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Gonyaulax excavata in the Bay of Fundy**

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Distribution and Abundance of the Toxic Dinoflagellate *Gonyaulax excavata* in the Bay of Fundy

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Water samples were collected for five consecutive summers (1980–84) in the Bay of Fundy at the surface and at 5 m to examine the distribution patterns of the motile stages of the toxic dinoflagellate *Gonyaulax excavata*, which has caused shellfish toxicity in this area for years, as well as occasional fish kills. In 1980 and 1981, 128 and 122 stations were sampled, respectively, and 84 and 41% of the samples contained *G. excavata* cells. Further sampling in 1982–84 was reduced to areas where most cells were observed in previous years. During this period, *G. excavata* was observed in 91–100% of the locations sampled. Despite variations in abundance of *G. excavata* cells from year to year, the overall distribution patterns were similar. The highest concentrations of cells occurred in the south-central and southwestern portions of the Bay in the area bounded by the Quoddy Region and Saint John, New Brunswick, and Digby, Nova Scotia. The distribution of various life cycle stages (planozygotes, vegetative duplets, and sexually fusing cells) was similar to that of individual motile cells, suggesting that the annual blooms in this region behave as one large population. Few or no *G. excavata* cells were found at the head of the Bay or at the seaward approaches. Results suggest the prevailing circulation in the Bay and the presence of tidal fronts are dominant factors in retaining *G. excavata* and its life cycle stages in the south-central and southwestern portion of the Bay and that this accounts for its perennial occurrence in this area.

Des échantillons d'eau ont été prélevés pendant cinq étés consécutifs (1980–1984) dans la baie de Fundy. Les échantillons, prélevés en surface et à 5 m de profondeur, ont servi à étudier les allures de la répartition des stades motiles du dinoflagellé toxique *Gonyaulax excavata* qui, pendant plusieurs années, a rendu les mollusques toxiques et, à l'occasion, provoqué des hécatombes de poissons dans cette région. En 1980 et 1981, respectivement 128 et 122 stations ont été échantillonnées. Des échantillons prélevés, 84 et 41 % contenaient des cellules de *G. excavata*. D'autres prélèvements ont été réalisés de 1982 à 1984 dans les zones où les plus grandes quantités de cellules avaient été décelées les années précédentes. Au cours de cette période, des *G. excavata* ont été découverts dans 91–100 % des endroits examinés. En dépit des variations annuelles de l'abondance des cellules de *G. excavata*, les modes de répartition généraux demeuraient semblables. Les concentrations les plus élevées ont été notées dans la partie centre-sud et sud-ouest de la baie, dans la zone se trouvant entre la région de Quoddy et Saint-Jean (Nouveau-Brunswick), et Digby (Nouvelle-Écosse). La distribution des cellules aux divers stades (planozygotes, doublets végétatifs et cellules en fusion sexuelle) était semblable à celle des cellules motiles individuelles, ce qui porte à croire que les individus qui pullulent annuellement dans cette région se comportent comme faisant partie d'une grande population. Peu ou pas de cellules de *G. excavata* ont été décelées dans le fond de la baie ou à son embouchure. Les résultats obtenus portent à croire que la circulation principale de la baie et la présence de fronts de marée sont les facteurs dominants qui retiennent *G. excavata*, à tous les stades de développement, dans la partie centre-sud et sud-ouest de la baie et en expliquent la persistance à cet endroit.

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The toxic marine dinoflagellate *Gonyaulax excavata*² (= *G. tamarensis* var. *excavata*) is responsible for paralytic shellfish poisoning (PSP, a potentially fatal food poisoning) on Canada's east coast. Blooms of this dinoflagellate are an annual occurrence in the Bay of Fundy and the St. Lawrence estuary. Shellfish toxicity records from the Bay of Fundy date to 1935 showing evidence of molluscan shellfish accumulating paralytic shellfish poisons while filter feeding, causing PSP in humans and other vertebrates when ingested. Fish kills can also

result from toxin transfer through the food web during intense blooms (White 1980, 1982, 1984).

Soft-shell clams (*Mya arenaria*) have been harvested in the Bay of Fundy for years with an annual seasonal closure due to unacceptable levels of paralytic shellfish toxins. Blue mussel (*Mytilus edulis*) harvesting has been prohibited in the entire Bay of Fundy for many years because of high toxin levels.

Gonyaulax excavata usually reproduces by means of asexual division, but a sexual phase can occur when gametes are formed that fuse to form a motile zygote or "hypnozygote." This large hypnozygote swims for a few days before developing into a cyst and settling to the bottom. This benthic resting cyst overwinters in the upper layers of sediment until a rise in water temperature induces germination to excystment into a vegetative cell

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²Taxonomy of this organism is in flux and the acceptable nomenclature is *Gonyaulax*, *Protogonyaulax*, or *Alexandrium*.

(Anderson 1980). Initially, newly excysted cells develop into large swimming cells or "planomeiocytes" which divide to produce vegetative cells.

During the winter of 1980–81, an extensive sampling survey of bottom sediments throughout the Bay of Fundy indicated *G. excavata* cysts present in low to moderate numbers in most offshore and intertidal areas. A rich deposit of cysts was found east and north of Grand Manan Island (White and Lewis 1982). This region of the Bay of Fundy serves as a major depositional area for silt/clay sediments and cysts. The results of this 5-yr survey on abundance and distribution of *G. excavata* and its major life cycle stages in the surface waters are discussed in relation to this natural cyst reservoir. Prior to our work, little was known of the patterns and distribution of *G. excavata* motile cells and their variation from year to year in the Bay of Fundy, thus prompting this survey to be initiated. The annual pattern of distribution is also discussed in relation to the retention mechanism provided by the circulation patterns and frontal regions within the Bay of Fundy.

Materials and Methods

Sampling

Plankton samples were collected for determination of *G. excavata* distribution and abundance throughout the Bay of Fundy for 5 consecutive yr. Sampling dates were August 14–20, 1980; July 31 – August 10, 1981; August 3–12, 1982; July 26–29, 1983; and July 10–26, 1984. Stations sampled are shown in Fig. 1. Sampling periods were determined by weekly monitoring of a sampling station off Campobello Island, a review of previous shellfish and toxicity records, and availability of ship time. Sampling areas varied from year to year as shown in Fig. 2.

An extensive surface water survey in 1980 and 1981 included the approaches as well as the entire Bay of Fundy, with 128

and 122 stations sampled, respectively (Fig. 2). Subsequent sampling in 1982 was reduced to 85 stations (Fig. 2). Sampling during 1983 and 1984 was limited to 55 and 43 locations, respectively (Fig. 2), where highest concentrations of cells had been observed in previous years. Samples at these locations were taken from the surface and a depth of 5 m to determine variability in cell abundance for the two depths. The water was sampled regardless of time of day for the years 1980, 1981, and 1983 whereas samples were collected only between 0700 and 2300 in 1982 and 1984.

Water was collected by bucket at the surface and 1.25-L Nansen bottle at 5 m for determination of temperature, salinity, and *G. excavata* abundance. The samples for *G. excavata* abundance were immediately preserved with 2.5% formalin – acetic acid (1:1) and subsequently a 50-mL subsample from each sample was settled in a chamber for counting with an inverted microscope. All plankton was identified, with *Gonyaulax* counts including all life cycle stages present. Reproduction of *G. excavata* is by asexual division of gametes forming duplets. As a bloom progresses, sexual fusing of gametes occurs, yielding a swimming zygote (planozygote) which becomes a nonmotile resting cyst or hypnozygote (Anderson and Wall 1978; Turpin et al. 1978; Anderson 1980). Fusing cells were distinguished from asexually dividing cells by the cingula of the fusing cells being at oblique angles to each other whereas the cingula of duplets are parallel. Planozygotes, fused gametes, duplets, triplets, quadruplets, and hypnozygotes were differentiated for all years excluding 1980 in which only total *Gonyaulax* numbers were recorded. Planozygotes were those cells with a length greater than or equal to 43 μm and differed from planomeiocytes in an absence of the characteristic red pigment of a newly germinated cell. All cysts identified in this study were newly formed in that they were completely filled with starch or lipid reserves.

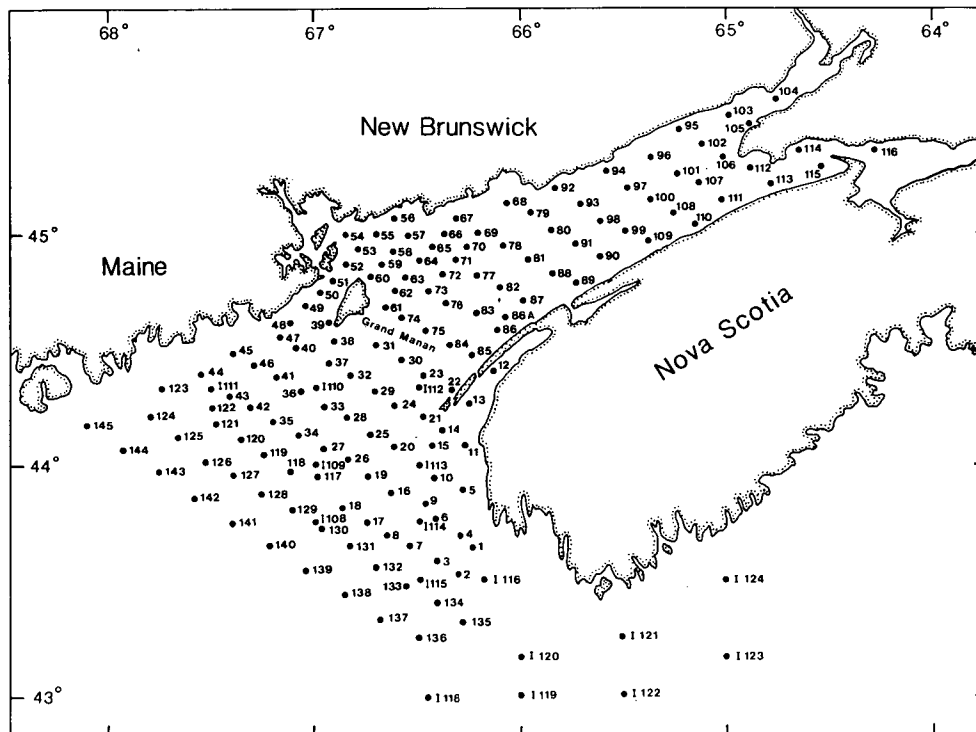


FIG. 1. Locations of sampling stations in the Bay of Fundy area.

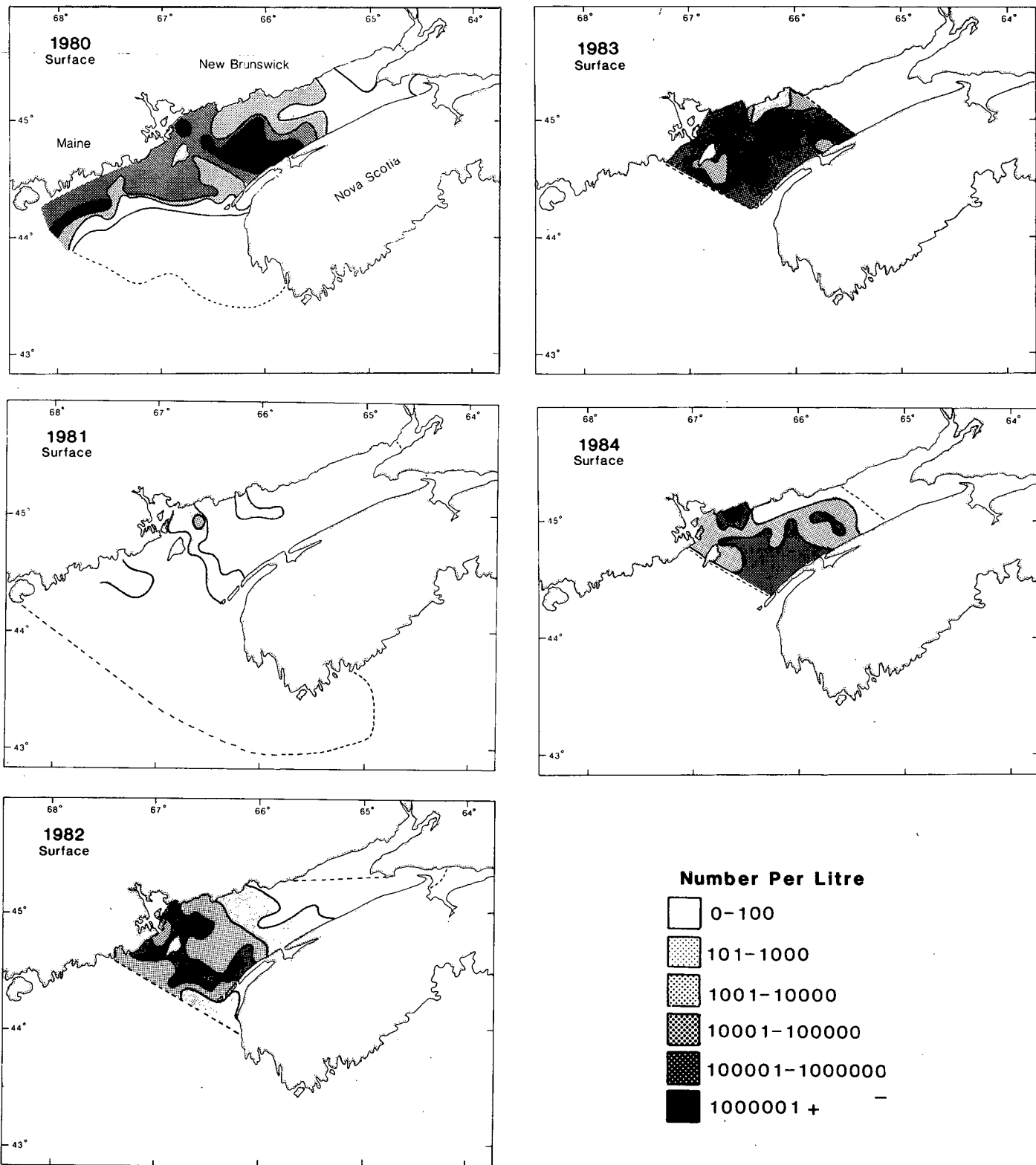


FIG. 2. Surface concentrations of *G. excavata* motile cells through the five sampling periods, 1980-84. Broken lines indicate outer limits of areas sampled.

Salinity was analyzed using a Guildline Instruments Limicea model 8400 salinometer. Map contouring for all figures was done both by hand and by computer using the Calcomp plotter. Similar results were obtained from both methods.

Results

Cell abundance is presented as though the samples were collected synoptically when collection times varied up to 2 wk,

depending on cruise tracks, weather conditions, and year sampled. The dominant organism from plankton material studied for this survey was *G. excavata*, with other dinoflagellates present to a lesser degree for each of the 5 yr. These included *Scrippsiella trochoidea*, *Ceratium longipes*, *C. minutum*, *C. furca*, *Gyrodinium aureoleum*, *Dinophysis* spp., and several species of large peridiniids. Tintinnids observed included *Helicostomella* spp., *Favella* spp., and *Ptychocylis* spp. The ciliate *Mesodinium rubrum* was observed at many locations. Mean temperatures for the surface waters were between 11.6 and 12.6°C for the five periods observed. Salinity values ranged from 30.0 to 32.0‰. Statistical analysis of temperature, salinity, and *Gonyaulax* number data for each year resulted in no statistically significant correlations between environmental variables and *Gonyaulax* abundance for the years 1980, 1981, 1982, and 1984. Since temperature and salinity did not vary appreciably during the five summers, the differences in cell numbers from year to year must have been related to other factors.

During all 5 yr, blooms of *G. excavata* were of sufficient magnitude to cause shellfish toxin levels to rise, resulting in a ban on harvesting. However, on August 23, 1980, shellfish toxicities reached levels as high as 8200 µg saxitoxin (STX) equiv./100 g in soft-shell clams (*M. arenaria*) at Crow Harbour, New Brunswick. For all following years, clams had detectable toxicity levels during July and August but at substantially lower levels.

Distribution maps for the incidence of *G. excavata* motile cells are given in Fig. 2. The 1980 bloom was very intense, with vegetative cells observed at 84% of the 168 stations during August 14–20. Cell concentrations as high as 1.8×10^7 cells/L which caused a reddish discoloration of the water were recorded at Station 86A (Fig. 1) in the southeastern Bay of Fundy. The greatest concentrations of *G. excavata* were found in the southeastern Bay of Fundy along the coast of Nova Scotia (Fig. 2). High concentrations in 1980 extended offshore to areas east and north of Grand Manan Island where highest concentrations of *G. excavata* cysts were observed during the winter of 1980–81 (White and Lewis 1982).

Gonyaulax excavata cells were observed at 41% of the 122 locations sampled during the summer of 1981 (Fig. 2). Total numbers of cells were low to nonexistent throughout the sampling area, with 1.06×10^3 cells/L at Station 58 being the highest concentration found. From these results, one might initially assume that sampling occurred during a nonbloom period. However, routine weekly monitoring of a station north of Grand Manan, Prince 5 (44°57'N, 66°51'W), was carried out between May and October of that year, indicating that the highest levels for 1981 were obtained during the week beginning July 13 with a concentration of 1.4×10^3 cells/L, and shellfish toxicity levels at Crow Harbour increased to 910 on August 10. The geographic sampling during 1981 was July 31 – August 10. Due to the low counts from the 1981 samplings, no fusing gametes or new hypnozygotes (cysts) were observed. Twenty duplets were found at Station 61, and 20 duplets were found at Station 129 (Fig. 1).

Results from the 1982 sampling showed 91% of the locations sampled to have *G. excavata* cells present. The sampling area for 1982 was reduced to 85 stations from the previous years to exclude the outer approaches to the Bay of Fundy and a portion of the inner Bay (Fig. 2). Normal vegetative cells dividing asexually (duplets) were more prevalent for this sampling period (Fig. 3) than sexually fusing gametes (Fig. 7) which were

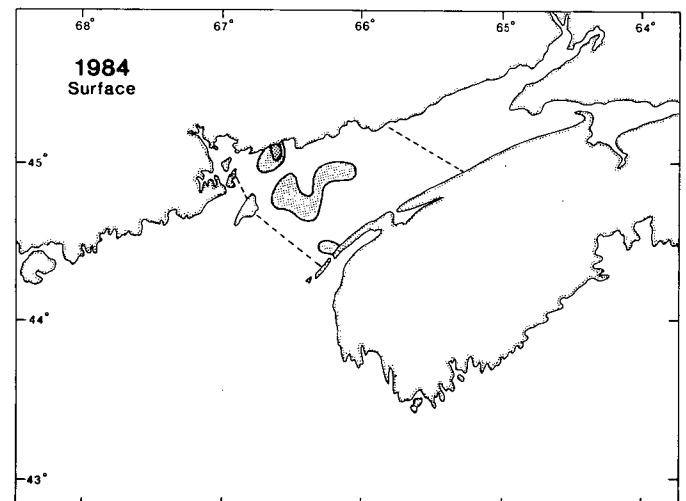
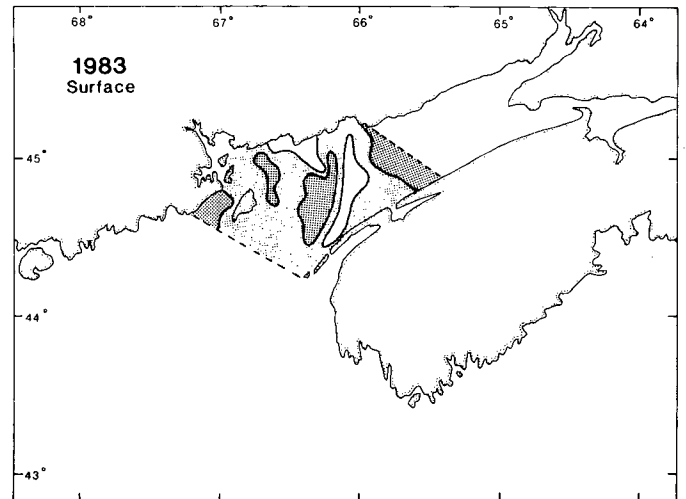
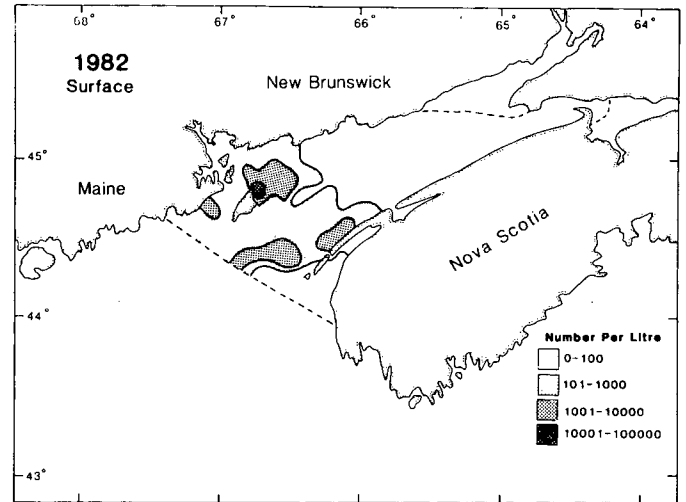


FIG. 3. Surface distribution and abundance of *G. excavata* asexually dividing cells (duplets).

observed at lower densities over much of the region. This high occurrence of duplets in asexual division indicates that sampling occurred in the early stages of bloom development. *Gonyaulax excavata* concentrations for this 1982 survey were at a maximum of 8.78×10^4 cells/L at Station 60.

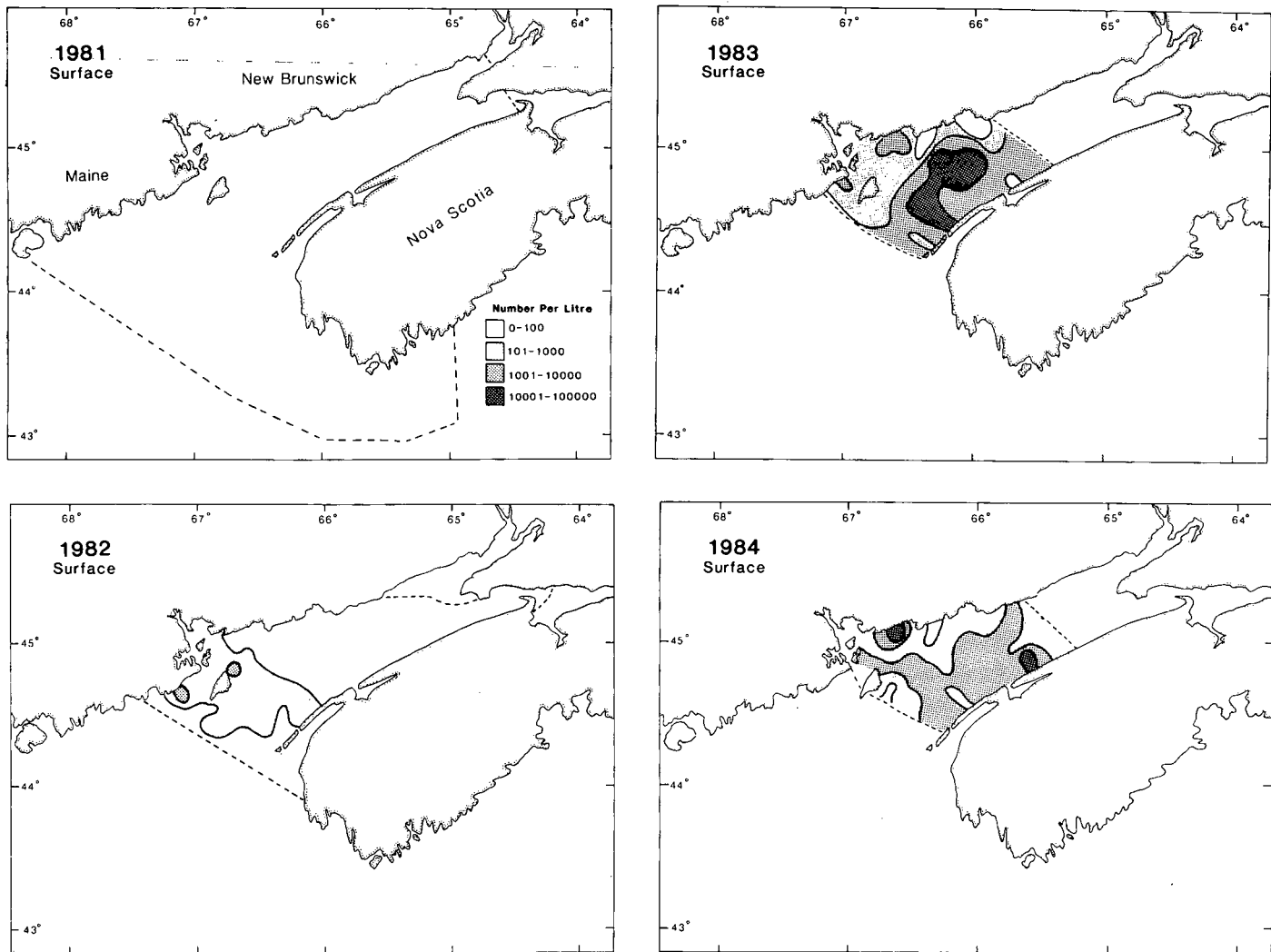


FIG. 4. Planozygote distribution at the surface.

Gonyaulax excavata motile cells were observed at all locations sampled both at the surface and at a depth of 5 m during 1983 and 1984 (Fig. 2, 5). The distributions for the surface and 5 m were similar for both years, with slightly higher concentrations observed in the surface samples. Highest concentrations in 1983 were 1.56×10^5 cells/L at Station 71. The greatest numbers of motile cells for 1984 were at Station 56 with 2.16×10^5 cells/L. Distribution and abundance for planozygotes for these 2 yr at both the surface and at 5 m are shown in Fig. 4 and 6. Ninety-four percent of all stations had planozygotes observed in 1983 and 97% in 1984. Sampling for 1983 seems to have occurred earlier during the bloom than 1984, since duplets were observed in 89% of the 1983 samples as opposed to 23% for the latter (Fig. 3).

No hypnozoogotes were observed during the 1981 or 1983 samplings. Forty newly formed cysts per litre were observed at Station 111 during 1982. Surface samples from nine locations (Stations 53, 60, 61, 84, 88, 90, 91, 98, 109) in 1984 had 20–40 cysts/L except Station 90 where 2.56×10^3 cysts/L were found. At the 5-m depth for the same year, cysts were observed at Stations 87 and 89 in concentrations of 20 and 60 cysts/L, respectively.

Discussion

The high concentration of *G. excavata* cells found in the cen-

tral Bay of Fundy (east of Grand Manan Island to Digby, Nova Scotia, and to Saint John, New Brunswick) is consistent with the direction of the currents and water patterns within the Bay of Fundy. Inflow from the Gulf of Maine eddy (located south of the Bay of Fundy to the east of Maine and southwest of Nova Scotia) occurs along the southern entrance to the Bay close to the coast of Nova Scotia (Bumpus 1960; Bumpus and Lauzier 1965). Much of this inflow crosses over to the north side of the Bay at an area northeast of Digby, Nova Scotia, to the Saint John area of New Brunswick (Godin 1968; Iles 1975; Greenberg 1984). The outflowing waters tend to run south and west along the New Brunswick coast to round Grand Manan Island to the east in a clockwise direction and flow either along the coast of Maine or cross the Bay and flow along the coast of Nova Scotia (Hachey and Bailey 1952). A cyclonic circulation of the surface and bottom waters occurs in the southwestern region of the Bay of Fundy east of Grand Manan. Tidal currents of 100 cm/s or greater from the region give rise to tremendous mixing throughout the waters, with tidal ranges of 8 m at the mouth of the Bay and 16 m at the head (Greenberg 1983; Daborn 1986).

During the 5-yr survey, the majority of *G. excavata* motile cells were observed between the mouth of the Bay of Fundy and an area between Saint John, New Brunswick, and northeast of Digby, Nova Scotia, which follows the current patterns deter-

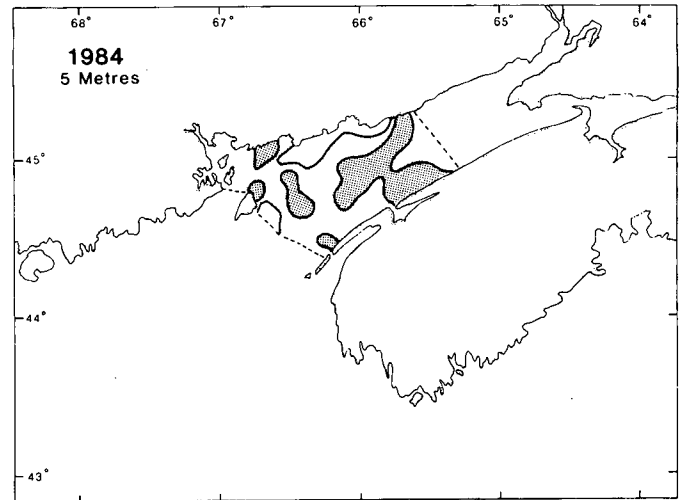
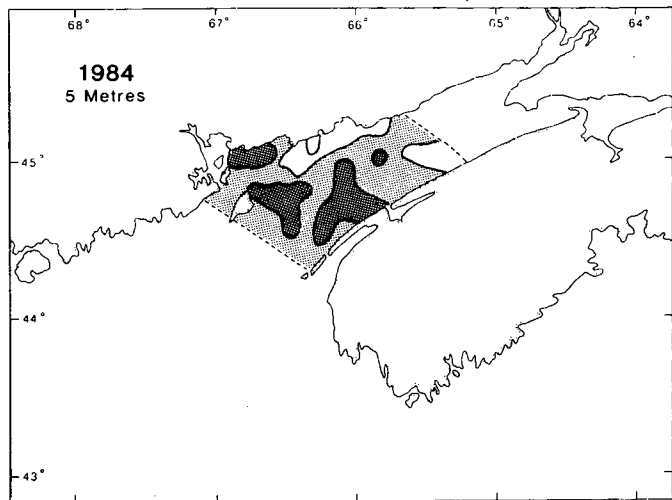
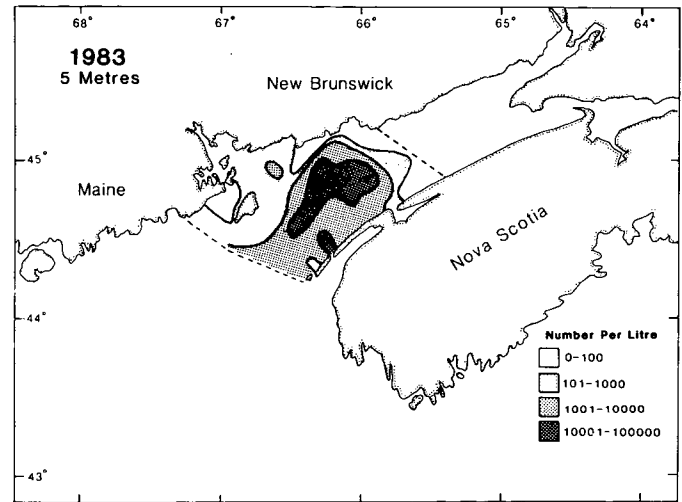
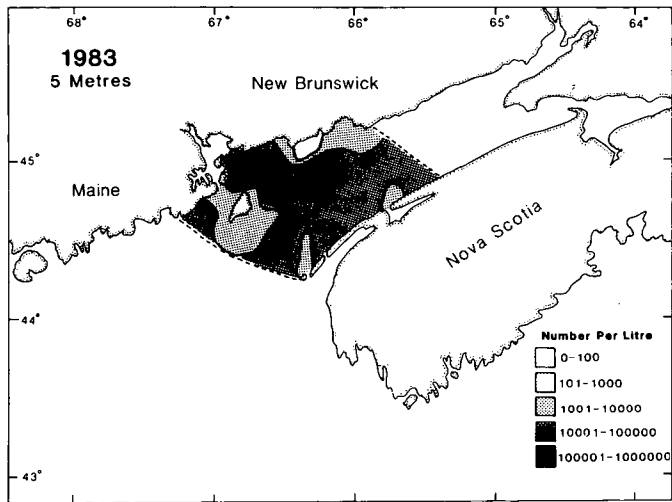


FIG. 5. Concentrations of *G. excavata* at a depth of 5 m.

FIG. 6. Distribution and abundance of planozygotes at a depth of 5 m.

mined for the Bay of Fundy (Godin 1968). The findings of low numbers of cells were consistent for the inner portions and basins at the head of the Bay (Fig. 2) where residual current patterns are not as prevalent as in the remainder of the Bay (Godin and Gutiérrez 1986).

The surface and bottom circulations in the Bay play an important role in the distribution of cysts, their distribution as they hatch into motile cells, and the retention of the cells within the system year after year. Cyst surveys of the Bay of Fundy during the winters of 1980–83 revealed moderate to low numbers of resting cysts occurring throughout most of the Bay and inshore, with rich deposits found offshore east and north of Grand Manan Island (White and Lewis 1982; J. L. Martin, unpubl. data). The fine silt/clay (LaHave clay) characteristic to this area is a result of active sediment deposition caused by relatively low tidal current velocities from the counterclockwise gyre of both surface and bottom water (Fader et al. 1977). Cysts are deposited to the area in a similar manner. The LaHave clay provides an ideal resting location as opposed to the Sambro sand (a net erosional sediment) along Nova Scotia and the glacial till in the central Bay (Fader et al. 1977) where few or no cysts were found during benthic surveys conducted during the winters of 1980–83. Highest concentrations of *G. excavata* motile cells were also located in the areas east and north of

Grand Manan Island, suggesting that this area serves as a major source for initiating summer blooms.

During August 1980, high concentrations of *G. excavata* cells causing red patches in the water were located in the southeastern region at Station 86A (Fig. 1, 2). This occurrence may be attributed to the circulation processes gathering hatching cysts from the LaHave clay beds and dispersing them to this particular area in the Bay. It has been established that water discolorations or high concentrations of dinoflagellates occur most often on hydrographic fronts or due to the convergent circulation systems induced about the fronts, and this could play a role in initiating dinoflagellate growth (Seliger et al. 1981). Pingree et al. (1975) discussed frontal regions as areas with combinations of high nutrients and a shallow upper mixed layer creating conditions suitable for rapid growth of phytoplankton. The three major frontal convergences within the Bay of Fundy are north of Grand Manan Island; south of Saint John Harbour, New Brunswick; and northwest of Digby, Nova Scotia, extending toward Saint John (Greenberg 1984; Loder and Greenberg 1986). However, frontal convergences, the local accumulations, and their effects alone cannot explain the wide distribution and patchiness of the *G. excavata* cells found during this sampling during five bloom periods. There is evidence for the years 1980, 1982, 1983, and 1984 of high concentrations of *G. excavata* motile cells located great distances from the deter-

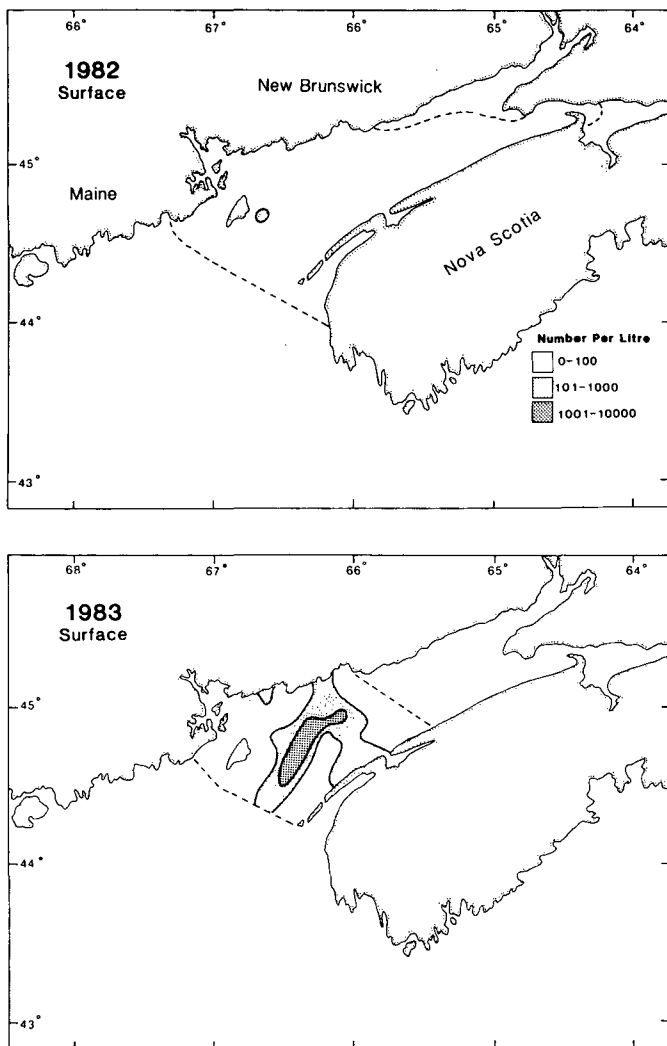


FIG. 7. Distribution and abundance of fusing cells at the surface.

mined frontal boundaries. A combination of winds, tidal mixing, frontal movements, and other physical effects that include a vertical transfer of water masses must play an important role in the dispersion of cells and nutrients. A significant correlation exists between shellfish toxicity and the 18.6-yr cycle of lunar modulation with the tides, indicating periods of intense toxicity in the mid-1940's, early 1960's, and late 1970's (White 1987).

Anderson et al. (1983) observed similar annual variations in abundance to those of the Bay of Fundy for 1980 and 1981 along the northeast coast of the United States. Similarly, *G. excavata* cells were present in high concentrations during 1980, with large numbers of new cysts deposited in surface sediments followed by a 1981 bloom period with a low percentage of the encysted population hatching, resulting in an almost non-existent bloom period. We assume that many cysts deposited are dormant from year to year without germination because the 1982, 1983, and 1984 bloom periods were considerably more productive than 1981.

Patchiness in cell distribution and abundance may be attributed to some extent to experimental error. Lund et al. (1958) estimated an error of $\pm 10\%$ when counting at least 400 cells. There is also a variation in cell number from two samples from the same location or in the pattern of sampling with samples taken at any phase of the tide. Vertical profiles for migration studies have proven that *G. excavata* cells in the Bay of Fundy

tend to remain at the surface both day and night, permitting continuous sampling (J. L. Martin, unpubl. data). In drawing the contours, there is an element of error where generalizations are made that all sampling locations within a designated contour actually fall into a particular category. However, the data do signify a real difference in areas with high concentrations of *G. excavata* as opposed to those with few. Although *G. excavata* was the predominant organism in samples counted, there was an additional error in distinguishing between *G. excavata* and *S. trochoidea*, as discussed by White (1986). For these counts, questionable cells were not counted as *G. excavata*, thus biasing towards an underestimation of actual cell numbers. Therefore, the contours may indicate slightly less cells than were actually present. However, samples with high numbers of *G. excavata* cells tended to have very few, if any, other organisms present. It must also be noted that sexual gametes were difficult to distinguish from vegetative cells unless they were fusing. All planozygotes were distinguished as cells greater than 43 μm .

Sampling during 1983 and 1984 carried out at both the surface and at 5 m shows very similar contouring for the surface and 5 m for each year, suggesting that the samplings for 1980, 1981, and 1982, although the surface was the sole depth of sampling, were representative of actual occurrences.

In summary, the offshore area in the southwestern Bay of Fundy seems to serve as the major source for *G. excavata* in the Bay and under ideal conditions along the northeastern coast of the United States. The high number of cells during one year resulting in numerous cysts deposited does not appear to be related to the size of the next year's bloom. Results from this survey suggest that further study is required to determine the cause of continued unacceptable shellfish toxin levels in the southern Bay of Fundy.

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References

- ANDERSON, D. M. 1980. Effects of temperature conditioning on development and germination of *Gonyaulax tamarens* (Dinophyceae) hypnozygotes. *J. Phycol.* 16: 166-172.
- ANDERSON, D. M., S. W. CHISHOLM, AND C. J. WATRAS. 1983. The importance of life cycle events in the population dynamics of *Gonyaulax tamarens*. *Mar. Biol. (Berl.)* 76: 179-190.
- ANDERSON, D. M., AND D. WALL. 1978. The potential importance of benthic cysts of *Gonyaulax tamarens* and *Gonyaulax excavata* in initiating toxic dinoflagellate blooms. *J. Phycol.* 14: 224-234.
- BUMPUS, D. F. 1960. Sources of water contributed to the Bay of Fundy by surface circulation. *J. Fish. Res. Board Can.* 17: 181-197.
- BUMPUS, D. F., AND L. M. LAUZIER. 1965. Serial atlas of the marine environment. Folio 7. American Geographical Society, New York, NY.
- DABORN, G. R. 1986. Effects of tidal mixing on the plankton and benthos of estuarine regions of the Bay of Fundy, p. 390-413. *In* J. Bowman, C. M. Yentsch, and W. T. Peterson [ed.] *Tidal Mixing and Plankton Dynamics*. Lecture Notes on Coastal and Estuarine Studies, 17. Springer-Verlag, Berlin and Heidelberg.
- FADER, G. B., L. H. KING, AND B. MACLEAN. 1977. Surficial geology of the eastern Gulf of Maine and Bay of Fundy. *Geol. Surv. Can. Pap.* 76: 17 p.

- GODIN, G. 1968. The 1965 current survey of the Bay of Fundy. A new analysis of the data and an interpretation of the results. Can. Dep. Energy Mines Resour. Mar. Sci. Branch MS Rep. Ser. 8: 97 p.
- GODIN, G., AND G. GUTIÉRREZ. 1986. Non-linear effects in the tide of the Bay of Fundy. Continental Shelf Res. 5: 379-402.
- GREENBERG, D. A. 1983. Modelling the mean barotropic circulation in the Bay of Fundy and Gulf of Maine. J. Physical Oceanogr. 5: 886-904.
1984. A review of the physical oceanography of the Bay of Fundy, p. 9-30. In D. C. Gordon Jr. and M. J. Dadswell [ed.] Update on the marine environmental consequences of tidal power development in the upper reaches of the Bay of Fundy. Can. Tech. Rep. Fish. Aquat. Sci. 1256.
- HACHEY, H. B., AND W. B. BAILEY. 1952. The general hydrography of the waters of the Bay of Fundy. Fish. Res. Board Can. MS Rep. 455: 62 p.
- ILES, T. D. 1975. The movement of seabed drifters and surface drift bottles from the spawning area of the "Nova Scotia" herring stock and the herring larval transport-retention hypothesis. Int. Counc. Explor. Sea C.M. 1975/C:37: 17 p.
- LODER, J. W., AND D. A. GREENBERG. 1986. Predicted positions of tidal fronts in the Gulf of Maine Region. Continental Shelf Res. 3: 397-414.
- LUND, J. W. G., KIPLING, C., AND E. D. LECREN. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 121: 143.
- PINGREE, R. D., P. K. PUGH, P. M. HOLLIGAN, AND G. R. FORSTER. 1975. Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. Nature (Lond.) 258: 672-677.
- SELIGER, H. H., K. R. MCKENLEY, W. H. BIGGLA, R. B. RIVKIN, AND K. R. H. ASPDEN. 1981. Phytoplankton patchiness and frontal regions. Mar. Biol. 61: 119-131.
- TURPIN, D. H., P. E. R. DOBEL, AND F. J. R. TAYLOR. 1978. Sexuality and cyst formation in Pacific strains of the toxic marine dinoflagellate *Gonyaulax tamarensis*. J. Phycol. 14: 235-238.
- WHITE, A. W. 1980. Recurrence of kills of Atlantic herring (*Clupea harengus harengus*) caused by dinoflagellate toxins transferred through herbivorous zooplankton. Can. J. Fish. Aquat. Sci. 37: 2262-2265.
1981. Marine zooplankton can accumulate and retain dinoflagellate toxins and cause fish kills. Limnol. Oceanogr. 26: 103-109.
1982. Intensification of *Gonyaulax* blooms and shellfish toxicity in the Bay of Fundy. Can. Tech. Rep. Fish. Aquat. Sci. 1064: 12 p.
1984. Paralytic shellfish toxins and finfish, p. 171-180. In E. P. Ragelis [ed.] Seafood toxins. ACS Symposium Series No. 262. American Chemical Society, Washington, DC.
1986. High toxin content in the dinoflagellate *Gonyaulax excavata* in nature. Toxicon 24: 605-610.
1987. Relationships of environmental factors to toxic dinoflagellate blooms. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 187: 38-46.
- WHITE, A. W., AND C. M. LEWIS. 1982. Resting cysts of the toxic red tide dinoflagellate *Gonyaulax excavata*. Can. J. Fish. Aquat. Sci. 39: 1185-1194.