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Oxygen distribution and aerobic respiration in the north and south eastern tropical Pacific oxygen minimum zones

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ABSTRACT

Highly sensitive STOX O_2 sensors were used for determination of in situ O_2 distribution in the eastern tropical north and south Pacific oxygen minimum zones (ETN/SP OMZs), as well as for laboratory determination of O_2 uptake rates of water masses at various depths within these OMZs. Oxygen was generally below the detection limit (few nmol L^{-1}) in the core of both OMZs, suggesting the presence of vast volumes of functionally anoxic waters in the eastern Pacific Ocean. Oxygen was often not detectable in the deep secondary chlorophyll maximum found at some locations, but other secondary maxima contained up to ~0.4 μmol L^{-1}. Directly measured respiration rates were high in surface and subsurface oxic layers of the coastal waters, reaching values up to 85 nmol L^{-1} O_2 h^{-1}. Substantially lower values were found at the depths of the upper oxycline, where values varied from 2 to 33 nmol L^{-1} O_2 h^{-1}. Where secondary chlorophyll maxima were found the rates were higher than in the oxic water just above. Incubation times longer than 20 h, in the all-glass containers, resulted in highly increased respiration rates. Addition of amino acids to the water from the upper oxycline did not lead to a significant initial rise in respiration rate within the first 20 h, indicating that the measurement of respiration rates in oligotrophic Ocean water may not be severely affected by low levels of organic contamination during sampling. Our measurements indicate that aerobic metabolism proceeds efficiently at extremely low oxygen concentrations with apparent half-saturation concentrations (K_m values) ranging from about 10 to about 200 nmol L^{-1}.

1. Introduction

Oxygen is a fundamental constraint on marine life, and it regulates many biological and chemical processes in the Ocean. Since oxygen is directly linked to carbon by photosynthesis and respiration, it is a diagnostic of the rate at which organic matter cycles in the Oceans (Keeling et al., 2010; Stramma, 2008). Its regulatory role is particularly evident in marine areas like oxygen minimum zones (OMZs) (Paulmier and Ruiz-Pino, 2009), where a combination of natural conditions, such as high productivity surface waters, stratification, and reduced circulation leads to extensive depletion of dissolved oxygen at intermediate depths of the water column (Wyrtki, 1962). The resulting oxygen gradients favor a complex succession of aerobic and anaerobic respiration processes with depth (Wright et al., 2012), that are tightly regulated by local O_2 levels and the presence of electron donors and alternative electron acceptors. The presence of OMZ regions was described in the early 1900s (Schmidt, 1925) and during recent decades their biogeochemical importance has been recognized, as they are estimated to account for 21–39% of the global oceanic nitrogen (N) loss and a similar percentage of oceanic N_2O emission (Bange, 2006; DeVries et al., 2012a; Kalvelage et al., 2013). Only recently we have gained the technical ability to resolve the O_2 distribution in the OMZ with satisfactory accuracy, and to determine the effect of nanomolar O_2 concentrations on biogeochemical cycling. Our ability to detect in situ oxygen concentration in the OMZ improved by about three orders of magnitude, as we progressed from the traditionally used Winkler titrations or electrochemical and optode sensors having detection limits around 1–2 μmol L^{-1}, to the Switchable Trace Oxygen (STOX) microsensor, that has a detection limit in the range of 1–10 nmol L^{-1} (Revsbech et al., 2009). The STOX sensor is an oxygen microsensor with front guard cathode,

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which enables in situ zero calibration, thus allowing measurement of near zero oxygen concentrations. Consequently the eastern tropical south Pacific (ETSP) OMZs as well as the OMZ in the Arabian Sea were renamed Anoxic Marine Zones (AMZs) (Ulloa et al., 2012), because no O_2 could be detected in the water layers occurring between 20 and 100 m depth and down to a few hundred meters depth. These totally anoxic water layers were shown to coincide with extensive NO_2^- accumulation (Canfield et al., 2010; Jensen et al., 2011; Thamdrup et al., 2012). Recent investigations have reported that the transitions between aerobic and anaerobic respiration in OMZs are regulated by O_2 levels in the nanomolar range. Even O_2 concentrations as low as 1 μmol L^{-1} or less appear to be inhibitory for anaerobic ammonium oxidation (anammox) and, to higher extent, for denitrification (Dalsgaard, personal communication); in addition both oxidations of ammonium and nitrite (Bristow, unpublished data) exhibit very low half-saturation concentrations for O_2 and these oxidation processes may occur at much lower oxygen concentrations than previously anticipated.

Forecasted decline in Ocean dissolved O_2 (Ocean deoxygenation) will likely lead to expansion, in area and volume of OMZs with widespread consequences (Keeling et al., 2010). Thus there is a need for more detailed data on the current O_2 distribution, dynamics and consumption rates in OMZ and AMZ waters, with focus on process regulation at low O_2 concentrations.

In this study we investigated the depth and regional variation of oxygen concentration, aerobic respiration in low oxygenated waters, and the potential for aerobic respiration in anoxic waters from the eastern tropical north and south Pacific (ETNP-ETSP) OMZs, through a combination of high sensitivity in situ and laboratory based STOX sensor measurements.

2. Material and methods

2.1. Experimental area and sampling

A total of three stations were investigated during two cruises in two main experimental areas: the eastern tropical north Pacific (ETNP) and the eastern tropical south Pacific (ETSP) (Fig. 1).

During the ETNP Spring Cruise (March and April 2012) aboard the R/V Thomas G. Thompson experiments were carried out at two main stations: one about 50 km from the Mexican coast, M1 (N 20° 03′ 50, W 106° 00′ 81), and an oceanic one (~700 km from the Mexican coast) M2 (N 16° 29′ 93, W 109° 59′ 00) (Fig. 1). In addition dissolved oxygen distribution was determined in two transects (Fig. 2 and S3). Profiles of physical variables were registered with a Seabird SBE-911 conductivity–temperature–depth (CTD) system, which was equipped with an SBE 43 oxygen sensor and an in situ STOX sensor unit (Unisense A/S). Seawater samples were collected using a 10-L Niskin bottle rosette.

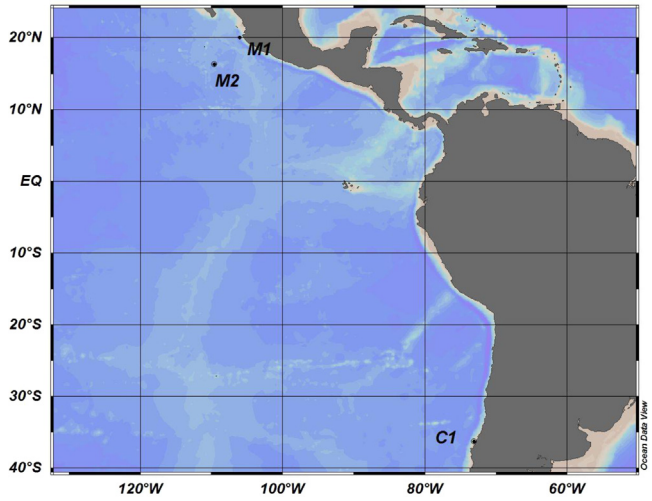

Fig. 1. *Map of the study area and sampling stations*. Study areas were located in the eastern tropical north and south Pacific, with three main sampling stations: M1, coastal Mexico; M2, off shores Mexico; C1, off Dichato, central Chile (Ocean Data View).

In the ETSP, Station C1 (S36°30′85, W73°07′75), ~18 km from the coast, was sampled during the MOOMZ4 cruise (March 2012) off Chile, using a pump profiling system (PPS) equipped with a Seabird SBE-25 CTD with an SBE 43 oxygen sensor package and an in situ STOX unit. Incubations were carried out in the Dichato laboratories of Universidad de Concepción.

High resolution oxygen profiling with the STOX sensor (Revsbech et al., 2009; Revsbech et al., 2011) was typically carried out on the first cast, together with nutrient measurements (Fig. S4), to characterize the water column at each station. We selected the depths for sampling mainly on the basis of in situ oxygen concentrations, detected by the STOX sensor and the two SBE 43 oxygen sensors, targeting seawater masses with naturally different oxygen concentrations. The main chosen primary sample depths were: oxygenated surface waters, partially oxygen depleted oxycline waters and completely oxygen depleted waters from below the oxycline. For each depth bottle incubations were performed shortly after sampling, as shown below.

2.2. Reactor experiments and STOX sensor

2.2.1. Measurements of community respiration rates

Experiments from stations M1, M2 and C1 were carried out in custom-modified Schott Duran® glass bottles of 1160 mL. The bottle design and filling procedure has been described previously (Tiano et al., 2014). During the incubations the bottles were kept in darkness and submersed in a water bath maintained at the desired temperature (12 °C for C1; 14 °C for M1 and M2). Continuous stirring was accomplished using glass coated magnets (Fisher Scientific®), while placing the container with the bottles on magnetic stirrers (IKA®). The seawater was partially or fully degassed by constant bubbling with He (Station C1) or N_2+0.04% CO_2 (stations M1 and M2) before being siphoned into the incubation bottles under a stream of N_2. If O_2 concentrations were too low for the specific experiment small volumes of water were added by a syringe with a long needle through the pressure compensation tube of the bottle. All experiments were conducted within 24 h of sampling with incubations for respiration rates normally lasting ~15 h. Before all experiments the glassware was washed in 0.1 M NaOH and subsequently in 0.1 M HCl to avoid organic contamination.

The STOX microsensors were built as described previously (Revsbech et al., 2009; Revsbech et al., 2011). Calibration was performed by injecting known volumes of air-saturated water into each bottle. The electronics applied for shipboard and laboratory based experiment were identical. The sensor currents were measured with a PA8000 eight-channel picoammeter (Unisense A/S), while the polarization and depolarization of the front guard were regulated by a custom-built timer-controlled switch-box with the timer set to cycles of 200 s on and 200 s off. The signals were collected by a Unisense ADC816 16-bit A/D converter, connected to a portable PC using the program Sensortrace Basic (Unisense A/S).

2.2.2. Effects of organic contamination and time on community respiration rates

Two sets of experiments were performed in order to investigate the effects of time (i) and organic contamination (ii) on CR rates in discrete bottle incubations. i) The effect of time solely was evaluated on water samples from 900 m depth that were incubated in two reactors for a total time of 37 h. ii) Organic