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Causes of decline of oyster production (*Crassostrea virginica*) in the Maryland portion of the Chesapeake Bay : A literature study

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RÉSUMÉ

Les causes du déclin de la production d'huîtres (*Crassostrea virginica*) dans la partie Marylandaise de la baie de Chesapeake: une étude bibliographique

L'analyse des données historiques des productions annuelles d'huîtres *Crassostrea virginica* a été réalisée pour la partie marylandaise de la Baie de Chesapeake. Les différentes tendances sont analysées parallèlement aux principaux évènements et aux stratégies d'aménagements qui ont été appliquées dans la baie. Trois périodes principales sont identifiées : (1) la période de forte production (1840 à 1890) avec des débarquements qui ont dépassé 600 000 tonnes. Elle est caractérisée par une forte surpêche entraînant la destruction de l'habitat des gisements d'huîtres provoquée par une utilisation abusive d'engins de récolte; (2) la période de décroissance et d'apports stables (1900 à 1980) due à l'échec du plan de repeuplement et au fort taux de sédimentation et les conditions estivales anoxiques n'a pas permis de dépasser une production de 80 000 tonnes; (3) la période de forte décroissance de la production (1981-1988) avec des apports annuels inférieurs à 15 000 tonnes est 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.

ABSTRACT

The historical landings of Eastern oyster *Crassostrea virginica* are described for the Maryland part of the Chesapeake Bay. The different trends are analyzed concurrently with the main events and management strategies which occurred. Three main periods are identified : (1) the great fishery when annual oyster landings from 1840 to 1890 reached 600,000 metric tons. This period was characterized by gross overfishing and the destruction of oyster habitat by the oyster gears; (2) the reduced but stable landings from 1900 to 1980, with failure of the reseeding plan connected to heavy sedimentation and anoxic summer conditions. Landings did not exceed 80,000 metric tons; (3) the large decrease of production (1981-1988), with landings as low as 15,000 metric tons since 1986, is caused by high mortalities related to diseases (MSX and *Perkinsus marinus*), predation and poor management practices. Alternative strategies for restoration of oyster production in the Chesapeake Bay are presented.

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INTRODUCTION

The Eastern oyster *Crassostrea virginica* (Gmelin, 1791) 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 (Table 1) (Truitt, 1925, 1927, 1931). Research was conducted on the effects of removal of cultch, and minimum size limits on adult oysters and regulations of the oystering season were enacted to try to restrict the overfishing. Investigators defined the sampling techniques now used for the systematic annual oyster bar survey. Krantz and Meritt (1977) stated that CBL staff conducted the surveys until the late 1950's (Beaven, 1955). Since then, the annual survey has been conducted by the Maryland Department of Natural Resources (MDNR). Intensive research has been done but only on limited aspects of oyster biology and ecology. Few reviews of the Eastern oyster and oystering in Chesapeake Bay have been yet published. Korringa (1952) and Galtsoff (1964) mainly described the biology of *Crassostrea virginica*. For the Virginia part of the bay, Haven *et al.* (1981a, 1981b) reviewed the oyster industry status and problems, while for the Maryland part, the only synthesis was published by Kennedy and Breisch (1981, 1983), and included biology, diseases effecs, management of the Maryland oyster industry, and an historical review. There is no specific analysis of the different causes for the production decline, which are generally described as 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. This paper aims to analyze the historical trends in oyster production in the Maryland portion of Chesapeake Bay in relation to overfishing, and the use of different gears, and their impact on the destruction of the physical characteristics of oyster bars.

Main Bay	
Length:	322 km
Greatest depth:	53 m
Average depth:	7.6 m
Surface:	569,800 ha
Volume:	68,109 m3
Total shoreline :	7,401 km
Tidal range:	0.9 m at mouth, 0.3 m at Annapolis
Salinity surface :	30 ppt at mouth, 10 ppt at Annapolis
Watershed	
Main tributaries: 8 Rivers. Susquehanna, Potomac, and James River contribute to 80 % of the freshwater runoff.	
Total tributaries:	419
Watershed area :	16,576,000 ha
Watershed population:	13 million in 1980 (projected in 2020: 16 million)

Table 1: Main Characteristics of Chesapeake Bay.

The State of Maryland has had an oyster repletion program in place since 1960. The program includes shell planting and seed oyster 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 diseases prevalence.

CHESAPEAKE BAY LANDINGS.

The methods for reconstitution of oyster landings have been developed by Héral *et at.* (1990). The Chesapeake Bay production, obtained by combining the Virginia and Maryland data, demonstrate a tremendous decline in oyster landings (Fig. 1). The oyster industry in Virginia has been well studied during the last decade (for review see Haven *et al.*, 1981a, 1981b; 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 3,600 ha of leased oyster ground representing 3 % of the oyster bottom (Jensen, 1981) (Fig. 2). In contrast, large areas are leased in Virginia for private use (i.e., 50,000 ha private vs. 97,200 ha public) (Haven and Whitcomb, 1986).

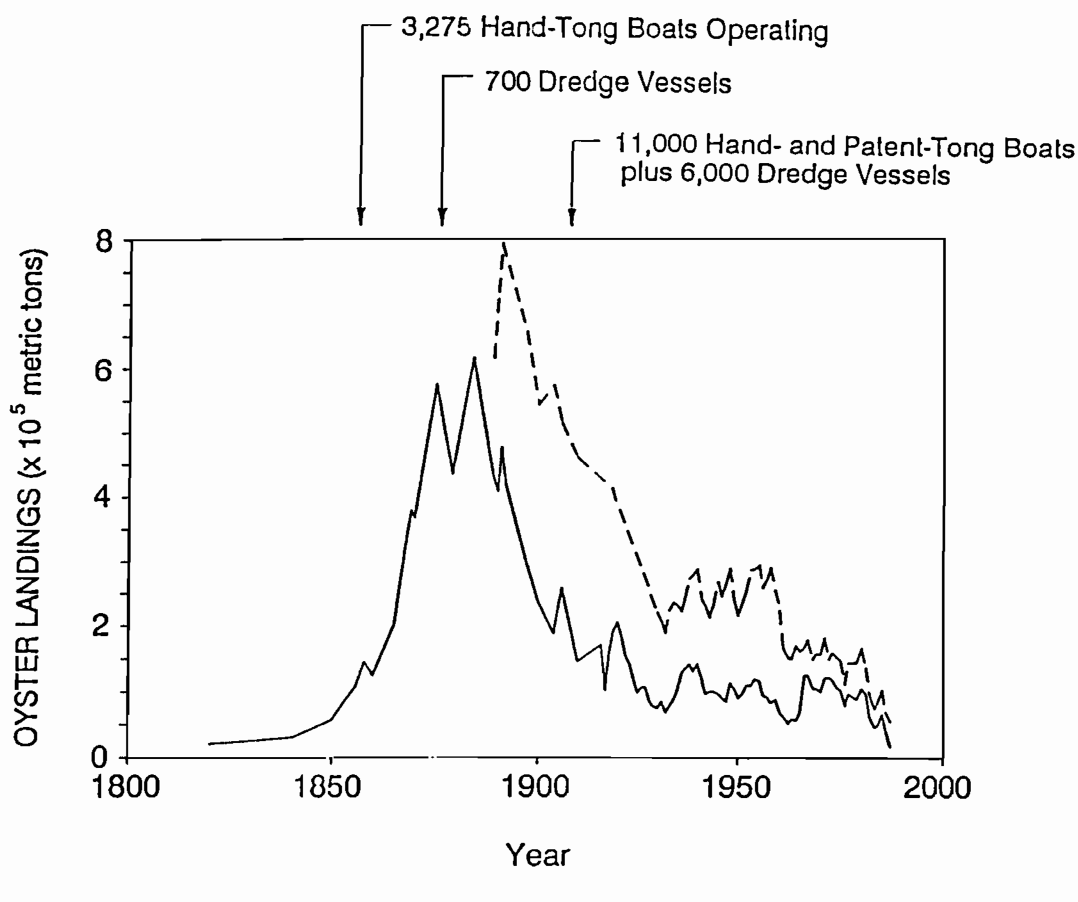

Figure 1. Trends in oyster production, total weight in M ıryland (solid line), and Chesapeake Bay (dashed).

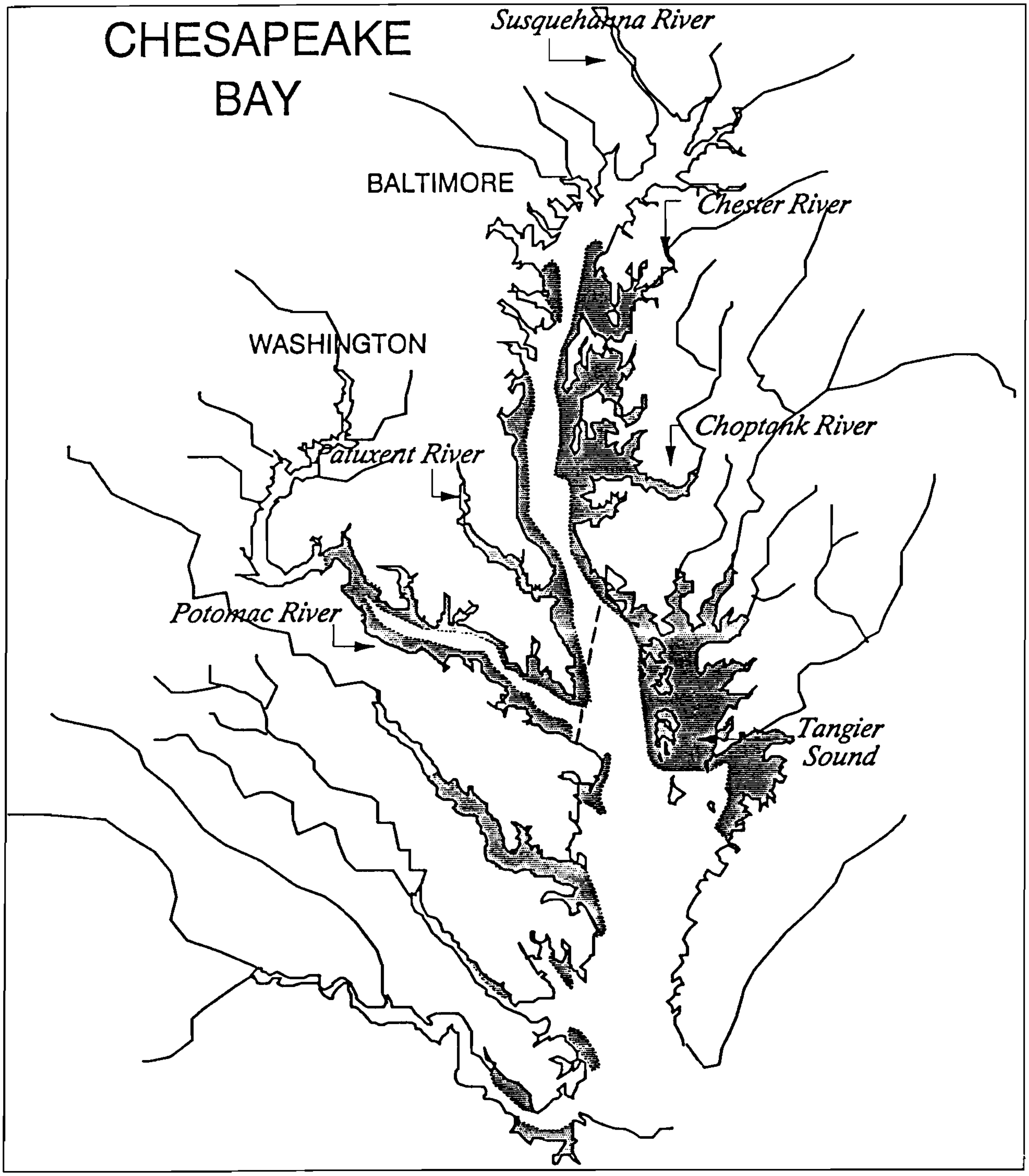

Figure 2. Location of the main public oyster bars in the Chesapeake Bay (stippled). Dashed line: 10 ppt salinity pycnocline.

The analysis of the Maryland oyster landings demonstrate that this fishery has passed through three stages of production:

Stage 1 : From 1840 to 1890 - The Great Fishery

Oysters were eaten by Indians, as demonstrated by large quantities of oyster shell near their camps. The early Maryland settlers easily gathered the abundant oysters. As the population, trade, and traffic (e.g., 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 (i.e., hand-tongs, dredges) (Fig. 1). Kennedy and Breisch (1981, 1983) indicated that the number of processing plants in the Baltimore area increased from one in 1834 to 80 by 1868. Ingersoll (1881) reported 98 packing plants with a production of 314,000 tons in 1879. The maximum landings were 615,000 tons in 1884 and the annual production stayed above 400,000 tons from 1872 to 1893. After reviewing old records, we conclude, like Christy (1964) and Kennedy and Breisch (1981, 1983), that the early harvests were probably not greatly over estimated and give a realistic idea of the production level supported by the entire bay. By comparing the oyster boat number in 1865 and in 1879, with an annual production of 200,000 tons, and 434,000 tons respectively, the fleet reached 2,555 and 3,275 boats with a total crew of 13,748 (Ingersoll, 1881). The fleet increased by 28% but the production doubled. The fishing efficiency was increased mainly by two means: 1) the fishery extension by discovering new bars. By way of example, the large reefs in Tangier Sound were discovered in 1840 (Kennedy and Breisch, 1983), and 2) the gear efficiency increase. 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 and also allowed fishing everywhere (Fig. 1).

The consequences of these large increases in the annual landings have been the destruction of the most productive beds. As in England and France, and despite regulations on the harvest season and boat type, and in 1868, a licensing system for the oyster boats, the fishing pressure remained high (Roche, 1897; Héral, 1989). We estimated the oyster mean density by dividing the maximum landings (i.e., 615,000 tons in 1884) by the total bar acreage (i.e., 111,600 ha), with an individual oyster weight of 150 g. It is nearly 3.7 oysters per m^2. Winslow (1884) found that the oyster mean density was 5.4 m^{-2} in 1879, and Brooks *et al.* (1884) found a 3.5 m^{-2} mean density. Therefore, the landings were at the same level as the total living stocks, meaning that the fishing pressure was too heavy. The landings could reach such a high level only because the different adult age classes of all oyster bars of the mainstem and tributaries were simultaneously 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 of the population to achieve adequate recruitment: (1) the removal of the juveniles: at that time, large quantities of spat were sold to other states for reseeding. By way of example, 89,329 tons of spat were sold in 1879 for bedding in northern waters from Delaware to Maine (Ingersoll, 1881); (2) the spat destruction attached to the adult oysters, by the packing houses, which did not reseed the young oysters; (3) the permanent cultch removal which was necessary for larval setting; the fishermen and the packing houses did not put shells or other hard substrate back on the oyster-beds; (4) the habitat destruction. 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 (Fig. 3). Winslow (1881) 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 reef height above the sediment. Following the intense fishery the bars were broader but with less relief, changing the physical characteristics of the oyster environment; a non-fished oyster reef is less subject to siltation as it is above the water sediment interface. The currents and the apparently increased turbulence in relation to the reef height prevented sedimentation and allowed oyster biodeposits to be transported away. This might explain Winslow's (1881) observations, who found that the overworked beds often had mud and sand among

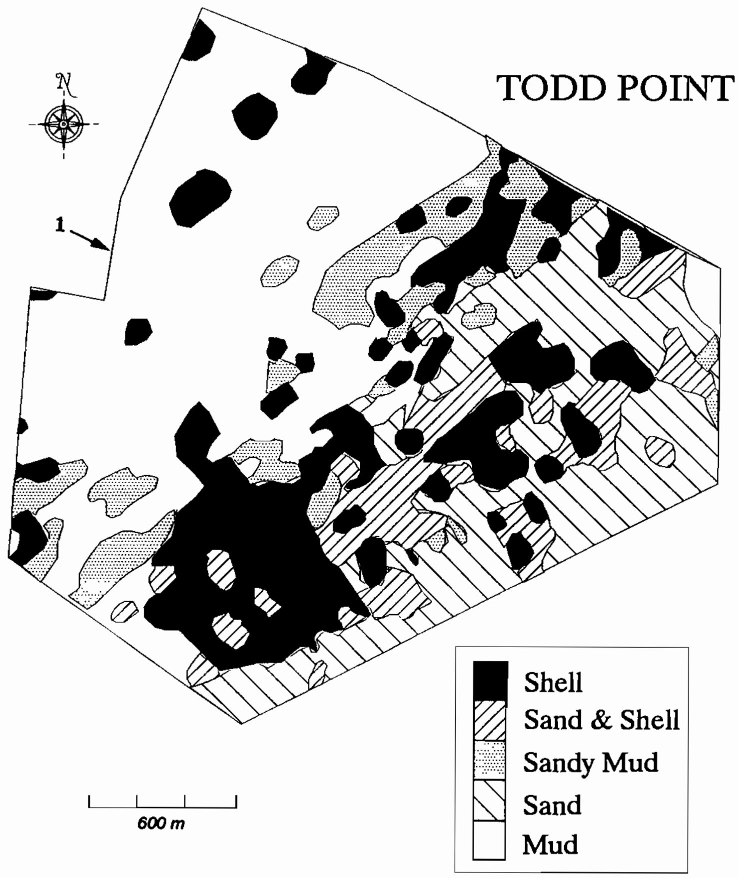

Figure 3. Comparison of the oyster bar 'Todd Point' bottom type between Yates survey (1913) and Rothschild *et al.* (1994) survey. The external limit (1) represents the shell extent in 1913, while shell in 1992 is drastically reduced.

the shells, and that spat settlement was reduced by a factor 3 in a fished bar than on a wild bar. Increased turbidity at the oyster vicinity has a deleterious effect on their growth rate resulting in negative production, and assimilation rate decrease (Héral *et al.*, 1983).

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

Stage 2 : Decreased but stable landings from 1900 to 1980

After a continuous decline in landings from 1890 to 1910, characterized by consistent overfishing, the harvest came to a stable phase fluctuating around 80,000 tons. Krantz and Meritt (1977) attributed the fluctuations to a reduced fishing effort during the 1960's. Landings variability was mainly related to recruitment intensity. For a given year-class, the main 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 (e.g., 1965 and 1980) (Fig. 4). Based upon the spat data set, the fishery has been supported by three main recruitment peaks during the last sixty years. At twenty year

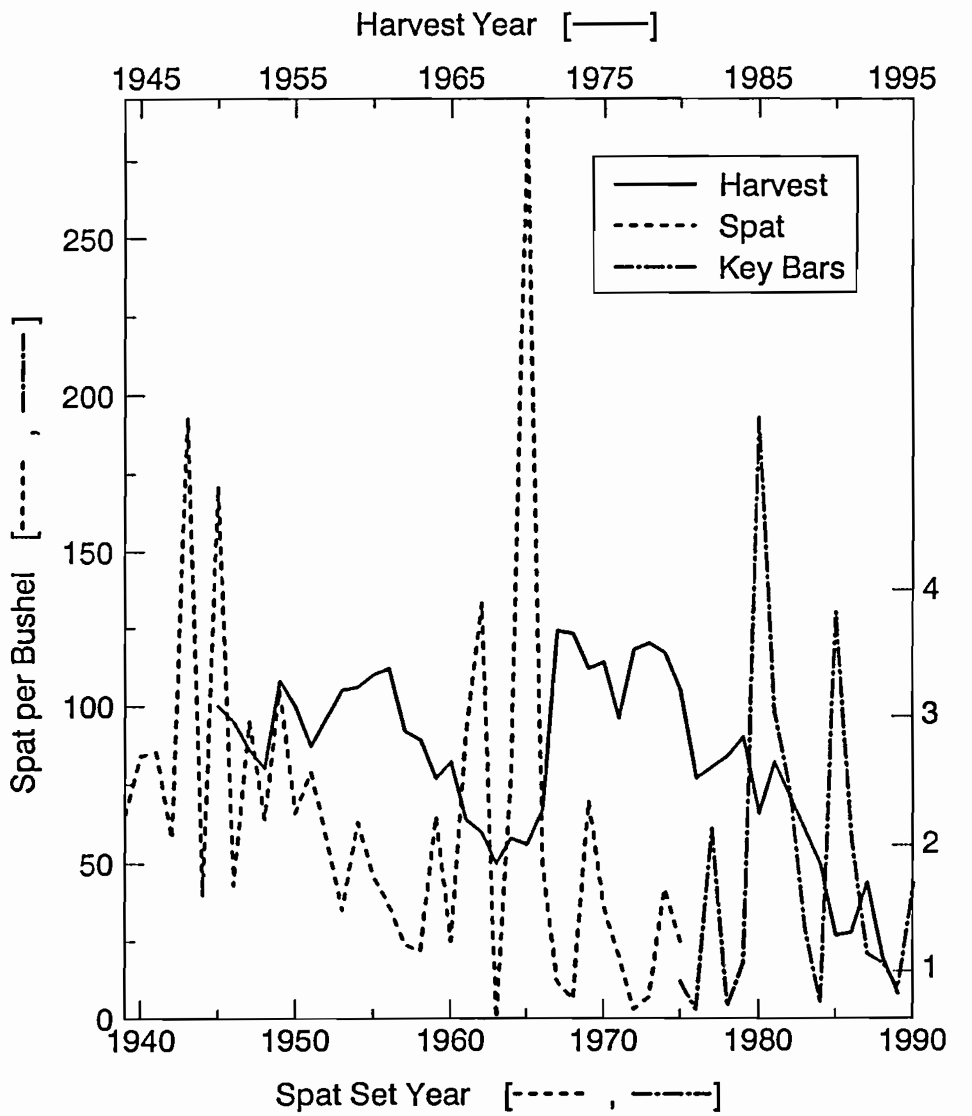

Figure 4. Time-series of an index of recruitment on shelled area: average number of spat per bushel in the Maryland part of the Chesapeake bay (from MDNR, 1987).

intervals, a major spat set has occurred, even in 1980 and 1985 with a very low stock size reduced by the diseases. First, the bay water quality was sufficient to permit a high survival rate for oyster larvae, and second, the stock-recruitment relationship still permitted a successful recruitment in 1985. For the first time, the 1940-1960 Virginia landings exceeded Maryland production and resulted from private production from leased bottoms while the harvest from public bottoms continued to decline (Hargis and Haven, 1988).

Different management operations have been used in Maryland to reverse the public oyster production trends. After the 1890 'Cull law', which required that shell 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 (1981, 1983) described how a 10% shell tax was

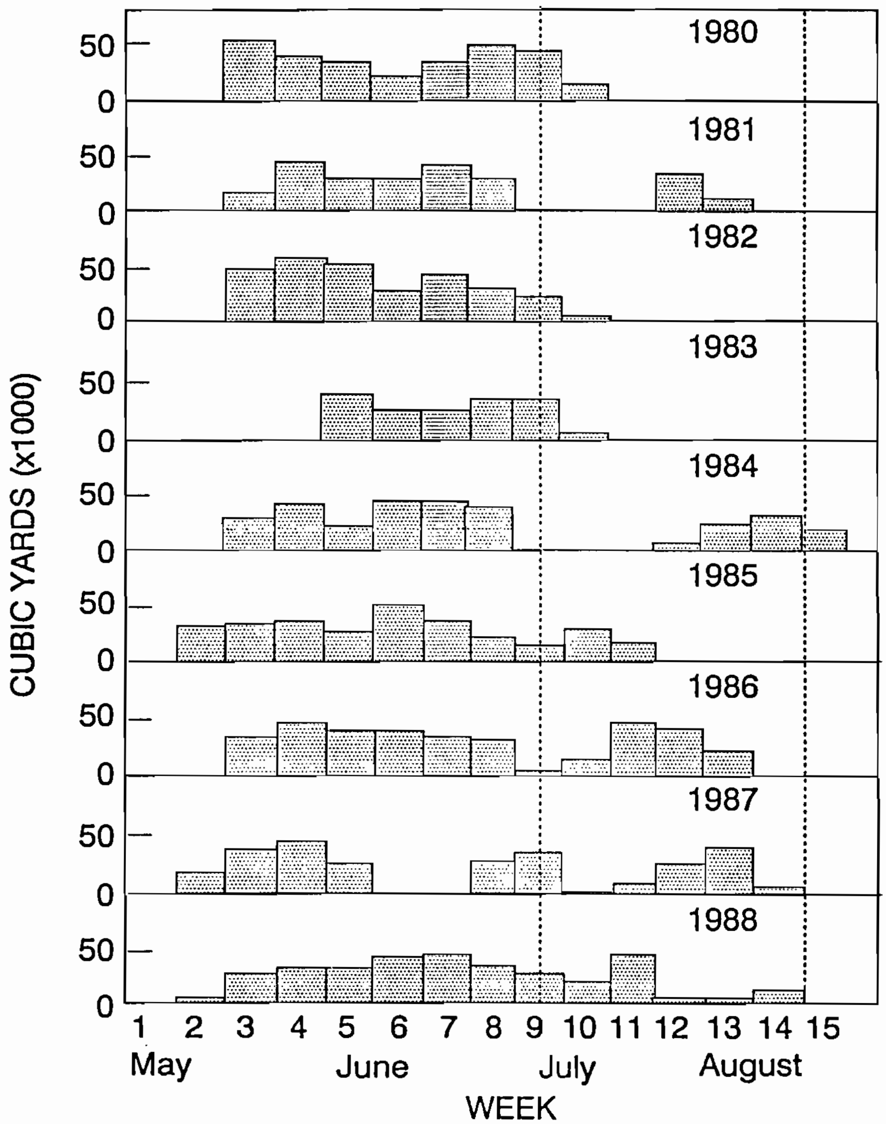

Figure 5. Comparison of weekly (MDNR) shell planting for the years 1980-1988 (vertical dash lines, period of oyster spawning).

charged in 1927, a 20 % shell tax in 1947, and in 1953, a law was enacted for a 50 % shell tax. Oyster packers and processors had to sell at least 50 % of their shucked shells to the State for redeployment. Funds for these operations came from a tax on each bushel of processed oysters. However, this program failed since the shells were not returned to the oyster bars (e.g., 1936), or the funds were not collected (e.g., 1948). Even after the 1953 law, the shell supply was still insufficient. For this reason the Maryland Department of Natural Resources (MDNR) made the decision in 1961 to use "fossil" shells for completing. Shells were 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, with a 360,000 tons record high in 1975. The available fresh shells represents only 3 % of the dredged shell quantity.

Truitt (1936) demonstrated that an overfished oyster bar could again become a productive area by using a properly managed shell planting program. Moreover, Abbe (1988) demonstrated that shell planting can be an effective mechanism for increasing oyster yield. Experimental shell planting was performed on oyster bars in the middle reach of Chesapeake Bay, and characterized by high current velocity and hard bottom. But the reseeding operation of dredged shells is a collective operation for the public Maryland oyster bars, and is performed by only one contractor who follows the allocation and the schedule defined by oyster committees and DNR biologists. Therefore, shell may be planted 2 or 3 months before the main spat settlement (Fig. 5). Spawning occurs in the Chesapeake Bay from June to August, but in some years the largest spat set may occur in September (Truitt, 1925; Shaw, 1969; Kennedy and Krantz, 1982). It is well known that oyster post-larvae set is more efficient on newly-planted, clean shell rather than on old shell, since fouling and siltation interact. For these reasons, Shaw (1967) recommended that shell should be planted in the first week of July, when the larvae are numerous. However, the scale of the public reseeding plan and the transplanting means dictate 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. By way of example, the Louisiana program lasts a week. In Long Island Sound, Korringa (1976) reported that private companies spread the shells in 4 days, which are chosen according to the larval abundance and developmental stage.

MacKenzie (1983) did a scuba survey in the Chesapeake Bay during the normal oyster setting period and reported that beds with high densities of oysters had much less silt than beds with only shell. Very often the Maryland beds had quantities of shells but partially covered by silt. Many management practices were recommended to avoid sedimentation before the oyster setting season; use of bagless dredges, mud-cleaning machines on boats, and use of quick lime to control fouling organisms. Our own observations on various substrates in the Patuxent River in 1989 showed a tremendous quantity of fouling both at the bottom and in the water column, particularly in June and July. All these observations indicate the necessary change for the planting schedule and the way it is performed to improve shell planting efficacy. Since the 'fossil' shells are very often broken and therefore of restricted value for spat settlement, there are not the best cultch material (Cabraal and Wheaton, 1981). Comparisons between shells of living oysters, fresh shells, old "fossil" shells and their efficiency in attracting spat settlement demonstrated that the spat densities were higher on living or fresh shells than on fossils shells. It could be due to an attractive shell protein effect (i.e., conchyolin). Using fresh clam shell instead of oyster shells might be of interest since the landings are important, and large amounts available. The cultch efficiency was demonstrated and used in the Louisiana oyster fishery because it was a light cultch and easier for the oysters to maintain their position on top of the soft sediment (Dugas, 1988; Korringa, 1976). Some use of clams shells is occurring to a limited extent in Chesapeake Bay. However, since the processed clam shells are "cooked", they might be of limited efficiency.

The Maryland DNR annually plants nearly 205,000 tons of oyster shells on natural bars to serve as substrates to maintain the recruitment. Following spat settlement, and if a 450 density per bushel is reached, oyster spat is transplanted from areas of high to low spat set areas with a 10 to 15% mortality rate (MDNR, 1987).

The shell to be planted should be allocated to areas where the highest probability of spat settlement is estimated regarding environmental conditions (Lough, 1975; Goulletquer *et al.*, 1993) (Fig. 6). Ulanowicz *et al.* (1980) demonstrated that variations in spat density were correlated with the cumulative high salinity during the spawning season. The spat abundance is generally highest in the mouths of the different tributaries, but cultch has also been planted in places where no recruitment has been observed for several years (Kennedy and Breisch, 1981, 1983). Christy (1964) assumed that shells were planted according to biological criteria, but shells are also placed where demanded by county politicians under pressure from the fishermen. To evaluate the reseeding plan efficiency, some rough calculations can be made. By analyzing the different estuaries and production trends 3 years later, with the quantities of shells and seed resources, it appears difficult

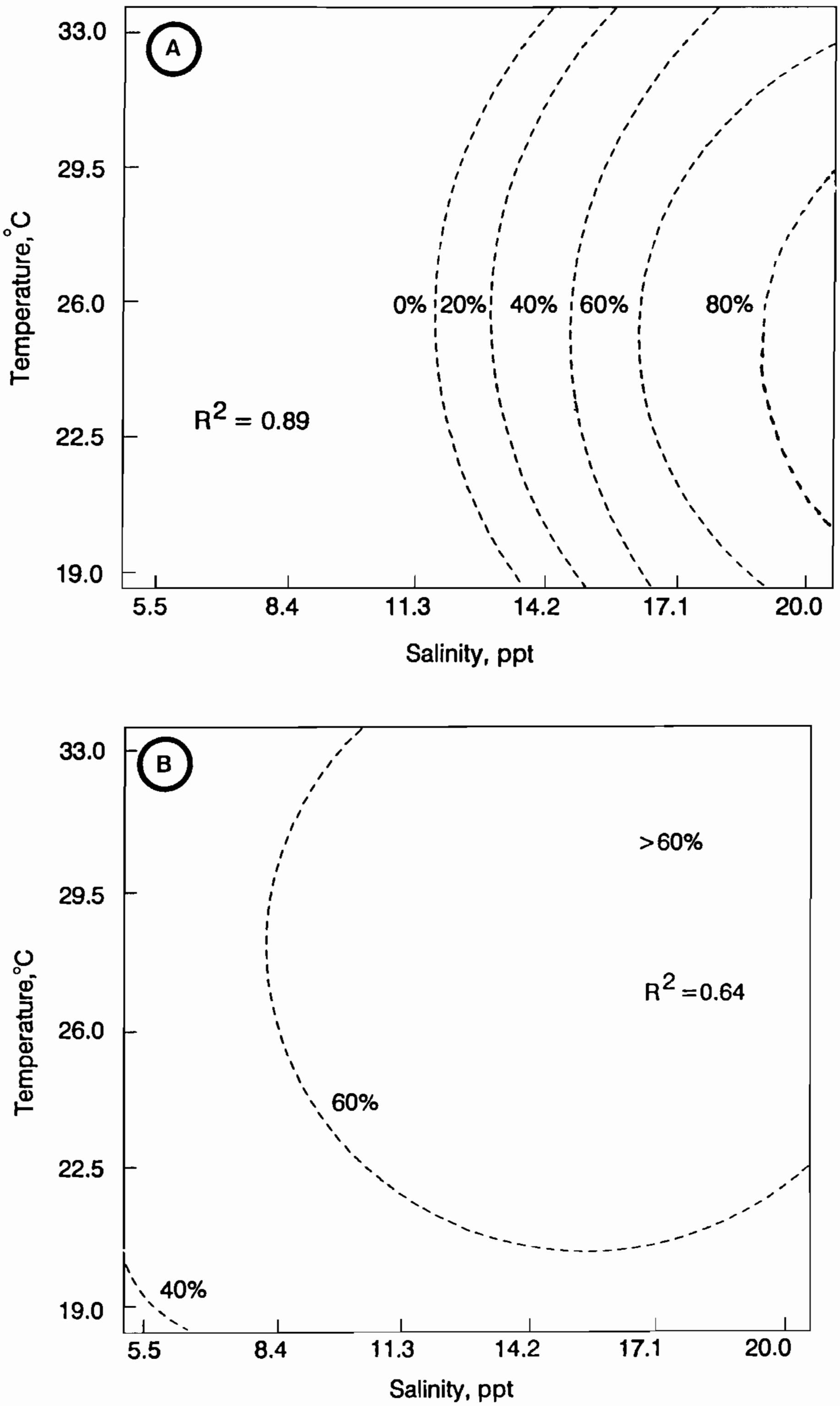

Figure 6. Percent survival estimate of *Crassostrea virginica* larvae, after 2 days (A) and 8 days (B) of development (Lough, 1975).

to assess percentage resulting from the fishing and from the reseeding plan. Moreover, the landings are still declining in several cases (e.g., Tangier sound) (Fig. 7). With 5,000,000 bushels deployed, a 200 spat density per bushel and a 10 % mortality rate per year, the expected production after three years would be 91,000 tons ranging between 80,000 and 120,000 tons. Although the harvest increased after some very high level of recruitment (e.g., 1945, 1965, 1980; + 61,500 tons, 5 years after 1965), it never went above 120,000 tons, which is 6 times less than the nineteenth century landings. Prosperity has not returned to the fishery despite the following regulation and management efforts on the public oyster bars: (1) the 3" (7.6 cm) market size limit; (2) restricting the fishing season from 15 September to 31 March; (3) the daily catch limits set by boat and gear type and the crew number; (4) the reseeding plan.

The fact that management has not worked appears to be mainly due to loss of suitable oyster habitat. Seliger and Boggs (1988a) demonstrated that there was a tremendous decline in 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 only 14 % of the surface still covered by oysters and shells in Chester River, Broad Creek and Tred Avon River. In a recent survey of the Virginia oyster bars, Haven and Whitcomb (1986) showed only 21.8 % of the oyster bars classified at the beginning of the century still survived. A study using a sonar and verified by sampling with hydraulic patent-tongs showed a similar trend in Pocomoke Sound with only 19.5 % of the original acreage of public oyster ground remaining (Whitcomb and Haven, 1987). In 1989-1991, we conducted an intensive systematic survey of eight oyster bars in Choptank River, which provided additional information. Only 48 % of the original listed acreage, based on Yates' survey (1913), was observed (Fig. 8). So, if nothing is done to recover the lost habitat, harvest can not return to a high level, even if there were cyclic recruitment successes.

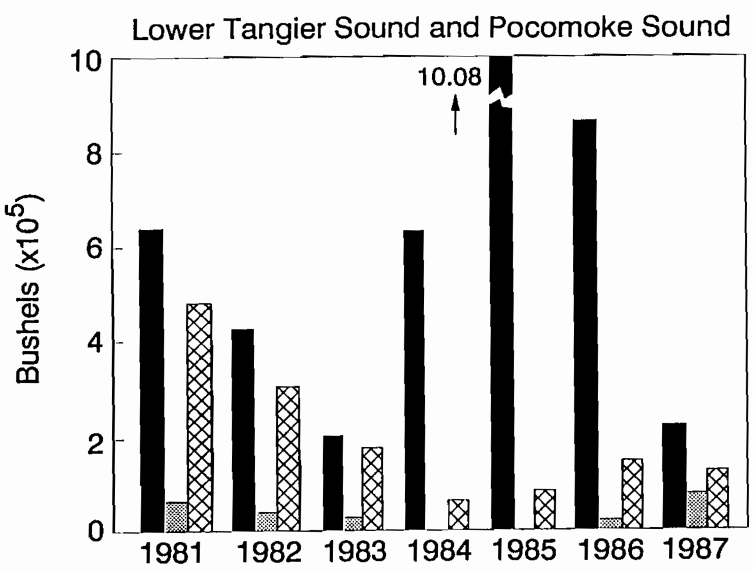

Figure 7. Example of management activity (planting oyster shell and seed) to harvest in Lower Tangier Sound: (cross hatched) bushels of shell, (stippled) bushels of seed, (solid) bushels harvested (MDNR, 1987).

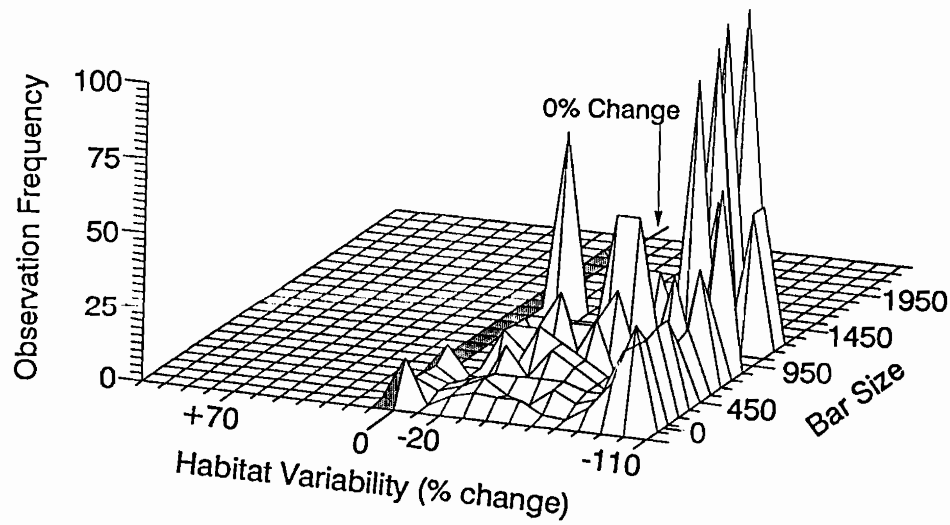

Figure 8. Observed changes in oyster bar habitat in the maryland portion of Chesapeake Bay determined by comparison of Yates' survey (1913) to the Maryland Department of Natural resources survey. The gray line represents the line of no change in habitat between the two surveys.

Furthermore, reductions in the reef elevation above the surrounding bottoms has apparently occurred because of fishing activity. Obviously overfishing and the gear type contributed to the destruction, but sedimentation can also be a major factor in the fishery decline. We have already described how the siltation limits the 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 Chesapeake Bay, suspended particulate matter inputs have mainly two origins; shore erosion, and the large rivers runoffs.

The 3,950 miles of shoreline in Maryland and its tributaries are constantly eroded by currents, tide effects, wind and storm effects, stream flows and possibly increased bottom activity (i.e., dredging 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 sediment output of 0.2 x 10^6 tons. Hurricanes (i.e., cyclonic storms) have tremendous erosion effects. In the Chesapeake Bay, Hurricane 'Agnes' in June 1972, was an obvious example which delayed the oyster recruitment and contributed to the clam fishery destruction. Hurricane 'Elena' in September 1985 destroyed a part of the oyster reefs in Florida, removing and burrying oysters, covering them with muddy sediment where they died (Berrigan, 1988). Moreover, agricultural practices contributed to increase siltation by watershed deforestation.

All the rivers flowing into the bay carry enormous loads of sediment. The Susquehanna River discharges 8.7 x 10^6 tons of suspended sediment per year, the Potomac River 2.3 x 10^6 tons per year, and the Patuxent River 0.6 x 10^6 tons per year (Schubel, 1968). The total amount of sediment coming from the land was estimated to 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 3 cm sedimentation rate per year was measured in Upper Bay. In the Patuxent River, 2.1 m of sediments were deposited 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 River 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; three depositional, one erosional, and one area of no apparent bathymetric change (Hill, 1988). There is 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. Deforestation and clearing for agriculture had multiplied the inputs by 4 to 8 times. Moreover, urbanization has promoted land erosion. Twenty-five to thirty percent of the one million tons reaching the Potomac estuary come from the Washington, D.C. area. Sedimentation rate on oyster bars can also be increased by dredging operations performed to maintain the ship channels into Baltimore harbor, and also in the tributaries to maintain and develop recreational activities (e.g., yachting, marinas). Several clam dredging boats working in the oyster bar vicinity can also contribute to a sedimentation rate increase on the bars. Therefore the oyster habitat is limited in Upper Bay and in the different tributaries by heavy siltation rate and sometimes by reduced salinity.

In deeper areas, oyster habitat is limited by the summer anoxic conditions. 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 Boggs, 1988b). The anoxia extent is directly related with the Susquehanna River flow. The freshwater flow induces spring and summer water stratification inhibiting vertical mixing. Respiration in benthic sediments and in the water column under the pycnocline consumes the oxygen until depletion. A severe summer anoxia in the Upper Bay occurred in 1984 in waters deeper than 6m (Seliger *et al.*, 1985). The anoxic waters may reach several tributaries mouth. Benthic organisms, living at depth greater than 6 m are killed, and only fast growing species showing all year round reproductive activity, are present in these areas when conditions are more favorable (Fig. 10). This is a strong factor limiting oyster habitat.

In the early 1960's MSX disease invaded Chesapeake Bay. The haplosporidian *Haplosporidium nelsoni* is the causative agent of MSX. The disease came from Delaware Bay after destroying its oyster population in 1957 (Haskin *et al.*, 1965). The disease outbreak reduced by 50 % Virginia oyster landings (Fig. 1). Since MSX activity was salinity-limited, mortalities were detected only in Tangier Sound in Maryland. MSX disease then regressed and virtually disappeared from the Maryland part of the bay from 1965 to 1981.

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

The annual MDNR survey recorded, between 1980 and 1982, mortality levels of 30 to 50 % for adult oysters, when adult mortality varied from 5 to 20 % during the 70's. A period of low mortality occurred from 1984 to 1985. But fall mortalities for adult oysters occurred in 1986 and increased in 1987-1988. The cumulative mortality of a single year class could reach 90 %. Meanwhile, harvest pressure remained high despite high mortality level, therefore causing the disappearance of most adult oysters. Since 1986, yearly production in the Maryland portion of the Chesapeake Bay has been lower than 10,000 tons per year.

Numerous factors can cause these high mortality levels, particularly predation, and water quality decline. Outbreaks of the two main diseases, the haplosporidium parasite *Haplosporidium nelsoni* (MSX) and the protozoan *Perkinsus marinus* are also related to mortalities.

MSX invaded the lower Chesapeake Bay in Virginia from 1961 to 1966. MSX requires salinity greater than 15 ppt. The infections remained low and disappeared below 10 ppt (Haskin and Ford, 1982). Later in 1981-1983, 1986-1987 a new MSX outbreak occurred in Virginia and Maryland during a particularly dry period which increased bay salinity. MSX prevalence rarely reached 20 %, but only a few bars were disease free and located in the Upper, low salinity, part of the bay (MDNR, 1987). High salinity conditions with warm winters favored MSX spread. Infection occurs mainly over a five month period in spring and summer. As well as the first year in 1961, mortalities occurred in Spring or at the Summer end, with a cumulative 30 % annual mortality rate (Andrews, 1966). Moreover, Newell (1985) reported a decline of the filtration rate in relation to MSX abundance, with a reduced condition index, fecundity decline and reduced glycogen storage (Barber *et al.*, 1988). Gametogenesis inhibition has been shown to occur in relation to prevalence, but there

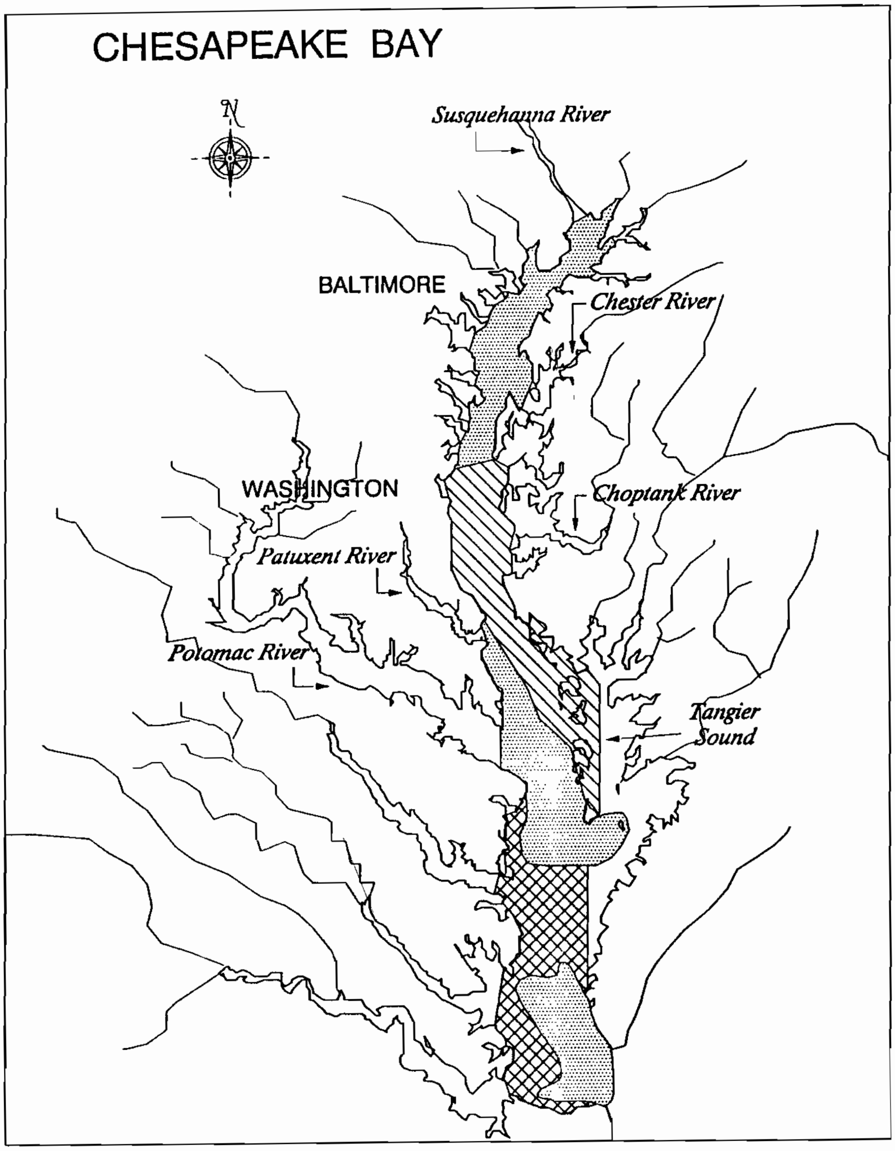

Figure 9. Gross deposition-erosion patterns determined by comparison of historic bathymetric data (hatched : erosional area, stippled : depositional area, cross-hatched : no change) (Hill, 1988).

was no correlation between annual fluctuation in rates of infection and oyster recruitment (Ford and Figueras, 1988).

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

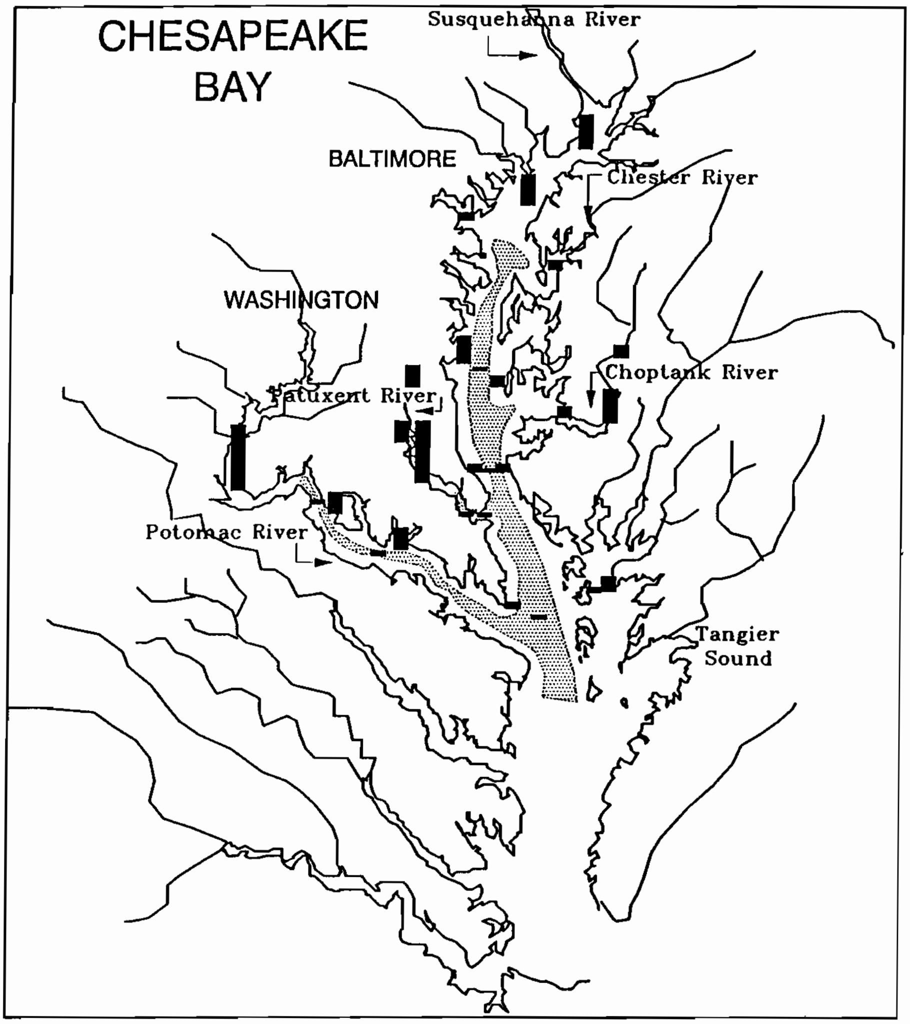

Figure 10. Spatial distribution of average annual benthic biomass, expressed in g ash free dry weight/m2, in relation with the region affected during summer by anoxic bottom waters (stippled) (Holland, 1987).

The "Dermo disease" *Perkinsus marinus* is present from the Gulf of Mexico coast to the Northeast Atlantic coast as far as Delaware Bay. It had been probably present in Chesapeake Bay before the first identification in 1949, and was widespread in the estuarine waters in lower Chesapeake Bay in 1957 (Mackin *et al.*, 1950; Andrews and Hewatt, 1957). *Perkinsus marinus* epizootic was studied in Maryland waters by Otto and Krantz (1976). The parasite is not salinity dependent compared to the oyster distribution. The MDNR survey during fall 1988, demonstrated the whole bay was contaminated with a very high prevalence rate; sometimes whole oyster populations were infested (Fig. 11). *Perkinsus marinus* is pathogenic during warm temperatures since the oysters expelled pathogens under 20°C (Andrews, 1984). This protozoan inhibits gonad development (Menzel and Hopkins, 1955). Perkinsus marinus abundance is correlated to the density of oyster populations since infections are caused by the parasites dispersion liberated in the water when the oysters die. Mobile vectors could also transmit the infection (White *et al.*, 1987-1989), in particular the ectoparasitic gastropod *Boonea impressa* (Say, 1821). In contrast to MSX, spat and young oysters are usually not infected by *Perkinsus marinus*.

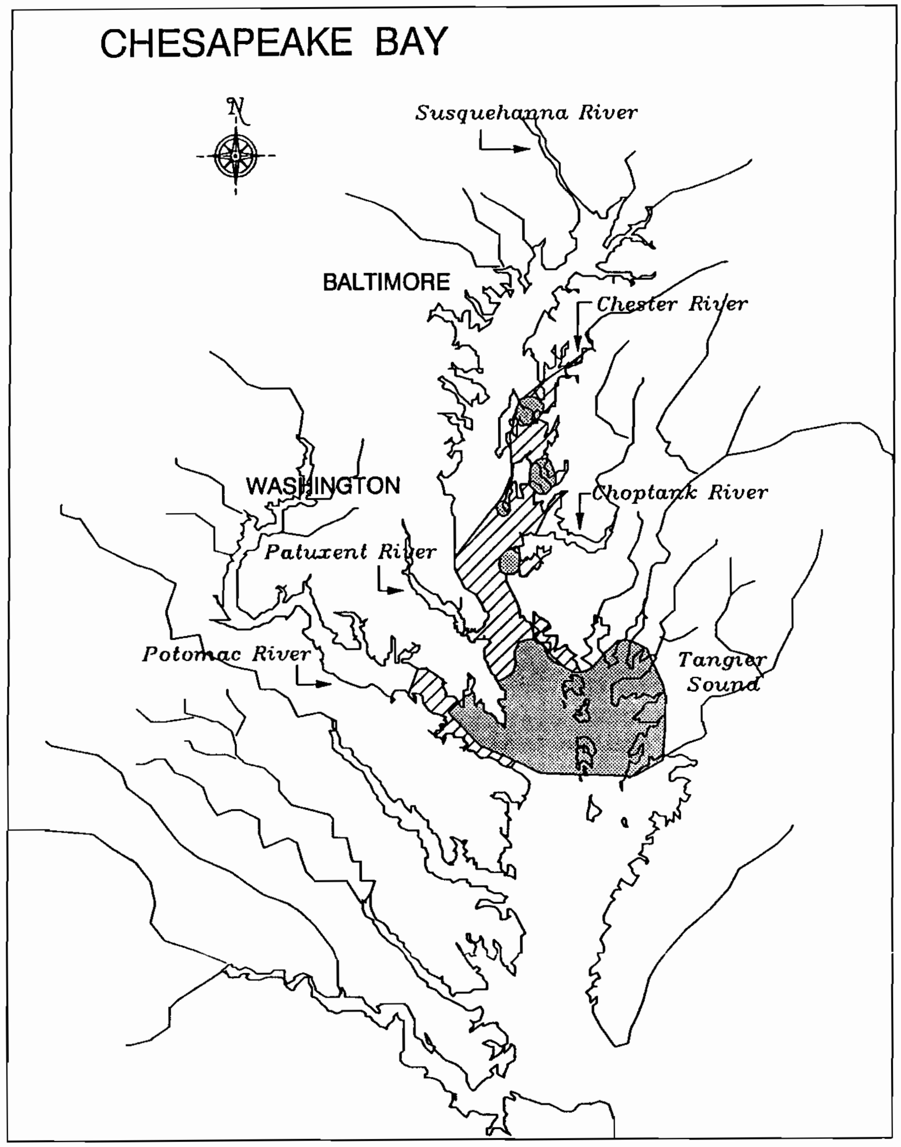

Figure 11. *Perkinsus marinus* distribution and prevalence during the fall 1988 survey, stippled > 50 %, hatched > 20 % (Krantz, 1989).

Superimposing the maps of oyster mortalities from 1981-1983, and 1986 and 1987, with respect to MSX and *Perkinsus marinus* abundance, emphasizes the correlations between prevalence and oyster mortality in various bay areas. Although mortalities higher than 20% occurred in 1981-1983 in the Upper Bay near Baltimore without MSX and *Perkinsus marinus* being abundant, these mortalities could be related to environmental conditions with unusually high temperatures in summer along with hypoxic conditions. Beaven (1947) demonstrated that in this area, many mortality incidents were correlated with high run-off of the Susquehanna River. Mortality rate is correlated to MSX abundance in Tangier Sound and the mouth of the Choptank River in 1981-1983, 1986 and 1987. In 1981-1983, MSX was abundant in Patuxent River mouth, but without abnormal mortality. In contrast, MSX was absent south of Potomac River in 1981-1983 and 1986, where high

Sound, mouth of Potomac River and in the mouth of Choptank River where *Perkinsus marinus* prevalence was above 50 % and MSX above 20 %. The mortalities (<25 %) were located in the upper part of the rivers and in the Upper Bay where MSX and *Perkinsus marinus* were less abundant (Krantz, 1989). Thus, it seems that high mortality levels are more closely related with *Perkinsus marinus* abundance, rather than with *Haplosporidium nelsoni.*

Many predators, despite the meso salinity of the bay, can also increase the oyster mortality rate. 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 inversely proportional to oyster size. Blue crabs could eat 16 spat per crab per day and large crabs can cause significant mortalities until oysters reach a shell height of 25 mm (Bisker and Castagna, 1987). Normally, blue crabs 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 occurs in summer 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 blue crabs landings exhibited a twofold increase between 1975 and 1981, remaining at an annual bay production higher than 40,000 tons until 1986 (Fig. 12). At least some of this increase resulted from an increase in the blue crab populations (Rothschild and Stagg, 1993). Therefore, the large increase in blue crab population could play a role in the increased oyster mortality rate since 1981. Although densities and trends are unknown, the mud crab *Panopeus herbstii* is present at high densities in Chesapeake Bay in salinities ranging from 10 to 34 ppt and is a more important predator than blue crab (Bisker and Castagna, 1987; Larsen, 1974; Schwartz and Cargo, 1960).

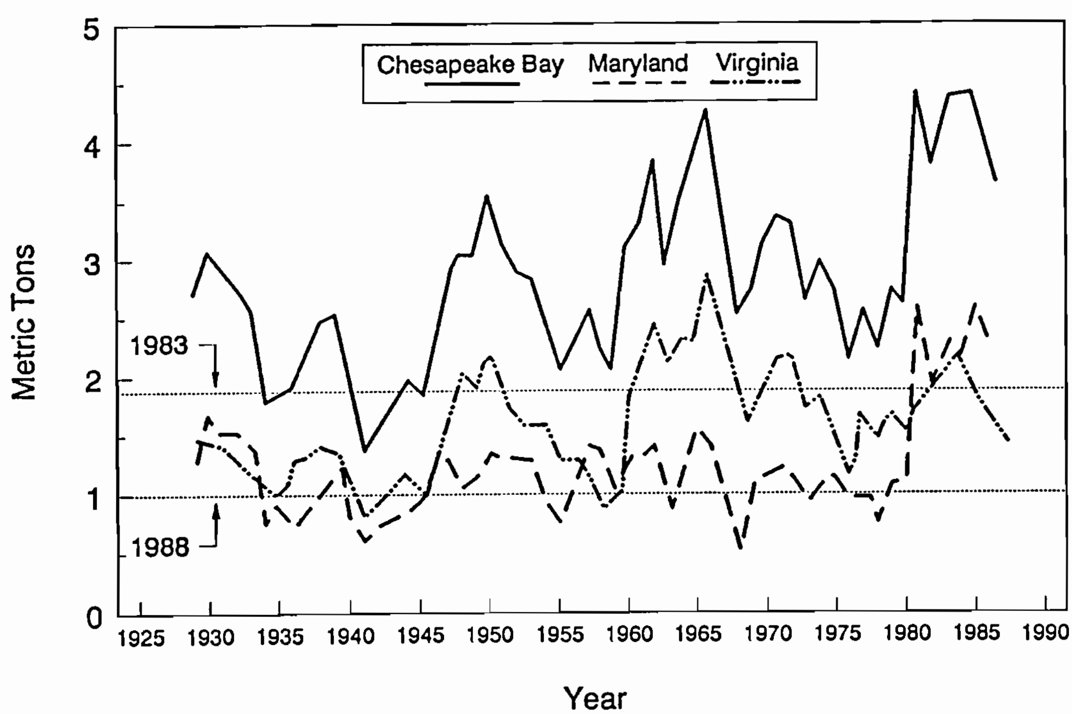

Figure 12. Evolution of the blue crab *Callinectes sapidus* commercial catch 1925-1987 in Virginia, Maryland and in the Chesapeake Bay expressed in 104 metric tons (Rothschild and Stagg, 1993).

The water quality degradation is very often given as an increasingly important factor of the oyster mortality rate, particularly by the watermen. Since pollutants affect bivalve larvae more than adults, it can be noted that the large spat sets which occurred in 1981 and 1985 demonstrate that summer environmental conditions permitted a normal growth rate and metamorphosis of the larvae. Large freshwater discharges into the Upper Bay, high sedimentation rate, and anoxic bottom waters can, either separately or together, cause mortalities. Heavy metals concentrations are below the level causing Eastern oyster larvae mortalities (Calabrese *et al.*, 1973, 1977; MacInnes and Calabrese, 1978). However, impact of organotin compounds should be studied in more detail 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 did not play a direct role in the increased mortality rate of oyster larvae or adults.

ALTERNATIVE STRATEGIES FOR RESTORATION OF OYSTER PRODUCTION IN THE CHESAPEAKE BAY

These recommendations mainly concern the Maryland part of the bay, but similar proposals could be applied to Virginia, especially for aquaculture on private bottoms. Alternatives can be developed along two lines, (i) within the repletion framework, by improving the present stock management, (ii) or external to this program by developing new intensive management, like oyster aquaculture. Hargis and Haven (1988) have already made strong recommendations to improve the oyster production of Virginia.

If the present management structure of the oyster fishery is maintained, reversing the production trends can be achieved by changing inadequate management practices which have contributed to the decline. For several decades oystermen have obviously practiced 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. Both are function of environmental conditions and management practices (e.g., shell planting, reseeding). Oyster overfishing in Chesapeake Bay is a different type of overfishing than that which occurs for fish. Overfishing results in not only taking more oysters than the stock can replenish, it also results in the habitat destruction. 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 the fishing season and enforcing a licensed boat system might not be enough. Developing sanctuaries in different areas where broodstocks are maintained, is of particular interest. 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, better estimates of the area with living oysters on the public bars is critical since maintaining and managing bottoms with mud and empty shells is useless. From 990 bars covering a total area of 116,000 ha, as estimated in 1912, we calculated the present acreage of the oysters bars to 55,600 ha by comparing with old and recent bay bottom charts, calibrated by our extensive survey (Rothschild *et al.*, 1992, 1993).

Based on these results, management efforts can focus on productive oyster bottoms. Knowing the spatial distribution of the stocks would also allow planned management of the fishery (e.g. 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. Oyster shell must be allocated with regards to biological and environmental constraints rather than social constraints. Diseases distribution must be considered for shell allocation to optimize the yields. Habitat must be favorable, in particular sedimentation must be low to keep the cultch as clean as possible and to guarantee high spat survival. Sites must be far away from anoxic bottom waters during summer, and in places where salinity remains high enough to facilitate the larval survivorship (Goulletquer *et al.*, 1993). Accordingly the large yearly variability in water quality can be responsible for success or recruitment failure (Fig. 13). The 10 ppt pycnocline shifts irregularly, extending or reducing the suitable area for spat settlement (cf. figure 2). Therefore, monthly water quality and larval abundance monitoring is likely to improve the overall management. Considerable scientific work and aquaculture practices have showed mainly in Japan and France, that to avoid fouling and sedimentation, it is best to employ spat collectors when the swimming oyster larvae are abundant, about 10 to 15 days before settlement (Héral et Deslous-Paoli, 1991). A positive correlation between the number of late-stage larvae and oyster set was also described in Chesapeake Bay by Engle (1955). Currently, shell is planted 2 to 3 months before the spawning period (Fig. 5) since only one private contractor performs the whole program. Within the existing fishery context, all the oyster fishermen who profit by the collective operation must help plant the cultch 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 improved yield might counterbalance the reduction. With regards to technical aspects of the reseeding plan, efficiency of different kinds of cultch (oyster shells, clam shells, concrete, slates, stones...) must be compared with the current dredged fossil shells. Comparison must be done in terms of biologic attraction for oyster larvae, hardness and stability of the cultch, behavior against fouling, and bottom rugosity 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. Optimization of the shell density in relation to the spat number and the cost and yield of the operation must be achieved.

Reseeding the spat in areas without recruitment, to places where growth rates are fast and mortality is low, can sustain the fishery but might also spread disease and reduce the spawning biomass. Before spat reseeding, diseases prevalence must be evaluated. 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 *Perkinsus marinus* are present, previously parasited oysters should be destroyed. How this could be accomplished is uncertain. This is particularly true for *Perkinsus marinus*, which contaminates oysters by proximity. Furthermore, the spat must be reseeded in places where the oyster habitat is the most favorable to its growth rate. Reseeded spat density must remain low to allow, optimum physiological conditions for resistance against the disease, and to avoid contamination by proximity, which is density dependant.

Since the landings are shrinking, demonstrating the failure of the oyster fishery, an alternative would be developing oyster aquaculture. This proposal would completely change the social characteristics of the Maryland watermen's community, since it will require by way of example, development of business enterprises, large investments. Therefore, an urgent need for sociological and economical research is required to estimate conditions and consequences of the development of oyster culture. From a biological point of view, the first problem with aquaculture is the choice of species. Since the native oyster is drastically affected by two diseases, it is not certain that aquaculturists must go with the Eastern oyster. Two main hypothesis could be investigated, (1) to proceed on *Crassostrea virginica*, or (2) to introduce another species like *Crassostrea gigas* (Thunberg, 1793).

With the Eastern 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 rates are obtained in suspension cultures. As market size oysters can be obtained in two years using these practices, high mortality rates occuring with MSX in three and four year-old oysters might be avoided. In this scheme it would be better to have natural spat if they were less expensive and more resistant to disease. A global analysis of oyster production development demonstrates clearly that leading countries depend on natural recruitment. In contrast, the history of production using juvenile mollusks produced in hatcheries is often unstable and to a

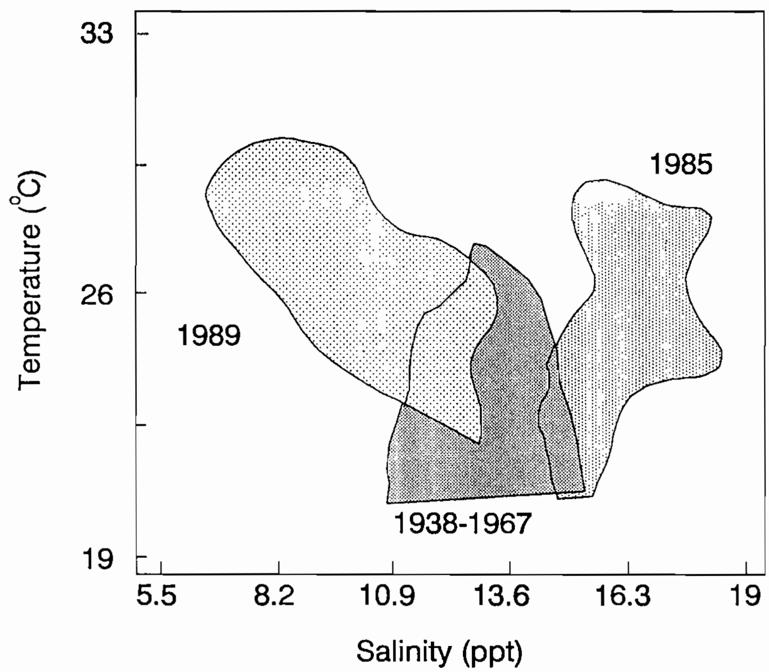

Figure 13. Comparison of temperature-salinity diagrams (June to September) at CBL's pier (mid-bay) in 1985, 1989 and an average based on 30 years. High oyster recruitment was observed in 1985, in contrast to the year 1989.

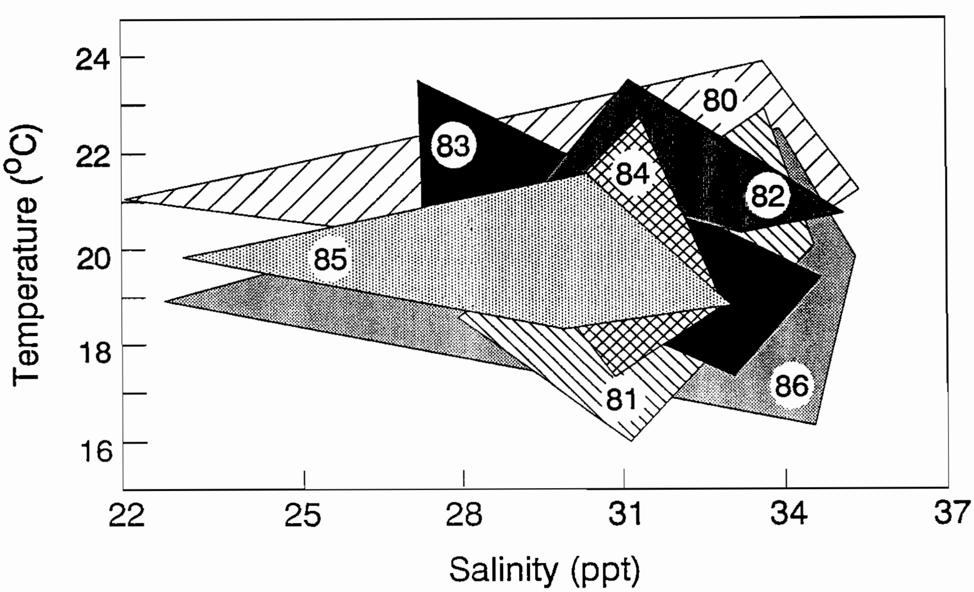

Figure 14. Temperature-salinity diagram in the Bay of Marennes-Oléron, during the evolution of *Crassostrea gigas* larvae (1980-1986) (Héral and Deslous-Paoli, 1991).

limited extent, compared to natural recruitment in spite of new techniques like remote setting using oyster larvae for settlement. This is mainly due to hatchery sizes, which cannot increase their production level, and also to diseases occuring frequently in overcrowded structures. By way of example, the amount of eyed larvae necessary to produce 160,000 tons of *Crassostrea gigas* by aquaculture in France, is estimated to be greater than 15 trillions! Reliance on hatcheries may be necessary when they are needed to produce some particular strain showing resistance to disease or fast growth, or even new "species" obtained by hybridization or by genetic manipulation.

For *Crassostrea virginica*, some selected strains are available. By selecting fast growing oysters and by crossing them together during several generations, a strain with fast growth (the market size could be reached after 12 to 18 months) is available to commercial hatchery (Paynter and Di Michele, 1990). Moreover, the MSX resistant strain developed by Rutgers University shows improved survivorship but still high susceptibility to *Perkinsus marinus* (Ford and Haskin, 1987; Burreson, 1991). Although, triploid yield produced in a sample may vary a lot, *Crassostrea virginica* triploids may be used to improve growth rates (Allen, 1986, 1993). Morover, Barber and Mann (1991) reported that *C. virginica* diploids and triploids were equally susceptible to *Perkinsus marinus.*

The introduction of another species must be evaluated. The Pacific oyster *Crassostrea gigas* yielding more than 70 % of total world production, is widely distributed in North America on the west coast but is not officially present on the east coast, even though Hargis and Haven (1988) reported that it is "now being processed or repacked in Virginia". Possible introduction of to the Chesapeake Bay has been extensively reviewed by Mann *et al.*, (1991). Reasons for choosing this species is that it is fast growing, reaching market size in one year when nutritional and temperature conditions are favorable (Héral, 1989), and its possible disease resistance to *Perkinsus marinus* and MSX. Also it is very resistant to various diseases, including the two viruses which destroyed the cupped European oyster *Crassostrea angulata* (Lamarck, 1819), and the protozoans *Marteilia refringens* and *Bonamia ostreae*, which caused severe damage to the European flat oyster *Ostrea edulis* Linné, 1758 (Grizel and Héral, 1990). Although there is some information regarding *C. gigas* resistance to *Perkinsus marinus*, none is available but urgently needed concerning *Haplosporidium nelsoni* effect (Meyers *et al.*, 1991; Barber and Mann, 1994). On the other hand, a new Bonamia-like disease inducing high mortalities in 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, several mortalities have been associated with vibrio and bacteria infecting the conchiolinous ligament and periostracum, a virus of *Crassostrea gigas* also affected larvae, causing large mortalities (Elston *et al.*, 1982; Elston *et al.*, 1985). In New-Zeland and France, an herpes virus-like has also affected larval culture (Comps *et al.*, pers. com.). In addition, large oyster mortalities, that may be due to a parasite, are now present in Japan. The risk associated with importing *C. gigas* from the west coast can be assessed using a disease survey. Importing diseases to Chesapeake Bay is a potential risk given the trade in Virginia between east coast and west coast. Imports could be made after an evaluation of sanitary quality of the oyster beds in countries showing disease free areas. Even if, for example, the historical case of *C. gigas* introduction 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 situations are not dramatically urgent, to take maximum precautions with imports and to follow ICES recommendations regarding species introduction for commercial or scientific purposes (e.g., quarantine, F1 hatchery production).

Another question about introducing *Crassostrea gigas* is the species behavior in the Chesapeake Bay. Habitat requirements of the Pacific oyster seems to be more marine than that of the Eastern oyster, and it might not reproduce regularly in the low salinities of the tributaries and the Upper Bay (Fig. 14). Moreover, *C. gigas* oysters are more sensitive to pollution than Eastern oysters. By way of example, a 2 $\mu g.l^{-1}$ organotin (TBT) exposure reduced the *C. virginica* growth rate without shell thickening. It affected *C. gigas* at concentrations from 1 $\mu g.l^{-1}$ to 0.01 $\mu g.l^{-1}$ (Héral *et al.*, 1989). TBT concentrations largely exceed this level in Chesapeake Bay, particularly in marinas and some tributaries (Hall, 1988), demonstrating that water quality could be a limiting factor for a different oyster species.

Use of *C. gigas* triploids would presumably limit their distribution since their reproductive effort is drastically reduced (Allen, 1986, 1993). Although inviable, hybridization between Eastern and Pacific oysters is possible since hybrids can survive 8-10 days but with reduced growth. Although direct genetic effects on *C. virginica* native range following *C. gigas* introduction are reduced (Allen, 1993; Allen *et al.*, 1993), this might still affect indirectly the reproductive capacity of the native species by trapping gametes.

Another alternative is a species change associated to a fishery management. To optimize production, the problems would be similar to the current difficulties of the Eastern oyster fishery.

It must be kept in mind that by changing the species, the whole ecosystem might be modified. If environmental conditions are optimal for a new species, it could spread very quickly, creating large oyster reefs and might, through increased filtration, reduce eutrophication, as happened in South San Francisco Bay (Officier *et al.*, 1982). This hypothesis was formulated 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 for successful spat settlement, therefore impeding full assessment regarding *C. gigas* introduction effects over the entire bay.

The next steps involve considering the possible fast improvements, such as making *C. virginica* management more rational and then considering in greater detail the choices or combinations among the management options - new species introduction - and intensified culture.

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