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Microbial Respiration, the Engine of Ocean Deoxygenation

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Microbial plankton respiration is the key determinant in the balance between the storage of organic carbon in the oceans or its conversion to carbon dioxide with accompanying consumption of dissolved oxygen. Over the past 50 years, dissolved oxygen concentrations have decreased in many parts of the world's oceans, and this trend of ocean deoxygenation is predicted to continue. Yet despite its pivotal role in ocean deoxygenation, microbial respiration remains one of the least constrained microbial metabolic processes. Improved understanding of the magnitude and variability of respiration, including attribution to component plankton groups, and quantification of the respiratory quotient, would enable better predictions, and projections of the intensity and extent of ocean deoxygenation and of the integrative impact of ocean deoxygenation, ocean acidification, warming, and changes in nutrient concentration and stoichiometry on marine carbon storage. This study will synthesize current knowledge of respiration in relation to deoxygenation, including the drivers of its variability, identify key unknowns in our ability to project future scenarios and suggest an approach to move the field forward.

Keywords: microbial respiration, respiratory quotient, ocean deoxygenation, ocean acidification, multiple stressors

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INTRODUCTION

Dissolved oxygen (O_2) is fundamental to all aerobic life and thus plays a major role in marine microbial ecology and the biogeochemical cycling of elements such as carbon, nitrogen, phosphorus and sulfur. The measurement of seawater O_2 began during the 1873–1876 *HMS Challenger* expedition, and O_2 continues to be the most commonly measured indicator of marine biogeochemistry, with the current global database amounting to millions of measurements (Keeling et al., 2010; Schmidtko et al., 2017). Time series data over the past 50 years show declining O_2 in many regions of the world's oceans, and a significant increase in the aerial extent of oxygen minimum zones (OMZs) in the eastern tropical North Atlantic (ETNA) and equatorial Pacific. Stramma et al. (2008) determined the decrease in O_2 for the region of the ETNA between 10–14°N and 20–30°W in the depth range 300–700 m to be 0.09–0.34 μmol kg^{-1} $year^{-1}$ between 1960 and 2008, while later studies revealed variations in this long term decline at interannual to multidecadal timescales consistent with natural climate variability (Brandt et al., 2015). The latest collation of global ocean dissolved oxygen data shows a decrease of more than 2% (4.8 $\pm$ 2.1 pmol), in the global oceanic oxygen content since 1960 (Schmidtko et al., 2017), however, at regional scales the changes are more complex. Deutsch et al. (2014) showed evidence for a decrease in the extent of oxygen minimum zones in the tropical Pacific Ocean over most of the 20th century. This was

related to weakening easterly trade winds in a warming climate which decrease the intensity of upwelling and therefore the magnitude of biological production, export of organic carbon and respiratory oxygen demand. In the coastal zone, low or zero oxygen conditions are induced by anthropogenic nutrient enrichment and eutrophication, with the number of these coastal zone hypoxic sites having increased by an order of magnitude since the 1960s (Diaz and Rosenberg, 2008). This "deoxygenation" of the open and coastal ocean is predicted to continue. Coupled climate – marine biogeochemical models all project a continued long term decrease in the global ocean O_2 inventory of between 1 and 7% by 2100 (Bopp et al., 2002; Keeling and Garcia, 2002; Keeling et al., 2010). Henson et al. (2017) investigated the trend in a multi-model mean ensemble of the Coupled Model Inter-comparison Project Phase 5 (CMIP5) output, run under a "business-as-usual" scenario (RCP8.5). This suggested that most of the world's oceans will experience a 1–2% decrease in the oxygen inventory per decade with respect to the mean of 1986–2005. However, the regions where temperature and O_2 changes are likely to have the greatest impact on marine ecosystems and biogeochemistry, the poles and the tropics, including the major eastern boundary upwelling systems where oxygen minimum zones occur (Gruber, 2011), are also the regions where inter-model agreement is low (Henson et al., 2017).

A number of physical, ecological, and biogeochemical mechanisms could contribute to the process of deoxygenation (**Figure 1**) including:

(1) The direct effect of increasing temperature reducing the solubility of oxygen in seawater. This physical chemical process is well constrained, with estimates of a decrease in O_2 of ca. 5 mmol m^{-3} for each 1°C increase in water temperature (Deutsch et al., 2011). Within the upper 1000 m, 50% of the observed O_2 loss is attributed to changes in solubility. This percentage decreases to 25% of the O_2 loss in the upper 2000 m and 15% of the O_2 loss over the full oceanic depth (Schmidtko et al., 2017).

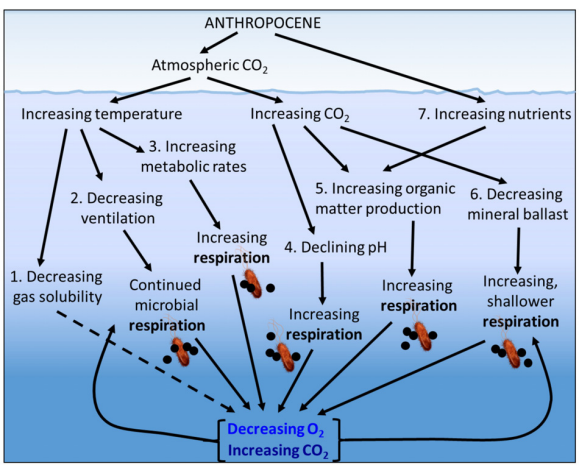

FIGURE 1 | Potential physical, ecological and biogeochemical mechanisms contributing to ocean deoxygenation in the Anthropocene.

(2) The indirect effect of increasing sea surface temperatures causing increased surface ocean stratification and reduced ventilation of the deep ocean, therefore increasing the length of time that deep water is separated from contact with the atmosphere. This delays the re-equilibration of dissolved oxygen to atmospheric concentrations while microbial degradation of organic matter associated with aerobic respiration consuming oxygen and producing carbon dioxide (CO_2) continues.

(3) The direct effect of increasing temperature on the metabolic rates of the plankton, with the expectation that for the same increase in temperature, heterotrophic processes such as microbial respiration which consume oxygen will increase more than autotrophic processes such as photosynthesis which produce oxygen (López-Urrutia et al., 2006; Wohlers et al., 2009), and that bacterioplankton growth efficiencies (the proportion of the carbon assimilated by bacterioplankton that is converted to biomass rather than being respired to CO_2) decrease with increasing temperature (Rivkin and Legendre, 2001). A warming ocean is therefore expected to change the depth distribution of oxygen consumption, with an increase in shallower warmer waters and a decrease at depth due to the reduced supply of organic matter. Whether this redistribution of oxygen consumption will lead to a decrease or increase in average oxygen concentrations remains uncertain.

(4) The direct effect of increasing CO_2 leading to increased bacterioplankton cell-specific respiration. The anthropogenically derived CO_2 in the atmosphere which is causing global warming is also dissolving in seawater, leading to increasing pCO_2 and decreasing seawater pH and carbonate ion concentration (ocean acidification). Elevated pCO_2 has been shown to increase the activity of bacterioplankton extracellular enzymes such as α and β–glucosidase (Piontek et al., 2010, 2013) and enhance bacterioplankton respiration (James et al., 2017).

(5) The indirect effect of increased photosynthesis caused by increasing concentrations of seawater CO_2. Increased CO_2 can enhance photosynthesis, producing an increased amount of particulate organic material (Riebesell and Tortell, 2011), a greater proportion of exudation of dissolved organic material (DOM; Engel et al., 2004) and increased carbon:nitrogen and carbon:phosphorus ratios of the DOM (Riebesell et al., 2007), leading to increased microbial respiration.

(6) The indirect effect of reduced calcium carbonate ballast due to decreasing seawater pH and carbonate ion concentration. The reduction in plankton extra-cellular calcium carbonate reduces the sinking rate of the plankton cells allowing respiration to occur at a shallower depth (Barker et al., 2003), and potentially allows a greater proportion of the exposed organic material to be respired in a given time.

(7) The indirect effect of increased coastal discharge of inorganic nutrients leading to increased primary production and thus increased phytoplankton derived particulate and dissolved organic carbon (or

eutrophication), which when degraded by heterotrophic bacteria supports increased microbial respiration. The indirect effect of increased discharge of inorganic nutrients and/or increased phytoplankton production of labile dissolved organic carbon "priming" the degradation of previously recalcitrant dissolved organic carbon (Jiao et al., 2011). The indirect effect of increased pollution-derived atmospheric deposition of soluble iron and fixed nitrogen leading to increased primary production and then increased respiration (Ito et al., 2016).

The inter-dependencies and feedbacks between these mechanisms mean that their individual effects on deoxygenation can be counteracted or exacerbated. For example, increased stratification due to increased surface temperature will reduce nutrient supply to the surface ocean, reducing primary production by an estimated 24% by the year 2300 when RCP8.5 predicts a fivefold increase in atmospheric CO_2 (Moore et al., 2018) which will offset the 27% increase in primary production due to carbon fertilization, estimated for a doubling of atmospheric CO_2 (Riebesell et al., 2007).

Apart from the temperature related decrease in oxygen solubility and ocean ventilation, all of these potential mechanisms causing deoxygenation depend on microbial aerobic respiration, the metabolic process driven by the degradation of dissolved and particulate organic carbon, which consumes oxygen, produces carbon dioxide and generates energy in the form of adenosine triphosphate (ATP). Midwater microbial communities – predominantly bacterioplankton, archaeoplankton and zooplankton – are therefore central to the challenge that is ocean deoxygenation because they both influence and are influenced by decreasing oxygen concentrations. Since the depletion of oxygen caused by microbial respiration is always accompanied by an increase in CO_2, ocean deoxygenation is always a dual stressor problem – both oxygen and CO_2 change (Brewer and Peltzer, 2009). Due to this complexity of feedbacks and interdependency, ocean deoxygenation is therefore a "wicked" problem contributing to the "super wicked" problem of climate change (Levin et al., 2012).

The aim of this paper is to explore this wicked problem from the perspective of microbial respiration, focusing on the key role that microbial respiration plays in enabling ocean deoxygenation and on how microbial respiration, and therefore the storage of carbon in the ocean, might be affected by ocean deoxygenation. I will build on previous reviews of microbial respiration (e.g., del Giorgio and Duarte, 2002; Robinson and Williams, 2005; Robinson, 2008; Arístegui et al., 2009; Regaudie-de-Gioux and Duarte, 2012, 2013) synthesizing what we know about midwater microbial respiration that could help us predict how microbial respiration might change in waters with reduced oxygen and increased carbon dioxide concentrations, and then identify areas of research that still need to be addressed and some emerging approaches that could be used.

MICROBIAL RESPIRATION

The magnitude and variability of marine microbial aerobic respiration is fundamental to deoxygenation, the formation of oxygen minimum zones and the efficiency of the biological carbon pump. Yet due to methodological limitations, the number of direct measurements and therefore our understanding of respiration, especially below the euphotic zone, is only loosely constrained.

Measurement Methods

The magnitude of midwater (i.e., between 100 and 1000 m depth range) respiration can be determined either from the oxygen consumption of an incubated water sample (Arístegui et al., 2005; Reinthaler et al., 2006; Baltar et al., 2010; Holtappels et al., 2014), from plankton electron transport system (ETS) activity (e.g., Packard et al., 2015; Osma et al., 2016; Martínez-García, 2017), from $^{14}CO_2$ production during incubations with ^{14}C labeled compounds (Hill et al., 2013), from measurements of bacterioplankton production and bacterioplankton growth efficiency (BGE = proportion of assimilated carbon used to produce bacterioplankton biomass) or from a time resolved estimate of the amount of oxygen consumed since a given water body left the sea surface where the dissolved oxygen concentration was in equilibrium with that in the atmosphere – the apparent (AOU; Sarmiento and Gruber, 2006), true (TOU) or evaluated (EOU; Duteil et al., 2013) oxygen utilization. Combining the estimate of oxygen utilization with an estimate of ventilation age from the distribution of tritium, radiocarbon or chlorofluorocarbons (CFCs), gives an average oxygen utilization rate (OUR; Jenkins, 1987). The efficiency of mesopelagic remineralization can also be inferred from the vertical profile of particle flux derived from underwater imaging, sediment trap data or thorium isotope disequilibria (Guidi et al., 2015) or reconstructed from large-scale ocean nutrient distributions (Weber et al., 2016).

Midwater respiration rates (60–300 $\mu mol\ O_2\ m^{-3}\ day^{-1}$) have been derived from direct measurements of oxygen consumption during incubations of 2–4 days. To minimize any potential artifacts due to such long incubations, data are only used when linearity in oxygen consumption and cell abundance are confirmed, or when significant relationships between oxygen consumption and bacterioplankton production during the incubations can be used with *in situ* bacterioplankton production measurements to "back-correct" the respiration to *in situ* values (Arístegui et al., 2005; Reinthaler et al., 2006; Mazuecos et al., 2015). The ETS method estimates the maximum activity (V_{max}) of the enzymes associated with the respiratory electron transport system of both eukaryotes and prokaryotes under substrate (NADH, NADPH) saturation, and is therefore a maximum "potential" respiration rate rather than the actual respiration rate. V_{max} is converted into rates of oxygen consumption using either an empirical relationship determined from bacterial cultures or application of an enzyme kinetic model (EKM). It therefore assumes an average relationship between enzyme mass and respiratory activity, and due to this assumption it has an estimated error of 31–38% (Packard et al.,

1988). A recent development of the ETS technique uses pyridine nucleotide concentrations and an EKM (Aguiar-González et al., 2012) to derive the actual respiration rate. This method has been used with cultured bacteria and zooplankton (Osma et al., 2016), but has not yet been tested in open waters.

A further modification of the ETS method derives respiration from the relationship between dissolved oxygen consumption and the *in vivo* reduction of 2-(p-iodophenyl)-3-(p-nitrophenyl)-5-phenyltetrazolium chloride (INT) to INT-formazan (Martínez-García et al., 2009). Martínez-García (2017) presents the first size-fractionated mesopelagic respiration data from station ALOHA in the North Pacific Subtropical Gyre using the INT technique, to show vertical and seasonal variability in respiration ranging from 56 to 107 μmol O_2 m^{-3} day^{-1} in the 100–1000 m depth horizon. These data are around an order of magnitude higher than earlier ETS estimates (1–7 mol O_2 m^{-2} y^{-1}; 3–25 μmol O_2 m^{-3} day^{-1}; Arístegui et al., 2003), which were calculated using a conversion factor derived from a senescent bacterial culture, suggesting that microbial communities in the mesopelagic ocean are much more active that previously assumed (Arístegui et al., 2009). Respiration can also be derived from the respiration of ^{14}C-leucine by bacterioplankton cells. Hill et al. (2013) determined respiration in the range 0.07–1.9 pmol leu L^{-1} h^{-1} between 20 and 160 m in the Atlantic Ocean after additions of ^{14}C-leucine at close to ambient (0.4 nmol L^{-1}) concentrations. Using ^{3}H-leucine bioassay isotope dilution to determine prokaryote production, and published estimates of prokaryote growth efficiencies, Giering et al. (2014) calculated depth integrated (50–1000 m) North Atlantic prokaryote respiration to be 71 mg C m^{-2} day^{-1}. Oxygen utilization rates including recent ones derived for the Pacific (Sonnerup et al., 2013, 2015) and Atlantic Oceans (Stanley et al., 2012) using transit time distributions, range from 0.3 to 50 μmol O_2 m^{-3} day^{-1} (0.03–18.2 mol O_2 m^{-2} y^{-1}; **Table 1**).

In the oxygen minimum zones (OMZ) where oxygen concentrations fall below 40 μmol L^{-1} or, in the most intense OMZs below 20 μmol L^{-1} (Paulmier and Ruiz-Pino, 2009), it is only relatively recently that techniques to accurately measure extremely low *in situ* oxygen concentrations and rates of oxygen consumption have become available. While Winkler titrations, electrochemical or optode sensors and oxygen isotope methods have detection limits around 0.1–1 μmol L^{-1}, the switchable trace oxygen (STOX) microsensor has a detection limit in the range 1–10 nmol L^{-1} (Revsbech et al., 2009, 2011), and in water bodies containing concentrations of O_2 less than 1 nmol L^{-1}, the ultra-sensitive Luminescence Measuring Oxygen Sensor (LUMOS) has a sensitivity of 7 pmol L^{-1} (Lehner et al., 2014, 2015). Good agreement was found between measurements of oxygen concentration and oxygen consumption made by STOX sensors, optode spots and membrane inlet mass spectrometric analysis of $^{18-18}O_2$ (Holtappels et al., 2014). Using these new nanomolar techniques, *in situ* oxygen and respiration measurements derived from consumption of oxygen, showed that aerobic respiration occurs efficiently at extremely low oxygen concentrations (Tiano et al., 2014; Kalvelage et al., 2015; Garcia-Robledo et al., 2016). As well as the difficulty in measuring very low oxygen concentrations and rates of oxygen consumption, the imperative to maintain *in situ* oxygen concentrations during shipboard sample collection, manipulation and analysis remains a significant challenge (Garcia-Robledo et al., 2016).

TABLE 1 | Recent midwater (100–1000 m) respiration estimates derived from dissolved oxygen consumption during a bottle incubation (ΔO_2), activity of the electron transport system (ETS), the reduction of the tetrazolium salt (INT), or the time resolved estimate of the amount of dissolved oxygen consumed since a water parcel was last in contact with the atmosphere, the oxygen utilization rate (OUR).

Region	Method	Respiration (μmol O_2 m^{-3} day^{-1})	Reference
NE Atlantic	ΔO_2	80–350	Arístegui et al., 2005
N Atlantic	ΔO_2	50–200	Reinthaler et al., 2006
Mediterranean Sea	ΔO_2	230–1650	Weinbauer et al., 2013
S Atlantic and Indian	ΔO_2	87–238	Mazuecos et al., 2015
NE Atlantic	ETS	120 ±14	Arístegui et al., 2005
N Atlantic	ETS	20–50	Reinthaler et al., 2006
Atlantic	ETS	66–88	Baltar et al., 2009a,b
N Atlantic	ETS	7–16	Fernández-Castro et al., 2016
Pacific coastal upwelling	ETS	3–750	Packard et al., 2015
N Pacific	INT	56–107	Martínez-García, 2017
Pacific	OUR	0.05–27	Feely et al., 2004
SE Pacific	OUR	5–55	Sonnerup et al., 2015
NE Pacific	OUR	0.3–30	Sonnerup et al., 2013
Atlantic	OUR	17 ± 3	Stanley et al., 2012

Apportionment to Microbial Group

In addition to bulk measurements of respiration, an appreciation of the proportion of respiration attributable to bacterioplankton or zooplankton and between particle-attached or free-living bacterioplankton is important for accurate predictions and projections of carbon remineralization and thus deoxygenation and marine carbon storage in a changing environment. Unfortunately, such apportionment of respiration to constituent plankton functional groups is hampered by the lack of a direct method able to differentiate the respiration of any component group from that of the rest of the plankton community. The post-incubation separation by filtration of a size class of the plankton community, coupled with the identification and enumeration of plankton within that size class, has become the pragmatic although imperfect field approach to infer the respiration of a particular group which dominates a particular size class. This is obviously problematic in environments where cells of the same size represent very different functional groups, for example, heterotrophic and autotrophic prokaryotes in the surface waters of oligotrophic gyres, but perhaps is less of a problem in coastal regions or in the mesopelagic.

The relative proportion of mesopelagic bacterioplankton and zooplankton respiration varies with euphotic zone productivity. Bacterioplankton respiration was 2- to 10-fold higher than zooplankton respiration at the oligotrophic ALOHA station in the North Pacific Subtropical Gyre, and up to fivefold higher at

the mesotrophic station K2 in the subarctic Pacific (Steinberg et al., 2008). Giering et al. (2014) found bacterioplankton respiration to dominate (70–92%) community respiration in the North Atlantic mesopelagic zone, while McDonnell et al. (2015) showed that the respiration rates of particle-associated microbes contributed 32–98% of the total respiration measured *in situ* at the Bermuda Atlantic Time-series Study site (BATS). Direct measurements of the oxygen consumption of microbes associated with phytodetrital aggregates collected using marine snow catchers in the northeast Atlantic, showed that the relative importance of particle-associated microbial respiration to the attenuation of particulate organic carbon (POC) increases from ∼8% in the upper mesopelagic (36–128 m) to ∼33% in the mid mesopelagic (129–500 m) as the rate of POC attenuation decreases (Belcher et al., 2016).

Influence of Environmental Conditions

Respiration rates vary in space and time depending on temperature, the quality and quantity of the organic substrate, availability of inorganic nutrients, and microbial community structure. Just like any other chemical reaction or metabolic rate, plankton respiration is related to temperature through an Arrhenius relationship. Mazuecos et al. (2015) derived mesopelagic respiration from oxygen consumption measurements and calculated a Q_{10} of 3.65 and an activation energy E_a of 0.90 eV for water temperatures between 8.7 and 14.9°C. This compared well with the temperature relationship of previously published mesopelagic respiration data (average Q_{10} of 4.07 and E_a of 0.98 eV), but is higher than the "optimal" Q_{10} values of between 1.5 and 2.6 of mesopelagic remineralization of particulate organic carbon derived from data-constrained modeling studies (DeVries and Weber, 2017; Laufkötter et al., 2017; Cram et al., 2018), and of activation energies determined for microbial respiration in surface waters (∼0.58 eV López-Urrutia and Móran, 2007; Yvon-Durocher et al., 2012).

Cell specific mesopelagic bacterioplankton respiration rates (**Table 2**) tend not to be correlated with temperature due to the ∼50-fold variability in cell specific respiration rates (0.1 to 5 fmol C cell^{-1} day^{-1}; Baltar et al., 2009a,b) related to the lack of a strong relationship between cell abundance and cell activity (del Giorgio and Gasol, 2008). For example, Reinthaler et al. (2006) found a threefold difference in bacterioplankton cell specific respiration rates in deep water masses of the east and west N Atlantic, with a general increase with depth, and with rates in the oxygen minimum zones intermediate between those in the more oxygenated water masses above and below.

Experiments which mimic the increase in pressure experienced by surface dwelling bacterioplankton as they descend to the mesopelagic zone associated with particles, show that rates of organic matter degradation decrease with increasing pressure (Tamburini et al., 2013). However, bacterioplankton which are endemic to the mesopelagic, adapt to conditions of high pressure, low temperature and low substrate availability, such that measurements of bacterioplankton production made at atmospheric pressure on decompressed samples underestimate *in situ* mesopelagic activity (Tamburini et al., 2013). As far as I am aware, measurements of mesopelagic bacterioplankton respiration have not yet been made at *in situ* pressures.

Nutrient addition experiments with oligotrophic and mesotrophic surface water plankton populations show increased plankton community and bacterioplankton respiration after addition of a mixture of glucose and amino acids (Martínez-García et al., 2013), and time series studies and data syntheses show significant correlations between bacterioplankton respiration and concentrations of dissolved organic carbon (Alonso-Sáez et al., 2008; Robinson, 2008). Bioavailability experiments with natural bacterioplankton communities and

TABLE 2 | Mesopelagic cell specific respiration (fmol C cell^{-1} day^{-1}) derived from measurements of electron transport system activity (ETS) or dissolved oxygen consumption (ΔO_2).

Region	Sample type	Cell specific respiration (fmol C cell^{-1} day^{-1})	Reference
Louisiana Shelf, United States	<1 μm, ΔO_2	2.4–8.7	Biddanda et al., 1994
Menai Strait, United Kingdom	<0.8 μm, ΔO_2	0.4–6.8	Blight et al., 1995
Gulf of Mexico, United States	<0.8 μm, ΔO_2	0.39	Jørgensen et al., 1999
Cardigan Bay, United Kingdom	0.2–12 μm, ΔO_2	4.28 ± 1.12	Mukhanov et al., 2003
North Sea	<0.8 μm, ΔO_2	0.3–3.6	Reinthaler et al., 2005
NW African coast	Whole sample, ΔO_2	0.2–2.0	Gasol et al., 2009
Temperate North Atlantic			Reinthaler et al., 2006
100–135 m	<0.6 μm, ΔO_2	Average 0.85	
402–725 m (O_2 minimum)	<0.6 μm, ΔO_2	Average 1.67	
1800–3000 m	<0.6 μm, ΔO_2	Average 2.74	
Southern Ocean			Obernoster et al., 2008
0–100 m	<0.8 μm, ΔO_2	0.5–1.9	
1000–4500 m	Whole sample, ΔO_2	0.23–6.9	
Subtropical North Atlantic			Baltar et al., 2009a
100 m	Whole sample, ETS	0.04–3.82	
200–1000 m	Whole sample, ETS	0.12–5.23	
1000–5000 m	Whole sample, ETS	0.43–7.66	
Subtropical North Atlantic			Baltar et al., 2009b
100 m	Whole sample, ETS	0.17–1.18	
200–1000 m	Whole sample, ETS	0.14–2.88	
1800–4500 m	Whole sample, ETS	0.23–6.90	

Adapted from Baltar et al. (2009b).

dissolved organic material harvested from cultures of four coastal diatoms under silicate and/or nitrate stress suggest that DOM remineralization and bacterioplankton growth efficiencies are influenced on time scales of a week by the nutrient stress under which the DOM is produced. However, on seasonal time scales, the diatom source species is more influential (Wear et al., 2015).

The interacting effect of increasing temperature and organic carbon supply on coastal bacterioplankton respiration and growth efficiencies has been studied recently in chemostats and turbidostats. In substrate limited conditions, growth efficiencies showed no trend with temperature, whereas under temperature limited, substrate replete conditions, bacterioplankton growth efficiencies increased with temperature (Maske et al., 2017). This contrasts with the meta-analysis of Rivkin and Legendre (2001) which showed a decrease in bacterioplankton growth efficiencies with increasing temperature.

In addition to the influence of nutrient availability and DOM composition, the bioavailability of DOM (and hence respiration rate) is also controlled by microbial community composition. Mesopelagic microbial communities in the eastern tropical South Pacific were able to utilize surface layer dissolved organic carbon which was recalcitrant to remineralization by surface microbial communities over time scales of 9–14 days (Letscher et al., 2015). Likewise, incubations of ambient seawater amended with DO^{13}C substrates including defined monosaccharides and exudates and lysates from ^{13}C-labeled *Synechococcus* cultures showed that each DOC substrate stimulated a different community growth response and a different rate of DOC removal (Nelson and Carlson, 2012). While *Synechococcus* exudates are incorporated by a wide diversity of bacterial taxa, defined monosaccharides and *Synechococcus* lysates were less bioavailable to ambient bacterioplankton.

RESPIRATORY QUOTIENTS

The relationship between the production of CO_2 and the consumption of O_2 during respiration is the respiratory quotient ($RQ = \Delta CO_2/-\Delta O_2$) and this varies depending on the stoichiometry of the organic substrate and the degree of oxidation or metabolic pathway used. Assuming complete oxidation, the RQ could range from 0.13 for lipid ($C_{40}H_{74}O_5$), 0.50 for methane (CH_4), 0.67 for saturated fatty acid (-CH_2-), 1.00 for glucose ($C_6H_{12}O_6$), 1.24 for nucleic acid ($C_1H_{1.3}O_{0.7}N_{0.4}P_{0.11}$), 1.33 for glycolic acid ($C_2H_4O_3$) and 4.00 for oxalic acid ($C_2H_2O_4$) (Rodrigues and Williams, 2001; Williams and del Giorgio, 2005; Berggren et al., 2011). Assuming the substrate is similar to the average composition of planktonic material, e.g., 65% protein, 19% lipid, 16% carbohydrate, or the typical composition of a phytoplankton cell, e.g., 40% protein, 40% carbohydrate, 15% lipid, 5% nucleic acid gives an RQ of 0.89 (Williams and del Giorgio, 2005). Quantifying the variability in RQ allows not only the production of CO_2 to be calculated from dissolved oxygen consumption, but also reveals shifts in plankton physiology that are not evident from any other measurement. Culture studies with marine bacteria (*Vibrio natriegens* and *Pseudomonas nautica*) show that the respiratory quotient varies with physiological state, metabolic pathway and carbon source (acetate or pyruvate) (Berdalet et al., 1995; Roy et al., 1999; Romero-Kutzner et al., 2015).

A systematic field study of the RQs of freshwater bacterioplankton showed large variability (1.2 ±0.45) with a significant negative correlation between RQ and *in situ* O_2 concentration and pH and a significant positive correlation between RQ and *in situ* pCO_2 (Berggren et al., 2011). Bacterioplankton RQs were low (average 0.81) in net autotrophic freshwater systems where reduced substrates derived from phytoplankton excretion are likely to dominate and higher (average 1.35) in net heterotrophic freshwater systems where oxidized substrates such as organic acids formed by photochemical processes could occur (Allesson et al., 2016). However, due to the low rates of oxygen consumption and CO_2 production by marine plankton, and the precision of methods to measure changes in dissolved inorganic carbon (DIC; ∼1–2 mmol m^{-3}), there has not been a systematic field study of the magnitude and variability of marine plankton RQs. Most studies of marine plankton respiration rely on measurements of dissolved oxygen consumption and assume a constant RQ of either 0.8 or 1.0 (e.g., Reinthaler et al., 2006; Nguyen et al., 2012; Teira et al., 2013), accepting that this introduces an error into the calculation of CO_2 production, since the RQ is likely to vary with environmental conditions and substrate availability.

Field measurements of the concurrent consumption of oxygen ($-\Delta O_2$) and production of DIC (ΔCO_2) of seawater samples incubated in the dark for 24h, can be used to derive an apparent respiratory quotient (ARQ; Angert et al., 2015). This is the integrative effect of not only the aerobic respiration of bacterio-, archaeo-, phyto-, and microzooplankton in the sample, but also all the other microbial metabolic processes which use or produce O_2 or CO_2, including nitrification (uptake of O_2 without production of CO_2), production of methane from acetate or methylamines (production of CO_2 without utilization of O_2), and production and dissolution of calcium carbonate (production or uptake of CO_2 without affecting O_2, respectively). The range of ARQs obtained from multiple field studies (Robertson, 1989; Wood, 1992; Robinson et al., 1999, 2002a,b; Sondergaard et al., 2000; Lefèvre et al., 2008 in **Figure 2**) spans the range of RQs calculated from the stoichiometry of potential substrates for microbial aerobic respiration with a median of 0.88 and an average of 1.11 ±0.76 (n = 149). There is some indication that higher ARQs occur in waters above the oxygen minimum zone in the Arabian Sea (Robinson and Williams, 1999) and lower ARQs occur during blooms of the coccolithophore *Emiliania huxleyi* (Holligan et al., 1993; Robertson et al., 1994). Until a more sensitive method is developed to measure CO_2 or DIC and a systematic study undertaken, derivation of CO_2 production from O_2 consumption will depend on using a constant $\Delta CO_2/-\Delta O_2$ ratio, accepting the potential 20–40% error (Reinthaler et al., 2006).

An apparent respiratory quotient integrated over longer time and larger space scales can also be derived from the relationship between DIC and AOU within a particular water mass. Measurements and models of the DIC:AOU ratio suggest a range between 0.51 and 0.85 depending on the composition

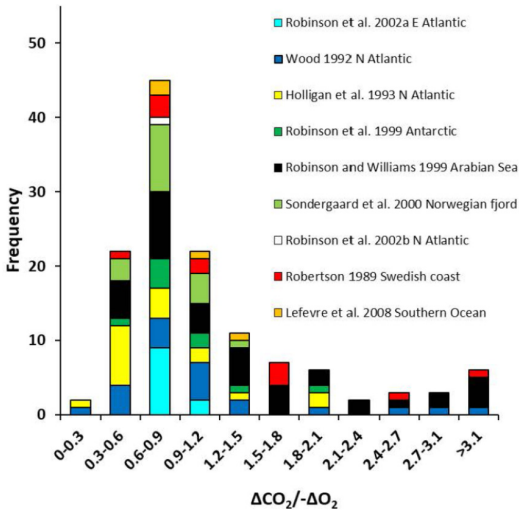

FIGURE 2 | Frequency histogram of apparent respiratory quotients (the ratio of oxygen consumption to production of dissolved inorganic carbon).

of the organic material being degraded – lower ratios are associated with the remineralization of labile and nitrogen-rich organic matter, higher ratios with remineralization of more recalcitrant organic matter (Thomas, 2002; Paulmier et al., 2009) – the combination of biogeochemical processes (e.g., respiration, nitrification, denitrification, anammox) occurring, and the history of the source water in terms of the different sensitivities of O_2 and DIC to changes in temperature and the different time scales of O_2 and CO_2 air-sea exchange (Anderson and Sarmiento, 1994; Thomas, 2002; Loucaides et al., 2012).

The ARQs of waters within oxygen minimum zones (and corresponding carbon maximum zones; Paulmier et al., 2011) vary between 0.6 and 1.5. Paulmier et al. (2011) determined the ARQ of waters in the shallow, very intense oxycline of Chilean coastal waters to be 1.1 ±0.3, potentially due to relatively higher rates of DIC production from more complete degradation of highly carbonated organic matter (Van Mooy et al., 2002; Paulmier et al., 2011).

SENSITIVITY TO DECREASING OXYGEN AND INCREASING CARBON DIOXIDE

Since the enzymes used during aerobic respiration require oxygen, at some level the rate of respiration will be directly sensitive to the ambient concentration of dissolved oxygen. In addition, dissolved oxygen concentration is a major determinant of microbial abundance and diversity (Wright et al., 2012) and will therefore indirectly affect the rate of respiration and other biogeochemical processes.

Hartnett et al. (1998), originally noted the strong negative relationship between sedimentary organic carbon preservation and length of exposure to oxygen, while Devol and Hartnett (2001) showed the influence of dissolved oxygen on midwater remineralisation. Calculated attenuation rates of particulate organic carbon flux for the oxic water column of the continental margin off Washington State were significantly higher than the attenuation rates calculated for the oxygen-deficient continental margin off northwest Mexico. A synthesis of attenuation length scale estimated from export flux and deep sediment trap data (Henson et al., 2012) shows clearly that mesopelagic remineralization is much reduced at low concentrations of dissolved oxygen (Sanders et al., 2016). Laufkötter et al. (2017) compiled particulate organic carbon flux measurements from 19 globally distributed sites and found that the attenuation of the flux of particulate organic matter depends on oxygen described by a half-saturation constant between 4 and 12 μmol L^{-1}. However, as well as any direct effect of reduced dissolved oxygen on aerobic microbial respiration, these attenuation rates will also include the indirect effect of reduced dissolved oxygen decreasing the depth of zooplankton diel vertical migration and so fragmentation, repackaging and respiration of organic carbon mediated by zooplankton (Cavan et al., 2016).

Due to the technical challenges of both measuring and maintaining extremely low oxygen concentrations, there are relatively few determinations of the oxygen sensitivity of aerobic respiration in low oxygen waters. Garcia-Robledo et al. (2016), using LUMOS optodes, found no apparent change in oxygen consumption rates at oxygen concentrations between ∼1.0 and 10 μmol L^{-1} in waters collected from the oxygen minimum zones of the eastern tropical Pacific Ocean and derived an apparent half saturation constant of 391 nmol O_2 L^{-1}. This agrees with a previous study using STOX microsensors which on average showed little oxygen dependence above oxygen concentrations of 500 nmol L^{-1} (Tiano et al., 2014). However, Kalvelage et al. (2015) showed an increase in aerobic respiration (from ∼0.1 to 8.0 μmol $L^{-1}d^{-1}$) with increasing ambient O_2 concentrations (from ∼1 to 20 μmol L^{-1}). This change in aerobic respiration is likely associated with changing community structure. Beman and Carolan (2013) sampled across oxygen gradients in the OMZ of the Gulf of California using pyrosequencing of 16S rRNA to show maximum values of bacterial richness on the edge of the OMZ where availability of oxidants and reductants contribute to functional and taxonomic diversity. Predicting the biochemical response of the microbial community to fluctuations in oxygen concentrations is extremely difficult, as both aerobic and anaerobic processes occur simultaneously, even in waters with undetectable oxygen concentrations (Bertagnolli and Stewart, 2018).

Since decreasing O_2 due to respiration will always be coupled with increasing CO_2, which leads to ocean acidification through decreasing pH and carbonate ion concentration, it is relevant to assess the positive or negative feedbacks associated with the direct and indirect effects of increasing CO_2 on plankton respiration. Many bacterial enzymatic processes involved in the utilization of organic compounds increase with increasing CO_2, or decreasing pH (e.g., Grossart et al., 2006; Piontek et al., 2010; Mass et al., 2013). Bunse et al. (2016) demonstrated upregulation of respiratory proton pumps at elevated CO_2 concentrations, presumably in order to export protons that invade the bacterioplankton cell as a result of low pH. Such proton exporting mechanisms are inherently energy demanding,

so that bacterioplankton would need to allocate more energy to cell maintenance instead of growth, implying a decrease in bacterial growth efficiency with increasing CO_2 (Bunse et al., 2016). This is consistent with measurements of the direct effect of increased CO_2 on bacterioplankton metabolism, revealing systematically greater cell-specific respiration in elevated CO_2 (James et al., 2017). This latter study also suggested that high CO_2 conditions may increase the ability of bacterioplankton to consume DOC, but with reduced growth efficiencies, leading to decreased storage of DOC.

Indirect effects of increased CO_2 on bacterioplankton respiration include increased respiration due to (1) the increased quantity and quality of phytoplankton derived particulate and dissolved organic carbon and/or (2) reduced calcium carbonate ballast enabling greater bacterial access to associated organic material. Mesocosm experiments in a range of nutrient regimes and plankton communities show equivocal results. Some show that bacteria benefitted both directly through enhanced enzymatic hydrolysis of organic matter and indirectly through increased availability of phytoplankton derived organic substrate (Grossart et al., 2006; Piontek et al., 2010), and that copepods increased their respiration rate at elevated CO_2 concentrations (Li and Gao, 2012). However, recent mesocosm and microcosm studies in an Arctic fjord, the Mediterranean Sea and the subtropical North Atlantic Ocean found no significant relationship between bacterioplankton or plankton community respiration and CO_2 concentrations (Motegi et al., 2013; Tanaka et al., 2013; Mercado et al., 2014; Maugendre et al., 2017; Filella et al., 2018), and Spilling et al. (2016) found a decrease in plankton community respiration at elevated CO_2 levels during a mesocosm experiment in the Baltic Sea.

As far as I am aware there have been no CO_2 manipulation studies of mesopelagic microbial communities or studies of the cumulative (additive, synergistic or antagonistic) effect of the combination of decreasing dissolved oxygen and increasing CO_2 on environmental genomics and plankton respiration, as have been undertaken for metabolic rates of invertebrate and vertebrate marine organisms (Gobler and Baumann, 2016).

KNOWN UNKNOWNS AND RECOMMENDATIONS FOR FUTURE RESEARCH

Current models do not reproduce the observed patterns of changes in dissolved oxygen, they underestimate the interannual to decadal variability in dissolved oxygen and they simulate only half of the oceanic oxygen loss inferred from observations (Oschlies et al., 2018). Increased *in situ* observations and quantitative mechanistic understanding of the influence of both physical and biological processes on dissolved oxygen changes are therefore required to develop and verify these numerical models. In particular, since these models account for the major physical and chemical processes involved in deoxygenation, but do not include some of the microbial processes and feedbacks discussed here, it is relevant to investigate whether including these microbiological processes would account for the additional decrease in oxygen needed to match the model outputs with the observations.

The major biological process influencing a decline in dissolved oxygen concentration is plankton respiration. Hence improved mechanistic understanding of the drivers influencing the variability of respiration, particularly those that are climate sensitive, or currently not represented in numerical models, is required. Examples would include the influence of changing inorganic nutrient concentrations and stoichiometry on plankton community structure including the proportion of respiration attributable to bacterioplankton or vertically migrating zooplankton and the size distribution and composition of exported particles, changes in the respiratory quotient, the interacting effects of increasing CO_2 and decreasing O_2 on bacterioplankton respiration, and the influence of warming and nutrient stoichiometry on the bacterial utilization of previously recalcitrant dissolved organic carbon (Jiao et al., 2010, 2014; Zhang et al., 2018). On a broader scale, this complex wicked problem also requires an appreciation of the potential feedbacks between primary production, nitrogen cycling, organic matter flux and oxygen consumption (Canfield, 2006; Boyle et al., 2013; Bristow et al., 2016). At the microbial scale, representation of symbiotic metabolic interactions (Wright et al., 2012), including the potential for cryptic oxygen cycling to occur within otherwise anoxic zones (Garcia-Robledo et al., 2017) is required.

A dedicated longtime and large spatial scale observational program is required, linked to a numerical modeling framework (Oschlies et al., 2018), and within which targeted manipulation experiments could take place. The observational program would include a range of methods for determining plankton respiration from the individual organism to the oceanographic region, including those already established (e.g., *in vitro* O_2 consumption, electron transport system activity, $^{14}CO_2$ production, AOU) and those currently in development (e.g., fluorescence, *in situ* respirometry, and derivation from optode measurements on moorings, gliders and biogeochemical Argo floats[1]), measured alongside the plankton community structure and organic/inorganic nutrient regime (e.g., Honjo et al., 2014; Collins et al., 2018). Metagenomic analysis coupled with trace chemical assays and isotope tracer experiments should be incorporated into the observational program to reveal the detail of low oxygen metabolic pathways (Bertagnolli and Stewart, 2018). In addition, established multidisciplinary time series and global surveys (e.g., OceanSITES[2] and GO-SHIP[3]) should begin to place as much emphasis on determining the plankton respiratory processes which utilize dissolved oxygen and convert organic carbon to CO_2, as they currently do on the autotrophic processes which produce dissolved oxygen and convert CO_2 to particulate and dissolved organic carbon. An implementation plan to specifically quantify the capacity for marine carbon storage through recalcitrant dissolved organic carbon (the microbial carbon pump), and the potential reduction in this capacity due to global change, leading to a positive

[1]http://www.argo.ucsd.edu/

[2]http://www.oceansites.org/index.html

[3]http://www.go-ship.org/index.html

feedback of increased oxygen consumption and CO_2 production, has recently been proposed (Robinson et al., 2018).

Isolation and cultivation of a greater number of microbes from low oxygen waters will help quantify the oxygen thresholds constraining chemical fluxes and identify the enzymes responsible (Bertagnolli and Stewart, 2018). A suite of single species and natural plankton community micro-, meso- and macro-cosm manipulation experiments should be embedded within the observational and modeling framework, specifically to confirm or refute proposed biological mechanisms of increasing ocean deoxygenation and the interacting effects of increasing CO_2 and decreasing O_2 on plankton metabolism (**Figure 1**). Since ocean deoxygenation is linked mechanistically to other ocean stressors (or drivers) including warming, acidification and nutrient availability and stoichiometry, these manipulation experiments will need to be multiple stressor experiments and follow appropriate best practice in design, implementation and statistical analysis (Riebesell and Gattuso, 2014; Boyd et al., 2016, 2018). The Scientific Committee on Oceanic Research (SCOR) working group 149 has recently released an open access decision support tool https://scor149-ocean.com/decision-support-tool/ to aid in design and interpretation of multiple stressor experiments, and a *Multiple Driver Best Practice Guide* will be launched in 2019.

The predictions and projections of the distribution and extent of ocean deoxygenation and the cumulative effects of other drivers of global change afforded by the observational verification of numerical models, need to also extend to predictions of the consequences of ocean deoxygenation on the ecosystem services and human livelihoods and welfare provided by the ocean (Breitburg et al., 2018). This aligns with the scientific objectives of the Integrated Marine Biosphere Research project (IMBeR) to *incorporate understanding of the drivers and consequences of global change on marine ecosystems and human societies at multiple scales into models to project and predict future states* (Hofmann and The IMBeR Scientific Steering Committee, 2016), and the Intergovernmental Oceanographic Commission (IOC) of UNESCO sponsored expert group, the Global Ocean Oxygen Network GO_2NE[4] which aims to improve ocean oxygen observation systems, identify and fill knowledge gaps, build capacity, and provide scientific advice to policy makers. GO_2NE also maintains the news site www.ocean-oxygen.org for scientists, stakeholders and the interested public.

Only through international co-ordination and collaboration will we be able to quantify the environmental, physiological and ecological drivers of variability in plankton respiration contributing to ocean deoxygenation, and hence predict and project the cumulative effect of ocean deoxygenation and other global change drivers on marine ecosystems and human societies.

[4] http://www.unesco.org/new/en/natural-sciences/ioc-oceans/sections-and-programmes/ocean-sciences/global-ocean-oxygen-network/

AUTHOR CONTRIBUTIONS

CR conceived and wrote the article.

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