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Oxygen minimum zones (OMZs) in the modern ocean

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ABSTRACT

In the modern ocean, oxygen minimum zones (OMZs) are potential traces of a primitive ocean in which Archean bacteria lived and reduced chemical anomalies occurred. But OMZs are also keys to understanding the present unbalanced nitrogen cycle and the oceans' role on atmospheric greenhouse control. OMZs are the main areas of nitrogen loss (as N_2, N_2O) to the atmosphere through denitrification and anammox, and could even indirectly mitigate the oceanic biological sequestration of CO_2. It was recently hypothesized that OMZs are going to spread in the coming decades as a consequence of global climate change. Despite an important OMZ role for the origin of marine life and for the biogeochemical cycles of carbon and nitrogen, there are some key questions on the structure of OMZs at a global scale. There is no agreement concerning the threshold in oxygen that defines an OMZ, and the extent of an OMZ is often evaluated by denitrification criteria which, at the same time, are O_2-dependent.

Our work deals with the identification of each OMZ, the evaluation of its extent, volume and vertical structure, the determination of its seasonality or permanence and the comparison between OMZs and denitrification zones at a global scale. The co-existence in the OMZ of oxic (in its boundaries) and suboxic (even anoxic, in its core) conditions involves rather complex biogeochemical processes such as strong remineralization of the organic matter, removal of nitrate and release of nitrite. The quantitative OMZ analysis is focused on taking into account the whole water volume under the influence of an OMZ and adapted to the study of the specific low oxygen biogeochemical processes.

A characterization of the entire structure for the main and most intense OMZs ($O_2 < 20$ μM reaching 1 μM in the core) is proposed based on a previously published CRIO criterion from the eastern South Pacific OMZ and including a large range of O_2 concentrations. Using the updated global WOA2005 O_2 climatology, the four known tropical OMZs in the open ocean have been described: the Eastern South Pacific and Eastern Tropical North Pacific, in the Pacific Ocean; the Arabian Sea and Bay of Bengal, in the Indian Ocean. Moreover, the Eastern Sub-Tropical North Pacific (25–52°N) has been identified as a lesser known permanent deep OMZ. Two additional seasonal OMZs at high latitude have also been identified: the West Bering Sea and the Gulf of Alaska. The total surface of the permanent OMZs is 30.4 millions of km^2 (~8% of the total oceanic area), and the volume of the OMZ cores (10.3 millions of km^3) corresponds to a value ~7 times higher than previous evaluations. The volume of the OMZ cores is about three times larger than that of the associated denitrification zone, here defined as NMZ ('nitrate deficit or NDEF > 10 μM' maximum zone). The larger OMZ, relative to the extent of denitrification zone, suggests that the unbalanced nitrogen cycle on the global scale could be more intense than previously recognized and that evaluation of the OMZ from denitrification could underestimate their extent.

1. Introduction

The interest in oxygen minimum zones (OMZs), characterized herein as O_2-deficient layers in the ocean water column, is quite recent, since the appearance of the name "OMZ" in Cline and Richards (1972). OMZs correspond to subsurface oceanic zones (e.g., at 50–100 m depth in the Arabian Sea; Morrison et al., 1999) and reaching ultra-low values of O_2 concentration (e.g. <1 μM; Karstensen et al., 2008). OMZs, because of their intensity and shallowness, are, a priori, different from the relatively well known "classical O_2 minimum", which is ~50 times more oxygenated than OMZs and found at intermediate depths (1000–1500 m) in all the oceans (Wyrtki, 1962). Note that in the present study, an OMZ is defined as being "more intense", when the O_2 concentrations in its core are lower.

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1.1. OMZ specificities for marine biogeochemistry and ecosystems

OMZs have been mainly known for playing an essential role in the global nitrogen cycle, in which various chemical species, according to their degree of oxidation (e.g. ammonium, NH_4^+; nitrite, NO_2^-; nitrate, NO_3^-; nitrous oxide, N_2O; dinitrogen, N_2), and different bacterial processes intervene. Under oxic conditions, but also at the upper boundary (oxycline) of an OMZ, nitrification transforms NH_4^+ into NO_3^-. But OMZs are especially associated with denitrification, which is a bacterial process occurring only in O_2-deficient regions (e.g., Codispoti et al., 2001). Denitrification converts NO_3^-, one of the main limiting nutrients in the ocean, into gaseous nitrogen (N as, for example, N_2O, N_2) which is lost to the atmosphere and contributes to the oceanic nitrate deficit (N/P $\approx$ 14.7; e.g., Tyrrell, 1999). However, recently, an unknown process in the ocean has been observed, first in sediments and then in the water column in the OMZs (e.g., Kuypers et al., 2003): the anaerobic oxidation of NH_4^+ using NO_2^- (anammox); this imposes a complete revision of the global nitrogen cycle (e.g., Arrigo, 2005). OMZs are also involved in the cycle of very important climatic gases: (i) production of ~50% of the oceanic N_2O (e.g., Bange et al., 1996); (ii) production of H_2 S (e.g., Dugdale et al., 1977) and CH_4 (e.g., Cicerone and Oremland, 1988), episodically or for OMZs in contact with sediments; (iii) limitation of atmospheric CO_2 sequestration by the ocean: directly as an end-product of remineralization (Paulmier et al., 2006) or indirectly through limitation of total primary production due to the N loss (see hypothesis of Falkowski, 1997); (iv) potential DMS consumption due to higher bacterial activity (Kiene and Bates, 1990). Chemically, OMZs are associated with acidification (low pH $\approx$ 7.5 SWS; Paulmier, 2005), and reduced conditions (Richards, 1965) favoring reduced chemical species (e.g., Fe(II) or Cu(I) potentially stimulating photosynthesis or N_2O production).

OMZs have also increased interest in biological and ecosystem studies. Because of similarities between Archean bacteria and those living in the OMZs (Zumft, 1997), OMZs could be considered as analogues of the primitive anoxic ocean in which life is widely thought to have first appeared. Transitions from high to low (the appearance of OMZs) oxygenation periods could stimulate biodiversity on a paleoclimatic scale (Rogers, 2000). OMZs can be a refuge for organisms specifically adapted to low O_2 concentration (e.g., giant Thioploca bacteria; Levin, 2002) from predation or competition with other species, and the lower OMZ boundary can even be among the richest habitats for the megafauna of the ocean. As a respiratory barrier, OMZs are associated with active vertical daily migration (e.g., for zooplankton; Fernández-Alamo and Färber-Lorda, 2006). But, for the main species (e.g., commercial fishes, such as anchovy), OMZs are considered as inhospitable. In the past, the Oceanic Anoxic Events (OAEs) have been associated with massive species extinction (e.g. during the Mid-Cretaceous). In the present, episodic anoxic events associated with eutrophicated waters are also inducing massive abnormal fish mortality (e.g., Chan et al., 2008).

1.2. Need for a reference state and an O_2 criterion for defining the OMZs extent

The intensity of all OMZ's perturbations and their potential feedback to climate and the marine ecosystem would depend on the OMZs extent. This extent would vary in response to climatic changes (lower ventilation due to stratification, and decreased O_2 solubility) and natural or anthropogenic fertilization (increased remineralization) through nutrient or metal inputs by upwelling, river discharge or atmospheric dust fall-out (e.g., Béthoux, 1989; Joos et al., 2003). In the past, OMZs have probably extended and contracted in warm (interglacial) and cold (glacial) periods, respectively (e.g., Cannariato and Kennett, 1999). Under present-day conditions, OMZs would increase or intensify, according to observations in recent decades (e.g., Stramma et al., 2008). But evaluations or predictions of OMZs variation over paleoclimatic periods, since the anthropocene era or in the future, cannot be validated without a reference state, and the report of all the existing OMZs detected in the modern ocean taking into account improvements in O_2-measurement techniques.

Despite the important role of OMZs in understanding primitive marine life and chemistry, as well as in the carbon (C) and nitrogen (N) cycles, little knowledge has been obtained on the extent and vertical structure of these oceanic "curiosities". This is mainly due to the following difficulties: (i) few available O_2 data obtained with a low enough detection limit (<1 μM) and accuracy (<2 μM), owing to the present limitations in the sampling and analysis techniques linked to the low O_2 concentration; (ii) the choice of a unique criterion for all OMZs, since the nature of this criterion often depends on research interest (e.g., specific low-O_2 biogeochemistry process studies have to take into account an O_2 concentration lower than 20 μM, but the influence of physical processes do not make it necessary to include suboxic and anoxic conditions); (iii) the criteria could be different for each OMZ region: for example, the OMZs in the Northeastern Atlantic ocean is excluded when a threshold of 20 μM is used (Helly and Levin, 2004). Different terms and thresholds have been used to described the overall low O_2 conditions. Suboxia has been mainly defined by biologists and biogeochemists as a transition layer from O_2- to NO_3^--respiration, with thresholds between ~0.7 μM (e.g., Yakusev and Neretin, 1997) and 20 μM (e.g., Helly and Levin, 2004). Hypoxia implies O_2 conditions under which macro-organisms cannot live: ~8 μM for Kamykowski and Zentara (1990), but up to 40 μM depending on the species considered, such as anchovy (e.g., Gray et al., 2002). Dysoxia (O_2 < 4 μM) and microxia (O_2 < 1 μM; Levin, 2002) are associated with a sharp O_2 transition for the large organisms, such as fishes. Anoxia (O_2 < 0.1 μM; Oguz et al., 2000) is defined by transition from NO_3-respiration to sulphate-reduction.

The first global study providing information on where water column OMZs can be located is that of Kamykowski and Zentara (1990) who produced maps of the distribution of hypoxia (O_2 < 8 μM) and of denitrification (Nitrate DEFicit or NDEF > 10 μM): ENP (Eastern North Pacific), ESP (Eastern South Pacific), AS (Arabian Sea) and BB (Bay of Bengal; see Fig. 1a). Without having a known evaluation of an OMZ's surface and vertical structure, Codispoti et al. (2001) concluded that the volume of suboxic zones could reach ~0.1% of the oceanic volume. OMZ areas have been considered to be similar to those of denitrification in several regional studies: ENP, ESP, AS (e.g., Codispoti et al., 2001). Hattori (1983) evaluated global oceanic denitrification (~8.45×10^6 km^2), obtained from separate previous evaluations using different criteria for each OMZ: NDEF > 10 μM (AS); secondary subsurface NO_2^- peak (ESP); O_2 < 5 μM (ENP). But from a qualitative comparison of hypoxia and denitrification maps, Kamykowski and Zentara (1990) concluded that the extent of the denitrification zone would be much less than the extent of the OMZ. Such a difference shows that the denitrification criterion could not be adapted to evaluating the size of the whole O_2-deficit zone. To validate this hypothesis, it is necessary to evaluate OMZs independently of the extent of the denitrification zone. Note also that the surface of OMZs that is in contact with sediments (1372×10^6 km^2; Helly and Levin, 2004) would be an order of magnitude lower than the global denitrification zone and the associated water-column OMZ surfaces.

Estimations of the extent of OMZs for biogeochemical studies are scarce and/or local (e.g., Morrison et al., 1999). Recently, the quantification of OMZs in the open ocean has been proposed by Karstensen et al. (2008). In the present study, three O_2 thresholds were used (the suboxic level of 4.5 μmol/kg, a more stringent 45 μmol/kg and a more relaxed level of 90 μmol/kg), and the anal-