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Trophic interactions between picophytoplankton and micro- and nanozooplankton in the western Arabian Sea during the NE monsoon 1993

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ABSTRACT: The grazing pressure of micro- and nanozooplankton on phytoplankton was estimated in serial dilution experiments in the northwestern Arabian Sea and its adjacent areas (the Somali Current, the Somali Basin, the Gulf of Aden and the southern Red Sea) during the NE monsoon 1992-1993. Microzooplankton grazing rates (g) on total phytoplankton (analyzed as chl a) were generally exceeded by phytoplankton growth rates (g = 0.2 to 1.19 d^{-1}, mean 0.48 d^{-1}; μ = 0.52 to 1.12 d^{-1}, mean 0.72 d^{-1}), resulting in an average daily consumption of 38% of the phytoplankton standing stock and 67% of the primary production. Microzooplankton grazing on 4 picophytoplankton groups (*Prochlorococcus* spp., *Synechococcus* spp., and 2 picoeukaryotes) analyzed by flow cytometry showed growth (μ = 0.27 to 0.92 d^{-1}, mean 0.68 d^{-1}) and grazing mortality rates (g = 0.26 to 0.73 d^{-1}, mean 0.67 d^{-1}) well in balance, with an average of 49% of the standing stock and 102% of the primary production grazed per day. Picophytoplankton growth and grazing mortality rates increased dramatically when grazers >10 µm were removed. These results suggest a control of the small grazers by larger ones (trophic cascade) and a close coupling between picoautotrophic prey and small grazers. The trophic cascade within the microbial food web of the nanoplankton encompasses 3 trophic levels: picoplankton – small HNF – larger flagellates and ciliates.

KEY WORDS: Grazing · Picophytoplankton · *Prochlorococcus* · *Synechococcus* · Picoeukaryotes Flow cytometry · Arabian Sea · Trophic cascade

INTRODUCTION

Photoautotrophic picoplankton (size 0.2 to 2 µm) often dominates the phytoplankton community within the euphotic zone of oligotrophic oceans (Campbell & Vaulot 1993, Fogg 1995), and particularly so during the inter-monsoon periods in the Arabian Sea (Burkill et al. 1993, Jochem 1995). The prokaryotic species *Prochlorococcus marina* (Chisholm et al. 1992) and *Synechococcus* spp. (Johnson & Sieburth 1979, Waterbury et al. 1979), as well as eukaryotic algae of various taxonomic groups (Johnson & Sieburth 1982, Simon et al. 1994) are the predominant autotrophs within this size class. In order to assess their role in oceanic carbon flux, information on their growth and grazing mortality rates is essential. Knowledge of the size of the principal predators of picoplankton is important as well, as size largely determines the fraction of carbon which is passed on to higher trophic levels (Sherr et al. 1986). Grazing can be assumed to be the most significant loss factor for these organisms, as direct sedimentation is unlikely due to their small size, although they may form a significant component in sinking aggregates (Lochte & Turley 1988). *Prochlorococcus*, reaching abundances of up to 350000 cm^{-3} in the euphotic zone of oligotrophic regions (Olson et al. 1990, Veldhuis & Kraay 1993, Lindell & Post 1995, Buck et al. 1996), cannot be discriminated reliably from heterotrophic bacteria by epifluorescence microscopy, due to their dim and fast-fading autofluorescence (Monger & Landry 1993), and many have been mistakenly counted as heterotrophic bacteria for that reason (Campbell et al. 1994, Sieracki et al. 1995). Although the occurrence of *Prochlorococcus* was shown in the NW Indian Ocean

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(Pollehne et al. 1993, Veldhuis & Kraay 1993, Jochem 1995), information on the dynamics of these tiny primary producers has been scarce. To date, information on *Prochlorococcus* growth rates is available only from the Sargasso Sea (Goericke & Welschmeyer 1993) and the equatorial Pacific (Vaulot et al. 1995); grazing estimates have been reported only from the equatorial Pacific (Landry et al. 1995a, b). Information on eukaryotic picoplankton dynamics is also rare. For *Synechococcus*, Burkill et al. (1993) reported high biomasses and turnover rates in the Arabian Sea during the autumn inter-monsoon period.

We report here specific phytoplankton growth and grazing mortality rates by microzooplankton (measured as bulk chl *a* and as separate picoautotrophic groups by flow cytometry: *Prochlorococcus*, *Synechococcus*, 2 picoeukaryotes, and occasionally 2 sub-populations of *Prochlorococcus* and *Synechococcus*) at different locations in the Somali Current, the Gulf of Aden, and the southern Red Sea during the NE monsoon period (January-February 1993). The standard dilution protocol of Landry & Hassett (1982) was modified in order to account for the respective grazing impact of different grazer size classes within the microzooplankton community (grazers <20, <10, <3 and <2 µm).

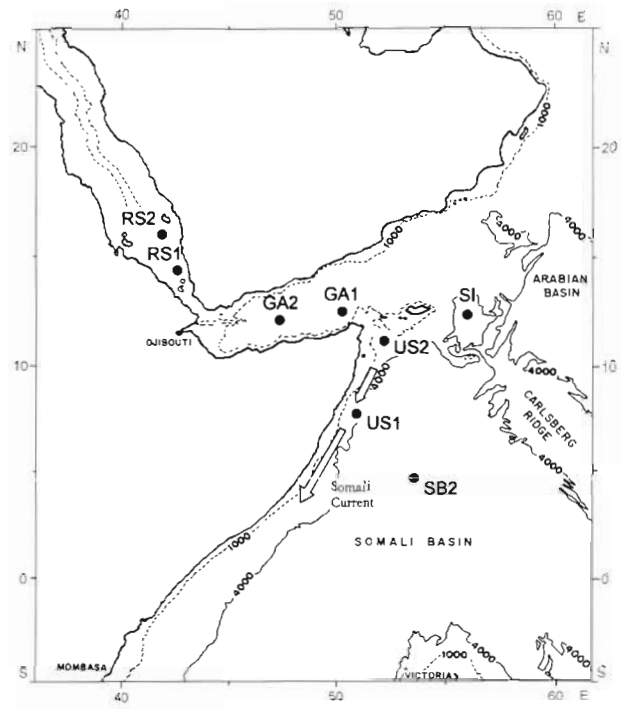

Fig. 1. Investigation area with stations in the Somali Current, the Gulf of Aden and the southern Red Sea. Arrows indicate the direction of the Somali Current during the NE monsoon

MATERIAL AND METHODS

Micro- and nanozooplankton grazing experiments (Landry & Hassett 1982) were carried out aboard RV 'Tyro' on cruise B2 of the Netherlands Indian Ocean Programme 1992-1993 (Baars et al. 1994) at 8 stations in the Arabian Sea off Somalia, in the Gulf of Aden and the Red Sea (Fig. 1) during the NE monsoon (January-February 1993). Water samples were taken from the upper mixed layer (10 to 30 m) on the uphaul with a Seabird CTD rosette water sampler equipped with 10.5 l NoEx bottles. Water samples were prescreened through a 200 µm mesh (to remove mesozooplankton) and diluted with particle-free seawater (prepared by sterile, preflushed 0.2 µm filter capsules; Nalgene) to give 4 dilution steps (100, 75, 50 and 25% original water) and incubated on board in 5 l glass bottles for 24 h, starting at sunrise. *In situ* conditions were simulated in a light-screened flow-through bath which ensured mixed layer temperatures and irradiances corresponding to the sampling depths (Table 1). For chl *a* analyses, samples (1 to 2.5 l) were filtered over a GF/F glass fibre filter (47 mm; Whatman) at the beginning and at the end of each respective experiment. Filters were stored at -80°C until fluorometric analysis according to Veldhuis et al. (1993).

Table 1 Locations, dates and ambient environmental conditions for the experiments in the Somali Basin (SB2 to SI), the Gulf of Aden (GA1, GA2) and the southern Red Sea (RS1, RS2) during the NE monsoon 1993. FC: flow cytometry

Expt	Phytoplankton analyzed by	Stn	Date (1993)	Simulated incubation depth (m)	Temperature (°C)	NO_3^- (µM)	Chl *a* (µg dm^{-3})
1	chl *a*, FC	SB2 (809-1)	Jan 15	20	26.9	0.13	0.35
2	chl *a*, FC	US1 (813-1)	Jan 18	20	26.7	0.23	0.28
3	chl *a*, FC	US2 (818-5)	Jan 21	20	26.0	0.80	0.30
4	chl *a*, FC	SI (820-1)	Jan 24	20	26.0	0.93	0.25
5	chl *a*	GA1 (826-4)	Jan 26	20	25.9	0.30	0.50
6	chl *a*, FC	GA2 (832-11)	Jan 30	20	25.4	1.53	0.46
7	chl *a*	RS1 (840-4)	Feb 02	10	25.7	0.02	0.95
8	chl *a*, FC	RS2 (842-14)	Feb 04	10	25.8	0.40	1.04

In parallel treatments, the standard serial dilution protocol was modified to the effect that in addition to grazers >200 µm, also grazers >20, >10, >3 and >2 µm were removed by prescreening in order to determine the respective grazing pressure of smaller grazer size classes on the picoautotroph community. The experimental water was siphoned from the CTD bottle into a light-screened 2 l plastic beaker by means of a submerged silicon tube. The water was prescreened by gravity through meshes (for the size fractions <20 and <10 µm) or presoaked polycarbonate filters (for the smaller fractions) and collected in dark plastic bottles. The prescreened water samples were then combined with particle-free seawater (prepared by preflushed encapsulated 0.2 µm syringe filters; Schleicher & Schuell Red Edge) from the beaker according to the 4 dilution steps (see above) and incubated in parallel in 60 ml polystyrene culture bottles on board under simulated *in situ* conditions (free floating in a light-screened container flushed with running seawater; see above) for 24 h, starting 1 h after sunrise. All experimental gear was washed thoroughly with 10% HCl and rinsed with 0.2 µm-filtered seawater. After incubation, the samples were counted immediately, or stored cool in the dark at 4°C until counted (up to 3 h). Cells were counted with a Coulter Epics CS flow cytometer as described by Veldhuis & Kraay (1993), with the difference that 458 nm instead of 488 nm was used as excitation wavelength.

Chl *a* and cell concentrations of the respective phytoplankton groups before and after the incubations were used to calculate apparent (k) and specific (μ) growth rates as well as specific grazing mortality rates (g) according to Landry & Hassett (1982). Linear regressions of dilution plots (apparent growth rates vs dilution factor) were considered significant at $p \leq 0.05$. Only those data were used for further calculations. Percentages of phytoplankton standing stock consumed per day were calculated as % cons. = $(1 - e^{g}) \times 100$; percentages of primary production consumed per day as % cons. = $(g/\mu) \times 100$. Absolute phytoplankton consumption rates were calculated using the average phytoplankton concentrations $\langle C \rangle$ in the incubation bottles according to Frost (1972): $C_{cons} = \langle C \rangle \times (1 - e^{g})$. Chl *a*-based total phytoplankton carbon consumption rates were estimated using a C:chl *a* conversion factor of 190 which was determined experimentally by relating flow cytometric cell counts (using the cell-to-carbon conversion factors) and red fluorescence intensities to fluorometrically measured chl *a* concentrations as described in detail by Veldhuis et al. (1997).

Cell numbers were converted to carbon biomass according to Veldhuis et al. (1997): *Synechococcus* 175 fg C cell^{-1} and *Prochlorococcus* 92 fg C cell^{-1}. Approximate picoeukaryotic cell sizes were calculated after examining polycarbonate filters retaining ca 50% of the respective picophytoplankton group (filters in the range of 8 to 0.45 µm pore size were used). Using a volume-to-carbon factor of 220 fg C µm^{-3} (Booth et al. 1988), and depending on the variation in scatter signals, a carbon content of 975 (Stn SB2), 1880 (Stn US1) and 2500 fg C cell^{-1} (other stations) was assumed for the small picoeukaryotes, and 5090 fg C cell^{-1} for the large picoeukaryotes.

RESULTS

Hydrography and phytoplankton composition

Strong northwesterly winds (4 to 7 Bft, average 5) prevailed during the investigation period. A sharp thermocline was detected only at the southernmost stations in the Somali Basin, and mixed layer temperatures ranged between 25.4 and 26.9°C. Mixed layer concentrations of nitrate were low but not depleted in the southern Somali Basin (0.13 to 0.23 µM), but increased substantially in the northern Somali Basin and the Gulf of Aden (0.8 to 1.53 µM), while in the southern Red Sea, concentrations were as low as 0.02 to 0.4 µM (Table 1). Generally, a distinct nutricline coincided with the thermocline. Meteorological conditions and decreasing water temperatures indicated a wind-induced entrainment of nutrient-enriched water from deeper layers into the surface layer, both in the northern Somali Basin (elevated concentrations at US2 and SI) and the Gulf of Aden (GA2). Mixed layer concentrations of phosphate (0.3 to 0.5 µM) and silicate (1.5 to 2.5 µM) were also low but not depleted.

Chlorophyll concentrations were low in the Somali Basin and Gulf of Aden (<0.5 µg dm^{-3}); only in the southern Red Sea did chl *a* concentrations exceed 1 µg dm^{-3} (Table 1). A distinct deep chlorophyll maximum was absent at all stations. Phytoplankton in the Somali Basin was dominated by picoplankton, specifically *Synechococcus*, *Prochlorococcus* and some unidentified pico- and nano-eukaryotes. At some stations, subgroups of *Synechococcus* and *Prochlorococcus* (dim and bright fluorescent) could be discriminated (Table 2). HPLC (high-performance liquid chromatography) pigment analysis indicated the presence of Prymnesiophyceae, Pelagophyceae, and *Micromonas*-type phytoplankton species (Veldhuis et al. 1994). Dinoflagellates were also abundant during the entire cruise (*Gymnodinium* and *Amphidinium* species), while cryptophytes were present only in low numbers. *Prochlorococcus* was present in the Somali Basin (up to 66000 cm^{-3}), but virtually absent in the inner Gulf of Aden and the southern Red Sea, while *Synechococcus* was present in high abundances (up to 142000 cm^{-3}) throughout the cruise. In the Gulf of Aden (GA2) and

Table 2. Cell concentrations (cells cm^{-3}) of photosynthetic picoplankton at the beginning of the experiments analyzed by flow cytometry. *Prochlorococcus* not analyzed; –: not detected

Expt	Stn	*Prochlorococcus*	Dim	Bright	*Synechococcus*	Dim	Bright	Small euks	Large euks
1	SB2	–*	–*	–*	67183	–	–	6420	–
2	US1	–*	–*	–*	51145	–	–	7686	–
3	US2	50239	26777	23462	43685	–	–	5396	–
4	SI	66253	40772	25481	53583	–	–	7172	812
6	GA2	13198	–	–	142225	92784	50504	18342	1601
8	RS2	–	–	–	47253	36845	10408	–	1162

Table 3. Results of chl *a*-based dilution grazing experiments (representing the total phytoplankton population). Growth and grazing coefficients derived from dilution plots (apparent growth rate vs dilution factor) according to Landry & Hassett (1982). Consumption rates calculated according to Frost (1972). ns: linear regressions of dilution plots not significant ($p > 0.05$)

Stn	Growth μ (d^{-1})	Grazing g (d^{-1})	Consumption of Chl *a* ($mg\ m^{-3}\ d^{-1}$)	Consumption of Carbon ($mg\ m^{-3}\ d^{-1}$)	r	n	p
SB2	0.653	0.192	0.07	14.16	0.442	12	ns
US1	0.595	0.042	0.02	3.22	0.076	12	ns
US2	0.520	0.201	0.08	15.33	0.630	12	<0.05
SI	0.928	0.503	0.18	34.69	0.729	12	<0.01
GA1	0.399	0.148	0.12	23.71	0.534	12	ns
GA2	0.742	0.708	0.40	75.56	0.741	12	<0.01
RS1	1.123	1.187	0.78	147.81	0.942	12	<0.01
RS2	0.681	0.383	0.59	111.74	0.733	12	<0.01

the southern Red Sea (RS2), a highly diverse phytoplankton community was found, consisting of large diatoms (*Chaetoceros*, *Nitzschia*, *Coscinodiscus*, *Biddulphia*), dinoflagellates (*Gymnodinium* and *Amphidinium*) and cryptophytes, as well as *Phaeocystis*-type colonies.

Phytoplankton growth and grazing mortality by microzooplankton

Results of microzooplankton dilution grazing experiments are summarized in Tables 3 & 4. Grazing on total phytoplankton (based on chl *a*) increased from the southern stations towards the northern Somali Basin, the Gulf of Aden and the southern Red Sea (Table 3). Total phytoplankton (chl *a*) grazing mortality rates were generally lower than specific growth rates, indicating an overall increase in phytoplankton biomass over time (Fig.2: chl *a*, open squares). However, in the Gulf of Aden (GA2) and the southern Red Sea (RS1), specific growth and grazing mortality rates were higher and grazing loss by microzooplankton roughly accounted for total phytoplankton biomass production, i.e. $\mu \approx g$ (Table 3). On average, phytoplankton (chl *a*) divided once a day ($\mu = 0.72$; Table 5). Flow cytometrically estimated specific picophytoplankton growth rates in the microzooplankton grazing treatments also showed 1 division d^{-1} on average ($\mu = 0.67$); however, picophytoplankton grazing mortality rates caused by microzooplankton were in the same range, resulting in a quasi-steady-state system with grazing losses compensated by growth (filled circles in Fig. 2, Table 5).

Total phytoplankton carbon consumption rates by microzooplankton increased from the Somali Basin (US2 and SI) towards the Gulf of Aden (GA2) and the southern Red Sea (RS1 and RS2; Table 3). There, carbon consumption by microzooplankton was highest (148 mg m^{-3} d^{-1} at RS1). Picophytoplankton carbon consumption was relatively conservative throughout the cruise and made up total phytoplankton consumption in the Somali Basin (Fig. 3A; US2 and SI). However, in

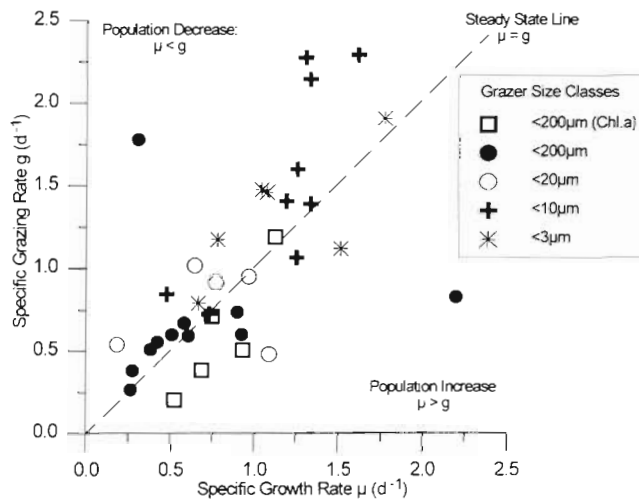

Fig. 2. Relationship between specific growth and grazing mortality rates for phytoplankton, as measured in the serial dilution experiments. Data from Table 4, sorted for the different grazer size class incubations (only data at $p \leq 0.05$ plotted). Dotted line represents steady-state conditions, where $\mu = g$

Table 4. As Table 3, but for picophytoplankton analyzed by flow cytometry in size-fractionation experiments. Results of experiments involving grazers <2 µm not shown (ns)

Stn	Growth μ (d^{-1})	Grazing g (d^{-1})	Consumption of Cells (no. cm^{-3} d^{-1})	Consumption of Carbon (mg m^{-3} d^{-1})	r	n	p
Grazers <200 µm							
Prochlorococcus							
US2	0.60	0.59	22555	2.08	0.93	8	<0.01
GA2	2.20	0.82	15932	1.47	0.68	12	<0.05
Synechococcus							
SB2	0.26	0.26	15558	2.72	0.93	12	<0.01
US1	0.38	0.51	19116	3.35	0.90	11	<0.01
US2	0.90	0.73	24659	4.32	0.95	8	<0.01
GA2	0.18	0.06	9469	1.66	0.16	12	ns
RS2	0.27	0.38	14159	2.48	0.85	12	<0.01
Small picoeukaryotes							
SB2	0.39	0.18	1157	1.13	0.44	12	ns
US1	0.51	0.60	3305	6.21	0.77	11	<0.05
US2	0.58	0.67	2516	6.29	0.91	8	<0.01
GA2	0.31	1.78	7985	19.96	0.75	12	<0.01
Large picoeukaryotes							
GA2	0.42	0.55	637	3.24	0.78	12	<0.01
RS2	0.92	0.60	619	3.15	0.85	12	<0.01
Grazers <20 µm							
Prochlorococcus							
US2	0.77	0.91	28008	2.58	0.95	6	<0.01
GA2	1.09	0.48	6473	0.60	0.76	8	<0.05
Synechococcus							
US2	0.97	0.95	27002	4.73	0.94	6	<0.01
GA2	0.56	0.35	26690	4.67	0.59	8	ns
Small picoeukaryotes							
US2	0.64	1.02	2872	7.18	0.92	6	<0.01
GA2	−0.09	0.13	1250	3.12	0.29	8	ns
Large picoeukaryotes							
GA2	0.18	0.54	480	2.45	0.75	8	<0.05
Grazers <10 µm							
Prochlorococcus							
US2	1.33	2.14	30398	2.80	0.79	8	<0.05
SI	1.33	1.39	48428	4.46	0.89	8	<0.01
GA2	1.25	1.06	8898	0.82	0.94	8	<0.01
Synechococcus							
US2	1.62	2.29	28595	5.00	0.79	8	<0.05
SI	1.19	1.40	36401	6.37	0.90	8	<0.01
GA2	0.47	0.84	38882	6.80	0.87	8	<0.01
Small picoeukaryotes							
US2	1.31	2.27	3101	7.75	0.79	8	<0.05
SI	1.26	1.60	4805	12.13	0.90	8	<0.01
GA2	−0.40	−0.07	−642	−1.60	0.15	8	ns
Large picoeukaryotes							
SI	0.73	0.72	418	2.13	0.82	8	<0.01
GA2	0.13	0.43	416	2.12	0.63	8	ns
Grazers <3 µm							
Prochlorococcus							
US2	0.43	0.07	3955	0.36	0.35	8	ns
SI	1.78	1.90	52981	4.87	0.97	8	<0.01
GA2	1.51	1.12	10203	0.94	0.99	8	<0.01
Synechococcus							
US2	0.61	0.10	5645	0.99	0.59	8	ns
SI	1.07	1.46	34160	5.98	0.98	8	<0.01
GA2	0.66	0.79	41829	7.32	0.98	8	<0.01
Small picoeukaryotes							
US2	0.24	0.02	123	0.31	0.12	8	ns
SI	1.04	1.47	4494	11.24	0.99	8	<0.01
GA2	−2.08	−2.31	−113808	−284.52	0.86	8	<0.01
Large picoeukaryotes							
SI	0.78	1.17	463	2.36	0.87	8	<0.01
GA2	−1.19	−1.04	−2328	−11.85	0.64	8	ns

Table 5. Growth and grazing mortality coefficients for total phytoplankton (measured as chl *a*) and picophytoplankton (analyzed by flow cytometry) in the different grazer size classes, averaged over all stations and picophytoplankton groups. Relative rate increments in the small fractions as compared to the <200 µm size class are given for the picophytoplankton

Grazer size class (µm)	Prey type	Growth μ (d^{-1})	Relative increment (%)	Grazing g (d^{-1})	Relative increment (%)	Consumption (% d^{-1}) of Stock	Prod.
<200	Total phytoplankton	0.72 ± 0.23		0.48 ± 0.39		38	67
<200	Picophytoplankton	0.67 ± 0.56		0.68 ± 0.39		49	102
<20	Picophytoplankton	0.73 ± 0.35	+9	0.78 ± 0.25	+15	54	107
<10	Picophytoplankton	1.17 ± 0.35	+75	1.52 ± 0.60	+124	78	131
<3	Picophytoplankton	1.14 ± 0.43	+70	1.32 ± 0.38	+94	73	115

the Gulf of Aden (GA2) and the southern Red Sea (RS2) an increasing amount of phytoplankton carbon was consumed as larger phytoplankton, which was not quantitatively accounted for in the flow cytometric analyses.

Within the picophytoplankton community, the relative importance of picoeukaryotes as food items sharply increased towards the high-chlorophyll Gulf of Aden and Red Sea stations; however, at RS2 they had disappeared completely (Table 2, Fig. 3B). The large picoeukaryotes significantly gained importance in the Gulf of Aden and the Red Sea, while the importance of *Prochlorococcus* decreased along this transect. Absolute carbon consumption rates were highest for the eukaryotic picoautotrophs (up to 20 mg m^{-3} d^{-1}, GA2), whereas *Synechococcus* (up to 4.3 mg m^{-3} d^{-1}, US2) and *Prochlorococcus* (up to 2.1 mg m^{-3} d^{-1}, US2) were generally less important as diet for microzooplankton. As an average over all stations and picophyoplankton groups, microzooplankton (<200 µm) was responsible for the removal of 49% of the picoautotrophic standing stock and 102% of picoautotrophic production from the water d^{-1} (Table 5). Relative and absolute picophytoplankton carbon consumption rates (Fig. 4) demonstrate that all groups were grazed according to their stocks, implying no apparent grazing preference for a specific group.

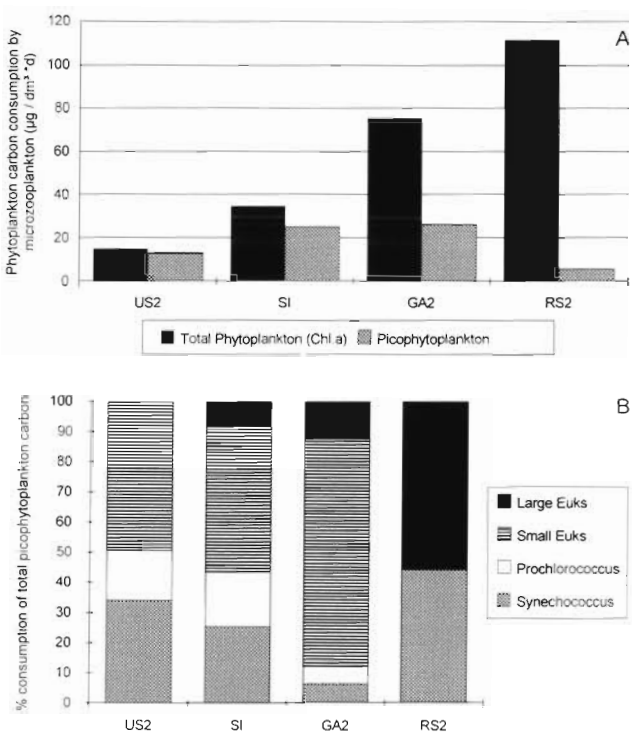

Fig. 3. Phytoplankton carbon consumption rates by microzooplankton i.e. grazers <200 µm (<10 µm at SI) at 4 stations in the Somali Current, the Gulf of Aden and the southern Red Sea. (A) Total phytoplankton (measured as chl *a*) and picophytoplankton (sum of all groups analyzed by flow cytometry) consumption rates, (B) relative proportions of the respective picophytoplankton groups to total picophytoplankton consumption

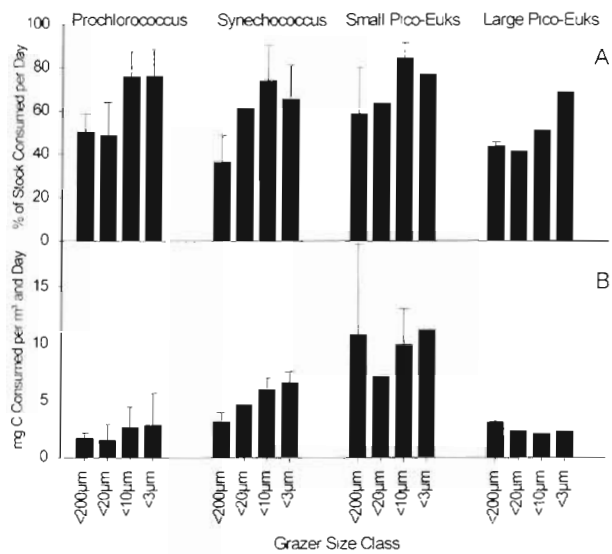

Fig. 4. (A) Relative and (B) absolute consumption rates of 4 picophytoplankton groups in the presence of different grazer size classes. Columns represent means of 2 to 5 experiments (data from Table 4), with standard deviations (only data at $p \leq 0.05$ plotted)

Picophytoplankton growth and grazing mortality by nanozooplankton

Removal of the microzooplankton and larger nanozooplankton (10 to 200 µm) from the incubation water resulted in a considerable increase of grazing pressure on the autotrophic picoplankton (Figs. 2 & 4, Table 4). In the samples containing the entire nano- (<20 µm) and microzooplankton (<200 µm), rates for all picoplankton groups were much lower and in the similar range as for chl *a* (Fig 2). Hence, the larger microzooplankton obviously exerted a strong control over first-order consumers of the picoplankton, thereby relieving the picoplankton from being grazed. As an average over all stations and picophytoplankton groups, grazers <10 and <3 µm consumed 78 and 73% of the picoautotrophic standing stock d^{-1}, and 131 and 115% of picoautotrophic production d^{-1}, respectively (Table 5). The prokaryotic genera *Prochlorococcus* and *Synechococcus*, as well as the small eukaryotic picoautotrophs, experienced the highest growth and grazing mortality rates in the small size fractions <10 and <3 µm; the rates for the large picoeukaryotes in these fractions were lower (Table 4).

At some stations, sub-populations of *Prochlorococcus* and *Synechococcus* could be analyzed, termed 'dim' and 'bright', according to their red fluorescence intensity (Table 2). While the 2 sub-groups of *Synechococcus* showed similar growth and grazing rates, the dynamics of the 2 sub-populations of *Prochlorococcus* were remarkably different: the 'dim' type showed growth rates slightly exceeding grazing mortality, whereas the 'bright' type virtually did not grow but experienced the same grazing pressure as the 'dim' type (Fig. 5), consequently it decreased in biomass. As for all analyzed picoautotrophic groups, growth and grazing mortality rates were dramatically elevated in the absence of grazers >10 µm.

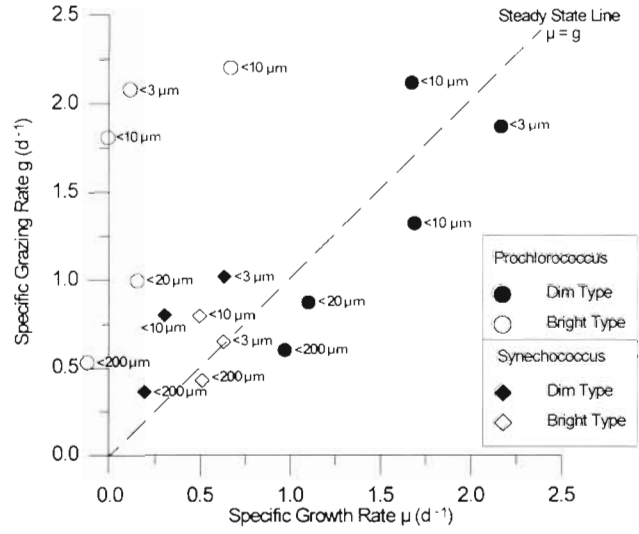

Fig. 5. As Fig. 2, for 2 *Prochlorococcus* and *Synechococcus* sub-populations ('dim' and 'bright' types). Respective grazer size classes are indicated for each data point (only data at $p \leq 0.05$ plotted)

DISCUSSION

Phytoplankton growth and grazing mortality by microzooplankton

Our data indicate a highly dynamic turnover of autotrophic picoplankton in the western Arabian Sea. Picophytoplankton divided roughly once a day, the same rate at which they were removed from the water column by microzooplankton grazing. This implies a balanced steady-state system with respect to this very small phytoplankton. However, we found that larger phytoplankton biomass could increase with specific growth rates exceeding grazing mortality rates. The same effect was described in the equatorial Pacific by Landry et al. (1995a, b), where they found chlorophyll-based growth rates exceeding grazing estimates, while the picoautotrophic community was more or less in balance or experienced a net decrease due to high grazing rates at concomitantly lower growth rates. As mesozooplankton, the potent grazers of the large phytoplankton, had been removed from the incubations (<200 µm), the large phytoplankton could increase in biomass. On the other hand, the microbial food web remained more or less unaffected in these treatments, resulting in a balanced system. The proportion of larger phytoplankton increased along the transect from the Somali Current into the Gulf of Aden and the Red Sea, and was increasingly utilized by microzooplankton, whereas the proportion provided by picoautotrophs remained relatively constant (Fig. 3A). As the C:chl *a* ratio we used (190) was determined by flow cytometry (Veldhuis et al. 1997), it may overestimate phytoplankton carbon values at stations rich in chlorophyll (Gulf of Aden and Red Sea) to a certain extent; for stations low in chlorophyll, however, such high ratios are reasonable (as discussed in detail by Buck et al. 1996). However, our interpretation with respect to the relative importance of the picoautotrophic organisms as a diet for the microzooplankton remains unaffected.

Within the picoautotrophic compartment, eukaryotes gained importance with increasing chlorophyll concentrations, while *Prochlorococcus* decreased in concentration along this gradient and was virtually absent in the southern Red Sea. This confirms recent

observations demonstrating *Prochlorococcus* to be a true open-ocean organism, largely restricted to oligotrophic warm stratified waters (Lindell & Post 1995, Suzuki et al. 1995, Buck et al. 1996). However, hardly any rate estimates have been published for *Prochlorococcus*. Goericke & Welschmeyer (1993) found relatively low growth rates in the Sargasso Sea (below 1 division d^{-1}), while Vaulot et al. (1995) report on division rates of 1 d^{-1} in the surface layer of the equatorial Pacific. Growth and grazing estimates from the same region are presented by Landry et al. (1995a, b): in their experiments, *Prochlorococcus* grazing mortality considerably exceeded specific growth rates, which were extraordinarily low (mostly $\mu = 0$ to 0.26 d^{-1}). The existence of 2 different strains of *Prochlorococcus* had been demonstrated earlier in the subtropical North Atlantic on the basis of pigment types (Goericke & Repeta 1993) and different chlorophyll and DNA contents at the HOT site (Hawaii, subtropical North Pacific; Campbell & Vaulot 1993). The data presented here suggest that the 2 sub-populations also may experience different growth characteristics, with an apparently healthy growing population ('dim') and a hardly active one ('bright'; Fig. 5).

Phytoplankton grazing estimates from the Arabian Sea have been reported so far only by Burkill et al. (1993). During the autumn inter-monsoon period, they found *Synechococcus* to be a highly abundant and dynamic component of the food web, with growth and grazing mortality well in balance. *Synechococcus* was the dominant picoautotroph during our investigations in terms of cell numbers, but the picoeukaryotes, due to their larger size, dominated in terms of carbon biomass. They were the most important picoautotrophic carbon source for the microzooplankton (Fig. 3B). *Prochlorococcus* was less abundant by a factor of 4 during the NE monsoon (up to 66000 cm^{-3}) than during the spring inter-monsoon (up to 276000 cm^{-3}; Veldhuis & Kraay 1993), so its contribution to micro- and nanozooplankton diet was rather low during this season. However, at abundances typical for oligotrophic conditions (up to 350000 cm^{-3}; e.g. Campbell & Vaulot 1993, Morel et al. 1993, Lindell & Post 1995, Buck et al. 1996), the nutritional importance of *Prochlorococcus* might be equal to, or even higher than, that of *Synechococcus* or the picoeukaryotes.

The size-fractionation experiments suggest that small heterotrophic nanoflagellates (HNF) are the main consumers of *Prochlorococcus*, *Synechococcus* and picoeukaryotes in the Arabian Sea. Epifluorescence analysis revealed that the vast majority of HNF (>90%) was smaller than 3 µm, with the biomass peak still within the <5 µm size range (data not shown). Small HNF are known to be mainly responsible for the removal of heterotrophic bacteria (e.g. Fenchel 1986), but are also able to consume coccoid cyanobacteria *in situ* (Caron et al. 1991). Parslow et al. (1986) reported that the small HNF *Pseudobodo* (2 × 4 µm) is capable of rapidly reproducing on the picoeukaryotic alga *Micromonas pusilla* (1 to 2 µm) as sole food source. Calculations assuming HNF to be the only consumers of picoautotroph carbon imply that they could well be able to satisfy their daily carbon demand exclusively from this source (up to 1200% of their own body carbon consumed d^{-1}; Table 6: daily ration). Although this assumption is a simplification (larger protozoa will probably contribute to the removal of picoautotroph carbon to a certain extent, and heterotrophic bacteria will still be a major diet for HNF), it nevertheless shows that <3 µm HNF may apply a vigorous grazing pressure on picophytoplankton. There is also direct microscopical evidence for the ingestion of autotrophic picoplankton by HNF: a large number of HNF <3 µm contained 1 or 2 whole or partly digested *Synechococcus* cells, which can be identified reliably by their bright yellow autofluorescence under blue excitation. Although some dinoflagellates also contained *Synechococcus* cells, their frequency was much lower than the *Synechococcus*-containing HNF. Ciliates containing *Synechococcus* cells were not detected.

Table 6. Absolute picophytoplankton carbon consumption rates as the sum of all picophytoplankton groups in the <200 µm fractions (SI: <10 µm) at 4 stations in the Somali Current, the Gulf of Aden, and the Red Sea. Ambient HNF and total protozoan biomasses (HNF + ciliates + heterotrophic dinoflagellates) are given to estimate daily rations of the grazers (prey carbon ingested as % of grazer body carbon). Protozoan biomasses were derived from epifluorescence counts (data not shown) according to the JGOFS protocols (Knap et al. 1994)

Stn	Picophytoplankton consumption (mg m^{-3} d^{-1})	HNF		Total protozoa	
		C biomass (mg m^{-3})	Daily ration of HNF (%)	C biomass (mg m^{-3})	Daily ration of protozoa (%)
US2	12.68	2.98	426	4.84	262
SI	25.08	2.12	1183	4.59	546
GA2	26.33	2.92	902	4.61	571
RS2	5.63	1.90	296	7.18	78

Multiple trophic interactions within the microbial food web

The number of trophic levels within the microzooplankton community and the size of the principal grazers of picoplankton are important variables when estimating carbon flux in picoplankton-dominated systems. Eukaryotic and prokaryotic bacterivores have been found in the bacterial size class, i.e. 0.2 to 2 µm (Fuhrman & McManus 1984, Guerrero et al. 1986). Wikner & Hagström (1988) presented experimental evidence for the existence of 4 trophic levels in the size class <12 µm, with the primary bacterivores being smaller than 3 µm and controlled by the larger protozoa. Glibert et al. (1992) found a similar effect in size-fractionated grazing and NH_4^+ regeneration experiments in Chesapeake Bay (USA) waters. When organisms >10 µm were removed from their incubations, ammonium regeneration rates increased significantly.

A linkage between the predators of the first-order consumers and the prey is a well-known feature in terrestrial ecology and limnology (trophic cascade; Carpenter et al. 1985, Strong 1992) and has recently also been described for marine pelagic food webs of different trophic conditions (Wikner & Hagström 1988, Weisse & Scheffel-Möser 1991, Hansen et al. 1993, reviewed in Verity & Smetacek 1996). For the Red Sea, Weisse (1989) reported on a 2-step protozoan food chain. heterotrophic bacteria profit from larger protozoa feeding on the major bacterivores, the HNF. Our data indicate that this effect also applies to the autotrophic picoplankton in the region. The enhanced grazing pressure on picophytoplankton in the absence of grazers >10 and >3 µm demonstrates that first-order consumers of picoplankton (i.e. the small HNF) are preyed upon by larger nanozooplankton and microzooplankton in the field, which act as carbon mediators from picoplanktonic autotrophs to higher trophic levels. The extent of this transfer largely depends on the metabolic rates of the primary consumers of the autotrophic picoplankton.

The elevated grazing rates in the fractions <10 µm may be due either to an increased per cell ingestion rate at constant grazer biomass, or to an increased grazer biomass at constant per cell ingestion rates. The former possibility seems unlikely as initial prey concentrations were identical in all parallel size fractionations; hence, an adjustment of the individual feeding effort as a reaction to different prey concentrations can be excluded. Moreover, extraordinarily high HNF growth rates have been measured in the absence of large predators by various authors ($\mu > 2$ d^{-1}, corresponding to more than 3 doublings d^{-1}; Sherr et al. 1983, Parslow et al. 1986, Kuosa 1991). Thus, if we assume that the increased grazing rates are symptomatic of an increased grazer biomass, it is possible to roughly estimate grazer growth and predation mortality rates from the size-fractionated experiments. It can then be estimated that grazers <10 µm more than doubled their biomass within 1 d when predators >10 µm were removed (increase of 124%; Table 5), which is a realistic figure (see above). When these results are extrapolated to field conditions, this means that small HNF, like their prey, divide once a day, and are removed by their predators at a similar rate. This is a strong indication for the presence of a trophic cascade encompassing at least 3 trophic levels within the nanoplankton: picoautotrophs – small HNF – larger protozoa.

In our experiments, the picophytoplankton also increased their specific growth rates when they were exposed to an increased grazing pressure (on average by 75% in the <10 µm fractions relative to the <200 µm fractions; Table 5, Fig 2). A close coupling between prey growth rates and grazing pressure (mediated by enhanced nutrient regeneration) has long been acknowledged as a prerequisite for the functioning of the microbial loop and has been demonstrated in laboratory and field experiments (i.e. Goldman & Caron 1985, Rassoulzadegan & Sheldon 1986, Berman et al. 1987, Wikner & Hagström 1988). Similar to our findings, Glibert et al. (1992) found ammonium regeneration rates to be substantially higher in their <10 µm fractions as compared to the <200 µm fractions, and Ferrier & Rassoulzadegan (1991) demonstrated that autotrophic pico- and nanoplanktonic growth was limited by protozoan standing stocks or their remineralizing, i.e. grazing, activity. Our data indicate that this linkage between grazer and prey may hold true also in the presence of considerable amounts of new nutrients, at least for the prokaryotic picoautotrophs and the small picoeukaryotes. Such a preferential uptake of ammonium in small phytoplankton cells in the presence of excess nitrate has been demonstrated in the field (Harrison & Wood 1988, Wheeler & Kokkinakis 1990, Price et al. 1994). These observations strongly substantiate the notion of the ubiquitous nature of this tight coupling between the smallest phytoplankton and their primary grazers, with grazing mortality and growth as the 2 sides of the coin.

Our data imply the existence of a multi-step food chain with respect to the small phytoplankton in the Arabian Sea, as had been demonstrated earlier for heterotrophic bacteria in the same region (Weisse 1989). On the one hand, this means that a certain amount of phytogenic carbon is forwarded from the autotrophic picoplankton via small heterotrophic flagellates and larger protozoa to the mesozooplankton; on the other hand, the high turnover rates and the size

of these first-order consumers indicate that this amount of picoplanktonic primary production reaching higher trophic levels will be smaller than in systems with larger herbivores. In such a system, where tiny primary producers (closely coupled to their grazers) represent the major fraction of primary production, recycling of nutrients and respiration within the euphotic zone will be quite high. As we believe that the mechanisms described also apply to other oceans, the resulting great potential to recycle CO_2 in the euphotic zone may help explain the minimal effect of iron fertilization on sea-surface CO_2 concentrations (Watson et al. 1994) within the framework of the IRONEX I experiment (Martin et al. 1994), as supposed by Banse (1995). Although IRONEX II (Coale et al. 1996) succeeded in triggering a diatom bloom (biomass increase 85×), associated with a considerable decrease of CO_2 in surface waters (Cooper et al. 1996), picophytoplankton only doubled in biomass, and was tightly coupled to microzooplankton (i.e. protozoan) biomass. This observation gives further evidence for a tightly coupled picophytoplankton-protozoa link which itself is rather loosely coupled to the food web involving larger organisms.

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