The frontal systems in the Iroise Sea: Development of Gyrodinium aureolum Hulburt on the inner front

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SUMMARY: Gyrodinium aureolum has been found responsible for a number of red tide outbreaks in northwest European shelf seas over the past decade, sometimes with adverse consequences on the ecosystem. The abundance of this species was followed up over several months in 1983 in the Bay of Douarnenez, from data obtained on a series of twelve cruises carried out from March 1983 to February 1984 and intended in the first place for the study of the influence of the Iroise coastal front on plankton production. High densities of Gyrodinium aureolum build up slowly: a three-month delay is observed from the appearance of the first cells in the Bay to the time when the abundance of the species reaches red tide concentrations. Different processes appear to have contributed to the generation of a red tide: Advection of low-salinity water into the Bay from the alongshore drift on the south coast of Brittany resulted in early stabilization of the water column and possibly introduced the species. Conditions favouring the dinoflagellate also persisted for several months, as thermal stratification (strong sunlight, no wind) replaced in June the spring haline stratification. The species could finally have benefited from intense regeneration which is shown to have taken place in the water mass below the thermocline.

Key words: Gyrodinium, fronts, dinoflagellates, red tides.

INTRODUCTION

In the recent years, the dinoflagellate Gyrodinium aureolum Hulburt has been responsible for a number of red water phenomena observed in the coastal waters of north-western Europe. Originally described from the east coast of the United States (HULBURT, 1957), this species was recorded for the first time in the European waters, when it was the causative organism for the intense red water phenomenon in the Norwegian coastal waters (BRAAARUD & HEIMDAL, 1970). Since then, numerous instances of Gyrodinium aureolum blooms have been recorded in European waters: in Norway (TANGEN, 1977; DAHL et al., 1982), in Sweden (LINDHALL, 1983), around British Isles (BALLANTINE & SMITH, 1973; HELM et al., 1974; OTTWAY et al., 1979; BOALCH, 1979; PYBUS, 1980), and along the French coast (GRALL, 1977; LASSUS, 1984). Gyrodinium aureolum blooms have often been accompanied by a mortality of pelagic or benthic organisms (TANGEN, 1977; FOSTER, 1979; GRIFFITHS et al., 1979; DAHL et al., 1982), as a result either of a toxin elaborated by the dinoflagellate (WIDDOWS et al., 1979; DAHL et al., 1982) or, more probably, of an oxygen deficit in the water column (TANGEN, 1977). On different occasions, G. aureolum has also been found to be abundant further offshore, in the vicinity of the thermal fronts which appear towards the end of spring in Celtic Sea and the Western English Channel (PINGREE et al., 1975, 1977; HOLLIGAN, 1979). According to PARKER et al. (1982), blooms of G. aureolum would develop first in the offshore waters. The frontal structures might then, play a crucial role in bringing them to the more coastal waters (AYRES et al., 1982).

In spite of the different observations cited above, conditions leading to development of Gyrodinium aureolum to the bloom stage are still poorly known: we neither know in detail the different sequences of the phenomenon, nor precisely the conditions prevailing at the moment of the initiation of the bloom.
itself. Most of the data available on the bloom situations are limited rather to the ultimate stages of the phenomenon, when the bloom becomes visible. This paucity of data on the initial stages of the bloom is because of the impossibility of predicting its incidence in space and time, and thus be able to monitor the entire sequence from initiation to the final stage of the phenomenon. During our studies on the hydrological, chemical and biological cycles in the Bay of Douarnenez (Fig. 1) between March 1983 and February 1984, we came across a G. aureolum bloom in the summer of 1983. Though originally our objective was to study the primary production of this Bay in relation to the seasonal establishment of the Iroise Inner Front, the fact we began our sampling much before the bloom, and continued, well thereafter, provides an opportunity to examine the different stages of the bloom in relation to physical, chemical and biological features, and forms the basis of this paper.

MATERIAL AND METHODS

Study site

Sampling was carried out at monthly intervals at five stations located in the Bay of Douarnenez and the adjacent sectors (Fig. 1). In July, when there was the Gyrodinium aureolum bloom, one additional series of sampling was done, and the areal coverage was extended to several more points within the Bay. However, the results presented here are only from the station D, selected as representative of the Bay of Douarnenez. Whilst the exception of some sites much nearer the coast, the Bay can be generally considered as free of pollution. Transport of nutrients through river flow into the Bay is very low, and the maximum nitrate concentrations in the Bay are usually < 10 µg at N l⁻¹. In spring and summer, a thermohaline front (haline in spring and thermal in summer) becomes established at the entrance of the Bay, which on its southern extremity penetrates well inside the Bay. This front sets the boundary between the zone of strong tidal currents where the water mass remains well-mixed and relatively less warm, and the zone where the tidal currents are weak resulting in a stratification. The presence of this front has an important role on the exchange between the Bay waters and the offshore waters. This front (called the Iroise inner front, Fig. 1) forms part of the complex frontal systems of the Iroise Sea, of which the Ushant front is the extensively studied one (for a review, see LE FÈVRE, 1986).

Hydrology-Nutrients

Water samples from four depths (0, 5, 10 and 25 m) were collected with 51 Niskin samplers. Temperature was measured with Richter and Wiese reversing thermometers (precision ± 0.01 °C). Salinity was measured in an Autosol 8400 Guildline salinometer, with a precision of ± 0.005 P.S.U. Density was calculated taking into consideration the precisions given by MILLERO & POISSON (1981). Dissolved oxygen content was estimated by the Winckler’s method (STRIKLAND & PARSONS, 1972), and its percentage saturation was calculated using the tables given by GREEN & CARRITT (1967). Samples for nutrients were pre-filtered on a 200 µm nylon mesh, and deep frozen until further analyses in a Technicon Auto-Analyzer II following the procedure given by TREGUER & LE CORRE (1975). Analytical precision for nitrate and silicate was ± 0.1 µg at l⁻¹, and for phosphate and nitrite, ± 0.01 µg at l⁻¹.

Phytoplankton

Samples for cell counts, chlorophyll and primary production were obtained from seven optical depths (100, 50, 25, 10, 7, 3, 1 % light penetration), and four standard hydrographic depths in every collection. Particulate matter filtered on a GF/C filter was extracted with 90 % acetone for fluorometric measurements of chlorophyll a and phaeopigments (YENTISCH & MENZEL, 1963) in a Turner model 111 fluorometer preliminarily calibrated, and their concentrations were calculated using LORENZEN’S (1966) equations. Samples for cell counts were preserved with acid lugol and counted following the Utermöhl method. Particulate matter for carbon and nitrogen measurements from the four hydrographic depths was recovered on pre-ignited (400 °C overnight) GF/C filters, and the analyses were made in a Perkin Elmer 240 elemental analyser.
RESULTS AND DISCUSSION

Hydrology

During winter and early spring, the water mass in the Douarnenez Bay remains homogenous (Figs. 2 and 3), directly as a result of the strong vertical mixing prevailing at this time of the year. Beginning from May, a strong stratification sets in which persists through the whole of the summer. This stratification has two different origins. In spring, it is predominantly of a haline nature and results from the presence of a low salinity water in the Bay (Fig. 3). This low-salinity water may arrive as a result of land or river runoff, or as a result of advection of an offshore water mass from the continental shelf. The latter assumption would seem the more likely, as there are no major rivers opening into the Bay. Again, this low-salinity water mass is totally nutrient-depleted (Figs. 11 and 12), suggesting a rather long transit before entry into the Bay, which would be possible if only the water mass has an external offshore origin. Hydrographic data collected on the Armorican continental shelf at this time of the year (SATIR cruises 83A and 83B, respectively in April and June 1983)

Fig. 4. — Vertical distribution of density (σt) at Station D.

also confirm the advection of a low-salinity water mass into the Douarnenez Bay. These show that, because of the unusually heavy rains in the spring of 1983, discharge of the Loire river was exceptionally high, and that this leads to the formation of a low-salinity water mass over the Armorican shelf which, then, moves westward along the coast and enters the Iroise Sea (Fig. 5). A part of these waters would probably have penetrated into the Bay of Douarnenez, and modified the usual hydrological structure of this Bay in 1983. It is also possible that some low-salinity water from the adjacent Rade of Brest flows into the Douarnenez Bay. In June, a thermal stratification succeeds the haline stratification. Thermocline was at relatively shallower depths (Fig. 2) and the pycnocline, as in spring, was located at about 10-15 m (Fig. 4). In summer, heating of surface waters is marked, more so in 1983 when the insolation was unusually high and, consequently, the mixing depth was shallow. Concomitant with the stratification in

Fig. 5. — Surface distribution of salinity (P.S.U.) on the Armorican shelf in June 1983 (SATIR 83B). The darker tones correspond to the low salinity waters.

Fig. 6. — Vertical distribution of the temperature (°C) at Station D from March 1983 to February 1984. The water column is well stratified from June to September.

Fig. 7. — Vertical distribution of salinity (P.S.U.) at Station D. Low-salinity waters are detected in surface in May 1983.
the Bay, a coastal front (the Iroise inner front, Fig. 6) appears in late spring at the entrance to the Bay. This front is thermohaline in spring and becomes primarily thermal in summer when freshwater flow into the Bay becomes lowest. This front plays an important role in the evolution of biological and chemical processes in the Bay in summer (MORIN, 1984) and, more particularly, in the incidence of red tides (LE FEVRE & GRALL, 1970).

Phytoplankton and primary production

The spring development of phytoplankton begins early, in March, well before the onset of the seasonal stratification (Fig. 7). Chlorophyll a concentrations, however, remain at modest levels (< 3 µg l⁻¹), and the phytoplankton cells, because of the vertical mixing, are uniformly distributed in the whole water column. The spring primary production maximum occurs in April (Fig. 8), with carbon fixation rates greater than 15 mg C m⁻³ h⁻¹ in the surface waters. This greater production with a comparatively lower phytoplankton biomass (Assimilation number = 4.97) suggests a healthy population and conducive growth conditions, as noted already by MORIN et al. (1985) also. At this time, the phytoplankton was constituted exclusively by diatoms, with Chaetoceros sp. dominating. *Gyrodinium aureolum* appears in the Bay only in May (1000 cells l⁻¹ in the surface waters), and is probably introduced along with the low-salinity waters advected into the Bay at this time. Diatoms are still dominant in May (about 250 000 cells l⁻¹, Fig. 9), and *Gyrodinium aureolum* represents only a fraction of Dinophyceae (approximately 30 %). *Dinophysis acuminata* also appears at this time, with densities of about 500 cells l⁻¹. Chlorophyll maximum attains a concentration of 5 µg l⁻¹ (Fig. 7) and is located at about the pycnocline. Primary production, however, decreases to values less than 10 mg C m⁻³ h⁻¹ in May. In June, diatoms continue to remain dominant, but *G. aureolum*, with a density of about 100 000 cells l⁻¹, becomes the major species of the dinophyceae (170 000 cells l⁻¹). In the subsequent weeks, *G. aureolum* develops rapidly and attains bloom proportions in July, with cells densities greater than 2.10⁶ l⁻¹ (Fig. 9). At this time, *G. aureolum* constitutes 95 % of the phytoplankton population contributing to the chlorophyll a maximum (13 µg l⁻¹). This chlorophyll maximum also corresponds to a primary production maximum, with a

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**Fig. 6.** Vertical distribution of temperature (°C) in the Iroise Inner Frontal area in August 1983.

**Fig. 7.** Vertical distribution of chlorophyll a (µg l⁻¹) at Station D.

**Fig. 8.** Vertical distribution of primary production (mg C m⁻³ h⁻¹) at Station D.

**Fig. 9.** Cell abundances of diatoms and *Gyrodinium aureolum* at the maximum of chlorophyll a at station D.
carbon fixation rate greater than 20 mg C m$^{-3}$ h$^{-1}$. This value is relatively low with respect to chlorophyll concentrations; so this coincidence does not necessarily imply an all specific growth of the phytoplankton population, since other mechanisms such as convergent motions can accumulate biological material (Le Fèvre & Grall, 1970; Pinoree et al., 1977). Self-shading in the bloom can also minimize photosynthesis (Jordan & Joint, 1984) and hence, primary production. In the following weeks, this chlorophyll maximum deepens progressively as the nitrate-depleted waters become deeper, and is no more associated with the pycnocline. Figures 7 and 11 clearly show this where the high densities of Gyrodinium aureolum are closely associated with the nitratecline. G. aureolum, thus, for the most part of the bloom period, is located in the relatively cool waters (14-16°C) under the pycnocline, where light levels and nutrient availability do not become limiting for its growth. Again, stratification plays an important role in the development of the G. aureolum bloom and its influence is indirect. In summer, only the superficial waters, up to a depth of 10 m, get stratified. Consequently, a part of the water column with favorable growth conditions of light (the 10% light depth coincides with the density discontinuity), nutrient availability and reduced mixing becomes isolated under the pycnocline. This unusual situation where both light and nutrients are available for photosynthesis and mixing is low favors dinoflagellates in their competition with diatoms (Margalef et al., 1979). These exceptional conditions associated with the stratification can, at least partly, explain the incidence of the Gyrodinium aureolum bloom in the Douarnenez Bay in 1983.

The growth of G. aureolum appears rather slow; our calculations based on cells counts show a doubling time of about seven days in the Douarnenez Bay. This doubling time can be considered as minimal since mechanisms as passive accumulation of cells are not taken into account. Under optimal growth conditions, Lindahl (1983) found a doubling time of 1 to 3 days, which was characteristic of an early stage in the development of G. aureolum. The assimilation ratio calculated for the chlorophyll maximum was low, being only 1.1 in late July, confirming the longer doubling time of the G. aureolum population at this period. It would appear thus that G. aureolum population was at an advanced stage of development in July. This suggests that an interval of two months is required between the appearance of the first cells of Gyrodinium and its development to bloom proportions. Thus, G. aureolum can attain high densities if only favourable conditions were maintained during a relatively longer period. This was the case in 1983 when the intrusion of low-salinity waters in spring produced and early stratification which was maintained and reinforced subsequently by favorable meteorological conditions (high insolation, low wind stress) throughout the summer. Besides, the nutrient stock available for assimilation in the summer of 1983 was also exceptionally high (see below).

High chlorophyll concentrations are associated with the frontal structure (Fig. 10). They do not occur directly on the front itself but rather at subsurface in the stratified waters. Frontal structures are well known for their ability to concentrate passively floating material, particularly phytoplankton (Rytler, 1955). The efficiency of such a mechanism has not been studied in the Iroise Inner Front but its presence (Le Fèvre & Grall, 1970) appears to be a favourable element for the formation of red tides.

**Nutrients**

In spite of the numerous observations, the exact influence of nutrients on the appearance of Gyrodinium aureolum blooms remains even now poorly known. Earlier studies have often been limited to the last phase of the phenomenon when the discoloration of seawater becomes visible. At this time, nutrients are usually totally depleted and hence no correlation between the nutrient concentrations and the incidence of the bloom can be detected. It would rather be preferable to determine the nutrient concentrations at the beginning than at its final phase. In fact, varying degrees of importance has been attributed to nutrients in initiating and leading to the development of the bloom. According to one school of thought, nutrients play a crucial role and hence, enrichment of surface waters with nutrients by processes like freshwater runoff, urban pollution, upwelling, etc., is essential for red tide formation. According to another school of thought, however, nutrients are of limited importance and physical processes, instead, are of primary importance; high phytoplankton densities need not necessarily result from high primary production, and their presence can, at least partially, be due to physical processes.

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**FIG. 10.** Vertical distribution of chlorophyll in the Iroise Inner Frontal area; the highest values are recorded on the stratified side of the front at the pycnocline level.
which tend to concentrate locally the phytoplankton cells (for a review, see Rounsefell & Nelson, 1966) or to the ability of the dinoflagellates to move vertically in the water column (Gran, 1929) and aggregate in a small volume of sea water. The ability of vertical migration also permits an efficient utilization of nutrients from a wider area. These models of red tide formation where mechanical concentration processes are advocated, need comparatively a lower nutrient stock than the typically “agricultural” model where the phytoplankton production occurs in situ. Our results on the evolution of nutrients before, during and after the bloom (Figs. 11 and 12), thus help to examine the importance of nutrients for a G. aureolum bloom.

The winter stock of nutrients in the Douarnenez Bay is relatively modest, with nitrate, silicate and phosphate concentrations being respectively lower than 10, 6 and 0.5 µg at 1\(^{-1}\). Nitrite and ammonium concentrations are also low (respectively < 0.3 and < 1.8 µg at 1\(^{-1}\)), and hence, these waters can be considered, as far as nutrients are concerned, as free of pollution. Nutrient assimilation begins in March and occurs in the whole of the water column. Continued assimilation through April and May reduces nutrient concentrations to very low levels (NO\(_3\)\(^-\) < 1.5 µg at 1\(^{-1}\) and Si(Oh)\(_4\) < 3.0 µg at 1\(^{-1}\)). The low-salinity waters appearing in the Bay at this time are already nutrient-depleted, as evidenced by the lack of any perturbation whatsoever in the changes of nitrate (Fig. 11) and silicate (Fig. 12). These nutrient-depleted waters, on the other hand, are enriched with particulate organic matter (organic nitrogen around 8 µg at N 1\(^{-1}\)) which probably results from an intense phytoplankton development when these waters were in transit on the continental shelf outside the Bay. The bay waters are thus fertilized with nitrogen but, unusually, this is in an organic form. Nutrient changes in summer are characterized by high silicate concentrations in the bottom waters (Si(Oh)\(_4\) > 9.0 µg at 1\(^{-1}\)). Associated with this there is a marked undersaturation of oxygen, down to less than 70 %, which is indicative of an active oxidation of organic matter and an intense nutrient recycling. Nevertheless, it can be noted that there is an absence of high concentrations of nitrate (NO\(_3\)\(^-\) < 2.0 µg at 1\(^{-1}\)) which should have been there as a result of nutrient regeneration. For example, according to the stoichiometric ratios of nutrient regeneration (Redfield et al., 1963), the measured deficit of dissolved oxygen in the bottom waters in summer (O\(_2\) > 2 ml 1\(^{-1}\)) should have resulted in a regeneration and accumulation of nitrate in excess of 10 µg at 1\(^{-1}\). This is not the case, and the only possible explanation can be that the nitrate is taken up by the Gyrodinium aureolum bloom as fast as it is regenerated. Recycling in 1983 in the Douarnenez Bay thus appears as a “discrete” source in space and time, and is very efficient in mineral nitrogen enrichment. The base material for this intense regeneration is probably the particulate organic matter brought in by the low-salinity waters in spring and settling out of the euphotic zone. While the high nutrient regeneration may play a decisive role in the initiation of the blooms, it does not, however, exclude the influence of other processes such as passive accumulation under the influence of an inner front or vertical migration, in the appearance of high densities of G. aureolum. The importance of nitrate becomes evident again in August: when the stratification becomes strongly marked (surface temperature > 18°C) in August, the bloom of G. aureolum collapses, and this coincides with the total depletion of nitrate in the entire water column in the Bay.

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