Regeneration of nutrients in the northern Benguela upwelling and the Angola-Benguela Front areas

Thorsten Dittmar*† and Matthias Birkicht*

Nutrient and dissolved organic carbon (DOC) distributions were determined in July 1999 in the northern Benguela upwelling and Angola-Benguela Front areas. Highest silicate and phosphate surface concentrations of up to 30 μM and 3.7 μM, respectively, were determined in recently upwelled waters between 19°S and 21°S off Namibia. Nitrate, on the other hand, exhibited there a local minimum, which indicates an advanced bloom of non-siliceous phytoplankton. Nitrate and DOC concentrations increased with distance from the upwelling centre (up to 15 μM and 720 μM, respectively), probably due to mineralization of phytoplankton-derived organic compounds, whereas silicate strongly decreased. Growth of siliceous phytoplankton, which covered their nitrogen requirements by nutrient recycling within the photic layer, probably caused this pattern in aged waters surrounding the upwelling. In contrast to primary production in the upwelling centre, this phytoplankton growth was therefore not 'new production'. Primary production was presumably limited by nitrate in recently upwelled waters and by silicate in aged waters. Phosphate was probably not limiting, indicated by low N/P ratios in surface waters (<10) and low surface depletion. Regeneration of silicate and phosphate was evident in source waters of upwelling in ~100 m depth. Silicate increased exponentially from off- to inshore by a factor of ~10, phosphate increased by ~30%. Regenerated silicate was ~25 μM, phosphate ~0.5 μM. Nitrate was not regenerated and oscillated apparently randomly between 11 μM and 24 μM at 100 m depth. Ammonium and nitrite increased exponentially from off- to onshore, indicating mineralization of nitrogenous compounds, but contributed only 3% to dissolved inorganic nitrogen on average. In the front area no evidence for nutrient trapping was found. The lack of nitrogen regeneration and strongly decreasing N/P and N/Si ratios shoreward are evidence for considerable nitrogen losses off Namibia. Denitrification, which is favoured by the oxygen deficit in source waters, is the probable reason for these losses. Since denitrification was disregarded in the past, the productivity of the northern Benguela and its role as a carbon sink have presumably been overestimated.

Introduction

The oceans contain about 90% of the carbon actively circulating in the biosphere.[1] Photosynthetic activity of marine phytoplankton removes carbon from the physical equilibrium between atmosphere and ocean. Dissolved organic matter in the oceans constitutes a total mass of carbon comparable with that of atmospheric CO_2.[2] Marine primary production therefore plays a key role in the global carbon cycle and is one of the control mechanisms for CO_2 concentration in the atmosphere. Knowledge of carbon fixation rates, and of the export of organic material from the photic layer and its preservation in the ocean, is therefore an essential prerequisite in the prediction of CO_2 dynamics and climate in the future.

Upwelling systems are characterized by the flux of nutrient-rich waters into the photic layer and belong to the most productive marine ecosystems. The extent of organic carbon export from these systems depends primarily on the proportion of 'imported new production' to total primary production.[3] Upwelling systems function mostly as an effective nutrient trap.[4] After upwelling, nutrients are assimilated by phytoplankton. During offshore transport, sinking organic particles of decaying phytoplankton are remineralized and the released nutrients transported back towards the upwelling centre. A considerable fraction of primary production is therefore based on nutrient recycling on the scale of the whole upwelling system ('secondary recycling') or within the photic layer itself ('primary recycling'). This fraction does not account to the productivity of the whole system. In this context, nutrient accumulation by 'secondary recycling' has been widely described in the major upwelling areas.[5–8]

The Benguela belongs to the world's most productive upwelling systems.[9] In the past, research was focused on the southern Benguela off South Africa and southern Namibia.[10] For the northern Benguela and the Angola-Benguela Front areas, published information on nutrient dynamics is rare. No data are available on either the regeneration of mineralized phosphate and silicate, or on the dynamics of organic compounds. Average nitrate concentrations have been estimated for the Benguela as a whole.[11] In this study, we present data on the distribution of silicate, phosphate and inorganic nitrogen compounds in the northern Benguela and the Angola-Benguela Front areas. Based on these data and the distribution of dissolved organic carbon (DOC), the driving forces behind nutrient patterns and regeneration rates are discussed.

During the period of sampling in austral winter 1999, upwelling occurred along most of the Namibian coast. The strongest upwelling of oxygen-deficient (~50 μM O_2) and cold (~14°C) thermocline waters from a depth of ~100 m was observed around 20°S near the coastline.[12] In the north, warm (>21°C) Angolan waters were advected in the photic layer southwards to ~16.7°S near the coast (~11.5°E).[13] To the west, at ~11.0°E, cold Benguela waters were advected northwards to ~15.7°S. A detailed description of Benguela Current dynamics can be found in the literature.[10] Oceanographic details during the period of sampling are given elsewhere in this issue.

Materials and methods

Sampling was performed along four cross-shelf transects in the northern Benguela upwelling area (20 stations) and three transects parallel to the coast in the Angola-Benguela Front system (17 stations) during the second leg of the FRS *Africana* cruise in July 1999.[35] For the exact positioning of sampling stations, the front was monitored using SST satellite images during the cruise (Fig. 1).

*Zentrum für Marine Tropenökologie, Fahrenheitstr. 6, D-28359 Bremen, Germany.
†Author for correspondence. Current address: Alfred-Wegener-Institut für Polar- und Meeresforschung, Am Handelshafen 12, 27570 Bremerhaven, Germany.
E-mail: tdittmar@awi-bremerhaven.de

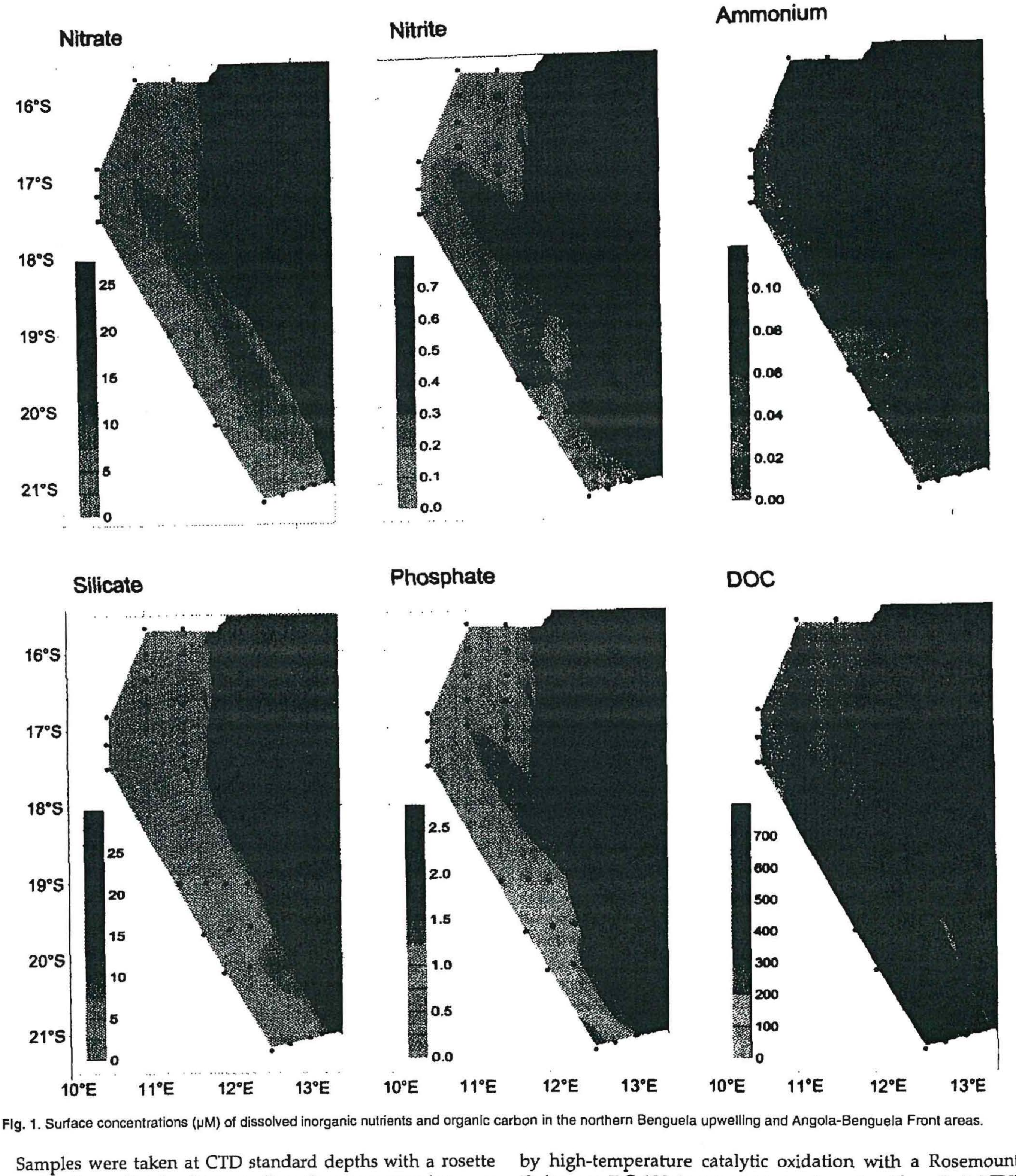
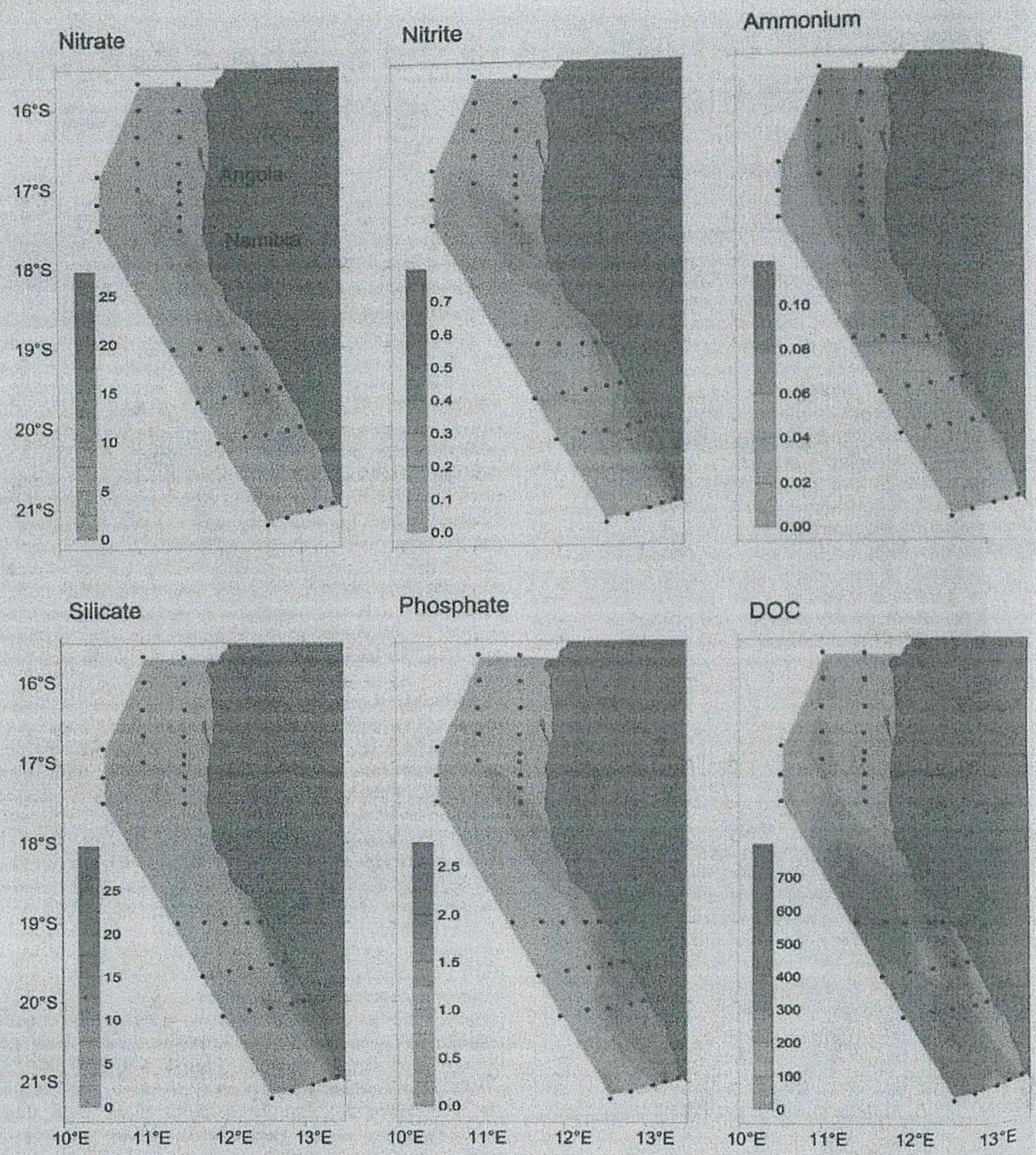


Fig. 1. Surface concentrations (μM) of dissolved inorganic nutrients and organic carbon in the northern Benguela upwelling and Angola-Benguela Front areas.

Samples were taken at CTD standard depths with a rosette sampler. Immediately after sampling, the water samples were passed through pre-combusted (4 h, 450°C) Whatman GF/C filters. Water aliquots for the analysis of inorganic nutrients were poisoned with $HgCl_2$ to a sample concentration of 100 mg l^{-1} and kept frozen in polyethylene bottles.[14] Samples for the determination of dissolved organic carbon were adjusted after filtration to pH 2 with 1 N HCl and kept frozen in pre-combusted sealed ampoules. Dissolved inorganic nutrients were measured by standard autoanalyser methods using a Skalar-SAN-plus system.[15] Dissolved inorganic nitrogen (DIN) was calculated as the sum of nitrate, nitrite and ammonium. DOC was determined by high-temperature catalytic oxidation with a Rosemount-Dohrman DC-190 instrument, equipped with a Fuji NDIR detector.[16,17] The relative standard deviations for each method and each run were less than 3.5% ($P = 0.05$; German standard method).[18] If a run exceeded this value or if the coefficient of variation between duplicates exceeded 5%, the determination was repeated. Detection limits (in μM) were: for nitrate 0.14, nitrite 0.01, ammonium 0.10, silicate 1.7, phosphate 0.14, and DOC 25.

Results

Nutrient concentrations of surface waters down and at 50 and 100 m depth are shown in Figs 1–3. Lowest concentrations were



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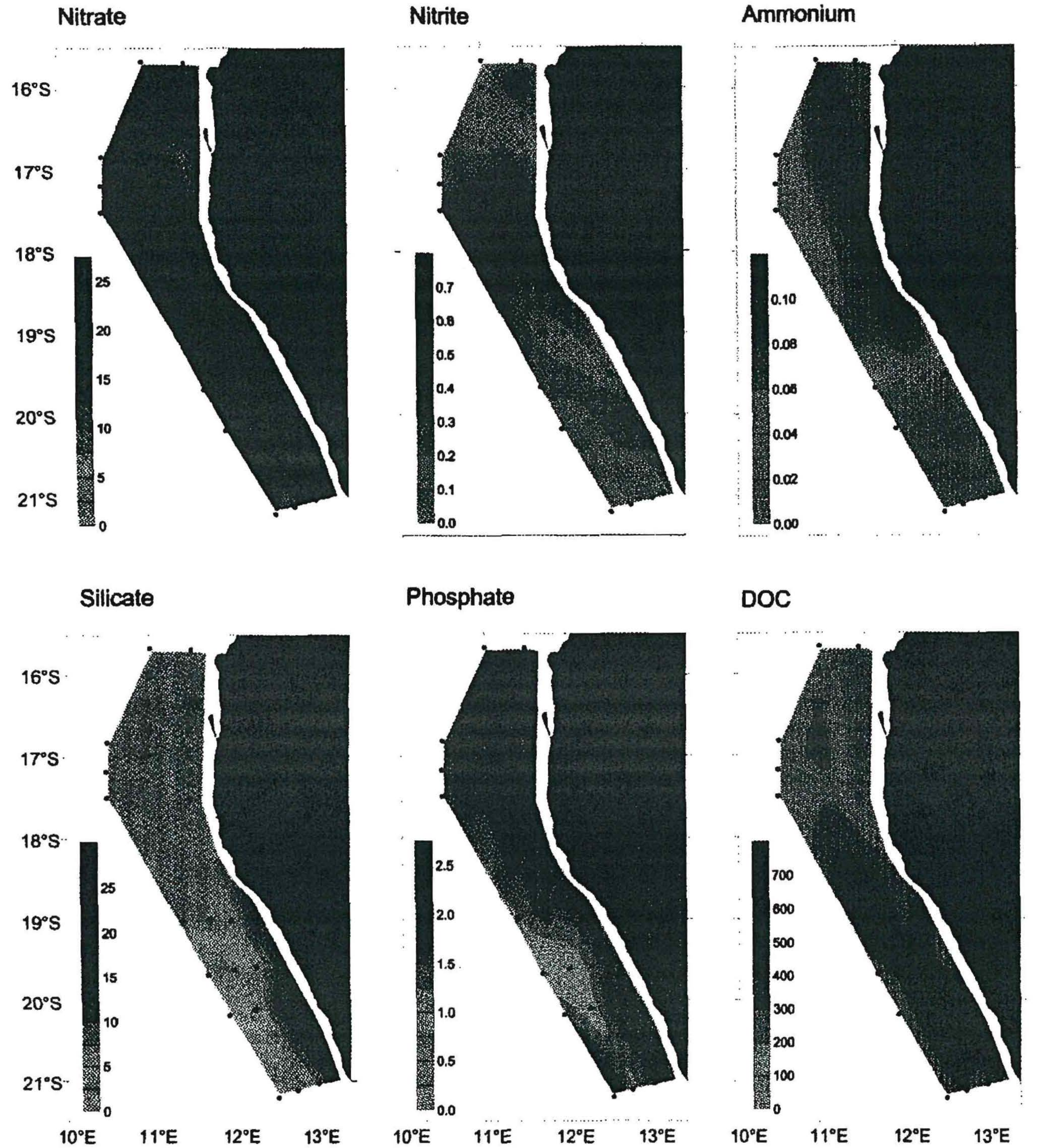
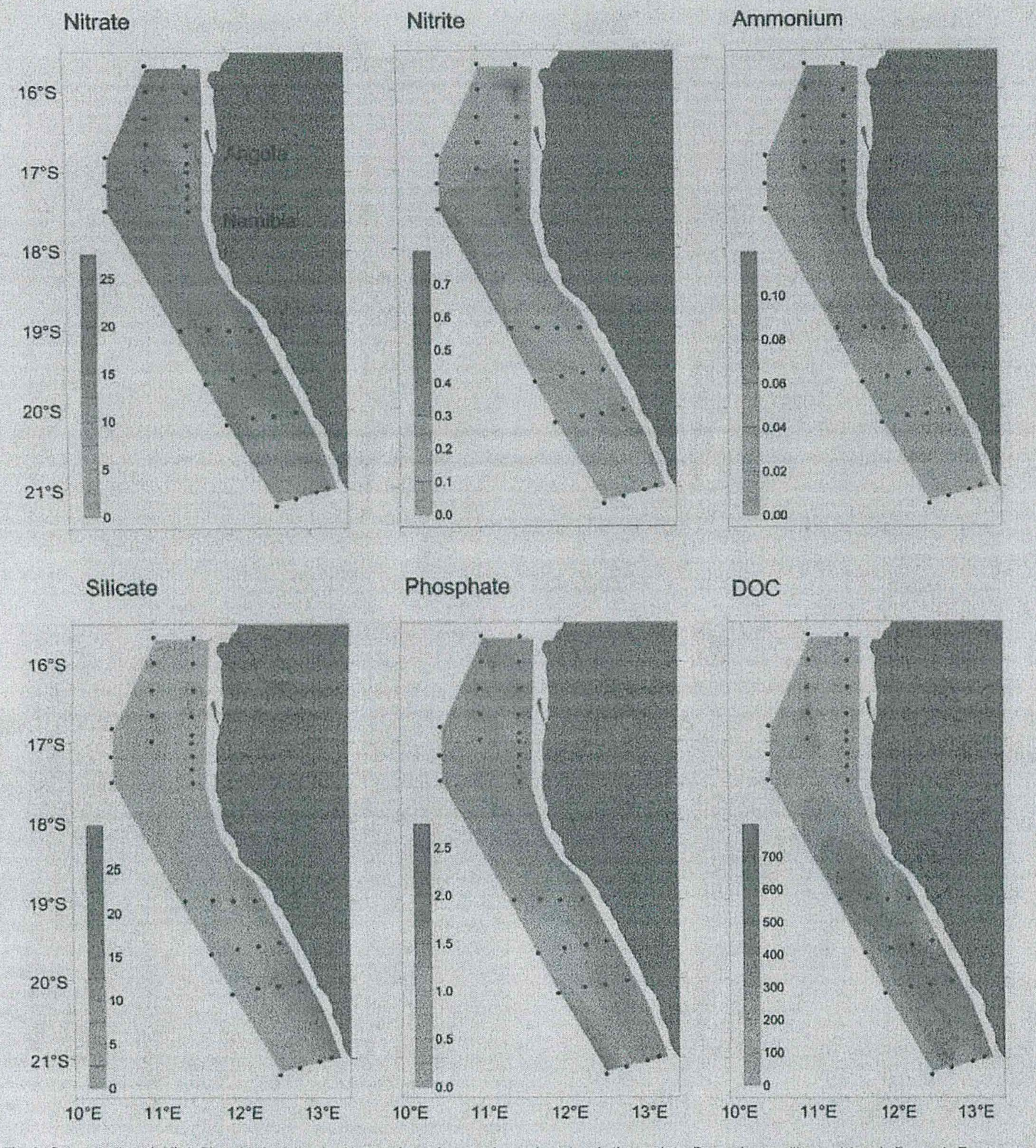


Fig. 2. Concentrations (µM) at 50 m depth of dissolved inorganic nutrients and organic carbon in the northern Benguela upwelling and Angola-Benguela Front areas.

usually measured north of 18°S. In the upwelling around 20°S, silicate and phosphate had highest surface concentrations, reaching values of 30 μM and 3.7 μM, respectively. Nitrate did not exhibit any response to the upwelling, ranging between 3.7 μM and 15 μM in Benguela surface waters. Off Angola, nitrate exhibited lower concentrations with minimum values close to the detection limit. Nitrite and ammonium did not contribute much to DIN, unlike nitrate, constituting 97% on average and at least 90%. Ammonium concentration was consistently near the detection limit.

Surface waters were highly depleted in nitrate and silicate. We used the ratio between surface and 100-m concentrations as a quantitative measure of surface depletion. In the Benguela area, the concentrations of both nutrients increased from the surface to a depth of 100 m by a factor of 3 on average. North of 18°S, they increased by a factor of ~6. Nitrate reached similar concentrations at 100 m in both areas, whereas silicate exhibited generally higher concentrations in Benguela waters than in waters off Angola. Despite the similar degree of surface depletion of silicate and nitrate on average, in the Benguela region the spatial patterns of their depletion were different. The ratio between the 100-m and surface nitrate concentrations gradually increased from ~2 near the coast to ~4 offshore, leading to a weak linear relationship between this ratio and distance from the coast



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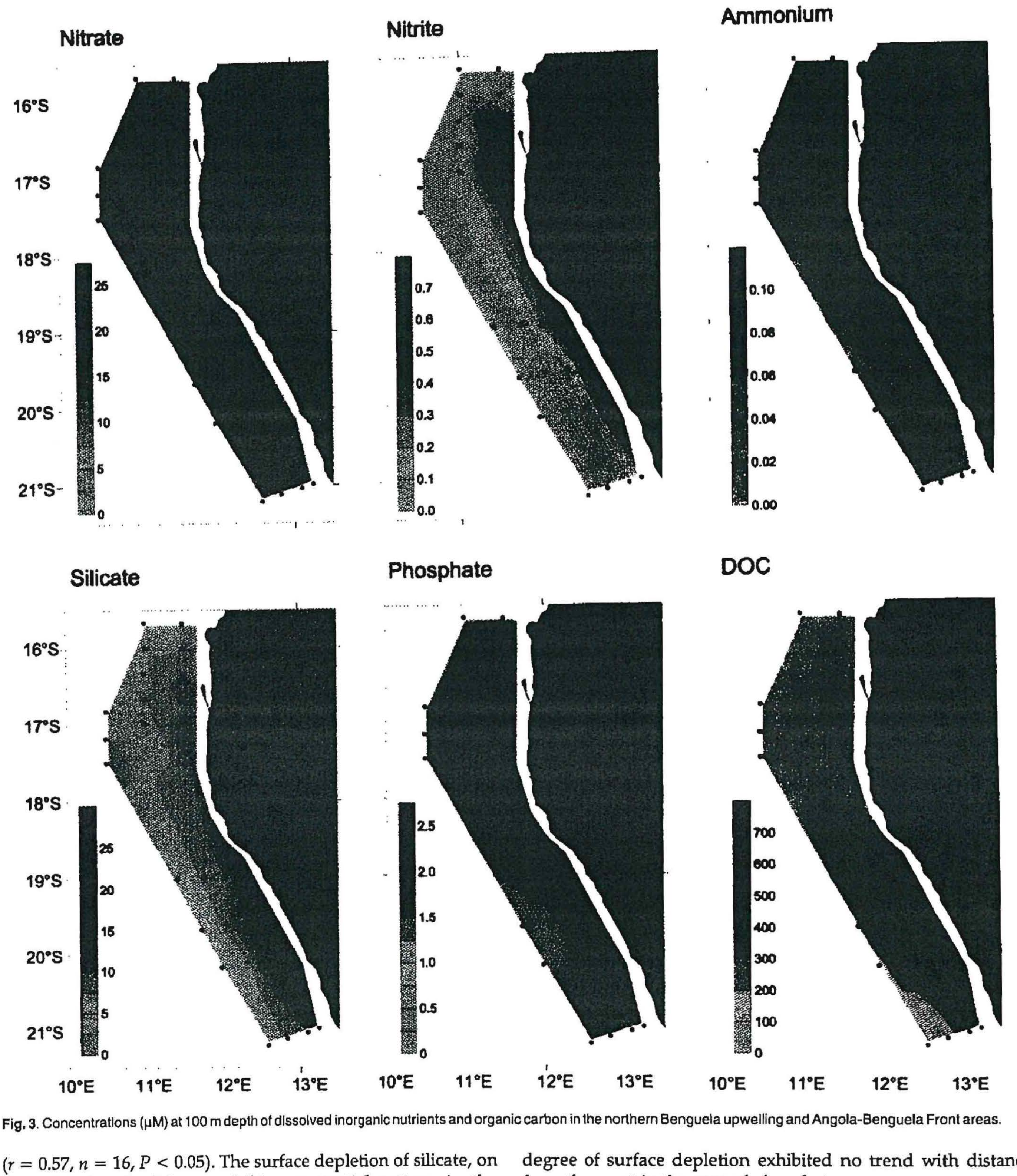
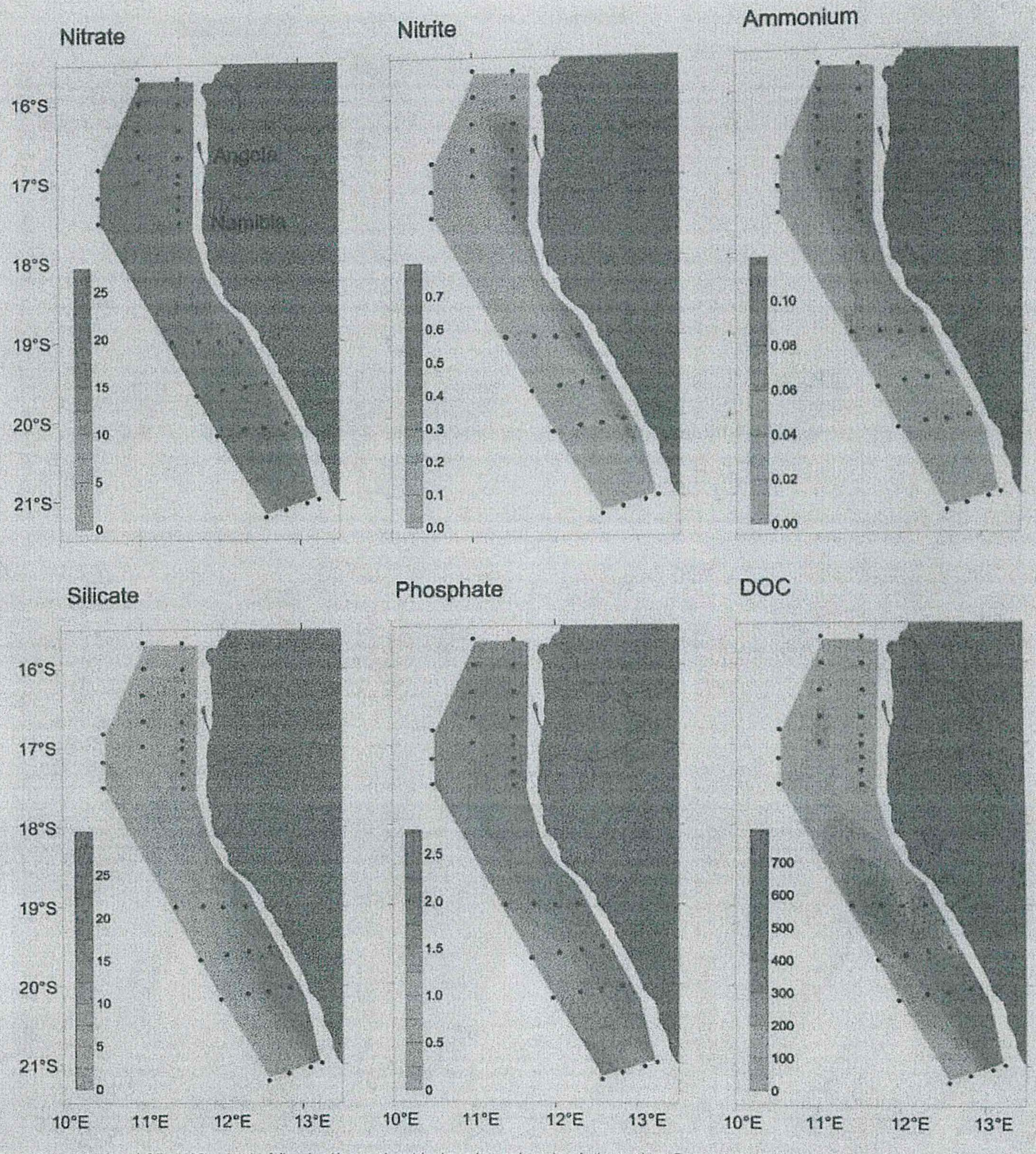


Fig. 3. Concentrations (μM) at 100 m depth of dissolved inorganic nutrients and organic carbon in the northern Benguela upwelling and Angola-Benguela Front areas.

($r = 0.57$, $n = 16$, $P < 0.05$). The surface depletion of silicate, on the other hand, did not exhibit any spatial pattern in the Benguela area. In contrast to nitrate, nitrite increased in Benguela surface waters, exhibiting at the surface about twice the 100-m concentration. Near the coast, the ratio between the surface and 100-m concentrations was ~1. With increasing distance from the coast it decreased to values close to 0. This ratio was linearly related to distance from the coast ($r = -0.64$, $n = 16$, $P < 0.01$). Off Angola, no trend with depth was observed for nitrite. Phosphate decreased at the surface less than DIN and silicate. The ratio of the surface and 100-m phosphate concentrations was ~1.5 in Benguela and ~2 in Angolan waters. The degree of surface depletion exhibited no trend with distance from the coast in the case of phosphate.

Although DOC exhibited a similar general pattern to inorganic nutrients in surface waters, with lower concentrations off Angola (<50–300 μM) and higher concentrations in the Benguela region (200–770 μM), the lowest concentrations in Benguela surface waters were measured in the upwelling around 20°S, in contrast to silicate and phosphate. The highest surface concentrations were found around the recent upwelling, mainly in the north and west. Some patches of elevated DOC surface concentrations with no distinctive pattern, were also observed at 70–80 km off Namibia and



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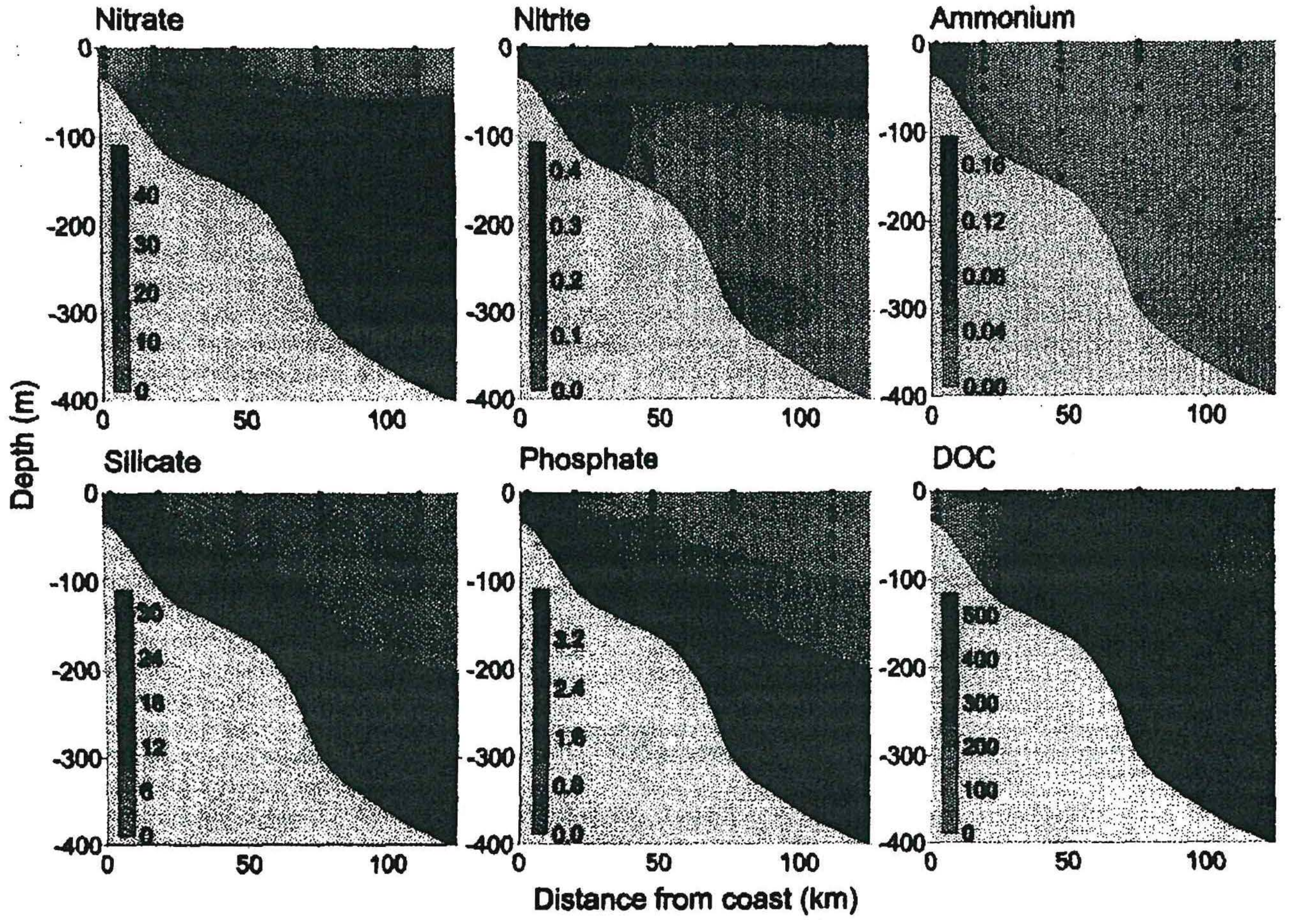


Fig. 4. Concentrations (μM) of dissolved inorganic nutrients and organic carbon in the northern Benguela upwelling area along a cross-shelf transect (~19.5°S).

Angola. DOC decreased slightly from the surface to a depth of 100 m by a factor of ~0.8 on average.

Nutrient concentrations in the water column were well-stratified (Figs 4, 5). Below the euphotic zone (30–50 m), nutrient concentrations generally increased sharply in the next 10 m. Concentrations continued to increase almost constantly to ~400 m or to the bottom. At the deeper stations, nitrate and phosphate reached maxima at ~400 m, whereas silicate increased down to the bottom. DOC in the Benguela area decreased approximately logarithmically down to 100 m and maintained an almost constant 150–350 μM at greater depth. North of 18°S, DOC continued decreasing with depth and reached values of about 50 μM at 400 m. At a distance of 70–80 km off Angola (around 11°E), where elevated surface concentrations were measured, concentrations decreased slightly with depth to minimum values of 180–210 μM (Fig. 5).

To evaluate possible regeneration processes in the northern Benguela upwelling system, we analysed nutrient and DOC concentrations at a depth of 100 m, for the source of upwelling being at this depth. Silicate concentration increased strongly from ~3.5 μM offshore (110 km) to ~29 μM near the coast; this trend followed a highly significant exponential function ($r = -0.97$, $n = 20$, $P < 0.001$) (Fig. 6). Phosphate increased only slightly from ~1.5 μM to ~2 μM, showing a weak linear relationship with distance from the coast ($r = -0.49$, $n = 19$, $P < 0.05$). Nitrate, on the other hand, did not exhibit any trend, ranging apparently randomly between 11 μM and 24 μM at a depth of 100 m, whereas nitrite and ammonium increased exponentially (nitrite: $r = -0.72, n = 20, P < 0.001$; ammonium: $r = -0.49, n = 20, P < 0.05$) from <0.1 μM offshore to concentrations of up to 0.5 μM (nitrite) and 0.16 μM (ammonium) onshore. The different

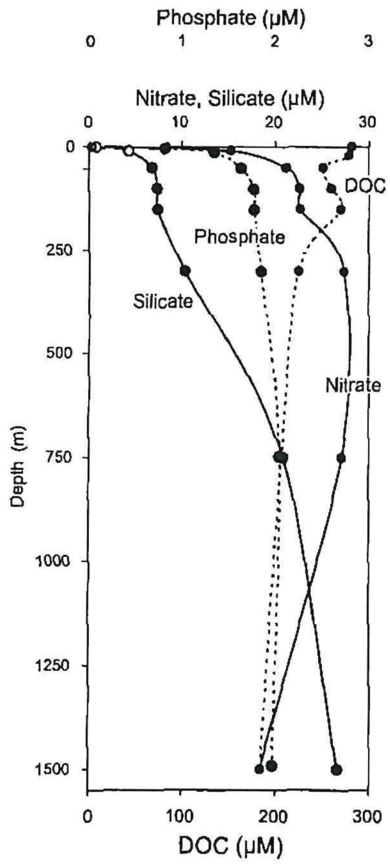
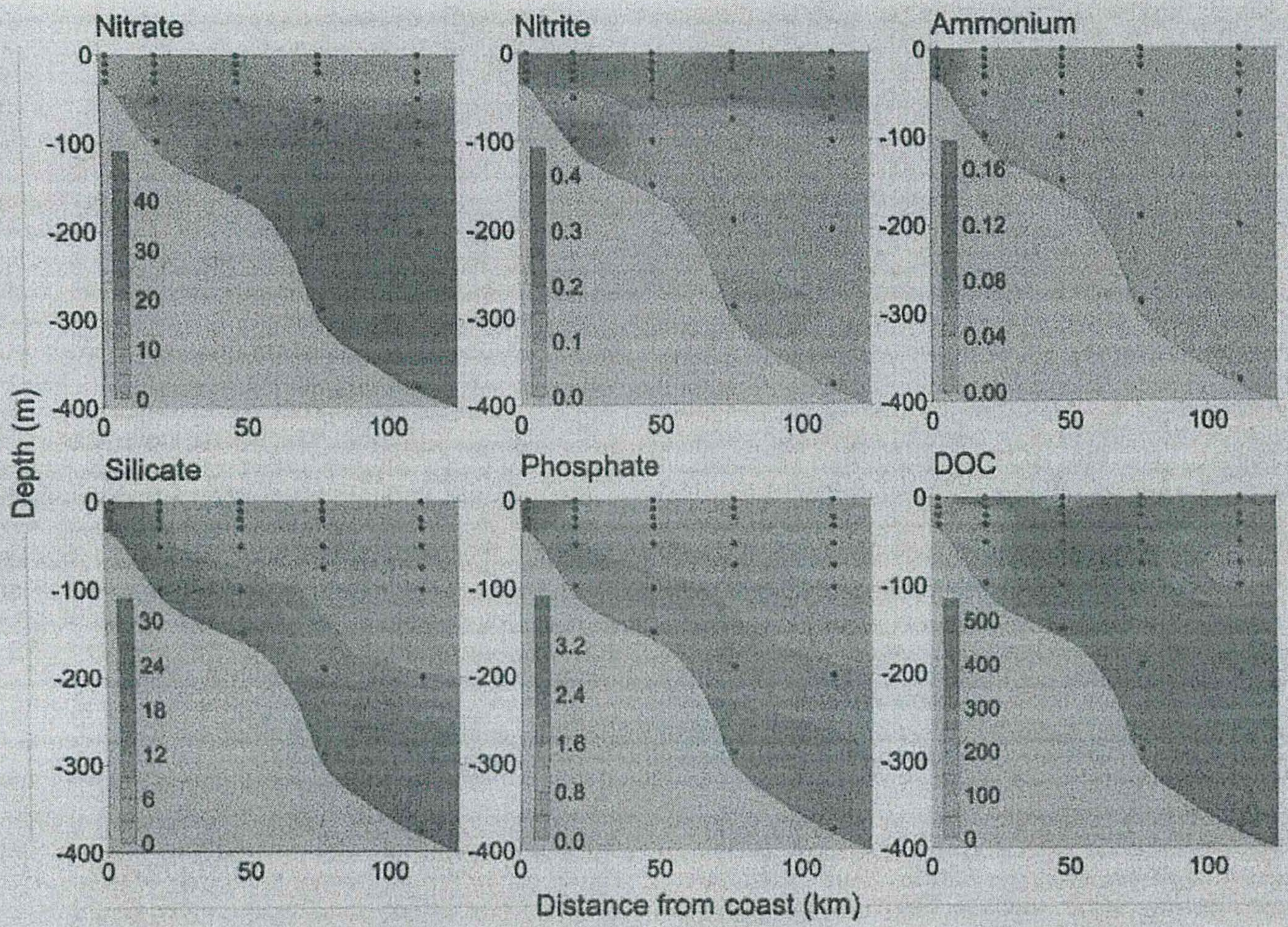


Fig. 5. Concentration profiles of dissolved inorganic nutrients and organic carbon in the Angola-Benguela Front area at 16.67°S, 11.01°E.



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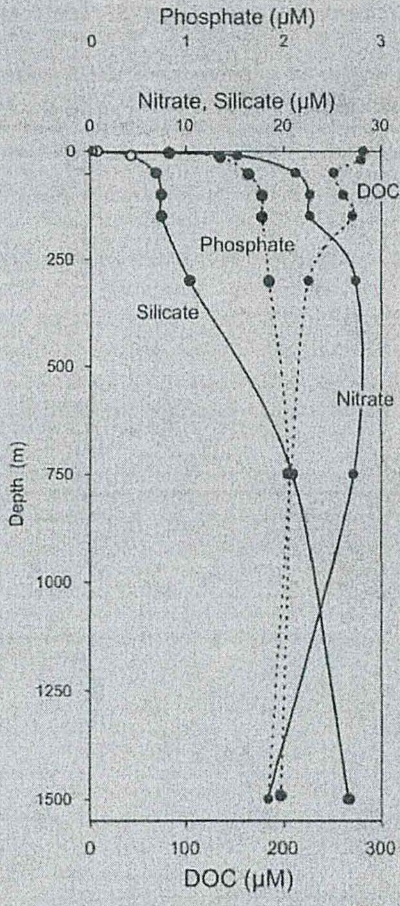

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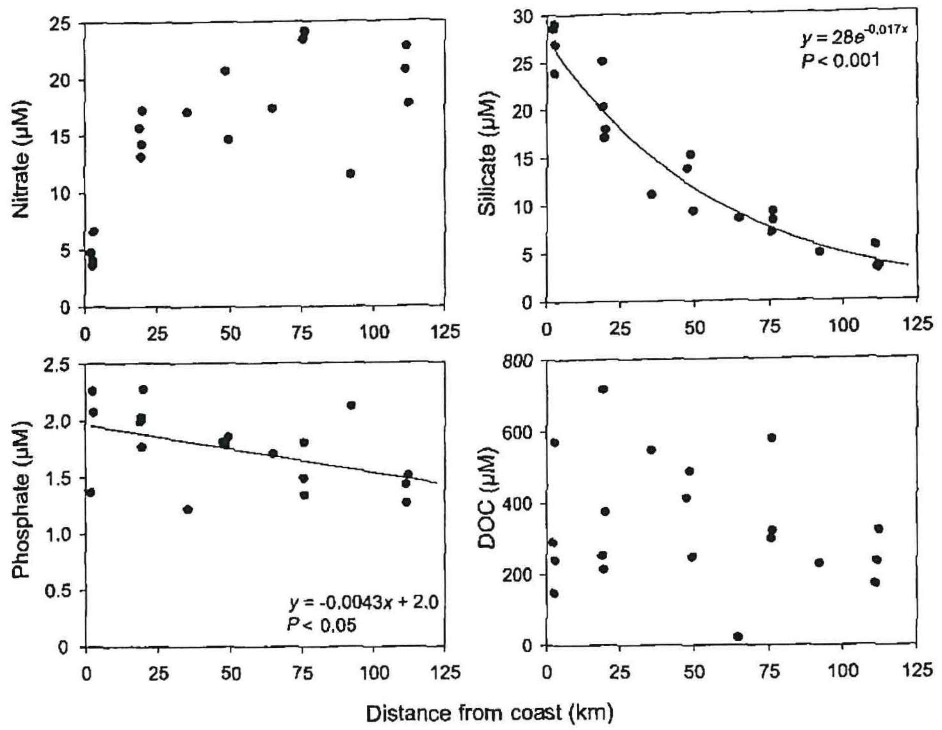

Fig. 6. Concentrations of dissolved inorganic nutrients and organic carbon at 100 m depth plotted versus distance from the coast in the northern Benguela upwelling area. For the stations closest to the coast, bottom concentrations (at ~30 m) are depicted.

behaviour of silicate, phosphate and nitrate caused pronounced changes of their molar ratios (Fig. 7). The N/Si ratio decreased linearly from off- to inshore ($r = 0.90$, $n = 20$, $P < 0.0001$) from values exceeding 4.5 to <0.2. The N/P ratio also decreased linearly ($r = 0.62$, $n = 20$, $P < 0.01$) from ~15 to ~6. DOC tended, in contrast to its surface concentrations, to higher values inshore. Around 20°S at the recent upwelling, this increase was most pronounced (from 170 μM offshore to 720 μM inshore). For the entire Benguela region on average, however, this trend was not statistically significant.

Discussion

The strong nitrate depletion in the area of recent upwelling around 20°S indicated an advanced phytoplankton bloom and the almost complete uptake of inorganic nitrogen. The comparatively slight surface depletion of phosphate suggested nitrogen rather than phosphate limitation of phytoplankton growth. Silicate was not taken up during that phytoplankton bloom. Its concentration was not depleted in the euphotic zone in the upwelling area. An abundant siliceous phytoplankton community, however, was evident from the highly reduced silicate concentration in the euphotic zone surrounding the upwelling. The nitrogen requirements of phytoplankton growth in these low-nitrogen aged upwelling waters were probably supplied by mineralization of organic nitrogen compounds, released during the bloom of non-siliceous phytoplankton in recently upwelled waters ('primary recycling'). Primary production in waters surrounding the upwelling is therefore most probably not 'new production', in the sense of primary production based on nutrient sources outside the euphotic zone. The nitrate concentration was higher in aged surface waters surrounding the upwelling than in recently upwelled waters, which was further evidence for nitrate being a product of organic matter mineralization in aged waters. Thus, low ammonium concentrations are not necessarily indicative for low 'regenerated production', as was assumed for the calculation of new production in Benguela waters[4,19]. The elevated nitrate concentrations in the zone of strong silicate uptake indicated that nitrogen regeneration there exceeded the demands of siliceous phytoplankton, and that silicate rather than nitrogen limited primary production, in contrast to recently upwelled waters. Phosphate, on the other hand, was less depleted in the euphotic zone than silicate and nitrate, suggesting that phosphate concentration was not the factor limiting phytoplankton growth. The N/P ratio in the photic layer, which was always <10 and thus nitrogen depleted relative to the biogeochemical composition of phytoplankton,[20–22] also indicated that phosphorus did not limit primary production, neither in recently nor in aged upwelled waters.

DOC, like nitrate, exhibited elevated surface concentrations in aged Benguela waters and was probably constituted of decay products of phytoplankton-derived organic matter. This coherent pattern of DOC and nitrate confirmed the suggestion that nitrate was a product of regeneration processes in the euphotic zone. The constant concentration of DOC with increasing depth at the outermost stations in the Benguela region and around 11°E off Angola suggests that some of the phytoplankton-derived DOC of at least 150 μM is not susceptible to fast mineralization. The production of non-labile organic

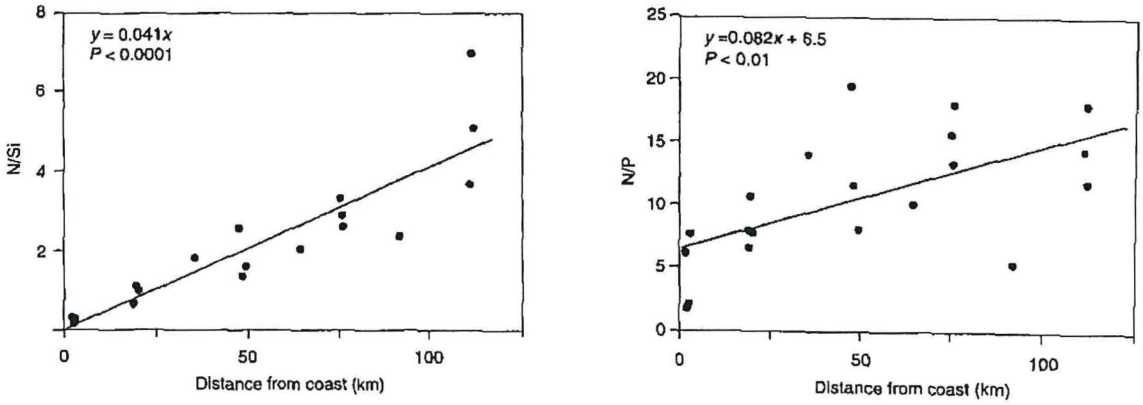

Fig. 7. Molar ratios of dissolved inorganic nutrients at 100 m depth plotted versus distance from the coast in the northern Benguela upwelling area. For the stations closest to the coast, bottom values (at ~30 m) are depicted.

compounds is a prerequisite for organic carbon export from the system. The elevated DOC concentrations off Angola coincided with near-surface currents of cold Benguela waters northwards to 15.7°S. Near the coast and offshore, warm Angolan waters, which were poor in DOC, flowed southwards. The elevated DOC concentrations at a depth of more than 1000 m around 11°E cannot be explained by advection of DOC-rich Benguela waters. It is more likely that microbial decay of sinking organic particles, originated from Benguela primary production, led to DOC release within the low-nutrient[21] and low-DOC[24] North Atlantic Deep Water at this depth. A considerable fraction of DOC released during bacterial production below the euphotic zone seems to be highly labile, since its concentration decreased strongly towards the surface during upwelling.

In the northern Benguela upwelling system, regeneration of nutrients was evident in source waters at 100 m depth. The oxygen depletion in the zone of upwelling and at depths > 100 m also is evidence for oxidative degradation processes. Microbial mineralization of sinking organic particles of decaying plankton from the euphotic zone, probably led to the increase of nutrient concentrations during the onshore flow of source waters ('secondary recycling'). Diffusion of mineralization products from bottom sediments also contributes to nutrient regeneration, as it was shown for upwelling in the northern[25] and southern[26] Benguela. The role of the latter mechanism for nutrient regeneration is supported by the strong silicate maxima measured close to the bottom (Fig. 4). In contrast to the upwelling system, no evidence was found for nutrient trapping in the front area off Angola.

In the Benguela Current, siliceous compounds exhibited the greatest mineralization. Silicate concentration at a depth of 100 m increased exponentially from offshore to inshore by a factor of ~10. Regenerated silicate was ~25 μM in upwelled water. Phosphate regeneration was only ~30% (~0.5 μM), and no evidence was found for the regeneration of inorganic nitrogen. Owing to these different rates, N/Si and N/P ratios decreased from offshore values, which were close to the worldwide average,[27,28] to considerably lower values inshore. Terrestrial input can be ruled out as the reason for the different regeneration rates, since there is no terrestrial runoff from the desert coastal region in Namibia. The predominant landward direction of the wind also precludes much aeolian input of minerals. Selective concentration of biogenic silica from decaying diatoms, different mineralization rates and incomplete mineralization of nitrogen and phosphorus are probable reasons for the different regeneration rates, as was found in other upwelling systems.[4,22] In view of the strong mineralization observed for silicon, however, it is very unlikely that nitrogen mineralization did not occur. The exponential increase of nitrite and ammonium concentrations at a depth of 100 m in the direction of the coast indicates mineralization of nitrogenous compounds. The estimated regeneration of nitrogen of 7 μM for the whole Benguela system[11] is probably compensated in the northern part by the antagonistic effect of a sink. Preferential retention and immobilization of nitrogenous compounds by bacteria during mineralization of phytoplankton-derived organic matter probably play a subordinate role. C/N ratios of bacteria and phytoplankton are very close,[29] and the release of carbonate species during oxidative degradation implicates nitrogen release.

Nitrogen losses through denitrification lead to N/P ratios as low as those determined in this study at several locations in the world oceans, in particular in upwelling systems.[28] The oxygen deficit in the northern Benguela favours the use of nitrate as an electron-acceptor and its conversion into N_2,[30] which would lead to an effective loss of nitrogen from the system and compensate nitrate release by mineralization. Denitrification has been identified as a major nitrogen sink in the upwelling systems of the equatorial Pacific[31,32] and in the Ubatuba upwelling area off southern Brazil.[33] Conversion of nitrate into gaseous products was disregarded in the past in the calculation of 'new production' in the Benguela system.[9,34] Productivity in the Benguela and its role as a carbon sink was overestimated in these calculations, since denitrification probably plays a considerable role in the nitrogen budget of the northern Benguela as indicated by the findings of the present study. Furthermore, the removal of nitrogen from the water column not only reduces potential new production in the northern Benguela, but also makes the upwelling system an effective nitrogen sink for the South Atlantic Ocean. Nitrogen is a limiting factor for primary production. Upwelling in the Benguela therefore acts as a regulatory mechanism affecting the South Atlantic Ocean's capacity to convert inorganic carbon into organic compounds and therefore affect the CO_2 budget on a global scale.

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Variability of chlorophyll profiles on the west coast of southern Africa in June/July 1999

B.A. Mitchell-Innes[a*], N.F. Silulwane[b] and M.I. Lucas[c,d]

The BENEFIT research training cruises on FRS *Africana* in June/July 1999 between Cape Columbine and Walvis Bay, and Walvis Bay and Cape Frio, provided an opportunity to examine vertical and horizontal variability of phytoplankton biomass in relation to the physical environment within four subprovinces of the Benguela upwelling system. Upwelling was evident inshore during the cruise and the upper mixed layer was generally deep. The shape of chlorophyll profiles generally changed from surface or near-surface peaks inshore to progressively weaker and deeper subsurface peaks offshore. Chlorophyll profiles were analysed in terms of a shifted-Gaussian curve, yielding four parameters describing the depth and height of the chlorophyll peak, the spread of the peak and the background chlorophyll concentration. Using a small set of data, this preliminary analysis provided chlorophyll profile shapes typical for shelf and slope waters of four Benguela subprovinces in winter, with the caveat that variability is high under upwelling conditions.

Studies of phytoplankton biomass and productivity are central to understanding the global biological carbon cycle. Phytoplankton, although forming only 1–2% of the total global biomass of primary producers, contributes 30–60% of the global fixation of carbon annually.[1] One of the objectives of the BENEFIT research training cruises[2] on FRS *Africana* in June/July 1999 was to examine spatial variation in phytoplankton biomass and productivity in the Benguela upwelling system between Cape Columbine and Cape Frio, a region little researched in winter. We examined phytoplankton distribution, both horizontal and vertical, in relation to the physical environment. One of our aims was to establish the shape of chlorophyll profiles typical for the Benguela. Profile shape is one of several parameters needed for the computation of water column productivity from remotely-sensed ocean colour towards regional and global estimates of productivity.[3–6]

Water column variability of phytoplankton is controlled by physical forcing, which ranges widely from microturbulence to large-scale oceanic circulation patterns.[7,8] These forcing functions control seasonal and other episodic cycles of stability and instability, thereby affecting exposure of phytoplankton to the underwater light field and supply of inorganic nutrients.[3,9] Based on regional differences in ocean physics, the oceans have been divided into four primary ecological domains and further subdivided into some 56 secondary ecological provinces.[3,4] The west coast of southern Africa, characterized by episodic wind-driven coastal upwelling,[10,11] forms the Benguela Current coastal province.[3,4] This includes the region between 14°S and 37°S,[11] encompassing seven upwelling cells as well as offshore filaments and eddy fields.[10,11] The Benguela has well-defined boundaries: the Angola-Benguela Frontal Zone (typically 14–17°S) in the north and the Agulhas Retroflection (typically 36–37°S) in the south.[11] The western boundary with the South Atlantic Tropical Gyre is formed by an often convoluted system of longshore thermal fronts which delimit the offshore extent of coastal upwelled water.[10,11] In winter these fronts may be diffuse, particularly in the southern Benguela.

The underlying premise of partitioning the oceans into provinces and subprovinces is that similar oceanographic processes prevail within each region, which result in similar biological processes and cycles. Since chlorophyll profiles are closely related to the structure of the water column, each hydrologically defined province will ideally have a typical chlorophyll profile or spectrum of profiles. Within this context, we examined the shape of these profiles in four regions covered by the BENEFIT cruise on the west coast of southern Africa in relation to winter hydrological conditions. Ultimately, we envisaged subdividing

[a]Marine and Coastal Management, Private Bag X2, Rogge Bay, 8012 South Africa.
[b]Marine Remote Sensing Unit, Oceanography Department, University of Cape Town, Rondebosch, 7701 South Africa.
[c]Zoology Department, University of Cape Town, Rondebosch, 7701 South Africa.
[d]George Deacon Division, Southampton Centre, Empress Dock, Southampton SO14 3ZH, U.K.
*Author for correspondence. E-mail: bminnes@mcm.wcape.gov.za