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Organic Matter Supply and Utilization in Oxygen Minimum Zones

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Abstract

Organic matter (OM) plays a significant role in the formation of oxygen minimum zones (OMZs) and associated biogeochemical cycling. OM supply processes to the OMZ include physical transport, particle formation, and sinking as well as active transport by migrating zooplankton and nekton. In addition to the availability of oxygen and other electron acceptors, the remineralization rate of OM is controlled by its biochemical quality. Enhanced microbial respiration of OM can induce anoxic microzones in an otherwise oxygenated water column. Reduced OM degradation under low-oxygen conditions, on the other hand, may increase the CO_2 storage time in the ocean. Understanding the interdependencies between OM and oxygen cycling is of high relevance for an ocean facing deoxygenation as a consequence of global warming. In this review, we describe OM fluxes into and cycling within two large OMZs associated with eastern boundary upwelling systems that differ greatly in the extent of oxygen loss: the highly oxygen-depleted OMZ in the tropical South Pacific and the moderately hypoxic OMZ in the tropical North Atlantic. We summarize new findings from a large German collaborative research project, Collaborative Research Center 754 (SFB 754), and identify knowledge gaps and future research priorities.

1. INTRODUCTION

Over the past 50 years, global oceanic oxygen content has declined by 2%, and the volume of waters with anoxic conditions has expanded fourfold (Schmidtko et al. 2017). The loss of oxygen in the ocean, termed ocean deoxygenation, disrupts marine ecosystems, fish stocks, and aquaculture and leads to loss of habitat and biodiversity (Oschlies et al. 2018a). In general, deoxygenation of a parcel of water occurs when oxygen consumption exceeds the physical supply. Respiration is the major loss term for oxygen in the subsurface ocean and is directly linked to the biological remineralization of organic matter (OM) to nutrients and CO_2, as indicated in the reaction equation for OM with the standard elemental stoichiometry:

$$(CH_2O)_{106}(NH_3)_{16}(H_3PO_4) + 138\ O_2 \longrightarrow 106\ CO_2 + 16\ HNO_3 + H_3PO_4 + 122\ H_2O,$$
$$\Delta G = -3{,}190\ \text{kJ mol}^{-1}. \qquad 1.$$

In the ocean, oxygen minimum zones (OMZs) have been associated mostly with regions where midwater oxygen levels fall below 60 μmol O_2 kg^{-1}, including hypoxic (5–60 μmol O_2 kg^{-1}), suboxic (<5 μmol O_2 kg^{-1}), and even anoxic (0 μmol O_2 kg^{-1}) waters. The hypoxic and suboxic thresholds are operational and to some extent arbitrary, but the physiological and behavioral performance of many zooplankton and nekton organisms are impacted below the hypoxic threshold, whereas specifically adapted species might use hypoxic areas as a refuge (Ekau et al. 2010, Seibel 2011, Hoving et al. 2020). Close to or below the suboxic threshold, aerobic microbial processes tend to be inhibited, and anaerobic processes set in (Codispoti et al. 2005, Kalvelage et al. 2015). Recent studies have demonstrated that OMZs harbor diverse metazoan and microbial communities that are specifically adapted to low or even absent oxygen (e.g., Ulloa et al. 2012, Wright et al. 2012, Wishner et al. 2018). Yet little quantitative information is available about their metabolic activity, including basic processes such as respiration and growth.

Oceanic OMZs are typically located at midwater depths (100–900 m), where oxygen supply via physical transport processes is low and respiration rates due to enhanced surface OM production and export flux are high. Those low-oxygen systems typically persist for extended periods of time. Four major oceanic OMZs are located in the Atlantic and Pacific Oceans (Chavez & Messié 2009) (**Figure 1**) and are associated with highly productive eastern boundary upwelling systems (EBUSs): one off Mauritania and Senegal in the North Atlantic, one off Angola and Namibia in the South Atlantic, one off California and Mexico in the North Pacific, and one off Chile and Peru in the South Pacific. In EBUSs, phytoplankton thrive on the continuous supply of new nutrients, and high autotrophic biomass is observed during periods of strong upwelling (Messié & Chavez 2015). EBUSs are responsible for ~25% of CO_2 uptake globally and are sites of high vertical carbon export (Jahnke 2010).

In the Atlantic, the northern and southern OMZs are well separated, as the energetic equatorial current system transports oxygenated water masses eastward (Brandt et al. 2012). In the Pacific, this separation is less obvious, and oxygen levels below 60 μmol O_2 kg^{-1} are found almost everywhere along the American coast. As the OMZs in both oceans are ventilated from the west, the larger longitudinal extent of the Pacific is the reason for the OMZ extending farther westward. Pronounced oceanic OMZs also exist in the Arabian Sea and the Bay of Bengal (for a review, see Rixen et al. 2020). The Baltic Sea and Black Sea, two enclosed marginal seas, also feature large OMZs due to limited water supply, and therefore ventilation, at depth.

Coherent data coverage, available since around 1960, shows a general expansion and intensification of oceanic OMZs (Schmidtko et al. 2017), predominantly due to global ocean warming and associated reduction of oxygen solubility. Superimposed is variability on decadal and

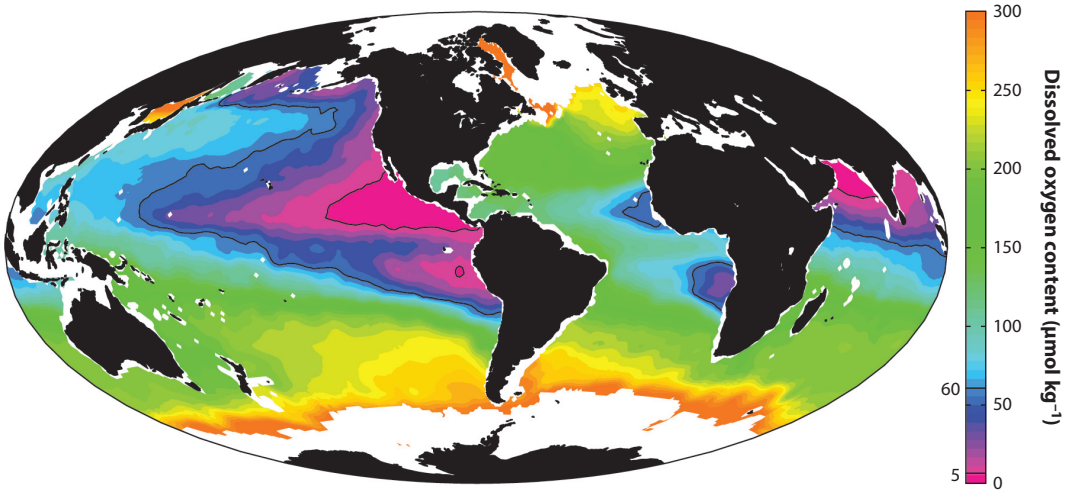


Figure 1

Global oxygen distribution at $\sigma_\theta = 27.05$ kg m^{-3} (~300–500-m depth), with 5 μmol O_2 kg^{-1} and 60 μmol O_2 kg^{-1} contours defining suboxic and hypoxic zones, respectively.

shorter timescales, often associated with climate variability such as the Pacific Decadal Oscillation (Deutsch et al. 2011, Stramma et al. 2020) or the Atlantic Multidecadal Variability (Brandt et al. 2021). Potential mechanisms of ocean deoxygenation have recently been reviewed by Oschlies et al. (2018b). Besides changes in oxygen solubility and physical transport, deoxygenation drivers also include a potentially enhanced supply of organic carbon to midwater depths and accordingly higher oxygen demand during remineralization.

Despite the general awareness that OMZs are determined by a delicate balance between oxygen supply and consumption, current Earth system models still fail to accurately reproduce present-day OMZs or the observed trends of deoxygenation due to a lack of quantitative knowledge of the involved mechanisms (Cabré et al. 2015) and difficulties in resolving processes at small temporal and spatial scales (Duteil et al. 2014). Recent evidence suggests that low-oxygen zones are more widespread in the ocean than expected and occur on different temporal and spatial scales below the system scale (**Figure 2**). To date, little is known about the frequencies and lifetimes of small and (sub)mesoscale low-oxygen zones and their contributions to the overall loss of oxygen in the ocean. Likewise, predictions of OMZ expansions in the future are inconclusive (Kwiatkowski et al. 2020).

For the assessment of the present-day oceanic oxygen content and for predicting future developments, such as deoxygenation, a sound mechanistic and quantitative understanding of physical transport processes for oxygen and of processes controlling OM supply and utilization in OMZs is a fundamental requirement. This article focuses on two major oceanic OMZs, located in the eastern tropical South Pacific (ETSP) off Peru and the eastern tropical North Atlantic (ETNA) off Mauritania. These regions were investigated in the frame of Germany's Collaborative Research Center 754 (SFB 754) as two extreme examples of oceanic OMZs, the already anoxic zone off Peru and the area off Mauritania, where oxygen concentrations are low but mostly above thresholds for anaerobic processes. Both systems are associated with highly dynamic, productive, and economically relevant EBUSs and are affected by ongoing deoxygenation (Grodsky et al. 2008, Stramma et al. 2008, Chavez & Messié 2009, Lam et al. 2012).

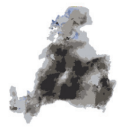
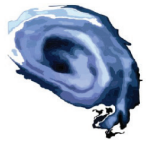
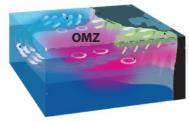
	Microscale 10^{-7} m – 10^{-2} m µm – cm	Mesoscale 10^{3} m – 10^{5} m 1 km – 100 km	Basin scale 10^{4} m – 10^{6} m 10 km – 1,000 km
	 Microzones in marine snow	 Dead-zone eddy	 EBUS OMZ
Typical enclosed volume (km^3)	10^{-16}–10^{-13} (Bianchi et al. 2018)	10^{2}–10^{3} (Karstensen et al. 2015)	10^{3}–10^{4} (Stramma et al. 2008)
Estimated global volume (km^3)	4×10^{2} (Bianchi et al. 2018)	Unknown	5×10^{5} (Bianchi et al. 2018)
Typical timescale	Days–weeks	Months–years	Centuries–millennia
Organic carbon (mg kg^{-1})	3.9×10^{1}–4.9×10^{1} (Alldredge 1998)	1.2×10^{-2}–3.6×10^{-1} (Fiedler et al. 2016)	1.2×10^{-2}–3.6×10^{-1} (this review)
Rate of oxygen loss (µmol kg^{-1} d^{-1})	6.7×10^{3}–1×10^{4} (Ploug 2001)	0.10–0.29 (Fiedler et al. 2016)	3×10^{-4}–2×10^{-3} (Stramma et al. 2008)

Figure 2

Zones of low oxygen. In marine snow, oxygen demand can greatly exceed diffusive oxygen transport; in already oxygen-reduced seawater, this may result in suboxic microzones with lifetimes of days to weeks. Mesoscale eddies detach from EBUSs and can maintain a low-oxygen dead zone for months to years. In oceanic OMZs, subsurface biological consumption and physical ventilation of oxygen nearly counterbalance over long timescales. Abbreviations: EBUS, eastern boundary upwelling system; OMZ, oxygen minimum zone.

2. SUPPLY OF ORGANIC MATTER TO OXYGEN MINIMUM ZONES

Oxygen loss in the subsurface ocean is ultimately linked to organic carbon supply and utilization. Three mechanisms are responsible for the transfer of OM into OMZs: (*a*) advective and diffusive transport of dissolved organic carbon (DOC) and particulate organic carbon (POC), (*b*) gravitational settling of POC, and (*c*) active transport by biota, mainly zooplankton, during vertical migrations (**Figure 3**). The second and third processes transport only OM, whereas the first also supplies oxygen to midwater depths.

2.1. Advective and Diffusive Transport Processes

Due to the presence of stratification in the thermocline, vertical solute and suspended OM fluxes can only be sustained by flow along sloping isopycnals or by vertical diffusion due to diapycnal mixing. Mesoscale eddies drive lateral export of OM from the EBUSs into the ocean interior. Similarly, submesoscale variability can lead to downward export of near-surface properties along isopycnals. Finally, DOC and suspended OM may be transported offshore within nepheloid layers.

Away from the mixed surface layer, fluxes of solutes and suspended particles across density surfaces are driven by turbulent motion. At the continental margins of EBUSs, elevated turbulence levels in the upper thermocline are sustained by breaking of internal waves resulting from the interaction of the sloping topography with tidal flows (e.g., Schafstall et al. 2010), favoring mixing across density surfaces (diapycnal mixing). Away from the ocean's boundary, turbulence levels are generally weaker by at least an order of magnitude. For dissolved or suspended components whose concentrations differ above and below the thermocline, diapycnal mixing results in net transport.

At the continental margin of the Peruvian EBUS, elevated downward fluxes of DOC (~30 mmol C m^{-2} d^{-1}) have been determined directly below the mixed layer (Loginova et al. 2019). Vertical DOC flux divergence, termed DOC supply in the following, was particularly strong in the upper 60 m, at >300 µmol C kg^{-1} y^{-1}. Budget estimates suggested that aerobic respiration of labile dissolved organic matter (DOM) (dissolved combined carbohydrates and dissolved

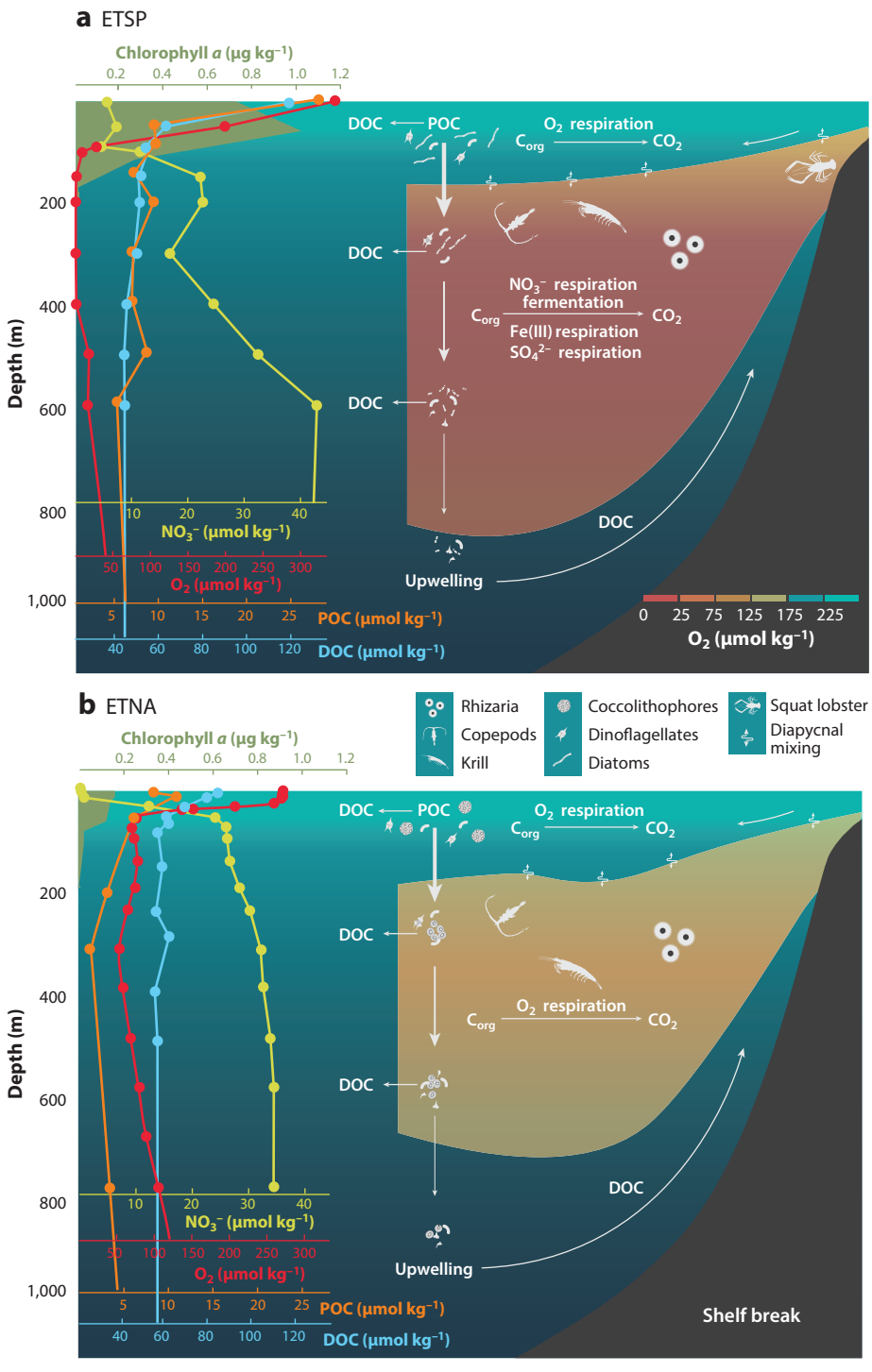


Figure 3

Schemes of the (*a*) ETSP and (*b*) ETNA OMZs, with profiles of water column biogeochemistry and the main pathways of organic matter supply and utilization. Abbreviations: DOC, dissolved organic carbon; ETNA, eastern tropical North Atlantic; ETSP, eastern tropical South Pacific; OMZ, oxygen minimum zone; POC, particulate organic carbon.

hydrolyzable amino acids), which contributed ~23% to DOC flux (Loginova et al. 2019), uses ~38% of the O_2 supply to this region. However, mean diapycnal fluxes of DOC were restricted to shallow depths and had already vanished at 50 m, suggesting that DOM utilization plays a significant role in shaping the upper oxycline in the ETSP. Even larger diapycnal DOM fluxes in the Peruvian upwelling region were reported by Maßmig et al. (2020), who determined a DOM supply of 410–1,240 μmol C kg^{-1} y^{-1} in the upper 40 m of the water column. Elevated diapycnal mixing at the continental margins of EBUSs also affects estimates of carbon export fluxes using ^{234}Th (Xie et al. 2020). Diffusive vertical fluxes of DOM to the OMZ in the ETNA have not been estimated.

Although OMZs are located in regions of sluggish ocean circulation (Wyrtki 1962), solute supply by the large-scale ocean circulation can be a dominant factor in the budgets of open ocean OMZs, such as their oxygen budgets (Karstensen et al. 2008). Estimating the advective supply to OMZs from observations requires knowledge of the transport of all currents flowing into and out of the OMZ at a given time and the respective DOM distributions at the OMZ boundaries. Due to a lack of data, the advective DOM supply by the large-scale circulation has not been determined.

Mesoscale eddies and mesoscale eddy variability have diverse roles in OMZs and EBUSs. The term mesoscale eddy is used to describe nonlinear mesoscale and submesoscale coherent vorticities with diameters of tens to hundreds of kilometers that trap water masses inside their cores and carry them westward into the open ocean (**Figure 2**); by contrast, the term mesoscale eddy variability describes a horizontal mixing process that acts to reduce gradients in ocean properties along isopycnals. This latter process provides an important supply process to open ocean OMZs. In EBUSs, mesoscale eddies are generated due to instabilities of the alongshore eastern boundary circulation or variability of local winds (Chelton et al. 2011). During their generation process, water masses from the proximity of the continental slope are trapped inside the eddy core and subsequently carried westward into the interior ocean (e.g., Nagai et al. 2015, Schütte et al. 2016a, Thomsen et al. 2016b). In the ETNA, these trapped water masses have large amounts of nutrients and OM but low oxygen concentrations. At continental margins, mesoscale eddies reduce biological production and enhance the lateral export flux of organic carbon into the open ocean (e.g., Gruber et al. 2011, Frenger et al. 2018). By contrast, mesoscale eddies are frequently associated with enhanced near-surface productivity and vertical carbon fluxes in the offshore OMZ (Fiedler et al. 2016, Schütte et al. 2016b). Due to their isolation from lateral exchange and enhanced respiration, water masses in the cores of ETNA eddies can become suboxic or even anoxic (Karstensen et al. 2015, Fiedler et al. 2016, Schütte et al. 2016b) (**Figure 2**).

Advective supply of OM from the surface mixed layer into the interior ocean along sloping isopycnals is known to occur in conjunction with submesoscale variability (1–10 km), such as the fronts and filaments that are common in EBUSs. Model studies suggest that this subduction process is particularly pronounced during the intensification or relaxation of fronts, generating vertical velocities of ~30 m d^{-1} (Spall 1995, Fox-Kemper et al. 2008). The sites of active subduction occupy a relatively small fraction of the surface area, rendering this process difficult to observe (Mahadevan et al. 2020). For the ETSP, Thomsen et al. (2016a) presented observational evidence for frontal subduction of OM-rich surface water to 40-m depth in a submesoscale cold filament that was subsequently advected offshore. An accompanying model study suggested that ~50% of the upwelled waters in the EBUSs subduct after a period of approximately five days. Recent model studies (e.g., Hauschildt et al. 2021) confirmed the above results and emphasized that the downward and offshore export of OM transport from the upwelling regions by submesoscale dynamics could also stimulate microbial activity in upper regions of the offshore OMZ below the euphotic

zone. In the North Atlantic, subduction of particulate organic matter from the surface to as deep as 350 m was observed at the periphery of an eddy (Omand et al. 2015). The authors suggested that approximately half of the total springtime export of POC may be achieved by subduction in submesoscale variability. Despite its potential importance for carbon export, a lack of observations has prevented estimation of advective solute or suspended OM supply due to this process.

Apart from mesoscale eddies and submesoscale features, another effective mechanism for transporting OM from the coastal upwelling system offshore takes place within nepheloid layers. Nepheloid layers are layers of elevated suspended sediment concentration that can be found near the surface and at intermediate depths extending from the continental shelves and slopes to several tens of kilometers into the interior ocean (e.g., Thorpe & White 1988, Inthorn et al. 2006). They are likely caused by enhanced bottom shear stresses due to the reflection of internal tides at near-critical continental slopes, which generates complex baroclinic velocity patterns, locally enhanced diapycnal mixing, and energetic rays in the water column just above the seafloor [see, e.g., the review by McPhee-Shaw (2006)]. The forcing mechanism for the lateral spreading of the resuspended sediments is thought to be either convergences of the upslope near-bottom diapycnal flow (Kunze et al. 2012) or the gravitational collapse of the locally well-mixed fluid patch at the boundary (McPhee-Shaw & Kunze 2006). On the shelf, particle accumulation and dissolution by benthic microorganisms and fauna may result in high fluxes of DOC from the seafloor into the OMZ (Loginova et al. 2016, Thomsen et al. 2016a). Moreover, efflux from the sediment pore waters may represent a source of OM to the water column. For the OMZ shelf off Peru, Loginova et al. (2020) showed that anoxic sediments release 0.2–2.5 mmol DOC m^{-2} d^{-1}. However, a substantial fraction of the released DOC was already remineralized at the sediment–water interface.

2.2. Gravitational Settling of Particles

Gravitational settling of organic particles from highly productive surface waters is the major export pathway for OM and is often determined using moored or drifting sediment traps, Underwater Vision Profilers, or deficits of the particle-reactive radioisotope ^{234}Th. Attenuation of particle flux over depth has been described by the coefficient b of a nonlinear decrease function (Martin et al. 1987), relating flux at depth z to flux at a reference depth (e.g., 100 m) below the mixed layer: $F_z = F_{100} \times (z/100)^{-b}$.

As for the ocean in general, most information on POC export fluxes (F_{POC}) in OMZ regions is derived from deep moored traps (>1,000 m) and hence is mostly from below low-oxygen midwater. Deep F_{POC} (>1,000 m) ranges between 5 and 20 mg C m^{-2} d^{-1} (Hebbeln et al. 2000, Fischer et al. 2010) for both the ETNA and the ETSP, supporting the idea of an efficient biological carbon pump in these regions (Honjo et al. 2008). F_{POC} shows pronounced inter- and intraannual variability, tightly associated with upwelling conditions and phytoplankton blooms (Hebbeln et al. 2000, González et al. 2004).

Limited information is available for F_{POC} and flux attenuation within the OMZ. Here, surface-tethered drifting sediment traps or neutrally buoyant traps have been used due to their better trapping efficiency in midwater depths (e.g., Martin et al. 1987, Van Mooy et al. 2002, Buesseler et al. 2007, Engel et al. 2017). Studies at ETSP stations (VERTEX II and VERTEX III off Peru; Martin et al. 1987) and off Mexico (Van Mooy et al. 2002) determined a reduced flux attenuation—i.e., lower b values (0.319–0.805) compared with the open ocean composite of 0.86 (Martin et al. 1987)—and therefore suggested that a greater proportion of OM escapes degradation while sinking through the OMZ. Using the ^{234}Th technique, Pavia et al. (2019) also reported lower b values (0.66 and 0.75) for the Peruvian OMZ stations compared with those of oxygenated water masses

farther east (1.11 to 1.52) and no statistically significant flux attenuation between 60- and 600-m depth. Potential explanations for reduced flux attenuation in OMZs include relatively reduced degradation rates of sinking particles by anaerobic microbes (Van Mooy et al. 2002, Le Moigne et al. 2017) and avoidance of suboxic regions by zooplankton flux and aggregate feeders (e.g., Wishner et al. 2018, Weber & Bianchi 2020). If particles are not fed upon, repackaged, or destroyed, they could sink faster through the OMZ, which would result in decreased degradation.

More recent results, however, have challenged the view of a generally reduced flux attenuation in suboxic waters of the ETSP. Analyzing time series from shallow sediment traps, Bretagnon et al. (2018) observed a high variability of particles entering the OMZ at 34 m (F_{POC} = 6.5–470 mg C m^{-2} d^{-1}) and estimated a wide range of attenuation coefficients ($b = -0.27$–2.97) between 34 m and the lower OMZ core (149 m). They concluded that particles are either preserved [a high transfer efficiency (T_{eff}) of >50%], partly remineralized (an intermediate T_{eff} of 20–50%), or mostly remineralized (a low T_{eff} of <6%) within the OMZ depending on the season, oxygen concentration, and OM quality. Their study suggested an efficient vertical transfer (T_{eff} > 50%) with extremely low O_2 concentrations and poor OM quality, while higher levels of O_2 or higher-quality OM, or less refractory OM at the oxycline, may strongly reduce OMZ transfer efficiency to below 50%. Multiple trap deployments farther offshore also did not show any generally reduced flux attenuation within the OMZ (A. Engel, C. Cisternas-Novoa, F.A. Le Moigne, H. Hauss & R. Kiko, manuscript in preparation).

In the ETNA, only a few export and attenuation profiles have been obtained for the OMZ, based on data from drifting traps (Engel et al. 2017), camera profiling, or moored traps (Iversen et al. 2010). F_{POC} values off Cape Blanc ranged from 100 to 200 mg C m^{-2} d^{-1} at 100-m depth and from 11 to 54 mg C m^{-2} d^{-1} at 1,200-m depth, indicating a loss of organic carbon from sinking particles (ΔF_{POC}) of 89–146 mg C m^{-2} d^{-1} (Iversen et al. 2010). In the open ocean OMZ in the Guinea Dome region, Engel et al. (2017) found a similar F_{POC}, with 240 ± 34 mg C m^{-2} d^{-1} at 100 m decreasing to 141 ± 8.8 mg C m^{-2} d^{-1} in the core of the OMZ (400 m), equivalent to a loss of ~100 mg C m^{-2} d^{-1}. Below the mixed layer, b values varied between 0.74 and 0.80 and were thus lower than the open ocean composite and lower than predicted from seawater temperatures within the upper 500 m (Marsay et al. 2015). Since oxygen in the ETNA is typically >40 μmol O_2 kg^{-1}, neither reduction of aerobic degradation processes nor zooplankton avoidance may explain a relatively efficient transfer through the OMZ. Instead, other mechanisms may play a role, in particular increased settling velocities of particles by aggregation with ballasting lithogenic material, which is introduced into the ETNA via atmospheric deposition of Saharan dust (Van der Jagt et al. 2018). However, as the number of studies in hypoxic systems like the ETNA is very small, this preliminary conclusion needs further investigation. This is especially important because little is known about flux attenuation in hypoxic waters, which are more widespread (~4% of ocean volume) and suggested to increase at a faster rate in response to global warming than suboxic waters (<0.05% of ocean volume).

In general, attenuation of OM export fluxes differs between fine and large particles due to the relatively longer residence time of fine particles at a given water depth. Macroscopic particles (>0.5 mm), such as marine snow or fecal pellets, form by physical or biological particle aggregation, respectively, and typically show high settling velocities (>100 m d^{-1}). Field studies revealed that OMZs feature particularly high loads of small particles (Whitmire et al. 2009, Rasse & Dall'Olmo 2019), probably representing centers of high microbiological activity and intense particle remineralization. Marine snow, on the other hand, may evolve specifically adapted microbiomes that are able to efficiently utilize OM under low-oxygen conditions (Wright et al. 2012). A better knowledge of particle size distribution and composition therefore may help us understand export fluxes of gravitationally settling particles into OMZs.

2.3. Transport by Vertical Migrations

Zooplankton and nekton conduct diel vertical migrations (DVMs) to midwater depths at nighttime in order to access the enhanced food supply in the productive epipelagic zone, which they then vacate during the daytime to avoid visual predators. These migrations can supply organic carbon to midwater depths, where organisms excrete, defecate, and die or are preyed upon. Under oxic and hypoxic conditions, migrators also contribute to oxygen consumption at depth and may codetermine OMZ formation due to their own respiratory activity (Bianchi et al. 2013) and by stimulating microbial respiration with fresh OM (e.g., fecal pellets).

In general, the distribution and activity of zooplankton and micronekton are strongly modulated by oxygen levels (Childress & Seibel 1998, Wishner et al. 2018). Some species that are less well adapted to low oxygen avoid OMZs and aggregate at the upper or lower oxycline (Wishner et al. 2013). Better-adapted species (e.g., some calanoid copepods and some euphausiids, as well as several gelatinous species) might thrive at low oxygen levels and/or migrate into suboxic and anoxic waters on a daily basis (Antezana 2010, Christiansen et al. 2018, Kiko & Hauss 2019, Hoving et al. 2020, Tutasi & Escribano 2020). Known adaptations that enable the exploitation of the OMZ niche are larger gill surface areas, thinner respiratory epithelia, and more effective respiratory pigments to extract oxygen at very low environmental concentrations (Childress & Seibel 1998). The capacity to downregulate metabolic activity and internally use anaerobic respiration pathways is another important adaptation that enables some species to "hold their breath" for a long time (Gonzalez & Quiñones 2002, Kiko et al. 2016, Seibel et al. 2016) and conduct migrations into severely hypoxic to anoxic zones. The described impact of low oxygen levels on zooplankton and micronekton migration and activity results in region-specific modulations of DVM-mediated fluxes.

Estimates of excretion and mortality fluxes for the ETNA have been obtained by combining biomass estimates from day–night pairs of MultiNet (Kiko et al. 2020) or Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) hauls (Hernández-León et al. 2019) with allometric functions (e.g., Ikeda 1985, Hirst & Kiørboe 2002). Oxygen concentrations in the ETNA normally do not fall below the hypoxia threshold of major migrators (Kiko et al. 2016), which enabled the use of the mentioned functions here, although these functions do not contain oxygen as a predictive variable. The combined carbon supply (DOC excretion, defecation, and mortality at depth) via DVM of zooplankton and nekton in the ETNA open ocean region is estimated at 1.57–3.56 μmol C kg^{-1} y^{-1} (Hernández-León et al. 2019, Kiko et al. 2020), which represents ~25–85% of the combined carbon supply via passive sinking and DVM. Inhibition of DVM was observed in this region in so-called dead-zone mesoscale eddies with oxygen levels of <1 μmol O_2 kg^{-1}(Hauss et al. 2016), highlighting the special nature of these features.

The suboxic to anoxic conditions of the ETSP require further adaptations of the allometric functions to also include oxygen as a predictor (as was done for respiration and NH_4 excretion in Kiko & Hauss 2019). Only very few highly abundant and highly adapted species, such as the euphausiid *Euphausia mucronata* and the copepod *Eucalanus inermis*, can migrate into suboxic and anoxic waters in the ETSP. Experiments showed that *E. mucronata* downregulates respiratory and excretory activity at ~5 μmol kg^{-1} (Kiko et al. 2016), and in situ video data indicate that this species is barely active in the OMZ core (Kiko et al. 2015; S. Sommer, H. Hauss & R. Kiko, unpublished data). Hence, their respiration and the excretions of DOC, dissolved organic nitrogen, and ammonium should be reduced within the OMZ (Kiko & Hauss 2019), whereas their gut flux—the transport of carbon to depth within the gut and the release of this gut content as fecal pellets—might be unaffected. Kiko & Hauss (2019) estimated the migrating zooplankton biomass off Peru at 1–4 g C m^{-2} d^{-1}. Assuming that gut flux and mortality at depth is 2% per day [1% gut flux

(recalculated from Schnetzer & Steinberg 2002) and 1% mortality as a very conservative estimate (e.g., Hirst & Kiørboe 2002)], one can estimate that ~3.2–12.8 μmol C kg^{-1} y^{-1} is transported to the 200–400-m depth layer via DVM. Antezana (2010) provided a median biomass estimate of 3 and a maximum of 8 g C m^{-2} d^{-1} for *E. mucronata* only, which would transport 9.5–25.2 μmol C kg^{-1} y^{-1} to depth. Antezana (2010) also provided estimates for the gut carbon content of *E. mucronata*, which is equivalent to 0.75% of the body mass. The above estimates indicate the potential magnitude of the carbon supply via DVM, as the gut content and mortality of migrators at depth are still largely unresolved.

3. UTILIZATION OF ORGANIC MATTER IN OXYGEN MINIMUM ZONES

3.1. Organic Matter Degradation

Rates of OM degradation depend on the concentration and chemical composition of OM and range from seconds to days for the most labile, from months to years for semilabile, and from decades to millennia for refractory components (Hansell 2013). Since the main source of OM is photosynthetic production, fresh, labile organic carbon is restricted mainly to the surface ocean, while refractory components, mainly in the form of DOC (~40 μmol L^{-1}), occur everywhere in the water column (Carlson & Hansell 2015). Accordingly, DOC turnover is fastest in the upper ocean (DOC turnover is responsible for up to 70% of oxygen consumption at <400 m; Doval & Hansell 2000) and slower at greater depths (DOC turnover is responsible for <10–20% of oxygen consumption in deep waters; Arístegui et al. 2002). Likewise, oxygen concentration itself affects the rate of OM remineralization (Nguyen & Harvey 1997, Devol & Hartnett 2001, Keil et al. 2016, Le Moigne et al. 2017), as anaerobic microbial respiration yields less energy and typically proceeds at a lower rate than aerobic remineralization (Strohm et al. 2007, Lam & Kuypers 2011). Whether oxygen is the primary limiting factor for OM degradation in the OMZ is still controversial. Several studies have suggested that OM availability may limit or colimit OM degradation under suboxic conditions (Lee 1992, Pantoja et al. 2009, Maßmig et al. 2020). Knowledge of interdependencies of OM and oxygen consumption in the field and of rates and thresholds of involved processes such as respiration, remineralization, and fermentation are highly relevant for estimating food web dynamics and biogeochemical cycling at regional and global scales.

Bioavailable OM enters the OMZ through advective and diffusive transport, sinking particles, and migrating biota (**Figure 3**). In the global ocean, the amount of POC exported to depths greater than 100 m is approximately five times that of DOC (Hansell et al. 2009). Vertical export of semilabile DOM by diapycnal mixing may be quantitatively important in highly productive EBUSs but is restricted to shallow depths (Loginova et al. 2019), whereas rapidly sinking particles and active transport by migrating biota dominate OM export deeper in the OMZ core. Within the OMZ, the composition and elemental stoichiometry of OM may differ from those in fully oxygenated systems. Specifically, nitrogen-rich components such as amino acids have been suggested to degrade faster in suboxic and anoxic waters (Van Mooy et al. 2002, Pantoja et al. 2004, Le Moigne et al. 2017), due to the elevated nitrogen demands of anaerobic bacterial processes such as anaerobic ammonium oxidation (anammox, i.e., the autotrophic oxidation of ammonium to N_2 via nitrite) and denitrification (the stepwise heterotrophic reduction of nitrate to N_2). Degradation of OM by heterotrophic denitrifiers is the main anaerobic process of organic carbon remineralization to CO_2 and releases ammonia, which in turn supports anammox (Sipler & Bronk 2015). Recent results indicate that the remineralization of small particles in particular fuels anammox in the Peruvian OMZ (Karthäuser et al. 2021). While the total amount of labile OM supplied to the OMZ controls the overall nitrogen loss from the OMZ (Ward et al. 2008, Kalvelage et al. 2013),

the C:N stoichiometry determines the nitrogen-loss balance between anammox and denitrification. For the average [POC]:[PON] stoichiometry of 6.6, the fraction of total nitrogen loss via anammox is expected to be 28% (Babbin et al. 2014). A higher supply with nitrogen-rich OM may accordingly enhance the proportion of anammox.

Preferential uptake of carbon- or nitrogen-rich compounds, such as dissolved combined carbohydrates and dissolved hydrolyzable amino acids, in response to the oxygen regime may result in a decoupling of the spatial covariance of those major biomolecules. In a study off Peru, the highest concentrations of dissolved combined carbohydrates occurred in fully oxygenated surface waters and steeply declined at shallow depths (i.e., within the oxycline), and there was a pronounced compositional change in the molar fractions of individual sugar monomers (Maßmig & Engel 2021). The concentrations of dissolved hydrolyzable amino acids were also highest close to the surface, but the attenuation over depth was less pronounced, and changes in composition as well as the production of specific free amino acids such as alanine and threonine also occurred under suboxic conditions (<5 μmol O_2 kg^{-1}), indicating an active nitrogen turnover within the OMZ.

It is well known that rates of microbial degradation and uptake of OM depend on the molecular composition and weight of the substrates (e.g., Amon & Benner 1996, Amon et al. 2001), with characterizable biochemicals (i.e., carbohydrates, amino acids, and lipids) being major components (Benner 2002, Sipler & Bronk 2015). Monomers such as free amino acids and single sugars are among the most labile components, while high-molecular-weight (>1 kDa), polymeric substances, such as dissolved combined carbohydrates and dissolved hydrolyzable amino acids, are semilabile (e.g., Fuhrman 1987, Amon et al. 2001, Davis et al. 2009). As cellular uptake of OM by bacteria is limited to compounds of low molecular weight (<600 Da), the first steps of OM degradation involve particle solubilization and hydrolytic cleavage, both of which are catalyzed by extracellular enzymes (Hoppe et al. 2002) (**Figure 4**). Enzymatic hydrolysis rates are controlled

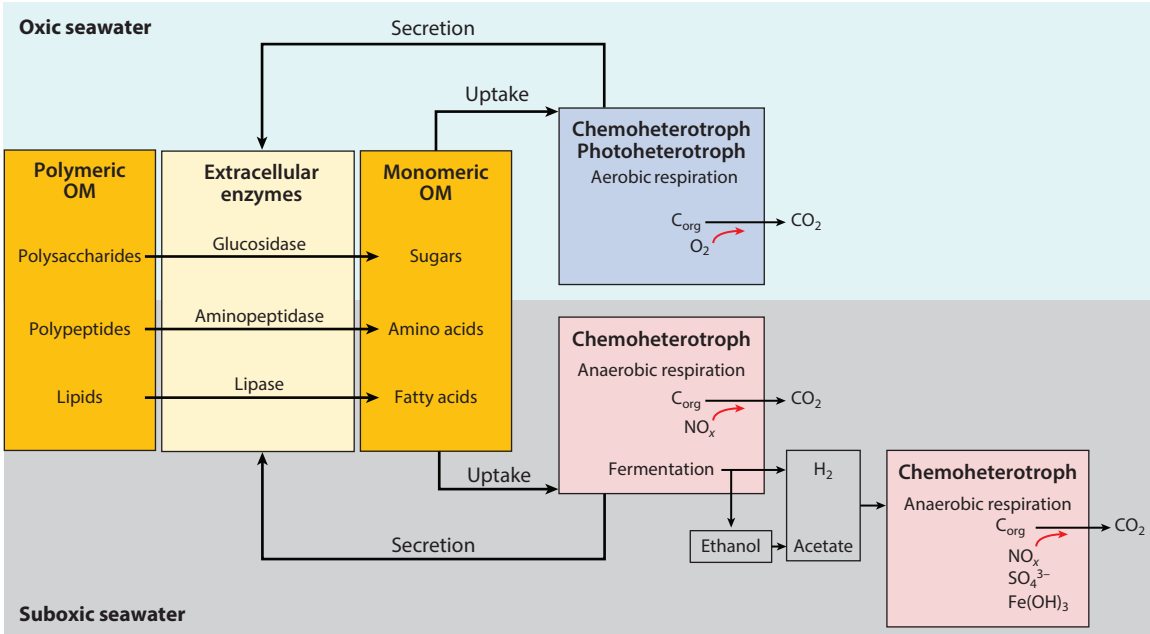


Figure 4

Aerobic and anaerobic pathways of OM degradation. Abbreviation: OM, organic matter.

by substrate concentration, temperature, and pH and can be actively regulated, e.g., in response to changing OM supply and quality (Hoppe et al. 2002). Little is known about the effect of oxygen concentration on extracellular enzyme activity in aquatic systems, and the findings so far are ambiguous, ranging from no effect of oxygen on rates of protein-hydrolyzing enzymes (peptidases) in Baltic Sea water (Hoppe et al. 1990) to a higher total activity in oxic compared with anoxic waters in the Cariaco Basin (Taylor et al. 2009) to enhanced cell-specific rates in anoxic waters off Peru (Maßmig et al. 2020) and in the Gulf of Mexico (Liu et al. 2017). Deciphering oxygen and other co-occurring controls (e.g., pH and temperature) of the activity of important hydrolytic enzymes, such as glucosidases, peptidases, and lipases, could help us to better understand variations in molecular composition as a consequence of microbial degradation in the OMZ.

The hydrolysis of biopolymers produces organic monomers that can be utilized by fermenting prokaryotic and eukaryotic microbes. Those microbes gain their energy from substrate-level phosphorylation and excrete products that are specific to the fermentation pathway (e.g., acetate, alcohols, and H_2) and are subsequently oxidized by anaerobic bacteria and archaea, e.g., during sulfate reduction and methanogenesis (**Figure 4**). A whole anaerobic food chain driven by a diverse microbial consortium may be involved in the final steps of OM decomposition (Kirchman 2012). Little is known about OM fermentation and the ecology of involved microbes in OMZs, in particular for the water column. Fermentation has been detected in substrate-enriched incubations of seawater collected from the OMZ, and fermentation products, mainly acetate, have been found in oxygen-deficient seawater off Chile and in the Cariaco Basin (Ho et al. 2002, Srain et al. 2020). Acetate is a final product of fermentation and can be derived from glucose, alcohol, or free amino acids. However, fermentation reactions may be energetically favorable or thermodynamically feasible only when reaction products are rapidly removed, as suggested for syntrophic consortia.

A close temporal and spatial coupling of OM degradation pathways may be realized in particle-associated microbial consortia (Wright et al. 2012), specifically in marine snow (**Figure 2**). Through the processes of particle aggregation and sedimentation, photosynthetically fixed carbon is removed from the surface and exported to the deep sea, thereby sequestering atmospheric CO_2 on long timescales (Siegenthaler & Sarmiento 1993). With concentrations of OM and abundances of microbiota being 10^2–10^3 times those of the surroundings, marine snow represents a hot spot of microbial activity (Simon et al. 2002). Accordingly, high respiration rates within marine snow and reduced solute exchange with the surrounding seawater can lead to oxygen-reduced microenvironments (Alldredge & Cohen 1987, Ploug et al. 1997, Moradi et al. 2018). The spatial proximity of oxic, suboxic, and anoxic microzones may favor the coexistence of microbial consortia capable of different redox-driven metabolic processes (Shanks & Reeder 1993, Wright et al. 2012, Stief et al. 2016). The co-occurrence of anaerobic and aerobic nitrogen cycling processes has been recently shown for dense cyanobacterial aggregates (Klawonn et al. 2015). Anoxia generated in particle aggregates may significantly expand the total volume of OMZs in the ocean (Stief et al. 2016, Bianchi et al. 2018) (**Figure 2**) and help to explain widespread chemolithotrophy in the water column despite apparently high oxygen concentrations (Swan et al. 2011). Moreover, respiration of OM associated with marine snow may contribute significantly to oxygen consumption in the deep sea (Bochdansky et al. 2010).

3.2. Estimating Oxygen Demand

Respiration of organic carbon to CO_2 requires electron acceptors. Oxic respiration has the highest theoretical energy yield ($\Delta G = -3{,}190$ kJ mol^{-1}; Equation 1) and is therefore prevalent in oxygenated water masses. When oxygen becomes depleted, alternative electron acceptors are

required for anaerobic respiration pathways (e.g., Fenchel & Finlay 1995, Lam & Kuypers 2011). The theoretical energy yields for anaerobic respiration range from −3,090 and −3,030 kJ mol^{-1} for MnO_2^- and NO_3^- respiration, respectively, to −380 and −350 kJ mol^{-1} for SO_4^{3-} and CO_2 respiration, respectively (Kirchman 2012).

The oxygen threshold for switching from aerobic to anaerobic respiration depends on the reaction and is likely controlled at the enzyme level. Aerobic respiration may proceed at low micromolar to nanomolar oxygen levels (microaerobic respiration) supported by high-affinity terminal oxidases with lower half-saturation constants (K_m of ~7 nmol O_2 kg^{-1}) compared with those of low-affinity terminal oxidases (~200 nmol O_2 kg^{-1}) (Morris & Schmidt 2013). Microaerobic respiration may be an important mode for remineralizing OM within apparently oxygen-free OMZs, e.g., in the ETSP. Denitrification has been shown for oxygen concentrations of up to 20 μmol O_2 kg^{-1}. Hence, aerobic and anaerobic respiration may co-occur in the OMZ, where small amounts of oxygen are occasionally provided through lateral intrusion and oxygenic photosynthesis of cyanobacteria at low light levels (Garcia-Robledo et al. 2017), with stable coexistence of aerobic and anaerobic microbial consortia being controlled by the relative supply rates of OM and O_2 (Zakem et al. 2020).

The amount of oxygen consumed for the respiration of organic carbon can be estimated by (*a*) directly measuring microbial and metazoan respiration, (*b*) calculating the amount of oxygen needed to fully oxidize and hence explain loss of organic carbon, and (*c*) indirectly estimating aerobic biological activity using the apparent oxygen utilization rate (aOUR).

Bacterial respiration rates in hypoxic and suboxic waters likely differ from those in oxygenated ones (Devol & Hartnett 2001, Kalvelage et al. 2013, Keil et al. 2016). Yet only a few direct measurements of aerobic respiration are available for OMZs. In particular, little is known about microaerobic respiration at concentrations below the detection limit of traditional methods (<5 μmol O_2 L^{-1}). Efforts to develop highly sensitive methods for detecting trace amounts of oxygen (>50–100 nmol kg^{-1}), such as switchable trace amount oxygen (STOX) sensors, have been undertaken over the past decade (Revsbech et al. 2009, Tiano et al. 2014) but need to be advanced and adopted more widely for high-frequency and robust measurements during field campaigns. Via uptake of added double-labeled $^{18-18}O_2$ during time series incubations with natural seawater, Kalvelage et al. (2015) determined high microaerobic respiration rates (up to 183 μmol O_2 kg^{-1} y^{-1}) at the upper oxycline of the OMZ off Peru, which also provided a substantial amount of the NH_4 (45–100%) required to explain anammox rates in this system. Even higher respiration rates (up to 1,200 μmol O_2 kg^{-1} y^{-1}) for the upper oxycline off Peru were determined by Maßmig et al. (2020), who estimated that microaerobic respiration may explain 19–31% of oxygen loss below the mixed layer.

For the ETNA, Baltar et al. (2009) estimated a potential microbial respiration of 29–33 μmol C kg^{-1} y^{-1} (25 μmol O_2 kg^{-1} y^{-1}) via the enzymatic electron transport system assay for the South Atlantic Central Water (~250–500-m depth). This method determines the maximum activity of the enzymes involved in respiratory electron transport and is therefore a maximum potential respiration rate.

Due to the lower energy yield per unit substrate consumed, anaerobic bacteria may be less active than their aerobic counterparts or, in contrast, enhance catabolic processes to compensate for the reduced energy gain. As a consequence, the bacterial growth efficiency—i.e., the amount of carbon biomass synthesized per amount of organic carbon taken up—may decrease with oxygen availability. While reduced bacterial growth efficiencies have been observed in anoxic lake sediments (Bastviken et al. 2003), little is known about those in marine OMZs. Maßmig et al. (2020) estimated a low average bacterial growth efficiency of 5% for the ETSP OMZ off Peru and suggested that it may be controlled by suboxia. However, experiments with microbial communities

from the Baltic Sea showed similar efficiency under high and low oxygen concentrations (Maßmig et al. 2019).

The bulk bacterial respiration rate also depends on cell growth, which is controlled not only by substrate availability and subsequent growth but also by bacterivore protozoa. Earlier studies have suggested that anoxia may suppress protozoa and favor bacterial biomass preservation in the OMZ (Lee 1992). However, anaerobic and microaerobic respiration is widespread in protozoa (Fenchel 2014), and the current database on protist grazing in oxygen-deficient waters is diverse (Medina et al. 2017). For instance, although total grazing rates were highest in oxic surface waters, specific grazing rates and hence impact on bacterial growth were more pronounced in suboxic waters of the ETSP (Cuevas & Morales 2006).

Metazoan respiration rates in OMZs are typically estimated from animals collected by net tows, subsequent determination of combined or individual biomass or size, and application of allometric functions. When using this approach, it is important to consider the inhibitory effects of low oxygen concentrations on metabolic activity (Kiko & Hauss 2019). From the hypoxic waters to waters below the oxycline of the ETSP, metazoan respiration is expected to be absent. Within the oxygenated top 50 m, mesozooplankton respiration rates of ~9–100 μmol O_2 kg^{-1} y^{-1} have been observed (Kiko & Hauss 2019). For the ETNA region, mesozooplankton respiration rates are estimated at ~0.3–1.0 μmol O_2 kg^{-1} y^{-1} at 300–600-m depth (Kiko et al. 2020). Further work is required to cover and combine all parts of the zooplankton size spectrum (microzooplankton, mesozooplankton, macrozooplankton, and nekton) to yield complete estimates of metazoan respiration rates.

An approximation of oxygen consumption rates can be derived from the difference in carbon flux between two depth levels (ΔF_{POC}). Collecting sinking particles during two drifting sediment trap deployments in the ETNA (~10°N, 21°W), Engel et al. (2017) observed ΔF_{POC} values of 6–11 μmol C kg^{-1} y^{-1} between 100 and 400 m (**Figure 5**). This indicates an oxygen demand of 5–13 μmol O_2 kg^{-1} y^{-1}, assuming a respiratory quotient of $[CO_2]$:$[O_2]$ of 0.89 (del Giorgio & Williams 2005). This approximation, however, includes only the fast-sinking particles that are typically captured with sediment traps and assumes that their loss from sinking fluxes is due to complete oxidation to CO_2 without significant production of suspended or dissolved OM. Another strategy to calculate the oxygen demand of detrital particles is via allometric approaches. Iversen & Ploug (2013) developed size-to-respiration-rate relationships for detrital particles, which were later adapted to calculate detrital particle respiration rates at different temperatures and oxygen levels (Kalvelage et al. 2015). These relationships allowed the calculation of respiration rates off Mauritania from in situ particle size distribution data (Thomsen et al. 2019). Particle-associated respiration rates (PARRs) of 146 μmol O_2 kg^{-1} y^{-1} above 50-m depth and of 40.15 μmol O_2 kg^{-1} y^{-1} at 50–200-m depth were estimated for offshore sampling stations (>70 km away from the coast) using in situ particle observations with an Underwater Vision Profiler 5, capturing all particles and zooplankton in the size range 0.1–16 mm.

The aOUR describes an integral rate of oxygen consumption within a water parcel that has occurred since the water parcel left the mixed layer. The approach is based on the apparent oxygen utilization (i.e., the difference between the in situ oxygen concentration and the oxygen saturation value at the surface) and on the age of the water mass (i.e., the time passed since it left the mixed layer) (e.g., Jenkins 1982). Water mass ages can be estimated with different approaches, such as methods based on concentrations of transient tracers (e.g., chlorofluorocarbon and SF_6) or ^{14}C. These methods often suffer from neglecting mixing processes along the water mass pathways, temporal limitations of transient tracers, and other effects, such as the impact of isotopic composition on radiocarbon dating (Karstensen et al. 2008).

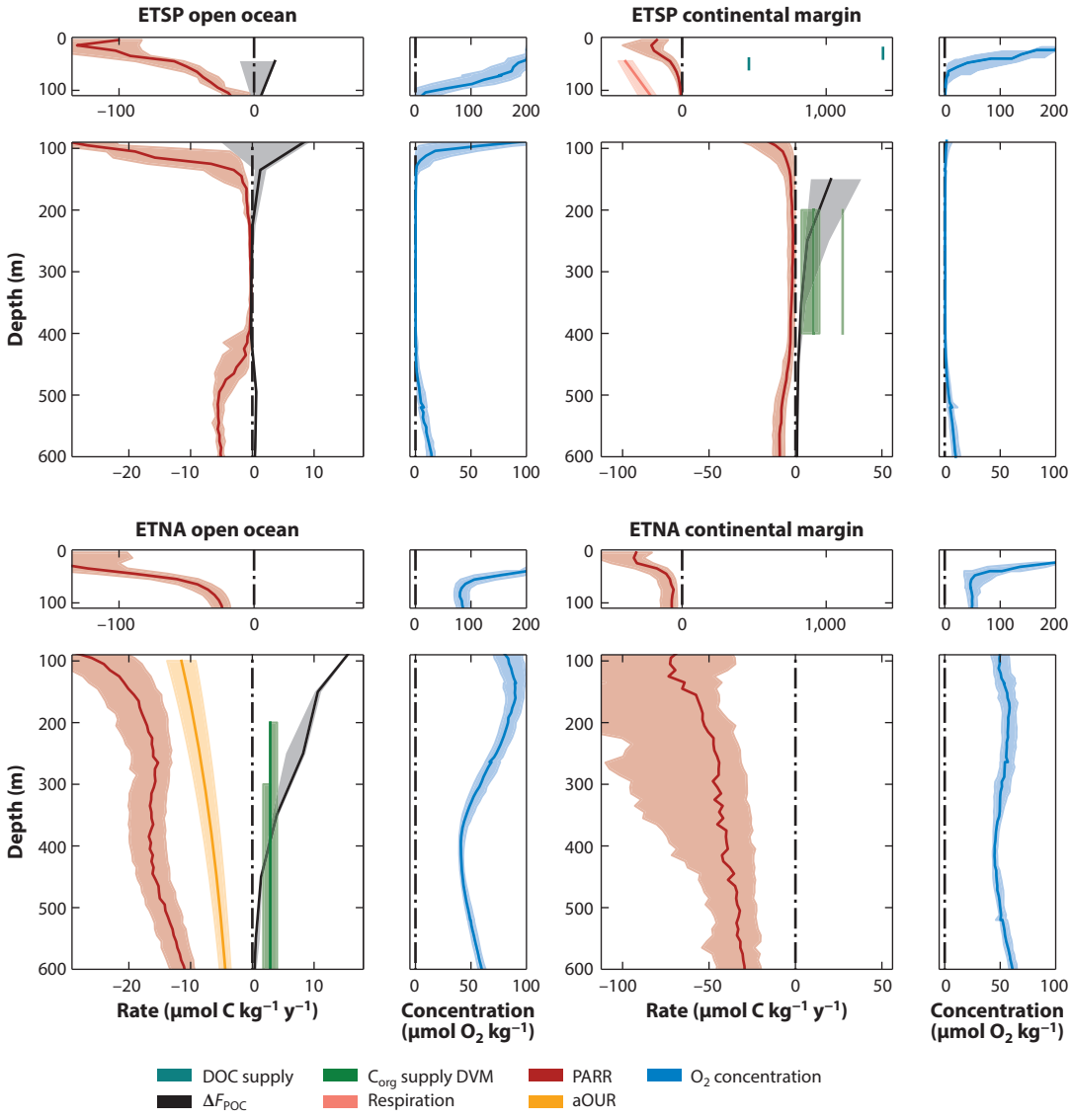


Figure 5

Carbon supply and demand rates as well as oxygen concentrations for the continental margin and the open ocean regions of the ETNA and ETSP. DOC supply data are from Maßmig et al. (2020). ΔF_{POC} data are from Engel et al. (2017), Pavia et al. (2019), and A. Engel, C. Cisternas-Novoa, F.A. Le Moigne, H. Hauss & R. Kiko (manuscript in preparation). Organic carbon supply via DVM are from Antezana (2010), Hernández-León et al. (2019), Kiko & Hauss (2019), and Kiko et al. (2020). Respiration (converted to carbon demand) data are from bottle incubations (Kalvelage et al. 2015). PARR is calculated according to the method described by Kalvelage et al. (2015) using Underwater Vision Profiler 5, temperature, and oxygen data from the respective regions (R. Kiko, M. Picheral, D. Antoine, M. Babin, L. Berline, et al., manuscript in preparation). aOUR data are from Karstensen et al. (2008); the shaded area indicates a 20% variability. Oxygen concentration data are from Germany's Collaborative Research Center 754 (SFB 754) cruises to the respective areas. The interquartile ranges for ΔF_{POC}, PARR, respiration, and O_2 are indicated by the shaded areas. Note the different *x*-axis scaling for the different regions and depth levels. Abbreviations: aOUR, apparent oxygen utilization rate; DOC, dissolved organic carbon; DVM, diel vertical migration; ETNA, eastern tropical North Atlantic; ETSP, eastern tropical South Pacific; PARR, particle-associated respiration rate.

Using oxygen distributions from the Atlantic and Pacific and water mass ages from the Global Ocean Data Analysis Project, Karstensen et al. (2008) derived a single aOUR distribution for the open ocean regions of both oceans. Anoxic regions were explicitly excluded in the derivation to avoid ambiguity. The results yielded an aOUR of ~9 μmol kg^{-1} y^{-1} at 100-m depth, decreasing to 4.7 μmol kg^{-1} y^{-1} at 400-m depth. More recently, Brandt et al. (2015) derived a lower aOUR in the upper 150 m of the water column using the concept of transit time distributions (e.g., Waugh et al. 2004) and allowing for mixing processes to determine water mass ages in the ETNA. They obtained an aOUR of 3–7 μmol kg^{-1} y^{-1} in the depth range 50–150 m. Values comparable to those of Karstensen et al. (2008) were found at >300-m depth. Much higher aOUR values have been detected in the hypoxic core of a productive anticyclonic mode water eddy that shed off the African coast (95 μmol O_2 kg^{-1} y^{-1} for 100-m depth; Fiedler et al. 2016).

3.3. Comparing the Supply and Utilization of Organic Matter and O_2 in the Eastern Tropical South Pacific and Eastern Tropical North Atlantic

To compare the amount of carbon supplied to the OMZ and utilized for aerobic respiration, we compiled relevant available information for the continental margin (<200 km off the coast with a water depth of >600 m) and open ocean (>200 km off the coast) of the ETNA and ETSP in **Figure 5**. Here, positive values indicate the supply of organic carbon via sinking particles (ΔF_{POC}) or DVM, and negative values denote aerobic respiration, converted to μmol C kg^{-1} y^{-1}. In this section, we also compare the carbon supply and demand with the oxygen supply and for this purpose convert oxygen supply rates in μmol O_2 kg^{-1} y^{-1} to carbon equivalents (CE, in μmol C kg^{-1} y^{-1}) using a conversion factor of 0.89. However, oxygen supply rates are not shown in **Figure 5**. For the ETSP open ocean, ΔF_{POC} derived from ^{234}Th approaches indicates no remineralization of POC in the OMZ core (Pavia et al. 2019), which is in accordance with the suggested inhibition of aerobic respiration under anoxic conditions and also indicated by negligible PARR estimates in the OMZ core (**Figure 5**). ΔF_{POC} increases again below the OMZ, but PARR values exceed this supply, which indicates that either PARR overestimates respiration at this depth or a carbon source is missing.

At the ETSP continental margin, oxygen decreases at a shallower depth than it does in the open ocean and remains undetectable down to ~450-m depth. In the top 60 m, the rates of DOC supply of 1,240 and 412 μmol C kg^{-1} y^{-1} at 20–40-m and 40–60-m depths, respectively, match or even exceed the rate of oxygen supply, which is estimated at 275 CE at 20–58-m depth (Loginova et al. 2019, Maßmig et al. 2019). Diapycnal oxygen supply at 87–115-m depth declines and is negligible, with only 1 CE (Loginova et al. 2019). Also, microbial respiration estimated by Kalvelage et al. (2015), as shown in **Figure 5**, agrees fairly well with the oxygen supply within the upper 100 m. ΔF_{POC} estimated from sediment trap deployments is clearly higher than it is in the open ocean and points to anaerobic remineralization or other unaccounted loss processes, as PARR estimates indicate that aerobic respiration is inhibited within the anoxic OMZ core. Moreover, carbon supply via DVM seems to be as important as the supply via sinking particles.

Few data are available for the ETNA continental margin. Here, PARR estimates are very high compared with those in the ETNA open ocean region. In the top 60 m, a diapycnal oxygen supply of ~700 CE at 25–45-m depth and ~160 CE at 45–60-m depth (Brandt et al. 2015) can easily satisfy the respiratory demand, as PARR estimates indicate that this is ~80 CE in the surface layer and then declines quickly (**Figure 5**). Yet no estimates of oxygen supply by the alongshore boundary circulation relevant for the deeper layers (Klenz et al. 2018) exist for this region.

For the ETNA open ocean region, aOUR values integrate over the entire subduction pathway and indicate a lower bound of oxygen consumption rates compared with PARR estimates, which

are twice as large (**Figure 5**). For this region, estimates of the relevant terms of the oxygen budget in the deeper water column (100–600-m depth) from long-term observations exist. Oxygen supply by mesoscale eddies is an important term in the budget, amounting to 1.7–2.2 CE for the depth range of 300–600 m and lower values at shallower depths (Hahn et al. 2014, Brandt et al. 2015). Advective oxygen supply to the OMZ was estimated by considering averaged zonal currents, resulting in 6.6 CE at 100–200-m depth, decreasing to ~1.8 CE at 200–400-m depth (Hahn et al. 2017). Due to low turbulent mixing rates (Banyte et al. 2012), diapycnal oxygen supply to the open ocean ETNA OMZ constitutes only 10–15% of the budget. Fischer et al. (2013) and Brandt et al. (2015) determined a supply of 0.4–0.8 CE at 300–500-m depth. Moreover, due to the presence of two oxygen minima in the ETNA (at approximately 100-m and 400-m depths) that cause reversing vertical oxygen gradients, the diapycnal supply acts as a sink of oxygen between 150 and 300 m. In total, the advective and diffusive oxygen supply from these studies is estimated at 4.9 ± 3.6, 4.2 ± 3.0, and 3.0 ± 3.2 CE at depths of 300–400 m, 400–500 m, and 500–600 m, respectively.

This total physical oxygen supply is able to balance the carbon supply by sinking particles and DVM of ~4.3 μmol C kg^{-1} y^{-1} at 300–600-m depth and also matches reasonably well with the aOUR of ~5 μmol C kg^{-1} y^{-1} at the same depth. PARR estimates, however, cannot be balanced below ~400-m depth (**Figure 5**). Despite major research efforts, it is therefore still difficult to fully constrain the O_2 and carbon loss and gain processes in this region, a statement that is even more valid for the ETNA continental margin and the ETSP.

4. CONCLUSION AND FUTURE PRIORITIES

It is clear from this review that knowledge of the full cycle of OM turnover—from carbon fixation at the surface to its degradation and respiration back to CO_2 at midwater depths—as well as of the physics involved in ventilating the ocean is fundamental to understanding the oxygen distribution in the ocean and assessing current and future expansions of OMZs. Recent climate change has altered the ocean and its ecosystems at a rate unprecedented in Earth history. Changes in the ocean's interior are often not obvious and progress slowly, as is the case for the expansion of oceanic OMZs. But their potential impacts on climate, air quality, marine life and productivity, and ultimately human well-being are massive. A joint effort by the scientific community is urgently needed to improve our basic understanding of the ocean as a highly sensitive coupled physical–chemical and biological system. Such a holistic approach also requires more certainty on supposedly well-known but actually understudied fundamental processes of carbon and oxygen cycling in marine systems and physical small- and large-scale transport.

FUTURE ISSUES

1. A significant increase is needed in the number of field observations of heterotrophic aerobic, microaerobic, and anaerobic respiration in oxygen minimum zones, their cores, and their boundaries, and the controlling factors must be understood and quantified.
2. The frequencies, spatial extents, and lifetimes of high-biomass, low-oxygen patches in the ocean need to be identified and understood in relation to physical forcing, and a better mechanistic understanding is needed of their formation and decay.
3. Multiple stressor impacts on organic matter cycling and oxygen consumption need to be resolved, and future climate–carbon cycle feedbacks should be estimated.

4. The supply rates of oxygen, dissolved organic carbon, and particulate organic carbon to oxygen minimum zones need to be determined at high spatial resolution over seasonal cycles.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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