

THE ENVIRONMENTAL CONTEXT OF A *GYRODINIUM AUREOLUM* BLOOM AND SHELLFISH KILL IN MAQUOIT BAY, MAINE, SEPTEMBER 1988

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ABSTRACT In September of 1988 a shellfish kill occurred in Maquoit Bay, Brunswick, Maine where clams, mussels and worms on the shellfish grounds suffered an estimated mortality of 30-40%. The dinoflagellate *Gyrodinium aureolum* was the dominant phytoplankton in water samples taken a few days after this event. Alternative origin and development scenarios for the bloom were considered based on the location where log phase growth may have occurred. The spatial and temporal events associated with the bloom and shellfish kill were examined by analysing meteorological data for the months of August and September, the geomorphology of Maquoit Bay, tidal data, the current patterns in Casco Bay, and other hydrographic data for the period. Our analysis suggests that a *G. aureolum* bloom of offshore origin was transported shoreward by a period of southerly winds enhanced by tidal action. Algal cells were further concentrated to around 1.4×10^8 cells l^{-1} by onshore winds and reduced tidal flushing in Maquoit Bay, a location with unique characteristics that may make it susceptible to such events. High mortality of marine organisms in Maquoit Bay may have been caused by the exposure of animals on the shellfish grounds to very low oxygen concentrations during the early morning hours over a period of 5 to 7 days. Mucous and toxin production by *G. aureolum* may have played a secondary role in the kill. Rapid decomposition of dead shellfish probably contributed an additional oxygen demand to that already present on the shellfish grounds.

INTRODUCTION

The 20th century has been a time of considerable anthropogenic change in ecosystems throughout the world. The socioeconomic activities of man have altered the structure and function of ecosystems both by changing the magnitude and extent of their controlling factors and by introducing or removing ecosystem components such as plants and animals (Elton 1958). The increasing frequency of toxic dinoflagellate blooms in some coastal and shelf seas, associated with increased eutrophication and pollution of coastal waters, (Prakash 1987, Nixon 1989) is an example of the results of such alterations. The effects of these alterations may be further illustrated by the presence of toxic dinoflagellate species in waters where they were formerly unknown. For example, since 1966 blooms of the dinoflagellate *Gyrodinium aureolum* have become common occurrences in the coastal seas of northwestern Europe where there is no prior record of the organism or the distinctive shellfish, fish and worm kills caused by its blooms (Tangen 1977, Boalch 1987, Gowen 1987, Holligan 1987).

G. aureolum was first identified and described by Hulburt (1957) who found it in a coastal pond near Woods Hole, Massachusetts. Since 1957 it has been reported from the following locations in the United States: North Carolina estuaries (Campbell 1973), the Chesapeake Bay (Marshall 1980), and a Long Island estuary (Chang and Carpenter 1985). We are not aware of any previous report of a shellfish kill associated with a *G. aureolum* bloom in U.S. waters.

Since the first identification of *G. aureolum* in Norwegian waters in 1966, (Braarud and Heimdal 1970), numerous subsequent blooms have been reported in Europe (Boalch 1979, Blake et al. 1981, Richardson and Kullenberg 1987) in which *G. aureolum* has been implicated in mortalities of finfish (Jones et al., 1982) and other marine organisms (Helm et al. 1974, Tangen 1977, Ottway et al. 1979). No specific toxin was previously reported in association with these events (Turner et al. 1987), but Partensky et al.

(1989) have recently identified a minor cytotoxin present in *Gymnodinium nagasakiensis*.

G. aureolum is phenotypically identical to *Gymnodinium nagasakiense* (Partensky et al. 1988), a common cause of "red tides" in Japan (Iizuka et al. 1989), where it has been associated with low oxygen events and shellfish kills (Ochi 1989). Partensky et al. (1988) noted that, despite the external similarity between these two species, there appear to be physiological and genetic differences between the two. The worldwide occurrences of such blooms has been summarized by Partensky and Sournia (1986), White (1988), and Shumway (1990).

Problem and Approach

On September 27, 1988 a shellfish kill in Maquoit Bay, Brunswick, Maine was reported to the Maine Department of Marine Resources (DMR). The softshell clam, *Mya arenaria* suffered 30-40% mortality on affected shellfish grounds. Marine worms of unspecified species and blue mussels, *Mytilus edulis*, were also affected. The extent of anoxia and advanced stages of decomposition observed in the dead shellfish suggested that the actual kill had occurred 7-10 days earlier (Brian Marcotte, pers. comm.). The lack of on-site observations before and during this event makes definitive determination of the actual cause of the mortalities impossible; however, the dinoflagellate, *Gyrodinium aureolum*, was the dominant algal species in the water of Maquoit Bay several days after the shellfish kill occurred (Selvin 1988, Haugen 1988). The presence of a dinoflagellate species, known to be associated with fish kills elsewhere, as the dominant phytoplankton just after a large shellfish kill is strong circumstantial evidence indicating its involvement in the incident.

In this paper we examined the spatial and temporal environment that produced a *G. aureolum* bloom in Maquoit Bay which in turn contributed to a shellfish and worm kill there. These results are used to reconstruct several possible scenarios that could ac-

count for this extraordinary event. The purpose of this research was to develop working hypotheses that can be used to guide future research on *G. aureolum* blooms in Maine and other U.S. coastal waters.

The analysis presented here was undertaken for several reasons. First, there are very few sets of observations that describe in detail the complete course of toxic dinoflagellate blooms and the observations which do exist are generally from the declining phase of the bloom making it difficult to unequivocally establish cause and effect (Holligan 1987). The technical and logistic difficulties associated with investigating ephemeral events (spatial scale of 10 km and temporal scale of 10 days) in coastal and shelf seas are in part responsible for this lack of detailed information on the physical environment of toxic bloom events (Holligan 1987). Second, the complex interactions of physical, chemical, and biological factors that control algal bloom dynamics are always hard to resolve and often require expensive field studies that have no guarantee of success. As a result of this lack of information, a general framework for assessing the physical context of these blooms cannot be developed at present (Holligan 1987). With so many difficulties preventing research on toxic and other algal blooms, scientists need viable working hypotheses around which to frame focused research proposals. Also, the economic impact of toxic and noxious algal blooms can be quite high, as it was to the shellfish industry in the case of the Maquoit Bay kill. Much higher costs may be incurred if the growing Maine salmon aquaculture industry is affected by *G. aureolum* blooms in the future. Therefore, high realized and potential economic impacts and the lack of a sufficient information base to establish, unequivocally, the cause of *G. aureolum* blooms make it necessary to use existing information and our knowledge of ecological principles to construct working hypotheses that could explain the Maquoit Bay kill.

Recognizing the variety of ways in which algal blooms can occur, we have developed two principal conceptual models to account for the presence of a *G. aureolum* bloom in Maquoit Bay. The Inshore Development model proposes that a bloom could have developed within the Bay as a result of local reproduction. A *G. aureolum* bloom which developed as a result of local reproduction was observed in the Carmens estuary of Great South Bay, Long Island in 1982 and 1983 (Chang and Carpenter 1985). The second, or Offshore Development, model, proposes the offshore development of a *G. aureolum* population associated with the stability and nutrient differences between stratified and mixed waters. In this case, the *G. aureolum* bloom must be transported into nearshore waters by favorable conditions of wind and tide. Holligan (1979) describes the processes that lead to *G. aureolum* blooms associated with density discontinuity fronts in the waters around the United Kingdom.

The Offshore Development model can, in turn, be divided into two alternative models based on whether log phase growth takes place on the surface or along subsurface density discontinuity fronts. Holligan (1979) describes a double peak pattern in the vertical distribution of chlorophyll which occurs when *G. aureolum* is brought to the surface and reproduces there. In the early summer, *G. aureolum* develops as part of the chlorophyll maximum flora on the stratified side of density discontinuity fronts in the western English Channel and is often found at the surface discontinuity between stratified and mixed waters (Holligan 1985). Alternatively, log phase growth could occur in the subsurface chlorophyll maximum layer as proposed by Richardson and Kullenberg (1987). Subsurface populations of *G. aureolum* occur

at lower cell densities than those in surface waters and this sub-model, therefore, depends on physical processes to concentrate the algal cells to bloom levels on the surface as well as to transport the bloom into nearshore waters. Lindahl (1987) presents evidence that offshore blooms of *G. aureolum* are concentrated in salinity fronts along the Norwegian coast.

METHODS

The methods used in this study were simple and direct. First, we compiled and reviewed existing bathymetric and hydrographic information on Casco Bay and Maquoit Bay. Second, we reconstructed the chronology of the shellfish kill from published accounts and conversations with eyewitness observers. Third, we assembled and interpreted existing information on temperature, wind, tide, and solar insolation to characterize environmental conditions before, during, and after the Maquoit Bay shellfish kill. This information was then used to develop two detailed scenarios based on the models described above.

RESULTS

Maquoit Bay

Maquoit Bay is an enclosed coastal embayment in the northeastern part of Casco Bay located at 70°00' west longitude and 43°55' north latitude (Fig. 1). The bay is shallow, the upper portion having a mean depth of 2–3 meters at mean high water (MHW) and approximately 81 hectares of mud flat are exposed at mean low water (MLW). The central portion of the bay has a mean depth of 3–4 meters at MLW. The bottom throughout the bay is predominantly soft mud, with eelgrass beds along the western and northern shores at or just below the MLW mark. Freshwater enters the bay from Bunganuc Brook on the western shore, which drains the western section of the town of Brunswick, including the now closed town dump, and from an unnamed brook which enters the head of the bay at Wharton Pt. at the northern extreme. A rather extensive marshy area exists on the northeastern shore which drains the Rossmore Road area.

The Bay is drained primarily through a channel between Sister Is. and Mere Pt. which is about 900 m wide. This opening is approximately 6% of the total perimeter of the Bay which is around 10 km² in area. When water leaves the Bay it tends to

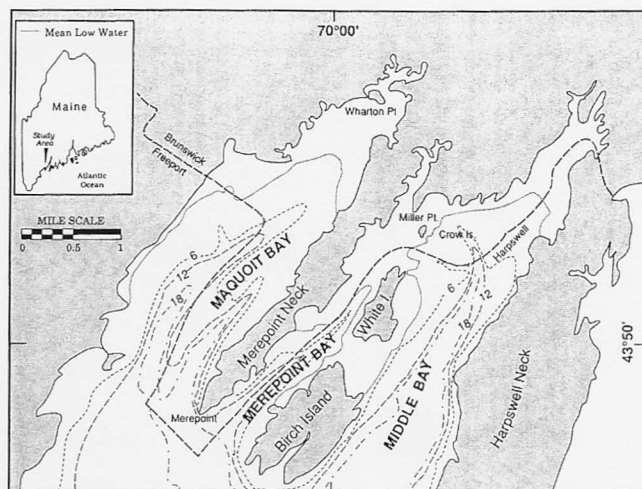


Figure 1. Maquoit and Middle Bay, Brunswick, Maine.

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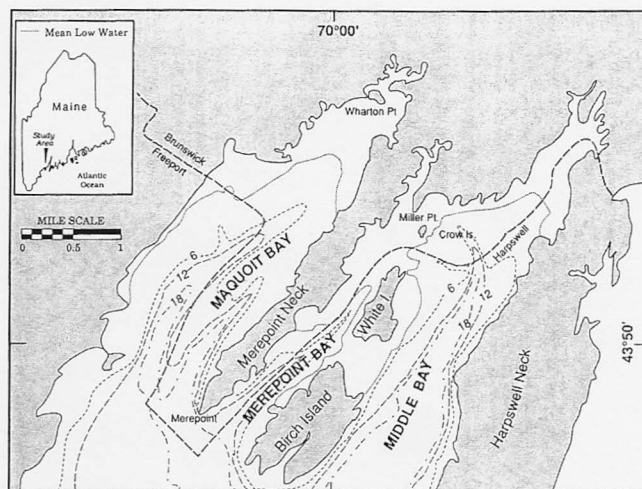


Figure 1. Maquoit and Middle Bay, Brunswick, Maine.

follow the depth contours shown in Figure 1, lying closer to the eastern side of the bay at low water. The water in Maquoit Bay is not flushed out as quickly as waters in neighboring Middle Bay which is widest at the mouth and becomes progressively narrower as it extends landward. Recent research by Gilfillian and others at Bowdoin College has produced a preliminary estimate of the flushing time in Maquoit Bay of 6 days, ranging from 5 to 15 days depending on stream flow and other conditions (Kresja 1990). Relatively slow flushing in Maquoit Bay may be a key to its high productivity, since phytoplankton are retained for longer times in the shallow, warm, fertile waters that are ideal for algal growth. The high productivity of Maquoit Bay is the reason for excellent growth of the resident shellfish population as well as the reason Maquoit Bay sediments are rich in organic matter with a shallow aerobic zone (Gilfillian et al. 1990). Historically, the Bay has been an extremely productive shellfish area for both the soft-shell clam, *Mya arenaria* and the northern quahog, *Mercenaria mercenaria*. Production in the bay for these species has been estimated at over \$1 million annually (Alan Houston, pers. comm.).

Hydrography of Casco Bay

The current patterns of Casco Bay were characterized as part of a larger study to assist in the prediction of oil spill trajectories (Parker 1982). Unfortunately, the upper reaches of Casco Bay, specifically Maquoit and Middle Bays, were not included in this study. Flow patterns of surface currents for ebb and flood tides for those areas studied in Casco Bay are summarized in Figures 2 and 3.

Most of the water entering Maquoit Bay and Middle Bay originates offshore and passes principally through Broad Sound, with a small component passing through Luckse Sound, and along the western shore of Whaleboat Island. Current velocities in Broad Sound during flood tide are quite high, ranging from 18–91 cm/sec

and averaging 25–30 cm/sec. In Luckse Sound current velocities range from 10–33 cm/sec with an approximate average of 15–20 cm/sec (Parker 1982).

Countercurrents exist during flood tide which flow in the opposite direction of that expected. Thus, flood tide in Casco Bay is of shorter duration than ebb tide and has slightly stronger average currents. Parker (1982) explains these unexpected reversals in current direction during the first two hours of the flood tide as being due to residual draining of the upper bays. Current flow patterns during ebb tide are more consistent with the expected direction. Southerly flowing water from both Maquoit and Middle Bays converge at the southern tip of Whaleboat Island and flow seaward, the principal flow passing through Broad Sound with a smaller flow exiting through Luckse Sound (Parker 1982).

Parker's late summer data also showed that a recirculating gyre occurred near West Cod Ledge and persisted throughout the tidal cycle. This gyre is characterized by strong vertical stability, a well defined thermocline between 5–10 meters, and low chlorophyll-a, which suggests nutrient deficiency and/or heavy grazing. Parker (1982) attributed the presence of this feature to the interference of West Cod Ledge with the north-south tidal flow and to the diversion of the southwesterly coastal current to the north and south of the ledge. The approximate position of this gyre is indicated by a plot of the temperature, density, stability, and chlorophyll-a fields (Fig. 4) in the vicinity of West Cod Ledge taken from Parker (1982).

Chronology, Observations, and Sample Analysis

On the morning of September 27th 1988 a report of a large clam, mussel, and worm kill in Maquoit Bay was received at the Maine Department of Marine Resources (DMR). Scientists were dispatched immediately and the area was surveyed and water samples taken that day. They estimated that shellfish in the Bay suf-

Surface Current Flood Tide

(after Parker 1982)

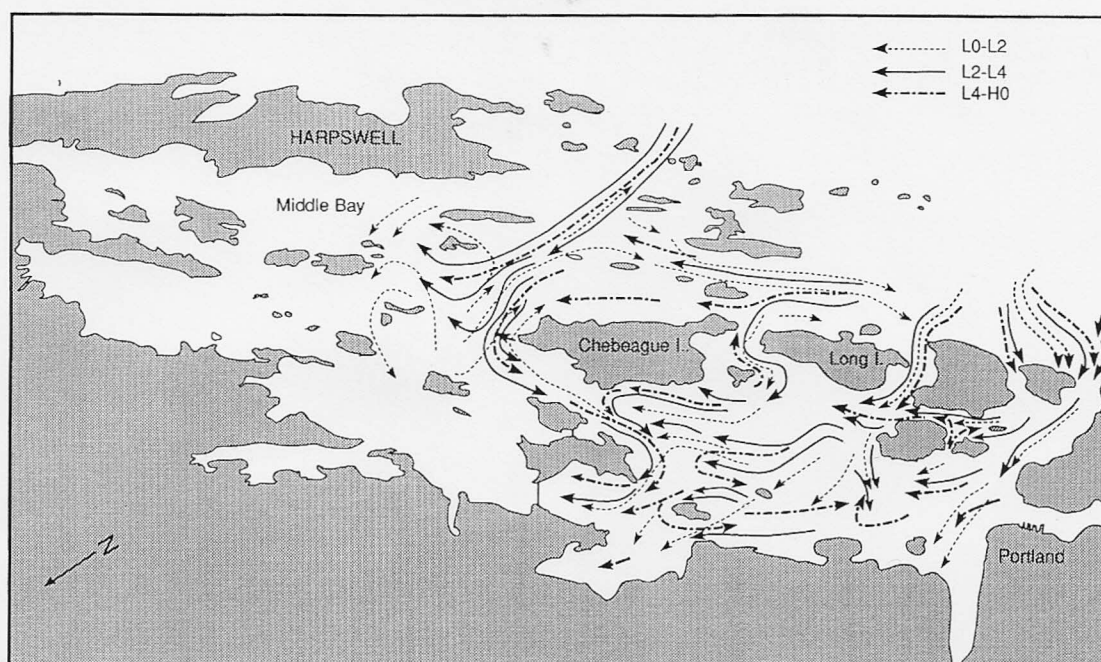


Figure 2. Casco Bay flood tide surface current patterns shown at two hour intervals from low water (LO) to high water (HO) (After Parker 1982).

Surface Current Ebb Tide

(after Parker 1982)

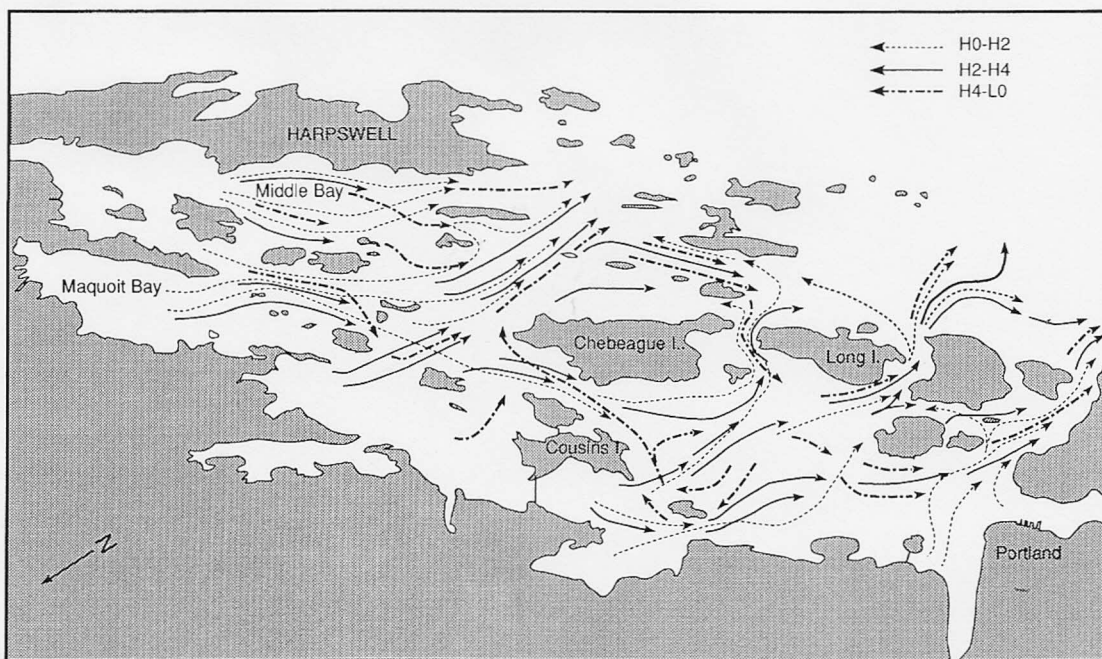


Figure 3. Casco Bay ebb tide surface current patterns shown at two hour intervals from high water (H0) to low water (L0) (After Parker 1982).

ferred 30–40% mortality, and that most shellfish had been dead for a week to ten days. This estimate roughly places the time of the kill between the 18th and 21st of September. Later estimates by Alan Houston, Shellfish Warden for the town of Brunswick, indicate that the destruction of marine life was most severe on the eastern side of the Bay where almost all of the *Mya arenaria* were killed. On the western side of the bay around 30–40% of these clams were killed. Houston reported that many marine worms were also killed but that the quahog *Mercenaria mercenaria* survived fairly well.

The phytoplankton population present in Maquoit Bay on the 27th was independently analyzed by two researchers at the Bigelow Laboratory for Ocean Sciences. The results of these analyses are summarized in Table 1. Both analyses showed a predominance of a dinoflagellate identified as *Gyrodinium aureolum*, at cell concentrations of 1.8×10^6 cells l^{-1} (Haugen, 1988), and 1.0×10^6 cells l^{-1} (Selvin, 1988). The number of algal cells present in the mixed community of dinoflagellates and diatoms in Maquoit Bay on the 27th was not unusually high for Maine coastal waters in September (Haugen, 1988).

Eye-witnesses described patches of brown or coffee-colored water in bays and around the islands of Casco Bay. Around September 20th, a fisherman observed a red to rust-colored patch concentrated near the ferry landing in a small cove on Chebeague Island, renown for its eddies (Dana Wallace, pers. comm.). Chebeague Island is approximately 15–17 kilometers from the head of Maquoit Bay and does not provide conditions conducive to the development of a bloom. Similar patches of brown or coffee-colored water were observed in Merepoint Bay around Birch Island on the outgoing tide on the 24th (Jan Derby, pers. comm.) and along the southern and eastern shores of White Island in Middle Bay on the outgoing tide on the 25th (Charles White, pers. comm.). In both cases the patches were considered to be discrete

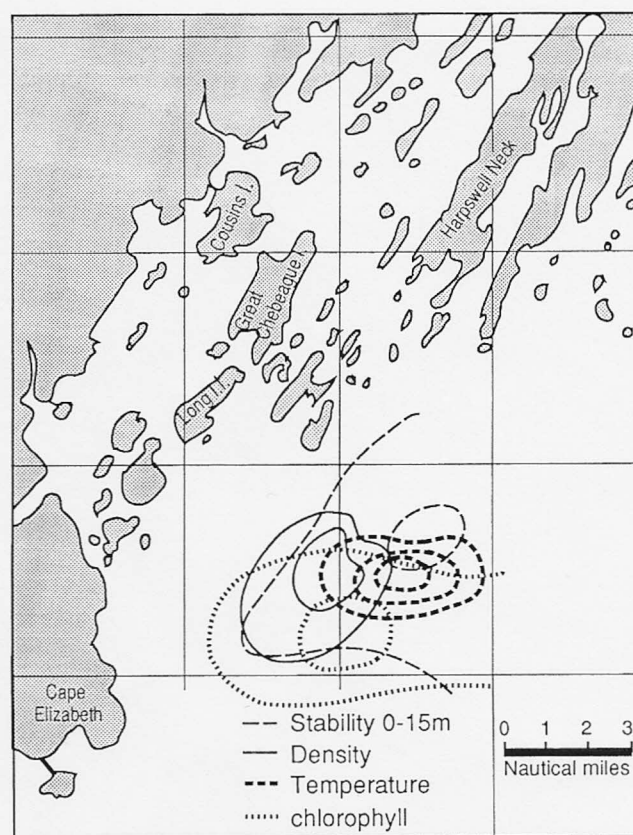


Figure 4. Approximate location of the West Cod Ledge gyre on ebb tide as indicated by stability, density, temperature, and chlorophyll-a fields (After Parker 1982.)

TABLE 1.
Phytoplankton analyses of Maquoit Bay samples.

	Rhonda Selvin	Elin Haugen
Analysis date	9/28-29/88	9/28/88
Species:		
Amphora sp.	Yes	—
Calycomonas sp.	Yes	—
Caetoceros cf. simplex	Yes	—
Chaetoceros spp.	—	Yes
Cryptomonad sp.	Yes	—
Dinophysis acuminata	Yes	Yes
Dinophysis sp.	Yes	—
Eutrepia lanowi	—	Yes
Gymnodinium sp.	Yes	—
Gyrodinium aureolum (Gyrodinium nagasakiense)	Yes $1.0 \times 10^6 \text{ l}^{-1}$	Yes $1.8 \times 10^6 \text{ l}^{-1}$
Gyrodinium spirale	Yes	—
Gyrosigma sp.	Yes	—
Heterocapsa sp.	Yes	—
Katodinium rotundatum	—	Yes
Leptocylindrus sp.	Yes	Yes $2.5 \times 10^5 \text{ l}^{-1}$
Navicula spp.	Yes	—
Nitzschia cf. closterium	Yes	Yes
Oxytoxum sp.	—	Yes
Prorocentrum micans	Yes	Yes $2.5 \times 10^5 \text{ l}^{-1}$
Prorocentrum minimum	Yes	Yes $8.3 \times 10^5 \text{ l}^{-1}$
Prorocentrum redfieldii	Yes	—
Protogonyaulax tamarensis	Yes	—
Rhizosolenia sp.	Yes	—
Scrippsiella sp.	Yes	Yes
Skeletonema costatum	—	Yes $2.8 \times 10^5 \text{ l}^{-1}$
Tetraselmis sp.	—	Yes
Thalassiosira cf. pseudonana	—	Yes
Thalassiosira sp.	Yes	—
Total chlorophyll cells		
8 μ filtration	—	$8.6 \times 10^6 \text{ l}^{-1}$
3 μ filtration	—	$9.0 \times 10^6 \text{ l}^{-1}$
0.4 μ filtration	—	$1.2 \times 10^7 \text{ l}^{-1}$
Total chlorophyll cells	—	$3.0 \times 10^7 \text{ l}^{-1}$
Total cyanobacteria	—	$4.2 \times 10^7 \text{ l}^{-1}$

in that they were surrounded by clear water at their peripheries. The reports of coffee-colored patches in the water described here are very similar to those reported for other *G. aureolum* blooms (Boalch 1979). Such patchiness would be consistent with the breaking up of a much larger algal mass as it passed around the numerous islands of Casco Bay during its shoreward movement; however, these algal patches could also have been produced by the leakage of cells on ebb tide from a population present in Maquoit Bay. For example, the patches observed around Merepoint on the 24th and in Middle Bay on the 25th could have resulted from the breakup and dispersion of a bloom in Maquoit Bay.

Environmental and Meteorological Conditions

Environmental conditions in Maquoit Bay on the 27th of September were not unusual for that time of year. Water temperatures were between 14° and 14.5°C, oxygen was 8 ppm, and salinity measured by a refractometer was around 33 parts per thousand. Sediments in Maquoit Bay were black and smelled of hydrogen

sulfide. Tests conducted by the Pathology section of DMR found no diseases or parasites in tissue samples taken from the Bay that could have been responsible for the kill. The shellfish taken from Maquoit Bay did not contain saxotoxin (John Hurst, pers. comm.), which is the primary toxin present in *Alexandrium tamarensis*, the species responsible for paralytic shellfish poisoning along the Maine coast. Tests for heavy metals, pesticides, herbicides, volatile and non-volatile organics performed by the State of Maine Public Health Laboratory on water and sediment samples from the bay showed normal levels of all pollutants except at one station where there were elevated concentrations of a volatile organic compound (Stuart Sherbourne, pers. comm.).

Meteorological data from both the Portland Jetport and the Brunswick Naval Air Station were obtained from the National Climatic Data Center, Asheville, North Carolina. Table 2 summarizes the wind speed and wind direction observations and other meteorological data taken at the Brunswick Naval Air Station during the month of September, 1988. Figure 5 shows meteorological observations for the months of August and September taken at the Portland Jetport and surface seawater temperature recorded at Boothbay Harbor, Maine for the same period.

The air temperature during the first fifteen days of August averaged 5.78°C warmer than the long term average (Fig. 5a). During the remainder of August and during the month of September air temperature oscillated around its long term average value. The warmer air temperatures of the first half of August are reflected in peak seawater temperatures of 17.9°C recorded at Boothbay Harbor during this period (Fig. 5b). Surface seawater temperature remained warm (around 15°C) until the 13th of September when strong winds resulted in vertical mixing which lowered it to 12.7°C at Boothbay Harbor. From the 7th to the 16th of September, more than 90% of the possible direct solar insolation was received on eight of ten days. A four day moving average of solar insolation was calculated to reflect the light conditions physiologically distinguishable by phytoplankton (Fig. 5c). The average light supporting algal growth was high and constant during this ten day period. In addition, from the 24th of August to the 5th of September 12.7 cm of rain fell at the Portland Jetport (Fig. 5d).

Wind patterns from Brunswick Naval Air Station (Table 2) were similar to those observed at the Portland Jetport (Figure 5e). Wind speed and direction are slightly different, but the general pattern of high wind days in September is the same. Based on the estimated shellfish kill date, local wind conditions during the period of September 18 to September 22 are highly significant. Beginning at 18:25 on September 20, and continuing to 05:12 September 21, winds were recorded out of the south at sustained

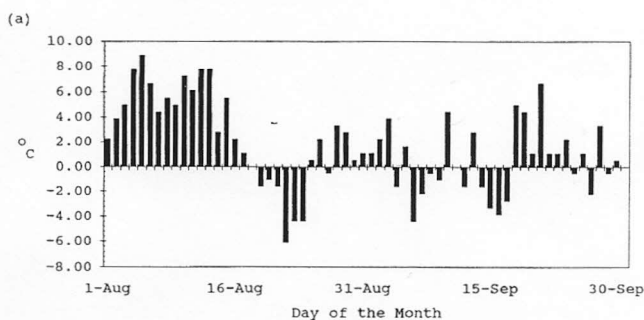


Figure 5a. Difference in air temperature from 30 yr. average for the period August 1 to September 30, 1988 at Portland, Maine.

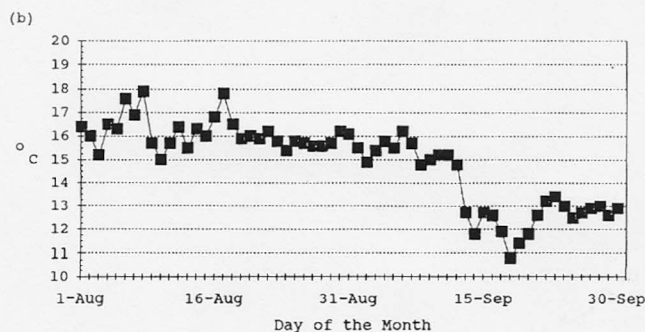


Figure 5b. Sea surface temperature at Boothbay Harbor, Maine for the period August 1 to September 30, 1988.

speeds of 10–20 knots with frequent gusts to 27 knots. On September 22 winds were moderate out of the northwest at 10–18 knots with intermittent gust from 18–26 knots.

The pattern of tidal exchange during August and September in Maquoit Bay shows that, at the estimated time of the shellfish kill, the difference between the highest low tide and the lowest high tide was a minimum (Fig. 5f). Under these conditions tidal exchange is minimal and water coverage of the shellfish beds is at a maximum.

Possible Bloom Scenarios

The daily mean wind speed during August and September, 1988 at the Portland Jetport shows seven days on which the average wind speed exceeded 5 m/sec. Based on calculation on vertical mixing, as presented in Campbell and Wroblewski (1986), we determined that, on these days, the wind energy was strong enough to produce a surface mixed layer 7.5 m thick by overcoming the density stratification in the center of the West Cod Ledge gyre observed by Parker (1982). Thus, water from the thermocline and chlorophyll maximum layer at 5–10 m would have been brought to the surface during this period. The vertical mixing which occurred on August 24th, September 5th, September 11th, September 13th, and September 15th plays an integral role in explaining the *G. aureolum* bloom and shellfish kill in Maquoit Bay. In addition to the effects of vertical mixing, the strong winds out of the northwest on the 11th and 15th could have augmented the upwelling which normally occurs near the seaward islands of Casco Bay (Parker 1982) resulting in additional deep water being brought to the surface. Based on these events and their potential effects, three possible bloom development scenarios were developed.

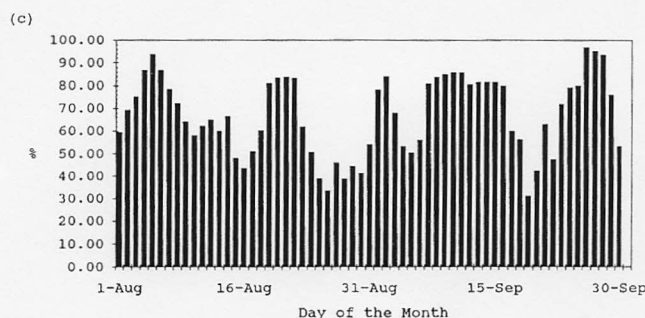


Figure 5c. Percent insolation at Portland, Maine for the period August 1 to September 30, 1988.

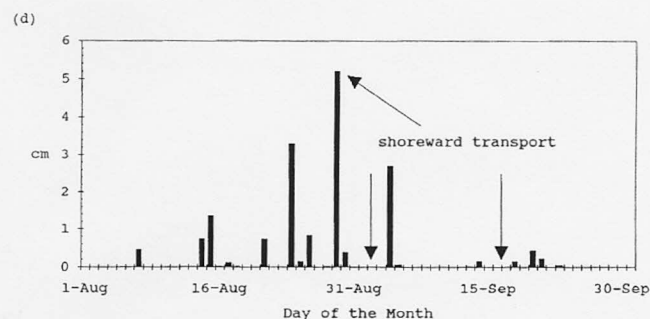


Figure 5d. Rainfall at Portland, Maine for the period August 1 to September 30, 1988.

Local Bloom Development

Several conditions which could have contributed to local bloom development may have been present in the late summer of 1988. A "seed" population of *G. aureolum* may have been introduced into the waters of Maquoit Bay either from the shoreward transport of a subsurface population found in stratified offshore waters, or by the resuspension of resting cysts present in the sediments of Casco or Maquoit Bays. However, the development of resting cysts by *C. aureolum* has never been demonstrated and we have no evidence that resting cysts of this organism exist in the sediments of Casco or Maquoit Bays, thus affording little support to the cyst resuspension alternative.

Examination of the wind data and calculations of Ekman transport show that a strong vertical mixing event could have occurred on August 24th followed by two periods of predominantly southerly winds from Aug. 26th to 29th and from September 1st to 4th. These latter winds could have resulted in shoreward transport sufficient to bring *G. aureolum* cells in offshore surface waters into Maquoit Bay. If a subsurface population of *G. aureolum* exists in the stratified waters of the West Cod Ledge gyre, cells might be regularly introduced into Casco Bay by routine upwelling events south of Jewell Island produced by the divergence of the flood tide surface flow as it enters Portland Harbor Channel, Hussey and Luckse Sounds (Parker 1982). Once transported into Maquoit Bay, these *G. aureolum* cells may have been subsequently retained in the bay if a sufficiently strong estuarine circulation pattern was produced in the bay by the 12.7 cm of rainfall from August 24th to September 5th. Persistent stratification within the Bay would have been required from September 5th through 17th to allow retention and growth of the population during the period of sunny

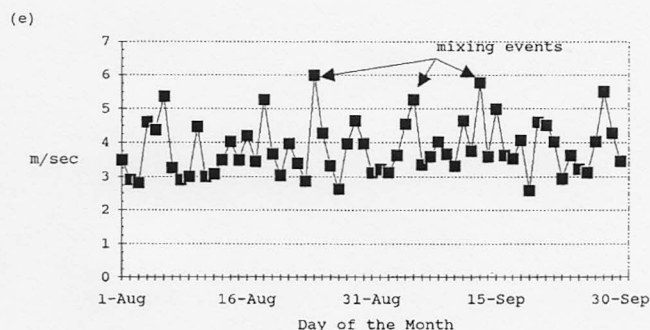


Figure 5e. Wind velocity at Portland, Maine for the period August 1 to September 30, 1988.

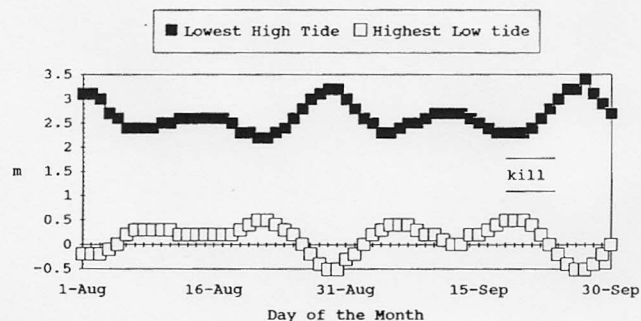


Figure 5f. Tidal amplitude at Portland, Maine for the period August 1 to September 30, 1988.

weather from September 6th to 17th. On September 17th a period of southerly winds began which could have resulted in the final concentration of *G. aureolum* cells at the head of Maquoit Bay. The resulting high cell concentration could, over a 5 day period of reduced tidal range, have caused a shellfish and worm kill either through oxygen depletion during nighttime respiration, mucous

TABLE 2.

Weather observations
Brunswick Naval Air Station (BNAS), Brunswick, Maine.

September 1988							
Wind*							
Date	Mean Speed	Mean Gust	Peak Speed	Direction (°true)	Temp. Max.	(°F.) Min.	Prec. (in.)
1	6.88	0.0	13	210	79	52	0.0
2	3.83	0.0	14	210	81	52	0.0
3	3.64	15.0	20	120	83	56	0.0
4	5.34	15.4	20	130	64	54	0.0
5	8.19	18.2	20	310	76	51	0.7
6	3.25	12.0	12	360	67	41	0.0
7	3.33	14.5	16	10	69	42	0.0
8	6.33	15.0	19	230	71	45	0.0
9	6.67	17.5	23	210	70	53	T
10	3.48	15.0	17	310	82	63	0.0
11	7.79	22.1	27	310	70	53	0.0
12	6.33	0.0	20	300	72	48	0.0
13	11.31	20.1	25	210	69	56	T
14	7.50	19.0	21	250	66	45	T
15	9.68	21.3	28	330	63	43	T
16	4.79	15.0	16	350	67	41	0.0
17	5.58	0.0	16	220	66	41	T
18	6.50	17.8	23	170	67	59	0.48
19	2.96	0.0	15	300	80	55	0.0
20	8.44	19.7	24	180	64	53	0.21
21	6.29	24.7	27	180	77	61	0.29
22	6.96	21.3	27	300	68	44	0.0
23	6.65	17.0	18	190	66	44	T
24	5.38	18.3	23	330	73	48	0.0
25	4.54	18.0	19	190	66	44	0.0
26	5.20	17.5	20	310	71	43	0.0
27	7.65	21.0	23	180	64	40	T
28	10.51	24.9	29	330	73	47	T
29	6.08	0.0	18	350	66	38	0.0
30	5.29	0.0	16	200	64	47	0.0

* Speeds in knots. T, trace amount.

production, toxicity, or more likely, a combination of one or more of these.

Offshore Surface Growth

The offshore development of a *G. aureolum* bloom may have proceeded either as surface growth seeded by subsurface cells or by subsurface growth in the chlorophyll maximum layer. In the surface growth model, wind mixing events on September 5th, 11th, and 13th would have been strong enough to overturn the stratified waters of the West Cod Ledge gyre to a depth of 7.5 m bringing nutrients and *G. aureolum* cells into the surface waters where growth was subsequently stimulated by the prolonged period of high and constant light which occurred from September 6th to 17th.

Offshore Subsurface Growth

Subsurface growth of *G. aureolum* also would have been stimulated by high and constant light conditions present at the thermocline from September 6th to 17th. As Holligan (1985) points out, dinoflagellates in northwestern European waters take advantage of the sunlight penetrating through the upper, clearer stratum while thriving on the nutrients which diffuse across the thermocline from the nutrient-rich waters below.

On September 11th and again on the 15th, strong northwest winds, gusting to 28 knots, blew for periods of 9 and 15 hours, respectively. These winds, particularly those of the 15th, may have been sufficiently strong and prolonged to disrupt the West Cod Ledge gyre and enhance the tidal-based upwelling at the entrance to Casco Bay bringing a subsurface bloom to the surface. Upwelling of deep water as a result of the seaward displacement of wind driven surface water is one mechanism that has been proposed to explain how subsurface algal blooms could be carried to the surface (Tangen, 1977). Subsurface growth of *G. aureolum* does not appear to reach the cell concentrations found in surface blooms. Thus, the subsurface growth model depends on physical processes to concentrate algal cells from a large area thereby producing bloom concentrations. Such a concentration of subsurface cells could have occurred through upwelling of water from the thermocline of the West Cod Ledge gyre at the entrance of Casco Bay.

Shoreward Transport of Offshore Bloom and Final Concentration

Both offshore bloom development alternatives rely on wind-driven shoreward transport for the bloom's final arrival in Maquoit Bay. During August and September three periods of southerly winds occurred that could have produced a shoreward Ekman transport of sufficient magnitude to shift the position of the West Cod Ledge Gyre so that it abutted the mouth of Broad Sound. These transport periods occurred on August 25–29, August 31–September 2, and September 17–20 as shown in Fig. 5d. The potential movement of the gyre under the influence of southerly winds on the 17th and 18th of September (Fig. 6) was large enough to allow water from the gyre to be drawn into Casco Bay through Broad Sound on the flood tide. A similar position of the gyre was obtained for the two earlier periods calculating water movement as in Parker (1982). Based on the location of the West Cod Ledge gyre and the normal tidal current path through Broad Sound described by Parker, along with the wind directions over these periods, Maquoit and Middle Bays are the most likely points of concentration for materials transported in the surface waters.

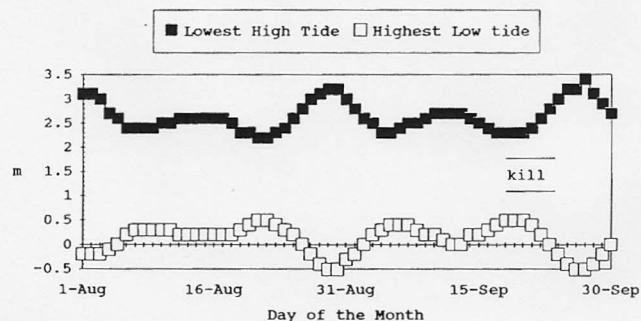


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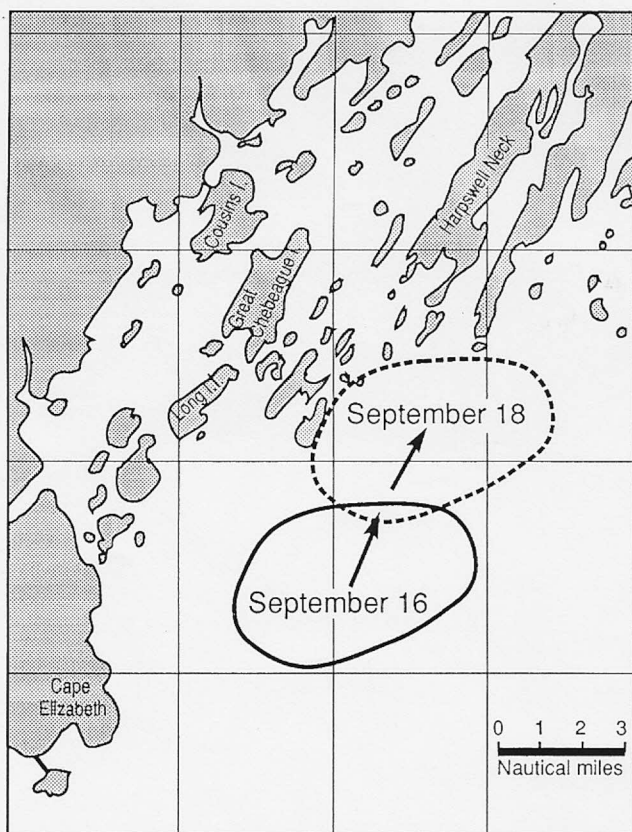


Figure 6. Estimated movement of the West Cod Ledge gyre under the influence of southerly winds on September 17–18, 1988.

In all growth scenarios, local wind patterns are responsible for concentrating *G. aureolum* cells on the shellfish grounds of Maquoit Bay. On the evening of September 20th strong southerly winds, with gusts between 24 and 27 knots, were recorded at Brunswick Naval Air Station and persisted through the early morning of the 21st. This period coincided with a +0.5 m low tide which would have afforded less than normal resistance to waters being moved by the opposing wind. These winds could also have pushed surface water up into the head of Maquoit Bay and over a large portion of the shellfish grounds, concentrating algal cells there. Winds from the northwest, gusting up to 27 knots on the 22nd, may have blown the concentrated bloom against the eastern side of the bay, thus accounting for the higher mortality found along that shore.

DISCUSSION

The association of phytoplankton with offshore gyres has been described by Pingree (1979). The West Cod Ledge gyre identified by Parker could provide ideal conditions for the development of *G. aureolum* blooms (Holligan, pers. comm.). The strong vertical stability of the gyre allows for the establishment of a discrete thermocline at a depth of approximately 5–10 meters between warm, nutrient-deficient surface water and cold, nutrient-rich water below. The transparency of the overlying water allows sunlight to penetrate deep into the upper layer. The combination of a discrete thermocline and adequate illumination provides the necessary requirements for the establishment of subsurface populations. Furthermore, the persistence of the gyre throughout most of the

tidal cycle suggests the possibility of the existence of a resident, subsurface population of *G. aureolum* immediately offshore of Casco Bay. If *G. aureolum* proves to be a permanent resident in the subsurface phytoplankton community of West Cod Ledge, it could be regularly available for seeding into Casco Bay through the upwelling of deep waters southwest of Cliff Is., as well as through wind driven horizontal and vertical transport events as mentioned earlier.

In the absence of any evidence of cyst formation by *G. aureolum*, we must assume that an offshore subsurface population served as a seed source of cells for the local growth as well as offshore growth alternatives. The existence of this species as a member of the phytoplankton community in the Gulf of Maine should be confirmed by field research and its spatial and temporal distribution determined.

Local Bloom Development

Chang and Carpenter (1985) observed a dense bloom of *G. aureolum* during the summers of 1982 and 1983 in the Carmans estuary of Long Island, New York. These blooms had potentially toxic cell concentrations of 2.0×10^7 cells l^{-1} , however, no ill effects were observed. For comparison, *G. aureolum* cell concentrations on the Maquoit Bay shellfish grounds could have been around 1.4×10^8 cells l^{-1} based on an initial seeding of 10^4 cells l^{-1} , (a log phase growth increase of $2000\times$ or approximately 1 division d^{-1}), and a wind driven volume concentration of $6.8\times$ within Maquoit Bay. Chang and Carpenter (1985) used a model based on observed rates of cell division, vertical migration of algal cells, and water movements to show that cells must move downward at the mouth of the estuary by either convergence of water or vertical migration of cells for the bloom to be maintained in the estuary. A stratified water column and estuarine type circulation pattern were necessary for the development and maintenance of this local bloom. The balance between cell growth and estuarine flushing determined whether or not the bloom could be maintained in the Carmans estuary. Based on these observations, we believe that the weakest link in the chain of circumstances supporting local growth of a bloom in Maquoit Bay is the assumption that a stratified water column, sufficiently stable to allow retention of the *G. aureolum* cells during growth of the bloom, existed in the bay from September 5th to September 17th. Any stratification that was present in the bay must have been based on 12.7 cm of rain that fell between August 24th and September 5th. Stratification in Maquoit Bay has been minimal for all currently observed conditions, but to date, these observations have not been related to fresh water input (Kresja, pers. comm.). A flushing rate of around 6 days may be too rapid to allow cell growth to keep up with cell losses from flushing, despite optimum sunlight conditions over an 11 day log growth period. This question could be resolved by a growth versus flushing model similar to that of Chang and Carpenter (1985). Additional information on the stratification and flushing of the bay under various conditions of fresh water input would allow the development of a relatively simple model to predict whether or not a bloom could have developed in Maquoit Bay as a result of local growth driven by the environmental conditions that existed in September 1988. The development of such a local bloom is certainly possible (Chang and Carpenter 1985), however, we must consider it doubtful without further proof that conditions in Maquoit Bay during September 1988 were sufficient to allow for the retention and growth of a *G. aureolum* blooms.

Offshore Surface Growth

Offshore surface growth provides another alternative explanation for the development of the *G. aureolum* bloom. The offshore origin of coastal blooms has been discussed by Tyler and Seliger (1978) and Lindahl (1985). The surface growth alternative is favored because the growth of *G. aureolum* is not inhibited by strong light as is the growth of many dinoflagellates (Richardson and Kullenberg 1987). Thus, this species would not reach its highest growth potential until exposed to surface light conditions (Richardson and Kullenberg 1987). In this alternative a vertical mixing event on September 5th brought nutrients and *G. aureolum* cells to the surface from a subsurface population at concentration of 10^4 cells l^{-1} , similar to that commonly observed in European waters (Holligan 1979). A $2000\times$ increase could have occurred through growth at the surface during 11 days of optimum light conditions (Iizuka et al. 1989) to result in an offshore concentration of 2.0×10^7 cells l^{-1} in the West Cod Ledge gyre. A further concentration of $6.8\times$ by the southerly winds over Maquoit Bay could have resulted in an effective concentration of 1.4×10^8 cells l^{-1} on the shellfish grounds.

Offshore Subsurface Growth

The concentration of subsurface *G. aureolum* cells to bloom levels by physical transport processes has been proposed as a mechanism to explain some blooms in the waters of Northwestern Europe (Richardson and Kullenberg 1987). Starting with a subsurface population of 10^4 cells l^{-1} , growth and transport would have to increase cell concentrations to approximately 2×10^7 cells l^{-1} to produce bloom concentrations with visible coffee colored patches (Tangen 1977). We assume that subsurface growth can account for a $100\times$ increase in cell numbers to account for a subsurface concentration of 1.0×10^6 cells l^{-1} similar to the maximum subsurface concentrations observed by Richardson and Kullenberg (1987). If all the water from the subsurface chlorophyll maximum layer was upwelled in the vertically mixed area in front of Casco Bay, this cell concentration would be increased approximately $4.5\times$. Cell concentrations could be increased an additional $6.8\times$ to 3.0×10^7 cells l^{-1} as a result of the concentration of *G. aureolum* cells over the shellfish beds of Maquoit Bay by southerly winds.

There are several problems with the subsurface growth alternative in explaining the development and transport of the bloom. The primary area of tidal divergence and upwelling (Parker 1982) that would be affected by northwest winds is to the south of Jewell and Cliff Islands which means that *G. aureolum* cells would have been supplied primarily to the Middle and Maquoit Bays area by the small flow entering through Luckse Sound. However, if *G. aureolum* cells were concentrated in this manner, we would also expect cells to be carried into the southwestern portion of Casco Bay in considerable quantities, but this was not observed. Further, the final concentration of cells on the shellfish beds of Maquoit Bay obtained under the assumptions used here is about 5 times smaller than that obtainable in the local growth and offshore surface growth alternatives. This difference is primarily attributable to the comparatively slow log phase growth rates which were assumed to apply for subsurface growth. The most important uncertainty in explaining bloom development by the subsurface growth alternative is the rate of algal growth in the chlorophyll maximum layer. Research is needed to show whether or not

growth rates of subsurface *G. aureolum* are faster or slower than our estimates of approximately 0.8 divisions d^{-1} .

The offshore surface growth alternative is a strong choice; however, it does not allow cells to reach Maquoit Bay as early as the subsurface growth option. The most uncertain assumption supporting the surface growth option is that sufficient nutrients would have been supplied from the September 5th mixing event to support 11 days of log phase growth. A more realistic picture may be provided if we assume that some combination of subsurface and surface growth occurred, perhaps with a double chlorophyll maximum as observed by Holligan (1979). The wind data shows that 4 vertical mixing events occurred during the 11 days of increased sunlight which could have kept surface nutrient concentrations high, but it would have redistributed algal cells according to the concentration difference between surface and bottom layers. Two of these wind events could have resulted in some enhancement of the upwelling at the entrance to Casco Bay. The transport of *G. aureolum* cells into Casco Bay may have been from both surface and subsurface growth regimes.

The Shellfish and Worm Kill

The mechanism by which shellfish and worms were killed in Maquoit Bay would have been the same for all growth alternatives. We can begin to understand how the kill occurred by examining more closely the environmental conditions which existed during the period from September 17th to September 23rd (Table 3). Marine organisms in Maquoit Bay could have been exposed to high concentrations of *G. aureolum* for five to seven of these days as discussed above. *G. aureolum* cells can negatively affect marine organisms by production of mucous, consumption of oxygen, and production of a weak toxin (Partensky et al. 1989).

Even though *G. aureolum* is a photosynthetic organism, oxygen consumption in the dark by dense algal concentrations has been shown to produce hypoxic conditions in shallow coastal waters (Odum and Wilson 1962). The normal cycle of diurnal oxygen concentration in shallow marine waters (Odum and Hoskin 1958) has a minimum in the early morning hours usually just after dawn. Table 2 shows that high tide occurred during the early morning hours from September 17th to 23rd and moderate southerly or southwesterly winds prevailed on six of seven days. Thus, a large proportion of the animals on the Maquoit Bay shellfish grounds were probably subjected to water loaded with highly concentrated, oxygen-consuming algae at the time of day when oxygen demand was highest. Under these conditions we may assume that sedentary

TABLE 3.

Summary of wind and tide data at the time of the shellfish kill.

Date	Tide		Wind Speed*	
	Time High Water	Minimum Range (m)	Resultant (m/s)	Direction (degrees)
Sept. 17th	0223	1.9	2.7	180
Sept. 18th	0310	1.8	2.8	180
Sept. 19th	0409	1.8	0.9	220
Sept. 20th	0514	1.8	4.2	170
Sept. 21st	0621	2.0	3.2	240
Sept. 22nd	0724	2.4	3.5	300
Sept. 23rd	0823	2.8	2.3	220

* Wind data from Portland Jetport; see Table 2 for local wind data.

marine organisms on the shellfish grounds were regularly exposed to severe oxygen stress over a period of 5 to 7 days. In addition, if *G. aureolum* cells settled out of the water column during slack water or migrated (Tangen et al. 1979) toward bottom waters on flood tide as implied by Chang and Carpenter (1985), the shellfish grounds would have been blanketed by a dense mat of algae with high oxygen demand. Since the aerobic sediment layer over much of Maquoit Bay is only a few millimeters thick (Maher 1991), we may assume this blanket of *G. aureolum* cells could have exposed marine organisms on the shellfish grounds to hypoxic conditions for up to six hours nightly over a period of 5 to 7 days. Mucous secretion and/or toxin production by such a mass of algae could have also contributed to the mortality of marine organisms during this time.

Hammen (1976) discusses the tolerance of many marine invertebrates to low oxygen levels. The time to 50% mortality under low oxygen conditions for various species tested ranged from less than one hour to 50 days. In general, crustaceans were most sensitive to low oxygen and mollusks least sensitive with marine worms in between. While mollusks are fairly tolerant of low oxygen conditions as a group, their tolerance for low oxygen is markedly less at higher temperatures. In addition, Theede (1973) demonstrated that the tolerance of marine invertebrates for oxygen deficiency decreased when the organisms were simultaneously exposed to hydrogen sulfide. We may assume that marine organisms on the Maquoit Bay shellfish beds were exposed to warm water (14.5–15°C), and to one or more of three additional stressors, hydrogen sulfide, mucous, and toxin. Given the potential synergistic effects of these adverse conditions we may further assume that marine invertebrates would have a minimum tolerance for low oxygen conditions on the grounds.

The toxic effects of *G. aureolum* on marine invertebrates have been demonstrated by Widdows et al. (1979), who challenged *Mytilus edulis* with high concentrations of *G. aureolum* in controlled tests of toxicity. In these experiments cell concentrations of 6.3×10^5 cells l^{-1} resulted in a marked decline in clearance rates along with cellular damage to the gut in experimental animals after only a few hours of exposure. This suggests that *G. aureolum* has a direct cytotoxic effect.

Turner et al. (1987) showed that *G. aureolum* produces a toxic substance which has cytological effects on fish. Nevertheless, considerable controversy exists concerning the exact mechanism involved in shellfish and other marine benthos mortalities associated with *G. aureolum* blooms. The prevailing view seems to be inclined towards deoxygenation of the water layer at the water-sediment interface resulting from the rapid decomposition of dead and dying cells, as well as the formation of mucoid slimes on the bottom, at the conclusion of a bloom (Helm et al. 1974, Tangen 1977, Tangen et al. 1979, Boalch 1979, Pybus 1980, Blake and Walker 1981). In the case of Maquoit Bay we must add low oxygen conditions brought on by a high oxygen demand produced by the wind-concentrated algal cells coincident with the normal diurnal oxygen minimum. Evidence of anoxic conditions was present in Maquoit Bay after the event in the form of black slime coating the bottom along the shore and the presence of the pungent odor of hydrogen sulfide, even though the water column was oxygen saturated. The fact that small clams and worms were seen scattered on the surface of the bottom suggests that conditions within the sediments became intolerable. Similar reactions have been reported in the lugworm, *Arenicola marina*, which appears to be particularly susceptible to the effects of *G. aureolum* blooms (Helm et al. 1974, Forster 1979). The severe anoxia that occurred

in Maquoit Bay sometime before September 27 may have been exacerbated by the decomposition of clams and other benthic forms which succumbed to the initial effects of the bloom.

Finally, the detrimental effects of the *G. aureolum* bloom on marine organisms were not restricted to Maquoit Bay. Mortalities among marine worms in Merepoint Bay were reported on September 29 (Wallace, pers. comm.) and, although observations of the mussel beds in upper Middle Bay in late September indicated only limited impact on the area, fisherman harvesting these beds later in the fall reported evidence of significant mortality which was initially attributed to the unusually hot summer. However, the magnitude of clam and worm mortalities in Maquoit Bay was larger and the area affected more extensive than observed elsewhere. Based on the direction of wind driven transport, Maquoit and Middle Bays should have been affected equally by the bloom. This was not the case because the geomorphology of the two bays is different. Maquoit Bay is a largely enclosed, shallow bay that empties through a narrow channel and has a fairly slow turnover time, whereas, Middle Bay is deeper and funnel shaped allowing faster and more complete flushing.

CONCLUSION

There are several common factors that occur in all of the proposed explanations for the Maquoit Bay shellfish kill that, when taken together, can serve to identify conditions favorable to *G. aureolum* blooms in the future. Warm temperatures favor *G. aureolum* in competition with other dinoflagellate species as evidenced by the fact that *G. aureolum* is most abundant during the warmest time of the year (Holligan 1985). The warmer than normal temperatures of August 1988 may have favored *G. aureolum* in competition with *Alexandrium tamarensis* or other dinoflagellate species in the subsurface waters of the West Cod Ledge gyre. The 11 days period of high and constant light conditions may also have favored *G. aureolum* in competition because it does not experience photoinhibition at high light levels as observed for many other dinoflagellate species (Richardson and Kullenberg 1987). The existence of winds favorable to the concentration of algal cells inshore was a necessary factor. Southerly winds on the 20th and 21st concentrated algal cells at the head of Maquoit Bay, and northwest winds on the 22nd further concentrated the *G. aureolum* cells on the eastern side of the Bay where the greatest damage was observed. Reduced tidal range in Maquoit Bay occurred from September 17th to 21st which produced a minimum in the capacity for water exchange. Onshore winds during this period further reduced the exchange of waters between Maquoit and Casco Bays. The occurrence of high water in the early morning from September 20th to 22nd caused a maximum coverage of the shellfish grounds with concentrations of oxygen consuming *G. aureolum* (through dark respiration) at the time of day when oxygen supplies are usually at a minimum. Finally, all explanations require an offshore source of *G. aureolum*, and the dispersion of bloom concentrations by increased tidal flushing from September 23rd to 27th, possibly aided by the wind. A similar combination of physical events has been associated with large shellfish kills in the past as described by Nixon (1989) for the great Narragansett Bay fish kill.

These unique characteristics of Maquoit Bay are in part responsible for its high phytoplankton and shellfish productivity, but they also set the stage for high mortalities of marine organisms in the presence of high concentrations of a noxious organism like *G. aureolum*. Although the nutrient loading of Maquoit Bay, as a

result of point or non-point sources of pollution, may not have contributed appreciably to this algal bloom, this does not imply that it could not precipitate a similar event involving this or another algae sometime in the future.

Clearly, further study is required in order to understand the origin and evolution of such blooms. For the immediate future, it

would be most valuable to determine if a resident, subsurface population of *G. aureolum* does indeed exist in the gyre off of Casco Bay. This is of particular interest in this case, for blooms of *G. aureolum*, in other parts of the world, particularly in Ireland and Norway, have historically repeated themselves in subsequent years after their initial observation.

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