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Do phytoplankton require oxygen to survive? A hypothesis and model synthesis from oxygen minimum zones

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Abstract

It is commonly known that phytoplankton have a pivotal role in marine biogeochemistry and ecosystems as carbon fixers and oxygen producers, but their response to deoxygenation has scarcely been studied. Nonetheless, in the major oceanic oxygen minimum zones (OMZs), all surface phytoplankton groups, regardless of size, disappear and are replaced by unique cyanobacteria lineages below the oxycline. To develop reasonable hypotheses to explain this pattern, we conduct a review of available information on OMZ phytoplankton, and we re-analyze previously published data (flow cytometric and hydrographic) on vertical structure of phytoplankton communities in relation to light and O_2 levels. We also review the physical constraints on O_2 acquisition as well as O_2-dependent metabolisms in phototrophs. These considerations, along with estimates of the photosynthetic capacity of phytoplankton along OMZ depth profiles using published data, suggest that top-down grazing, respiratory demand, and irradiance are insufficient to fully explain the vertical structure observed in the upper, more sunlit portions of OMZs. Photorespiration and water–water cycles are O_2-dependent pathways with low O_2 affinities. Although their metabolic roles are still poorly understood, a hypothetical dependence on such pathways by the phytoplankton adapted to the oxic ocean might explain vertical patterns in OMZs and results of laboratory experiments. This can be represented in a simple model in which the requirement for photorespiration in surface phytoplankton and O_2-inhibition of OMZ lineages reproduces the observed vertical fluorescence profiles and the replacement of phytoplankton adapted to O_2 by lineages restricted to the most O_2-deficient waters. A high O_2 requirement by modern phytoplankton would suggest a positive feedback that intensifies trends in OMZ extent and ocean oxygenation or deoxygenation, both in Earth's past and in response to current climate change.

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

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Deoxygenation in oceans is a growing phenomenon associated with anthropogenic climate change with several interacting causes that include changes in circulation and mixing, decreased solubility of oxygen (O_2) as temperature increases, and possibly biogeochemical changes (Ito et al., 2017; Schmidtko et al. 2017; Oschlies et al. 2018). The first evidence of a decline in dissolved O_2 was recorded in the 1980s (Horak et al. 2016; Ito et al. 2017). Oxygen minimum zones (OMZs) are naturally occurring zones where O_2 in sub-surface waters drops below a threshold that varies among authors but is

usually between 20 μmol kg^{-1} (Gilly et al. 2013) and 70 μmol kg^{-1} (Breitburg et al. 2018). Regional expansion of OMZs, and a further decrease in the global ocean O_2 inventory, are predicted over the next century (Keeling et al. 2010; Stramma et al. 2010; Grégoire et al. 2021; but see Auderset et al. 2022). Slight changes of O_2 can have significant biological effects (Levin 2018), especially for those organisms living near their physiological limits (Wishner et al. 2018).

Phytoplankton are estimated to contribute about half of global phototrophic primary production, and are thus major contributors to O_2 on Earth (Field et al. 1998; Rousseaux and Gregg 2014; Huang et al. 2021; Mattei et al. 2021). Their growth, interspecies competition, and resulting community structure in the ocean have long been studied in relation to factors such as temperature, irradiance, salinity, and nutrient availability (Tilman et al. 1982; Geider et al. 1997; Litchman et al. 2010). Despite being O_2 producers, phytoplankton can be exposed to dynamic conditions where O_2 varies from an aerobic state (oxic) to deficiency (hypoxic/suboxic), or even a total absence (anoxic), and their distributions along the vertical O_2 gradient of OMZs are distinctive (Aldunate et al. 2020). Since there are no clear and universally used definitions for the terms describing O_2 concentration in the water column, here we use the 10 μM threshold as the boundary between hypoxic and suboxic, which has often considered an approximate boundary for identifying waters in which O_2 might begin to be replaced as the principal electron acceptor in prokaryotic communities (Brewer et al. 2014; Pinti 2022; but see Canfield and Thamdrup 2009; Zakem and Follows 2017). We here use the term O_2-limited (including hypoxic and suboxic) waters to refer to waters with O_2 below 60 μM. This hypoxic threshold is often used to identify waters with critically low O_2 levels for aerobic animal communities, although individual species can have higher or lower critical O_2 thresholds (Chu and Gale 2017; Grégoire et al. 2021). We assume that the proportion of the plankton community affected by O_2 limitation rises steeply as O_2 declines below this threshold, when considering both microbes and animals as well as their interactions (such as grazing or predation). For some oceanic OMZs, where O_2 levels are undetectable and nitrite levels are high, we use the term anoxic marine zones (AMZ; Ulloa et al. 2012). We use the term AMZ oxycline to define the oxycline above water where anoxia occurs, even though turbulence or local production can result in detectable O_2 in layers that are normally anoxic. Below these AMZ oxyclines, all surface phytoplankton, regardless of size, disappear and, when sufficient sunlight penetrates, are replaced by unique AMZ cyanobacterial lineages below the oxycline (sensu secondary chlorophyll maximum (SCM); Lavin et al. 2010; Ulloa et al. 2021). The depth and abundance of these unique communities in the water column vary with OMZ thickness (Sarma et al. 2020).

Most knowledge of the ocean's ecological and biogeochemical function is from the conditions of high O_2 and low CO_2 (relative to most of Earth history) that currently dominate. In addition to present-day OMZs that exhibit low O_2 and high CO_2 states, we can look into Earth's past to understand how processes may be impacted in a future low O_2 and high CO_2 state. The appearance of oxygenic photosynthesis in cyanobacteria in the middle of the Archaean Eon culminated in the first step in the oxidation of the planet (Holland 2006; Kump 2008; Luo et al. 2016; Oliver et al. 2021). The banded iron formations of the proterozoic are commonly interpreted as the result of the alternation between an anoxic ocean rich in soluble Fe(II), and an ocean with sufficient O_2 to oxidize soluble Fe(II) to insoluble Fe(III), which precipitated in coastal water on continental crust (Klein 2005; Sessions et al. 2009). The Archaeplastida appears to have originated at least 1–1.6 Ga ago (e.g., crown-group Rhodophytes, Bengtson et al. 2017; *Bangiomorpha pubescens*, Gibson et al. 2018), that is, not later than the Mesoproterozoic, when the eukaryotic ancestor acquired photosynthesis by an endosymbiotic cyanobacterium that became the chloroplast (Ponce-Toledo et al. 2017; Sánchez-Baracaldo et al. 2017). Planktonic green algae, which are larger and sink faster, and sequester more carbon, than cyanobacteria, have been credited with the late proterozoic increase in O_2 (neoproterozoic oxidation event) that allowed the evolution of animals and the Cambrian explosion (Saltzman et al. 2011). During the Phanerozoic, there have been episodes of deep ocean deoxygenation, massive OMZs, and even global anoxic events (Falkowski et al. 2004, 2011; Levin 2018). Nevertheless, current marine phytoplankton includes major lineages that have evolved since the Proterozoic (Falkowski et al. 2004) in an ocean where at least the surface mixed layer is O_2-rich. How sensitive are modern phytoplankton to high CO_2 and low O_2 states that may become more common in the Anthropocene?

Phytoplankton communities in the OMZs in relation to depth, light, and O_2

OMZs provide unique systems to investigate the effects of low O_2 and high CO_2 states on phytoplankton composition and ecological dynamics. In certain core regions and depths of OMZs, O_2 in the water column becomes undetectable by sensors with limits of detection in the nanomolar (nM) range, while gene expression suggests most microorganisms are using anaerobic metabolisms (Stewart et al. 2012; Ulloa et al. 2012). When at sufficiently shallow depths, the upper layers of the apparently anoxic waters include a cryptic O_2 cycle driven by *Prochlorococcus* performing photosynthesis in a seemingly SCM found below the AMZ oxycline (Garcia-Robledo et al. 2017). Between the primary chlorophyll maximum (PCM) above the oxycline, composed of a diversity of eukaryotic and cyanobacterial phototrophs, and the SCM, composed exclusively of AMZ specific lineages of *Prochlorococcus* (Lavin et al. 2010; Ulloa et al. 2021), there is a chlorophyll/fluorescence minimum, which also corresponds to a transparency maximum (Fig. 1B). The eukaryotic phytoplankton disappear completely in the oxycline, while *Synechoccocus* and

Prochlorococcus abundances reach a minimum at the chlorophyll minimum/transparency maximum (Fig. 1C), despite the fact that nutrients are plentiful and sufficient light (between 0.1% and 1% of surface light) for photosynthesis is available (Garcia-Robledo et al. 2017; Aldunate et al. 2020). A strikingly similar pattern has been documented in the freshwater Lake Tanganyika, where a PCM in oxic surface waters is dominated by eukaryotes, they disappear in the oxycline, and are replaced by cyanobacteria-dominated community (*Synechococcus*) and green sulfur bacteria (Chlorobiaceae; obligate anaerobic phototrophs) below the oxycline, resulting in a minimum of chlorophyll and a SCM below (Callbeck et al. 2021).

To explore more quantitatively the relationship between phytoplankton, O_2, and light penetration along the oxyclines, we analyzed a total of 147 depth profiles made with conductivity-temperature-depth (CTD) instruments that included dissolved O_2 and fluorescence data from research cruises in the eastern tropical North Pacific (ETNP: NH1410 and RB1603) and the eastern tropical South Pacific (ETSP: AT2626, Lowphox, and NBP1305) OMZs (Fig. S1 and Table S1). We measured the depth and O_2 concentration in the PCMs, averaging over the depths at which in vivo fluorescence was within 90% of the maximum value recorded at each station. We defined the oxycline operationally to be within the thresholds of 10% and 85% of the maximum O_2 concentration at the specific station. 99% of 147 PCMs were within the upper half of the oxycline and 56% of the PCMs formed above the oxycline (Fig. S2). It is important to note that an SCM is not always found in OMZs; it has been proposed that they only exist when there is 1% downwelling blue light overlapping with anoxia (Cepeda-Morales et al. 2009). A clear SCM was observed in 87 profiles, always occurring below the oxycline where O_2 was below the limits of the CTD O_2 sensors, and therefore we considered all to be SCMs, permitting us also to characterize fluorescence minimums in these profiles.

Light plays an important role in the distribution and composition of phytoplankton (Schwaderer et al. 2011; Edwards et al. 2015) and supports O_2 generation when these phytoplankton photosynthesize. Light availability down the water column is dependent on the surface irradiance, and optical properties of the water, which can be different among locations and time. In order to directly compare the role of light penetration vs. O_2 concentration in the vertical structuring of phytoplankton, we normalized depth by light penetration using optical depth (OD; the light attenuation coefficient divided by depth). Attenuation coefficients (K_d) were estimated from the Copernicus-GlobColour satellite product with daily gap-free resolution (DOI. 10.48670/moi-00281), based on merging of remote sensing from the platforms SeaWiFS, MODIS-Aqua, MERIS, VIIRS-SNPP & JPSS1, OLCI-S3A & S3B

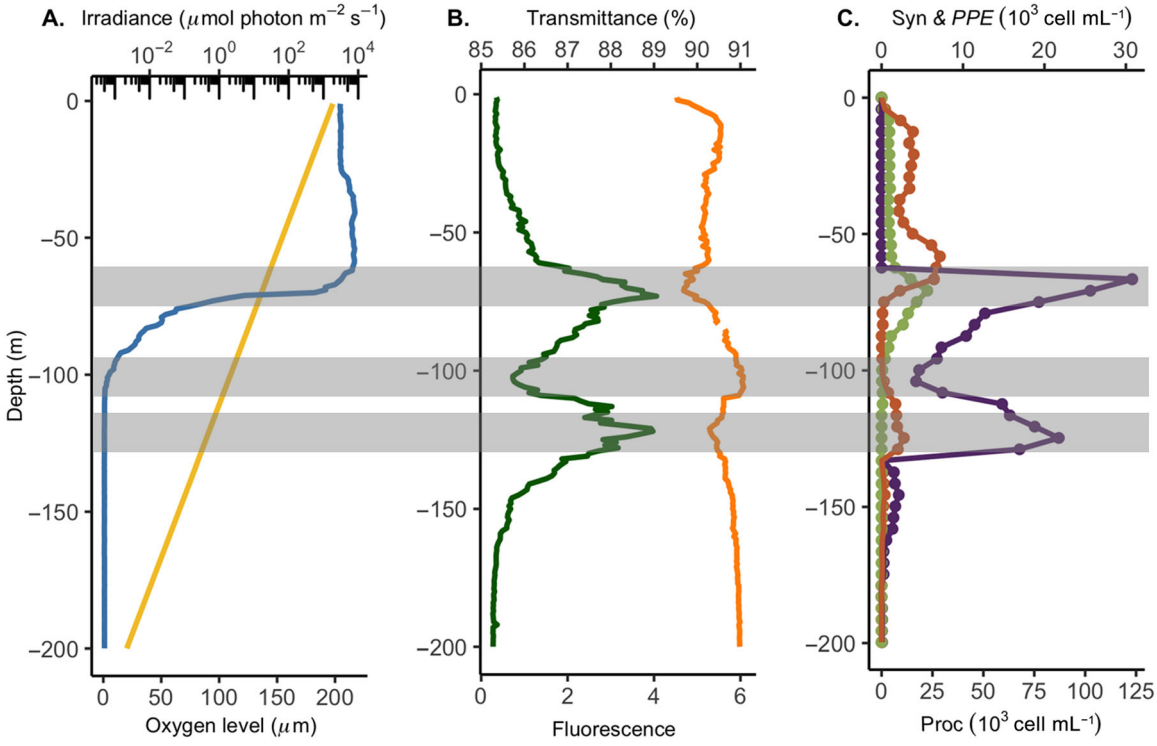

Fig. 1. An example of typical depth profiles at one of the investigated stations, RB1603-ST11. (**A**) O_2 concentration (blue) and irradiance in log scale (yellow), (**B**) fluorescence (green) and transmittance (orange) along the oxycline, and (**C**) cytometric profiles highlighting the abundance of *Prochlorococcus* (Pro; purple), *Synechococcus*-like (Syn + Pro; brown), and the photosynthetic picophytoeukaryotes (PPE; green). Gray boxes enclosed PCM (top), chlorophyll minimum (middle), and SCM (bottom).

following Garnesson et al. (2019), using the coordinates and date of sampling from each station (3 × 3 pixels and 3-day average). We note that similar results were obtained in some cases where data from a transmissometer in the CTD package was available to directly calculate attenuation coefficients (not shown).

The majority of the chlorophyll minima occurred at a light level higher than 1% of surface irradiance (Fig. 2A). In general, phytoplankton are unlikely to be limited by light at such depths, as both eukaryotic and cyanobacterial lineages are known to thrive at such light levels. Prymnesiophytes and low-light (LL) adapted *Prochlorococcus* are well known to be found at the lower margin of the euphotic zone (1% of surface irradiance), or at even deeper depths (e.g., Goericke et al. 2000; Haidar and Thierstein 2001; Quinn et al. 2005; Ras et al. 2008). Likewise, diverse assemblages of large diatoms are important contributors to deep photosynthetic biomass and these "shade flora" organisms are especially important for exporting carbon in the deep sea (Kemp and Villareal 2013). Thus, both eukaryotic and cyanobacterial phytoplankton can thrive at much lower light levels, so light alone is not limiting the vertical distribution of phytoplankton in such shallow oxyclines.

Chlorophyll fluorescence minima between the PCM and SCM occurred at the median O_2 of 3.5 μM (90% quantile between 2.1 and 21.3 μM; Table S1), with only minor variation among cruises (Fig. 2B). When the oxycline was shallow, the depths where the PCM started to decline with depth followed closely the depths at which the oxycline started (Fig. 2C). The relationship became less strong the deeper the oxycline formed, suggesting that when the oxycline was deep, low light appeared to limit PCM depth, but when the oxycline was shallow, the PCM depth was not based on light limitation but instead by an interaction with low O_2 that begins above a threshold assumed for hypoxia.

These observations indicate that vertical zonation of phytoplankton closely follows O_2. When light is low but not below the requirements for oxygenic phototrophs, low O_2 somehow appears to limit the accumulation of planktonic phototrophs found in most of the ocean. As phytoplankton are O_2 producers, such a limitation would create a feedback between the depth of the PCM and the oxycline depth.

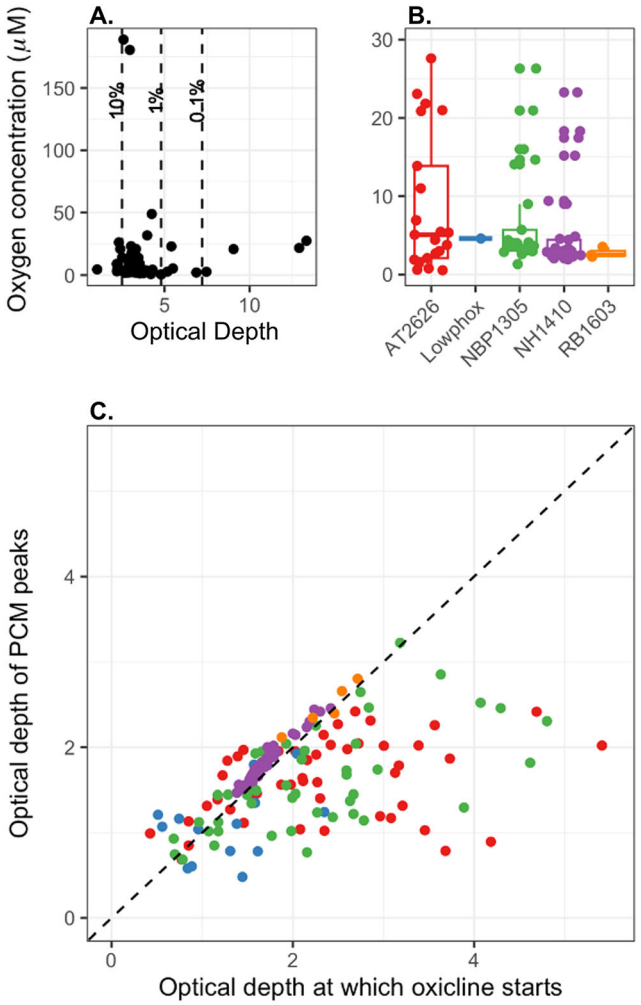

Fig. 2. (**A**) O_2 concentration and OD of chlorophyll minimums (when the SCM was present). Dotted lines represent 0.1%, 1%, and 10% of surface irradiance based of euphotic zone. (**B**) Box and whisker plot of O_2 concentration at chlorophyll minimum with respect to each of five cruises. Cruises AT2626, Lowphox, and NBP1305 in the ETSP in front of Peru and/or Chile; Cruises NH1410 and RB1603 in the ETNP in front of Mexico (map and ID of stations sampled in each cruise can be found in Fig. S1 and Table S2). When data from all cruises are averaged, the mean was 3.5 μM O_2, with the 90% quantile between 2.1 and 21.3 μM). (**C**) Relationship between the depth of the PCM (90% intensity) and the depth where the oxycline starts (including all stations, even when the SCM was not present). Dotted line represents a 1 : 1 correlation, r2 = 0.88. AT2626 (red), Lowphox (blue), NBP1305 (green), NH1410 (purple), and RB1603 (orange).

Could O_2-control of grazing cause the early disappearance of phytoplankton in the oxycline?

Mechanisms such as grazing and sinking rates could also govern the community structure of phytoplankton (Finkel et al. 2010; Litchman et al. 2010). The transmission maximum, which coincides with the fluorescence minimum between the PCM and SCM, may correspond to a general minimum in both phototrophic and nonphototrophic microbes in the picoplankton and nanoplankton size categories, as light transmission is mostly affected by smaller particles in these size ranges (Ehlers et al. 2012). If O_2 levels become low enough to limit planktonic grazers (e.g., heterotrophic and mixotrophic nanograzers and micrograzers, larger zooplankton groups), could decreased grazing explain the formation of an SCM? Grazers are not completely excluded because diel vertical migration has been observed in several types of zooplankton (i.e., mostly amphipods, large eucalaniid copepods, and salps), which spend a substantial amount of time in

O_2-limited subsurface layers, and even anoxic water within the core OMZ (Vargas and Madin 2004; Maas et al. 2014; Riquelme-Bugueño et al. 2020; Tutasi and Escribano 2020). However, smaller copepods, the primary control of heterotrophic microzooplankton (e.g., ciliates and flagellates), could decrease or undergo diapause in response to the drop in O_2 (Wishner et al. 2020). If animal zooplankton are excluded at higher levels of O_2 than protist grazers, this could result in a trophic cascade where heterotrophic flagellate grazers increase in the oxycline and then decrease below the oxycline, resulting in a local minimum in picoplankton and nanoplankton in the oxycline (and the observed transparency maximum). A trophic cascade might enhance heterotrophic flagellates in the oxycline, resulting in a local minimum in picoplankton and nanozooplankton. In euphotic layers of the ETSP OMZ, the impact of unicellular grazers is significant, explaining up to 13% of primary production in picophytoplankton ($< 2\ \mu$m, mostly cyanobacteria), 49% in nanophytoplankton (2–20 μm, mostly photosynthetic nanoflagellates), and 36% in microphytoplankton ($> 20\ \mu$m, mostly diatoms; Cuevas et al. 2004; Cuevas and Morales 2006). Moreover, substantial populations of microzooplankton were observed in *Prochlorococcus*-dominated depths of the Arabian Sea and ETNP OMZs (Goericke et al. 2000; Gowing et al. 2003; Peng and Valentine 2021), in support of the top-down control hypothesis. Indeed, a recent metabolic model supported the possibility that O_2-limited grazing could result in a chlorophyll minimum within the oxycline (Zakem et al. 2020). Nevertheless, although grazing may play an important role and might partly explain the fluorescence minimum, three points of evidence argue that top-down control is insufficient to explain the observed vertical distributions of phytoplankton in OMZ waters, particularly the changes in community assemblage between the PCM and the SCM.

First, Cuevas and Morales (2006) reported that heterotrophic nanoflagellates decrease in a monotonic manner through the oxycline. Although the decline was less steep than that of autotrophic nanoflagellates, there was no evidence for a maximum in heterotrophic flagellates at the depths where most phytoplankton disappear. More recently, Fuchsman et al. (2022) did observe a high increase of metagenomic reads from Acantharea and Radiolarians at the base of the oxycline, and these heterotrophic protists might be important grazers, but their role here is still not clear.

Second, among *Prochlorococcus* strains, the LL lineages of *Prochlorococcus*, which are abundant in the deep euphotic zone of the rest of the tropical and subtropical ocean, exhibit very low abundances in the dimly sunlit waters below the oxycline in AMZs, where only AMZ-specific lineages dominate (Lavin et al. 2010; Astorga-Eló et al. 2015; Ulloa et al. 2021). The existence of distinct cyanophage communities in the SCM could be important in the mortality of cyanobacteria (Fuchsman et al. 2019). However, although further investigation of cyanophage roles is needed, it is not clear if there might be a mechanism whereby cyanophages, or cyanophage infection, might respond to O_2 or O_2-deficiency in a way that could select AMZ-lineages over typical LL *Prochlorococcus* below the oxycline and/or inhibit the penetration upwards of AMZ-lineages. Hence, there is no evidence yet to suggest either -grazing or O_2-responsive cyanophage infection could explain the dominance of AMZ-lineages instead of LL lineages of *Prochlorococcus* below the oxycline.

Third, as mentioned previously, much of the typical "shade flora" at or below deep chlorophyll maxima in the open ocean is composed of diverse eukaryotic phytoplankton, including large diatoms such as *Thalasiothrix* and *Coscinodiscus* (Kemp et al. 2000; Kemp and Villareal 2013), and coccolithophores or other prymnesiophytes (Haidar and Thierstein 2001; Quinn et al. 2005; Ras et al. 2008). These groups should be subject to different grazer pressures, yet neither are part of the "shade flora" of the OMZ, which is a layer of exclusively cyanobacteria at the SCM (Garcia-Robledo et al. 2017). In fact, the overall diversity of eukaryotic assemblages reaches a minimum at the upper boundary of the OMZ ($\sim 10\ \mu$M; $\sim$ 70–100 m). Species richness then increases and peaks when the O_2 continues to drop ($< 5\ \mu$M; $\sim$ 100–400 m), especially for the smaller size fraction (Parris et al. 2014; Duret et al. 2015). The subsurface peak in diversity occurs at depths assumed to be anoxic based on nitrite accumulation and studies with high sensitivity O_2 sensors in the zones studied (Ulloa et al. 2012; Garcia-Robledo et al. 2017). Several factors are suggested to be operative at lower depths, such as trophic lifestyle (Jing et al. 2015; Peng and Valentine 2021). The increase of eukaryotic communities below the oxycline is not due to phototrophs, and peaks well below the SCM (> 200 m). If the local minimum of chlorophyll and fluorescence in the oxycline were due to a local maximum of protist grazing at these depths, the SCM should be composed of a rich community of phototrophs including eukaryotes, but this is not the case.

How phytoplankton deal with low O_2 conditions

If the vertical patterns can be explained by direct physiological responses of phytoplankton to O_2, two very distinct effects must be invoked. First is whether low O_2 can inhibit phytoplankton adapted to the oxic layers of the ocean, and second is what excludes the AMZ lineages from the oxic zones both vertically, as they disappear with decreasing depth in the oxycline, and horizontally, as they are not found in oxygenated low light waters in the rest of the ocean. We focus primarily on the first possibility as it has the broadest implications.

Since phytoplankton cannot photosynthesize in the dark, they rely on other mechanisms to supplement their O_2 requirements in low or no O_2 conditions when light is inadequate. For example, microalgae form resting stages such as spores to survive in anoxic sediments (Yang et al. 2015), so one strategy is to greatly reduce metabolism. There is also evidence that many microalgae and cyanobacteria can maintain

metabolic activity in low O_2. *Prochlorococcus* could possibly survive dark anoxic conditions through the use of organic compounds (Coe et al. 2016; Biller et al. 2018) by "helper-bacterium" (Morris et al. 2008; Roth-Rosenberg et al. 2020) and fermentation in AMZ *Prochlorococcus* (Ulloa et al. 2021) may represent additional features to supplement their required carbon and energy requirements under low O_2. Many eukaryotic microalgae are able to transform energy from stored organic carbon by fermentation under dark anoxic conditions (Catalanotti et al. 2013). Diatoms may be particularly adept at tolerating low O_2 as they have been reported to use nitrate-respiration (i.e., dissimilatory nitrate reduction; Kamp et al. 2011) when kept in dark and very low O_2 conditions. Thus, at least in the dark, both cyanobacterial and eukaryotic phytoplankton have a variety of alternative strategies to perform heterotrophic metabolism when O_2 is limiting.

Enhanced ATP production through cyclic electron flow is a way for phytoplankton to utilize less O_2 in oxidative phosphorylation. Cyclic electron flow around photosystem I (PSI) occurs in all marine phytoplankton organisms, with associated active H^+ flux into the thylakoid lumen from the stroma in eukaryotes and cytosol in cyanobacteria (Larkum et al. 2017, 2018). The H^+ pumped per electron moving from the reducing to the oxidizing end of the PSI is taxonomically variable, with corresponding influence on the quantity of ATP produced when the pumped H^+ moves downhill through the ATP synthase to the stroma or cytosol (Larkum et al. 2017, 2018). This means that the quantity of ATP synthesized per absorbed photon allocated to PSI is taxon dependent (Larkum et al. 2017, 2018). With a fixed allocation of absorbed photons between the two photosystems, this would involve additional energy dissipation at photosystem II (PSII), which may not be a problem at the relatively low irradiances associated with ocean suboxic zones. However, state transitions can alter the distribution of absorbed photons between PSII and PSI (Wollman 2001). Another possibility of O_2-independent photoproduction of ATP is cyclic electron flow around PSII, which might also decrease O_2 production by competing for absorbed photons. However, it is still not established whether such electron flow is coupled to pumping H^+ into the thylakoid lumen (Ananyev et al. 2017; Kedem et al. 2021). ATP synthesis coupled to PSI cyclic electron transport could, in the light, replace ATP production by fermentation under anoxia in the photic zone (Gfeller and Gibbs 1984).

Some types of photosynthesis do not produce O_2. For example, cyanobacteria can use hydrogen sulfide instead of water as the electron donor for photosynthesis under anoxic conditions, generating sulfur (S^0) instead of O_2 (Cohen et al. 1975, 1986; Garlick et al. 1977; Oren and Padan 1978; Nagy et al. 2014; Grim and Dick 2016; Hamilton et al. 2018; Liu et al. 2020). The genes for anoxygenic photosynthesis have not been found in the AMZ *Prochlorococcus* (Ulloa et al. 2021). But the top of the anoxic layer does have a peak in H_2S oxidation and high rates of dark CO_2 assimilation, attributed to a group of diverse sulfide-oxidizing microbes (Fuchsman et al. 2017; Saunders et al. 2019; Raven et al. 2021). A cryptic sulfur cycle (Canfield et al. 2010) and a cryptic O_2 cycle (Garcia-Robledo et al. 2017) act in this AMZ anoxic photic zone.

Ion-pumping rhodopsins provide another possibility of O_2-independent transduction of absorbed photons with production of ion (H^+, Na^+, or Cl^-) electrochemical differences across a membrane (Larkum et al. 2018; Gómez-Consarnau et al. 2019). Ion-pumping rhodopsins occur in some marine Archaea and Bacteria, but not in marine cyanobacteria (Hasegawa et al. 2020); they also occur in some eukaryotic phytoplankton, but apparently not in membranes that contain ATP synthase, so their active ion transport can only be used to drive solute cotransport across the rhodopsin-containing membrane (Larkum et al. 2018). Accordingly, rhodopsin-based energy transduction in phytoplankton cannot completely replace fermentation in the light under anoxia (Gómez-Consarnau et al. 2019; Munson-McGee et al. 2022).

Thus, it would appear that a variety of mechanisms are distributed among extant phototrophs that should permit a diverse group to tolerate and even thrive under low O_2. In fact, when sufficient light is present for photosynthesis, a lower O_2/higher CO_2 level would be expected to be stimulatory, through the releasing of photorespiration pressure (reviewed in more detail below). Enhanced photosynthesis and growth were indeed observed in the estuarine diatom *Thalassiosira weissflogii* (*Conticribra weissflogii*) when O_2 was lowered and CO_2 raised (Sun et al. 2022). This makes it surprising that such eukaryotic phytoplankton are not flourishing in the oxycline above the AMZs.

To date, we are aware of three studies that have reported that low O_2 can inhibit growth in phytoplankton. A study on another diatom, *T. psuedonana*, reported that its growth rate was moderately enhanced by 150 μM O_2 but moderately inhibited by 40 μM O_2 compared to O_2 saturation reported as 310 μM O_2 (Chen et al. 2021). In addition to slightly lower O_2 than the study by Sun et al. (2022), Chen et al. (2021) used lower light (150 vs. 200 μmol photons m^2 s^{-1}) and reported that the inhibitory effect was enhanced when was grown under 8 : 16 instead of 16 : 8 light : dark cycle, which suggests that low light also should be considered in future studies.

The second study, a nanoflagellate, the haptophyte *Immantonia* sp., was reported to suffer severe growth inhibition and even mortality when exposed to low O_2 (56 μM) and low pH (7.5) (Piscoya et al. 2022), conditions designed to mimic the oxycline above the ETSP OMZ. This study is especially interesting both as the strain tested was isolated from directly above the oxycline in question and as it is so far the only study to consider the combination of low O_2 and low pH/high CO_2 conditions that occur in nature.

The third study examined the response of *Prochlorococcus* strain MED4, a "high light" strain representative of cyanobacterial phytoplankton typical of surface communities,

to much lower O_2 levels, with and without CO_2 limitation (Bagby and Chisholm 2015). Although their focus was on CO_2 limitation, and they did not test the combination of low O_2 and high CO_2, it is interesting to note that growth was inhibited and chlorophyll fluorescence dropped under their 0% O_2 treatment with all CO_2 conditions they tested. Low O_2 (< 0.001%–10%) disrupted both growth and the ability to buffer light stress for normal photosynthetic electron transport in this organism. Photosynthetic O_2 supply also could not meet cellular demand even under sufficient CO_2 and light at low O_2. With rapid loss of O_2 from diffusion to the surrounding anoxic water, there was little O_2 available to plastoquinol terminal oxidase (PTOX), which serves as an electron sink when carbon fixation is insufficient. This suggests the potential role of exogenous O_2 in a cell's capacity to respond and recover from excessive reducing equivalents. Only 4 genes out of 2096 tested were detected as differentially expressed specifically under low O_2 (in comparison to 296 genes under low CO_2 and 261 genes specific to the combination of low O_2 and low CO_2. These four genes were annotated as "Possible high light inducible protein Hli14," and three hypothetical proteins, so none offer a clear indication of what functions are affected by low O_2. Unfortunately, this study did not test the combination of low O_2 and low pH/high CO_2, however, it provides powerful evidence that non-AMZ lineages of *Prochlorococcus* may be severely inhibited in the extremely low O_2 where the AMZ lineages dominate.

It is curious that both *Immantonia* sp. And HL *Prochlorococcus* appeared to be much more sensitive to low O_2 than the two diatoms tested. This would suggest that sensitivity to low O_2 may vary among lineages as well as being affected by interactions with pH/CO_2 and light.

A review on O_2 requirements relevant to phytoplankton metabolism

To search for possible hypotheses that might explain these observations, we review the known roles of O_2 in autotrophs, examining what metabolic processes might determine the success of organisms under O_2-limiting conditions. Since relevant information on phytoplankton is limited, information from flowering plants is also reviewed, with attention to the caveat of the phylogenetic and functional differences among photosynthetic organisms.

Respiratory demand

The internal O_2 concentration of phytoplankton is controlled energetically through respiration and photosynthesis. The O_2/H_2O pair possesses a high oxidation potential and allows more H^+ to be pumped per electron transferred from NADH, and thus more ATP synthesis, than electron transfer to lower potential acceptors. Respiratory O_2 uptake is briefly enhanced after illumination, which is called light-enhanced dark respiration (LEDR; Stone and Ganf 1981; Weger and Turpin 1989; Beardall et al. 1994). LEDR is variable and related to their carbon storage/light history during the previous day (Markager and Sand-Jensen 1989). Raven and Beardall (1981) discussed earlier work showing that dark respiration can be subdivided into growth and maintenance. Growth can only be achieved when there is enough energy and other resources for the synthesis of various cellular materials and division. Maintenance respiration (R_0) represents the energy demand of a cell to maintain viability, and is correlated with the intracellular pool of organic matter (Langdon 1993). Respiration rate of phytoplankton is variable: highest after sunset, reaching a minimum gradually and a slight increase before sunrise (Markager and Sand-Jensen 1989). However, there are still deviations from observed patterns that remain to be directly characterized (Bender et al. 2022).

It is practically challenging to measure respiration accurately in nature. Direct measurement using microsensors or membrane-inlet mass spectrometer systems have only proved possible for relatively large colonial planktonic organisms (Hoch and Kok 1963; Ploug et al. 1999) or indirectly with the use of in vitro electron transport activity measurements. Gerard and Falk (1931) demonstrated that respiration rate is independent of O_2 concentration until it is below a threshold value, the critical O_2 tension. Apparent half saturation constant for O_2 uptake has later been adopted as a true kinetic parameter to define O_2 affinity. The terminal oxidase of *Vibrio*, cbb3, has a higher affinity for O_2 than cytochrome aa3, which is the highest affinity terminal oxidase of eukaryotes (Gong et al. 2018). From the literature, the half-saturation constant (K_M) for cytochrome-c oxidase (COX) is between 1 and 69 μM for cyanobacteria (Jensen and Cox 1983), 17–21 μM for Rhodophyta (Furbank and Rebeille 1986), and only around 0.1 μM for flowering plants (Gupta et al. 2009). Other studies have shown that dinoflagellates have a higher O_2 requirement per ATP produced in oxidative phosphorylation compared to other phytoplankton as a result of the absence of a H^+-pumping Complex I in their mitochondria (Tang 1996; Raven and Beardall 2017), yet dinoflagellates may be one of the more abundant protist groups below the oxycline (e.g., Fuchsman et al. 2022).

At least for the smallest phytoplankton, respiratory demands should be met by very low O_2 concentrations, in the range of 1–10 nM or less (Tiano et al. 2014). We performed similar calculations for three classes of nanoplankton and phytoplankton using a simple model (Table 1; Jumars et al. 1993). Besides illumination, the respiratory demand for O_2 is also related to temperature, cell size (López-Sandoval et al. 2014), and is taxon-specific (Tang 1996). O_2 is transported into and out of the cell via diffusion, which is affected by cell size and the composition of cell membranes (Ploug et al. 1999). Larger cells may be more prone to O_2 limitation when the cell is deficient in O_2, due to a lower surface-to-volume ratio and a thicker diffusion boundary layer around the cell. The peptidoglycan layer and outer cell membrane of

Table 1. $[O_2]_{env}$ derived from Jumars et al. (1993) with an assumption of the diffusivity of O_2 (D) in seawater at 25°C (Jähne et al. 1987). Parameters of phytoplankton groups (size, maintenance respiration, and Chl *a* content) are compiled from the literature (Jørgensen 1966; Prézelin and Sweeney 1977; Pelley and Bannister 1979; Falkowski 1980; Laws and Bannister 1980; Owens et al. 1980; Rivkin et al. 1982; Verity 1982; Barlow and Alberte 1985; Falkowski et al. 1985; Geider et al. 1986; Geider and Osborne 1986; Langdon 1987; Sakshaug et al. 1991; Collier and Grossman 1994; Polle et al. 2000; Brunet et al. 2006 and Table S3).

				Cyanobacteria	
		Chlorophyceae	Bacillariophyceae	*Synechococcus*	*Prochlorococcus*
Diffusivity (D)	$\times 10^{-9}$ m^2 s^{-1}	2.53			
Size (radius; r_0)	μm	10	5	0.6	0.3
Respiration (Ro)	μmol O_2/μg Chl *a*/h	0.003–0.011	0.002–0.005	0.017	
Chl *a* content	$\times 10^{-8}$ μg Chl *a*/cell	154	50	1.94	0.04–0.16
Influx (J_D)	$\times 10^{-9}$ μmol O_2/cell/h	9.73	1.50	0.33	0.017
$[O_2]_{env}$	Nmol/L	8.50	2.62	4.80	0.50
Range $[O_2]_{env}$	Nmol/L	4.03–14.8	1.75–4.37	2.97–6.63	0.22–0.77

cyanobacteria are very porous and freely permeable for O_2 molecules (Ligeza et al. 1998; Kihara et al. 2014). The lipid components of the plasma and thylakoid membrane are also not a significant barrier to O_2 diffusion, but proteins embedded in the membranes could reduce the permeability of the membranes (e.g., 30% in the plasma membrane and 80% in the thylakoid; Kirchhoff et al. 2002; Kihara et al. 2014). Nevertheless, here we ignore membranes as they are not expected to be a major limiting factor that might distinguish among cells (Kihara et al. 2014).

Diffusion rate of O_2 (J_D, mol cell^{-1} h^{-1}) from bulk seawater to the surface of a sphere where O_2 is consumed is determined by Fick's Law:

$$J_D = -4\pi r_0 D\left([O_2]_{env} - [O_2]_0\right) \quad (1)$$

where r_0 is the cell radius (μm), D is the diffusivity of O_2 (m^2 s^{-1}), $[O_2]_0$ and $[O_2]_{env}$ are the concentrations of O_2 at the cell surface (assumed 0) and in the environment. As shown in Table 1, respiratory demands should be met by nanomolar (nM) O_2 levels in these organisms. Therefore, it would seem that O_2-limitation of respiration would not be sufficient to explain observed patterns.

O_2-dependent cell constituents

The biosynthesis of some phytoplankton metabolites requires O_2, particularly tetrapyrrole pigments and sterols. Studies have shown a close link between these compounds and the rise of terrestrial O_2, which resulted in diversification of biosynthetic alternatives or as a result of adaptive response. Tetrapyrroles are described as the "pigments of life" (Battersby 2000; Bryant et al. 2020), as these pigments are essential in the capture of light and photosynthesis in phytoplankton. Although information on the K_M for O_2 for pigment biosynthesis is not known, we would expect it to be in a similar range as for respiration. Additionally, the capacity to synthesize pigments in the absence of O_2 should be ancestral and may still be present in some phytoplankton lineages. AMZ *Prochlorococcus*, which may represent the metabolic capabilities of the ancestral lineages originating in anoxic oceans (although molecular phylogenetic studies suggest that *Prochlorococcus* originated at the NOE ~ 1.8 Ga after the GOE: Sánchez-Baracaldo and Cardona 2020), have complementary enzymes for pigment biosynthesis that work under O_2-limiting conditions (three genes: $hemN_2$, $acsF_2$, and ho_2; encode secondary versions of enzymes involved in heme, chlorophyll, and phycocyanobilin biosynthesis), and retained phycobilisomes as light-harvesting antennae (Ulloa et al. 2021). In other organisms, alternative pathways were also found to synthesize the same end-products in the absence of O_2 (Bryant et al. 2020), which also include hemes that are produced in a similar manner to chlorophyll via the tetrapyrrole synthesis pathway (Chapman et al. 1997).

Evidence shows that the evolution of sterols is linked to the availability of molecular O_2 in the atmosphere (Bloch 1983; Galea and Brown 2009), as well as an early defense mechanism against O_2. The synthesis of sterols is an O_2-intensive process; one molecule of cholesterol, ergosterol, and phytosterol require 11, 12, and 11 molecules of O_2, respectively (Summons et al. 2006). Sterol is an essential constituent of eukaryotic membranes, and plays multiple roles in membrane organization, dynamics, function, and sorting (Lindsey et al. 2003). Sterols are very diverse in microalgae, with diatoms containing more than 40 identified sterols. Some algae have a single sterol that predominates, others possess mixtures of 10 or more sterols (Volkman 2005). Yet, certain dinoflagellates do not contain any sterol (Kokke et al. 1981; Goad and Withers 1982; Teshima et al. 1983), and it has been debated that cyanobacteria do not synthesize sterols (reviewed by Volkman 2005). There is only information on K_M for O_2 available for yeast, in which it is around 0.3–4 μM for the first O_2 integration by squalene monooxygenase (also called squalene epoxidase; Jahnke and

Klein 1983). Thus, the ranges of O_2 that limit sterol biosynthesis may be of a similar order of magnitude to those of respiration.

Photorespiration

Photorespiration is an O_2-demanding metabolic pathway with a low affinity for O_2. It is one of the pathways that have evolved in response to the declining atmospheric $CO_2 : O_2$ ratio since the global oxidation event in the early Proterozoic (Rickaby and Eason Hubbard 2019). Photorespiration, or the C_2 cycle, is integral to photoautotrophic organisms given the promiscuous chemistry of ribulose 1,5-bisphosphate (RuBP) carboxylase/oxygenase (RuBisCO) (Tcherkez 2016). RuBisCO evolved in the Archean before there was significant O_2 in the atmosphere, and selective pressure on RuBisCO kinetics was a response to the declining atmospheric $CO_2 : O_2$ ratio. The $CO_2 : O_2$ selectivity of RuBisCO means that, oxygenase activity is unavoidable in photosynthetic cells during the day (which also operates in the dark in chemolithotrophs) when CO_2 entry is by diffusion from the present atmosphere (Lorimer and Andrews 1973). For similar kinetics of RuBisCO, diffusive limitation of CO_2 assimilation is greater in organisms lacking carbon dioxide concentrating mechanisms (CCMs), especially in aquatic organisms with CO_2 and O_2 diffusion coefficients in water 10^{-4} that in air. The presence of a CCM increases the steady state $CO_2 : O_2$ concentration ratio at the active site of RuBisCO, and thus the photosynthesis : photorespiration ratio is higher (Raven et al. 2012; Raven and Beardall 2017; Van de Waal et al. 2019; Rickaby and Eason Hubbard 2019). Yet, the presence of CCMs does not fully suppress 2-phosphoglycolate (2PG) synthesis from oxygenation. Photorespiratory metabolism is functionally important to detoxify and recycle or complete oxidize 2PG, and is indispensable for oxygenic photosynthesis (Tolbert 1997; Eisenhut et al. 2008; Hagemann et al. 2016).

When there is no O_2, 2PG will not be generated by RuBisCO and there should be no need for downstream photorespiration pathways. Nevertheless, there are discussions that photorespiration may play other essential roles in some phototrophic organisms (Eisenhut et al. 2008; Bauwe et al. 2012; Fernie and Bauwe 2020). In plants, photorespiration provides reducing equivalents and substrates for ATP production and redox balance, although this does not compensate for the higher ATP and NADPH requirement per net CO_2 fixed by photosynthesis plus photorespiration than for the photosynthesis without photorespiration (Gardeström and Wigge 1988; Kromer et al. 1993; Wingler et al. 2000; Lim et al. 2020). Photorespiration also interacts with other carbon metabolisms as well as nitrogen assimilation (Gilbert et al. 2016; Eisenhut et al. 2019). In terms of carbon recovery, the enzymes catalyzing the conversion of glycolate to glycerate have been found in some algal species (Chlorophyceae, Euglenophyceae, and Treboxiophyceae), via the photorespiratory pathway most similar to that of higher plants (Bruin et al. 1970; Merrett and Lord 1973; Tolbert 1974). There are alternative pathways that convert glyoxylate to increase CO_2 in the chloroplast through the tartronate semialdehyde pathway, and complete decarboxylation (Niessen et al. 2007; Eisenhut et al. 2008; Dalal et al. 2015; Ahmad et al. 2016; South et al. 2018). For example, the carbon flow of the diatom *Cylindrotheca fusiformis* branches after the oxidation of glycolate to glyoxylate, with a second pathway that involves glyoxylate carboligase and involves no amino acid intermediates (Paul and Volcani 1976). It allows a more direct shuttling of carbon back to glycerate, but further examination is required to determine the importance of each pathway.

As in plants (Bloom 2015), a possible coupling between photorespiration and nitrogen metabolism has also been proposed in diatoms (Keys et al. 1978; Allen 2005). However, any such coupling must be very different from what might be found in flowering plants, as diatoms possess a complete urea cycle similar to that of metazoans but which is absent in green algae and plants. The urea cycle is important to diatom nitrogen metabolism, turn-over, and signaling. It has been speculated that the urea cycle could recover the photorespiratory derived NH_3 and CO_2 (Armbrust et al. 2004; Allen et al. 2006, 2011). For example, reassimilation of NH_3 is catalyzed by glutamine synthetase II (GSII) in the chloroplast (Beardall 1989), or by cytosolic GSIII (Parker and Armbrust 2005). There is only limited research on the functional role of photorespiration in the overall cellular energy balance, C and N status and turnover in diatoms, but evidence has shown differences from that of well-studied green-lineage organisms.

These photorespiratory pathways are shown to be variable among taxa, and are affected differently by abiotic factors. Glycolate dehydrogenase is stimulated by light in *Euglena* (Codd and Merrett 1971; Davis and Merrett 1975), and its activity is dramatically reduced under nitrogen starvation in the green algae *Chlamydomonas reinhardtii* (Cooksey 1971). For the diatom *C. fusiformis*, glycolate oxidation activity is maintained at a continuous level and does not correlate with photosynthetic activity, only the later step that both glyoxylate-glutamate aminotransferase and glyoxylate carboligase are regulated by conditions which affect photorespiration (Paul and Volcani 1976). In *C. weissflogii*, whether glycolate produced from photorespiration is being released or metabolized downstream is dependent on temperature, light, and nitrogen source (Parker et al. 2004; Parker and Armbrust 2005). Under high light conditions, photorespiration and nitrate reduction were proposed as a mechanism to dissipate excess energy, especially under low temperature when the Calvin cycle enzymes are inhibited. Chen et al. (2021) reported differential expression of some genes related to photorespiration under low O_2 in the diatom *T. pseudonana* (see both their main text and their Table S5) including PG phosphatase, glycolate oxidase, glutamate-glyoxylate aminotransferase, glyceraldehyde-3-phosphate dehydrogenase, and glycine dehydrogenase. Some genes, such as glycolate oxidase, were moderately upregulated under O_2-limited compared to normoxic conditions when grown on 8 : 16 LD, but

downregulated under O_2-limited conditions compared to normoxic conditions when grown on 16 : 8 LD. Other genes, such as glutamate-glyoxylate aminotransferase, were unchanged between O_2-limited and normoxic conditions under 16 : 8 LD but either also unchanged or only slightly upregulated under O_2-limited conditions when grown on 8 : 16 LD. The patterns are not easily interpretable but do suggest an interaction between light and O_2. An important lesson here is that how photorespiration is integrated into other metabolic processes, and thus how or if it might be essential beyond 2PG disposal or impacted by interactions with other factors such as nutrients or light, must be highly variable among phototrophs.

Water–water cycles

In addition to LEDR and photorespiration in oxygenic photosynthetic organisms, light-dependent O_2 uptake occurs in water–water cycles (Raven et al. 2020). Here, electrons flow from water oxidation in the O_2 evolving complex of PSII, via electron and hydrogen redox agents, to O_2. The simplest water–water cycle is plastoquinol terminal oxidase or plastid terminal oxidase (PTOX), where electrons from the reducing end of PSII reduces plastoquinone to plastoquinol, which is then oxidized by PTOX, reducing O_2 to water (Raven et al. 2020). The other two water–water cycles involve both PSII and PSI. The longest known of these water–water cycles is the Mehler ascorbate peroxidase (MAP) reaction, also known as the Asada–Halliwell–Foyer pathway (Raven et al. 2020). In this pathway, two electrons from the reducing end of PSI combine with two O_2 to produce two superoxide anions, and using superoxide dismutase, one H_2O_2 and one O_2.. H_2O_2 is metabolized via ascorbate peroxidase, ultimately generating two H_2O using another two electrons from the reducing end of PSI (Raven et al. 2020). More recently characterized is the flavodi-iron pathway, where four electrons from the reducing end of PSI are transferred, via a flavodi-iron protein, to O_2 to produce two H_2O (Raven et al. 2020).

The electron transport pathways of the water–water cycles are coupled to H^+ transport across the thylakoid membrane. For PTOX, four H^+ are transported from the stroma (cytosol in cyanobacteria) to the thylakoid lumen per O_2 evolved from PSII and O_2 reduced by PTOX (Raven et al. 2020). For the MAP and flavodi-iron water–water cycles, 12 H^+ are transported from the stroma to the thylakoid lumen per O_2 evolved from PSII and O_2 reduced by PSI (Raven et al. 2020). Since there is no evidence of an uncoupling protein that transfers H^+ from the thylakoid lumen to the stroma (cytosol in cyanobacteria) with energy dissipation rather than coupling to energy transduction, it is assumed that H^+ return to the stroma (eukaryotes) or cytosol (cyanobacteria) via the CF_OCF_1 ATP synthase (Raven et al. 2020). Such an obligatory coupling to ATP synthesis constrains the rate of the water–water cycles to the rate at which the ATP they produce can be used. This limits the extent to which water–water cycles can act in, for example, dissipation of excess excitation energy from PSII at high irradiances. The H^+ : electron ratio of one for PTOX makes this water–water cycle variant more useful in energy dissipation under conditions of limited ATP requirement than the two water–water cycles that have a H^+ : electron ratio of three (Raven et al. 2020). Under conditions of greater ATP requirement, the water–water cycles involving both photosystems with their H^+ : electron ratio of three would provide a 50% higher ATP output per absorbed photon, assuming a fixed allocation of absorbed photons between the two photosystems, that is, no state transitions (Wollman 2001). One alternative to water–water cycles in ATP production in the light without corresponding ferredoxin or $NADP^+$ reduction is mitochondrial respiration (Bailleul et al. 2015; Raven et al. 2020), but that has relatively high affinity O_2 uptake.

In summary, both photorespiration and water–water cycles have low O_2 affinities in phytoplankton. It is likely that one or both of these processes would disappear below higher minimum O_2 concentrations than respiration or other known metabolisms. However, the allocation of the observed electron flux to O_2 among the various pathways, that is, light-enhanced mitochondrial respiration, photorespiration, and water–water cycles, is complicated and poorly understood. Metabolic inhibitors and gene knock-outs specific for a particular O_2 uptake process can result in compensatory changes in other pathways (Raven et al. 2020). There are major challenges in our capacity to resolve the roles and interactions of these pathways, but we have sufficient evidence for the importance of O_2 to phytoplankton and proceed to develop a model to explore whether such a pathway might be critical.

Could O_2-dependent metabolisms explain the missing photosynthetic growth in the oxycline?

Our goal was to explore if inhibition by low O_2 of phytoplankton from the oxic ocean might explain the vertical patterns observed in OMZs in nature. We chose to test the simplest model with the minimum possible assumptions. This approach also allowed an order-of-magnitude estimation of the potential impact on energy flow represented by the fluorescence minimum.

We started by predicting the depth-variation of photosynthesis considering only light and assuming an organism with light-acclimated photophysiology similar to those documented for *Prochlorococcus*. Photosynthesis is predicted to vary with light according to Platt et al. (1980):

$$P^{\mathrm{B}}(E) = P_{\mathrm{s}}{}^{\mathrm{B}}\left[1 - \exp\left(-\frac{\alpha E}{P_{\mathrm{s}}{}^{\mathrm{B}}}\right)\right]\exp\left(-\frac{\beta E}{P_{\mathrm{s}}{}^{\mathrm{B}}}\right) \quad (2)$$

where P^{B} is the photosynthetic rate at irradiance E, normalized to chlorophyll/per cell, α is the initial slope, and β defines the degree of inhibition at high intensities. $P_{\mathrm{s}}{}^{\mathrm{B}}$ is the potential

maximum photosynthetic rate normalized to chlorophyll/per cell; it is related to the observed maximum rate

$$P_m{}^B \quad \text{(as)}$$

$$P_s{}^B = P_m{}^B \left(\frac{\alpha}{\alpha+\beta}\right)\left(\frac{\beta}{\alpha+\beta}\right)^{\beta/\alpha} \quad (3)$$

Photosynthetic parameters (α and $P_m{}^B$) were adopted from *Prochlorococcus* populations (Ulloa et al. 1997). As β was not reported, it was estimated by R package "phytotools" with data extracted with WebPlotDigitizer (version 4.4) from the reported P-E curves. A is within 0.0249–0.0834; β is within 0.0091–0.0117. While there are no data on β for AMZ *Prochlorococcus*, estimated α from AMZ *Prochlorococcus* (Garcia-Robledo et al. 2017) are not outside the ranges reported for non-AMZ *Prochlorococcus* ($\alpha = 0.052$–0.088; $\beta = 0.0009$–0.0182). Thus, we assume the lineages of phytoplankton adapted to oxic and anoxic waters have similar α and β. As we are concerned with the highly stratified conditions of the oxycline, we assume phytoplankton at each depth are fully acclimated to their light environment, and an exponential curve was assumed to account for the depth variations in α and β (Partensky and Hoepffner 1993).

We simulated the light environment of several OMZ stations with the SCM, and compared them with the observed fluorescence profile. Surface light was assumed to be 1580 μmol photon m^{-2} s^{-1} (surface PAR from MODIS, year 2016, at N15.96–17.54 W103.88–112.96). Attenuation coefficients were either measured directly from transmissometer measurements (averaging from the surface to below the SCM) or from MODIS and converted to k_{PAR} by a model of (Morel et al. 2007). Six stations from cruise RB1603, with varying size of SCMs, are shown in Figs. 3, 4 and Figs. S3–S8), where the measured chlorophyll fluorescence is shown in panels (A). In panels (B), the predicted photosynthesis based only on light is shown (orange). If growth is proportional to predicted photosynthesis, clearly, light alone is unlikely to explain the double maxima in photosynthetic organisms, with a low fluorescence minimum and transmission maximum in between.

We chose to model a high dependence on O_2 through photorespiration as there is more knowledge of this process than other candidate low affinity O_2 metabolisms such as water–water cycles, and thus it is simpler to incorporate. The oxygenation rate per RuBisCO molecule (R_{Ox}), when RuBP is in saturation, is predicted to vary with CO_2 and O_2 concentrations according to (Savir et al. 2010),

$$R_{Ox} = \frac{v_O}{1 + \frac{K_O}{[O_2]} + \left(\frac{K_O}{K_C}\right)\left(\frac{[CO_2]}{[O_2]}\right)} \quad (4)$$

where v_O is the maximal rate of oxygenation, and K_C and K_{Ox} are the effective affinities of the CO_2 and O_2 molecules to the RuBisCO–RuBP complex. The constants v_O, K_C, and K_{Ox} were assumed to be 0.78/s, 309 μM, and 1400 μM, respectively, based on values for *Prochlorococcus* from the literature following Savir et al. (2010). The drop in O_2 with depth in the oxycline is parallel to a rise in CO_2, and Eq. 4 predicts that these synergistic effects would result in a steep decline in R_{Ox} in the oxycline.

As far as we know, there are no data to estimate a possible growth dependence of phytoplankton on RuBP oxygenation. For an initial exploration of how such a dependence might impact surface organisms, we assumed a direct dependence. At the lowest O_2 levels (at the base of the oxycline), a Monod-type dependence would approximate such a direct dependence, but this might lead to an over-estimation of the inhibition of photosynthesis at the upper side of the oxycline. At very low O_2 levels, inhibition of other O_2-dependent pathways, such as pigment or lipid biosynthesis, might also contribute, but are not explicitly modeled here. As expected, a direct relationship between growth rate, predicted photosynthesis, and R_{Ox} results in a steep decrease of the upper organism with depth in the oxycline.

The primary goal of our model is to demonstrate that upper layer organisms in the oxic ocean may be O_2 limited. However, an inhibition of surface phototrophs by low O_2 would by itself be insufficient to explain the chlorophyll minimum and transmission maximum within the oxycline. Limiting the penetration upwards into the oxycline by AMZ lineages might be explained by using a combination of the grazer effect (Zakem et al. 2020) and inhibition by high light. Alternatively, AMZ *Prochlorococcus* might not be inhibited by O_2 but simply outcompeted for reduced N by organisms such as Thaumarcheota, which are highly competitive for reduced N (e.g., ammonia and urea; Martens-Habbena et al., 2009). The simplest possible model is to assume the phototrophs from suboxic or anoxic layers are themselves inhibited by O_2; a trait that is common for many organisms adapted to low O_2 environments. Genes potentially related to PG metabolism were found in both AMZ and non-AMZ *Prochlorococcus* genomes (Ulloa et al. 2021; see Data S1 and Tables S4–S6). One difficulty to get more information from searches of genomes is that most or all of the genes are for enzymes whose function is used in more than one pathway. For example, genes for enzymes involved in the pathways from glycolate produced by photorespiration are also found in nonphotosynthetic organisms such as humans (Vignaud et al. 2007) and *Escherichia coli* (Lord 1972; Pellicer et al. 1996). A second difficulty is that it is challenging to identify true orthologs, and enzymes catalyzing very different reactions can be closely related evolutionarily, such as the glycolate oxidases/lactate oxidases (Kern et al. 2020). Available evidence does not explain why AMZ *Prochlorococcus* are excluded from oxic waters, and it may be an indirect effect (e.g., exclusion of AMZ microbes on which it depends metabolically). Further studies will require going beyond the conservation of genes among AMZ organisms to direct experiments. However, for the

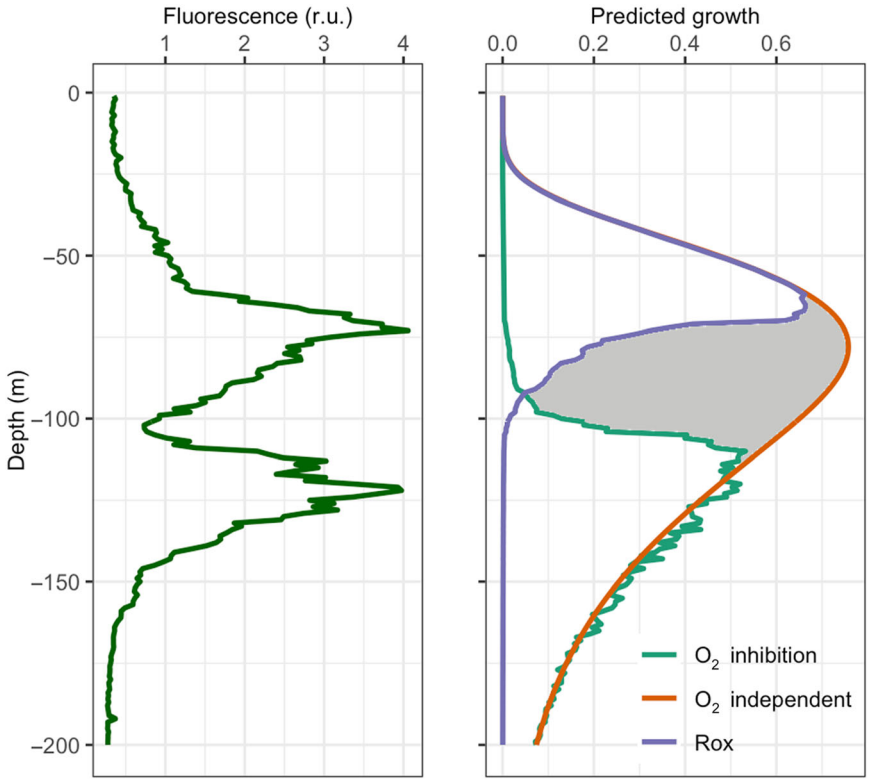

Fig. 3. Cruise RB1603 station ST11 (**A**) Measured fluorescence vs. depth. (**B**) Predicted growth of phytoplankton populations based on light and O_2: independent from O_2 concentration (orange), with a half-inhibition constant of 1 μM (green), and restricted by oxygenation of RuBP (Rox; purple). Missing photosynthesis (gray area) = 27%.

purposes of the demonstration here, we assume a simple direct inhibition by O_2.

For the AMZ *Prochlorococcus* below the oxycline, we assumed Haldane-type inhibition of growth by O_2 following Bush et al. (2017):

$$h_i(O_2) = 1/\left(1 + \left(O_2/H_{jO_2}\right)\right) \quad (5)$$

where the inhibition function $h_i(O_2)$ is related to the O_2 concentration and the half-inhibition constant H_{j,O_2}. A half-inhibition constant for O_2 for strict anaerobes was assumed to be 1 μM (Loesche 1969), although we also tested 10 μM for all the simulated stations (Figs. S3–S8). While AMZ *Prochlorococcus* are excluded from oxic low light conditions in the rest of the ocean, they did remain active at up to 400 nM O_2 (the highest tested) in short-term bottle microcosm incubations (Garcia-Robledo et al. 2017). Thus, half-inhibition constants in the range of 1–10 μM are reasonable assumptions for this purpose and are not ruled out by available evidence.

As expected, adding a population of phototrophs that are inhibited by O_2 produces an SCM below the oxycline (green, Fig. 3B). In general, the lower O_2 half-inhibition constant decreases penetration of shallow waters of the AMZ lineages and also their peak abundances (7%–15%, Figs. S3–S8).

Importantly, this relatively simple model produced predicted depth varying photosynthesis that showed qualitative similarity to many of the observed fluorescence profiles from OMZ waters, in terms of producing a PCM and SCM separated by a minimum, as well as often matching roughly the depths and relative sizes of the PCM and SCM (compare Figs. 3, 4), although we also show three cases where the SCM was clearly over-estimated by the simple model (Figs. S5–S7). We have not included processes such as diel variation in irradiance, turbulence or internal waves, and we expect that in nature there may be more complicated relationships along the oxycline, including interactions of O_2 with light, nutrients, and/or grazing effects (Martens-Habbena et al. 2009; Fuchsman et al. 2019, 2022). We caution that the purpose was not to test a particular metabolic hypothesis. Instead, the point is that the observed vertical patterns could be easily explained by hypothesizing that most surface phytoplankton have an unexpectedly high requirement for O_2 for growth in the light.

This simple model also allowed estimating that shallow OMZ conditions might result in a substantial decrease (on the order of one fifth to one third) in water column-integrated photosynthetic growth (missing photosynthetic growth) compared to what would be expected in comparable oxic waters. These very approximate results would likely be obtained by

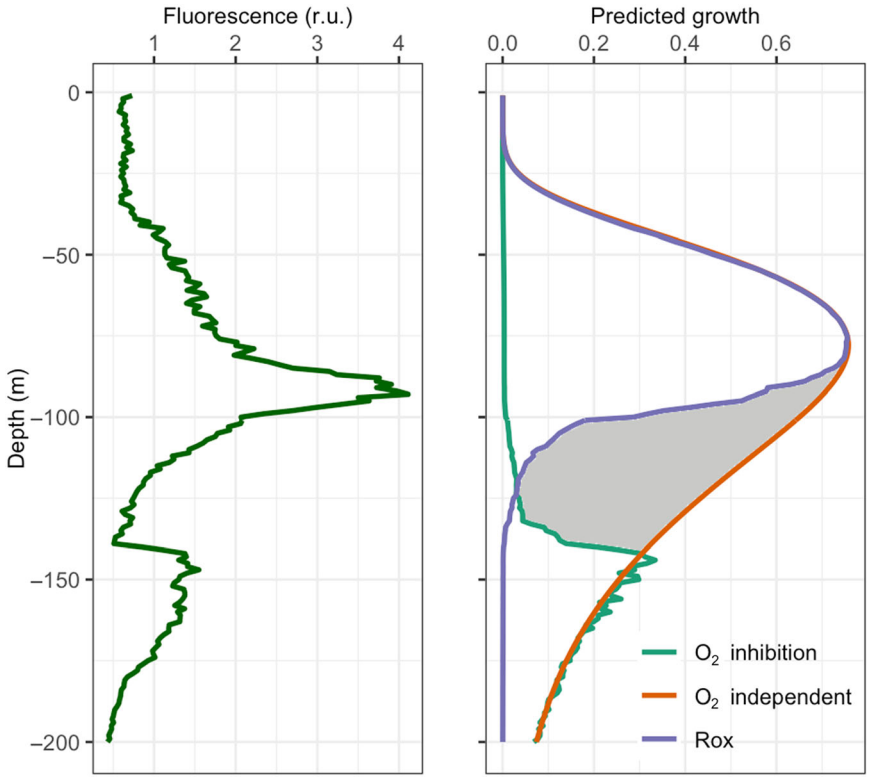

Fig. 4. Cruise RB1603 station ST11 (**A**) Measured fluorescence vs. depth. (**B**) Predicted growth of phytoplankton populations based on light and O_2: independent from O_2 concentration (orange), with a half-inhibition constant of 1 μM (green), and restricted by oxygenation RuBP (Rox; purple). Missing photosynthesis (gray area) = 22%.

other models that could reproduce the vertical structures observed in photosynthetic communities, and are not meant to be interpreted with precision. Expansion and shoaling of suboxic or anoxic conditions have been documented by a number of studies (Stramma et al. 2010; Horak et al. 2016). This class of mechanisms could represent a novel climate feedback where deoxygenation results in decreased ocean primary productivity.

Conclusion

Vertical structures of phytoplankton communities in OMZs are not sufficiently explained by top-down grazing pressure, or bottom-up processes such as light and/or nutrient limitation. This implies that phytoplankton may actually have a higher-than-expected direct requirement for O_2 or are indirectly inhibited by low O_2 conditions. Knowledge of phytoplankton responses to low O_2 and high CO_2 conditions characteristic of these zones is still very limited, investigation of the effects of O_2 on microalgal photosynthesis have traditionally focused on high O_2 conditions. Nevertheless, the current body of evidence, including a few recent studies showing inhibition of growth by low O_2 in both cyanobacterial and eukaryotic phytoplankton, permits the formulation of testable hypotheses. Unraveling these interactions is important to understanding how marine ecosystem function has evolved from the Proterozoic through the Phanerozoic. Additionally, simple models suggest that this previously unrecognized effect of low O_2 on modern phytoplankton might result in an important inhibition of total water column photosynthesis, resulting in a possible unrecognized feedback in OMZ expansion. Indeed, some observations suggest that OMZs may be becoming shallower (Horak et al. 2016). Thus resolving these processes will be imperative for predicting the ecological and biogeochemical responses to ongoing loss of O_2 by the ocean.

Data availability statement

The authors confirm that the data supporting the findings of this study are available within the article and/or its supplementary materials.

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Conflict of Interest

None declared.

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