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Effects of N:P:Si ratios and zooplankton grazing on phytoplankton communities in the northern Adriatic Sea. III. Zooplankton populations and grazing

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ABSTRACT: As part of mesocosm experiments to study effects of nutrients and zooplankton grazing on phytoplankton communities from the northern Adriatic Sea, we monitored metazoan zooplankton fluctuations in enclosures and performed grazing experiments in May and June of 1993. An effort was made to increase zooplankton abundances up to 10 times above normal levels in May, whereas in June, we attempted to initially exclude zooplankters >100 µm in size. Neither manipulation mattered since, in both cases, a cohort of copepodites rapidly developed from eggs and nauplii added during initial filling of enclosures. Declines in abundances of nauplii, with concurrent increases in copepodites, during both experiments likely resulted from a combination of nauplii molting into copepodites, and possibly cannibalism of nauplii by copepodites and adults. In May copepodites were almost exclusively *Acartia clausi*, whereas in June, both *A. clausi* and particularly *Oithona similis* copepodites increased in enclosures after 6 to 7 d. Grazing rates by *A. clausi* adults and copepodites were low in both months (0.01 to 0.35 ml copepod^{-1} h^{-1} in May, and <0.21 ml copepod^{-1} h^{-1} in June). Zooplankton community grazing had minimal impact, in that phytoplankton growth continued unabated until nutrients were exhausted.

KEY WORDS: Zooplankton · Grazing · Adriatic Sea · Copepod

INTRODUCTION

Zooplankton grazing is a potentially important aspect of phytoplankton ecology, because variations in the degree of grazing impact may allow or prevent blooms of certain phytoplankters. Zooplankton community grazing impact is variable, ranging from negligible to substantial (Dagg & Turner 1982, Morales et al. 1993, Landry et al. 1994, Sautour et al. 1996, and references therein), and may be particularly important in relation to seasonal or unusual phytoplankton blooms (Turner & Tester 1997). Reduced grazing pressure has been implicated in allowing development of various blooms (Martin 1970, Sellner & Olson 1985, Smayda & Villareal 1989, Bautista et al. 1992, Malej & Harris 1993), whereas zooplankton grazing pressure has also been linked to termination of other blooms (Turner & Anderson 1983, Nielsen 1991, Nakamura et al. 1996). Thus, attempts to understand the ecology of phytoplankton blooms should incorporate information on zooplankton grazing upon such blooms (Turner et al. 1998).

As part of the mesocosm experiments described by Granéli et al. (1999, in this issue) and Carlsson & Granéli (1999, in this issue), which were designed to study the interacting effects of nutrient additions and mesozooplankton grazing on growth and community

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succession of northern Adriatic phytoplankton in 100 l mesocosms, we examined zooplankton grazing and population development in mesocosms in May and June of 1993. In May we attempted to increase grazing pressure by adding elevated abundances of zooplankton, whereas in June, we attempted to remove mesozooplankton prior to filling mesocosms. In both cases, the results were unanticipated.

METHODS

May 1993. Natural phytoplankton assemblages from the northern Adriatic, off Fano, Italy, were sieved through 100 µm mesh to remove larger mesozooplankton, and mesocosms were immersed in a large pool to maintain natural temperature. Light intensity was reduced by screens over the surfaces of enclosures to prevent photoinhibition. Various nutrient regimes (nitrate, phosphate and silicate limiting, and nitrate, phosphate and silicate replete) were added to mesocosms in excess. The following nutrient additions were made to all cylinders: NO_3: Day 1, completed to 10 µM, Days 2 and 5, 10 µM added; PO_4: Day 1, completed to 1 µM, Days 2 and 5, 1 µM added; Si: Day 2, 15 µM added, Day 5, 20 µM added. Daily samples were taken for phytoplankton and zooplankton quantification and identification and measurements of amounts of chlorophyll and nutrients.

Zooplankton were collected with 333 µm mesh nets off Fano. In May, the net was allowed to sink to 5 m depth and then pulled upward through the water column. This, combined with the net mouth diameter (0.5 m), allowed semi-quantitative estimates of zooplankton abundance. After 2 h of allowing dead or damaged animals to sink to the bottom of containers (17 to 18°C, gentle bubbling), live actively swimming zooplankton were added to mesocosms at levels of natural abundance (1×), 5 times natural abundance (5×) and 10 times natural abundance (10×). Water for controls was sieved through 100 µm mesh, and left without added zooplankton. There were 4 replicate mesocosms for each of 4 treatments (total = 16 mesocosms). Zooplankton were removed from the mesocosms each day (2 l samples), concentrated onto 64 µm mesh screens and counted and staged.

Using some of the copepods from the Day 1 and Day 6 samples, feeding experiments were performed using 10 adult female *Acartia clausi* in a bottle from each of the 16 mesocosms, 200 ml total volume. Experimental duration was 12 h. Phytoplankton cell counts were performed on 25 ml of settled material from initial, control, and experimental containers, following the protocols of Turner & Tester (1989).

Egg production experiments were performed at room temperature (18 to 21°C), but the copepods had been in water at 17.5 and 19.5°C on Days 1 and 6, respectively. Between 10 and 20 adult female *Acartia clausi* were placed in 500 ml aliquots from each mesocosm. Day 1 egg production experiments were of 24 to 27 h duration, and those of Day 6 were 17 h.

June 1993. In June 1993, experiments were performed that were similar to those of the previous month with 1 important exception: instead of adding zooplankton to mesocosms, an effort was made to remove all larger mesozooplankton by sieving water through 100 µm mesh prior to filling mesocosms. Daily samples were taken from all mesocosms for phytoplankton, chlorophyll and nutrient analyses, as well as for zooplankton counts and identifications. Mesocosm treatments, as described by Granéli et al. (1999) were P deficient (Tanks 1 to 3), N-deficient (Tanks 4 to 6), Si-deficient (Tanks 7 to 9) and nutrient sufficient (Tanks 10 to 12). In addition, grazing experiments were performed on 17, 18, 19, and 20 June using water from 1 tank of each type of nutrient addition, and copepods freshly collected from approximately 2 km offshore from Fano. In these grazing experiments, either 15 *Acartia clausi* CI + CII copepodites (17, 19 and 20 June), or 10 *A. clausi* females (18 June) were added to each container (150 ml) in mesocosm water that had been screened through 100 µm mesh, and incubated in the dark at ambient temperature (21.4°C) for (18.63 to 23.39 h). Experiments were terminated by preservation with Utermöhl's solution, and phytoplankton remaining in the jars were concentrated by sedimentation and counted and identified microscopically. Ingestion and filtration rates were determined for major phytoplankton taxa as well as for the total phytoplankton assemblage using the formulae of Frost (1972). Unlike the May 1993 experiments, no egg production experiments were performed in June.

Table 1 May 1993 grazing experiments (data for total phytoplankton cells). F: filtration rate (ml copepod^{-1} h^{-1}) and I: ingestion rate (cells copepod^{-1} h^{-1}). SD: standard deviation of 3 replicates

Treatment	Mean F	SD F	Mean I	SD I
Day 1				
Control	0.75	0.35	36.7	3.5
1×	0.54	0.21	30.3	8.2
5×	0.57	0.15	31.8	6.5
10×	0.63	0.08	34.9	3.1
Day 6				
Control	0.30	0.01	280	65
1×	0.24	0.09	228	76
5×	0.26	0.11	231	87
10×	0.26	0.11	238	85

RESULTS

May 1993

Zooplankton abundance

The zooplankton assemblage in May was essentially a monospecific population of the copepod *Acartia clausi*. This copepod is usually dominant late spring-early summer in the northern Adriatic (Cataletto & Fonda Umani 1994, Cataletto et al. 1995). Numbers of adult copepods increased only slightly between Days 1 and 6, but copepodites exhibited a substantial increase (Figs. 1 & 2). Since all stages of copepodites were not retained quantitatively by 333 µm mesh, these copepodites cannot be considered to have been added quantitatively at 1×, 5×, and 10×, concentrations which applied to adults. Numbers of nauplii were initially much higher than those of adults and copepodites, and since zooplankton for additions had been collected with 333 µm mesh nets, which most nauplii would have passed through, these nauplii were already in the natural unconcentrated water that was added to the enclosures (i.e. controls).

By Day 6, the relative distributions and total abundances of various stages of *Acartia clausi* in the mesocosms had changed dramatically (Figs. 1 & 2). Numbers of nauplii had declined precipitously from levels of approximately 30 to 150 l^{-1} on Day 1 to <10 l^{-1} by Day 6. Numbers of adults had increased somewhat, but abundances of copepodites had increased substantially (Figs. 1 & 2). The most likely explanations for these changes are a combination of (1) many nauplii moulting into copepodites, and (2) possible cannibalism of nauplii by adults and copepodites. Since egg production was proceeding throughout these experiments, but no second cohort of *Acartia* nauplii appeared, we suspect that the initial cohort of nauplii that developed into the copepodites recorded on Day 6, and the second cohort of nauplii that would have replaced the first were cannibalized by the copepodites of the preceeding generation.

Grazing and egg production experiments

Copepods were active during grazing experiments, had pigment in their guts and were producing abundant fecal pellets. Feeding rates were about 33 phytoplankton cells *Acartia* h^{-1} and were uniform over the experimental treatments. On Day 6 the number of cells ingested was nearly 7 times higher, but the filtration rate had slowed, probably due to the fact that phytoplankton cell concentrations were much higher on Day 6 (Table 1).

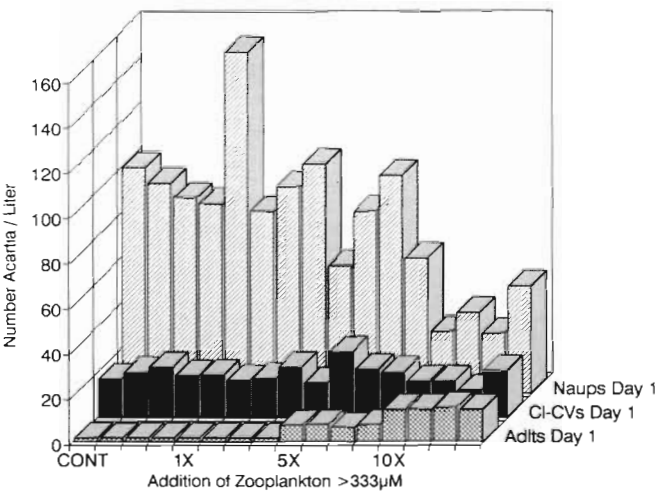

Fig. 1. May 1993. Abundance of *Acartia clausi* adults, combined CI–CV copepodites and nauplii in mesocosms (4 replicates of each treatment) of control (CONT) water with zooplankton removed by screening, natural abundance (1×), 5 times natural abundance (5×) and 10 times natural abundance (10×) on Day 1 of the experiment

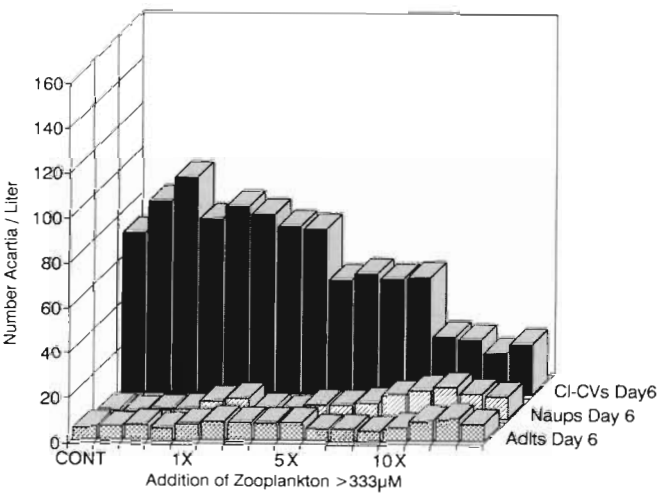

Fig. 2. Legend as in Fig. 1 but for Day 6

Egg production on Day 1 was low but increased by Day 6 (Fig. 3). The difference of 2 to 3°C was likely an important factor since food was abundant both days.

June 1993

Zooplankton abundance

Despite attempts to remove zooplankton by sieving through 100 µm mesh prior to addition of water to mesocosms, considerable numbers of copepod nauplii were present in all enclosures by Day 1 (Fig. 4). Some

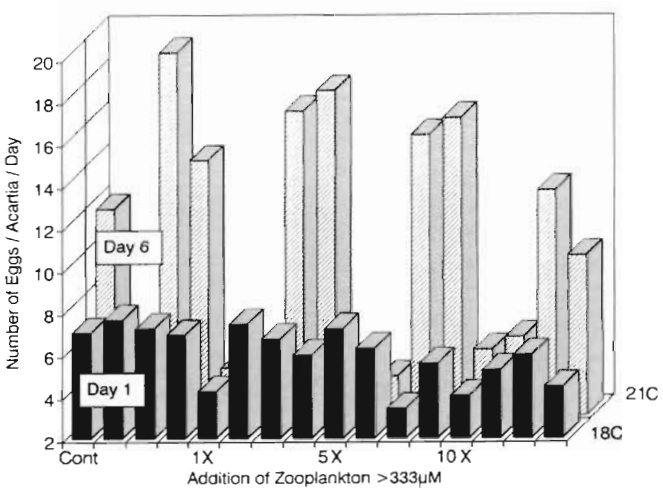

Fig. 3. May 1993. Rates of egg production for *Acartia clausi* females from mesocosms (4 replicates of each treatment) of control (CONT) water with zooplankton removed by screening, natural abundance (1×), 5 times natural abundance (5×) and 10 times natural abundance (10×) on Days 1 and Day 6 of the experiment

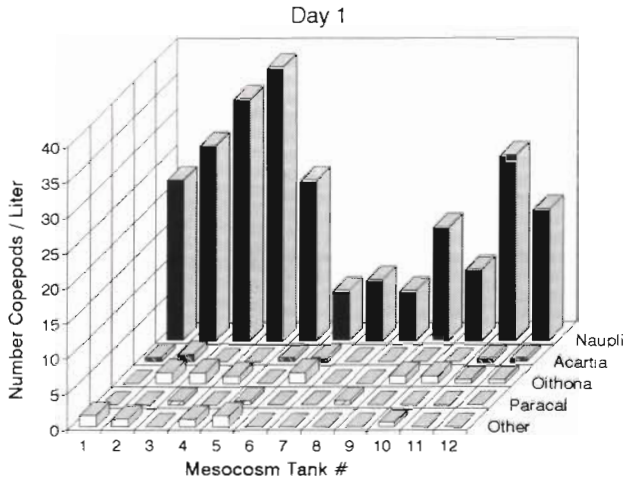

Fig. 4. June 1993. Abundance of copepods (combined adults + copepodites) of the genera *Acartia*, *Oithona*, *Paracalanus*, and all other genera combined, and combined copepod nauplii (all stages and species) in the 12 mesocosm tanks on Day 1 of the experiment

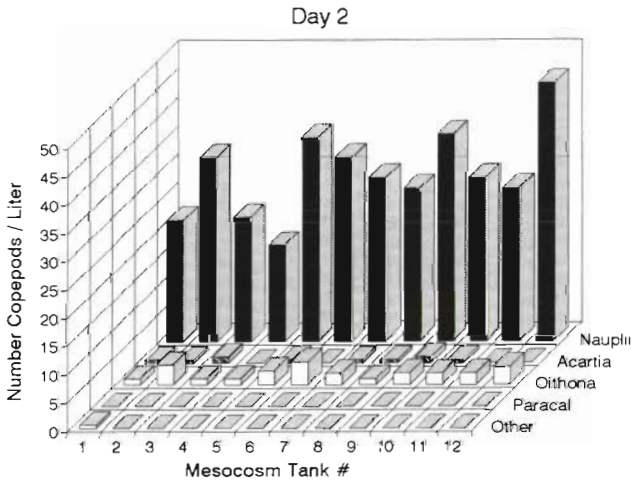

Fig. 5. Legend as in Fig. 4 but for Day 2

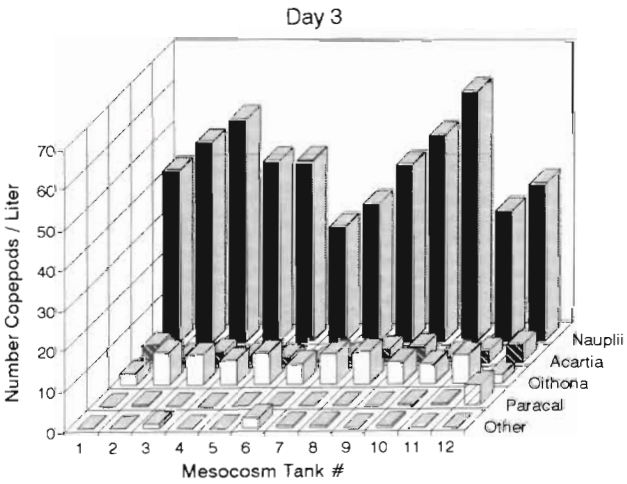

Fig. 6. Legend as in Fig. 4 but for Day 3

smaller nauplii <100 µm in size undoubtedly entered mesocosms during initial filling, whereas others passed through the mesh as eggs and hatched into nauplii within the first 24 h of the incubations. It is clear that this initial cohort of nauplii went through its naupliar molts over the course of the 7 d of the experiment, progressively declining to near absence by Day 7 (Figs. 4 to 10). Since individual naupliar stages were not distinguished on each day, total abundances were generally the same for the first 4 d, and started to decline noticably only after Day 4, as late-stage nauplii made the transition to copepodites by Days 4 to 5.

The progressive decline of the nauplii was mirrored by a progressive increase in *Acartia*, almost all of which were copepodites, as the experiment proceeded from Day 1 to 6 (Figs. 4 to 10). This trend undoubtedly reflects *Acartia* nauplii moulting into copepodites, again most pronounced by Day 4.

Unlike the May experiment, in which the zooplankton was virtually a monospecific *Acartia clausi* population, in June, other taxa such as *Oithona similis* and *Paracalanus* sp. were also present (Figs. 4 to 10). Over the first 3 d of the experiment, numbers of nauplii (all stages and species) remained relatively high, and numbers of *A. clausi*, *O. similis*, and *Paracalanus* sp.

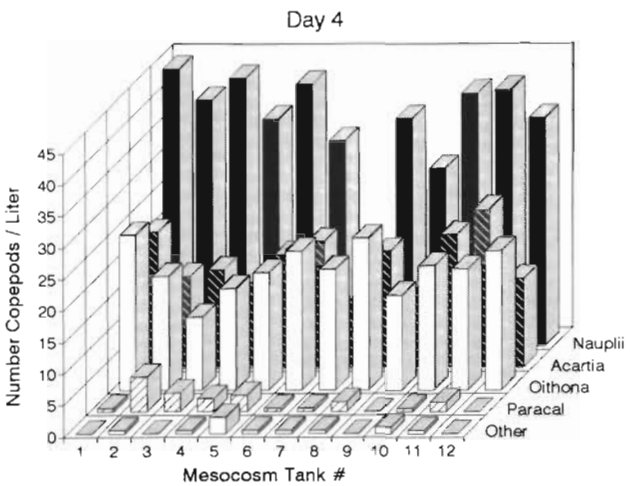

Fig. 7. Legend as in Fig. 4 but for Day 4

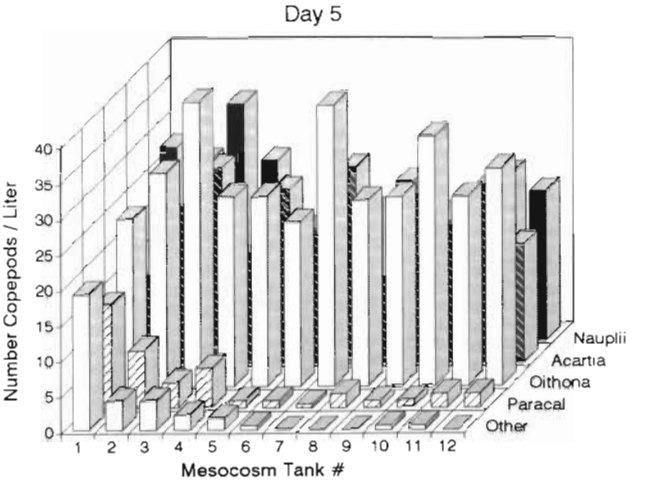

Fig. 8. Legend as in Fig. 4 but for Day 5

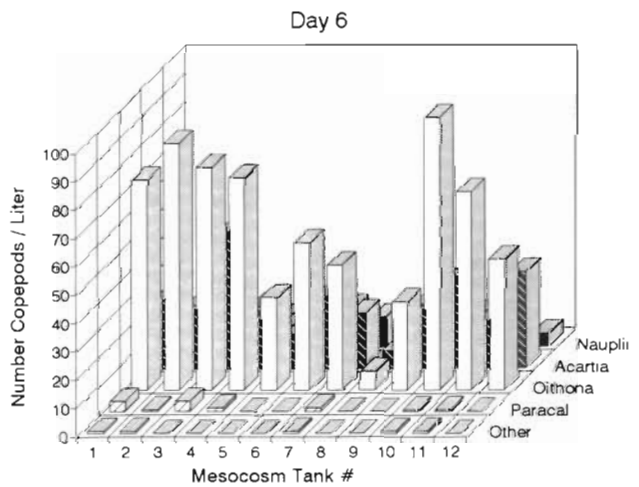

Fig. 9. Legend as in Fig. 4 but for Day 6

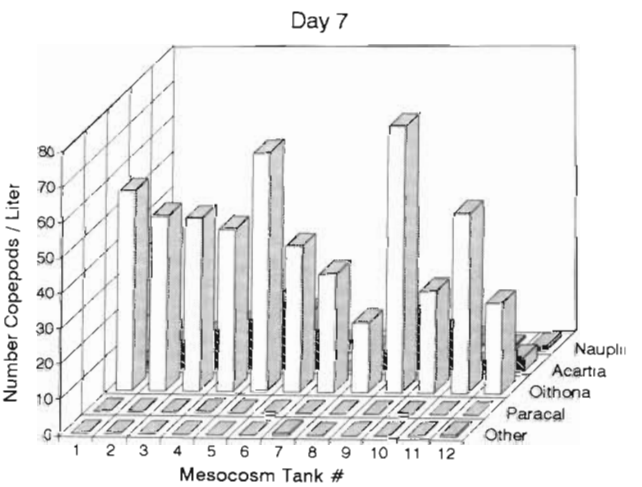

Fig. 10. Legend as in Fig. 4 but for Day 7

(primarily copepodites) remained low, but showed steady increases (Figs. 4 to 6). By Day 4, however, numbers of *A. clausi* and *O. similis* copepodites exploded (Fig. 7), generally increasing 2- to 3-fold. By Day 5 (Fig. 8), this trend had continued, and numbers of nauplii had declined precipitously. By Days 6 (Fig. 9) and 7 (Fig. 10), *O. similis* had taken over the enclosures, and abundances of *A. clausi* and nauplii had declined to minimal levels.

These trends are due to a combination of factors. Since many of the nauplii had to be those of *Oithona*, which were the basis of the population increase of copepodites of this genus, much of the coincident declines in nauplii and increases in copepodites were due to moulting of nauplii into copepodites as they progressed through their developmental stages. However, since various species of *Oithona* have been shown to be heavily carnivorous on naupliar stages of their own and other copepod species (references in Turner 1994), some of the naupliar decline is possibly due to cannibalism of nauplii by the developing cohort of *Oithona* copepodites and adults.

Grazing experiments

Due to the neccessity of screening water from enclosures through 100 µm mesh to remove extraneous grazers prior to use of this water in grazing experiments, the phytoplankton assemblages in grazing experiments were often quite different from those recorded by Carlsson & Granéli (1999) for the total

Table 2. June 17 to 20 grazing experiments (data for total phytoplankton cells). F: filtration rate (ml copepod^{-1} h^{-1}) and I: ingestion rate (cells copepod^{-1} h^{-1}). SD: standard deviation of 3 replicates

	Mean cells ml^{-1} (initial)	Mean F	SD F	Mean I	SD I
Day 1 (17 June) (*Acartia clausi* CI + CII copepodites)					
Tank 3 (–P)	35633	0.212	0.063	4.777	1190
Tank 5 (–N)	21045	0	0	0	0
Tank 7 (–Si)	28150	0.021	0.020	636	393
Tank 12 (+P,N,Si)	25513	0.038	0.087	631	1606
Day 2 (18 June) (*Acartia clausi* adult females)					
Tank 3	34440	0	0	0	0
Tank 5	24032	0	0	0	0
Tank 7	34866	0	0	0	0
Tank 12	58326	108.6	153.4	19313	15232
Day 3 (19 June) (*Acartia clausi* CI copepodites)					
Tank 3	44350	0.068	0.033	2426	1123
Tank 5	33524	0.142	0.077	3332	1528
Tank 7	60000	0.123	0.061	5023	2369
Tank 12	25712	0.059	0.045	1257	922
Day 4 (20 June) (*Acartia clausi* Ci copepodites)					
Tank 3	24008	0	0	0	0
Tank 5	19256	0.034	0.021	636	394
Tank 7	32023	0	0	0	0
Tank 12	49949	0	0	0	0

unscreened assemblages, because screening removed large or chain-forming taxa such as *Chaetoceros* spp., *Rhizosolenia fragilissima*, and larger dinoflagellates. The phytoplankton used in the June grazing experiments was dominated by small cells such as athecate microflagellates and *Nitzschia closterium*. Grazing data for ingestion of these cells by *Acartia* CI copepodites (17, 19, and 20 June) and adult females (18 June) (Table 2) revealed minimal grazing. Filtration rates were either undetectable or generally <0.2 ml copepod^{-1} h^{-1}. For experiments performed at 21°C, these are extremely low rates. Possible reasons are that cell numbers in enclosures (see Table 2) vastly exceeded those found in nature, and copepods became clogged in 'phytoplankton soup'. Further, except for 1 day (18 June) these copepods were CI copepodites, unlike the adult females used in the May experiments. The only substantial grazing recorded was by adult females on 18 June in Tank 12, which was replete with nitrate, phosphate and silicate. Despite the high per individual grazing rates recorded on that date, it is likely that this grazing effort was inconsequential, since adult females were such a small component of the total zooplankton assemblage in the tanks.

In terms of whether there was preferential grazing on *Nitzschia closterium* versus microflagellates or other phytoplankton taxa, no clear trends were evident, since overall grazing was so diminished.

Nutrients and chl *a*

May 1993

Since nutrient and chl *a* data for the May 1993 experiment were not presented by Granéli et al. (1999), but are pertinent to the zooplankton grazing studies, these data are summarized in Fig. 11. In control, 1×, 5×, and 10× natural zooplankton abundance tanks, silicate and nitrate levels increased over the first 3 d after nutrient addition, declined over the next 2 d, increased again by Day 6, and plummeted by Day 7. Chl *a* levels increased through Day 4 (as nitrate and silicate declined), remained constant or declined slightly by Day 5, and increased dramatically over Days 6 and 7. The meteoric rise in chl *a* on Day 7 in all tanks coincided with a precipitous decline in nitrate and silicate, suggesting heavy nutrient utilization. It is unfortunate that this experiment had to be terminated after 7 d because we do not know if chlorophyll levels would have crashed in response to nutrient depletion. What is clear, however, is that the grazing impact by zooplankton in the enclosures appeared to have minimal effect on development of high chl *a* levels (approximately 80 µg l^{-1}) in all mesocosms.

June 1993

Although extensive details on nutrient and chl *a* fluctuations in mesocosms have been presented by Granéli et al. (1999), they are briefly summarized here in Fig. 12, within the context of zooplankton grazing and population fluctuations.

Levels of added nutrients increased in all enclosures over the first 2 d, but thereafter declined precipitously between Days 4 and 6. These nutrient depletions were concurrent with chlorophyll increases which substantially declined by Day 7. As in the previous month, there was no apparent relationship between zooplankton and chl *a* fluctuations, the latter seemingly more related to nutrient exhaustion than to zooplankton grazing.

DISCUSSION

Despite the differences in experimental design of the May experiments (when zooplankton were added) versus the June experiments (when an attempt was made to exclude zooplankton), the overall results of the two were similar from the phytoplankton grazing impact perspective. Simply stated, when phytoplankton communities are allowed to develop under nutrient-enriched conditions, zooplankton grazing cannot keep

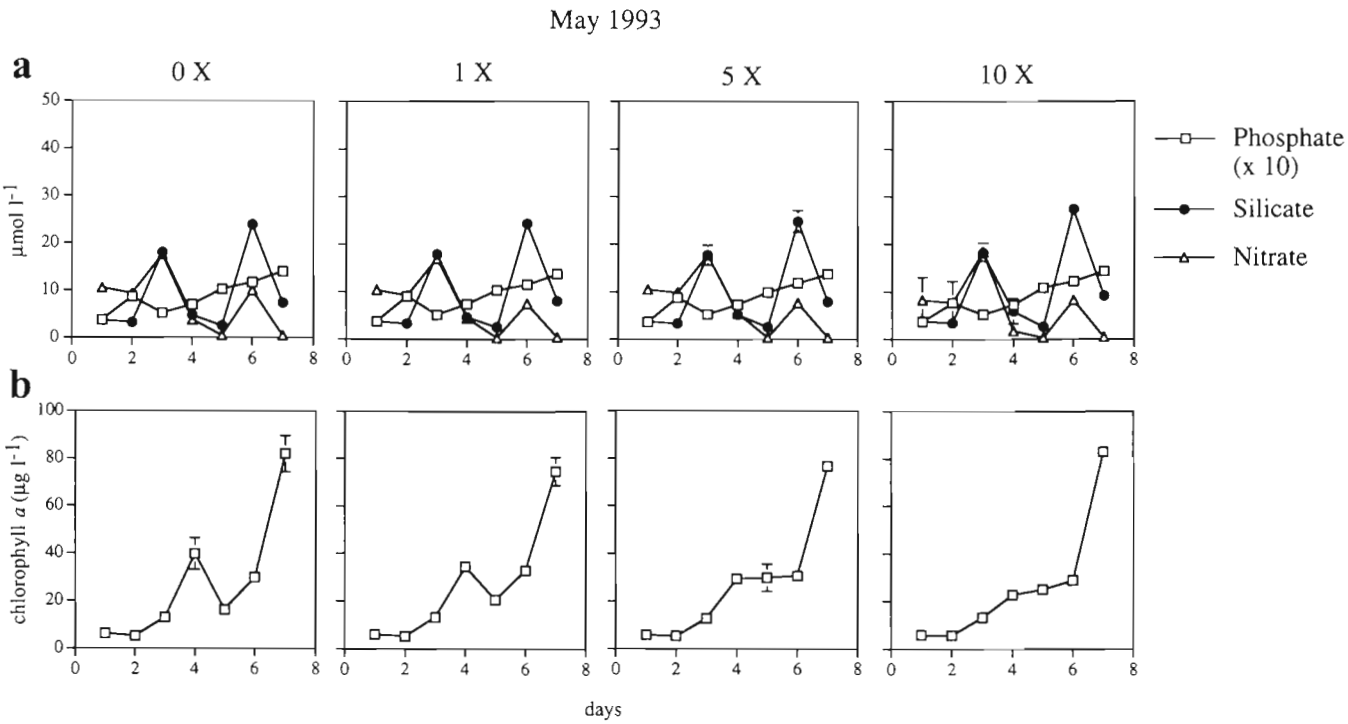

Fig. 11. May 1993. Fluctuations of (a) nutrients and (b) chlorophyll *a* in mesocosms of control (0×) water with zooplankton removed by screening, natural abundance (1×), 5 times natural abundance (5×) and 10 times natural abundance (10×) on Days 1 to 6 of the experiment (data points are means of 3 replicates, ±SD)

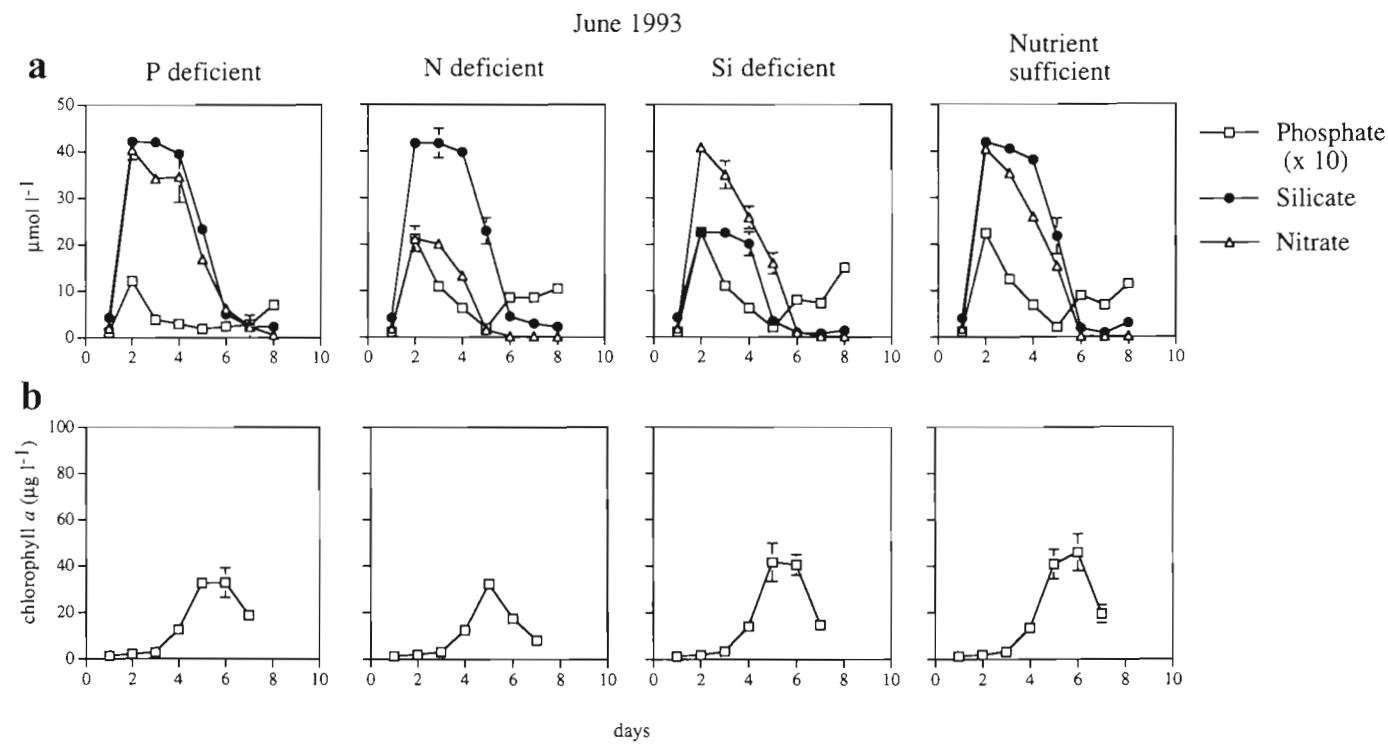

Fig. 12. June 1993. Fluctuations of (a) nutrients and (b) chlorophyll *a* in mesocosms of P-deficient, N-deficient, Si-deficient and nutrient-sufficient waters on Days 1 to 7 of the experiment (data points are means of 3 replicates, ± SD)

up with phytoplankton growth. Even though grazing by *Acartia clausi* adults in May was considerably higher than by CI and CII copepodites in June (compare data in Tables 1 & 2), overall grazing in both cases was inconsequential. Despite the fact that zooplankton populations were increasing throughout both experiments in most enclosures, and even though animals were usually grazing in both situations, phytoplankton populations continued to increase until nutrients were exhausted, and then (at least in June) they crashed (Figs. 11 & 12). Thus, in terms of the importance of 'top-down' versus 'bottom-up' influences on phytoplankton growth, in these experiments the 'bottom-up' impact of nutrient enrichment clearly dominated over the extremely minimal 'top-down' impact of zooplankton grazing.

These experiments also reveal something else of importance. It is clear from our results that screening of plankton communities through meshes of plankton netting did not accomplish the desired exclusion of metazoan grazers. In both May and June, copepod eggs and/or nauplii passed through the initial screening of 100 µm and subsequently developed into the dominant components of the zooplankton assemblages in both experiments. Thus, attempts to add adults collected with 333 µm mesh in May, or to exclude metazoan zooplankters in June, proved inconsequential, inasmuch as the 'contaminant' eggs and nauplii resulted in population increases that took over the mesocosms in both cases. Screening to remove extraneous grazers from water to be used in grazing experiments also compromised those experiments, since abundant chain-forming phytoplankters that would likely have been heavily grazed (*Chaetoceros* spp.) were removed by seiving that was designed to remove their predators.

In terms of zooplankton fluctuations within the enclosures, it appears that, in both May and June, fluctuations were most related to a combination of nauplii developing into copepodites, which possibly cannibalized the next generation of nauplii. Thus, even if the initial impact of zooplankton grazing on the phytoplankton had been high, by cannibalizing the subsequent generation of copepods that would have replaced them at the end of their life spans, the initial cohort of copepodites and adults ensured that the grazing impact of future generations would be even less than theirs had been.

We conclude that the impact of grazing by metazoans such as copepod adults, copepodites and nauplii upon the nutrient-enriched phytoplankton assemblages in our enclosures was negligible. The same result nas been obtained in several other similar mesocosm studies (Riemann et al. 1990, Olsson et al. 1992, Turner & Granéli 1992, Granéli et al. 1993, Carlsson et al. 1995). Conversely, Ryther & Sanders (1980) found that copepod grazing caused significant reductions in phytoplankton abundance and changes in species composition in estuarine enclosures, although those enclosures were not nutrient enriched. Although grazing by zooplankton protists may exceed that of copepods (reviewed by Pierce & Turner 1992) the message from these experiments is clear: under nutrient-enriched conditions of purposeful eutrophication, the water turns green until nutrients are exhausted, regardless of the abundance and grazing activities of grazers. Thus, the solution to anthropogenic eutrophication, in the Adriatic or elsewhere, likely lies in a reduction of nutrient loading.

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