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Moderate increase in the biomass of omnivorous copepods may ease grazing control of planktonic algae

Olav Vadstein[1,*], Herwig Stibor[2], Bettina Lippert[2], Kjetil Løseth[3], Wendy Roederer[2], Line Sundt-Hansen[3], Yngvar Olsen[3]

[1]Department of Biotechnology, and [3]Department of Biology, Trondhjem Biological Station, Norwegian University of Science and Technology, 7491 Trondheim, Norway

[2]Department of Biology II, Section of Aquatic Ecology, University of Munich, 80333 Munich, Germany

ABSTRACT: Copepods and ciliates are 2 functionally different types of herbivores that dominate marine ecosystems. Ciliates have a higher reproductive capacity than copepods, but copepods can graze on ciliates. Hence we have an omnivorous system in which the inferior grazer can graze on its competitor. We conducted a 3^2 factorial mesocosm experiment with natural plankton communities to explore how the copepod–ciliate interaction affects algal development on the timescale relevant for algal blooms. We used nutrient load and copepod biomass as the experimental variables. Ciliate biomass was positively correlated to nutrient addition and negatively correlated to copepod biomass, with copepod biomass as the predominant factor at the highest densities tested. Both increasing copepod biomass and nutrient addition resulted in increased algal biomass, with the strongest effect on nanoalgae. The mechanism involved was carnivory by copepods and a resulting trophic cascade through ciliates to algae. We conclude that even a moderately high biomass of copepods may promote algal blooms when the initial size distribution of the algal community is appropriate (i.e. dominance of algae eaten primarily by ciliates).

KEY WORDS: Copepoda · Ciliata · Phytoplankton · Algae · Omnivory · Grazing · Predation · Zooplankton

INTRODUCTION

Predator–prey interactions are fundamental for successions and ecosystem functioning (Begon et al. 1996), and are also important for management practice (Gulati et al. 1990). Most theoretical and field studies have focused on linear food chains or on 2 predators that share the same prey. In planktonic food webs, some exceptional situations may occur, because many grazers select food primarily on a size basis, and grazers of greatly different sizes may have overlapping prey size spectra due to different feeding strategies (i.e. phagotrophy, filter-feeding, ambush predation).

Whether or not an increased input of nutrients to aquatic systems will give rise to algal blooms is dependent on the food-web structure of the system, and in particular on the herbivores present and the number of trophic levels present (Hairston et al. 1960). Experiments in lakes have shown that a high biomass of herbivorous zooplankton can dramatically suppress algal blooms in food chain-dominated ecosystems (Lampert et al. 1986, Reinertsen et al. 1989, Gulati et al. 1990). Marine ecosystems are primarily of the food-web type, dominated by 2 functionally different types of herbivores—metazoans (primarily copepods) and protozoans (primarily ciliates) (Pierce & Turner 1995, Sherr et al. 1996). In a non-steady state situation following (e.g.) a nutrient perturbation, maximum growth rate, size selectivity and differential mortality rates are the most important characteristics determining the succession for algae, ciliates and copepods. Maximum growth rates of algae and ciliates are comparable, and

*Email: olav.vadstein@biotech.ntnu.no

2 to 20 times faster than those of copepods (Gismervik et al. 1996, Hansen et al. 1997). Thus, whereas algae and ciliates form a tight predator–prey coupling, algae may outgrow copepods. Due to differences in feeding mechanisms, ciliates and copepods have an overlapping prey size spectrum, even though they differ in size by 2 to 3 orders of magnitude (Hansen et al. 1994, Gismervik et al. 1996). When the whole life history of copepods is taken into consideration, the overlap is even greater, as copepod nauplii reduce the lower size limit of prey exploited by the copepods. Because of their large differences in size, ciliates and copepods experience different predation-mortality rates. In particular, the typical size of ciliates (10 to 40 µm) is well within the prey size range of copepods (Stoecker & Capuzzo 1990, Kleppel 1993, Hansen et al. 1994, Pierce & Turner 1995, Gismervik et al. 1996). It has also been demonstrated that some copepods may switch from filter-feeding to search-feeding (Tiselius & Jonsson 1990, Gismervik & Andersen 1997), and may therefore selectively feed on ciliates as these are relatively large food items. Thus in these food webs we have an omnivorous system in which copepods may exert a high selective mortality rate on ciliates and hence counteract the competitive superiority of the ciliates. The result may be a less tight grazing control of algal biomass.

We hypothesised that on the timescale of normal algal bloom development the biomass increase of planktonic algae following an increased nutrient supply would be positively correlated with copepod biomass, because a high copepod biomass would result in strong predation on ciliates and therefore indirectly reduce the grazing pressure on algae. Ciliates are the only group of grazers that algae cannot outgrow. We tested this hypothesis in a 3^2 factorial mesocosm experiment with natural populations of marine plankton using nutrient supply rate as the first factor and mesozooplankton (copepod) biomass as the second.

MATERIALS AND METHODS

Experimental and sampling methods. The experiment was arranged as a 3^2 factorial experiment, with nutrient supply rate as the first factor and mesozooplankton (copepod) biomass as the second. The experiment was carried out over 10 d in August–September 2000 in the landlocked coastal bay Hopavågen (63° 36′ N, 9° 33′ E) west of Trondheim, central Norway. We moored 9 mesocosms made from polyethylene in floating stands. The volume of the bags was ca. 4 m^3, with a diameter of 0.9 m and total depth 6.5 m, and consisted of a 6 m straight tube and a conical bottom. Each mesocosm was filled the evening preceding the experiment (Day 0) by lifting them from ca. 7 m depth to the surface. Mesozooplankton biomass was adjusted by addition or removal of zooplankton. Of the 9 mesocosms, 3 were kept at ambient zooplankton concentrations, 3 were amended by adding zooplankton carefully collected by net hauls (200 µm) in Hopavågen, and 3 were reduced by removing zooplankton (see 'Results').

For each mesozooplankton concentration, 3 different nutrient addition regimes where applied: no, normal and high addition. The no-addition regime entailed a slight oligotrophication due to sedimentation of matter. The normal addition regime was comparable to the natural load in the system (O. Vadstein et al. unpubl. data), but resulted in a slight enrichment as the mesocosms were closed systems and advective losses were zero. Nutrients were added in an atomic ratio of 16:16:1 for Si:N:P. Si was added as silicate, P as phosphate, and N as nitrate and ammonia (1:1). The daily doses of added P were 0, 0.5 and 2.5 µg P l^{-1} d^{-1} (0, 16 and 40 nmol P l^{-1} d^{-1}). Nutrients were added on the evening of Day 0, and each evening thereafter.

Integrated composite water samples were taken daily to represent the whole mesocosms from 0 to 6 m depth between 07:00 and 08:00 h. The sample was taken with a 2 m long Ramberg tube sampler (Ramberg 1976) covered with black plastic to protect the plankton from light exposure, transferred to 25 l low-transparency bottles, and used for sub-sampling. Samples for determination of ciliate biomass and the size spectrum of plankton were fixed with acid Lugol's solution (1% final conc.) and stored in the dark. The particulate matter >200 µm from 11 l was collected quantitatively and analysed for particulate phosphorus. Samples for determination of mesozooplankton species composition (0 to 6 m) were collected with a Ramberg sampler on Days 1, 5 and 10. From each mesocosm a 21 l sample was concentrated in a 35 µm net, transferred to a 250 ml plastic vial, and fixed with acid Lugol's iodine to a final concentration of 1%.

Chemical analysis. Samples for analysis of chlorophyll *a* were collected on Whatman GF/F glass-fibre filters, extracted in methanol, and quantified by fluorometry using a Turner Designs fluorometer (Strickland & Parsons 1972). Before filtration, the water was screened through a 200 µm screen to remove larger organisms; 2 replicates were analysed per sample. For 6 of the mesocosms (normal and high nutrient addition) chlorophyll *a* was analysed also for the size fractions <20 and <2 µm. Fractionation was done sequentially by means of a 20 µm plankton net and a 2 µm polycarbonate filter. Determinations of dissolved inorganic nutrients were done on samples filtered through preignited and acid-washed Whatman GF/F filters. Nitrate, ammonia, silicate, phosphate and particulate phospho-

rus in the >200 µm fraction were analysed according to Grasshoff et al. (1983).

Determination of biomass. Samples for determination of ciliate biomass were settled in 10 or 50 ml Utermöhl chambers and counted in an inverted microscope. Cells were counted and sized at appropriate magnification, and cell volumes were calculated using simple geometrical formulas. Normally >200 cells (never <100) were counted per sample, which should give a coefficient of variation of <7%. Ciliate volumes were converted to units of carbon by a factor of 0.19 pg C μm^{-3} (Putt & Stoecker 1989). The size spectrum of the plankton was determined with a Casy 1 TTC particle counter (Schäerfe Systems). Mesozooplankton samples were identified and counted with a Leitz MZ3 dissecting microscope. The initial experimental mesozooplankton biomass was calculated from average particulate phosphorus >200 µm during the first 7 d of the experiment using a conversion factor of 27 ± 1.6 µg P [mg C]$^{-1}$ (±SE; our unpubl. data based on 20 independent measurements of mesozooplankton P:C ratio in Hopavågen using microscopic counting and P analysis). There is no significant response in mesozooplankton biomass on this timescale, and the average of 7 determinations with this method gives higher precision in biomass estimation than 2 estimates based on counts of 21 l fixed samples. Standard errors of means were 8 to 17 and 5 to 46% for the P-based and count-based methods, respectively. For regression analysis, algal biomass was calculated from chlorophyll *a* using a conversion factor of 64 µg C [µg chl *a*]$^{-1}$ (our unpubl. data from a mesocosm experiment in 1997).

Statistical analysis. Multiple regression was used to quantify the effect of the 2 experimental variables (nutrient dose and initial mesozooplankton biomass) on the main dependent variables, i.e. ciliate biomass, and algal biomass in total or in the size fractions <20 and >20 µm. Copepod biomass (copepod P) and nutrient additions (added P) were included in the model in phosphorus units (µg P l^{-1} and µg P l^{-1} d^{-1}, respectively). The regressions were done in carbon biomass for the dependent variables. Average values of the dependent variables for the period Days 6 to 9 was used in the regressions, as in most mesocosms the biomass of both algae and ciliates levelled off during this period. To compensate for variable variance, the averages were weighted with the inverse of the standard deviation (weighted least-squares; Box et al. 1978). A model of Type $R = a + bZ + cN + dZN$ was used, where R is response parameter, Z is copepod biomass, N is nutrient addition regime and a, b, c and d are coefficients. Inclusion of terms in the regression model was based on the appearance of relationships (intercepts and differences in slopes; cf. Figs. 3 & 4), and confirmed by stepwise regression using both forward and backward selection. All statistical analysis was done using SYSTAT Version 10.

RESULTS

The initial mesozooplankton gradients in the experiment estimated from particulate P >200 µm spanned a total range of 14 to 60 µg C l^{-1} (cf. *x*-axis and data points in Figs. 2 & 3). The calanoid copepod community consisted of *Temora longicornis*, *Centropages* sp., *Pseudocalanus elongatus* and *Acartia longiremis*. More than two-thirds of the biomass was comprised of copepods of the genera *Temora* and *Pseudocalanus*, which were fairly equal in biomass. In mesocosms with ambient mesozooplankton biomass, the densities of calanoid copepods averaged 16 individuals (ind.) l^{-1}. In addition, the cyclopoid copepod *Oithona similis* was present in all mesocosms. Its density was approximately the same in all treatments and was always below 5 ind. l^{-1}. Non-crustacean zooplankton consisted mainly of bivalve veliger larvae and polychaetes (*Tomopteris* sp.). They never exceeded 4 ind. l^{-1} and did not show major changes in abundance or composition during the experiment.

Dissolved inorganic nutrients remained fairly stable and low in the mesocoms receiving no nutrient addition, with averages for the period Days 7 to 10 of 1 ± 0.4, 8 ± 3 and 25 ± 16 µg P, N and Si l^{-1}, respectively (data not shown). Some accumulation of dissolved inorganic nutrients occurred in the mesocosms that received the highest nutrient dose: towards the end of the experiment the concentrations were typically a factor of 5 above the concentrations in the mesocosms receiving no nutrients. In mesocosms receiving the low dose of nutrients the silicate concentrations were a factor of 3 above the concentration in mesocosms receiving no nutrients, whereas for inorganic nitrogen only a slight increase (~50%) was observed. For inorganic phosphorus no differences were observed, and the concentrations in mesocosms with no or low nutrient addition were in fact close to the detection limit. Phosphorus was therefore most probably the primary limiting nutrient. The addition of nutrients entailed an increase in total phosphorus (dissolved + particulate) by an average of 18 and 76% in systems with low and high nutrient addition, respectively. As a consequence the carrying capacity of the systems increased with increasing nutrient addition.

The time course of ciliate biomass, chlorophyll *a* and the fraction of chlorophyll *a* <20 µm for the various mesocosms is shown in Fig. 1. The addition of nutrients indirectly caused an increase in the biomass of ciliates due to increased primary productivity (primary production data not shown). This response was evident after 2

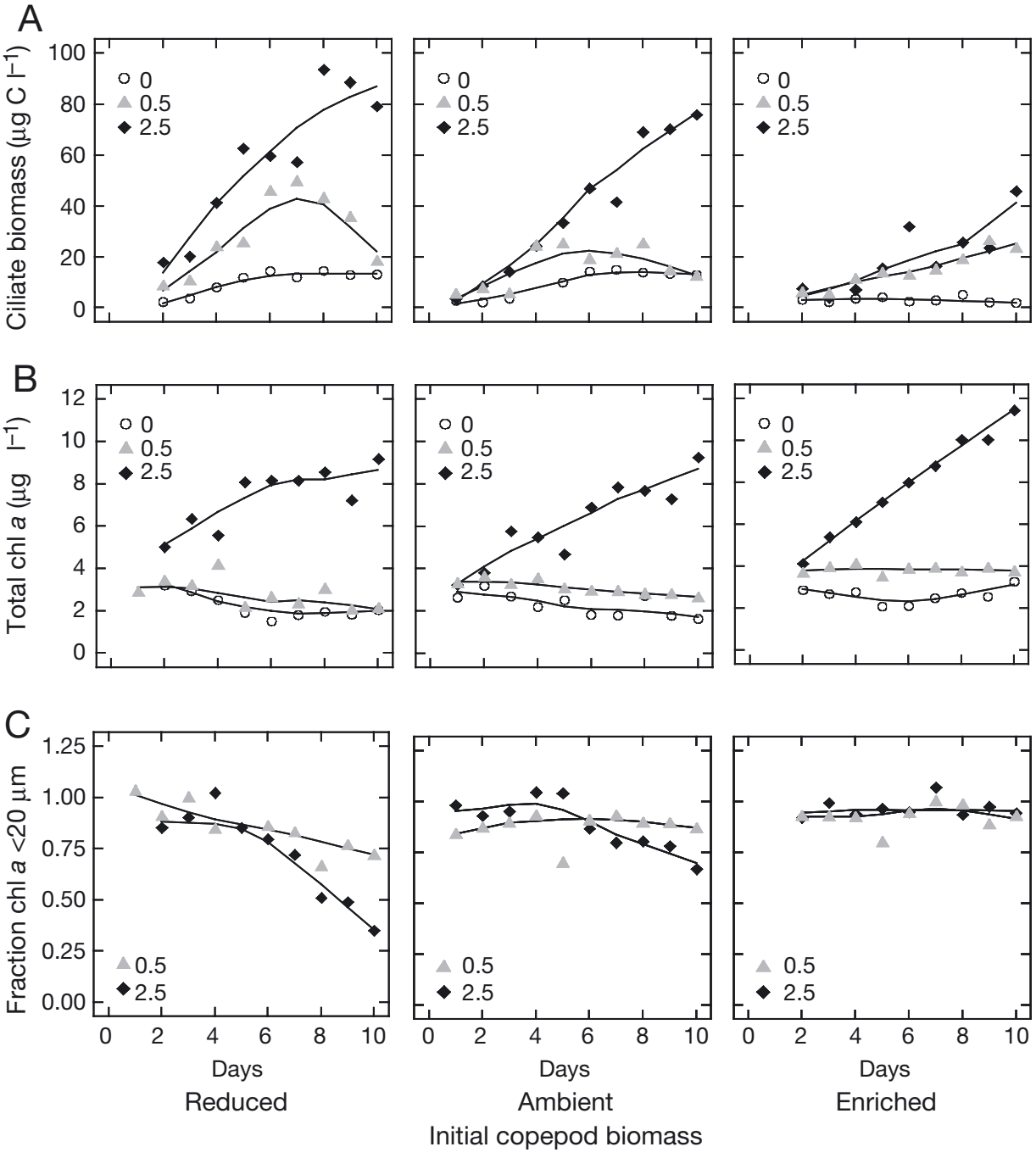

Fig. 1. Time course in mesocosms of ciliate biomass, total chlorophyll *a* and fraction of chlorophyll *a* <20 µm. Different nutrient addition regimes are indicated µg P l^{-1} d^{-1} by different symbols. Curves drawn using LOWESS smoother

to 3 d, but the ciliate biomass peaked after 1 wk in many cases. The biomass of copepods affected the ciliates negatively. This was demonstrated further by plotting ciliate biomass versus initial copepod biomass day by day (Fig. 2). Already from Day 2 a clear negative impact of copepod biomass on ciliate biomass was observed. The strength of this negative correlation reached its maximum on Day 7 (Fig. 2). The opposite effect of the 2 experimental variables is revealed by data for Days 6 to 9 (Fig. 3). The rate of nutrient addition had a positive effect on the ciliate biomass and there was an interaction effect for the 2 experimental variables. This is evident from the increase in ciliate biomass and the steeper slopes in Fig. 3 with increased nutrient input. Most of the scatter in data in Fig. 2, can be explained by nutrient addition (Fig. 3). If for each nutrient addition

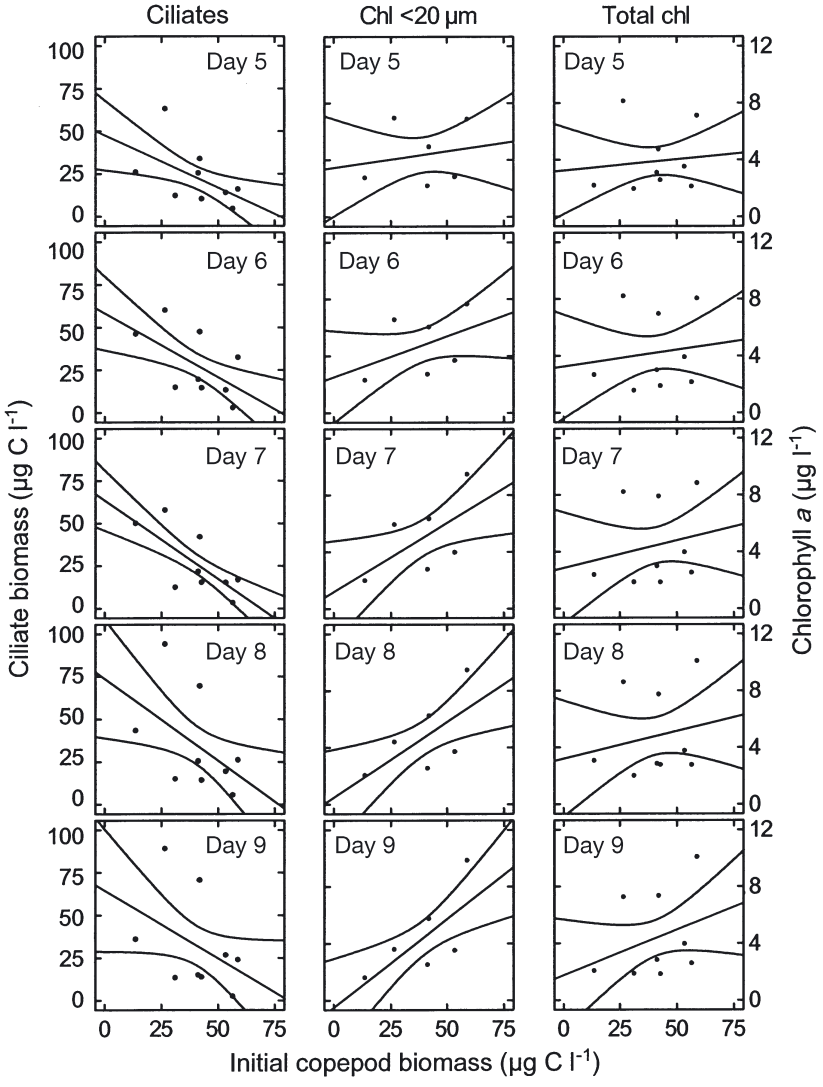

Fig. 2. Development of ciliate biomass and chlorophyll *a* concentration as a function of initial mesozooplankton (copepod) biomass from Days 5 to 9. Chlorophyll *a* concentrations given for total chl *a* and for particles passing 20 µm net. Lines are linear regressions showing means and 0.50 confidence intervals

regime, ciliate biomass is normalized to the ciliate biomass in the mesocosm with ambient copepod biomass, the data from all 9 mesocosms can be adequately described by 1 line (R^2 of 0.82 to 0.88, N = 9 for Days 7 to 9). High copepod biomass resulted in a significant ~50% decrease in the average size of the ciliates, with averages (±95 CI, N = 9) during Days 6 to 9 of 3.1 ± 1.0 × 10^3 µm^3 and 5.2 ± 1.0 × 10^3 µm^3 for mesocosms with high and low initial copepod biomass, respectively. Also, reduced food availability caused by zero addition of nutrients caused a significant one-third reduction in average size of ciliates. Average volumes (±95 CI, N = 9) during Days 6 to 9 were 3.1 ± 0.7 × 10^3 µm^3 and 4.7 ± 1.1 × 10^3 µm^3 for mesocosms with zero and high nutrient additions, respectively.

Chlorophyll *a* concentrations showed limited change with time in mesocosms with no or a low amount of added nutrients (Fig. 1B). In mesocosms receiving the high dose of nutrients, the chlorophyll level increased more or less linearly to a level that was a factor of 3 to 4 above the initial level. Whereas most of the chlorophyll passed a 20 µm net at the beginning of the experiment and in mesocosms enriched with copepods, large algae became more important with reduced copepod biomass (Fig. 1C). This effect was strongest for the high nutrient addition, where chlorophyll *a* <20 µm amounted to less than one-third of the total. As hypothesised, algal biomass (measured as chlorophyll *a*) increased with increasing copepod biomass (Fig. 2). (The average initial algal biomass was 3 µg chl *a* l^{-1}.) This was observed from Day 4, but with the strongest effects towards the end of the experiment. However, the impact of initial zooplankton biomass on chlorophyll *a* was weak and with considerable scatter in the data. Again the second experimental variable (rate of nutrient addition) explained most of the scatter observed for total chlorophyll in Fig. 2. A significant accumulation of algae with time was found only in the mesocosms with a high input of nutrients. These general trends are exemplified by data for Days 6 to 9 in Fig. 4. With the experimental conditions used in the present study, the nutrient input had a stronger impact on total chlorophyll than the copepod biomass. For the total biomass of algae the effect of nutrient addition and copepod biomass was additive (no interaction effect), as indicated by the equal slopes for each nutrient addition regime (Fig. 4A). However, the impact of copepod biomass on algal biomass was much stronger when the larger algae (not easily available to the ciliates) were excluded (Figs. 2 & 4B). Moreover, the scatter in Fig. 2 is much less for chlorophyll <20 µm than for total chlorophyll. The positive effect of both experimental variables on chlorophyll <20 µm is evident when Days 6 to 9 are considered (Fig. 4B), and with a multiplicative (positive interaction) effect for the 2 experimental variables. The difference in the effects on total algae versus algae <20 µm was most evident for the mesocosms with the highest nutrient addition. In these mesocosms, the slope of the chlorophyll *a* line

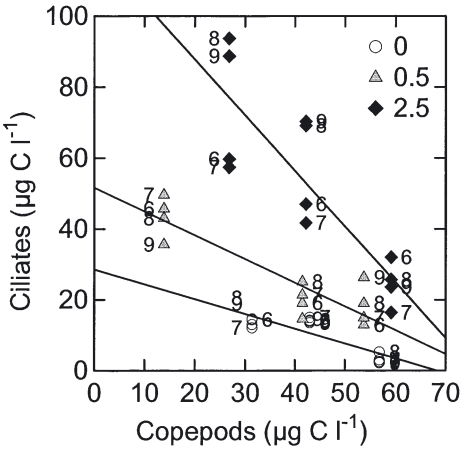

Fig. 3. Ciliate biomass in mesocosms as a function of initial mesozooplankton (copepod) biomass on Days 6 to 9 (number next to each data point = sampling day). Nutrient addition regimes (µg P l^{-1} d^{-1}) represented by different symbols. Regression lines are drawn for each nutrient addition regime separately and based on all observations

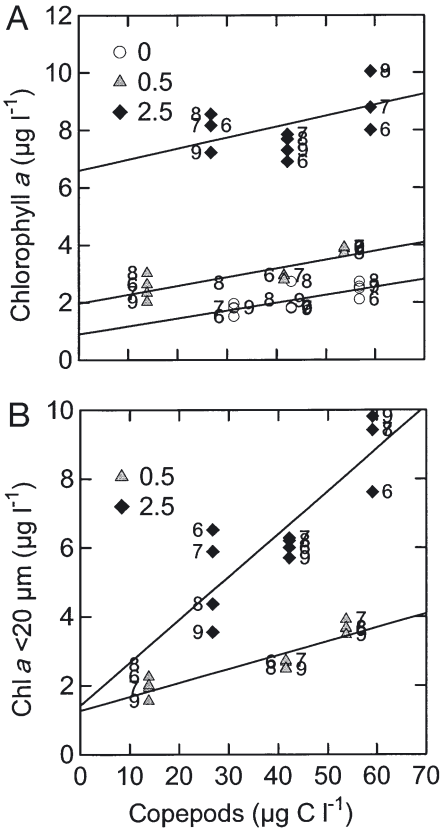

Fig. 4. Concentration of (A) chlorophyll *a* and (B) chlorophyll *a* <20 µm in the mesocosms as a function of initial mesozooplankton (copepod) biomass on Days 6 to 9. Further details as in Fig. 3

was 3 times higher for the <20 µm fraction than for total chlorophyll, and the intercept of the regression line with the chlorophyll axis was 1.4 for the <20 µm fraction compared to 6.5 µg l^{-1} for total chlorophyll (Fig. 4).

The impact of low copepod and high ciliate biomass on the accumulation of larger algae is further illustrated for the mesocosms with high nutrient addition (Fig. 5). Algae >20 µm were almost absent in the mesocosm with high copepod biomass and hence low ciliate biomass. At the lowest copepod biomass and hence highest ciliate biomass, the 2 size fractions were comparable. Chlorophyll *a* retained on a 20 µm filter constituted generally 30 to 60% of the total when ciliate biomass was >45 µg C l^{-1}, compared to 5 to 10% at the start and when ciliate biomass was below this limit (Fig. 1). The particle size distribution of the plankton (Fig. 6) demonstrated a considerably higher biomass of plankton for all size classes <10 µm equivalent spherical diameter (ESD) in the mesocosm with high than in that with low copepod biomass. The mesocosm with high ciliate biomass, however, had more plankton in the size classes >10 µm ESD, but this difference was not pronounced. The differences in size spectrum were further illustrated by calculating the difference in the 2 size spectrums (Fig. 6B). The peak found at an ESD of ~18 µm corresponds to the dominant size class of ciliates.

DISCUSSION

The initial mesozooplankton biomass in the mesocosms (range 14 to 60 µg C l^{-1}) was within the normal range observed in Hopavågen during summer. Mesozooplankton biomass based on weekly samplings during summer (June to September) for the period 1996–2000 was normally in the range of 10 to 115 µg C l^{-1}, with yearly summer averages of 30 to 70 µg C l^{-1} (I. Gismervik et al. unpubl. data). Moreover, our data are consistent from day-to-day and within the 3^2-matrix. We therefore claim that our observations should be relevant for natural pelagic communities also. The responses are, however, dependent on the initial conditions of the plankton community (Stibor et al. 2004, this issue).

We have quantified the impact of our 2 experimental variables on the main response parameters by regression analysis. To make the experimental variables more comparable, both were included in terms of phosphorus units in the regressions. The regression models adequately describe the biomass of both ciliates and algae (Table 1). The coefficients for the ciliate regression model indicate that nutrient addition had a positive impact on ciliate biomass, whereas the impact of copepods was negative. However, the negative interaction effect means that the impact of nutrient addition diminishes with increasing copepod biomass. Thus ciliate biomass was determined by co-occurring

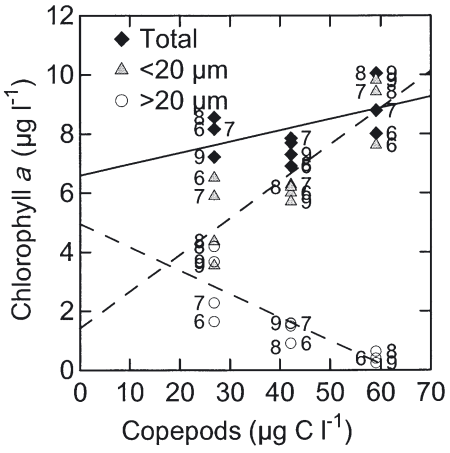

Fig. 5. Concentration of chlorophyll *a* in 2 size fractions in mesocosms with high nutrient addition as a function of initial mesozooplankton (copepod) biomass on Days 6 to 9 (number next to each data point = sampling day). Regression lines are drawn for each size fraction separately

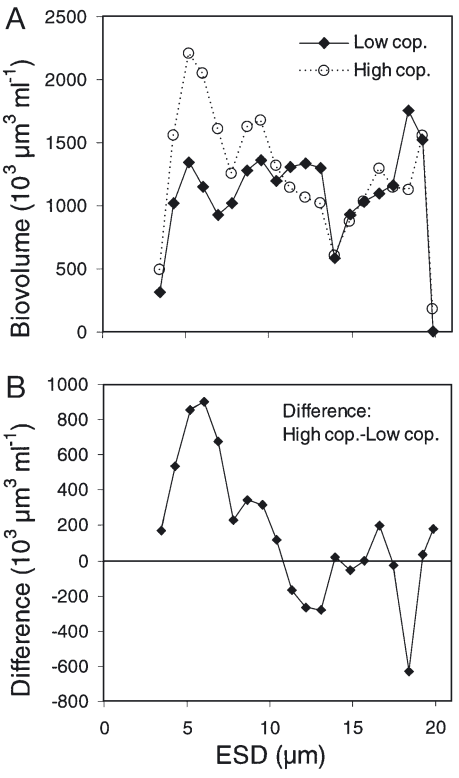

Fig. 6. Size-frequency spectrum of plankton biomass in mesocosms with high nutrient addition. Data are averages for Days 8 and 9. Particles sorted according to equivalent spherical diameter (ESD). (A) Size spectrum in mesocosms with high and low copepod biomass; (B) difference between size spectrum in mesocosms with high and low copepod biomass (positive values indicate more biomass of that size fraction in mesocosm with high copepod biomass)

bottom-up and top-down regulation, but the top-down regulation was the predominant process at the highest copepod biomasses used in the experiment. On a timescale sufficient to give a numerical response for the top predator (longer than this 10 d experiment) top-down regulation could be even stronger (Hairston et al. 1960).

It is an unresolved question in both marine and limnetic systems to what extent food limitation (bottom-up) and/or predation (top-down) regulates the biomass of ciliates, and also how these 2 factors interact. There are a few reports on the stimulation of ciliate biomass as an indirect result of nutrient addition, but some studies have concluded that the biomass of ciliates is normally controlled by predation (see Nielsen & Kiørboe 1994, Kivi et al. 1996). Our experiment clearly demonstrates that this is not an either/or situation, as both factors affected the biomass of ciliates simultaneously (Fig. 3 , Table 1). Moreover, the relative strength of bottom-up versus top-down control is highly dynamic. Kivi et al. (1996) and Levinsen & Nielsen (2002) made similar observations. The negative interaction effect in the ciliate regression model indicates that the copepods affect ciliate abundance not only via direct grazing. An explanation for this is that copepods and ciliates have overlapping food-size spectra, and at higher copepod densities an increasing fraction of this

Table 1. Results of multiple linear regressions with ciliate and algal biomass as dependent (response) variables. Model of Type $R = a + b\,Z + c\,N + d\,Z\,N$ was used, where R is response parameter, Z is copepod biomass, N is nutrient addition regime and a, b, c and d are coefficients. All regression coefficients are given with ± SE. Copepod biomass (Copepod P) and nutrient additions (Added P) are included in regression model in phosphorus units (µg P l^{-1} and µg P l^{-1} d^{-1}, respectively). Averages of data for Days 6 to 9 were used in all regressions. N = 9 for ciliates and total algae; N = 6 for algal size fractions. All coefficients are significantly different from zero ($p < 0.005$), except constant for the algal regression ($p = 0.3$). For all regressions $p < 0.0002$. ni: term not included

Variable	Constant	Copepod P	Added P	Cross term	R^2	*F*-ratio
Ciliates	30.4 ± 6.0	−16.0 ± 5.1	38.0 ± 8.1	−18.6 ± 6.1	$R^2 = 0.943$	$F_{3,5} = 27.5$
Algae[a]	35.6 ± 31.3	81.9 ± 25.8	154.0 ± 10.7	ni	$R^2 = 0.972$	$F_{2,6} = 105.5$
Algae <20 µm[ab]	122.2 ± 14.3	ni	ni	102.5 ± 12.3	$R^2 = 0.945$	$F_{1,4} = 69.2$
Algae >20 µm[ab]	ni	ni	119.7 ± 9.7	−72.7 ± 7.9	$R^2 = 0.986$	$F_{2,4} = 140.5$

[a]Calculated from chlorophyll *a* assuming 64 µg C (µg chlorophyll *a*)$^{-1}$
[b]Does not include mesocosms without addition of nutrient, due to lacking data

shared food is consumed by copepods. Empirical data on the size selectivity of ciliates and copepods supports this reasoning (Hansen et al. 1994).

Both nutrient addition and copepod density had a significant positive effect on total algal biomass (Table 1). However, the nutrient addition rates applied created larger variation in algal biomass than the density of copepods used. It must be remembered that these results are relevant only for a timescale on which the copepods are not able to increase significantly in biomass. It is difficult to give the regression model an ecological interpretation, as the copepods have a dual, size-dependent impact on algae. This is shown by the great difference in the regression models for the 2 size fractions of algae (Table 1). For algae <20 µm, a positive multiplicative dependence on the 2 experimental variables was found. Thus the biomass of these smaller algae is dependent on both experimental variables. A possible reason for this is that grazing on these smaller algae is relieved due to high grazing by copepods on ciliates. For algae >20 µm the interaction effect is negative and larger by a factor of 5 than the negative interaction effect for the ciliates. Moreover, nutrient addition had a strong positive impact. Thus the regression model for algae >20 µm is qualitatively similar to the ciliate regression model, except that the constant and the copepod term are not required. As a result, the biomass of algae >20 µm is predicted to be zero without nutrient addition. This prediction may be an artefact due to lack of fractionated chlorophyll data from the mesocosms without nutrient addition. However, in the initial situation chlorophyll *a* >20 µm was <0.2 µg l^{-1} in the mesocosms, which corresponds to <13 µg C l^{-1}.

The classical grazing chain (sensu Steele 1974) predicts a negative relationship between copepod and algal biomass, and most numeric ecosystem models have until recently been based on such an understanding. Our experiment revealed a positive correlation between algae and copepods, in particular for algae <10 to 20 µm (Figs. 1, 4, 5 & 6). To our knowledge no comparable studies have been published. However, some studies support our observations and conclusions. In the MERL (Marine Ecosystems Research Laboratory) eutrophication experiment, high numbers of ciliates coincided with an increase in diatoms and a decline in <10 µm flagellates and monads (Oviatt et al. 1989). Results from 1 d incubation experiments suggested that copepod predation on ciliates may promote blooms of single-celled *Phaeocystis* spp. (Hansen et al. 1993). Kivi et al. (1996) made observations similar to those in the present study in a 2^2 factorial experiment with ± nutrient addition and ± mesozooplankton at concentrations 100-fold above natural concentrations. The responses in their experiment on algal biomass and size distribution were, however, not as dramatic as those reported here.

To our knowledge, no one has demonstrated the stimulatory effect that natural densities of copepods can have on algal biomass as a consequence of an easing of grazing pressure. Thus, in marine ecosystems the role of carnivory by copepods, and the resulting trophic cascade through ciliates and heterotrophic dinoflagellates to algae, is as important in shaping algal communities as herbivory by copepods. In addition to the studies cited above (Oviatt et al. 1989, Hansen et al. 1993, Kivi et al. 1996, Levinsen & Nielsen 2002), some recent reports indirectly support our findings (Stoecker & Capuzzo 1990, Gismervik & Andersen 1997, Burns & Schallenberg 2001), but limited attention has been given to trophic cascades in marine ecosystems (Verity & Smetacek 1996). The presence of an omnivory link in the marine copepod–ciliate–algae food-web system not only determines how tight the grazing control of algae is and, hence, the possibility of bloom formation by nanoalgae (2 to 20 µm), but will also affect the structure and diversity of the algal community because of differences in the preysize that can be exploited by copepods and ciliates. However, later work shows that the quality and the strength of the trophic cascade and its significance for algal community structure is dependent on the initial algal community structure (Stibor et al. 2004). We conclude that top–down effects and trophic cascades in marine systems can be as important as in limnetic systems, but due to more complex food webs they are more difficult to detect.

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