Blooms of a Dinoflagellate *Gyrodinium cf. aureolum* in New Jersey Coastal Waters and Their Occurrence and Effects Worldwide

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ABSTRACT

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A dinoflagellate we identified as *Gyrodinium* cf. *aureolum* Hulburt bloomed extensively and persistently in southern New Jersey coastal waters in the summers of 1984 and 1985. This paper documents the New Jersey events, and reviews the occurrence and effects of blooms of the species elsewhere in the world. The New Jersey blooms were the first of the species reported in United States neritic waters. One certain consequence of these incidents was greatly diminished aesthetic quality of the coastal water. Mild sickness in humans, and kills of blue mussel, *Mytilus edulis*, and lady crab, *Ovalipes ocellatus*, coincided with the presence of both blooms but direct association was not established. The species currently is not considered a major threat in the United States, although it bloomed at least five times in the northeast region between 1982 and 1988. In Europe, however, it has flourished in estuarine, neritic and oceanic waters since 1966, and has caused numerous mass mortalities of marine fauna. Exceptional physiological versatility offers a possible explanation for its success in diverse environments. *Gyrodinium aureolum* is euryhaline, eurythermal, and can use efficiently both high and low light regimes. It apparently is vigorously phototactic, so it has the potential to position itself in favorable light levels. Major questions, such as how *G. aureolum* changed from a newly identified species to one of great importance in thirty years, and how it adversely affects marine fauna, remain to be answered.

ADDITIONAL INDEX WORDS: *Gyrodinium cf. aureolum, dinoflagellate blooms, marine fauna kills.*

INTRODUCTION

Extensive blooms of an unarmored dinoflagellate, which we identified as *Gyrodinium* cf. *aureolum* Hulburt, resulted in greenish or yellow-green water discolorations along the southern New Jersey coast in the summers of 1984 and 1985. These were the first documented blooms of the species in United States neritic waters. Their most obvious consequence was diminished aesthetic enjoyment of the affected New Jersey beaches. Following exposure to the discolored water, however, some persons reported mild sickness, and marine fauna may have been adversely affected.

The first reported *G. aureolum* blooms in the U.S. prior to the ones we describe were in the Carmans River, New York, in 1982 and 1983 (CHANG and CARPENTER, 1985). The latest *G.* cf. *aureolum* bloom in the northeast, and the only additional reported occurrence in this country thus far, was in Maquoit Bay, Maine, in the fall of 1987, and this is suspected to have caused a kill of benthic fauna (HAUGEN, *personal communication*). The incidence and effects of the *G.* cf. *aureolum* blooms in the northeast U.S. between 1982 and 1988 do not suggest a critical situation. Nevertheless, major importance of the species in the region, with accompanying detriment to marine life, should be considered a possibility. In Europe,

since its first reported bloom in 1966, it has become the most important dinoflagellate in the North Sea and in coastal waters around Ireland, England, Denmark, Sweden and Norway (SELIGER and HOLLIGAN, 1985). Many of the *G. aureolum* blooms in the coastal zone in Europe are associated with mortalities of marine fauna, and the variety of affected species is considerable (PARTENSKY and SOURNIA, 1986).

The section of New Jersey coastline where *G. cf. aureolum* was most concentrated is a prime recreational area, and the persistence of the blooms aroused considerable concern. This, and the fact that *G. aureolum* blooms have had catastrophic results elsewhere in the world, dictated that the New Jersey occurrences be examined. We document the New Jersey blooms, and review information on the causative species and the development and effects of its blooms worldwide. Detailed information on the study region and discussion of the probable factors contributing to the development of the New Jersey blooms is provided in U.S. EPA (1986, 1987).

BLOOMS OF *G. aureolum* AND OTHER SPECIES IN NEW JERSEY

The *G. cf. aureolum* blooms we report occurred from mid-August to mid-September, 1984 and from mid-July to mid-August, 1985. Surveys were conducted by boat and helicopter. In 1984, the bloom was first seen, and subsequently was most intense, along approximately 43 km of the New Jersey coast, from Long Beach Island to Ocean City (Figure 1). It also occurred, with less intensity and shorter duration, southward and northward of this zone. In 1985, the earliest sighting of the bloom was in two locales, Ocean City and Hereford Inlet. Soon after, it was evident northward to Atlantic City. The bloom then persisted in the Ocean City—Atlantic City area, and was less intense north of this zone than in 1984. In both years, the blooms were most intense from the shore out to about 1 km, but extended seaward 2 to 8 km, especially around the plumes of Great Egg Inlet and, in 1984, Little Egg Inlet (Figure 1). We observed the bloom water to enter local inlets only occasionally, this being with flooding tides. Cell concentrations in the bloom zones between Sandy Hook and Island Beach,

New Jersey, ranged $1.5-36 \times 10^6 \, 1^{-1}$; the geometric mean cell concentration was $3.4 \times 10^6 \, 1^{-1}$. Cell concentrations in areas where the bloom discoloration plainly was visible generally ranged $10-20 \times 10^6 \, 1^{-1}$. On a few clear days, when a *G. cf. aureolum* bloom was present, we observed the yellow-green discoloration to be most vivid during mid-day; the same areas appeared greenish-brown several hours earlier in the morning.

Salinities ranged 30-34 ‰ and 32-35 ‰, respectively, in the regions of the 1984 and 1985 blooms. Water temperatures were 21-25° C. In the summer of 1984, dissolved oxygen concentrations in New Jersey coastal waters were generally high, including during the time span, and in the geographical zone, of the blooms (U.S. EPA, 1985). Levels in the bloom zone during August–September ranged $2.9-7.4$ mg 1^{-1}; concentrations < 4 mg 1^{-1} (likely to be stressful to components of the fauna) were infrequent. In 1985, however, dissolved oxygen levels < 4 mg 1^{-1} were common, and depressed levels persisted for up to two months. Decomposition of the bloom likely exacerbated the condition. Most of the oxygen concentrations in the bloom zone from late July to early September were < 4 mg 1^{-1}, and many were < 3 mg 1^{-1}.

Symptoms in humans coincidental with exposure to the bloom water included nausea, sore throat, eye irritation and lung congestion (MARINO, *personal communication*). Complaints were primarily from individuals, such as lifeguards, who had relatively extensive contact with the bloom water, or who were on the beaches for long periods when it was present. During both events, isolated kills of blue mussel, *Mytilus edulis*, and lady crab, *Ovalipes ocellatus*, were observed on beaches and in the surf, coincident with presence of the bloom water. The Long Beach Township Health Department observed thousands of dead mussels on the beach at Harvey Cedars, August 15–17, 1984, and the Ocean City beach patrol reported a kill of mussels and crabs on the beach during July 24–August 7, 1985 (FLICKER, *personal communication*). Fish may have avoided the bloom water; personal observation and reports from sport fishermen suggested that fish catches were greatly diminished in a 7 km-wide area of bloom water off Little Egg Inlet in early September 1984.
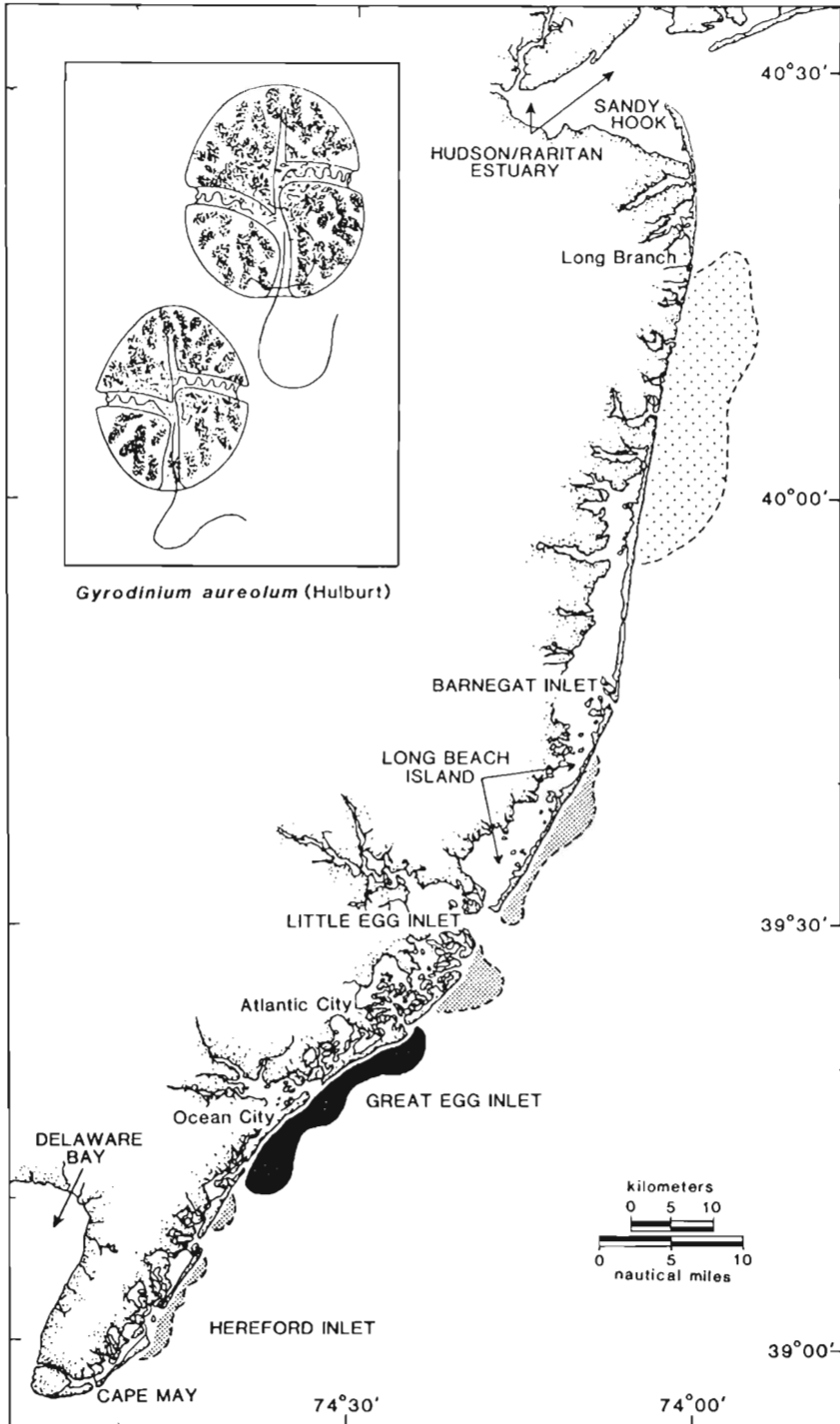
Figure 1. Map of the New Jersey coastline with approximate areas of *Gyrodinium aureolum* bloom distribution, 1984–1985. The dark to light shading indicates dense to moderate or patchy presence of the species. The insert shows the species' two major morphological types, elliptical (upper) and fusiform (lower); redrawn from Hulburt (1957).

There are major estuaries at the northern and southern ends of the New Jersey coast (Figure 1), and these at times are the sources for populations of phytoplankton which bloom in parts of the coastal region. Phytoplankton assemblages found along the northern New Jersey coast often resemble those in the Hudson-Raritan estuary (OLSEN and COHN, 1979), reflecting such estuarine contribution and the characteristically southward direction of the Hudson-Raritan plume. The Delaware estuary is a less likely source of phytoplankton for the New Jersey coast than the Hudson-Raritan but, according to BUMPUS (1969), its plume can flow northward during periods of low runoff and southerly winds. Nevertheless, the 1984–1985 G cf. *aureolum* blooms in south-central New Jersey apparently developed in the neritic waters of this region, because we did not observe dense populations of the species in the Hudson-Raritan estuary, Delaware Bay, or in the back bays and estuaries adjacent to the area where the blooms were most intense.

In the zone of greatest G. cf. *aureolum* bloom intensity, encompassing 43 km of coastline (15 km north and 28 km south of Atlantic City), there are five inlets (Figure 1), and these permit a greater tidal exchange than in any equivalent length of the New Jersey coast. Major nutrient input from the estuarine and coastal areas to adjacent nearshore environs likely promoted bloom development; weather and New York Bight inner shelf circulation patterns probably also were contributory factors (U.S. EPA, 1986, 1987).

We have monitored phytoplankton assemblages and nuisance blooms of various phytoplankton, including the phytoflagellates *Olisthodiscus luteus, Katodinium rotundatum,* and *Prorocentrum micans,* in northern New Jersey estuarine and coastal waters for over two decades. None of these were acutely toxic but some caused nausea and respiratory discomfort to bathers (MAHONEY and McLAUGHLIN, 1977), and mortality of fauna due to dissolved oxygen depletion when the blooms collapsed (OGREN and CHESS, 1969). A major hypoxia of bottom waters following the collapse of a large bloom (areal distribution at least 13,000 km^2) of the dinoflagellate *Ceratium tripos* in 1976 resulted in the greatest recorded kill of marine fauna off the New Jersey coast (MAHO-

NEY and STEIMLE, 1979; SWANSON and SINDERMANN, 1979).

Intense spring diatom blooms in New Jersey waters are usually dominated by a few species including *Skeletonema costatum, Thalassiosira nordenskioldii,* and *Asterionella glacialis* (OLSEN and COHN, 1979). In summer, minute coccoid chlorophytes, including *Nannochloris atomus,* dominate the phytoplankton in the inner New York Bight, especially in the Hudson-Raritan estuary and adjacent coastal waters. In 1985 and 1986, dense blooms of these chlorophytes resulted in pale green water along much of the New Jersey coast. In 1985, the chlorophyte bloom overlapped the area of the G. cf. *aureolum* bloom. Major phytoplankton related water discolorations in general, however, have been rare along the southern New Jersey coast. The first documented dinoflagellate bloom in this region was a late-June, early-July 1978 occurrence of *Dinophysis acuta,* that extended from Brigantine, just north of Atlantic City, to Ocean City (FIGLEY, 1979). The G. cf. *aureolum* blooms, therefore, were not uniquely important in New Jersey waters, but were the most important in the affected region.

DESCRIPTION OF *G. AUREOLUM,* AND TAXONOMIC DIFFICULTIES

Gyrodininium aureolum (Figure 1) was first described from Cape Cod, Massachusetts by HULBURT (1957). Hulbert's description of this unarmored dinoflagellate is:

"body essentially globular, its dorsi-ventral outline either somewhat ellipsoidal or somewhat fusiform, slightly dorsi-ventrally flattened, with subequal epicone and hypocone. Length 27-34 μm, width 17-32 μm. Epicone hemispherical to broadly conical, sometimes slightly truncate. Hypocone similar, but usually distinctly truncate, with antapex faintly indented at times. Girdle wide, moderately deep, displaced 0.20 body length. Sulcus reaching from just behind apex all the way to antapex, with slight left deflection in girdle region, rather narrow on epicone, wide on hypocone. Anterior flagellar chamber a posteriorly pointed, fingershaped cavity; posterior flagellar chamber an underhollowing of left sulcal margin opposite right girdle

limb. Anterior flagellum completely encircling body; posterior flagellum very long, up to two body lengths. Numerous yellow-brown chromatophores present, elliptical in shape, usually arranged in a somewhat radiating manner. Nucleus spherical, or wider than long, with elongate chromatin corpuscles."

Gyrodinium aureolum is recognized generally to be strongly pleomorphic. TANGEN (1977) found that the morphology of *G. aureolum* cells from a major bloom along the Norwegian coast in 1976 agreed with Hulburt's original description, but morphological variability was relatively great. The ranges of cell dimensions were wider (length 19-37 μm, width 19-35 μm), and dorsi-ventral flattening of cells greater, than reported by Hulburt. Girdle displacement varied from ¼ to ½ the cell length, although it was most often ⅓ the cell length, as reported by Hulburt. Tangen observed numerous elliptical yellow-brown chloroplasts, as did Hulburt, but also found globular or irregular chloroplasts. These were only sometimes in a radiating arrangement, whereas Hulburt reported this to be the typical situation. The high degree of pleomorphism exhibited by an unarmored dinoflagellate, which appeared to be *Gyrodinium mirabile* when first cultured, and later resembled *Gyrodinium fissum*, led KIMBALL and FERGUSON WOOD (1965) to suspect that *Gyrodinium aureolum, Gymnodinium nelsoni,* and *Gyrodinium resplendens* are synonymous with *G. mirabile* or *G. fissum*.

PARTENSKY and SOURNIA (1986) regarded the problem of *G. aureolum* identification to be complex and currently unresolvable. Contributing to the difficulty is the fact that various taxonomists may not study the same cytological features and may not conduct their observations in the same manner. They proposed the general adoption of a standardized checklist of cytological characteristics for the species and suggested the use, until firm taxonomic features are found, of the cautionary designation *Gyrodinium* cf. *aureolum* for the species found in northern European waters. More recently, PARTENSKY *et al.* (1988) suggested replacement of the latter appellation with *Gymnodinium* cf. *nagasakiense* for the species currently called *Gyrodinium aureolum* in the literature.

Our identification of *G.* cf. *aureolum* in the New Jersey blooms was based primarily on examination of live cells by P. Olsen and M. Cohn using light microscopy. Preserved material also was examined but this was not relied on because standard preservative such as Lugol's iodine resulted in cell distortion. Previous identification of *G. aureolum* in the New York Bight by M. Cohn was confirmed by H. Marshall (MARSHALL and COHN, 1981). We accept the advice of PARTENSKY and SOURNIA (1986), however, and regard our identification as presumptive pending resolution of the taxonomic difficulties.

Cells of *G.* cf. *aureolum* in our field collections from southern New Jersey coastal waters in general conformed to Hulburt's description but, reminiscent of Tangen's findings, there was considerable variation in size of cells and degree of roundness of epicone and hypocone. In live specimens, the fusiform shape (Figure 1) predominated. Numerous yellow-green chromatophores, elliptical in shape, were randomly distributed.

Gyrodinium cf. *aureolum* cells from the New Jersey blooms moved with a steady, spiralling motion. Live cells in sample bottles in the laboratory tended to concentrate near the water surface when lighted from above, suggesting positive phototaxis. Senescent cells readily settled out forming a flocculent mass; a clear gelatinous sheath often was apparent around individual senescent cells.

HULBURT (1957) and TANGEN (1977) observed the chloroplasts in *G. aureolum* to be yellow-brown but TAYLOR (1985) reported them to be pale green. TANGEN and BJORNLAND (1981) described *G. aureolum* as a species with variable pigmentation, unlike most other photosynthetic dinoflagellates. Although the chloroplasts appeared yellow-green in cells examined from the 1984–1985 blooms off southern New Jersey, they were yellow-brown in *G.* cf. *aureolum* cells cultured in 1984 at the Sandy Hook Laboratory from a bloom on the southeastern shore of Long Island, New York. HULBURT (*personal communication*) does not regard chromatophore color to be a critical taxonomic criterion in this species. POTTS and EDWARDS (1987) reported on August 1986 bloom of *G. aureolum* off Plymouth, England that appeared greenish-brown in color.

Because of the taxonomic difficulties, pub-

lished information on *G. aureolum* may refer to that species, different strains of the species, or to closely related different species. We believe, however, that the large size, and the seriousness of the associated detrimental effects, of many of the blooms in Europe, and the possibility of such blooms occurring chronically in northeast U.S. waters, indicate the need for immediate attention on the species and its blooms in this country. We, therefore, have reviewed currently available information to reach some general conclusions, and assume that any possible errors regarding particular identifications, events, *etc.* eventually will be resolved. PARTENSKY *et al.* (1988) and BALECH (1988) believe that both genera and species are likely to be revised within the next few years.

SPECIES DISTRIBUTION AND BLOOM OCCURRENCE

When *G. aureolum* was first described by HULBURT (1957), he discussed the distribution of phytoplankton species on both eastern and western sides of the North Atlantic Ocean. At that time, it apparently had not been found in Europe because he regarded it as a new species, and definitive antecedent description has not emerged. SILVA (1959), however, described an unfamiliar *Gyrodinium* sp. in Portugal, common in the Obidos Lagoon in autumn and early winter, that BRAARUD and HEIMDAL (1970) suspected was likely *G. aureolum*.

The first recorded bloom of *G. aureolum* anywhere, and also the first time the species was reported in European waters, was a huge occurrence in 1966 (BRAARUD and HEIMDAL, 1970) along the Norwegian south and southwest coasts (Figure 2). It currently is the most abundant dinoflagellate in the North Sea, particularly the east and southeast regions, and in coastal waters around Ireland, England, Denmark, Sweden, and Norway (SELIGER and HOLLIGAN, 1985). Elsewhere in Europe, it has been reported in France (LASSUS *et al.*, 1985), Germany (PARTENSKY and SOURNIA, 1986; cautionary identification), and northwest Spain (FRAGA and SANCHEZ, 1985). Its distribution also ranges to the South Atlantic because it has been reported in Brazil (ROSA and BUSELATO, 1981). In the Pacific Ocean, a red tide organism in Japan identified as *Gymnodinium*

nagasakiense is considered by some investigators to be conspecific with *G. aureolum* (TANGEN, 1977; TAYLOR, 1985). PARTENSKY *et al.* (1988) and MATSUOKA *et al.* (1989), however, regard morphological characters alone to be inadequate to resolve this. PARTENSKY *et al.* (1988) found differences between the two, including greater DNA complement in the Japanese taxon, and formation by the European taxon of subpopulations of large and small cells, which cause them to doubt conspecificity.

In the western North Atlantic, the species has been in the New York Bight for more than a decade. It first was identified in the New York Bight in a 1974–1978 phytoplankton survey of the Hudson-Raritan estuary and adjacent New Jersey northern shore waters (OLSEN and COHN, 1979). In 1978 (MARSHALL and COHN, 1981), and 1981 (COHN, unpublished information) surveys of phytoplankton assemblages in the northeast coastal and shelf region, *G. aureolum* was reported at seven nearshore sites in the New York Bight, including three sites within 32 km of shore between Little Egg and Hereford Inlets. CAMPBELL (1973) identified the species in Gales Creek, North Carolina, MARSHALL (1980) reported it in Chesapeake Bay, and HAUGEN (*personal communication*) identified it in Maquoit Bay, Maine. Therefore, assuming that the various identifications were of the same species, the known range of *G. aureolum* in the eastern United States extends from North Carolina to Maine.

Blooms of *G. aureolum* in the Carmans River in Long Island, New York, in 1982 and 1983 persisted for about two months, primarily in July and August of those years; concentrations were as high as 2×10^7 cells 1^{-1} (CHANG and CARPENTER, 1985). Blooms probably of *G. aureolum* were observed on the western south shore of Long Island in the summers of 1983 and 1984 (FREUDENTHAL, *personal communication*). These were more widespread than those in the Carmans River, extending as much as 9.5 km along the coast. Two other blooms we suspect were of *G*. cf. *aureolum* occurred on the New Jersey coast in 1980 and 1982, but these were localized and of short duration. The *G*. cf. *aureolum* blooms in southern New Jersey coastal waters in 1984 and 1985 were considerably larger than the Long Island occurrences (Figure 1).

Figure 2. Map of northwestern Europe with regions indicated where known *G. aureolum* blooms have occurred.

DETRIMENTAL EFFECTS OF *G. aureolum* BLOOMS

The potential threats of *G. aureolum* blooms currently are not clear. An absence of documented poisoning of humans associated with the species suggests that a serious public health problem is unlikely. Standard assays have not detected paralytic shellfish toxin in this species in Europe (BRAARUD and HEIMDAL, 1970; HELM *et al.*, 1974; BOALCH, 1979; OTTWAY *et al.*, 1979). This, however, does not eliminate the possibility that other toxins that can affect humans may be produced by *G. aureolum*. *Gyrodinium aureolum* appears to be closely related to *Gymnodinium flavum, Gymnodinium venefi-*

cum and *Ptychodiscus brevis*, which are all toxic to fish (TAYLOR, 1985). Reports during the last 20 years on the effects of *G. aureolum* blooms on marine animals offer varied conclusions and suggest a complex situation.

Major blooms off Norway in 1966 and 1976 were accompanied by extensive mortalities of fish and shellfish. Norwegian investigators determined that their *G. aureolum* strains were not icthyotoxic and believed that the mortalities likely were due to anoxia from high respiratory consumption of oxygen by the dinoflagellates (TANGEN, 1979). Subsequently, however, workers in Scotland (TURNER *et al.*, 1984) detected ichthyotoxin in cultures from Norway (Oslofjord); the level of toxin produc-

tion in the cultures was mediated by the level of biotin in the growth medium. TURNER et al. (1984) thought this may have important implications regarding the occurrence of toxic or non-toxic blooms of the species. They found that in rainbow trout, *Salmo gairdneri*, exposure to *G. aureolum* grown in high-biotin medium resulted, progressively, in darkening of skin, loss of equilibrium, and death. The gills showed generalized necrosis and sloughing of the epithelium, with hypertrophy and congestion of branchial vessels. Again with a Norwegian culture, ROBERTS et al. (1983) found all five concentrations of *G. aureolum*, ranging from $1-11 \times 10^6$ cells 1^{-1}, to be lethal to 8 cm rainbow trout in 24 hours; gills displayed marked degeneration and necrosis of the lamellar epithelium. The presence of biotoxins has been confirmed in *Gyrodinium* cf. *aureolum* (PARTENSKY and VERBIST, unpublished data, cited in PARTENSKY et al., 1988). The use of inappropriate assays might explain inconsistencies in the detection of toxins associated with *Gyrodinium* (JONES et al., 1983). Assessment of water quality with an oyster embryo bioassay, during and after a late June-early September 1982 bloom in Plymouth Sound, England, showed that water quality was poor during the bloom and did not return to normal until 3-4 weeks after the bloom ended (THAIN and WATTS, 1984).

There have been periodic *G. aureolum* blooms in waters around the United Kingdom and Ireland, many with associated marine fauna kills. Some investigators reported that oxygen depletion had a role in certain of the incidents, but others have provided evidence that the species can produce lethal concentrations of toxin(s). A *G. aureolum* bloom in September and October 1971 was accompanied by mass mortality of lugworm, *Arenicola marina*, and urchin, *Echincardium cordatum*, along the North Wales coast (HELM et al., 1974). HELM et al. concluded that the mortalities were not directly related to the bloom but could have been the consequence of climatic conditions that resulted in an oxygen depletion, possibly aggravated by the bloom. In contrast, investigation of a 1978 bloom along the south coast of England that resulted in mortalities of fish and invertebrates revealed the water to be cytotoxic to blue mussel, *Mytilus edulis* (WIDDOWS et al., 1979). Mussels experimentally exposed to cell concentrations of 1 to 3×10^5 1^{-1} of *G. aureolum* had acute reduction

of clearance rate and marked cellular damage in the gut.

Accidental exposure of pond-reared salmon, *Salmo salar*, to *G. aureolum* bloom water caused a mass mortality in Scotland in 1980 (JONES et al., 1982). Pathology investigations showed that death of the fish resulted from extensive damage to the gills and gut, and mouse bioassays suggested that a necrotizing toxin was present in the *G. aureolum* cells. The first *G. aureolum* bloom in Irish waters, in late July to mid-August 1976, resulted in kills of *Arenicola marina* and other marine life in several areas on the south coast of Ireland (OTTWAY et al., 1979). In Youghal, where the effects were most serious, besides mortalities of lugworm, large numbers of moribund fishes such as plaice, *Pleuronectes platessa*, moved into the shallows. Shellfish, including cockles, *Cerastoderma edule*, also washed ashore. Much of this fish and shellfish was consumed by local people and, perhaps coincidentally, diarrhea was prevalent in the area.

Marine fauna kills associated with *G. aureolum* blooms also occurred on the south and southwest coasts of Ireland in August–September, 1978 (LEAHY, 1980) and September–October 1979 (CROSS and SOUTHGATE, 1980). Oxygen depletion was not considered to be the cause of the mortalities because dissolved oxygen did not fall below saturation levels; the mortalities often occurred along open coastlines with strong mixing, and many species of benthic infauna were not harmed. Extensive mortalities of a wide range of taxa including grazers (chiefly gastropods and echinoids), predators (*Nucella lapillus*, crabs, fish and asteroids), and filter feeders (*Mytilus* spp., *Anomia* spp. and ascidians) resulted from a 1979 bloom in Dunmanus Bay (CROSS and SOUTHGATE, 1980). Individual blooms did not always cause widespread or catastrophic marine fauna kills. SOUTHGATE et al. (1984) observed inconsistent effects of *G. aureolum* blooms in Pointabulloge, Dunmanus Bay, because neither 1978 nor 1980 blooms resulted in detectable mortalities at that site. LEAHY (1981) generally found little damage to littoral animals in Roaringwater Bay associated with the 1978 bloom but, in one area where the bloom was densest, 50% of the limpets (*Patella* sp.) and 80% of the winkles (*Littorina* sp.) were killed in about 5 days.

The species also has been implicated in iso-

lated marine fauna kills elsewhere in Europe and in other regions of the world. LASSUS *et al.* (1985) found an association between a bloom of *G. aureolum* and 75% mortality among cultured mussels in Douarnenez Bay, France in late summer of 1982. An extensive *G. aureolum* bloom was accompanied by mortality of marine fauna on the coast of Rio Grande do Sol, Brazil (ROSA and BUSELATO, 1981). *Gymnodinium nagasakiense*, which TAYLOR (1985) considers synonymous with *G. aureolum*, has caused marine fauna kills in the coastal waters of Korea and Japan (TAKAYAMA and ADACHI, 1984). No fish or invertebrate kills were observed or reported associated with the *G. aureolum* blooms in the Carmans River, New York (CHANG and CARPENTER, 1985).

PHYSIOLOGY AND NUTRITION

Salinity Tolerance

Gyrodinium aureolum is euryhaline. In the seas of northwest Europe, the species blooms in waters having a salinity range of 25-35 0/00 (TANGEN, 1977). CAMPBELL (1973) found it in salinities from 18 to 24 0/00 in Gales Creek, North Carolina. CHANG and CARPENTER (1985) reported *G. aureolum* survival in salinities from 0 to 20 0/00 during 1982–1983 blooms in the Carmans River, New York; cell concentrations were lower in waters having salinities in the extremes of this range but otherwise were comparable.

Temperature Tolerance

The species tolerates a wide range of temperatures, 6-20° C, in European waters (HOLLIGAN, 1985). During a bloom in southwest Ireland, the *G. aureolum* population concentrated in higher temperature water (above 13° C) and apparently avoided water colder than 11° C (RODEN *et al.*, 1981). Carmans River, New York blooms began at a "critical" temperature level of about 24-27° C, persisted to 30° C (the highest water temperature measured), and terminated when the temperature declined to 19-22° C (CHANG and CARPENTER, 1985).

Light Requirements

Gyrodinium aureolum can grow well in low light and is particularly well suited to exploit dynamic light environments, which are typical in ocean front regions (RICHARDSON and KULLENBERG, 1984). In high, non-saturating light regimes, photosynthesis per cell was higher when pretest acclimation was in low rather than high light. Light saturation occurred at approximately the same level (around 200 uE m^{-2} s^{-1}), however, for both low and high light acclimated cells. Therefore, low-light adapted *G. aureolum* has the unusual capability to utilize low light efficiently while retaining its ability to photosynthesize maximally if the level of available light becomes high. *G. aureolum* was not photoinhibited by high light intensities (to 500 uE m^{-2} s^{-1}), and its light saturation level is higher than that of many other dinoflagellates.

Growth Characteristics

In the July–August 1983 bloom in the Carmans River, New York (water temperature 24.5-27.0° C, initially), *G. aureolum* rate of cell division peaked just after sunrise. In the beginning of the bloom, it also had a second peak at midnight. The growth rate was 1.3 (divisions per day) at first, decreased to 0.57 at mid-bloom and, was 0.4 when the bloom began to decline (CHANG and CARPENTER, 1985). Mean growth rate over a three week incubation in 1 m diameter *in situ* plastic tubes in the Rosfjord, southern Norway (water temperature 13-15° C) was 0.27 division per day (DAHL and BROCKMAN, 1985). In laboratory cultures the growth rate was approximately 0.25 division per day; unlike other dinoflagellate species, *G. aureolum* can survive for several months in stationary phase of culture growth (PARTENSKY and SOURNIA, 1986).

Nutrition

The natural distribution of *G. aureolum* suggests that it prefers an an environment where nitrate or ammonium, or both, are available in the daytime, and its blooms have initiated primarily in areas where nitrate is adequate in the upper water layers (PAASCHE *et al.*, 1984). In laboratory studies, nitrate was not taken up in the dark unless the cells were N-starved; ammonium was taken up in the dark but only at approximately one-fifth of the rate in the light. Uptake of nitrate was coupled with pho-

tosynthetic carbon assimilation and, apparently, even very low light intensities are sufficient for the nitrogen uptake necessary for this species (PAASCHE *et al.*, 1984). Nitrate uptake by *G. aureolum* in large *in situ* enclosures was highest in the daytime, and ammonium was assimilated faster than nitrate (BROCKMAN *et al.*, 1985). Nutrient supply appears to be very critical for the species because nutrient depletion for four days caused a reduction in cell numbers, not reversible by subsequent nutrient addition. *Gyrodinium* cf. *aureolum* can grow in medium F/2 (GUILLARD and RYTHER, 1962), which is prepared from natural sea water supplemented with nutrients, chelated metals mix and vitamins (PARTENSKY and SOURNIA, 1986). Addition of earth extract to this medium, however, or utilization of Erdschreiber medium (GROSS, 1937), which contains earth extract, resulted in increased culture yield. There currently is no evidence that *G. aureolum* has the ability to utilize organic nitrogen and phosphorus, which could provide the species an advantage in nutrient-deficient environments (PARTENSKY and SOURNIA, 1986).

G. aureolum BLOOM DEVELOPMENT

PARTENSKY and SOURNIA (1986) outlined certain common features of the *G. aureolum* blooms in Europe. The blooms most often appeared after a period of calm and warm weather sufficient to result in a well established thermocline. In certain instances, this ensued after wind-induced vertical mixing of the water column. Low turbulence appears, therefore, to be a determining factor, although dense populations of *G. aureolum* may sometimes persist for a substantial period in turbulent waters. *G. aureolum* generally develops after the spring diatom blooms in environments that are relatively impoverished so that nutrient replenishment is a prerequisite. Vertical and horizontal concentration factors can be important because multiplication of the population often is insufficient to explain the observed very rapid increase in cell concentration in the bloom waters. The occurrence of a bloom in the coastal zone generally appears to be due to the transport of an offshore population shoreward to the vicinity of a front or other hydrologic discontinuity, and subsequent concentration. Bloom decline, in the majority of

cases, is due to hydrologic and/or meteorological changes: wind, temperature decline, disappearance of the thermocline.

Various modes of *G. aureolum* bloom development have been observed or postulated for the outbreaks of this species in areas on both sides of the Atlantic. These include growth of an *in situ* population in an estuarine habitat with ample ambient nutrients; growth of an *in situ* population in coastal waters, previously nutrient enriched by upwelling; transport of the bloom inoculum from elsewhere with subsequent development and landward transport; and growth of a subsurface population which eventually extends to the surface.

BRAARUD and HEIMDAL (1970) attributed the 1966 *G. aureolum* bloom in Norwegian coastal waters to wind-driven upwelling that transported nutrient-rich deep water to the surface. With the consequent breakdown of stratification, *G. aureolum*, being a motile phototactic species, had an advantage over diatoms in counteracting vertical transport to below the euphotic zone. Later, heavy rainfall and land drainage reduced the salinity of surface layers, which restored stratification, and the bloom proceeded in these waters. Essentially the same hydrological situation promoted a similar bloom in 1976 (TANGEN, 1977).

An explanation proposed by LINDAHL (1983) for 1982–1983 blooms of the species in the Skagerrak (an arm of the North Sea) and along the Swedish and Norwegian coasts (Figure 2) is that the bulk of the algae grew offshore and ultimately concentrated in the salinity front along the coast. Lindahl found an association between the 1982 occurrence of *G. aureolum* and high salinity surface water along the Swedish coast and concluded that the 1982 bloom populations originated offshore and were brought into the Skagerrak by the Jutland current. Once in the Skagerrak they were transported landward by wind-induced currents. During the autumn of 1983, the main part of the *G. aureolum* population first was found along the front between offshore (Skagerrak) water and low salinity Baltic current water and, as in 1982, later was transported landward, entrained in a wind-driven surface current (LINDAHL, 1984).

In the western English Channel (Figure 2), *G. aureolum* first becomes abundant in the early summer as a component of a subsurface mixed

dinoflagellate assemblage (HOLLIGAN, 1985). This subsurface population primarily develops at a tidal front, within a shallow thermocline between a well-illuminated, nutrient-deficient surface layer and a poorly-illuminated, nutrient-rich bottom layer. G. aureolum continues to increase during the mid and later summer, eventually extends to the surface, and can comprise > 90% of the phytoplankton biomass. The timing and degree of development of the bloom phase is variable from year to year. Development generally takes about one month, and the bloom may persist for another month. Other phytoplankton species are found at densities comparable with those under non-bloom conditions, so there is no evidence for competitive exclusion by G. aureolum. According to Holligan, frontal convergences, Langmuir circulation and internal waves are important in defining patchiness within the bloom area.

During a G. aureolum bloom in Norway in 1976, TANGEN (1977) observed that in Ardalsfjorden, the cells concentrated at the surface in daytime in a layer which varied from 10 cm to a few meters in thickness, most often 1 m thick; bloom patches were about 100 m wide. In calm weather there was a 10-20 cm layer of clear water over the bloom patches. Tangen hypothesized lessened vertical stratification of the bloom during the night. HICKEL et al. (1971) observed nighttime bloom population maxima in the Helgoland Bight at around 6 m.

In an August–September 1978 G. aureolum bloom off the south coast of Ireland, concentrations of nitrate, nitrite and ammonium were all low, sometimes below detection limits, when the bloom was intense, but they increased greatly as the bloom declined (PYBUS, 1980). Phosphorus concentrations also increased but not dramatically so. No overall pattern of change in concentration of silicate, organic nitrogen and organic phosphorus was apparent. Pybus concluded that nitrate was likely the nutrient which limited development of the bloom. Silicate levels suggested lack of utilization, as might be expected in a dinoflagellate bloom. Nitrogen also may have limited a bloom on the Swedish west coast in 1982 (LINDAHL, 1983). DAHL et al. (1984) examined the role of nitrogen from precipitation and runoff in the development of a 1981 G. aureolum bloom along the southern coast of Norway; these sources supplied just 6-15% of the nitrogen that sup-

ported the bloom. The authors concluded, therefore, that most of the nitrogen came from the sea, probably from upwelling, and this possibly was supplemented by nitrogen obtained during diel vertical migration of the dinoflagellates.

Blooms in 1982 and 1983 in the nitrogen-rich Carmans River, New York (CHANG and CARPENTER, 1985), were very localized. The visible part of the bloom was only about 1 km long, although the species was distributed throughout the estuary. Bloom patches moved up and down river with the tidal current but never extended beyond the river mouth. Temperature was a major factor controlling the bloom (as outlined earlier). The G. aureolum population initially developed within one to two weeks, persisted at a level of about 10^7 cells l^{-1} for about two months and then declined rapidly in late summer. Late summer decrease in temperature and light lowered the growth rate below that needed to sustain the population. These blooms are considered never to have been nutrient limited.

DISCUSSION

In summary, G. aureolum is a versatile species that has flourished in a variety of habitats. Its distribution in the seas of northern Europe suggests that the species is essentially neritic but its consistent presence in waters well away from the coast indicates that this dinoflagellate is also capable of surviving in a purely oceanic ecosystem (PARTENSKY and SOURNIA, 1986). It seems to be particularly adapted to growth along ocean fronts (RICHARDSON and KULLENBERG, 1984). Various attributes contribute to its success. It is euryhaline (TANGEN, 1977) and eurythermal (HOLLIGAN, 1985). It can survive with little light and can efficiently exploit dynamic light conditions (RICHARDSON and KULLENBERG, 1984). The species seems to be vigorously phototactic (BRAARUD and HEIMDAL, 1970; TANGEN, 1977), which provides potential for it to position itself in favorable light. It thrives in environments where nitrate or ammonium or both are available in the daytime (PAASCHE et al., 1984); some of the blooms apparently have been nitrogen limited (PYBUS, 1980; LINDAHL, 1983). Additional information on G. aureolum nutrition, as it is developed, will likely provide further explanation of why it is so successful.

Mean growth rate when nutrient supply, light, and temperature are favorable is high compared to that of other net phytoplankton, in general, but is comparable to growth rates in similar species.

Its structural fragility is in contrast to all the apparently advantageous attributes the species has. Calm habitats are more suitable than turbulent waters. Although *G. aureolum* flourishes in a diversity of habitats, bloom development in offshore waters is more common than initial development in estuarine or coastal waters. Available evidence (HOLLIGAN, 1985) suggests that the apparent toxicity of *G. aureolum* may not provide it a competitive advantage because, in the English Channel blooms, it was superimposed on but did not replace the usual phytoplankton assemblage.

A complete explanation is not available, as yet, for the transition of *G. aureolum* from being a newly identified species in 1957 to currently being the most important dinoflagellate in the eastern North Atlantic. Explanation, likewise, is not on hand for the recent occurrence of its blooms elsewhere in the world, such as the northeast U.S., in recent years. Its sudden world-wide importance raises some fundamental questions. If the species had been endemic, but so scarce that it escaped notice, then what promoted its current success? And if it previously had had limited distribution, then what enabled it to rapidly migrate around the world?

The increased incidence of *G. aureolum* in the northeast U.S. may have its basis in both far reaching and local influences. This is suggested by the first two blooms in Norwegian coastal waters. Major regional change in water quality might have favored a native *G. aureolum* population. Alternatively, an immigrant population transported cross-ocean might have been favored by changed or unchanged North Sea water quality and/or transported in cross-ocean. This permitted the first bloom in 1966 and subsequent rapid spread of *G. aureolum* throughout the North Sea. The next bloom in Norway, however, did not occur until 1976. The ten year gap between these blooms is not fully understood but it is known that essentially the same local hydrological situation promoted both events.

The close taxonomic relationship of *G. aureolum* to well documented ichthyotoxic species,

including Florida's *Ptychodiscus brevis* (former appellation, *Gymnodinium breve*) (TAYLOR, 1985), as well as an accumulation of observational and experimental evidence from Europe indicating such toxicity, suggests that this aspect should be examined whenever it blooms. In the New York Bight, *G. aureolum* blooms in the Carmans River (CHANG and CARPENTER, 1985) did not cause marine fauna kills, but there were reports of kills of crabs and mussels coincident with the blooms in New Jersey. Mortality of marine fauna was reported associated with the *G.* cf. *aureolum* bloom in Maine in 1987 (HAUGEN, *personal communication*). If the New Jersey and Maine blooms and observed mortalities were associated, the inconsistency with the Long Island blooms is not surprising because European workers find varied toxicity. The apparent relationship between biotin level in the sea water (TURNER *et al.*, 1984) and toxicity of *G. aureolum* blooms is an important area of inquiry.

ACKNOWLEDGEMENTS

LITERATURE CITED

BALECH, E., 1988. *Los Dinoflagelados del Atlantico Sudoccidental.* Publicaciones Especiales No. 1. Instituto Espanol de Oceanographia. Madrid, 310p.

BRAARUD, T. and HEIMDAL, B. R., 1970. Brown water on the Norwegian coast in autumn 1966. *Nytt Magasin Botanikk*, 17, 91–97.

BROCKMAN, U.H.; DAHL, E., and EBERLEIN, K., 1985. Nutrient dynamics during a *Gyrodinium aureolum* bloom. *In:* D.M. ANDERSON; A.W. WHITE and D.G. BADEN (eds.), *Toxic Dinoflagellates, Proceedings of Third International Conference on Toxic Dinoflagellates*, New York, NY: Elsevier, pp. 239–244.

BUMPUS, D.F., 1969. Reversals in the surface drift

in the Middle Atlantic Bight area. *Deep Sea Research*, 16 (suppl.), 17–23.

CAMPBELL, P.H., 1973. *Studies on Brackish Water Phytoplankton. University of North Carolina Sea Grant Publication 73–07*, 403p.

CHANG, J. and CARPENTER, E.J., 1985. Blooms of the dinoflagellate *Gyrodinium aureolum* in a Long Island estuary: box model of bloom maintenance. *Marine Biology*, 89, 83–93.

CROSS, T.F. and SOUTHGATE, T., 1980. Mortalities of fauna of rocky substrates in south-west Ireland associated with the occurrence of *Gyrodinium aureolum* blooms during autumn 1979. *Journal of the Marine Biological Association of the United Kingdom*, 60, 1071–1073.

DAHL, E.; DANIELSSEN, D.S.; SEMB, A., and TANGEN, K., 1984. Precipitation and run-off as a fertilizer to a *Gyrodinium aureolum* Hulburt bloom. *ICES B7. Special Meeting on the Causes, Dynamics and Effects of Exceptional Marine Blooms and Related Events*, 20p.

DAHL, E. and BROCKMAN, U.H., 1985. The growth of *Gyrodinium aureolum* Hulburt in *in situ* experimental bags. *In*: D.M. ANDERSON; A.W. WHITE and D.G. BADEN (eds.), *Toxic Dinoflagellates, Proceedings of Third International Conference on Toxic Dinoflagellates*, New York, NY: Elsevier, pp. 233–238.

FIGLEY, W., 1979. Biochemical monitoring of New Jersey's nearshore ocean waters: June 1977 to June 1978. *New Jersey Technical Report No. 42M*. N.J. Department of Environmental Protection, Nacote Creek Research Station, Nacote Creek, N.J., 171p.

FRAGA, S. and SANCHEZ, F.J., 1985. Toxic and potentially toxic dinoflagellates found in Galacian Rias (NW Spain). In: D.M. ANDERSON; A.W. WHITE and D.G. BADEN (eds.), *Toxic Dinoflagellates, Proceedings of Third International Conference on Toxic Dinoflagellates*, New York, NY: Elsevier, pp. 51–54.

GROSS, F., 1937. Notes on the culture of some marine plankton organisms. *Journal of the Marine Biological Association of the United Kingdom*, 21, 753–768.

GUILLARD, R.R.L. and RYTHER, J.H., 1962. Studies of marine planktonic diatoms. 1. *Cyclotella nana* (Hustedt) and *Detonula confervacea* (Cleve). *Canadian Journal of Microbiology*, 8, 229–239.

HELM, M.M.; HEPPER, B.T.; SPENCER, B.E., and WALNE, P.R., 1974. Lugworm mortalities and a bloom of *Gyrodinium aureolum* Hulburt in the eastern Irish Sea, autumn 1971. *Journal of the Marine Biological Association of the United Kingdom*, 54, 857–869.

HICKEL, W.; HAGMEIER, E. and DREBES, G., 1971. *Gymnodinium* blooms in the Helgoland Bight (North Sea) during August, 1968. *Helgolander Wissenschaftliche Meeresuntersuchungen*, 22, 401–416.

HOLLIGAN, P.M., 1985. Marine dinoflagellate blooms—growth strategies and environmental exploitation. *In*: D.M. ANDERSON; A.W. WHITE and D.G. BADEN (eds.), *Toxic Dinoflagellates, Proceedings of Third International Conference on Toxic*

Dinoflagellates, New York, NY: Elsevier, pp. 133–139.

HULBURT, E.M., 1957. The taxonomy of unarmored dinophyceae of shallow embayments on Cape Cod, Massachusetts. *Biological Bulletin*, 112, 196–219.

JONES, K.J.; AYERS, P.; BULLOCK, A.M.; ROBERTS, R.J., and TETT, P., 1982. A red tide of *Gyrodinium aureolum* in sea lochs of the Firth of Clyde and associated mortality of pond-reared salmon. *Journal of the Marine Biological Association of the United Kingdom*, 62, 771–782.

KIMBALL, JR., J.F. and FERGUSON WOOD, E.J., 1965. A dinoflagellate with characters of *Gymnodinium* and *Gyrodinium*. *Journal of Protozoology*, 12, 577–580.

LASSUS, P.; BARDOUIL, M.; TRUQUET, I; TRUQUET, P.; LEBAUT, C., and PIERRE, M.J., 1985. *Dinophysis acuminata* distribution and toxicity along the southern Brittany coast (France): correlation with hydrological parameters. *In*: D.M. ANDERSON; A.W. WHITE and D.G. BADEN (Eds.), *Toxic Dinoflagellates, Proceedings of Third International Conference on Toxic Dinoflagellates*, New York, NY: Elsevier, pp. 159–164.

LEAHY, P., 1980. The effects of a dinoflagellate bloom in 1978 on the invertebrate fauna of the sea shore in Dunmanus Bay, Co. Cork, Ireland. *Journal of Sherkin Island*, 1, 119–125.

LEAHY, P., 1981. The effect of the red tide on shore invertebrates in Roaringwater Bay, Summer 1978, *In*: PARKER, M. (ed.), *Red Tides*. Fisheries Seminar Ser. No. 1. Dublin, p. 12.

LINDAHL, O., 1983. On the development of a *Gyrodinium aureolum* occurrence on the Swedish west coast in 1982. *Marine Biology*, 77, 143–150.

LINDAHL, O., 1984. The connection between the occurrence of *G. aureolum* and water of high salinity. *ICES A5. Special Meeting on the Causes, Dynamics and Effects of Exceptional Marine Blooms and Related Events*, 6p.

MAHONEY, J.B. and McLAUGHLIN, J.J.A., 1977. The association of phytoflagellate blooms in Lower New York Bay with hypertrophication. *Journal of Experimental Marine Biology and Ecology*, 28, 53–65.

MAHONEY, J.B. and STEIMLE, JR., F.W. 1979. A mass mortality of marine animals associated with a bloom of *Ceratium tripos* in the New York Bight. *In*: D.L. TAYLOR and H.H. SELIGER (eds.), *Toxic Dinoflagellate Blooms*, New York, NY: Elsevier, pp. 225–230.

MARSHALL, H.G., 1980. Seasonal phytoplankton composition in the lower Chesapeake Bay and Old Plantation Creek, Cape Charles, Virginia. *Estuaries*, 3, 207–216.

MARSHALL, H.G. and COHN, S., 1981. Phytoplankton community structure in northeastern coastal waters of the United States. *NOAA Technical Memorandum NMFS-F/NEC-8*, Woods Hole, MA, 57p.

MATSUOKA, K.; ITZUKA, S.; TAKAYAMA, H.; HONJO, T., FUKUYO, Y., and ISHIMARU, T. 1989. Geographic distribution of *Gymnodinium nagasakinese* Takayama et Adachi around west Japan. *In*: T. OKAICHI; D.M. ANDERSON and T. NEMOTO

(eds.), *Red Tides: Biology, Environmental Science and Technology*. New York, NY: Elsevier, pp. 101–104.

OGREN, L. and CHESS, J., 1969. A marine kill on New Jersey wrecks. *Underwater Naturalist*, 6, 4–12.

OLSEN, P. and COHN, M.S., 1979. Phytoplankton in Lower New York Bay and adjacent New Jersey estuarine and coastal areas. *Bulletin of the New Jersey Academy of Sciences*, 24, 59–70.

OTTWAY, B.; PARKER, M.; McGRATH, D. and CROWLEY, M., 1979. Observations on a bloom of *Gyrodinium aureolum* Hulburt on the south coast of Ireland, summer of 1976, associated with mortalities of littoral and sublittoral organisms. *Irish Fisheries Investigations*, Ser. B. No. 18, 9p.

PAASCHE, E.; BRYCESON, I., and TANGEN, K., 1984. Interspecific variation in dark nitrogen uptake by dinoflagellates. *Journal of Phycology*, 20, 394–401.

PARTENSKY, F. and SOURNIA, A., 1986. Le dinoflagelle *Gyrodinium* cf. *aureolum* dans le plancton de l'Atlantic Nord: identification, ecologie, toxicite. *Cryptogamie Algologie*, 7, 251–275.

PARTENSKY, F.; VAULOT, D.; COUTE, A., and SOURNIA, A., 1988. Morphological and nuclear analysis of the bloom-forming dinoflagellates *Gyrodinium* cf. *aureolum* and *Gymnodinium nagasakiense*. *Journal of Phycology*. 24, 408–415.

POTTS, G.W., and EDWARDS, J.M., 1987. The impact of a *Gyrodinium aureolum* bloom on inshore young fish populations. *Journal of the Marine Biological Association of the United Kingdom* 67, 293–297.

PYBUS, C., 1980, Observations on a *Gyrodinium aureolum* (Dinophyta) bloom off the south coast of Ireland. *Journal of the Marine Biological Association of the United Kingdom*, 60, 661–674.

RICHARDSON, K. and KULLENBERG, G. 1984., Physical and biological interactions leading to plankton blooms: A review of *Gyrodinium aureolum* blooms in Scandinavian waters. *ICES A2. Special Meeting on the Causes, Dynamics and Effects of Exceptional Marine Blooms and Related Events*, 13p.

ROBERTS, R.J.; BULLOCK, A.M.; TURNER, M.; JONES, K., and TETT, P., 1983. Mortalities of *Salmo gairdneri* exposed to cultures of *Gyrodinium auroleum*. *Journal of the Marine Biological Association of the United Kingdom*, 63, 741–743.

RODEN, C.M.; LENNON, H.J.; MOONEY, E.; LEAHY, P. AND LART, W., 1981. Red tides, water stratification and phytoplankton species succession around Sherkin Island, southwest Ireland, in 1979. *Journal of Sherkin Island*, 1, 105–118.

ROSA, Z.M. and BUSELATO, T.C., 1981. Sobre ocorencia de floracao de *Gyrodinium aureolum* Hulburt (Dinophyceae) no litoral sul do Estado do Rio Grande do Sul, Brazil. *Iheringia*, 28, 169–179.

SELIGER, H.H. and HOLLIGAN, P.M., 1985. Sampling criteria in natural phytoplankton populations. In: D.M. ANDERSON; A.W. WHITE and D.G. BADEN, (eds.), *Toxic Dinoflagellates, Proceedings of Third International Conference on Toxic Dinoflagellates*, New York, NY: Elsevier, pp. 540–544.

SILVA, E.S., 1959. Some observations on marine dinoflagellate cultures. I. *Prorocentrum micans* Ehr. and *Gyrodinium* sp. *Notas Estudos Instituto Biologia Maritima*, 21, 1–15.

SWANSON, R.L. and SINDERMANN, C.J. (eds.), 1979. Oxygen depletion and associated benthic mortalities in New York Bight, 1976. *NOAA Professional Paper 11*. Rockville, MD 345p.

SOUTHGATE, T.; WILSON, K.; CROSS, T.F., and MYERS, A.A., 1984. Recolonization of a rocky shore in S.W. Ireland following a toxic bloom of the dinoflagellate, *Gyrodinium aureolum*. *Journal of the Marine Biological Association of the United Kingdom*, 64, 485–492.

TAKAYAMA, H. and ADACHI, R., 1984. *Gymnodinium nagasakiense* sp. nov., a red-tide forming dinophyte in the adjacent waters of Japan. *Bulletin Plankton Society of Japan*, 31, 7–14.

TANGEN, K., 1977. Blooms of *Gyrodinium aureolum* (Dinophyceae) in north European waters, accompanied by mortality in marine organisms. *Sarsia*, 63, 123–133.

TANGEN, K., 1979. Dinoflagellate blooms in Norwegian waters. In: D.M. ANDERSON; A.W. WHITE, and D.G. BADEN (eds.), *Toxic Dinoflagellates, Proceedings of Third International Conference on Toxic Dinoflagellates*, New York, NY: Elsevier, pp. 179–182.

TANGEN, K. and BJORNLAND, T., 1981. Observations on pigment and morphology of *Gyrodinium aureolum* Hulburt, a marine dinoflagellate containing 19'-hexanoylofucoxanthin was a main carotenoid. *Journal of Plankton Research*, 3, 389–401.

TAYLOR, F.J.R., 1985. The taxonomy and relationships of red tide flagellates. In: D.M. ANDERSON; A.W. WHITE and D.G. BADEN (eds.), *Toxic Dinoflagellates, Proceedings of Third International Conference on Toxic Dinoflagellates*, New York, NY: Elsevier, pp. 11–26.

THAIN, J.E. and WATTS, J., 1984. The use of a bioassay to measure changes in water quality associated with a bloom of *Gyrodinium aureolum* (Hulburt). *ICES D3. Special Meeting on the Causes, Dynamics and Effects of Exceptional Marine Blooms and Related Events*, 14p.

TURNER, M.F.; BULLOCK, A.M.; TETT, P., and ROBERTS, R.J., 1984. Toxicity of *Gyrodinium aureolum*: some initial findings. *ICES D11. Special Meeting on the Causes, Dynamics and Effects of Exceptional Marine Blooms and Related Events*, 15p.

U.S. ENVIRONMENTAL PROTECTION AGENCY, 1985. *New York Bight Water Quality Summer of 1985*. United States Environmental Protection Agency Region II—Surveillance and Monitoring Branch. Edison, NJ 08837, 112 p.

U.S. ENVIRONMENTAL PROTECTION AGENCY, 1986. *An Environmental Inventory of The New Jersey Coast/New York Bight Relevent to Green Tide Occurrence*. Prepared by Science Applications International Corp. for U.S. Environmental Protection Agency, Region II, 26 Federal Plaza, New York, New York 10278, 156p.

U.S. ENVIRONMENTAL PROTECTION AGENCY,

1987. *Green Tide Monitoring Survey for 1986—Results.* Prepared by Science Applications International Corp. for U.S. Environmental Protection Agency, Region II, 26 Federal Plaza, New York, NY 10278, 156p.

WIDDOWS, J.; MOORE, M.N.; LOWE, D.M. and SALKELD, P.N., 1979. Some effects of a dinoflagellate bloom *(Gyrodinium aureolum)* on the mussel, *Mytilus edulis. Journal of the Marine Biological Association of the United Kingdom*, 59, 522–524.

□ RESUMEN □

Un dinoflagelado que hemos identificado como *Gyrodinium* cf. *aureolum* Hulburt se ha desarrollado extensiva y persistentemente en las costas del Sur de New Jersey en los veranos de 1984 y 1985.

Este articulo documenta los sucesos de New Jersey y revisa las ocurrencias y efectos de otros floricimientos de especies en otras partes del mundo. El caso de New Jersey fue el primero informado en las aguas neriticas de USA. Una consecuencia indudable de estos incidentes fue la disminución de la calidad estética de las aguas costeras. Coincidiendo con ambos florecimientos, se registraron ligeras indisposiciones en los usuarios humanos y la muerte del mejillón azul, Mytilus edulis, y del cangrejo Ovalipes Ocellatus, aunque no se ha establecido una asociación directa entre ambos sucesos. La progresión de las especies no se considera una amenaza importante en USA aunque han florecido al menos cinco veces en la región Nordeste entre 1982 y 1988. En Europa, sin embargo, han florecido en aguas de estuarios, neriticas y oceánicas, desde 1966 y han causado numerosas mortalidades masivas de la fauna marina. La excepcional versatilidad biológica ofrece una posible explicación de su éxito en distintos ambientes. El Girodynium aureolum es eurihalino, euritermal y puede utilizar eficientemente tanto regimenes luminosos altos como bajos. Aparentemente es fototácico, es decir, tiene la capacidad de poder situarse en los niveles de luz favorables. Las principales preguntas, como con el cómo G. aureolum ha cambiado a partir de especies recientemente identificadas para convertirse a la fauna marina, están todavia sin responder.—*Department of Water Sciences, University of Cantabria, Santander, Spain.*

□ ZUSAMMENFASSUNG □

Eine dinoflagellate, die wir als *Gyrodinium* cf. *aureolum* (Hulburt) identifizierten, breitete such in den Küstengewässern des südlichen New Jersey weitflächig und dauerhaft in den Sommern von 1984 und 1985 aus. Dieser Artikel dokumentiert das Ereignis in New Jersey und gibt einen Überblick über das Auftreten und die Auswirkungen der Blüten dieser Algenart in anderen Teilen der Welt. Die Blüten in New Jersey waren die ersten der gennanten Dinoflagellate, über die aus den neritischen Gewässern der USA berichtet wurde. Eine direkte Konsequenz dieser Ereignisse was die deutlich verminderte äesthetische Qualität der Küstengewässer. Leichtere Krankheiten bei Menschen und das Abtöten von Miesmuscheln *(Mytilus edulis)* und Krabben *(Ovalipes ocellatus)* ereigneten sich gleichzeitig mit den beiden Algenblüten, aber ein direkter Zusammenhang konnte nicht beweisen werden. In den USA wird gegenwärtig diese Art nicht als eine wesentliche Bedrohung angesehen, obwohl sie zwischen 1982 und 1986 mindes tens fünfal in der nordöstlichen Region blühte. Allerdings breitete sie sich in Europa seit 1966 in ästuarinen, neritischen und ozeanischen Gewässern stark aus und führte dort zum Massenterben zahlreicher marine r Faunen. Die außergewöhnliche physiologische Vielseitigkeit bietet eine Erklärung für ihre erfolgreiche Vermehrung in unterschiedlichen Lebensräumen. *Gyrodinium aureolum* ist euryhalin, eurythermal und kann sich gut sowohl an hole als auch an niedrige Lichtverhältnisse anpassen. Offenbar ist diese Art stark phototakisch, so daβ sie die Fähi gkleit besitzt, sich selbst in vorteilhaften Lichtniveaus zu plazieren. Wichtige Fragen, etwa wieso *G. aureolum* in 30 Jahren von einer neu identifizierten Spezies zu groβer Bedeutung kommen konnte und wie sie nachteilig die marine Fauna beeinfluβt, sind noch unbeantwortet.—*Helmut Brückner, Geographisches Institut, Universität Düsseldorf, F.R.G.*

□ RÉSUMÉ □

Un dinoflagellé que nous avons identifié comme *Gymnodinium* cf. *aureolum* Hulburt a présenté des efflorescences importantes et persistentes dans les eaux côtières du sud du New Jersey durant les étés 1984 et 1985. Ce papier rapporte ces évènements et recense l'apparition et les effets des efflorescences de cette espèce dans le monde. Les efflorescences du New Jersey sont les premières de cette espèces concernant les eaux néritiques des Etats-Unis. Une conséquence certaine de ces évènements fut de diminuer de beaucoup la qualité esthétique des eaux. Des intoxications modérées des personnes, des mortalités de la moule bleue *Mytilus edulis* et du crabe *Ovalipes ocellatus*, ont coincidé avec la présence des deux efflorescences mais aucune association directe n'a été établie. L'éspèce n'est pas habituellement considérée comme une grande menace aux Etats-Unis, bien que au moins cinq efflorescences aient été observées dans la region nord-est entre 1982 et 1988. En Europe, au contraire, elle est apparue dans les eaux estuariennes, côtières et océaniques depuis 1966 et a causé de nombreuses mortalités massives de la faune marine. Une souplesse physiologique exceptionelle offre une explication possible de son succès dans des environments variés. *Gyrodinium aureolum* est euryhaline, eurytherme et peut utiliser efficacement tant les forts régimes lumineux que les faibles. Elle semble être fortement phototactique, ce qui lui permet de se situer aux niveaux lumineux favorables. Des questions importantes restent posées, et en particulier la façon dont *Gyrodinium aureolum* est passée en trent ans du statut d'espèce nouvellement identifié à celui d'espècede grande importance, et comment elle nuit à la faune marine.—*Bruno Delesale, École Practique des Hautes Études, Lab. Biologie Marine et Malacologie, Centre Biologie Ecologie Trop. et Med., Université de Perpignan, Avenue de Villeneuve, 66025 Perpignan, France.*