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BASIC FACTORS INFLUENCING RED TIDES¹

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ABSTRACT

Ecologically, there are three aspects common to all toxic red tides. First, there is an increase in population size, called here initiation. Secondly, there is support, e.g., suitable salinity, temperature, nutrients and growth factors, and finally, in many red tides, the maintenance and transport of blooms by hydrologic and meteorologic forces. The first two aspects are often considered inseparable. However, with recent advances in dinoflagellate life cycle work, specifically, detection and description of sexual phases and viable benthic cysts, the possibility of benthic seed populations and the factors influencing their development should be primary research objectives. The locality of initiation is also critical. For example, *Gymnodinium breve* blooms are initiated about 16 to 64 km off southwest Florida in 12 to 37 m, and it is suggested that if a dormant stage exists, then seed populations or seed "beds" possibly can be delineated within this zone. Present data indicate gradual motile population increases, not sudden population "explosions" due to increased cell division rates. Once initial increases occur, specific chemical and physical conditions are necessary to support these blooms. Lastly, as evidenced by many dinoflagellate blooms, winds, currents, and organism migrations are important transport and concentrating mechanisms.

INTRODUCTION

Toxic dinoflagellate blooms are common in coastal and/or estuarine waters around the world, particularly temperate and subtropical regions. Ecologically, there are at least three aspects common to such blooms. First, there is an increase of initial motile populations above background levels, which in the case of *Gymnodinium breve* blooms, are not due to increased cell division rates. Secondly, water conditions must be optimal for support of such blooms either by land run-off, upwelling, submarine spring discharge, preceding biological conditioning, or possibly some other regulatory factor. The third progressional aspect in this proposed general concept concerns the maintenance and transport of blooms by meteorologic and hydrologic forces.

It is the first stage, initiation, that we think is critical to understanding red tides, or for that matter, many coastal and estuarine dinoflagellate blooms. This does not imply that subsequent stages are insignificant. On the contrary, they are essential to whether or not red tide conditions are established, how long they last, and what areas can be affected.

Data (1,2) suggest that *G. breve* blooms annually in Gulf of Mexico coastal waters (> 16 km offshore) and that probably 3/4 of these blooms terminate offshore without developing into major outbreaks. Others are transported to nearshore waters where they can become established and cause severe economic distress (3, 4). Once in nearshore waters, the offshore blooms which evidently seed nearshore blooms can continue (e.g. 1968) or subside (e.g. 1967). Occasionally, as in 1974, the nearshore blooms will subside but can be

reestablished sporadically by continuing offshore blooms of low to moderate concentrations. The point to be made here is that the zone of initiation and the status of the original "seed" population offshore should be evaluated to determine "triggering" factors. It is our contention that toxic dinoflagellate blooms are life cycle phenomena and to understand red tides, researchers need to concentrate on alternation of cytological and/or morphological generations and the environmental parameters which influence these stages.

The recent investigations of Dr. David Wall (Woods Hole Oceanographic Institution) and Dr. H. A. von Stosch (Phillips University, Marburg) on dinoflagellate life stages lends credence to the speculation that pelagic, toxic dinoflagellate blooms might originate from dormant stages and that these stages might be associated with certain bottom sediments. This then brings up the question, if benthic resting stages of certain dinoflagellates actually "seed" coastal red tides, are there localized areas of accumulation, or what we could call "seed beds"?

DISCUSSION

Sexuality and Resting Stages

There are at least ten dinoflagellates known to have sexual and asexual cycles involving cytological and/or morphological alternation of generations. These include the armored species *Ceratium cornutum*, *C. horridum*, *Glenodinium lubiniensiforme*, *Helgolandinium subglobosum*, and the unarmored species *Amphidinium carterae*, *Gymnodinium microadriaticum*, *G. pseudopalustre*, *Noctiluca scintillans*, *Oxyrrhis marina*, and *Woloszynskia apiculata*. (5,6,7,8,9). This list represents six marine and four freshwater species. The marine species are homothallic and either isogamous or anisogamous. The zygotes show a wide diversity ranging from resting cysts to motile cells bearing a close resemblance to their vegetative haplont counterpart. Although sexuality has been painstakingly described from laboratory experiments, the actual stages in fusion, zygote formation, meiosis, etc., can easily be missed *in situ* because of the time frame and the fact that very little cytological work has been done with field specimens. All dinoflagellate species known to have sexual cycles are haplontic with the exception of *Noctiluca*, which is diplontic.

The importance in discussing sexuality lies in the recent revelations that at least several benthic resting cysts (freshwater species) are actually hypnozygotes, and that sexual cycles could possibly account for seasonal appearances of certain bloom organisms. Braarud (10) speculated, "It would not seem unreasonable to assume that the seasonal distribution pattern of the meroplanktonic species may be influenced by a periodicity in sexual reproduction which may vary from one species to another."

Based on the work of Dr. Wall and others (11) there are at least 59 dinoflagellate taxa (38 marine, 21 freshwater) with described resting cysts isolated from sediments. Representatives have been documented for the armored genera *Cachonina*, *Ceratium*, *Diplopetopsis*, *Diplopsalis*, *Enciculi-*

fera, *Fragilidium*, *Gonyaulax*, *Helgolandinium*, *Heterocapsa*, *Peridinium*, *Pyrodinium*, *Pyrophacus*, *Scrippsiella*, and the unarmored genera *Gymnodinium*, *Gyrodinium* (?), and *Woloszynskia*. The majority of these cysts are thick-walled stages; however, there are several exceptions, including *Gonyaulax tamarensis*, which have thin walls and no ornamentation (12). Dormancy is known for several freshwater species, a few marine species, and is speculated for the remainder of those species which produce benthic cysts (8, 13, 14). This is an extremely important aspect of the life history which needs verification and experimentation to determine what exogenous and/or endogenous factors stimulate onset of or emergence from dormancy. Of the described cysts, at least ten represent bloom species including the toxic *Gonyaulax tamarensis*, *G. polyedra* and *Pyrodinium bahamense*. *Gonyaulax catenella* is said to produce cysts, but no descriptive work is published.

The hypothesis that such benthic cysts, whether they are zygotes or asexual stages, represent dormant "seed" populations in coastal and estuarine sediments is intriguing; however, two points should be stressed. First, not all zygotes are nonmotile benthic cysts; they can vary from nonmotile to motile pelagic stages. Secondly, benthic cysts have not been positively shown to function as seed populations in marine ecosystems, although it has been suggested by several researchers.

Zone of Initiation

Most toxic dinoflagellate blooms, e.g. *Gonyaulax tamarensis*, *G. polyedra*, *G. catenella*, *Pyrodinium bahamense*, and *Gymnodinium breve*, are coastal in origin (15, 16, 17, 18, 19), although some can become established in estuaries depending on hydrologic conditions. These species are characterized as neritic based on frequency of occurrence and distribution. Depending on continental shelf topography, neritic can mean 2 km to 160 km or more, and in the case of broad, shallow shelves, it becomes important to pinpoint origin of blooms to evaluate initiation versus support, particularly if initiation is "offshore".

Gymnodinium breve red tides along Florida's west coast have been assumed to originate close to shore near passes (3); however, monthly data from 1964-1965 along four transects up to 32 km and monthly data from 1965-1967 for transects up to 164 km indicate that *G. breve* blooms originate at greater than 16 km and are associated with an initiation zone 16 to 64 km offshore in depths of 12 to 37 m. Offshore blooms in these two instances had population increases above background levels (< 1,000 cells/liter) and involved counts up to several hundred thousand per liter, which during 1967 were associated with fish kills. Since motile *G. breve* are common to both inshore and offshore coastal waters at low background levels throughout non-red tide years, a sampling program to detect where initial population increases are occurring should extend far offshore. Inshore sampling programs in bays and nearshore waters would not give adequate forewarning of a red tide outbreak, whereas extended programs could detect red tides in their early stages.

Dragovich and Kelly (20) concluded from their 1964-1965 data representing stations out to 32 km, "...incidence of *G. breve* was highest at the 27.8-km (15-mile) stations and least at the 9.3-km (5-mile) stations." Summarizing unpublished data representing 28 monthly collections of 504 live samples up to 75 km and 16 live samples over 8 months at 139 and 164 km off two widely separated geographic points (Tampa Bay and Sanibel Island), Steidinger (11) showed that a 1967 red tide originated from blooms first detected 16 to 37 km off the Tampa Bay area with other sampling stations inshore and offshore of this detection area having less than 100 *G. breve*/liter. *Gymnodinium breve* (< 100/liter) was recorded only once at one of the two stations on the outermost shelf (164 km at 73 m) and this isolated occurrence was coincident with the 1967 red tide. These monthly data plus the fact that one station, 75 km offshore, was sampled biweekly rather than monthly, indicated that the 1967 red tide was not seeded from further offshore than the proposed zone of initiation 16 to 64 km. Data also suggest that initial blooms are localized.

Physical Factors

After initiation and support, currents can occasionally transport blooms long distances. In November 1972, the first *G. breve* red tide along the southeast Florida coast was attributed and documented to transport of bloom concentrations from off Sanibel Island through the Florida Keys into the Florida Straits and up the east coast via the Gulf Stream (21). Data from a Loop Current anomaly (22), *G. breve* counts, and satellite imagery suggested that an unusual current pattern set up in the lower eastern Gulf acted as an initial transport mechanism. Since *G. breve* can be transported by oceanic currents, this incidence has raised the question of whether or not *G. breve* is recruited from the Caribbean through the Yucatan Straits. However, in 34 live, 5-gallon water samples over a two year period (1967-1969) from 12 stations in the Yucatan Straits and open Gulf waters directly above the Straits, Ms. J. Williams (FDNR, personal communication) did not observe any motile *G. breve*.

Although currents, including tides, can transport blooms, the receiving waters must be suitable for survival. For example, data from two of the three red tides that have established in Tampa Bay, Florida, indicate that the normally low salinity barrier of the Tampa Bay System was nonexistent at these times because of drought conditions. Salinities in upper bay reaches, e.g. Old Tampa Bay, during the summer of 1971 were as high as 31⁰/oo when normally salinities of 25⁰/oo or less would be characteristic. In early months of 1974, the salinities were normal, up to 25⁰/oo in Old Tampa Bay. Consequently, high salinity conditions in 1971 allowed *G. breve* blooms, once in the estuary, to penetrate and survive in upper reaches in Old Tampa Bay while salinities in 1974 were at the lower limit for *G. breve* tolerance and blooms never became established in that part of the bay system, although blooms and fish kills were common in higher salinity waters of the lower bay reaches.

Gymnodinium breve during these two outbreaks originally gained access to Tampa Bay via the ship channel and cell counts showed it to be progressively moving up the bay. Once in Tampa Bay or the lower bays, e.g. Boca Ciega, winds and tides were instrumental in transporting and dispersing blooms. The importance of these mechanisms was obvious. On high tide in a back canal of Boca Ciega Bay with gentle winds from the SSW, surface samples from a distinctly discolored patch moving with the tide had 11 million *G. breve*/liter and 18" below the surface only 370,000/liter. The patch was oriented perpendicular to the wind direction. Five days later at the same time, same station, and with similar wind conditions, *G. breve* was 21 million/liter at the surface and 16.7 million/liter about 15" below. On the turn of the tide, the patch dissipated and counts at that station were 330,000/liter. It should be stressed however, that normally in coastal or estuarine waters, although there can be higher concentrations at the surface during daylight hours, fish-killing concentrations in the hundreds of thousands usually exist throughout the water column and mortality of fishes associated with bottom waters is common.

CONCLUSIONS

Gymnodinium breve red tides start offshore. The status of the seed population is not known, although there is a motile, planktonic population throughout the year at less than 1,000 cells/liter. No detailed cytological work has been attempted with this population, or even bloom populations, to determine whether specimens are haploid or diploid. If there is even the slightest possibility of toxic dinoflagellate blooms having their initiation from benthic resting cysts which may be hypnozygotes, it would seem that this avenue of research should have a high priority among phytoplankton systematists and ecologists.

The possibility of benthic seed populations and even seed beds for at least some *Gonyaulax* and *Pyrodinium* has a higher probability than for *Gymnodinium breve*. Again, however, no detailed cytological work has been attempted to determine whether these naturally occurring *Gonyaulax* and *Pyrodinium* cysts are zygotes. The only support for the possibility of *G. breve* also having a benthic stage is: 1) freshwater *Gymnodinium* and *Woloszynskia* have such stages and 2) Wall and Dale (23) described three marine benthic cysts, which on excystment produced a *Gymnodinium*, a *Gyrodinium* (?), and another member of the Gymnodiniales. Natural cycles in toxic as well as nontoxic dinoflagellate blooms should be clarified. This is an opportunity to look at the sediment/water interface, its community structure and regulating mechanisms in depths to about 46 m. Many coastal phytoplankters are said to be meroplanktonic (14, 24, 25), but evidence that the meroplanktonic cycle influences species succession, distribution, and abundance is minimal for open coastal waters.

The second aspect of blooms, nutritive support, also needs careful scrutiny because it is still not conclusive whether such planktonic populations are being supported by preceding biological conditioning, upwelling, or enrichment from land discharge, whether it be runoff from rivers (26) or discharge from submarine springs. (27). Plankton community metabolism *in situ* is difficult to assess, but much progress has been made in culture on basic growth requirements for individual species. Yet, little is known concerning community interactions. For example, what factors allow a single species, or a species complex now that hybridization is a possibility, to dominate plankton biomass to the exclusion of other plankters for long periods of time, e.g. months? Is it lack of natural predators, excretion of inhibitory substances, or competitive exclusion? Why, in other words, do we have monospecific dinoflagellate blooms covering vast areas of open coastal waters? I, for one, envision such coastal blooms as having occurred sporadically for centuries and consider them natural phenomena, an aspect of an ecosystem we do not fully understand rather than an imbalance of nature.

Modeling such phenomena becomes a precarious task, because we essentially do not know the regulatory mechanisms. Models based solely on nutrients or solely on hydrologic factors negate the interaction of the three proposed aspects, namely initiation, nutritive support, and physical maintenance and concentration. One such model stressed the importance of water column vertical stability over horizontal convection mechanisms (28). It is difficult to separate these two aspects because the influence of winds, vertical stability and organisms migrations are interrelated. Direction and intensity of winds play an extremely important role in horizontal transport and concentration of daytime, surface-concentrated *G. breve* blooms, either by surface currents, tidal penetration of bays, or convection mechanisms (1). This is not to say that vertical stability is not an influencing parameter in dinoflagellate blooms. Rather, vertical stability is only one factor and should be considered along with temperature, salinity, winds, currents, nutrients and growth factors, tropism, light, metabolic requirements and efficiencies, life cycles, community interactions, etc. Red tides are an interdisciplinary problem and require an interdisciplinary approach by biologists, chemists, physicists, and geologists.

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