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The effect of zooplankton grazing on estuarine blooms of the toxic dinoflagellate *Gonyaulax tamarensis*

Carl J. Watras[1], Veronique C. Garcon, Robert J. Olson, Sallie W. Chisholm and Donald M. Anderson[2]

48-425 Ralph M. Parsons Laboratory, Massachusetts Institute of Technology, Cambridge, MA 02139, and [2]Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

[1]*Present address: Trout Lake Laboratory, Center for Limnology, University of Wisconsin, Boulder Junction, WI 54512, USA*

Abstract. A series of short-term *in situ* experiments was conducted in two Cape Cod embayments to estimate mortality rates of the toxic dinoflagellate, *Gonyaulax tamarensis*, resulting from grazing by zooplankton. Rates of grazing by the whole zooplankton community and by specific zooplankton populations were measured at various points in the *G. tamarensis* bloom cycle. The planktonic larvae of the spionid polychaete *Polydora ligni* and the tintinnid ciliate *Favella* sp. were important grazers in the systems studied. *Gonyaulax*-specific clearance rates effected by *Polydora* ranged from 0.02 to 0.5 ml individual^{-1} h^{-1}; for *Favella* the range was about an order to magnitude lower. Peak population densities were close to 900 and 400 individuals l^{-1} for *P. ligni* and *Favella*, respectively. Whether measured directly or predicted as the product of individual clearance rates and numerical abundance, rates of grazing were often higher than estimated algal division rates in years when blooms failed to develop. A simulation model corroborated the results of the field study, demonstrating that grazing can be a significant source of mortality during blooms, and can suppress bloom development when grazers are abundant.

Introduction

The toxic dinoflagellate *Gonyaulax tamarensis* Lebour blooms sporadically in small estuarine embayments on Cape Cod and in other areas of southern New England (Anderson *et al.*, 1982). These blooms are initiated by the germination of benthic cysts during vernal warming (Anderson and Wall, 1978; Anderson and Morel, 1979) after which the population increases to a maximum over a 1–2 month period and then decreases rapidly (Anderson *et al.*, 1983). Temperature and salinity are thought to be the most important factors influencing *G. tamarensis* growth in these embayments during the period of bloom development (Watras *et al.*, 1982). These factors remain optimal during the period of rapid bloom decline indicating a shift in the dominant regulatory factors at the time of peak cell densities (Anderson *et al.*, 1983). Mechanisms which may contribute to bloom decline include: parasitism, episodic advective losses from the tidal estuaries into coastal waters, mortality due to grazing and a population shift to sexual reproduction resulting in cyst formation.

In years when major blooms failed to develop at our study sites, we have not seen marked differences in the physical or chemical characteristics of the embayments relative to bloom years. This raises two questions: (i) what factors suppress blooms in certain years? and (ii) what is reponsible for the rapid decline of the blooms in years when they do occur? We hypothesize that changes in the rates of cell loss from the system, rather than changes in cell growth capacity, dominate the bloom dynamics. The pur-

pose of this study was to estimate the extent to which grazing might contribute to this loss rate, using both direct measurements and model simulations.

Evidence suggesting the importance of grazing on *G. tamarensis* populations appears in several previous studies, particularly in the Bay of Fundy (see Prakash *et al.*, 1971). Needler (1949) was the first to propose that summer populations of *G. tamarensis* were regulated by *Favella* grazing. Prakash (1963), Prakash *et al.* (1971) and White (1979) made similar observations. White (1980, 1981) has also demonstrated that *Evadne*, *Balanus* nauplii and *Acartia* ingest *Gonyaulax* cells. More recently, Turner and Anderson (1983) presented data from 24-h laboratory incubations of natural communities which indicated that zooplankton grazing could have a significant impact on *G. tamarensis* abundance.

Our objective was to build on these studies by obtaining direct estimates of grazing pressure at various phases during *Gonyaulax* bloom development. The short-term, *in situ* methodology used was similar to that used by Haney (1971, 1973) and by Roman and Rublee (1981). In contrast to these studies, however, our objective was to measure the death rate of the dinoflagellate, rather than the feeding dynamics of the zooplankton.

Although not the central focus of this study, we also report estimates of the *in situ* intrinsic growth rate of *G. tamarensis* for comparison with our estimates of mortality rates. The results of a simulation model of the bloom dynamics are also described.

Methods

Field survey

Routine sampling of the study sites was initiated in 1980. A detailed description of the embayments, the methods of collection and the processing of samples is presented in Anderson *et al.* (1983). Briefly, Perch Pond and Salt Pond, small embayments on Cape Cod (surface area: 0.07 and 0.8 km^2; mean depth: 1.5 and 3.5 m, respectively), were sampled weekly from early spring to mid-summer, 1980 – 1983. Phytoplankton and zooplankton concentrations, temperature, and salinity were measured in the samples. The methods for collecting biological samples were modified somewhat from year to year, particularly as our interest in the zooplankton increased. In 1980, vertically integrated whole-water samples were collected at a single station to estimate *G. tamarensis* abundance. Zooplankton were collected with a net (73-μm mesh; 30 cm diameter; flow-metered) in duplicate tows along a transect near the centre of each embayment. In 1981, *G. tamarensis* sampling was expanded to six stations and zooplankton were collected from the surface, mid-depth, and bottom at a central station with a Niskin bottle and concentrated with a 64 μm nitex ringnet. In 1982 and 1983, both *G. tamarensis* and zooplankton were collected in vertically integrated, whole-water samples taken at multiple stations in each embayment; the zooplankton were concentrated with a 35 μm nitex ringnet.

In situ growth rates

Measurements of carbon fixation by individual *G. tamarensis* cells over the course of a day were used to estimate the intrinsic growth rate of these cells in Perch Pond in 1981. Water samples were collected at dawn using a 5-foot integrating water sampler. [^{14}C]Bicarbonate was added (3 μCi ml^{-1}) and the samples were incubated *in situ* in

vertical 4-foot Pyrex tubes (25 mm diameter) sealed with silicone-rubber stoppers. The incubations were begun at dawn, and were terminated at sunset or the following dawn. To stop the incubation, the phytoplankton were gently concentrated on a 10-μm nitex mesh and then rinsed with 2 vol. of filtered pond water. Single cells were isolated from 1 ml of this concentrate using a micropipette, and placed into scintillation vials. Similar volumes of samples free of *G. tamarensis* cells were taken to estimate background ^{14}C levels due to inadvertently harvested small cells or dissolved organic carbon. The scintillation vials were fumed with concentrated HCl for 12 h, air-dried, and counted for radioactivity after the addition of scintillation fluor.

The amount of radioactivity incorporated by individual cells over the incubation period was reasonably consistent from cell to cell, as indicated by the linear relationship between total activity of a sample and the number of cells counted (Figure 1). Also, the consistency of the data from the dawn-to-sunset with that of the dawn-to-dawn incubation periods indicates that there was an insignificant loss of radioactivity due to respiration.

Specific activity of the ^{14}C bicarbonate in each sample was determined by counting the ^{14}C activity in 10 μl of water. The carbon content of the cells was estimated from cell volume according to the method of Eppley *et al.* (1970). This estimate was corroborated by direct measurements of the carbon content of cultured *G. tamarensis* cells using a CHN analyser. Specific growth rates of the cells were calculated as the ratio of the amount of carbon incorporated per cell per day to the carbon content of the cells.

Grazing experiments

Our objective was to estimate the specific mortality rate of *G. tamarensis* due to zooplankton grazing, under nearly natural conditions. Our basic methodology was modified from that of Haney (1971), who used radiolabelled yeast cells as a food tracer in short-term (i.e., minutes), *in situ* incubations. Since our goal was to measure only the ingestion

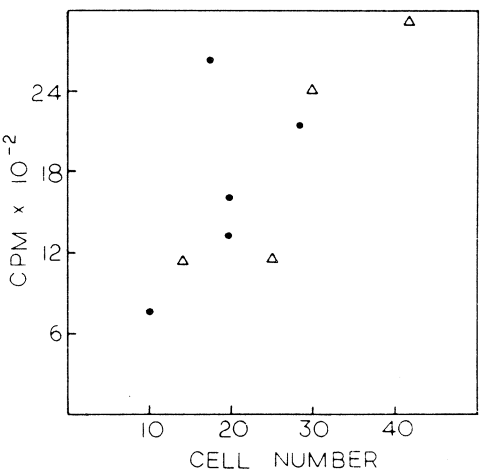

Fig. 1. [^{14}C] Bicarbonate uptake by *G. tamarensis* on 23 April 1981 in Perch Pond after *in situ* incubation of whole water samples from dawn-to-dawn (△) or dawn-to-sunset (●), individual *G. tamarensis* cells were isolated with a micropipette, and their radioactivity was counted. Average carbon fixation per cell was calculated using the average c.p.m. per cell from these data.

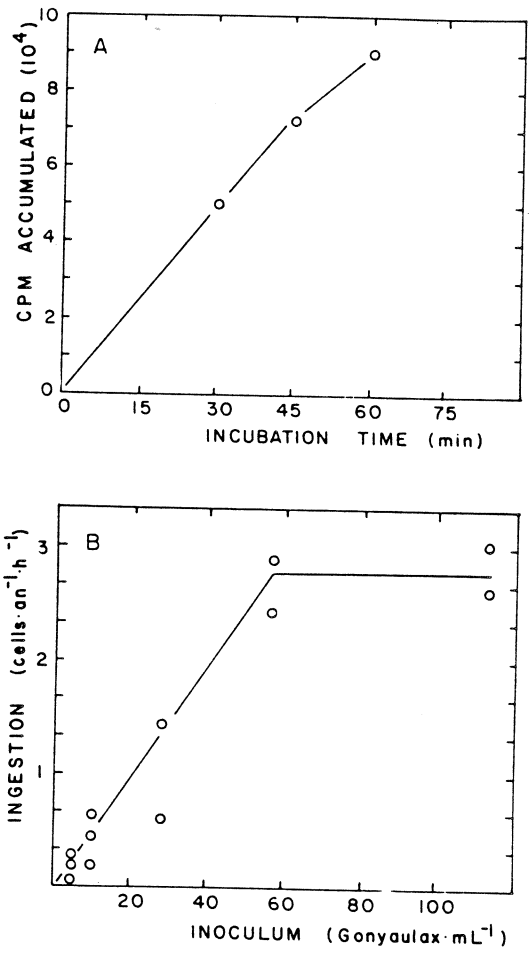

Fig. 2. Effects of incubation time on radioactivity accumulated by the whole zooplankton community **(A)** and effect of inoculum size on ingestion rate of individual *P. ligni* **(B)** in grazing experiments. Data in **(B)** from groups of 20–30 *Polydora*. Inoculum size in **(A)**: 14 cells ml^{-1}; incubation time in **(B)**: 30 min.

of *G. tamarensis* by the zooplankton, however, we used ^{14}C labelled *G. tamarensis* cells in our incubations. These cells had been isolated from a local embayment (clone GTMP; D.Anderson). They were cultured to late log phase in f/2-Si medium (Guillard, 1975), spiked with 1–3 μCi ml^{-1} $NaH^{14}CO_3$ and incubated for an additional 2–4 days. Before inoculation of the grazing chambers, the cells were gently rinsed with sterile filtered seawater (10× dilutions, repeated six times) above a 10-μm nitex mesh.

The incubation time of grazing experiments was generally 30 min and the concentration of labelled *G. tamarensis* in the chambers ranged from 5 to 20 cells ml^{-1}. Our intent was to provide sufficient incubation time and labelled cells to obtain adequate counts in the zooplankton, without exceeding their gut passage time. An *in situ* time-series experiment (Figure 2a) indicated that tracer uptake by the whole zooplankton

community was indeed linear with a zero intercept for incubations up to 45 min. A concentration-series run simultaneously showed that feeding by *Polydora ligni* larvae (often the most abundant zooplankter) was not saturated until the inoculum size reached 50 cells ml^{-1} (Figure 2b). Thus, inocula below this concentration probably constituted tracer additions relative to total available particles, and we saw no evidence of tracer recycling in 30-min incubations. In some cases we were adding large quantities of *G. tamarensis* cells relative to those present *in situ*, but the additions were always low relative to bloom concentrations and to total algal biomass (see Anderson *et al.*, 1983).

Grazing experiments were conducted in two ways. In the first set of experiments, 3-l clear plastic bottles were filled with a composite water sample taken with a vertically integrating sampler at several points along a transect. The bottles were sealed and suspended in the pond for a 30-min acclimation period. They were then inoculated with labelled cells, and resuspended for the feeding period. In later experiments, Haney-type grazing chambers (Haney, 1971) were used to measure clearance rates of individual species with minimal disturbance of the grazers.

At the end of the feeding period the zooplankton were removed by screening, washed into plastic vials, and preserved with formalin (4%). The samples were processed within 30–60 min after fixation. The zooplankton were either collected *in toto* on 8-μ Nuclepore filters, or individual species were isolated with a pipette; in several cases, the sample was split and treated both ways. The animals were then digested overnight in 1 ml Protosol at 40°C, neutralized with 50 μl glacial acetic acid and counted overnight in 10 ml Scintiverse fluor. The mandatory fixation step in our procedure may have resulted in the leaching of some tracer from the organisms (Holtby and Knoechel, 1981), which would cause an underestimation of grazing rates. Thus, our estimates of grazing may be conservative.

Whole community grazing rates on *G. tamarensis* were calculated from the filtered samples using the formula:

$$G = \frac{R_z}{R_g\, t} \tag{1}$$

where G is the grazing rate (day^{-1}), R_z are the total c.p.m. in zooplankton, R_g are the total c.p.m. available as *G. tamarensis* in the chamber, and t is the incubation time in days. These rates are specific mortality rates for the *G. tamarensis* population due to consumption by zooplankton.

In order to calculate population grazing rates for individual species, clearance rates for given species were calculated using a similar formula:

$$F = \frac{R_z\, v}{R_g\, t} \tag{2}$$

where F is the *Gonyaulax*-specific clearance rate (i.e., volume swept clear of *G. tamarensis* in ml animal $^{-1}h^{-1}$), R_z is c.p.m. per individual animal, R_g is the same as equation 1, v is the volume of the chamber in ml, and t is the incubation time in h. Population grazing rates (or the mortality rate attributable to a given zooplankton species) are then given by:

$$g = F \times n \times 24 \text{ h day}^{-1} \tag{3}$$

where n is the zooplankton population abundance in animals ml^{-1}, and g is the grazing rate expressed in units of day^{-1} for ease of comparison with the phytoplankton growth rate data.

Since activity rhythms (i.e., diel vertical migrations and diel grazing rhythms) have been documented for many zooplankton species (e.g., Haney and Hall, 1975) and since these rhythms may be linked to environmental periodicities such as light or tides, the grazing experiments were usually conducted several times during a 24- or 36-h period. The light intensity (as incident PAR in μ Einsteins m^{-2} s^{-1}) and the tidal cycle were monitored continuously.

Model formulation

We attempted to simulate the observed bloom dynamics in Salt Pond with a simple, time-dependent model using the population densities and estimated grazing rates of two numerically important zooplankters. The intrinsic growth rate of the *G. tamarensis* population was modelled as an empirically determined function of ambient temperature and salinity, as described in Watras *et al.* (1982). A residual loss term, β, was estimated by analysis of the discrepancy between the observed *G. tamarensis* population dynamics and that which could be accounted for by subtracting losses due to grazing from the intrinsic growth potential of the cells.

The equation governing the evolution of the dinoflagellate population over time was:

$$dN/dt = (\mu - F_p n_p - F_f n_f - \beta) N \quad (4)$$

where $N = N(t)$ is the vegetative cell density of *G. tamarensis* (cells l^{-1}), t is time (day), μ is the specific growth rate of the dinoflagellate population (day^{-1}), n_p and n_f are the concentrations of *P. ligni* and *Favella* sp. in the ponds (animals ml^{-1}), F_p and F_f are the clearance rates of *P. ligni* and *Favella* sp., respectively (ml $animal^{-1}$ day^{-1}), and β is the residual mortality rate (day^{-1}).

We chose the simplest possible formulation for the grazing component of the model: the clearance rates, F_f and F_p, were assumed constant, corresponding to increasing ingestion rates with increasing food concentrations. A feeding threshold, when used, was implemented by simply delaying the onset of grazing by the zooplankters until the cell density of *G. tamarensis* reached the defined threshold level. Although we have no experimental evidence for the existence of such a threshold, preliminary simulations (Garcon and Anderson, 1984) indicated that it could play a critical role in the early stages of bloom development.

The values used for the clearance rates of the two species were selected from a subset of values measured in this study and from existing literature. Clearance rates for *Favella* sp. have been observed to range between 3 and 24 μl $animal^{-1}$ h^{-1} in laboratory studies (Stoecker and Guillard, 1982; Aelion, 1983), which is within the range of field measurements made in this study (see below). We chose from these data a constant clearance rate of 10 μl $animal^{-1}$ h^{-1}, which was used throughout the simulations. The majority of reported clearance rates for *P. ligni* grazing on *G. tamarensis* fall between 0.03 and 0.09 ml $animal^{-1}$ h^{-1} (Turner and Anderson, 1983; and this study). Simulations were run using both the high and the low value for this species, to describe the envelope of possible results. The value for the residual mortality rate, β, was deter-

mined by iteration to the best fit to the observed rate of bloom decline.

The initial conditions of the state variable N were taken from the measured cell concentrations when *G. tamarensis* first appeared in the pond. The time series for temperature was developed using multiple regression analysis of the field data from Anderson *et al.* (1983). Daily zooplankton concentrations were generated from the weekly field data assuming linear variation between sampling dates.

Results

Field survey

Only one bloom of *G. tamarensis* ($\geq 10^4$ cells l^{-1}) occurred in Perch Pond during the four-year period (1980) whereas three blooms were observed in Salt Pond (1980, 1982, 1983) (Figure 3). The development of *G. tamarensis* populations in both embayments, however, had some strikingly consistent characteristics during the four-year period. Every year in both ponds, planktonic cells appeared in late March or early April and were last seen in early June. In Perch Pond, peak population abundance always occurred in late April; in Salt Pond all three blooms peaked within the 10-day period between 23 May and 2 June.

Three taxa dominated the spring zooplankton communities of both embayments: larvae of the benthic spionid polychaete, *P. ligni* (Blake, 1969), tintinnid ciliates (*Favella* sp.) and rotifers (*Synchaeta* sp.). Copepods (often *Acartia*) were present, but were relatively less abundant (Turner and Anderson, 1983; C.J.Watras, unpublished data). The population dynamics of two of the zooplankton species (*P. ligni* and *Favella* sp.) are compared with the dynamics of *G. tamarensis* in Figure 3. *Polydora ligni* were relatively abundant during all four years in Perch Pond. During this time there was only one *G. tamarensis* bloom, which declined rapidly at the time of peak *P. ligni* abundance. In Salt Pond, high *G. tamarensis* concentrations corresponded to low *P. ligni* abundance in two years (1980 and 1983). When *P. ligni* were abundant, either no bloom occurred (1981) or it occurred after *P. ligni* had declined (1982). Although such correlations do not imply causality, they suggest that polychaete abundance might be linked to bloom suppression during the development phase.

Favella sp. shows striking fluctuations in both embayments (Figure 3). The tintinnid populations were monitored for only two years (1982 and 1983) of this study, but an ephemeral late spring population comprising several hundred animals per litre appeared in both years. In Salt Pond, the peaks in *Favella* and *G. tamarensis* populations were almost simultaneous. Again, this does not indicate a causal relationship, but the data do suggest that *Favella* could play a role in the decline of these blooms.

We conclude from the survey data that if grazing is an important loss factor for *G. tamarensis* populations in Perch Pond, *P. ligni* is the zooplankton species of interest. In Salt Pond, *P. ligni* may be a factor in bloom suppression, but the survey data indicate that bloom decline is more probably influenced by *Favella*. Without measuring the magnitude of the potential grazing pressure relative to *G. tamarensis* growth rates, however, these correlations are only suggestive.

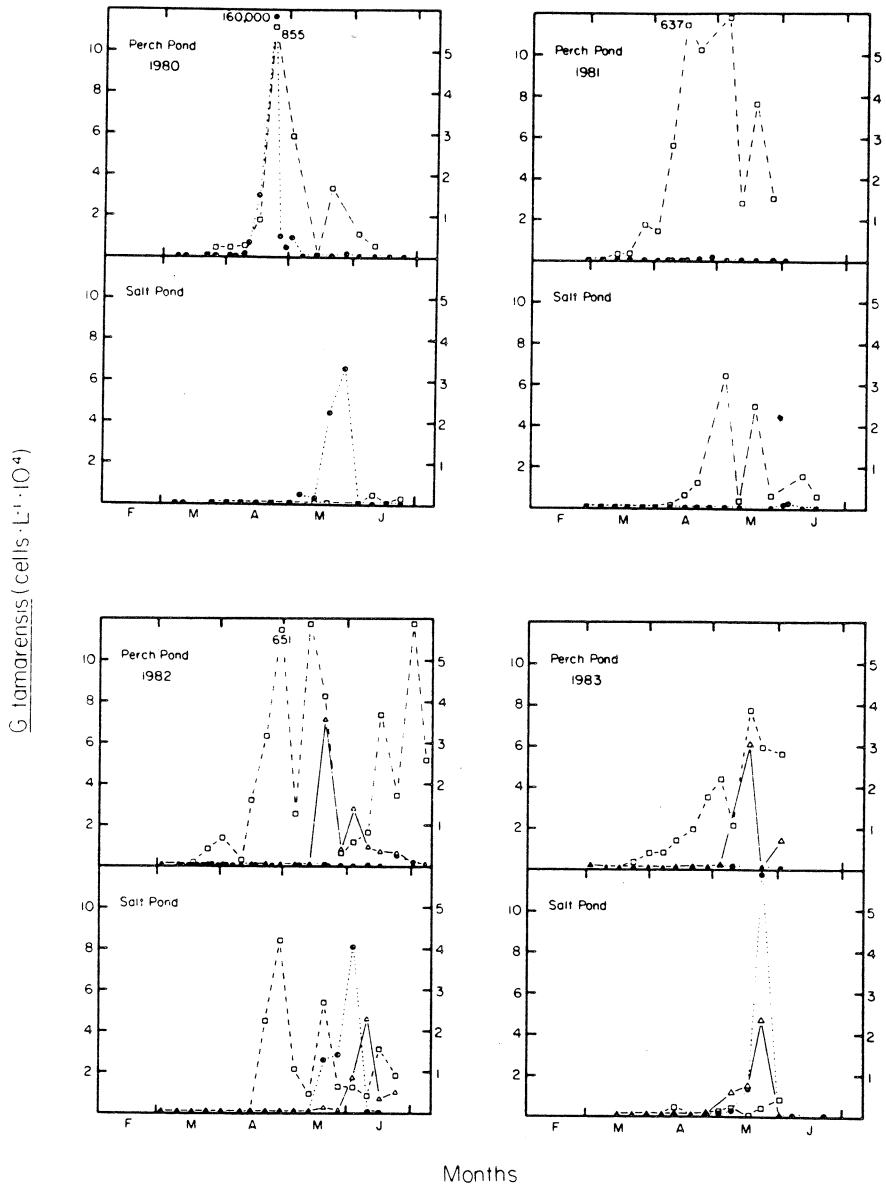

Fig. 3. Population dynamics of *G. tamarensis* ●---● *P. ligni* larvae □---□, and *Favella* sp. △—△ in Perch Pond and Salt Pond, 1980 – 1983. Filled squares and triangles: overlapping points. Note: *Favella* were not monitored until 1982.

In situ growth rates

Estimating the significance of grazing mortality to the overall growth dynamics of *G. tamarensis* populations depends heavily on knowledge of the intrinsic growth rate of the algal cells in the ponds. The results of our single cell, ^{14}C measurements in Perch

Table I. Estimates of whole community grazing rates on *G. tamarensis* from six *in situ* experiments, 1981

Date	Embayment	Time of day (h)	Grazing rate (G, day^{-1})
23 April	Perch	12.00	1.1
		21.00	2.3
5 June	Perch	11.00	0.3
		22.00	1.0
4 June	Salt	15.00	0.2
		22.00	0.6

Pond (Figure 1) gave us an estimate of the *G. tamarensis* growth rate of 0.15 day^{-1}. This rate was calculated based on a specific activity of ^{14}C of 2.9×10^{11} c.p.m. g C^{-1}, an average ^{14}C incorporation of 86 c.p.m. $cell^{-1}$ day^{-1} (from Figure 1), and thus a carbon fixation rate of 3.0×10^{-10} g C $cell^{-1}$ day^{-1}. This value was divided by an average value for the carbon content of the cells (2.0×10^{-9} g C $cell^{-1}$), to arrive at the specific growth rate. Although this value is directly dependent upon the cellular carbon content of *G. tamarensis*, which can be quite variable, we are encouraged by the agreement between this value and the range of growth-rate values measured by Rubin (1981) using measurements of the mitotic index of *G. tamarensis* populations in this same system. Moreover, a growth rate of about 0.15 day^{-1} is only slightly less than what one would predict for Perch Pond at this time of year, based on the relationship between growth rate and temperature determined in the laboratory (Watras *et al.*, 1982). We acknowledge that generalization based on such a limited number of observations is presumptuous. The consistency of these estimates, however, inspires some confidence that intrinsic growth rate of *G. tamarensis* is not highly variable, and is not significantly constrained by factors other than temperature and salinity during the bloom development phase.

In situ grazing

The first series of grazing experiments was conducted during spring 1981 (Table I), a year when there was no bloom in either embayment. These were bottle incubations done around midday and midnight near the dates when (i) we expected peak *G. tamarensis* concentrations in both embayments (based on the 1980 field data) and (ii) at the time when *G. tamarensis* cells disappear from the plankton in Perch Pond. The data show relatively high grazing rates (Table I) which exceed the expected growth rate of *G. tamarensis* populations at each point in time. The data also show consistently higher grazing rates at night. The tentative conclusion, then, is that grazing by zooplankton could have suppressed bloom development in these embayments in 1981.

During 1982, all grazing experiments were conducted on Perch Pond, again using bottle incubations. Our goals were to further examine the diel periodicity evident in the 1981 data and to identify specific grazer populations through size-fractionation and species isolation. In the first experiment, we again saw very high grazing rates (Figure 4a), relative to the intrinsic growth rate of *G. tamarensis*. Grazing was highest at dusk, intermediate at midnight, low during morning and midday with an increase in late afternoon of the second day. This pattern followed the light cycle, and showed no corre-

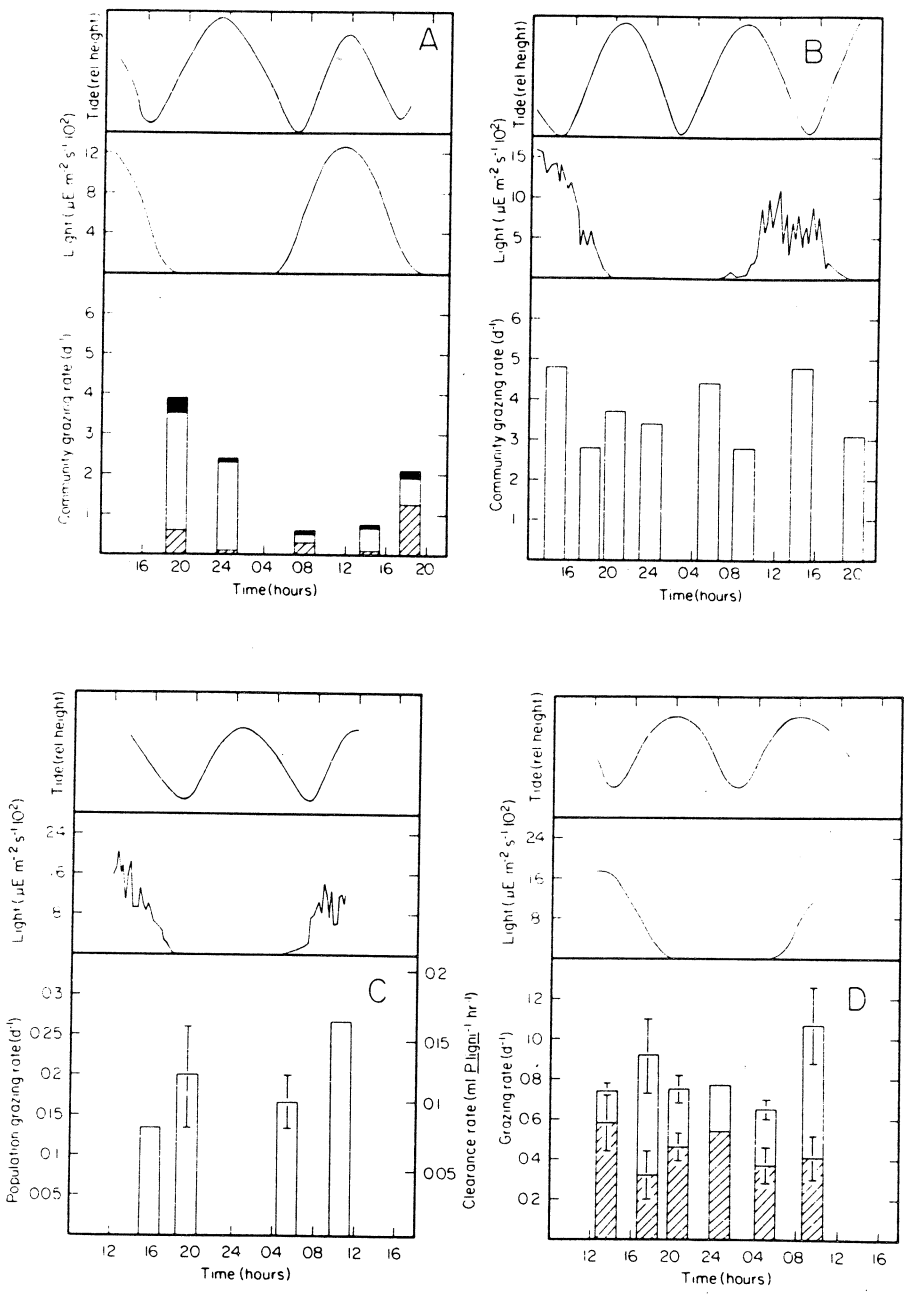

Fig. 4. *Gonyaulax*-specific grazing rates, photocycle and tidal cycle during *in situ* experiments, Perch Pond. **(A)** Whole community grazing rates (G) for three size fractions split with 53 μm (hatched), 80 μm (open) and 253 μm (solid) nitex ringnets (23 – 24 April 1982). **(B)** Grazing rates of zooplankton in the 80-μ size fraction (18 – 19 May 1982). **(C)** Grazing rates of *Polydora* larvae estimated from picked samples; data are means with range of duplicate groups comprising ~30 larvae each (14 – 15 April 1983). **(D)** Comparison of grazing by whole zooplankton community (unshaded) and *Polydora* population (hatched); data are means with standard error (5 – 6 May 1983).

Table II. Zooplankton retention by different size meshes in sieve series, 24 April 1982, Perch Pond. Data are relative frequencies obtained by assigning most abundant class a value of 100

Zooplankton	Mesh size (μm)		
	53	80	253
Polydora ligni	10	100	0.2
Favella sp.	0	0	0
Rotifers	1	4	0
Copepod nauplii	12	77	0
Copepodids	1	4	1

Table III. Comparison of whole-community grazing rates with those of the *P. ligni* population on *G. tamarensis* (12 June 1982, Perch Pond)

Time (h)	*Polydora* sp.			Community
	Clearance (ml larva^{-1} h^{-1})	Abundance (n l^{-1})	Grazing rate (g, day^{-1})	Grazing rate (G, day^{-1})
15.00	0.08	100	0.19	0.17 (0.05)
18.30	0.52	60	0.75	0.72 (0.24)

Whole community comprises zooplankton retained by 151 μm mesh. At this time, 80–90% of this community was large *P. ligni* larvae. (Data are means, with range of duplicate experiments in parentheses.)

lation with the tidal cycle. Size-fractionation of the zooplankton with 53, 80 and 253 μm nitex ringnets showed that the intermediate size class (80–253 μm) was most active. Most of the zooplankton were found in this size class and 90% of these were *P. ligni* larvae (Table II). We repeated this experiment four weeks later with closer experimental intervals, looking only at the size class >80 μm (Figure 4b). Again, the grazing rates were roughly an order of magnitude greater than the growth potential of *G. tamarensis*. The diel pattern observed previously (Figure 4a) was not evident on this date.

A third experiment was conducted in mid-June specifically to look at the *P. ligni* population. A 151 μm ringnet was used to isolate a size fraction containing mostly large *P. ligni* larvae. Aliquots of this fraction were either counted *in toto* or in groups of 20–30 individuals isolated by pipette. The agreement between results of these methods was quite good (Table III), and again a dramatic evening increase in the grazing rate was evident.

During 1983, our experiments focussed on the *P. ligni* population in Perch Pond and the *Favella* sp. population in Salt Pond. Haney chambers were used to minimize disturbance of the grazers. In the first experiment on Perch Pond, the grazing rate of the *P. ligni* population was relatively low, averaging about 0.2 day^{-1} (Figure 4c), but potentially high enough to retard significantly the growth of the *G. tamarensis* population which had developed to about 1500 cells l^{-1} at this time. In a second experiment conducted three weeks later, the *P. ligni* population had grown and dominated the zooplankton community numerically (Table IV). Population grazing rates were correspondingly higher (Figure 4d), constituting 40–80% of the whole community rates

Table IV. Zooplankton abundance [animals l^{-1} (standard error)] in grazing chambers during *in situ* experiments on 5–6 May 1983 at Perch Pond

Zooplankton	Time of experiment					
	13.30	17.30	20.30	00.30	05.00	09.30
Polydora ligni	684(84)	479(117)	357(38)	751	393(31)	289(78)
Favella sp.	0	2(2)	0	0	2(2)	34(34)
Rotifers	54(11)	58(9)	58(15)	300	68(12)	73(22)
Copepod nauplii	17(6)	11(4)	19(6)	17	21(4)	13(13)
Copepodids	2(2)	0	2(20)	0	2(2)	0
Number of experiments	4	4	4	1	4	2

Table V. Individual clearance rates for *P. ligni* larvae determined during *in situ* experiments on 5–6 May 1983, Perch Pond

Time (h)	N[a]	Clearance rate [b] (ml animal^{-1} h^{-1})
13.30	7	0.04 (0.010)
17.30	7	0.03 (0.006)
20.30	8	0.06 (0.009)
00.30	1	0.03 (–)
05.00	6	0.04 (0.013)
09.30	4	0.06 (0.008)

[a]Number of samples picked (20–40 larvae per sample).
[b]Mean (standard error).

Table VI. Grazing by *Favella* sp. on *G. tamarensis* during bloom development and at the beginning of bloom decline in Salt Pond, 1983

Date	Bloom phase	Time of day	Clearance rate (μl *Favella*$^{-1}$ h^{-1})	Abundance (*Favella* l^{-1})	Population grazing rate (g,d^{-1})
12 May	Development	05.30	5.3	70	0.008
		12.15	9.3	70	0.015
		19.30	3.7	70	0.007
24 May	Initial decline	08.15	20.0	235	0.11
		14.00	15.0	235	0.08
		21.00	45.0	235	0.25
		05.00	20.0	235	0.11

measured simultaneously. Individual clearance rates were somewhat lower than those measured in previous experiments and there was no clear diel pattern to their variability (Table V). Overall, grazing mortality ranged from 0.7 to 1 day^{-1} at this time (Figure 4d), well above the growth potential of *G. tamarensis*. The field survey data (Figure 3) show that as the *P. ligni* population increased to around 400 animals l^{-1} the *G. tamarensis* population waned. Again, there was no bloom in 1983 (Figure 3).

Grazing by *Favella* sp. in Salt Pond was measured on two dates in 1983 (Figure 2): once during bloom development and again when the bloom began to decline (Table VI). The *P. ligni* population was relatively low in this year. During bloom development, both the abundance and individual clearance rates of *Favella* sp. were also low. This resulted in minor grazing mortality, which is consistent with the rapid development of the bloom (Figure 3). At the peak of *G. tamarensis* abundance, however, *Favella* abundance and clearance rates showed dramatic increases (Table VI). Although this produced a much higher mortality due to grazing just as the bloom began to subside, the magnitude of this loss rate is not large relative to the observed rate of population decline. In both 1982 and 1983, the rate of *G. tamarensis* decline from peak abundance was roughly 0.9 day^{-1}; maximal measured loss to *Favella* was 0.25 day^{-1} (Table VI).

Model simulation

A simple simulation model was constructed to obtain a better assessment of the degree to which the dominant grazers could affect the overall bloom dynamics of *G. tamarensis*. Our goal was to see whether we could mimic the development and decline of a bloom while assuming that the net population growth of the alga was dictated by a balance between vegetative growth and mortality due to grazing by *Favella* and *P. ligni*. We then used the discrepancy between the observed and simulated population dynamics to estimate the magnitude of residual loss terms required to explain the rapid bloom decline. The simulations of Salt Pond data in 1981 and 1982 are presented here as representative of both 'non-bloom' and 'bloom' years. A more detailed account of the modelling exercise can be found in Garcon and Anderson (1984).

We first attempted to fit the time course of bloom development in each of the two years by varying the magnitude of the clearance rates of the zooplankton within a range that has been observed experimentally (see Methods). We also examined the influence that a threshold food concentration for the onset of feeding would have on the timing of the bloom. Threshold values of 1000, 5000 and 10 000 cells l^{-1} were examined in preliminary simulations, and the lowest value was shown to be the only one that could provide a reasonable fit to the data (Garcon and Anderson, 1984).

The first conclusion from the simulations was that if all loss terms were neglected, *G. tamarensis* growth developed too rapidly in both years (Figure 5). In the 'bloom' year, 1982, the best fit to the observed data on population development was achieved using a relatively low clearance rate for *P. ligni* (0.03 ml animal^{-1} h^{-1}), and a feeding threshold of 1000 cells l^{-1}. These same parameter values resulted in an excellent fit to the *G. tamarensis* data for Salt Pond in 1980, and a good (but one week delayed) fit for the 1983 data (Garcon and Anderson, 1984). When higher grazing rates were used, or the threshold was eliminated, the simulated bloom was eliminated or significantly delayed relative to that actually observed. In the 'non-bloom' year, 1981, the higher clearance rate value (0.09 ml animal^{-1} h^{-1}) was sufficient to delay and suppress the bloom to the degree required to match the data.

Thus, by varying the clearance rate of *P. ligni* within a realistic range, and with the inclusion of a threshold concentration for the onset of grazing, the observed population dynamics of *G. tamarensis* can be well reproduced by the model up to the point of population decline in both years. The reasons behind these results become obvious when

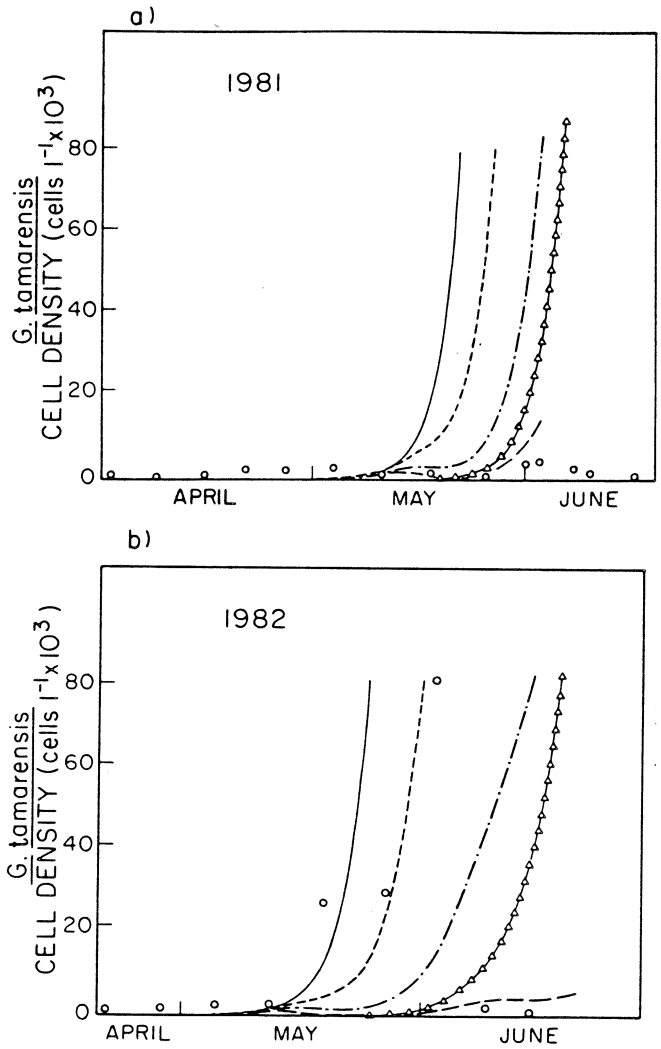

Fig. 5. Model sensitivity to changes in *P. ligni* clearance rate (F_P) and to the inclusion of a 1000 cells l^{-1} feeding threshold concentration for **(a)** 1981 and **(b)** 1982. Observed *G. tamarensis* cell densities (○), predicted densities with no grazing (—); predicted *G. tamarensis* cell densities with threshold included and F_p = 0.03 (---), 0.06 (— · —), 0.09 (— —) ml *Polydora*$^{-1}$ h^{-1}; with no feeding threshold and F_p = 0.03 (△——△) ml *Polydora*$^{-1}$ h^{-1}. 1982 simulations with threshold and F_f = 10 μl animal^{-1} h^{-1}.

calculated loss rates due to zooplankton grazing (the product of the clearance rate and the density of the zooplankton in the ponds) are plotted along with the simulated temperature-dependent intrinsic growth rate of the *G. tamarensis* cells (Figure 6). This presentation also points out why the feeding threshold is required for the goodness of fit. With the threshold in effect, the animals were not able to begin feeding on *G. tamarensis* until late April in 1981, and mid-May in 1982 (see arrows in Figure 6). This delay in the onset of feeding eliminated an interval when grazing mortality would

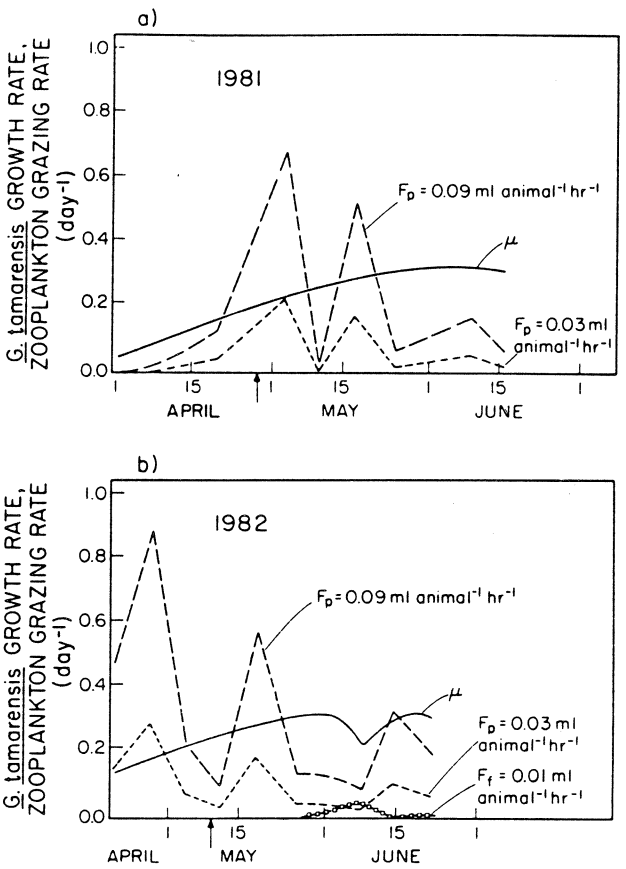

Fig. 6. Evolution over the spring season of the simulated *G. tamarensis* growth rate and zooplankton grazing rates of **(a)** 1981 and **(b)** 1982. μ, intrinsic cell division rate (−); *P. ligni* grazing rate with F_p = 0.01 (---), 0.09 (— —) ml animal^{-1} h^{-1}; *Favella* sp. grazing rate with F_f = 10 (□↔□) μl animal^{-1} h^{-1}. Arrow indicates when the threshold food concentration is reached.

have been greater than the growth capacity of *G. tamarensis* in 1982, which would have greatly retarded the development of the bloom.

The results shown in Figure 6 also display the sensitivity of the system to the range of clearance rates used in the simulations. In both years, the lower clearance rate allows bloom development, but at the higher rate, grazing can surpass the growth rate of the cells enough to suppress the bloom. Grazing by *P. ligni*, therefore, could be important in regulating the early bloom dynamics in these ponds.

Examination of the relative rates of growth and mortality (Figure 6) during the period of bloom decline (which began in early June in 1982), makes it immediately obvious that grazing cannot account for the net loss of cells from the pond during this interval. The potential growth rate is always greater than the grazing rate, when the clearance rate used to simulate the early stages of the bloom is maintained. Under these conditions, an additional loss term (β) is required to force the model to mimic the observed decline in the *G. tamarensis* population. In 1982, as well as 1980 and 1983 (Garcon and Ander-

son, 1984) the value of β required to force the observed rate of bloom decline was 0.5 day^{-1}.

Discussion

Our overall conclusion is that mortality due to zooplankton grazing can play a significant role in regulating the timing and magnitude of blooms of *G. tamarensis* in Cape Cod embayments. Zooplankton grazing also appears to have some influence on the rate of bloom decline, but does not appear to be the dominant factor during this interval. These conclusions are based on a comparison of our estimates of grazing pressure in the ponds over a 3-year period with the growth capacity of the *G. tamarensis* population during the bloom season. Our conclusions concur with those of Turner and Anderson (1983) and, in a very general way, with those of Wyatt and Horwood (1973), Fiedler (1982) and Huntley (1982) which indicate that a reduction in grazing pressure may be critical to the development and maintenance of dinoflagellate populations. However, our conclusions rest heavily on the assumption that the intrinsic growth rate of the *G. tamarensis* population in the ponds does not exceed the values measured in the laboratory at comparable temperatures and salinities (Watras *et al.*, 1982). Our measurement of the *in situ* growth rate of *G. tamarensis* during this study, and the estimates of Rubin (1981) from earlier years, are consistent with this assumption.

The community grazing rates measured *in situ* were in general quite large relative to the calculated intrinsic growth rate of *G. tamarensis*, and often exceeded 1 day^{-1}. With the exception of the measurements made in Salt Pond in 1982, our grazing experiments were performed in years and/or ponds in which major blooms of *G. tamarensis* did not occur. This was not by design, but it is noteworthy that such high grazing rates were observed in these low density years. Our simulations utilizing the zooplankton census data illustrate the rather delicate balance that seems to exist between the zooplankton and *G. tamarensis* populations in these ponds (Figure 6). If, for example, the high clearance rate for *P. ligni* (0.09 ml $animal^{-1}$ h^{-1}) is used in the simulations during a bloom year, the development of the bloom can be eliminated. In contrast, if the low clearance rate (0.03 ml $animal^{-1}$ h^{-1}) is used, both the timing and magnitude of the bloom can be matched quite nicely. In other words, a bloom may or may not develop in a given year, depending upon which end of a rather narrow range of grazing rates is realised *in situ*.

When blooms do occur in these ponds, the *G. tamarensis* population typically decreases in the late spring at a rate of $\sim$ 1.0 day^{-1} (Anderson and Morel, 1979; Anderson *et al.*, 1983). Although a few of our measured whole-community grazing rates during 'non-bloom' years could match this loss rate (Figure 4, Table I) we have no actual measurements of such high rates during the bloom decline interval. The model simulations consistently demonstrate that grazing accounts for a relatively small fraction of the observed population decline unless the highest measured clearance rate for *Favella* is used throughout the simulation (Garcon and Anderson, 1984). The conservative conclusion then is that other factors must be important in regulating the rapid decline of the *G. tamarensis* population at the end of a bloom.

There are several processes that may contribute to the rapid decline of the blooms in these ponds including parasitism, encystment, and enhanced tidal advection. On

average, advective losses have been estimated to be small (0.07 day^{-1}) in Salt and Perch Ponds (Anderson *et al.*, 1983), and we have no evidence of storm events at the time of bloom decline in all years. Losses due to parasitism are impossible to quantify at present, but it is noteworthy that infestation of *G. tamarensis* by *Amoebophyra ceratii* was recently noted during blooms in Perch and Salt Ponds (D.M.Anderson, unpublished data).

Decreases in population size due to encystment of the vegetative *G. tamarensis* cells comes from two factors: changes in the population division rate, and the sedimentation of cells as resting cysts. The losses due to cyst deposition have been estimated to be of the order of 0.06 day^{-1} (Anderson *et al.*, 1983). Since the motile population in the late stages of a bloom would be a mixture of dividing vegetative cells and non-dividing gametes and planozygotes (the precursors to cysts) the assumed population growth rate predicted by our model (0.3 day^{-1}) is clearly too high. Gametes are not yet distinguishable from vegetative cells, but planozygotes were observed to be a relatively constant 30–35% of the motile populations at the onset of bloom decline (Anderson *et al.*, 1983). If we make the assumption that 50% of the observed motile cell population consisted of non-dividing sexual stages, the intrinsic growth rate of the population would be correspondingly reduced, decreasing the magnitude of the required composite loss term, β.

Because our data are incomplete in various aspects of this overall study, we hesitate to attempt to quantify further the factors regulating the rate of disappearance of *G. tamarensis* cells from these embayments. We feel confident, however, with the qualitative statement that grazing by itself is seldom sufficient to account for the rate of bloom decline. It is our impression that no one factor dominates this process, despite the rather consistent pattern of population decline from year to year in the various ponds.

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