Journal of Plankton Research Vol.20 no.3 pp.571–584, 1998

Comparative growth rates and yields of ciliates and heterotrophic dinoflagellates

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Abstract. Growth rates, ingestion rates and grazer yields (grazer volume produced/prey volume consumed) were measured for six protozoan species (ciliates: *Favella* sp., *Strombidinopsis acuminatum*, *Uronema* sp.; heterotrophic dinoflagellates: *Amphidinium* sp., *Gymnodinium* sp., *Noctiluca scintillans*) in laboratory batch culture experiments. Comparative growth data indicate that the prymnesiophyte *Isochrysis galbana*, the prasinophyte *Mantoniella squamata*, two cryptophyte species and several autotrophic dinoflagellate species were suitable foods for these grazers. When grown on optimized diets at 13°C, maximum ciliate growth rates (range 0.77–1.01 day^{-1}) uniformly exceeded maximum heterotrophic dinoflagellate growth rates (range 0.41–0.48 day^{-1}). A compilation of published data demonstrates that this growth rate difference persists across a range of ciliate and dinoflagellate taxa and cell sizes. Comparison of volume-specific ingestion rates and yields for the six species studied here showed that there was no single explanation for this growth rate disparity. Heterotrophic dinoflagellates exhibited both low ingestion rates and, in one case, low yields; ciliates were able to achieve higher growth rates via either higher ingestion rates or higher yields, depending on ciliate species. Volume yield increased over time throughout the exponential growth phase in nearly all experiments, suggesting variation in response to changing food concentrations or long-term acclimation to culture conditions. Higher maximum ciliate growth rates mean that these grazers have the potential to exercise tighter control over incipient blooms of their prey than do heterotrophic dinoflagellates.

Introduction

Experimental work over the past decade has demonstrated that protozoans are major grazers of both bacteria and algae in many ocean regions (summarized by Pierce and Turner, 1992; Sherr and Sherr, 1993). This finding was forecast by Pomeroy (1974), who postulated that the abundant small producers in the ocean (e.g. bacteria and ultraphytoplankton) must support active communities of small consumers. As herbivores, protozoa are capable of ingesting cells ranging from <1 μm photosynthetic prokaryotes to large chain diatoms (e.g. Landry *et al.*, 1984; Campbell and Carpenter, 1986; Jacobson and Anderson, 1986; Strom and Strom, 1996). Further, protozoan population growth rates can be high (>2 doublings day^{-1}), such that increases in grazer biomass can potentially keep pace with increases in algal prey (Banse, 1992). These grazing and growth capabilities, along with the results of field grazing rate assessments, demonstrate that protozoan grazers are important regulators of algal biomass and species composition in the sea.

Despite their evident importance in planktonic food webs, we still know little of the basic biology of planktonic protozoa. Taxonomy, life cycles, successional patterns and effects of environment on ecological rates remain poorly described. Contrast this with the situation for the other major group of planktonic grazers: the metazooplankton. The large amount of biological information available for many of these species has enabled researchers to describe the implications for

elemental and energy cycling of communities dominated by, for example, small copepods, larvaceans or krill (Michaels and Silver, 1988; Verity and Smetacek, 1996). A similarly wide range of taxonomy, morphology and behavior characterizes the planktonic protozoa, with equally large implications for the structure and function of planktonic food webs.

Here we present comparative data on rates of growth and ingestion by six species of planktonic protozoans: three ciliates and three heterotrophic dinoflagellates. Ciliates and heterotrophic dinoflagellates can be dominant members of planktonic grazer communities, particularly in coastal and polar regions (Garrison, 1991; Lessard, 1991; Pierce and Turner, 1992). Although it has been hypothesized that ciliates have higher potential population growth rates than heterotrophic dinoflagellates (Strom, 1991; Hansen, 1992), no previous studies have compared the two experimentally. We found that, when provided optimized diets, ciliates consistently grew at higher rates than heterotrophic dinoflagellates. No single underlying parameter sufficed to explain growth rate differences; rather, both ingestion rates and grazer yields contributed to the growth rate disparity between these two protozoan groups.

Method

Unialgal stock cultures (Table I) were maintained in f/2 medium without added silicate (Guillard and Ryther, 1962). Protozoa (Table I), isolated from Oregon coastal waters (*Uronema* sp.) or northern Puget Sound (all others), were maintained on algal mixtures in a trace metal-enriched seawater medium (Gifford, 1985). Preliminary experiments were conducted to determine which single algal species would support survival or growth of protozoa. Protozoa were combined with algae in cell well plates or tissue culture flasks (Table II) and visually inspected at 1–2 day intervals for survival or growth. Additional food trials were then conducted with all possible paired combinations of algal species that, singly,

Table I. Dimensions of species used in experiments. n = 40 (algae) or 50 (grazers); values in parentheses are lorica dimensions for *Favella* sp. All cells were preserved in 5% (final concentration) acid Lugol's. Length (L) and width (W) are in μm, volume (Vol) is in μm^3

Expt	Alga	L	W	Vol	Grazer	L	W
1	*Gymnodinium simplex*	11.2	6.7	265	*Favella* sp.	80.5	51.7
	Pyrenomonas salina	8.0	4.7	93		(161.1)	(77.5)
2	*Prorocentrum minimum*[a]	11.1	10.0	337	*Strombidinopsis*	108.7	49.9
	Prorocentrum minimum[b]	16.1	14.6	1035	*acuminatum*		
	Pyrenomonas salina	9.0	4.9	111			
3	*Isochrysis galbana*	4.0	3.7	28	*Amphidinium* sp.	21.8	15.5
	Pyrenomonas salina	9.4	5.0	125			
4	*Isochrysis galbana*	3.8	3.6	25	*Uronema* sp.	13.7	10.5
	Pyrenomonas salina	9.2	5.0	122			
5	*Isochrysis galbana*	3.9	3.8	29	*Gymnodinium* sp.	10.5	9.0
6	*Prorocentrum micans*[c]	41.6	26.8	8703	*Noctiluca scintillans*	271.2	254.8

[a]Dimensions of cell contents.
[b]Dimensions of thecae.
[c]Thecae completely filled by cell contents

Table II. Growth responses for six species of protozoa fed a variety of algal species

Algal taxon↓	Grazer taxon →	S a	F sp	U sp	G sp	A sp	N s
Prymnesiophyta	*Isochrysis galbana*	o	–	+	+	+	o
	Emiliania huxleyi	nd	nd	o	–	+	o
Cryptophyta	*Cryptomonas* sp.	o	+	nd	nd	+	nd
	Pyrenomonas salina	o	+	+	+	+	+
Dinophyta	*Gymnodinium simplex*	–	nd	–	o	–	o
	Prorocentrum minimum	+	–	nd	nd	nd	nd
	Heterocapsa niei	nd	o	o	–	–	+
	Prorocentrum micans	nd	nd	nd	nd	nd	+
Chlorophyta	*Nannochloris oculata*	nd	nd	–	–	o	–
	Mantoniella squamata	nd	nd	+	+	+	o
Cyanophyta	*Synechococcus* sp. strain G	nd	nd	+	o	o	o

S a, *Strombidinopsis acuminatum*; F sp, *Favella* sp.; U sp, *Uronema* sp.; G sp, *Gymnodinium* sp.; A sp, *Amphidinium* sp.; N s, *Noctiluca scintillans*. o, survival (no growth); –, no survival; +, growth; nd, not determined.

supported survival or growth. For the experiments described below, protozoa were fed paired algal species if those supported higher growth rates than any single species. Otherwise, only a single algal species was used. In all cases, the single or paired algal species supporting the highest observed growth rate (the 'optimized diet') for that protozoan species was used (Table I).

Grazing experiments were conducted in six or eight replicate 23 l polycarbonate carboys containing 11–23 l initial volume, depending on the experiment. Algal stock cultures in late exponential phase were added to sterile filtered (0.2 μm) seawater (salinity 29–30‰) in all carboys for initial total concentrations of 190–390 μg C l^{-1}. For experiments using two algal species, the goal was a 1:1 mixture of the two, although this was not always achieved (Figure 1). Protozoan grazers were added to half the carboys at initial concentrations of 0.1–106.6 cells ml^{-1} (Figure 1). Larger species (*Favella* sp., *Strombidinopsis acuminatum*, *Noctiluca scintillans*) were pre-concentrated by reverse filtration before addition to minimize carry-over of stock culture medium and algal food. Smaller species could be grown to sufficient density in stock cultures such that carry-over was minimal.

Carboys were incubated at 13°C in dim light (≤1 μmol photons m^{-2} s^{-1}) with a 12:12 h light:dark cycle. After gentle mixing, subsamples (single: Experiments 3, 4 and 6; duplicate: Experiments 1, 2 and 5) for the determination of algal and grazer abundance were withdrawn initially and every 12–24 h for 6–10 days, until algae were nearly gone in grazer-containing carboys. Additional subsamples were withdrawn for pigment analysis by high-performance liquid chromatography (HPLC); pigment methodology and results will be presented elsewhere (Strom *et al.*, 1998).

Algal abundance samples (20 ml) were fixed with 1 ml of 10% glutaraldehyde and stored under refrigeration. Slides for epifluorescence microscopy were prepared within 24 h of sample collection; preliminary tests showed significant species-dependent losses of glutaraldehyde-fixed algal cells after 24 h refrigerated storage. Slides were prepared by filtering 1–20 ml of the glutaraldehyde-preserved

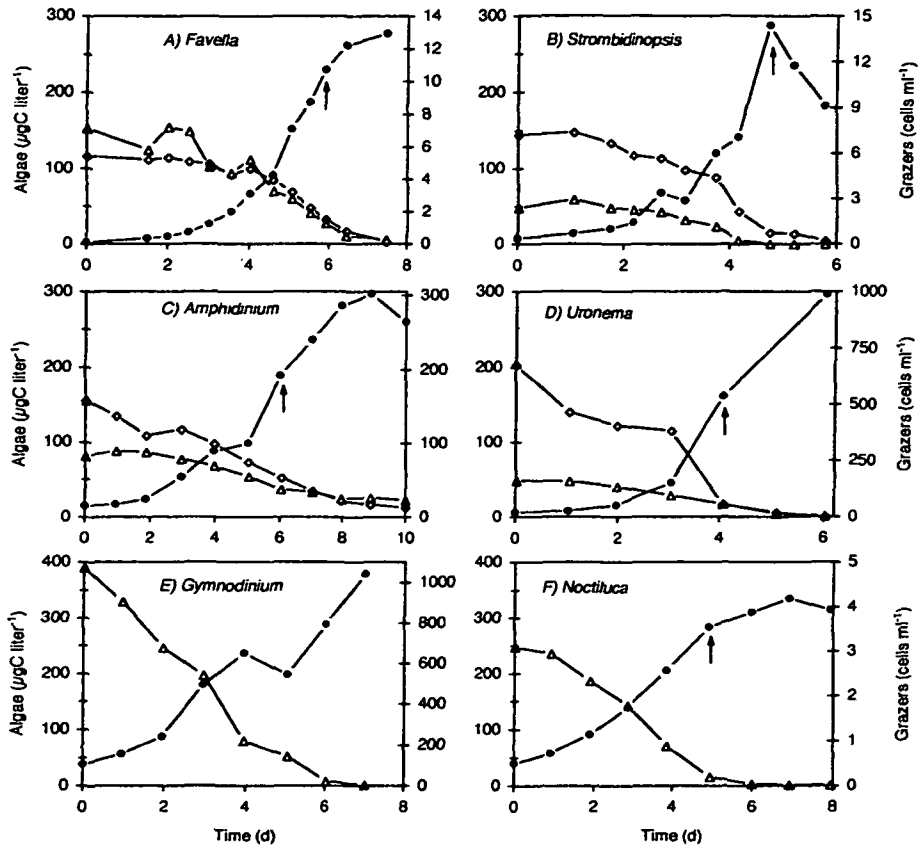

Fig. 1. Changes in algal and grazer concentration over time during experiments. Points are means ($n = 3$ or 4); error bars are omitted for clarity. ◇, *Pyrenomonas salina*; △, *Gymnodinium simplex* (**A**), *Prorocentrum minimum* (**B**), *Isochrysis galbana* (**C–E**), *Prorocentrum micans* (**F**); ●, grazers. Arrows indicate the end of the grazer exponential growth phase.

subsample onto a 1.0 µm pore size 25 mm polycarbonate membrane filter with a 1.2 µm cellulose backing filter. Gentle vacuum (≤125 mmHg) was used. Filters were mounted with immersion oil (Cargille type DF) and stored frozen (–20°C) for later counting. Algae were enumerated using epifluorescence microscopy (Sherr *et al.*, 1993); contents of at least 50 grids per slide were counted at 100–400× magnification (total algal counts usually >150). In some cases, particularly later time point samples from Experiment 6, the entire filter area was counted.

Grazer abundance samples (20–200 ml) were fixed with acid Lugol's solution (5% final concentration). Variable volumes of fixed subsample were transferred to 10 ml settling chambers and the contents enumerated using inverted microscopy. For early time points of Experiments 1, 2 and 6, entire 200 ml subsamples were poured through a 20 µm mesh screen and back-washed into the 10 ml settling chamber. Preliminary tests showed complete recovery of cells by this method.

Algal and grazer cell dimensions were measured on acid Lugol's-preserved samples from intermediate experiment time points. A Sony SSC-D7 CCD camera and Bioscan Optimas software were used to image cells and measure dimensions. A minimum of 40 algal cells and 50 grazer cells were measured (Table I). Cell volumes were estimated from dimensions using standard geometric formulae; algal carbon contents were estimated from Lugol's-fixed cell volumes according to Montagnes *et al.* (1994).

Growth rates were calculated by linear regression from the linear portion of plots of the natural log of cell density versus time. Note that, strictly speaking, these are division rates, as they do not account for changes in grazer cell size during the incubations. Grazer abundance during each time interval was calculated from a logarithmic average; grazer-specific clearance and ingestion rates were then calculated for each time interval in each carboy using the equations of Frost (1972). Volume yield (grazer cell volume produced/algal cell volume ingested) was calculated based on total growth and ingestion from the beginning of the experiment to the end of the exponential growth phase. Cumulative yields (grazer volume produced/algal volume ingested from the beginning of the experiment to each subsequent time point) were also determined.

Results

Food quality

Isochrysis galbana, *Mantoniella squamata* and the two cryptophytes were the highest-quality foods tested, supporting survival or growth in nearly every grazer species (Table II). *Isochrysis galbana* and *M.squamata* supported growth of all three small grazer species. Most of the autotrophic dinoflagellates, with the exception of *Gymnodinium simplex*, were suitable foods for the larger grazers, but no one dinoflagellate species was best for all. Note that although *G.simplex* was not tested singly on *Favella* sp., in combination with the cryptophyte *Pyrenomonas salina* it represented the best diet for this grazer. *Emiliania huxleyi* and *Synechococcus* sp. were lower-quality foods, supporting survival, but not growth, in most tested grazers. *Nannochloris oculata* was a poor-quality food. Some prey types that are potentially important in natural waters, including diatoms and heterotrophic nanoflagellates, were not tested in this study. Thus, our 'optimized' diets (Table I) cannot necessarily be considered 'optimal' (i.e. the best possible).

Growth and ingestion rates

Maximum growth rates of ciliates (range 0.77–1.01 day^{-1}) were consistently higher than maximum growth rates of heterotrophic dinoflagellates (range 0.41–0.48 day^{-1}) (Table III). Differences in growth rate between the two groups were significant (*t*-test, $P < 0.001$). The food concentration at which exponential growth ceased (here termed the limiting food level, or LFL) varied widely among the grazer species (Figure 1, Table III). *Amphidinium* sp. entered stationary phase at a food concentration of 89 μg C l^{-1}, while *Gymnodinium* sp. was still

Table III. Summary of rate and yield data for protozoa (c, ciliate; hd, heterotrophic dinoflagellate). All values are averages from replicate carboys, with 1 SD in parentheses ($n = 3$ or 4)

Grazer	Taxon	μ	Yield	LFL	I(200)
Favella sp.	c	0.86 (0.02)	0.57 (0.13)	60	3.8
Strombidinopsis acuminatum	c	0.77 (0.04)	0.64 (0.21)	15	5.4
Uronema sp.	c	1.01 (0.05)	0.28 (0.02)	34	5.9
Gymnodinium sp.	hd	0.48 (0.08)	0.15 (0.03)	≤5	3.6
Amphidinium sp.	hd	0.47 (0.01)	0.46 (0.08)	89	3.0
Noctiluca scintillans	hd	0.41 (0.02)	14.22 (5.19)	16	nd

μ is growth rate (day^{-1}). Yield (calculated to end of exponential phase) is total grazer volume produced/total algal volume ingested. LFL (limiting food level, μg C l^{-1}) is the algal concentration at which the grazer population entered the stationary phase. I(200) is the estimated volume-specific ingestion rate (day^{-1}) at an algal concentration of 200 μg C l^{-1}. nd, not determined.

growing exponentially at the conclusion of Experiment 5, when the algal concentration was ~5 μg C l^{-1}. There was no clear relationship between LFL and grazer size, taxon or feeding mode.

Volume-specific ingestion rates [(μm^3 algae ingested) (μm^3 grazer)$^{-1}$ day^{-1}] ranged from 0 to 12 over all experiments (excluding Experiment 6). Ingestion showed either a linear or an exponential increase with food concentration over the experimental range (Figure 2). Predicted volume-specific ingestion at an algal concentration of 200 μg C l^{-1} was calculated for each experiment as a means of comparing ingestion rates among grazers. Predicted values ranged from 3.0 to 5.9 day^{-1}, with the two dinoflagellate grazers and *Favella* exhibiting relatively low rates, and the remaining ciliate grazers (urotrich and *Strombidinopsis*) exhibiting higher rates (Table III; Figure 2, arrows). Because *Noctiluca* is highly vacuolated and variable in size, volume-specific ingestion rates were extremely low, difficult to interpret, and not directly comparable to those of other grazers. Therefore, they were excluded from this analysis.

Grazer yield

Volume-based grazer yield varied from 0.15 to 0.64, except for *Noctiluca*, which yielded 14 units of grazer volume for each unit of algal volume consumed (Table III). As for LFL, there was no obvious relationship between yield and grazer size or taxon. These yield estimates represent total grazer volume produced/total algal volume ingested from the beginning of each experiment to the onset of the stationary phase. Cumulative yield was also calculated to examine changes in this ratio over the incubation period. Yield was observed to increase over time in most experiments (Figure 3).

We considered the possibility that the observed continuous increases in yield could be an artifact of uncoupled ingestion and growth (sometimes termed unbalanced growth). In other words, it seemed possible that time lags between ingestion and resulting growth, combined with increasing grazer population size, could create apparent increases in yield over time in our batch culture system. To evaluate this possibility, a simple model was created. Given a specific ingestion rate of

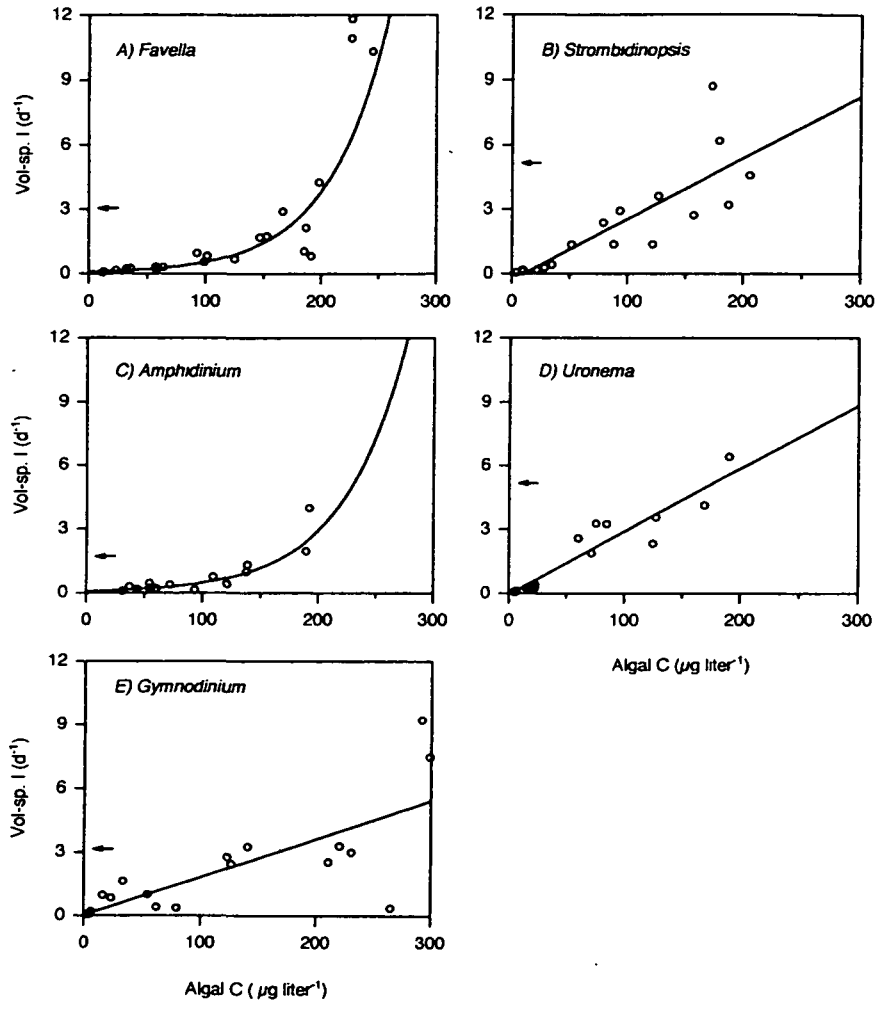

Fig. 2. Volume-specific ingestion rates as a function of algal concentration (calculated as the average for each time interval). Data from replicate carboys were pooled, and early time points were excluded from the analysis because algal concentration changes were too small to measure ingestion accurately. *y*-axis arrows show estimated ingestion rates at 200 μg algal C l^{-1}. (**A**) $y = 0.080(10)^{0.0084x}$; $r^2 = 0.88$. (**B**) $y = -0.306 + 0.028x$; $r^2 = 0.70$. (**C**) $y = 0.076(10)^{0.0079x}$; $r^2 = 0.79$. (**D**) $y = -0.063 + 0.030x$; $r^2 = 0.90$. (**E**) $y = 0.025 + 0.018x$; $r^2 = 0.57$.

2 day^{-1}, an actual yield of 0.4, and unlimited prey availability, we calculated cumulative yield versus time for various values of deferred grazer production. Deferred grazer production was defined as the fraction of grazer production based on ingestion during time interval t that was not realized until time interval $t + 1$. Unbalanced growth, modeled as described above, did indeed cause an erroneous estimate of yield: estimates ranged from 0.4 (= actual yield) to 0.22 for fraction of deferred production ranging from 0.0 to 0.9. These underestimates, however, were not time dependent, i.e. unbalanced growth did not cause yield to change

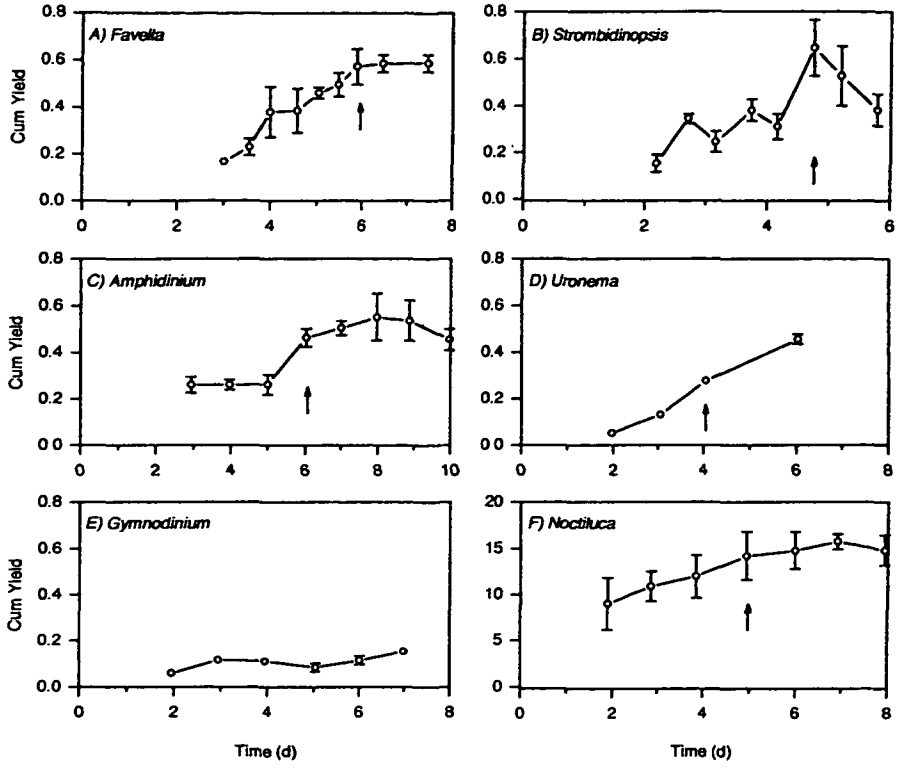

Fig. 3. Cumulative volume yield (grazer cell volume produced/algal cell volume ingested) over time; points represent means (n = 3 or 4) ± 1 SE (error bars are sometimes smaller than symbols). Early time points were excluded from analysis, as for Figure 2. Arrows indicate the end of the grazer exponential growth phase.

over time during modeled experiments as it did during actual experiments (Figure 4). For each value of deferred production, model output quickly converged on an estimate of yield that was invariant for the remainder of the modeled experiment. In general, a high value of deferred production (0.9) caused a 50% underestimation of actual yield in this batch culture scenario.

Discussion

Our major finding was that, during these experiments, ciliates consistently exhibited higher maximum growth rates than heterotrophic dinoflagellates. Furthermore, taxon-based differences greatly outweighed sized-based differences in growth rate (Figure 5A). These growth rate differences agree with previous conclusions (Strom, 1991; Hansen, 1992), although the current study is the first to optimize diets and then apply these, using a consistent experimental design, to members of both grazer groups.

The same few algal species constituted the best diets for most of the protozoan

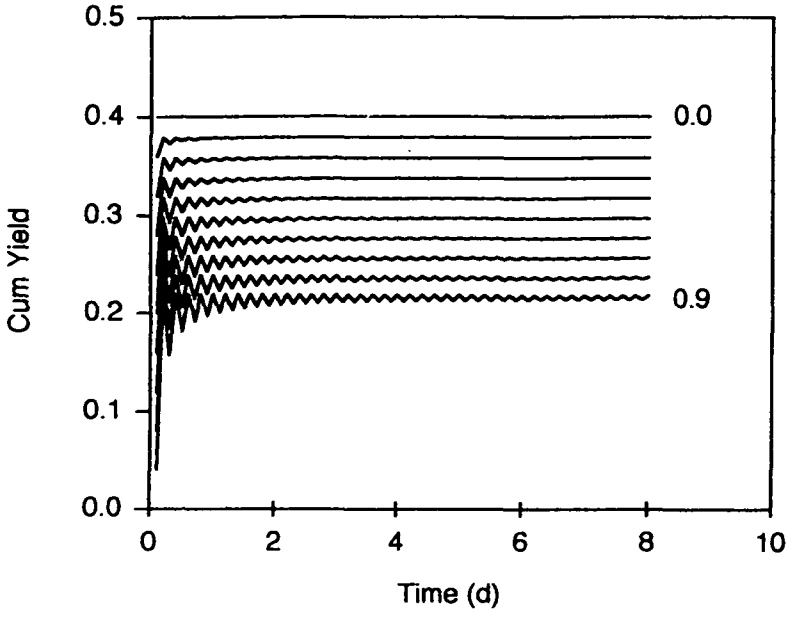

Fig. 4. Results of the grazing model predicting cumulative yield as a function of time for fraction of deferred production ranging from 0.0 to 0.9. See the text for details.

grazers, regardless of grazer taxon. The prymnesiophyte *I.galbana* and the prasinophyte *M.squamata* were suitable foods for all the smallest grazers, while the cryptophyte *P.salina* was a suitable food for all grazers tested (5/6). Various autotrophic dinoflagellate species supported growth when fed to the larger grazers, though no one species was best for all (Table II). This dietary consistency across grazer taxa, as well as our efforts to optimize experimental diets, indicate that absence of key dietary nutrients during experiments is not a likely explanation for observed differences in ciliate and heterotrophic dinoflagellate growth rates.

Protozoan growth rate differences must be based on differences in either ingestion rate or gross growth efficiency (GGE; Fenchel, 1982; Hansen, 1992). Lower ingestion rates on the part of the dinoflagellates would point to differences in feeding mechanisms or digestion rates as underlying causes for growth differences. Lower GGEs would indicate differences in biomass synthesis requirements; for example, growth in heterotrophic dinoflagellates may be more energetically demanding, or require more of a scarce dietary nutrient, than growth in ciliates. We calculated ingestion and yield (a proxy for GGE) on a cell volume basis because there are few data available on the carbon or energy content of ciliates and, especially, heterotrophic dinoflagellates. Any extrapolation from this volume-specific approach to a mass- or energy-based approach assumes that grazer and prey unit volume mass or energy content are similar.

The heterotrophic dinoflagellates *Amphidinium* and *Gymnodinium*, and the ciliate *Favella*, had low volume-specific ingestion rates at most studied food levels.

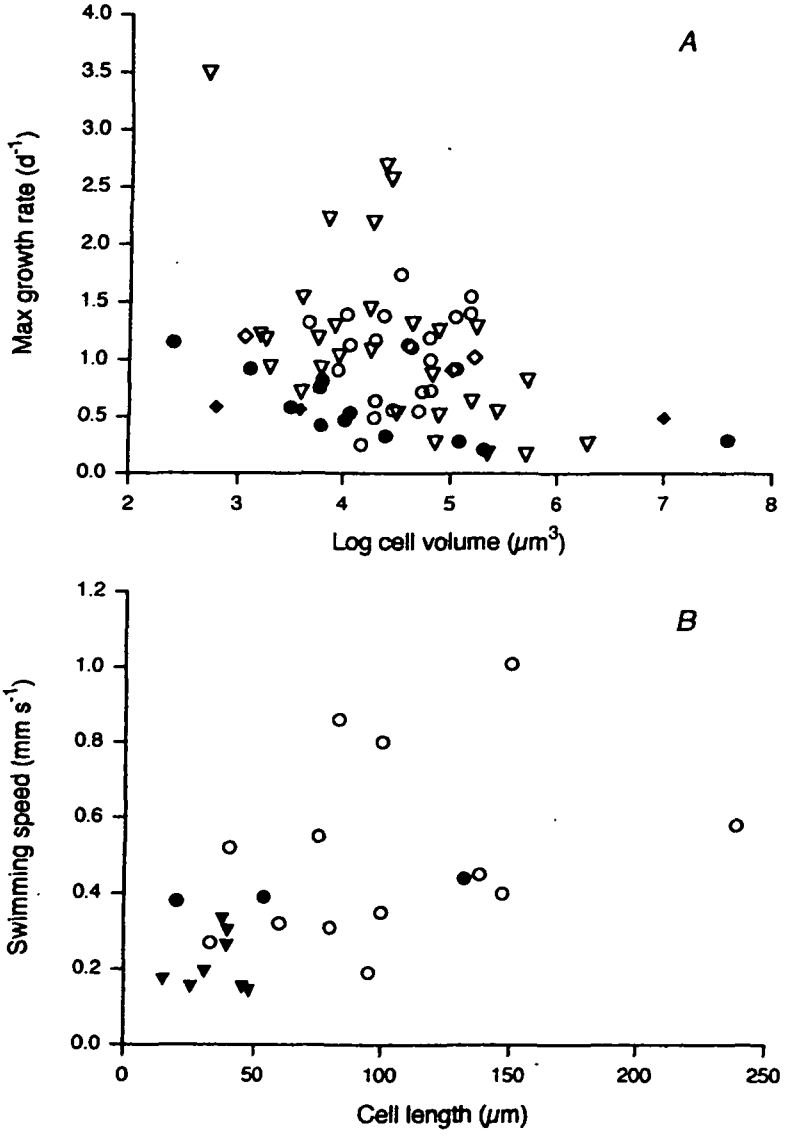

Fig. 5. (**A**) Protozoan growth rate as a function of cell volume (log μm^3). Filled symbols, heterotrophic dinoflagellates; open symbols, ciliates (circles, choreotrichs; triangles, all other ciliates); diamonds, data from this study. Sources for ciliates: compilation of Montagnes (1996, his Table 4), Fenchel (1968), Hamilton and Preslan (1970), Finlay (1977), Heinbokel (1978), Taylor (1978), Stoecker *et al.* (1983), Verity (1985), Muller and Geller (1993), this study; for dinoflagellates: Goldman *et al.* (1989), Strom (1991), Hansen (1992), Jacobson and Anderson (1993), Strom and Buskey (1993), Jeong and Latz (1994), Buskey (1995), this study. Cell volumes of Lugol's-fixed cells were divided by 0.7 to convert to live cell volumes (Jerome *et al.*, 1993); all growth rates were adjusted to 15°C using a Q_{10} of 2.5. Growth rates measured at temperatures of >20 or <10°C were excluded due to the likelihood that Q_{10} varies with temperature (Muller and Geller, 1993). (**B**) Protozoan swimming speeds as a function of cell length. Closed symbols, dinoflagellates (circles, heterotrophs; triangles, autotrophs); open symbols, ciliates. Sources: Kamykowski *et al.* (1992), Buskey *et al.* (1993). All speeds were measured at 20°C.

Favella, though, exhibited very high ingestion rates (>9 day^{-1}) at high food levels. Thus, relatively low ingestion rates were consistently, though not exclusively, associated with dinoflagellate grazers during this study.

As for ingestion, yield varied widely over the course of each experiment, tending to increase over time to the end of the exponential phase. Recall that Figure 3 shows cumulative yield, plotted as a means of smoothing the data. Because populations were growing exponentially, cumulative yield at any given time point was dominated by population yield during the immediately preceding time interval. Excluding *N.scintillans*, grazer yield generally ranged from 0.1 to 0.4 during exponential growth. The ciliates *Favella* and *Strombidinopsis* exhibited even higher values of ~0.6 near the end of the exponential phase. In contrast to most of the grazer species, the dinoflagellate *Gymnodinium* exhibited low yields (<0.2) throughout the experiment. Ingestion rate and yield data taken together indicate that there is no single explanation for low dinoflagellate growth rates; further, the conclusion of Hansen (1992) that low GGEs are the cause is not strongly supported by our data. In our study, the two dinoflagellate grazers *Amphidinium* sp. and *Gymnodinium* sp. had relatively low ingestion rates. Furthermore, only one of the dinoflagellate species grew with a consistently low yield. By the same token, the ciliates studied here supported relatively high growth rates by various combinations of high ingestion rates and high yields.

The contrast between low heterotrophic dinoflagellate and high ciliate growth rates holds across a range of species and cell sizes. A data compilation (Figure 5A) shows that, for cells of a given size, dinoflagellate growth rates are nearly always lower than ciliate growth rates. A large range of maximum rates at any given cell volume is also apparent. This may be due in part to experiments that did not use an optimal diet (i.e. the true maximum growth rate of the species was not realized), and in part to real variation in potential growth rate among the diverse ciliate taxa. Banse (1982), in a comparison of ciliates and autotrophic dinoflagellates, also concluded that ciliates consistently grew faster, with an overall weak dependence of growth rate on cell size.

A comparison of ciliate and heterotrophic dinoflagellate swimming speeds using the limited data available shows that while there is an overall dependence on cell size, there is no difference in swimming speeds between the two grazer groups (Figure 5B). Thus, differences in ingestion and resulting growth rates are unlikely to be due to differences in encounter rates between grazer and prey. Slower digestion of prey by dinoflagellates is another possible cause of differences in ingestion and hence growth. Verity (1991), who used a modeling approach to explore differences in maximum tintinnid growth rates, attributed low growth rates on 'poor-quality' prey to slower digestion of these species. A more fundamental cause is suggested by observation of photosynthetic dinoflagellates, which consistently have lower maximum growth rates than similarly sized cells from other algal taxa [Tang (1996) and references therein]. Attempts have been made to relate the lower growth rates of these algae to cell chlorophyll content or photosynthetic capacity (Chan, 1978; Tang, 1996). The consistency with which both photosynthetic and heterotrophic dinoflagellates exhibit low maximum growth rates, however, indicates that the cause transcends processes specific to

trophic mode (e.g. digestion, photosynthesis) and is rooted in more fundamental cellular processes. Tang (1996) hypothesized that the large dinoflagellate genome is likely to require much material and energy for maintenance, leaving less for catalytic activity. Reduced availability of energy and material for biomass synthesis should be evident as reduced growth efficiencies, as observed in one case here. Conversely, ciliates may achieve high growth rates through nuclear dualism, with sexual and vegetative metabolic activity segregated between the micro- and macronuclei, respectively (Taylor and Shuter, 1981).

A consistent feature of our data is the increase in yield with time in nearly all experiments. The model developed here shows that this increase is not an artifact of temporally uncoupled ingestion and growth. Such uncoupling can cause an underestimation of yield, an important consideration in the study of species with diel or otherwise synchronous division patterns. This underestimation is constant with time in a batch culture scenario, however, and unbalanced growth does not give rise to the continuously increasing yields seen here.

Other possible sources of yield variation include changes in food concentration and acclimation to algal diets. Although numerous studies (e.g. Heinbokel, 1978; Stoecker and Evans, 1985; Jonsson, 1986; Grover, 1990; Strom, 1991; Jacobson and Anderson, 1993) have shown GGE to increase with decreasing food levels (as seen here), many others show contrasting trends, and few general conclusions can be drawn. Adamson and Shapiro (1996) showed that preconditioning the heterotrophic dinoflagellate *Oxyrrhis marina* on different algal foods had a large effect on the GGE expressed during subsequent grazing experiments. In our study, while all stock culture diets were similar to experimental diets, only three out of six (those for the heterotrophic dinoflagellates) were identical. The three ciliate grazers, which exhibited the largest yield changes over time, were also raised on stock culture diets that differed from experimental diets either by addition or deletion of algal species. Progressive acclimation to the experimental diet could have resulted in the observed temporal increases in yield.

The higher maximum growth rates of ciliates compared with heterotrophic dinoflagellates have implications for whole planktonic communities. The growth rate disparity means that ciliate populations have the potential to increase more rapidly in response to increases in prey biomass. Considering maximum growth rates alone, ciliates should be better able than dinoflagellates to control incipient blooms of their prey. Such predation control may be modified by other ecological relationships, including the responses of ciliates and heterotrophic dinoflagellates to very low prey abundances (Montagnes, 1996) and the extent of predation upon the two groups.

In conclusion, the hypothesis that ciliates have higher maximum growth rates than heterotrophic dinoflagellates is supported by our observations. There was no single explanation for the contrast between ciliate and heterotrophic dinoflagellate growth rates, although dinoflagellates did exhibit relatively low volume-specific ingestion rates and, in one case, low yields. These growth rate differences may arise from fundamental differences in nuclear structure and function, and may enable ciliates to exercise tighter control over blooms of prey species.

Acknowledgements

The *Uronema* sp. culture was graciously provided by B. and E.Sherr. We thank W.Arthurs, J.Holmes and K.Thompson for assistance with culture maintenance, cell counts and food quality assessments. General laboratory support was provided by G.McKeen, and the manuscript was improved by comments from the SPMC Plankton Group and two anonymous reviewers. This research was supported by NSF grant OCE 9301698.

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Received on January 28, 1997; accepted on November 10, 1997