Limnol. Oceanogr., 36(2), 1991, 219–234

Physiological characteristics and food-web dynamics of *Synechococcus* in Lakes Huron and Michigan

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Abstract

Single *Synechococcus* cells accounted for an average of 10% (range 1–26%) of surface mixed-layer primary production in Lakes Huron and Michigan in 1986–1988. Maximal photosynthetic rates (P_{max}) were relatively low (range = 1.9–6.0 fg C cell^{-1} h^{-1}) and no significant photoinhibition was found at irradiances as high as 3.0 Einst m^{-2} h^{-1}. *Synechococcus* growth rates estimated by four techniques (ampicillin, ^{14}C uptake, dilution, and small inocula) ranged from 0.1 to 0.9 d^{-1} with a mean of 0.37. Although substantial variability was noted among techniques on any one date, on average all estimates were in reasonable agreement with the exception of the dilution estimates which were significantly lower ($P < 0.01$). Three techniques for estimating grazing loss rates (ampicillin, dilution, and ^{14}C-labeling of *Synechococcus*) provided similar estimates ranging from 0.1 to 0.7 d^{-1}. On specific dates, grazing loss rates were 33–120% of growth rates, suggesting that grazing was the major loss for *Synechococcus* populations in these lakes. Most of the grazing loss (68%) was attributable to small (4–10 μm), heterotrophic flagellates and ciliates. Crustaceans and rotifers accounted for only a small percentage of total grazing loss (5–21%) even when *Daphnia* accounted for 40% of crustacean biomass.

Chroococcoid cyanobacteria of the genus *Synechococcus* are important contributors to pelagic freshwater and marine ecosystems (Joint 1986; Stockner and Antia 1986). In both, *Synechococcus* abundance can exceed 100,000 cells ml^{-1} and its contribution to total primary production can exceed 20% (Fahnenstiel et al. 1986; Waterbury et al. 1986; Iturriaga and Marra 1988). The contribution of *Synechococcus* to primary production usually increases in more oligotrophic environments (Stockner and Antia 1986). Few genera of phytoplankton are such important contributors to primary production in both freshwater and marine ecosystems.

Because the widespread occurrence of *Synechococcus* was first noted in the last decade (Waterbury et al. 1979), its ecology is not yet fully understood (Glover 1985; Stockner and Antia 1986). Even though it is abundant in both freshwater and marine environments, most of the information on its ecology in pelagic systems is from the marine environment (Glover 1985; Stockner and Antia 1986). The existing information suggests substantial variability in the ecology of *Synechococcus* with regard to

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Acknowledgments

L. Herche and J. Cavaletto provided technical assistance. We also appreciate comments by W. Gardner, L. Herche, M. McCormick, and two anonymous reviewers.

GLERL Contribution 700.

photosynthetic characteristics, growth, and grazing loss rates. Maximal photosynthetic rates (P_{max}) have been reported to range from 2 to 40 fg C cell^{-1} h^{-1} (Fahnenstiel et al. 1986; Prézelin et al. 1986, 1987), and growth rates have been reported to range from 0.1 to 8.9 d^{-1} (*see* Stockner and Antia 1986). Reported grazing rates are less variable, ranging from 0.1 to 1.3 d^{-1} (Landry et al. 1984; Iturriaga and Mitchell 1986; Weisse 1988). It is difficult to determine the significance of this variability because several different techniques have been used for these estimates.

Growth rates have been estimated by incorporation of ^{14}C (Iturriaga and Mitchell 1986; Fahnenstiel et al. 1986), by abundance changes in diluted and antibiotic-treated samples (Campbell and Carpenter 1986*a*; Weisse 1988), and by the frequency of dividing cells (Campbell and Carpenter 1986*b*). Likewise, grazing rates have been estimated by abundance changes in diluted and antibiotic-treated samples and by the ingestion of ^{14}C-labeled cells (Campbell and Carpenter 1986*a*; Iturriaga and Mitchell 1986; Weisse 1988). These methodological differences are noteworthy because significant variability has been noted among techniques (Campbell and Carpenter 1986*b*; Iturriaga and Marra 1988).

Although grazing by heterotrophic organisms appears to be an important loss for *Synechococcus* populations (Campbell and Carpenter 1986*b*; Iturriaga and Mitchell 1986), very little quantitative information exists for the role of specific grazers (Joint 1986). Much of the available information is qualitative, focusing on observations of ingestion by specific grazers (Caron et al. 1985; Fahnenstiel et al. 1986; Iturriaga and Mitchell 1986).

We investigated the photosynthetic characteristics, growth rates, and grazing loss rates of single *Synechococcus* cells. This study is novel because we based all rate estimates on examinations of individual cells and not on bulk determinations of specific size fractions, thus providing more accurate rate estimates. Furthermore, we used live *Synechococcus* cells to measure filtering rates of all potential grazers (i.e. protozoans to metazoans) simultaneously. Finally, we compared the more commonly used techniques for estimating *Synechococcus* growth and grazing loss rates. Because of the deep and relatively oligotrophic nature of Lakes Huron and Michigan, this information provides useful comparisons to more frequently studied environments such as the open ocean.

Materials and methods

Sampling was conducted at offshore stations in Lake Huron (42°56′N, 82°21′W; max depth, 70 m) and Lake Michigan (43°1′11″N, 86°36′48″W; max depth, 100 m) from March 1986 to November 1988. On the basis of biological and chemical characteristics, these lakes have been classified as oligotrophic (Beeton 1965; Dobson et al. 1974). During the spring isothermal mixed period in both lakes, total P concentrations are ~4–8 μg liter^{-1} and phytoplankton chlorophyll concentrations range from 1.0 to 3.0 mg m^{-3} (Dobson et al. 1974; Fahnenstiel et al. 1989).

Water was collected from the surface mixed layer with clean 5- or 30-liter PVC Niskin bottles. Picoplankton samples for microscopic analysis were transferred into 250-ml amber bottles and preserved with glutaraldehyde (1% final concn) buffered with sodium cacodylate (0.1 M final concn). Preserved samples were kept cold (~5°C), and duplicate slides were prepared (Waterbury et al. 1979) and frozen immediately (−20°C). These slides were counted within a few days to minimize errors due to the fading of autofluorescence. We estimated picoplankton biomass and composition on each slide by enumerating a minimum of 500 individuals with a Leitz Laborlux epifluorescent microscope (1,250×) equipped to distinguish the dominant autofluorescent emission of an individual cell. The microscope was equipped with both blue (450 nm) and green excitation (530–560 nm) filter blocks. For our procedures, counting error that included slide preparation typically averaged 5% (C.V.).

Both unicellular and colonial (≥8 cells per colony) forms of picocyanobacteria (<3 μm) were observed. During the 3 yr of this study, ~78% of all picocyanobacteria were single coccoid, phycoerythrin-containing (P-

E) cells ~1.0 μm in diameter. Clumped P-E-containing cells (<8 cells per clump) were rare (<5% of coccoid P-E picocyanobacteria) as were phycocyanin-containing picocyanobacteria (<0.5% of total P-E picocyanobacteria). For this study, *Synechococcus* cells were defined as single (noncolonial), chroococcoid, P-E-containing cyanobacteria of ~1 μm. An isolate of these cells from Lake Huron was found to divide in one plane, thus confirming their designation as *Synechococcus* (Stanier et al. 1971). Recently divided single cells (i.e. daughter cells still attached) were counted as single cells.

The length and breadth of 20 individuals from both lakes were measured from projections of photomicrographs twice during each of the major seasons. Cell volumes were calculated via simple geometric approximations, and these estimates were subsequently converted to C with a conversion factor of 121 fg C μm^{-3} (Iturriaga and Mitchell 1986).

Primary production and autoradiography—Primary production was estimated with the ^{14}C technique as modified by Fahnenstiel and Scavia (1987) and Fahnenstiel et al. (1989). Water collected from the surface mixed layer was dispensed immediately into shaded, 2-liter polycarbonate bottles, inoculated with 2–220 μCi of $NaH^{14}CO_3$, and incubated briefly (1–2 h) at ambient temperature in a shipboard photosynthesis-irradiance (*P-I*) incubator (Fahnenstiel et al. 1989). After incubation, subsamples (100 ml) were filtered onto membranes (0.22-μm Millipore), decontaminated with 0.5 ml of 0.5 N HCl for 4–6 h, placed in scintillation vials with 12 ml of scintillation cocktail, and assayed with a Packard Tri-Carb scintillation counter. Counting efficiencies were determined with external standards. Temperature, pH, and alkalinity were used to determine dissolved inorganic C (DIC) concentrations. Also, a subsample from each low-activity experimental bottle was filtered through a 2-μm Nuclepore filter and retained for autoradiography.

Autoradiographs were prepared by preserving the <2-μm fraction with 1% glutaraldehyde buffered with 0.1 M sodium cacodylate. Subsamples of 5–20 ml were immediately concentrated onto 0.2-μm Nuclepore membranes, transferred onto gelatin-coated coverslips, and then dipped and developed for track autoradiography (Carney and Fahnenstiel 1987). ^{14}C loss associated with preservation was monitored by time-series filtration and did not exceed 5%. Tracks per cell were converted to C-specific uptake rates with the procedures of Carney and Fahnenstiel (1987).

Photosynthetic rates of *Synechococcus*, expressed per cell, were used to construct *P-I* curves (Fahnenstiel et al. 1989). The simple two-parameter model (α = initial slope and P_{max} = maximal light-saturated rate) was used because values for β were not significant ($P > 0.05$). The procedure used to calculate *P-I* parameters is described by Fahnenstiel et al. (1989). Cell-specific *P-I* parameters were combined with hourly incident irradiance values and extinction coefficients to determine rates of daily cellular C production (Fahnenstiel and Scavia 1987). Exponential growth rates were determined by combining daily production rates with cellular C estimates.

Growth experiments—A 4-liter polycarbonate bottle containing prefiltered lake water (<0.2 μm, Gelman capsule) was inoculated with lake water (100 ml) previously passed through a 3-μm Nuclepore filter. This bottle was incubated in a shipboard incubator that simulated light and temperature regimes at 5 m. Samples for picoplankton analysis were taken at 0, 24, 36, and 48 h. Growth rates from these experiments are referred to as small-inocula growth (SIG) estimates. Other growth rate estimates were provided from primary production experiments (*see above*) and from dilution and ampicillin-treated grazing experiments (*see below*).

Grazing experiments—Three independent techniques were used to estimate microzooplankton grazing on *Synechococcus*. First, microzooplankton (grazers) abundances were manipulated through a series of bottle dilutions, and then changes in *Synechococcus* abundance were measured in each bottle (Landry et al. 1984; Campbell and Carpenter 1986*a*). Bottle dilutions (10-, 8-, 5-, 3-, and 0-fold dilutions) were performed by mixing appropriate volumes of

prescreened lake water (<153 μm) with filter-sterilized lake water (<0.2 μm) in 4-liter polycarbonate bottles augmented with PO_4^{3-} (0.6 μM) to compensate for potential nutrient recycling between herbivores and algae associated with the dilution manipulations. P was added to the bottles because it is the limiting nutrient in both lakes (Schelske et al. 1974; Lin and Schelske 1981). Bottles were incubated in the same shipboard incubator described above, which simulated light and temperature conditions at 5 m. Because increasing bottle dilution alleviates grazing pressure, the slope of the growth rate of *Synechococcus* (dependent variable) across dilution treatments (independent variable) is an estimate of the grazing loss rate, and the intercept is an estimate of *Synechococcus* growth rate.

A second set of enclosure experiments to estimate *Synechococcus* grazing loss and growth rate involved the use of the procaryotic inhibitor, ampicillin (Campbell and Carpenter 1986*a*). We tested the effect of ampicillin on an isolate of *Synechococcus* from Lake Huron by adding ampicillin to a culture in log-phase growth. Cell division appeared to stop without causing cell lysis; the slope of the ampicillin treatment (growth rate) was not significantly different than zero (F-test, $P > 0.05$, $F = 6.6$, df = 5). In the 1988 experiments, whole water was passed through several screens to examine the grazing of different size classes (<153, <30, and <8 μm); experiments in 1987 were performed only on the <153-μm size class. The prescreened water was dispensed into duplicate 4-liter polycarbonate bottles; ampicillin was added to one bottle and the second served as control. Bottles were incubated for 48 h and sampled over time (0, 2, 12, 24, 36, and 48 h) to determine the abundance of *Synechococcus*. The time-zero sample from the ampicillin bottle was taken at 1 h to allow for the lag in effect of the inhibitor (Sherr et al. 1986). The slope of the natural log of abundance vs. time from the ampicillin treatment is the loss rate, while the difference in slopes between the ampicillin and control treatments is the growth rate. Because no eucaryotic inhibitor was used in conjunction with the procaryotic inhibitor in the control bottle to inhibit both grazing and growth, these estimates of grazing loss may be conservative.

Finally, we used ^{14}C-labeled *Synechococcus* to determine *Synechococcus* grazing losses by all predators. First, an isolate of *Synechococcus* from Lake Huron was grown in BG-11 culture medium (Stainer et al. 1971). During late log phase, cells were given 1–3 mCi of ^{14}C as $NaHCO_3$, then incubated for 4–8 h. At the end of the incubation, all extracellular ^{14}C was removed by rinsing the labeled cells three times via centrifugation followed by resuspension in filtered (0.2 μm) lake water. With this procedure, on average 97% of the ^{14}C was incorporated in the cells, and cellular activities ranged from 0.02 to 0.20 dpm $cell^{-1}$. No significant cell damage or loss of incorporated radioactivity occurred with centrifugation. Furthermore, viability of centrifuged cells tested by resuspending these cells in BG-11 and then following growth showed that cells continued in exponential growth after a stationary period of several hours.

Grazing experiments were initiated by inoculating 20-liter carboys containing whole lake water with ^{14}C-labeled *Synechococcus* at ~5–10% of natural abundance. The first carboy was processed as soon as labeled cells were added and served as a time-zero control (blank). Two carboys (one for community fractionation and one for species-specific grazing rates) were processed after a 1–2-h incubation at ambient temperature and light.

Community fractionation estimates were determined from a complete fractionation series. First, the entire contents of each carboy were passed through a 153-μm Nitex screen. Subsequently, 4-liter subsamples of the <153-μm filtrate were passed through a 30-μm Nitex screen, 500-ml subsamples of the <30-μm filtrate through a 8-μm Nuclepore filter, and 150-ml subsamples of the <8-μm filtrate through 2- and 3-μm Nuclepore filters. The organisms retained on the 30- and 153-μm screens were narcotized with club soda, filtered (Whatman GF/A), and transferred into scintillation vials with 0.5 ml of NCS tissue solubilizer. These samples were digested for 24 h at 45°C, after which 12 ml of scintillation cocktail was added to each vial along with 0.1 ml of gla-

cial acetic acid to reduce chemical quenching. Organisms retained on the 2-, 3-, and 8-μm filters were processed by placing each filter into a scintillation vial containing 0.2 ml of methyl chloride and ethanolamine, followed by the addition of scintillation cocktail. Loss rates for *Synechococcus* were calculated from

$$L = \frac{\ln\{1 + [(F - B)/A]\}}{T}$$

where L is loss rate (d^{-1}), F is activity on filter (dpm ml^{-1}), B is blank activity (dpm ml^{-1}), A is activity added (dpm ml^{-1}), and T is length of incubation (d^{-1}). Specific activity and cell abundances of ^{14}C-labeled *Synechococcus* added to the carboys did not change significantly during the 1–2-h incubation (<5%); therefore, no correction for these factors was included in our loss calculations.

Species-specific grazing rates on ^{14}C-labeled *Synechococcus* were estimated by screening the contents of each carboy through the fractionation series described above. Individuals retained on the 153- and 30-μm screens were narcotized, preserved with 1% Lugol's solution, separated and identified, placed in scintillation vials (several specimens of the same taxon), and radioassayed. The loss associated with preservation was monitored by comparing activity in the unpreserved community fraction (>153 μm) to the sum of activities of the individuals from the preserved species carboy; loss upon preservation averaged 20%. *Synechococcus* uptake by organisms retained on the 2-, 3-, and 8-μm screens was evaluated by gently transferring the organisms onto gelatin-coated coverslips or slides, and then dipping and developing the slides and coverslips for track autoradiography (Carney and Fahnenstiel 1987).

Filtering rates (μl ind.$^{-1}$ h^{-1}) for individual grazers were determined with the equation

$$\mathrm{FR} = \frac{D}{A \times T}$$

where D is activity per grazer (dpm ind.$^{-1}$).

The C content of protozoans was determined by converting cell volumes, based on measurements of individual cells, to C with a conversion factor of 0.15 g C ml^{-1}. C contents of rotifers and crustaceans were calculated as 0.5 × dry wt. Dry weights were determined previously from Lake Michigan specimens (D. Scavia and T. Nalepa unpubl. data).

Results

P-I *parameters and contribution to primary production*—The *P-I* relationship of *Synechococcus* was adequately described with a two-parameter model (Fig. 1), which explained >92% of the total variation for any one experiment (Table 1). Maximal rates of photosynthesis (P_{max}) ranged from 1.9 to 6.0 fg C $cell^{-1}$ h^{-1} with a mean of 3.8. The α or initial slope of the *P-I* relationship at low irradiances ranged from 3.5 to 28.9 fg $cell^{-1}$ m^2 $Einst^{-1}$ with a mean of 14.8. I_k values ranged from 0.15 to 0.54 Einst m^{-2} h^{-1}. Lowest values of P_{max} and α were observed during summer stratification, whereas values were highest during spring isothermal mixing.

The contribution of *Synechococcus* to areal surface mixed-layer primary production varied from 1 to 9% in 1988 (Table 1). Because *Synechococcus* abundance was unusually low in 1988 during April to July (6–13 × 10^3 cell ml^{-1}) as compared to the abundances in 1986 and 1987 (10–50 × 10^3 cells ml^{-1}, G. Fahnenstiel unpubl. data), a better estimate of the contribution of *Synechococcus* would be obtained using photosynthetic rates from 1988 combined with abundances from the entire 1986–1988 period and comparing these *Synechococcus* production estimates to total primary production. This comparison yields *Synechococcus* contributions ranging from 1 to 26% with a mean of ~10%. The contribution was maximal on 13 September 1987 in Lake Michigan.

Growth rates—Except for two dates in 1987 when growth rates measured by the dilution technique were negative (29 July and 20 August), exponential growth rates ranged from 0.11 to 0.92 d^{-1} (Table 2). About 80% of the growth rates were between 0.1 and 0.5 d^{-1}, and the highest were found during thermal stratification. Furthermore, growth rates between lakes were not significantly different ($t = 0.85$, $P > 0.3$, $n = 47$).

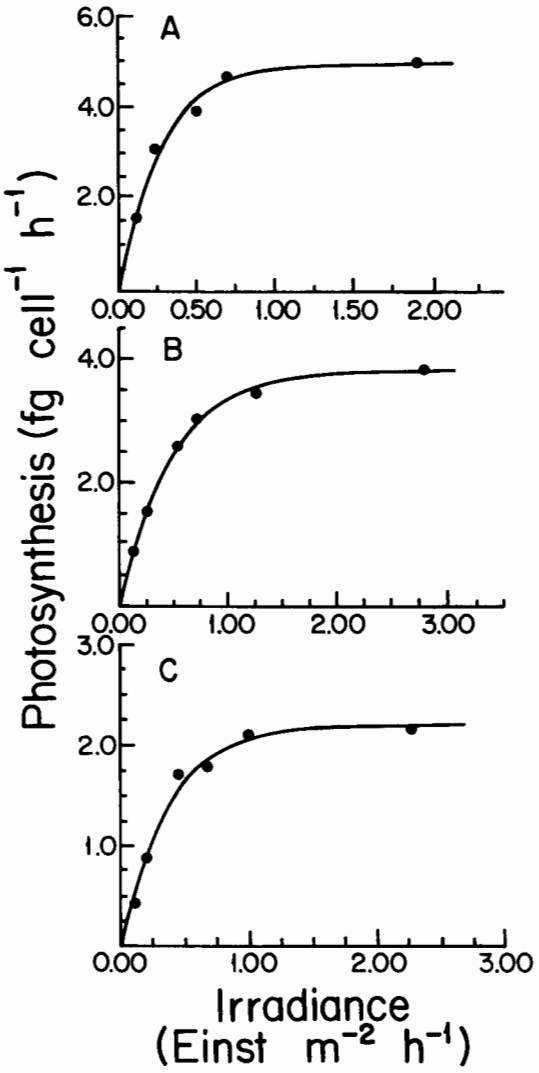

Fig. 1. *P-I* curves for *Synechococcus* spp. determined by track autoradiography: A—Lake Michigan, 11 April 1988, 5 m; B—Lake Michigan, 14 June 1988, 5 m; C—Lake Huron, 26 July 1988, 5 m.

Although there was substantial variability in growth estimates on any one date, most techniques provided similar estimates (Table 2). A one-way ANOVA blocked by thermal period (thermal periods defined by Fahnenstiel et al. 1989: spring isothermal, intermediate stratification, and midstratification) was used to examine overall and seasonal paired differences between estimates with the different techniques. Overall, all techniques provided similar growth rates with the exception of dilution; SIG, ampicillin, and ^{14}C were not significantly different (SIG vs. amp., $P > 0.5$; SIG vs. ^{14}C, $P > 0.1$; amp. vs. ^{14}C, $P > 0.1$) while dilution estimates were lower than SIG and ampicillin estimates (SIG vs. dilution, $P < 0.01$; amp. vs. dilution, $P < 0.001$). Moreover, substantial seasonal variability was noted among most techniques, but again significant differences were primarily associated with the dilution estimates (SIG vs. amp., $P = 0.05$; SIG vs. ^{14}C, $P > 0.05$; amp. vs. ^{14}C, $P > 0.10$; whereas SIG vs. dilution, $P < 0.05$; amp. vs. dilution, $P < 0.001$). Differences between dilution and the other estimates were largest during thermal stratification. Although sample sizes for these comparisons were small ($n = 4$), dilution growth rates were not significantly different than SIG growth rates during spring isothermal mixing (paired-$t = 2.8$, $P > 0.05$) but were significantly different during thermal stratification (paired-$t = 4.2$, $P < 0.05$).

Grazing loss rates—Although variable results among methods were observed on some dates, on average all three measures of grazing loss produced remarkably similar and repeatable results between lakes and between the 2 yr studied (Table 3; Figs. 2 and 3). For microzooplankton, grazing loss estimates from the dilution and ampicillin techniques were not significantly different (paired-$t = 0.75$, $P > 0.40$, $n = 9$). Furthermore, grazing loss rates for both macro- and microzooplankton as determined from labeled cells were not significantly different than grazing losses due to microzooplankton alone (one-way ANOVA of paired differences blocked by thermal periods as described earlier, amp. vs. dilution, $P > 0.5$; amp. vs. ^{14}C, $P > 0.05$). Also, no significant seasonal differences among techniques were noted (amp. vs. dilution, $P > 0.5$; amp. vs. ^{14}C, $P = 0.1$). These results suggest that macrozooplankton were not major grazers of *Synechococcus*. This idea was confirmed by results from the labeled-cell experiments (*see below*). Grazing losses were low during isothermal periods (0.11–0.20 d^{-1}) and increased during summer stratification (0.33–0.54 d^{-1}).

Grazing appeared to be the major loss affecting *Synechococcus* populations, ac-

Table 1. *P-I* parameters and contribution to total primary production for single *Synechococcus* cells in 1988. Units: P_{max}—fg C cell^{-1} h^{-1}; α—fg C cell^{-1} m^2 Einst^{-1}; I_k—Einst m^{-2} h^{-1}. R^2 of regression and percent contribution of *Synechococcus* to primary production (PP%) are also given. Error estimates are standard errors.

	P_{max}	α	I_k	R^2	PP%
Lake Michigan					
11 Apr	4.9±0.2	17.3±2.0	0.28	0.98	2
11 May	6.0±0.5	28.9±8.1	0.21	0.93	1
14 Jun	3.8±0.1	7.8±0.3	0.49	0.99	4
Lake Huron					
22 Jun	1.9±0.2	3.5±0.4	0.54	0.97	5
26 Jul	2.2±0.1	6.0±0.6	0.37	0.98	5
13 Oct	3.8±0.3	25.5±5.2	0.15	0.93	9

counting for 33–120% of growth rate on any given date, Substantial variability was associated with each estimate as on all individual dates; growth and grazing rates were not significantly different ($P > 0.05$).

Grazing loss rates of *Synechococcus* by specific predators were also assessed with ampicillin and ^{14}C-labeled cells. Both techniques produced similar results and demonstrated little spatial or temporal variation in the percent loss attributable to various size fractions. Prefractionated water treated with ampicillin demonstrated that the <8-μm fraction accounted for 55–73% of total grazing loss of *Synechococcus* (mean 65%), while the 8–30- and 30–153-μm fractions accounted for an average of 25 and 10%, respectively, of total grazing loss (Table 4). Similarly, experiments with ^{14}C-labeled cells showed that the 2–8-μm size fraction comprised the dominant grazers on *Synechococcus* (mean 68%), whereas larger size fractions became increasingly less important (Table 5).

Autoradiography of the <8-μm fraction revealed that the dominant grazers were small (4–10 μm) protists (flagellates and ciliates) that did not exhibit chlorophyll fluorescence. Heterotrophic protists also were the dominant grazers in the 8–30-μm size class. Although mixotrophic protozoans were observed, their contribution to total protozoan grazing was minor (<8%). In the 30–153-μm fraction, heterotrophic protists

Table 2. Exponential growth rates (d^{-1}) for *Synechococcus*. Experimental procedures are described in the text. Error estimates are standard errors. LH—Lake Huron; LM—Lake Michigan.

	SIG	Ampicillin	Dilution	^{14}C-autorad.
29 Apr 86—LH	0.43±0.12	—	—	—
30 Apr 86—LH	0.23±0.14	—	—	—
22 Jun 86—LH	0.93±0.06	—	—	—
17 Aug 86—LH	0.92±0.13	—	—	—
1 May 87—LM	—	0.33±0.07	—	—
18 May 87—LH	—	0.28±0.02	0.40±0.10	—
23 Jun 87—LM	0.43±0.12	0.67±0.14	0.20±0.01	—
29 Jul 87—LH	0.46±0.06	0.65±0.16	−0.02±0.08	—
20 Aug 87—LM	0.48±0.05	0.50±0.09	−0.11±0.05	—
15 Oct 87—LH	0.36±0.09	0.28±0.07	0.13±0.04	—
2 Nov 87—LM	0.28±0.08	0.21±0.09	0.20±0.04	—
11 Apr 88—LM	0.21±0.07	0.19±0.01	0.20±0.03	0.46
10 May 88—LM	0.21±0.13	0.11±0.03	0.15±0.02	0.67
18 May 88—LH	0.28±0.09	0.16±0.02	0.15±0.01	—
13 Jun 88—LM	0.35±0.10	0.17±0.06	—	0.37
21 Jun 88—LH	0.39±0.09	0.40±0.05	—	0.18
11 Jul 88—LM	0.18±0.06	0.36±0.03	—	—
26 Jul 88—LH	0.30±0.08	0.26±0.05	—	0.26
13 Oct 88—LH	0.25±0.10	0.33±0.03	—	0.40
Mean	0.39±0.05	0.33±0.04	0.14±0.05	0.39±0.07

Table 3. Heterotrophic grazing loss rates (d^{-1}) for *Synechococcus*. Dilution and ampicillin estimates are for organisms <153 μm and labeled-cell estimates are for all organisms. Error estimates are standard errors.

	Ampicillin	Dilution	Labeled cells
1 May 87—LM	−0.11±0.01	—	—
18 May 87—LH	−0.11±0.04	−0.35±0.15	—
23 Jun 87—LM	−0.34±0.20	−0.23±0.01	—
29 Jul 87—LH	−0.36±0.19	−0.69±0.17	—
20 Aug 87—LM	−0.50±0.08	−0.32±0.12	—
15 Oct 87—LH	−0.22±0.06	−0.19±0.07	—
2 Nov 87—LM	−0.13±0.12	−0.11±0.09	—
11 Apr 88—LM	−0.20±0.03	−0.32±0.05	−0.23
10 May 88—LM	−0.12±0.02	−0.16±0.03	−0.09
18 May 88—LM	−0.15±0.02	−0.11±0.02	—
13 Jun 88—LM	−0.18±0.06	—	−0.27
21 Jun 88—LH	−0.54±0.05	—	−0.25
11 Jul 88—LM	−0.49±0.04	—	−0.21
26 Jul 88—LH	−0.33±0.02	—	−0.46 and −0.19
13 Oct 88—LH	−0.36±0.06	—	−0.28
Mean	−0.27±0.04	−0.27±0.06	−0.25±0.01

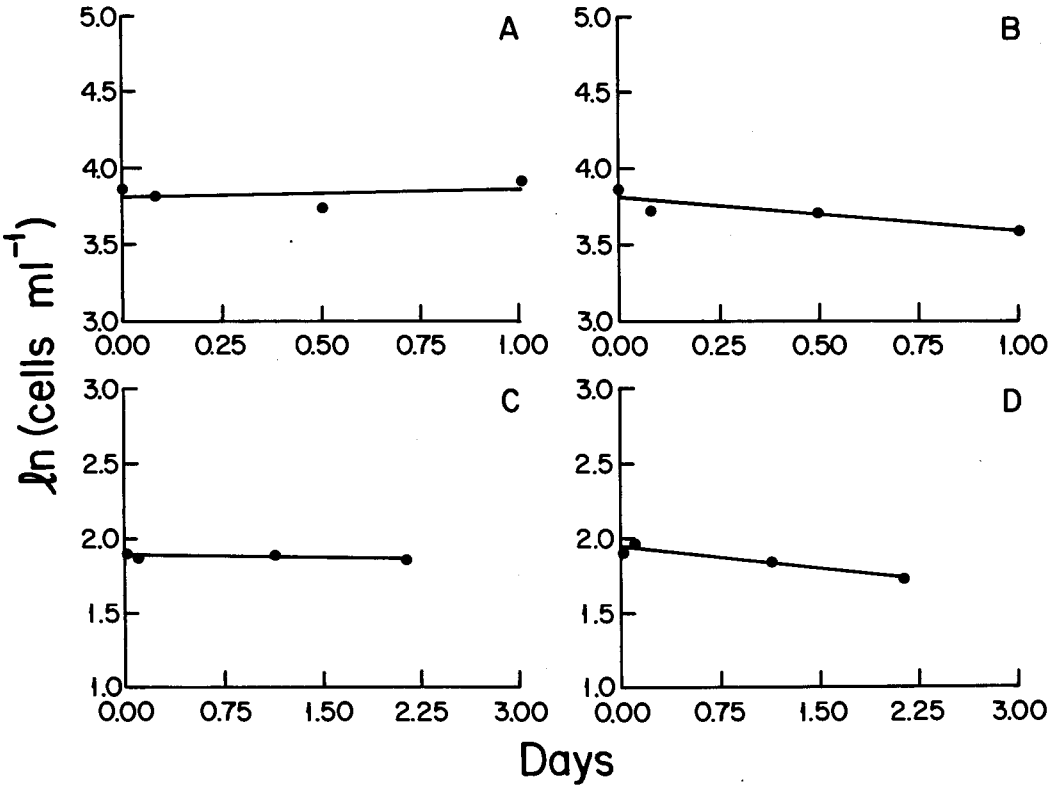

Fig. 2. Examples of results from ampicillin antibiotic experiments. The grazing rate is the difference between slopes of the control and ampicillin treatments. Lake Huron, 15 October 1987: A—control treatment, $r^2 = 0.12$, $Y = 0.06X + 3.81$; B—ampicillin treatment, $r^2 = 0.80$, $Y = -0.22X + 3.81$. Lake Michigan, 10 May 1988: C—control treatment, $r^2 = 0.63$, $Y = -0.01X + 1.89$; D—ampicillin treatment, $r^2 = 0.98$, $Y = -0.12X + 1.93$.

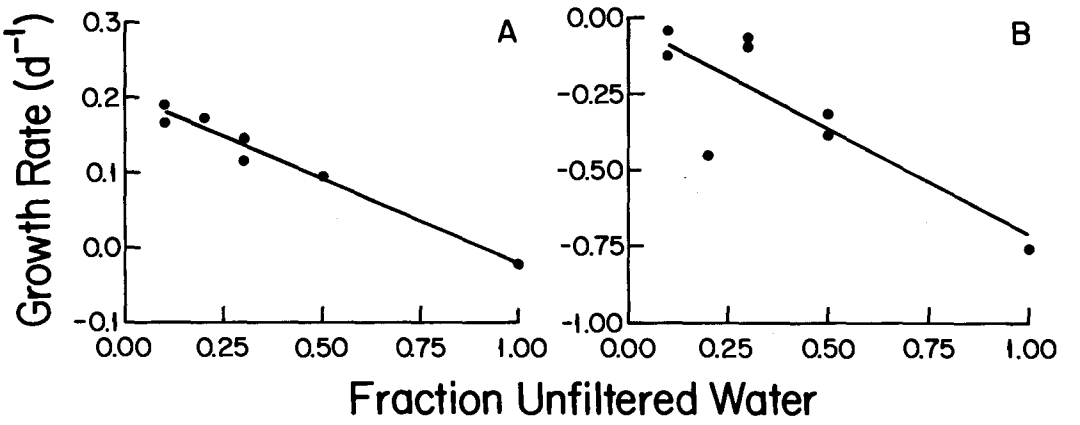

Fig. 3. Examples of results from dilution experiments where the slope represents the grazing rate and the intercept is the growth rate: A—Lake Michigan, 23 June 1987, $r^2 = 0.97$, $Y = -0.28X + 0.20$; B—Lake Huron, 29 July 1987, $r^2 = 0.68$, $Y = -0.69X - 0.02$.

and rotifers were the dominant grazers; in the >153-μm fraction, crustaceans were the only grazers noted. The greatest contribution of the >153-μm fraction to total grazing loss was only 10% and this occurred when *Daphnia* (i.e. *Daphnia retrocurva* and *Daphnia galeata*) constituted 40% of total crustacean biomass. The average contributions of the >153- and 30–153-μm fractions to total *Synechococcus* loss were 2.4 and 7.4%.

Species-specific filtering rates for selected grazers, as determined by assaying individual organisms for the uptake of ^{14}C-labeled *Synechococcus,* were quite variable among and within taxonomic groups (Table 6). In general, the cladocerans had the highest individual filtering rates; copepods, rotifers, and protozoans exhibited much lower filtering rates. *Daphnia galeata* and *D. retrocurva* exhibited the highest filtering rates, which were at least an order of magnitude higher than rates for any other taxon (Table 6). Within the same taxonomic group, pronounced differences in filtering rates were observed. For example, the smallest rotifer listed in Table 6, *Keratella cochlearis,* exhibited the highest mean filtering rate of any rotifer. Filtering rates for *Diaptomus minutus* were 2× higher than rates for *Diaptomus sicilis* and *Diaptomus ashlandii.* In some cases the most pronounced variability for relatively similar organisms was noted for the protozoan community. Several hetero-

Table 4. Grazing loss rates (d^{-1}) for *Synechococcus* by size classes of grazers in 1988. Percent of total grazing loss (<153 μm) also is estimated for each size class. Estimates were determined by prefractionated ampicillin experiments, and error estimates are standard errors.

	Fraction		
	0.2–8 μm	0.2–30 μm	0.2–153 μm
11 Apr—LM	0.11±0.04 (55%)	0.17±0.01 (85%)	0.20±0.02
21 Jun—LH	0.33±0.03 (61%)	0.49±0.04 (91%)	0.54±0.09
11 Jul—LM	0.33±0.02 (67%)	0.41±0.02 (84%)	0.49±0.04
26 Jul—LH	0.24±0.06 (73%)	0.30±0.03 (91%)	0.33±0.02
13 Oct—LH	0.24±0.01 (67%)	0.35±0.05 (97%)	0.36±0.06
Mean (%)	65	90	100

Table 5. Percent of total *Synechococcus* grazing loss by size fraction in 1988. Grazing loss rates were determined by the addition of ^{14}C-labeled *Synechococcus* cells.

	Fraction			
	2–8 μm	8–30 μm	30–153 μm	>153 μm
18 May—LH	72.6	19.3	7.5	0.5
13 Jun—LM	69.5	8.0	18.0	3.3
21 Jun—LH	66.0	25.0	4.2	1.4
11 Jul—LM	70.8	13.5	5.4	10.2*
25 Jul—LH	60.5	33.9	5.3	0.2
27 Jul—LH	72.6	22.2	4.2	1.1
13 Oct—LH	61.0	31.4	7.4	0.2
Mean	67.6	21.9	7.4	2.4
	2–12 μm	12–30 μm		
11 Apr—LM	87.0	12.0	0.7	0.2

* *Daphnia* constituted 40% of total crustacean biomass.

trophic flagellates had relatively high filtering rates, while others did not seem to ingest *Synechococcus* at all.

The differences among individual grazers must be considered in relation to their size and biomass as lengths of individual grazers varied from 6×10^{-3} mm to 2.3 mm. To facilitate comparisons, we calculated C-specific filtering rates for several individual grazers. In contrast to absolute rates, the highest C-specific filtering rates were found for the smallest organisms; protozoans exhibited the highest rates followed by rotifers, cladocerans, and copepods. *Ochromonas* exhibited a C-specific filtering rate at least 15× greater than *Keratella*; the *Keratella* C-specific rate was almost 10× greater than the *Daphnia* rate.

Discussion

Production, growth, and P-I *characteristics*—Although there is much variability in the contribution of *Synechococcus* and similar chroococcoid cyanobacteria in other aquatic environments, values from Lakes Huron and Michigan are similar to values reported from other freshwater environments and on the low end of values reported from marine environments. In Lakes Huron and Michigan, *Synechococcus* contributed on average 10% of surface mixed-layer primary production. Maximum contributions (as high as 26%) occurred during the period of thermal stratification which also was the period of maximum *Synechococcus* abundance (G. Fahnenstiel unpubl. data). Similarly, in three oligotrophic to mesotrophic lakes, *Synechococcus* or chroococcoid cyanobacteria contributed from 1 to 38% of

Table 6. Filtering rates (μl ind.$^{-1}$ h^{-1}) of selected grazers on ^{14}C-labeled *Synechococcus* cells.

	Mean	Range	*N*	Grazer length (mm)
Rotifers				
Asplanchna	0.6	—	1	0.7
Keratella cochlearis	1.6	0.8–3.4	6	0.1
Polyarthra dolichoptera	0.4	0.1–1.0	7	0.1
Crustaceans				
Daphnia retrocurva	250	—	1	1.0
Daphnia galeata	249	128–335	4	1.1
Bosmina	10.9	7.7–17.2	5	0.3
Diaptomus minutus	11.2	7.9–16.6	5	1.0
Diaptomus sicilis	4.7	—	1	1.6
Diaptomus ashlandii	4.5	1.9–6.9	4	1.2
Limnocalanus macurus	2.6	—	1	2.3
Cyclops bicuspidatus	1.2	0.8–1.6	2	1.0
Diaptomus C1–C5	4.8	1.0–9.8	8	0.8
Nauplii	0.7	0.1–1.0	7	0.3
Protozoans				
Katablepharis	14.4×10^{-3}	$5.0–30.1\times10^{-3}$	6	0.008×10^{-3}
Ochromonas	29.0×10^{-3}	$12.0–40.0\times10^{-3}$	5	0.006×10^{-3}
Rhodomonas minuta	0.3×10^{-3}	$0.0–0.6\times10^{-3}$	3	0.012×10^{-3}
Urotricha	23.5×10^{-3}	$15.0–30.0\times10^{-3}$	3	0.015×10^{-3}
Strobolidium	19.0×10^{-3}	$6.0–62.0\times10^{-3}$	3	0.010×10^{-3}
Strombidium	1.0×10^{-3}	$0.0–2.0\times10^{-3}$	2	0.040×10^{-3}

primary production (Caron et al. 1985; Fahnenstiel et al. 1986; Weisse 1988). However, in marine environments, the contribution of *Synechococcus* has been reported to be from 5 to 95% with highest values from the open oceans (Glover et al. 1986; Waterbury et al. 1986; Iturriaga and Marra 1988). Some of the variability in marine values may be related as much to methods as to environmental variability. The commonly used postincubation differential filtration can produce artificially high estimates of the contribution of picoplankton such as *Synechococcus* (Waterbury et al. 1986; G. Fahnenstiel unpubl. data). Thus, the very high estimates based solely on postincubation differential filtration may need further evaluation.

Estimates of *Synechococcus* growth may also be method-dependent. Although SIG, ampicillin, and ^{14}C estimates of growth rate were relatively similar (ANOVA of paired differences, all values of $P > 0.1$), dilution growth rates were lower than the other estimates ($P < 0.01$), particularly during thermal stratification. Moreover, substantial variability was noted among all estimates on any one date (Table 2). The lower dilution growth rates may have been caused by the nutrient addition (0.6 μM P liter^{-1}) given to each incubation bottle to ensure a constant growth rate between dilution treatments. Large nutrient additions to nutrient-limited cells, such as those found during thermal stratification in Lakes Huron and Michigan, can cause a shift from photosynthesis to nutrient uptake (Healey 1979). This metabolic shift may have contributed to the lower growth estimates in dilution experiments.

Our growth rates for *Synechococcus* were lower than most values reported for *Synechococcus* from other aquatic environments. If dilution growth rates are excluded, the mean growth rate of *Synechococcus* in Lakes Huron and Michigan was ~0.37 d^{-1} with a range of 0.1–0.9. Values >0.5 d^{-1} were observed for only 10% of the experiments (Table 2). However, *Synechococcus* growth rates in the marine environment ranged from 0.4 to 8.9 d^{-1} with most values between 0.5 and 2.0 (*see* Stockner and Antia 1986; Campbell and Carpenter 1986*b*; Iturriaga and Marra 1988). Growth rates from freshwater environments are generally lower than marine estimates, but still range from 0.1 to 1.5 d^{-1} with mean values of 0.6 and 1.0 d^{-1}, respectively (Fahnenstiel et al. 1986; Weisse 1988). Because there was significant overlap in the techniques used among studies (ampicillin and ^{14}C uptake) and because numerous estimates were made in Lakes Huron and Michigan, our lower estimates are noteworthy and probably reflect differences between clones or environments.

As might be expected by our lower growth rates, our P_{max} values for *Synechococcus* were on the low end of values reported from other aquatic environments. Our P_{max} values for *Synechococcus* ranged from 1.9 to 6.0 fg C cell^{-1} h^{-1} with a mean of 3.8 (Table 2), whereas P_{max} for *Synechococcus* from the marine environment ranged from 2 to 40 fg C cell^{-1} h^{-1} with most values around 10 (Prézelin et al. 1986, 1987; Iturriaga and Marra 1988). P_{max} values of 6 and 7 fg C cell^{-1} h^{-1} were reported from Lake Superior (Fahnenstiel et al. 1986).

Earlier work in the marine environment suggested that *Synechococcus* generally was adapted to low irradiance as indicated by its susceptibility to photoinhibition (Barlow and Alberte 1985) and by saturation of growth at low irradiances (Morris and Glover 1981). More recent work, in which no photohibition was found at irradiances as high as 7 Einst m^{-2} h^{-1}, has suggested that *Synechococcus* is euryphotic (Kana and Glibert 1987). Our work suggests that *Synechococcus* from Lakes Huron and Michigan is euryphotic and well adapted to irradiances found in the surface mixed layer. Although our maximal incubation irradiances were only 2–3 Einst m^{-2} h^{-1}, we did not detect photoinhibition in any of our experiments. Also, I_k values for *Synechococcus* ranged from 0.15 to 0.54 Einst m^{-2} h^{-1}; values in this range are common for temperate phytoplankton and do not suggest any specific adaptation to low light (Harris 1978). *Synechococcus* can also do well at low irradiances in these lakes as demonstrated by its abundance maximum at the depths of 0.5–5.0% isolumes during thermal stratification (G. Fahnenstiel unpubl. data).

Grazing loss—The relatively good agree-

ment among techniques for estimating grazing in our study (Table 3) is consistent with previous evaluations of the dilution and antibiotic techniques where more mixed results were found (Campbell and Carpenter 1986*b*; Saunders and Porter 1986; Sherr et al. 1986). The conditions in our study, i.e. high *Synechococcus* abundance and low grazing rates, contributed to the good agreement among techniques. Campbell and Carpenter (1986*b*) compared dilution and ampicillin techniques and found good agreement between estimates at a coastal station where *Synechococcus* abundances were relatively high, but at a warm-core eddy site with lower *Synechococcus* abundances only the ampicillin technique produced significant grazing estimates. The poor agreement at the warm-core site was related to low *Synechococcus* abundances and a threshold grazing effect. The abundance of *Synechococcus* in Lakes Huron and Michigan is generally above this threshold and in the range of values reported for the coastal station (G. Fahnenstiel unpubl. data). Furthermore, several investigators have questioned the use of antibiotic inhibitors because eucaryotic organisms may also be affected (Saunders and Porter 1986; Sherr et al. 1986). Because the effect of antibiotics is species-specific, it is difficult to extrapolate the work of Saunders and Porter (1986) and Sherr et al. (1986) to other environments; none of the ciliates studied by Saunders and Porter are common in Lakes Huron and Michigan (Carrick and Fahnenstiel 1990). Finally, the relatively large error associated with each estimate in our study (C.V. = 20–66%), makes discrimination among techniques difficult.

Grazing by heterotrophic organisms is an important loss for *Synechococcus* in Lakes Huron and Michigan as grazing loss rates ranged from 0.10 to 0.69 d^{-1}. For individual experiments, grazing balanced 33–130% of the growth rate (Table 7) suggesting that grazing was a major process controlling *Synechococcus* abundance. Maximal grazing rates were found during the June–August period of thermal stratification and were likely caused by increased abundances of the dominant grazers, protozoans (Carrick and Fahnenstiel 1989), and by increased filtering rates of these grazers.

Table 7. Combined best estimates (d^{-1}) of *Synechococcus* growth (A) and grazing (B) and the percent of growth that is balanced by grazing. Growth estimates are the mean from SIG, ampicillin, and ^{14}C-uptake experiments and grazing loss estimates are the mean from ampicillin, dilution, and ^{14}C-labeled *Synechococcus* experiments. Errors estimates are standard errors.

	A	B	B/A (%)
1 May 87	0.33±0.07	0.11±0.01	33
18 May 87	0.28±0.02	0.23±0.12	82
23 Jun 87	0.55±0.12	0.28±0.06	51
29 Jul 87	0.56±0.10	0.52±0.16	93
20 Aug 87	0.49±0.01	0.41±0.09	84
15 Oct 87	0.32±0.04	0.20±0.02	62
2 Nov 87	0.24±0.03	0.12±0.01	50
11 Apr 87	0.29±0.09	0.25±0.04	86
10 May 88	0.33±0.17	0.12±0.02	36
18 May 88	0.22±0.06	0.13±0.02	59
13 Jun 88	0.30±0.06	0.22±0.04	73
21 Jun 88	0.32±0.07	0.40±0.14	125
11 Jul 88	0.27±0.09	0.35±0.14	130
26 Jul 88	0.27±0.01	0.33±0.08	122
13 Oct 88	0.33±0.04	0.32±0.03	97

Grazing also plays a major role in controlling *Synechococcus* and chroococcoid cyanobacteria populations in other environments. In Lake Constance, grazing rates on phototrophic picoplankton, which were predominantly chroococoid cyanobacteria, were similar to growth rates (Weisse 1988). At two stations in the northwest Atlantic Ocean and at a third station in Long Island Sound, Campbell and Carpenter (1986*a*) examined the coupling between growth and grazing for *Synechococcus*. Growth and grazing were roughly balanced at a coastal Gulf of Maine station, but grazing accounted for 30–60% of growth at stations in a warm-core eddy and in Long Island Sound. From two studies in the North Pacific Ocean, grazing rates were ~15–40% of growth rates (Landry et al. 1984; Iturriaga and Mitchell 1986).

Few data exist for the quantitative role of specific grazers of *Synechococcus*, because most previous studies have focused on qualitative observations of ingestion by potential predators. Various organisms, i.e. microflagellates and rotifers, were found to ingest chroococcoid cyanobacteria in freshwater environments (Caron et al. 1985;

Fahnenstiel et al. 1986). Similarly, experiments with ^{14}C-labeled *Synechococcus* and autoradiography demonstrated that a diverse assemblage of micrograzers consumed and metabolized *Synechococcus* in the North Pacific Ocean (Iturriaga and Mitchell 1986).

It is clear from our results that qualitative observations on the grazing potential of various predators are of very limited value; most organisms examined had the ability to ingest *Synechococcus* (Table 6). However, organisms that passed an 8-μm screen were responsible for most (mean = 68%, range = 60–73%) grazing throughout our study (Tables 4 and 5). The dominant grazers in the <8-μm screen were heterotrophic protozoans (flagellates and ciliates) of 4–10-μm size. The importance of larger organisms decreased with increasing body size; the largest class (>153 μm, exclusively crustaceans) was responsible for only an average of 2.4% of the total grazing loss.

Small heterotrophic protozoans were consistently the major grazers despite substantial changes in the abundance and composition of the metazoan community. During the course of our study, rotifer and crustacean biomass varied from 0.1 to 2.0 and 10 to 150 μg liter^{-1}, respectively, and crustacean composition varied from 0 to 40% *Daphnia*; yet crustaceans and rotifers (>30 μm; Table 4) consistently accounted for only a small percentage (5–21%) of the total grazing on *Synechococcus*. When *Daphnia* was most abundant, there was a slight increase in the percent of *Synechococcus* grazed by organisms >153 μm, but protozoans were still responsible for most grazing (Table 5).

Our results are less dramatic than those noted for bacterial populations during food-web manipulations in a eutrophic lake (Riemann 1985). Major changes in bacterivory were noted when zooplankton abundance was manipulated through the removal or addition of fish. Zooplankton consumed 35–41% of the available bacteria when fish were removed and zooplankton biomass increased but consumed only 4–6% when fish were added and zooplankton biomass decreased. Most of this increased bacterivory by zooplankton occurred in the >140-μm size fraction. It should be noted, however, that these manipulations produced significant variability in the abundance of microflagellates (at least 20-fold) which is unlike any natural variability found in Lakes Huron and Michigan (Carrick and Fahnenstiel 1989). Therefore, the differences in responses of metazoan grazing on picoplankton populations between our study and those of Riemann (1985) are probably related to the differential food-web structure of the two environments and to the extreme conditions produced by the experimental manipulation.

The importance of small, heterotrophic protozoans in Lakes Huron and Michigan is further demonstrated by their relatively high C-specific filtering rates. C-specific clearance rates for the protozoan *Ochromonas* were at least one order of magnitude greater than the *Keratella* filtering rate and at least two orders of magnitude greater than the *Daphnia* filtering rate.

Previous information on filtering rates of various grazers on *Synechococcus* is limited mostly to rotifer and crustacean communities (Bogdan and Gilbert 1984; Lampert and Taylor 1985). Bogden and Gilbert (1984) examined the filtering rates of metazoan grazers on laboratory cultures of *Synechococcus*. Although their *Synechococcus* was significantly larger than ours (2 vs. 0.6 μm^3), the patterns of filtering rates among groups of organisms were similar to the results of our study. The filtering rates for rotifers and *Bosmina* were in the range of values reported here, but their rates for *D. minutus* were slightly higher than ours, perhaps due to the larger *Synechococcus* used in their study. Moreover, Lampert and Taylor (1985), in a study of the dominant herbivores in a small eutrophic lake, found *Daphnia* filtering rates on *Synechococcus* of ~250 μl animal^{-1} h^{-1}, which are similar to our filtering rates for *Daphnia* (Table 6).

Despite limited information about filtering rates on *Synechococcus*, much information exists for filtering rates of a variety of grazers on bacterial populations (DeMott and Kerfoot 1982; Porter et al. 1983; Sherr et al. 1989). This information can be used for comparisons to rates on *Synechococcus* even though heterotrophic bacteria are generally smaller and more abundant than *Syn-*

echococcus in most environments (Stockner and Antia 1986). The filtering rates we observed for various groups of grazers on *Synechococcus* are in the range of values reported for similar organisms grazing on bacteria. Filtering rates for similar-sized *Daphnia* and *Bosmina* have been reported to range from 10 to 1,300 μl animal^{-1} h^{-1} for *Daphnia* (Peterson et al. 1978; DeMott and Kerfoot 1982; Porter et al. 1983) and from 4 to 210 μl animal^{-1} h^{-1} for *Bosmina* (DeMott and Kerfoot 1982; Porter et al. 1983). Protozoan filtering rates on bacteria have been reported to range from 14 to 308 nl animal^{-1} h^{-1} for ciliates (Sherr et al. 1989) and from 1 to 336 nl animal^{-1} h^{-1} for microflagellates (Sherr et al. 1986).

Bacterivory by ciliates and phytoflagellates has received much attention during the last few years because earlier work suggested that these organisms were not significant grazers of bacteria (Azam et al. 1983). More recently, Sherr et al. (1986) and Sherr and Sherr (1987) reported high filtering rates of ciliates on bacteria and suggested that ciliates were major consumers of them. Our work extends the observations on the importance of ciliate grazing to *Synechococcus* populations. Ciliates exhibited filtering rates comparable to flagellates and accounted for a significant fraction of total grazing by protozoa (Table 6). Also, previous investigators have noted bacterivory by microflagellates that contained chlorophyll and have suggested that these phytoflagellates may be responsible for most bacterivory (Porter 1988). Although we noted ingestion of *Synechococcus* by phytoflagellates, phytoflagellates were responsible for only a small percentage (<8%) of total protozoan grazing. Filtering rates for the one phytoflagellate listed in Table 6, *Rhodomonas minuta,* were at least one order of magnitude lower than rates of two smaller heterotrophic flagellates, *Katablepharis* and *Ochromonas.*

In conclusion, *Synechococcus* is an important contributor to primary production in Lakes Huron and Michigan, especially during thermal stratification. The role of *Synechococcus* in the Great Lakes food web is different than the role of larger (>5 μm), more frequently studied phytoplankton such as diatoms, filamentous blue-greens, greens, and flagellates. *Synechococcus* exhibits higher growth rates (0.1–0.9 d^{-1}), and grazing is the principal loss, whereas larger phytoplankton exhibit lower growth rates (0.05–0.40 d^{-1}, Fahnenstiel and Scavia 1987; G. Fahnenstiel and H. Carrick) and several loss pathways (sedimentation, grazing, and autolysis) are important (Scavia and Fahnenstiel 1987). Furthermore, small heterotrophic protozoans (<10 μm) are the dominant grazers of *Synechococcus,* whereas metazoans are the dominant grazers of larger phytoplankton (Scavia and Fahnenstiel 1987). Thus, because of their small size and their consumption by small grazers, *Synechococcus* probably plays a more important role in the recycling and retention of C within the euphotic zone rather than in the transfer of C to higher trophic levels, i.e. zooplankton and fish.

References

AZAM, F., AND OTHERS. 1983. The ecological role of water-column microbes in the sea. Mar. Ecol. Prog. Ser. **10:** 257–263.

BARLOW, R. G., AND R. S. ALBERTE. 1985. Photosynthetic characteristics of phycoerythrin-containing marine *Synechococcus* spp. Mar. Biol. **86:** 63–74.

BEETON, A. M. 1965. Eutrophication of the St. Lawrence Great Lakes. Limnol. Oceanogr. **10:** 240–254.

BOGDAN, K. G., AND J. J. GILBERT. 1984. Body size and food size in freshwater zooplankton. Proc. Natl. Acad. Sci. **81:** 6427–6431.

CAMPBELL, L., AND E. J. CARPENTER. 1986*a*. Estimating the grazing pressure of heterotrophic nanoplankton on *Synechococcus* spp. using the sea water dilution and selective inhibitor techniques. Mar. Ecol. Prog. Ser. **33:** 121–129.

———, AND ———. 1986*b*. Diel patterns of cell division in marine *Synechococcus* spp. (Cyanobacteria): Use of the frequency of dividing cells technique to measure growth rate. Mar. Ecol. Prog. Ser. **32:** 139–148.

CARNEY, H. J., AND G. L. FAHNENSTIEL. 1987. Quantification of track and grain density autoradiography and evaluation of ^{14}C loss on preservation. J. Plankton Res. **9:** 41–50.

CARON, D. A., F. R. PICK, AND D. R. S. LEAN. 1985. Chroococcoid cyanobacteria in Lake Ontario: Vertical and seasonal distributions during 1982. J. Phycol. **21:** 171–175.

CARRICK, H. J., AND G. L. FAHNENSTIEL. 1989. Biomass, size structure, and composition of phototrophic and heterotrophic nanoflagellate communities in Lakes Huron and Michigan. Can. J. Fish. Aquat. Sci. **46:** 1922–1928.

———, AND ———. 1990. Planktonic protozoa in

lakes Huron and Michigan: Seasonal abundance and composition of ciliates and dinoflagellates. J. Great Lakes Res. **16:** 319–329.

DEMOTT, W. R., AND W. C. KERFOOT. 1982. Competition among cladocerans: Nature of the interaction between *Bosmina* and *Daphnia*. Ecology **63:** 1949–1966.

DOBSON, H. F. M., M. GILBERTSON, AND P. G. SLY. 1974. A summary and comparison of nutrients and related water quality in Lakes Erie, Huron and Superior. J. Fish. Res. Bd. Can. **31:** 731–738.

FAHNENSTIEL, G. L., J. F. CHANDLER, H. J. CARRICK, AND D. SCAVIA. 1989. Photosynthetic characteristics of phytoplankton communities in Lakes Huron and Michigan: P-I parameters and end-products. J. Great Lakes Res. **15:** 394–407.

———, AND D. SCAVIA. 1987. Dynamics of Lake Michigan phytoplankton: Primary production and growth. Can. J. Fish. Aquat. Sci. **44:** 499–508.

———, L. SICKO-GOAD, D. SCAVIA, AND E. F. STOERMER. 1986. Importance of picoplankton in Lake Superior. Can. J. Fish. Aquat. Sci. **43:** 235–240.

GLOVER, H. E. 1985. The physiology and ecology of the marine cyanobacterial genus *Synechococcus*. Adv. Aquat. Microbiol. **3:** 49–107.

———, L. CAMPBELL, AND B. B. PRÉZELIN. 1986. Contribution of *Synechococcus* spp. to size-fractionated primary productivity in three water masses in the northwest Atlantic Ocean. Mar. Biol. **91:** 193–203.

HARRIS, G. P. 1978. Photosynthesis, productivity, and growth: The physiological ecology of phytoplankton. Ergeb. Limnol. **10:** 1–171.

HEALEY, F. P. 1979. Short-term responses of nutrient-deficient algae to nutrient additions. J. Phycol. **15:** 289–299.

ITURRIAGA, R., AND J. MARRA. 1988. Temporal and spatial variability of chroococcoid cyanobacteria *Synechococcus* spp. specific growth rates and their contribution to primary production in the Sargasso Sea. Mar. Ecol. Prog. Ser. **44:** 175–181.

———, AND B. G. MITCHELL. 1986. Chroococcoid cyanobacteria: A significant component in the food web dynamics of the open ocean. Mar. Ecol. Prog. Ser. **28:** 291–297.

JOINT, I. R. 1986. Physiological ecology of picoplankton in various oceanographic provinces, p. 287–309. *In* Photosynthetic picoplankton. Can. Bull. Fish. Aquat. Sci. 214.

KANA, T. M., AND P. M. GLIBERT. 1987. Effect of irradiances up to 2000 μE m^{-2} s^{-1} on marine *Synechococcus* WH7803—1. Growth, pigmentation, and cell composition. Deep-Sea Res. **34:** 479–495.

LAMPERT, W., AND B. E. TAYLOR. 1985. Zooplankton grazing in a eutrophic lake: Implications of diel vertical migration. Ecology **66:** 68–82.

LANDRY, M. R., L. W. HAAS, AND V. L. FAGERNESS. 1984. Dynamics of microbial plankton communities: Experiments in Kaneohe Bay, Hawaii. Mar. Ecol. Prog. Ser. **16:** 127–133.

LIN, C. K., AND C. L. SCHELSKE. 1981. Seasonal variation of potential nutrient limitation to chlorophyll production in southern Lake Huron. Can. J. Fish. Aquat. Sci. **38:** 1–9.

MORRIS, I., AND H. E. GLOVER. 1981. Physiology of photosynthesis by marine coccoid cyanobacteria—some ecological implications. Limnol. Oceanogr. **26:** 957–961.

PETERSON, B. J., J. E. HOBBIE, AND J. F. HANEY. 1978. *Daphnia* grazing on natural bacteria. Limnol. Oceanogr. **23:** 1039–1044.

PORTER, K. G. 1988. Phagotrophic phytoflagellates in microbial food webs. Hydrobiologia **159:** 89–97.

———, Y. S. FEIG, AND E. F. VETTER. 1983. Morphology, flow regimes, and filtering rates of *Daphnia, Ceriodaphnia,* and *Bosmina* fed natural bacteria. Oecologia **58:** 156–163.

PRÉZELIN, B. B., H. E. GLOVER, AND L. CAMPBELL. 1987. Effects of light intensity and nutrient availability on diel patterns of cell metabolism and growth in populations of *Synechococcus* spp. Mar. Biol. **95:** 469–480.

———, M. PUTT, AND H. E. GLOVER. 1986. Diurnal patterns in photosynthetic capacity and depth-dependent photosynthesis-irradiance relationships in *Synechococcus* spp. and larger phytoplankton in three water masses in the Northwest Atlantic Ocean. Mar. Biol. **91:** 205–217.

RIEMANN, B. 1985. Potential importance of fish predation and zooplankton grazing on natural populations of freshwater bacteria. Appl. Environ. Microbiol. **50:** 187--193.

SAUNDERS, R. W., AND K. G. PORTER. 1986. Use of metabolic inhibitors to estimate protozooplankton grazing and bacterial production in a monomictic eutrophic lake with an anaerobic hypolimnion. Appl. Environ. Microbiol. **52:** 101–107.

SCAVIA, D., AND G. L. FAHNENSTIEL. 1987. Dynamics of Lake Michigan phytoplankton: Mechanisms controlling epilimnetic communities. J. Great Lakes Res. **13:** 103–120.

SCHELSKE, C. L., E. D. ROTHMAN, E. F. STOERMER, AND M. A. SANTIAGO. 1974. Responses of phosphorus-limited Lake Michigan phytoplankton to factorial enrichments with nitrogen and phosphorus. Limnol. Oceanogr. **19:** 409–419.

SHERR, B. F., E. B. SHERR, T. L. ANDREW, R. D. FALLON, AND S. Y. NEWELL. 1986. Trophic interactions between heterotrophic protozoa and bacterioplankton in estuarine water analyzed with selective metabolic inhibitors. Mar. Ecol. Prog. Ser. **32:** 169–179.

SHERR, E. B., F. RASSOULZADEGAN, AND B. F. SHERR. 1989. Bactivory by pelagic choreotrichous ciliates in coastal waters of the NW Mediterranean Sea. Mar. Ecol. Prog. Ser. **55:** 235–240.

———, AND B. F. SHERR. 1987. High rates of consumption of bacteria by pelagic ciliates. Nature **325:** 710–711.

STANIER, R. Y., R. KUNISWAWA, R. MANDEL, AND G. COHEN-BAZIRE. 1971. Purification and properties of unicellular blue-green algae (Order Chroococcales). Bacteriol. Rev. **35:** 171–205.

STOCKNER, J. G., AND N. J. ANTIA. 1986. Algal picoplankton from marine and freshwater ecosys-

tems: A multidisciplinary perspective. Can. J. Fish. Aquat. Sci. **43**: 2472–2503.

WATERBURY, J. B., S. W. WATSON, R. R. L. GUILLARD, AND L. E. BRAND. 1979. Widespread occurrence of a unicellular, marine, planktonic cyanobacterium. Nature **277**: 293–294.

———, ———, F. W. VALOIS, AND D. G. FRANKS. 1986. Biological and ecological characterization of the marine unicellular cyanobacterium *Synechococcus*, p. 71–120. *In* Photosynthetic picoplankton. Can. Bull. Fish. Aquat. Sci. 214.

WEISSE, T. 1988. Dynamics of autotrophic picoplankton in Lake Constance. J. Plankton Res. **10**: 1179–1188.

Submitted: 23 March 1990
Accepted: 3 December 1990
Revised: 8 January 1991