International Council
for the Exploration
the Sea

C.M. 1990/K : 20
Shellfish Committee

DECLINE OF OYSTER PRODUCTION IN THE MARYLAND PORTION OF THE CHESAPEAKE BAY:

CAUSES AND PERSPECTIVES

by
Maurice Héral*
Brian J. Rothschild**
Philippe Goulletquer**

*Institut Francais de Recherche pour l'Exploitation de la Mer (IFREMER),
Laboratoire Ecosystèmes Conchylicoles (LEC),
La Tremblade BP 133 17390 France

**University of Maryland
Center for Environmental and Estuarine Study
Chesapeake Biological Laboratory (CBL)
Solomons, Maryland 20688 USA

ABSTRACT : The historical landings of the oyster production are described for the Maryland part of the Chesapeake Bay. The different trends are analysed concurently with the main events and management strategies which occured on the bay. Three main periods are identified :

- the greatest fishery from 1840 to 1890 with a large overfishing and the destruction of the oyster habitat caused by the oyster gears,
- the decrease and stable landings from 1900 to 1980 due to the failure of the reseeding plan connected to the heavy sedimentation and the anoxic summer conditions,
- the large decrease of the production (1981-1988) caused by high mortalities related to diseases (MSX and *Perkinsus marinus*) predation and management practices.

Alternative strategies for restoration of oyster production in the Chesapeake Bay are discussed.

RESUME : L'analyse des données historiques des productions annuelles d'huîtres a été réalisée pour la Baie de Chesapeake, en particulier pour l'état du Maryland. Les différentes tendances sont analysées parallèlement aux principaux évènements et aux stratégies d'aménagements qui ont été appliquées dans la baie. Trois périodes principales ont été identifiées :

- La période de forte production (1840 à 1890) avec une forte surpêche entraînant la destruction de l'habitat des gisements huîtres provoquée par une utilisation abusive d'engins de récolte,
- la période de décroissance et d'apportas stables (1900 à 1980) due à l'échec du plan de repeuplement en liaison avec le fort taux de sédimentation et les conditions estivales anoxiques,
- la période de forte décroissance de la production (1981-1988) caractérisée par les fortes mortalités liées aux parasites (MSX et *Perkinsus marinus*), à la prédation et aux pratiques d'aménagement.

Des stratégies alternatives pour la restauration de la production d'huîtres en Baie de Chesapeake sont discutées.

Introduction

The American oyster (Crassostrea virginica) has historically been the most valuable fishery in Chesapeake Bay. At the turn of the century, more oysters were landed in Maryland than anywhere in the world. The fishery has long been followed and studied by biologists (Ferguson et al., 1880 ; Ingersoll, 1881 ; Yates, 1913). From the beginning of this century until the present, landings have declined steadily and the industry is now in crisis.

The Chesapeake Biological Laboratory (CBL) of the University of Maryland was built in 1925 to study the cause of the decline in production of oysters in the Bay (see Table 1 for main characteristics) (Truitt, 1925, 1927, 1931). Research was conducted on the effects of removal of cultch, placing size limits on adult oysters available to be captured and open season limits, to try to restrict the overfishing. Investigators defined the sampling techniques now used for the systematic annual oyster bar survey. Krantz and Merritt (1977) stated that the personnel of the CBL conducted the surveys until the late 1950's (Beaven 1954). Since then, annual survey has been conducted by the Maryland Department of Natural Resources (DNR). Intensive research has been done but only on limited aspects of oyster biology, fishery ecology. Not many reviews of the American oyster and oystering in Chesapeake Bay have been published. Korringa (1952) and Galtsoff (1964) described mainly the biology of Crassostrea virginica. For the Virginia part of the bay, Haven et al. (1981a) reviewed the status and problems of the oyster industry, while for the Maryland part, the only synthesis on oysters has been that of Kennedy and Breisch (1983), which includes the biology, the main diseases of oyster populations, management of the Maryland oyster industry, and an historical review. There is no specific analysis of the different causes for the decline of production, which are generally described in brief terms like overfishing, predation, water quality, sediment modifications or consequences of diseases.

Contributing further to the uncertainty, attempts to protect the resource and to reverse the substantial decline have obviously been unsuccessful. In this paper, our aim is to analyze the historical trends in oyster production in the Maryland portion of Chesapeake Bay in relation to overfishing, the use of the different gears, and their impact on the destruction of the physical characteristics of oyster bars.

Table 1 : Main Characteristics of Chesapeake Bay.

Main Bay	
Length :	322 Km
Greatest depth :	53 m
Average depth :	7.6 m
Surface :	569,800 ha
Volume :	68,109 m^3
Total shoreline :	7,401 km
Tidal range :	0.9 m at mouth 0.3 m at Annapolis
Salinity surface :	30 ‰ at mouth 15‰ at Annapolis
Watershed	
Main tributaries	8 Rivers (Susquehanna, Potomac, and James contribute 80 % of freshwater flow)
Total tributaries	419
Area of watershed	16,576,000 ha
Population of watershed	13 millions in 1980 (projected in 2020 : 16 millions)

The State of Maryland has had an oyster repletion program in place since 1960. The program includes shell planting and seed shell transplanting components. We will discuss the techniques and time of shell planting in relation to the physical and biological characteristics of the Chesapeake Bay, and propose new research to optimize the management of Maryland oyster production despite the prevalence of diseases.

I. Methods for reconstitution of oyster landings

For the Virginia part of the Chesapeake Bay, data on production came from a very exhaustive paper by Hargis and Haven (1988), who detailed how they rebuilt data for Virginia. For the Maryland part of the Chesapeake Bay, harvest data from 1820 to 1917 came from Grave (1912) and Yates (1913). Ingersoll (1881) and Stevenson (1894) gave the detailed statistics based upon the production of the different Maryland packing houses, the exportation of oysters shipped North, mainly for planting in Delaware Bay and Providence River, and for immediate consumption in New York and Delaware Bay. These data are compared with an estimate of the number of boats licensed or not and their yield. The data after 1912 came from different reports in the CBL library, from the Maryland Department of Natural Resources, and from the Fisheries Statistics

Branch of the National Marine Fisheries Service. Krantz and Haven (1982) and Stagg (1985) have, however, demonstrated that the present landings are underreported.

For comparison with other US regions, the following conversions are used : A US standard bushel is 2,150.4 cubic inches, Maryland bushel is 2,800.9 cubic inches, and a Virginia bushel is 3,200.1 cubic inches. To convert Maryland data to in U.S. bushels we multiply by 1.3, and Virginia bushels by 1.49. In the fisheries statistics, it is stated that in a US bushel the wet weight of oysters flesh varies with the season and ranges from 5.10 to 5.95 US pounds. A mean of 5.5lbs. is retained. Results in pounds are converted to Kg by dividing by 2.2 and then expressed in metric tons.

Thus a Maryland bushel contains 3.25 Kg wet weight of oyster tissue, a Virginia bushel 4.10 Kg, and a US standard bushel 2.5 Kg. These results can be compared with some values found in the literature (Table 2).

Table 2 : Estimated wet weight of oyster flesh per bushel from the literature

Unit Authors	Wet Weight in Kg of Oyster Tissue
US Standard Bushel MacKenzie, 1983	2.2
Maryland Bushel Truitt, 1945	3.64
Maryland Bushel Haven et al., 1981a	2.64
Virginia Bushel Haven et al., 1981a	3.18

Our data are in a good agreement with Truitt (1945) and MacKenzie (1983) but the Haven et al. (1981a) conversion rates are nearly 20 % low.

To compare the productions at various locations in the US with the production of other countries, it is necessary to use the same unit of measure. The one that we have chosen follows the FAO recommendation, i.e., the total weight of the oyster. By comparing the US statistics in pound of wet weight flesh and the FAO statistics in metric tons of total weight over the last 10 years, the percentage of the wet weight ranges from 7.4 % to 8 %. Our data obtained in the field (Patuxent River) showed that for market size oysters this percentage varies from 5 to 9 % in relation to the physiological condition of the oysters. If we use the percentage of 8 %, a US standard bushel corresponds to nearly 31 Kg, a Maryland bushel to 41 Kg, and a Virginia bushel to 51 Kg, total weight. DNR reports indicate that a Maryland bushel contains nearly 350 oysters, since the weight of market-sized oysters (3 inches) is 120 g - 130 g. For a bushel this converts to between 42 Kg to 45 Kg which is very close to the data obtained by our conversions.

Table 3 : Principal conversion rates for different jurisdictions.

Wet Weight in Kg Units Oyster tissue	Total Weight of Oyster in Kg	Volume of oyster in liters
US Standard Bushel 2.50	31	35.2
Maryland Bushel 3.25	41	45.9
Virginia Bushel 4.10	51	52.4

II. Trends in the World Production of Oysters

During the last ten years the total world production of oysters in the world (aquaculture and fisheries) has increased by 20%, from 859,682 tons in 1977 to 1,011,079 tons in 1986. This rise is due to the fact that production has increased in Korea by 68 %, in France by 57 %, and in Japan by 25 %. However, US production has decreased by 25 % since 1982.

The US was first in oyster landings until 1986 when it was passed by Japan and Republic of Korea. Since 1986 Korea has been first in world production of oysters (Fig. 1).

Those three countries (Japan, Korea, France) which practice oyster aquaculture, are increasing their production in contrast to the US, which mainly fishes for oysters. It is interesting to note that these four countries produced nearly 87 % of the world total.

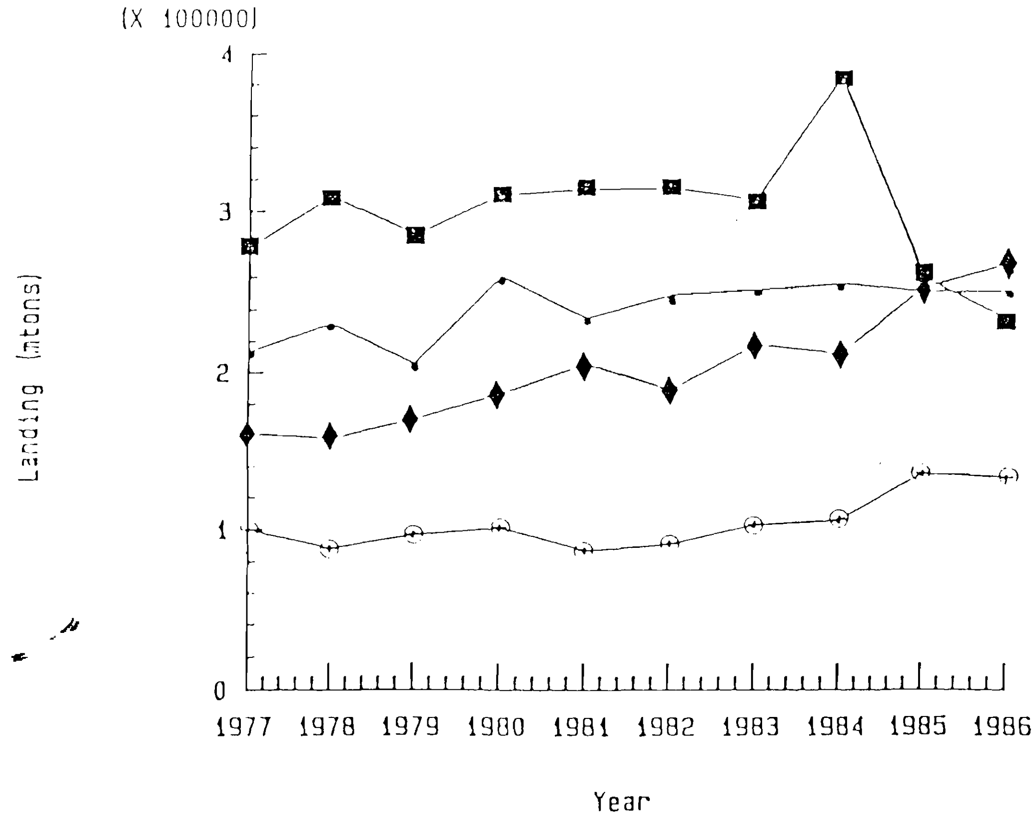

Figure 1 : Trends in the production of oysters for USA (■), Japan (•), Korea (♦) and France (⊕) expressed in 1*10 5 tons of total weight.

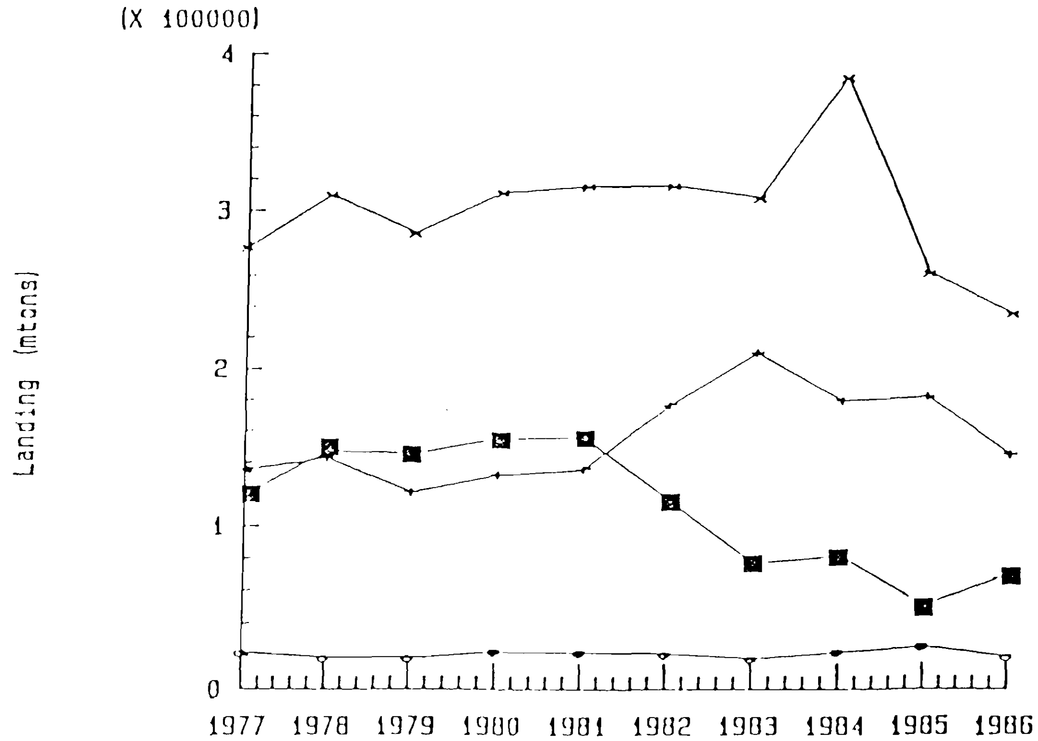

Figure 2 : Trends in US production of oysters (×), gulf (+), east coast (■) and west coast ( ) expressed in 1*10 5 tons of total weight.

III. Evolution of the United States Production

From the US landings it appears that the production of the Japanese oyster (Crassostrea gigas) on the west coast is stable with an annual mean of 22,000 tons and representing 8 to 10 % of the total production of oysters despite some recent disease caused by a Bonamia-like protozoan. In the east, Gulf of Mexico production (Florida, Texas and mainly Louisiana) fluctuated from 120,000 tons to 210,000 tons, with a maximum in 1983, and a mean of 156,000 tons (fig. 2). The Gulf of Mexico, which produced about 45 % of the US harvest until 1981 now represents 60 to 65 % of the total production. The Texas production has increased from 3 % to 12 % and the Louisiana production rose from 13 % to 30 %, making it the leading state in oyster production. Variation in the Louisiana oyster production mainly reflect adverse environmental factors such as hurricanes and dredging. The high salinity conditions of recent years gave highly successful oyster sets on shells, which were reseeded by the Department of Wildlife and Fisheries (Keithly and Roberts, 1988 ; Dugas, 1988).

The US east coast production, comprised mainly landing from the Chesapeake Bay, but includes Delaware Bay, Narragansett Bay and Long Island Sound, has declined from 155,994 tons in 1981 to 50,442 tons in 1985. This represents only 19 % of the total US landings whereas these regions formerly produced 40 to 50 % of the total production. This large decline in production of the northeast coast is responsible for the decline of the US landings.

IV. Chesapeake Bay Landings

The Chesapeake Bay production, obtained by combining the Virginia and Maryland data, demonstrate a tremendous decline in oyster landings (Fig. 3). The oyster industry in Virginia has been well studied during the last decade (for reviews see Haven et al., 1981a, and Hargis and Haven, 1988).

The Maryland oyster fishery was the greatest in the world at the end of the last century, with 990 public oyster bars spread over 111,600 ha. (Yates, 1913). The private use of the bottom is not developed with only 3600 ha of leased oyster ground representing 3 % of the oyster bottom, (Jensen, 1981) (fig.4). In contrast, large areas are leased in Virginia for private use (50,000 ha private vs. 97,200 ha public) (Haven and Whitcomb, 1986).

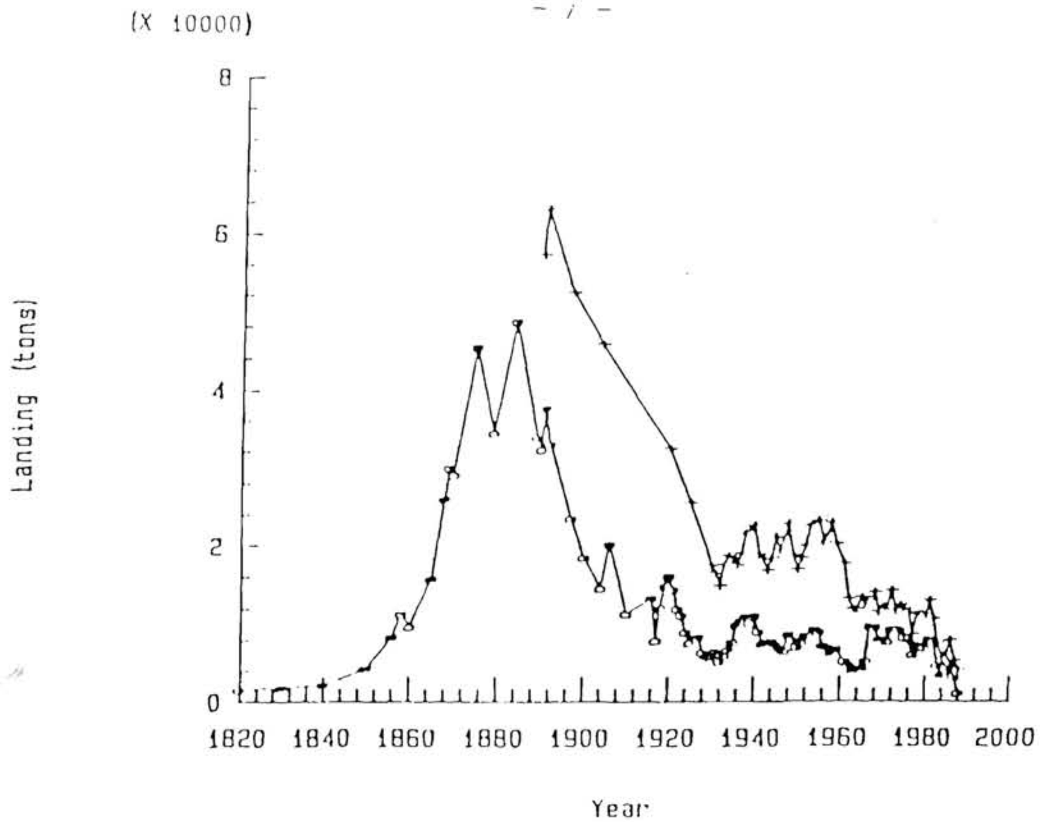

Figure 3 : Trends in oyster production, in wet weight of flesh, Maryland part (+), Chesapeake bay (▫).

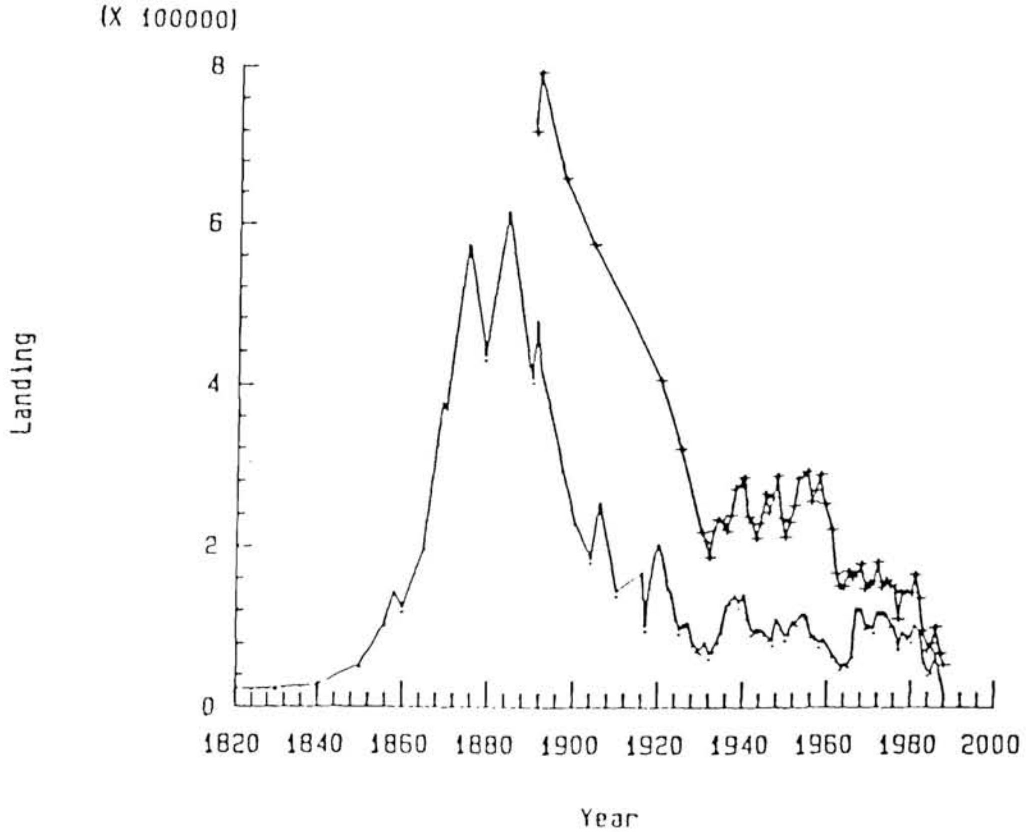

Figure 5 : Trends in the oyster production, in total weight Maryland part (•), Chesapeake Bay (+).

The analysis of the Maryland oyster landings demonstrate that this fishery has passed through 3 stages of production (Fig. 3) :

Stage 1 : From 1840 to 1890--The Greatest Fishery

Oysters were eaten by Indians, as evidenced by the large quantities of oyster shells near their camps. The early Maryland settlers easily gathered oysters since they were very abundant. As the population, trade, and traffic (boats, roads, railways) increased at the end of the nineteenth century, the demand for oysters went up. From hand picking, a very active fishery developed using new gears to fish the underwater populations of oysters (hand-tongs and dredges). Kennedy and Breisch (1983) indicated that the number of processing establishments in the Baltimore area increased from one in 1834 to 80 by 1868. In 1879, Ingersoll (1881) reported 98 packing plants with a production of 314,000 tons. The maximum landings in this period was 615,000 tons in total weight in 1884. The annual production stayed above 400,000 tons in total weight during 20 years from 1872 to 1893. After an examination of the old records, we conclude, like Chritsy (1964) and Kennedy and Breish (1983), that the early harvests were probably not greatly over estimated and give a realistic idea of the level of production which was supported by the bay and the tributaries. If we compare the number of boats fishing oysters in 1865 with an annual production of 200,000 tons, and in 1879 with an annual production of 434,000 tons, there were, respectively, 2,555 and 3,275 boats with a total crew of 13,748 (Ingersoll, 1881). The number of boats increased by 28 % but doubled the production. The efficiency of the boats was increased by two main means :

- extension of the fisheries by discovery of new bars. For example, the large reefs in Tangier Sound were discovered in the year 1840 (Kennedy and Breisch, 1983)

- increase of the efficiency of the gears. After 1865 large dredges became legal, making it possible to fish deeper than 7 meters, a depth which could not be reached by hand- tongs. Patent-tongs came on the market in 1887 (Fig. 6) and also allowed fishing everywhere.

The consequences of these large increases in the annual landings have been the destruction of the most productive beds. As in England and France (Roche, 1887 ; Héral, 1989), despite regulations on the harvest season, on the type of boat and in 1868, a licensing system for the oyster boats, the fishing pressure remained intensive.

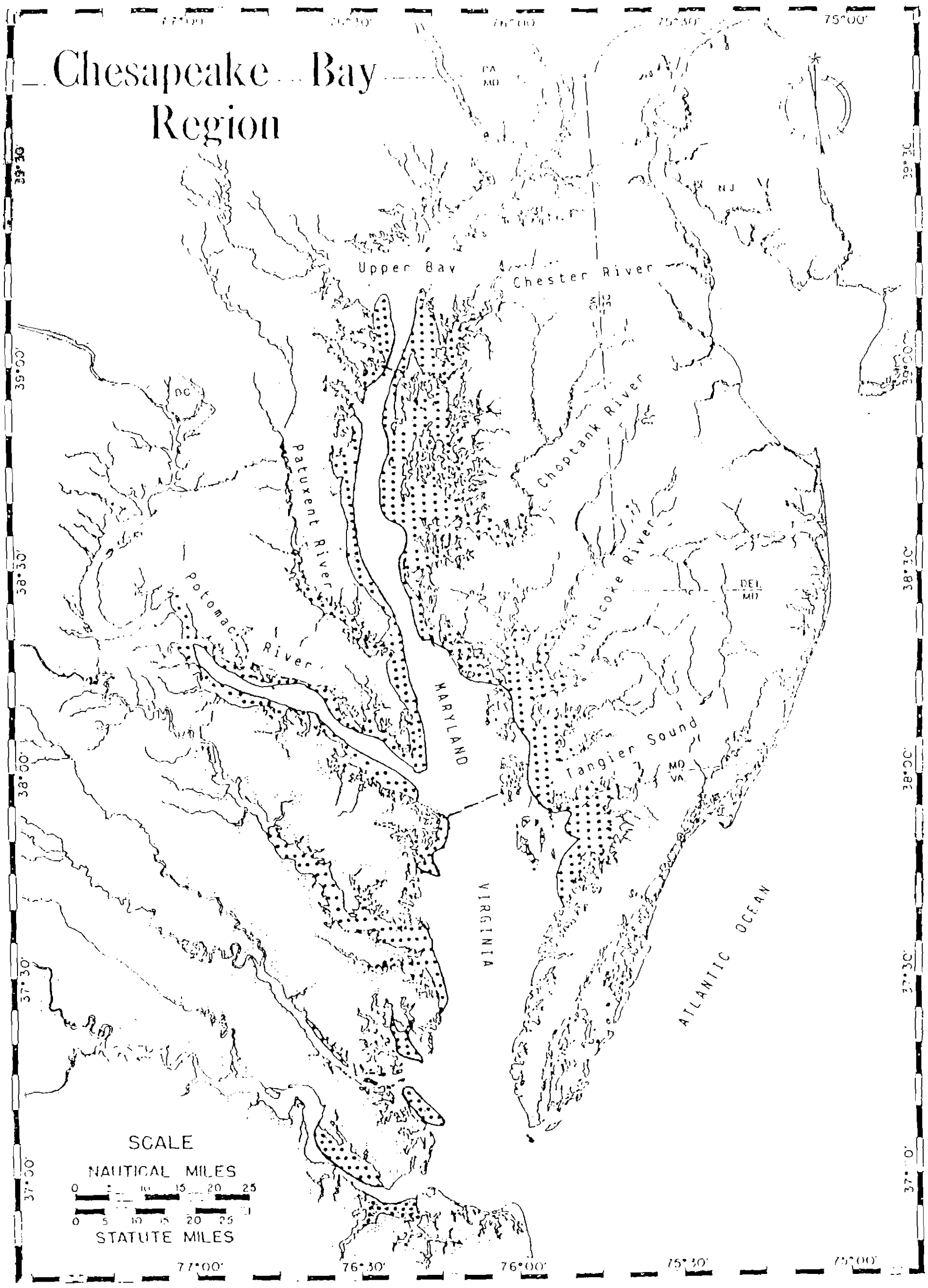

Figure 4 : Location of the main public oyster bars in the Chesapeake bay (::::::).

By dividing the maximum landing (615,000 tons in 1889) by the total surface of the oyster bars described at this period (111,600 ha), with an individual oyster weight of 150 g, the mean density of the population is obtained. It is nearly 3.7 oysters per square meter. Winslow (1884) found that the mean density of the oyster bars was $5.4/m^2$ in 1879, and Brooks et al. (1884) found a mean density of $3.5/m^2$. These results demonstrate that the landings were at the same levels as the total living stocks, meaning that the fishing pressure was extremely heavy. The fisheries could reach such a high level only because the different adult age classes of all the oyster bars of the Chesapeake Bay and its tributaries were exploited. The capital in biomass of all the previous years (an oyster can live more than 15 years) was consumed.

Several reasons could explain the failure to adequate reproduction :

- the fishing of the juveniles : during this period large quantities of spat were sold to other states for reseeding. For example, in 1879, 89,329 tons of spat were sold for bedding in northern waters from Delaware to Maine (Ingersoll, 1881),

- the destruction of the spat attached to the adult oysters, by the packing houses which did not reseed the young oysters,

- the permanent removal of cultch which was necessary for setting of the larvae; the fishermen and the packing houses did not put shells or other hard substrate back on the oyster-beds,

- the destruction of the habitat. Before the intensive fishery, the oyster reefs were very sharply defined and often elevated above the hard bottom. They could be of considerable thickness below and above the surface, even being exposed at low tide. In the Gulf of Mexico, Bouma (1976) demonstrated that the base of the oyster reef was buried shell, deposited over several thousand years. Commercial harvesting has changed the nature of the oyster bars. Winslow (1887) assumed that dredging enlarged the bars by dispersing the dredged oysters out of the reef onto soft bottoms. The dredges and the patent tongs dispersed the shell and reduced the height of the reefs above the sediment. The bars were, after the intensive fisheries, broader but with much less relief. This modified the physical characteristics of the environment around the oysters ; a non-fished oyster reef was less subject to siltation as it was above the water sediment interface. The currents and the apparently increased turbulence in relation to the height of the reef prevented sedimentation and allowed the biodeposits of the oyster populations to be transported away. This might explain the observations of Winslow

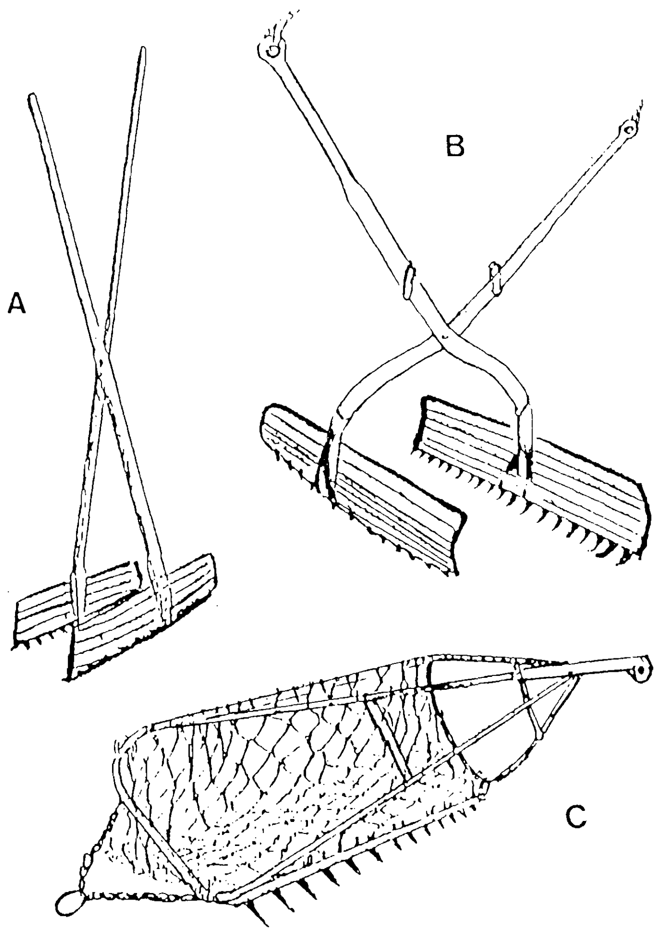

Figure 6 : Gears for catching oysters in the Chesapeake Bay : (A) hand tongs, (B) patent tongs, (C) dredge.

(1887), who found that the overworked beds had often mud and sand among the shells and that the settlement of the spat was three times less in a fished bar than on a wild bar. It has now been shown that increased turbidity in proximity of the oysters has a deleterious effect on their growth rate, causes negative production, and a decrease in the assimilation rate (Héral et al, 1983).

All these factors combined together to cause the destruction of the most productive beds. In 1881, Ingersoll stated that the famous beds of Tangier and Pocomoke sounds were exhausted, and Winslow (1887) suggested that old beds which were overfished should be rebuilt with scattered materials, but these recommendations were not followed. Truitt (1927) established that the overfishing of oyster beds brought about a complete depletion of one-fifth of the oyster bars and near exhaustion of one-third of the original oyster bars.

Level 2 : Decreasing and stable landings from 1900 to 1980

After a continuous decline in landings from 1890 to 1910, characterized by permanent overfishing, the harvest came to a stable phase which fluctuated around 80,000 tons. Krantz and Meritt (1977) described the fluctuations with a decline in harvest during the 1960's. It appeared that variations in landings were mainly related to recruitment intensity. For a given year, the majority of the production was fished 4 to 5 years after settlement. Periods of low recruitment, 1952-1960, and 1966-1978, were followed by years of high spat set (1965 and 1980) (fig. 7). With this data on spat set, it appears that during the last sixty years, the fishery has been supported by three main peaks of recruitment. At twenty year intervals, a major spat set has occured, even in 1980 and 1985 with a very low stock size in relation to the diseases. Though, first the water quality of the bay was sufficient to permit high survival rate for oyster larvae and secondly the relation stock-recruitment permitted still a good record in 1985. Ulanowicz (1980) demonstrated that variations in spat density were correlated with the cumulative high salinity during the spawning season.

It is interesting to note that Virginia landings for the period 1940-1960 for the first time exceeded Maryland production. Hargis and Haven (1988) noted that it was due to private production from leased bottoms while the harvest from public bottoms continued to decline.

Different management operations have been used in Maryland to try to increase the public oyster production. After the cull law of 1890, which required that the shells with spat and young oysters be returned to the oyster bars, legislation for shell planting initiated an annual placement of shell as cultch for seed on the bars. Kennedy and Breisch (1983) described how a 10% shell tax was charged in 1927, a 20 % shell tax in 1947, and in 1953 a law was enacted for a 50 % shell tax. It required that the oyster packers and processors had to sell at least 50 % of their shucked shells to the State, which collected and reseeded the fresh shells. Funds for these operations come from a tax on each bushel of processed oysters. These regulations and laws were all failures. The shells were not returned to the oyster bars (1936), or the funds to sow the oyster shells were not collected (1948). Even after the law of 1953, the supply in shells was still insufficient. For this reason the Maryland Department of Natural Resources (DNR) made the decision in 1961 to use "fossil" shells dredged by a contractor who would plant them from May to, normally, the end of June. The mean quantity of dredged shells is 205,000 tons per year. The largest amount of shell, 360,000 tons, was planted in 1975. The state always attempts to buy all the fresh shells available, but which now represents only 3 % of the dredged shells.

It was well demonstrated by Truitt (1936) that an overfished oyster bar could again become a productive area by using a properly managed shell planting program. Also, Abbe (1988), working on an oyster bar, near Calvert Cliffs Nuclear Power Plant, on hard bottom, a place where the velocity of the current was high, demonstrated that shell planting can be an effective mechanism for increasing oyster yields. But this operation of reseeding the dredged shells is a collective operation for the public Maryland oyster bars, and is done by only one contractor who follows the allocation and the schedule defined by the oyster committees and DNR biologists. The shells may be planted 2 or 3 months before the main settlement. Spawning occurs in the Chesapeake Bay from June to August (Shaw 1969, Kennedy and Krantz 1982), but in some years the largest spat set may occur in September, (Truitt, 1925). It is well known that oyster post-larvae set on newly-planted, very clean shells better than on old shells because of the fouling and the siltation. For these reasons, Shaw (1967) recommended for the Chesapeake Bay shells should be planted in the first week of July when the larvae are numerous. The problem for the Maryland oyster fishery is the size of the public reseeding plan and the means by which the shells are moved, which dictated that the operations begin too early in the season. In other states, it appears that private oyster companies working on their own grounds are more efficient. For example, in Louisiana it takes a week to deploy the shells. In Long Island Sound, Korringa (1976) reported the private companies spread the shells in 4 days, which are chosen according to the abundance and developmental stage of the larvae in the plankton.

MacKenzie (1983) did a scuba survey in the Chesapeake Bay during the normal oyster setting period. He observed that beds with high densities of oysters had much less silt than beds with only shells. Very often the Maryland beds had quantities of shells but they were partially covered by silt. Many management practices were recommended for avoiding sedimentation by silt before the oyster setting season: use of dredges without bags, mud-cleaning machines on boats and the employment of quick lime to control fouling organisms. Our own observations during 1989 showed a tremendous quantity of fouling both at the bottom and in the water column, on different substrates in the Patuxent River, particularly in June and July. All these observations indicate the same thing : to make shell planting more efficient for settlement, it is necessary to change the planting schedule and the way in which it is done.

The "fossil" shells are not the best cultch material (Cabraal and Wheaton, 1981). They are very often broken and therefore of minimal value for spat settlement. Comparisons between shells of living oysters, fresh shells, old "fossil" shells and their efficiency in attracting spat settlement demonstrated that the densities of spat were higher on living or fresh shells than on fossils shells. It could be due to an attractive effect of the conchyolin, the protein of the shell. It would be interesting to use fresh clam shells instead of oyster shells, as the landings are important, and large amounts of clam shells are available. This cultch is good and was used in the Louisiana oyster fishery (Dugas, 1988), because it was not a heavy cultch and it was easier for the oysters to maintain their position on top of the soft sediment (Korringa, 1976). In facts, some use of clam shells is occuring in Chesapeake Bay, but reports on their efficiency are not available. One problem is that the processed clam shells are "cooked", possibly limiting their efficiency.

The Maryland DNR annually plants nearly 205,000 tons of oyster shells on natural bars to serve as substrates to maintain the recruitment. Shells are planted in areas of good settlement and used to carry the oyster seed from areas of high spat set to areas of low settlement. When the density of spat is higher than 300 per bushel, they are transplanted with a mortality of 10 to 15 % (DNR, 1987).

The shell to be planted should be allocated to areas where the highest densities of spat have been observed in the previous years (for example, fig. 8). The spat abundance is generally highest in the mouth of the different tributaries, but cultch has also been planted in places where no recruitment has been observed for several years (Kennedy and Breisch, 1983). Christy (1964) assumed that shells were planted according to biological criteria, but shells are also placed where demanded by county politicians under pressure of the watermen. To evaluate the efficiency of the reseeding plan, some rough calculation can be made. By inspection of the different estuaries and comparing the trends in production 3 years after, with the quantities of shells and seed resources, it appears impossible to know which part is due to fishing and which part to the reseeding plan. Then, very often, the landings are still declining (fig. 8, example of the Tangier sound). With a seeding of 5,000,000 bushels, a maximum spat density of 200 per bushel (fig. 7) and a mortality rate of 10 % per year (DNR, 1985) the expected production after three years would be 91,000 tons, with a range between 80,000 and 120,000 tons. Although the harvest increased after some very high level of recruitment (1945, 1965, 1980) (+ 61,500 tons, 5 years after 1965), it never went above 120,000 tons, which is 6 times less than the landings of the end of the nineteenth century. Prosperity has not returned to the fishery despite the following regulation and management efforts on the public oyster bars :

- the market size limit of 7.6 cm,
- restricting the fishing season from 15 September to 31 March,
- daily catch limits set by boat and gear type and the number of crew,
- the reseeding plan.

The fact that management has not worked appears to be mainly due to the loss of suitable oyster habitat. Seliger and Boogs (1988a) demonstrated that there was a tremendous decline of the surface area of oyster bars in the tributaries. By comparing the results of Yates survey (1913) and their survey obtained with echosounder calibrated by sampling with dredge and by scuba diver, they found that only 14 % of the surface was still covered by oysters and shells in Chester River, Broad creek and Tred Avon River. In a recent survey of the Virginia part of the oyster bars, Haven and Whitcomb (1986) showed that only 21.8 % of the oyster bars classified at the beginning of the century still survived. A study using an underwater microphone and verified by sampling with hydraulic patent–tongs showed the same tendency in Pocomoke Sound with only 19.5 % of the original surface of public oyster ground remaining (Whitcomb and Haven, 1987). In 1989, we conducted an intensive systematic survey on eight oyster bars in Choptank River, which provided additional information. Only 48 % of the original listed acreage, based on Yates survey (1913), was observed. So, if nothing is done to recover the lost habitat, harvest could not reach again a high level, even if there were cyclic recruitment successes.

Furthermore, the elevation of oyster reefs above the surrounding bottoms has apparently declined because of fishing activity. Obviously the overfishing and the type

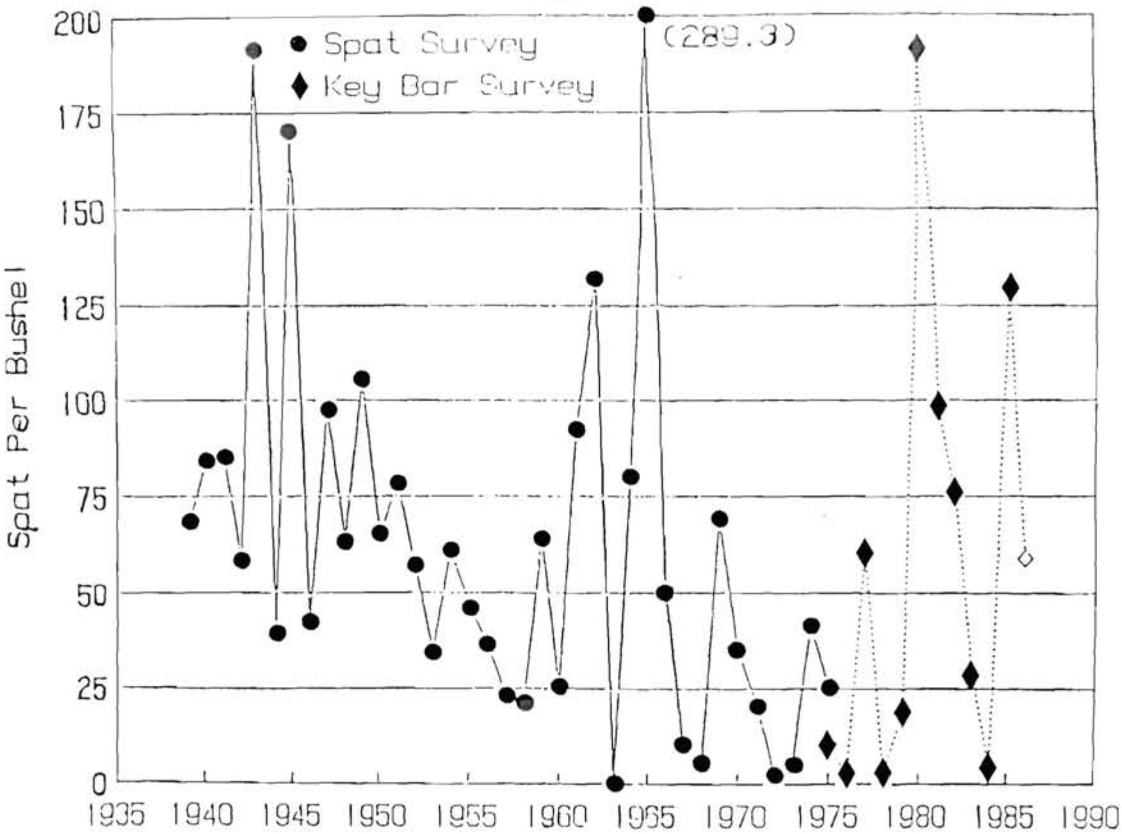

Figure 7 : Time–series in an index of recruitment : average number of spat per bushel in the Maryland part of the Chesapeake bay (from DNR 1987).

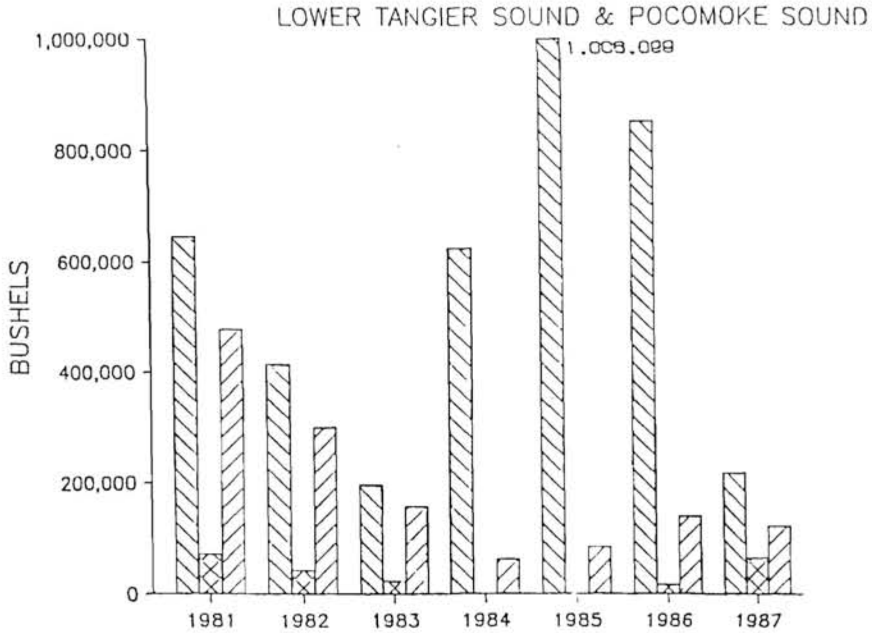

Figure 8 : Example of management activity (planting oyster shell and seed) to harvest in Lower Tangier Sound ▨ bushels of shell, ⊠ bushels of seed, ▧ bushels harvested (from DNR 1987).

of gears used contributed to the destruction, but sedimentation can also be a major factor in the reduction of oyster harvest. We have already described the action of siltation upon the decline of spat settlement particularly in relation to the reseeding plan. Galtsoff (1964) described how many productive oyster bottoms along the East Coast had been destroyed by siltation. In the Chesapeake Bay the inputs of suspended particulate matter has mainly two origins : erosion of the shore, and the large input from the rivers.

The 3,950 miles of shoreline in the Maryland part of the Chesapeake Bay and its tributaries are constantly eroded by currents, tide effects, wind and storm effects, stream flows and possibly increased bottom activity. Wolman (1968) calculated that about 2,400 ha of land have been eroded during nearly a century, which gives an average loss of 6.5 ha per Km of shoreline and an annual output of 0.2 x 10^6 tons. Hurricanes (cyclonic storms) have tremendous erosion effects. In the Chesapeake Bay, Hurricane Agnes in June 1972, was an obvious example which delayed the recruitment of oysters and which contributed to the destruction of the clam fishery. Hurricane Elena in September 1985 destroyed a part of the oyster reefs in Florida. It removed and buried the oysters, covering them with muddy sediment where they died (Berrigan, 1988).

All the rivers flowing into the bay carry enormous loads of sediment. For example the Susquehanna River, discharges 0.6 x 10^6 tons of suspended sediment per year, the Potomac River 2.3 x 10^6 tons per year and the Patuxent River 8.7 x 10^6 tons per year (Schubel, 1968). The total amount of sediment coming from the land was estimated to be 8 million tons per year (Wolman, 1968). Seventy percent of the inputs come during the time of peak runoff from February to May. Thus, a sedimentation rate of 3 cm per year was measured in the channels up to Chesapeake Bay Bridge. In Patuxent River the sedimentation rate reached 2.1 m from 1859 to 1966 at Upper Marlboro. Schubel (1968) found that all the sediment carried by the Susquehanna was deposited in the upper bay. But the Potomac carries its sediment a very long distance into the Bay. Figure 9 shows the predominant erosion-deposition patterns within given main stem areas of the Bay. There are five major areas of bathymetric changes ; three depositional, one erosional, and one area of no apparent change (Hill, 1988). There is in the Chesapeake Bay a natural tendency for sedimentation in the channels and erosion on the borders, but the influence of man's activity on the sedimentation rate in the bay is important. The deforestation and clearing for agriculture had multiplied the inputs by 4 to 8 times. In addition, urbanization has promoted erosion of the land. Twenty five to thirty percent of the one million tons reaching the Potomac estuary come from the area of Washington, D.C. After a thunderstorm, what is typical is the sudden changing of the colour of the

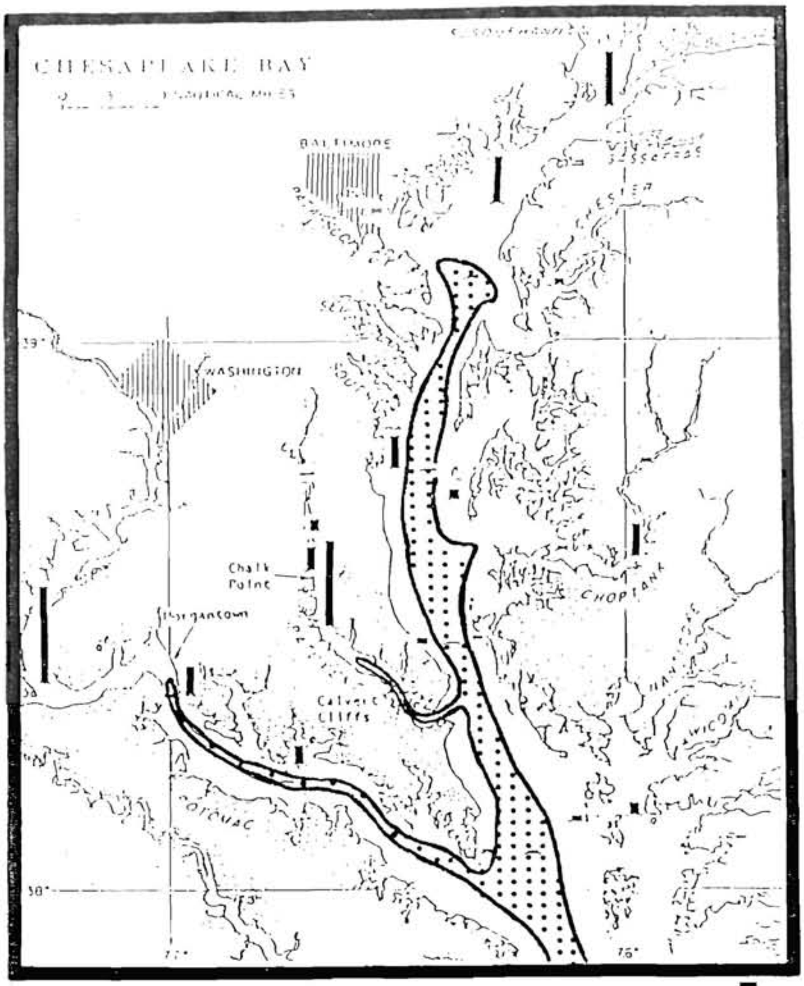

Figure 10 : Spatial distribution of average annual benthic biomass in relation with the region affected during summer by an -xic bottom waters from Holland (1987).

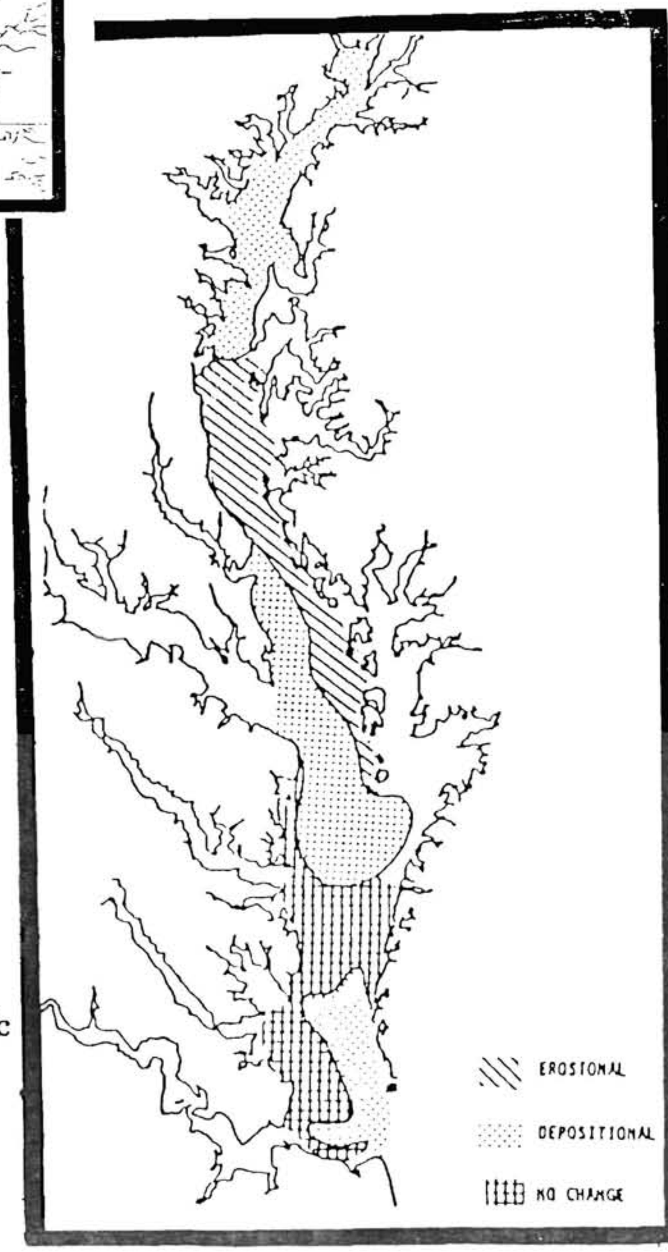

Figure 9 : Gross deposition-erosion patterns determined by comparison of historic bathymetric data from Hill (1988).

bay becoming yellow grey. The sedimentation rate on oyster bars can also be increased by dredging operation which is practiced to maintain the ship channels into Baltimore harbour and in all the tributaries to maintain and develop recreational activities (yachting, marinas...). Several clam dredging boats working in the vicinity of oyster bars, in places where the velocity of the current is little, can also contribute to an increase of the sedimentation rate on the bars. So, it appears clearly that the oyster habitat is limited in the upper bay and in the different tributaries, by heavy siltation rate and sometimes reduced salinity.

In deeper areas, oyster habitat is limited by the anoxic conditions which occur in summer. A review of the anoxia problems since 1950 demonstrated that the annual volume of anoxic bottom waters in the Chesapeake Bay shows no statistically significant increase (Seliger and Boogs, 1988b). The extent of anoxia is directly related with the flow of the Susquehanna River. The freshwater flow induces stratification in spring and summer which inhibits vertical mixing. Respiration in benthic sediments and the water column under the pycnocline consume the available oxygen until it is totally depleted. A severe summer anoxia in the upper Chesapeake Bay occurred in 1984 in waters deeper than 6m (Seliger et al., 1985). The anoxic waters, when the conditions are severe, may reach the mouth of the different tributaries. Benthic organisms living at depth greater than 6m are killed, only fast growing species which can reproduce all year are present in such areas when conditions are more favorable (Holland, 1987; Fig. 10). Thus this appears to be another strong limiting factor on the habitat available to oysters.

In the early 1960's MSX disease invaded the Chesapeake Bay. The haplosporidian Haplosporidium nelsoni came from Delaware Bay after destroying the oyster population there in 1957 (Haskin et al., 1965). This disease had a very severe impact on Virginia oyster landings (Fig. 3), which declined by 50 %. In Maryland, as MSX activity was salinity-limited, it caused mortalities only in Tangier Sound's. MSX disease then regressed and virtually disappeared from the Maryland part of the Bay from 1965 to 1981.

Level 3 : 1981 - 1989 : Large decrease in production caused by high mortalities

The annual survey by MDNR biologists recorded, between 1980 and 1982, mortality levels of 30 to 50 % for adult oysters. Normally, using the same sampling design from 1970 to 1980, the oyster adult mortality varied from 5 to 20 %. A period of low mortality occured from 1984 to 1986. But fall mortalities for adult oysters occured in 1986 and increased in 1987-1988. The cumulative mortality of a year class could reach

90 %. During that period the harvest pressure remained permanent despite the high levels of oyster mortality which caused the disapearance of most of the adult oysters. Since 1986, the production in the Maryland portion of the Chesapeake Bay has been 15,000 tons per year.

Numerous factors can cause these high levels of mortalities particularly diseases, predation or degradation of water quality. Two main diseases are related to mortalities in the Chesapeake Bay, the haplosporidium parasite Haplosporidium nelsoni (MSX) and the protozoan Perkinsus marinus.

MSX invaded the lower Chesapeake bay in Virginia from 1961 to 1966. MSX requires salinity greater than 15 ‰. The infections remained low and disapeared below 10 % (Haskin and Ford, 1982). Later in 1981-1983 and again in 1986-1987 a new MSX outbreak occured in Virginia and Maryland during a particularly dry period which caused salinity increases in the Bay. The prevalence of MSX infections were not very high, rarely above 20 %, but only a few bars in the upper, low salinity, part of the bay were free of disease (DNR, 1987). High salinity conditions with warm winters created good conditions again for MSX. The infection occurs mainly in spring and summer over 5 months. As early as the first year in 1961, mortalities occured at the end of the summer and the year after at the end of the winter, with a cumulative annual mortality rate of 30 % (Andrews, 1966). Furthermore, the MSX infections acted upon the physiology of the oysters. Newell (1985) reported a decline of the filtration rate in relation with MSX abundance with a reduced condition index, reduction of the fecundity and a reduced glycogen stores (Barber et al., 1988). A clear inhibition of gametogenesis has been shown in relation with intensity of infection but there was no correlation between annual fluctuation in rates of parasitism and oyster recruitment (Ford and Figueras, 1988).

Resistant strains of American oyster have been obtained by Ford and Haskin (1987) by crossing oysters from natural populations which survived the MSX epizootic for 6 generations. These oysters had delayed infections and mortality rather than being immune to infection, but these strains could provide practical interest to watermen. Unfortunately, there are infected as the natural oyster population by the second disease occuring in the Bay (Krantz, pers. com.).

This second most important parasite is Perkinsus marinus. "Dermo disease" as it is called, is present from the Gulf coast to the Northeast Atlantic coast as far as Delaware bay. This disease was reported for the first time in Maryland by Otto and

Krantz (1976) in the lower Chesapeake bay. The parasite is not salinity dependant. The DNR survey during fall 1988, demonstrated clearly that the whole bay was contaminated (fig. 11) with a very high prevalence rate, sometimes whole oyster populations were infested. Perkinsus marinus is pathogenic during warm temperatures ; under 20°C, the oysters expelled the pathogens (Andrews, 1984). This protozoan inhibits gonad development (Menzel and Hopkins, 1955). The abundance of this Dermo disease is correlated to the density of oyster populations, because infections are caused by the dilution and dispersion of the parasites free in the water when the oysters die. Mobile vectors could also transmit the infection, in particular the ectoparasitic gastropod Boonea impressa (White et al., 1987-1989). Contrary to the case with MSX, spat and young oysters are not usually infected by Perkinsus marinus.

Superimposition of the maps of the oyster mortalities, from 1981-1983, and 1986 and 1987, with the respective abundance of MSX and Dermo disease will emphasize the correlations between prevalence of the diseases and mortalities in the different areas. Although mortalities higher than 20 % occured in 1981-1983 in the Upper Bay near Baltimore without MSX and Dermo being abundant. These mortalities could be related to environmental conditions with unusually high temperatures in summer along with hypoxic conditions. Beaven (1946) demonstrated that for this area, many incidents of mortality were correlated with high run-off of the Susquehanna River. There was a good agreement between mortality rate and MSX abundance for Tangier Sound and the mouth of the Choptank river in 1981-1983, 1986 and 1987. But in 1981-1983, MSX was abundant in the mouth of the Patuxent river, but without abnormal mortality. In contrast, MSX was absent in the South of Potomac River in 1981-1983 and 1986, places where high mortalities occured. In fall 1987, mortalities largely increased and reached 75 to 100 % in Tangier Sound, mouth of the Potomac river and in the mouth of the Choptank river where the prevalence of Dermo was above 50 % and MSX above 20 %. The mortalities, which did not exceed 25 %, were located up the river and in the upper bay where MSX and Dermo disease were less abundant (Krantz, 1989). Thus, it seems that high mortality levels are more closely related with Perkinsus marinus abundance than with Haplosporidium nelsoni.

Many predators, despite the meso salinity of the bay, can also increase the mortality rate of oyster populations. Webster and Medford (1959) noted that the flatworm Stylochus ellipticus could be a very active predator on young spat in the Chesapeake bay, while oyster drills are not abundant in the Maryland part of the bay because of the low salinity. But the most important predation could be the blue crab, Callinectes sapidus. The predation rate is directly proportional to crab size and

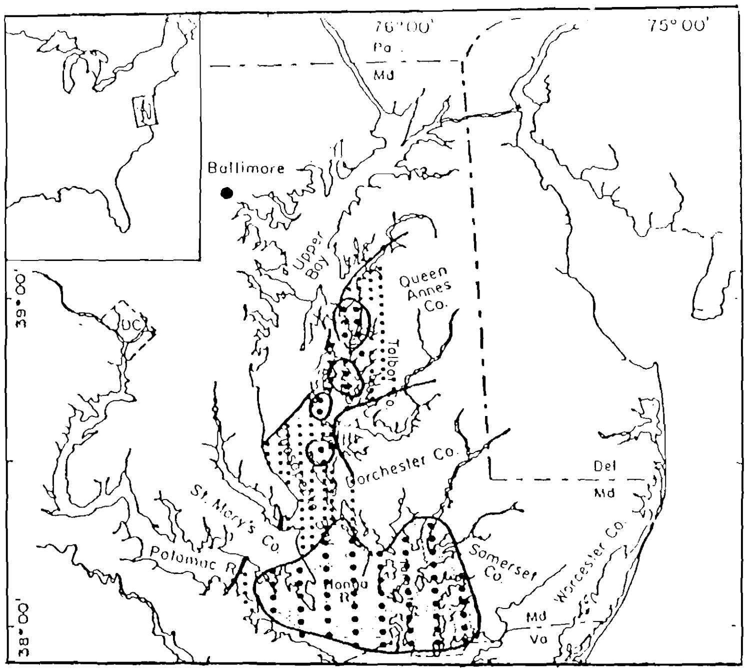

Figure 11 : Perkinsus marinus distribution during the fall 1988 survey (from DNR unpublished data). > 50% , > 20% .

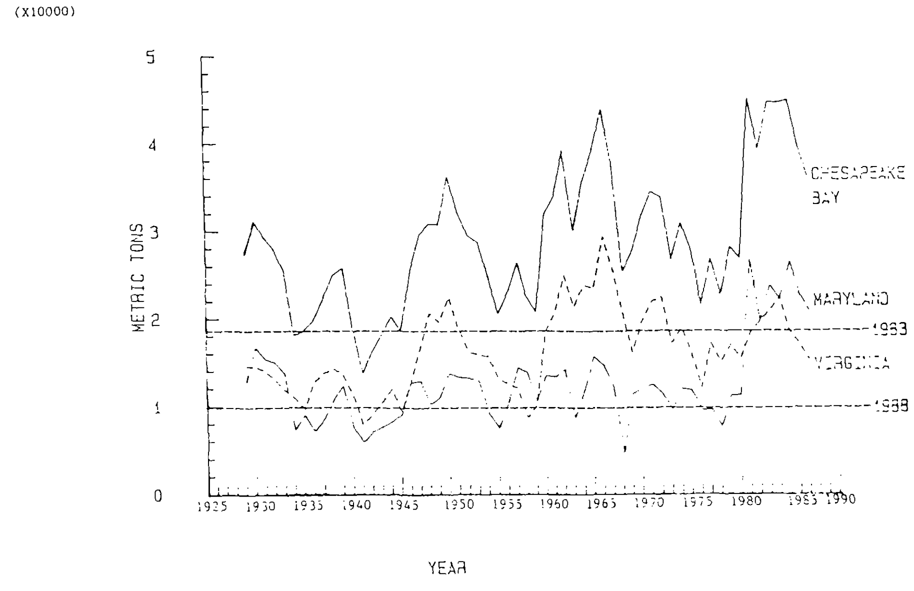

Figure 12 : Evolution of the blue crab commercial catch 1925-1987 in Virginia, Maryland and in the Chesapeake Bay expressed in ten thousand metric tons from Rothschild and Staag, 1990.

inversely proportional to oyster size (Bisker and Castagna, 1987). These authors demonstrated that blue crabs could eat 16 spat per crab per day and large crabs can cause significant mortalities until oyster reach a shell height of 25 mm. Normally, blue crab cannot successfully eat adult oysters except when they are thin-shelled (Lunz, 1947). Larsen (1974) found blue crab densities up to $13m^2$ in the James river. It is interesting to note that the highest densities of blue crab occures in summer time on the margins and in the tributaries of the Chesapeake bay. The blue crab fishery is one of the most important in Maryland with both commercial and large recreational fisheries. Commercial landings of blue crabs exhibited a twofold increase between the year 1975 and 1981 (fig. 12), remaining at an annual production higher than 40,000 tons for the bay until 1986. At least some of this increase resulted from an increase in the blue crab populations (Rothschild and Stagg, 1990). The mud crab Panopeus herbstii is also present at high densities in the Chesapeake Bay (Larsen, 1974) in salinities ranging from 10 to 34 % (Schwartz and Cargo, 1960). This crab is a more important predator than blue crab (Bisker and Castagna, 1987) but the densities in the whole bay and their evolution are not known. However, the large increase of blue crab population could play a role in the increment of the mortality rate of the oyster since 1981.

The degradation of water quality is very often given, as an increasing factor of the oyster mortality rate, particularly by the watermen. As the pollutants affect bivalve larvae more than adults, it can be noted that large spat sets which occured in 1981 and 1985 demonstrate that summer environmental conditions permit a normal growth rate and metamorphosis of the larvae. Large discharges of fresh water in the upper bay, the high sedimentation rate, and anoxic bottom waters can, either separately or together, cause mortalities. The concentrations of heavy metals in the bay are below the level which causes mortalities of American oyster larvae (Calabrese et al., 1973, 1977 ; MacInnes and Calabrese, 1978). The impact of organotin compounds should be studied in more details as this pollutant affects oyster larvae at very low concentrations (for a review on oysters see Héral et al., 1989). Tributyltin (TBT) concentrations in the water column of Chesapeake Bay marinas were above the toxicity limit for Crassostrea virginica larvae (Hall, 1988). But in non-marina areas the reported concentrations were not toxic for oyster larvae in terms of acute toxicity. So it appears that chemical pollutants, and particularly heavy metals and their salts, could not play a direct role in the increased mortality rate of oyster larvae or adults.

IV. Alternative strategies for restoration of oyster production in the Chesapeake Bay

These reflections mainly concern the Maryland part of the bay, but similar proposals could be applied to Virginia especially for aquaculture on private bottoms. However Hargis and Haven (1988) have already made strong recommandations to improve the oyster production of this state.

If the present management structure oyster fishery is retained, restoration of production can be achieved by changing inadequate management practices which have contributed to the decline. For several decades oystermen have obviously practised overfishing, which has had a more noticeable impact in recent years. More adult oysters are removed each year than are recruited to the coming year class minus the cumulative mortality, which are both functions of natural conditions and management operations (shell planting, reseeding...). It is important to remember the overfishing of oyster in Chesapeake Bay is a different type of overfishing than that which occurs for finfish. In particular, for oysters overfishing results in not only taking more oysters than the stock can replenish, it also results in the destruction of habitat. Overfishing plus natural mortalities have established critical conditions in several rivers which lacking adequate populations of adult oysters, creates severe conditions for spat set in the vicinity. Limiting the landings by shortening fishing season and enforcing a licenced boat system might not be enough. It would be interesting to develop the sanctuary concept in different parts of the bay in which stocks for reproduction are maintained. Furthermore, fisheries should be controlled by closing bars and rotating the opening every four or five years (time of the mean growth rate) for the most productive oyster bars.

To assist management it would be very useful to have a better estimate of the area of the public bars with living oysters. It is unnecessary for the state to maintain and try to manage bottoms with mud and empty shells. From 990 bars with a total area of 116,000 ha, as estimated at the beginning of the century, what is the real numbers of bars and size of oysters grounds at the present time ?

By eliminating from management - at least temporarly - oyster bottoms which are not more productive could enabled focus on those grounds that are productive. Knowing the spatial distribution of the stocks, would allow planned management of the fisheries (sanctuaries, rotation), and the reseeding plan could be optimized.

Before placing cultch in the reseeding plan, the right place, the right time and the right means must be chosen. The allocation of shell must not be decided mainly by social constraints but for biological reasons. The habitat must be favourable, in particular they must be far away from anoxic bottom waters during summer, and in places where salinity remains high enough to facilitate the survival of the larvae. Sedimentation must be low, first to keep the cultch as clean as possible, secondly to guarantee a good survival rate of the young spat. Sectors of high spat settlement in the past years must have priority, but new areas at the vicinity of the sanctuaries which would be created must be found.

Considerable scientific work and aquaculture practices have showed, around the world, but mainly in Japan and France that it is best to employ spat collectors when the swimming oyster larvae are abundant, about 10 to 15 days before the settlement, to avoid fouling and sedimentation. In contrast, in Chesapeake Bay, Maryland, shell is planted 2 to 3 months before the spawning period. This delay is mainly because the Department of Natural Ressources of Maryland (DNR) uses only one private contractor for the whole bay. In the existing fishery context, we propose that all the oyster fishermen who profit by the collective operation, plant the cultche in 15 days, when the biologists find that oyster larvae are abundant in the water. While it is certain that by this strategy, the total amount of shell planted might be substantially reduced, the gain in efficiency might counterbalance the reduction.

Regarding the technical aspects of the reseeding plan, the efficiency of different kinds of cultch (oyster shells, clam shells, concrete, slates, stones...) must be compared with dredged fossil shells, which are actually used. The comparison must be done in terms of biologic attraction for oyster larvae, hardness and stability of the cultch, behaviour against fouling, and rugosity of the bottom covered with the cultch to avoid siltation. As a matter of fact the depth of the shell layer could be very often reduced, since spat that are buried do not survive. Optimisation of the density of shell in relation to the number of spat and the cost and yield of the operation must be achieved.

Reseeding the spat in areas without recruitment, in places where growth rates are very fast and mortality is low, can be good management, but it might also spread disease. Before spat is reseeded, sampling for the abundance of diseases must be done. Even if the spat is not directly infested by a parasite, it could carry the disease as a host. Similarly, before reseeding spat in areas where MSX and Dermo are present, it is necessary to eradicate previously parasited oysters by removing all the oysters. How this could be acomplished is uncertain. This is particularly true for Dermo disease, which contaminates oysters by proximity. Furthermore, the spat must be reseeded in places where the habitat of the oyster is the most favourable to its growth rate. The density of the reseeded spat must remain low to permit, first good physiological conditions to resist against the disease, secondly to avoid contamination by proximity, which is directly related with density.

Since the landings have remained very low several years, demonstrating the failure of the oyster fishery, an alternative would be a development of oysters aquaculture. This proposal would completely change the social characteristics of the Maryland watermen's community, since it will require development of business enterprises, large investments, etc. So there is urgent need for sociological and economical research to estimate the conditions and the consequences of the development of oyster culture in this area. From a biological point of view, the first problem with aquaculture is the choice of species. Since the native oyster is attacked mainly by two diseases, it is not certain that aquaculturists must go with the American oyster. Two main hypothesis would be investigated; to proceed on Crassostrea virginica, or to introduce another species like Crassostrea gigas.

With the American oyster, natural spat can be collected on bottoms or with collectors in suspension. Everywhere in the world, collectors are more efficient when they are suspended. In addition, faster growth rate are obtained in different suspensions culture. As market size oysters can be obtained in two years with this type of structure, it avoids the high mortality rates which occur with MSX in three and four year-old oysters. In this scheme it would be better to have natural spat if they were less expensive and more resistant to disease. An analysis of the global development in oyster production demonstrates clearly that the countries producing the most oysters depend on natural recruitment. In contrast the history of production using juvenile molluscs produced in hatcheries is often unstable and at a low level, compared to natural recruitment even with new techniques like "eyed larvae" and remote setting. This is mainly due to the size of the hatcheries, which cannot always increase their level of production, and also to diseases, which frequently occur in the overcrowded structures. For example, the amount of eyed larvae, necessary for sustaining a production of 160,000 tons of Crassostrea gigas by aquaculture in France, is estimated to greater than 15 trillions ! Relying on hatcheries may be necessary when they are needed to produce some particular strain showing resistance to disease or fast growth rate, or even new "species" obtained by hybridization or by genetic manipulation.

For Crassostrea virginica, some selected strains are available. By selecting of fast growth oyster and by breeding them together during several generations, a strain with fast growth (the market size could be reached after 12 to 18 months) is now commercialised at the Piney Point hatchery under contract with DNR. Moreover the strain resistant to MSX (Ford and Haskin, 1987) shows to reduce mortality. Triploïds of Crassostrea virginica may also be used to give better growth rates compared with diploïds by using the energy which normally would go into growth of gonads (Allen, 1986). But the percentage of triploïds produced in a sample may vary a lot.

The introduction of another species must be evaluated. The species which yields more than 70 % of total world production is the Japanese oyster Crassostrea gigas. This species is widely distributed in North America on the west coast but is not officially present on the east coast, even if, in the Chesapeake Bay, Hargis and Haven (1988) reported that this oyster, cultivated on the west coast were "now being processed or repacked in Virginia." The choice of this species could be explained first by the fast growth rate of this oyster, which can reach market size in one year when nutritionnal and temperature conditions are favourable (Héral, 1989). Secondly, this oyster is very resistant to different diseases, including the two viruses which destroyed the cupped European oyster Crassostrea angulata (Grizel and Héral, 1990), and the protozoans Marteilia refringens and Bonamia ostreae which caused severe damage to the european flat oyster Ostrea edulis. There is no litterature regarding the resistance of Crassostrea gigas to Perkinsus marinus and Haplosporidium nelsoni. These experiments are urgently needed. On the other hand, a new Bonamia-like disease which caused hight mortalities on adult oysters has appeared on the US west-coast (Bauer, pers. com.). Morphology and immunodiagnostic studies demonstrate that this parasite is a new species different from the microcells of the flat oyster (Boulo and Hervio, pers. com.). In west-coast hatcheries which there are also mortalities associated with vibrios and bacteria infect the conchiolinous ligament and periostracum (Elston et al., 1982), a virus of Crassostrea gigas also affected larvae, causing large mortalities (Elston et al., 1985).

After a disease survey it can be calculated the risk associated with importing C. gigas from the west coast. The danger of importing diseases to Chesapeake Bay is now very large given the trade in Virginia between east coast and west coast. Imports could be made from Japan where no diseases are described at the present time for the cupped oyster. Even if, for example, the historical case of C. gigas implantation in France remains a success, it is important to emphasize that this type of operation can present considerable danger, particularly from the zoosanitary point of view (Grizel and Héral, 1990). Also, it is necessary, when the situations are not dramatically urgent, to take maximum precautions with importations and to follow the recommendation of ICES on introduction of species for commercial or scientific purposes (quarantine, production in hatcheries of F1, etc...)

Another question about the introducing Crassostrea gigas is the behavior of this species in the Chesapeake Bay. The habitat requirements of the Japanese oyster seem to be more marine than that of the American oyster (Heral and Deslous-Paoli, 1990). It appears that this oyster might not reproduce regularly in the low salinities of the tributaries and the upper bay. Moreover, C. gigas oysters are more sensitive to pollution than american oysters. For example, exposure to organotin (TBT) reduced the growth rate of Crassostrea virginica at only 2 $\mu g.l^{-1}$ without shell thickening. It affected on C. gigas under 1 $\mu g.l^{-1}$ until 0.01 $\mu g.l^{-1}$ (Héral et al., 1989). The TBT concentrations largely exceed this level in the Chesapeake Bay, particularly in marinas and some tributaries (Hall, 1988). This demonstrates that the quality of the water could be a limiting factor for a different species of oyster.

As for Crassostrea virginica, if triploïds of Crassostrea gigas were used (Allen, 1986) since they are not able to reproduce it would prevent their escape from culture. Hybrids of American oyster and Japanese oyster could be produced, but the resistance to disease is not known. By comparison, hybrids of Crassostrea angulata and Crassostrea gigas have the same characteristics as the parents for growth and disease resistance (Bougrier et al., 1986).

Another alternative is to change the species but to manage it in a fishery. To optimize production, the problems would be the same as we have presented at the beginning of this paragraph for the American oyster fishery.

It must be kept in mind that by changing the species, the whole ecosystem of the bay might be modified. If environmental conditions are optimal this oyster can spread very quickly creating large oyster reefs and might through increased filtration, reduce eutrophication, as has been done in South San Francisco Bay (Officier et al., 1982) and proposed by Newell (1988) for the Chesapeake Bay. However, as we have already pointed out, it is unlikely that optimal conditions can be achieved in the Northern Bay and because this is difficult then to prognosticate the effects for the entire Bay.

The next steps involve taking into account what can be presently accomplished such as rationalizing the management of Crassostrea virginica and then considering in more details the choices or combinations amoung the rationalized management - introduction of new species - and intensified culture.

Acknowledgment : We thank Martin Wiley for his technical review of this manuscript. Thanks are also due to W.P. Jensen for his helpful comments and encouragements. This study was funded by the National Oceanic and Atmospherie Administration, by the Maryland Department of Natural Resources under contract F 166-89-008 and by the Institut Français de Recherche pour l'Exploitation de la Mer.

REFERENCES

Abbe G.R., 1988. Population structure of the american oyster, Crassostrea virginica, on an oyster bar in central Chesapeake Bay : changes associated with shell planting and increased recruitment. J. Shellfish Res., 7 (1) : 33-40.

Allen S.K., 1986. Gametogenesis in three species of triploids shellfish : Mya arenaria, Crassostrea gigas, Crassostrea virginica. EIFAC/FAO/86/ Symp. E20, 19 p.

Andrews J.D., 1966. Oyster mortality studies in Virginia. V. Epizootiology of MSX, a protistan pathogen of oysters. Ecology, 47 : 19-31.

Andrews J.P., 1984. Epizootiology of hasplosporidian diseases affecting oysters. In: Comparative Pathobiology, vol. 7. Pathogens of invertebrates. Edit. by J.C. Cheng, Plenum Press : 243-266.

Barber B.J., Ford S.E., Haskin H.H., 1988. Relationships among condition index, glycogen level, reproductive effort and intensity of MSX (Haplosporidium nelsoni) infection in oysters Crassostrea virginica. J. Shellfish Res., 7 (1): 25-318

Beaven G.F., 1946. Effect of Susquehanna River stream flow on Chesapeake Bay salinities and history of past mortalities on Upper Bay bars. Convention Adresses of Proc. Natl. Shellfish Assoc.: 38-41.

Beaven G.F., 1955. Various aspects of oyster setting in Maryland. Proc. Natl. Shellfish Assoc., 45: 29-37.

Berrigan M.E., 1988. Management of oyster resources in Apalachicola Bay following Hurricane Elena. J. Shellfish Res., 7 (2): 281-288.

Bisker R., Castagna M., 1987. Predation on single spat oysters Crassostrea virginica (Gmelin) by blue crabs Callinectes sapidus (Rathbun) and mud crabs Panopeus herbstii (Milne-Edwards). J. Shellfish Res., 6 (1): 37-40.

Bougrier S., Raguenes G., Bachère E., Tigé G., Grizel H., 1986. Essai de réimplantation de Crassostrea angulata en France. Résistance au chambrage et comportement des hybrides C. angulata - C. gigas. Cons. Inter. Explor. Mer CM 1986/F 38 : 6 p.

Bouma A.H., 1976. Subbottom characteristics of San Antonio Bay. In: Shell dredging and its influence in Gulf Coast Environment Houston, Gulf Publishing : 132 - 148.

Brooks W.K., Waddell J.I., Legg W.H., 1884. Report of the oyster commission of the state of Maryland. Edit. by J.B. Ehlers and Co, Baltimore 193 p.

Cabraal R.A., Wheaton F.W., 1981. Production functions for the Maryland oyster fishery. Trans. Amer. Soc. Agric. Eng., 24 : 248-252.

Calabrese A., Collier R.S., Nelson D.A., Mac Innes J.R., 1973. The toxicity of heavy metals to embryos of the American oyster, Crassostrea virginica. Mar. Biol., 18 : 162-166.

Calabrese A., MacInnes J.R., Nelson D.W., Miller J.E., 1977. Survival and growth of bivalve larvae under heavy-metal stress. Mar. Biol., 41 : 179-184.

Christy F.T., 1964. The exploitation of a common property natural resource : the Maryland oyster industry. PhD. University of Michigan, 222 p.

Department of Natural Resources, 1985. Preliminary review : Current status of Maryland's oyster Ressources, Maryland DNR Report, 64 p.

Department of Natural Resources, 1987. Status and trends 1987 : Maryland's Oyster Resources. Maryland DNR Report, 63 p.

Dugas R.J., 1988. Administering the Louisiana oyster fishery. J. Shellfish Res., 7 (3): 493-499.

Elston R., Elliot E.L., Colwell R.R., 1982. Conchiolin infection and surface coating vibrio shell fragility, growth depression and mortalities in cultures oysters and clams, Crassostrea virginica, Ostrea edulis and Mercenaria mercenaria. J. Fish Diseases, 5 : 265-284.

Elston R.A., Wilkinson M.T., 1985. Pathology, management and diagnosis of oyster velar virus disease (OVVD). Aquaculture, 48 : 189-210.

Engle J.B., 1955. Ten years of study on oyster setting in a seed area in upper Chesapeake Bay. Proc. Natl. Shellfish. Assoc., 45: 88-99.

Ferguson T.B., Hughlett T., Brook W.K., Winslow F., 1880. Report of the Commissioners of Fisheries of Maryland, 397 p.

Ford S.E., Haskin H.H., 1987. Infection and mortality patterns in strains of oysters Crassostrea virginica selected for resistance to the parasite Haplosporidium nelsoni, MSX. J. Parasit., 73 : 368-376.

Ford S.E., Figueras A.J., 1988. Effects of sublethal infection by the parasite Haplosporidium nelsoni (MSX) on gametogenesis spawning and sex ratios of oysters in Delaware Bay, USA. Dis. Aquat. Org., 4 : 121-133;

Galtsoff P.S., 1964. The American oyster Crassostrea virginica Gmelin. Fish. Bull., 64 : 1-480.

Grave C., 1912. A manual of oyster culture in Maryland. Fourth Rep. Board Shell Fish. Com., Baltimore : 279-348.

Grizel H., Héral M., 1990. Introduction in France of the Japanese oyster Crassostrea gigas. Journal du Conseil : in press.

Hall L.W., 1988. Tributyltin environmental studies in Chesapeake Bay. Mar. Pollut. Bull., 19 : 431-438.

Hargis W.J., Haven D.S., 1988. Rehabilitation of the troubled oyster industry of the lower Chesapeake Bay. J. Shellfish Res., 7 (2): 271-279.

Haskin H.H., Ford S.E., 1982. Haplosporidium nelsoni (MSX) on Delaware Bay seed oyster beds : a host parasite relationship along a salinity gradient. J. Invertebr. Pathol., 40 : 388-405.

Haskin H.H., Canzonier W.J., Myhre J.L., 1965. The history of MSX on Delaware Bay oyster grounds, 1957-1965. Am. Malacol. Un. Bull., 32 : 20-21.

Haven D.S., Whitcomb J.P., 1986. The public oyster bottoms in Virginia : an overview of their size, location and productivity. Am. Malacol. Un. Bull., Special edition, 3 : 17-23.

Haven D.S., Hargis W.J., Kendall P.C., 1981a. The oyster industry of Virginia : its status, problems and promise. A comprehensive study of the oyster industry in Virginia. Va, Inst. Mar. Sci., Spec. Paper Mar. Sci. n@4, 1024 p..

Haven D.S., Whitcomb J.P., Kendall P., 1981b. The present and potential productivity of the Baylor grounds in Virginia. Vol. 1 (167 p) and II (154 p). Va, Inst. Mar. Sci., Spec. Rep. Appl. Mar. Sci., Ocean Eng., 243.

Héral M., 1989. L'ostréiculture française traditionnelle. Aquaculture. Edit. by G. Barnabé, Lavoisier Paris, 2ème édition : 348-397.

Heral M., Deslous-Paoli J.M., 1990. Oyster culture in European countries. In : Estuarine and Marine Bivalve Mollusc Culture. Edit. by W. Menzel, C.R.C. Press, (in press).

Héral M., Deslous-Paoli J.M., Sornin J.M., 1983. Transferts énergétiques entre l'huître Crassostrea gigas et la nourriture potentielle disponible dans un bassin ostréicole : premières approches. Océanis, 9 (3) : 169-194.

Héral M., Alzieu C., Deslous-Paoli J.M., 1989. Effect of organotin compounds (TBT) used in antifouling paints on cultured marine molluscs. A litterature study. Aquaculture. A biotechnology in progress 1989. Edit. by N. De paw, E. Jaspers, H. Ackefors, W. Wilkins. European Aquaculture Society, Bredene, 1081-1089.

Hill J.M., 1988. Physiographic distribution of interstitial waters in Chesapeake Bay. Maryland Geological Survey, report of investigations # 49, 32p..

Holland F., 1987. Habitat Requirements for Chesapeake Bay Living Resources Ed. by Chesapeake Bay Living Resources Task Force D1-D13, 63p.

Ingersoll E., 1881. The history and present condition of the fishery industries. The oyster industry 10th Census of the US Washington DC Dept of Interior : 156-180.

Jensen W.P., 1981. Leased bottoms and the Maryland oyster fishery. Ed. by D. Webster. Oyster culture in Maryland 1980. A proceedings Univ. Maryland Coop. Ext. Serv., UM SG MAP 81-01 : 117-127.

Keithly W.R., Roberts K.J., 1988. The Louisiana oyster industry : economic status and expansion prospects. J. Shellfish Res., 7 (3): 515-526

Kennedy V.S., Krantz L.B., 1982. Comparitive gametogenic and spawning patterns of the oyster Crassostrea virginica (Gmelin) in Central Chesapeake Bay. J. Shellfish Res. 2 (2): 133-140.

Kennedy V.S., Breisch L.L., 1983. Sixteen decades of political management of the oyster fishery in Maryland's Chespeake Bay. Environmental Management, 16 : 153-171.

Korringa P., 1952. Recent advances in oyster biology. Quart. Rev. Biol., 27 : 266-308 and 339-365.

Korringa P., 1976. Farming the cupped oysters of the genus Crassostrea. Elsevier, New-York : 208 p.

Krantz G.E, 1989. Maryland Oyster Population Status Report. State of Maryland, Dept. of Natural Resources, 23p..

Krantz G.E., Meritt D.W., 1977. An analysis of trends in oyster spat set in the Maryland portion of the Chesapeake Bay. Proc. Natl. Shellfish Assoc., 67 : 53-59.

Krantz G.E., Haven D.S., 1982. A study of the present state of oyster statistics in Chesapeake Bay and suggested remedial measures In : Report of Workshop on Chesapeake Bay Fisheries Statistics ed. by E. Cronin UMCEES-CBL : 44-52.

Larsen P.F., 1974. Quantitative studies of the macrofauna associated with the mesohaline oyster reefs of the James River. PhD.Disseration. School of Marine Science, College of William and Mary, Virginia, 182p..

Lough R.G., 1975. A reevaluation of the combined effects of temperature and salinity on survival and growth of Bivalve larvae using response surface techniques. Fish. Bull., 73 (1) : 86-94.

Lunz G.R., 1947. Callinectes versus Ostrea. J. Elisha Mitchell Sci. Soc., 63 : 81.

MacInnes J.R., Calabrese A., 1978. Response of embryos of the American oyster, Crassostrea virginica to heavy metals at different temperatures. In : Physiology and behaviour of marine organisms. Edit. by D.S. Mc Lusky and A.J. Berry. Proc. 12 th Eur. Mar. Biol. Symp.,Pergamon Press, Oxford 195-202.

Mac Kenzie C.L., 1983. How to increase oyster production. Marine Fisheries Review, 45 : 1-22.

Menzel R.W., Hopkins S.H., 1955. The growth of oysters parasitized by the fungus Dermocystidium marinum and by the trematode Bucephalus cuculus. J. Parasitol. 41 : 333-343.

Newell R.I.E., 1985. Physiological effects of the MSX parasite Haplosporidium nelsoni (Haskin, Stauber and Mackin) on the American oyster Crassostrea virginica (Gmelin). J. Shellfish Res., 5 (2): 91-96.

Newell R.I.E., 1988. Ecological changes in Chesapeake Bay : are they the result of overharvesting the American oyster, Crassostrea virginica. In : Understanding the Estuary : Advances in Chesapeake Bay Research. Chesapeake Research Consortium, Publication 129. CBP/TRS 24/88 : 536-546.

Officier C.B., Smayda T.J., Mann R., 1982. Benthic filter feeding : a natural eutrophication control. Mar. Ecol. Prog. Ser. 9 : 203-210.

Otto S.V., Krantz G.E., 1976. An epizootic of "Dermo" disease in oysters in the Maryland portion of the Chesapeake Bay. Proc. Natl. Shellfish Assoc., 67 : 121.

Roche G., 1897. La culture des mers. Ed. Bibliothèque Scientifique Internationale, Tours : 162-312.

Rothschild B.J., Staag C., 1990. Populations dynamic of the Blue crab Callinectes sapidus in Chesapeake Bay, ms.

Schubel J.R., 1968. Suspended sediment of the Northern Chesapeake Bay. Chesapeake Bay Institute, Technological Report 35, 68-2, 264 p..

Schwartz F.J., Cargo D.G., 1960. Recent records of the xanthid crab, Panopeus herbstii from Maryland and Virginia waters. Chesapeake Sci., 1 : 201-202.

Seliger H.H., Boogs J.A., 1988a. Evidence for loss of suitable benthic habitats for oysters in Tributaries of the Chesapeake Bay. In: Understanding the Estuary : Advances in Chesapeake Bay Research. Research Consortium, Publication 129. CBP/TRS 24/88 : 111-127.

Seliger H.H., Boogs J.A., 1988b. Long term pattern of anoxia in the Chesapeake Bay. In: Understanding the estuary : Advances in Chesapeake Bay Research. Chesapeake Research Consortium, Publication 129. CBP/TRS 24/88 : 570-583.

Seliger H.H., Boggs J.A., Biggley W.H., 1985. Catastrophic anoxia in the Chesapeake Bay in 1984. Science, 228 : 70-73.

Shaw W.N., 1967. Seasonal fouling and oyster setting on asbestos plates in Broad creek, Talbot County, Maryland 1963-65. Chesapeake Sci., 8 : 228-236.

Shaw N.N., 1969. Oyster setting in two adjacent tributaries of Chesapeake Bay. Trans. Am. Fish. Soc., 98 : 309-314.

Stagg C., 1985. An evaluation of the information available for managing Chesapeake Bay Fisheries : Preliminary stock assessments. Chesapeake Bay Commission, Md : 11-43.

Stevenson C.H., 1894. The oyster industry of Maryland. Bull. US Fish. Commission for 1892 : 205-297.

Truitt R.V., 1925. Oyster problem inquiry of Chesapeake Bay. Third Annu. Rep. Conserv. Dep., State of Maryland, Baltimore, MD : 25-55.

Truitt R.V., 1927. A policy for the rehabilitation of the oyster industry in Maryland. Annual Rep. Md. Conserv. Com., 5 p.

Truitt R.V., 1931. Recent oyster researches on Chesapeake Bay in Maryland. Chesapeake Biological Lab., 3 : 28 p.

Truitt R.V., 1936. Annual Report of the Chesapeake Biological Laboratory, State Press, contribution n° 8 Department of Research and Education.

Truitt R.V., 1945. The oyster. Bios, 15, 12 p.

Ulanowicz R.E., Caplins W.C., Dunnington E.A., 1980. The forecasting of oyster harvest in central Chesapeake Bay. Estuar. Coast. Mar. Sci., 11 : 101-106.

Webster J.R., Medford R.Z., 1959. Flatworm distribution and associated oyster mortality in Chesapeake Bay. Proc. Natl. Shellfish. Assoc., 50 : 89-95.

Whitcomb J.P., Haven D.S., 1987. The physiography and extent of public oyster grounds in Pocomoke sound, Virginia. J. Shellfish Res., 6 : 55-65.

White M.E., Powell E.N., Ray S.M., Wilson E.A., 1987. Host to host transmission of Perkinsus marinus in oyster (Crassostrea virginica) populations by the ectoparasitic snail Boonea impressa (Pyramidellidae). J. Shellfish. Res., 6 (1): 1-5.

White M.E., Powell E.N., Wilson E.A., Ray J.M., 1989. The spatial distribution of Perkinsus marinus a protozoan parasite, in relation to its oyster host (Crassostrea virginica) and an ectoparasitic gastropod (Boonea impressa). J. Mar. Biol. Ass. U.K., 69 : 703-717.

Winslow F., 1884. Present condition and future propects of the oyster industry. Trans. Amer. Fish. Soc., 13 : 148-163.

Winslow F., 1887. Deterioration of American oyster-beds; Pop. Sci. Monthly 20 : 29-43 and 145-156.

Wolman M.G., 1968. The Chesapeake Bay. Geology and geography. In: Proceedings of the governor's conference on the Chesapeake Bay.

Yates C.C., 1913. Summary of survey of oyster bars of Maryland 1906–1912. US Coast and geodetic Survey. Washington DC, 81 p.