

Reduced nitrogen fixation in the glacial ocean inferred from changes in marine nitrogen and phosphorus inventories

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To explain the lower atmospheric CO₂ concentrations during glacial periods, it has been suggested that the productivity of marine phytoplankton was stimulated by an increased flux of iron-bearing dust to the oceans^{1,2}. One component of this theory is that iron—an essential element/nutrient for nitrogen-fixing organisms—will increase the rate of marine nitrogen fixation, fuelling the growth of other marine phytoplankton and increasing CO₂ uptake. Here we present data that questions this hypothesis. From a sediment core off the northwestern continental margin of Mexico, we show that denitrification and phosphorite formation—processes that occur in oxygen-deficient upwelling regions, removing respectively nitrogen and phosphorus from the ocean—declined in glacial periods, thus increasing marine inventories of nitrogen and phosphorus. But increases in phosphorus were smaller and less rapid, leading to increased N/P ratios in the oceans. Acknowledging that phytoplankton require nitrogen and phosphorus in constant proportions, the Redfield ratio³, and that N/P ratios greater than the Redfield ratio are likely to suppress nitrogen fixation^{4,5}, we suggest therefore that marine productivity did not increase in glacial periods in response to either increased nutrient inventories or greater iron supply.

Denitrification of fixed nitrogen represents a substantial loss of biologically available nitrogen from the ocean. It occurs mostly in oxygen-deficient zones where large settling fluxes of organic detritus in coastal upwelling areas near continental margins leads to consumption of oxygen in subsurface waters at rates that exceed resupply from horizontal and vertical mixing. This leads to water-column denitrification because, in the absence of oxygen, NO₃⁻ is used as an electron acceptor in the bacterially mediated degradation of organic matter. Because the gaseous products of denitrification (N₂O and N₂) are to a large extent lost to the atmosphere, this process constitutes a net loss of fixed nitrogen from the ocean^{6,7}. Water-column denitrification occurs today primarily in three areas: off northwestern Mexico in the eastern tropical North Pacific Ocean, off Peru–Chile in the eastern tropical South Pacific Ocean and in the Arabian Sea⁸. The loss of fixed N in these three regions accounts for almost one-half of the total oceanic nitrogen loss of 200 Tg N yr⁻¹ (ref. 6).

For the marine phosphorus inventory, the precipitation of carbonate fluorapatite (CFA) in organic-rich sediments constitutes an important mode of removal of biologically available P from the ocean, accounting for some 10–15% of the total P removal⁹. Phosphogenesis in the contemporary ocean occurs mainly in the eastern tropical Pacific and Arabian Sea, and to a minor extent off Namibia and western Australia (Table 1). (The term phosphogenesis is used here exclusively with reference to relatively large P enrichments in margin sediments with porewater HPO₄²⁻ levels exceeding CFA saturation, although we recognize that

CFA occurs at trace levels elsewhere in deep-sea and margin sediments⁹. The marked spatial correspondence between phosphogenesis and water-column denitrification suggests that these processes are promoted by conditions prevailing in oxygen-deficient upwelling margins⁸.

The eastern tropical North Pacific hosts the most extensive coastal upwelling area and the largest mass of denitrifying waters in the world's oceans, and phosphogenic sediments are common in the bordering margins off Central America⁸. Off northwest Mexico, the oxygen minimum has near-zero oxygen concentrations extending from approximately 150 to 800 m water depth (Fig. 1a). Denitrification is a major respiration process in subsurface waters, as indicated by a large nitrate deficit in the water column that corresponds with the oxygen-deficient zone (Fig. 1b). Denitrification preferentially reduces ¹⁴N, and as a result the residual nitrate is progressively enriched in ¹⁵N in the denitrifying waters¹⁰ (Fig. 1c). This signal is transmitted to the sediments by upwelling of isotopically heavy nitrate into surface waters, its assimilation by phytoplankton, and the subsequent sinking of organic detritus to the sea floor^{6,11}. As a result, δ¹⁵N values in box cores are heavy, ranging between 9‰ and 10‰ across the margin⁸.

Contents of sedimentary organic carbon in box cores on the Mexican continental slope increase from 2 wt% on the outer shelf (shelf break ~150 m) to ~10% at 1,000 m depth (Fig. 1d). The sediments that are accumulating between 150 and ~800 m water depth are distinctly laminated, and contain high concentrations of P (Fig. 1e) owing to the presence of CFA as disseminated grains and discrete unconsolidated laminae typically < 1 cm thick. The CFA-enriched layers are also defined by large spikes in down-core P concentration profiles (plotted as maximum P contents in Fig. 1e), which cannot be accounted for by P contained in organic or lithogenous material. A close correspondence between increased interstitial dissolved HPO₄²⁻ concentrations and CFA precipitation can be seen in Fig. 1e and f. Thermodynamic calculations indicate that interstitial dissolved phosphate concentrations exceeding 40 μM should cause supersaturation with respect to CFA solubility in these sediments¹². The increased porewater P concentrations of phosphogenic sediments, which exceed CFA solubility by an order of magnitude, are attributed primarily to a large P supply to the sediments by way of settling biogenic debris and to some extent to the cycling of remineralized/redissolved P in suboxic sediments¹³. Although the roles of fish-bone dissolution, Fe-oxyhydroxide cycling and inhibited bioturbation in promoting CFA precipitation are being debated^{14,15}, phosphogenesis and porewater phosphate levels exceeding CFA saturation occur almost exclusively in organic-rich, suboxic upwelling margin sediments that underlie oxygen-deficient/denitrifying bottom waters (Fig. 1; refs 12–15).

A 10-m-long piston core (NH15P; 425 m water depth) raised from the upper slope of the Mexican margin provides a detailed history of productivity, denitrification and phosphogenesis on glacial–interglacial timescales (Fig. 2a–e). This core site is located where the oxygen minimum and denitrification are the most

Table 1 Estimated rates of burial of phosphogenic P in the modern ocean

Location	P burial*	Area (10 ⁶ km ²)
ETNP (off Mexico–Guatemala)†	0.3 to 1.6	0.5
ETSP (off Peru–Chile)† ¹³	0.8 to 6.3	0.2
Arabian Sea (off Oman and Indo-Pakistan) ¹⁵	0.076 to 1.04	0.4
Southwest Africa (Namibian shelf) ²³	2.8 to 3.3	0.03
West Australian shelf ²⁴	NA	<0.02
Global phosphogenic P burial‡	1.2 × 10 ¹⁰ mol yr ⁻¹	

* In units of μmol cm⁻² yr⁻¹, except where shown.

† Rates estimated from P contents in Mexican margin box cores (Fig. 1). Area calculated on the basis that phosphogenesis is occurring on the shelf and upper slope of the eastern North Pacific (ETNP), the eastern South Pacific (ETSP) and the Arabian Sea, and on the shelf off Namibia and West Australia.

‡ Estimated by extrapolating median P burial of 1 μmol cm⁻² yr⁻¹ over a total phosphogenic sediment area of 1.2 × 10¹⁰ km². NA, not available.

intense, and where CFA is precipitating in the modern sediments. X-radiographs reveal alternating cycles of laminated and bioturbated intervals down core that closely match glacial–interglacial cycles (Fig. 2a). Laminated sediments are confined to interglacial stages (1, 3 and 5), while glacial-age sediments are bioturbated (stages 2 and 4). Contents of organic carbon and opal are significantly higher in interglacial intervals compared to glacial sediments (Fig. 2c and d). Phosphorus-enriched layers are invariably confined to laminated interglacial sediments rich in organic carbon and opal (Fig. 2b–d). The lack of P-enrichment in glacial horizons suggests that phosphogenesis did not occur at the position of the modern oxygen minimum off northwest Mexico at these times.

Measurements of $\delta^{15}\text{N}$ in the core show cyclic variations, with particularly enriched values ($> 8\text{‰}$) being largely confined to the interglacials (Fig. 2e). This suggests that large-scale denitrification occurred in this region only during the interglacials and was absent during the glacial periods^{6,11}. The close correspondence between the bioturbated (unlaminated) sections of the core and lighter $\delta^{15}\text{N}$ values indicates that waters overlying the core site were relatively well oxygenated and the sediments were less reducing during the deposition of these intervals. Such glacial–interglacial contrasts in the accumulation rates of organic carbon, opal, biogenic barium and $\delta^{15}\text{N}$ values are seen across the continental slope in this same area. This has led to the suggestion that biological productivity and upwelling rates diminished over the margin during the glacial periods^{6,16}. Relatively low export production during the glacial periods resulted in a decreased supply of settling biogenic debris and enhanced oxygenation of the water column and superficial sediments. These conditions in turn seem to have inhibited denitrification in the water column and sedimentary CFA precipitation.

These processes seem to have operated on other highly productive continental margins. Off Peru, sedimentary phosphorites in

laminated organic-rich sediments invariably formed during interglacial periods, and evidence for phosphogenesis is absent in glacial intervals^{17,18}—which are marked by reduced productivity and denitrification and increased oxygenation of sub-thermocline waters⁶. On the Arabian Sea margins, very high P contents are confined to interglacial sediments in contact with oxygen-deficient waters on the upper slope, and phosphogenesis seems to have decreased during glacials^{15,19} in response to reduced production and increased oxygenation of the water column^{6,20}.

The concomitant declines in phosphogenesis and denitrification during glacial periods should have had a much larger effect on the oceanic inventory of N than of P. Given that the continental margins bordering the eastern Pacific and the Arabian Sea account for more than 90% of the total area that supports phosphogenesis in the modern ocean (Table 1), the elimination of phosphogenesis in these regions during glacial stages should have resulted in a reduction in P burial of up to 10% of the modern total burial rate (about $8\text{--}12 \times 10^{10} \text{ mol P yr}^{-1}$; ref. 9). Assuming that the P removal rate in other oceanic regions is proportional to the P concentration in sea water, this would only account for an approximately 10% increase over the modern P inventory of the ocean ($3.2 \times 10^{15} \text{ mol P}$; ref. 9). In addition, the decline in P burial ($\sim 10\%$) due to diminished phosphogenesis is likely to have been compensated to some extent by increased P burial in glacial sediments in non-phosphogenic areas. Glacial–interglacial changes in reactive P input in the ocean—from the erosion of continental shelf sediments exposed during lowstands²¹, or from terrestrial biomass or soils—are poorly constrained. However, such changes are likely to be much smaller in magnitude, and the changes in P transfer rates at glacial–interglacial transitions much slower, than required to account for rapid changes in temperature and partial pressure of CO_2 recorded in ice cores⁶. Thus, the glacial increase in oceanic P inventory could not have been

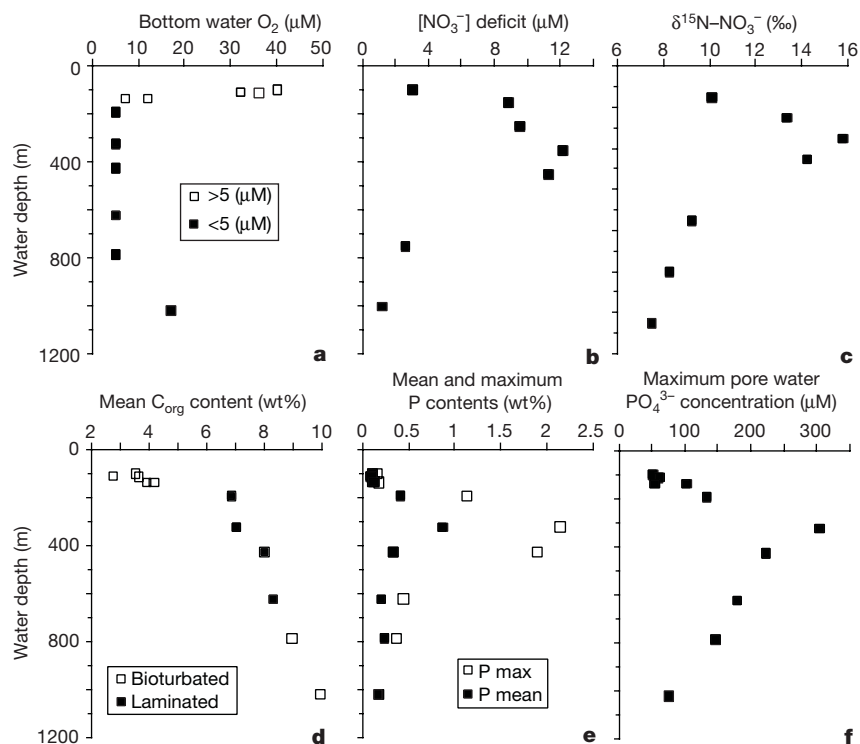


Figure 1 Water column and sediment properties across the continental shelf and slope off northwest Mexico. **a–c**, Water-column profiles of oxygen, nitrate deficit and the $\delta^{15}\text{N}$ of nitrate originally reported in ref. 8. **d**, Mean wt% of organic carbon (C_{org}) in box cores that were typically 15–30 cm long and were sectioned at 1–2-cm intervals. Down-core core changes in organic carbon content are within 1 wt% in most box cores. **e**, Mean and maximum wt% P in the box cores plotted against water depth. The large difference

between mean and maximum P contents indicates the occurrence of CFA enriched laminae in sediments. **f**, Maximum phosphate concentrations in pore waters²⁵. Total carbon was determined by Carlo-Erba CNS analyser, and carbonate carbon by coulometry. Organic carbon was obtained by difference with a combined precision of $\pm 3.9\%$. P was determined using an automated Phillips PW1400 X-ray fluorescence spectrometer with precision better than $\pm 5\%$.

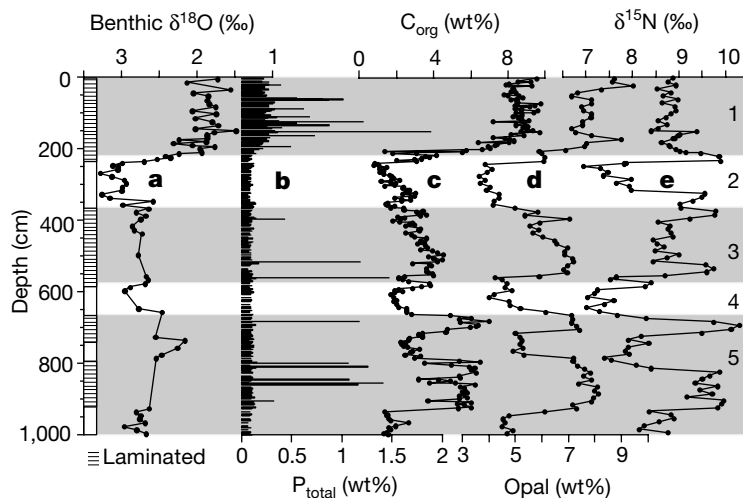


Figure 2 Records of $\delta^{18}\text{O}$ of benthic foraminifera, weight per cent phosphorus and organic carbon, and $\delta^{15}\text{N}$ of bulk sediments in Core NH15P (425 m water depth; 22° 41.0' N, 106° 28.8' W). Hatched bars on the left margin indicate the presence of visible laminations in X-radiographs. Isotope stage boundaries are based on 13 AMS- ^{14}C dates and benthic foraminiferal oxygen isotope stratigraphy¹⁶. Isotope stages are indicated near the right margin of the panels and interglacial stages are shaded grey. **a**, $^{18}\text{O}/^{16}\text{O}$ ratios were measured on *Bolivina* spp., using a VG PRISM mass spectrometer equipped with a VG Autocarb common-bath sample preparation system. The results are reported in the δ notation, $\delta^{18}\text{O} = [(^{18}\text{O}/^{16}\text{O})_{\text{sample}} / (^{18}\text{O}/^{16}\text{O})_{\text{standard}}] - 1$, in units of per mil, where the standard is PDB. The analytical precision for these measurements is $\pm 0.04\%$. **b**, Phosphorus contents are presented as bar graphs with each bar representing a 2-cm sampling interval (see Fig. 1 legend for analytical details). Some of the most elevated P concentrations occur in intervals corresponding with layered structures, where the presence of CFA is identified by X-ray powder diffraction. Note that sample intervals with CFA laminae contain up to 3 wt% P, which corresponds to a CFA content of roughly 25% (pure CFA contains ~ 13 wt% P; ref. 26). The intervening sediments are also enriched in P

more than 10% of the present value, whereas the glacial increase in fixed nitrogen due to reduced water-column denitrification was probably substantial (about 50% of the modern value; see, for example, ref. 6). In addition, the oceanic residence time for N (3 kyr; ref. 4) is much shorter than that for P (20–30 kyr; ref. 9), and therefore the N content could rise much faster than that of P during glacial periods.

On the basis of the above inferences, we propose two models for nutrient contents of the glacial ocean. First, the rising glacial dissolved N/P ratio rapidly shifted ecological advantage from nitrogen-fixers (diazotrophs) to non-nitrogen-fixing algae⁴, counteracting the effect of decreased denitrification and effectively anchoring the N to the P inventory. This would restore the Redfield ratio. Implicit in this argument, however, is the assumption that the ecological response by nitrogen fixation is as immediate as the increase in N/P ratio. The second model involves slow compensation by nitrogen fixation for variations in N/P ratios, as has been suggested recently⁵. In this case, glacial N contents would have rapidly increased until the N/P ratio was high enough to subjugate nitrogen fixation, allowing the seawater N/P ratio to gradually return to its Redfield value.

But regardless of which of the above two models is correct, they allow two important conclusions to be drawn. First, nitrogen fixation in glacial times is likely to have been lower (and not higher) than interglacial nitrogen fixation—owing to P limitation (higher N/P)—and therefore the ice-age flux of aerosol iron to oligotrophic regions of the sea is unlikely to have been as biogeochemically important as suggested previously^{1,2}. This is consistent with recent observations that nitrogen fixation could be phosphorus-limited in Fe-replete conditions²². Second, glacial increases in ocean productivity resulting from changes in nutrient inventory

to varying degrees due to the presence of dispersed CFA grains. The P accumulation rate in the Holocene sediments of Core NH15P is on the order of $0.6 \mu\text{mol cm}^{-2}\text{yr}^{-1}$ (calculated as the product of the sedimentation rate (17 cm kyr^{-1}), an average P content of 0.33 wt%, P atomic wt 30.97, and a dry bulk density of 0.35 g cm^{-3}). More than 80% of this is in the form of reactive P (CFA + organic P), based on comparison of the P/Al ratio in CFA-free and organic-free detritus (~ 0.0088 ; ref. 26) and the mean in the Holocene section of NH15P (0.044). In contrast, P burial in the Last Glacial Maximum (LGM) sediments in Core NH15P was approximately $0.1 \mu\text{mol cm}^{-2}\text{yr}^{-1}$ (4 cm kyr^{-1} ; 0.09 wt% P; 0.7 g cm^{-3} ; 0.013 P/Al), of which the dominant host, based on normative calculations, is lithogenic detritus. **c**, Organic carbon determination is described in Fig. 1 legend. **d**, Opal determinations were made by colorimetry after leaching sediments with 2 M Na_2CO_3 at 85 °C for 3 h. Analytical precision is $\pm 6\%$. **e**, Nitrogen isotope ratios were determined using a Carlo-Erba CHN analyser interfaced directly to the mass spectrometer. $\delta^{15}\text{N} = [(^{15}\text{N}/^{14}\text{N})_{\text{sample}} / (^{15}\text{N}/^{14}\text{N})_{\text{standard}}] - 1$, in units of per mil, where the standard is atmospheric nitrogen; the precision of this measurement is better than $\pm 0.3\%$.

and their influences on the partial pressure of CO_2 are likely to have been small, having been fundamentally dictated by the slight and slow increase in P inventory. □

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Competing interests statement

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The effect of millennial-scale changes in Arabian Sea denitrification on atmospheric CO₂

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Most global biogeochemical processes are known to respond to climate change, some of which have the capacity to produce feedbacks through the regulation of atmospheric greenhouse gases¹. Marine denitrification—the reduction of nitrate to gaseous nitrogen—is an important process in this regard, affecting greenhouse gas concentrations directly through the incidental production of nitrous oxide, and indirectly through modification of the marine nitrogen inventory and hence the biological pump for CO₂. Although denitrification has been shown to vary with glacial–interglacial cycles^{2,3}, its response to more rapid climate change has not yet been well characterized. Here we present nitrogen isotope ratio, nitrogen content and chlorin abundance data from sediment cores with high accumulation rates on the Oman continental margin that reveal substantial millennial-scale variability in Arabian Sea denitrification and productivity during the last glacial period. The detailed correspondence of these changes with Dansgaard–Oeschger events recorded in Greenland ice cores⁴ indicates rapid, century-scale reorganization of the Arabian Sea ecosystem in response to climate excursions, mediated through the intensity of summer monsoonal upwelling. Considering the several-thousand-year residence time of fixed

nitrogen in the ocean, the response of global marine productivity to changes in denitrification would have occurred at lower frequency and appears to be related to climatic and atmospheric CO₂ oscillations observed in Antarctic ice cores between 20 and 60 kyr ago⁵.

Denitrification occurs under suboxic conditions when bacteria utilize NO₃⁻ as an electron acceptor and in doing so convert it primarily to N₂ gas. This process is the primary loss mechanism for combined nitrogen from the biosphere, and thus has an important role for the nitrogen cycle and the biogeochemical cycles linked to it. In the ocean, denitrification occurs in organic-rich continental margin sediments and in intermediate waters within intense oxygen–minimum zones. Of the latter, the Arabian Sea supports approximately one-third of marine water-column denitrification⁶. Denitrification also strongly fractionates nitrogen isotopes, leaving the remaining NO₃⁻ enriched in ¹⁵N (refs 7 and 8). A palaeoceanographic record for denitrification intensity is created when ¹⁵N-enriched NO₃⁻ is transported to surface waters and consumed by phytoplankton, with subsequent downward transport of organic matter and preservation in the sediments. When there is good-to-excellent preservation of organic matter at the sea floor due to either suboxic bottom water and/or high sediment accumulation rates, sediment δ¹⁵N faithfully records the δ¹⁵N of sinking organic matter⁹.

Previous studies have shown strong coupling between variations in denitrification intensity and climate change at orbital periodicities (> 19 kyr) for the Arabian Sea^{2,3}, as well as during glacial–interglacial transitions in other major regions for water-column denitrification¹⁰. Here we take advantage of two deep-sea cores from the Oman margin (Fig. 1) with relatively high sediment accumulation rates (~15 cm kyr⁻¹) to examine possible high-frequency variability in denitrification and productivity and their relationship to climate change. Sampling every 1 cm achieved an

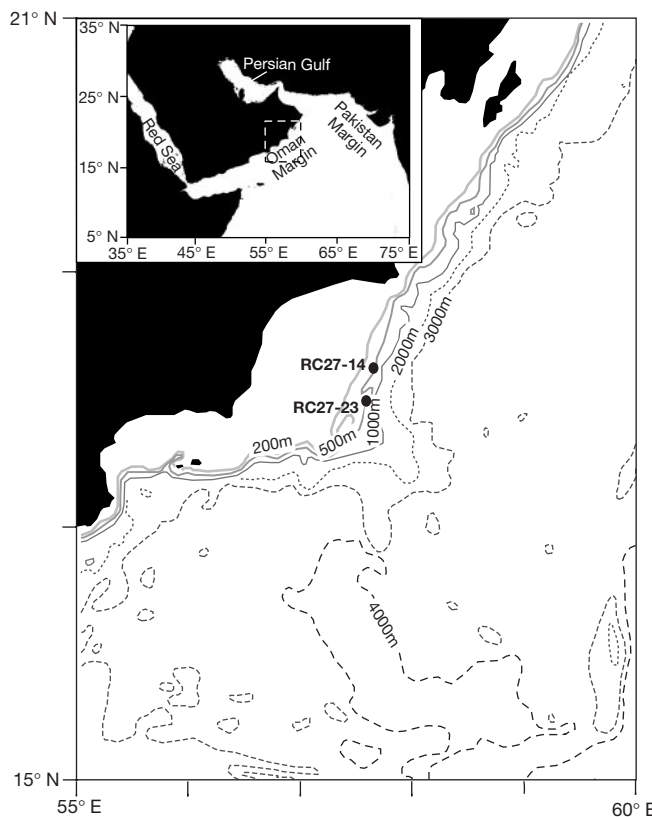


Figure 1 Location of sediment cores on the Oman margin, and (inset) the location of the Oman margin within the Arabian Sea. Both sites (RC27-14: 18° 15.2' N, 57° 39.3' E, 596 m water depth; RC27-23: 17° 59.6' N, 57° 35.4' E, 820 m water depth) lie at depths inside the oxygen–minimum zone, which impinges on the continental slope between 200 and 1,200 m water depth.