# Ecological Changes in Chesapeake Bay: Are They The Result of Overharvesting the American Oyster, *Crassostrea virginica*?

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## ABSTRACT

Standing stocks of the American oyster (Crassostrea virginica) in Chesapeake Bay were as high as $188 \times 10^6$ Kg dry tissue prior to the major harvests of the late 19th Century. Due to continued overfishing and the effects of disease, the population has declined to a current level of about $1.9 \times 10^6$ Kg dry tissue. Crassostrea virginica is a suspension feeder, removing suspended organic and inorganic particles >3 $\mu$m in diameter with high efficiency. As it only assimilates approximately 70% of the filtered organic material, its dense mucus-bound biodeposits can provide a food resource for benthic organisms. Thus the oyster can form an important link between pelagic and benthic food webs.

It is possible that this decline in oyster biomass, and consequent reduction in their cropping of phytoplankton populations, may be a strong contributing factor to the apparent shift to microbial food webs and resultant summer anoxia in the deeper waters of the Bay. In addition, it is possible that planktonic suspension-feeding organisms, such as copepods and microzooplankton, have increased in abundance in response to this reduction in competition for phytoplankton. Such an increase in zooplankton would be expected to lead to a rise in the biomass of their predators, such as ctenophores and jellyfish. An increase in the oyster population by management and aquaculture could significantly improve water quality by removing large quantities of particulate carbon.

## INTRODUCTION

The development during the summer of brief periods of anoxia in the bottom waters of Chesapeake Bay was first reported by Newcombe et al. (1939) in the 1930's. Since then, the duration and extent of such anoxic conditions may have expanded until by the mid-

1980's much of the water beneath the pycnocline is anoxic for extended periods during the summer (Officer et al. 1984). Such a deterioration in water quality in the Bay imposes a stress on the biota, which is usually fatal to benthic invertebrates, including many commercially valuable species. Thus, over the last decade a considerable amount of research has been directed toward understanding the causes and consequences of these changes in water quality (Taft et al. 1980, Officer et al. 1984). The general consensus from these investigations is that an increase in inorganic nutrient inputs, from both point and non-point sources, has led to enhanced levels of primary production throughout the Bay. It is the utilization and respiration of these abnormally high levels of organic material by the benthos and heterotrophic bacteria that reduces the dissolved oxygen concentration in the bottom waters (Kemp and Boynton 1984), and when a strong summer pycnocline prevails, anoxia can become very widespread (Malone et al. 1986, Officer et al. 1984). Therefore, in 1987 legislation to reduce nutrient inputs into the Chesapeake Bay by 40% was enacted which, it is thought, will reduce many of the consequences of eutrophication.

Extant benthic invertebrate populations are now recognized to be extremely important in nutrient recycling and benthic pelagic coupling (Rhoads 1974, Boynton et al. 1980, Dame et al. 1980) and molluscan suspension feeders may even act as a natural control on the adverse effects of eutrophication in estuaries (Cloern 1981, Cohen et al. 1984, Officer et al. 1982). The objective of this paper is to explore the possibility that the effects of nutrient enrichment on the Chesapeake Bay ecosystem have been exacerbated by the decline over the last century in the American oyster population. In an effort to quantify the role of oysters in Chesapeake Bay, I have compared the time it would take the oyster populations at their pre-exploitation densities, and in 1988, to filter the entire volume of the Bay. This method has previously been used to demonstrate the role of extant populations of suspension feeders in other estuaries (e.g. Dame et al. 1980, Biggs and Howell 1984). I have then taken these calculations a stage further by determining what proportion of the current daily primary production the original oyster populations could have removed from the water column. From this information I have calculated what proportion of the carbon that could have been used by the original high densities of oysters is now available for other organisms, such as pelagic suspension feeders.

## OYSTER STANDING STOCKS

The American oyster, <u>Crassostrea virginica</u> is a well adapted estuarine species that produces large oyster beds in localities with salinities that range from 5 to 30 ppt (Galtsoff 1964). The oyster also requires firm substrates to form substantial populations; thus it is incapable of living on the softer muds often found in the >9 m deep channels of both the main-stem Chesapeake Bay and upper bay tributaries, except in certain exceptional localities (e.g. at 37-40 m near Point Patience in the Patuxent river [Kennedy and Breisch 1981]). The oyster was once so abundant in Chesapeake Bay that 18th century contemporary accounts suggest that oyster reefs were a significant navigational hazard (Wharton 1957). The subsequent decline in abundance is thought to be primarily due to continuous overexploitation (Kennedy and Breisch 1981) and, secondarily, due to the effects of disease.
Despite the economic importance of the oyster there is little reliable information on oyster biomass in Chesapeake Bay. Instead, I have estimated biomass from information on oyster landings in Maryland and Virginia, although it is widely regarded that oyster landings are significantly under-reported (Krantz and Haven 1982, Stagg 1985). Also, harvest statistics only give information for commercial size oysters (>7 cm) and are subject to other errors that give rise to inconsistences between supposedly identical records (Haven et al. 1978).

The most complete record for oyster landings in Maryland were compiled by Kennedy and Breisch (1981). From their data (Figure 1) I have calculated that 304 x $10^6$ Maryland bushels of oysters were harvested between 1870 and 1895. Contemporary surveys of the major oyster growing regions during the late 19th Century show that there was a precipitous decline in oyster stocks and an irreversible change in many oyster beds as a result of the harvest activities, such that many were no longer conducive to oyster larval settlement (for review see Kennedy and Breisch 1981). After these large harvests, landings declined to a fairly stable level of about 3 x $10^6$ bushels a year for the next four decades. The stability of these subsequent harvests suggest that this was the annual level of recruitment to the population and the earlier annual harvests of over 10 x $10^6$ bushels were of a standing stock that had built up over many years in areas where recruitment occurred infrequently. Similarly, Davis et al. (1976) suggested that in certain localities within the Bay the abundance of oysters depends on a successful recruitment that occurs only every 10-15 years. Thus, if an annual recruitment of 3 x $10^6$ bushels is subtracted from the landings for the 25-year period 1870-1895 it indicates that there was a standing stock of 229 x $10^6$ bushels of oysters in Maryland prior to 1870. I used a yield factor of 2.64 Kg wet weight of oyster tissue per Maryland bushel (Haven et al. 1978), and that an oyster has an 80% water content (Newell, unpublished data), to calculate that the dry weight biomass of oysters in Maryland prior to the major harvests was 120.5 x $10^6$ Kg. Unfortunately, there is no information available on oyster landings in Virginia prior to 1880. Thus, oyster stocks cannot be calculated from reported landings for the period of the major harvest. Instead, I have calculated from National Marine Fisheries Service statistics (Figure 1) that in 1880, 1888, 1890 and 1891 the Virginia landings were, on average, 56% of those in Maryland. Assuming that the fishing pressure on the oyster stocks during this period was the same between the two states, the standing stock in Virginia would be 56% of the calculated value for Maryland i.e. 67.4 x $10^6$ Kg dry oyster tissue.
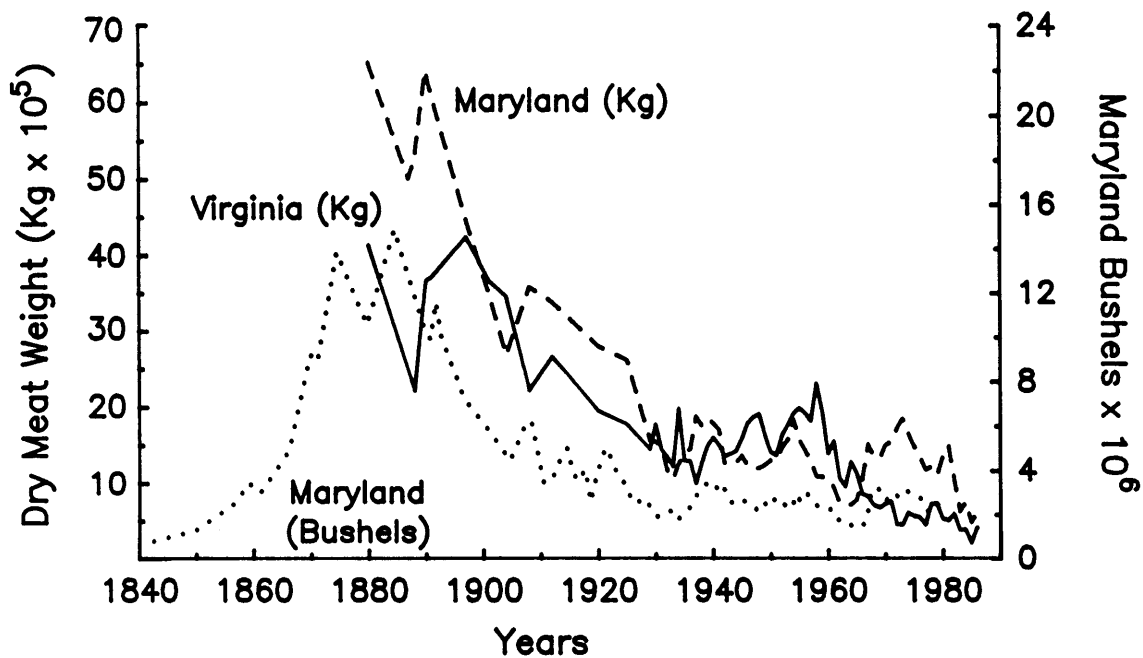


Figure 1. Oyster landings (dry tissue weight) for Maryland (- - -) and Virginia (——) [source: NMFS statistics for oyster landings, converted to dry weight: see text for details] and bushels x $10^6$ landed in Maryland (. . . .) (Redrawn from Kennedy and Breisch 1981).

A second method for estimating pre-harvest oyster stocks is to use an estimate of what percentage of the total population was being harvested annually and apply this to the data on landings. In the early 1970's this exploitation rate was extremely high, reaching over 30%, because the oyster stocks were small (Cabraal 1978). In order to obtain a conservative estimate of the oyster biomass I have applied a moderately high exploitation rate of 10% to the peak harvest data of 1880 for Maryland and Virginia (Figure 1) to calculate that in 1880 Maryland had a stock of $65.3 \times 10^6$ Kg and Virginia $41.4 \times 10^6$ Kg dry tissue.

By 1975 the oyster stocks in Maryland had declined to $5.26 \times 10^6$ Kg dry tissue (Cabraal 1978) and in 1988 are about 1.05 Kg dry tissue (pers. comm., Dr. S.J. Jordan, Maryland Department of Natural Resources). The Virginia oyster population in 1988 was estimated to be about $1.5 \times 10^6$ bushels ($0.85 \times 10^6$ Kg dry tissue) (pers. comm., Dr. R. Mann, Virginia Institute of Marine Science).

## ESTIMATION OF THE FEEDING ACTIVITY OF CRASSOSTREA VIRGINICA

The oyster is an active suspension feeder, removing particles > 3 $\mu$m with high efficiency (Haven and Morales-Alamo 1970). Subtidal oysters in the Chesapeake Bay feed for over 23 h per day with no diurnal rhythm (Newell, unpublished data). Feeding activity varies seasonally but rates of $5\ l \cdot h^{-1} \cdot g^{-1}$ dry tissue weight are typical for oysters during the summer (Newell, unpublished data). Thus oysters have an average summer filtration rate of $0.115\ l \cdot kg^{-1} \cdot d^{-1}$.

For Chesapeake Bay, and Maryland's portion of the Bay, the total volumes ($71.5 \times 10^9$ and $27.3 \times 10^9$ m$^3$, respectively), and volumes <9m in depth ($53.8 \times 10^9$ and $17.8 \times 10^9$ m$^3$, respectively), of the regions with salinities >5 ppt (in which oysters flourish), were calculated from Cronin and Pritchard (1975).

The pre-1870 oyster populations in the Chesapeake Bay could potentially filter the entire water column during the summer in less than 3 to 6 days and the <9m water every 2 to 4.5 days (Table 1). However, with the current oyster stocks, these turnover times have dramatically increased to 325 days and 244 days, respectively (Table 1).

Table 1. Number of days required by the oyster population, prior to the major harvests (pre-1870 and 1880 oyster stock estimates) and today, to filter both the entire water column and the water shallower than 9 m, both in Maryland's portion of the Bay and in the entire Chesapeake Bay.

| Date | Oyster Biomass (Kg x 10⁶ Dry Tissue Wt) | Volume of Water Filtered (L x 10¹² d⁻¹) | Turnover Time (d) Total Water Column | <9m Zone |
|---|---|---|---|---|
| Maryland's Portion of Chesapeake Bay | | | | |
| Pre-1870 | 120.5 | 13.86 | 2.0 | 1.3 |
| 1880 | 65.3 | 7.51 | 3.6 | 2.4 |
| 1975 | 5.3 | 0.61 | 44.8 | 29.2 |
| 1988 | 1.1 | 0.12 | 227.5 | 148.3 |
| Entire Chesapeake Bay | | | | |
| Pre-1870 | 188.0 | 21.62 | 3.3 | 2.5 |
| 1880 | 106.8 | 12.27 | 5.8 | 4.4 |
| 1988 | 1.9 | 0.22 | 325.0 | 244.5 |

## THE ROLE OF OYSTERS IN CARBON CYCLING

Harding et al. (1986) measured the daily rate of carbon production by phytoplankton along the main stem of Chesapeake Bay in the spring, summer and fall of 1982. From their data I have calculated an average carbon production of $1.08 \pm 0.25(S.E.)$ g C . $m^{-2}$ . $d^{-1}$ (range 0.14 - 2.65) for the >5 ppt regions of the Bay where oysters can grow. Malone et al. (1986) reported a slightly higher rate of phytoplankton carbon production of 1.44 g C . $m^{-2}$ . $d^{-1}$ during the summer and early fall of 1984 in the main stem of the Bay near the mouth of the Choptank river.

The total area of Chesapeake Bay with salinities >5 ppt is $10.7 \times 10^9$ . $m^{-2}$ and the area within Maryland is $3.66 \times 10^9$ . $m^{-2}$ (Cronin 1971). Thus, using the value of $1.08 \pm 0.25(S.E.)$ g C . $m^{-2}$ . $d^{-1}$ (Harding et al. 1986), the average total daily planktonic carbon production during 1982, in the entire Bay, and in Maryland's portion, was calculated to be $11.5$ g $\times 10^9$ g and $3.95 \times 10^9$ g, respectively. Malone et al. (1984) reported that the euphotic zone ranged in depth from 3 to 6 m and was confined to the mixed layer above the pycnocline. Therefore, in order to convert the areal daily carbon production to carbon per litre I have assumed that phytoplankton production is confined to waters shallower than 9 m waters (This is generally also the maximum depth in which oysters live in the Bay). Thus, there is an average daily carbon production of $2.2 \times 10^{-4}$ g . $l^{-1}$ in the Chesapeake Bay.

The metabolic carbon requirements of an oyster feeding at 5 l . $h^{-1}$ . $g^{-1}$ are 0.537 mg C respired $h^{-1}$, calculated from its rate of oxygen consumption of 1 ml $O_2$ . $h^{-1}$ . $g^{-1}$ (Newell and Langdon 1986). Assuming that respiratory carbon demands are 75% of total carbon requirements (Bayne and Newell 1983), the oyster's total carbon requirements are 17.3 mg C . $d^{-1}$. Using these estimates of carbon requirements, together with those for 1982 phytoplankton carbon production, the pre-1870 oyster stocks in Maryland would have been capable of removing 77% of the 1982 daily carbon production in the <9 m waters (Table 2); about 70% of the filtered carbon would be used to satisfy their metabolic demands while the other 30% would have been egested as compacted biodeposits available to the benthic food web (Table 2). Even the conservative estimate of the original oyster population in Maryland suggests that they could remove 42% of the 1982 daily carbon production from the <9 m water column. Overall, the entire population of oysters that existed in Chesapeake Bay prior to their heavy exploitation by man might have been capable of removing between 23% and 41% of the 1982 phytoplankton carbon production.

By 1975 the population of oysters that existed in Maryland's portion of Chesapeake would have been capable of removing only 3.4% of the 1982 daily carbon production in the <9 m waters. By 1988 the oyster population had declined to such an extent that it is only capable of removing about 0.7% of the daily carbon from Maryland's waters and 0.4% baywide (Table 2).

Unfortunately, it is difficult to assess from my calculations the relative impact of the pre-exploitation oyster populations on benthic pelagic coupling in the main stem of Chesapeake Bay, where about 35% of the area is >9 m deep (Pritchard 1952), compared to its shallower tributaries. Even in the main-stem, however, oyster densities were extremely high on both the western and eastern shores, with particularly extensive populations at the mouths of each tributary, and in Eastern Bay and Tangier Sound (Kennedy and Breisch 1981). Generally, oyster beds are concentrated in areas of high water flow and scour, such as occur along the edges of channels, where water movement is sufficient to bring in food and remove biodeposits (Lund 1957). This water circulation would have enhanced the ability of oysters to filter large amounts of particulate material, even from the main-stem Chesapeake Bay. In addition, the pre-

Table 2. For Maryland's portion of the Bay and the entire Chesapeake Bay, prior to the major period of oyster harvest (pre-1870 and 1880 oyster stock estimates) and today, a) percent of the daily phytoplankton carbon production filtered by oysters; b) weight of carbon filtered by oysters from the <9 m water column; c) the total carbon assimilated; and d) the amount of carbon, in the form of oyster biodeposits, sedimented. All calculations are based on 1982 daily carbon production estimates of $39.5 \times 10^8$ and $115.6 \times 10^8$ g carbon for Maryland's portion of the Chesapeake Bay, and the entire Bay, respectively.

| Date | % Daily Carbon Production Removed | Carbon Removed <9m Zone $(g \times 10^8 \, d^{-1})$ | Assimilated Carbon $(g \times 10^8 \, d^{-1})$ | Carbon Sedimented $(g \, m^{-2} \, d^{-1})$ |
|------|------|------|------|------|
| | Maryland's portion of Chesapeake Bay | | | |
| Pre-1870 | 77.2 | 30.5 | 20.7 | 0.267 |
| 1880 | 41.7 | 16.5 | 11.2 | 0.145 |
| 1975 | 3.4 | 1.34 | 0.9 | 0.012 |
| 1988 | 0.7 | 0.26 | 0.2 | 0.002 |
| | Entire Chesapeake Bay | | | |
| Pre-1870 | 41.2 | 47.6 | 32.2 | 0.144 |
| 1880 | 23.4 | 27.0 | 18.3 | 0.081 |
| 1988 | 0.4 | 0.48 | 0.3 | 0.002 |

exploitation oyster reefs were such large accretions of shell and living oysters that they must have enhanced turbulent mixing and created changes in the local water currents. Again this would enable the oyster community to intercept a larger proportion of the water flow, compared to other benthic suspension feeders that can only feed in the region of low flow associated with the benthic boundary layer.

## ECOLOGICAL CHANGES IN CHESAPEAKE BAY

In Chesapeake Bay the extant macrobenthic invertebrates are both numerous and diverse, with many communities dominated by suspension feeding molluscs (Holland et al. 1987). Unfortunately, there is no direct data available to indicate whether the biomass of these communities has changed as a consequence of the decrease in the oyster population. However, currently one of the most abundant suspension feeding molluscs in the mesohaline regions is the wedge clam, Rangia cuneata. This species :as only become a dominant member of the benthos in the last two decades, and was thought to be extinct on the east coast prior to 1955 (Hopkins and Andrews 1969). In the oligohaline to freshwater reaches of the Potomac river, the Asiatic clam, Corbicula fluminea, which was introduced in the last decade, is so abundant that its feeding activity causes a significant decrease in the phytoplankton population (Cohen et al. 1984). In contrast to the increase in some species of benthic invertebrates it is possible that in some localities the benthic biomass is lower today as a consequence of the reduction in oyster biodeposition. The feces and pseudofeces produced by the oyster contain a large proportion of organic matter (Newell and Jordan 1983) which can form an important energy source for bacteria and benthic invertebrates feeding at the sediment water interface (Haven and Morales-Alamo 1966, 1968; Jordan 1987).

Indeed, Holland et al. (1987) have speculated that benthic communities at some locations within Chesapeake Bay are currently food limited. Also, the original oyster beds provided a major source of firm substrate for other benthic invertebrates, such as mussels, barnacles, and tunicates that cannot live on the generally muddy bottom of the Bay.

Pelagic suspension feeders, such as zooplankton may have increased in abundance as a result of the decline in oyster stocks. Zooplankton, which are relatively short-lived and opportunistic animals, can respond rapidly to an increase in the supply of phytoplankton. Zooplankton and meroplankton in Chesapeake Bay can attain high densities and currently consume nearly 100% of the daily phytoplankton production during August in the mesohaline portion of the Bay (White and Roman 1988). This suggests that during the summer the zooplankton community is a major consumer of the phytoplankton population, a position that could once have been filled by the adult oyster and its planktotrophic larvae.

The major consumers of zooplankton are fish larvae, certain species of adult fishes, ctenophores (Mnemiopsis leidyi), and jellyfish, e.g., the sea nettle (Chrysaora quinquecirrha); the sea nettle also preys on the ctenophore. In a detailed review by Wharton (1957) of the historical literature available on colonial fisheries in Virginia there is little mention of the now-abundant sea nettle. Given the current attention paid to the sea nettle by fisherman and boaters it is plausible to equate the lack of reference in the historical diaries with the idea that sea nettles might not have been very abundant during that period. I speculate that the current high abundance of sea nettles may be due, in part, to an increase in their zooplankton food supply, which is a consequence of a reduction in oyster stocks. However, sea nettles have probably always been present within Chesapeake Bay, perhaps relying on the once abundant oyster larvae as a prey item.

It is currently thought that increased nutrient inputs and reduced light levels are encouraging the growth of small species of phytoplankton in Chesapeake Bay (for review see Verity 1987). There is no information available concerning the size structure of the phytoplankton community in Chesapeake Bay a century ago when oysters were abundant. However, oysters are capable of removing cells <3 $\mu$m, albeit with relatively low efficiency (Haven and Morales-Alamo 1970). In contrast, Acartia tonsa, which is usually the dominant pelagic suspension feeder during the summer (Heinle 1966, White and Roman 1988), cannot feed efficiently on cells <7 $\mu$m (Richman et al. 1977, Ryther and Sanders 1980). Thus, in systems such as Chesapeake Bay that are dominated by zooplankton herbivores, it is likely that there will be a shift to smaller phytoplankton species simply as a result of selective effects of zooplankton grazing (Richman et al. 1977, Ryther and Sanders 1980).

Oysters, in common with other bivalve molluscs, are efficient suspension feeders and can have a considerable impact on particle concentrations because of their ability to pump large volumes of water across the ciliated surfaces of their gills (Jorgensen 1966). They are also long-lived animals that overwinter and increase their feeding activity in the spring in response to rising water temperature. Thus the pre-harvest oyster population would have been an important consumer of the spring phytoplankton bloom. In contrast, the copepod Acartia tonsa is not able to overwinter as an adult in the Chesapeake Bay, due to low winter temperatures. Other members of the zooplankton population are meroplanktonic e.g., polychaete larvae which in August are second only to copepods in their consumption of phytoplankton (White and Roman 1988). As a consequence of the low zooplankton biomass in the spring a large proportion of the spring phytoplankton bloom currently remains ungrazed. It is the provision of this pulse of carbon to the benthic invertebrate and bacterial communities

beneath a strong pycnocline (when it develops) that is responsible for the anoxic conditions in the bottom waters of the Bay (Kemp and Boynton 1984).

In addition to their role in cropping phytoplankton populations, the pre-exploitation oyster populations may also have been important in controlling turbidity, by reducing both the particulate inorganic material (PIM) and organic material (POM) suspended in the water column. The oyster removes PIM and POM with high efficiency and ejects the undigested material as mucus-bound biodeposits. Thus, the grain size of the PIM is effectively increased, making the PIM more resistant to erosion and resuspension (Haven and Morales-Alamo 1968, Jordan 1987). Increased turbidities in the Bay that have occurred since colonial times have principally been attributed to anthropogenic factors (e.g., land clearing) increasing the rate of terrestrial erosion in the watershed, and a decline in the seagrass communities that not only trap suspended sediments but can also serve to stabilize sediments (Short and Short 1986). However, the decline in the oyster population over the last century may have exacerbated suspended particulate concentrations simply by reducing rates of biodeposition.

Currently the euphotic zone in Chesapeake Bay lies between 3-6 m deep (Malone et al. 1986) and although primary production is high it is generally considered to be light and not nutrient limited (Harding et al. 1986, Verity 1987). Thus phytoplankton production may also have been high prior to 1870 because of increased light penetration, as well as the rapid recycling of nutrients via the oysters metabolic processes (Rhoads 1974, Boynton et al. 1980). My calculations for the amount of carbon required by the pre-1870 oyster population in Maryland (Table 2) indicate that the oysters required about 52% of the 1982 daily carbon production to satisfy their own requirements. These calculations suggest that only 25% of the 1982 carbon production would be directly available, and another 25% indirectly in the form of oyster biodeposits, for all other herbivores and detrivores in Chesapeake Bay. This suggests that the Bay must have been an extremely productive system prior to 1870 in order to support both the oyster population and the other animal species. It is possible that it was even food limited on some occasions.

## SUMMARY

From my calculations it is apparent that oyster stocks were once abundant enough to be the dominant species filtering carbon from the water column in Chesapeake Bay. Harding et al. (1984) estimated that phytoplankton doubling times during the summer in Chesapeake Bay are on the order of 0.8 to 4.3 days. This is very similar to the summer filtration times for the <9 m water column of 1.3-4.4 days that I estimated for the original oyster populations (Table 1). From the rationale of Officer et al. (1982), this suggests that the oyster could have exerted a major influence on the phytoplankton population in Chesapeake Bay. I believe that these calculations provide insights into the role that a flourishing oyster population once played in the ecology of Chesapeake Bay. Even if the figures are not absolute, the relative magnitude of the changes associated with the over-exploitation and decline of the oyster stocks cannot be ignored. Consideration of the former trophic role oysters may have played in the Chesapeake Bay ecosystem is instructive since it suggests a valuable biological role that restored oyster populations can play in future water quality restoration efforts. This is in addition to the well recognized importance of the oyster to commercial fisheries. If it is impossible to restore Crassostrea virginica, due to its susceptibility to two major oyster diseases (MSX and Perkinsus) that are present in the Bay, perhaps we should consider introducing a non-native oyster species, such as the Pacific oyster Crassostrea gigas. Officer et al. (1982) make the point that is the introduced species of bivalve molluscs in South San Francisco Bay that are controlling the detrimental effects of eutrophication. Restoring an abundant population of filter

feeding oysters to the shallow waters of Chesapeake Bay and its tributaries might really help lend new meaning to the phrase "Clean up the Bay".

## ACKNOWLEDGEMENTS

## LITERATURE CITED

Bayne, B.L. and R.C. Newell. 1983. Physiological energetics of marine molluscs. In: The Mollusca, Vol 4, Physiology, Part I. A.S.M. Saleuddin, K.M. Wilbur, eds. Academic Press, New York, p.407-515.

Biggs, R.B. and B.A. Howell. 1984. The estuary as a sediment trap: Alternate approaches to estimating its filtering efficiency. In: The estuary as a filter. V.S. Kennedy, ed. Academic Press, Orlando, Fl. p. 107-129.

Boynton, W.R., W.M. Kemp and C.G. Osbourne. 1980. Nutrient fluxes across the sediment-water interface in the turbid zone of a coastal plain estuary. In: Estuarine Perspectives. V.S. Kennedy, ed. Academic Press, New York. p. 93-109.

Cabraal, R.A. 1978. Systems analysis of the Maryland oyster fishery: production, management, and economics. Ph.D. dissertation, University of Maryland, College Park. 318pp.

Cloern, J.E. 1981. Does the benthos control phytoplankton biomass in South San Francisco Bay? Mar. Ecol. Prog. Ser. 9:191-202.

Cohen, R.R.H., P.V. Dresler, E.J.P. Philips, and R.L. Cory. 1984. The effect of the asiatic clam, Corbicula fluminea on phytoplankton of the Potomac River, Maryland. Limnol. Oceanogr. 29:170-180.

Cronin, W.B. 1971. Volumetric, areal, and tidal statistics of the Chesapeake Bay estuary and its tributaries. Chesapeake Bay Institute. Special Report. No 20.

Cronin W.B. and D.W. Pritchard. 1975. Additional statistics on the dimensions of the Chesapeake Bay and its tributaries: Cross section widths and segment volumes per meter depth. Chesapeake Bay Institute. Special Report. No 42.

Dame, R., R. Zingmark, H. Stevenson and D. Nelson. 1980. Filter feeder coupling between the estuarine water column and benthic subsystems. In: Estuarine Perspectives. V.S. Kennedy, ed. Academic Press. New York. p. 521-526.

Davis, J., D. Haven, K.G. Drobeck and E.A. Dunnington. 1976. Plans for the Management of the Fisheries of the Tidal Potomac River. Univ. of Maryland, Solomons, Md. CEES Ref No.76-123CBL. 38pp.

Galtsoff, P.S. 1964. The American oyster Crassostrea virginica (Gmelin). U.S. Fish Wildl. Serv. Fish. Bull. 64:1-480.

Harding, L.W., B.W. Meeson and T.R. Fisher. 1986. Phytoplankton production in two east coast esturies: Photosynthesis-light functions and patterns of carbon assimilation in Chesapeake and Delaware Bays. Estuar. Coastal Shelf Sci. 23:773-806.

Haven, D., and R. Morales-Alamo. 1966. Aspects of biodeposition by oysters and other invertebrate filter-feeders. Limnol. Oceanogr. 11:487-498.

Haven, D., and R. Morales-Alamo. 1968. Occurrence and transport of faecal pellets in suspension. Sed. Geo. 2:141-151.

Haven, D., and R. Morales-Alamo. 1970. Filtration of particles from suspension by the American oyster Crassostrea virginica. Biol. Bull. 139:248-264.

Haven, D.S., W.J. Hargis and P.C. Kendall. 1978. The oyster industry of Virginia: its status, problems and promise. VIMS Spec. Papers Mar. Science No. 4 1024pp.

Heinle, D.R. 1966. The production of a calanoid copepod, Acartia tonsa, in the Patuxent estuary. Ches. Sci. 7:59-74.

Holland, A.F., A.T. Shaughnessy and M.H. Hiegel. 1987. Long-term variation in mesohaline Chesapeake Bay benthos: Spatial and temporal patterns. Estuaries 10:227-245.

Hopkins, S.H., and J.D. Andrews. 1969. Rangia cuneata on the east coast: Thousand mile range extension, or resurgence? Science 167:868-869.

Jordan, S.J. 1987. Sedimentation and remineralization associated with biodeposition by the American oyster Crassostrea virginica (Gmelin). Ph.D. Dissertation Thesis. University of Maryland, College Park.

Jorgensen, C.B. 1966. The Biology of Suspension Feeding. Pergamon Press, London. 357pp.

Kennedy. V.S. and L.L. Breisch. 1981. Maryland's Oysters: Research and Management. Maryland Sea Grant, University of Maryland, College Park, MD. 286pp.

Kemp, W.P. and W.R. Boynton. 1984. Spatial and temporal coupling of nutrient inputs to estuarine primary production: the role of particulate transport and decomposition. Bull. Mar. Sci. 35:242-247.

Krantz, G.E., and D.S. Haven. 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. L.E. Cronin, ed., UMCEES-CBL. p.44-52.

Lund, E.J. 1957. Self silting by the oyster and its significance for sedimentation geology. Publ. Inst. Mar. Sci. Univ. Texas 4:320-327.

Malone, T.C., W.M. Kemp, H.W. Ducklow, W.R. Boynton, J.H. Tuttle and R.B. Jonas. 1986. Lateral variation in the production and fate of phytoplankton in a partially stratified estuary. Mar. Ecol Prog. Ser. 32:149-160.

Newcombe, C.L., W.A. Horne, and B.B. Sheperd. 1939. Studies on the physics and chemistry of estuarine waters in Chesapeake Bay. J. Mar. Res. 2:87-116.

Newell, R.I.E. and S.J. Jordan. 1983. Preferential ingestion of organic material by the American oyster Crassostrea virginica. Mar. Ecol. Prog. Ser. 13:47-53.

Newell, R.I.E., and C.J. Langdon. 1986. Digestion and absorption of refractory carbon from the plant Spartina alterniflora by the oyster Crassostrea virginica. Mar. Ecol. Prog. Ser. 34:105-115.

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

Officer, C.B., R.B. Biggs, J.L. Taft, L.E. Cronin, M.A. Tyler, W.R. Boynton. 1984. Chesapeake Bay Anoxia: Origin, development and significance. Science 223:22-27.

Pritchard, D.W. 1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. J. mar. Res. 11:106-123.

Rhoads, D. 1974. Organism-sediment relations on the muddy sea floor. Oceanogr. Mar. Biol. Ann. Rev. 12:263-300.

Richman, S., D.R. Heinle and R.Huff. 1977. Grazing by adult estuarine calanoid copepods of the Chesapeake Bay. Mar. Biol. 42:69-84.

Ryther, J.H. and J.G. Sanders. 1980. Experimental evidence of zooplankton control of the species composition and size distribution of marine phytoplankton. Mar. Ecol. Prog Ser. 3:279-283.

Short, F.T., and C.A. Short. 1986. The seagrass filter: Purfication of estuarine and coastal waters. In: The estuary as a filter. V.S. Kennedy, ed. Academic Press, Orlando, Fl. p. 395-413.

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

Taft, J.L., W.R. Taylor, E.D. Hartwig, and E.D. Loftus. 1980. Seasonal oxygen depletion in Chesapeake Bay. Estuaries 3:242-247.

Verity, P.G. 1987. Factors driving changes in the pelagic trophic structure of estuaries, with implications for the Chesapeake Bay. In: Perspectives on the Chesapeake Bay: Advances in Estuarine sciences. M.P. Lynch, ed. Chesapeake Research Consortium, Gloucester Point, Va. p. 33-56

Wharton, J. 1957. The Bounty of the Chesapeake. Fishing in Colonial Virginia. Univ. Press of Virginia, Charlottesville, Va. 78pp.

White, J.R. and M.R. Roman. 1988. Grazing and egg production by Chesapeake Bay zooplankton in spring and summer. Abstract In: Understanding the Estuary: Advances in Chesapeake Bay Research. M. Lynch, ed. Chesapeake Research Consortium, Gloucester Point, Va.