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Spatial and temporal aspects of *Gyrodinium galatheanum* in Chesapeake Bay: distribution and mixotrophy

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Abstract. *Gyrodinium galatheanum* (Braarud) Taylor 1995 is a common bloom-forming, potentially toxic photosynthetic dinoflagellate in Chesapeake Bay, USA. Abundance of this dinoflagellate achieved densities >4 × 10^3 cells ml^{-1} in the mid- and upper Bay during late spring and early summer of 1995 and 1996. Ingestion of cryptophytes by this dinoflagellate was detected in most samples collected from the Bay. During late spring and early summer, mean number of ingested cryptophytes per *G.galatheanum* was as high as 0.46 for dinoflagellate populations located in surface waters of the mid- and upper Bay where dissolved inorganic phosphorus was low. Observations on the distribution of *G.galatheanum* in Chesapeake Bay show that populations of this dinoflagellate were usually restricted to waters with salinities ranging from 7 to 18 psu, seasonally progressed up the estuary, and usually co-occurred with cryptophytes. Correlation analysis indicates that abundance of *G.galatheanum* and incidence of feeding was negatively correlated with dissolved inorganic phosphorus, and that incidence of feeding was positively correlated with abundance of cryptophyte prey. These results indicate that *G.galatheanum* is an important component of the Chesapeake Bay phytoplankton during the spring and summer. Our results suggest that the phagotrophic capability possessed by this phototrophic dinoflagellate may contribute to its success in a varying-resource environment like Chesapeake Bay.

Introduction

In most years, blooms of relatively large, photosynthetic dinoflagellates occur in Chesapeake Bay or its tributaries. Usually, these blooms occur in late spring to early fall in response to nutrient input from terrestrial run-off. At times, surface abundances of dinoflagellates are high enough to visibly discolor the water, causing red tides. Dinoflagellate blooms can represent a major portion of local phytoplankton biomass and production (Loftus *et al.*, 1972; Sellner and Brownlee, 1990). Several species are reported to be involved in the formation of blooms in Chesapeake Bay, including *Prorocentrum minimum* (synonyms, *P.mariae-lebouriae*, *P.triangulatum*), *Gymnodinium sanguineum* (synonyms, *G.splendens*, *G.nelsonii*), *Gyrodinium uncatenum* and *Ceratium furca* (Tyler and Seliger, 1978; Bockstahler and Coats, 1993a). None of these dinoflagellates are reported to be toxic in the mid-Atlantic region, but dense blooms can nevertheless have harmful effects. High concentrations of dinoflagellates are reported to inhibit feeding of zooplankton and invertebrate larvae and to alter coastal food webs (Shumway, 1990; Turner and Tester, 1997). Sedimentation and decomposition of senescent blooms can lead to low oxygen in bottom waters, causing fish kills and losses of benthic invertebrates (Sellner and Brownlee, 1990; Shumway, 1990; Hallegraeff, 1993; Turner and Tester, 1997).

In 1994, we noticed red tide patches caused by a small (<20 μm) non-thecate photosynthetic dinoflagellate in mesohaline waters of Chesapeake Bay (Li *et al.*, 1996). Isolates of this species were identified as *Gyrodinium galatheanum* (Brauud) Taylor 1995 (synonym, *Gymnodinium galatheanum*) using scanning electron microscopy (Steidinger, personal communication). *Gyrodinium galatheanum* had not been previously reported from the Bay, but with light microscopy it is easily confused with *Gyrodinium estuariale* (synonym, *Gymnodinium estuariale*) which has been reported from Chesapeake Bay (Marshall, 1980, 1994).

Blooms of *G.galatheanum* have been recorded since 1950 in coastal waters of Southwest Africa, and thereafter in European waters (Johnsen and Sakshaug, 1993; Nielsen, 1996). *Gyrodinium galatheanum* has been considered toxic because blooms of this species are often associated with mortality of fish (Larsen and Moestrup, 1989; Hallegraeff, 1993). Laboratory studies have also shown that high densities of this species inhibit the growth of mussels (Nielsen and Stromgren, 1991) and can kill cod larvae (Nielsen, 1993). However, not until recently has this dinoflagellate been noticed along the southeast coast of the USA. Blooms of *G.galatheanum* have been associated with fish kills in aquaculture ponds and small tributaries in the Chesapeake Bay region and elsewhere in the south east [(Terlizzi, 2000) and personal communication; Steidinger personal communication]. However, to date, fish kills have not been reported in association with blooms in the mainstem of Chesapeake Bay. In contrast with European populations, little quantitative information is available on distribution and other ecological aspects of this species in American waters.

An important feature of this phototrophic dinoflagellate is its phagotrophic capability. Field and laboratory experiments have demonstrated that it is able to eat a variety of other protists, including cryptophytes, with which it commonly co-occurs in Chesapeake Bay (Li *et al.*, 1996). Mixotrophy (i.e. simultaneous nutritional mode of heterotrophy and autotrophy) appears common among dinoflagellates (Sanders and Porter, 1988; Bockstahler and Coats, 1993a; Jacobson and Anderson, 1996; Li *et al.*, 1996), and has been proposed to contribute to their success under varying environmental conditions (i.e. light and nutrient limitation) (Stoecker *et al.*, 1997). Whether mixotrophy in *G.galatheanum* could influence its survival, distribution and bloom formation in the Bay remains largely unknown.

The goal of this research was to document and analyze spatial and temporal patterns in the distribution of *G.galatheanum* (Braarud) Taylor 1995, cryptophytes, and ingestion of cryptophytes by *G.galatheanum*. In this study, we document variations in seasonal and spatial distributions of *G.galatheanum* and cryptophyte prey in Chesapeake Bay based on a two-year survey. We also investigate the possible role of physical, chemical and biological factors in regulating the distribution and feeding patterns of *G.galatheanum*.

Method

Samples were collected during monthly cruises in Chesapeake Bay between May and September 1995, and between April and September 1996. On each cruise

aboard the RV 'Cape Henlopen', vertical casts of CTD (conductivity, temperature, depth, plus fluorescence) with Niskin bottles were made at each station during daylight to profile the water column. Samples were taken at 2–3 m intervals from the surface to near bottom at routine stations along the main-stem of the Bay (Figure 1). Samples were also taken from lateral transect stations in the mesohaline region of the Bay (Figure 1).

For estimating abundance of *G.galatheanum* and phycoerythrin-containing cryptophytes, whole-water samples (20 ml for each) were immediately preserved

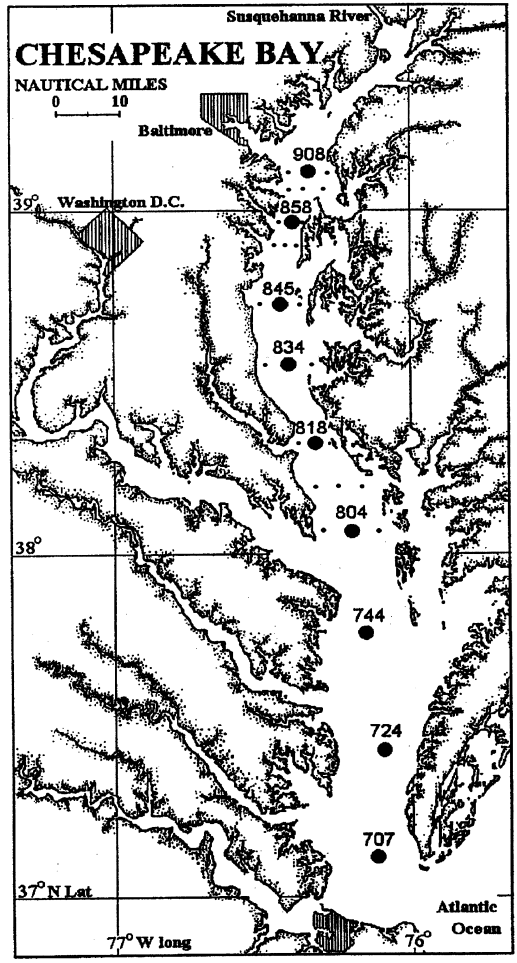

Fig. 1. Map of Chesapeake Bay showing locations of the mainstem stations (•) and the cross-bay transect stations (•) for cruises in 1995 and 1996. Station designations from the south to the north are 707 (37°07′ N; 76°07′ W); 724 (37°24′ N; 76°05′ W); 744 (37°44′ N; 76°11′ W); 804 (38°04′ N; 76°13′ W); 818 (38°18′ N; 76°17′ W); 834 (38°34′ N; 76°26′ W); 845 (38°45′ N; 76°26′ W); 858 (38°08′ N; 76°23′ W); 908 (39°08′ N; 76°20′ W). In the text, the following regions of the bay are defined as: the upper bay (or the northern bay) – above 39°N, the mid-bay – between 39°N and 37°48′ N, and the lower bay (or the southern bay) – below 37°48′ N.

with glutaraldehyde at a final concentration of 1% and stored at 4°C until 5–10 ml sub-samples were filtered onto 2 μm pore black membrane filters (Poretic Corp.). Filters were mounted on glass slides with immersion oil (Resolve©) and capped with a cover slip. Slides were stored frozen at –20°C and subsequently examined with epifluorescence microscopy at room temperature (Zeiss filter set 487709; BP450–490 exciter filter, FT 510 dichromatic beam splitter, and LP520 barrier filter). *Gyrodinium galatheanum* and orange-fluorescent cryptophytes were enumerated at 400× (Li *et al.*, 1996).

The absence or presence of food vacuoles with ingested orange-fluorescent cryptophytes was recorded for the first 100 *G.galatheanum* cells encountered on each slide. Feeding data were expressed as the number of ingested cryptophytes per *G.galatheanum*.

For inorganic nutrient analyses (ammonia, nitrate, nitrite and dissolved phosphate), duplicate samples were gently filtered through GF/F filters and stored frozen (–20°C) in acid-washed scintillation vials until analysis (Technicon Autoanalyzer II, Bran and Luebbe detector, TAOS software). Because gains or losses of ammonia may occur when samples are not analyzed within a few hours after sampling (Parsons *et al.*, 1984), the ammonia data are not as accurate as those for the other dissolved inorganic nutrients.

Correlation analysis for abundance of *G.galatheanum* and mean number of ingested cryptophyte per *G.galatheanum* cell with biological (cryptophyte densities and *in vivo* fluorescence), physical (temperature, salinity and depth) and chemical (concentrations of ammonia, nitrate and nitrite, and phosphate) variables were made using Spearman rank order correlation with SigmaStat Version 2.0 (Jandel Scientific software). A polynomial regression (quadratic surface) gridding method was used to develop vertical salinity contour plots; other contour plots were developed by Kriging, a geostatistical gridding method provided with Surfer Version 6.00 (Golden Software, Inc).

Results

Gyrodinium galatheanum distribution

At times, *G.galatheanum* was widely distributed in the Bay (Figures 4 and 5), but usually it was restricted to waters with salinities ranging from 7 to 18 (Figures 2–5). In May 1995, highest density of this dinoflagellate occurred in the mid-Bay between Station 818 and Station 858 (Figures 4 and 5). Peak density was associated with the 8–14 isohalines, with a subsurface maximum density of about 4×10^3 cells ml^{-1} at Station 845 (Figures 2–5). Several weeks later, peak density still coincided with the 8–14 isohalines, but the bloom had moved several km northward, with a surface maximum density of approximately 3×10^3 cells ml^{-1} to the west of Station 858. By July, two localized areas of high density of *G.galatheanum* were evident, one of which was located several km northward from Station 858 and the other southward from Station 858 to Station 845. Cell densities at that time had begun to decline, with a surface maximum density of approximately 1×10^3 cells ml^{-1}. By August, the Bay showed more stratification relative to that in July

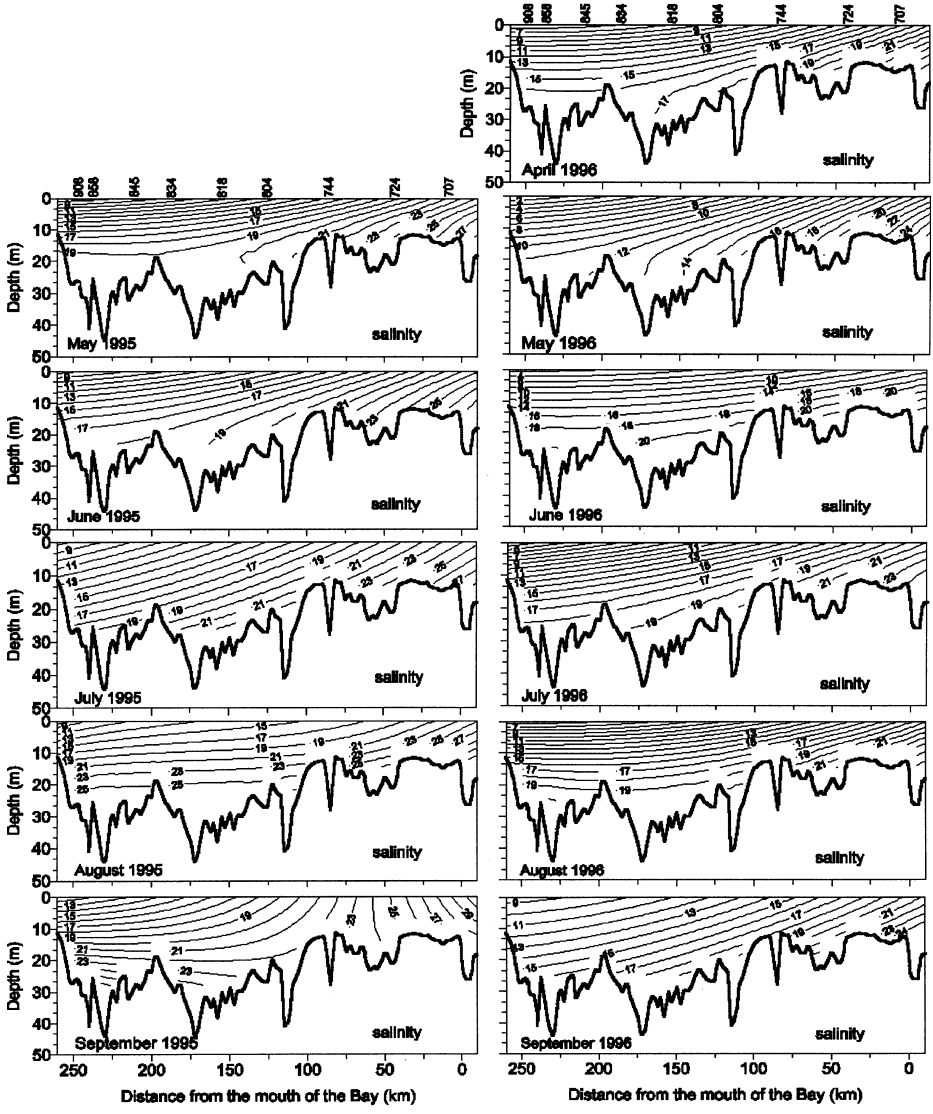

Fig. 2. Vertical salinity isopleths along the mainstem of Chesapeake Bay for 1995 and 1996 cruises. Station numbers are given at the top of the panels.

and September, and the bloom had dissipated (Figures 2 and 4). Cell densities above 50 cells ml^{-1} were only encountered in a surface patch in the upper Bay (Figure 4). In September, mixing was observed near the mouth of the Bay and a second bloom appeared in surface waters in the upper Bay, but cell densities were significantly lower (maximum of about 800 cells ml^{-1}) than during the May bloom (Figures 4 and 5).

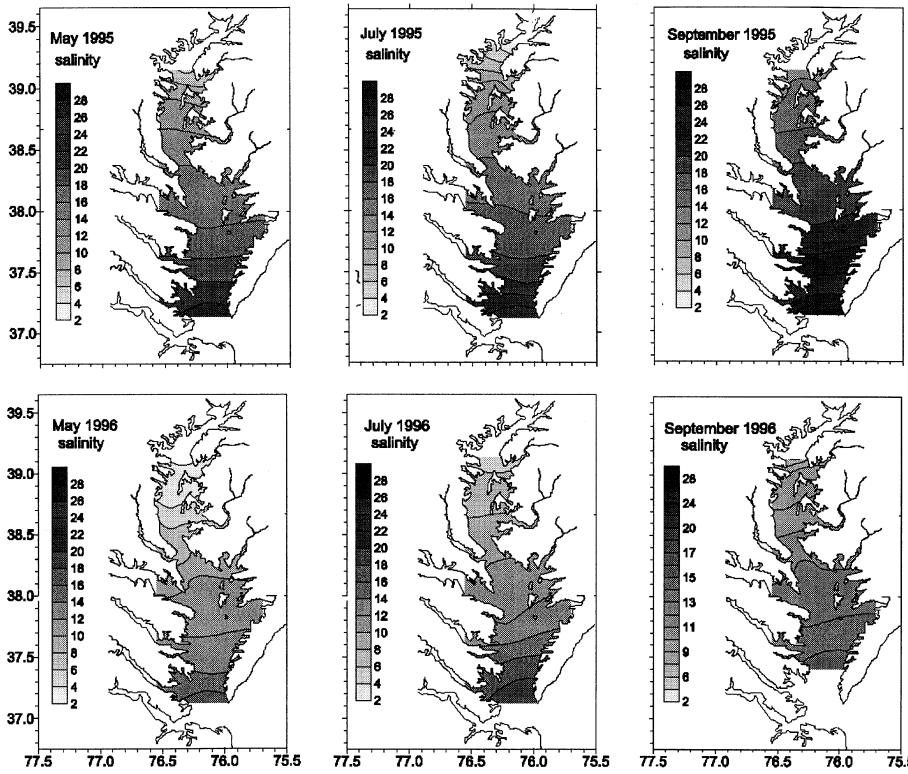

Fig. 3. Horizontal distribution maps of salinity isopleths in the surface waters of Chesapeake Bay for 1995 and 1996 cruises.

In 1996 cruises, we were able to record the whole process from *G.galatheanum* bloom initiation to termination (Figures 4 and 5). Lower salinity and stronger stratification were observed in the Bay in 1996 than in 1995 (Figures 2 and 3). In April 1996, *G.galatheanum* was restricted to the southern part of the Bay and was present at only a few cells ml^{-1} (Figure 4). By May, the center of the *G.galatheanum* population had shifted northward to the mid-Bay, with abundances up to 200 cells ml^{-1}. The highest densities were located at the pycnocline (Figure 4). In June, the peak density was still located in the mid-Bay, but accumulations of cells were observed just above the pycnocline, and a subsurface patch was observed at Station 818 (Figure 4). By July, two localized density maxima (>200 cells ml^{-1}) of *G.galatheanum* occurred in surface waters in the mid-Bay (Figures 4 and 5). Over the next month, abundance of *G.galatheanum* significantly declined and the density peaks continuously shifted towards the north (Figure 4). Elevated cell densities (>200 cells ml^{-1}) re-occurred in September, as in the previous year, in surface water in the mid- to upper Bay (Figures 4 and 5).

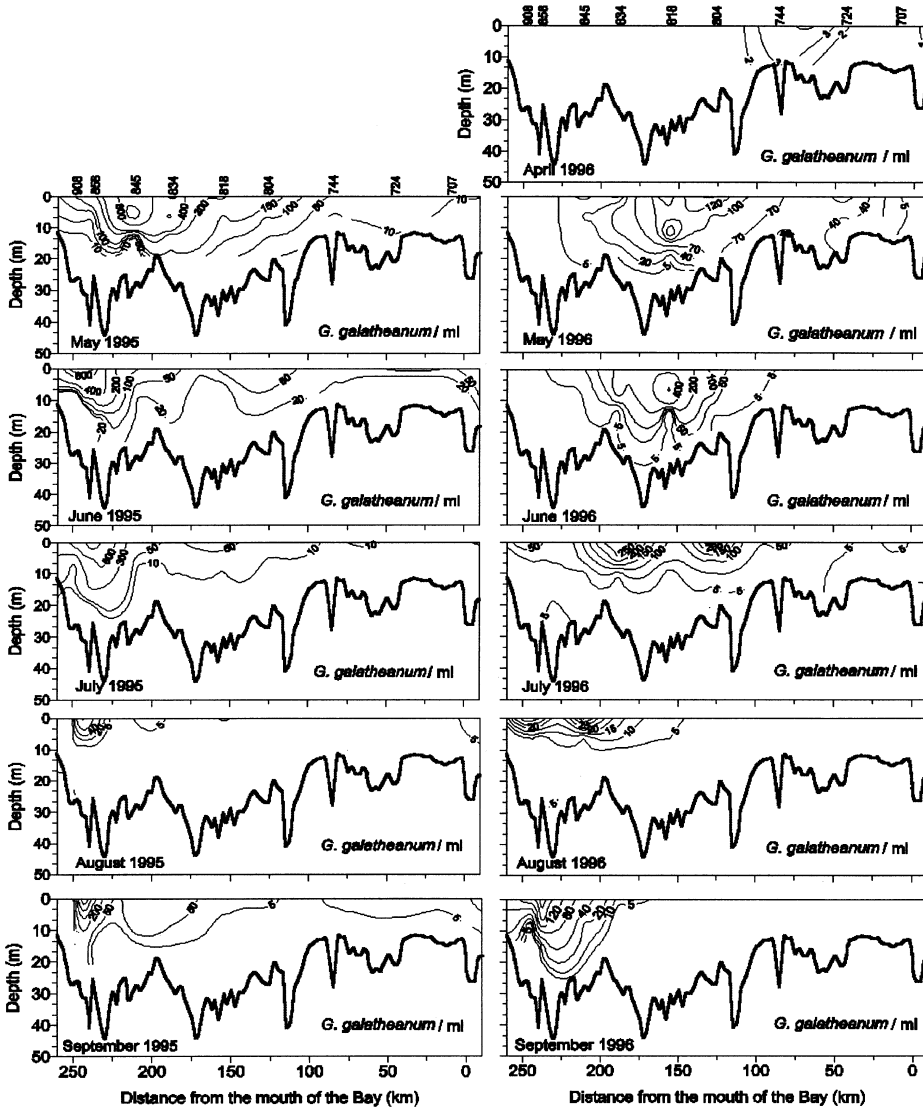

Fig. 4. Vertical distribution maps showing the abundance of *Gyrodinium galatheanum* along the mainstem of Chesapeake Bay for 1995 and 1996 cruises. Station numbers are given at the top of the panels.

Cryptophyte distribution

The vertical and horizontal distribution of phycoerythrin-containing cryptophytes in Chesapeake Bay for the 1995 and 1996 cruises are illustrated in Figures 6 and 7, respectively. Cryptophytes were widely distributed in the Bay and often formed density peaks in different areas and during different months. In 1995, two

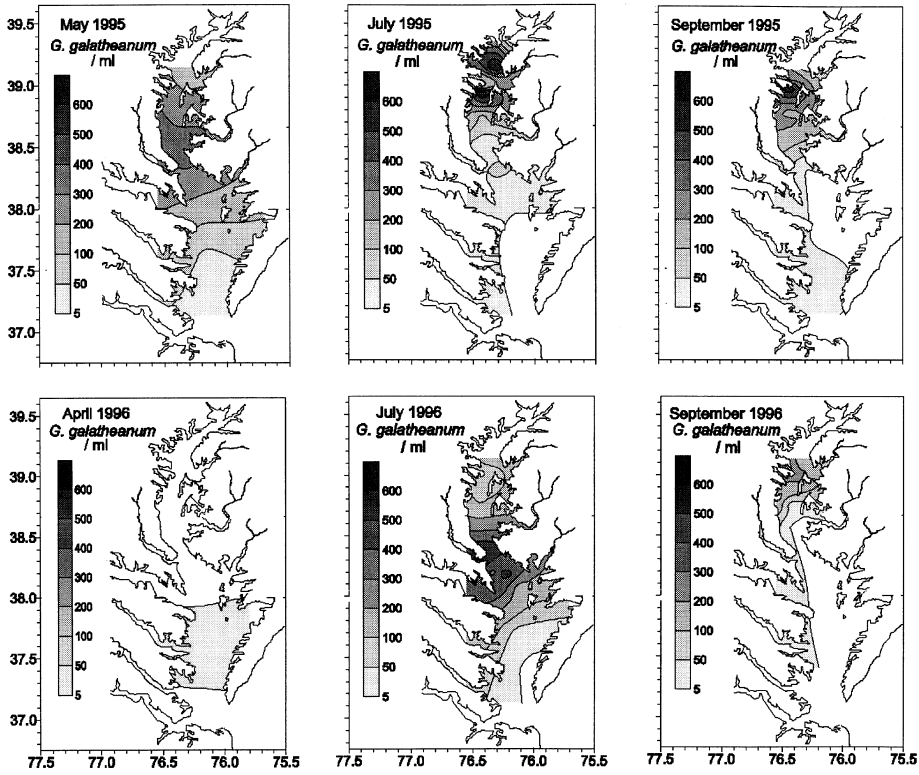

Fig. 5. Horizontal distribution maps showing the abundance of *Gyrodinium galatheanum* in the surface waters of Chesapeake Bay for 1995 and 1996 cruises.

localized density maxima of cryptophytes were found in May and June in the mid- and upper Bay (Figures 6 and 7). In the following months, only one density maximum of cryptophytes was observed in the mid- and upper Bay, with the highest density >6 $\times$ 10^3 cells ml^{-1} found in July (Figures 6 and 7). A similar pattern of seasonal distribution was found in 1996, i.e. density of cryptophytes progressively increased from spring to summer when bloom concentrations reached >7 $\times$ 10^3 cells ml^{-1}, and then cryptophyte abundance declined in September (Figures 6 and 7).

Feeding of Gyrodinium galatheanum *on cryptophyte prey*

The feeding patterns of *G.galatheanum*, as indicated by mean number of ingested phycoerythrin-containing cryptophytes per *G.galatheanum*, are presented in Figures 8 and 9. In May 1995, two localized areas with high incidences of feeding were observed, one of which (>0.3 ingested cryptophytes per *G.galatheanum*) was located in surface waters in the mid- to upper Bay and the other (>0.3 ingested cryptophytes per *G.galatheanum*) in the lower Bay (Figures 8 and 9). Both of

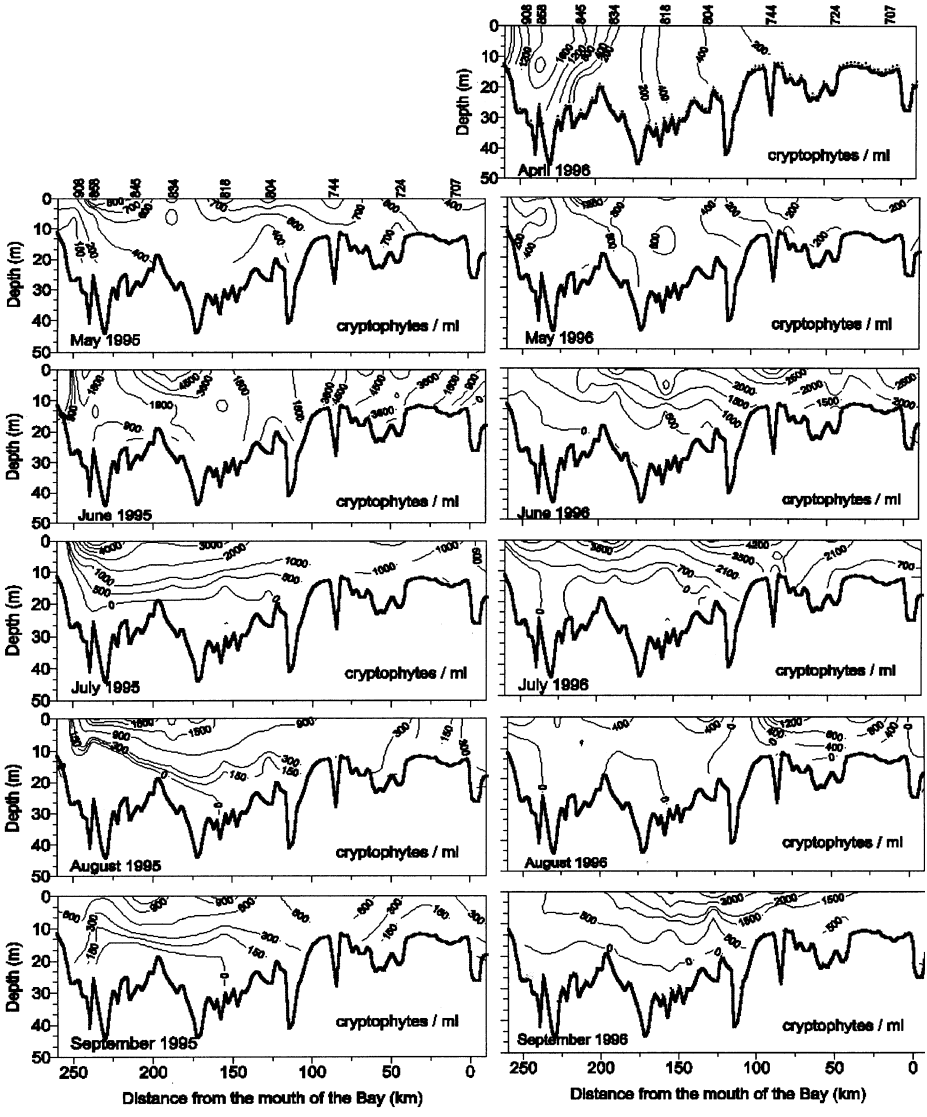

Fig. 6. Vertical distribution maps showing the abundance of phycoerythrin-containing cryptophytes along mainstem of Chesapeake Bay for 1995 and 1996 cruises. Station numbers are given at the top of the panels.

these areas of high feeding were associated with high densities of the cryptophyte prey (>700 cryptophyte cells ml^{-1}) (Figures 6 and 7). As the summers progressed, areas of high feeding on cryptophytes shifted northward in the Bay, with one area of high feeding located in surface waters in the upper Bay and another centered at the pycnocline of Station 845 in the mid-Bay region (Figures 8 and 9). By July

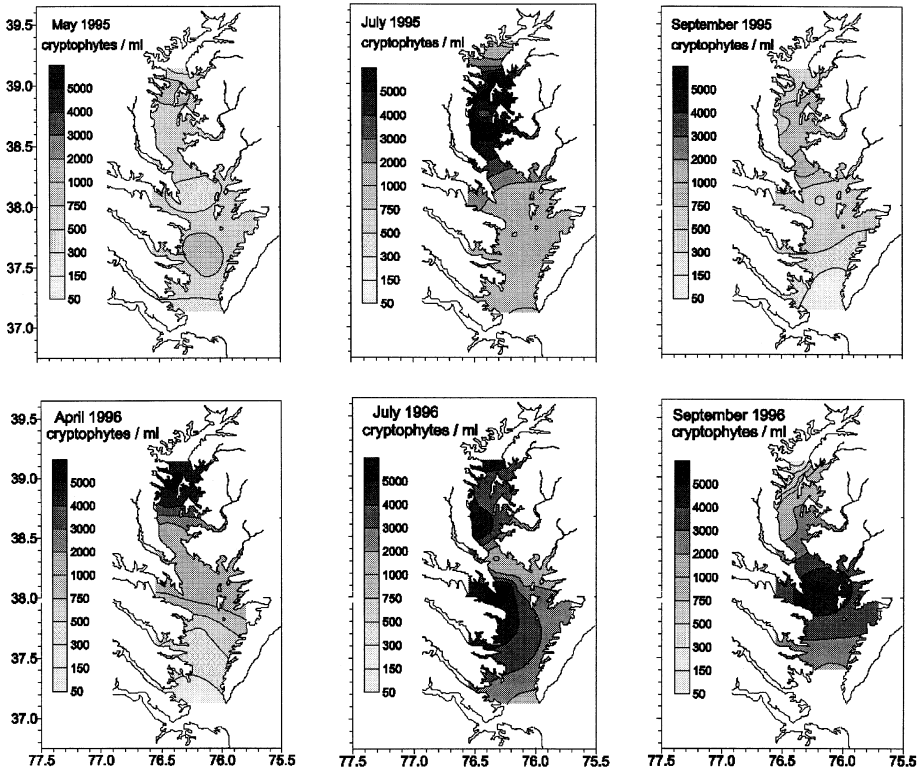

Fig. 7. Horizontal distribution maps showing the abundance of phycoerythrin-containing cryptophytes in surface waters of Chesapeake Bay for 1995 and 1996 cruises.

1995, two peak areas of feeding were still evident and associated with cryptophytes (Figures 6–9), but the number of ingested cryptophytes per *G.galatheanum* was much lower than observed in May and June (Figures 8 and 9). With the decline in abundance of *G.galatheanum* and cryptophytes in August, lower incidences of feeding by *G.galatheanum* were observed (Figure 8). By September, reoccurrence of relatively high incidences of feeding (>0.1 ingested cryptophytes per *G.galatheanum*) was found in surface waters in the upper Bay (Figures 8 and 9).

During 1996, feeding by *G.galatheanum* progressively increased from April until July, when highest feeding (>0.3 ingested cryptophytes per *G.galatheanum*) was found in surface waters in the mid-Bay (Figures 8–9). In the late summer and fall, incidence of feeding declined significantly and the areas of highest feeding were shifted toward the north (Figures 8 and 9). Two peak areas of feeding activity were still evident, and the locations of these peaks were still coincident with the locations of cryptophyte maxima (Figures 8 and 9).

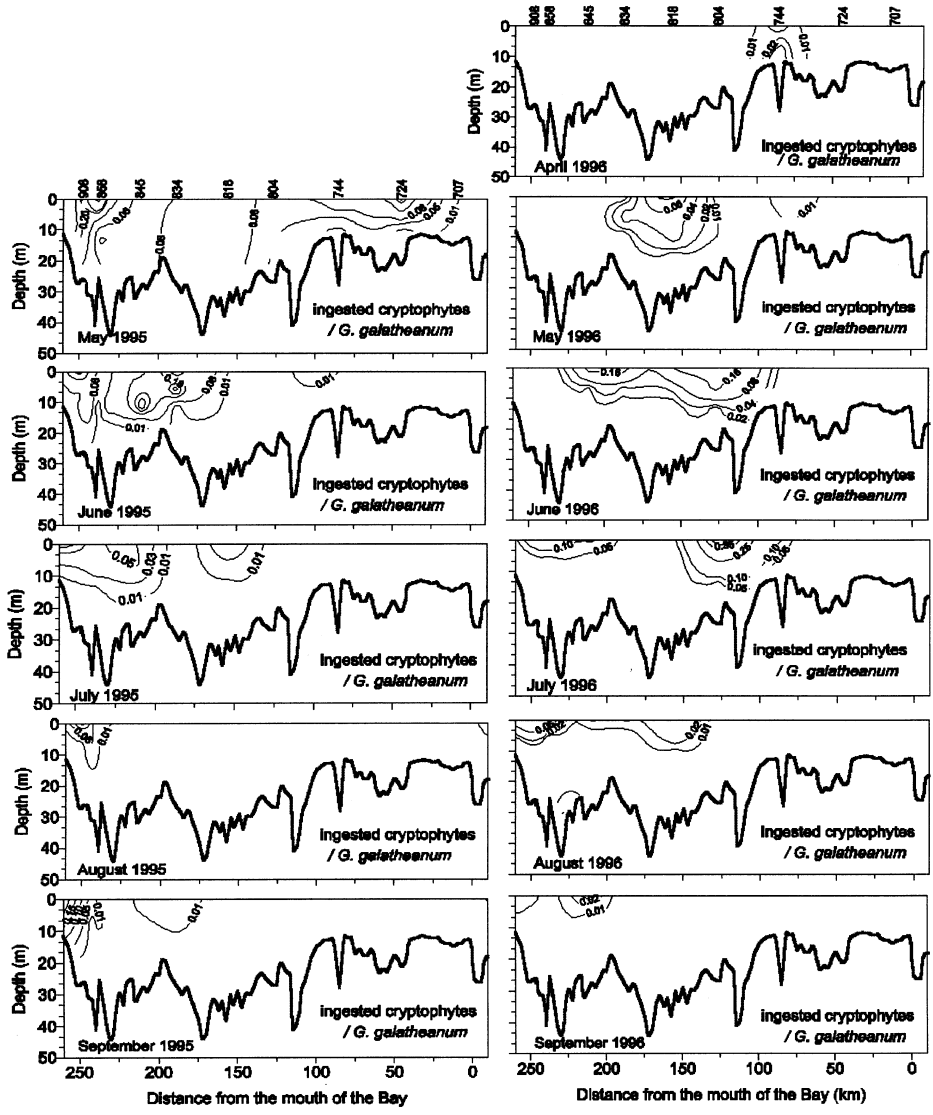

Fig. 8. Vertical distribution maps showing the number of ingested cryptophytes per *Gyrodinium galatheanum* along mainstem of Chesapeake Bay for 1995 and 1996 cruises. Station numbers are given at the top of the panels.

Factors that affect the distributions and feeding patterns of Gyrodinium galatheanum

In order to investigate the possible role of biological, physical and chemical factors in regulating the distribution and feeding patterns of *G.galatheanum*, a Spearman rank order correlation analysis was carried out on variables measured

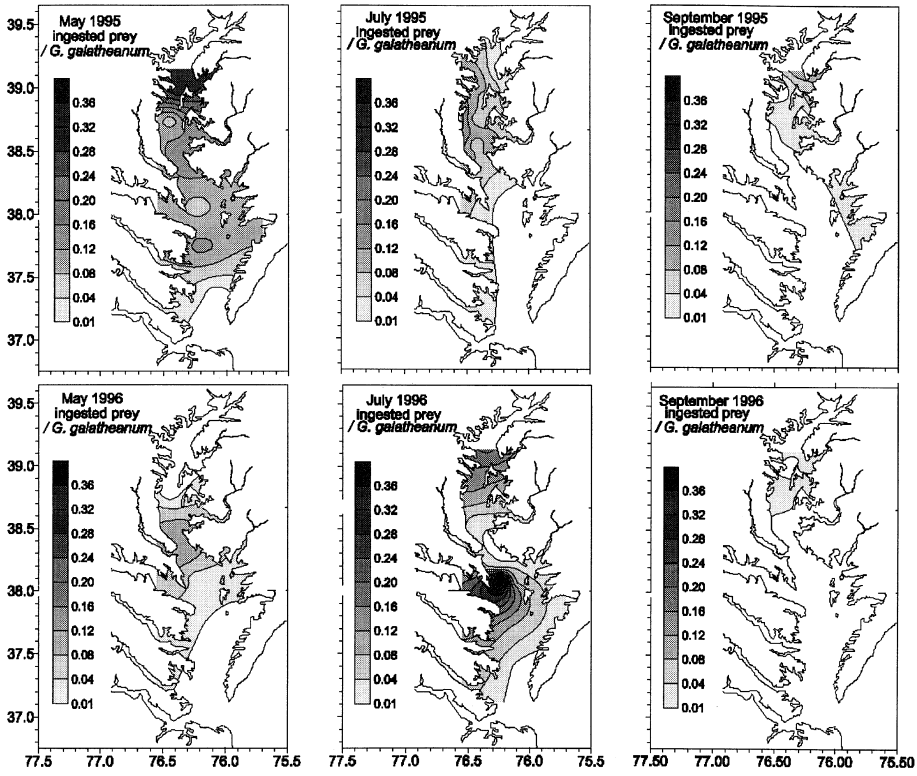

Fig. 9. Horizontal distribution maps showing the number of ingested cryptophytes per *Gyrodinium galatheanum* in surface waters of Chesapeake Bay for 1995 and 1996 cruises.

during our cruises (Table I). Dinoflagellate abundance positively correlated with abundance of cryptophytes and *in vivo* fluorescence (Table I). There was marginally significant correlation between *G.galatheanum* abundance and temperature, but cell densities did reflect seasonal variation in temperature (Table I, Figure 10A). Abundance of *G.galatheanum* was negatively correlated with salinity (Table I) and high abundances of this dinoflagellate were only found at salinities ranging from 7 to 16 (Figure 10B). Abundance of *G.galatheanum* was also negatively correlated with dissolved inorganic phosphorus (DIP), but positively correlated with dissolved inorganic nitrogen (DIN) (Table I). In addition, the DIP:DIN ratio was negatively correlated with the abundance of *G.galatheanum* (Table I).

Several factors were significantly correlated with incidence of feeding by *G.galatheanum*. Our data show that there is a significant, although relatively weak, positive correlation (r = 0.38) between number of ingested prey per dinoflagellate and prey abundance (Table I). The mean numbers of ingested cryptophytes per *G.galatheanum*, when plotted as a function of prey abundance, exhibit a considerable scatter (Figure 10C). Ingestion of cryptophytes by *G.galatheanum*

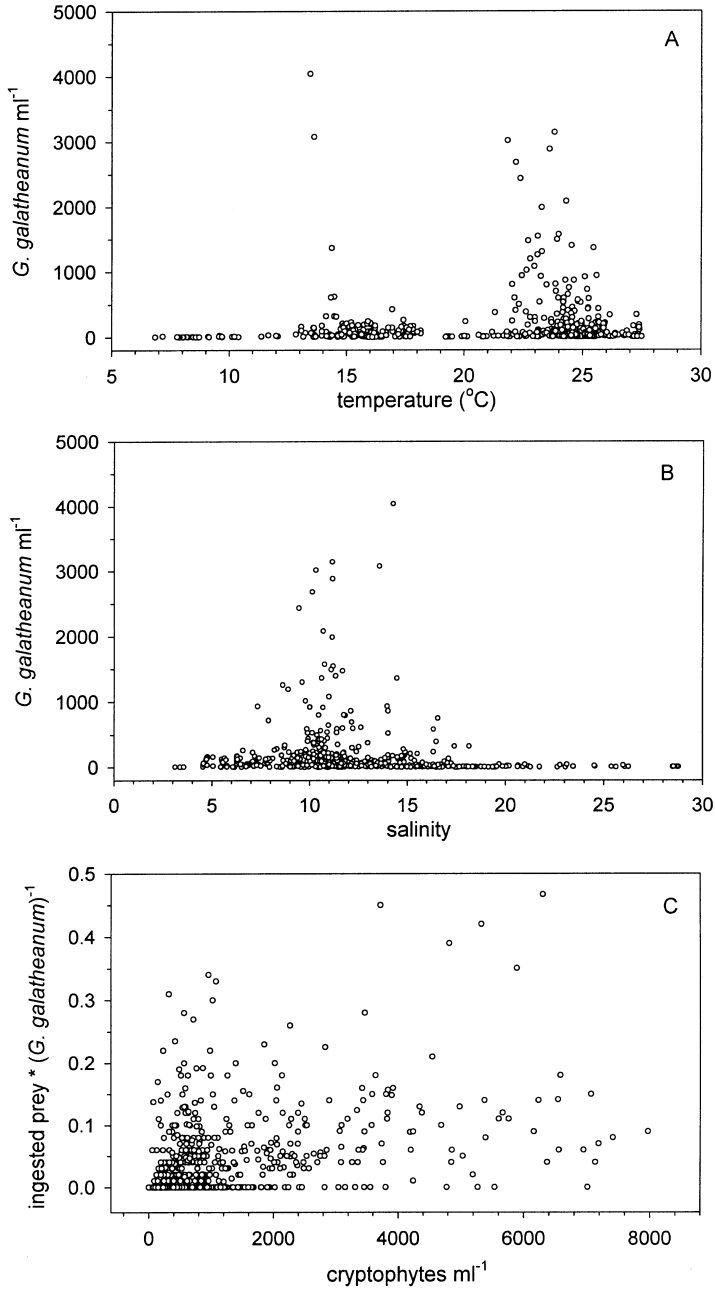

Fig. 10. Relationships of abundance of *Gyrodinium galatheanum* with temperature and salinity are illustrated in (**A**) and (**B**), respectively. The mean number of ingested cryptophytes per *G.galatheanum* plotted as a function of abundance of phycoerythrin-containing cryptophytes is presented in (**C**).

Table I. Spearman rank order correlation analysis of abundances and incidences of feeding of *Gyrodinium galatheanum* with biological, chemical and physical variables

	G.galatheanum ml^{-1}		Ingested cryptophytes per *G.galatheanum*	
	Coef.	*n*	Coef.	*n*
G.galatheanum ml^{-1}			0.51 (**)	572
Cryptophytes ml^{-1}	0.28 (**)	572	0.38 (**)	572
In vivo fluorescence	0.36 (**)	561	0.28 (**)	561
Temperature (°C)	0.13 (**)	561	–0.02 (ns)	561
Salinity	–0.34 (**)	561	–0.39 (**)	561
Depth (m)	–0.35 (**)	561	–0.33 (**)	561
[NH_4^+], μmol l^{-1}	0.03 (ns)	236	0.05 (ns)	236
[NO_2^-] + [NO_3^-], μmol l^{-1}	0.27 (**)	236	0.41 (**)	236
DIN, μmol l^{-1}	0.16 (*)	236	0.38 (**)	236
DIP, μmol l^{-1}	–0.16 (*)	236	–0.40 (**)	236
DIP:DIN, (mol:mol)	–0.25 (**)	236	–0.58 (**)	236

Coef. = Correlation coefficient; probability is indicated as ns = not significant ($P > 0.05$), * $P < 0.05$ and ** $P < 0.01$; *n* = number of samples.

and depth were negatively correlated, indicating that higher feeding occurred in surface waters than in deeper waters (Table I). In addition, feeding of this dinoflagellate was negatively correlated with salinity (Table I), suggesting that feeding usually occurred near the surface of the mid- and the northern Bay where salinity was relatively low. *In vivo* fluorescence was positively, but weakly, correlated with *G.galatheanum* ingestion (Table I). Significant positive correlation between total DIN and ingestion of cryptophytes, but negative correlations between total DIP or DIP:DIN and ingestion of the cryptophytes by *G.galatheanum*, were evident (Table I).

Discussion

Our results indicate that *G.galatheanum*, a species that can form harmful algal blooms, is an abundant summer species in Chesapeake Bay. Although fish kills have not been reported in association with *G.galatheanum* in the mainstem of the Bay, this species, when it reaches densities of around 1×10^5 cells ml^{-1}, has been associated with fish kills, particularly in aquaculture facilities, in the Chesapeake Bay region and elsewhere [(Nielsen, 1993, 1996; Terlizzi, 2000); Steidinger, personal communication]. The highest abundances we observed in open waters of the Chesapeake Bay during 1995 and 1996 were about 4×10^3 cells ml^{-1}, lower than those densities reported to kill fish but high enough to discolor surface waters (Li, personal observation). This density is in the upper range of total photosynthetic nanoflagellate (2–20 μm range) densities in the Bay between April and October (Dolan and Coats, 1990), indicating that *G.galatheanum* can dominate the 2–20 μm nanophytoplankton. *Gyrodinium galatheanum* densities were similar to those reported for *Prorocentrum minimum*, a well known bloom-forming species in Chesapeake Bay (Tyler and Seliger, 1978, 1981), during 1995 and 1996 (Stoecker *et al.*, 1997). Larger-size bloom-forming dinoflagellates, such

as *Gymnodinium sanguineum*, *Ceratium furca* and *Gyrodinium uncatenum*, usually occur at densities of <100 cells ml^{-1} in Chesapeake Bay during summer [data in (Bockstahler and Coats, 1993b)]. Our investigation indicates that *G.galatheanum* is an important component of the Chesapeake Bay phytoplankton during the spring and summer. Because *G.galatheanum* is a harmful species at high densities, it is important to understand the factors that regulate its spatial and temporal abundance.

From 2 years of field observations in Chesapeake Bay, we found that *G.galatheanum* had wide salinity (3–29 psu) and temperature (7–28°C) tolerances (Figures 10A and 10B). However, abundance peaks of this species usually followed salinity isopleths of 8–14 psu, with highest cell density found near 10–11 psu, suggesting that the optimal salinity for net population growth of this dinoflagellate is approximately 10 psu (Figure 10B). The optimal salinity of about 10 psu also indicates that *G.galatheanum* populations may grow well in tidal tributaries, even when the mainstem salinity is >10 psu in the lower- and mid-Bay during summer. Relatively high densities of *G.galatheanum* are sometimes observed in tributaries of Chesapeake Bay during summer (Stoecker, personal observation). Some of the patterns we observed (e.g. higher cell densities of *G.galatheanum* and cryptophytes found on the western side than on the eastern side of the Bay) may have resulted from the changes in salinity and inorganic nutrient loading from major river drainages, such as from Potomac (Figures 3, 5 and 7).

In contrast to field observation, Nielsen (Nielsen, 1996) found that the optimal salinity and temperature for a culture of *G.galatheanum* isolated from the Oslofjord, Norway were 24 and 20–24°C, respectively. These discrepancies may imply that net population growth of *G.galatheanum* in the Bay may be determined largely by factors other than salinity and temperature, such as nutrient availability or predator–prey interactions. An alternate explanation may be that the *G.galatheanum* found in these two places are different physiological strains or geographical subspecies. However, no information is available on physiological variability within this species.

Although our sampling frequency was not enough to document detailed temporal changes in environmental parameters and abundance and distribution, differences between 1995 and 1996 were apparent. Susquehanna River flow is the primary source of freshwater and nutrient input to the mainstem of Chesapeake Bay. This flow largely controls spatial and temporal patterns in the distribution of salinity and nutrients, and is important to inter-annual variation in the timing, position and magnitude of phytoplankton blooms (Fisher *et al*., 1992; Harding, 1994; Malone *et al*., 1996). The mean annual freshwater flow of the Susquehanna was extremely low, 69×10^6 m^3 day^{-1} in 1995, a drought year, but extremely high, 156×10^6 m^3 day^{-1} in 1996 (Smith, 2000). This is reflected in the lower salinity (Figures 4 and 5) and higher nutrient levels in the mainstem of the Bay in 1996 than in 1995 (Smith, 2000). The centers of distribution of *G.galatheanum* and cryptophytes occurred further down the Bay in 1996 than in 1995 (Figures 4–7), probably due to these differences in the distribution of salinity and nutrients. It is interesting that although input of inorganic nutrients to the mainstem of the

Bay was higher in 1996 than 1995 (Smith, 2000) in most months, *G.galatheanum* and cryptophytes did not appear to be more abundant in 1996 than in 1995 (Figures 4–7). In 1995, the spring bloom was dominated by dinoflagellates, which, along with cyanobacteria, also dominated the summer phytoplankton assemblage. In contrast, during the high flow year, 1996, the spring bloom was dominated by diatoms, which continued to be important throughout the summer (Smith, 2000).

Changes in inorganic nutrient availability may partially explain the seasonal cycles and annual variations of dinoflagellate abundance observed. In Chesapeake Bay, primary producers often experience seasonal and spatial limitations by nitrogen or phosphorus (Fisher *et al.*, 1992; Glibert *et al.*, 1995; Malone *et al.*, 1996). It has been reported that at the extremes of low and high salinity in the Bay, ratios of N to P lie above or below the Redfield value (N:P = 16:1), respectively, and phytoplankters are limited by P or N, respectively, through the year (Fisher *et al.*, 1992). Studies have also shown that P limits primary production during spring when river flow dominates nutrient inputs to Chesapeake Bay, and N:P values during spring are much higher than the Redfield value (N:P = 16:1) (Fisher *et al.*, 1992; Malone *et al.*, 1996). During the rest of the year, as salinity increases due to exchanges with coastal waters, the N:P values are lower than 16:1, and N supply determines the activity of primary producers. As a primary producer, *G.galatheanum* is probably affected by variations of inorganic nutrient availability, in a similar manner as found in other phytoplankton.

Mixotrophic nutrition could be an important physiological attribute to consider in terms of understanding the distribution of *G.galatheanum* in Chesapeake Bay. We found a negative correlation between DIP:DIN and abundance of *G.galatheanum* (Table I), suggesting that this species experienced P limitation during most of the spring and summer in 1995 and 1996. In addition, there is negative correlation between DIP:DIN and incidence of feeding (Table I), suggesting that high feeding occurred when *G.galatheanum* populations in the Bay were probably P-limited. In laboratory experiments, feeding of *G.galatheanum* is stimulated more by P deficiency than N deficiency (Li *et al.*, 2000). These relationships suggest that *Gyrodinium galatheanum* does relatively well in P-limited environments due to its phagotrophic activity, and that this mixotrophic dinoflagellate may have a competitive advantage over other species in P-limited environments, although it appears to have a high internal P:N ratio (Nielsen 1996; Li *et al.* 2000).

Although *G.galatheanum* is an obligate phototroph (Li *et al.*, 1999), it is able to ingest a variety of nanoplankters, including phycoerythrin-containing cryptophytes (Li *et al.*, 1996). In this present study, we dealt with the ingestion of the phycoerythrin-containing cryptophytes, because they usually co-occur with *G.galatheanum* in the Bay and because they are easily detected microscopically due to their orange fluorescence. Thus, we could detect feeding on this type of prey and examine the abundance of the prey and the dinoflagellate at the same time. Feeding on other types of prey, however, occurs in field populations, but it is difficult to detect this feeding without adding labeled prey (Li *et al.*, 1996). Consequently, the feeding capability of this dinoflagellate species is

underestimated in the present study because only easily detected prey, cryptophytes, were considered. Even within the same category of prey (i.e. the phycoerythrin-containing cryptophytes), specific species or sizes may be selectively ingested by this dinoflagellate. Prey selection may explain why incidence of feeding sometimes coincides with density peaks of cryptophytes while sometimes it does not (Figures 6 and 8).

In Chesapeake Bay, there was a relatively weak correlation (r = 0.38) between cryptophyte abundance and incidence of feeding on cryptophytes (Table I). The feeding capability of *G.galatheanum* was also correlated with population density, depth and availability of inorganic nutrients (Table I). In culture, *G.galatheanum* contains higher cellular phosphorus than other dinoflagellates and other groups of phytoplankton (Nielsen, 1996; Li *et al.*, 2000), suggesting that this species has a higher P requirement for its growth than most phytoplankton. In addition, in the laboratory, feeding of *G.galatheanum* is positively correlated with cellular C content and C:N ratio and negatively correlated with cellular chlorophyll content (Li *et al.*, 2000). In culture, we have observed that light is required for inducing feeding, and that high light and inorganic nutrient limitation (N or P or both) stimulate feeding, suggesting that *G.galatheanum* is a primarily photosynthetic species that becomes more phagotrophic when faced with nutrient limitation (Li *et al.*, 1999, 2000). Thus, it is not surprising that cryptophyte prey density is weakly correlated with feeding of *G.galatheanum i*n Chesapeake Bay, as other environmental factors as well as biochemical composition of the grazer can be important to feeding.

Several mixotrophic, bloom-forming dinoflagellates attain high concentrations in the middle and the northern regions of Chesapeake Bay (Tyler and Seliger, 1978, 1981; Harding, 1988; Harding and Coats, 1988; Bockstahler and Coats, 1993a; Stoecker *et al.*, 1997). Among these species, a subsurface transport mechanism for *Prorocentrum minimum* in the Bay has been hypothesized (Tyler and Seliger 1978, 1981; Harding and Coats, 1988). It is interesting to note that *G.galatheanum* may also participate in an annual subsurface transport from the southern Bay to the mid- and upper Bay, where it forms blooms in the surface water. In 1995, we observed a subsurface cell density maximum at a mid-Bay station in May, and the maximum was subsequently shifted to the surface waters at northern Bay stations during the summer (Figures 4 and 5). During 1996, it was clearer that the center of the *G.galatheanum* population shifted, as a subsurface layer, from the lower Bay in the spring to the mid-Bay in the early summer. It was also evident in 1996 that in the mid-summer, populations of this dinoflagellate shifted from subsurface to the surface in the mid-Bay and thereafter formed a surface bloom (Figures 4 and 5).

Mixotrophy is very common among dinoflagellates (Stoecker, 1999) and it is interesting that many harmful algal species are mixotrophic (Smayda, 1997). In Chesapeake Bay, almost all of the photosynthetic, bloom-forming dinoflagellates are capable of feeding, including *Gymnodinium sanguineum*, *Gyrodinium uncatenum*, *Gyrodinium galatheanum*, *Ceratium furca* and *Prorocentrum minimum* (Bockstahler and Coats, 1993a, 1993b; Li *et al.*, 1996; Stoecker *et al.*, 1997). Feeding on other phytoplankton by mixotrophic dinoflagellates may have

significant ecological impacts on the organization and function of microbial food webs and on dinoflagellate population dynamics. The investigations of Bockstahler and Coats (Bockstahler and Coats, 1993b) and Jeong *et al.* (Jeong *et al.*, 1997) indicate that mixotrophic dinoflagellates could be important grazers/predators on other plankton, and suggest that mixotrophic dinoflagellates could compete with zooplankton and other consumers of phytoplankton for the food supply. Consequently, competition for inorganic nutrients between mixotrophic flagellates and other phytoplankton, and competition for particulate prey between these flagellates and zooplankton, could co-exist (Rothhaupt, 1996; Thingstad *et al*., 1996; Stickney *et al.*, 2000). For example, feeding greatly enhances the growth of the mixotrophic dinoflagellate, *Fragilidium subglobosum* (Skovgaard, 1996). In culture, mixotrophic growth rates of *G.galatheanum* are about twice as high as strictly phototrophic growth rates at the same irradiance (Li *et al.*, 1999). Although grazing may be important to the growth of *G.galatheanum* in Chesapeake Bay, grazing by this species appears to have only a minor impact on cryptophyte prey populations, removing an estimated 0–4% of the cryptophyte standing stock daily (Li *et al.*, unpublished data). However, too little information is available to evaluate the overall significance of feeding by photosynthetic dinoflagellates to trophodynamics. To better understand the mechanisms of bloom formation and persistence of dinoflagellates, more research examining the impact of mixotrophy on dinoflagellate photophysiology, toxicity, as well as the potentially important role of mixotrophic dinoflagellates in food web dynamics, is needed.

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