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REGULATION OF GROWTH IN AN ESTUARINE CLONE OF *GONYAULAX TAMARENSIS* Lebour: SALINITY-DEPENDENT TEMPERATURE RESPONSES[1]

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Abstract: Batch-culture experiments with *Gonyaulax tamarensis* Lebour indicated variations in population growth rate and cell size as a function of temperature and salinity. The data on population growth were used to formulate a simple model which predicts bloom development in the absence of other regulatory factors. The agreement between observed and predicted results is quite good for field populations of *G. tamarensis* in Cape Cod embayments during 1977 and 1980. Although other factors may undoubtedly complicate population dynamics, this agreement indicates that in some cases one can account for the development of blooms in this region simply on the basis of salinity-dependent temperature regulation of cell division rates.

In our cultures, cell size was found to change with population growth rate; small cells dominated in populations growing rapidly. However, the larger cell size in the slower growing cultures failed to compensate for the reduced population growth rates when rates of biosynthesis were compared. The potential use of cell size variability in estimating in situ growth rates, and its role in bloom decline through size-selective grazing by zooplankton are considered.

INTRODUCTION

Along the coast of New England and eastern Canada, sporadic blooms of the toxic dinoflagellate *Gonyaulax tamarensis* occur during spring and summer months, often causing paralytic shellfish poisoning (PSP) (Prakash, 1967; Hartwell, 1975; Hurst & Yentsch, 1981). Although much of the region is affected by widespread coastal blooms, on Cape Cod the organism has been confined to isolated estuaries where accumulated resting cysts of *G. tamarensis* are found in sediments (Anderson & Wall, 1978; Anderson *et al.*, in press). Germination of the cysts in these locations effectively inoculates the overlying waters with a seed population (Steidinger, 1975) that initiates the bloom cycle.

Many of the affected estuaries on Cape Cod are pond-like with small shallow inlets which limit tidal exchange. Their physical characteristics make them suitable for comparative field studies of *G. tamarensis* bloom dynamics (Anderson & Wall, 1978; Anderson & Morel, 1979). Results of a recent field study indicated that the pattern of

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G. tamarensis bloom development was highly correlated with water temperature and salinity (Anderson *et al.*, unpubl. data). In two of these salt ponds, the warming trends, salinity, and bloom development were strikingly similar (Fig. 1). In a third pond, the

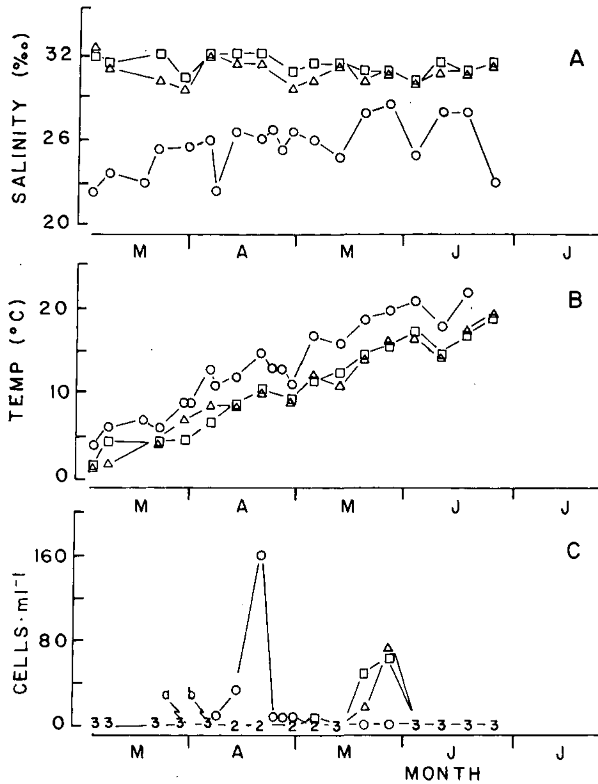

Fig. 1. Salinity (A), temperature (B) and *Gonyaulax tamarensis* population density (C) in three estuarine systems during 1980: ○, Perch Pond, Falmouth, MA; □, Salt Pond, Orleans, MA; △, Mill Pond, Orleans, MA; numerals indicate overlapping points; a, first cells Salt, Perch Ponds (500 cells $\cdot$ l^{-1}); b, first cells Mill Pond (20 cells $\cdot$ l^{-1}).

G. tamarensis population reached peak density ≈35 days before the populations in the other two ponds (Fig. 1C). Although warming at the same rate as Salt and Mill Pond, Perch Pond was ≈3 °C warmer on any given day (Fig. 1B). This corresponds to a 20-day differential in temperature development (see p. 31), which by itself is inadequate to account for the 35-day difference in *G. tamarensis* population growth. However, since salinity also varied systematically in the three estuaries (Fig. 1A), we hypothesized that temperature and salinity together could play a key regulatory role.

Indeed, early work has suggested that the physiological effects of temperature and salinity were critical in the development of north-eastern red tides (see Prakash, 1967). Later studies, however, have contested this, stressing instead the complex interaction

of hydrodynamics and nutrients (e.g., Hartwell, 1975; Mulligan, 1975; Yentsch *et al.*, 1975). Recently, attention has been refocused on salinity–temperature interactions because of their purported effect on the timing and spatial distribution of *Prorocentrum mariae–lebouriae* blooms in the Chesapeake Bay (Tyler & Seliger, 1981).

In the present study, a factorial experiment using batch cultures of *Gonyaulax tamarensis* (Lebour) was designed to examine the salinity dependence of temperature effects on growth rate. The results were used to simulate population growth under field conditions. The correspondence between observed and predicted patterns of bloom development was considered a test of the hypothesis that, in certain estuarine environments, temperature and salinity may regulate the development of *G. tamarensis* blooms through their effect on rates of cell division.

The effect of temperature on the average size of individual cells was also assessed in relation to (1) temperature-independent biomass production (Eppley, 1972; Goldman, 1977), (2) in situ growth rate estimates, and (3) population decline through size selective grazing.

METHODS

ORGANISM AND MEDIUM

Gonyaulax tamarensis (clone GTMP), isolated from Mill Pond by D. Anderson in 1977, was cultured in 25-mm diameter, acid-washed, borosilicate-glass tubes containing 25 ml f/2-Si medium (Guillard, 1975). The presence of a ventral pore indicates that this clone is probably *G. tamarensis* var *excavata* (Schmidt & Loeblich, 1979). Salinities approximating the average levels in the estuaries (Salt and Mill Ponds: 32.5‰; Perch Pond 25.5‰) were obtained using natural sea water and appropriate amounts of distilled water. Experimental tubes were inoculated with 300 to 900 cells $\cdot$ ml^{-1} from cultures acclimated for at least a week at or near (in the case of extreme temperatures) the experimental temperature and salinity.

TEMPERATURE CONTROL

A thermal gradient was established in an aluminum bar (48 × 6 × 1 in.) so that 30 experimental tubes could be monitored simultaneously at 10 temperatures. A 300-W cartridge heater imbedded in one end of the bar, and cold water ($\approx 1\,°C$) circulated through the other end, served as the heat source and sink. Ten rows of 25-mm diameter holes drilled through the bar held three culture tubes at each temperature: 26.5, 24.5, 22.5, 20, 18, 16, 13, 10.5, 8.5, and 5.5 °C. The bar was sandwiched between layers of Styrofoam insulation in a wooden box to minimize temperature variation and block extraneous light. A clear Plexiglas sheet allowed controlled light to reach the cultures from below. Detailed descriptions of similar temperature-gradient bars can be found in the literature (see Blankley & Lewin, 1976).

LIGHT

Three 40-W cool white fluorescent lamps delivered $\approx 170\ \mu E \cdot m^{-2} \cdot s^{-1}$ (PAR) to the bottom of each culture tube (SD: $9\ \mu E \cdot m^{-2} \cdot s^{-1}$; range: 150 to $178\ \mu E \cdot m^{-2} \cdot s^{-1}$). The lamps were set on a 14 : 10 (LD) photocycle. Because heat from the lamps was incompletely filtered, this light regime produced slight diel temperature fluctuations in the culture tubes, roughly $\pm 0.5\ ^\circ C$.

POPULATION GROWTH

Population growth was monitored over 6 to 12 days using in vivo fluorescence measured with a Turner Designs model 10 fluorometer equipped with a 25-mm cuvette holder. The technique was identical to that described by Brand *et al.* (1981). Briefly, fluorescence was measured in each tube at the same time every day following a 15-min exposure to reduced light ($\approx 50\ \mu E \cdot m^{-2} \cdot s^{-1}$). The tubes were gently shaken to distribute the cells uniformly in the medium before measuring fluorescence.

A specific growth rate, μ ($\cdot$ day^{-1}), was calculated from a semi-log plot of relative fluorescence units (ln rfu) vs. time (days) using regression techniques. Fluorescence decline at extreme temperatures was not quantified and was considered to represent a zero growth rate.

CELL NUMBER AND CELL VOLUME

For cells cultured at 25.5‰ salinity, cell density (cells $\cdot$ ml^{-1}) and cell volume ($\mu m^3 \cdot$ cell^{-1}) were determined following the final fluorescence reading of each experiment. Although the population growth rate may have declined slightly at this point

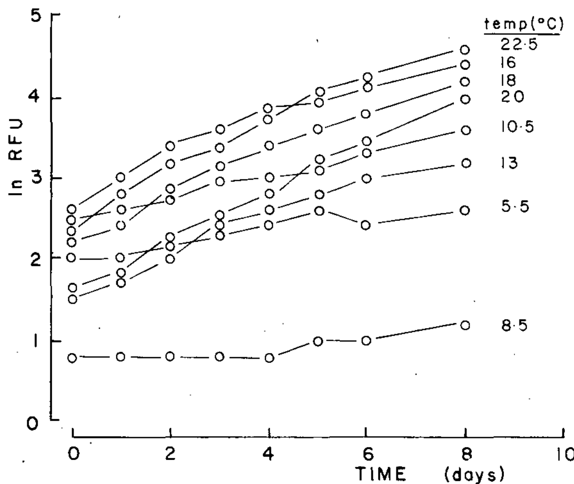

Fig. 2. Typical growth curves for *Gonyaulax tamarensis* using in vivo fluorescense: RFU, relative fluorescence units.

(Fig. 2), a control experiment demonstrated that cell volumes measured at this time were representative of those existing throughout the growth of acclimated cultures. The particles were counted and measured on a Coulter model Zf Electronic Particle Counter with a 100-μm aperture tube and a Coulter model P128 Size Distribution Analyzer interfaced with a Zapple 8k Basic computer. These data were used to estimate the relationship between rates of fluorescence change and rates of cell division as well as the relationship between temperature, cell size, and biomass production.

Results

POPULATION GROWTH: RATES OF CELL DIVISION

A typical family of population growth curves, resulting from one series of cultures (10 tubes) on the temperature-gradient bar, is shown in Fig. 2. Periodic cell counts showed a good correspondence between fluorescence and cell concentration, indicating that the rate of fluorescence change was a valid measure of cellular division rate (Fig. 3). In general, the temperature limits for growth were between 6 and 25 °C. Around 6 °C, fluorescence remained relatively constant and a sparse population of motile cells was always visible. Above 25 °C, fluorescence dropped rapidly to background and no motile cells remained visible in cultures. At intermediate temperatures, growth rate increased gradually to a broad optimum (13 °C < $T_{\mu max}$ < 23 °C). Reducing salinity from 32.5 to

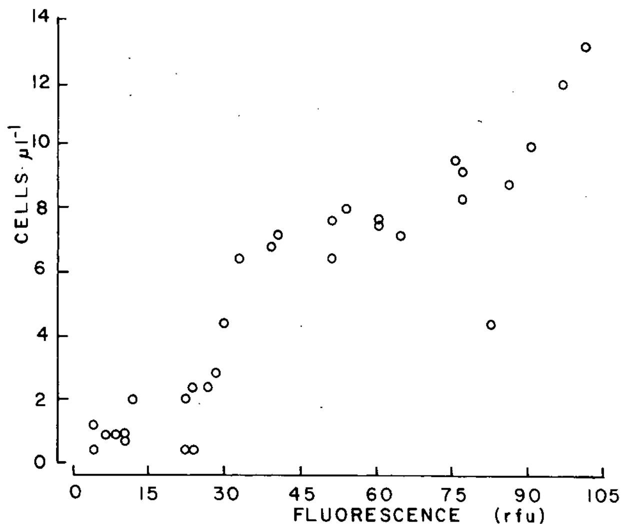

Fig. 3. Relationship between cell concentrations and in vivo fluorescence in *Gonyaulax tamarensis* cultures: the regression equation, $Y = 59.7 + 116X$ accounted for 84% of the variation, but the intercept was not significantly different from zero ($P < 0.001$); fitted without this constant, the equation $Y = 117X$ remains highly significant ($P < 0.001$).

25.5‰ elevated division rates at all but the lowest temperature without affecting the general shape of the temperature response (Fig. 4).

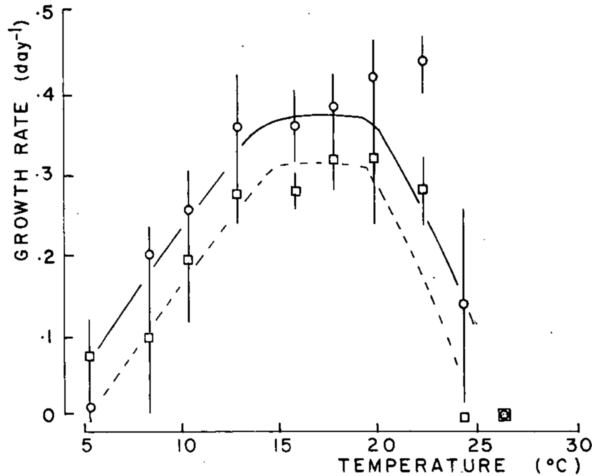

Fig. 4. Relationship between population growth rate (μ) and temperature for *Gonyaulax tamarensis* cultured at two salinities: means ± SD; curves from polynomial regression, as described in text (solid line, circle, 25.5‰ broken line, rectangle, 32.5‰).

Polynomial regression techniques were used to quantify the functional relationship between temperature, salinity, and growth. A cubic equation of the form

$$\mu = b_o + b_1 T^2 + b_2 T^3 + b_3 S \,, \tag{1}$$

where μ = population growth rate ($\cdot$ day^{-1}), T = temperature (°C), and S is an indicator variable designating the salinity (0 for 32.5‰, 1 for 25.5‰), provided the best fit to the data ($R = 0.89$, 80 d.f.). The fitted constants were: $b_o = -9.79 \times 10^{-2}$, $b_2 = -1.52 \times 10^{-4}$, and $b_3 = 7.26 \times 10^{-2}$. Since the curve described by Equation (1) with these coefficients declines gradually above 20 °C, rather than dropping sharply around 23 °C (Fig. 3a), the fit was poor at high temperatures. This is inconsequential to our modelling efforts, however, because field temperatures rarely exceeded 20 °C when *G. tamarensis* was present.

Bloom development in the three estuaries was simulated by combining Equation (1) with two additional functions:

$$N_t = N_o e^{\mu t} \tag{2}$$

$$T = b_o + b_1 t + b_2 X \,, \tag{3}$$

where N = population density (cells $\cdot$ l^{-1}), t = time (d), and X is an indicator variable designating the pond ($X = 1$ for Perch Pond; 0 for Salt and Mill Pond). The function describing temperature change in the ponds, Equation 3, was estimated using multiple

regression techniques with the data shown in Fig. 1B. Results of this analysis indicated that (1) the ponds were warming at the same rate (0.165 ± 0.015 °C · day^{-1}; 95% CI), (2) that warming in Salt and Mill Ponds could be described by the same line ($P < 0.05$), and (3) that Perch Pond was, on the average, 3 ± 1 °C (95% CI) warmer than Salt or Mill Pond.

Given the above temperature function, population growth rates could be calculated using Equation (1). Initial cell concentrations measured in each pond (Fig. 1) were then used as the starting point for simulating ΔN with time. Assuming exponential growth, (Equation 2), population density was determined for each sampling date during 1980.

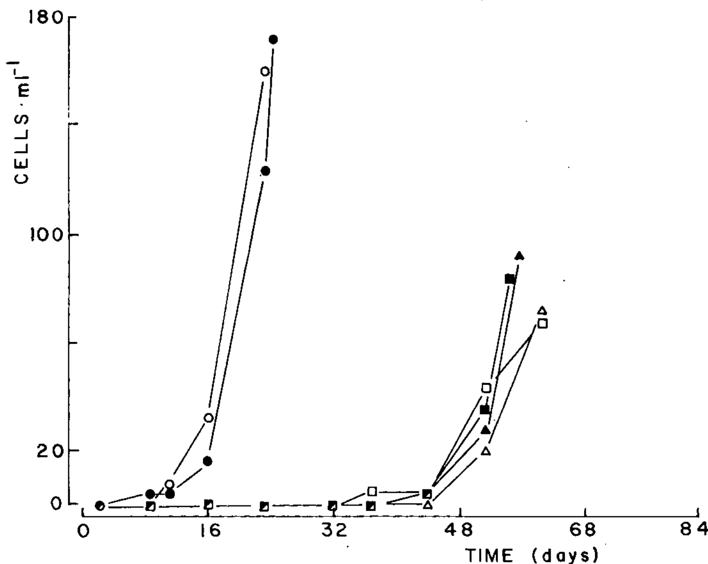

Fig. 5. Comparison of observed and predicted *Gonyaulax tamarensis* population growth during bloom development in three Cape Cod estuaries, 1980: Perch Pond: ○ obs., ● pred.; Salt Pond: □ obs., ■ pred.; Mill Pond: △ obs., ▲ pred.

As shown in Fig. 5, the observed and predicted population levels were very similar up to the point of peak abundance in all three systems. We conclude from the close agreement between the 1980 data and the model that the development of these *G. tamarensis* blooms can be predicted simply on the basis of salinity dependent temperature regulation of population growth.

CELL VOLUME CHANGE

In addition to differences in division rate, average cell-size also varied in cultures grown at different temperatures. Plotted as a function of temperature, the change in average cell volume mirrored the change in population growth rate (Fig. 6). When rates of cell division were high, average cell volume was small (Fig. 7). No obvious skew or

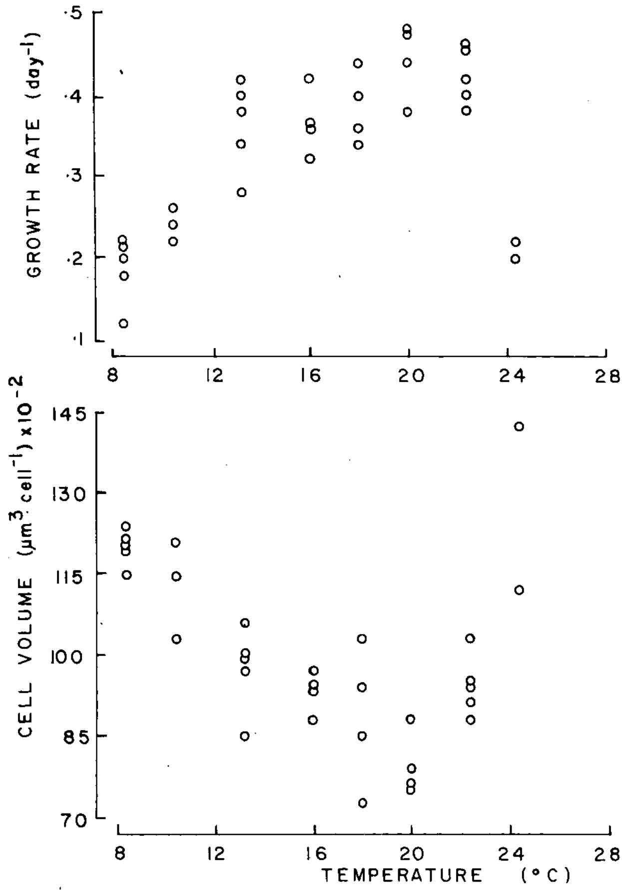

Fig. 6. Effect of temperature on population growth rate (μ) and mean cell volume for *Gonyaulax tamarensis* cultured in the laboratory.

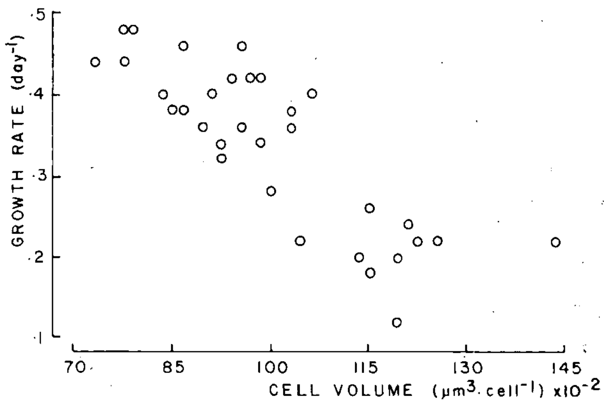

Fig. 7. Relationship between population growth rate and mean cell volume for *Gonyaulax tamarensis* in the laboratory.

bimodality was evident in the size-frequency distributions, thus it seems unlikely that the differences in average cell size were due to the production of sexual stages (Anderson, 1980).

In terms of biosynthesis, these differences in cell-size compensate to some extent for the temperature induced changes in division rate. Theoretically, large, slowly dividing cells could produce organic matter at rates comparable to small, rapidly dividing cells. However, the relative magnitudes of the growth rate and volume changes in our study (Fig. 6) suggest that although biosynthesis was less sensitive to temperature change than was population growth, it was not constant at all temperatures (assuming that cellular density, $\mu g \cdot cell^{-1}$, did not also change). For example, biomass production ($\mu m^3 \cdot cell^{-1} \cdot day^{-1}$), calculated as the product of mean growth rate and mean cell volume, was 2283, 3501, 4032, and 1664 at 8.5, 13, 22.5, and 24.5 °C, respectively.

Discussion

Although other factors undoubtedly influence the dynamics of *G. tamarensis* populations in natural systems, our data on population growth rates support the hypothesis that, in some instances, salinity and temperature can be the principal determinants of the development rate of *G. tamarensis* blooms. In effect, these two parameters set the upper limit to population growth in the ponds; a limit which is apparently reached in certain blooms.

The general response to temperature observed in this study was similar to that reported by others working with *G. tamarensis* (Prakash, 1967; Yentsch *et al.*, 1975), and the overall pattern of change in μ with increasing temperature (i.e., gradual increase, broad optimum (≈ 10 °C), steep decline) seems characteristic of many unicellular marine algae (Jitts *et al.*, 1964). The observed salinity effect agrees more closely with the results of Prakash (1967) than White (1978). Prakash reported a salinity optimum between 15 and 23‰ at 10 °C. White's regression equation, also for data collected at 10 °C, predicts a 5% increase in growth rate as salinity increases from 25.5 to 32.5‰. Our model indicates that the growth rate of our clone should decline by 24% at 10 °C. The reason for this discrepancy is unclear.

Our model does not predict the dramatic population decline seen in the field. Temperature and salinity conditions remained favorable for population growth throughout the sampling season in all the ponds, thus other factors must control abundance beyond these peaks. Since the concentration of major nutrients (*N* and *P*) also remained sufficient for continued growth (Anderson *et al.*, unpubl. data), grazing, encystment, tidal advection or micronutrients (either through limitation or toxicity; Anderson & Morel, 1978) must eventually override the effects of temperature and salinity on division rates. The usefulness of our model at this point, then, is in estimating a maximal expected growth rate for populations of estuarine *G. tamarensis* (sensu Eppley, 1972) thus predicting the earliest probable date for the onset of toxic conditions.

The general applicability of our model was tested against two additional published

sets of data on *G. tamarensis* blooms, one for Perch Pond during 1977 (Anderson & Morel, 1979), and one for the Bay of Fundy during 1962 (Prakash *et al.*, 1971). For Perch Pond, the close agreement between observed and predicted results (Fig. 8)

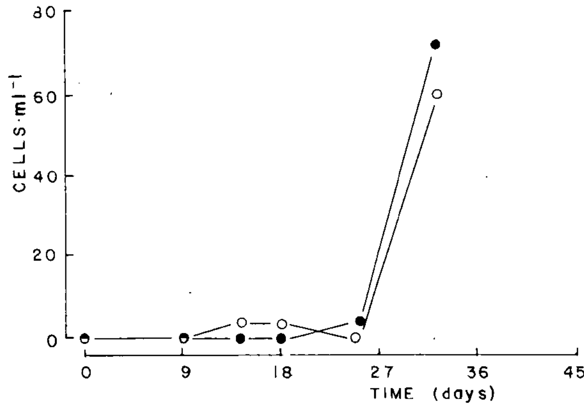

Fig. 8. Comparison of observed (○) and predicted (●) *Gonyaulax tamarensis* population growth in Perch Pond, 1977: data from Anderson & Morel, 1979.

indicates again that, up to the point of peak abundance, the 1977 population was growing as if regulated primarily by temperature and salinity. Although surprising to us, the results suggest that other regulatory factors, such as advection, nutrients, or grazing, seem to have little effect in the early phase of population development and that an empirical model based on salinity-dependent temperature regulation may prove generally applicable during this phase in small estuaries.

For the Bay of Fundy, the agreement between observed and predicted cell concentrations was not as good (Fig. 9). This may result from (1) clonal differences, (2) the

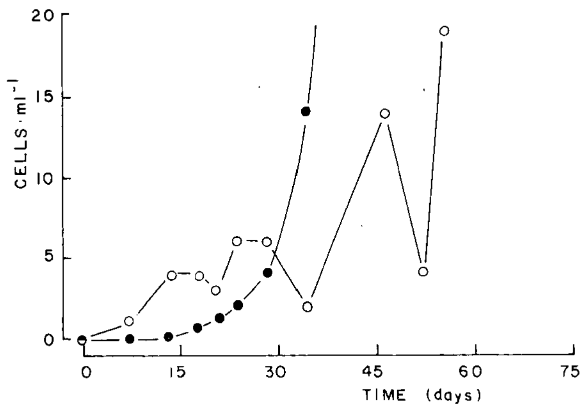

Fig. 9. Comparison of observed (○) and predicted (●) *Gonyaulax tamarensis* population growth in the Bay of Fundy, 1962: data from Prakash *et al.*, 1971.

inadequacy of surface temperature data and sampling problems due to patchiness in deep-water environments, or (3) the increased importance of other regulatory factors, such as grazing or temperature-nutrient-light interactions in coastal waters (Rhee & Gotham, 1981a,b).

The observations on changes in cell-size with temperature indicate that cellular growth and cell division are not tightly coupled in *G. tamarensis*; temperature affects division rates more than net rates of biosynthesis. This is apparently not uncommon for marine phytoplankton. Goldman (1977) found that cell biomass in *Phaeodactylum tricornutum* and *Dunaliella tertiolecta* in continuous culture increased at temperatures above and below the optimum for cell division as we have found with *Gonyaulax tamarensis*. Eppley (1972) compiled evidence for several species showing that decreased temperatures resulted in increased cellular biomass. For *Ditylum brightwellii* and *Dunaliella tertiolecta*, $C \cdot cell^{-1}$ and $C \cdot Chl\ a^{-1}$ roughly doubled as temperature was decreased 10 to 15 °C. Similarly, we found a near two-fold change in the average cell volume of *Gonyaulax tamarensis* over a comparable temperature range (Fig. 6).

Ecologically, morphological variation due to temperature may be mechanistically related to bloom decline. Limited evidence suggests that the decline of several red-tide populations was due to grazing by protozooplankton and/or rotifers (e.g., Prakash, 1963; Holmes *et al.*, 1967). Such grazers, especially tintinnids, may prey selectively on dinoflagellates provided the cells are small enough for ingestion (Stoecker *et al.*, 1981). In theory, then, small *G. tamarensis* may suffer higher predation rates than large morphs, particularly when the major grazers are microzooplankton. If so, one would expect increasing grazing pressure to occur at temperatures > 13 °C, when the cultured cells were the smallest. It is noteworthy that *G. tamarensis* population decline in the study ponds began as water temperatures exceeded this potential grazing threshold.

The strong correlation between μ and cell volume (Fig. 7) invites consideration of cell size as an index of in situ growth rates. Although we urge caution here, precise measurements of vegetative cell size might provide relative estimates of μ through time in field populations. Supported by more sensitive but laborious techniques (e.g., the mitotic index approach, Rubin, 1981; McDuff & Chisholm, in press) such data would help further clarify the ways that physiological responses to environmental conditions affect estuarine blooms of *Gonyaulax*.

In summary, our laboratory data show that the effects of temperature and salinity on population growth are sufficient to account for the timing of four estuarine blooms. The data also show that changes in cell size offset the effects of temperature on population growth, but that cellular growth is not sufficiently enhanced to maintain constant biomass production at all temperatures. The significance of the empirical model we have constructed lies in its simplicity. We do not suggest that it constitutes a general model for red tides, but rather the simplest quantitative expression for predicting maximal rates of bloom development. As such, it can serve as a basic formulation to which other regulatory factors can be added in developing a more general predictive model of *G. tamarensis* blooms in New England's coastal waters.

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