PERGAMON

Deep-Sea Research II 46 (1999) 1665–1690

DEEP-SEA RESEARCH
PART II

Phytoplankton growth and mortality during the 1995 Northeast Monsoon and Spring Intermonsoon in the Arabian Sea

David A. Caron*, Mark R. Dennett

Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

Received 1 September 1997; received in revised form 3 July 1998; accepted 10 August 1998

Abstract

Phytoplankton growth rates and mortality rates were experimentally examined at eight stations in the Arabian Sea along the U.S. JGOFS cruise track during the 1995 Northeast Monsoon (January) and Spring Intermonsoon (March–April). Instantaneous growth rates averaged over an entire cruise were approximately twice as high during the NE Monsoon than during the Spring Intermonsoon period (overall averages of 0.84 ± 0.29 (s.d.) versus $0.44 \pm 0.19\ d^{-1}$). Average herbivore grazing (mortality) rates, however, were quite similar for the two seasons (overall averages of 0.35 ± 0.18 and $0.30 \pm 0.17\ d^{-1}$ for the NE Monsoon and Spring Intermonsoon, respectively). The absolute amounts of phytoplankton biomass consumed during each season also were similar (29 and 25% of standing stock consumed d^{-1} for the January and March–April cruises, respectively), as were the geographical trends of this removal. These seasonal trends in growth and removal rates resulted in net phytoplankton growth rates that were considerably higher during the January cruise ($0.48\ d^{-1}$) than during the March–April cruise ($0.14\ d^{-1}$). That is, phytoplankton production was more closely balanced during the Spring Intermonsoon season (87% of daily primary production consumed) relative to the NE Monsoon season (49% of daily primary production consumed). Station-to-station variability was high for rate measurements during either cruise. Nevertheless, there was a clear onshore–offshore trend in the absolute rate of removal of phytoplankton biomass (μg chlorophyll consumed $l^{-1}\ d^{-1}$) during both cruises. Coastal stations had removal rates that were typically 2–4 times higher than removal rates at oceanic stations.

* Corresponding author. Fax: 001-508-457-2169.
E-mail address: dcaron@whoi.edu (D.A. Caron)

0967-0645/99/$ - see front matter
PII: S0967-0645(99)00039-9

1. Introduction

Microbial herbivory is recognized as a major source of phytoplankton mortality in pelagic food webs (Caron and Finlay, 1994; Sherr and Sherr, 1994). One recent overview of investigations examining herbivory in marine ecosystems has indicated that microbial predation is similar in magnitude to meso- and macrozooplankton predation (Sherr and Sherr, 1994). Average values in the studies cited in that review indicated that approximately 60% of daily primary production is consumed by microbial herbivores. As a consequence, a considerable amount of research has been undertaken in recent years to measure microbial herbivory because of the large role that this process plays in determining the fate of primary production in aquatic ecosystems.

Primary production that is consumed directly by microbial predators in plankton communities is believed to be retained largely within biogeochemical cycles in surface waters of the world ocean. Heterotrophic microbial activities in surface waters are considered to contribute principally to recycling processes rather than to the production of rapidly sinking particles that dominate flux to the deep ocean (Michaels and Silver, 1988). The conceptual basis for this argument is that production by very small phytoplankton is consumed primarily by protozoa that release dissolved materials or small particles with slow sinking speeds (Stoecker, 1984; Caron et al., 1985; Elbrächter, 1991; Nagata and Kirchman, 1992). The general paradigm continues that these minute phytoplankton must be transferred through several trophic steps before this material reaches a size sufficient to result in significant sinking speeds (Azam et al., 1983). The existence of complex microbial food webs, and remineralization processes that take place at each trophic transfer, reduce the amount of energy and biomass available to each subsequent trophic level (Goldman and Caron, 1985). Thus, the amount of microbial biomass that is transformed into rapidly sedimenting particles may be a small percentage of the original quantity of primary production.

The magnitude of the role that microbial consumers play as herbivores in pelagic ecosystems, and their role (outlined above) in determining the fate of primary production in marine biogeochemical cycles, has focused attention on the activities of these assemblages within the context of the Joint Global Ocean Flux Study, JGOFS (SCOR, 1990). Studies of phytoplankton growth and mortality were conducted within the context of the JGOFS in the northern Arabian Sea during 1995. We report here on our studies to obtain estimates of phytoplankton growth rates and mortality (herbivory) by nanozooplankton (2–20 μm) and microzooplankton (20–200 μm) in the upper water column at selected stations throughout the study area. Estimates of the abundance and biomass of the nano-sized and micro-sized phytoplankton and zooplankton in the upper water column during these seasons have been presented elsewhere (Dennett et al., 1999).

2. Materials and methods

2.1. Sample locations and collection procedures

Phytoplankton growth rates and mortality rates were examined at eight stations during TN043 (January 8–February 4) and at seven stations during TN045

(March 14–April 10) of the US JGOFS Arabian Sea program. These cruises corresponded to the Northeast (NE) Monsoon and Spring Intermonsoon periods, respectively, in the Arabian Sea (Fig. 1 shows station locations). The same stations were occupied during both cruises in a clockwise fashion starting with station N4 on TN043 or station N7 on TN045. Most of the data comparisons presented here group these stations as "northern" (N4–N11) and "southern" (S2–S15) transects by agreement among the investigators in the US JGOFS program because the cruise tracks constitute two nearshore–offshore transects through different hydrographic regimes.

Samples for herbivory experiments were collected using 30-l Go-Flo® bottles held in a resin-coated rosette frame designed to minimize trace metal contamination. Seawater was collected using 2–3 bottles per depth. Water from the bottles was combined into a 50-l carboy using wide-bore silicone tubing inserted all the way to the bottom of the carboy to minimize bubbling and physical disturbance. Water was collected at two depths in the euphotic zone at each station and processed separately. Our strategy in this research program was to obtain an index of phytoplankton growth and grazing in the upper and lower portions of the euphotic zone at each station.

2.2. Initial chemical analyses and microbial counts

Pertinent chemical parameters (nutrients, chlorophyll *a*) were obtained at the time of collection for the seawater used in the herbivory experiments. Physical parameters (temperature, depth) were obtained from sensors deployed on the rosette. Measurements of total dissolved inorganic nitrogen (DIN = NH_4^+, NO_3^-, NO_2^-), PO_4^{-3} and dissolved silica in the samples at the time of collection were provided by the US JGOFS Arabian Sea hydrographic team. Chlorophyll *a* concentrations at the beginning of the experiments were measured for the unfiltered seawater and seawater passed through Nitex® nylon screening to obtain < 5, 5–20, and $> 20\,\mu m$ size fractions. Samples were caught on Gelman® GF/F filters. Chlorophyll *a* was extracted in 100% (TN043) or 90% (TN045) acetone at $-20^\circ C$ overnight in the dark and measured flurometrically using a Turner Designs fluorometer.

Initial population abundances of pico- (0.2–2.0 μm), nano- (2.0–20 μm) and microplanktonic (20–200 μm) phytoplankton, as well as nanoplanktonic and microplanktonic zooplankton (protozoa and micrometazoa) were determined from flow cytometric or microscopical analyses of samples collected in 10-l Niskin bottles. These samples were collected as a part of the effort to characterize microbial abundance and biomass during the Arabian Sea program (Dennett et al., 1999). Samples for phototrophic picoplankton counts were preserved with paraformaldehyde and stored in liquid nitrogen. Abundances were determined by flow cytometry (counts provided by Dr. Lisa Campbell, Texas A&M University). Samples for nanoplankton counts were preserved with formalin and prepared for epifluorescence microscopy within 24 hr (Sherr et al., 1993). Microplankton samples were preserved with Lugols preservative and counted using inverted light microscopy.

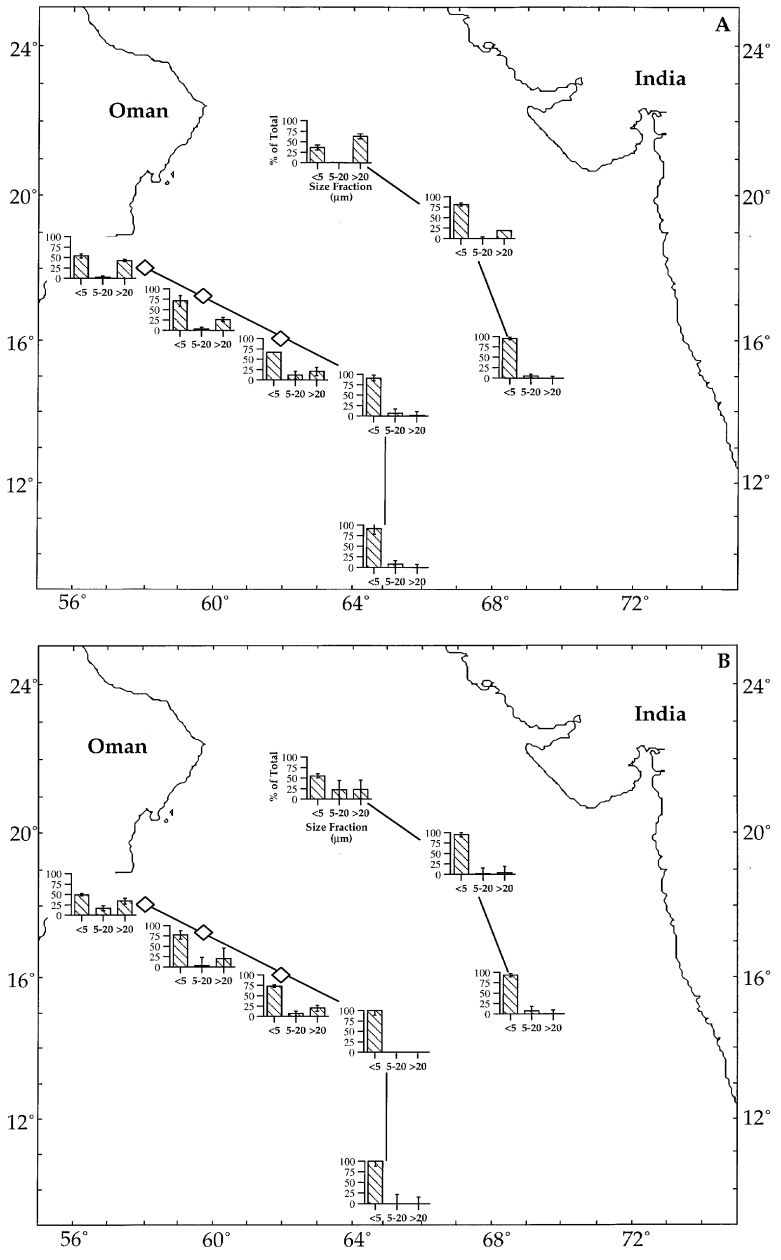

Fig. 1. Chlorophyll concentrations (expressed as a percent of total) in three size fractions at the beginning of each dilution experiment performed in the shallow euphotic zone (A,C) and deep euphotic zone (B,D) during the 1995 NE Monsoon (A,B) and Spring Intermonsoon (C,D). See Table 1 for sample depths. Error bars are ± one standard deviation.

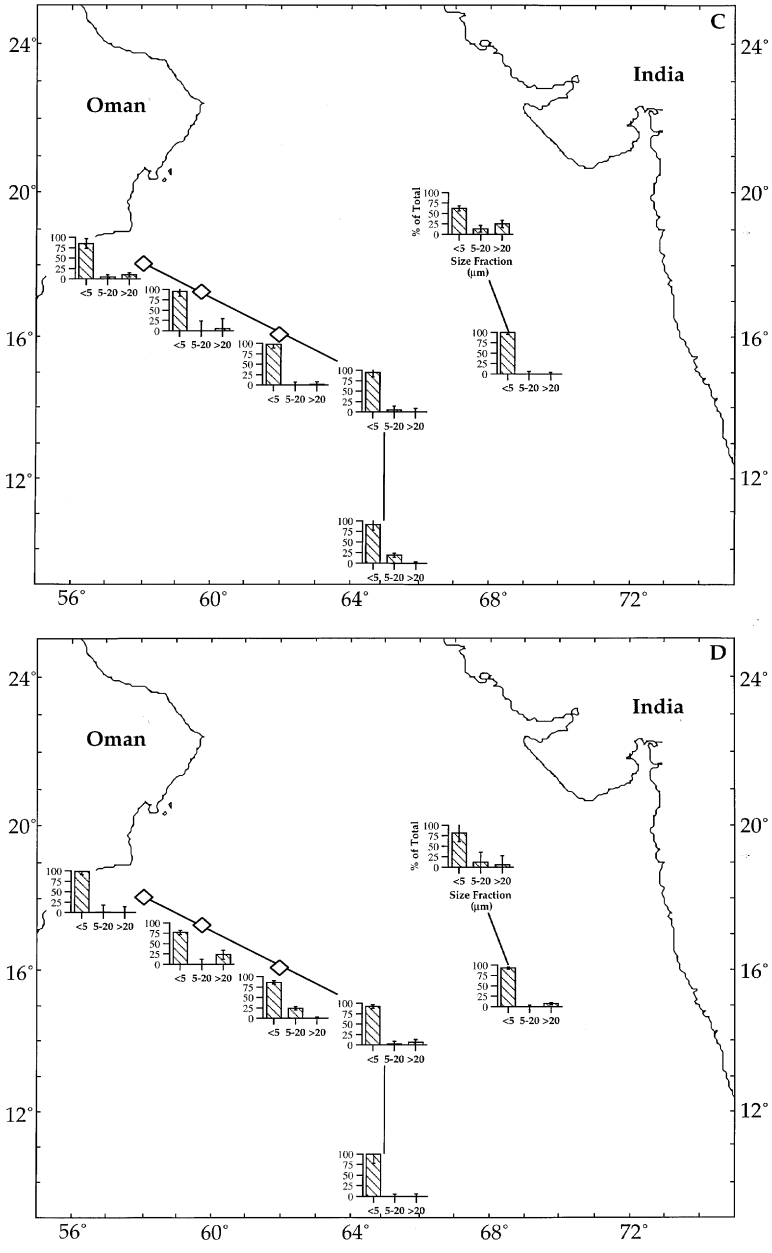

Fig. 1. Continued.

2.3. Microbial herbivory

Microbial herbivory was examined using a modified dilution technique (Landry and Hassett, 1982; Landry, 1993; Landry et al., 1995b). All tubing, carboys, experimental flasks and filters were soaked in 10% HCl and rinsed in distilled–deionized water prior to each experiment. Special care was taken to reduce bubbling in all filtrations and sample transfers in order to minimize damage to delicate phytoplankton and protozoa. Measured volumes of diluent were added to the incubation bottles first for all diluted samples, and then unfiltered seawater was added to a prescribed level without bubbling using wide bore silicone tubing. Filtrate for all experiments was prepared using acid-soaked Gelman® cartridge filters (0.2 μm pore size) using only gravity filtration. These filters produce large volumes of filtrate in short periods of time with very little head, and apparently with little cell breakage. Measurements of dissolved organic carbon (courtesy of Dr. Dennis Hansell) and inorganic nutrients (courtesy of the US JGOFS Arabian Sea hydrographic team) in unfiltered seawater and filtrate showed no measurable changes in these constituents as a result of the filtration process.

Containers for the herbivory experiments were 1.2-l clear polycarbonate bottles filled to the neck to reduce agitation during incubations. The dilution series consisted of bottles containing 100, 80, 60, 40 and 20% unfiltered seawater with nutrient enrichment (10 μM NH_4^+ and 1 μM PO_4^{-3}). Duplicate sets of bottles with unfiltered seawater without nutrient additions were prepared and incubated, as well as diluent controls (filtrate from the cartridge filter) to measure residual chlorophyll in the filtrate and any changes in these controls during the incubations. Chlorophyll concentrations in the controls were typically two orders of magnitude lower than experimental bottles (near the limit of detection) and never showed measurable increases in concentrations during any of the experiments. All dilution bottles were prepared and incubated in triplicate.

Incubations were conducted in two on-deck incubators covered with blue acrylic plastic to reduce PAR light intensity to 30% of the incident value. The incubator that held the samples collected from the deeper euphotic zone also was covered with a layer of grey window screening to reduce light intensity further to 15% of the incident value. Incubations were performed for approximately 24 h, and then all bottles were resampled and analyzed for changes in chlorophyll concentration. Samples from the upper euphotic zone generally were obtained from depths that were similar to the light intensity recreated in the incubator used to incubate these samples. Samples from the lower euphotic zone, however, were often collected near significant subsurface features such as deep chlorophyll maxima that had in-situ light intensities that were sometimes lower than the intensities in the incubator employed for these samples (15% of I_o).

Growth and mortality rates of phytoplankton were calculated from changes in chlorophyll concentrations over the length of the dilution experiments using linear regression analysis. Our terminology follows that of Landry et al. (1995a,b). Growth rates of the phytoplankton assemblages in the enriched bottles (μ_n) were determined from the Y-intercepts of the regressions of apparent growth rate in the bottles versus

dilution. Phytoplankton mortality rates (m) were determined from the slopes of the regressions. Phytoplankton growth rates in the unenriched bottles (μ_o) were determined from net (apparent) growth rates of the phytoplankton in the unenriched, undiluted bottles (k) and the mortality rates ($\mu_o = k + m$).

3. Results

3.1. Initial Chemical/Physical/Biological Parameters

Temperatures at the two depths sampled for the phytoplankton growth and mortality experiments were similar over the entire study area during both cruises (overall range 24.4–28.6°C; Table 1). Concentrations of DIN, phosphate and silicate in these samples occurred at measurable levels for most samples (Table 1). Greatest between-cruise variability (factor of 2.7X) was observed for DIN (overall average = 2.67 μM, range = 0.06–5.01 μM for the NE Monsoon; overall average = 0.98 μM, range = undetectable-4.14 μM for the Spring Intermonsoon). Average DIN values were similar for shallow and deep water samples during the NE Monsoon (2.42 versus 2.92 μM), while average DIN for the shallow samples was approximately $\frac{1}{3}$ that for the deep samples during the Spring Intermonsoon (0.51 versus 1.46 μM). Lowest DIN concentrations were observed at the southernmost station of the southern transect (station S15).

Initial concentrations of chlorophyll averaged over each cruise were remarkably similar (NE Monsoon = 0.48 $\mu g\, l^{-1}$; Spring Intermonsoon = 0.44 $\mu g\, l^{-1}$). Ranges of chlorophyll concentrations spatially were nearly identical for the two cruises (overall range for both cruises 0.1–1.4 $\mu g\, l^{-1}$). Chlorophyll averaged for shallow and deep samples was similar for the NE Monsoon (0.54 and 0.41 $\mu g\, l^{-1}$) but shallow samples for the Spring Intermonsoon averaged approximately $\frac{1}{2}$ the average of the deep samples (0.28 $\mu g\, l^{-1}$ for shallow samples versus 0.60 $\mu g\, l^{-1}$ for deep samples). These differences mirror trends observed for initial values of DIN (i.e., lower DIN concentration correlated with lower chlorophyll concentration).

Size-fractionated chlorophyll analyses indicated the size distribution of phytoplankton during the study (Fig. 1). In general, these analyses indicated that most samples were dominated by small nanoplanktonic and picoplanktonic algae (< 5 μm). However, significant contributions of microplanktonic (> 20 μm) phytoplankton were observed at several stations and depths during each cruise. In particular, phototrophic microplankton made signficant contributions to phytoplankton biomass at stations N4, S2, S4 and S7 during the NE Monsoon (Fig. 1A and B) and stations N7 and S4 during the Spring Intermonsoon (Fig. 1C,D). This station-to-station variability in the size distribution of chlorophyll was also apparent in the relative contributions of phototrophic picoplankton, nanoplankton and microplankton to total phytoplankton biomass (Campbell et al., 1998; Dennett et al., 1999). The small sample size (270 ml) used to the perform size-fractionated chlorophyll measurements may have underestimated the importance of microplanktonic algae in some samples.

Table 1
Station/sample information, initial nutrient concentrations and initial phototroph abundances for dilution experiments performed during cruises TN043 (NE Monsoon, January 1995) and TN045 (Spring Intermonsoon, March–April 1995) in the Arabian Sea. See Fig. 1 for station locations. DIN = dissolved inorganic nitrogen (nitrate, nitrite, ammonium); PPIC = (0.2–2.0 μm algae; *Prochlorococcus* and *Synechococcus*); PNAN = phototrophic nanoplankton (2.0–20 μm algae); PMIC = phototrophic microplankton (algae > 20 μm). *Values of PPIC provided by Drs. Lisa Campbell (Texas A&M University, Austin) and Mike Landry (University of Hawaii). Chl = Chlorophyll

Date	Station	Depth (m)	Station location	Temp (°C)	DIN (μM)	PO_4 (μm)	Si (μM)	Phototroph abundances			
								PPIC* Cells ml^{-1}	PNAN Cells ml^{-1}	PMIC Cells l^{-1}	CHl ($\mu g\, l^{-1}$)
NE Monsoon											
10 Jan	N4	5	21°11′N	24.9	1.82	0.54	1.1	5.09×10^4	1.23×10^3	1.20×10^5	1.39
		66	63°33′E	24.9	2.66	0.62	1.3	2.60×10^4	6.13×10^2	3.03×10^4	0.49
13 Jan	N7	8	19°12′N	24.8	3.51	0.64	3.3	4.42×10^4	7.05×10^2	4.25×10^3	0.55
		59	67°10′E	24.8	4.51	0.71	4.1	2.21×10^4	2.04×10^2	8.92×10^3	0.33
15 Jan	N11	8	15°23′N	26.3	1.51	0.44	1.5	1.21×10^5	4.72×10^2	2.96×10^3	0.43
		69	68°45′E	26.3	1.71	0.48	1.5	1.15×10^5	5.31×10^2	4.00×10^3	0.32
17 Jan	S15	7	10°00′N	27.2	0.06	0.27	2.1	2.34×10^5	2.80×10^2	5.04×10^2	0.16
		69	64°54′E	27.2	1.47	0.40	2.7	8.53×10^4	7.42×10^2	1.96×10^3	0.40
20 Jan	S11	8	14°27′N	25.8	3.17	0.53	3.8	1.02×10^5	4.13×10^2	2.80×10^3	0.31
		49	65°00′E	25.7	3.25	0.54	3.8	1.18×10^5	5.60×10^2	2.40×10^3	0.30
24 Jan	S7	8	16°02′N	25.1	5.00	0.66	2.1	1.50×10^5	9.04×10^2	1.70×10^4	0.40
		28	62°00′E	25.0	5.01	0.66	2.1	9.71×10^4	9.19×10^2	1.15×10^4	0.39
27 Jan	S4	3	17°12′N	24.9	1.92	0.49	2.0	7.82×10^4	6.06×10^2	4.41×10^4	0.34
		22	59°46′E	24.7	2.37	0.53	2.2	6.32×10^4	7.27×10^2	2.78×10^4	0.31
29 Jan	S2	3	18°05′N	24.4	2.37	0.55	2.4	6.12×10^4	2.00×10^3	5.59×10^4	0.77
		22	58°00′E	24.4	2.43	0.55	2.2	2.88×10^4	1.67×10^3	5.62×10^4	0.78

18 Mar	N7	10	19°12′N	25.3	1.57	0.43	1.0	2.00×10^5	9.63×10^2	2.08×10^4	0.46
		40	67°10′E	24.9	4.14	0.57	1.5	2.89×10^4	8.41×10^2	3.95×10^4	0.26
21 Mar	N11	10	15°23′N	27.4	1.23	0.44	1.8	2.15×10^5	7.42×10^2	2.88×10^3	0.15
		80	68°45′E	25.4	1.83	0.46	2.2	7.19×10^4	9.34×10^2	6.64×10^3	0.28
23 Mar	S15	10	10°00′N	28.6	0.05	0.19	2.0	2.18×10^5	3.43×10^2	1.13×10^3	0.12
		60	64°54′E	28.5	un	0.38	2.8	2.87×10^5	7.76×10^2	2.01×10^3	0.31
26 Mar	S11	10	14°27′N	27.6	0.14	0.27	1.9	2.07×10^5	1.87×10^2	2.21×10^3	0.11
		70	65°00′E	26.5	1.37	0.46	1.4	1.22×10^5	6.88×10^2	4.49×10^3	0.48
31 Mar	S7	10	16°02′N	26.9	0.20	0.37	0.8	4.01×10^5	3.35×10^2	1.70×10^3	0.34
		35	62°00′E	25.9	1.26	0.50	0.8	1.92×10^5	5.64×10^2	3.42×10^3	0.62
2 Apr	S4	10	17°12′N	26.3	0.23	0.38	1.1	7.55×10^4	7.11×10^2	4.81×10^3	0.48
		30	59°46′E	25.0	1.20	0.50	1.6	6.86×10^4	1.07×10^3	1.19×10^4	1.33
5 Apr	S2	10	18°05′N	26.5	0.15	0.33	1.2	3.91×10^5	9.99×10^2	3.72×10^3	0.32
		50	58°00′E	24.7	0.39	0.39	1.2	1.14×10^5	7.45×10^2	9.89×10^3	0.91

Nano- and microzooplankton abundances in the Arabian Sea during this study were typical of oceanic waters. Heterotrophic nanoplankton (HNAN) ranged up to 6.87×10^2 ml^{-1} while total heterotrophic microplankton (HMIC) ranged up to $2–3 \times 10^3$ l^{-1} (Table 2). Heterotrophic dinoflagellates and non-loricate ciliates numerically dominated the HMIC, particularly at the nearshore stations, but substantial numbers of foraminifera, actinopods, tintinnid ciliates and copepod nauplii were present at most stations. There were no clear differences in HNAN or HMIC abundances between the two cruises.

3.2. Phytoplankton Growth and Mortality

Phytoplankton growth rates in the unenriched bottles of the dilution series (μ_o) differed by approximately a factor of two between the two cruises (Table 2). Growth rates averaged over all experiments during the NE Monsoon were 0.84 ± 0.29 d^{-1} (± 1 standard deviation), while rates averaged for the Spring Intermonsoon were 0.44 ± 0.19 d^{-1}. Growth rates from individual experiments varied greatly. Overall ranges were 0.02–1.44 d^{-1} for the NE Monsoon and 0.13–0.82 d^{-1} for the Spring Intermonsoon. The fastest rates corresponded to approximately two doublings per day. There were no consistent differences between the growth rates averaged separately for shallow and deep samples.

In contrast, phytoplankton mortality rates (m) averaged over all stations for each cruise were quite similar. Average mortality rates were 0.35 ± 0.18 d^{-1} (range = 0.11–0.82 d^{-1}) for the NE Monsoon and 0.30 ± 0.17 d^{-1} (range = undetectable slope-0.70 d^{-1}) for the Spring Intermonsoon. Rates in the shallow samples were somewhat higher than rates in the deep samples for the monsoon (0.44 ± 0.20 versus 0.26 ± 0.12 d^{-1}) and intermonsoon (0.36 ± 0.18 and 0.24 ± 0.15 d^{-1}) but variability within each subset was substantial.

Net phytoplankton growth rates in the unenriched bottles ($k = \mu_o - m$) reflected the differences in phytoplankton growth between the two cruises (Table 2). Values for the January cruise averaged 3.5X the rates measured during the March-April cruise (0.48 versus 0.14 d^{-1}). Phytoplankton growth averaged over all samples and stations exceeded mortality for both cruises, but net growth was 57% of growth rate (μ_o) during the NE Monsoon while it was 32% of μ_o during March–April.

Nutrient enrichment enhanced phytoplankton growth rates in many but not all of the dilution experiments (μ_n; Table 2). The most consistent effect occurred in the shallow samples collected during the Spring Intermonsoon. Phytoplankton growth rates for unenriched bottles from the shallow samples of this cruise averaged approximately $\frac{1}{2}$ the growth rates in the enriched bottles from the same samples. This ratio (μ_o/μ_n) averaged for the deep samples from the Spring Intermonsoon was 0.85, and 0.88 for all samples from the NE Monsoon.

Comparison of k, μ_o and m on a station-by-station basis indicated few obvious trends in the spatial pattern of these parameters (Fig. 2). Rates of growth consistently exceeded mortality among the stations during the NE Monsoon, except for the "oligotrophic" station S15. Growth rates during the Spring Intermonsoon generally were lower than rates during January (again with the exception of station S15), and

Table 2
Initial heterotroph population abundances and summary of results for dilution experiments performed during the 1995 NE Monsoon and Spring Intermonsoon in the Arabian Sea. See Table 1 and Fig. 1 for station locations. HNAN = heterotrophic nanoplankton (2.0–20 μm); HMIC = heterotrophic microplankton (20–200 μm; heterotrophic dinoflagellates, tintinnid and non-loricate ciliates, foraminfera + actinopods, copepod nauplii); μ_n = phytoplankton growth rate in nutrient-amended bottles (d^{-1}); μ_o = phytoplankton growth rate in unenriched bottles (d^{-1}); k = net phytoplankton growth rate in unenriched bottles (d^{-1}); m = grazing mortality (d^{-1}); r^2 = regression coefficient

Date	Station	Depth (m)	HNAN Cells ml^{-1}	HMIC					μ_n (d^{-1})	k (d^{-1})	μ_o (d^{-1})	m (d^{-1})	r^2
				Hetero. Dinoflag. Cells l^{-1}	Tintinnid Ciliates Cells l^{-1}	Non-lor. Ciliates Cells l^{-1}	Forams & Actin. Cells l^{-1}	Copepod Nauplii Indiv. l^{-1}					
NE Monsoon													
10 Jan	N4	5	4.03×10^{2}	4.58×10^{2}	6.35×10^{1}	5.11×10^{2}	5.53×10^{1}	2.24×10^{1}	0.92	0.37	0.85	0.48	0.91
		66	2.81×10^{2}	3.96×10^{2}	2.53×10^{1}	2.87×10^{2}	1.53×10^{1}	9.41×10^{0}	0.80	0.54	0.65	0.11	0.26
13 Jan	N7	8	4.33×10^{2}	1.11×10^{3}	5.53×10^{1}	8.32×10^{2}	7.18×10^{1}	1.06×10^{1}	1.13	0.46	1.06	0.60	0.89
		59	2.92×10^{2}	6.88×10^{2}	5.88×10^{1}	6.24×10^{2}	2.94×10^{1}	1.29×10^{1}	1.03	0.60	1.05	0.45	0.93
15 Jan	N11	8	2.63×10^{2}	7.16×10^{2}	5.65×10^{1}	7.00×10^{2}	3.65×10^{1}	2.12×10^{1}	1.43	0.62	1.44	0.82	0.82
		69	2.84×10^{2}	8.18×10^{2}	1.29×10^{1}	5.16×10^{2}	4.23×10^{1}	1.06×10^{1}	1.01	0.71	0.86	0.15	0.51
17 Jan	S15	7	2.92×10^{2}	2.11×10^{2}	4.00×10^{1}	4.01×10^{2}	3.53×10^{1}	2.35×10^{0}	0.69	−0.21	0.02	0.19	0.37
		69	2.46×10^{2}	5.95×10^{1}	1.76×10^{1}	1.61×10^{2}	2.47×10^{1}	3.53×10^{0}	0.38	0.33	0.55	0.22	0.67
20 Jan	S11	8	1.90×10^{2}	4.60×10^{2}	5.53×10^{1}	9.27×10^{2}	8.47×10^{1}	1.18×10^{1}	1.01	0.63	0.97	0.34	0.77
		49	2.88×10^{2}	2.71×10^{2}	4.82×10^{1}	1.32×10^{3}	4.11×10^{2}	3.06×10^{1}	0.98	0.67	0.84	0.17	0.58
24 Jan	S7	8	3.01×10^{2}	3.71×10^{2}	5.53×10^{1}	9.28×10^{2}	4.35×10^{1}	2.47×10^{1}	0.98	0.56	0.85	0.29	0.78
		28	2.76×10^{2}	1.83×10^{2}	3.88×10^{1}	5.12×10^{2}	4.24×10^{1}	2.00×10^{1}	0.99	0.63	0.89	0.26	0.68
27 Jan	S4	3	1.32×10^{2}	5.10×10^{2}	4.12×10^{1}	1.11×10^{3}	7.88×10^{1}	4.47×10^{1}	1.07	0.41	0.74	0.33	0.94
		22	1.89×10^{2}	1.05×10^{2}	1.29×10^{1}	4.76×10^{2}	1.14×10^{2}	3.06×10^{1}	1.04	0.60	1.02	0.42	0.98
29 Jan	S2	3	6.77×10^{2}	1.32×10^{3}	6.71×10^{1}	6.79×10^{2}	6.71×10^{1}	1.77×10^{1}	1.02	0.42	0.92	0.50	0.80
		22	4.62×10^{2}	2.12×10^{3}	9.29×10^{1}	7.09×10^{2}	1.22×10^{2}	3.06×10^{1}	0.82	0.42	0.73	0.31	0.66

Table 2. Continued.

Date	Station	Depth (m)	HNAN Cells ml^{-1}	HMIC					μ_n (d^{-1})	k (d^{-1})	μ_o (d^{-1})	m (d^{-1})	r^2
				Hetero. Dinoflag. Cells l^{-1}	Tintinnid Ciliates Cells l^{-1}	Non-lor. Ciliates Cells l^{-1}	Forams & Actin. Cells l^{-1}	Copepod Nauplii Indiv. l^{-1}					
Spring Intermonsoon													
18 Mar	N7	10	2.80×10^2	7.20×10^2	5.29×10^1	4.65×10^2	5.88×10^0	1.88×10^1	1.21	0.12	0.82	0.70	0.89
		40	4.16×10^2	1.69×10^2	1.77×10^1	1.41×10^2	5.65×10^1	3.06×10^1	0.59	0.38	0.55	0.17	0.84
21 Mar	N11	10	2.94×10^2	8.51×10^2	2.35×10^1	3.18×10^2	6.12×10^1	3.76×10^1	1.50	−0.06	0.28	0.34	0.89
		80	2.12×10^2	2.95×10^2	3.53×10^1	1.46×10^2	2.12×10^1	1.18×10^1	0.37	0.37	0.37	ND*	–
23 Mar	S15	10	1.24×10^2	3.84×10^2	1.18×10^0	1.94×10^2	2.82×10^1	5.88×10^0	0.96	0.54	0.71	0.17	0.75
		60	2.64×10^2	4.07×10^2	1.18×10^1	2.00×10^2	9.41×10^0	1.41×10^1	0.63	−0.19	0.15	0.34	0.77
26 Mar	S11	10	2.74×10^2	5.82×10^2	2.82×10^1	2.73×10^2	4.47×10^1	1.88×10^1	1.07	0.30	0.52	0.22	0.68
		70	3.00×10^2	7.95×10^2	2.35×10^1	4.21×10^2	7.41×10^1	1.76×10^1	0.32	0.30	0.46	0.16	0.46
31 Mar	S7	10	3.35×10^2	2.70×10^2	6.59×10^1	6.59×10^2	4.47×10^1	2.24×10^1	0.76	0.12	0.37	0.26	0.46
		35	2.95×10^2	9.73×10^2	8.47×10^1	7.72×10^2	3.65×10^1	1.65×10^1	0.56	0.26	0.53	0.27	0.91
2 Apr	S4	10	5.63×10^2	2.50×10^2	9.65×10^1	3.20×10^2	8.59×10^1	1.18×10^1	0.65	0.01	0.38	0.37	0.95
		30	6.87×10^2	3.53×10^3	1.71×10^2	3.91×10^2	5.06×10^1	2.00×10^1	0.15	−0.13	0.13	0.26	0.69
5 Apr	S2	10	3.57×10^2	1.74×10^3	4.71×10^1	5.82×10^2	8.00×10^1	2.35×10^1	0.84	−0.10	0.33	0.43	0.94
		50	5.11×10^2	2.54×10^3	1.68×10^2	5.15×10^2	2.12×10^1	4.71×10^0	0.52	0.00	0.49	0.49	0.86

ND* = < 0.10 level of significance.

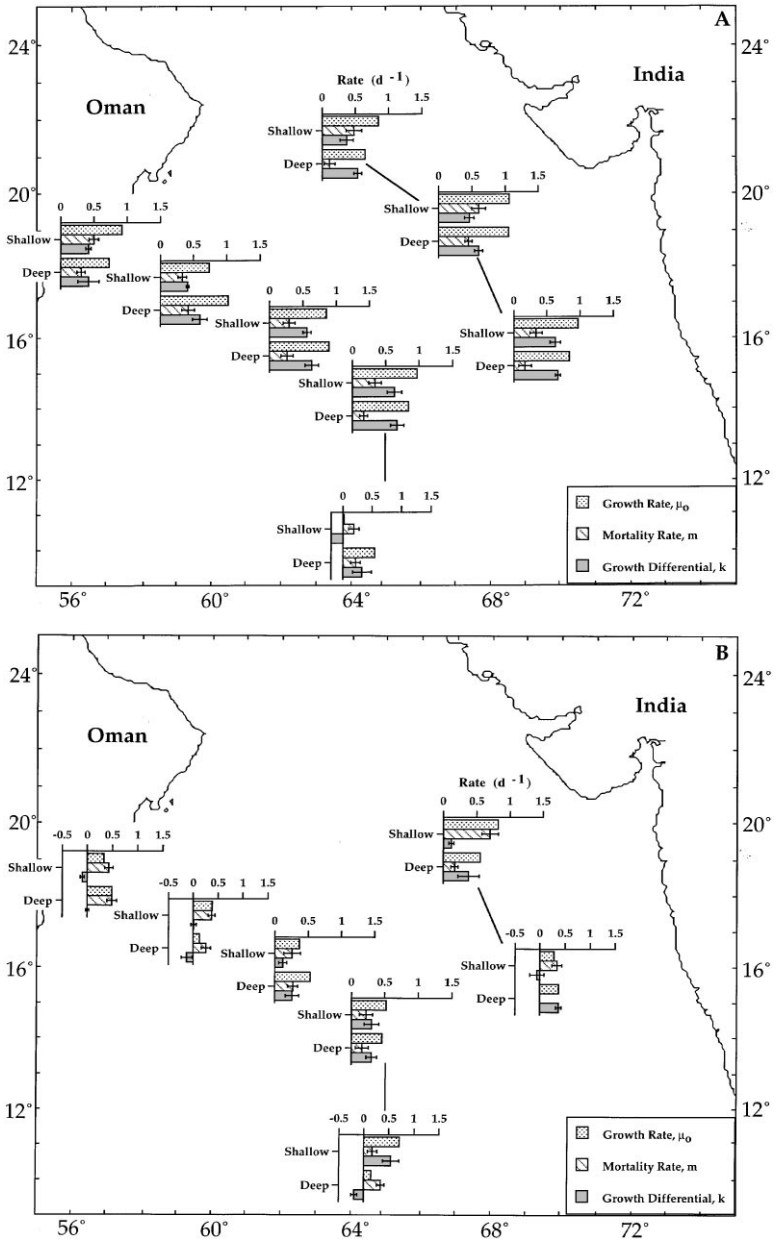

Fig. 2. Summary of phytoplankton growth rates (μ_o), mortality rates (m) and growth differential (net phytoplankton growth rate, ($k = \mu_o - m$) during the 1995 NE Monsoon (A) and Spring Intermonsoon (B). See Table 1 for sample depths. Error bars represent the standard error.

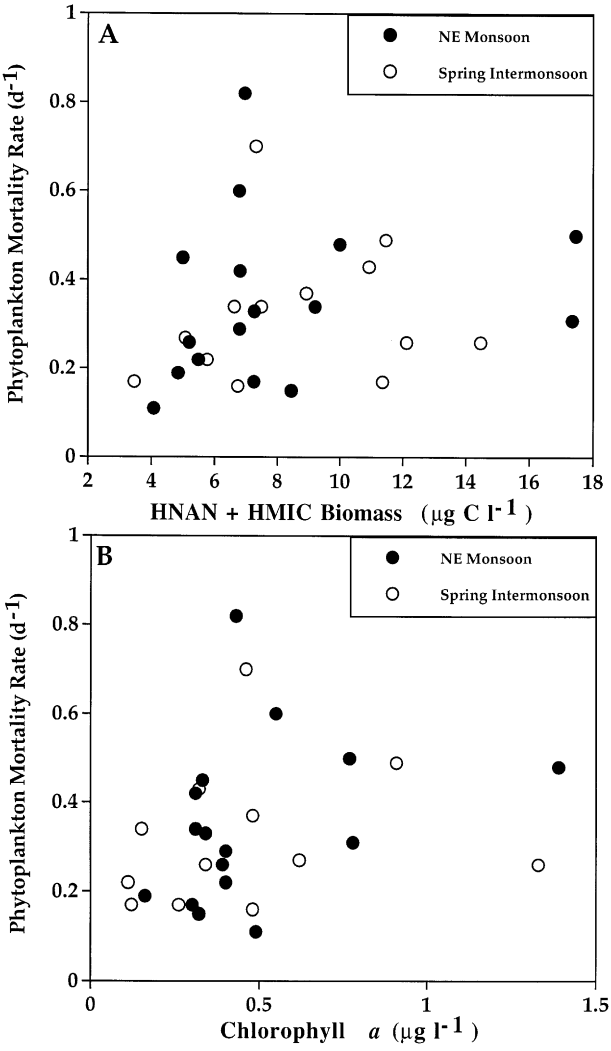

Fig. 3. Phytoplankton mortality rate (m) expressed as a function of the biomass of (A) heterotrophic nano- and microplankton (consumers 2–200 µm in size) and (B) chlorophyll concentration at the beginning of dilution experiments performed in the Arabian Sea during the 1995 NE Monsoon and Spring Intermonsoon seasons.

the growth differential (i.e., net growth rate, $k = \mu_o - m$) was lower during the Spring Intermonsoon. Balanced growth and grazing rates were particularly evident at the nearshore stations (S2, S4) during the March–April cruise.

Phytoplankton mortality rate showed little or no relationship to various facets of the microbial community within or between cruises. For example, mortality rate did not vary in any consistent manner with HNAN + HMIC biomass (Fig. 3a) although

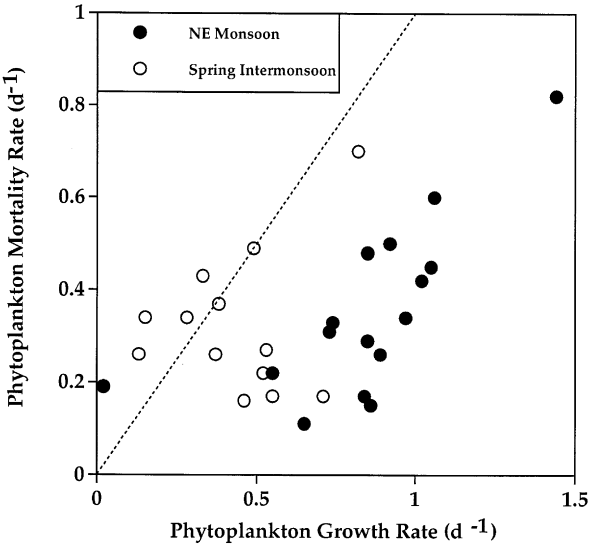

Fig. 4. Phytoplankton mortality rate (m) expressed as a function of phytoplankton growth rate (μ_o) for dilution experiments performed in the Arabian Sea during the NE Monsoon and Spring Intermonsoon seasons 1995. The dotted line indicates the line of one-to-one correspondence between growth and mortality rates.

there were clearly bounds within which the values occurred. This lack of correlation may be a consequence of several factors including other sources of phytoplankton mortality not included in our estimates of HNAN + HMIC, or variability in the cell^{-1} grazing activities of these consumers during the study periods. Similarly, there was little correspondence between mortality rate and total phytoplankton biomass as indicated by chlorophyll concentration (Fig. 3b).

A poor correlation also was observed between phytoplankton mortality and phytoplankton growth rate (Fig. 4). Few experiments showed one-to-one correspondence between mortality and growth (dotted line in Fig. 4), although the data for the experiments performed during the Spring Intermonsoon were somewhat evenly dispersed on either side of this line. Interestingly, the data for the experiments from the NE Monsoon showed a fair correlation between mortality and growth rate ($r^2 = 0.68$, with one data point omitted), but all data points except one occurred to the right of the line of one-to-one correspondence. This finding indicates significant net growth of phytoplankton during the January cruise.

Although station-to-station variability for mortality rates was not strongly related to distance from shore along the two transects for either cruise as described above (Fig. 2), the absolute amounts of phytoplankton standing stock consumed showed consistent changes along the nearshore–offshore transects (Fig. 5). Removal rates (μg chlorophyll a l^{-1} d^{-1}) were calculated from mortality rates and chlorophyll concentration for each experiment. Removal rates estimated in this manner varied several fold along the southern transect during either cruise, with highest removal rates

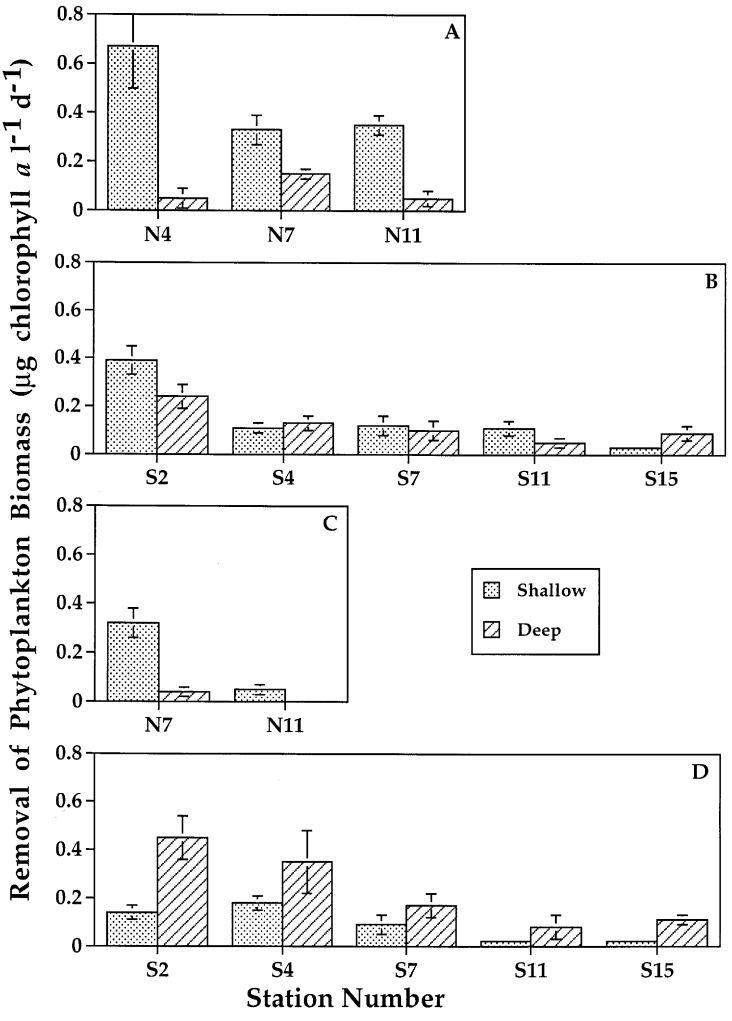

Fig. 5. Phytoplankton mortality (expressed as µg chlorophyll a consumed $l^{-1}\,d^{-1}$) during dilution experiments performed in the Arabian Sea during the 1995 NE Monsoon (A, B) and Spring Intermonsoon (C, D).

observed at coastal stations. Both the absolute removal rates and the general geographical patterns of removal were similar for the two cruises. Averaged over all depths and stations, chlorophyll removal rates were 0.15 and 0.13 µg chlorophyll *a* $l^{-1}\,d^{-1}$ for the NE Monsoon and Spring Intermonsoon, respectively.

Removal of chlorophyll expressed as a percentage of the standing stock was similar for the two cruises when averaged over all stations (Table 3). The removal rates given above corresponded to averages of 29 and 25% of the phytoplankton standing stock removed each day. Removal of phytoplankton production, however, differed

Table 3
Daily removal of phytoplankton (expressed as a percentage of chlorophyll standing stock) and primary production during the 1995 NE Monsoon and Spring Intermonsoon in the Arabian Sea based on mortality rates obtained from regression analysis of dilution experiment results. Station locations are given in Table 1

NE Monsoon				Spring Intermonsoon			
Station	Depth (m)	Chlorophyll consumed (%)	Production consumed (%)	Station	Depth (m)	Chlorophyll consumed (%)	Production consumed (%)
N4	5	38	67				
	66	10	22				
N7	8	45	69	N7	10	50	90
	59	36	56		40	16	37
N11	8	56	73	N11	10	29	118
	69	14	24		80	UN	UN
S15	7	17	874[a]	S15	10	16	31
	69	20	47		60	29	207
S11	8	29	46	S11	10	20	49
	49	16	28		70	15	40
S7	8	25	44	S7	10	23	74
	28	23	39		35	24	58
S4	3	28	54	S4	10	31	98
	22	34	54		30	23	188
S2	3	39	65	S2	10	35	124
	22	27	51		50	39	100
Average = 29			49[a]	Average = 25			87
S.D. ± 12			± 16	S.D. ± 12			± 59

[a]One high value excluded from average. UN = undetectable, included as "0" in the calculation of the average rates

substantially between the two cruises because of the different growth rates of phytoplankton during the cruises. Mortality removed an average of only 49% of daily phytoplankton production during the NE Monsoon, but 87% of daily production during the Spring Intermonsoon period (Table 3).

Higher phytoplankton growth rates during the NE Monsoon (Table 2) may have been a consequence of more nutrient replete conditions for the phytoplankton assemblages during that season (Fig. 6). A comparison of phytoplankton growth rates in unenriched and enriched bottles (μ_o/μ_n; expressed as a percent of enriched growth rate μ_n) showed that this ratio was quite high for samples from the January cruise (overall average of 88%; 94% with one very low value excluded). Therefore, nutrient enrichment did not greatly enhance phytoplankton growth rate in these samples. In contrast to the NE Monsoon results, μ_o/μ_n for the experiments performed during the Spring Intermonsoon season averaged 71%, which indicated that nutrient enrichment resulted in at least a mild stimulation of phytoplankton growth in most samples. Particularly low μ_o/μ_n ratios (average = 51%) characterized the shallow samples during March-April. Low μ_o/μ_n ratios during the Spring Intermonsoon, and for one of

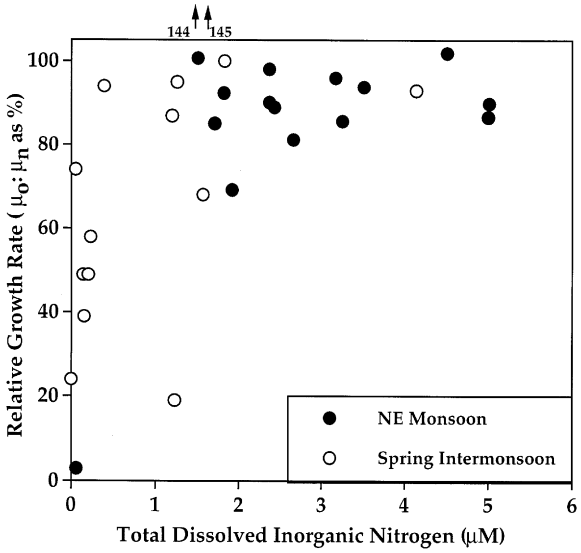

Fig. 6. Ratios of phytoplankton growth rates in unenriched and enriched bottles (μ_o/μ_n; expressed as a percentage of enriched growth rates) as a function of the total dissolved inorganic nitrogen concentration during dilution experiments performed in the Arabian Sea.

the samples from the NE Monsoon, corresponded to samples in which total dissolved inorganic nitrogen concentrations were low (Fig. 6).

4. Discussion

4.1. Phytoplankton growth in on-deck incubators

Phytoplankton growth rates (μ_o, μ_n and k) observed in this study are in good agreement with the observations of other studies using the dilution technique in the Arabian Sea (Burkill et al., 1993; Reckermann and Veldhuis, 1997; Landry et al., 1998). These values should be extrapolated to nature with care, however, because there is a potential for biasing these rates during shipboard incubations. For example, measurements of phytoplankton growth rates in shipboard incubators are susceptible to artifacts caused by changes in chlorophyll cell^{-1} as a consequence of photoadaptation (McManus, 1995). Such changes in chlorophyll cell^{-1} during the incubations would be misinterpreted as "growth" or "mortality" of phytoplankton, but of course are unrelated to actual changes in abundance or biomass of the phytoplankton assemblage. Additionally, the incubation of the samples at a light intensity different than in situ conditions could affect photosynthetic rate of the phytoplankton in the incubated samples, and thus result in growth rates that are not indicative of in-situ rates.

We speculate that phytoplankton growth rates were minimally affected in this study for the samples collected from the shallow euphotic zone because light intensity and spectral quality in that incubator were similar to conditions at the sampling depth. Growth rates obtained in our study for these latter samples were in agreement with growth rates obtained during the NE Monsoon cruise using the pigment-labeling method (Goericke, personal communication). However, that method also is susceptible to bias as a consequence of photoadaptation.

Photoadaptation and/or changes in photosynthetic rate for the samples collected from the lower euphotic zone may have occurred during the incubation period. Some of these samples were collected from specific hydrographic features (e.g., deep chlorophyll maxima) at light intensities below $\approx 15\%$ of incident light intensity used in our on-deck incubators. Photoadaptation to the higher light intensity in the incubator presumably would act to decrease the amount of chlorophyll cell^{-1} (resulting in an underestimation of their growth rate), while it also might stimulate their growth rate (relative to growth at the lower in situ light intensities). Therefore, interpretation of the growth rates resulting from these counteracting effects is not straighforward.

We compared growth rates measured for the samples from the deep euphotic zone in our study with rates obtained for samples collected during the 1995 SW Monsoon and late Fall Intermonsoon/early NE Monsoon (Landry et al., 1998) in order to determine the degree to which light intensity in our incubator may have affected photosynthetic rates of our deep samples. Deep euphotic zone samples in the latter study were incubated at a light intensity comparable to in situ light intensity ($\leqslant 6\%$). Overall averages for these rates were very similar between the two studies. Average values for all deep euphotic zone samples in our study were $0.62\,d^{-1}$ for μ_o and $0.68\,d^{-1}$ for μ_n. Respective growth rates for the deep samples from Landry et al. (1998) were 0.53 and $0.62\,d^{-1}$. The similarity between these results may be fortuitous, but they do not indicate a strong bias of μ_o or μ_n in the present study due to light intensity in the incubator used to hold the samples from the deep euphotic zone.

4.2. *Phytoplankton growth, mortality and size distribution*

Phytoplankton growth rates determined in this study using the dilution technique during the 1995 NE Monsoon averaged approximately 2X the rates for the subsequent Spring Intermonsoon. This difference is not surprising given the very different hydrographic regimes that result seasonally from strong physical forcing in this area (Banse, 1987,1994). It is interesting, however, that while average growth rates varied two-fold, the average chlorophyll concentrations (Table 1) and phytoplankton biomass (Dennett et al., 1999) were remarkably similar for the two seasons.

Our results indicated a relationship between dissolved inorganic nitrogen concentration in the samples at the time of collection and the nutrient sufficiency of the phytoplankton community (Tables 1 and 2; Fig. 6). Phytoplankton growth rates in the enriched bottles (μ_n) were stimulated in most samples with low DIN concentrations (lowest μ_o/μ_n ratios in Fig. 6). This situation was more prevalent during the Spring

Intermonsoon than the NE Monsoon in the present study, and is in agreement with the expectation of more oligotrophic conditions during the intermonsoonal periods.

In contrast to phytoplankton growth rates, grazing mortality rates (m) averaged over an entire cruise in this study were nearly identical for the NE Monsoon and Spring Intermonsoon (Table 2; overall averages were 0.35 and 0.30 d^{-1}, respectively). This correspondence in average mortality rates in the study area for the two seasons, and the overall equity in phytoplankton standing stocks, resulted in an absolute amount of phytoplankton biomass consumed daily that was similar for the two seasons (Fig. 5).

The similarity in mortality rates but dissimilarity in phytoplankton growth rates resulted in an average net phytoplankton growth rate (k) during the NE Monsoon that was 3.4X greater than net growth rate during the Spring Intermonsoon (0.48 versus 0.14 d^{-1}, respectively). We hypothesized that the larger net phytoplankton growth rates during the NE Monsoon in our study may have been a result of a shift during the monsoon to larger phytoplankton species which might be less susceptible to microbial grazing. Reckermann and Veldhuis (1997) in the western Arabian Sea and Landry et al. (1995a,b) and Latasa et al. (1997) in the central equatorial Pacific have argued that grazing activity in their studies appeared to keep picoplanktonic algal growth in check while total net phytoplankton growth rates (indicated by changes in chlorophyll concentrations) often were high. These results imply that growth of the larger phytoplankton in those studies exceeded grazing pressure and might account for most of the net phytoplankton growth.

Reckermann and Veldhuis (1997), for example, measured phytoplankton growth and mortality rates in the Red Sea, western Arabian Sea and Somali Current during the NE Monsoon in 1993. Total net phytoplankton growth rates in that study varied from approximately 0.4 to 1.1 d^{-1}. Their ratios of phytoplankton growth rates to mortality rates (m/μ_o) averaged 24% for two stations in the western Arabian Sea, and 35% when two more stations from the Somali Current were included. That is, phytoplankton growth exceeded grazing impact by a factor of 2.9. However, picoplankton populations in the Reckermann and Veldhuis study were heavily grazed (i.e. production $\approx$ removal) even though growth rates of the total phytoplankton community exceeded mortality. A similar result (i.e., grazing on small algae balanced growth while growth rates of larger phytoplankton exceeded mortality rates) also was observed in the equatorial Pacific Ocean (Latasa et al., 1997).

Many of the samples during the two cruises in the present study were dominated by picoplanktonic and small nanoplanktonic phytoplankton (Fig. 1; also, see Campbell et al., 1998). The predominance of small algae in the Arabian Sea is consistent with the findings of other studies (Burkill et al., 1993; Jochem et al., 1993; Reckermann and Veldhuis, 1997; Veldhuis et al., 1997). However, large phytoplankton (especially diatoms) dominated nanoplankton and microplankton biomass sporadically at some of the stations during both the NE Monsoon and the Spring Intermonsoon of 1995 (Dennett et al., 1999). Algae > 20 μm comprised $\geqslant 20\%$ (up to 63%) of the chlorophyll in 10 out of 30 samples during this study (Fig. 1). Based on these data and the

reasoning above, therefore, we anticipated that we might observe a correlation between net phytoplankton growth rate (k) and the size structure of the phytoplankton assemblage in our data set.

This relationship was not conspicuous in our data. Although there were significant shifts in the proportion of small and large algae among the samples examined in this study (Fig. 1), we observed no clear relationships between the concentration of chlorophyll > 20 μm and net growth rate (k), grazing pressure (m) or the ratio of mortality to growth (m/μ_o; data not shown). Nevertheless, averaged over the entire study area during each cruise, the contribution of large (> 20 μm) phytoplankton to the total phytoplankton standing stock was greater during the NE Monsoon compared to the Spring Intermonsoon (averages of algae > 20 μm were 17 and 6%, respectively, based on data in Fig. 1), as were phytoplankton net growth rates (k). We conclude that large phytoplankton may play a role in establishing net phytoplankton growth rates in dilution experiments, but that other factors such as the composition of the microbial consumer assemblage may tend to obscure this relationship.

4.3. Microbial herbivory and particle flux

The degree to which planktonic production is consumed by microbial grazers has significant consequences for particle flux. A low mortality:growth ratio (m/μ_o) implies a situation in which the potential for carbon export (sinking) from surface waters is high. The theoretical underpinning for this reasoning is that the portion of the phytoplankton community that is consumed directly by microbial grazers is largely recycled in surface waters and thus does not contribute significantly to sinking particle flux (Michaels and Silver, 1988). A high m/μ_o ratio was observed for the Spring Intermonsoon in the present study (87%). Based on the above reasoning, this ratio implies that most of the phytoplankton production during this period was consumed directly by grazers (i.e., did not contribute notably to flux). In contrast, the low ratio (39%) observed during the mid-late NE Monsoon indicates a greater potential for flux during that period relative to the intermonsoon season.

The average m/μ_o ratios observed in this study during the 1995 NE Monsoon and by Reckermann and Veldhuis (1997) during the 1993 NE Monsoon were approximately half of the average observed by Landry et al. (1998) during the 1995 SW Monsoon (39 and 35% versus 70%). Total flux and carbon flux out of surface waters observed using sediment traps during the 1995 US JGOFS field study, on the other hand, were significantly higher during the SW Monsoon (Buesseler, 1998) than the preceding NE Monsoon. If m/μ_o ratios are interpreted literally, then the above ratios are in conflict with sedimentation patterns observed during this JGOFS program. It is possible that fine-to-small scale spatial variability in growth, grazing and flux may obscure a direct relationship between m/μ_o and particle flux. Ratios of mortality rate to growth rate were variable spatially during this study. It is equally probable, however, that low ratios of microbial herbivory to phytoplankton growth (m/μ_o) should not be considered indicators of the absolute amount of sinking carbon, but rather as indicators of the conditions under which high particle fluxes are possible. Specific aspects of food web structure and trophodynamics (e.g., meso- and

macrozooplankton abundance and activity) may be overriding factors controlling the amount of primary production that sinks from surface waters (Rivkin et al., 1996).

4.4. Microbial herbivory in (and out of) the Arabian Sea

Our study and the investigation of Landry et al. (1998) working along the same transects lines observed similar patterns of phytoplankton growth in the northern Arabian Sea during 1995. Growth rates were 0.84 versus 0.44 d^{-1} in the present study during the 1995 NE Monsoon and Spring Intermonsoon, respectively. Rates for two cruises conducted during the 1995 SW Monsoon and the late Fall Intermonsoon/early NE Monsoon were 0.79 versus 0.66 d^{-1} (Landry et al., 1998). Similarities also exist for the rates of phytoplankton mortality obtained by the two studies. Averaged over the entire study area, comparable phytoplankton mortality rates were obtained during both cruises in the present study (0.35 and 0.30 d^{-1}). Landry et al. (1998) also observed similar average mortality rates during two cruises later in 1995 (0.55 and 0.57 d^{-1}) although rates in the latter study were nearly twice the values that we observed. Mortality rates in both studies were lower in the deep euphotic zone compared to rates in surface waters.

Taken at face value, the results of these two studies indicate somewhat similar responses of the primary producer and microbial consumer communities in this oceanic ecosystem throughout the study period. Phytoplankton growth rates during the NE and SW Monsoon were greater than the rates of grazing mortality, resulting in significant net phytoplankton growth rates during these two monsoonal seasons. Decreases in phytoplankton growth rates during intermonsoon periods, but retention of mortality rates comparable to the preceding monsoonal seasons, resulted in low net phytoplankton growth rates.

The results of these studies are also indicative of a microbial consumer population that is responsive to strong seasonal fluctuations in phytoplankton production. The rate of herbivory (i.e. mortality) during the SW Monsoon (Landry et al., 1998) was approximately twice the rate observed during the present study. Although microbial grazers did not keep up with phytoplankton growth in either monsoonal season, there was a clear 'shift up' in the mortality rates observed during the SW Monsoon (Landry et al., 1998) relative to the NE Monsoon (this study). The higher rates of mortality observed during the SW Monsoon, together with higher standing stocks of phytoplankton (0.72 chlorophyll *a* l^{-1} versus 0.54 μg chlorophyll *a* l^{-1} during the NE Monsoon) imply that microbial herbivores consumed a substantially larger absolute amount of phytoplankton biomass during the SW Monsoon.

A fundamental goal of the JGOFS program has been to provide information concerning the production and fate of organic carbon in the global ocean. Phytoplankton mortality estimates in the Arabian Sea, observed as part of the present study, aid in the development of that global picture of carbon biogeochemistry (Fig. 7). Although chlorophyll concentrations measured in the present study do not represent the highest values observed in the Arabian Sea (Landry et al., 1998), the values that we measured

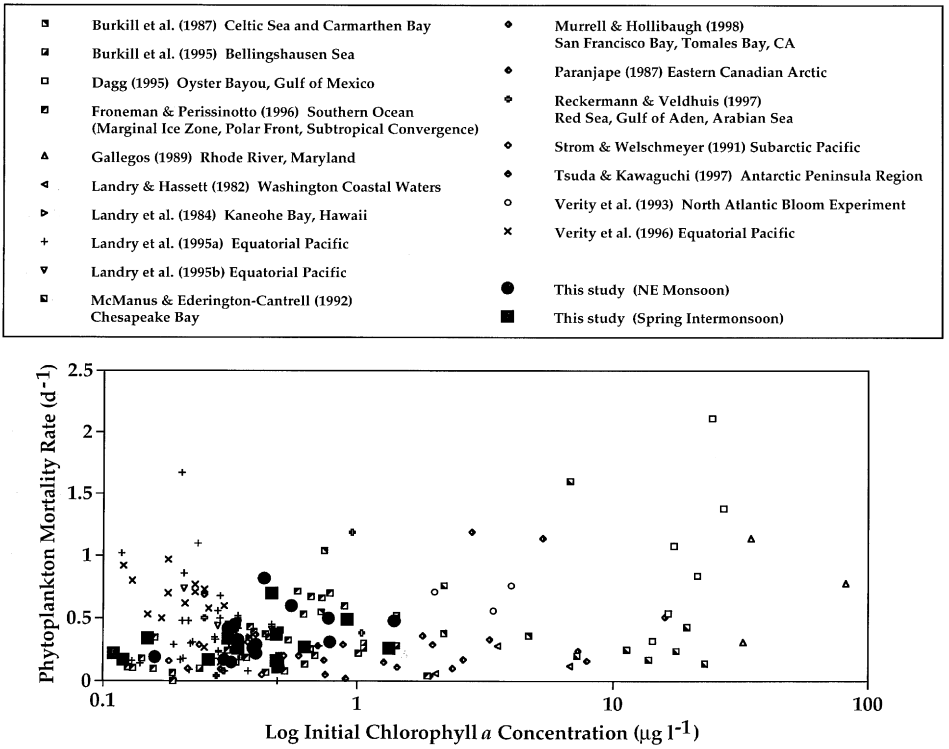

Fig. 7. Summary of studies examining phytoplankton mortality by the dilution technique. Mortality rates are plotted against the initial Chlorophyll *a* concentrations in the samples. Non-significant regression results have not been plotted. References and geographical locations are provided in the key.

were not unusually high relative to other highly productive oceanic ecosystems (e.g., North Atlantic Bloom Experiment, and some Arctic and Antarctic waters), or as low as those representative of highly oligotrophic waters (horizontal range in Fig. 7). Likewise, phytoplankton mortality rates observed in this study were completely within the range of values that have been observed in numerous experiments from other locations (vertical range in Fig. 7).

The conclusion arising from these observations is that phytoplankton growth and mortality due to microbial predation in the Arabian Sea represent intermediate situations to these rate processes in highly oligotrophic or eutrophic ecosystems. While phytoplankton mortality rates (expressed either as turnover rate of the phytoplankton assemblage, or as absolute amount of phytoplankton biomass consumed per day) were substantial in the present study, they were not remarkable compared to rates that have been observed, for example, in the North Atlantic Bloom Experiment or the Equatorial Pacific efforts of the JGOFS program

(Verity et al., 1993,1996; Landry et al., 1995a). Based on preliminary comparisons of these data sets, a consensus is emerging that microbial predation constitutes a substantial source of phytoplankton mortality, and thus an important factor in global carbon cycling.

Acknowledgements

We gratefully acknowledge the assistance of the captain and crew of the R/V *Thomas G. Thompson* and the US JGOFS Office for logistical and cruise support. We thank the US JGOFS Arabian Sea hydrographic team for nutrient analyses, Dr. Lisa Campbell for phototrophic picoplankton abundances, and Peter Countway for technical assistance during cruise TN045. This study was supported by National Science Foundation grant OCE-9310693. Contribution No. 9566 from Woods Hole Oceanographic Institution. U.S. JGOFS contribution number 414.

References

Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., Thingstad, F., 1983. The ecological role of water-column microbes in the sea. Marine Ecology Progress Series 10, 257–263.

Banse, K., 1987. Seasonality of phytoplankton chlorophyll in the central and northern Arabian Sea. Deep-Sea Research 34, 713–723.

Banse, K., 1994. Overview of research efforts and results in the Arabian Sea, 1960–1990. Biogeochemical processes in the Arabian Sea 7–25.

Buesseler, K.O., Ball, L., Andrews, J., Benitez-Nelson, C., Belastock, R., Chai, F., Chao, Y., 1998. Upper ocean export of particulate organic carbon in the Arabian Sea derived from thorium-234. Deep-Sea Research 45, 2461–2487.

Burkill, P.H., 1987. Analytical flow cytometry and its application to marine microbial ecology. In: Sleigh, M. (Ed.), Microbes in the Sea. Ellis Horwood Ltd, Chichester, pp. 139–166.

Burkill, P.H., Edwards, E.S., Sleigh, M.A., 1995. Microzooplankton and their role in controlling phytoplankton growth in the marginal ice zone of the Bellingshausen Sea. Deep-Sea Research 42, 1277–1290.

Burkill, P.H., Leakey, R.J.G., Owens, N.J.P., Mantoura, R.F.C., 1993. Synechococcus and its importance to the microbial foodweb of the northwestern Indian Ocean. Deep-Sea Research 40, 773–782.

Campbell, L., Landry, M.R., Constantinou, J., Nolla, H.A., Liu, H., Brown, S.L., Caron, D.A., 1998. Response of microbial community structure to environmental forcing in the Arabian Sea. Deep-Sea Research 45, 2301–2325.

Caron, D.A., Finlay, B.J., 1994. Protozoan links in food webs. In: Hausmann, K., Hülsmann, N. (Eds.), Progress in Protozoology, Proceedings of the IX International Congress of Protozoology, Berlin 1993, Gustav Fischer Verlag, Stuttgart, pp. 125–130.

Caron, D.A., Goldman, J.C., Andersen, O.K., Dennett, M.R., 1985. Nutrient cycling in a microflagellate food chain. II. Population dynamics and carbon cycling. Marine Ecology Progress Series 24, 243–254.

Dagg, M.J., 1992. Ingestion of phytoplankton by the micro- and mesozooplankton communities in a productive subtropical estuary. Journal of Plankton Research 17, 845–857.

Dennett, M.R., Caron, D.A., Mursov, S., Polikarpov, I.G., Gavrilova, N.A., Georgieva, L.V., Kuzmenko, L.V., 1999. Abundance and bimass of nano- and microplankton during the 1995 Northeast Monsoon and Spring Intermonsoon in the Arabian Sea. Deep-Sea Research 46, 1691–1717.

Elbrächter, M., 1991. Faeces production by dinoflagellates and other small flagellates. Marine Microbial Food Webs 5, 189–204.

Froneman, P., Perissinotto, R., 1996. Microzooplankton grazing in the Southern Ocean: implications for the carbon cycle. P.S.Z.N.I.: Marine Ecology 17, 99–115.

Gallegos, C.L., 1989. Microzooplankton grazing on phytoplankton in the Rhode River, Maryland: non linear feeding kinetics. Marine Ecology Progress Series 57, 23–33.

Goldman, J.C., Caron, D.A., 1985. Experimental studies on an omnivorous microflagellate: implications for grazing and nutrient regeneration in the marine microbial food chain. Deep-Sea Research 32, 899–915.

Jochem, F.J., Pollehne, F., Zeitzschel, B., 1993. Productivity regime and phytoplankton size structure in the Arabian Sea. Deep-Sea Research 40, 711–735.

Landry, J.R., Brown, S.L., Campbell, L., Constantinou, J., Liu, H., 1998. Spatial patterns in phytoplankton growth and microzooplankton grazing in the Arabian Sea during monsoon forcing. Deep-Sea Research 45, 2353–2368.

Landry, M.R., 1993. Estimating rates of growth and grazing mortality of phytoplankton by the dilution method. In: Kemp, P.F., Sherr, B.F., Sherr, E.B., Cole, J.J. (Eds.), Handbook of Methods in Aquatic Microbial Ecology. Lewis Publishers, Boca Raton, pp. 715–722.

Landry, M.R., Constantinou, J., Kirshtein, J., 1995a. Microzooplankton grazing in the central equatorial Pacific during February and August, 1992. Deep-Sea Research 42, 657–671.

Landry, M.R., Haas, L.W., Fagerness, V.L., 1984. Dynamics of microbial plankton communities: experiments in Kaneohe Bay. Hawaii. Marine Ecology Progress Series 16, 127–133.

Landry, M.R., Hassett, R.P., 1982. Estimating the grazing impact of marine microzooplankton. Marine Biology 67, 283–288.

Landry, M.R., Kirshtein, J., Constantinou, J., 1995b. A refined dilution technique for measuring the community grazing impact of microzooplankton, with experimental test in the central equatorial Pacific. Marine Ecology Progress Series 120, 53–63.

Latasa, M., Landry, M.R., Schlüter, L., Bidigare, R.R., 1997. Pigment-specific growth and grazing rates of phytoplankton in the central equatorial Pacific. Limnology and Oceanography 42, 289–298.

McManus, G.B., 1995. Phytoplankton abundance and pigment changes during simulated in situ dilution experiments in estuarine waters: possible artifacts caused by algal light adaptations. Journal of Plankton Research 17, 1705–1716.

McManus, G.B., Ederington-Cantrell, M.C., 1992. Phytoplankton pigments and growth rates, and microzooplankton grazing in a large temperate estuary. Marine Ecology Progress Series 87, 77–85.

Michaels, A.F., Silver, M.W., 1988. Primary production, sinking fluxes and the microbial food web. Deep-Sea Research 35, 473–490.

Murrell, M.C., Hollibaugh, J.T., 1998. Microzooplankton grazing in northern San Francisco Bay measured by the dilution method. Aquatic Microbial Ecology 15, 53–63.

Nagata, T., Kirchman, D.L., 1992. Release of macromolecular organic complexes by heterotrophic marine flagellates. Marine Ecology Progress Series 83, 233–240.

Paranjape, M.A., 1987. Grazing by microzooplankton in the eastern Canadian arctic in summer 1983. Marine Ecology Progress Series 40, 239–246.

Reckermann, M., Veldhuis, M.J.W., 1997. Trophic interactions between picophytoplankton and micro- and nanozooplankton in the western Arabian Sea during the NE Monsoon 1993. Aquatic Microbial Ecology 12, 263–273.

Rivkin, R.B., Legendre, L., Deibel, D., Tremblay, J.-E., Klein, B., Crocker, K., Roy, S., Silverberg, N., Lovejoy, C., Mesple, F., Romero, N., Anderson, M.R., Matthews, P., Savenkoff, C., Vezina, A., Therriault, J.-C., Wesson, J., Berube, C., Ingram, R.G., 1996. Vertical flux of biogenic carbon in the ocean: is there food web control? Science 272, 1163–1166.

SCOR 1990. The joint global ocean flux study: science plan. JGOFS Report Number, vol. 5, 61pp.

Sherr, E.B., Caron, D.A., Sherr, B.F., 1993. Staining of heterotrophic protists for visualization via epifluorescence microscopy. In: Kemp, P., Sherr, B., Sherr, E., Cole, J. (Eds.), Handbook of Methods in Aquatic Microbial Ecology. Lewis Publishers, Boca Raton, pp. 213–227.

Sherr, E.B., Sherr, B.F., 1994. Bacterivory and herbivory: key roles of phagotrophic protists in pelagic food webs. Microbial Ecology 28, 223–235.

Stoecker, D., 1984. Particle production by planktonic ciliates. Limnology and Oceanography 29, 930–940.

Tsuda, A., Kawaguchi, S., 1997. Microzooplankton grazing in the surface water of the Southern Ocean during an austral summer. Polar Biology 18, 240–245.

Veldhuis, M.J.W., Kraay, G.W., van Bleijswijk, J.D.L., Baars, M.A., 1997. Seasonal and spatial variability in phytoplankton biomass, productivity and growth in the norhtwestern Indian Ocean: the southwest and northeast monsoon, 1992-1993. Deep-Sea Research 44, 425–449.

Verity, P.G., Stoecker, D.K., Sieracki, M.E., Nelson, J.R., 1993. Grazing, growth and mortality of microzooplankton during the 1989 North Atlantic spring bloom at 47°N, 18°W. Deep-Sea Research 40, 1793–1814.

Verity, P.G., Stoecker, D.K., Sieracki, M.E., Nelson, J.R., 1996. Microzooplankton grazing of primary production at 140°W in the equatorial Pacific. Deep-Sea Research 43, 1227–1255.