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Nitrogen utilization by phytoplankton in the Namibian upwelling region during an austral spring

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Abstract—The uptake of NO_3^-, NH_4^+ and urea by phytoplankton populations was investigated off the Namibian coastline between 20° and 26°30′S during the spring, 1985. The region was characterized by intense upwelling with resultant penetration of high nutrient concentrations into adjacent oceanic waters. In spite of the high ambient NO_3^- concentrations, nitrogen was taken up primarily as NH_4^+ and urea in accordance with phytoplankton preference. Measured *f*-ratios (NO_3^- uptake/total nitrogen uptake) were correspondingly lower than expected, with a mean value of 0.32. Ratios calculated from integrated data for the photic zone (*f*′-ratio) proved to be positively correlated with phytoplankton biomass (Chl *a*) and production.

Factors such as NO_3^- concentration, light, temperature and recycled nutrient concentration were considered as potential influences on the *f*-ratio. No obvious relationship was evident between *f*-ratios and either NO_3^- concentrations or concentration ratios. Temperature (mean upper mixed layer) was well correlated with nutrient uptake but not with the *f*-ratio. Temperature coefficients (Q_{10}) were considerably larger than expected, suggesting control of nutrient uptake by factors other than temperature. Light limitation, though probably influencing individual depth profiles of *f*-ratios, could not explain inter-station variability in *f*′-ratios. The *f*-ratio, however, was negatively affected by increasing concentrations of recycled nutrients both for discrete depths and for depth-integrated values.

It is proposed that the high nutrient and low chlorophyll conditions that prevailed over much of the region were the result of an inhibition of phytoplankton bloom development by zooplankton grazing and deep mixing. The nitrogen excretory products of zooplankton (NH_4^+ and urea) in turn were preferentially utilized by phytoplankton with the resultant suppression of NO_3^- uptake, explaining the low measured *f*-ratios.

INTRODUCTION

THE Benguela upwelling system off the west coast of Africa is one of the four major eastern boundary current systems in the world ocean (BARBER and SMITH, 1981). The northern limit of the Benguela system is defined by a zone of strong convergence that is subject to seasonal shifts within 15° and 18°S. To the south the Benguela system can extend as far as Cape Agulhas (35°S) during the summer upwelling period (SHANNON, 1985). The northern region has been the subject of a number of recent reviews including aspects of its physical oceanography (NELSON and HUTCHINGS, 1983; SHANNON, 1985), chemical oceanography (CHAPMAN and SHANNON, 1985) and biological oceanography (SHANNON and PILLAR, 1986). The broader Benguela region is characterized by a number of important upwelling centres of which the Luderitz zone centred around 26°S is the most conspicuous. Although a seasonal signal is evident in upwelling intensity

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throughout the region (BOYD and AGENBAG, 1985), upwelling off the Namibian coastline is the most persistent, with a slight maximum in spring and minimum in autumn (STANDER, 1964). The region to the north of the Luderitz upwelling cell supports an important pelagic fishery (SHELTON *et al.*, 1985).

In spite of the obvious inherent interest in an oceanographic region such as the Namibian upwelling system, there exists to date only a few studies on primary production and its regulation in this region (SHANNON and PILLAR, 1986; ESTRADA and MARRASE, 1987). Upwelling water here and further south is considerably enriched during its passage over the biogenically rich shelf sediments, resulting in larger nutrient concentrations in upwelled water relative to source water (CALVERT and PRICE, 1971; BAILEY, 1985). Although nitrogen is the nutrient most often implicated in the limitation of primary production, no direct measurements of its utilization by phytoplankton in this region have been made.

The present study was undertaken to quantify the importance of upwelled nitrogenous nutrients (NO_3^-) to primary producers during the spring maximum in upwelling. Environmental correlations with the fraction of total nitrogen taken up as NO_3^- (*f*-ratio) have been emphasized in light of the biogeochemical implications of this ratio. Conceptually the *f*-ratio is an important measure in that it can provide insight to the partitioning of primary production between major oceanic sinks. Under steady-state conditions it indicates the proportion of primary production that can be exported from the euphotic zone (mainly through sinking of particles) without depleting the system (DUGDALE and GOERING, 1967). This proportion of primary production, termed new production, depends principally on upwelling and the turbulent diffusion of nutrients from deeper waters to replenish losses from the euphotic zone. Different productivity regimes therefore can be distinguished on this basis, ranging from oligotrophic systems with a low *f*-ratio (<0.1) to upwelling systems with their typically higher *f*-ratios of about 0.5 and larger (EPPLEY and PETERSON, 1979; EPPLEY, 1981). Recent studies, however, indicate typical *f*-ratios for open ocean systems might be larger than previously thought, necessitating a scaling up of estimates for new production in these regions (PLATT and HARRISON, 1985). Similarly, measured *f*-ratios for eastern boundary current systems, at times such as during upwelling events, may be significantly smaller than expected (MINAS *et al.*, 1986).

METHODS

Sampling

Experimental measurements of ^{15}N uptake were carried out on board the R.V. *Africana* between 16 September and 6 October 1985 during the Spanish/Namibian Environmental Cruise—85 (SNEC—85). This was the first of two collaborative ventures between the Institut de Ciencies del Mar, Barcelona, and the Sea Fisheries Research Institute, Cape Town. Most of the stations occupied during SNEC—85 for ^{15}N experiments were located over the continental shelf and slope (Fig. 1).

Water samples were collected using a rosette of 5-1 Niskin bottles at varying depths between the surface and the bottom for Chl *a* and nutrient analyses. Experiments with ^{15}N were generally started around midday using water from the surface, 25%, 10% and 1% light penetration depths. At most stations sampling depths were determined by means of a Lambda LI–192S underwater quantum light sensor, although a Secchi disc

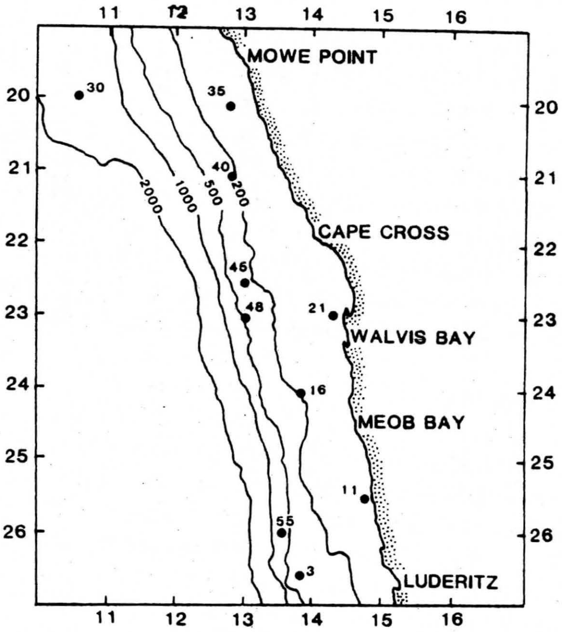

Fig. 1. Station locations in continental shelf and slope waters off the Namibian coastline.

was used on occasion. Water samples were not screened prior to incubations in simulated *in situ* deck boxes cooled with flowing surface seawater. A calibration exercise carried out after the cruise revealed that incubators originally designed for transmittances of 25, 10 and 1% were actually 16, 5 and 3%, respectively. However, aerial integrations were carried out using the depth of sampling, not the depth corresponding to the actual light level during incubation. Using the latter approach had very little effect on the present results. Temperature and salinity data were obtained from the ship's CTD system (Neil Brown Mark III).

Analytical

Nitrate concentrations (corrected for NO_2^-) were analysed on board ship by a Technicon AutoAnalyser (Mostert, 1983). Urea and NH_4^+ concentrations were determined in triplicate according to the manual methods described in Grasshoff *et al.* (1983), scaled down to 5 ml. Ammonium determinations were made immediately on sampling while urea samples were stored frozen and analysed after the cruise. Standards treated in the same manner as urea samples showed no significant alteration of urea concentration during storage. Chlorophyll *a* was measured fluorimetrically on clarified extracts of particulate matter concentrated onto Whatman GF/C filters (Yentsch and Menzel, 1963; Strickland and Parsons, 1972). Particulate nitrogen was measured with a Heraeus CHN analyser after collection on a Whatman GF/F filter and desiccation at 60°C for 24 h.

Nitrogen flux experiments

Urea and NO_3^- uptake rates were determined according to Dugdale and Goering (1967). ^{15}N was added as either $Na^{15}NO_3$ (99.6 at. %) or $CO(^{15}NH_2)_2$ (99.1 at. %) to 1-

litre samples. Urea was added at a constant concentration of 0.04 μg-at. N l^{-1} to all samples, resulting in an enrichment of ambient concentration seldom exceeding 40%. In the case of NO_3^- uptake experiments, prior knowledge of ambient concentration was available; thus the amount of ^{15}N added could be adjusted to keep enrichments at desirable levels (*ca.* 10%). Incubations were run for 4–6 h in borosilocate glass bottles and were terminated by filtration onto Whatman GF/F filters. The filters were rinsed with filtered seawater and stored frozen. ^{15}N content was determined using a Jasco N-150 ^{15}N Analyser after Kjeldahl/Rittenberg oxidation (Fiedler and Proksch, 1975). All enrichments were corrected for contamination from chemicals used in the analyses as determined from ^{15}N dilution of standards carried through the digestion and distillation procedures.

Ammonium uptake rates at Stas 45, 48 and 55 were measured in a similar manner to NO_3^- and urea after addition of 0.05 μg-at. $N^{15}NH_4Cl$ (99.7 at. %) to 1-litre. At the remaining stations correction was made for isotope dilution allowing simultaneous calculation of uptake and regeneration rates (Harrison, 1978). Uptake rates were calculated according to Glibert *et al.* (1982c) and regeneration rates following the Blackburn—Caperon model (Blackburn, 1979; Caperon *et al.*, 1979). Exactly 2-l were spiked with 0.1 μg-at. $^{15}NH_4$-N, 1-litre being filtered immediately and the other placed in the appropriate incubator. A portion of the filtrate was used in NH_4^+ determinations, and 900 ml was spiked with 10 μg-at. N of carrier NH_4Cl. These samples were stored frozen for later recovery of aqueous NH_4^+ by diffusion (Probyn, 1987). All NH_4^+ uptake incubations lasted 4–6 h and were terminated by filtration. Filters were treated for subsequent ^{15}N measurements and, after removal of an aliquot for NH_4^+ concentration measurement, 900 ml of the filtrate was spiked and frozen as at the start. As before, ^{15}N enrichments of both aqueous and particulate (after Kjeldahl digestion) samples were determined according to the Rittenberg oxidation procedure.

RESULTS

Hydrographic features

The hydrographic features during SNEC—85 were indicative of intense upwelling (Fig. 2). Sections at 26°, 23° and 20°S indicate more vigorous upwelling to the south in the vicinity of Luderitz and yet higher NO_3^- concentrations in the upper 50 m farther north. Nitrate concentrations appreciably larger than typical for upwelling source water (South Atlantic Central Water) were present at the shelf and upper slope sediment–water interface (see Bailey, 1985).

Nitrogen uptake

A summary of the specific uptake rates (h^{-1}) for NO_3^-, NH_4^+ and urea at the different light levels is given in Table 1. It is apparent that specific rates for the reduced nitrogen sources were not affected by sample depth. In contrast, NO_3^- uptake rates were reduced below the 10% light level. Total nitrogenous nutrient uptake rates were calculated by assuming dark/light uptake ratios of 0.5 for NH_4^+, 0.3 for urea and 0.1 for NO_3^- (Harvey and Caperon, 1976; Price *et al.*, 1985) and a 12/12 h light/dark cycle. Growth rates, in daily doublings of particulate nitrogen, calculated from these data indicate a consistency within the euphotic zone, with an average of 0.22 doublings day^{-1}.

Depth profiles of absolute rates of nitrogen uptake and Chl *a* concentrations together with nutrient concentrations and thermal structure at two of the stations sampled are

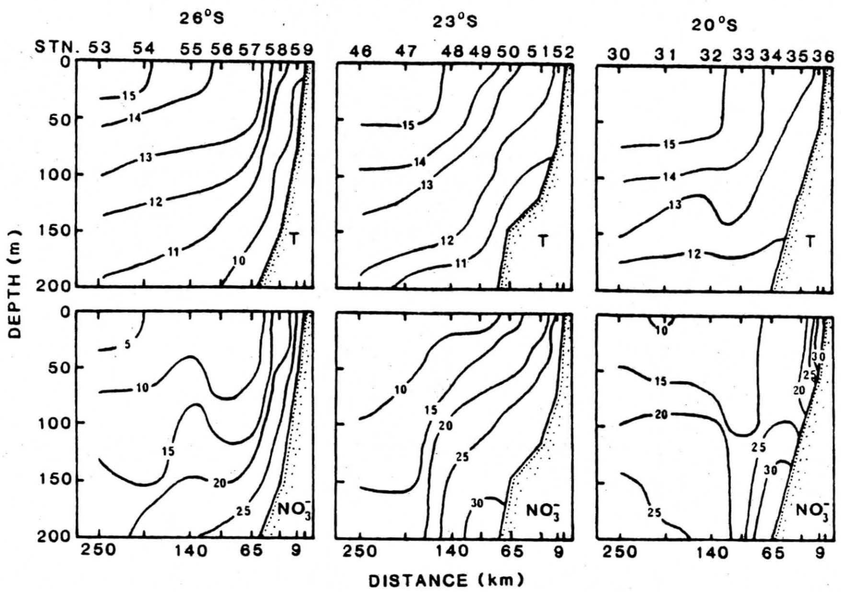

Fig. 2. Section of temperature (°C) and NO_3^- (mg-at. N m^{-3}) to a depth of 200 m for transects at 26°, 23° and 20°S extending 250 km offshore.

Table 1. *Mean specific nitrogen uptake rates* (±95% *confidence limit*) *normalized to particulate nitrogen* (h^{-1}) *at the four light penetration depths. Doublings of particulate nitrogen* (day^{-1}) *were calculated from the combined uptake rates for all three nutrients*

Light depth (%)	Specific uptake rates (h^{-1})			Total N uptake (day^{-1})	Doublings (day^{-1})
	NH_4^+	Urea	NO_3^-		
100	0.0043 (±0.0014)	0.0019 (±0.0007)	0.0041 (±0.0015)	0.1625	0.23
25	0.0042 (±0.0015)	0.0020 (±0.0009)	0.0043 (±0.0018)	0.1649	0.24
10	0.0047 (±0.0008)	0.0020 (±0.0009)	0.0027 (±0.0009)	0.1525	0.22
1	0.0045 (±0.0017)	0.0019 (±0.0009)	0.0018 (±0.0009)	0.1352	0.22

shown in Fig. 3. Interestingly, NO_3^- uptake was negatively correlated with ambient NO_3^- concentrations ($r = 0.39$, $P < 0.05$), whereas there was no significant relationship between uptake and concentration for NH_4^+ and for urea.

Phytoplankton preferences for the uptake of individual nitrogen sources were quantified as a relative preference index as formulated by McCarthy *et al.* (1977). The relative preference index (RPI) provides an expression of the uptake rates of a particular nitrogen source relative to its concentration in the total nitrogenous nutrient pool. RPI values of unity indicate utilization rates in accordance with relative availability. A RPI > 1 indicates preference and a RPI < 1 reflects rejection of a particular nitrogenous nutrient (McCarthy *et al.*, 1977). In all cases RPI values for NH_4^+ were >1, indicating NH_4^+ was without exception the preferred nitrogen source, whereas RPI values for NO_3^- were <1 (Fig. 4). Urea was generally a preferred substrate during this study, but at the low end of the total nitrogen concentration range it occasionally was rejected. The results fit the generally recognized hierarchy of preferential uptake where NH_4^+ > urea > NO_3^-.

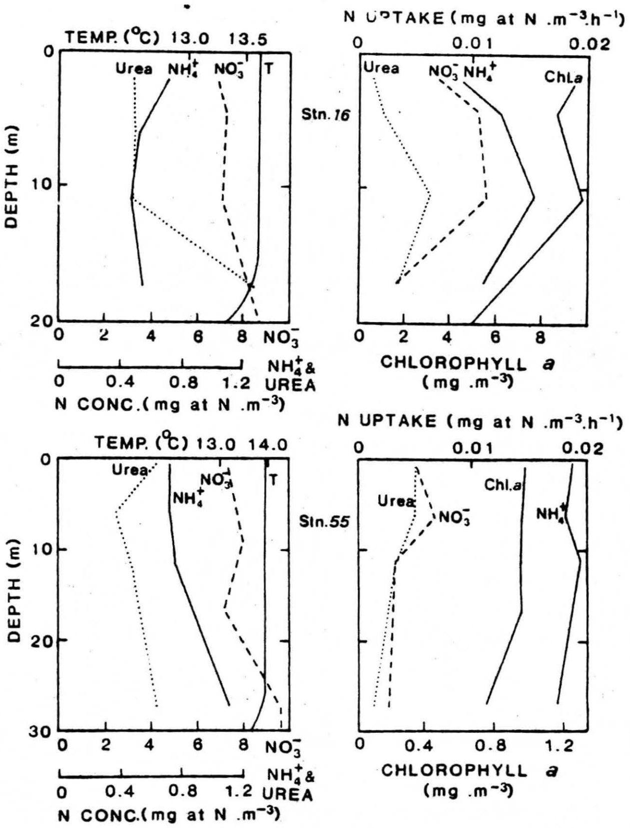

Fig. 3. Vertical distribution of nutrient concentrations, nitrogen uptake rates and Chl *a* concentrations as related to thermal structure at Stas 16 and 55.

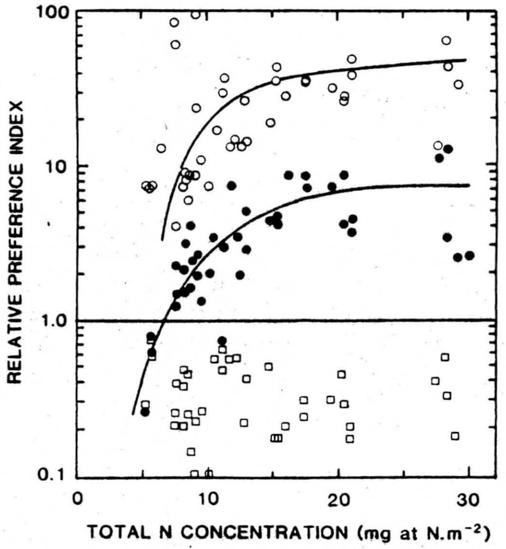

Fig. 4. Relative preference indices for NO$_3^-$ (□), NH$_4^+$ (○) and urea (●) uptake as a function of their combined concentrations. Curves were fitted visually.

Table 2. *Nitrogen productivities, concentration ratios* (NO_3^-/total N) *and* f'*-ratios and Chl* a *integrated over the euphotic zone. The depth of the upper mixed layer* (Z_m) *and* 1% *light penetration depth* (Z_e) *are included*

			N uptake rates (mg at. N m^{-2} h^{-1})					
Sta.	Z_m (m)	Z_e (m)	NH_4^+	NO_3^-	Urea	NO_3^-/ total N	f'-ratio	Chl *a* (mg m^{-2})
3	18	42	0.1572	0.0553	0.1651	0.74	0.15	41.88
11	29	19	0.1145	0.0523	0.0274	0.94	0.27	28.71
16	30	17	0.1605	0.1334	0.0587	0.82	0.37	96.70
21	40	17	0.0809	0.0496	0.0285	0.96	0.31	31.65
30	45	18	0.2705	0.3271	0.1676	0.91	0.43	37.88
35	21	32	0.2425	0.1389	0.2033	0.95	0.24	25.67
40	31	11	0.4341	0.3279	0.0649	0.81	0.40	90.53
45	50	28	0.2302	0.1479	0.0633	0.92	0.34	55.91
48	45	22	0.1858	0.3029	0.0579	0.94	0.55	105.90
55	29	29	0.4965	0.1000	0.0996	0.86	0.14	23.43

A plot of integrated uptake rates (Table 2) against mean temperatures for the upper mixed layer (Fig. 5) illustrates the non-linear increase in the uptake of NO_3^- ($r = 0.87$, $P < 0.005$), NH_4^+ + urea ($r = 0.71$, $P < 0.05$) and the total of all three nutrients ($r = 0.85$, $P < 0.005$) with temperature. Data from Sta. 3, which was characterized by a euphotic zone depth (Z_e) considerably deeper than the upper mixed layer depth (Z_m), were excluded from this analysis. A temperature coefficient (Q_{10}) calculated over the range of mean temperature for the upper mixed layer encountered in this study (10.7–15.3°C) varied between 52.5 for NO_3^- uptake, 11.4 for recycled nitrogen uptake and 19.3 for total nitrogen uptake. It is evident that recycled nitrogen uptake rates were faster than NO_3^- uptake rates at a given temperature.

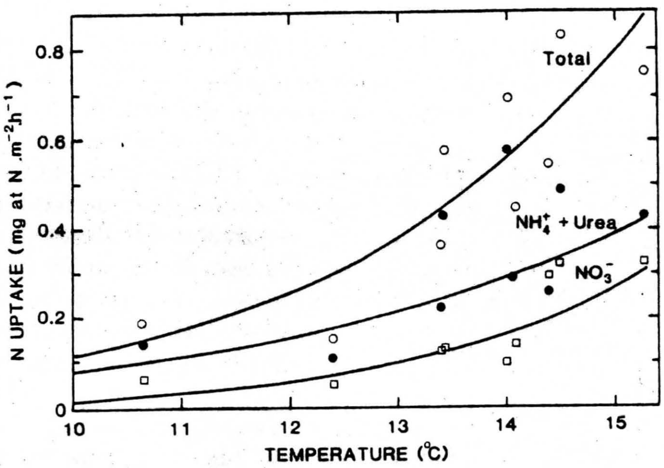

Fig. 5. The relationship between mean upper mixed layer temperature (T) and integrated uptake rates for NO_3^- (□), for NH_4^+ plus urea (●) and for the total of all three nutrients (○) as described by NO_3^- uptake $= 0.00026\ e^{0.463T}$, NH_4^+ + urea uptake $= 0.004\ e^{0.306T}$, and total N uptake $= 0.003\ e^{0.373T}$, respectively.

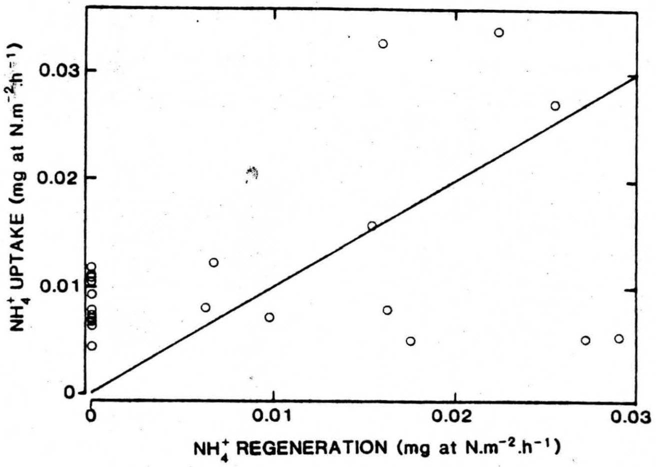

Fig. 6. A plot of NH_4^+ uptake rates against NH_4^+ regeneration rates. Line indicates a 1 : 1 relationship.

Ammonium regeneration by the plankton

In contrast to a number of other studies (HARRISON, 1978; GLIBERT, 1982; HARRISON *et al.*, 1983; COCHLAN, 1986; PROBYN, 1987) NH_4^+ uptake and regeneration rates were not well correlated (Fig. 6). With the exception of two stations (Stas 21 and 30), NH_4^+ uptake from discrete depths always exceeded regeneration, indicating a shortfall in supply during incubation. These comparatively slow rates of *in situ* NH_4^+ regeneration taken together with the relatively short incubation times (4–6 h) would minimize the potential error associated with isotope dilution at those stations where it was not measured directly (Stas 45, 48 and 55). On average NH_4^+ uptake would have been underestimated by 11% if isotope dilution were not accounted for. The potential error, however, was occasionally quite appreciable (66%).

The f*-ratio*

The quantitative importance of new nitrogen to primary production is given by the *f*-ratio, the ratio of NO_3^- uptake to the combined uptake of NO_3^-, NH_4^+ and urea (EPPLEY and PETERSON, 1979). The variation in *f*-ratio with depth (Fig. 7) indicates a general trend towards maxima in near-surface waters (25% light penetration) and minima towards the base of the euphotic zone. Primary production showed a similar trend, also reaching a maximum at the 25–50% light levels (M. ESTRADA, unpublished results). The *f*-ratio also can be shown to vary with the concentration of reduced nitrogen ([NH_4^+ + urea]), both for the discrete depths and for integrated values for the euphotic zone (Fig. 8). Also shown in Fig. 8 are *f*-ratios integrated over the euphotic zone (f') as a function of integrated NH_4^+ plus urea concentrations ([NH_4^+ + urea]'). Excluding Sta. 3, where the euphotic zone depth (Z_e) was considerably deeper than the mixed layer depth (Z_m), from the regression analysis, resulted in a significant negative linear correlation between the f'-ratio and [NH_4^+ + urea]' ($r = -0.68$, $P < 0.05$). A summary of nitrogen uptake rates and, *f*-ratios and concentration ratios integrated for the euphotic zone is shown in Table 2.

The larger f'-ratios were characteristic of those stations with a high algal biomass. In

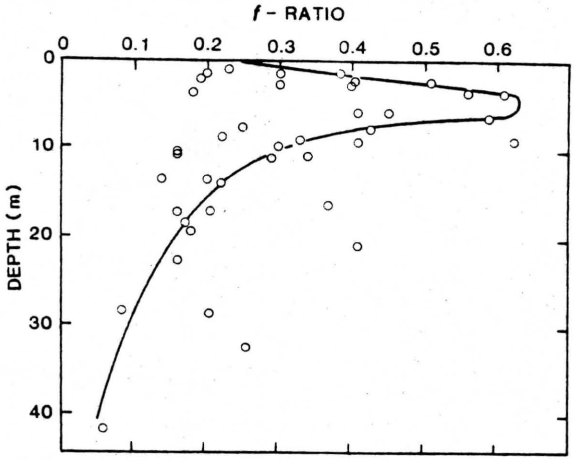

Fig. 7. Vertical distribution of f-ratios. Line represents a visual smoothing of the data.

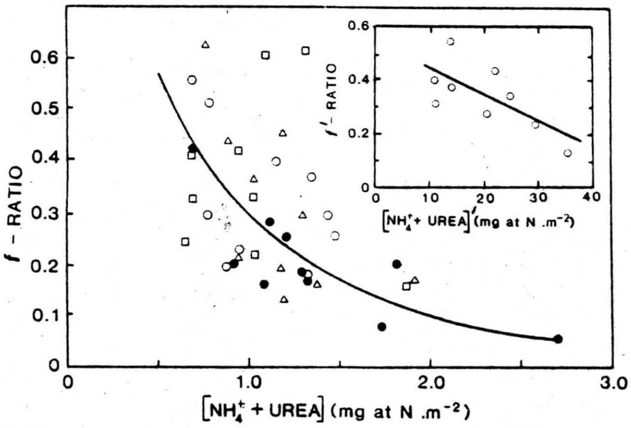

Fig. 8. The effect of recycled nutrient concentrations ([NH_4^+ + urea]) on f-ratios measured at the 100% (○), 25% (□), 10% (△) and 1% (●) light penetration depths. These data can be described by $f = 0.996\,e^{-1.046[NH_4^+ + \text{urea}]}$. Inset shows this relationship integrated over the euphotic zone with Sta. 3 excluded: $f' = 0.534 - 0.004\,[NH_4^+ + \text{urea}]'$.

fact there was a good positive correlation ($r = 0.73$, $P < 0.02$) between f'-ratios and Chl *a* standing crops (Fig. 9). Considering that chlorophyll levels are likely to have a major effect on Z_e, it is not surprising that the f'-ratio was negatively correlated ($r = -0.64$, $P < 0.05$) with Z_e (Fig. 10). This situation contrasts with the studies by Harrison *et al.* (1983) in the Mid-Atlantic Bight where they demonstrated a positive relationship between the f'-ratio and Z_e. A positive correlation ($r = 0.69$, $P < 0.02$), however, did exist between the f'-ratio and Z_m in the present study (Fig. 10): low f'-ratios characterized those stations where Z_e was similar to or deeper than Z_m. Conversely the highest f'-ratios recorded in this study occurred when Z_m was deeper than Z_e. This relationship between the f'-ratio and Z_m may be misleading, as it is quite likely that if uptake measurements had been performed routinely down to the base of the upper mixed layer a

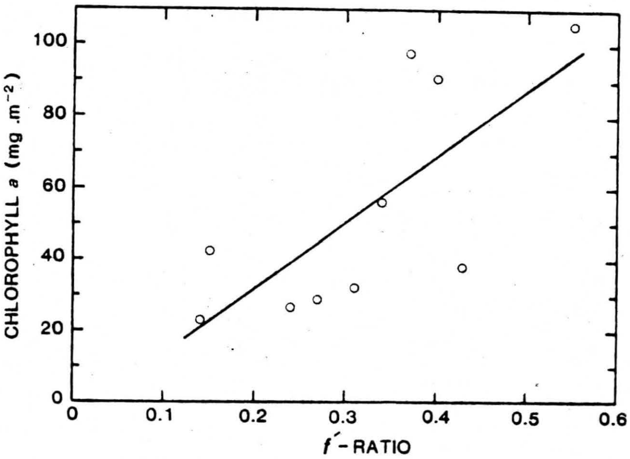

Fig. 9. The relationship between the f'-ratio and Chl a integrated over the euphotic zone (Chl $a = -5.0 + 183.8\,f'$).

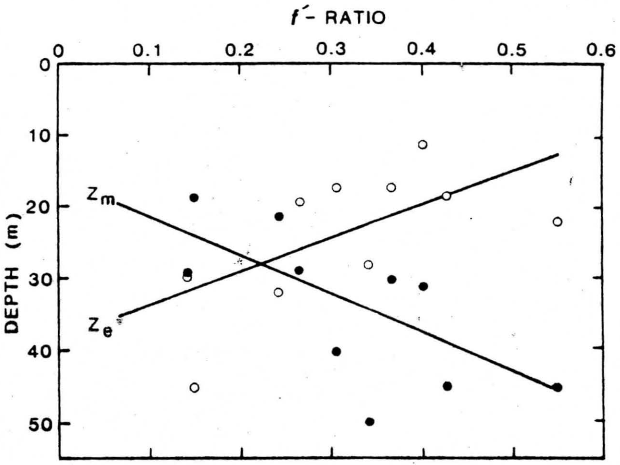

Fig. 10. The relationship between the f'-ratio and Z_e (○), the depth of the euphotic zone ($Z_e = 38.35 - 46.40\,f'$) and Z_m (●), the depth of the upper mixed layer ($Z_m = 15.06 + 58.58\,f'$).

different set of f'-ratios would have emerged. One set of measurements that was extended down to Z_m did in fact reveal a smaller f'-ratio than for the euphotic zone.

DISCUSSION

The hydrographic and chemical features during SNEC—85 illustrate the intense upwelling characteristic of the region in the spring (Fig. 2; Maso and Manriquez, 1986; Estrada and Marrase, 1987). These conditions were similar to the high nutrient and low chlorophyll situation also described by Minas *et al.* (1986) for a spring season in the Namibian upwelling region. The effect of upwelling was detectable well offshore of the continental shelf, as shown by the considerable quantity of NO_3^- present at the outermost stations (Fig. 2). Nitrate levels, integrated to a depth of 50 m (within the upper mixed layer) 250 km offshore, ranged from 261 mg-at. N m^{-2} at 26°S to as high as 719 mg-at. N m^{-2} at 20°S. These figures represent an important potential nitrogen productivity, particularly in the northern part of the region, extending into the surrounding oceanic waters.

The f*-ratio*

In spite of large ambient NO_3^- concentrations, the mean f'-ratio of 0.32 (mean f-ratio = 0.31) was somewhat smaller than expected from the relationship given in EPPLEY and PETERSON (1979), for a coastal upwelling system. Off southern California f-ratios of about 0.2–0.8 have been recorded (EPPLEY *et al.*, 1979), and in the Peruvian upwelling system ratios range between 0.5 in freshly upwelled waters to nearly 0.9 for maturing phytoplankton assemblages (MACISAAC *et al.*, 1985). The relationships between f-ratio and ambient NO_3^- concentrations described by HARRISON *et al.* (1987) indicate that in waters off Peru and southern California f-ratios from discrete depths generally fall between 0.5 and nearly 1.0 at NO_3^- concentrations similar to those encountered in the present study. Large f-ratios, in excess of 0.8, also have been recorded for recently upwelled water off the coast of Washington and Oregon (KOKKINAKIS and WHEELER, 1987). The comparatively low f-ratios measured here are explained at least partially by the fact that urea uptake was not taken into account in the majority of the other studies, thereby over-estimating the f-ratio. However, excluding urea from the present data set results in a mean f'-ratio of 0.39, still at the low end of the range expected for coastal upwelling systems.

The calculation of new production from the product of the f-ratio and total production assumes that current ^{15}N techniques measure predominantly phytoplankton-mediated uptake. Microheterotrophic assimilation of reduced nitrogen compounds, and not nitrate, will thus result in an underestimate of an effective f-ratio (see discussion in HARRISON *et al.*, 1987). One might expect a relatively greater contribution of microheterotrophs to nitrogen assimilation towards the end of phytoplankton bloom rather than in maturing upwelled waters. As the Namibian upwelling region during the spring is characterized by nitrate-rich, relatively recently upwelled waters for the large part (Fig. 2), microheterotrophs probably did not have a significant influence on the f-ratio during SNEC—85.

Recently the practise of labelling a particular ocean province as oligotrophic or eutrophic has been questioned on the bases of measured and calculated temporal variations in f'-ratio (PLATT and HARRISON, 1985). The measured f'-ratios presented here, being in some cases typical of the impoverished open ocean, emphasize the additional complication of spatial variability within a particular oceanographic region.

PLATT and HARRISON (1985) and HARRISON *et al.* (1987) have demonstrated an asymptotic increase in f-ratio with an increase in ambient NO_3^- concentrations for a particular ocean area. No obvious trend was evident in the SNEC—85 data, suggesting little effect of NO_3^- availability on the f-ratio. Similarly, HARRISON *et al.* (1987) have formulated a linear relationship between f-ratios and concentration ratios for a number of different regions. In the present study the NO_3^- concentration ratio was large and relatively constant ($\bar{x}$ = 0.88 ± 0.03, 95% confidence limits), precluding a significant correlation ($P > 0.10$) with the variable f-ratio. Such domination of the nitrogenous pool by NO_3^- belies its relatively small contribution to primary production, a situation similar to that found in Antarctic waters. Bearing in mind the conceptual importance of new production to our understanding of sedimentation rate and yield at higher trophic orders, it is pertinent to consider other potentially important environmental influences on the *f*-ratio.

Factors affecting the *f*-ratio inevitably should be similar to those that affect uptake rates of individual nitrogen sources. An important consideration is phytoplankton preferences for individual nitrogen resources. Phytoplankton populations during SNEC—85 (Fig. 4) displayed the usual preference for NH_4^+ and urea, and rejection of NO_3^- (e.g. MCCARTHY *et al.*, 1977; GLIBERT *et al.*, 1982b; PROBYN, 1985). Exceptions to this general pattern of nutrient preference, however, are not infrequent (e.g. FURNAS, 1983; HARRISON *et al.*, 1985; COCHLAN, 1986). In these studies NO_3^- was taken up preferentially and urea rejected for water masses with a low concentration of total nitrogenous nutrients (<1 mg-at. N m^{-3}). The trends in Fig. 3 suggest that the RPI's for all nutrients similarly approach unity at the low end of the range of total nitrogen concentrations (*ca.* 5 mg-at. N m^{-3}), indicating utilization equitable with ambient concentration. These trends can be explained both by the suppression of NO_3^- RPI's at NH_4^+ concentrations >1 mg-at. N m^{-3} (MCCARTHY *et al.*, 1977; FURNAS, 1983; PROBYN, 1985) and by the domination of the total nitrogen pool by NO_3^-. Available information thus indicates that in upwelling environments with their characteristic high nutrient concentrations, NO_3^- generally will be rejected and reduced nitrogen selected by phytoplankton populations.

It should be remembered that RPI's are an expression of the qualitative aspects of nitrogen assimilation that may or may not be related to absolute rates of uptake. Since it is the latter that is used in the formulation of the *f*-ratio, RPI's can give a misleading impression of the quantitative aspects of nitrogen utilization.

A number of studies have shown the dependence of maximum nitrogen uptake rates on temperature (FISHER *et al.*, 1981; GLIBERT *et al.*, 1982b; PAASCHE and KRISTIANSEN, 1982; KANDA *et al.*, 1985; CARPENTER and DUNHAM, 1985). A similar exponential relationship between temperature and nitrogen uptake in the field was formulated in the present study (Fig. 5). The temperature coefficients (Q_{10}) for uptake of different nitrogen sources in thus study (11.4–52.5) were substantially larger than expected if temperature alone were the controlling variable. Previous measurements of photosynthetic rates (EPPLEY, 1972) and ammonium uptake rates for natural populations (PAASCHE and KRISTIANSEN, 1982; GLIBERT *et al.*, 1982b) indicate a Q_{10} value typically between 1.9 and 3.2. The present findings suggest an over-riding influence of factors other than temperature on nitrogen uptake rates. Considering the relationship between temperature and nitrogen uptake might lead one to expect a similar relationship between temperature and the f'-ratio. There was, however, no significant relationship between the two variables ($P > 0.1$). The lack of any apparent differential effect of temperature on oxidized or reduced nitrogen uptake (Fig. 5) is a possible explanation.

Depth profiles of *f*-ratios with minima generally occurring at the 1% light level and maxima nearer the surface (Fig. 7) suggest light may be an important factor in determining these ratios. A similar decrease in *f*-ratio with depth in the euphotic zone has been demonstrated in areas with enriched surface NO_3^- concentrations (GOERING *et al.*, 1970; OLSON, 1980). These findings may be an indication of the greater light requirement for NO_3^- uptake than for NH_4^+ uptake (MACISAAC and DUGDALE, 1972;

BATES, 1976; CAPERON and ZIEMANN, 1976). In contrast, HARRISON *et al.* (1983) in the Mid-Atlantic Bight, found the *f*-ratio paralleled NO_3^- concentrations, increasing to a maximum at the base of the euphotic zone (HARRISON *et al.*, 1983; PLATT and HARRISON, 1985). In an analysis of a wide range of field data, HARRISON *et al.* (1987) concluded light had little effect on the *f*-ratio by comparison with the effect of ambient NH_4^+ concentrations. However, considering the large surface water NO_3^- concentrations (ESTRADA and MARRASE, 1987) and the lack of any obvious depth-related effect of recycled nitrogen (see below), light most probably had an important influence on the individual depth profiles of *f*-ratios during SNEC—85, either directly or indirectly through its effect on primary production. Similar conclusions might apply to the findings of OLSON (1980) in the NO_3^--rich Antarctic waters where the *f*-ratio was shown to be reduced at the 10% light level relative to the surface. However, when making comparisons between the different stations it appears that depth-integrated ratios were not affected by average light levels. The highest f'-ratios were measured at those stations with $Z_m > Z_e$, conditions likely to reduce the average light level experienced by a phytoplankton cell.

The concentration of recycled nitrogen has a potentially major effect on the *f*-ratio. In fact the relationship of *f*-ratios with ambient NO_3^- concentrations and with nitrogen concentration ratios is affected by ambient NH_4^+ concentrations (PAASCHE and KRISTIANSEN, 1982; HARRISON *et al.*, 1987). A more direct effect is shown in the decrease in *f*-ratio with increasing NH_4^+ concentration (OLSON, 1980; GLIBERT *et al.*, 1982a; COCHLAN, 1986). In the present study it was the concentration of NH_4^+ plus urea rather than NH_4^+ alone that appeared to affect the *f*-ratio, as is to be expected with urea uptake included in the calculations (Fig. 8). This effect is presumably a result of the often described suppression of NO_3^- uptake by NH_4^+ (MCCARTHY and EPPLEY, 1972; HARVEY and CAPERON, 1976; CAPERON and ZIEMANN, 1976; MCCARTHY *et al.*, 1977) and by urea (MCCARTHY and EPPLEY, 1972). In agreement with OLSON (1980), integrated values of the *f*-ratio and recycled nutrient concentrations were more strongly correlated than data from discrete depths, indicating nitrogen uptake rates were coupled more closely with processes (e.g. nutrient regeneration) occurring throughout the euphotic zone than those occurring at the different depths. Assuming that rates obtained from incubations are a good approximation of *in situ* rates, this example demonstrates how responses of phytoplankters are averaged out over their life times as a result of mixing within the euphotic zone.

New production

The f'-ratio has been demonstrated to be related in a non-linear fashion to total primary production both between (EPPLEY and PETERSON, 1979) and within (EPPLEY *et al.*, 1979; PLATT and HARRISON, 1985) different oceanographic regions. Using the primary production data of ESTRADA and MARRASE (1987) one can formulate a positive relationship between the f'-ratio and integrated primary production ($r = 0.64$, $P < 0.05$) and integrated new production ($r = 0.93$, $P < 0.001$) for the northern Benguela region (Fig. 11). As one might expect, the f'-ratio was better correlated with new production than with total primary production. However, an increase in the amount of spurious correlation, similar to that described for ratios (ATCHELY *et al.*, 1976), must be considered when a product (new production) is correlated with one of its variables (f'-ratio).

It has been proposed (SHANNON, 1985) that intense upwelling in the Luderitz area forms an environmental barrier between the northern and southern Benguela. However, AGENBAG and SHANNON (1988) recently suggested that the biological discontinuity

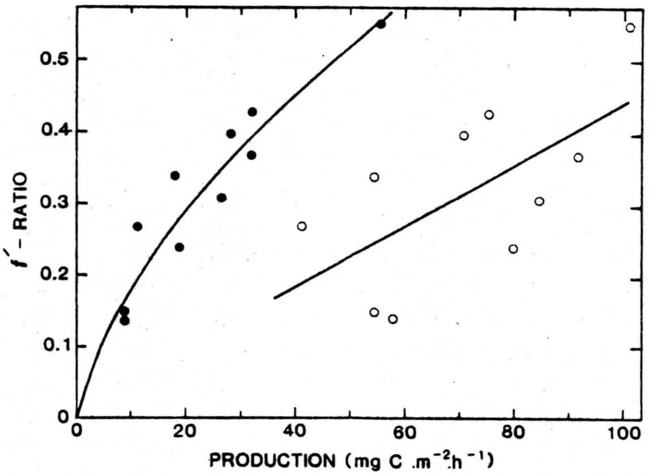

Fig. 11. Variation in f'-ratio with total primary production (○) and with new production (●). The relationships are described by $f' = 0.021 \times 0.004$ (total production) and $f' = 0.043$ (new production)$^{0.638}$. Primary production rates recorded during SNEC—85 are given in ESTRADA and GUITERREZ (1987).

(for pelagic fish) may actually lie farther north in the vicinity of Meob Bay (Fig. 1), due to decreased turbulence levels north of this site. Although sampling was too superficial to draw any firm conclusions, the trends in measured f-ratios and new production do support a claim for such a discontinuity. At Stas 3, 11 and 55, located south of Meob Bay, new production was on average 9.11 ± 1.5 mg C m^{-2} h^{-1} (95% confidence limits), while at the remainder of the stations it was calculated at 30.71 ± 9.4 mg C m^{-2} h^{-1}. Assuming the measured f'-ratios are indicative of processes occurring over longer averaged time, these data suggest considerably faster fluxes to the sediment (new production) north of Meob Bay than was the case in the south during this period of active upwelling. The predominance of biogenically enriched sediments over the shelf and upper slope north of Meob Bay (CALVERT and PRICE, 1970; BREMNER, 1983) supports the notion that these short-term measurements of new production are consistent with long-term trends in sedimentation rates.

Regenerated production

Primary production in excess of new production is based on nutrients recycled within the upper water column by animal excretion and bacterial decomposition (DUGDALE and GOERING, 1967). Calculated f'-ratios (Table 1) indicate that recycled nutrients supplied the major share of phytoplankton requirements (45–86%). Quantitatively NH_4^+ proved to be the most important nutrient resource, accounting for a mean of 47 ± 7% (95% confidence limits) of measured nitrogen uptake rates. The contribution of urea to total uptake ($\bar{x} = 20 \pm 7\%$) was significant but generally lower than measured for other regions, including coastal upwelling systems (MCCARTHY, 1972; PROBYN, 1985), coastal embayments (HARVEY and CAPERON, 1976; KRISTIANSEN, 1983; KAUFMAN *et al.*, 1983), high latitude ecosystems (HARRISON *et al.*, 1985; PROBYN and PAINTING, 1985) and oligotrophic oceanic waters (EPPLEY *et al.*, 1973).

Other studies have shown that most of the recycled nitrogen in shelf waters and deeper is regenerated in the upper water column, generally by organisms <200 μm (HARRISON *et al.*, 1983; PROBYN, 1987). During this study NH_4^+ uptake most often exceeded regeneration in the euphotic zone (Fig. 5), indicating a non-steady situation that would lead to NH_4^+ depletion. Such findings conflict with the field situation where measurable NH_4^+ was present in the euphotic zone ($\bar{x} = 0.34$ mg-at. N m^{-3}) at all the nitrogen productivity stations. Bearing in mind that Z_m was, with the exception of Sta. 3, considerably deeper than Z_e, it is possible, invoking substantial NH_4^+ regeneration below the euphotic zone, that uptake and regeneration rates integrated over Z_m would be in better agreement. The time constraint on the tracer experiments also may have contributed towards the imbalance between uptake and regeneration. It is likely that ammonium (and urea) regeneration rates would have exceeded uptake rates at night due to a light-cued decrease in assimilation. Vertical migration of zooplankters and subsequent excretion in the upper water column will similarly enhance supply during the dark hours. Thus uptake and regeneration rates may well be similar when averaged for a 24 h period (e.g. CAPERON *et al.*, 1979; GLIBERT, 1982).

The chlorophyll–nutrient poise

In contrast to the situation at the end of the austral summer (ESTRADA and MARRASE, 1987), the Namibian upwelling region during the spring is characterized by high nutrient and low Chl *a* concentrations, indicating a slow rate of development of phytoplankton populations in upwelled water during offshore transport. An appealing explanation for the establishment of these conditions is by the appearance of herbivores soon after an upwelling event which, through grazing pressure, maintains algal biomass at comparatively low levels and hence retards the consumption of new nutrients (MINAS *et al.*, 1986). The relatively large contribution of heterotrophic excretory (and decomposition) products to primary production (= regenerated production) found in this study indirectly indicates an active zooplankton component that could arguably have maintained algal biomass at low levels.

Deep mixing also would have contributed towards establishing these conditions of high nutrient and low Chl *a* concentrations. Mixing penetrating deeper than Z_e, as was typical for the region during SNEC—85, would have promoted both nutrient entrainment from deeper waters and retarded primary production. Deep mixing is also relevant to the light-induced increase in physiological activities (shift-up) that phytoplankton undergo in a post-upwelling phase (MACISAAC *et al.*, 1985; WILKERSON and DUGDALE, 1987). During shift-up, biomass-specific NO_3^- uptake rates increase downstream of the upwelling site to a maximum and then decrease in response to moderate nutrient depletion. Initial limiting nutrient concentrations (NO_3^- or silicate) and mixed-layer depths may affect the rate of acceleration of NO_3^- uptake, the maximal level achieved and the duration of this phase (MACISAAC *et al.*, 1985; WILKERSON and DUGDALE, 1987; ZIMMERMAN *et al.*, 1987). The slow specific NO_3^- uptake rates reported here (Table 1) indicate incomplete shift-up in spite of the extended spatial and temporal scales under consideration. Deep mixing rather than initial nutrient concentrations is thought to be the cause, as NO_3^- (and silicate concentrations) in fresh upwelling water were large, generally in excess of 25 mg-at. N(Si) m^{-3}.

CONCLUSIONS

In spite of the large ambient concentrations of NO_3^- present in the euphotic zone in the Namibian upwelling region during the austral spring, nitrogen appeared to be assimilated primarily in its reduced forms. The restricted consumption of new nutrients over the continental shelf resulted in their penetration far offshore, thereby increasing the potential nitrogen productivity of adjacent slope waters. A combination of herbivory and deep mixing is thought to retard phytoplankton blooms and hence nutrient consumption. Under these conditions the production of reduced nitrogen within the euphotic zone by grazers and decomposers counteracts the favourable NO_3^- concentrations and is therefore regarded as the most important factor dictating the unexpectedly small f'-ratios. In this respect these findings are in direct agreement with the studies of MINAS *et al.* (1986). Other factors, such as light and temperature, appear to be relatively unimportant. Preliminary findings indicate that short-term measurements of new production may well be indicative of long-term trends in sedimentation rates.

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REFERENCES

AGENBAG J. J. and L. V. SHANNON (1988) Suggested physical explanation for the existence of a biological boundary at 24°30′S in the Benguela System, *South African Journal of Marine Science*, **6**, 119–132.

ATCHELY W. R., C. T. GASKINS and D. ANDERSON (1976) Statistical properties of ratios. I. Empirical results. *Systematic Zoology*, **25**, 137–148.

BAILEY G. W. (1985) Distribution and cycling of nutrients at four sites in the Benguela system. *Proceedings of the International Symposium on the Most Important Upwelling Areas off Western Africa (Cape Blanco and Benguela), Barcelona, Spain, November* 1983. *Instituto de Investigaciones Pesqueras*, **1**, 119–148.

BARBER R. T. and R. L. SMITH (1981) Coastal upwelling ecosystems. In: *Analysis of marine ecosystems*, A. R. LONGHURST, editor, Academic Press, London, pp. 31–68.

BATES S. S. (1976) Effects of light and ammonium on nitrate uptake by two species of estuarine phytoplankton. *Limnology and Oceanography*, **21**, 212–218.

BLACKBURN T. H. (1979) Method for measuring rates of NH_4 turnover in anoxic marine sediments, using a ^{15}N-NH_4 dilution technique. *Applied Environmental Microbiology*, **37**, 760–765.

BOYD A. J. and J. J. AGENBAG (1985) Seasonal trends in the longshore distribution of surface temperatures off Southwestern Africa 18–34°S, and their relation to subsurface conditions and currents in the area 21–24°S. *Proceedings of the International Symposium on the Most Important Upwelling Areas off Western Africa (Cape Blanco and Benguela), Barcelona, Spain, November* 1983. Instituto de Investigaciones Pesqueros, **1**, 119–148.

BREMNER J. (1983) Biogenic sediments on the South West African (Namibian) continental margin. In: *Coastal upwelling. Its sediment record. Part B: sedimentary records of ancient coastal upwelling*, J. THIEDE and E. SUESS, editors, Plenum Press, New York, pp. 73–103.

CALVERT S. E. and N. B. PRICE (1970) Minor metal contents of recent organic-rich sediments off South West Africa. *Nature*, **227**, 593–595.

CALVERT S. E. and N. B. PRICE (1971) Upwelling and nutrient regeneration in the Benguela Current, October, 1968. *Deep-Sea Research*, **18**, 505–523.

CAPERON J. and D. A. ZIEMAN (1976) Synergistic effects of nitrate and ammonium ion on the growth and uptake kinetics of *Monochrysis lutheri* in continuous culture. *Marine Biology*, **36**, 73–84.

CAPERON J., D. SCHELL, J. HIROTA and E. LAWS (1979) Ammonium excretion rates in Kaneohe Bay, Hawaii, measured by a ^{15}N isotope dilution technique. *Marine Biology*, **54**, 33–40.

Carpenter E. J. and S. Dunham (1985) Nitrogenous nutrient uptake, primary production, and species composition of phytoplankton in the Carmans River estuary, Long Island, New York. *Limnology and Oceanography*, **30** 513–526.

Chapman P. and L. V. Shannon (1985) The Benguela ecosystem, Part II. Chemistry and related processes. *Oceanography and Marine Biology, Annual Review*, **23**, 183–251.

Cochlan W. P. (1986) Seasonal study of uptake and regeneration of nitrogen on the Scotian Shelf. *Continental Shelf Research*, **5**, 555–577.

Dugdale R. C. and J. J. Goering (1967) Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography*, **12**, 196–206.

Eppley R. W. (1972) Temperature and phytoplankton growth in the sea. *Fisheries Bulletin U.S.*, **70**, 1063–1085.

Eppley R. W. (1981) Autotrophic production of particulate matter. In: *Analyses of marine ecosystems*, A. R. Longhurst, editor, Academic Press, London, pp. 343–361.

Eppley R. W. and B. J. Peterson (1979) Particulate organic matter flux and planktonic new production in the deep ocean. *Nature*, **282**, 677–680.

Eppley R. W., E. H. Renger, E. L. Venrick and M. M. Mullin (1973) A study of plankton dynamics and nutrient cycling in the central gyre of the North Pacific Ocean. *Limnology and Oceanography*, **18**, 534–551.

Eppley R. W., E. H. Renger and W. G. Harrison (1979) Nitrate and phytoplankton production in southern California coastal waters. *Limnology and Oceanography*, **24**, 483–494.

Estrada M. and C. Marrase (1987) Phytoplankton biomass and productivity off the Namibian coast. In: *Benguela* 86, A. I. L. Payne, J. A. Gulland and K. H. Brink, editors, *South African Journal of Marine Science*, **5**, 347–356.

Fieldler R. and G. Proksch (1975) The determination of nitrogen-15 by emission and mass spectrometry in biochemical analysis: a review. *Analytica Chimica Acta*, **78**, 1–62.

Fisher T. R., P. R. Carlson and R. T. Barber (1981) Some problems in the interpretation of ammonium uptake kinetics. *Marine Biology Letters*, **2**, 33–44.

Furnas M. J. (1983) Nitrogen dynamics in lower Narragansett Bay, Rhode Island. I. Uptake by size-fractionated phytoplankton populations. *Journal of Plankton Research*, **5**, 657–676.

Glibert P. M. (1982) Regional studies of daily, seasonal and size fraction variability in ammonium remineralization. *Marine Biology*, **70**, 209–222.

Glibert P. M., D. C. Biggs and J. J. McCarthy (1982a) Utilization of ammonium and nitrate during austral summer in the Scotia Sea. *Deep-Sea Research*, **29**, 837–850.

Glibert P. M., J. C. Goldman and E. J. Carpenter (1982b) Seasonal variations in the utilization of ammonium and nitrate by phytoplankton in Vineyard Sound, Massachusetts, USA. *Marine Biology*, **70**, 237–249.

Glibert P. M., F. Lipshultz, J. J. McCarthy and M. M. Altabet (1982c) Isotope dilution models of uptake and remineralization of ammonium by marine plankton. *Limnology and Oceanography*, **27**, 639–650.

Goering J. J., D. D. Wallen and R. M. Nauman (1970) Nitrogen uptake by phytoplankton in the discontinuity layer of the eastern subtropical Pacific Ocean. *Limnology and Oceanography*, **15**, 789–796.

Grasshoff K., M. Ehrhardt and K. Kremling (1983) *Methods of seawater analysis*, 2nd edn, Verlag Chemie, Weinheim, pp. 127–187.

Harrison W. G. (1978) Experimental measurements of nitrogen remineralization in coastal waters. *Limnology and Oceanography*, **23**, 684–694.

Harrison W. G., D. Douglas, P. Falkowski, G. Rowe and J. Vidal (1983) Summer nutrient dynamics of the Middle Atlantic Bight: nitrogen uptake and regeneration. *Journal of Plankton Research*, **5**, 539–556.

Harrison W. G., E. J. H. Head, R. J. Conover, A. R. Longhurst and D. D. Sameoto (1985) The distribution and metabolism of urea in the eastern Canadian Arctic. *Deep-Sea Research*, **32**, 23–42.

Harrison W. G., T. Platt and M. R. Lewis (1987) *F*-ratio and its relationship to ambient nitrate concentration in coastal waters. *Journal of Plankton Research*, **9**, 235–248.

Harvey W. A. and J. Caperon (1976) The rate of utilization of urea, ammonium, and nitrate by natural populations of marine phytoplankton in a eutrophic environment. *Pacific Science*, **30**, 329–340.

Kanda J., T. Saino and A. Hattori (1985) Nitrogen uptake by natural populations of phytoplankton and primary production in the Pacific Ocean: Regional variability of uptake capacity. *Limnology and Oceanography*, **30**, 987–999.

Kaufman Z. G., J. S. Lively and E. J. Carpenter (1983) Uptake of nitrogenous nutrients by phytoplankton in a barrier island estuary: Great South Bay, New York. *Estuarine, Coastal and Shelf Science*, **17**, 483–493.

Kokkinakis S. A. and P. A. Wheeler (1987) Nitrogen uptake and phytoplankton growth in coastal upwelling regions. *Limnology and Oceanography*, **32**, 1112–1123.

Kristiansen S. (1983) Urea as a nitrogen source for the phytoplankton in the Oslofjord. *Marine Biology*, **74**, 17–24.

MASO M. and M. MANRIQUEZ (1986) Preliminary hydrological results of the "Spanish Namibian Environmental Cruise" survey, SNEC—1. *Collection of Scientific Papers. International commission for the south east Atlantic Fisheries*, pp. 137–151.

MCCARTHY J. J. (1972) The uptake of urea by natural populations of marine phytoplankton. *Limnology and Oceanography*, **17**, 738–748.

MCCARTHY J. J. and R. W. EPPLEY (1972) A comparison of chemical, isotopic, and enzymatic methods for measuring nitrogen assimilation of marine phytoplankton. *Limnology and Oceanography*, **17**, 371–382.

MCCARTHY J. J., W. R. TAYLOR and J. L. TAFT (1977) Nitrogenous nutrition of the plankton in the Chesapeake Bay. 1. Nutrient availability and phytoplankton preferences. *Limnology and Oceanography*, **22**, 996–1011.

MACISAAC J. J. and R. C. DUGDALE (1972) Interactions of light and inorganic nitrogen in controlling nitrogen uptake in the sea. *Deep-Sea Research*, **19**, 209–232.

MACISAAC J. J., R. C. DUGDALE, R. T. BARBER, D. BLASCO and T. T. PACKARD (1985) Primary production cycle in an upwelling center. *Deep-Sea Research* , **32**, 503–529.

MINAS H. J., M. MINAS and T. T. PACKARD (1986) Productivity in upwelling areas deduced from hydrographic and chemical fields. *Limnology and Oceanography*, **31**, 1182–1206.

MOSTERT S. A. (1983) Procedures used in South Africa for the automatic photometric determination of micronutrients in sea water. *South African Journal of Marine Science*, **1**, 189–198.

NELSON G. and L. HUTCHINGS (1983) The Benguela upwelling area. *Progress in Oceanography*, **12**, 333–356.

OLSON R. J. (1980) Nitrate and ammonium uptake in Antarctic waters. *Limnology and Oceanography*, **25**, 1064–1074.

PAASCHE E. and S. KRISTIANSEN (1982) Nitrogen nutrition of the phytoplankton in the Oslofjord. *Estuarine, Coastal and Shelf Science*, **14**, 237–249.

PRICE N. M., W. P. COCHLAN and P. J. HARRISON (1985) Time course of uptake of inorganic and organic nitrogen by phytoplankton in the Strait of Georgia: comparison of frontal and stratified communities. *Marine Ecology, Progress Series*, **27**, 39–53.

PLATT T. and W. G. HARRISON (1985) Biogenic fluxes of carbon and oxygen in the ocean. *Nature*, **318**, 55–58.

PROBYN T. A. (1985) Nitrogen uptake by size-fractionated phytoplankton populations in the southern Benguela upwelling system. *Marine Ecology, Progress Series*, **22**, 249–258.

PROBYN T. A. (1987) Ammonium regeneration by microplankton in an upwelling environment. *Marine Ecology, Progress Series*, **37**, 53–64.

PROBYN T. A. and S. J. PAINTING (1985) Nitrogen uptake by size-fractionated phytoplankton populations in Antarctic surface waters. *Limnology and Oceanography*, **30**, 1327–1332.

SHELTON P. A., A. J. BOYD and M. J. ARMSTRONG (1985) The influence of large-scale environmental processes on neritic fish populations in the Benguela Current System. Cal COF1 Rep 26, pp. 72–92.

SHANNON L. V. (1985) The Benguela ecosystem, Part I. Evolution of the Benguela, physical features and processes. *Oceanography and Marine Biology, Annual Review*, **23**, 105–182.

SHANNON L. V. and S. C. PILLAR (1986) The Benguela ecosystem, Part III. Plankton. *Oceanography and Marine Biology, Annual Review*, **24**, 65–170.

STANDER G. H. (1964) The Pilchard of South West Africa. The Benguela current off South West Africa. *Investigational Report Marine Research Laborarory, South West Africa*, **12**, 120 pp.

STRICKLAND J. D. H. and T. R. PARSONS (1972) *A practical handbook of seawater analysis*, Fisheries Research Board of Canada, Ottawa, pp. 201–206.

WILKERSON F. P. and R. C. DUGDALE (1987) The use of large shipboard barrels and drifters to study the effects of coastal upwelling on phytoplankton dynamics. *Limnology and Oceanography*, **32**, 368–382.

YENTSCH C. S. and D. W. MENZEL (1983) A method for the determination of phytoplankton chlorophyll and phaeophytic by fluorescence. *Deep-Sea Research*, **10**, 221–231.

ZIMMERMAN R. C., J. N. KREMER and R. C. DUGDALE (1987) Acceleration of nutrient uptake by phytoplankton in a coastal upwelling ecosystem: A modelling analysis. *Limnology and Oceanography*, **32**, 359–367.