboard data on wind speed, sea surface temperature (SST) and salinity (SSS) that were spatially interpolated using the ordinary kriging procedures as outlined for pCO₂. The annual mean CO₂ exchange coefficients, sea surface pCO₂ and flux rates for the northern and southern Benguela Upwelling System that we used in this study are presented in Table 1.

4 Results and discussion

4.1 Effect of bottom trawling on benthic fluxes and upwelling source waters

4.1.1 Benthic fluxes

According to published estimates across the northern and southern upwelling region of the BUS (Sala et al., 2021), the

amount of CO₂ released during the remineralization of resuspended sediment after bottom trawling added up to 4.35 and 0.64 Tg C year⁻¹ ($3.62*10^{11}$ and $5.33*10^{10}$ mol C year⁻¹), respectively. Hereby, the CO₂ release was highest from regions with water depths of 200-400 m, contributing over 50% to the trawl-induced benthic CO₂ efflux, adding DIC into bottom waters overlying the sediment surface. To take note of the associated release of nutrients like nitrate due to bottom trawling, we applied the average molar carbon to nitrate (C/N) ratio (9.16) found within the top layer of the sediment as derived from multicore samples across the NBUS region (Table 2). This resulted in $3.95*10^{10}$ mol N year⁻¹ (= $3.62*10^{11}$ mol C year⁻¹/9.16) for the NBUS and $5.82*10^9$ mol N year⁻¹ for the SBUS, respectively, that are assumed to be released during the remineralization of resuspended sediment into bottom waters.

Hereby, a preferential remineralization of nitrogen containing compounds should have led to an increase in the C/N ratio of suspended organic matter (SPM) in the water column. SPM collected along the continental shelf break at water-depths between 200 and 1000 m showed C/N ratios between 2.7 and 15.0 (see Supplementary Figure 2). Apart from two exceptions with a C/N ratio above 10, the maximum C/N ratios increase with a decreasing distance to the surface sediments, reflecting an increased contribution of resuspended sediments to the SPM. With C/N ratios of SPM hardly exceeding 9.6, there appears to be no preferential remineralization of nitrogen containing compounds that would have otherwise significantly increased C/N ratios within the SPM.

One of the factors controlling the benthic CO₂ efflux is the reactivity of organic carbon in sediments. Hereby, high reactivity values, as applied by Sala et al. (2021) for the BUS, can be traced back to environmental factors limiting OM degradation due to enhanced vertical or lateral transfer of OM to the seafloor, or due to factors impeding OM degradation directly, such as diminished oxygen availability (Arndt et al., 2013). In case of the BUS, the presence of OMZs could be responsible for highly reactive, fresh OM settlement at the sediment surface as implicated by k values derived from the sediment samples. Together with other studies reporting intermediate to highest values for organic matter reactivity in the BUS (Arndt et al., 2013; Pika et al., 2023; Xu et al., 2023), the applicability of k = 1, and amount of the trawlinduced benthic CO2 efflux, appear plausible. However, the spatial variability in OM reactivity as seen in our DI estimates and seasonal variability in poorly oxygenated SACW inflow exerting control over the OMZ highlights the need to refine the reaction constant on a higher spatio-temporal resolution.

A further concern with the approach of Sala et al. (2021) is that both natural and bottom trawl-induced remineralization of organic carbon across the sediment-water interface are being accounted for in calculating the trawl-related benthic CO_2 efflux, therefore overestimating the CO_2 release after bottom trawling [Hiddink et al., (2023)]. In this regard, the bottom trawl-induced nitrate efflux of $3.95*10^{10}$ mol N year⁻¹ in the NBUS corresponds to more than ten times the diffusive benthic nitrate efflux of $3.5*10^9$ mol N year⁻¹ as calculated by Neumann et al. (2016) based on pore water gradients across the inner-shelf mud belt off Namibia. Thus, the amount of nutrients released after bottom trawling seems to be higher than the natural benthic efflux from inner-shelf sediment that is profoundly rich in fresh organic matter, which, together with the rise in bottom water DIC concentrations, highlights the intrusive nature of bottom trawling on the benthic-pelagic coupling. Hereby, it should be noted that we only accounted for the nutrients associated with the remineralization of resuspended organic matter, which we derived via applying the C:N ratio to the benthic CO_2 efflux by Sala et al. (2021). Hence, we neglected the dissolved nutrients within pore waters that could be released during bottom trawling as shown by a study in the Gulf of Lion, where 2-5 orders of magnitude more nutrients were released from pore waters of muddy sediments after trawling as compared to the natural benthic efflux (Durrieu de Madron et al., 2005).

However, results of other studies displayed the trawl-released nutrients to only affect nutrient availability on a short timeframe without long-term consequences for the overall nutrient budget (Trimmer et al., 2005), while others noted elevated nutrient concentrations to be detectable even within a 100 m distance to the trawl track (Bradshaw et al., 2021). These partially contradicting outcomes are likely site-specific, with sediments being subject to various factors governing their response to trawl-induced disturbances, such as sediment type (cohesive vs. non-cohesive) (Palanques et al., 2014; Hale et al., 2017), trawl frequency and gear type (Eigaard et al., 2016; Depestele et al., 2019). Hereby, studies on trawl-induced carbon and nutrient releases found remineralization of particulate organic matter at sites with muddy sediments to be either enhanced by the deposition of fresh organic matter on a nutrientdeprived trawled area (Paradis et al., 2019), or decreased with the degradation of sedimentary habitats and depletion in organic matter content (Pusceddu et al., 2014). Further contradicting findings were reported for sedimentary organic carbon concentrations, which either showed an increase (Pusceddu et al., 2005; Palanques et al., 2014; Sciberras et al., 2016) or decrease (Mayer et al., 1991; Hale et al., 2017; Tiano et al., 2019) in the aftermath of bottom trawling, as well as for organic matter degradation pathways to be increased (Polymenakou et al., 2005; Paradis et al., 2019) or decreased (Tiano et al., 2019), with no clear effects on sedimentary organic carbon reported along the Southern Benguela Upwelling System (Atkinson et al., 2011). In addition, remineralization of organic matter after trawling events was found to be enhanced if resuspended from low oxygenated sediment environments into well oxygenated bottom waters (Sciberras et al., 2016; Bradshaw et al., 2021). In this context, oxygen-depleted zones within the BUS might limit remineralization of resuspended sediments which could reduce the effect of bottom trawling on benthic carbon and nutrient fluxes, or might be promoted by trawl-induced OM oxidation, especially with the entrainment of oxygen-depleted SACW into the NBUS shelf system (Mohrholz et al., 2008).

4.1.2 Upwelling source waters

On the basis of the published benthic CO_2 efflux (Sala et al., 2021), we estimated the increase of DIC and nutrients within the upwelling source waters due to bottom trawling by dividing the release of sedimentary carbon and nitrate (in mol year⁻¹) by the annual volume of waters (in Sverdrup, Sv) that are being upwelled within the NBUS and SBUS region. With an upwelling volume of 0.9 Sv (= $10^6 \text{ m}^3 \text{ s}^{-1}$) for the NBUS (Muller et al., 2014; Bordbar et al., 2021) and 0.4 Sv for the SBUS (Bordbar et al., 2021), we estimated 2.83* 10^{13} and 1.26* 10^{13} m^3 year⁻¹ of water masses to

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be upwelled, respectively. Dividing the benthic efflux of $3.62^{*10^{11}}$ and $5.33^{*10^{10}}$ mol C year⁻¹ of the NBUS and SBUS by the volume of upwelling waters (m³ year⁻¹) resulted in a DIC enrichment of 12.8 and 4.3 µmol kg⁻¹ per year, respectively. Nitrate concentrations would be enhanced by 1.39 and 0.47 µmol kg⁻¹ year⁻¹ in the NBUS and SBUS, respectively, making up ~5 and ~2% of the corresponding average source water nitrate concentrations of 26.49 ± 1.04 and 21.06 ± 0.2 µmol kg⁻¹ year⁻¹ (Table 1).

Although our average source water mass DIC concentration might already be influenced by bottom trawling activities, we add the trawl-induced release of CO_2 and nutrients to our respective DIC and N concentration of the upwelling source water masses, as bottom trawling is an ongoing fishing practice where carbon and nutrients are being released from the sediment-water interface.

4.2 Biological response and feedback to air-sea gas exchange

To estimate the impact of bottom trawling on the biological productivity, we applied the bottom-up approach to calculate new production rates for each subsystem within the BUS based on respective upwelling volumes and benthic nitrate concentrations released into the upwelling source waters after bottom trawling (NBUS: 1.39 μ mol N kg⁻¹, SBUS: 0.47 μ mol N kg⁻¹). Quantifying this amount of N available within the euphotic zone and translating it into equivalent grams of C using the Redfield-ratio (6.6) resulted in new production rates of 3.14 and 0.47 Tg C year⁻¹ for the NBUS and SBUS, respectively. Compared to new production rates based on average DIC and N concentrations of the source water masses (NBUS: 59.83 Tg C year⁻¹, SBUS: 21.14 Tg C year⁻¹), the release of N in the aftermath of bottom trawling could increase new production by 5.25% in the NBUS and 2.22% in the SBUS.

However, compared to the corresponding benthic CO_2 efflux of 4.35 and 0.64 Tg C year⁻¹ in the north and south, only 2/3 of the benthic CO_2 emissions could be recaptured and assimilated into organic matter by benthic nutrients as a result of the difference in C: N ratios between the sediment (Table 2) and surface biomass (Redfield, 6.6). Although this could support the overall productivity of the system, the remaining 1/3 of the benthic CO_2 emissions could lead to an ongoing enrichment of DIC and rise of pCO₂ in the surface region. To elaborate the latter, we estimated the impact of enhanced DIC and nutrient concentrations through bottom trawling on the air-sea gas exchange through sea surface pCO₂ simulations using CO2SYS. We therefore compared our results with the measured and simulated pCO₂ of the NBUS and SBUS coastal and offshore region as presented in Siddiqui et al. (2023).

According to Siddiqui et al. (2023), highest pCO_2 prevails in the coastal region (Figures 3A, C) where the upwelling of carbon-rich waters fosters the outgassing of CO₂, as also indicated by elevated pCO_2 measurements. Hereby, the average modelled pCO_2 in the upwelled water lies within the upper range of the nearshore measured pCO_2 (NBUS:294 – 1012 µatm, SBUS: 334 – 610 µatm). This implies biologically-mediated nutrient consumption and fixation of DIC into biomass to occur simultaneously with coastal upwelling, as also indicated by increased chlorophyll concentrations that have been

observed by satellites along a narrow belt across the coastal region within the BUS (Weeks et al., 2006; Demarcq et al., 2007; Lamont et al., 2019). In addition, pCO2 measurements were taken during different times of the year, covering (non-) upwelling seasons and variable intensities of solar radiation that could have led to variabilities in the warming of upwelling waters and its effect on sea water CO2 solubility. The latter is addressed by considering the effect of the biologically-mediated nutrient consumption on pCO2 within the offshore region, while also accounting for the warming of upwelled waters in a subsequent stage. This caused a decrease in pCO₂ with respect to the coast due to degassing and the biologically-mediated uptake of CO₂ within the offshore flowing waters (Figures 3B, D). Hereby, the simulated pCO₂ falls into the spectrum of measured estimates in cases when the surface warming effect is being accounted for. Depending on its strength, pCO₂ can be drawn below or above the atmospheric pCO₂, which, in the end, controls the regional CO₂ sink and source functionality of the two subsystems (Siddiqui et al., 2023).

In order to account for the impact of bottom trawling, we repeated the simulations of pCO_2 for the coast and offshore regions by adding the bottom trawl-induced efflux of DIC and nutrients as previously outlined to the given source water concentrations. The effect of bottom trawling thereby led to an additional increase in pCO_2 at the coast of +100 and +20 µatm in the NBUS and SBUS, respectively, that gradually decreased towards offshore, where pCO_2 was merely raised by 5 µatm in the north and 3 µatm in the south.

Given the increase in pCO₂ through bottom trawling by 5 μ atm in the NBUS, the corresponding annual CO₂ flux would increase by ~1 Tg C year⁻¹, resulting in 17.13 (-2.64 – 77.25) Tg C year⁻¹ that would be emitted into the atmosphere. In the SBUS, the bottom trawl-induced rise in pCO₂ would offset the annual CO₂ flux by 0.3 Tg C year⁻¹, leading to a comparatively lower CO₂ uptake of -2.79 (-4.55 – 4.25) Tg C year⁻¹. Thus, an additional release of sedimentary carbon into upwelling source waters could on average reduce the SBUS's sink functionality of atmospheric carbon by ~10%, and increase the rate of outgassing by 6.5% in the NBUS.

These values are in the order of CO_2 emissions by land use and land cover changes as ascribed to the AFOLU (agriculture, forestry, and other land use) sector for Namibia, which takes into account carbon stocks of coastal reservoirs like mangrove forests, tidal marshes, and seagrass meadows ("blue carbon") (Rixen et al., 2023). The bottom trawl-induced release of CO_2 into the atmosphere within the BUS (~1Tg C year⁻¹) corresponds to ~3% of the CO_2 currently stored by AFOLU (-30.6 Tg C year⁻¹) (Rixen et al., 2023), showing the scale to which bottom trawling could potentially alter CO_2 emissions in coastal settings.

Hence, the efficiency of the biological carbon pump in sequestering and storing atmospheric CO_2 is likely affected by bottom trawling: On the one side, such fishing practices impair the sink function of the BUS by reactivating ~5 Tg C year⁻¹ previously stored in the sediment of which 2/3 may be transformed back into organic matter. On the other side, the trawl-induced release of sedimentary CO_2 into upwelling source water masses can potentially foster an additional outgassing of ~1 Tg C year⁻¹ into the atmosphere. Hereby, our estimations are representative for an upper limit, assuming the entirety of the benthic CO_2 efflux and associated nutrients to be upwelled into



FIGURE 3

Simulations of the sea surface partial pressure of CO₂ with CO2SYS (Lewis and Wallace, 1998; Humphreys et al., 2020) as estimated from bottom trawling activities within the Benguela Upwelling System. Measured sea surface pCO_2 (in µatm) normalized to reference year 2020 (Takahashi et al., 2009, 2014) and modelled pCO_2 during coastal upwelling and nitrate (N) consumption through biologically-mediated CO₂ uptake across the shelf and offshore boundary for the (**A**, **B**) NBUS and (**C**, **D**) SBUS, adapted from Siddiqui et al. (2023), licensed under CC BY 4.0. The simulated pCO_2 after biological consumption is shown without (Model 1) and with (Model 2) the surface warming effect. The effect of bottom trawling on pCO_2 as simulated in this study is shown in blue. The grey dashed line mirrors atmospheric pCO_2 of the reference year 2020 based on Mauna Loa records (414 µatm). Sea surface pCO_2 are presented as the standard deviation, whereas uncertainties in the modelled pCO_2 are based on the standard error of the average source water mass characteristics.

the surface region and assimilated into organic matter, while neglecting any processes hampering the biologically-mediated CO₂ uptake, such as light and iron limitations or water column denitrification. The rise in pCO₂ through bottom trawling is thereby related to the efficiency at which benthic nutrients and DIC are recaptured and assimilated into organic matter after being released from the sediment and upwelled into the surface region. Thus, using a constant stoichiometric carbon to nutrient ratio further disregards any variability in nutrient utilization and remineralization, which, in the end, is a pivotal factor that constitutes the recapture efficiency of the bottom trawl-induced CO2 efflux. Additionally, the amount of the benthic CO₂ efflux and associated nutrients as elucidated for the BUS are subject to uncertainty because underlying calculations of the labile carbon fraction and remineralization were based on basin-scale average values that curtailed spatial variabilities within the BUS (Sala et al., 2021; Epstein et al., 2022). In this regard, the remineralization potential is related to oxygen availability, with oxygen-rich environments likely promoting organic matter degradation and oxygen deficiencies limiting remineralization (Sciberras et al., 2016; Bradshaw et al., 2021). Hereby, a potential expansion of Oxygen Minimum Zones (OMZs) could add further pressure on benthic ecosystems under the influence of bottom trawling by impeding the recovery potential and protection of benthic flora and fauna, which would otherwise have a stabilizing effect on the sediment and increase its resistance to physical disruptions (Roberts et al., 2017). Hence, in addition to monitoring of hydrographic changes and benthic ecosystem responses, higher spatially resolved data is needed to account for heterogeneity in sedimentary carbon characteristics and to refine trawl-induced benthic carbon and nutrient effluxes within the BUS.

5 Conclusion

In this study, we examined how coastal sediments exposed to trawl-induced disturbances may impact the biological carbon pump efficiency of the Benguela Upwelling System by applying the bottomup approach to simulate benthic C and N pathways from the bottom trawled seafloor to the sunlit surface via coastal upwelling of source water masses encompassing the bottom shelf region. Using shipboard data on sea surface and water column characteristics and published benthic CO_2 emission estimates from bottom-trawled sediments, we estimated a release of ~5 Tg C year⁻¹ from the trawled sediment into bottom waters within the BUS, together with nutrient inputs that could enhance source water nitrate concentrations by ~2-5%. Despite of supporting the biological productivity, benthic nitrate inputs merely lead to 2/3 of CO₂ released from bottom trawling to be recaptured into organic matter due to stoichiometric C:N ratio differences between the sediment (~9) and surface biomass (Redfield, 6.6), impeding the biological carbon pump efficiency in sequestering atmospheric CO₂ by ~1.3 Tg C year⁻¹. Hence, our results suggests that C:N stoichiometry should be considered when determining how trawl-induced disturbances at the seafloor may affect carbon and nutrient cycling in coastal upwelling ecosystems. Hereby, the heterogeneity in sediment type and hydrographic changes affecting OM remineralization give further incentive to refine sedimentary and pelagic C and N variabilities in order to better understand effects of trawl-induced sediment resuspension on the biological carbon pump.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation. We have adopted the python code previously published by Siddiqui et al. (2023) for sea surface pCO_2 simulations (thermally and nonthermally controlled pCO_2), CO_2 flux calculations and new production calculations. These codes incorporate all necessary equations and parameters for reproducing the output of this study. The python code is available in Figshare under the accession code doi:10.6084/m9.figshare.21436494.

Author contributions

CS: Conceptualization, Investigation, Visualization, Writing – original draft, Writing – review & editing. TR: Conceptualization, Supervision, Writing – review & editing. NL: Investigation, Writing – review & editing. TL: Writing – review & editing. AvdP: Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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