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MASS MORTALITIES OF OYSTERS (<u>CRASSOSTREA GIGAS</u>) DURING SPRING 1988 IN THE BAY OF MARENNES-OLERON, RELATED TO ENVIRONMENTAL CONDITIONS.

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ABSTRACT : Mass mortalities of oysters were recorded in the South of the Bay of Marennes-Oleron, during Spring 1988. The percentages of mortality averaged 50 % and reached up to 90 % in some areas of bottom culture. The losses were estimated to 7 800 tonnes. This paper present the results of the investigations carried out in several fields. Among them, pathological examination revealed that no pathogenic agent or parasitic infestation could be evoked to explain these mortalities. Analyses of pollutants were either negatives, or the concentrations were far below the toxicity levels. Climatological and hydrological observations showed that rainfalls were twice more abundant then the average, for a period of 6 months preceding the mortalities. The salinity was low and fluctuating in the area, and the temperature was warmer, then the average during the same period. Phytoplanktonic blooms were recorded only by the end of May, latter then usual. These ecological changes resulted in a poor physiological condition of the oysters, which became critical for the grounds located at the South of the bay. Both their high tidal position and low quantities of phytoplankton are characteristic of this area. The high densities of oysters in the parks were also evoked as contributing to the establishment of such critical conditions.

INTRODUCTION

Mass mortalities of cultivated bivalves have been commonly observed, from long time and throughout the world (Sindermann, 1976). They have often resulted in significant reductions in the production. Until recent years, there causes were often classified as of "unknown origin", the identification of precise causes being very difficult. But the development of pathological research in the past ten years allowed to identify several pathogenic organisms as causative organisms of mortalities, on populations of molluscs. Among them, <u>Minchinia nelsoni</u> and <u>M. costalis</u> on <u>Crassostrea virginica</u> (Glude, 1975), <u>Bonamia ostreae</u> and <u>Marteilia refringens</u> on <u>Ostrea edulis</u>, have received a considerable attention.

Mortalities of molluscs were sometimes related to the action of factors other than pathogenic agents. Populations of predators can dramatically increase in abundance, and some changes in the physical environment may result in localized mass mortalities, involving restricted geographic areas, such as river mouths (Nikolic, 1964). More recently, environmental disturbances were mentionned as a causative agent of oyster mortalities, both as the result of ecological crisis (eutrophication) or the impact of pollutants.

Following Sinderman (1976), oyster mortalities and their effects may be classified in three groups. (1) Background mortalities, occurring at any stage of the life history. (2) "Localized mass mortalities, affecting restricted geographic areas and killing up to 100 % of the populations in those areas." (3) Extensive mass mortalities, affecting large geographic areas and resulting in significant decreases of the oysters productions in those areas.

Mortalities pertaining to the last category were encountered in the recent time along the French coast, at least for the two cultivated species of oysters. The portuguese oyster (<u>Crassostrea angulata</u>) was affected in 1967 by a so called "gill disease" which was first reported by Marteil (1968) in Arcachon Bay. Almost simultaneously the same disease was reported from Portugal (Vilela, 1968 ; Alderman, 1969). After heavy mortalities, the Portuguese oyster was then replaced by the Japanese oyster, <u>Crassostrea gigas</u>, imported from British Columbia and Japan. However the viral disease still affect the previous species (Bougrier et al., 1986). The populations of the European flat oyster, <u>Ostrea edulis</u>, also suffered high mortalities, approximately at the same time. Two different organisms were identified as contributing to the mortalities of the flat oyster, although with a different etiology. The first is <u>Marteilia refringens</u> heavy economic losses for the French oyster industry (Meuriot and Grizel, 1984). They are not eradicated yet, and the French annual production of flat oyster is merely the tenth of the values recorded 20 years ago.

In the bay of Marennes-Oléron, background mortalities are usually high from 1984–1986, because of the intensive development of reared stocks which now exceed the carrying capacity of the ecosystem, as was demonstrated by Héral et al. (1986) by means of empirical modelling. These mortalities may reach a value of 21 % per year (Bodoy, 1986).

In early Spring of 1988, mortalities began to noticeably exceed the average values computed the previous years, in an area already know to suffer higher losses then elsewere in the bay (Bodoy, op. cit.). As these mortalities developed, a study was performed to measure their extend, and to understand their origins. The present paper reports the results obtained, with some insight on the different factors which may have contributed to these mortalities.

MATERIALS AND METHODS

In the Bay of Marennes-Oléron, oyster culture developed into the large, sheltered intertidal areas (fig. 1). The whole bay benefit from a nutrient enrichment linked with the input of fresh waters from the Charente river. The heavy mortalities recorded in Spring 1988 were encountered at the South part of the bay, far from the mouths of Charente river. A bathymetric survey performed in 1985 (Anonymous, 1986) allowed to characterize the altitude of this site, and to compare it with other productive areas within the bay. The elevation of the highest point of several areas was expressed in metres, above the reference level of marine charts (Extrem Water Level of Springs, ELWS). The surface of areas located at different elevations was computed from cartographic results, in order to characterize the average elevation of these sites.

Water currents in the bay, including the intertidal areas when these are covered, were recorded previously (Anonymous, 1979) and a mathematical model in two dimensions, was built.

Local, meteorological parameters (average daily air temperature, rainfall, periods of sunshine) were available at the Departemental Climatological Office (unpublished results). Monthly averages were computed on a period of 28 years for the same area.

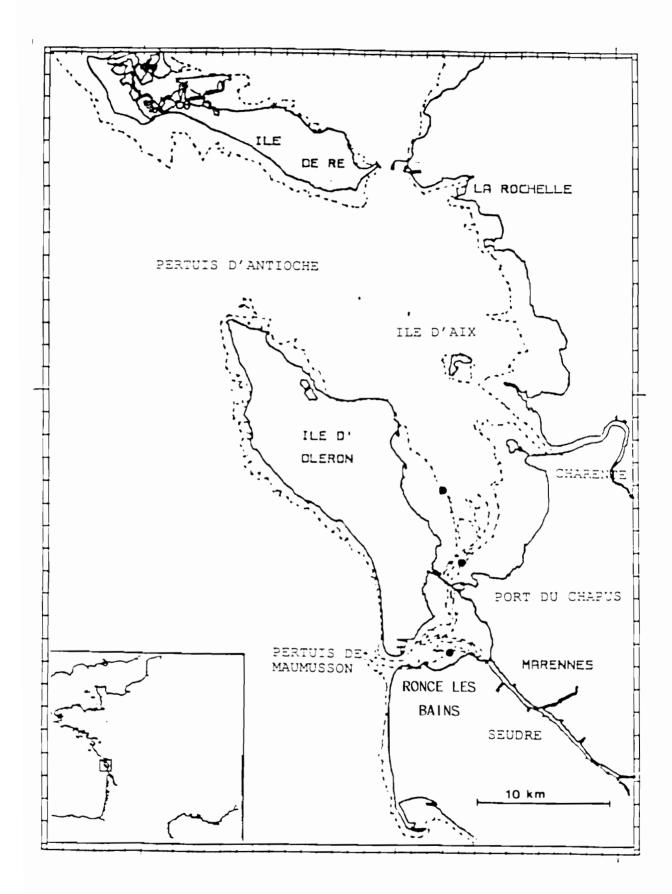


Figure 1 : Location of the oysters grounds in the bay of Marennes-Oleron. The dashed lines correspond to the limits of the intertidal areas. = sampling sites located at the same tidal level (tide coefficient = 70/120).

Hydrological parameters have been recorded in this area for 12 years. 5 points have been sampled every two weeks near the surface and at the bottom of the water column. The results given concern a sampling site near the grounds of Ronce Les Bains. Water temperature and salinity were measured in situ, particulate organic and inorganic matter were collected on GF/C filters and measured by weighing, before and after ignition at 450°C for one hour. Chlorophyll and pheopigments were measured by fluorometry (Yentsch and Menzel, 1963), after extraction in acetone 90 %.

Growth, mortality and biochemical composition of oysters have been measured for 4 years at the same 5 points, on a monthly basis. Total weight and mortality were assessed on trays of 50 labelled oysters (Bodoy, 1986), while other biometric parameters and biochemical composition were assessed by a seasonal sampling. Carbohydrate and glycogen analyses were performed using the method of Dubois et al. (1956).

Pathological analyses were performed on samples of surviving oysters and in unaffected areas, in order to reveal any infectious etiology. Anatomo-pathological aspects were also searched in these samples both by optic and electron microscopy. These analyses were made at the Laboratory of Pathology and Genetic of Molluscs (IFREMER, La Tremblade).

Chemical pollutants which might have caused or contributed to the mortalities were also analyzed in the flesh of oysters. A list of the commercial products which are currently utilized in the neighbouring area was established with agricultural technical advisers, and other suspected products were also searched. The analyses were performed by a reference laboratory.

The results of the French National Network for the observation of the marine environmental quality (oceanic data) for the bay were also utilized. 13 organic micro pollutants have been analyzed in the water and 6 metallic micropollutants have been analyzed both in the water and in living organisms (zooplankton and oysters) since 1976. The results of a survey of toxic, phytoplanktonic algae, which may be responsible for bivalves mortalities (<u>Gyrodinium sp.</u>) or for DSP and PSP syndrome are also available on this area.

RESULTS

The oysters leases which are part of the ground of Ronce les Bains, are located at the South of the bay (fig. 1). The cultivated surface was estimated to measure 115 ha, corresponding to 13.4 % of the total surface exploited in the bay of Marennes-Oléron (Bodoy and Geairon, 1987). The bottom culture took place on 87 ha, while stick and trays (bag) cultures developped on 28 ha. All these surfaces correspond to intertidal areas.

If compared with the reference level (ELWS) the grounds of Ronce les Bains culminated at 3.5 m, which is far higher then any other oyster ground within the bay, since most of them culminated at less then 2 m. 45 ha, corresponding to more then 50 % of bottom culture had an altitude higher then 3 m. In terms of water coverage, it was computed that the oysters were covered only 72 % of the time, on an annual basis. This oyster ground is then located very high on the intertidal range.

The water currents are predominantly of a tidal origin. The results (fig. 2) obtained by modelling the tidal influence show that the water bodies circulate first in the North part of the bay. A ventage point was found in the middle of the bay indicating that the water bodies are finally going from North to South. It takes from 5 days (Spring tides) to 9 days (Neap tides) for the water to cross the entire bay and to be expelled at the South Mouth (Pertuis de Maumusson). There, the flood tide only brings half the volume of waters then the ebb tide does.

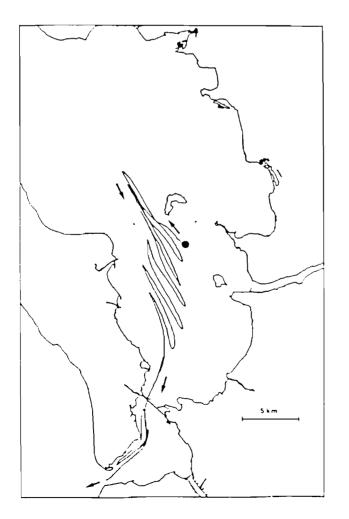


Figure 2 : Trajectories of the water during tidal excursions (Spring tides) from the North to the South of the Bay of Marennes-Oleron. Ventage point. (after Bacher, 1989). The mortalities measured during the past three years and Spring 1988 are shown in figure 3. They were recorded in five areas, at the same tidal level (Tide coefficient = 70). These monthly mortalities are usually higher in the area of Ronce les Bains then elsewere in the bay, excepted in 1986. A peak of monthly mortality (higher then 3 per cent) was often observed during Spring. During the year 1985 the annual mortality (background mortality) during the year 1985 was of 27.3 % at Ronce les Bains and in average 15 % at the other sites. During 1986, it was 16 % against 13 % and during 1987, it was 16 % against 6.5 %. Therefore the area of Ronce les Bains, even for oyster leases located at the same tidal levels, was usually affected by higher mortalities then the rest of the bay.

Abnormal mortalities were recorded early, in April 1988 in Ronce les Bains, with a monthly rate of 6 % (fig. 3) while it was less then 3 % in the other areas. These mortalities extended dramatically in May 1988 and reached a peak during the second spring tide of that month. An extensive survey of the area showed that 25.7 % of surviving oysters died during those few days. Current mortalities recorded afterwards were unusually high, and by the end of July 1988, average cumulated mortalities from the beginning of the year reached 50 % for the bottom culture, and 30 % for the off-bottom culture. The most affected parks were all located in the upper part of the area, with mortalities reaching 90 % in some of them. This part formed a stripe parallel to the shore line.

The bottom culture was estimated to 13 171 tonnes before the mortalities (and to only 10 762 tonnes one year before) while for the off-bottom culture, 4 048 tonnes were present before the mortalities. The losses at the end of July 1988 were estimated to 7 800 tonnes, corresponding to a value of 74.1. millions F.F.

The physiological status of oysters may be characterized through the changes in flesh weight and in their proximate biochemical composition (fig. 4). A marked seasonality has currently been observed in the life cycle of oysters in the bay (Deslous-Paoli and Héral, 1988). For oysters reared in trays on different sites of the bay from March 1987, growth expressed in terms of life weight appeared to be continuous in the North part of the bay, with an average weight of 75 g obtained before spawning, in August 1988. The same oysters only reached an average weight of 54 g in the central part, and no growth was observed for the whole year. In Ronce les bains, the final weight was of 46 g before spawning, no growth occurred during Winter and the final emaciation was more pronounced then in the central part. The ash-free dry weight (AFDW) of the same oysters exhibited a more marked seasonality. In Summer 1987, an intense decrease corresponding to the gametes release, was observed simultaneously in all parts of the bay.

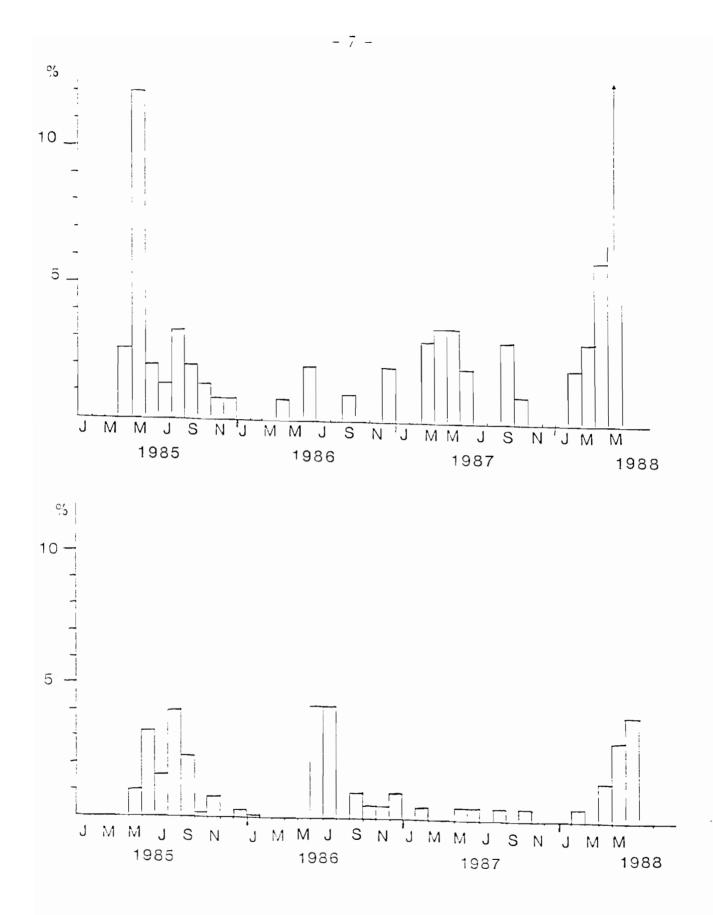


Figure 3 : Evolution of the current monthly mortalities measured from 1985 to 1988 on the five sampling sites.

- A: Values observed in the South (Ronce Les Bains).
- B : Average values of the four other sites.

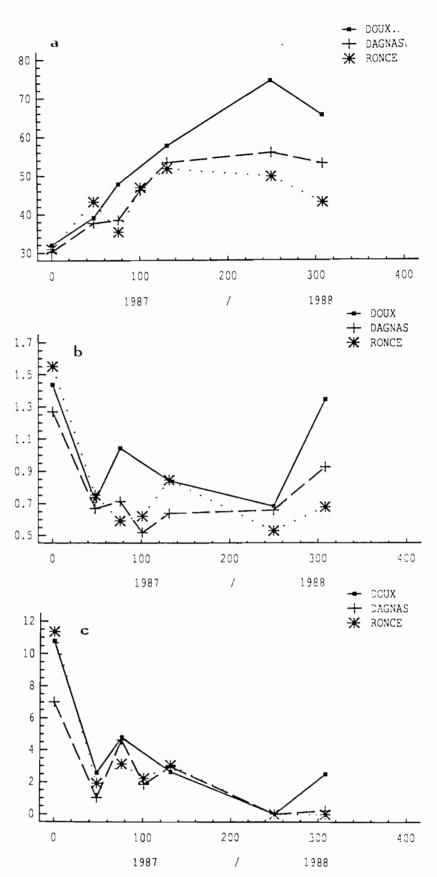


Figure 4 : Average changes in live weight (a), Ash-Free Dry Weight (b) and glycogen content in per cent of AFDW (c) of individual oysters reared at the same tidal level, in three sites located at the North (Doux), at the centre (Dagnas) and at the South (Ronce) of the bay of Marennes-Oleron.

During Autumn, some growth was observed for the northern oysters and those in the central part. During Winter, an emaciation was observed everywhere, although it was more intense in the South. The main geographical differences were observed in Spring 1988, when the average AFDW was of 1.35 g in the North, 0.95 g in the Centre and only 0.65 g in the South, which is approximately half of the AFDW measured in the North. On the highest parts of the ground in Ronce les Bains, a continuous loss of AFDW was even recorded on a separate sampling performed during the field assessment of mortalities. Even at the same tidal level, growth was then slower in the South at Ronce les Bains, with marked differences before and after the mortalities.

Among the biochemical components, carbohydrates and more specifically the glycogen are involved in seasonal metabolism (Gabbott, 1983). Its change as energetic storage is shown in figure 4. The high initial content, linked with the beginning of gametogenesis (Deslous-Paoli and Héral, 1988) then fell, after the gamete release (August). A period of storage of glycogen occured in Automn 1987, which was less intense for the Centre of the bay. During Winter, a decline in glycogen content was observed in all parts and the values did not significantly differed from zero in March 1988. The rise observed after that month only concerned the North and the Centre of the bay. Very low glycogen contents, not significantly different from zero were observed at Ronce les bains from November 1987 to May 1988, thus indicating that no energetic reserves were available during these six months.

The monthly values of climatologic parametres for the first semester of 1988 are given in figure 5, as well as the monthly average computed locally for a period of 28 years. The air temperature in 1988 was always higher then the average, the difference being approximately of 1°C. January 1988 was even 4.5°C warmer then the average. On the same period, the rainfall was always more abundant then the monthly average precipitations (fig. 6). The excess ranked from 23.8 % in february 1988 to 159 % in January. April and June were also characterized by heavy rainfalls. Sunshine was therefore reduced during that period.

Anatomic examinations performed by several scientists did not reveal any abnormal clinical figure. The branchial gills remained unaffected, the mantle margins were thick and well pigmented, and the muscles were normally strong. The genital gland was well developped, with a brown pigmentation. Some green spots were observed, which proved to be caused by hemocytes accumulation.

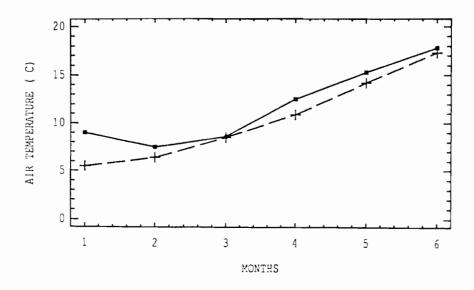


Figure 5 : Average monthly values of the air temperature for the six first months of the year, computed on a period of 28 years () and values observed during the year 1988 (+------+).

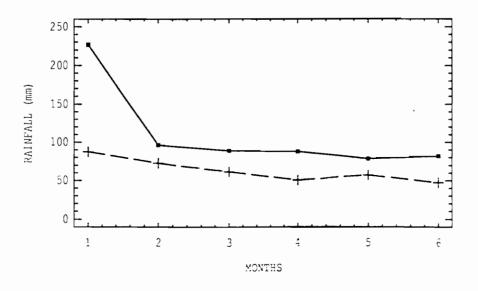


Figure 6 : Average monthly values of the rainfalls for the six first months of the year, computed on a period of 28 years (•----•) and values observed during the year 1988 (+--+).

Microscopic examinations (photonic and electronic) confirmed a general good condition. No lesion of stomachal epithelium and digestive diverticula were observed, as has sometimes been the case, during Summer mortalities (Maurer et al., 1986). Blood cells had a normal size and were abundant. By far the most important, no pathogenic agent (parasitic bacterial or viral) was detected, nor infectious syndroma, excepted for a kyste, on the mantle of a unique oyster, which contained a bacterial colony.

The water temperature was higher then the average from Summer 1987 (fig. 7 and 8). The most noticeable event was observed during Winter, when water temperatures below 10°C where recorded only once. After this mild Winter, the rise during Spring was also faster then what is usually observed.

Among the hydrological parametres, the salinity was the most affected, since the records from January to April 1988 significantly differed from the average computed on 12 years, while the 1987 records were not different, excepted in April 1987. Salinities as low as 19 ppm were recorded in March 1988, and normal conditions were not reestablished by June 1988. The decrease in salinity was sudden, thus creating a stress for the oysters. After that time, salinity remained low and fluctuating. This was another factor of stress for the molluscs, which may have difficulties to adapt.

At the same period, the content in particulate inorganic matter was high, as is usual in this bay. The monthly average values ranked from 30 to 45 mg.l-1. During the year 1987 and the beginning of 1988, similar values were observed, some being even lower. As is often observed on short period of samplings for this parametre, variability was high.

The concentration of chlorophyllic pigments, considered as representative of the available food for the molluscs, usually exhibited a peak in April, in these sampling sites (fig. 9). The monthly average contents are higher then 3 mg.m⁻³, and may reach values up to 13 mg.m⁻³. During the period under particular observation (fig. 10), the chlorophyllic pigment were often found at concentrations lower then the average computed on the 12 years period. The year 1987 was characterized by negative differences, which became acute during Spring 1988. By the end of May, values as low at 4 mg.m⁻³ were still found in this area. Afterward the pigments content exhibited a sharp rise, up to 22 mg.m⁻³, during the month of June, that is just after the peak of mortalities. Values lower then the average were still found during Summer months.

Areas of intensive culture are mainly localised near the coasts, and around the continental shore line of the bay. The Seudre River receives wastes of inlands and

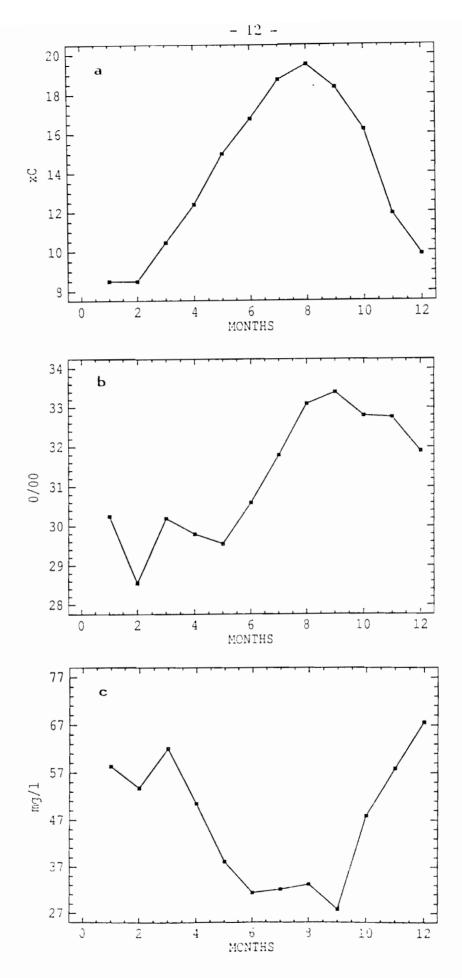


Figure 7 : Average monthly values of sea temperature (a), salinity (b) and total particulate matter (c) computed over a period of 12 years, in a sampling point located near the oyster parks of Ronce Les Bains.

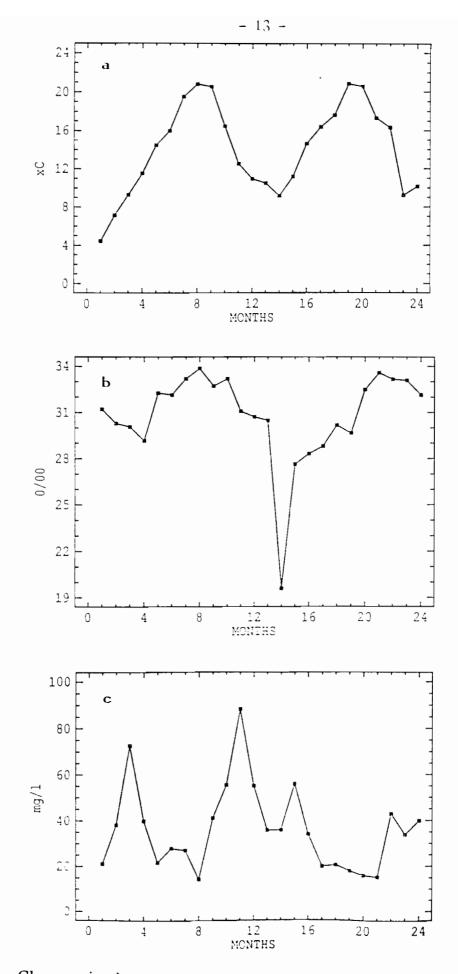


Figure 8 : Changes in the values of water temperature (a), salinity (b) and total particulate matter (c) observed from 1987 to june 1988 near the parks of Ronce Les Bains.

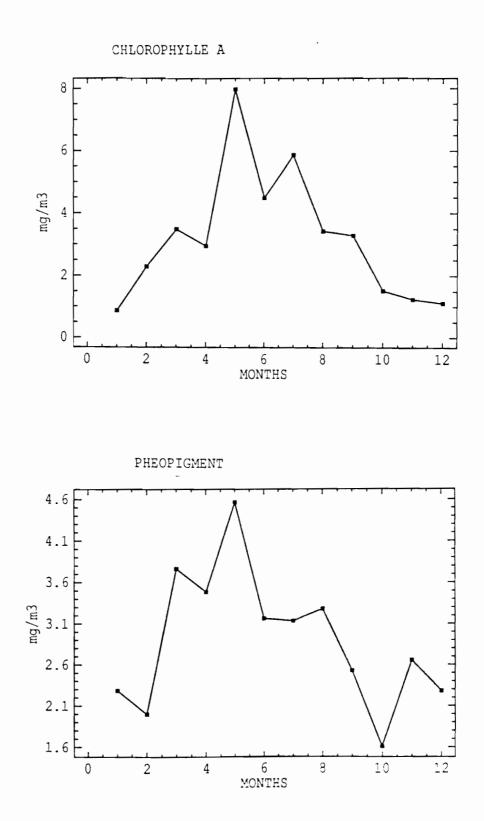


Figure 9 : Average monthly values of phytoplanktonic pigments, computed on a period of 12 years near Ronce Les Bains.

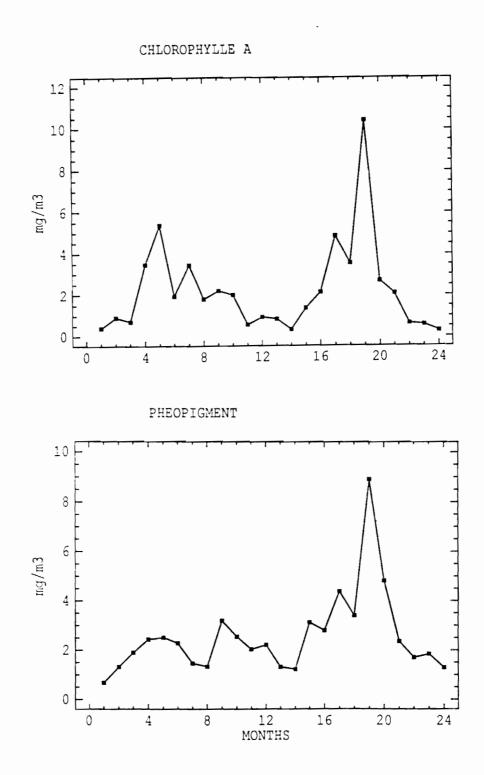


Figure 10 : Changes in the values of phytoplanktonic pigments observed from 1987 to june 1988 near Ronce Les Bains.

sharp rise, up to 22 mg.m⁻³, during the month of June, that is just after the peak of mortalities. Values lower then the average were still found during Summer months.

Areas of intensive culture are mainly localised near the coasts, and around the continental shore line of the bay. The Seudre River receives wastes of inlands and marshes, occupied by corn and sunflower culture. The main reject is located 10 kilometers far from its mouths. Analyses of pesticids, herbicids and a molluscicid ; performed on the flesh of surviving oysters collected during the peak of mortality at Ronce les Bains, are shown in table 1.

<u>Table 1</u>: Concentration of organic pollutants in the flesh of oysters, collected at Ronce les Bains, the 27 mai 1988. N.D. = not detected. Detections levels and concentrations are given in nanogrammes per gramme of frozen flesh.

Chemicals	Detection level nanogramme/gramme	Concentration nanogramme/gramme
Chlormephos	5	N.D.
Lindane	5	8
Deltamethrine	5	N.D.
Propiconazole	35	N.D.
Bromoxynil	5	N.D.
Ioxynil	10	N.D.
Mercaptodimethur	35	N.D.

Lindane was the only chemical which was detected in the flesh of oysters at Ronce les Bains. All the other pollutants searched were not detected. Another sample was taken at the same time, on an oyster bed located only 1 km far from the reject of the agricultural area. While the tidal currents regularly brings these waters to the oyster bed nearby, no mortalities were observed there, and the analyses of the same pollutants were all negative.

DISCUSSION

High rates of mortalities are not uncommon in the bay of Marennes-Oléron, as in major areas of oyster culture. The most recent episode occurred during october 1987. It was due to a storm, which, in some areas of bottom cultures, removed oysters, out of the leases and scattered them. Another noticeable mortalities with a rate of 10 % occurred during Spring 1983. But the most important crisis occurred in 1967-1970 when the portuguese oyster, <u>Crassostrea angulata</u>, was concerned with heavy losses whose etiology proved to be successively caused by the gill disease (Comps, 1970) and by an iridovirus (comps et al., 1976). They resulted in the complete regression of the culture of this species in Northern Europe and its replacement by the imported Japanese oyster, <u>Crassostrea gigas</u>. Before these mortalities, the total quantity of Portuguese oysters reared in the bay of Marennes-Oléron has been estimated to 200 000 tonnes (Héral, 1987; Héral et al., 1986).

The mortality recorded on oysters in Spring 1988 showed most of the characteristics of an acute mortality, pertaining to the second group as defined by Sindermann (1976). The phenomenon was effectively well localized, since mortalities only developped on an area representing merely 13 % of the total cultivated surfaces in the bay. Furthermore, high rates of mortality were recorded in a short, well defined period of time. Finally there was no spread in other neighbouring areas, nor on other oyster culture sites along the European coasts. Therefore the facts strongly differed from the observations made on the same area in 1967–1968, when the gill disease affected the Portuguese oyster.

Among the causative factors of mortalities, the action of pathogens or parasites is known to produce heavy economic losses (Meuriot and Grizel, 1984; Grizel and Héral, 1990). The control of such factors remains very difficult, and even sometimes impossible. Before the implementation of genetically resistant strains, some positive results may be obtained by technical managements. Lowering the densities resulted in some improvements for the cultivation of the european flat oyster <u>Ostrea edulis</u>, parasited by <u>Bonamia ostreae</u> on the Brittany coasts.

The results of the anatomo-pathological analyses showed that no pathogen or parasites were observed in the samples. The subsequent evolution of the population, during Summer 1988, showed that the normal mortality rates for this area were progressively obtained. Oysters transplanted to other grounds culture recovered a healthy condition, during the months of September and October, and no other abnormal mortalities were recorded after. These facts confirmed that the observed mortality was not due to a pathogenic agent able to cause an epizooty.

The analyses of pollutants were all negative, excepted for the lindane. It was found at concentrations far lower then the acute toxicity level for molluscs. Its high remanence may explain its detection, while it should not be currently utilized, in this area excepted against white ants. The tribulyltin oxyde (TBT) used in antifouling paints is know for its very high toxicity, either at the acute level (Gendron, 1985), or during chronic exposure (Thain, 1983). But the observations differed from what may be observed with a pollution caused by this chemical : absence of growth, shell thickening, perturbation of reproduction (Alzieu and Heral, 1984), or histopathological alterations (Chagot et al., 1990). Monitoring studies of TBT showed that the area was now preserved. The only contamination recorded was found in 1979–1982 at the Northern part of the bay of Marennes-Oleron (Martial et al., 1990).

Still remains the hypothesis of an unidentified, acute pollution. The mapping of mortalities, performed during the survey, showed the highest rates were found at the upper part of this site. As a deep channel surrounds the whole ground, even at low tide, the probability for a continental, acute pollution to produce such remote, concentric aspects remains low. In such case, highest mortalities would have been observed on the individuals nearest of the reject point (shore-line).

Climatological and hydrological observations performed during the first semester of 1988 differed on a great extent from the average. As was previously noted, the quantity of rainfalls were twice as much as this average and the air temperature was always 1°C warmer at least. This mild and very humid weather induced higher water temperatures and lower salinities in this sheltered and shallow bay. In spite of its location near the Southern mouths (Pertuis de Maumusson), by the vicinity of the opensea, the ground culture of Ronce les Bains was not protected against these trends, since the residual currents are directed southward throughout the bay. Furthermore, Seudre river usually has a very low flow, its stream being stopped by locks. But during that period, the heavy rains made necessary to open them several times. Such actions may have originated the sharp decline in salinity observed in March 1988, and may be related with the salinity fluctuations in April and May.

Ecological consequences of these abnormal variations primarily concerned the phytoplanktonic production. Phytoplanktonic blooms in the bay generally occur at the beginning of April (Héral et al., 1987), while during the year 1988 these were recorded only by the end of May. This may be related with the low water temperatures and with the increase of fresh water input from the Charente river, and the resultant dilution of nutrients into the marine ecosystem, together with higher turbidity. As the main area of primary production within that bay is located near the mouths of Charente estuary, lower contents in chlorophyllic pigments were observed during this period. This resulted in less food available for the oyster populations within the bay. Another ecological consequence may be found on the fluctuating salinities which may have stressed the oyster. Because of the impact of Seudre river, the culture ground located at the South of the bay were most affected by these low and fluctuating salinities. As mixing of water is often difficult in case of flooding, the upper oyster leases may have been heavily concerned by the low salinities.

The last ecological consequence concerned the oyster populations. Warmer water temperatures encountered during this winter stimulated the metabolisms of oyster (Mann, 1979), more then usual. The energetic storage, which is constituted by glycogen accumulated into the mantle (Gabbott, 1983) was then utilized at a faster pace. The glycogen content was very low, early before the mortalities, during winter, and this was more pronounced for the Southern areas. Glycogenic storages were totally exhausted by the end of April, when the contents did not significantly differ from zero. During the recovering period, the glycogen content rose rather in the North (Doux) then in the South (Ronce), indicating that the food available for growth was more abundant in the North of the bay. This fact was even clearer when considering the fresh weight of the flesh, with a growth more intense in the North (Doux) then at the center (Dagnas), while an emaciacion was still observed in the South of the Bay (Ronce).

Together with these ecological changes, other geographic and human factors may have acted to create critical and even lethal conditions. The high background mortalities which are currently observed in the South, at Ronce-les-Bains (Bodoy, 1986), are linked with the direction of residual currents within the bay and thus the average availability of food. The oyster beds ware estimated to a total of 93,700 tonnes in 1987 (Bodoy and Geairon, 1988), or 76,500 tonnes if the Southern grounds were not included. After circulating on these, the available food is reduced in the South, while tidal inputs of phytoplankton from the open sea through the South strait are usually poor (Heral et al., 1986). A part from these observations which all concern oysters reared at the same tidal level, topographic features constituted also a factor of mortality. The portuguese oyster was first cultivated in the grounds of Ronce-Les-Bains, high on the tidal range, as everywhere in the French production centers. The replacement by C. gigas led oysterman to use preferably the lower parks, since the Japanese oyster apparently does not afford such long emergence. The trend towards the use of lower tidal levels has been general, excepted for the grounds of Ronce-Les-Bains. Its high elevation make them therefore highly sensitive to any perturbation because of a reduced time available for feeding and average poor condition.

The last factor to be considered is a human action. Technical rules for the bottom culture in the bay indicates that an average density of 10 kilogramme per square meter should not be exceeded. Stock measurements indicated that in Ronce Les Bains 13 171 tonnes of oysters were cultivated on 87 hectares which correspond to an average density of 15.14 kilogramme per square meter. The grounds of bottom culture were then overloaded in 1988. The increase from 1987 (10 762 tonnes) was of 22.4 %.

All these ecological, geographic and technical factors contributed to the establishment of lethal conditions which were encontered at a time of the year when metabolic requirements of the oysters were high and when energetic reserves were exhausted and available food was scarce.

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