

Top-down control of phytoplankton biomass and community structure in the monsoonal Arabian Sea

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Abstract

During the 1995 monsoons, phytoplankton biomass was low over large areas of the Arabian Sea in spite of often high concentrations of inorganic nutrients, characteristics typical of high-nutrient, low-chlorophyll (HNLC) areas. The objective of this study, a part of the Arabian Sea U.S. JGOFS program, was to elucidate controls of phytoplankton biomass and community structure in these areas, using primarily pigment-based methods. Unlike other HNLC areas, phytoplankton biomass and growth rates in the monsoonal Arabian Sea were not likely limited by the availability of trace nutrients but rather controlled by grazers. Evidence for this conclusion is high concentrations of iron, the nutrient likely limiting phytoplankton biomass in other HNLC areas; phytoplankton growth rates clearly not limited by concentrations of inorganic nutrients; blooms during grow-out experiments in the absence of mesozooplankton; rates of microzooplankton and mesozooplankton grazing that approached rates of primary production; and the absence of blooms in situ in spite of persistently high concentrations of inorganic nutrients. A more detailed look at shifts of phytoplankton community structure with increasing levels of phytoplankton biomass, in situ and during grow-out experiments, shows that diatoms were the only group of organisms capable of blooming in the absence of mesozooplankton, i.e., their abundance in situ was likely controlled by mesozooplankton grazing. Changes in the abundance of different picocautotroph taxa with increasing levels of phytoplankton biomass suggest that their biomass was controlled within tight bounds by microzooplankton grazing, rather than by the availability of resources. Thus, these results are consistent with the hypothesis that phytoplankton abundance and community structure in the HNLC areas of the monsoonal Arabian Sea are controlled by top-down forces, grazing, rather than bottom-up forces, availability of resources.

The phytoplankton of the open ocean is usually a complex assemblage of up to hundreds of species. These species are drawn from diverse taxonomic groups characterized by dramatically differing physiologies. Understanding and predicting the structure of a community at the species level is virtually impossible. However, viewing ‘the phytoplankton’ as a single ecological and physiological unit neglects attributes of different groups of phytoplankters that can have important impacts on cycles of energy and matter in the ocean. The problem is an aggregation problem: Even though systems are most accurately represented by the assemblage of their species populations, such an approach is not feasible if the number of these populations is large (O’Neill et al. 1986). Instead, aggregates of the species populations have to be defined such that the properties of these aggregates and their interactions with the rest of the system can be used to ex-

plain the phenomena under investigation.

The type of aggregate chosen as a unit of study depends on the phenomena of interest, e.g., rates of primary production, controls on biomass. Approaches based on size capture some of the functional differences between groups of phytoplankters but fall short at times, as dramatic physiological and ecological differences between large diatoms and large dinoflagellates illustrate. Taxonomic units defined by taxon-specific pigments represent an alternative approach that has been used extensively over the last 30 yr to describe the structure of marine phytoplankton communities (Jeffrey et al. 1997). Yet, evidence that these pigment-defined taxa represent ecologically meaningful units has been scarce, primarily because the methods that allow us to study the physiological characteristics of these taxa have become available only recently, i.e., the Landry and Hassett (1982) dilution method coupled with pigment analysis and the carotenoid-labeling method (Gieskes and Kraay 1989; Goericke and Welschmeyer 1993a). Studies based on these two methods have shown consistent physiological differences between pigment-defined taxa.

It is the objective of this study to characterize the distribution and abundance of algal taxa in the monsoonal Arabian Sea and to elucidate the factors and forces that control phytoplankton biomass and community structure. During the monsoons, the Arabian Sea is unlike any other tropical or subtropical open ocean. Physical forcing dominates the system during both monsoon seasons (Smith et al. 1998). Mixed-layer concentrations of macronutrients are high over large areas, in particular during the northeast monsoon (Morrison et al. 1998). However, phytoplankton biomass is low,

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as characteristic of high-nutrient low-chlorophyll (HNLC) areas (Barber et al. 2001). Unlike other HNLC regions, iron is most likely not the nutrient limiting phytoplankton biomass (Measures and Vink 1999) since an ample aeolian supply exists (Tindale and Pease 1999). These observations suggest that phytoplankton biomass in the monsoonal Arabian Sea could be controlled by grazers, i.e., by top-down forces. A corollary of this hypothesis is that rates of phytoplankton growth and microzooplankton and mesozooplankton grazing are balanced. Indeed, the results of Caron and Dennett (1999), Landry et al. (1998) and Roman et al. (2000) suggest that this is the case. To complete this argument, I will show here that phytoplankton growth rates were high, likely unconstrained by the availability of resources, and that the phytoplankton had the potential to bloom in the absence of grazers. Data on the abundance and growth rates of different taxa suggest that the biomass of picoautotrophs was controlled by microzooplankton and that the biomass of diatoms was controlled by mesozooplankton. These observations constitute strong circumstantial evidence that phytoplankton biomass and community structure in the HNLC regions of the monsoonal Arabian Sea were primarily controlled by the grazing of microzooplankton and mesozooplankton, rather than physical and chemical parameters, i.e., this is a system that is controlled by top-down forces (grazing) rather than bottom-up forces (availability of resources).

Methods

Pigment analysis—Samples for pigment analysis by high-pressure liquid chromatography (HPLC) were collected and processed as described previously (Goericke and Repeta 1993): To summarize, 1 to 4 liters of seawater were filtered on glass fiber filters (25 mm Whatman GF/F), which were stored in liquid nitrogen until analysis aboard the ship or ashore. Filters were extracted in 1.5-ml acetone (soak-grind-soak) and analyzed by C8 column reverse-phase HPLC (rp-HPLC). Samples from the mixed layer were also run on a C18 column based rp-HPLC system for the quantitation of zeaxanthin and lutein. Concentrations of the taxon-specific pigments chlorophyll *a* (Chl a_1), divinyl-chlorophyll *a* (Chl a_2), chlorophyll *b* (Chl b_1), divinyl-chlorophyll *b* (Chl b_2), zeaxanthin, lutein, fucoxanthin, 19'-butanoyloxyfucoxanthin (but-fucox), 19'-hexanoyloxyfucoxanthin (hex-fucox), peridinin, prasinoxanthin, and alloxanthin were determined, as well as nonspecific pigments Chl $c_{1,2}$, Chl c_3 , diadinoxanthin, diatoxanthin, α -carotene, and β -carotene. Contributions of chemotaxonomically defined taxa to total chlorophyll *a* (TChl a = Chl a_1 + Chl a_2) were calculated as described previously (Goericke and Montoya 1998). The Chl a_1 /pigment ratios (K) that were used are $K(\text{peridinin}) = 1.40$ for dinoflagellates, $K(\text{fucoxanthin}) = 1.43$ for diatoms, $K(\text{hex-fucox}) = 1.27$ for prymnesiophytes, $K(\text{but-fucox}) = 1.21$ for pelagophytes, $K(\text{zeaxanthin}) = 0.66$ for *Synechococcus*, $K(\text{neoxanthin}) = 7.31$ for chlorophytes, and $K(\text{alloxanthin}) = 5.03$ for cryptophytes. The ancillary ratios were $K(\text{hex-fucox/fucox}) = 0.097$ for prymnesiophytes, $K(\text{hex-fucox/but-fucox}) = 0.22$ for pelagophytes, and $K(\text{Chl } a_2/\text{zeaxanthin}) = 1.08$ for *Prochlorococcus*. Tests for independence

from initial conditions were carried out by performing optimizations using widely varying initial pigment ratios.

The above approach assumes that diatoms are the only group that have fucoxanthin as their major accessory pigment; this assumption does not hold perfectly since some strains of *Phaeocystis* exist that have fucoxanthin, rather than hex-fucox, as their major accessory pigment (Jeffrey and Wright 1994). Indeed, blooms of *Phaeocystis* were observed in the Arabian Sea during the late southwest monsoon (cruise TN50) but not during the late northeast monsoon (cruise TN43; Garrison et al. 2000); information for the early southwest monsoon (cruise TN49) is not available. However, it is unknown whether *Phaeocystis* sp. present during TN43 and TN49 were strains with fucoxanthin or hex-fucox; Latasa and Bidigare (1998) presented evidence that *Phaeocystis* sp. present during the late southwest monsoon had some fucoxanthin. It is possible to test for the presence of *Phaeocystis* sp. with high concentrations of fucoxanthin (Latasa and Bidigare 1998). If such strains contribute significantly to biomass, ratios of Chl c_3 and prymnesiophyte + pelagophyte pigment biomass are expected to be unusually high. During TN43, TN49, and TN54 the average ratio was 0.19 ± 0.07 ($n = 219$). At one station (TN49, S2) values of 0.63 to 0.68 were observed; at all other stations values ranged from 0.09 to 0.42. The latter values are well within the range of Chl c_3 /Chl a_1 values reported for different strains of prymnesiophytes (Jeffrey and Wright 1994) and thus suggest that *Phaeocystis* sp. with fucoxanthin did not contribute significantly to pigment biomass. The higher ratio of 0.65 at station S2 during TN43 suggests that *Phaeocystis* sp. with significant concentrations of fucoxanthin may have been present at this one station.

Grow-out experiments—Water for grow-out and pigment-labeling experiments (*see below*) was collected using a trace-metal clean rosette until it was lost midway during TN49 (Barber et al. 2001). After the loss a normal rosette was used. The water was transferred from GoFlo or Niskin bottles into acid-cleaned and Milli-Q-water rinsed polycarbonate bottles using silicone tubing; the water was not pre-screened. The bottles were incubated aboard the ship in a seawater-cooled Plexiglas incubator covered with window-screen, which attenuated the irradiance. For grow-out experiments seawater with high levels of nutrients (1.5–13 μM nitrate) was incubated in 2.8-liter bottles. For daily sampling, the contents of a whole bottle were partitioned into four 50-ml samples (one for nutrient analysis and three for TChl *a* analysis by fluorometry) and the residual was filtered, as described above, for pigment analysis by HPLC. During TN43, experiments were performed at 60 and 36% of the surface irradiance (I_0) and treatments (time point, irradiance) were not replicated except for the time zero (duplicate). No significant difference was observed between the 60 and 36% irradiance treatments (data not shown), and these were treated as replicates, i.e., each time point represents the results of two independent incubations. During TN49, incubations were only carried out at 60% I_0 but each time point was replicated. Thus, a total of five experiments were performed; each experiment consisted of a time zero and three or four replicated time points. Taxon-specific net

growth rates (d^{-1}) were determined by fitting pigment concentrations (P) to the equation $P(t) = P_0 \exp((\mu - g)t)$, where $\mu - g$ represents the net growth rate, i.e., the difference between the instantaneous rate of growth (μ) and the phytoplankton-biomass-specific rate of grazing (g).

Pigment-labeling experiments—Water was sampled and incubated for pigment-labeling experiments as described above, except that 4.4- or 8.8-liter polycarbonate bottles were used. The incubation bottles were inoculated with ^{14}C -labeled bicarbonate at first light and incubated for 24 h. Light in the incubation bottles was attenuated to 60 and 36% surface irradiance using nickel-density screens. Primary production experiments were also carried out at the same time in situ on the array described by Barber et al. (2001). Samples from pigment-labeling experiments were processed and instantaneous growth rates (μ) were calculated from rates of ^{14}C pigment labeling as previously described (Goericke and Welschmeyer 1993a,b). Growth rates of diatoms, green algae, dinoflagellates, prymnesiophytes, pelagophytes, cyanobacteria, and *Prochlorococcus* sp. were calculated from the labeling of fucoxanthin, lutein, peridinin, hex-fucox, but-fucox, zeaxanthin, and Chl a_2 , respectively. Phytoplankton community growth rates, to be reported elsewhere, were calculated from the labeling of Chl a_1 and Chl a_2 . During the northeast monsoon, Caron and Dennett (1999) measured phytoplankton growth and microzooplankton grazing rates using the Landry-Hassett dilution method. On average, the two measurements of growth rates were identical with a ratio of 1.02 ± 0.22 ($n = 7$, excluding Caron's growth rate of $-0.02 d^{-1}$ for Sta. S15). This comparison shows that the set of data consisting of pigment-labeling- and dilution-method-derived growth rates is internally consistent.

Strictly speaking, pigment-labeling methods only allow one to measure specific rates of pigment synthesis that equal rates of growth only if growth is balanced (Goericke and Welschmeyer 1993a). Thus, results for photosynthetically active pigments can be biased if the algae photoacclimate during the incubation. Since mixed layers were deep at some stations (Gardner et al. 1999), it is possible that phytoplankton sampled at these stations were adapted to an irradiance lower than the irradiance where these were incubated. As a consequence, growth rates derived from the labeling of photosynthetically active pigments may be negatively biased. However, growth rates derived from the labeling of pigments that are not photosynthetically active, such as zeaxanthin, are not expected to be biased. Thus, a sign for an acclimation to a higher irradiance during the incubation would be a higher specific rate of pigment synthesis for low-light incubations compared to high-light incubations for pigments such as Chl a_1 and the absence of such a difference for pigments such as zeaxanthin. The differences between specific rates of zeaxanthin synthesis at 60 and 36% I_0 are plotted in Fig. 1 against the differences between specific rates of Chl a_1 synthesis at 60 and 36% I_0 . Light limitation of growth would move the data points into the upper right quadrant, and photoinhibition would move the data into the lower left quadrant, assuming that cyanobacteria and other autotrophs are similarly affected. Acclimation to a higher irradiance would lead to higher Chl a_1 growth rates at low light but would

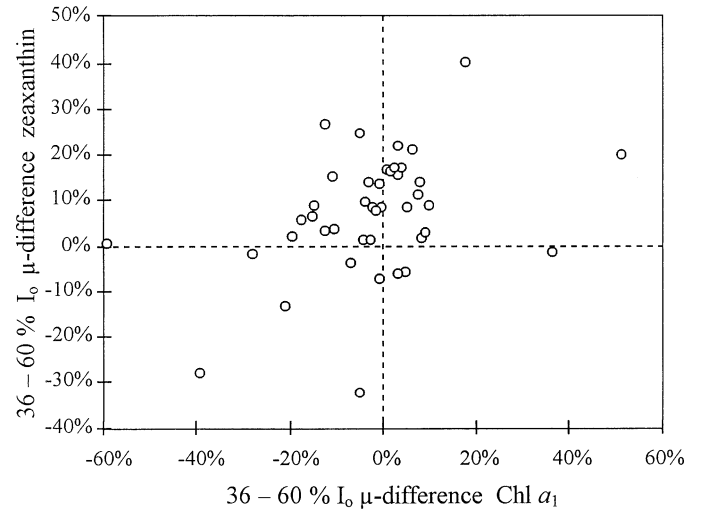


Fig. 1. The percentage difference between the zeaxanthin-based growth rate at 36 and 60% I_0 is plotted against the percentage difference between the Chl a_1 -based growth rate at 36 and 60% I_0 to determine the effects of photoacclimation on pigment-labeling-method based measurements of phytoplankton growth rates.

not affect growth rates based on zeaxanthin, i.e., would shift data into the two left quadrants. Since the percentage difference between the 60 and 36% I_0 Chl a_1 growth rates is on the average 0% for TN43 and -5% for TN49, it can be concluded that the effect of photoadaptation on measurements of growth rates was small if present at all. There were only very few large differences between the specific rates of Chl a_1 synthesis at 60 and 36% I_0 that were not matched by similarly large differences between specific rates of zeaxanthin synthesis at 60 and 36% I_0 (Fig. 1), which suggests that growth rates determined from the labeling of photosynthetically active pigments were not severely biased by photoadaptation.

Statistical tests—Standard errors of averages are designated by \pm in the text. Linear least squares regressions were performed on some data sets to obtain functions that best describe the dependence of one variable on another. Note that this procedure, as opposed to significance testing, does not require any assumptions regarding the distributions of the data. The significance of these linear relationships (b not equal to 0) was tested using a nonparametric test, Spearman's ρ (Conover 1999). Monod kinetics were used to explore the dependence of taxon-specific growth rates on concentrations of inorganic nutrients present at the beginning of the incubations; e.g., concentrations of nitrate ($[NO_3]$),

$$\mu = \mu_{\max} \frac{[NO_3]}{k_{NO_3} + [NO_3]} \quad (1)$$

to determine maximum growth rates (μ_{\max}) and the apparent half-saturation constant (k_{NO_3}) of growth with respect to concentrations of nitrate. To explore the colimitation of growth by concentrations of nitrate and ammonia ($[NH_4]$), the data were also fitted to a formulation given by Cullen et al. (1992),

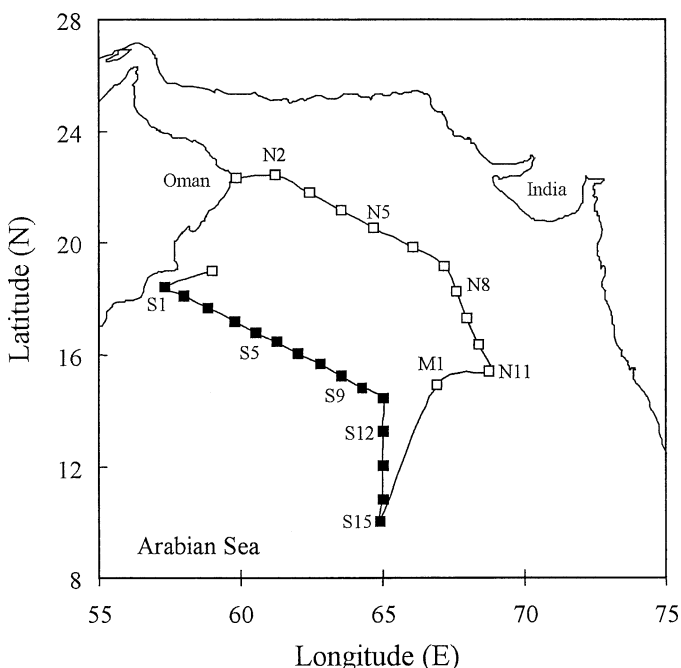


Fig. 2. A map of the Arabian Sea with the cruise track and station names.

$$\mu = \mu_{\max} \frac{N}{1 + N} \quad \text{for } N = \frac{[\text{NO}_3]}{K_{\text{NO}_3}} + \frac{[\text{NH}_4]}{K_{\text{NH}_4}} \quad (2)$$

The parameters K_{NO_3} and K_{NH_4} are effective half-saturation constants for growth on NO_3 and NH_4 . The Solver module of Microsoft Excel, with the minimization of least squares as a conversion criterion, was used to determine these parameters through nonlinear curve fitting (Goericke and Welschmeyer 1993b).

Results

The physical environment—This study is based on data collected as part of the U.S. JGOFS Arabian Sea program during the northeast monsoon (TN43, January 1995) and the first half of the southwest monsoon (TN49, July–August 1995). Data from the beginning of the 1995/1996 northeast monsoon (TN54, November–December 1995) are also included in some data sets (pigments, physical variables). Data will be presented for a northern transect (Fig. 2 stations N1–N11, M1) and a southern transect (Fig. 2 stations S1–S15).

During the northeast monsoon in 1995, convective overturning deepened mixed layers (Fig. 3A) and entrained nutrient-rich water over large areas of the study domain into the surface layer. As a consequence, concentrations of inorganic nutrients were high at almost all stations (Fig. 3B). Convective overturning as well as Aeolian deposition enriched the mixed layer with trace metals; concentrations of iron ranged from 0.48 to 2.4 nM (Measures and Vink 1999). Oligotrophic conditions were only observed at the southernmost station, S15. Surprisingly, phytoplankton biomass (i.e., TChl *a* Fig. 3C) only ranged from 0.4 to 1.0 $\mu\text{g Chl } a \text{ L}^{-1}$ in the offshore areas.

During the southwest monsoon upper ocean dynamics were dominated by wind-driven entrainment. Deep mixed layers were observed throughout the study domain, but particularly in the offshore areas (Fig. 3D). Concentrations of nitrate were more variable compared to the northeast monsoon, ranging from low or undetectable values along the eastern or southern portions of both transects to values as high as 12 μM in a filament at station S6 (Morrison et al. 1998) and closer to the coast (Fig. 3E). Aeolian input of trace metals to the surface ocean was particularly important during this time; concentrations of iron in the mixed layer ranged from 0.6 to 2.4 nM (Measures and Vink 1999). In spite of the large variability of inorganic nutrient concentrations, TChl *a* was remarkably constant along both transects, ranging from 0.25 to 0.75 $\mu\text{g L}^{-1}$, but for areas close to the coast values as high as 1.6 $\mu\text{g L}^{-1}$ were observed (Fig. 3F).

A systematic relationship was observed between sea surface temperature (SST) and concentrations of nitrate in the mixed layer (Fig. 4A), as is typical for upwelling regions (Morrison et al. 1998). Concentrations of nitrate and ammonia were significantly correlated (Fig. 4B), although variance in nitrate concentrations explained by concentrations of ammonia was small, 22%. Concentrations of nitrate and ammonia covaried more tightly in a data set confined to those stations where growth rate experiments were performed, particularly for $[\text{NO}_3] < 5 \mu\text{M}$ (data not shown). TChl *a* was significantly related to SST and concentrations of nitrate, but the predictive relationships were weak (Fig. 4C,D).

Phytoplankton community structure—Contributions of different taxonomic groups to TChl *a* were calculated from concentrations of taxon-specific pigments as measured by HPLC. The taxonomic units delineated by these taxon-specific pigments are variable, ranging from a single genus in the case of *Prochlorococcus* sp. (i.e., Chl *a*₂) to classes such as dinoflagellates (peridinin) or cryptophytes (alloxanthin). The contributions of the different taxonomic groups to TChl *a* were quite similar for the two monsoon seasons along both transects (Fig. 5) with the exception of *Prochlorococcus*, which contributed significantly to phytoplankton biomass only during the southwest monsoon along the N transect. Prymnesiophytes, characterized by hex-fucox, were the most abundant group of autotrophs in the offshore areas. Prymnesiophytes, characterized by fucox, i.e., some strains of *Phaeocystis* sp., may have been present only at Sta. S2 during the early southwest monsoon (see *Methods*). At stations close to the coast, diatoms contributed up to 60% to TChl *a*. Offshore the contribution of diatoms was smaller, except for the southernmost portions of both transects (M1, S13–15) during the southwest monsoon. The abundance of diatoms covaried significantly, but not strongly, with concentrations of nitrate and mixed-layer depth but did not covary significantly with concentrations of silicate (Fig. 6).

Contributions of *Prochlorococcus* to TChl *a* were highly variable, ranging from undetectable close to the coast to more than 50% of the total during the southwest monsoon along the N transect (Fig. 5). During the northeast monsoon, the highest contributions of *Prochlorococcus* to TChl *a* were observed at the southern ends of the transects. The contri-

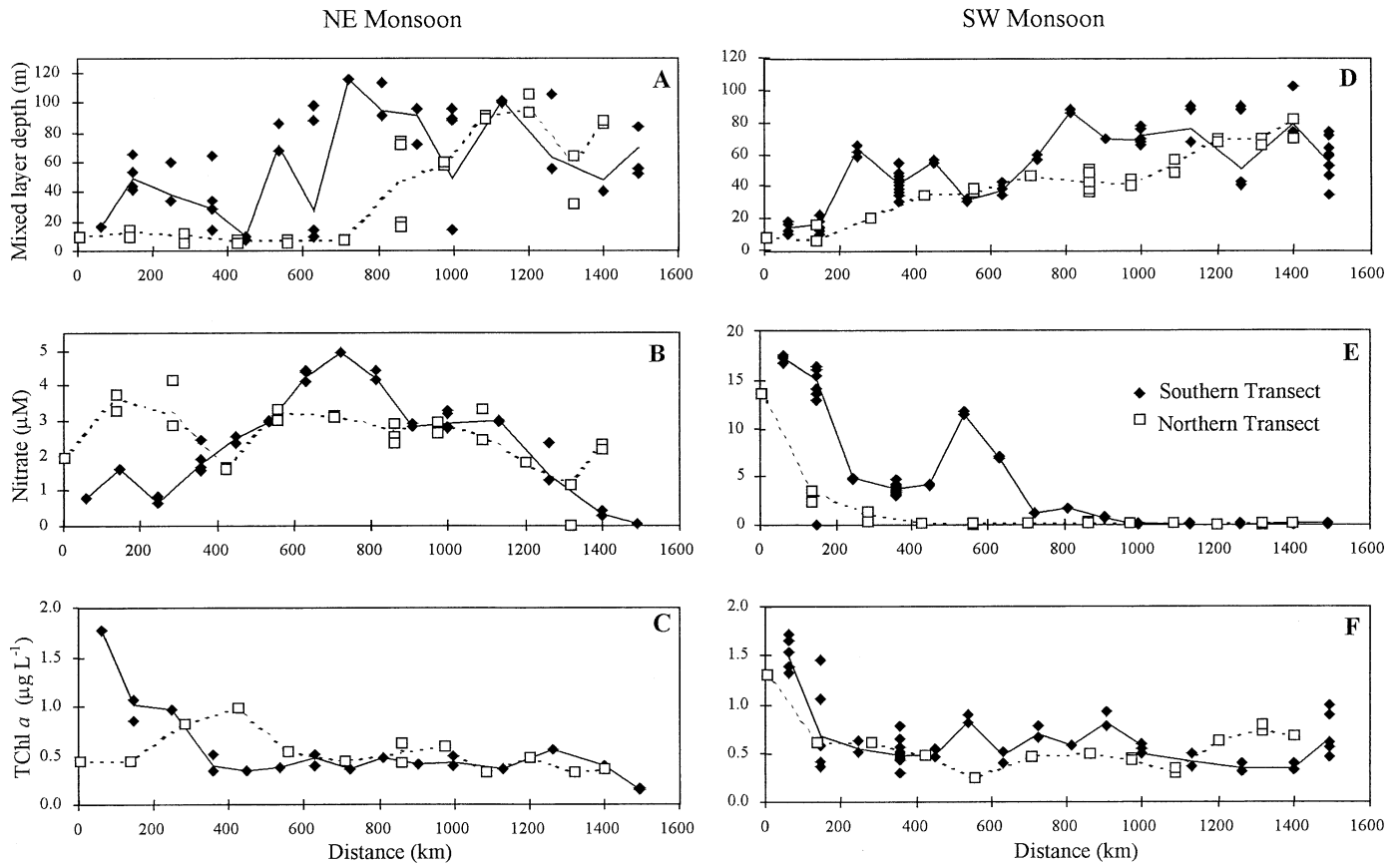


Fig. 3. Mixed-layer depth (A, D; data from Gardner et al. 1999), average mixed-layer concentrations of nitrate (B, E; from Morrison et al. 1998), and average mixed-layer concentrations of the sum of chlorophyll *a* and divinyl-chlorophyll *a* (i.e., TChl *a*; C, F). Data for the northeast and early southwest monsoon cruises are plotted, respectively, in the left and right columns of the figure. Data from individual casts are given by symbols (solid diamond, southern transect; open squares, northern transect). Lines (solid, southern transect; dotted, northern transect) connect station averages. Distances along transects are from the coast along the track.

bution of cyanobacteria (exclusive *Prochlorococcus*), in contrast, varied little along the offshore portions of the transect and ranged from 10 to 20% of TChl *a*. The abundance of *Prochlorococcus* was primarily related to temperature; it was restricted to a SST $>24^{\circ}\text{C}$, linearly increasing with temperature (Fig. 7A), and it was negatively related to concentrations of ammonia (data not shown). However, it is likely that SST, which was significantly correlated with ammonia, interfered with this statistical analysis. A weak positive effect of ammonia on the abundance of *Prochlorococcus* is evident from a significant, albeit weak, relationship between residuals of the *Prochlorococcus*-SST regression and concentrations of ammonia (Fig. 7B). Cyanobacterial biomass did not covary significantly with temperature (Fig. 7C). For temperatures $>24^{\circ}\text{C}$, this covariation was significant but weak, accounting for only 2% of the variance. The same results hold for the covariation of cyanobacterial biomass and concentrations of nitrate (data not shown). There was no significant relationship between cyanobacterial abundance and ammonia (Fig. 7D).

Contributions of the different groups of autotrophs to TChl *a* varied in almost all cases systematically with TChl *a* (Fig. 8). Contributions of all groups but *Prochlorococcus* sp. and Cyanobacteria (excluding *Prochlorococcus* sp.) in-

creased with increasing TChl *a*. Diatoms, chlorophytes, cryptophytes, and pelagophytes may have had a lower abundance threshold at TChl *a* of $\sim 0.2 \mu\text{g L}^{-1}$, i.e., below this threshold their abundance was a negligible fraction of the total. The abundance of prymnesiophytes, dinoflagellates, and pelagophytes increased with increasing TChl *a* up to a point and saturated at levels substantially less than TChl *a* and did not increase any further as TChl *a* increased. The abundance of diatoms, chlorophytes, and cryptophytes steadily increased with increasing TChl *a*, i.e., it did not saturate. However, for chlorophytes this response was driven by stations close to the coast (circles in Fig. 8). Once these data points are excluded from the analysis, chlorophyte biomass also approaches asymptotic values, similar to those observed for the other groups. Diatoms are the bloom species in this system, i.e., the group that will dominate the phytoplankton community for high values of TChl *a*. The contributions of cyanobacteria to TChl *a* did not vary with TChl *a*. The abundance of *Prochlorococcus* was inversely related to TChl *a*, a relationship mirroring that of *Prochlorococcus* abundance and temperature (cf. Fig. 7A).

Grow-out experiments—At stations along the southern transect, seawater with naturally high levels of nutrients was

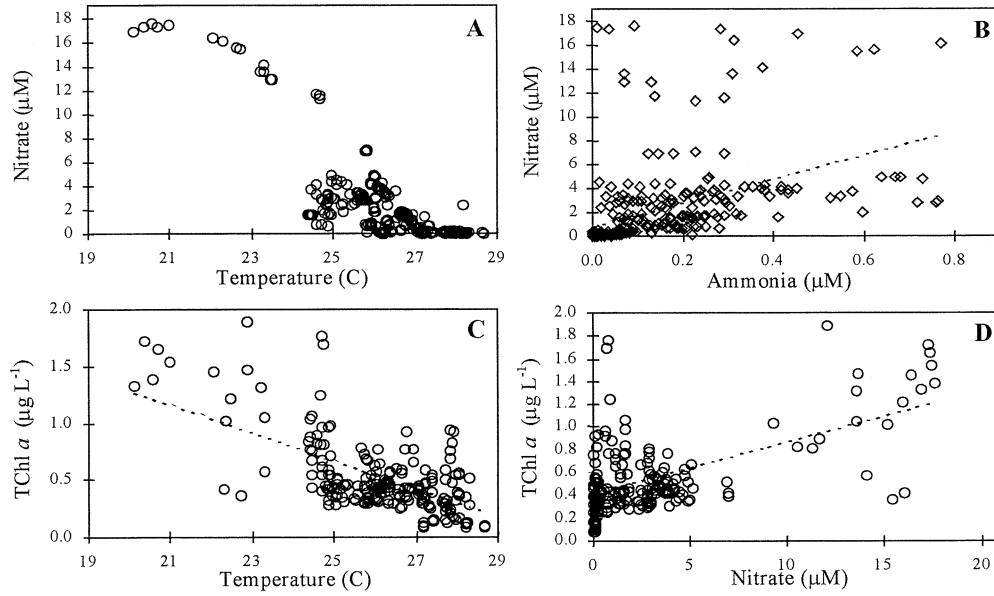


Fig. 4. Property plots for the mixed layers of TN43, TN49, and TN54. (A) Nitrate versus SST. (B) Nitrate versus ammonium. (C) TChl *a* versus temperature. (D) TChl *a* versus nitrate. Linear regressions of the data are represented by dotted lines ([B] $r^2 = 0.22$, $df = 307$, $P < 0.01$; [C] $r^2 = 0.40$, $df = 218$, $P < 0.01$; [D] $r^2 = 0.34$, $df = 218$, $P < 0.01$).

incubated without any manipulation, e.g., addition of nutrients, for up to 4 d. The objective of these experiments was to determine the response of the phytoplankton community to reduced levels of mesozooplankton grazing, which are not efficiently sampled using Niskin or GoFlo bottles. Phyto-

plankton biomass, i.e., TChl *a*, increased in all cases exponentially in the incubation bottles over the first 2 to 3 d, and nutrients were taken up (e.g., Fig. 9). A lag period in the response was not observed. On the average, the uptake of 1- μM inorganic nitrogen produced 0.34 μg TChl *a*. During

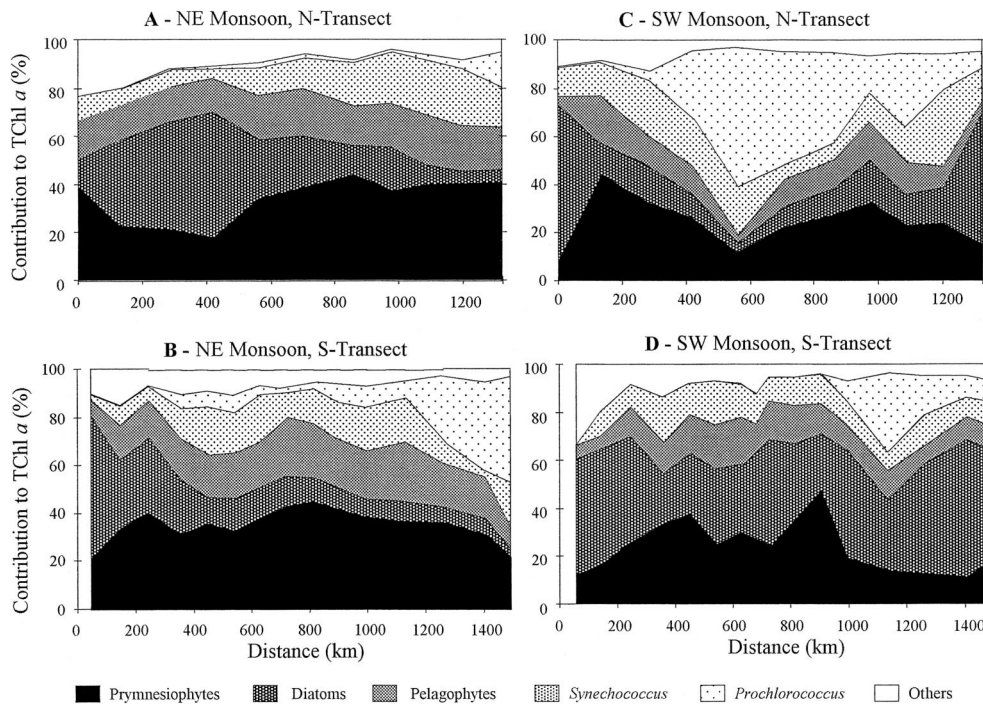


Fig. 5. Relative contributions of different groups of algal taxa as defined by taxon-specific pigments to TChl *a* along the northern and southern transects during the northeast and southwest monsoons.

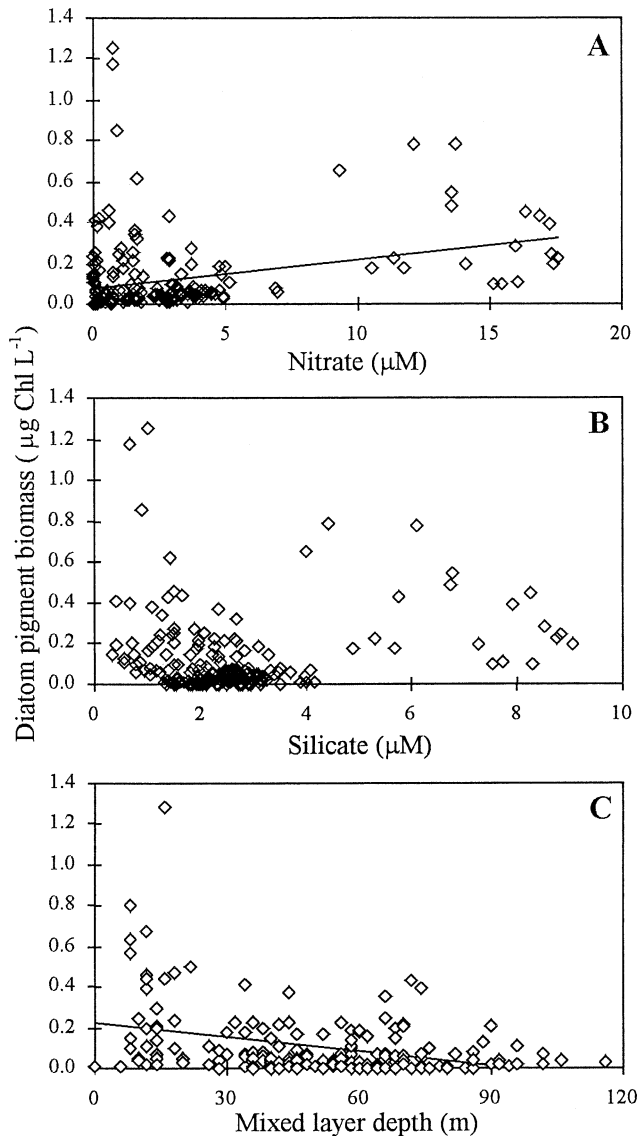


Fig. 6. The pigment biomass of diatoms plotted against concentrations of (A) nitrate, (B) silicate, and (C) mixed-layer depth. Dotted lines indicate regressions of diatom pigment biomass against the independent variable in case regressions were significant ([A] $r^2 = 0.10$, $df = 218$, $P < 0.01$; [B] $r^2 = 0.01$, $df = 218$, $P > 0.05$; [C] $r^2 = 0.13$, $df = 170$, $P < 0.01$).

the southwest monsoon, almost $12\text{-}\mu\text{M}$ nitrate were taken up within 4 d, which suggests that the community was growing rapidly. Most of the biomass increase was due to the growth of diatoms (e.g., Fig. 9B and Table 1A); net growth rates of these ranged from 0.44 to 0.84 d^{-1} . Net growth rates of pelagophytes, dinoflagellates, and cryptophytes were significantly different from zero as well, but these groups were not large contributors to TChl a (Table 1A,B). The biomass of prymnesiophytes, *Prochlorococcus*, and cyanobacteria (excluding *Prochlorococcus*) did not change significantly over the 3- to 4-d incubation periods. However, during the first 24 h of the experiments the biomass of cyanobacteria and *Prochlorococcus* increased significantly with average net

growth rates of 0.84 and 0.47 d^{-1} , respectively, but declined subsequently.

To compare changes of phytoplankton community structure during the grow-out experiments with changes observed in situ, contributions of the different groups of autotrophs to biomass were plotted against TChl a along with bin averages derived from the in situ data (symbols and lines, respectively, in Fig. 10). Changes of the biomass of different groups with TChl a during the grow-out experiments are for most groups very similar to biomass variations of these groups observed in situ. The one exception is chlorophytes. However, since in situ patterns for chlorophytes at TChl $a > 1\text{ }\mu\text{g}$ are primarily driven by coastal data (Fig. 8), the difference between the kinetics for in situ and grow-out experiments simply reflects a difference between coastal and off-shore system.

Taxon-specific growth rates—Instantaneous growth rates of different groups of autotrophs were measured using the pigment-labeling method (Goericke and Welschmeyer 1993a). These rates are determined from the incorporation of ^{14}C into carotenoids and Chl a_2 , i.e., biomarkers associated with living autotrophs. Thus, these measurements are not affected by grazing that occurs in the incubation bottles. All data presented here are averages from shipboard incubations at 36 and 60% I_0 , which are considered here the average growth rate for the surface layer. Rates of primary production measured in bottles incubated aboard the ship at 60% I_0 were virtually identical to rates of primary production measured in situ at $\sim 75\%$ I_0 (Fig. 11).

Growth rates were highly variable, within taxa for different stations and among taxa at any one station. At most stations concentrations of lutein were too low for measurements of chlorophyte growth rates except for three S-transect stations close to the coast during the southwest monsoon, where concentrations of nitrate ranged from 13 to $18\text{ }\mu\text{M}$. The average chlorophyte growth rate at these stations was $0.77 \pm 0.13\text{ d}^{-1}$. Growth rates of other groups of autotrophs covaried with concentrations of inorganic nitrogen. For example, during the southwest monsoon growth rates of diatoms, when plotted against $[\text{NO}_3]$ (Fig. 12A), show saturation patterns typical of Monod-growth kinetics (Eq. 1). However, deviations of growth rates from Monod kinetics for high $[\text{NO}_3]$ varied systematically with $[\text{NO}_3]$. To explore this systematic deviation, residuals for $[\text{NO}_3] > 2\text{ }\mu\text{M}$ were plotted against SST (Fig. 12B). Indeed, as expected from a temperature dependence of maximum growth rates (Eppley 1972), a systematic variation of residuals with temperature was found. A 10°C increase of temperature increased growth rates by 30%; a very small effect compared to the effect of temperature on the maximum growth rates of any one species (Eppley 1972). To correct growth rate data for temperature effects and explore the dependence of growth rates on concentrations of nutrients in more detail, rates shown in Fig. 12A were normalized by the temperature-dependent maximum growth rates as predicted from the data in Fig. 12B and plotted against concentrations of nitrate (Fig. 12C). This normalization resulted in a slightly better fit of Monod kinetics to the data. Residuals of this fit did not vary systematically with concentrations of ammonia or silicate (data

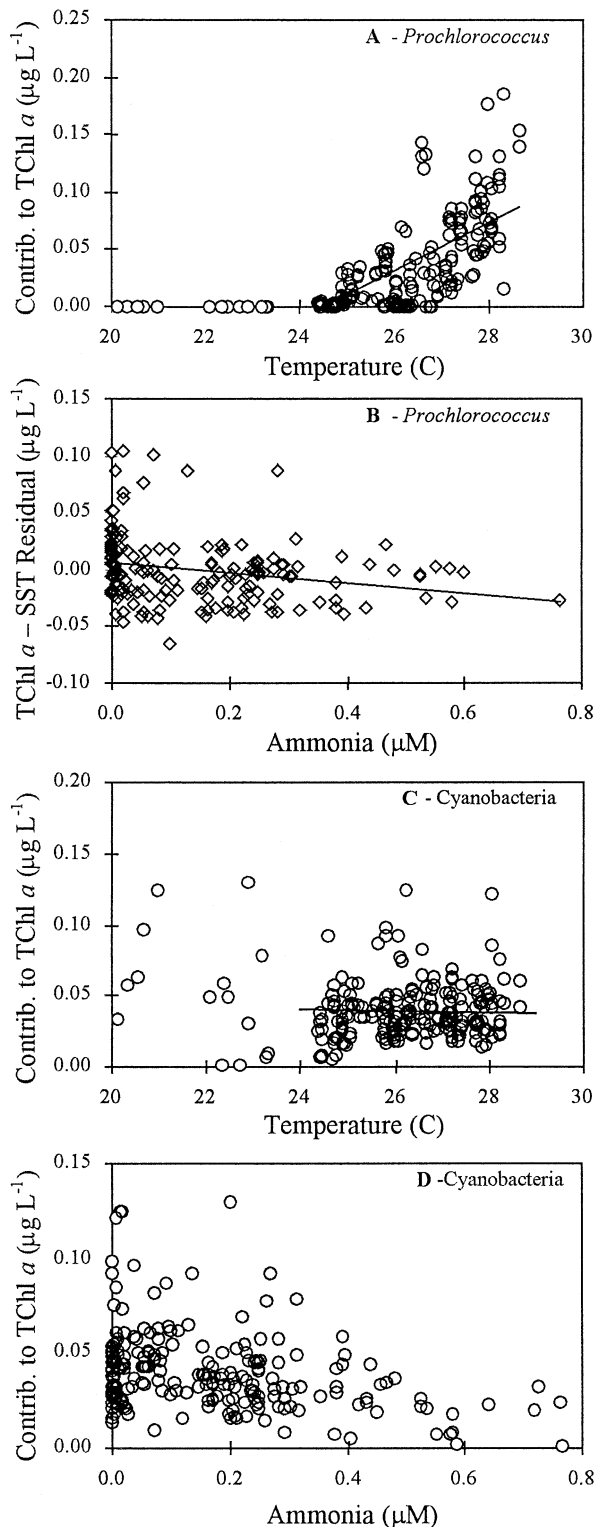


Fig. 7. Pigment biomass of *Prochlorococcus* sp. and cyanobacteria (exclusive *Prochlorococcus*) plotted against SST (A, C, respectively) and residuals of the *Prochlorococcus* sp.—SST regression and biomass of cyanobacteria plotted against concentrations of ammonia (B, D, respectively). Lines indicate regressions of pigment biomass against the independent variable in case these were significant ([A] only data for SST > 24°C, $r^2 = 0.49$, $df = 177$, $P < 0.01$; [B] $r^2 = 0.06$, $df = 179$, $P < 0.01$. The regression of cyano-

not shown). This result, however, does not imply that ammonia and silicate did not affect growth rates; it is possible that such a relationship is hidden in the covariation of these and nitrate.

Growth rates of other chemotaxonomically defined groups of autotrophs, when plotted against $[\text{NO}_3]$, also show saturation patterns typical of Monod-growth kinetics (Fig. 13). Maximum growth rates of these groups of autotrophs, determined by fitting Monod kinetics to the data, differed dramatically, ranging from 1.1 d^{-1} for diatoms to 0.36 d^{-1} for dinoflagellates (Table 2). Half-saturation constants of growth with respect to $[\text{NO}_3]$ ranged from 0.01 to $0.19 \mu\text{M}$ (Table 2). The assumption that only nitrate limits phytoplankton growth in this system is unrealistic; rather $[\text{NO}_3]$ should be viewed as a proxy for the availability of inorganic nutrients since most of these covaried in this system. The colimitation of growth by nitrate and ammonia was explored by fitting Eq. 2 to the data. Fits of Eq. 2 to the growth rates of cyanobacteria resulted in a slightly better fit to the data than fits based on NO_3 or NH_4 alone; however, the variance explained by the different models did not differ substantially (Table 2). Differences in the variance explained when using either model were similar for other groups of autotrophs or smaller (Table 2). Half-saturation constants of growth on nitrate and nitrate and ammonia combined (Table 2) are well within the range of constants determined from laboratory experiments (McCarthy 1981). However, it is questionable that the half-saturation constants determined are physiologically meaningful, since other nutrients covaried with nitrate and ammonia. Nonetheless, values of such coefficients are potentially useful for the parameterization of models that assume phytoplankton growth to be dependent only on concentrations of nitrate or nitrate and ammonia.

Discussion

Bottom-up and top-down control of autotroph biomass—An unusual aspect of the monsoonal Arabian Sea was elevated concentrations of inorganic nutrients over large areas of the basin and low levels of phytoplankton biomass compared to concentrations of inorganic nutrients. During the northeast monsoon, concentrations of nitrate in the surface layer averaged $2.4 \mu\text{M}$. Rates of nitrate uptake and TChl *a* synthesis observed during grow-out experiments suggest that the available nitrate could have supported the production of an additional $1 \mu\text{g TChl } a \text{ L}^{-1}$, at least transiently. Yet the observed average TChl *a* during the northeast monsoon was $0.55 \mu\text{g Chl } a \text{ L}^{-1}$. Nutrient concentrations were higher and more variable during the southwest monsoon along the southern transect up to 1,000 km offshore, yet TChl *a* along this section, excluding coastal stations, was only $0.65 \mu\text{g L}^{-1}$ on the average. Clearly, large areas of the monsoonal Arabian Sea were high-nutrient low-chlorophyll (HNLC) areas. Two hypotheses have been advanced to explain the

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bacterial biomass and SST restricted to values >24°C is given by $r^2 = 0.02$, $df = 202$, $P < 0.01$).

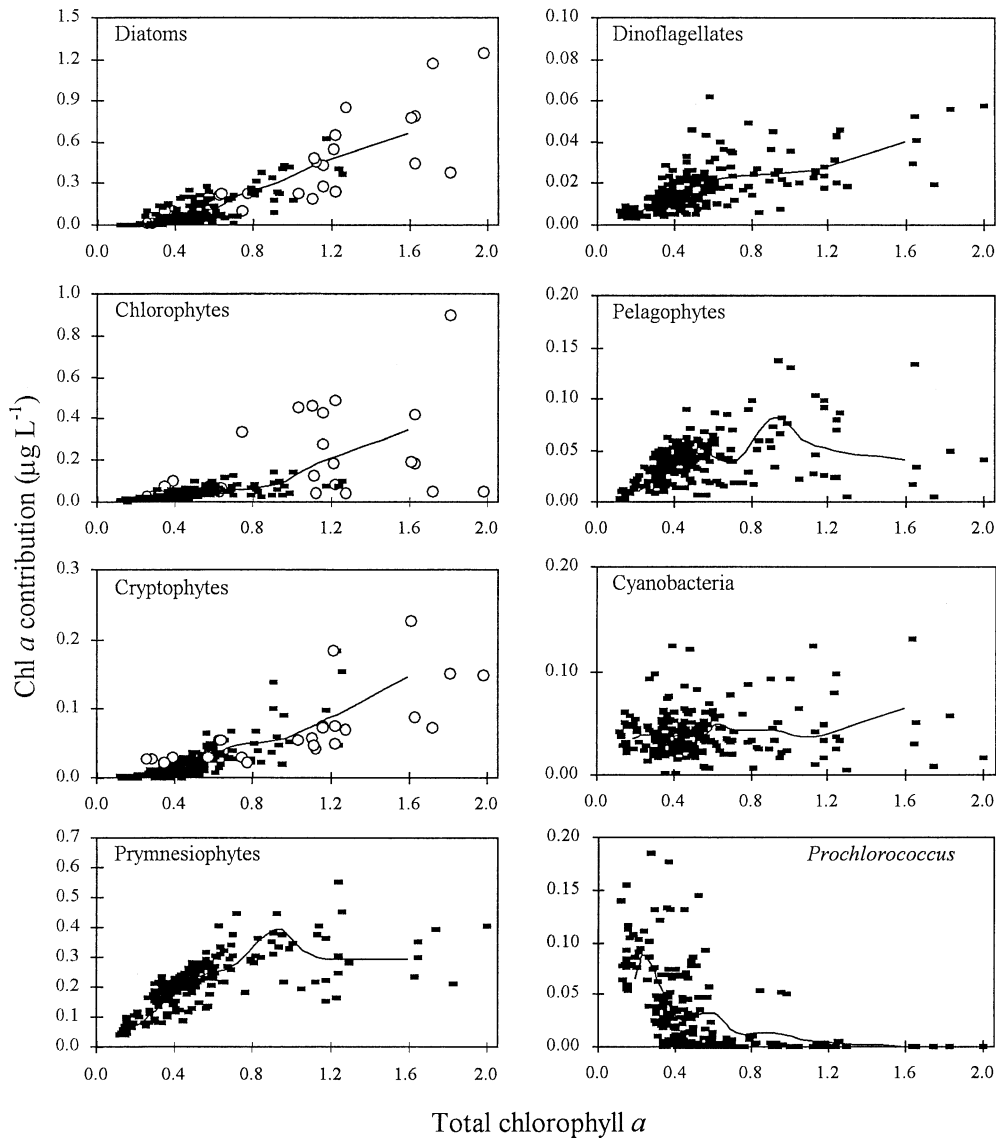


Fig. 8. The contributions of different groups of algal taxa to TChl a are plotted against TChl a . Shown are data for the mixed layers of all stations sampled during the 1995 northeast, 1995 early southwest, and 1995/1996 early northeast monsoon cruises. Circles in diatom, chlorophyte, and cryptophyte panels represent coastal stations. Lines connect the bin averages of the data. Note that the abscissa differ between plots, ranging from 0.2 to 2 μg TChl a .

HNLC phenomenon in the open ocean; limitation of phytoplankton biomass and growth rates by trace metals—i.e., control by resources or bottom-up control—and limitation of phytoplankton biomass, but not growth rates, by grazers—i.e., top-down control (Chisholm and Morel 1991). The first hypothesis predicts that in situ phytoplankton growth rates are well below their temperature-constrained physiological maxima. The second hypothesis predicts that phytoplankton growth rates are near maximal when concentrations of critical nutrients are high and that rates of growth and grazing are balanced.

Results of the U.S. JGOFS program do not suggest that there was a single nutrient or suite of nutrients that could have limited phytoplankton biomass or growth rates during

the monsoon seasons in areas where high concentrations of macronutrients were observed. Inorganic nitrogen-to-phosphate ratios were substantially lower than the Redfield ratio throughout the Arabian Sea, which suggests that inorganic nitrogen was more important than phosphate as a nutrient potentially limiting phytoplankton biomass and growth (Morrison et al. 1998). Concentrations of iron, the nutrient that likely controls phytoplankton biomass and/or rates of growth in other high-nutrient low-chlorophyll regions (Martin et al. 1991, 1994), were not sufficiently low to be limiting to primary production or phytoplankton growth (Measures and Vink 1999; Barber et al. 2001). Concentrations of silicate, a nutrient essential to the growth of diatoms, were never depleted relative to concentrations of inorganic nitrogen

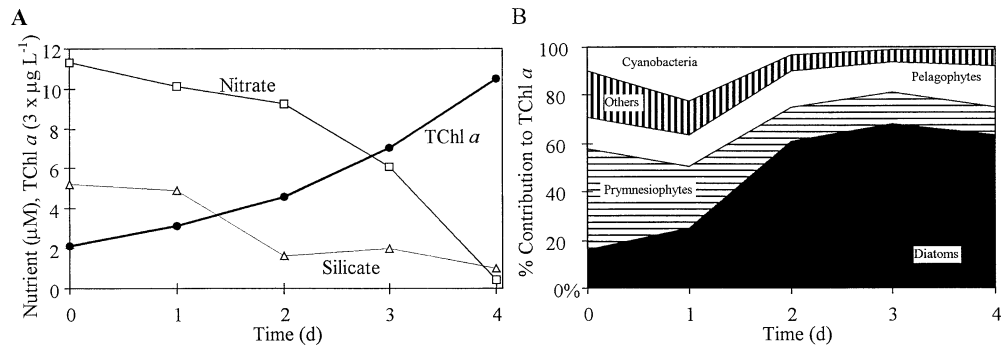


Fig. 9. An example of a grow-out experiment: Seawater with naturally high levels of inorganic nutrients (TN49 Sta. S6) was incubated for 4 d and sampled daily. Plotted are (A) concentrations of TChl *a* (multiplied by 3), nitrate, and silicate, and (B) the relative contributions (%) of different groups of algae to TChl *a*. Net growth rates of the different groups of algae for this and other experiments are shown in Table 1.

during the northeast and first half of the southwest monsoon at stations where concentrations of inorganic nitrogen were high (Morrison et al. 1998). This implies that silicate could not have limited phytoplankton biomass or growth rates at these stations during these two time periods. These considerations suggest that phytoplankton growth was not constrained by the availability of inorganic nutrients in the HNLC areas of the monsoonal Arabian Sea.

Rates of phytoplankton growth saturating with increasing concentrations of inorganic nutrients (e.g., nitrate, Fig. 13), also suggest that phytoplankton growth was not limited by

inorganic nitrogen or by other nutrients covarying with inorganic nitrogen in the HNLC areas of the Arabian Sea. The tight relationship observed between inorganic nitrogen and phytoplankton growth rates also suggests that some other nutrient limiting growth did not exist, such as a trace metal or a vitamin, since concentrations of critical nutrients varying independently of $[\text{NO}_3^-]$ would have caused a higher variability of growth rates for $[\text{NO}_3^-] > 2 \mu\text{M}$. Considering these observations one must ask "Why were no phytoplankton blooms observed in situ?"

Such blooms were indeed observed during grow-out ex-

Table 1. Results from grow-out experiments performed during the northeast and southwest monsoons. The pigments on which the measurements are based are listed below the group's name. (A) The averages and the 95% confidence levels of the relative contributions of the different groups of autotrophs to Tchl *a* at the beginning (t_0) and the end of the third day of the experiment (t). (B) The average ($n = 2$) net growth rates (specific rates of pigment concentration change, d^{-1}) of the different taxa for the individual experiments and the average and their 95% confidence levels. Stations and cruise names where experiments were performed are given in the first column of section B. The autotrophs are diatoms (Diat), prymnesiophytes (Prymn), pelagophytes (Pelago), dinoflagellates (Dino), cryptophytes (Cryp), chlorophytes (Chloro), cyanobacteria (Cyano), and *Prochlorococcus* sp. (PRO). Net growth rates are based on changes of pigment concentrations over the first 3 d of the experiment. Average net growth rates of cyanobacteria and *Prochlorococcus* over the first 24 h of the experiment were 0.84 ± 0.29 and $0.47 \pm 0.18 \text{ d}^{-1}$.

	Diat fucox.	Prymn hexfucox.	Pelago butfucox.	Dino peridinin	Cryp allox.	Chloro. neox.	Cyano zeax.	PRO Chl a_2
A								
Average t_0	26%	38%	11%	3%	4%	10%	7%	2%
95% confidence	16%	11%	3%	1%	1%	2%	6%	2%
Average t	54%	16%	8%	3%	6%	5%	6%	2%
95% confidence	17%	9%	2%	2%	2%	3%	5%	1%
B								
TN43 S07	0.66	0.02	0.20	0.27	0.33	0.12	0.22	-0.14
TN43 S04	0.59	0.09	0.26	0.37	0.59	0.13	-0.16	-0.07
TN43 S02	0.44	-0.06	0.17	0.20	0.22	-0.07	0.39	0.18
TN49 S06	0.84	-0.01	0.30	0.23	0.18	-0.15	-0.42	n.d.
TN49 S02	0.63	0.02	0.25	0.26	0.58	0.07	0.21	n.d.
Average	0.63	0.02	0.23	0.27	0.38	0.02	0.05	-0.01
95% confidence	0.13	0.05	0.05	0.06	0.17	0.11	0.29	0.19

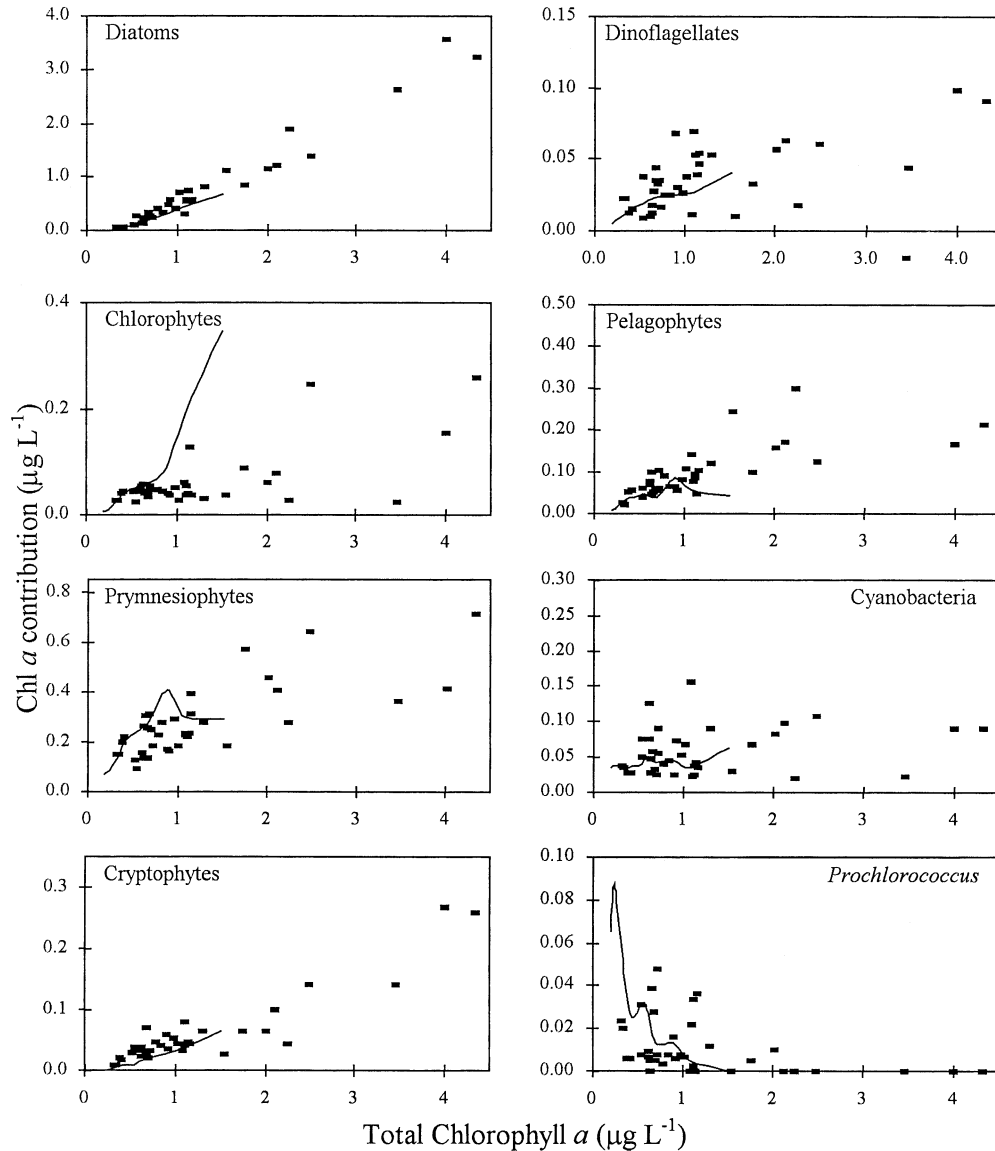


Fig. 10. As Fig. 8 but the contributions of different groups of algal taxa to TChl *a* plotted against TChl *a* for all grow-out experiments. Lines represent the bin averages of the data presented in Fig. 8, showing that changes of community structure with increasing TChl *a* are similar during grow-out experiments and in the field.

periments. During these experiments the phytoplankton assimilated up to 12- μM inorganic nitrogen in 4 d and phytoplankton pigment biomass increased up to fivefold, clearly demonstrating that the phytoplankton had the capacity to bloom, at least during grow-out experiments. Could this result be an artifact due to the confinement of natural communities in incubation bottles? There is no doubt that in situ experiments are to be preferred over bottle experiments to study the phytoplankton community, but should one really dismiss results of bottle incubations summarily? An interesting result of the highly successful in situ iron enrichment experiments was that they basically corroborated conclusions that were drawn from earlier bottle-incubation experiments (Martin et al. 1994; Coale et al. 1996). Similarly, long-term incubations in the subarctic Pacific (Goericke and

Welschmeyer 1993a) showed that even though the phytoplankton community changed dramatically over 4 to 5 days, growth rates of different phytoplankton taxa did not change over the incubation period. These results suggest that confinement in bottles per se is not detrimental to phytoplankton, unless the bottles are toxic or have toxic residues.

Dramatic changes in phytoplankton community structure were also observed during 3- to 4-d grow-out experiments in the Arabian Sea. Are those changes observed in incubation bottles representative of in situ processes? Plots of the contributions of the different autotrophs to pigment biomass versus TChl *a* delineate the response of communities to nutrient enrichment or release from grazing (Fig. 10). The surprising result of the grow-out experiments was that community changes with increasing TChl *a* in incubation bottles

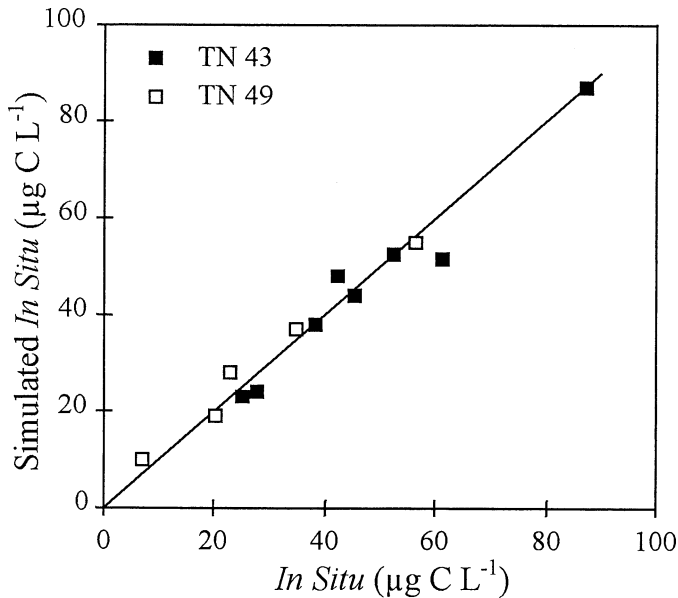


Fig. 11. Comparison of rates of primary production measured in situ and in shipboard incubators (simulated in situ). Incubations were carried out in parallel for the 60% I_0 (simulated in situ) and 75% I_0 (in situ) light treatments. The line designates the 1:1 relationship.

were virtually identical to community changes in situ (Fig. 8). These results support the hypothesis that in the Arabian Sea community processes in incubation bottles were very similar to community processes in situ with one important difference: Blooms of phytoplankton were only observed close to the coast and in incubation bottles but not in the offshore areas where high concentrations of inorganic nutrients were found, but levels of biomass were consistently 3 to 5 times less than those observed at the end of the grow-out experiments.

An important difference between conditions in situ and in incubation bottles is the absence of mesozooplankton in bottles, since mesozooplankton can avoid capture by rosette-mounted sampling bottles. I suggest that release from mesozooplankton grazing allowed the phytoplankton to bloom in the incubation bottles and that mesozooplankton grazing in situ prevented the phytoplankton from blooming. The predicted consequence of mesozooplankton control of phytoplankton biomass in situ is an imbalance between rates of phytoplankton growth and microzooplankton grazing in incubation bottles. Such an imbalance was indeed observed during the grow-out experiments and during 24-h pigment-labeling experiments at 36 and 60% I_0 . The average net growth rate for the latter experiments when $[\text{NO}_3^-]$ was larger than $1 \mu\text{M}$ was $0.33 \pm 0.23 \text{ d}^{-1}$ in 4.4-liter incubation bottles (Goericke unpubl. data). These results are corroborated by results from dilution experiments for stations with $[\text{NO}_3^-] > 1 \mu\text{M}$: Caron and Dennett (1999) reported an average net growth rate of phytoplankton of $0.48 \pm 0.11 \text{ d}^{-1}$ for stations with $[\text{NO}_3^-] > 1 \mu\text{M}$ during the northeast monsoon (TN43, $n = 7$). Net growth rates calculated from data reported by Landry et al. (1998, i.e., $\mu_0 - m$) were $0.50 \pm 0.14 \text{ d}^{-1}$ and $0.50 \pm 0.79 \text{ d}^{-1}$ for corresponding experiments performed during

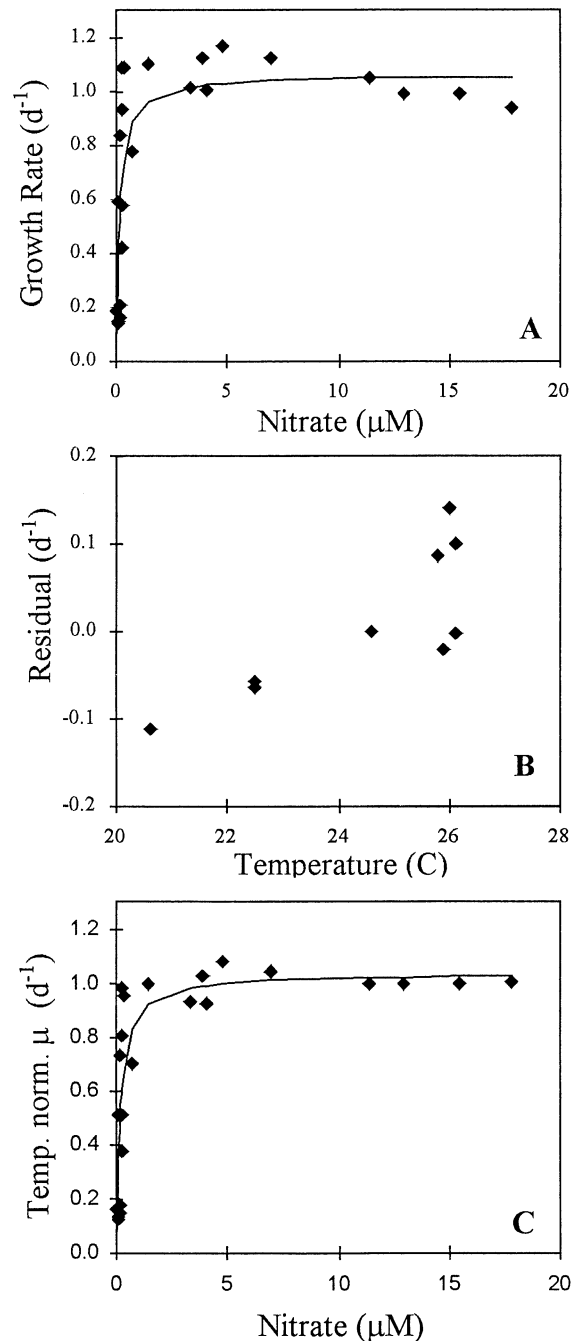


Fig. 12. Growth rates of diatoms during the early southwest monsoon (TN49): (A) growth rates plotted against $[\text{NO}_3^-]$. The solid line represents a fit of Monod kinetics to the data ($\mu_{\text{max}} = 1.08 \text{ d}^{-1}$, $k_{\text{NO}_3} = 0.15$, $r^2 = 0.74$). (B) Residuals for the fit of Monod kinetics to growth rates for $[\text{NO}_3^-] > 2 \mu\text{M}$ along the southern transect (stations S1–S10) plotted against SST. (C) The growth rate data shown in (A) normalized by the maximum growth rate predicted for the SST plotted against $[\text{NO}_3^-]$. The solid line represents a fit of Monod kinetics to the data ($\mu_{\text{max}} = 1.03 \text{ d}^{-1}$, $k_{\text{NO}_3} = 0.18$, $r^2 = 0.80$).

the early northeast monsoon (TN54, $n = 5$) and the second half of the southwest monsoon (TN50, $n = 6$), respectively.

The imbalance between rates of phytoplankton growth and microzooplankton grazing in incubation bottles contrasts

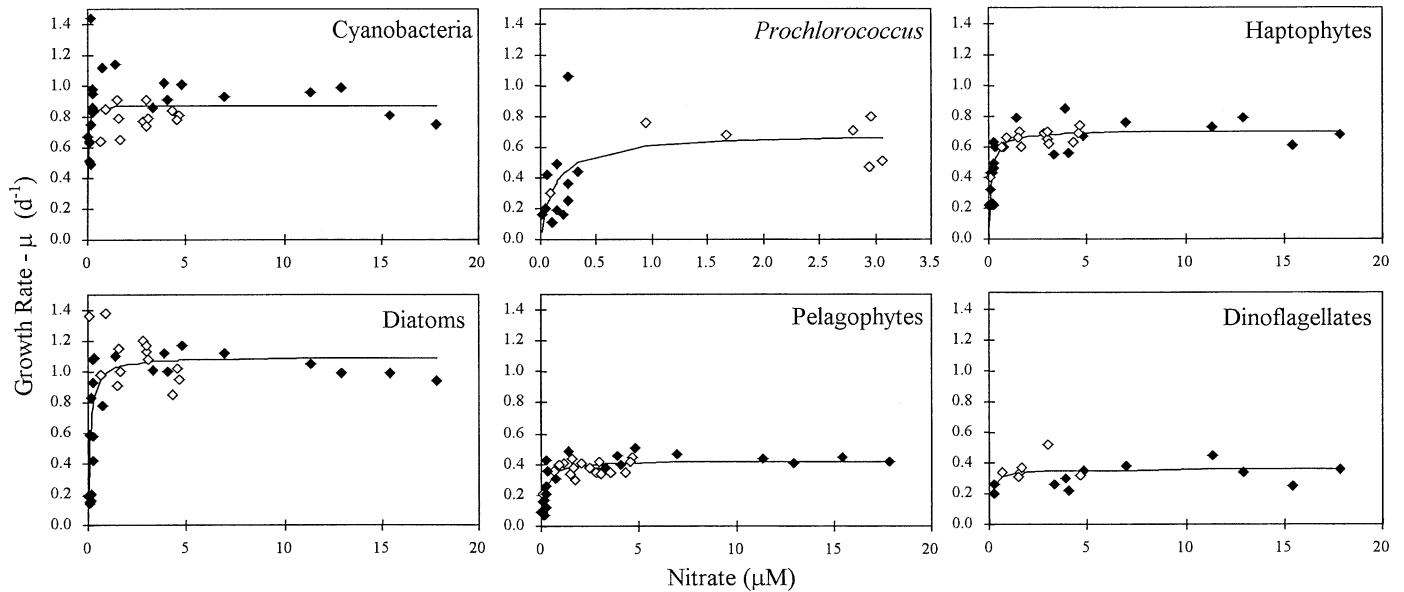


Fig. 13. Taxon-specific growth rates plotted against $[\text{NO}_3]$. Open and solid diamonds represent data from the northeast and southwest monsoons, respectively. Each data point is the average of data from incubations at 60 and 36% surface irradiance. The solid lines are fits of Monod-growth kinetics. Parameters and statistics for these data are given in Table 2.

with concentrations of TChl *a* varying little in the offshore areas of the Arabian Sea, in particular during the northeast monsoon. These observations suggest that in situ rates of growth and loss were balanced. Roman et al. (2000) reported that in the Arabian Sea phytoplankton was a major prey item for mesozooplankton, contributing ~80% to their diet, and calculated that mesozooplankton ingestion of phytoplankton accounted for ~32% of the primary production per day. Comparing rates of mesozooplankton and microzooplankton (74% of the primary production) ingestion, the authors concluded that phytoplankton growth and grazing were balanced to within 10% in the Arabian Sea. Note, however, that for the late northeast monsoon such an apparent balance did not exist: Roman et al. (2000, their Fig. 10) calculated that me-

sozooplankton and microzooplankton consumption accounted for $27 \pm 5\%$ of primary production, and Caron and Dennett (1999) reported that microzooplankton grazing accounted for $40 \pm 10\%$ of phytoplankton growth at stations corresponding to those of Roman et al. (2000), which leaves $33 \pm 15\%$ of growth or primary productivity unaccounted for. Nonetheless, most of the evidence presented here supports the hypothesis that phytoplankton biomass in the HNLC areas of the monsoonal Arabian Sea was controlled by grazers, i.e., by top-down forces.

Taxon-specific growth rates—This study is based on taxa as delineated by taxon-specific pigments, which results in

Table 2. Maximum growth rates (μ_{\max}) and half saturation constants (K_{nutrient}) for growth on nitrate (NO_3) and nitrate and ammonia combined (*N*), calculated assuming Monod kinetics of growth, i.e., Eq. 1 and Eq. 2, respectively. The maximum growth rates obtained did not vary significantly between the two models. Growth rates for IronEx II are from Landry et al. (2000) and were measured using the dilution method.

Taxon	μ_{\max}	NO_3		<i>N</i>			IronEx II
		K_{NO_3}	r^2	K_{NO_3}	K_{NH_4}	r^2	
diatoms	1.10	0.10	0.48	0.12	0.06	0.49	1.2–1.9
prymnesiophytes	0.71	0.12	0.65	0.13	0.07	0.66	0.3–1.4
pelagophytes	0.43	0.19	0.73	0.20	0.42	0.74	0.7–1.4
cyanobacteria	0.89	0.01	0.44	0.03	0.01	0.57	0.8–1.2
<i>Prochlorococcus</i>	0.69	0.12	0.39	0.15	0.03	0.43	0.0 & 0.9‡
dinoflagellates	0.36	0.11	0.18		n.d.†		0.1–1.4
chlorophytes	0.77*		n.d.		n.d.		n.d.§

* Growth rates based on the labeling of lutein were only obtained at three stations.

† A solution was not obtained using the *N*-growth model (Eq. 2).

‡ Initially one growth rate of 0.9 d^{-1} was obtained during the experiment, but subsequent rates averaged to less than zero.

§ No rates based on lutein were reported. Rates based on Chl *b* clustered around 0.45 during the early part of the experiment and ranged from 0.3 to 1.7 subsequently.

rather broad categories, usually at the class level (Jeffrey et al. 1997). I believe that the data presented here demonstrate convincingly, at least for the offshore Arabian Sea, that groups defined by taxon-specific pigments are physiologically and ecologically distinct units. The strongest data supporting this suggestion are the data on taxon-specific growth rates. The growth rates of all taxonomic groups follow Monod kinetics when plotted against increasing concentrations of inorganic nutrients (Figs. 12, 13). Maximum growth rates, observed when inorganic nutrients were likely replete, $[\text{NO}_3] > 2 \mu\text{M}$, varied dramatically among groups, ranging from high values of 1.1 d^{-1} for diatoms and 0.9 d^{-1} for cyanobacteria to values as low as 0.4 d^{-1} for dinoflagellates and pelagophytes (Table 2). The small variability of growth rates within any group for $[\text{NO}_3] > 2 \mu\text{M}$ suggests that the maximum growth rate of any taxonomic grouping did not vary substantially across the offshore portions of the Arabian Sea. For example, the growth rates of diatoms at stations with $[\text{NO}_3] > 2 \mu\text{M}$ ranged from 0.9 to 1.2 d^{-1} (average $1.1 \pm 0.1 \text{ d}^{-1}$, $n = 20$), an extremely small range, attesting to the physiological homogeneity of 'the diatoms' in the offshore Arabian Sea and also to the precision of the pigment-labeling method. Growth rates of cyanobacteria at $[\text{NO}_3] > 2 \mu\text{M}$ showed a similarly tight clustering. However, a substantially higher growth rate was observed for cyanobacteria at station N7 during the northeast monsoon, 1.44 d^{-1} for $[\text{NO}_3] = 0.15 \mu\text{M}$. Brown et al. (in press) measured slightly higher growth rates for these groups under nutrient replete conditions using the dilution method during the late southwest and early northeast monsoons, which suggests that the physiological characteristics of the phytoplankton community may have changed with time. Differences in the methods used are not a likely cause, since a very good correspondence was achieved during the northeast monsoon (TN43) between growth rates measured using the dilution method (Caron and Dennett 1999) and the pigment-labeling method (this study). With the exception of pelagophytes, growth rates of different taxa achieved under nutrient replete conditions in the Arabian Sea were slightly less than those measured during IronEx II in the equatorial Pacific in the iron patch (Landry et al. 2000, see Table 2), i.e., when phytoplankton was hypothesized to grow under nutrient replete conditions. Growth rates of pelagophytes in the Iron Ex II patch were two to three times higher than rates in the Arabian Sea under nutrient replete conditions.

Maximum growth rates reported in this and the studies by Landry et al. (2000) and Brown et al. (in press) are similar to maximum growth rates of autotrophs isolated from the subtropical and tropical open ocean. The maximum growth rate of 0.69 d^{-1} determined for *Prochlorococcus* is quite similar to the average maximum growth rate of high-light adapted strains of *Prochlorococcus* in the laboratory, $0.76 \pm 0.07 \text{ d}^{-1}$ (Moore and Chisholm 1999). Maximum growth rates of prymnesiophytes, diatoms, and cyanobacteria isolated from the Sargasso Sea, 1.1 , 1.8 , and 1.3 d^{-1} , respectively (Brand et al. 1986; Moore et al. 1995), were slightly higher than maximum growth rates of these groups in the Arabian Sea, 0.7 , 1.1 , and 0.9 d^{-1} , which is not surprising considering that the former are laboratory isolates. These results clearly show that maximum growth rates of auto-

trophs in the open tropical and subtropical ocean are substantially lower, by factors of 2 to 5, compared to maximum growth rates that *could* be expected given the ambient temperature (Eppley 1972). Landry et al. (1998) reached a similar conclusion, based on measurements of nutrient-amended growth rates measured using the dilution technique. These results clearly constrain rates of carbon cycling in the tropical and subtropical open ocean (cf. Goldman 1988; Banse 1995).

It has to be stressed that this conclusion only holds for open ocean environments. There is ample evidence that autotrophs found in coastal environments can grow at substantially higher rates. For example, Landry et al. (1998) measured a growth rate of 2.7 d^{-1} close to the coast of Oman during the southwest monsoon at a station where diatoms dominated the phytoplankton community when $[\text{NO}_3]$ was $19 \mu\text{M}$. Waterbury et al. (1986) reported extremely high growth rates for *Synechococcus* off Woods Hole, ranging from ~ 1.8 to 2.8 d^{-1} . The compilation of phytoplankton in situ growth rates by Furnas (1990) and the high maximum growth rates of coastal isolates in culture also suggest that coastal communities can have substantially higher maximum growth compared to oceanic communities.

The tight clustering of growth rates for $[\text{NO}_3] > 2 \mu\text{M}$ reported here is in stark contrast to the large variability of these at $[\text{NO}_3] < 2 \mu\text{M}$. Physiological considerations suggest that this variability is real, rather than an artifact. Phytoplankton growth is not directly controlled by concentrations of inorganic nutrients in the environment, but rather by intracellular concentrations (McCarthy 1981). Thus, if in situ concentrations of critical nutrients are high, growth rates will be high as well and close to maximum growth rates; however, if in situ concentrations are low, we are not able to make any inferences about the intracellular nutrient concentrations since the phytoplankton may have experienced high concentrations of nutrients recently. This uncertainty about the nutritional history of the populations we studied will impact our ability to interpret the in situ relationships between phytoplankton growth rates and nutrient concentrations. In spite of this uncertainty—we are not able to assume steady state as is the case in a chemostat—observed relationships are as good as many of those determined for single species in chemostats.

Phytoplankton community structure—The covariation of the abundance of the different groups of autotrophs with TChl *a* further supports the contention that groups delineated by taxon-specific pigments are ecologically distinct units. The observed patterns show that phytoplankton community structure in the monsoonal Arabian Sea varies in a predictable fashion with TChl *a* (Fig. 8). Some groups of phytoplankters have abundance thresholds that constrain their abundance. Above these thresholds their biomass increases with increasing TChl *a* to saturate eventually at different levels. The exceptions are the bloom species, diatoms in the offshore Arabian Sea, whose abundance increases with TChl *a* without apparent limitation, not only in the field (Fig. 8) but also during grow-out experiments (Fig. 10).

The data provide evidence for the presence of at least two different communities of chlorophytes, a coastal and an off-

shore community, since in situ chlorophyte biomass was only high close to the coast, again suggesting that the phytoplankton coastal community differs significantly from the offshore communities. Patterns quite similar and even more distinct, because the data sets encompassed larger values of TChl *a*, have been observed in the California current and in a Southern California nearshore environment (Goericke unpubl. data), which suggests that such patterns of abundance are a general feature of maritime phytoplankton communities.

Patterns of abundance appear to vary significantly and predictably among different taxa. The observed patterns for the different groups of autotrophs are similar to variations of TChl *a* in different size classes as a function of TChl *a* (Chisholm 1992). For example, Raimbault et al. (1988) and Riegman et al. (1993) observed that the total amount of Chl *a* in successively larger size classes has upper limits, and that beyond certain thresholds Chl *a* can only be added to the system in the form of larger size classes. It appears that the phytoplankton community of the Arabian Sea follows similar rules, except that it is possible to formulate these rules in terms of taxonomic units as delineated by taxon-specific pigments rather than size classes. Such taxon- or size-based patterns, if generally valid, are powerful predictors of phytoplankton size structure or phytoplankton community structure. The patterns observed here for individual classes of phytoplankters, once generalized to the world's ocean or specified for different regions thereof, could be used as empirical rules governing the assembly of model communities.

Control of phytoplankton community structure—Physical and chemical parameters described above and elsewhere (Lee et al. 2000) varied significantly on the mesoscale <100 km. In contrast, variables characterizing the phytoplankton community varied coherently along more than 1000 km long transects. Indeed, physical and chemical variables were only weakly related to TChl *a* and to the abundance of individual groups of taxa, e.g., diatoms and cyanobacteria. Only *Prochlorococcus* displayed a strong relationship between pigment biomass and temperature. The lack of strong relationships between physical variables and most biological properties during the monsoon seasons suggests that phytoplankton biomass and community structure were controlled by biological factors, and among these not phytoplankton physiology alone.

Earlier I concluded that phytoplankton biomass was controlled by mesozooplankton grazing in the high-nutrient areas of the monsoonal Arabian Sea (*see above*). This conclusion can now be refined by considering the different groups of autotrophs present. Clearly, picoautotrophs are not directly controlled by crustacean mesozooplankton; the latter only graze efficiently on particles larger than 5–8 μm (Mauchline 1998). However, their abundance must be constrained by some factor, since the biomass of, e.g., pelagophytes and cyanobacteria appears to saturate with increasing TChl *a* at values ranging from ~ 0.1 to $0.25 \mu\text{g Chl } a \text{ L}^{-1}$ (*see Fig. 8*). Consistent with these in situ observations are results of the grow-out experiments, since the biomass of picoautotrophs changed very little during these experi-

ments—net growth rates of these were consistently below maximum growth rates of these groups, at times even zero, Table 2—even though their growth rates were highest when concentrations of inorganic nutrients were high. These results suggest that growth of picoautotrophs in the incubation bottles was balanced by microzooplankton grazing.

I suggest that the same mechanism also operates in situ: picoautotroph biomass and rates of growth are limited by some inorganic nutrient when $[\text{NO}_3^-]$ are low (0.05 to 0.5 μM). When $[\text{NO}_3^-]$ are $>1 \mu\text{M}$, rates of growth are at or near their physiological maxima; these rates must be balanced by grazing, preventing picoautotroph biomass from accumulating as the system becomes enriched with nutrients. The consistently low biomass of the picoautotrophs is likely maintained at high TChl *a* by a balance between picoautotroph growth rates, rates of loss these suffer from microzooplankton grazing, growth rates of microzooplankton, and rates of loss these suffer from mesozooplankton grazing.

The monsoonal Arabian Sea is, as pointed out above, unusual because blooms of phytoplankton, in particular those of diatoms, were not observed during the northeast and first half of the southwest monsoon. Even though the high concentrations of inorganic nutrients created an environment conducive to the bloom of diatoms, diatoms only contributed 20 to 40% to phytoplankton biomass in the high-nutrient, low-Chl *a* areas (Fig. 5). Unlike other autotrophs, diatoms also require silica for growth, which is taken up by diatoms approximately in a 1:1 ratio with nitrogen (Brzezinski and Nelson 1995). The uptake of silicate is not as efficient as the uptake of inorganic nitrogen as a concentration threshold of about 1- μM silicate exists below which diatom growth is inhibited (Brzezinski and Nelson 1995). In the monsoonal Arabian Sea, particularly during the northeast monsoon, concentrations of silicate reached values as low as 1 μM , which suggests that diatom growth could have been limited at some stations by the availability of silicate (Morrison et al. 1998); however, at these stations concentrations of nitrate were low as well. Blooms of diatoms tend to shift the ratio of dissolved inorganic nitrogen and silica to values larger than 2; such elevated ratios are evidence of past diatom blooms. During TN43 and TN49 ratios of inorganic nitrogen and silicate in the surface layer were consistently below values of 2 in the offshore areas, suggesting that diatom blooms had not occurred (Morrison et al. 1998). This analysis of nutrient distributions suggests that diatom blooms should have occurred in the HNLC areas of the Arabian Sea but did not occur during TN43 and TN49 or prior to those cruises.

The growth rate data presented here also suggest that diatom growth was not limited by the availability of inorganic nutrients in the HNLC areas of the monsoonal Arabian Sea. Indeed, diatoms were the group with the highest growth rate, but nonetheless they did not bloom in situ. The grow-out experiments clearly showed that diatoms had the capacity to bloom as these dominated the phytoplankton community at the end of the 3- to 4-d experiments. These results suggest that loss processes, rather than growth rates, controlled the abundance of diatoms in this system. One significant loss process is respiration, which is particularly important in this system because of the, at times, deep mixed layers. If re-

spiratory losses in deep mixed layers, or other losses related to mixed-layer depth, affected communities of diatoms more than other autotrophs, one would expect the contribution of diatoms to TChl *a* to be negatively related to the depth of the mixed layer. The weak, albeit significant, relationship between diatom abundance and mixed-layer depth (Fig. 6C), suggests that diatoms were not disproportionately affected by the presence of deep mixed layers.

Other rates of loss affecting standing stocks of diatoms are grazing by smaller zooplankton and sinking. If grazing by larger protozoa and small metazoa were important, these would have to be well represented in the large incubation bottles used. Thus, effects of these two groups would be attributed to microzooplankton. Sinking of diatoms out of the mixed layer represents an additional loss process that is currently difficult to estimate directly. However, since rates of export production relative to rates of primary production were extremely low along the offshore transects during the northeast and early southwest monsoon, 2 to 5% of primary production with one value of 10% (Buesseler et al. 1998), large losses due to sinking are unlikely.

In the absence of other processes that could control the abundance of diatoms, I suggest that grazing by mesozooplankton controlled the abundance of diatoms. Indeed, Roman et al. (2000; *see above*) demonstrated that mesozooplankton ingestion, primarily grazing on phytoplankton, had the potential to control diatom growth. For example, during the late northeast monsoon (TN43), diatom biomass in the study domain averaged $3.4 \mu\text{g C L}^{-1}$ (Garrison et al. 1998). Assuming an average mixed-layer depth of 75 m, this value translates to 21 mM C m^{-2} . Assuming a growth rate of 1.1 d^{-1} (this study; clearly an overestimate of the actual growth rate since light became limiting to primary production in the upper 20 m of the water column, Barber et al. 2001) and constant levels of diatom biomass, the daily diatom productivity is estimated as $23 \text{ mM C m}^{-2} \text{ d}^{-1}$. This value is substantially lower than the late northeast monsoon average mesozooplankton phytoplankton-ingestion rate of $34 \text{ mM C m}^{-2} \text{ d}^{-1}$, which demonstrates that mesozooplankton grazing was of the proper order of magnitude to control diatom abundance. Interestingly, a similar conclusion was reached by Dam et al. (1995) for the equatorial Pacific.

To conclude, the evidence presented here supports the hypothesis that both phytoplankton biomass and community structure in the HNLC-areas of the monsoonal Arabian Sea were controlled by top-down forces, grazers, rather than bottom-up forces, resources. This result sets the monsoonal Arabian Sea apart from other open ocean environments where phytoplankton biomass is likely limited by the availability of resources, i.e., inorganic nitrogen, phosphorus, or iron (Chisholm and Morel 1991). Grazers exert control over phytoplankton community structure through the grazing of mesozooplankton on diatoms and the grazing of microzooplankton on picoautotrophs. Grazer control of picoautotroph biomass may well be a universal feature of meso- and eutrophic environments (Chisholm 1992) and a consequence of trophic dynamics (Thingstad 1998). The prerequisites of mesozooplankton control of diatom biomass in the monsoonal Arabian Sea are still unknown and may have to await a more detailed understanding of the seasonal successions

and life cycles of the dominant zooplankton species of this region (Smith 2002).

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