Limnology (2001) 2:111–117

RESEARCH PAPER

Maiko Kagami · Jotaro Urabe

Phytoplankton growth rate as a function of cell size: an experimental test in Lake Biwa

Received: August 24, 2000 / Accepted: March 2, 2001

Abstract It is well known that algal growth rates decrease with increasing cell size. Most of these findings were, however, obtained under laboratory conditions. It is not clear if these allometric relationships are also applicable to in situ conditions. In the present study, the relationship between growth rates and cell size of algal species was examined seasonally in Lake Biwa by in situ dilution bioassays. The bioassays revealed that the highest growth rate of each species throughout the experiments was negatively correlated with cell size consistent with known allometric relationships. At each incubation experiment, however, growth rates were not necessarily correlated with cell size. This was true even when both macro- and micronutrients were added, although a substantial number of species responded to nutrient enrichment. These results showed that nutrient supplies affected algal species differently regardless of cell size and that factors other than nutrient supplies limited the growth rate of some algal species. Due to such species-specific differences in limiting factors, at any given time in situ growth rates of algae are not determined exclusively by cell size.

Key words Allometry · Growth rate · Cell size · Phytoplankton · Nutrient limitation

Introduction

The size structure of the phytoplankton community is an important component of food-web dynamics in aquatic habitats (Porter 1977; Sieburth et al. 1978; Lampert and Sommer 1997), since food preferences of herbivores (DeMott 1990; Sterner 1989a) and the vertical flux due to sinking depend strongly on algal size (Smayda 1970; Reynolds 1984; Kiørboe 1993). It is, therefore, crucial to clarify how algal growth rate relates to cell size in natural habitats. A biological law states that smaller organisms are metabolically more active (Peters 1983). In accordance with this law, mass-specific nutrient uptake and photosynthetic rates decrease with increasing algal cell size (Malone 1980). This trend suggests that growth rates should also change according to cell size. Indeed, a large number of studies have shown that algal growth rates decrease exponentially with increasing cell size (e.g., Reynolds 1984; Chisholm 1992; Tang 1995). However, these studies examined algal growth rates in laboratory cultures where sufficient light and nutrients were supplied. It is not clear whether the growth–size relationships of algae found in laboratory cultures also hold in natural habitats. In lakes, environmental conditions may not necessarily be constant or optimal for any algal species: nutrients, lights, and other factors would differently limit the growth of different algal species (Sommer 1988, 1989a). If factors that limit algal growth rates differ among species, growth–size relationships in situ may differ from those in culture studies. To understand algal size structure in particular habitats, therefore, it is essential to examine how algal cell size relates to growth rate under natural conditions.

In Lake Biwa, the largest lake in Japan, large-sized phytoplankton such as *Staurastrum dorsidentiferum* var. *ornatum* Glönbl dominate in biomass and contribute more than 50% of total primary production in most seasons (Tezuka 1984; Kawabata and Nakanishi 1994). If small phytoplankton species grow much faster than large phytoplankton species, then a dominance of large phytoplankton in Lake Biwa is explainable only if the large phytoplankton have extremely low loss rates. In fact, these large species are believed to be less preferentially grazed by zooplankton (Kawabata 1987; Urabe et al. 1996). However, large phytoplankton species are abundantly found even during the period when zooplankton biomass is limited, and therefore grazing pressure for small phytoplankton species is expected to be low. Thus, unlike the growth–size relationships established in laboratory cultures (Reynolds 1984; Chisholm 1992; Tang 1995), large phytoplankton species in Lake Biwa may grow at rates as fast as small cell species in

M. Kagami (✉) · J. Urabe
Center for Ecological Research, Kyoto University, Kamitanakami Hirano-cho 509-3, Otsu, 520-2113 Japan
Tel. +81-77-549-8240; Fax +81-77-549-8201
e-mail: kagami@ecology.kyoto-u.ac.jp

Table 1. Range and concentration of nutrients added to the bioassay bottles

Nutrient	Concentration (μM)
Macronutrients	
KH_2PO_4	2.5
$(NH_4)_2SO_4$	18.0
Na_2SiO_3 diluted by 0.1% Na_2CO_3	20.0
Micronutrients	
$CuSO_4 \cdot 5H_2O$	0.004
$ZnSO_4 \cdot 7H_2O$	0.080
$CoCl_2 \cdot 6H_2O$	0.050
$MnCl_4 \cdot 4H_2O$	0.900
$Na_2MoO_4 \cdot 2H_2O$	0.090
Na_2SeO_3	0.012
Na_3VO_4	0.010
$FeCl_3 \cdot 6H_2O$	3.70
$Na_2EDTA \cdot 2H_2O$	11.70

the lake. In the present study, we examined this possibility. For this purpose, incubation experiments with diluted lake water were performed in situ, and the growth rates of several algal species were estimated in relation to cell size.

Methods

Incubation experiments were performed on nine occasions during the periods from May to November 1997 and April to May 1998 at a pelagic site (35°11′N, 135°56′N) in the north basin of Lake Biwa. Lake water for experiments was collected from 2.5 m depth by a modified Van Dorn sampler and filtered through a 100-μm screen to remove large zooplankton. An aliquot of the filtrate was fixed with 0.4% acid Lugol's solution to determine the initial algal concentration. The remaining water was used for experiments. Water temperature was measured with a multiple vertical profiler (Sea Bird Electronics, SBE-25).

To initiate the experiments, <100 μm lake filtrate with plankton was further diluted 1:6.6 with 0.2 μm filtered lake water from the same depth to reduce the abundance of algal grazers passed through 100-μm mesh net and the possibility of nutrient depletion during the incubation. This dilution water was prepared by gentle filtration through 0.2-μm capsule filters (Gelman No. 12140). The diluted water was poured into four 250-ml polycarbonate bottles. Both micro- and macronutrients (Table 1) were added to two of these bottles (enriched treatment). The concentrations of phosphorus and nitrogen added to the bottles were based on previous studies (Urabe et al. 1995; Gurung and Urabe 1999). The composition of enriched micronutrients was determined according to COMBO (Kilham et al. 1998). The other two bottles received no nutrients and served as unenriched treatments. The bottles were incubated at 2.5 m depth where lake water was collected. We chose this depth as representative of the productive layer, because peaks of primary production rate and algal biomass were frequently found at 2.5 m depth in Lake Biwa (Nakanishi 1976; Kagami 1999). Incubation was performed for 48 h from 11:00 a.m. At the end of the incubation, samples were collected from each bottle to determine the final concentration of algae.

For enumeration, 100-ml plankton samples were concentrated to 1 ml by sedimentation for at least 2 days. All algal cells in the sample were then counted using a 1-ml Sedgwick-Rafter chamber at 200× and 400× magnification. In the present study, picoplankton was not included because the conventional method for algal counts could not enumerate them precisely at the species level. Cell volumes of algal species in Lake Biwa were obtained from the data of Ichise et al. (1995) if they were listed. For algal species that were not listed, cell volume was estimated as in Ichise et al. (1995). In short, cell volume was estimated from length measurements of at least 50 cells applied to common geometric shapes (Willen 1976). Since we used Lugol preserved samples, estimated values were converted to fresh cell volume with a conversion factor of 1.33 (Montagnes et al. 1994). As in Ichise et al. (1995), the cell volume of each algal species was estimated at various dates. Since temporal changes in cell volume of algal species were much smaller compared with the growth rate, we used average cell volume over seasons for each species.

Growth rates of phytoplankton (μ, day^{-1}) during 2-day incubations were estimated assuming exponential growth as follows:

$$\mu = (\ln N_2 - \ln N_0)/2 \quad (1)$$

where N_2 and N_0 are the cell densities of phytoplankton at the beginning and the end of the 2-day incubation. Growth rate was estimated for algal species that gave counts of more than 30 cells per single sample. Significant differences in algal growth rates between enriched and unenriched treatments were examined statistically by a one-tailed *t*-test, since we had expected higher growth rates in response to enrichment. Kendall's rank correlation test was applied to examine if the relationship between cell size and growth rate was significant in each experiment. In this analysis, we use μ calculated for each bottle rather than the mean value within treatments. We defined the highest growth rate of a given species throughout the course of the experiments, $\mu_{highest}$. To quantify the effect of cell size on $\mu_{highest}$, the data were fitted to the following power function:

$$\mu_{highest} = \alpha W^{\beta} \quad (2)$$

where $\mu_{highest}$ is the highest growth rate (day^{-1}), W is cell volume ($\mu m^3\ cell^{-1}$), and α and β are regression coefficients. Significant differences in the slope (β) and elevation (α) of the power function between unenriched and enriched treatments were examined by analysis of covariance (ANCOVA). These statistical tests were performed with the aid of a computer program package (StatView ver 5, SAS Institute Inc., Cary, North Carolina, USA).

Results

During the study period, the water temperature ranged from 11.9°C to 25.6°C at 2.5 m depth (Fig. 1). The highest

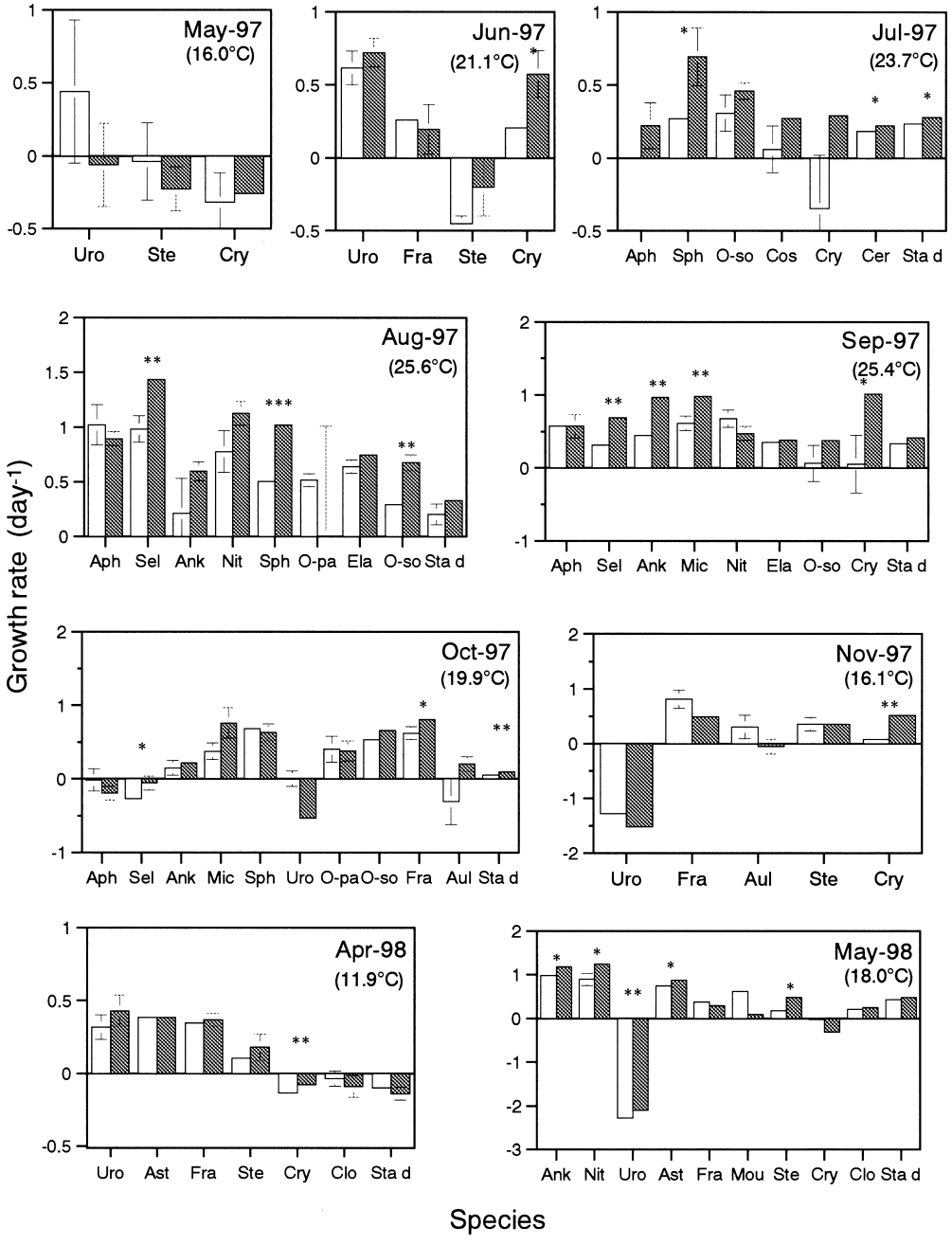

Fig. 1. Growth rate of each algal species in treatments with (*shaded bars*) and without (*open bars*) nutrient enrichment. A key to abbreviations for the phytoplankton species is given in Table 2. Cell size of phytoplankton shown in the X-axis increases from left to right. *Vertical lines* are the range of two measurements. Significant differences between treatments are denoted by *asterisks*: $*P < 0.05$, $**P < 0.025$, $***P < 0.0005$. The temperature at 2.5 m depth is indicated for each date

temperature was found in August 1997 and the lowest in April 1998. In spring, the dominant phytoplankton species in terms of biovolume was *Fragilaria crotonensis*, while *Staurastrum dorsidentiferum* dominated in summer to autumn. The number of species in which enough could be counted to estimate growth rate (>30 cells per sample) was 19 over all the experiments (Table 2). The cell volumes of these algal species ranged over five orders of magnitude from 2 μm^3 (*Aphanothece* sp.) to 32000 μm^3 (*Staurastrum dorsidentiferum*). Among these species, *Mougeotia* sp., *Cosmocladium constrictum*, and *Ceratium hirundinella* appeared abundantly in only one experiment. The other species occurred in sufficient abundance to estimate growth rates in more than two experiments.

Incubation experiments showed that growth rate (μ) differed markedly among species (Fig. 1). For example, in the experiments conducted in October, when 11 species were abundant, their growth rates varied from −0.3 to 0.7 day^{-1} in unenriched treatments. A similar range of variation in growth rate among species could be found in any experiment regardless of treatments. Growth rate also varied markedly between experiments within a single species. Growth rates of *Fragilaria crotonensis* were lower than 0.3 day^{-1} in June, but as high as 0.6 day^{-1} in October and November. In addition, *Aphanothece* sp. and *Selenastrum* sp. showed growth rates close to 1.0 day^{-1} in August, but their growth rates were almost zero in October.

Table 2. Cell volumes and abbreviations for the 19 phytoplankton species sufficiently abundant to be counted in the 2-day incubation experiments

Taxon	Abbreviation	Biovolume (μm^3)
Bacillariophyceae		
Asterionella formosa Hassal	Ast	350[a]
Aulacoseira granulata (Ehrenberg) Simonsen	Aul	1500[a]
Fragilaria crotonensis Kitton	Fra	755
Nitzschia spp.	Nit	30[a]
Stephanodiscus carconensis Grunow	Ste	4200[a]
Chlorophyceae		
Ankistrodesmus sp.	Ank	11
Closterium aciculare var. *subpronum* W.et G.S. West	Clo	9200[a]
Cosmocladium constrictum (Archer) Joshua	Cos	1600[a]
Mougeotia sp.	Mou	1086
Oocystis parva W.et G.S. West	O-pa	100
O. solitaria Wittrock	O-so	530[a]
Selenastrum sp.	Sel	12
Sphaerocystis schroeteri Chodat	Sph	74
Straurastrum dorsidentiferum var. *ornatum* Gronbl	Sta d	32000[a]
Chrysophyceae		
Uroglena americana (Calkins) Lemmermann	Uro	98[a]
Cryptophyceae		
Cryptomonas sp.	Cry	5337
Cyanophyceae		
Aphanothece sp.	Aph	2[a]
Microcystis sp.	Mic	14[a]
Dinophyceae		
Ceratium hirundinella (O.F. Muller) Schrank	Cer	30000[a]

[a] From Ichise et al. (1995)

The highest growth rates throughout the experiments in unenriched treatment were found for four species in August 1997 and May 1998. In October and November, three species had their highest growth rates. The highest growth rates were found for two species in June and for only one species in September. In May and July 1997 and April 1998, however, no species showed the highest growth rate in unenriched treatments.

The response of algae to nutrient enrichment differed among experiments. Growth stimulation by nutrient enrichment was not found at all in May 1997 and was found for only one species in June and November 1997 and in April 1998. However, 5 out of 10 species showed higher growth rates in enriched than in unenriched treatments in May 1998. In other months, the growth rates of three or four species were stimulated by nutrient enrichment.

In the present study, negative growth rates were sometimes detected for *Uroglena americana* and *Cryptomonas* sp. *U. americana* had negative growth rates in two of six cases in the unenriched treatment, and four times in the enriched treatment. Growth rates of *Cryptomonas* sp. were negative in four of seven cases in the unenriched treatments and three times in the enriched treatment. It should be noted that these two are mixotrophic species (Sanders and Porter 1988).

Rank correlation analysis revealed that growth rates were not always correlated with cell volume (Table 3). In unenriched treatments, growth rates correlated significantly with cell size only in August 1997 and in April and May 1998. In enriched treatments, significant correlation between these was found in April alone. The highest growth rates ($\mu_{highest}$) throughout the experiments correlated significantly with cell volume in both unenriched ($\tau = -0.560$, $P < 0.001$) and enriched ($\tau = -0.478$, $P < 0.001$) treatments.

Table 3. Rank correlation coefficients between growth rates (μ) and cell size (V) in treatments with (+N) and without (−N) nutrient enrichment

Month	*n*	τ	
		−N	+N
1997			
May	6	−0.596	−0.149
Jun	8	−0.54	−0.231
Jul	14	0.023	−0.357
Aug	18	−0.404*	−0.337
Sep	18	−0.337	−0.202
Oct	22	0.257	0.177
Nov	10	−0.047	0.471
1998			
Apr	14	−0.686**	−0.755**
May	20	−0.369*	−0.238

* $P < 0.05$
** $P < 0.01$

When the highest growth rate ($\mu_{highest}$) of each species was plotted against cell volume (V, μm^3), a significant negative correlation was found in both enriched and unenriched treatments (Fig. 2). These relationships could be described as follows:

$$\mu_{highest} = 1.24\, V^{-0.15} \ (r^2 = 0.441,\ P < 0.001) \quad \text{in unenriched treatment} \tag{3}$$

$$\mu_{highest} = 1.38\, V^{-0.13} \ (r^2 = 0.325,\ P < 0.001) \quad \text{in enriched treatment} \tag{4}$$

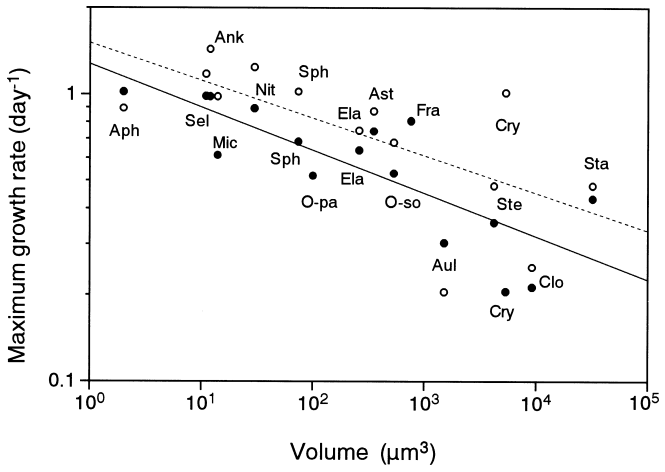

Fig. 2. Relationship between the highest growth rate (μ_{max}) and cell volume of various phytoplankton species in unenriched (*closed circles* and *thin line*) and enriched treatment (*open circles* and *dotted line*). A key to abbreviations for the phytoplankton species is given in Table 2

ANCOVA revealed that these two treatments did not differ significantly in either slope ($P = 0.62$) or elevation ($P = 0.69$).

Discussion

Several studies have shown that growth rates of phytoplankton species decrease with increasing cell size (e.g., Reynolds 1984; Chisholm 1992; Tang 1995). In the present study, the highest growth rate throughout in situ experiments was also lower for algal species with larger cell size. The exponent of the power function estimated in this study, −0.15 to −0.13, coincided closely with the value (−0.150) established by Tang (1995), who analyzed a total of 126 observations on growth rates of various algal taxa in culture experiments. This concordance suggests that the highest growth rate of algal species in situ is related to cell size in the same way as has been found in laboratory culture. Compared with the maximum growth rate in culture experiments (Tang 1995; Reynolds 1984), however, the highest growth rate at given cell size was lower in the present study. Several studies examining in situ growth rates of various algal species with different cell sizes showed that the highest growth rates generally ranged from 0.4 to 1.1 day^{-1} in mesotrophic to eutrophic lakes (Sommer 1988, 1989a, 1991; Sterner 1989b; Sterner and Grover 1998; Grover et al. 1999). The highest growth rates in the present study fell within this range. Thus, in natural habitats, most algae may not grow at the maximum rate found in laboratory cultures, even when environmental conditions are favorable.

Unlike the highest growth rates, algal growth rates in each experiment were not always correlated with cell size. This was true even when the samples were enriched with nutrients. Thus, the allometric relationship between growth rate and cell size does not necessarily hold for algal communities at a given time in natural habitats. In the present study, a substantial number of species did not respond to nutrient enrichment, although their growth rate was not high. In addition, the effects of nutrient enrichment differed among experiments even within the same species. The results suggest that nutrient limitation was important to some species but not to all.

Other than nutrient supplies, temperature, irradiance, and photoperiod are important factors regulating algal growth rates. It is known that these factors affect algal species differently, depending on the requirement of each species (Eppley 1972; Schlesinger et al. 1981; Langdon 1988). Laws (1975) suggested that under low light conditions, large phytoplankton species grow better than small species because of their low mass-specific respiration rate. This inference implies that the growth rate of algae is less related to cell size under low light conditions. In the north basin of Lake Biwa, the growth rates of algal communities have been shown to be limited mainly by phosphorus (Tezuka 1984, 1985; Frenette et al. 1996) and sometimes by nitrogen (Tezuka 1984). Urabe et al. (1999) suggested that not only nutrients but also light limited phytoplankton communities in a large part of the epilimnion in Lake Biwa. According to their results, phytoplankton were light limited at depths greater than 1 m. Since growth responses to light intensity differ among phytoplankton species, and since light and temperature as well as nutrient supplies differ seasonally, it is most likely that limiting factors differ among species at a given time in the natural habitat. Therefore, algal growth–size relationships would not be clear in most experiments.

In some experiments, significant relationships between growth rates and cell size were found. In August, when water temperature was high, many species grew at their highest rates under ambient conditions. Therefore, growth–size relationships could be detected in the unenriched treatment. In enriched treatments, however, algal growth was not correlated significantly with cell size. In this month, three out of nine species responded to nutrient enrichment with increased growth rates, but other species did not at all. This large difference in the response to nutrient enrichment among species might have made the growth–size relationship unclear. Similarly, a significant correlation between growth rate and cell size was found only in unenriched treatments in May 1998. In enriched treatments, different species might become limited by factors other than nutrients, such as light and temperature, because they were released from nutrient limitation. In April 1998, when no algal species responded to nutrient enrichment, their growth rates were correlated with size in both unenriched and enriched treatments. Since water temperature was low in this month, it is likely that the growth of most algal species was limited by water temperature. It is well known that algal growth rate depends highly on water temperature (e.g., Reynolds 1984). However, it is not clear how changes in water temperature affect growth–size relationships of algal species. The clear growth–size relationships found in April suggest that low water temperature might limit growth of most algal species to the same degree relative to their maximum growth rates.

It should be noted that removal of grazers >100 μm alone may have led to an underestimation of the growth rates of the smaller algae, because smaller grazers tend to ingest smaller algae (Lampert and Sommer 1997). In the present study, however, we diluted the lake filtrate with 0.2 μm lake water. This dilution would result in lower concentrations of smaller grazers and reduce grazing pressure on phytoplankton. Indeed, few metazoans and ciliates were found in samples collected at the end of 2-day incubations. However, we could not reject the possibility that heterotrophic nanoflagellates (HNF) might increase during the 2-day incubations because their growth rates are high (e.g., Gurung et al. 2000). However, these flagellated protozoans ingest mainly picoplankton (Porter 1996), which were not included in the present analysis. Thus, effects of small grazers that might be passed through a 100-μm screen would not be large in the present study.

One may suspect that unclear relationships between growth rate and cell size in enriched treatments might be due to species-specific differences in delay of response to nutrient enrichment or ability to store nutrients within the cell due to luxury uptake (Sommer 1989b). Frenette et al. (1996) suggested that differences in light and nutrient history caused unclear relationships between algal size and their nutrient uptake rates. These possibilities imply that algal species do not respond equally to changes in environmental conditions at the same time scale. Thus, algal growth rates would not be correlated with cell size at a given time in their natural habitat.

During the study period, negative growth rates were sometimes observed, especially for algae with a phagotrophic mode of nutrition, such as *Uroglena americana*. In enriched treatments, their growth rates might be negatively affected by the addition of nutrients, since these species are known to be sensitive to changes in mineral concentrations (Lehman 1976; Sandgren 1988). However, negative growth rates were also found even when no nutrients were added. Thus, we could not attribute the negative growth rate to nutrient enrichment alone. Dilution with 0.2 μm lake filtrate might contribute to lower growth rates of mixotrophic algae, because the dilution decreased bacterial concentrations. In other experiments performed in Lake Biwa, we found that growth rates of *U. americana* depended on bacterial concentration (Urabe et al., in preparation).

The mechanism behind the relationships between growth rate and cell size among phytoplankton species was originally explained by surface to volume ratio (S/V) as Rubner's surface rule (Bertalanffy 1951). In the present study, cell size was expressed as cell volume. The morphology of algal species is, however, diverse and differs largely from a sphere. Some species, such as *Staurastrum* sp., have long, hornlike projections, and other algal forms have platelike or ellipsoidal shapes. These morphological characteristics change S/V even if cell volume is the same. It should be noted that only 45% of the variance of the highest growth rates of phytoplankton was explained by cell volume or carbon content. If size were expressed as surface/volume, more variance in highest growth rates might be explained.

In conclusion, although the highest growth rates of algal species are a function of cell size, it does not necessarily hold that smaller species have higher growth rates in situ. The absence of a clear relationship between algal growth rate and cell size probably stems from the fact that the effects of nutrients, light, and water temperature differ among algal species regardless of algal size. In Lake Biwa, large phytoplankton such as *Staurastrum dorsidentiferum* and *Closterium aciculare* are abundant, dominate in biomass, and contribute to more than 50% of total primary production in most seasons (Tezuka 1984; Kawabata and Nakanishi 1994). Dominance of these large phytoplankton species has sometimes been explained by low vulnerability to zooplankton grazing (e.g., Kilham 1988; Sterner 1989a). In Lake Biwa, the growth rates of these large phytoplankton species were not always lower than those of smaller species and were sometimes higher. Thus, species-specific factors regulating growth rate may also contribute to the dominance of large phytoplankton species in Lake Biwa.

Acknowledgments We appreciate Dr. S. Kilham's reviewing our manuscript. We thank Mr. T. Koitabashi, Mr. T. Ueda, T.B. Gurung, and T. Yoshida, for their help during the experiments. We are grateful to M. Nakanishi, S. Flöder, and members of the aquatic ecology seminar group in CER, Kyoto University, for their invaluable discussions. This study was supported by a Grant-in-Aid for scientific research (A) No. 10308025 and a Japanese Ministry of Education, Science and Culture, Grant-in-Aid for Creative Basic Research (09NP1501).

References

Bertalanffy LV (1951) Metabolic types and growth types. Am Nat 85:111–117

Chisholm SW (1992) Phytoplankton size. In: Falkowski PG, Woodhead WD (eds) Primary productivity and biochemical cycles in the sea. Plenum Press, New York, pp 137–213

DeMott WR (1990) Retention efficiency, perceptual bias, and active choice as mechanisms of food selection by suspension-feeding zooplankton. In: Hughes RN (ed) Behavioral mechanisms of food selection. Springer-Verlag, Berlin, Heidelberg, pp 569–594

Eppley RW (1972) Temperature and phytoplankton growth in the sea. Fish Bull 70:1063–1085

Frenette JJ, Vincent WF, Legendre L, Nagata T (1996) Size-dependent phytoplankton responses to atmospheric forcing in Lake Biwa. J Plankton Res 18:371–391

Grover JP, Sterner RW, Robinson JL (1999) Algal growth in warm temperate reservoirs: nutrient-dependent kinetics of individual taxa and seasonal patterns of dominance. Arch Hydrobiol 145:1–23

Gurung TB, Urabe J (1999) Temporal and vertical difference in factors limiting growth rate of heterotrophic bacteria in Lake Biwa. Microb Ecol 38:136–145

Gurung TB, Nakanishi M, Urabe J (2000) Seasonal and vertical difference in negative and positive effects of grazers on heterotrophic bacteria in Lake Biwa. Limnol Oceanogr 45:1689–1696

Ichise S, Wakabayashi T, Matsuoka Y, Yamanaka S, Fujiwara N, Tanaka K (1995) A simple method for the estimation of phytoplankton biomass based on cell morphology in Lake Biwa. Rep Shiga Pref Inst Pub Hlth Environ Sci 30:27–35

Kagami M (1999) Dyanamics and functions of large phytoplankton in Lake Biwa. Master's thesis, Kyoto University (in Japanese)

Kawabata K (1987) Ecology of large phytoplankters in Lake Biwa: population dynamics and food relations with zooplankters. Bull Plankton Soc Jpn 34:165–172

Kawabata K, Nakanishi M (1994) Food web structure and biodiversity in lake ecosystems. In: Abe T, Levin SA, Higashi M (eds) Biodiversity: an ecological perspective. Springer, Berlin, pp 203–213

Kilham SS (1988) Phytoplankton responses to changes in mortality rates. Verh Int Ver Theor Angew Limnol 23:677–682
Kilham SS, Kreeger DA, Lynn SG, Goulden CE, Herrera L (1998) COMBO: a defined freshwater culture medium for algae and zooplankton. Hydrobiologia 377:147–159
Kiørboe T (1993) Turbulence, phytoplankton cell size, and the structure of pelagic food webs. In: Blaxter JHS, Southward AJ (eds) Advances in Marine Biology. Vol 29. Academic Press, London, pp 1–72
Lampert W, Sommer U (eds) (1997) Limnoecology: the ecology of lakes and streams. Oxford University Press, New York
Langdon C (1988) On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton. II. A general review. J Plankton Res 10:1291–1312
Laws EA (1975) The importance of respiration losses in controlling the size distribution of marine phytoplankton. Ecology 56:419–426
Lehman JT (1976) Ecological and nutritional studies on *Dinobryon* Ehrenb.: seasonal periodicity and the phosphate toxicity problem. Limnol Oceanogr 21:646–658
Malone TC (1980) Algal size. In: Morris I (ed) The physiological ecology of phytoplankton. Blackwell Scientific Publications, Oxford, pp 433–463
Montagnes DJS, Berges JA, Harrison PJ, Taylor FJR (1994) Estimating carbon, nitrogen, protein and chlorophylla from volume in marine phytoplankton. Limnol Oceanogr 39:1044–1060
Nakanishi M (1976) Seasonal variations of chlorophyll *a* amounts, photosynthesis and production rates of macro and microphytoplankton in Shiozu Bay, Lake Biwa. Physiol Ecol Japan 17: 535–549
Peters RH (ed) (1983) The ecological implications of body size. Cambridge University Press, Cambridge
Porter KG (1977) The plant-animal interface in freshwater ecosystems. Am Sci 65:159–170
Porter KG (1996) Integrating the microbial loop and the classic food chain into a realistic planktonic food web. In: Polis GA, Winemiller KO (eds) Food web. Chapman & Hall, New York, pp 51–59
Reynolds CS (ed) (1984) The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge
Sanders RW, Porter KG (1988) Phagotrophic phytoflagellates. In: Marshall KC (ed) Advances in Microbial Ecology. Vol 10. Plenum, New York, pp 167–192
Sandgren CD (1988) The ecology of chrysophyte flagellates: their growth and perennation strategies as freshwater phytoplankton. In: Sandgren CD (ed) Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press, Cambridge, pp 9–194
Schlesinger DA, Molot LA, Shuter BJ (1981) Specific growth rates of freshwater algae in relation to cell size and light intensity. Can J Fish Aquat Sci 38:1052–1058
Sieburth JM, Smetacek V, Lenz J (1978) Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. Limnol Oceanogr 23:1256–1263
Smayda TJ (1970) The suspension and sinking of phytoplankton in the sea. Oceanogr Mar Biol Annu Rev 8:353–414
Sommer U (1988) Does nutrient competition among phytoplankton occur in situ? Verh Internat Verein Limnol 23:707–712
Sommer U (1989a) Nutrient status and nutrient competition of phytoplankton in a shallow, hypertrophic lake. Limnol Oceanogr 34:1162–1173
Sommer U (1989b) The role of competition for resources in phytoplankton succession. In: Sommer U (ed) Plankton ecology: succession in plankton communities. Springer, Berlin, pp 57–106
Sommer U (1991) A comparison of the Droop and the Monod models of nutrient limited growth applied to natural populations of phytoplankton. Funct Ecol 5:535–544
Sterner RW (1989a) The role of grazers in phytoplankton succession. In: Sommer U (ed) Plankton ecology: succession in plankton communities. Springer, Berlin, pp 107–170
Sterner RW (1989b) Resource competition during seasonal succession toward dominance by cyanobacteria. Ecology 70:229–245
Sterner RW, Grover JP (1998) Algal growth in warm temperate reservoirs: kinetic examination of nitrogen, temperature, light, and other nutrients. Water Res 32:3539–3548
Tang EP (1995) The allometry of algal growth rates. J Plankton Res 17:1325–1335
Tezuka Y (1984) Seasonal variations of dominant phytoplankton, chlorophyll *a* and nutrient levels in the pelagic regions of Lake Biwa. Jpn J Limnol 45:26–37
Tezuka Y (1985) C:N:P ratios of seston in Lake Biwa as indicators of nutrient deficiency in phytoplankton and decomposition process of hypolimnetic particulate matter. Jpn J Limnol 46:239–246
Urabe J, Nakanishi M, Kawabata K (1995) Contribution of metazoan plankton to the cycling of nitrogen and phosphorus in Lake Biwa. Limnol Oceanogr 40:232–241
Urabe J, Kawabata K, Nakanishi M, Shimizu K (1996) Grazing and food selection of zooplankton community in Lake Biwa during BITEX '93. Jpn J Limnol 57:27–37
Urabe J, Sekino T, Nozaki K, Tsuji A, Yoshimizu C, Kagami M, Koitabashi T, Miyazaki T, Nakanishi M (1999) Light, nutrients and primary productivity in Lake Biwa: an evaluation of the current ecosystem situation. Ecol Res 14:233–242
Willen E (1976) A simplified method of phytoplankton counting. Br Phycol 11:265–278