Vol. 29: 105–115, 1986 | MARINE ECOLOGY – PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published February 27

Grazing of phototrophic nanoplankton by microzooplankton in Narragansett Bay

Peter G. Verity

Graduate School of Oceanography, University of Rhode Island, Kingston, Rhode Island 02882, USA

ABSTRACT: Daily photosynthetic nanoplankton (< 10 μm and < 5 μm) growth rates and microzooplankton (10 to 202 μm) grazing rates were measured at weekly intervals for 1 yr using size-fractionated natural populations incubated *in situ* in lower Narragansett Bay. Changes in < 10 μm and < 5 μm chlorophyll *a* in the presence and absence of 10 to 202 μm microzooplankton were used to calculate growth and grazing rates. NH_4, NO_3, PO_4, and $Si(OH)_4$ concentrations measured within the dialysis bags before and after *in situ* incubations indicated that nutrient availability was adequate to meet uptake requirements during these short experiments. Chl *a* growth rates ranged from 0 to 2.2 doublings d^{-1} (< 10 μm) and 0 to 2.1 doublings d^{-1} (< 5 μm), and increased with temperature. Microzooplankton grazing rates ranged from 0 to 2.2 μg chl *a* l^{-1} d^{-1} (< 10 μm) and 0 to 2.1 μg chl *a* l^{-1} d^{-1} (< 5 μm). Grazing was linearly related to chl *a* standing stock and production in each size fraction. Annual mean microzooplankton grazing represented 62 % of < 10 μm and < 5 μm chl *a* production. Grazing impact was elevated when low temperatures limited nanoplankton production, suggesting that microzooplankton grazing contributed to seasonal variations in relative importance of different size fractions of phytoplankton in Narragansett Bay.

INTRODUCTION

Evaluating rates of *in situ* production by phytoplankton populations and transfer to higher trophic levels has long been a problem in plankton ecology. Methods of measuring productivity of natural phytoplankton communities include incorporation of radioactive labels (Steemann Nielsen 1952, Redalje 1983) and stable isotopes (Hama et al. 1983); measurement of changes in dissolved gases (Williams et al. 1983); calculation of water column net oxygen utilization rates (Jenkins 1982); and measurement of rates of synthesis of community biomass tracers such as ATP (Sheldon & Sutcliffe 1978) and RNA (Karl et al. 1981). All of the methods which involve manipulating samples must minimize or avoid 'bottle effects' or containment problems which yield artificial results (Venrick et al. 1977, Eppley 1980). *In situ* incubation of natural phytoplankton populations in cage cultures after screening out grazers permits direct measurement of growth rates with a minimum of artifacts (Sakshaug & Jensen 1978, Furnas 1982).

Methods of estimating the grazing impact of natural zooplankton populations include extrapolation from production rates and energy requirements (Durbin & Durbin 1981); extrapolation from laboratory- or field-determined grazing rates of abundant species to population estimates (Heinbokel & Beers 1979); and large-volume containment studies (Thompson et al. 1982). Small-volume incubations with macrozooplankton are generally not feasible due to low abundances, unless they are artificially concentrated (Roman & Rublee 1981). However, microzooplankton have high specific feeding rates (Heinbokel 1978, Verity 1985) and are sufficiently numerous that small-volume incubations of natural populations are feasible. A major problem is that confinement in bottles results in the demise of ciliate populations (Venrick et al. 1977). Dialysis bags, on the other hand, have been used successfully to measure grazing and growth rates of natural microzooplankton communities (Landry & Hassett 1982, Verity 1986).

Phytoplankton passing a 10 μm mesh contributed 36 % of annual chl *a* standing stock in lower Narragansett Bay (Verity 1984), where microzooplankton are abundant year-round (Hargraves 1981, Verity 1984). Their small size, rapid metabolic rates, and preference for food particles that are inefficiently filtered by larger

0171-8630/86/0029/0105/$ 05.00

zooplankton (Nival & Nival 1976) suggest that microzooplankton provide an important link in the transfer of photosynthetic nanoplankton production to higher trophic levels (Porter et al. 1979). In the present study, *in situ* incubations of <10 µm nanoplankton in the presence and absence of 10 to 202 µm microzooplankton were conducted at weekly intervals for 1 yr to assess the grazing impact of microzooplankton on phototrophic nanoplankton populations in Narragansett Bay.

METHODS

Experiments were conducted at weekly intervals (n = 52) between March 1982 and March 1983 at a station located in lower Narragansett Bay, Rhode Island (41° 30′ N, 72° 23′ W) in 7 m of water. On the morning of an experiment, 4 lengths of large-diameter dialysis tubing (90 mm inflated diameter, MW cutoff 12,000) were autoclaved and rinsed in distilled water to remove glycerin. Each length of tubing was tied off at one end and transported to the experimental site, where a surface sample was collected using a 20 l plastic bucket with a 202 µm mesh across the mouth. Three of the 4 dialysis tubes were filled with <202 µm plankton by slowly raising them through the bucket. The <10 µm community was prepared by filling an acid-cleaned glass beaker with the <202 µm fraction and allowing a plexiglass cylinder with 10 µm Nitex mesh on one end to sink by gravity. The <10 µm community inside the cylinder was siphoned into the fourth dialysis tube. The entire process took ca 20 min, and the 4 bags were moored at 1 m for 24 h. Experiments were generally initiated between 1000 and 1200 h, as diel experiments indicated no significant differences in microzooplankton growth rates. Dialysis bags were used because preliminary experiments indicated persistent declines in ciliate populations incubated in Pyrex containers. Plexiglass cages with polycarbonate membranes were difficult to manipulate and quantitatively sample, due to changes in volume when the cages were withdrawn from water.

A portion of the <202 µm sample was returned to the laboratory for determination of initial chlorophyll *a* (chl *a*) and nutrient concentrations and microzooplankton abundance. Chl *a* was measured in triplicate in the <153 µm, <10 µm, and <5 µm fractions by filtration onto Gelman A/E 0.45 µm glass fiber filters. Comparison of Narragansett Bay plankton communities collected on Gelman A/E and Whatman GF/F filters revealed no significant differences in chl *a* over an annual cycle (Smayda unpubl.). One l of the <202 µm community was preserved with seawater-buffered formalin and concentrated by settling to a final volume of 5 to 10 ml for determination of microzooplankton abundance. Another portion of the <202 µm fraction was filtered and frozen for subsequent determination of NH_4, NO_3, PO_4, and $Si(OH)_4$ concentrations. Comparison of NH_4 concentration in fresh (phenol-hypochlorite method) and frozen (automated analysis) samples, ranging from undetectable to 36 µM, showed a mean loss of only 7 % (n = 149) in frozen samples (Verity & Smayda unpubl.).

Chl *a* and microzooplankton abundance were measured after 24 h in each of the 3 dialysis bags containing <202 µm plankton, and chl *a* in the bag containing <10 µm plankton. Chl *a* in the <10 µm and <5 µm fractions was determined after gently passing aliquots from the <202 µm and <10 µm bags through 10 µm and 5 µm meshes and filtering them in triplicate on glass fiber filters. Microzooplankton from the 3 dialysis bags containing <202 µm plankton were preserved and concentrated as previously described. Aliquots from each of the 4 bags were also filtered and frozen for subsequent measurement of nutrient concentrations.

Chl *a* was extracted by grinding in 90 % acetone and measured fluorometrically before and after acidification using the method of Holm-Hansen et al. (1965). NH_4, NO_3, PO_4, and $Si(OH)_4$ concentrations were determined on a Technicon Autoanalyzer II using automated methods (Grasshoff 1966, Pavlou 1972). Ciliate and metazoan microzooplankton were enumerated in a Sedgwick-Rafter chamber, with a minimum of 3 replicate 1 ml counts from the 5 to 10 ml concentrates. Heterotrophic dinoflagellates and microflagellates were not enumerated.

Chl *a* production and grazing by microzooplankton was calculated using the equations of Frost (1972), and treating the <10 µm plankton community as a control lacking grazers of autotrophic cells. Calculations of mean grazing and growth rates were made for both <10 µm and <5 µm chl *a* in each experiment. The chl *a* growth rates represent net increases in the presence of heterotrophs passing a 10 µm mesh; grazing rates represent ingestion by 10 to 202 µm microzooplankton. Growth rates of autotrophic nanoplankton in bags with and without 10 to 202 µm microzooplankton are assumed to be identical (see 'Discussion').

Incident irradiance was measured at the Eppley Laboratories in Newport, located 7 km from the experimental site. Light extinction was determined using a Secchi disk, and the extinction coefficient (k) was calculated as $k = 1.44/z$, where z (m) was the depth of disappearance of the Secchi disk (Holmes 1970). Light measurements inside the bags using a Biospherical Instruments QSL-100 quantum sensor indicated that autoclaved dialysis membranes transmitted 85 % of surface incident irradiance.

Correlations between rate and biomass measurements were analyzed using functional regressions as

both variables were subject to measurement error (Ricker 1973, Laws & Archie 1981). All statistical tests were performed according to Snedecor & Cochran (1967). Significance levels were $p < 0.05$ unless otherwise noted.

RESULTS

Tintinnids were the most abundant ciliate microzooplankton in the dialysis bags (Table 1). Their annual minimum (90 l^{-1}) coincided with *Olisthodiscus luteus*

Table 1. Initial abundance of microzooplankton (no. l^{-1}) in the dialysis chambers containing <202 μm plankton

Date	Tintinnids	Other Protozoa	Mesodinium	Nauplii	Copepodites	Rotifers
8 Mar 1982	3186	120		63		27
15 Mar	1620	33		10		3
23 Mar	573	60		60		3
26 Mar	200	217		47		7
14 Apr	164	70		40		
27 Apr	220	177		40		
4 May	330	850	530	100		
12 May	1332	1000	573	93		17
17 May	2826	433	287	23		20
25 May	2706	220	233	23	7	
2 Jun	4863	1073	590	127	10	
10 Jun	7660	2753	2340	57	3	
18 Jun	694	1477	3503	33	3	3
21 Jun	2111	117	417	30		
28 Jun	176	396		44	8	
6 Jul	123	370		27	10	
12 Jul	90	1440		90	7	
21 Jul	550	430		53		
1 Aug	8181	1360	670	40	3	3
4 Aug	4407	1647	1057	183		
11 Aug	1286	1254	243	93		
18 Aug	1144	1310	450	67		
27 Aug	2624	1707	7100	50		
1 Sep	2500	1257	2537	40		
5 Sep	4828	2097	2530	17	3	
15 Sep	2711	2803	70	43	3	7
23 Sep	1899	150	27	60	3	43
2 Oct	958	83	130	80	3	7
15 Oct	249	63	73	23	7	
19 Oct	784	107	23	47	3	
28 Oct	670	247	50	27	3	
1 Nov	1770	10		20	3	
8 Nov	1131	30		17	3	
15 Nov	803	20		20	3	
22 Nov	476	420	1050	53	10	6
30 Nov	2040	120	713	73	10	
7 Dec	1270	143		60	10	
14 Dec	222	137		50	7	
20 Dec	626	450		77	7	
27 Dec	491	113		93	7	
1 Jan 1983	346	26				
9 Jan	427	117		40		
17 Jan	247	83		20		
25 Jan	634	127		83		
30 Jan	767	50		57		
14 Feb	429	10		40		
22 Feb	306	5		100		6
27 Feb	263	33		90	7	3
8 Mar	2280	140		90	3	7
20 Mar	400	23		83		7
24 Mar	618	163		133		3
29 Mar	714	8		10	4	

blooms in late June and early July; maximum tintinnid abundances were found immediately before (7.6×10^3 l^{-1}) and after (8.2×10^3 l^{-1}) these blooms. With the exception of dates with high *O. luteus* concentrations, tintinnids consistently exceeded 10^3 l^{-1} from May through September; the annual mean abundance was 1.5×10^3 l^{-1} (SD = 1.8×10^3, n = 52). Nine genera representing 26 species were found ; *Tintinnopsis* was the most important genus in terms of both abundance and species number (Verity 1984). Protozoa other than tintinnids, predominantly holotrich and 'sheathed' (e.g. *Laboea*) and 'nonsheathed' (e.g. *Lohmanniella*) oligotrich ciliates, were numerically second in importance with an annual mean of 530 l^{-1} (SD = 720, n = 52). Their seasonal abundance cycle was similar to that of tintinnids, with highest numbers occurring in May, early June, August, and September, and lowest abundances during mid-summer and winter. The photosynthetic gymnostome ciliate, *Mesodinium rubrum,* bloomed during May-June and August-September when temperatures ranges from 10 to 23 °C. Maximum abundance was 7.1×10^3 l^{-1}, and the annual mean was 485 l^{-1} (SD = 1.2×10^3, n = 52). Copepod nauplii, predominantly the genus *Acartia,* were present year-round, with an annual average of 52 l^{-1} (SD = 35, n = 52). Highest abundances occurred in June, August, and February-March; minima were observed in November and January. Rotifers and copepodite stages of copepods each averaged 3 l^{-1} on an annual basis. Rotifers were generally present during the winter and spring; copepodites occurred during summer and fall. Benthic invertebrate larvae rarely passed the 202 µm mesh and were seldom observed in the dialysis bags.

The experiments were initiated at the termination of the winter-spring diatom bloom in March 1982, and chl *a* in the <153 µm, <10 µm, and <5 µm size fractions was low until late-May (Fig. 1). *Olisthodiscus luteus* and several uncharacterized microflagellates were abundant throughout June and July; the majority of these cells passed a 10 µm mesh. The annual peak in nanoplankton standing stock occurred on August 1, when chl *a* was 8.9 and 6.2 µg l^{-1} in the <10 µm and <5 µm fractions, respectively. Chain-forming diatoms were abundant during September and peaked in early October with <153µm chl *a* of 14.2 µg l^{-1}. An extensive bloom of small *Thalassiosira* species, primarily *T. constricta,* was present during November and December; most of these cells passed 10 µm mesh but were retained on 5 µm netting. Chl *a* levels were low during the remainder of the winter, with the exception of short blooms of *T. constricta* in January and several uncharacterized microflagellates in mid-March. The annual mean chl *a* concentration in the <153 µm fraction was 3.7 µg l^{-1} (range: 0.5 to 14.2); chl *a* passing 10 µm and 5 µm meshes averaged 50 and 24 %, respectively.

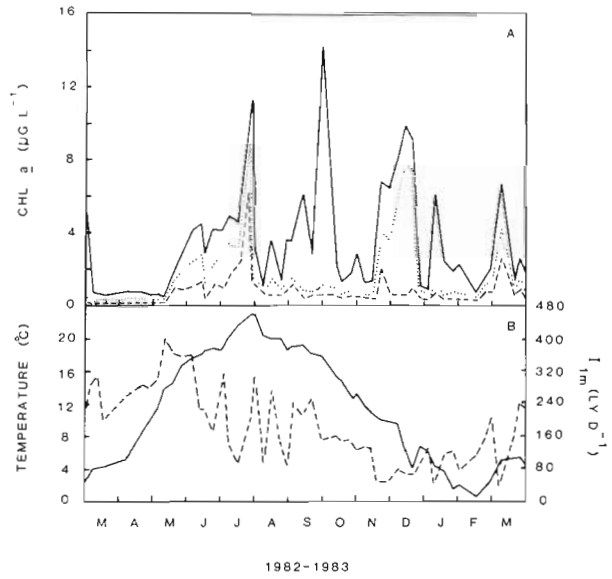

Fig. 1. (A) Chl *a* in the <153 µm (——), <10 µm (· · · · ·), and <5 µm (- - -) size fractions. (B) Surface water temperature (——) and estimated *in situ* irradiance at 1 m (- - -) at the experimental site

Chl *a* growth rates ranged from 0 to 2.2 (<10 µm) and 0 to 2.1 (<5 µm) doublings d^{-1} (Fig. 2). Growth was highest in the summer, with secondary peaks in late

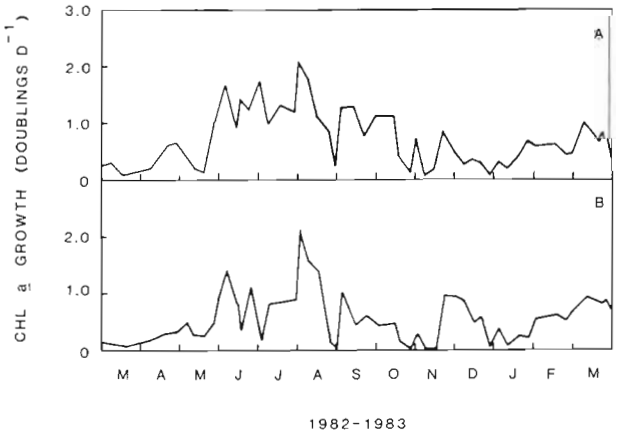

Fig. 2. Seasonal growth rates of chl *a* in the (A) <5 µm and (B) <10 µm size fractions in dialysis bags containing only <10 µm plankton

fall and late winter. Chl *a* in the <5 µm fraction persistently doubled 1 to 2 times daily from early June to mid-October. Microzooplankton grazing on chl *a* in the <10 µm fraction exhibited distinct peaks during the late-winter and summer flagellate blooms, and the late-fall *Thalassiosira* bloom (Fig. 3). The maximum ingestion of 2.2 µg chl *a* l^{-1} d^{-1} occurred in early

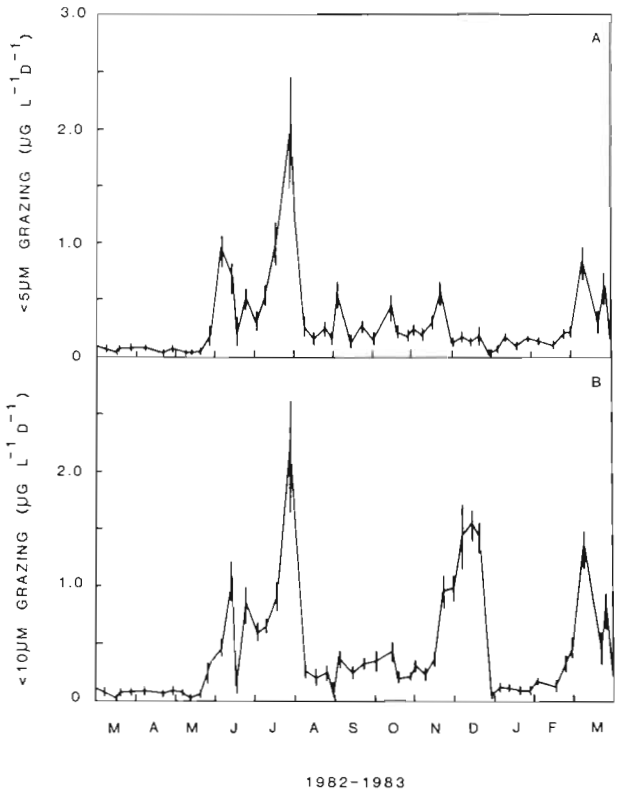

Fig. 3. Seasonal microzooplankton grazing rates on the (A) <5 µm and (B) <10 µm size fractions. Error bars represent ±1 SD

August; minimal grazing was observed in mid-winter and early spring. Grazing of <5 µm chl *a* was heaviest during the summer, with removal rates up to 2.1 µg l^{-1} d^{-1}. The fall *Thalassiosira* bloom was dominated by cells 5 to 10 µm in effective size, so that ingestion of <5 µm cells was relatively low.

The highest chl *a* growth rates coincided with elevated temperatures (Fig. 4), although a considerable range in growth rates occurred at a given temperature.

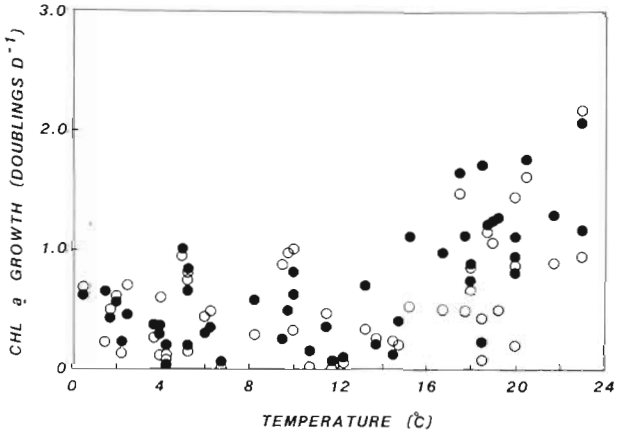

Fig. 4. Growth rates of chl *a* in the <10 µm (○) and <5 µm (●) size fractions as a function of temperature

An exponential fit of the log-transformed maximum growth rate (K_m) at each temperature (T) yielded:

$$K_m = 0.48e^{0.05(T)},\ n = 21,\ r^2 = 0.50. \quad (1)$$

The exponent is equivalent to a Q_{10} of 1.7. Whereas phytoplankton growth was temperature-dependent, microzooplankton grazing rates were not clearly related to temperature (Fig. 5): elevated ingestion

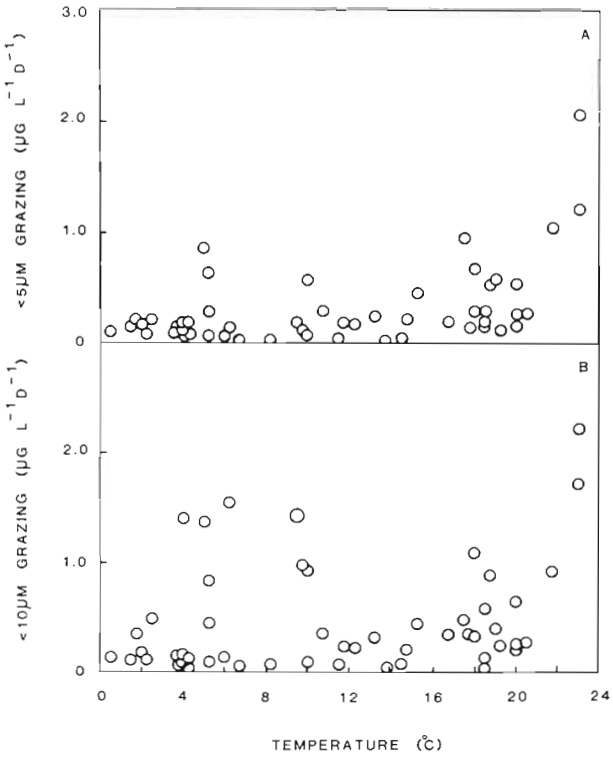

Fig. 5. Microzooplankton grazing rates on the (A) <5 µm and (B) <10 µm size fractions as a function of temperature

occurred during the fall *Thalassiosira* event (4 to 10 °C) and the summer flagellate blooms (18 to 24 °C).

Daily chl *a* production in dialysis bags containing only <10 µm plankton ranged from 0 to 8.2 (<10 µm cells) and 0 to 7.8 (<5 µm cells) µg l^{-1} d^{-1}. The standing stock of chl *a* in each size class was linearly related to the daily production rate (Fig. 6): high nanoplankton concentrations were observed when production was elevated, and low chl *a* levels coincided with low production. Microzooplankton grazing on both size fractions exhibited significant ($p < 0.05$) linear relations with the standing stock (Fig. 7) and production rates (Fig. 8) of phototrophic nanoplankton in Narragansett Bay. Increased phytoplankton productivity was associated with enhanced transfer to the microzooplankton community, an effect especially evident in the <10 µm size class. In the <5 µm fraction, a single experiment exhibited very high nanoplankton abun-

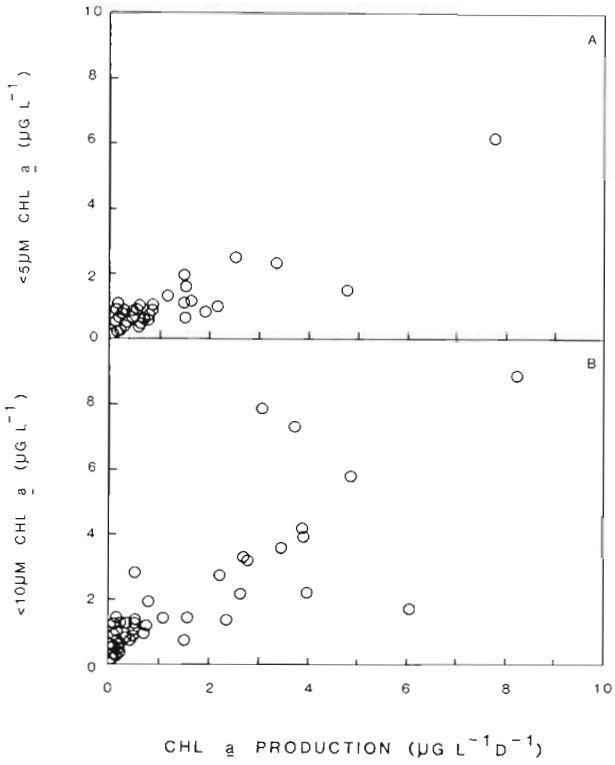

Fig. 6. Chl *a* concentration in the (A) <5 µm and (B) <10 µm fractions as a function of chl *a* production. <5 µm chl *a* = 0.29 + 0.68 (<5 µm chl *a* production), r^2 = 0.77, n = 52, $p < 0.05$. <10 µm chl *a* = 0.32 + 1.08 (<10 µm chl *a* production), r^2 = 0.71, n = 52, $p < 0.05$

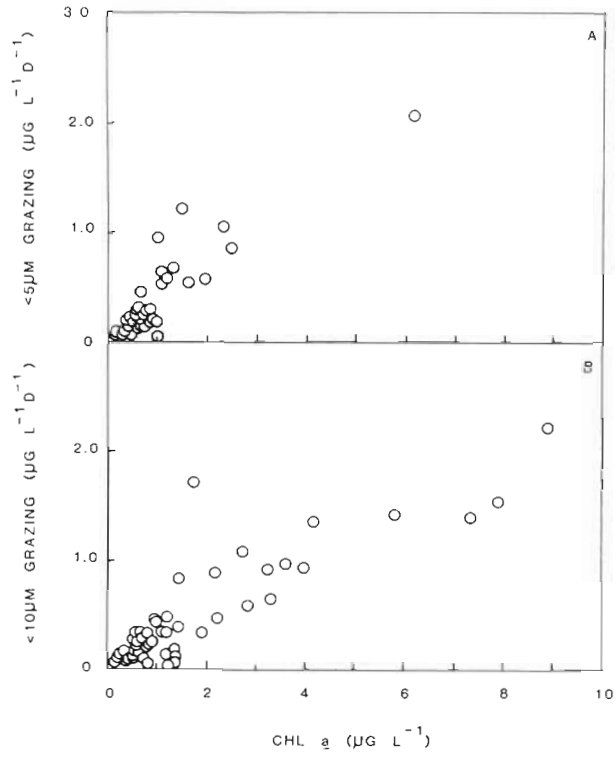

Fig. 7. Microzooplankton grazing rates on the (A) <5 µm and (B) <10 µm size fractions as a function of chl *a* concentration in each size class. <5 µm grazing rate = −0.03 + 0.41 (<5 µm chl *a*), r^2 = 0.80, $p < 0.01$. <10 µm grazing rate = 0.02 + 0.26 (<10 µm chl *a*), r^2 = 0.77, $p < 0.05$

dance, production, and grazing by microzooplankton. Comparison of slopes calculated with and without this experiment indicated no significant differences, nor are the intercepts significantly different from zero in either case.

DISCUSSION

Grazing rates were measured as differences in chl *a* concentrations after 24 h in the presence and absence of 10 to 202 µm microzooplankton. Two assumptions are inherent in these calculations. The first is that <10 µm phytoplankton grew at the same rate in bags containing <10 µm and <202 µm plankton. This would seem a valid assumption because the temperature and light fields were similar for both communities within a given experiment. Nitrogen is the major nutrient limiting phytoplankton growth in lower Narragansett Bay (Smayda 1974). Similar nitrogen concentrations were present in the <10 µm and <202 µm bags, and NO_3 or NH_4 was always detectable after 24 h (Fig. 9). In addition, PO_4 and $Si(OH)_4$ were present in excess relative to dissolved inorganic nitrogen, and initial and final concentrations were generally similar (Fig. 10). These data indicate that transport across the dialysis membrane and remineralization within the bags was sufficient to meet uptake requirements during the 24 h incubations. Thus the assumption of similar photosynthetic nanoplankton growth rates in dialysis bags with and without 10 to 202 µm microzooplankton appears justified.

A corollary is that phytoplankton species interactions influencing phototrophic nanoplankton growth were similar in bags with and without microzooplankton. Relevant literature is scarce, with the classic example being the apparent reciprocal co-dominance of *Skeletonema costatum* and *Olisthodiscus luteus* in Narragansett Bay. This effect was originally attributed to excretion of low molecular weight (<2,000) inhibitory compounds by *O. luteus* (Pratt 1966, Stuart 1972); however, more recent analysis suggests that these events may be mediated more by selective grazing than phytoplankton interactions (Tomas 1980). Dialysis membranes permit passage of compounds of higher molecular weight (<12,000), so that in the present study external metabolites derived from phytoplankton cells should have affected all the bags equally.

The second assumption is that significant grazing on

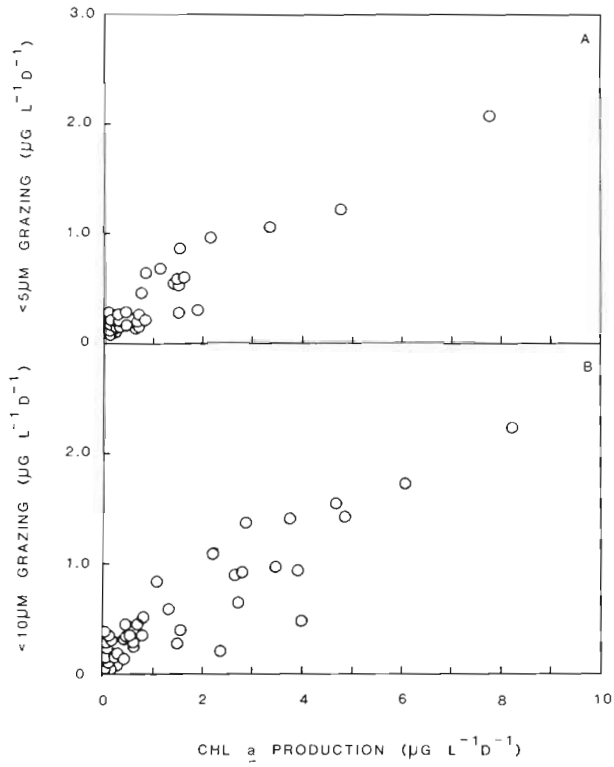

Fig. 8. Microzooplankton grazing rates on the (A) <5 μm and (B) <10 μm size fractions as a function of chl *a* production rates in that size class. <5 μm grazing rate = 0.09 + 0.28 (<5 μm chl *a* production), $r^2 = 0.89$, $p < 0.01$. <10 μm grazing rate = 0.10 + 0.28 (<10 μm chl *a* production), $r^2 = 0.85$, $p < 0.01$

autotrophic phytoplankton did not occur in the control (<10 μm) bags. Regular inspection of the <10 μm plankton communities indicated that few ciliates passed a 10 μm mesh and rarely increased in abundance, in agreement with similar observations of summer nanoplankton populations in Narragansett Bay (Furnas 1982). The impact of <10 μm heterotrophic microflagellates and dinoflagellates on photosynthetic nanoplankton is unknown. The latter may be significant grazers in tropical oceanic waters (Lessard & Swift 1985), but most coastal forms exceed 10 μm in effective size. Heterotrophic microflagellates are considered to be primarily bacterivorous (Fenchel 1982), although at least one species fed equally well on bacteria and selected phytoplankton (Goldman & Caron 1985). Zooflagellates are a potential food source for ciliates (Sieburth & Davis 1982), and the seasonal cycle and abundance of apochlorotic flagellates in Narragansett Bay is similar to that of photosynthetic nanoplankton (Davis et al. 1985). Although Narragansett Bay tintinnids did not survive in culture on a diet of heterotrophic microflagellates (Verity unpubl.), to the extent that herbivory by heterotrophic nanoplankton and predation on these heterotrophs by 10 to 202 μm microzooplankton was important, both the photosynthetic nanoplankton growth and microzooplankton grazing rates were conservative estimates.

Tintinnids were the most abundant ciliate microzooplankton at the experimental site in lower Narragansett Bay. The seasonal pattern of maximal abundances

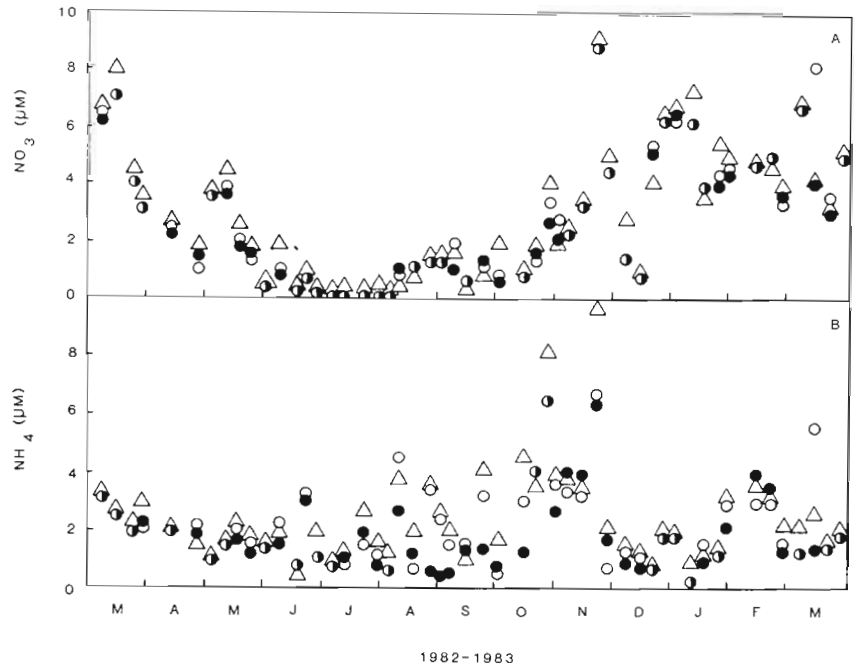

Fig. 9. (A) NO_3 and (B) NH_4 concentrations at the initiation of each experiment (△) and after 24 h in the <202 μm (○) and <10 μm (●) dialysis bags

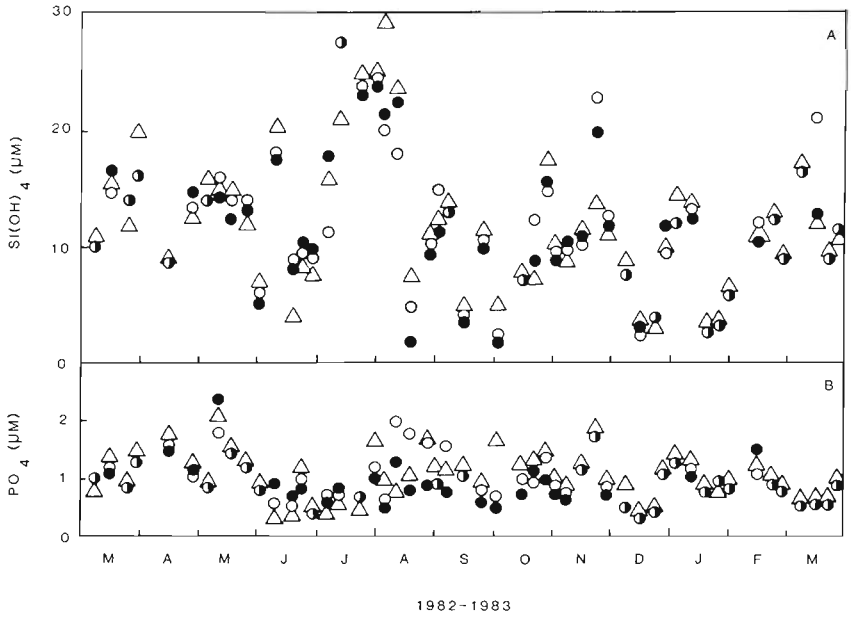

Fig. 10. (A) $Si(OH)_4$ and (B) PO_4 concentrations in the dialysis bags. Symbols as in Fig. 9

in spring and late-summer, separated by mid-summer and winter minima, is similar to previous findings in Narragansett Bay (Hargraves 1981, Verity 1984). The summer decline is due to the toxicity of the flagellate *Olisthodiscus luteus* to tintinnids (Verity & Stoecker 1982). The winter minimum reflects reduced food availability and growth rates at low temperatures (Verity 1985, 1986). Tintinnid abundance was not significantly different ($p < 0.05$) from the 3 yr mean for another site in lower Narragansett Bay, and was comparable to that observed in other shallow coastal waters (see summary in Verity 1984).

Protozoa other than tintinnids, predominantly oligotrich and holotrich ciliates, were second in numerical importance, consistent with observations in other shallow temperate waters (Capriulo & Carpenter 1980, Burkhill 1982). Occasional comparisons of counts on living and preserved material from Narragansett Bay indicated good agreement, as low levels of detritus did not obscure settled ciliates (Dale & Burkhill 1982). Non-loricate ciliates are generally more abundant than tintinnids in offshore waters (Beers & Stewart 1970, Johansen 1976). *Mesodinium rubrum*, a gymnostome ciliate containing photosynthetic symbionts (Taylor et al. 1971), bloomed in spring and late-summer in Narragansett Bay over a temperature range of 10 to 23 °C. The oral cone of this ciliate is reduced and the mouth is vestigial, lacking oral tentacles; *M. rubrum* is considered a functional autotroph (Smith & Barber 1979). These ciliates did not pass a 10 µm mesh, so that nanoplankton chl *a* growth rates in <10µm dialysis bags are independent of *M. rubrum* population dynamics.

Copepod nauplii, primarily *Acartia* NI-IV, were the most abundant metazoan microzooplankton. They were characterized by highest abundances in the spring *(A. hudsonica)* and late summer *(A. tonsa)*, in agreement with previous investigations (Durbin & Durbin 1981). The general absence of older nauplii reflects their reduced abundance and body lengths sufficient for some to be excluded by the 202 µm mesh. Copepodite stages were found in low numbers, and other microzooplankton occurred infrequently.

Grazing rates on the <10 µm and <5 µm chl *a* size fractions were highest during mid-summer and late-winter microflagellate blooms. Microzooplankton then ingested nanoplankton at rates in excess of 1 µg chl *a* l^{-1} d^{-1}. In addition, many of these herbivores potentially fed on phototrophic cells >10 µm in effective size, so that the present removal rates provide only a conservative estimate of their total grazing impact. Tintinnids were the most abundant ciliate microzooplankton during the coincident periods of high grazing rates and microflagellate blooms. Grazing on the <10 µm fraction was also elevated during a 5 wk bloom of small *Thalassiosira* species in November and December. Most of these diatoms passed a 10 µm mesh but were retained by 5 µm netting, as found by Furnas (1982). Tintinnids were not abundant during this period, and laboratory experiments indicated that *Thalassiosira* is an unsuitable food for coastal species (Verity & Villareal 1985). The most important grazers at this time were probably copepod nauplii and copepodites.

Grazing by microzooplankton was proposed as a mechanism regulating nanoplankton populations in

Canadian waters (Blackbourn 1974, Johansen 1976), but estimates of their grazing impact are indirect and range from <10 to 100 % of net primary production. The only annual estimates suggest consumption of 60 % of total phytoplankton production in the Solent estuary (Burkhill 1982) and 27 % of production in Long Island Sound (Capriulo & Carpenter 1983). In Narragansett Bay, the slope of the functional regression of grazing rate on chl *a* production indicated that 28 % of <10 μm and <5 μm chl *a* production was consumed by microzooplankton. However, when grazing impact is calculated for each experiment and summed for all, an annual mean grazing impact of 62 % of production in both size fractions is obtained. The discrepancy reflects the fact that grazing by microzooplankton equalled or exceeded nanoplankton growth at low temperatures (Fig. 11) and low production rates (Fig. 12). Below 4 °C, the grazing impact invariably exceeded 60 % of nanoplankton production. Below 15 °C, microzooplankton ingested a minimum of 25 % of daily production, and, in 13 of the 34 experiments, all of the chl *a* production was ingested. Production was <0.5 μg l^{-1} d^{-1} in every experiment in which grazing equalled or exceeded production. Above 15 °C, grazing did not match phytoplankton growth. The net result was that the standing stock of chl *a* in the <10μm and <5μm fractions exhibited significant ($p < 0.05$) linear relations with the difference between production and grazing (Fig. 13). For much of the year, microzooplankton grazing kept pace with temperature-limited phytoplankton growth, and nanoplankton community biomass remained low. Nanoplankton growth rates increased with temperature during the spring and summer, and microzooplankton grazing accounted for a smaller fraction of production; high nanoplankton standing stocks were found at this time. Thus, microzooplankton grazing contributed to seasonal variations in the size structure of phytoplankton communities in Narragansett Bay. High grazing impact on nanoplankton during the cold months coincided with netplankton (>10 μm) dominance of phytoplankton community biomass; low grazing impact during the summer was associated with nanoplankton

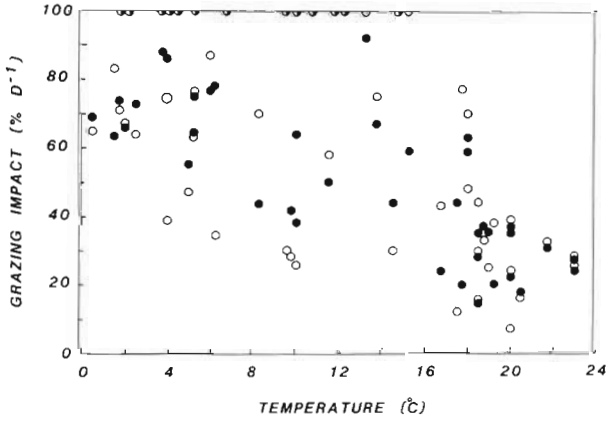

Fig. 11. Microzooplankton grazing impact (% chl *a* production per day) on the <10 μm (○) and <5 μm (●) size fractions as a function of temperature

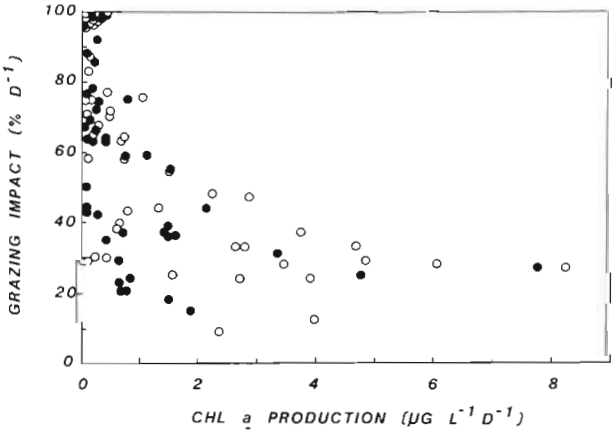

Fig. 12. Microzooplankton grazing impact as a function of chl *a* production in each size fraction. Symbols as in Fig. 11

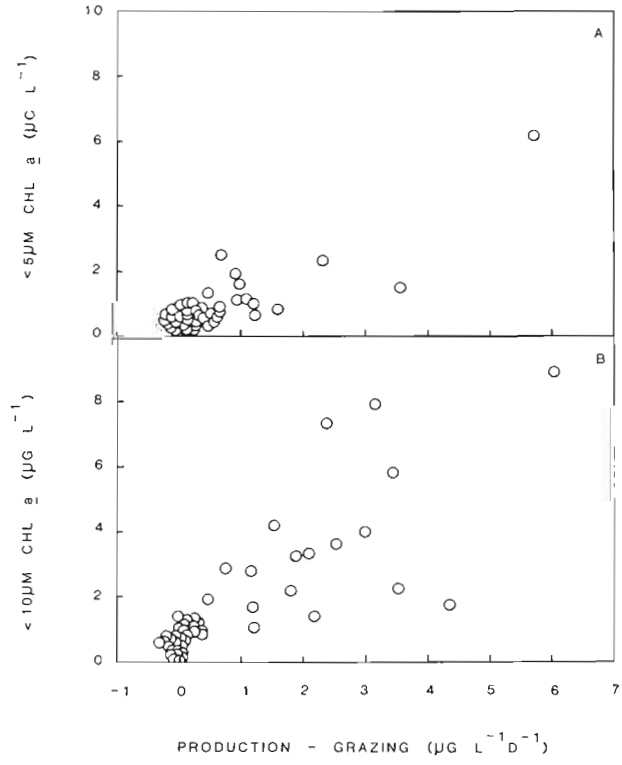

Fig. 13. Chl *a* standing stock in the (A) <5 μm and (B) <10 μm size fractions as a function of the difference between chl *a* production (P) and grazing (G) rates in each size class. <5 μm chl $a = 0.38 + 0.92$ (<5 μm P−G), $r^2 = 0.72$, $p < 0.01$. <10 μm chl $a = 0.49 + 1.44$ (<10 μm P−G), $r^2 = 0.66$, $p < 0.01$

dominance. The low microzooplankton grazing impact at higher temperatures, coupled with rapid reductions of copepod filtering efficiency on <10 μm particles (Nival & Nival 1976), suggest that zooplankton grazing alone cannot regulate nanoplankton populations during the summer in Narragansett Bay. Additional factors such as benthic grazing (Officer et al. 1982) may be important at this time.

Acknowledgements. I thank C. Griswold and T. Villareal for sampling assistance, and D. French and T. Villareal for sharing hours on the Autoanalyzer. N. Hairston, Jr., P. E. Hargraves, S. Levings, J. McN. Sieburth, T. J. Smayda, D. Stoecker, and 2 anonymous reviewers made valuable comments on various drafts. This work was supported by the Department of Commerce (NOAA) Grant No. NA80RA-00064 awarded to T. J. Smayda.

LITERATURE CITED

Beers, J. R., Stewart, G. L. (1970). The ecology of the plankton off La Jolla, California, in the period April through September 1967. VI. Numerical abundance and estimated biomass of microzooplankton. Bull. Scripps Inst. Ocenogr. 17: 67–87

Blackbourn, D. J. (1974). The feeding biology of tintinnid Protozoa and some other inshore microzooplankton. Ph. D. thesis, Univ. British Columbia, Vancouver

Burkhill, P. H. (1982). Ciliates and other microplankton components of a nearshore food web: standing stocks and production processes. Ann. Inst. océanogr. Paris 58 (S): 335–349

Capriulo, G. M., Carpenter, E. J. (1980). Grazing by 35 to 202 μm microzooplankton in Long Island Sound. Mar. Biol. 56: 319–326

Capriulo, G. M., Carpenter, E. J. (1983). Abundance, species composition, and feeding impact of tintinnid micro-zooplankton in central Long Island Sound. Mar. Ecol. Prog. Ser. 10: 277–288

Dale, T., Burkhill, P. H. (1982). Live counting – a quick and simple technique for enumerating pelagic ciliates. Ann. Inst. océanogr. Paris 58 (S): 267–276

Davis, P. G., Caron, D. A., Johnson, P. W., Sieburth, J. McN. (1985). Phototrophic and apochlorotic components of picoplankton and nanoplankton in the North Atlantic: geographic, vertical, seasonal, and diel distributions. Mar. Ecol. Prog. Ser. 21: 15–26

Durbin, A. G., Durbin, E. G. (1981). Standing stock and estimated production rates of phytoplankton and zooplankton in Narragansett Bay, Rhode Island. Estuaries 4: 24–41

Eppley, R. W. (1980). Estimating phytoplankton growth rates in the central oligotrophic oceans. In: Falkowski, P. G. (ed.) Primary productivity in the sea. Plenum Press, New York, p. 231–242

Fenchel, T. (1982). Ecology of heterotrophic microflagellates. IV. Quantitative occurrence and importance as bacterial consumers. Mar. Ecol. Prog. Ser. 9: 35–42

Frost, B. W. (1972). Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. 17: 805–819

Furnas, M. J. (1982). Growth rates of summer nanoplankton (<10 μm) populations in lower Narragansett Bay, Rhode Island, USA. Mar. Biol. 70: 105–115

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

Grasshoff, K. (1966). Automatic determination of fluoride, phosphate, and silicate in seawater. In: Skiggs, L. T. (ed.) Automation in analytic chemistry. 1965 Technicon Symposium, Mediad, New York, p. 304–307

Hama, T., Miyazaki, T., Ogawa, Y., Iwakumi, T., Takahashi, M., Otsuki, A., Ichimura, S. (1983). Measurement of photosynthetic production of a marine phytoplankton population using a stable ^{13}C isotope. Mar. Biol. 73: 31–36

Hargraves, P. E. (1981). Seasonal variations in tintinnids (Ciliophora: Oligotrichida) in Narragansett Bay, Rhode Island, USA. J. Plankton Res. 3: 81–91

Heinbokel, J. F. (1978). Studies on the functional role of tintinnids in the Southern California Bight. I. Grazing and growth rates in laboratory cultures. Mar. Biol. 47: 177–189

Heinbokel, J. F., Beers, J. R. (1979). Studies on the functional role of tintinnids in the Southern California Bight. III. Grazing impact of natural assemblages. Mar. Biol. 52: 23–32

Holmes, R. W. (1970). The Secchi disk in turbid coastal waters. Limnol. Oceanogr. 15: 688–694

Holm-Hansen, O., Lorenzen, C. J., Holmes, R. W., Strickland, J. D. H. (1965). Fluorometric determination of chlorophyll. J. Cons. 25: 115–128

Jenkins, W. J. (1982). Oxygen utilization rates in North Atlantic subtropical gyre and primary production in oligotrophic systems. Nature, Lond. 300: 246–248

Johansen, P. L. (1976). A study of tintinnids and other Protozoa in eastern Canadian waters, with special reference to tintinnid feeding, nitrogen excretion, and reproduction rates. Ph. D. thesis, Dalhousie Univ., Halifax

Karl, D. M., Winn, C. D., Wong, D. C. L. (1981). RNA synthesis as a measure of microbial growth in aquatic environments. II. Field applications. Mar. Biol. 64: 13–21

Landry, M. R., Hassett, R. P. (1982). Estimating the grazing impact of marine microzooplankton. Mar. Biol. 67: 283–288

Laws, E. A., Archie, J. W. (1981). Appropriate use of regression analyses in marine biology. Mar. Biol. 65: 13–16

Lessard, E. J., Swift, E. (1985). Species-specific grazing rates of heterotrophic dinoflagellates in oceanic waters, measured with a dual-label isotope technique. Mar. Biol. 87: 289–296

Nival, P., Nival, S. (1976). Particle retention efficiencies of an herbivorous copepod, *Acartia clausi*: effects on grazing. Limnol. Oceanogr. 21: 24–38

Officer, C. B., Smayda, T. J., Mann, R. (1982). Benthic filter-feeding: a natural eutrophication control. Mar. Ecol. Prog. Ser. 9: 203–210

Pavlou, S. (1972). Phytoplankton growth dynamics. Technical Series I. Chemostat methodology and chemical analyses. Dept. Oceanogr., Univ. Wash. Spec. Rep. No. 52, 1–130

Porter, K. D., Pace, M. L., Battey, J. F. (1979). Ciliate protozoans as links in freshwater food chains. Nature, Lond. 277: 563–565

Pratt, D. M. (1966). Competition between *Skeletonema costatum* and *Olisthodiscus luteus* in Narragansett Bay and in culture. Limnol. Oceanogr. 11: 447–455

Redalje, D. G. (1983). Phytoplankton carbon biomass and specific growth rates determined with the labelled chlorophyll *a* technique. Mar. Ecol. Prog. Ser. 11: 217–225

Ricker, W. E. (1973). Linear regressions in fishery research. J. Fish. Res. Bd Can. 30: 409–434

Roman, M. R., Rublee, P. A. (1981). A method to determine *in situ* zooplankton grazing rates on natural particle assemblages. Mar. Biol. 65: 303–309

Sakshaug, E., Jensen, A. (1978). The use of cage cultures in studies of the biochemistry and ecology of marine phytoplankton. Oceanogr. mar. Biol. A. Rev. 16: 81–106

Sheldon, R. W., Sutcliffe, W. H. (1978). Generation time of 3 h for Sargasso Sea microplankton determined by ATP analysis. Limnol. Oceanogr. 23: 1051–1055

Sieburth, J. McN., Davis, P. G. (1982). The role of heterotrophic nanoplankton in the grazing and nurturing of planktonic bacteria in the Sargasso and Caribbean Sea. Ann. Inst. océanogr. Paris 58 (S): 285–296

Smayda, T. J. (1974). Bioassay of the growth potential of the surface water of lower Narragansett Bay over an annual cycle using the diatom *Thalassiosira pseudonana* (oceanic clone 13–1). Limnol. Oceanogr. 19: 889–901

Smith, W. O., Jr., Barber, R. T. (1979). A carbon budget for the autotrophic ciliate *Mesodinium rubrum*. J. Phycol. 15: 27–33

Snedecor, G. W., Cochran, W. G. (1967). Statistical methods. Iowa State Univ. Press, Ames

Steemann Nielsen, E. (1952). The use of radioactive carbon (^{14}C) for measuring organic production in the sea. J. Cons. perm. int. Explor. Mer 18: 117–140

Stuart, M. (1972). The effects of *Olisthodiscus luteus* Carter on the growth of *Skeletonema costatum* (Grev.) Cleve. M. S. thesis, Univ. Rhode Island, Kingston

Taylor, F. J. R., Blackbourn, D. J., Blackbourn, J. (1971). The red water ciliate *Mesodinium rubrum* and its incomplete symbionts: a review including new ultrastructural observations. J. Fish. Res. Bd Can. 28: 391–407

Thompson, J. M., Ferguson, A. J. D., Reynolds, C. S. (1982). Natural filtration rates of zooplankton in a closed system: the derivation of a community grazing index. J. Plankton Res. 4: 545–560

Tomas, C. R. (1980). *Olisthodiscus luteus* (Chrysophyceae). V. Its occurrence, abundance and dynamics in Narragansett Bay, Rhode Island. J. Phycol. 16: 157–166

Venrick, E. L., Beers, J. R., Heinbokel, J. F. (1977). Possible consequences of containing microplankton for physiological rate measurements. J. exp. mar. Biol. Ecol. 26: 55–76

Verity, P. G. (1984). The physiology and ecology of tintinnids in Narragansett Bay, Rhode Island. Ph. D. thesis., Univ. Rhode Island, Kingston

Verity, P. G. (1985). Grazing, respiration, excretion, and growth rates of tintinnids. Limnol. Oceanogr. 30: 1268–1282

Verity, P. G. (1986). Growth rates of natural tintinnid populations in Narragansett Bay. Mar. Ecol. Prog. Ser. 29: 117–126

Verity, P. G., Stoecker, D. (1982). Effects of *Olisthodiscus luteus* on the growth and abundance of tintinnids. Mar. Biol. 72: 79–87

Verity, P. G., Villareal, T. A. (1985). The relative food value of diatoms, dinoflagellates, flagellates, and cyanobacteria for tintinnid ciliates. Arch. Protistenk. (in press)

Williams, P. J. LeB., Heinemann, K. R., Marra, J., Purdie, D. A. (1983). Comparison of ^{14}C and O_2 measurements of phytoplankton production in oligotrophic waters. Nature, Lond. 305: 49–50

This paper was submitted to the editor; it was accepted for printing on December 17, 1985