

Distribution of the Toxic Dinoflagellate *Gonyaulax tamarens* in the Southern New England Region^a

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Based on the presence or absence of cysts in sediment samples from selected estuarine and coastal locations in southern New England and Long Island, a population distribution is described for the toxic dinoflagellate *Gonyaulax tamarens* Lebour. This distribution is influenced by hydrography and shoreline configuration, with accumulations predominantly offshore in the Cape Ann and Massachusetts Bay regions, and within estuarine embayments on Cape Cod. Three locations in Connecticut and six on Long Island also accumulated cysts, despite a history free from paralytic shellfish poisoning (PSP). It would appear that a massive coastal red tide in 1972 introduced *G. tamarens* into numerous embayments in previously unaffected areas. However, discovery of cysts of this organism in 11 locations with no history of PSP supports an alternative hypothesis that isolated populations of *G. tamarens* existed in the region prior to 1972. Whether these newly discovered populations represent a continuation of a southward dispersal of the toxic organism cannot be resolved at this time.

These data suggest different mechanisms for the initiation and development of *G. tamarens* populations responsible for PSP in the study area. While cysts on Cape Cod are found in close proximity to the toxic shellfish, other areas are apparently exposed to motile populations of this species originating further afield. Extreme localization of cysts on Cape Cod has remained essentially unchanged over a 3-year period, despite recurrent

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outbreaks. The patchy distribution of cysts and motile cells in the southern New England region may reflect physical and chemical constraints or may simply be a manifestation of relatively recent 'colonization'.

Introduction

One view of the recent history of toxic dinoflagellate blooms (red tides) in New England is that of a gradual southward dispersal of the causative organism *Gonyaulax tamarensis*. Although paralytic shellfish poisoning (PSP) was documented in north-eastern Canada nearly 100 years ago (Ganong, 1889), the first New England outbreak occurred in eastern Maine in 1958 (Hurst, 1975). This remained the only state with a shellfish toxicity problem until 1972 when a massive bloom affected the coasts of Maine, New Hampshire and Massachusetts (Mulligan, 1975; Yentsch *et al.*, 1975). Subsequently, these states have experienced recurrent PSP closures. In 1979, mussel beds were closed when PSP was detected in Narragansett Bay, Rhode Island (*Providence Journal—Bulletin*, 30 June 1979). The causative organism was not identified.

If these events are indicative of a southward dispersal of *G. tamarensis*, a large part of the species' success can be attributed to a benthic cyst stage in the organism's life cycle. The resting cysts (hypnozygotes) can overwinter in the sediments and germinate to inoculate overlying waters (Dale, 1977; Anderson & Wall, 1978). Such cysts had been postulated as seed populations for bloom initiation and dispersal (Prakash, 1967; Steidinger, 1975; Wall, 1975), but none was identified until recently. In retrospect, a tenable hypothesis is that the massive 1972 bloom along the New England coast introduced cyst populations into previously unaffected areas, with those dispersed into favorable environments establishing localized, persistent populations (Dale, 1977; Anderson & Wall, 1978).

An alternative explanation for recent outbreaks of PSP is suggested by Alam *et al.* (1979) who reported a tenfold variation in toxicity per cell between three Massachusetts clones of *G. tamarensis*. Low-toxicity cells could thus be present in numbers undetectable by routine PSP bioassays or by symptoms in humans. Conditions leading to elevated population densities (or perhaps higher toxicity/cell) could result in PSP in what appeared to be a previously unaffected area, resulting in the unjustified conclusion that spreading had occurred. An example of 'latent' PSP detection may be Perch Pond, Massachusetts, where shellfish toxicity first occurred in 1976 after 4 years of negative testing following the 1972 coastal bloom (Anderson & Wall, 1978). The Perch Pond clone of *G. tamarensis* is approximately one-tenth as toxic as an isolate from the 1972 event (Alam *et al.*, 1979).

Further support for the existence of localized populations prior to 1972 can be found in older phytoplankton records which document *G. tamarensis* (described as *G. orientalis*) off the Maine coast in 1932 and 1935 (Gran, 1933; Gran & Braarud, 1935), and in southern Massachusetts coastal waters in 1935 (Lillick, 1937). Nevertheless, the lack of published or rumored accounts of shellfish poisoning prior to 1972 is in sharp contrast to the present situation.

Any evaluation of the possible spreading of *G. tamarensis* requires a baseline population distribution. State PSP records cannot be used in this respect since mouse bioassays are designed to measure shellfish toxicity, are not widespread geographically and, more importantly, cannot detect small, relatively harmless populations. Similarly, systematic water samples and cell counts would indicate the presence or absence of *G. tamarensis* at given locations but are not feasible for an extensive survey. Alternatively, since this species forms resting cysts, sediment samples from carefully selected deposition sites can locate cyst accumulations. Recognizing a detection limit determined by the sampling location,

technique, and the quantity and depth of sediment examined, one sample can nevertheless provide a reliable record of the cyst-forming dinoflagellates deposited in an area over an extended period of time (Dale, 1976; Anderson & Wall, 1978).

It is thus the main objective of this paper to describe a baseline population distribution to the north and south of the organism's proven southern limit (Massachusetts) against which future spreading can be assessed. These data can also be used to evaluate the role of cysts in the development of shellfish toxicity in different hydrographic regimes within the region. Finally, we can consider the potential for future PSP outbreaks in new locations due either to the introduction of motile or encysted populations of *G. tamarens* or to the unexpected growth of an unnoticed, localized population.

Methods

Sampling locations

Sediment samples were collected from 362 stations (Figures 1-3). Detailed locations are available on request. Where possible, every station from a similar 1976 survey of southern Cape Cod (Anderson & Wall, 1978) was sampled again, with new stations added in that region to provide more coverage. In other areas, stations were located where local hydrography indicated that deposition of fine-grained materials was likely. These latter sites were often selected either through the advice of shellfish wardens or by onsite inspection. In all cases, samples were from soft, muddy locations rather than hard, sandy areas subject to scour and erosion.

Sediment collection

Due to the large area covered by this survey, sampling was conducted on various dates: Stations 1-52 between 10/78 and 3/79; 53-238 between 7/79 and 9/79; 239-270 between 3/80 and 6/80; 271-309 during 9/80 or 6/81; 310-350 during 10/80 or 6/81; 351 and 352 on 28/7/81, and 353-362 on 3/11/80.

Sampling methods varied with the depth of the water, ease of boat access and sediment type. Where possible, a plankton net was towed gently across the sediment surface, either from a boat or while wading. Another method used a bilge pump connected to a hose that was lowered to the sediments and moved laterally while the sediment surface was 'vacuumed'. Deeper samples were collected with either a VanVeen grab sampler or a box corer. In each case, only a subsample of the surface sediments was examined.

All samples were stored in jars containing local seawater, with temperature maintained at the sediment temperature. Processing consisted of sonication and 20-80- μ m size fractionation (Wall & Dale, 1968). Although sediment types differed significantly, approximately 0.4 g of sediment (dry weight) were processed, concentrated and examined for each station. This generally involved inspection of 3 ml of the size-fractionated sample, with *G. tamarens* cyst detection verified using additional slides. No attempts were made to enumerate cysts because of the non-quantitative sampling methods. Data are thus expressed on a presence vs. absence basis.

The *G. tamarens* cyst distribution reported here is based solely on light microscope examination for morphological characteristics described by Dale (1977) and Anderson & Wall (1978). To date, there are no published descriptions of other dinoflagellate cysts that could be confused with *G. tamarens* using this type of examination. Clearly, however, positive identification and toxin determination require germination and culturing, which was undertaken for samples of special interest.

Results

Of the 362 sediment samples examined, 51 contained cysts of *G. tamarensis* (Figures 1-3). Specific details will be presented by geographic region.

North-eastern Massachusetts (Figure 1)

In marked contrast to estuaries further south on Cape Cod, the Essex, Annisquam and Plum Island Sound estuaries contained very few *G. tamarensis* cysts, despite a recurrent shellfish toxicity problem. Where cysts were found, concentrations were so low that verification was difficult. Sediment samples were very sandy, reflecting the extensive flushing (mean tidal excursion 2.7 m). *G. tamarensis* cysts were numerous, however, in nearly all offshore stations, with the highest numbers found in Gloucester Harbor (Station 262). Offshore sampling depths ranged from 10 to 50 m.

In this Cape Ann region, PSP is often first detected in early June, continuing to rise for several weeks and decreasing thereafter. Toxin levels are generally undetectable from late July through the fall and winter. During some years, however, PSP has been detected in September, although spring outbreaks are more frequent and severe. It is noteworthy that the first locations to show positive PSP scores are those near the mouth of the Annisquam River (near Station 35).

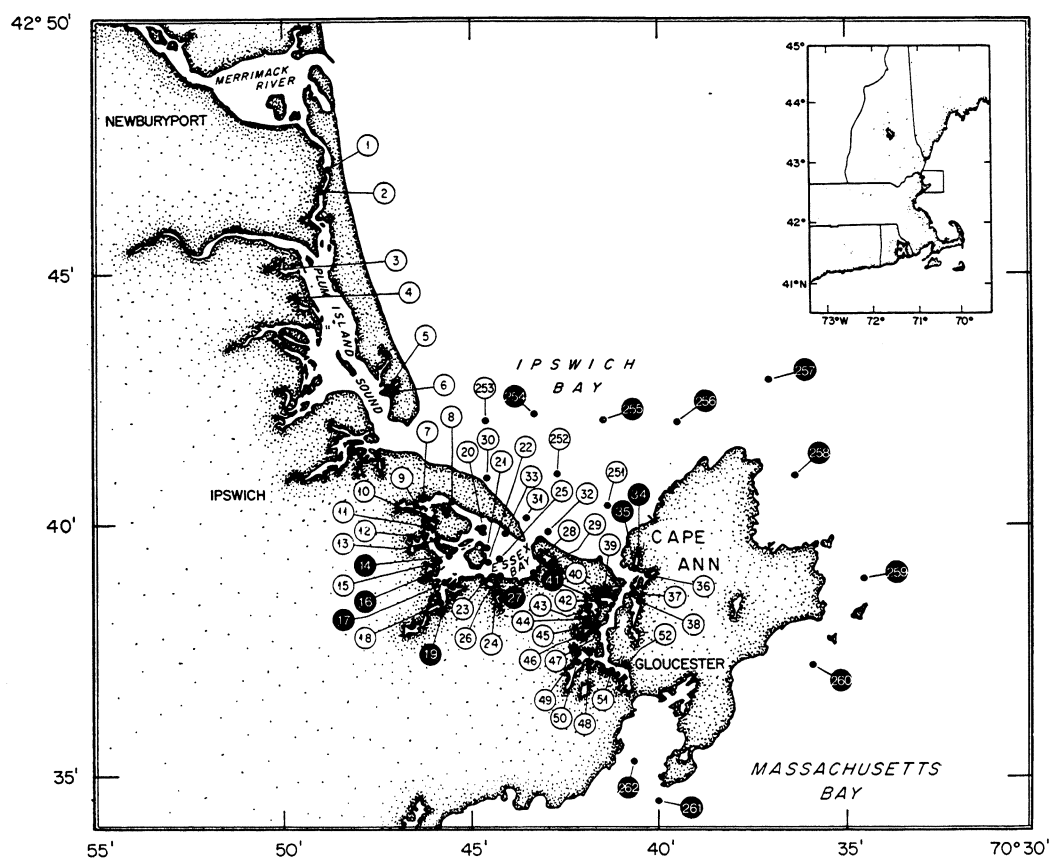


Figure 1. Distribution of *Gonyaulax tamarensis* cysts (blackened circles) in the Cape Ann region of northern Massachusetts. Numbers are for station identification.

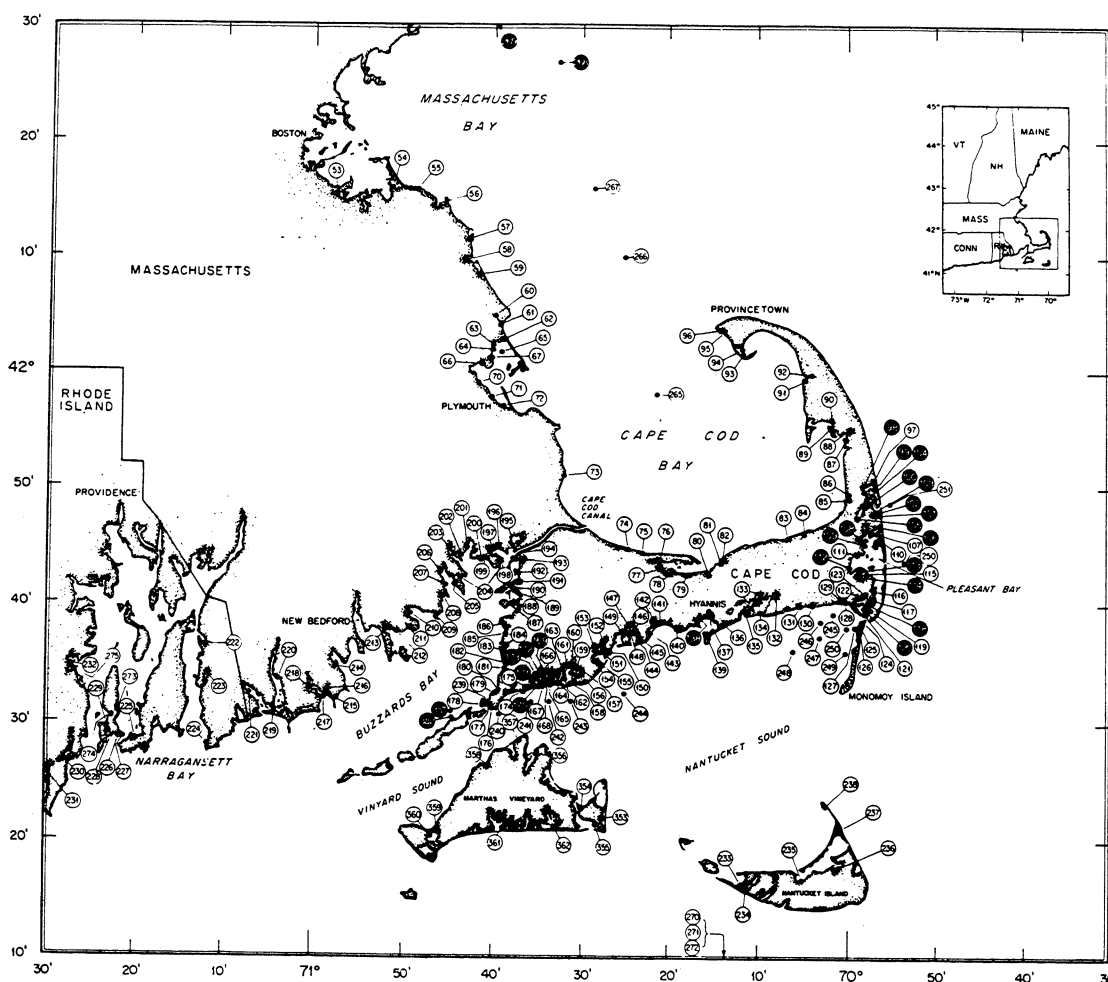


Figure 2. Distribution of *Gonyaulax tamarensis* cysts (blackened circles) between Boston and Narragansett Bay, Rhode Island.

South-eastern Massachusetts (Figure 2)

Proceeding south across Massachusetts Bay from Cape Ann, *G. tamarensis* cysts were present in samples 268 and 269 at depths approaching 100 m. Three other stations in the Bay (265–267) contained no cysts, but microscopic examination suggests that surface sediments were lost in grab sampling. *G. tamarensis* cysts were not found in estuarine samples from Boston to Provincetown, although they were numerous on the east side of Cape Cod (Stations 97–128). Affected areas in that region were generally small embayments with restricted inlets and muddy sediments. Nearby areas subject to stronger currents were very sandy and predictably devoid of cysts. On southern Cape Cod, *G. tamarensis* cysts were found in Hyannis (Station 138) and in several embayments in the Falmouth area (Stations 169–173). Estuarine samples from Martha's Vineyard and Nantucket Island and from locations along the coast west of Falmouth around Buzzards Bay to the Rhode Island border were all negative. Offshore samples to the east and south of Cape Cod contained coarse sand, relatively little organic matter and no cysts, indicative of the high energy

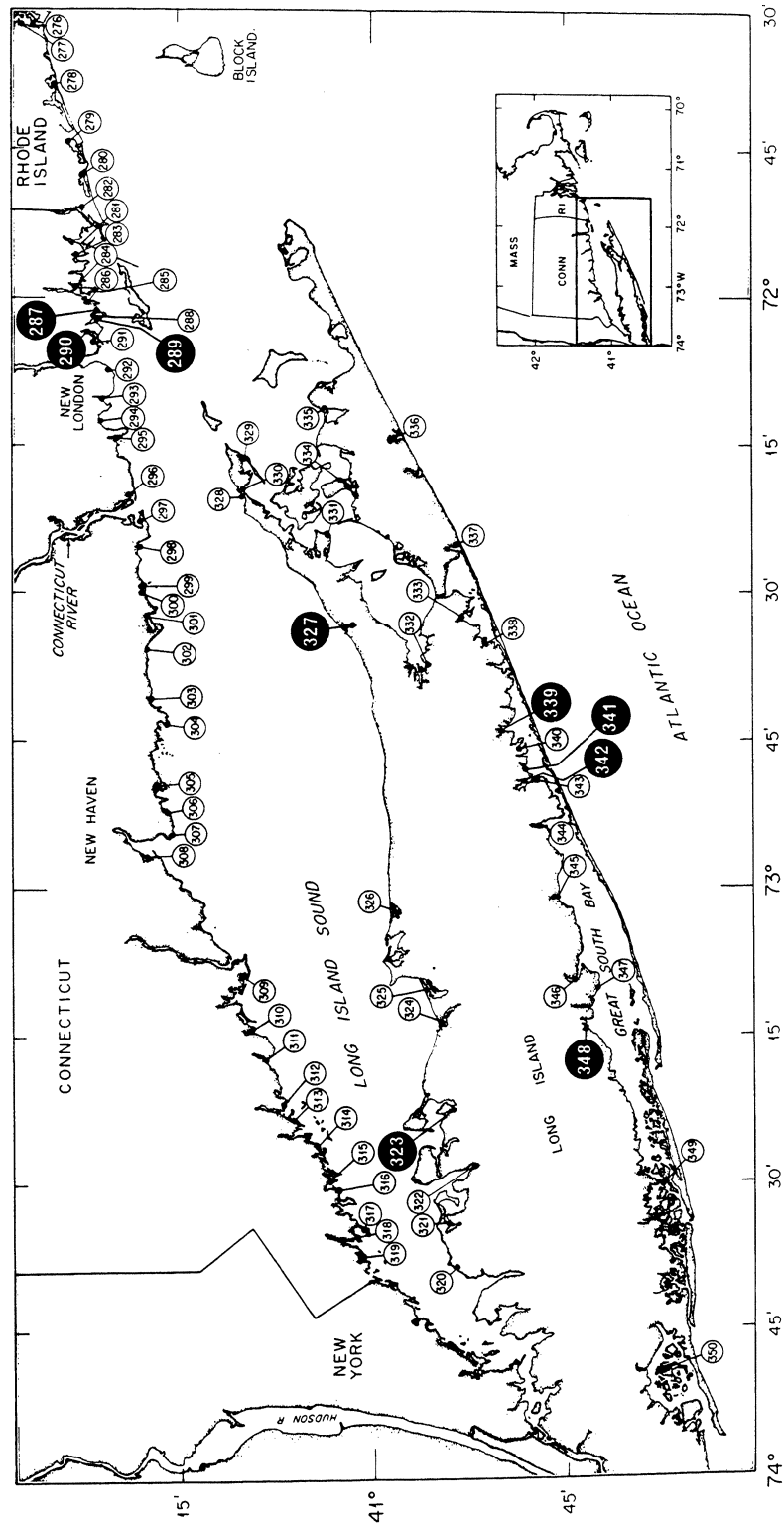


Figure 3. Distribution of *Gonyaulax tamarensis* cysts (blackened circles) in Connecticut and Long Island.

current regime along the coast. Samples (270–272) taken far offshore in a known deposition site termed the ‘mud patch’ (Bothner *et al.*, 1981) were also negative. Offshore *G. tamarensis* cysts were detected to the west of Cape Cod in Buzzards Bay (Stations 351 and 352).

Shellfish toxicity in this region is as localized as the cyst distribution. Between Boston and the Cape Cod Canal, PSP is often detected first along the open coast in June, with most estuarine areas relatively unaffected. Two early warning areas, Strawberry Point (near Station 56) and Manomet Point (north of Station 73) are rocky with hard sandy bottoms and direct exposure to coastal currents.

In contrast, PSP on Cape Cod occurs much earlier, first within sheltered embayments and salt ponds, spreading to nearby areas with time. Toxicity is often detected in May or early June. Key early warning stations are Salt Pond, Mill Pond, Hornes Marina and Perch Pond (near Stations 98, 102, 116 and 173 respectively.) Shellfish toxicity has never been reported in the Hyannis area, although *G. tamarensis* cysts are present and isolates are toxic. PSP has never been reported within Massachusetts to the west of Perch Pond.

Rhode Island, Connecticut and Long Island

Gonyaulax tamarensis cysts were found in nine estuarine locations in this region (Figure 3). No offshore samples were collected. In Rhode Island, samples were all negative including two (226, 227) taken near the site of a 1979 PSP outbreak in Narragansett Bay. In Connecticut, *G. tamarensis* cysts were found in three neighboring embayments to the east of New London. Cultures established from these cysts were *G. tamarensis* (var. *tamarensis*) and were toxic (Shimizu, personal communication; Anderson, unpublished). Equally noteworthy was the presence of cysts in six widely dispersed stations on Long Island. Only cultures from Mud Creek (Station 341) have been tested to date, but isolates are toxic (Shimizu, personal communication) and again are *G. tamarensis* (var. *tamarensis*) (Anderson, unpublished).

The above results are interesting since these two states have no PSP history. The only reported shellfish toxicity in this region was in 1979 in Narragansett Bay, Rhode Island. The shellfish were from Station 226, which is rocky and exposed.

Discussion

Based on the presence or absence of *G. tamarensis* cysts in sediment samples, a population distribution can be described to the north and south of the known southern limit of this toxic organisms’ geographic range in New England. When this survey is linked to that of Lewis *et al.* (1979) in Maine, the *G. tamarensis* cyst distribution is seen to be widespread to the north, with extensive offshore and estuarine accumulations. Proceeding south to Cape Cod, the distribution becomes patchy and localized within key estuaries, dwindling to a few scattered ‘seedbeds’ in Connecticut and Long Island. These later results document the presence of *G. tamarensis* in waters with no previous history of PSP and suggest a significant potential for future outbreaks.

An obvious question arises concerning the resolution of this method—if *G. tamarensis* cysts are not detected in a sample, is the result indicative of the area represented by that station? While acknowledging a detection limit determined by sampling and processing protocol, we feel that the method is far more sensitive than other alternatives and is both reproducible and reliable. With the exception of very sandy environments, samples generally contained many pollen grains, a variety of dinoflagellate cysts and abundant particulate organic material. The lack of *G. tamarensis* cysts in such samples is considered noteworthy.

Cyst distribution and shellfish toxicity

The most obvious correlation between cyst distribution and shellfish toxicity is on Cape Cod where the two are tightly coupled. *G. tamarensis* cysts were not found in 17 offshore samples, but were numerous in sheltered embayments (higher than in any region surveyed). Shellfish toxicity is generally confined to these same estuaries in the immediate vicinity of the cyst accumulations. Anderson & Wall (1978) and Anderson & Morel (1979) proposed that motile *G. tamarensis* populations originate within these embayments, inoculated by the germination of cysts from such 'seedbeds' (Steidinger, 1975), a conclusion consistent with the cyst distribution in Figure 2. An interesting exception to this pattern is the detection of *G. tamarensis* cysts in nearshore waters to the west of Cape Cod in Buzzards Bay—a large embayment where PSP has never been reported. Although all estuarine sediment samples were negative, the two deeper stations (15–20 m) did contain *G. tamarensis*. The ultimate fate of motile populations originating in that area is unknown, but here again there is a potential for future PSP outbreaks in a previously unaffected embayment.

Outside Cape Cod, the coupling is less direct between cysts and motile populations affecting shellfish. Cape Ann, for example, has experienced numerous PSP outbreaks since 1972, yet the estuaries are relatively free of *G. tamarensis* cysts, presumably due to extensive tidal flushing. Cysts were numerous in nearly all offshore samples, so an offshore seed bed hypothesis is plausible given the extensive coastal upwelling and vertical mixing in this region (Bigelow, 1927; Graham, 1970; Hartwell, 1975). A *G. tamarensis* cyst survey by Lewis *et al.* (1979) also showed extensive offshore cyst accumulations further north in Maine.

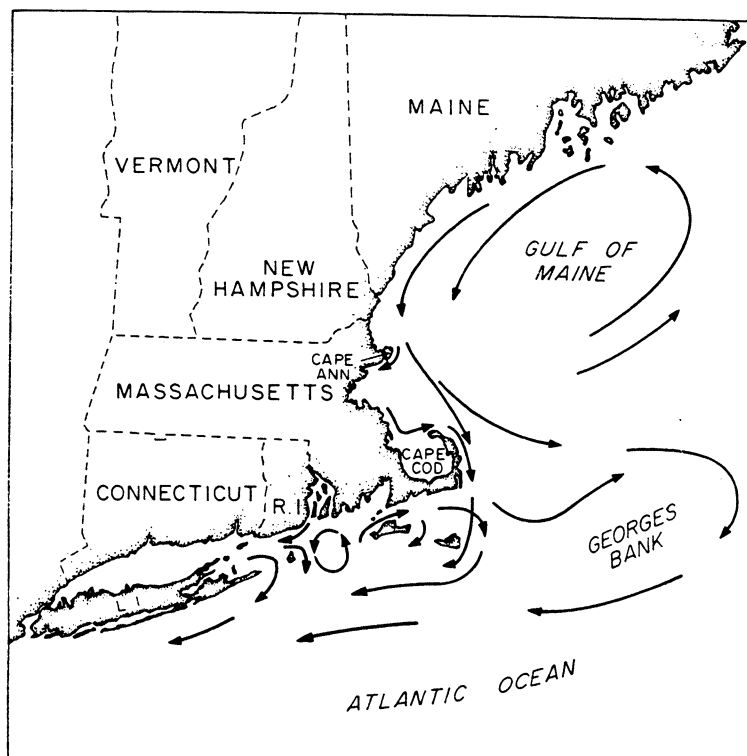


Figure 4. Schematic representation of the non-tidal circulation in the study area. Redrawn from Bigelow (1927), Bumpus & Wehe (1949) and Bumpus (1973).

Transport of motile *G. tamarensis* populations to Cape Ann from their origins to the north has been hypothesized, with advection driven by persistent north-east winds (Hartwell, 1975; Seliger *et al.*, 1979). The general summer and early fall circulation in the Gulf of Maine (Figure 4) is counterclockwise (Bigelow, 1927; Hartwell, 1975), which could also carry established populations from Maine and New Hampshire south. Although this north-south transport may occur, the more general temporal trend is one that results in PSP moving from south to north in a given year. For example, an early warning station for PSP in Maine is Hampton, New Hampshire, a station to the south and west of the Maine border (Hurst, 1975). Further, a massive outbreak in August 1980 closed the entire Maine coastline, yet no closures occurred on Cape Ann at that time. PSP concentrations had peaked early that summer, well before the outbreak in Maine. It is thus probable that *G. tamarensis* populations in the Cape Ann region originate offshore, but not from distant locations. Cysts found in nearshore waters may serve this function.

Between Cape Ann and Cape Cod, *G. tamarensis* populations apparently originate offshore as well. These may be cells advected from Cape Ann, or they may be more localized within Massachusetts Bay, but they presumably do not originate within estuaries, since (a) no cysts were found in the estuaries of this region, but were found offshore instead (Figure 2); (b) the earliest toxicity is detected on promontories exposed to coastal currents; and (c) PSP is first detected on Boston's south shore approximately 1 week after it occurs on Cape Ann.

With the exception of the 1979 episode in Narragansett Bay, Rhode Island, PSP has not been reported south or west of Perch Pond, Falmouth (Station 173). This is in obvious contrast to the presence of *G. tamarensis* populations at nine stations in that region (with isolates from three locations already proven toxic). The non detection of PSP may reflect a very recent spreading to these areas, a lack of conditions suitable for sufficiently dense *G. tamarensis* blooms, low toxicity populations (Alam *et al.*, 1979), or a shortage of shellfish resource and thus limited harvesting during bloom periods. Unfortunately, insufficient background information is available to resolve these possibilities.

Spreading of Gonyaulax tamarensis

There is only one record of *G. tamarensis* in southern New England coastal waters prior to 1972, despite numerous observations in the Gulf of Maine (Gran, 1933; Gran & Braarud, 1935; Prakash, 1967). This one report was from Vineyard Sound (west of Station 240) in 1935 (Lillick, 1937). The absence of documented or rumored PSP-like shellfish poisonings in southern New England is consistent with the apparent scarcity of *G. tamarensis* prior to 1972. As this study has verified, however, absence of PSP events does not imply the absence of toxic *G. tamarensis*, so we cannot rule out the prior existence of localized populations within the region. Nevertheless, there is little doubt that the 1972 bloom introduced *G. tamarensis* cells into previously unaffected areas in southern New England. The recurrent nature of the toxic outbreaks and the dangerously high PSP scores measured in popular clamming areas since then both suggest a significant change.

A similar lack of baseline data makes it difficult to ascertain whether spreading has occurred since 1972. Comparison of this study with a 1976 survey of southern Cape Cod (Anderson & Wall, 1978) indicates that *G. tamarensis* cysts remain localized within the same embayments along the eastern and southern shores of Cape Cod, but that they are also now present at a station in between (Station 138) that was not examined in 1976. Further evaluation of the spreading of *G. tamarensis* awaits surveys that refer to the more extensive data base presented here.

Looking to other regions for future dispersal of the species, it is likely that this toxic dinoflagellate could survive in estuarine waters to the south and west of the area covered in this study. Within estuaries with characteristics similar to those already supporting *G. tamarensis* growth, *G. tamarensis* cysts would germinate as waters warm in the spring (Anderson & Wall, 1978; Anderson & Morel, 1979), effectively selecting a suitable temperature regime. Thus the species could theoretically grow in waters far to the south given sufficient seasonal temperature variation. In this respect, the discovery of *G. tamarensis* cysts in Connecticut and Long Island is not surprising.

Given the apparently large geographic range with potentially suitable environments, why then is the species localized and patchy in southern New England? One answer may reflect the time needed to establish a sizeable seed population. The widespread cyst distribution in Maine (Lewis *et al.*, 1979) may reflect that regions' 20-year exposure to *G. tamarensis*, whereas the patchiness in southern New England is consistent with a more recent colonization.

It is also possible that natural advection restricts species dispersal to the south. Several circulation studies (e.g. Bigelow, 1927; Bumpus & Wehe, 1949; Bumpus *et al.*, 1971; Bumpus, 1973) suggest that *G. tamarensis* populations in Massachusetts coastal waters would be carried along the eastern portion of Cape Cod and into the higher salinity offshore environment (Figure 4). A similar fate would befall populations flushed from estuaries on southern Cape Cod. Transport towards land would then be affected by complex eddies to the south, with considerable dispersion and dilution of the population expected. Surface waters in Long Island sound, for example, have a net eastward flow away from land (Riley, 1956).

North of Cape Ann, the bathymetry indicates a highly irregular and glacially scoured bottom with intervening sediment-filled valleys and small basins (Tucholke *et al.*, 1972). To the south, the bottom is hummocky and rough but becomes relatively smooth and flat near Plymouth (Schlee *et al.*, 1973). The bedform morphology south of Cape Cod (O'Hara, 1980) indicates active scour and erosion, with deposition expected only in the northeast portion or in Nantucket Bight. (Samples from this deposition zone contained finer sediments and organic detritus, but no *G. tamarensis* cysts.) Buzzards Bay to the west has a muddy bottom subject to extensive deposition (Rhoads & Young, 1970). The smooth, gently sloping topography and dynamic hydrographic regime near Cape Cod may thus account for the occurrence of *G. tamarensis* cysts only within estuaries, whereas the offshore basins and topographical depressions to the north and west provide ideal accumulation sites.

The patchiness may also reflect trace metal sensitivity (Anderson & Morel, 1978). As shown by Anderson & Morel (1979), *G. tamarensis* cysts germinating into Vineyard Sound water could not produce viable motile populations without chelator additions while those incubated in water from nearby estuaries were viable without additions. The implication is that certain locations or times may provide suitable conditions for *G. tamarensis* growth, while others may be inhibitory. For this as yet unproven hypothesis to apply to southern New England, there must be significant variations in trace metal speciation as one proceeds from restricted embayments to the open coastal waters. Unfortunately, present analytical techniques cannot resolve this issue.

In summary, this study has examined the distribution of the toxic dinoflagellate *G. tamarensis* in the southern New England region. In addition to providing a baseline against which future spreading events can be assessed and pinpointing several unaffected areas where PSP may occur, the results suggest a varying spatial correlation between cyst 'seed-beds' and estuarine shellfish toxicity. The continued localization of *G. tamarensis* populations in key embayments at the southern limit of the species geographic range is noteworthy,

but the underlying mechanisms remain obscure. The potential for future spreading from both natural advection and human activities in the coastal zone (e.g. dredge and fill operations, shellfish seeding) is real, however, and should be monitored closely.

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References

- Alam, M. I., Hsu, C. P. & Shimizu, Y. 1979 Comparison of toxins in three isolates of *Gonyaulax tamarensis* (Dinophyceae). *Journal of Phycology* **15**, 106-110.
- Anderson, D. M. & Morel, F. M. M. 1978 Copper sensitivity of *Gonyaulax tamarensis*. *Limnology and Oceanography* **23**, 283-295.
- Anderson, D. M. & Morel, F. M. M. 1979 The seeding of two red tide blooms by the germination of benthic *Gonyaulax tamarensis* hypnocyts. *Estuarine and Coastal Marine Science* **8**, 279-293.
- Anderson, D. M. & Wall, D. 1978 The potential importance of benthic cysts of *Gonyaulax tamarensis* and *Gonyaulax excavata* in initiating toxic dinoflagellate blooms. *Journal of Phycology* **14**, 224-234.
- Bigelow, H. B. 1927 Physical Oceanography of the Gulf of Maine. *Bulletin of the U.S. Bureau of Fisheries* **40**, 511-1027.
- Bothner, M. H., Spiker, E. C., Johnson, P. P., Rendigs, R. R. & Aruscavege, P. J. 1981 Geochemical evidence for modern sediment accumulation on the continental shelf off southern New England. *Journal of Sedimentary Petrology* **51**, 281-292.
- Bumpus, D. F. 1973 A description of the circulation on the continental shelf of the east coast of the United States. *Progress in Oceanography* **6**, 111-158.
- Bumpus, D. F. & Wehe, T. J. 1949 Hydrography of the Western Atlantic: coastal water circulation off the east coast of the United States between Cape Hatteras and Florida. *Woods Hole Oceanographic Institution Reference No. 49-6*, 11 pp.
- Bumpus, D. F., Wright, W. R. & Vaccaro, R. F. 1971 Sewage disposal in Falmouth, Massachusetts: II. Predicted effect of the proposed outfall. *Journal of the Boston Society of Civil Engineers* **58**, 255-277.
- Dale, B. 1976 Cyst formation, sedimentation, and preservation: factors affecting dinoflagellate assemblages in Recent sediments from Trondheimsfjord, Norway. *Review of Palaeobotany and Palynology* **22**, 39-60.
- Dale, B. 1977 Cysts of the toxic red-tide dinoflagellate *Gonyaulax excavata* Balech from Oslofjorden, Norway. *Sarsia* **63**, 29-34.
- Ganong, W. F. 1889 The economic mollusca of Acadia. *Bulletin of the Natural History Society of New Brunswick* **8**, 116 pp.
- Graham, J. J. 1970 Coastal currents in the western Gulf of Maine. *International Commission of the North Atlantic Fisheries, Research Bulletin* **7**, 19-31.
- Gran, H. H. 1933 Studies on the biology and chemistry of the Gulf of Maine. *Biological Bulletin* **74**, 159-182.
- Gran, H. H. & Braarud, T. 1935 A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine. *Journal of the Biological Board of Canada* **1**, 1-279.
- Hartwell, A. D. 1975 Hydrographic factors affecting the distribution and movement of toxic dinoflagellates in the western Gulf of Maine. In *Toxic Dinoflagellate Blooms* (LoCicero, V. R., ed.), *Proceedings of the 1st International Conference, Massachusetts Science and Technology Foundation*. pp. 47-68.
- Hurst, J. W. Jr. 1975 History of paralytic shellfish poisoning on the Maine coast. In *Toxic Dinoflagellate Blooms* (LoCicero, V. R., ed.), *Proceedings of the 1st International Conference, Massachusetts Science and Technology Foundation*. pp. 525-528.

- Lewis, C. M., Yentsch, C. M. & Dale, B. 1979 Distribution of *Gonyaulax excavata* resting cysts in the sediments of Gulf of Maine. In *Toxic Dinoflagellate Blooms* (Taylor, D. L. & Seliger, H. H., eds). *Proceedings of the 2nd International Conference*. Elsevier/North Holland, Amsterdam. pp. 235-238.
- Lillick, L. C. 1937 Seasonal studies of the phytoplankton off Woods Hole Massachusetts. *Biological Bulletin* **73**, 488-503.
- Mulligan, H. F. 1975 Oceanographic factors associated with New England red-tide blooms. In *Toxic Dinoflagellate Blooms* (LoCicero, V. R., ed.). *Proceedings of the 1st International Conference, Massachusetts Science and Technology Foundation*. pp. 23-40.
- O'Hara, C. J. 1980 Bedform morphology of Nantucket Sound, Massachusetts. *United States Geological Survey Administrative Report*.
- Prakash, A. 1967 Growth and toxicity of a marine dinoflagellate *Gonyaulax tamarensis*. *Journal of the Fisheries Research Board of Canada* **24**, 1589-1606.
- Rhoads, D. C. & Young, D. K. 1970 The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* **28**, 150-177.
- Riley, G. A. 1956 Oceanography of Long Island Sound, 1952-1954. 2. Physical oceanography. *Bulletin of the Bingham Oceanographic Collection* **15**, 15-46.
- Schlee, J. S., Folger, D. W. & O'Hara, C. J. 1973 Bottom sediments on the Continental Shelf off Northeastern United States—Cape Cod to Cape Ann, Massachusetts. *United States Geological Survey Miscellaneous Geological Investigation Map* I-746.
- Seliger, H. H., Tyler, M. A. & McKinley, K. R. 1979 Phytoplankton distributions and red tides resulting from frontal circulation patterns. In *Toxic Dinoflagellate Blooms* (Taylor, D. L. & Seliger, H. H., eds). *Proceedings of the 2nd International Conference*. Elsevier/North Holland, Amsterdam. pp. 239-248.
- Steidinger, K. A. 1975 Basic factors influencing red tides. In *Toxic Dinoflagellate Blooms* (LoCicero, V. R., ed.). *Proceedings of the 1st International Conference, Massachusetts Science and Technology Foundation*. pp. 153-162.
- Tucholke, B. E., Oldale, R. N. & Hollister, C. H. 1972 Map showing echo-sounding survey of Massachusetts Bay and Cape Cod Bays, western Gulf of Maine. *United States Geological Survey Miscellaneous Geological Investigation Map* I-716.
- Wall, D. & Dale, B. 1968 Modern dinoflagellate cysts and evolution of the Peridinales. *Micropaleontology* **14**, 265-304.
- Yentsch, C. M., Cole, E. J. & Salvaggio, M. G. 1975 Some of the growth characteristics of *Gonyaulax tamarensis* isolated from the Gulf of Maine. In *Toxic Dinoflagellate Blooms* (LoCicero, V. R., ed.). *Proceedings of the 1st International Conference, Massachusetts Science and Technology Foundation*. pp. 163-180.