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Size-fractionated uptake of nitrogenous nutrients and carbon by phytoplankton in the North Sea during summer 1994

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ABSTRACT: The growth of 2 different algal size classes was studied in July/August 1994 along a transect from the Dogger Bank to the Shetland Islands in the thermally stratified part of the North Sea. Size-differential growth rates were estimated on the basis of independent measurements of carbon and nitrogen uptake. In general, the major nutrients were low in the upper mixed layer. At 10 m depth, average values for phosphate, ammonium, urea, and nitrate were 0.047 ± 0.019 (n = 32), 0.17 ± 0.05 (n = 27), 0.15 ± 0.09 (n = 26), and 0.16 ± 0.13 (n = 27) µM, respectively. Nitrate, urea, and ammonium uptake by the total plankton community were 9, 31 and 60% of the total nitrogen uptake, respectively. The <5 µm fraction showed a comparable speciation of nitrate, urea and ammonium uptake being 8, 32 and 60%, respectively. The average chlorophyll *a* (chl *a*) concentration was 0.68 ± 0.47 µg l^{-1} (n = 34), and 71% of the total chl *a* was in the <5 µm fraction. The average specific growth rate of <5 µm phytoplankton (0.39 ± 0.17 d^{-1}; n = 19) was not significantly different (0.25 > p > 0.1) from the specific growth rate of the >5 µm fraction (0.43 ± 0.12 d^{-1}; n = 15). At 40 m depth, i.e. just below the chl *a* maximum near the thermocline, major nutrients were present at non-limiting concentrations and photosynthetic active radiation (PAR) ranged between 2 and 5% of the surface PAR. Average values for phosphate, ammonium, urea, and nitrate were 0.40 ± 0.13 (n = 32), 1.40 ± 0.90 (n = 34), 0.15 ± 0.06 (n = 34), and 2.61 ± 1.79 (n = 34) µM, respectively. At 40 m depth, more nitrate was consumed than at 10 m depth: nitrate, urea, and ammonium uptake by the total community were 17, 16 and 67% of the total nitrogen uptake, respectively. The <5 µm fraction showed a lower preference for nitrate with nitrate, urea and ammonium uptake being 12, 14 and 74% of the total nitrogen uptake by this size fraction, respectively. The average chl *a* at 40 m was 0.63 ± 0.42 (n = 34), and also at this depth 71% of the total chl *a* was in the <5 µm fraction. The average specific growth rate of phytoplankton was lower at greater depth: 0.17 ± 0.09 d^{-1} (n = 15) for the <5 µm fraction. The specific growth rate of the phytoplankton >5 µm was 0.10 ± 0.06 d^{-1} (n = 15), which was significantly lower than the value for the smaller size fraction (p < 0.025). Net primary production showed large variation amongst the stations with average values for the <5 µm fraction and the total community of 0.37 ± 0.19 g C m^{-2} d^{-1} (n = 20) and 0.50 ± 0.26 g C m^{-2} d^{-1} (n = 20), respectively. In combination with the companion paper it is concluded that size-partitioning of algal growth rate appears to depend on the character of the growth rate limiting factor. Smaller algae showed faster growth than larger ones in light-controlled environments, regardless of the nitrogen source predominantly used. In the nutrient-controlled surface layers, no size-partitioning of algal growth rate was present when ammonium was the major nitrogen source. At some stations, where nitrogen limitation co-occurred with enhanced nitrate consumption, larger algae did grow faster than smaller ones. However, the algal biomass in different size classes was not related to the estimated growth rates of these different categories. Apparently, larger algae do not dominate during summer in the surface layers of the stratified central North Sea, since mesozooplankton densities are high compared to spring and vertical mixing in the photic zone is low. At the lower part of the photic zone, the larger algae do not dominate since they grow much slower than the smaller species due to light-limitation.

KEY WORDS: Phytoplankton growth · Size fractionation · Nitrogen uptake · Carbon uptake · North Sea

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INTRODUCTION

In the companion study, we described size-fractionated nitrogen uptake and phytoplankton growth along a transect from the Dogger Bank (North Sea) to the Shetland Islands during spring, when typically light-controlled phytoplankton growth occurred (Riegman et al. 1998, in this issue). It was found that, although the spring bloom mainly consisted of larger species, smaller algae (< 5 µm) grew faster than the larger ones. These findings consolidated the concept of size-differential control of phytoplankton communities (Thingstad & Sakshaug 1990) under typical spring bloom conditions which originally was demonstrated in a coastal area (Riegman et al. 1993). During summer, the northern part of the North Sea is thermally stratified, exhibiting a major nutrient-depleted surface layer (Woodward & Owens 1990), a chlorophyll *a* (chl *a*) maximum near the thermocline at 30 to 35 m depth (Riegman et al. 1990a), and deeper water layers where low irradiances and temperature prevail and inorganic nutrients are still available. An inflow of nutrient-rich ocean water occurs near the Shetland Islands which occasionally may trigger *Emiliania huxleyi* or cyanobacterial blooms (Van der Wal et al. 1995, Timmermans et al. 1998) in the surface layers. In the central North Sea, the major nutrient sources are internal recycling and entrainment from below the thermocline. Primary production is about 0.8 to 1.2 g C m^{-2} d^{-1} at chl *a* levels of 0.4 µg l^{-1} (Gieskes & Kraay 1984, Riegman & Colijn 1991). Over the northern slope of the Dogger Bank, where the water column is 30 to 40 m, enhanced chl *a* near the bottom has been reported (Riegman et al. 1990a, Nielsen et al. 1993). The locally associated enhanced primary production has been ascribed to interaction between wind and tidal mixing at this particular site, promoting the net upwards transport of major nutrients (Riegman et al. 1990a). Generally, phytoplankton is dominated by species < 5 µm during summer. Especially in the most oligotrophic central North Sea they contribute up to 75% of the primary production in the surface layers (Owens et al. 1990). Either nitrogen or phosphorus has been found to limit the growth rate of algae (Riegman et al. 1990b) in the central North Sea, whereas near the Shetlands a potential iron limitation of nitrate reduction has been reported (Timmermans et al. 1998). The dominance of smaller algae in stratified, nutrient-controlled waters is usually explained by their reduced losses by sedimentation compared to larger species (Margalef 1978) and the ability of smaller species to compete for nutrients as a consequence of their relatively higher surface to volume ratio (Blasco et al. 1982, Grover 1989). It can be argued that species with a high surface to volume ratio are good competitors under steady state conditions, but under transient state conditions the storage capacity for the growth rate limiting nutrient becomes an additional factor that determines the competitive ability of the species. It has been demonstrated that, due to their higher storage capacity, larger diatoms were better competitors for nitrate (under fluctuating supply rates and nitrogen limiting growth conditions) than smaller diatoms (Stolte et al. 1994, Stolte & Riegman 1995). On the other hand, when ammonium (which could not be stored in the vacuole in large quantities) was supplied instead of nitrate, there was no size-differential growth observed when the nutrient supply was fluctuating. In mixed algal species cultures, it was observed that smaller species usually competed better for nutrients than larger ones (Riegman et al. 1996). Extrapolation of these laboratory results is hampered by the lack of quantitative information on the variability of nutrient concentrations that individual algal cells experience in their natural environment.

Field observations on the specific growth rate of algae in different size classes within the same sample in nutrient-controlled environments are rare. In some reports, small algae were growing faster and were more heavily grazed than the larger species (Strom & Welschmeyer 1991, McManus & Ederington-Cantrell 1992, Riegman et al. 1993, Kamiyama 1994, Landry et al. 1995, Gallegos et al. 1996), whereas in other studies (Verity 1986, Paranjape 1990) no indications were found for size-differential growth and grazing rates. Also, some studies illustrate the tendency of small and large cells to prefer reduced and oxidized forms of nitrogen, respectively (Probyn 1985, Probyn & Painting 1985, Harrison & Wood 1988, Probyn et al. 1990), whereas other studies do not (Chisholm 1992, Dauchez et al. 1996). Estimated growth rates of natural phytoplankton assemblages (Riegman et al. 1993, Kristiansen et al. 1994) are usually lower than the maximum growth rate potentially achievable at the *in situ* temperature (Eppley 1972), indicating that natural populations usually are limited in their growth rate by light and/or nutrient availability.

Primary production in the upper layer of stratified and nutrient-controlled waters is usually mainly dependent on the internal regeneration of nitrogen, indicated by the uptake of ammonium and urea (sensu Dugdale & Goering 1967), and the import of nitrogen from below the photic zone, where nitrate uptake as percentage of the total nitrogen uptake (*f*-ratio; Eppley & Peterson 1979) is considered as indicative for the ratio between new and regenerative production. *f*-ratios have been reported for the central North Sea during summer stratification ranging between 12 and 55% in the surface layers (Owens et al. 1990). However, these data were established without the consideration of urea uptake, which may have resulted in a

40% overestimation of new production (Wafar et al. 1995).

Here we describe a study along a transect from the Dogger Bank area to the Shetland Islands (North Sea) during summer on size-fractionated growth rate of phytoplankton, estimated from ^{14}C-bicarbonate and ^{15}N-ammonium, urea, and nitrate uptake. In an earlier study during spring, it was found that, in the absence of stratification, new production was higher than regenerative production and algae <5 µm grew faster than larger ones in this typically light-controlled environment (Riegman et al. 1998). During the summer cruise, we investigated size-fractionated algal growth rates and the uptake of different nitrogen sources in the same area, when stratification and major nutrient availability controlled the phytoplankton communities. During summer, nitrogen is the main controlling nutrient in the upper layer of the photic zone in offshore areas of the North Sea (Riegman et al. 1990b).

MATERIAL AND METHODS

The cruise track and the location of the stations between the northern slope of the Dogger Bank (Stn H1: 55° 29' 68" N, 2° 52' 68" E) and the Shetland Islands (Station H7: 61° 00' 24" N, 0° 46' 19" E) is presented in Riegman et al. (1998). Along the transect there were 7 main stations (H0 to H7). Additionally, there were 6 sub-stations (N1 to N6) located in between these main stations, and 16 sub-stations located 32 km eastwards (E0 to E7) and westwards (W0 to W7) of the main stations. At all stations CTD profiles were obtained to provide information on temperature, light attenuation, turbidity and fluorescence between 25 July and 11 August 1994. At various depths, samples were taken with NOEX bottles for carbon fixation and chl *a* (10 and 40 m), and nutrients (at 12 different depths).

Incident solar irradiance was measured for 2 wk on board ship, using a Kipp Solarimeter. The photosynthetically available radiation (PAR) was calculated from the average daily irradiance assuming PAR to be 45% of the total irradiance and expressed as J m^{-2} s^{-1} (Lüning 1981). Light reflection at the sea surface was assumed to be 3% of the total irradiance (Vermij 1987). The underwater attenuation coefficient (K_d, m^{-1}) was calculated from underwater quantum measurements (PAR sensor, Biospherical) and fitted according to the Lambert-Beer law.

NH_4, NO_3, urea, and phosphate were measured with a TRAA autoanalyser system. NH_4 was detected immediately after sampling as indo-phenolblue-complex (pH 10.5) at 630 nm (Helder & de Vries 1979); NO_3 was reduced in a copper cadmium coil to nitrite (using imidazole as a buffer) and then measured as nitrite. NO_2 was detected after diazotation with sulphanilamide and N-(1-naphtyl)-ethylene diammonium dichloride as the reddish purple dye complex at 540 nm (Grasshoff 1967). Urea was determined within 1 mo after storage at −30°C and measured at 520 nm after condensation with diacetylmonoxime to form a pink coloured complex using thiosemicarbazide to intensify and ferrichloride to stabilize the colour. Phosphate was determined according to Strickland & Parsons (1972).

Samples for chl *a* analysis were collected by filtration (Whatman GF/F for unfractionated phytoplankton and by polycarbonate filters [Poretics, 5 µm] for the >5 µm fraction) and analyzed on board fluorometrically according to the method of Holm-Hansen et al. (1965).

Carbon fixation was estimated using the ^{14}C technique (Riegman & Colijn 1991).

Water samples were taken from 2 different depths (10 m and 40 m below the surface) and subdivided in 50 ml subsamples. Prior to incubation 5 µCi $NaH^{14}CO_3$ (Amersham) was added to subsamples in a thermostated irradiance gradient incubator at ambient temperatures. The incubator was illuminated with an Osram metallogen HMI 1200 W lamp, the spectrum of which closely resembles that of natural sunlight (Colijn 1983). Different irradiances were achieved using neutral density filters (Lee, Andover, UK). The side walls of the incubation vessels (tissue culture bottles; Greiner, Solingen, Germany) were covered with black tape to ensure illumination exclusively from the front. It was concluded from previous tests that this precaution improved the reproducibility of P/I (photosynthesis/irradiance) measurements. Irradiances were measured prior to every incubation using a Licor LI-192 SA underwater Quantum sensor. Calculation of the average irradiance of each vessel was based on in- and outcoming irradiance which was measured for each incubation series. For the establishment of 1 P/I relationship at least 7 irradiances (ranging from 10 to 3000 µE m^{-2} s^{-1}) were used. After incubation for 2 h, samples were filtered through 5 µm pore size Poretics polycarbonate membrane filters and the filtrate across Whatman GF/F filters with a gentle filtration pressure (−12 kPa relative to atmospheric pressure) to obtain size-fractionated carbon fixation rates. Filters were fumed over conc. HCl for at least 10 min and counted in a liquid scintillation counter after addition of 10 ml Instagel II (Packard Canberra). Total inorganic carbon was determined with a TOC analyzer (model 700; IO Corporation, College Station, TX, USA).

Filter absorption was found to be negligible. Dark values, never exceeding 5% of the maximum photosynthesis rate, were not subtracted from light values (Mortain-Bertrand et al. 1988).

P/I curves were fitted according to Platt et al. (1980). Daily carbon fixation profiles were calculated from the average PAR, K_d, the measured P/I relationship, and corrected for the vertical distribution of phytoplankton as indicated by the fluorescence measurements. This incubator method has been found to deviate by less than 10% from *in situ* measurements (Riegman & Colijn 1991).

Nitrate, ammonium and urea incorporation rates were estimated using ^{15}N. From 10 and 40 m depth, 1 l samples were spiked with either $^{15}NH_4^+$, $^{15}NO_3^-$ or ^{15}N-urea added in trace amounts and incubated in polycarbonate bottles. We enriched the samples with 10% of the ambient concentration, subject a minimum of 0.1 µM, to prevent isotope dilution effects during the 2 h incubation period. We corrected for this enrichment assuming that the nutrient uptake rate is linearly related to its concentration. The bottles were incubated at *in situ* temperature (9 to 12°C at 40 m and 13 to 18°C at 10 m depth) and a photon flux density of 80 µE m^{-2} s^{-1} corresponding to 10 m depth and 15 µE m^{-2} s^{-1} corresponding to 40 m depth. After 2 h, the incubation was terminated by filtration of 300 ml samples using maximally ~12 kPa. Filtration through a precombusted Whatman GF/F filter was performed to obtain the uptake by the total particulate material. The < 5 µm fraction was collected on a precombusted Whatman GF/F filter after filtration through a 5 µm pore size polycarbonate filter (Poretics). The filters were stored at −50°C for no longer than 3 mo before analysis. Filters were then dried and acidified twice with 7% H_2SO_3 to remove inorganic carbon. Particulate carbon, nitrogen and $\delta^{15}N$ were determined using a Carlo Erba Instruments NA 1500 Series 2 CNS Analyzer on line with a VG Isotech Optima Stable Isotope Mass Spectrometer. ^{15}N incorporation rates were calculated after Dugdale & Goering (1967).

The specific growth rate of phytoplankton (μ_N), based on hourly nitrogen uptake in the light, was calculated by dividing the total inorganic nitrogen uptake rate by chl *a* and assuming a cellular N/chl *a* ratio of 19 µg µg^{-1} (10 m samples) and 6.05 µg µg^{-1} (40 m samples). This ratio was calculated from the average total particulate N/total chl *a* ratio measured at all stations. Application of an average N/chl *a* ratio was chosen since there might be a variable variation in this ratio due to a contribution of non-phytoplankton species to the particulate N fraction. This could cause wrong estimates at some stations, especially when heterotrophs were much more abundant than algae.

The hourly based specific growth rate was converted to a daily rate by multiplying by $^3/_4$. This irradiance factor was introduced on the assumption that the algae experienced light only for 16 h of the day, during which time they would take up nitrogen at the same rate as under the experimental conditions. However, nitrogen uptake shows diel variability (Glibert & Garside 1992). Therefore, it was assumed that, during the 8 h dark period, the N uptake rate would be 25% of the measured uptake rate in the light (Cochlan et al. 1991).

The specific growth rate of algae, based on the measured inorganic carbon fixation rates, was calculated by dividing the daily carbon fixation of the water column by the depth of the photic zone, the chl *a* content of the photic zone, and assuming a C/chl *a* ratio of 60 (Gieskes & Kraay 1984). Additionally, this apparent growth rate was multiplied by 0.66 to yield the estimated specific growth rate. This factor was based on the assumption that during the 8 h dark period no carbon was fixed, and storage products are converted into new cell material with an efficiency in cell synthesis of 33% in order to maintain the same growth rate in the dark period (Riegman 1985). Primary production over the photic zone was calculated as the product of the specific growth rate (calculated from nitrogen uptake rate; µN), the depth of the photic zone, chl *a* and a C/chl *a* ratio of 60 for the upper mixed layer and 25 for the lower part of the photic zone around the thermocline. Statistics were performed using Student's *t*-test.

RESULTS

According to the CTD profiles, the water column was stratified at all stations along the transect. Near the Dogger Bank, at Stns H1 to H2, the thermocline was between 20 and 28 m depth. At the other stations, the thermocline was located at 30 to 40 m depth. A detailed hydrographical description of the area is presented elsewhere (Kuipers & Witte 1998). In general, the major nutrients were low in the upper mixed layer. At 10 m depth, average values for phosphate, ammonium, urea, and nitrate were 0.047 ± 0.019 (n = 32), 0.17 ± 0.05 (n = 27), 0.15 ± 0.09 (n = 26), and 0.16 ± 0.13 (n = 27) µM, respectively. In contrast to ammonium and urea, which were low along the entire transect (Table 1), nitrate was enhanced (up to 1.05 µM at Stn E7) near the Shetland Islands. At 40 m depth, i.e. 2 to 6 m below the fluorescence maximum near the thermocline, PAR was 2 to 5% of the surface PAR. At these reduced irradiances, the average levels of phosphate, ammonium, urea, and nitrate were higher compared to the 10 m values: 0.40 ± 0.13 (n = 32), 1.40 ± 0.90 (n = 34), 0.15 ± 0.06 (n = 34), and 2.61 ± 1.79 (n = 34) µM, respectively. Ammonium at 40 m varied amongst the stations, urea was below 0.5 µM, and nitrate was higher than 3 µM at all stations in the northern part of the transect (W5 to W7; Table 1).

Table 1. Dissolved nitrogen concentrations and nitrogen uptake rates (V) at 10 m and 40 m depth at the various stations along the transect from the Dogger Bank to the Shetland Islands in August/July 1994

Station no.	10 m NH_4^+	10 m NO_3^-	10 m Urea	40 m NH_4^+	40 m NO_3^-	40 m Urea	10 m $V_{NH_4^+}$	10 m $V_{NO_3^-}$	10 m V_{urea}	40 m $V_{NH_4^+}$	40 m $V_{NO_3^-}$	40 m V_{urea}
	(µM)			(µM)			(mg N m^{-3} h^{-1})			(mg N m^{-3} h^{-1})		
H1	0.14	0.11	0.20				0.089	0.015	0.105			
H1	0.10	0.09	0.05	0.14	0.10	0.11	0.017	0.007	0.045	0.038	0.023	0.075
E1				0.15	0.09	0.11				0.078	0.028	0.045
W1				0.25	0.31	0.15				0.095	0.041	0.030
N1	0.24	0.10	0.19	2.15	4.71	0.35	0.143	0.014	0.008	0.059	0.041	0.011
H2	0.22	0.10	0.12	2.05	0.87	0.21	0.424	0.010	0.094	0.137	0.023	0.070
E2	0.12	0.09	0.10	1.15	1.39	0.16	0.144	0.014	0.094			
W2	0.16	0.09	0.13	1.08	2.94	0.28				0.192	0.279	0.141
N2	0.17	0.13	0.22	0.63	0.31	0.08	0.217	0.013	0.131			
H3	0.20	0.07	0.12	0.21	0.10	0.07	0.061	0.009	0.003	0.042	0.006	0.003
E3	0.20	0.09	0.07	0.20	3.45	0.12	0.115	0.010	0.009			
W3				1.01	2.74	0.21				0.065	0.003	0.017
N3				2.43	2.91	0.28				0.049	0.010	0.003
H4	0.14	0.08	0.10	2.68	1.78	0.13	0.089	0.013	0.023			
E4				0.74	1.67	0.09				0.040	0.006	0.003
W4	0.20	0.08	0.22	1.72	1.50	0.26	0.256	0.037	0.197			
N4	0.22	0.12	0.25	0.67	1.36	0.10	0.250	0.030	0.258			
H5	0.16	0.09	0.05	0.36	0.33	0.08	0.287	0.026	0.056	0.047	0.004	0.006
E5	0.13	0.07	0.07	0.55	.023	0.12	0.196	0.020	0.057			
W5	0.11	0.08	0.11	0.34	3.62	0.13	0.154	0.018	0.088			
N5	0.02	0.04	0.06	1.57	3.78	0.12	0.039	0.020	0.069			
H6	0.12	0.07	0.12	2.01	6.38	0.12	0.232	0.055	0.129	0.020	0.005	0.001
E6	0.26	0.04	0.12	2.60	5.63	0.19	0.559	0.032	0.212			
W6	0.30	0.05	0.25	2.45	5.43	0.22	0.346	0.030	0.309			
N6	0.16	0.33	0.07	2.72	3.33	0.26	0.179	0.090	0.074	0.024	0.003	0.003
H7	0.28	0.69	0.03	2.12	6.04	0.09	0.017	0.043	0.008	0.017	0.004	0.001
E7	0.21	1.05	0.06	2.23	6.00	0.17				0.012	0.002	0.001
W7	0.16	0.26	0.04	2.78	4.88	0.15						

Chl *a* (Table 2) showed 2 opposite trends at the 2 different depths. In the upper layer, the highest chl *a* values were found near the Shetland Islands, whereas at 40 m the highest values were recorded near the northern slope of the Dogger Bank. The average value for total chl *a* along the entire transect was 0.68 ± 0.47 (n = 34) at 10m and 0.63 ± 0.42 (n = 34) at 40 m. At stations with enhanced chl *a*, the size distribution reflected in the <5 µm fraction and total chl *a* fraction was similar between most stations (Table 2). At both depths 71% of the total chl *a* was in the <5 µm fraction.

The nitrogen uptake rate (Table 1) showed a comparable distribution as chl *a*. At 10 m, lower values were found at the oligotrophic stations H1 to E3 than at W3 to E7 for ammonium and nitrate uptake. The average total nitrogen uptake rate (i.e. the sum of ammonium, urea, and nitrate uptake) was 0.31 ± 0.15 mg N m^{-3} h^{-1} (n = 24) for the total communities, and 0.23 ± 0.11 mg N m^{-3} h^{-1} (n = 22) for the fraction <5 µm. Lower nitrogen uptake rates were observed at 40 m depth: the average total nitrogen uptake was 0.12 ± 0.09 mg N m^{-3} h^{-1} (n = 17) for the total communities, and 0.10 ± 0.08 mg N m^{-3} h^{-1} (n = 15) for the fraction <5 µm. In this deeper layer, the highest activity was near the Dogger Bank (Stns H1 to W2).

The main inorganic nitrogen component taken up by the plankton was ammonium. The relative contribution of the different inorganic nitrogen substrates to the total nitrogen uptake is presented in Fig. 1.

At 10 m, nitrogen uptake by the total plankton community (Fig. 1b) for nitrate, urea, and ammonium were 9, 31 and 60% of the total nitrogen uptake, respectively (Table 3). The <5 µm fraction (Fig. 1a) showed a comparable speciation for nitrate, urea and ammonium uptake, being 8, 32 and 60%, respectively. Along the entire transect, the f-ratio for nitrate remained low in the surface layer for both size fractions. At 40 m, more nitrate, relative to the reduced nitrogen sources, was used. The nitrogen uptake of the total plankton community (Fig. 1d) for nitrate, urea, and ammonium was 17, 16 and 67% of the total nitrogen uptake, respectively (Table 3). Especially at the northern slope of the Dogger Bank, the f-ratio for nitrate was enhanced in the deeper layer (on the average 23% [n = 7] at Stns H1 to N2). Plankton in the <5 µm fraction showed also a higher relative uptake of nitrate at greater depth (Fig. 1c): at 40 m nitrate, urea, and ammonium contributed 12, 14 and 74%, respectively, to the total N uptake. At Stns H1 to N2, the f-ratio for nitrate of the <5 µm fraction (14%, n = 6) was lower than the f-ratio

Table 2. Total chl *a* and chl *a* of the particle size fraction <5 µm sampled at 10 m and 40 m depth, and gross Carbon Fixation Rate (CFR) at the various stations along the transect from the Dogger Bank to the Shetland Islands in August/July 1994

Station no.	10 m Chl *a* <5 µm	10 m Chl *a* Total	40 m Chl *a* <5 µm	40 m Chl *a* Total	CFR <5 µm	CFR Total
	(µg l^{-1})		(µg l^{-1})		(g C m^{-2} d^{-1})	
H1	0.31	0.37	0.75	1.15	0.68	0.97
E1	0.28	0.35	0.81	1.88	0.82	1.16
W1	0.27	0.30	0.99	1.45	0.61	0.80
N1	0.41	0.51	0.48	0.67	0.87	1.12
H2	0.19	0.24	0.94	1.11	0.73	1.13
E2	0.37	0.43	0.60	1.29	0.82	1.74
W2	0.33	0.44	0.50	0.97	0.35	0.80
N2	0.21	0.27	0.61	0.71	0.64	0.99
H3	0.12	0.16	0.79	0.89	–	–
E3	0.20	0.29	1.01	1.10	0.63	0.89
W3	0.25	0.31	0.48	0.62	0.83	1.03
N3	0.09	0.22	0.17	0.84	0.33	0.92
H4	0.44	0.58	0.04	0.05	0.86	1.24
E4	0.54	0.63	0.45	0.54	1.11	1.49
W4	0.33	0.40	0.19	0.32	0.82	1.06
N4	0.24	0.27	0.72	1.01	0.62	0.88
H5	0.22	0.28	0.21	0.39	0.84	1.16
E5	0.37	0.45	0.26	0.48	0.67	0.95
W5	0.22	0.29	0.36	0.41	0.77	1.18
N5	0.34	0.54	0.42	0.59	0.54	1.22
H6	1.00	1.29	0.04	0.06	0.70	1.03
E6	1.03	1.50	0.18	0.22	1.00	1.36
W6	0.58	1.06	0.10	0.13	1.37	2.16
N6	1.27	1.64	0.14	0.17	1.14	1.80
H7	1.63	2.17	0.12	0.15	0.96	1.82
E7	1.41	1.93	0.12	0.14	0.99	1.41
W7	1.65	2.43	0.04	0.11	0.88	1.86

of the total community, indicating that especially the algae >5 µm attributed to the enhanced nitrate uptake at greater depth near the Dogger Bank.

The average particulate molar C:N ratio along the transect was 6.89 ±1.26 (n = 281).

Gross carbon fixation rates were between 30 and 42 mg C m^{-3} d^{-1} at 10 m with the highest values near the Shetland Islands (Fig. 2a). A carbon fixation maximum near the thermocline (Fig. 2a) never exceeded the fixation rates at the surface. The carbon fixation rate of the <5 µm fraction showed a distribution (Fig. 2b) which was comparable to the activity of the total communities. Along the entire transect (Stns H1 to H7), the average carbon fixation rate for the total communities was 1.22 ± 0.28 g C m^{-2} d^{-1} (n = 33). On average, the <5 µm fraction contributed 65% (0.79 ± 0.18 g C m^{-2} d^{-1}, n = 33) of the total carbon fixation rate.

Relating nitrogen uptake rates and carbon fixation rates to algal biomass yielded estimates of specific algal growth rates along the transect. In general the specific algal growth rate (based on nitrogen uptake and presented as μ_N in Fig. 3) varied amongst the different stations without any significant trend. However, the specific growth rate of the communities at 40 m were generally lower than the specific growth rate of the communities at 10 m depth (Fig. 4). The average algal growth rate was 0.39 ± 0.17 d^{-1} (n = 19) for the smaller size fraction at 10 m. The larger size fraction had a slightly higher average specific growth rate (0.43 ± 0.12 d^{-1}; n = 15). For the sub-surface communities (at 40 m), a lower μ_N was observed: 0.17 ± 0.09 d^{-1} (n = 15) for the <5 µm fraction. At this greater depth, the larger phytoplankton were growing significantly more slowly ($p < 0.025$) than the smaller species: μ_N = 0.10 ± 0.06 d^{-1} (n = 15) for the >5 µm fraction.

The chl *a* specific carbon uptake rates (μ_C), which yielded estimates of the specific growth rate (averaged

Table 3. Values for chl *a*, nutrients, nitrogen uptake rates and specific growth rates, averaged for all stations along the transect from the Dogger Bank to the Shetland Islands in August/July 1994, measured at 10 m and 40 m depth. Data are presented as mean value ± standard deviation (number of samples)

	10 m	40 m	Units
Chl *a* (<5 µm)	0.50 ± 0.33 (34)	0.43 ± 0.29 (34)	µg l^{-1}
Chl *a* (total fraction)	0.68 ± 0.47 (34)	0.63 ± 0.42 (34)	µg l^{-1}
Ammonium	0.17 ± 0.05 (27)	1.40 ± 0.90 (34)	µM
Urea	0.15 ± 0.09 (26)	0.15 ± 0.06 (34)	µM
Nitrate	0.16 ± 0.13 (27)	2.61 ± 1.79 (34)	µM
Total N-uptake rate (<5 µm)	0.23 ± 0.11 (22)	0.10 ± 0.08 (15)	mg N m^{-3} h^{-1}
Total N-uptake rate (total fraction)	0.31 ± 0.15 (24)	0.12 ± 0.09 (17)	mg N m^{-3} h^{-1}
f-ammonium (<5 µm)	60 ± 13 (22)	74 ± 15 (16)	% of total N uptake by <5 µm fraction
f-urea (<5 µm)	32 ± 14 (22)	14 ± 11 (16)	% of total N uptake by <5 µm fraction
f-nitrate (<5 µm)	8 ± 4 (22)	12 ± 9 (16)	% of total N uptake by <5 µm fraction
f-ammonium (total fraction)	60 ± 12 (24)	67 ± 15 (17)	% of total N uptake by total fraction
f-urea (total fraction)	31 ± 13 (24)	16 ± 11 (17)	% of total N uptake by total fraction
f-nitrate (total fraction)	9 ± 5 (24)	17 ± 7 (17)	% of total N uptake by total fraction
μ_N (<5 µm)	0.39 ±0.17 (19)	0.17 ±0.09 (15)	d^{-1}
μ_N (total fraction)	0.38 ±0.16 (17)	0.12 ±0.11 (15)	d^{-1}

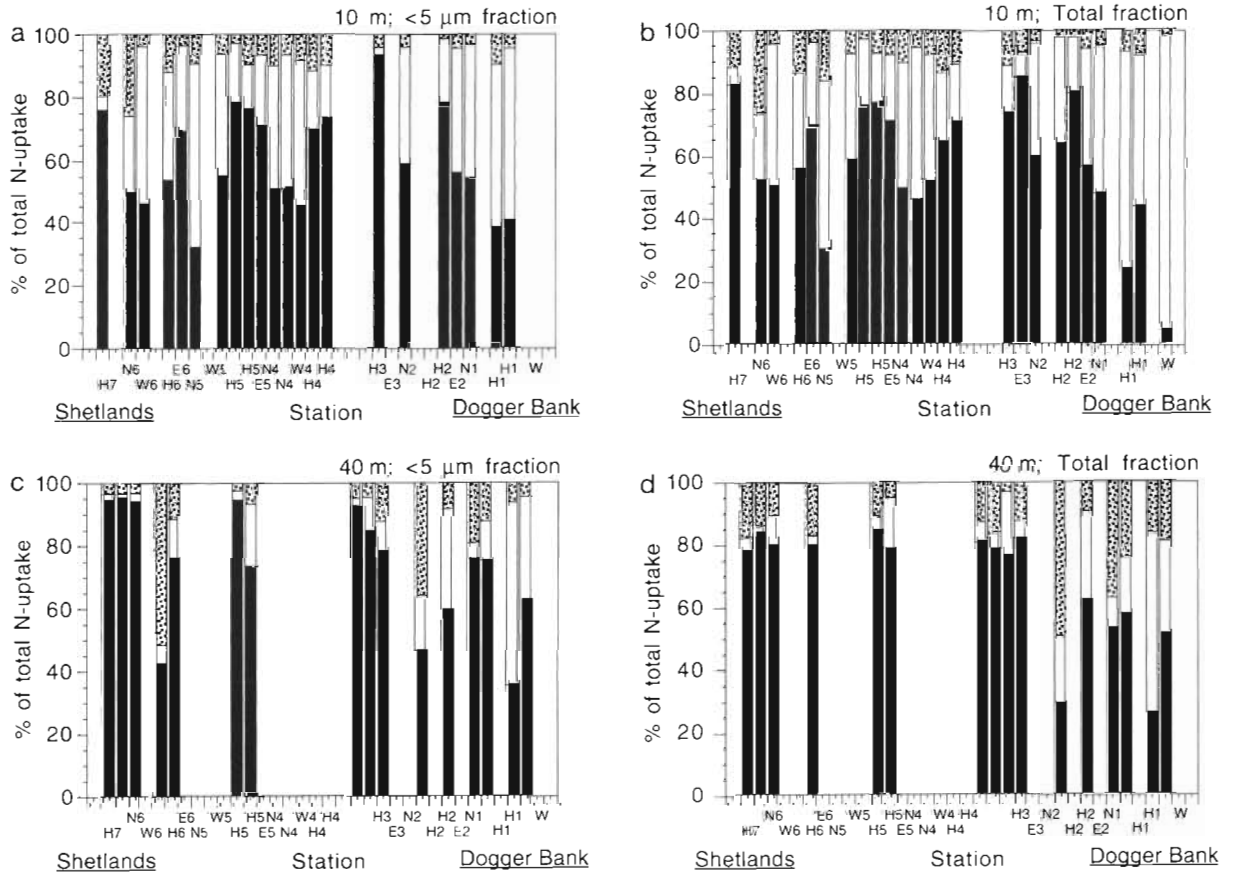

Fig. 1. Relative uptake rates of nitrate (upper, dotted), urea (middle, white), and ammonium (lower, black), calculated as percentage of the total nitrogen uptake rate by the specified fraction, at the different stations for: (a) the <5 µm fraction at 10 m, (b) the total community at 10 m, (c) the <5 µm fraction at 40 m, and (d) the total community at 40 m

over the photic zone), showed an even stronger variation than μ_N (Fig. 5). A significantly higher ($0.1 > p > 0.05$), specific growth rate (μ_C) for the total communities was found (0.47 ± 0.21 d^{-1} [n = 32] versus 0.41 ± 0.14 d^{-1} [n = 33] for the >5 µm size fraction). These calculated specific growth rates, based on inorganic carbon uptake, were in reasonably good agreement with the data calculated from nitrogen uptake.

Apparently, the smaller algae grew faster than the larger ones only in the typically light-controlled deeper layers. However, in the nutrient-controlled surface layer the larger species grew as fast as, or even faster than, the smaller species.

Primary production, defined as the daily net biomass production by phytoplankton, was calculated from the specific phytoplankton growth rate (estimated from

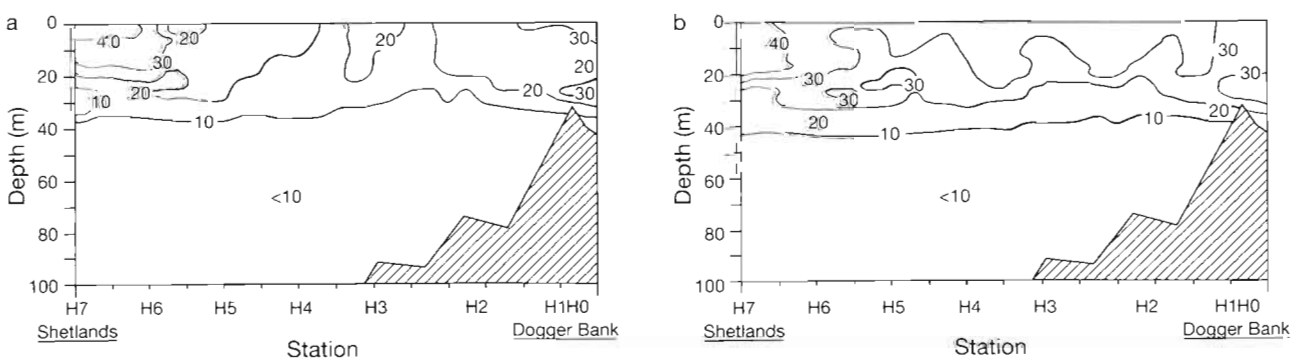

Fig. 2. Carbon fixation rates (mg C m^{-3} d^{-1}) by (a) the <5 µm fraction and (b) the total communities along the transect during summer 1994

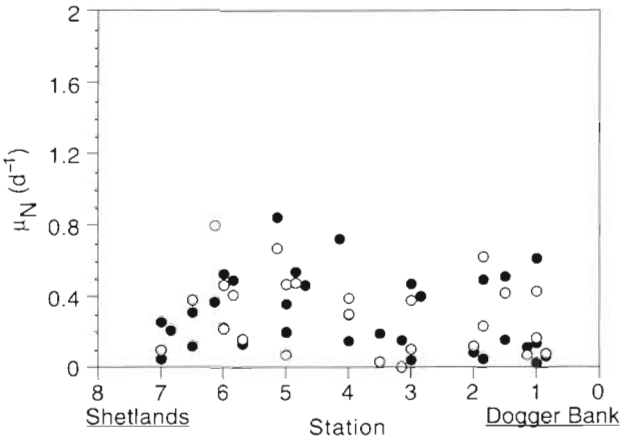

Fig. 3. Specific growth rate of phytoplankton, calculated on the basis of nitrogen uptake (μ_N), for the algae <5 µm (●) and the total phytoplankton communities (○). Data from 10 m and 40 m samples

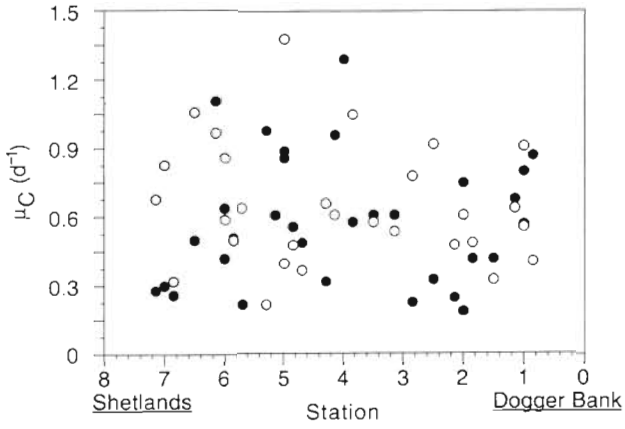

Fig 5. Specific growth rate of phytoplankton, calculated on the basis of inorganic carbon uptake (μ_C), for the algae <5 µm (●) and the total phytoplankton communities (○)

nitrogen uptake) and the actual biomass of the populations. Along the entire transect, primary production varied up to a factor 8 between the different stations (Fig. 6). Average values for the <5 µm fraction and the total community were 0.37 ± 0.19 g C m^{-2} d^{-1} (n = 20) and 0.50 ± 0.26 g C m^{-2} d^{-1} (n = 20), respectively.

DISCUSSION

In combination with previous findings along the same transect during spring (Riegman et al. 1998), 3 essentially different environments can be distinguished. First, in spring, the phytoplankton was irradiance controlled, the main nitrogen source was nitrate, and the algae <5 µm grew faster than the larger ones. Second, in summer, at 40 m depth, major nutrients were in excess and low irradiance levels prevailed. Just below the thermocline the community was irradiance controlled, the main nitrogen source was ammonium, and again the algae <5 µm grew faster than the larger ones. Third, at 10 m depth during summer stratification, major nutrients were depleted, irradiance in excess (Riegman et al. 1990a), and reduced nitrogen (ammonium + urea) was the main nitrogen source. Here, algae in the small size class grew at a similar rate to the larger ones.

From this comparison it could be concluded that in light-controlled environments smaller algae grow

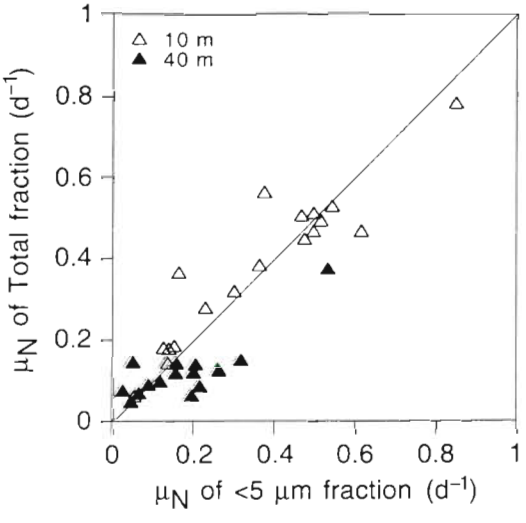

Fig. 4. Relationship between the specific growth rates of the total communities and the specific growth rates of the <5 µm fraction (both estimated from chl *a* specific nitrogen uptake), collected at 10 m (△) or 40 m (▲) depth

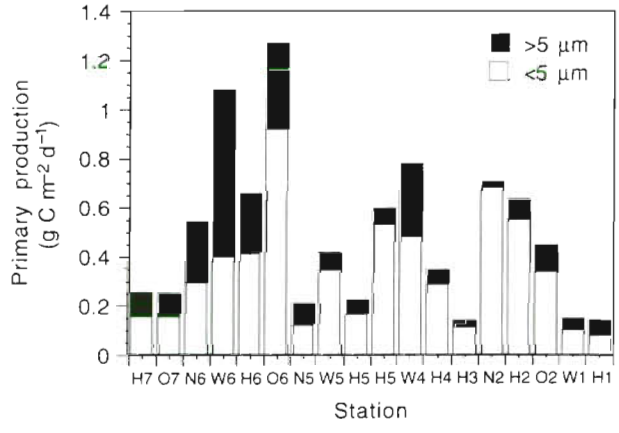

Fig. 6. Primary production, presented cumulatively, of the >5 µm phytoplankton (black) and the <5 µm size fraction (grey), calculated as the product of algal biomass and their specific growth rates estimated from nitrogen uptake, along the transect

faster than larger ones, irrespective of whether ammonium or nitrate was consumed. This conclusion is in agreement with the theoretical prediction of Raven (1984), who calculated the growth rate of algal cells on the basis of their size-related irradiance harvesting and cell synthesis efficiency. Basically, he concluded that larger cells should be poorer competitors for light than smaller ones, since the ratio between cellular photon absorption and the energy requirement for cell synthesis decreases with cell size. Apparently, the redox status of the consumed nitrogen had no differential effect on the growth rate of algal size classes under light limitation. This is in agreement with former laboratory studies (Thompson et al. 1989, Levasseur et al. 1993) which showed that the use of ammonium rather than nitrate is of little energetic importance in terms of growth rate at low photon flux densities. Despite their higher specific growth rate, the <5 µm algae were not capable of building up biomass to the same extent as the >5 µm species. We observed the same phenomenon during a spring bloom in Dutch coastal waters, where the biomass of the smallest and fastest growing algal size fraction was kept under microzooplankton grazing control, thereby gradually channelling the nutrients into the poorly grazed size fraction of larger algae (Riegman et al. 1993).

During summer stratification, ammonium, nitrate and urea were present in equal, and low, amounts (Table 3) in the upper layers. Yet, there was a preference for nitrogen in the reduced form, as indicated by the contribution of ammonium and urea, being 60 and 32%, respectively, of the total nitrogen uptake for the <5 µm fraction and 60 and 31%, respectively, for the total community. According to experimental research, large algae can accumulate nitrogen just as fast as smaller cells under nitrogen limitation, if reduced nitrogen is the major nitrogen source (Stolte et al. 1994). Our field data consolidate these findings: the specific growth rate of the <5 µm fraction (0.39 d^{-1}) was comparable to the specific growth rate of the >5 µm fraction (0.38 d^{-1}). However, it should be kept in mind that there is another possible explanation for the observation of the absence of size differential growth rates. The >5 µm fraction may have been dominated by colonies or chains of small cells expressing the same physiological activities as cells in the <5 µm fraction. Unfortunately, we have no microscopical information to exclude this alternative explanation.

It has been argued that the advantage of larger algal species having a higher storage capacity for nitrate in their vacuole will only result in higher growth rates of larger species than smaller ones when nitrate is the major nitrogen source under fluctuating, nitrogen limiting conditions (Stolte & Riegman 1995). This situation may have prevailed at the stations near the Shetland Islands (N6 to W7), where enhanced nitrate levels were present in the photic zone and the highest *f*-ratios for nitrate (26.3 to 27.1 %) in the surface layers were found. Here, the specific growth rate of the algae >5 µm was much higher (0.43 d^{-1}) than that of the <5 µm fraction (0.10 d^{-1}).

The algal biomass distribution (estimated from chl *a*) between the different size fractions did not reflect the differences in specific growth rates. This indicates that loss factors may have been more decisive for the observed size distribution in biomass than growth properties. During spring, reduced losses due to sedimentation and grazing in a well-mixed water column with a low abundance of mesozooplankton (Fransz et al. 1998) may have resulted in the dominance of larger algal species (Kuipers & Witte 1998, Riegman et al. 1998). Picoalgae biomass is usually fairly constant over the entire range of total chl *a* in water masses (Raimbault et al. 1988, Søndergaard et al. 1991), increasing only occasionally above 1 µg l^{-1} (Søndergaard et al. 1991). During summer, a stratified water column may have facilitated a shift in biomass towards smaller algae, due to their lower sedimentation losses in this type of environment compared to larger algae (Kiørboe et al. 1990, Kiørboe 1993). Also, mesozooplankton biomass was much higher during summer as compared to spring, which may have facilitated additional grazing losses of the larger algae (Banse 1994).

There are several indications that the difference between large and small phytoplankton in taking up new nitrogen is less clear than previously thought. Apart from differences between size classes in their acclimation of nitrogen uptake, being dependent on the controlling factor as argued above, biomass distribution, being affected by loss factors, will have an additional impact on size fractionated nitrogen uptake. For example, if the spring bloom is largely dominated by large phytoplankton, most of the new production (i.e. nitrate uptake) will be performed by these algae, even if they grow somewhat more slowly than the smaller species. Vice versa, an autumn bloom, which follows a period of stratification and a more than 80% predominance of small species, may show the highest new production in the smallest size class, even if the larger algae, being much lower in abundance, have a higher affinity for nitrate (as observed by e.g. Dauchez et al. 1996).

The nitrate *f*-ratio of the total communities was on average 10% higher than the *f*-ratio of the <5 µm fraction. This may very well have been due to bacterial nitrogen uptake with a preference for reduced nitrogen, which would be most pronounced in the smallest size fraction (Harrison & Wood 1988). In the surface layers with equal amounts of ammonium, nitrate, and urea, ammonium was taken up twice as fast as urea. This is in agreement with findings in the Barents Sea

(Kristiansen et al. 1994), in Antarctica (Cochlan et al. 1993), in the Skagerrak (Karlson et al. 1996) and earlier measurements (Eppley & Peterson 1979). However, it should be mentioned that the contribution of urea (amongst others produced by heterotrophic microflagellates) (Andersson et al. 1985) to the total nitrogen uptake can vary from 3% to more than 91% (McCarthy 1972, McCarthy et al. 1977, Bury et al. 1995, Takahashi et al. 1995).

New production was 9 and 17% in the surface and deeper layers, respectively. In a comparable study on the thermally stratified central North Sea in 1987, Owens et al. (1990) also identified ammonium as the major nitrogen source assimilated, with a nitrate *f*-ratio of 25% in the surface waters. Urea uptake was not included in this study. Non-inclusion of urea uptake would have led to a 44% overestimation of the nitrate *f*-ratio according to our data, which is comparable to the expected 42% as reported for oceanic waters (Wafar et al. 1995). Correction of the data from Owens et al. (1990) for urea uptake yields a *f*-ratio for nitrate of 17%, which is somewhat higher than we measured 7 yr later. In general, new production near the thermocline was twice that near the surface. Net primary production, calculated on the basis of nitrogen uptake, was 42% of the gross ^{14}C fixation rates, and showed a considerable variation amongst the different stations. This variation indicates that carbon fixation is quite uncoupled from algal growth in nutrient-controlled systems.

Summarizing, it can be stated that size-partitioning of algal growth rate appears to depend on the character of the growth rate limiting factor. Smaller algae grew faster than larger ones in light-controlled environments, regardless of the nitrogen source which was consumed.

In typically nitrogen-controlled surface layers, no size partitioning of algal growth rate was present when ammonium was the major nitrogen source. At some stations, where nitrogen limitation co-occurred with enhanced nitrate consumption, larger algae did grow faster than smaller ones.

The algal biomass in different size classes was not related to the estimated growth rates of these different categories. Apparently, larger algae do not dominate during summer in the surface layers of the stratified central North Sea, since mesozooplankton densities are high compared to spring and vertical mixing in the photic zone is low. In the lower part of the photic zone, the larger algae do not dominate since they grow much slower than the smaller species due to light limitation.

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