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**THE DECLINE OF CHESAPEAKE BAY OYSTER POPULATION:
A CENTURY OF HABITAT DESTRUCTION AND OVERFISHING**

by

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ABSTRACT

The oyster population in the Maryland portion of the Chesapeake Bay has declined by more than 38-fold since the early part of the century. Although the effects of fishing have been implicated, the decline has been attributed primarily to water quality and recently oyster disease. The decline has also been thought to have affected the biota and chemistry of the Bay. Our analysis provides a quantitative demonstration that the long-term declines are largely the result of habitat loss related to overfishing early in the century, stock overfishing, early in the century through the recent times. Furthermore, the major ecological effects on Chesapeake Bay occurred well-before World War II, before industrialization and the prevalence of disease.

The American oyster (Crassostrea virginica) stock in Chesapeake Bay is at historically low levels (1). This decline is often attributed to reduced water quality, disease and fishing. This report shows that much of the decline during the period 1884 to 1990 results from destruction of habitat by fishing, and by stock overfishing which has been occurring since early in the century (2), rather than reduced water quality or disease.

The peak catch of oysters in Maryland was 615,000 metric tons in 1884-85 (Figure 1). In the 19th century this was the bulk of world production. The catch, which is correlated with the oyster population abundance, declined almost steadily reaching a steady state of about 10⁵ metric tons per year in the 1920's (the 1990 catch was only about 16,000 metric tons). The decline occurred before water quality or oyster disease concerns were evident. Reenforcing the notion that the decline in catch reflected a decline in apparent abundance (or catch per unit effort) was the 1900 observation that the dredges practically exhausted the bars before the end of the season (2).

The decline in Maryland oyster abundance can be associated with the destruction of oyster habitat by increasingly intensive and mechanized fishing. From the mid-17th century to 1865, the principal oyster fishing gear was hand tongs (3). About 3,275 small dories and row boats fished with hand-tongs in the late 1860's (3). These boats fished locally and the hand tongs had only a marginal effect on the oyster reefs, more or less "picking" oysters from the reef.

After 1865 large oyster dredges were legalized (4). The dredges not only caught oysters but destroyed the physical integrity of the oyster-reef, centuries-old oyster shell accretions. The oyster dredge has teeth up to 10 cm in length which rake the bottom. The dredges covered more extensive area than hand tongs since the dredges were used on large sail-powered vessels including sloops, schooners, and later the famous Chesapeake Bay skipjacks. By the late 1870's 700 dredge vessels had dramatically increased the absolute intensity of fishing and its areal extent.

In 1887, the hand-operated patent tong was introduced. The hand-operated patent tong consists of two articulated "jaws" that are dropped to the bottom and when closed upon retrieval remove both oysters and some of the substrate upon which the oysters live. This gear enabled capturing oysters in waters deeper than those that could be operated with hand-tongs. The effects of the patent tong on the entire population were intensified because steam power enabled extension of the range and fishing efficiency of the fleet to previously unfished deep-water reefs. Attempts to constrain total fishing effort by restricting the dredge gear to only sail-powered vessels and to state public waters were of limited effectiveness because by 1890 the fleet of large sail-powered craft

had increased to greater than 1000 vessels. In 1900 more than 5,714 dredges and 11,191 hand-tongs and hand-operated patent tongs were operating in the oyster fishery (5). This implies 10-fold and fourfold increases in dredge and tong nominal-fishing mortality, respectively.

By 1950 an even more destructive (per unit area) gear was introduced, the hydraulic powered patent-tongs. The hydraulic patent-tong is like a jawed bucket and is much heavier than the hand operated patent-tongs. When it is dropped to the bottom, the jaws are hydraulically closed removing a "bite" from the oyster-reef structure (6).

The destruction of oyster bars by the various gears can be assessed by comparing data taken during c.1907 and c.1980 surveys which examined the areal extent of oyster habitat (7). In the 1906-1912 Yates survey, boundaries of oyster bars were defined by triangulation. Samples were taken inside this boundary by hand-tongs to increase the resolution of the estimates of the areas of oyster habitat. In the 1974-1982 Maryland Department of Natural Resources survey, shelled areas were defined as oyster bars. We compared the two surveys by superimposing the charts produced from each and then calculating the difference in bar area (B) between the early 1900's and 1980's. Percent habitat change for each bar was calculated as: $[(B_{1982} - B_{1912})/B_{1912}] \times 100\%$.

Figure 2 shows the frequency distribution of percent habitat reduction from the early part of the century to the present time classified by 1906-1912 100-acre bar size-classes. The acreage of oyster bars has declined by more than 50 percent from 1912 to 1982 (8,9). In addition to the substantial decline in acreage, the character of the bars must have been affected (10,11). For example, when the European explorers first visited Chesapeake Bay (c.1600) they found extensive reefs exposed at low tide and in shallow waters (12). It is thought that recruitment of oysters to these shallow reefs would be enhanced because of reduced predation by blue crabs (Callinectes sapidus) (13). The decline in habitat obviously eliminates substrate upon which young oysters can grow. However, the effects have a more far-reaching influence in that existing reefs are also affected. Natural oyster reefs rise several feet above the surrounding bottom and generate complex flow patterns (15). Portions of reefs where higher oyster growth occurs are associated with relatively intense currents that prevent the negative effects of siltation and biodeposition (2, 16, 17). In addition, some authors suggest that the building of an oyster bar is enhanced by frictional turbulence and higher water velocities over the bar produced by tidal movement which eliminates silt and increases feeding encounters (10, 14). For example, productive oyster bars in Choptank River are located at areas with strong bathymetric gradients (10).

Changes in the vertical profiles of oyster reefs caused by fishing have made oysters more susceptible to the effects of other environmental problems. In particular, mechanical destruction and reduction of prime oyster beds in the historically productive areas have exacerbated the direct effects of erosion and sedimentation (19). The current habitat with lowered vertical profile is now subject to heavy siltation (20) probably arising from urbanization, and associated declines of water currents due to decreased turbulent mixing.

A modification of the reef profile affects the dynamics of sedimentation on and around the reef. The sediment which has origins both as faeces and pseudofaeces and from sources external to the reefs are noxious to the oysters (21). Sediments reduce gill function and reduce metabolic efficiency through increased production of pseudofaeces. If oysters are associated with sediment then their growth decreases, mortality increases, reproductive efficiency decreases and possibly the susceptibility to disease increases (22). Siltation is also responsible for the lack of suitable habitat for "spat" (recruiting juvenile oysters) settlement during the reproductive season (14, 23). Such large changes in reef structure understandably affect other populations that support other food chains and may very well be related to the decline of the striped bass (Morone saxatilis).

Evidence for stock overfishing is determined from yield-per-recruit and spawning-stock biomass isopleths (24). Fishing mortality, particularly on smaller oysters has been sufficiently intense to reduce the yield per recruit and spawning stock biomass to less than optimum levels. Isopleths are calculated using estimates of i) natural mortality, ii) growth, iii) length (largest dimension of shell length) and weight, iv) length and age at maturity, v) fishing mortality, and vi) the minimum length distribution of oysters taken by the fishing gear.

Natural mortality estimates are based on long-term studies (25) which agree with our own field observations suggesting that the instantaneous coefficient of natural mortality is about 0.15 (26). In terms of growth, it is surprising that there are virtually no data on oysters larger than 85 mm. Our observations (27) and those of a number of authors (12,25,26,27,29) suggested that an oyster 85 mm in shell length is about three years old. It appears from our examination of 20,000 oysters that 150 mm in length is a reasonable estimate of the average maximum length of an oyster (27,28,30). This results in the growth curve, $L_t = 150\text{mm}(1 - e^{-\beta t})$ (32). Biomass can be obtained from length using the conversion $W_t = \alpha L_t^\beta$; where $\alpha = 3.94 \times 10^{-4}$ and $\beta = 2.80$, where weight at some age t is expressed in grams (27,32).

Size and age at maturity are used for computing the spawning stock biomass. According to Galtsoff (34) and our own results (27), the size of sexual maturity is 31 mm or about one year of

age.

Instantaneous fishing mortality rate is based upon estimates of total instantaneous mortality which is based on the average length (36). In 1890 the mean length of oysters in the catch was 73 mm (37). The size at first capture was 64 mm (2.5"). Using the growth curve, these lengths correspond to 2.5 and 2.1 years, respectively. The total instantaneous mortality rate based upon the reciprocal of the age difference was therefore 2.5. The instantaneous rate of fishing mortality is estimated at 2.35. In our 1990 survey the mean length was 88 mm and the size at first capture 76 mm. This corresponds to ages of 3.2 and 2.6 years, respectively. Total instantaneous mortality is therefore 1.7 and the fishing mortality is 1.6. So fishing mortality in recent years, although very high, is substantially lower than it was at the turn of the century. The smaller size at first capture at the turn of the century and in 1990 was related to minimum size regulations. In response to general concern with declining oyster catches, a 2.5" size limit was imposed in 1890 to conserve the resource. However, catches still continued to decline and the minimum was raised to 3.0" in 1927; it remains in effect today. Also note that prior to 1890 even smaller oysters (<2.5") may have been taken in large quantities to supply the oyster seed fishery for northern states where the beds were already exhausted by overfishing (e.g. Connecticut) (3).

The calculations above enable the computation of the yield-per-recruit and spawning-stock biomass isopleths (Figure 3). These show that early in the century and in 1990 high fishing mortality and the relatively low size at first capture reflects substantial overfishing. The effects of fishing have evidently reduced the spawning efficiency per unit biomass of the oyster population. The oyster is evidently a protandric hermaphrodite, there is a predominance of females at larger oyster sizes (35,35'), suggesting that high levels of fishing mortality may affect the "natural" sex ratio of oysters. The magnitude of fishing mortality may have a significant effect on the sex ratio and hence spawning capability of the oyster. As fishing mortality increases, the average length of the oyster population decreases and as a result the proportion of females decreases, resulting in a male-dominated population, supported by the field studies of Kennedy (35). An increase in the size of first capture to 117 mm would result in roughly double the yield-per-recruit and quintuple the spawning stock biomass.

The effects of a diminished oyster population certainly must have had an effect on the ecology of Chesapeake Bay, although these effects must have become evident at the time of the maximum stock decline (1884-1910), rather than only in recent times (38). Effects at that time must have included the oysters reduced capacity to filter the water column (39). This implies that increased quantities of dead phytoplankton which when settled to the bottom, increased bacteria abundance, contributing to anoxia

(40), a situation which again must have begun well before World War II (41).

We conclude that currently habitat is probably 50% or less than it was a century ago, due to overfishing and exacerbated by environmental degradation and diminished water quality. There was once shell or other substrate where oysters could grow, these areas are now covered with silt and are not suitable substrate for oysters, impeding any recovery. In addition there has been a history of stock overfishing. The stock overfishing may very well be related to recruitment overfishing (42,43). In this regard an increase in spawning stock biomass would compensate to some extent for the reduction in reef structure. It is interesting to observe that a substantial reduction in fishing mortality would not increase the oyster equilibrium yield-per-recruit; rather, more substantial gains would accrue from an increase in the size of capture, facts of considerable economic significance to the management of the public fishery.

Although considerable concern is voiced regarding Chesapeake Bay water quality and the effects of disease on oysters, the effects of fishing probably have had a much greater influence on the long-term decline of the oyster. The problem is however complex because the negative effects of siltation, for example, are exacerbated by reductions in reef profile. A repletion program has been operated for a number of years, but we have shown that it could be improved to a considerable degree (27). Management measures to restore reefs de novo may not be cost-effective, but more targeted repletion combined with scientifically regulated and managed fishing are likely to at least partially restore the reefs, important habitat for oysters, and other commercial and recreational species, such as blue crabs and striped bass.

REFERENCES AND NOTES

1. Kennedy V.S. and Breisch L.L. 1981. Sea Grant Program Publi. UM-SG TS. 81-04. Univ. of Maryland. 286p. Héral M., Rothschild B.J., Gouilletquer P. 1990. ICES. C.M./K:20. 37p.
2. The decline in Maryland stock can be viewed as roughly proportional to landings from 615,000 metric tons in 1884 to 16,195 metric tons in 1989 (one Maryland bushel equals 0.041 metric ton). Review of historical oyster production shows that the major decline began well prior to any significant outbreak of disease (i.e. the protozoan parasites Minchinia nelsoni (MSX) and Perkinsus marinus (Dermo)), which occurred in the 1950's-1960's.
2. Grave, C. 1907. Shellfish Commission of Maryland. First Report, 231p. By the time the dredging season (November 1 to March 15) was one-third over, the bars were exhausted but worked many times in one season.
3. Ingersoll, I. 1881. Census of the U.S. Department of the Interior:156-180; Winslow, F. 1881. Pop. Sci. Monthly 20:29-43 & 145-156.
4. The dredges were used as early as 1812 by a schooner fleet coming from northern States, but were recognized as destructive to the habitat and quickly prohibited by Maryland in 1820. Stevensen, C.H. 1894. Bull. U.S. Fish Commission for 1892: 205-297.
5. U.S. Commission of Fisheries, Part XXVI. Commissioner's Report 1900:268-287.
6. Continually declining catches stimulated diver harvesting of oysters in 1978.
7. Yates, C.C. 1913. Summary of Survey of Oyster bars in Maryland, 1906-1913. Department of Commerce. 80p. Anon. 1982. Unpublished charts from the Maryland Department of Natural Resources Bay Bottom Survey.
8. The Yates (7) survey was extensively conducted during the period 1906-1912, where 279,000 acres of natural oyster bar were surveyed and charted, which represented 25% of the bay bottom at that time. Sounding chains were used for locating shelled-areas and hand-tong samples were used to calibrate assessments. The Maryland Department of Natural Resources survey principally used hydroacoustics for determining bottom sediment composition in the Maryland portion of the bay. Although the Yates and MDNR surveys varied slightly in methodology, their results are comparable because the hydroacoustic data derived from the MDNR survey was "ground truthed" by bottom sediment grabs. This allowed calibration of the hydroacoustic signals and accurate identification of

shelled-area assessments. Our habitat loss estimates are conservative because our comparisons used Yates' data which were collected post-1907, after the principal decline of oyster catches.

9. Our oyster bottom surveys in 1989 and 1990 confirmed a continuation of habitat loss (27). More than 30 oyster bars estimated during Yates' survey were systematically sampled for stock assessment during 1989 and 1990 by using patent-tongs (30). We used linear regression to estimate the loss of shelled-areas, first between the Yates and MDNR surveys, and then the MDNR and CBL surveys. The regressions were highly correlated for both studies ($R^2=0.94$ and $R^2=0.98$, respectively). Habitable acreage continued to decline between 1980 to 1990.
10. Other authors have also suggested that habitat diminution has continued even after 1980. Seliger, H.H. and J.A. Boggs. 1988. Understanding the Estuary. Advances in Chesapeake Bay Research. CBP/TRS 24/88:111-127.
- 10'. There is no apparent evidence that reduction in oyster bar production was singly caused by periodic bouts of anoxia, algal blooms, and siltation as there is no evidence of high profile mounds covered with dead oysters and silt. This would suggest that the effects of overfishing reduced the high profile of the oyster bars and thus eliminated habitat. In our surveys we found a heterogeneous substrate composed of mixed sand, mud and oyster shell in areas where oyster bars once existed. The lack of prominent physical structure and homogenous accretions of shell suggests deleterious physical effects of fishing.
11. Winslow, F. 1881. Pop. Sci. Monthly 20:29-43 & 145-156; Whitcomb, J.P. and D.S. Haven. 1987. Virginia J. Shellfish Res. 6:55-65; Mackenzie, C.L. 1983. Marine Fisheries Review 45(3):1-22; Truitt, R.V. 1927. Annual. Rep. MD Conserv. Com., 5p; Hammer, R.C. 1948. Proc. Natl. Shellfish Assoc., 1947:8-10; Marshall, N. 1954. Proc. Natl. Shellfish Assoc., 44:113-122.
12. Kennedy V.S., Breisch L.L. 1983. Jour. of Envir. Managt. 16:153-171; Kennedy V.S. 1989. Marine invertebrate fisheries, their assessment and management. John Wiley & Sons, Inc.:455-477.
13. Lower predation pressure is still observed in Virginia locations where the majority of the oyster resource is in the intertidal zone (R. Mann, pers. com, 14).
14. Keck, R., Maurer, D., Watling, L. 1973. Hydrobiology 42:369-379.

15. Chestnut, A.F. 1974. Coastal Ecological Ecosystems of the United States, Vol. II: 171-203; Dame, R.F. and B.C. Patten. 1981. Mar. Ecol. Prog. Ser. 5:115-124.; Grave, C. 1905. Report of the U.S. Commission of Fish and Fisheries for 1903:247-351; Copeland, B.J. and H.J. Hoese. 1966. Publication Inst. Mar. Sci., Univ. Texas 11:149-158.
16. Lund, E.J. 1957. Publ. Inst. Mar. Sci. Texas:320-327.
17. According to Bahr (18), the living portion of a typical reef is generally thicker at the edges than in the center. On natural bars the turbid waters slow down while passing over a reef and thus the settlement of suspended matter inhibits the oyster growth, increasing the mortality.
18. Bahr, L.M. 1976. Ecology 57:121-131.
19. Hill, J.M. 1988. Maryland Geological Survey, Report of Investigations; 49, 32p.
20. Schubel J.R. 1972. Jour. of the Wash. Acad. of Sciences. 62(2):56-87; Mackenzie, C.L. 1983. Marine Fisheries Review 45(3):1-22; Mackenzie, C.L. 1989. Marine Fisheries Review 51(3):1-47.
21. Loosanoff, V.L. and F.D. Tommers. 1948. Science 107 (2768):69-70; Héral, M., Deslous-Paoli, J.M., and J.M. Sornin. 1983. Océanis 9(3):169-194; Lund, E.J. 1957. Publ. Inst. Mar. Sci. Texas:320-327; Winter, J.E. 1978. Aquaculture 13:1-33; Bahr, L.M. 1976. Ecology 57:121-131.
22. Héral, M., Deslous-Paoli, J.M., Sornin, J.M. 1983. Océanis 9(3):169-194; Gouilletquer, P., Bacher, C., 1988. Aquat. Liv. Res. 1: 141-154.
23. Mackenzie, C.L. 1983. Marine Fisheries Review 45(3):1-22; Mackenzie, C.L. 1989. Marine Fisheries Review 51(3):1-47; Bahr, L.M. 1976. Ecology, 57:121-131.
24. Beverton, R.J.H. and S.J. Holt. 1957. Fish. Invest. Minist. Agric. Fish. Food UK (Series 2), 19. 533p.
25. Abbe, G. 1987. Ecological studies in the Middle Reach of Chesapeake Bay. Springer Verlag. 23:142-164.
26. Several investigators (25,27,29) have held various size classes of small (<100 mm) oysters over time in containers and estimated the cohort survivorship. We estimated $M=0.15$ and this is roughly the average of other studies. However, under severe epizootic conditions and predation, instantaneous coefficient of natural mortality may reach 0.46 according to McHugh and Andrews (1955). When disease (Dermo and MSX) is rampant the natural mortality rate would be expected to be elevated (G. Krantz, pers. comm.).

27. Rothschild, B.J. et al. 1990. UMCEES[CBL] 90-131. 258p.
28. Kent, B.W. 1988. Making dead oysters talk. Maryland Historical Department. 107p
29. Beaven, G.F. 1950. Proc. Natl. Shellfish. Assoc. 1949:43-49; Beaven, G.F. 1953. Proc. Natl. Shellfish Assoc. 43:90-98; Butler, P.A. 1953. Proc. Natl. Shellfish. Assoc. 43:157-162; McHugh, J.L. and Andrews, J.D. 1955. Proc. Natl. Shellfish. Assoc. 45:217-239; Shaw, W.N. 1966. Proc. Gulf Carib. Fish. Inst. 19:108-115; Shaw, W.N. 1966. Proc. Natl. Shellfish. Assoc. 56:59-63; Shaw, W.N. and Merrill, A.S. 1966. Proc. Natl. Shellfish. Assoc. 56:67-72; Prou J., Gouilletquer P., Bacher C. 1991. CBL-IFREMER Report, 20p.
30. Goode, G.B. 1884. U.S. Commission of fish and fisheries. The fishery industry of the United States, 895p. Webster, J.R. 1953. Proc. Natl. Shellfish. Assoc. 1952:113-120; Goode and archeological observations of Indian midden sites around the Chesapeake Bay have uncovered shells of up to 200-230 mm length, suggesting that L_{∞} may have been larger in the past. Our own field work has found living oysters of up to 185 mm in different tributaries of the Chesapeake Bay (Choptank, Patuxent, Potomac, Honga Rivers, Tangier Sound and in the Mainstem of the Bay. Plasticity of molluscan growth to environmental variables has been recognized by many authors (31), suggesting that animals growing at higher densities and on soft bottoms tend to extend their growth in shell length rather than putting on shell depth and greater weight per unit of surface area (Krantz, pers. com., 28, 29).
31. Caddy, J.F. 1989. Marine Invertebrate Fisheries, 665-700.
32. The coefficient K of the von Bertalanffy growth model can be estimated from solving simultaneous equations between two constrained points corresponding to the age and lengths at time zero and some older age λ yielding $K=1/(t_{\lambda}-t_0)\ln[(L_{\infty}-L_0)/(L_{\infty}-L_{\lambda})]$. Thus, K was estimated as $K=[1/3]\ln[150/(150-85)]=0.28$.
33. Conversion of the growth curve to weight-at-age is accomplished by inserting L_{∞} for L_t in $W_{\infty}=\alpha L_{\infty}^{\beta}$ and expanding the growth curve to the power β . Biomass-at-age is computed as $B_t=N_t W_t$ and then sum across all ages for population biomass B. Yield in weight Y_w is assumed proportional to population biomass as $Y_w=FB$, where fishing mortality F is the proportionality constant.
34. Galtsoff, P.S. 1964. Fish Bull. 64:480p.
35. Kennedy, V.S. 1983. The Veliger. 25 (4): 329-338.
36. Ehrhardt, N.M. and J.S. Ault. (in press). Trans. Am. Fish. Soc.

37. Brooks, W.K. 1905. The Oyster. John Hopkins Press. 255p.
38. Seliger H.H. and J.A. Boggs. 1988. Understanding the Estuary: Advances in Chesapeake Bay Research. CBP/TRS 24/88:570-583.
39. Newell, R.I.E. 1988. Understanding the Estuary. Advances in Chesapeake Bay Research. CBP/TRS 24/88:536-546.
40. Kemp, W.P. and W.R. Boynton. 1984. Bull. Mar. Sci. 35:242-247.
41. Newcombe, C.L. and W.A. Horne. 1938. Science 88:80.
42. Rothschild, B.J. 1986. Dynamics of Marine Fish Populations. Harvard. 277p.
43. Stock overfishing occurs when the vector of fishing mortality (see Rothschild et al., 1986) results in less than maximum yield per recruit. Recruitment overfishing occurs when spawning stock biomass produces less than maximum recruitment. Strict maxima do not always occur. Stock overfishing and recruitment overfishing may influence one another (42). Though increased fishing intensity will increase the number of oysters caught (that is above the present levels), their average weight in the population will steadily decrease, and so, ultimately, will the total weight of the catch.
44. We thank the scientists who critically reviewed the manuscript and offered suggestions, including G. Abbe, V. Kennedy, G. Krantz, R. Mann, and R. Ulanowicz. This study was supported by Maryland Department of Natural Resources grants F-166-89-008 and F-199-90-008. This is Center for Environmental and Estuarine Studies contribution XXXX.

Figure 1: Time series of Maryland oyster landings. The panel segments show corresponding evolution of the fishing gears: (A) use of hand tongs (HT), (b) introduction of dredges (DR) (note peak in production occurred in 1884), (C) introduction of patent tongs (PT) which corresponds with the beginning of the catch decline, (D) introduction of the hydraulic patent tong (HPT) in 1950, (E) the addition of diver harvesting (DI) in 1980.

Figure 2: Percent loss of oyster reefs in the Maryland portion of the Chesapeake Bay determined by comparison of the 1907 survey of Yates (5,6) to the 1980 Maryland Department of Natural Resources bay bottom survey (5). The gray stippled region represents the line of zero change in bar habitat area between the two surveys.

Figure 3: Yield-per-recruit and spawning stock biomass isopleths expressed as functions of fishing mortality rate F and age of first capture t_c for the Chesapeake Bay Oyster stock. Spawning stock biomass is expressed as a fraction of the unexploited stock (i.e. fishing mortality rate equals zero). Point A shows roughly the 1900 position of the fishery, and B shows roughly the 1990 position. The rectangular area shows the range of the fishery over the last century. Parameters for generation of the isopleths were: $M=0.15$, $W_e=488.5$ grams, $K=0.28$ yr⁻¹, $t_m=0.92$ years.

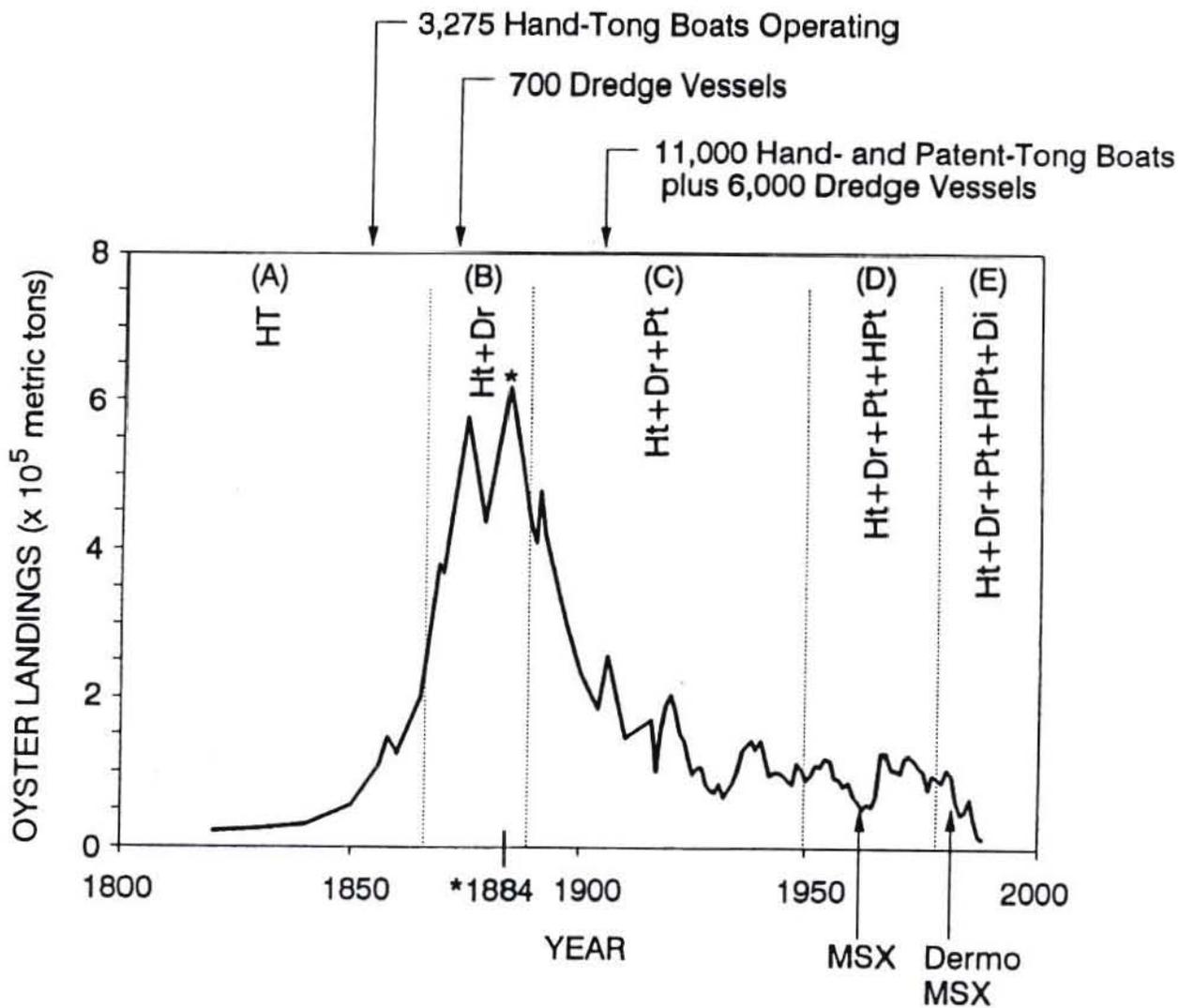


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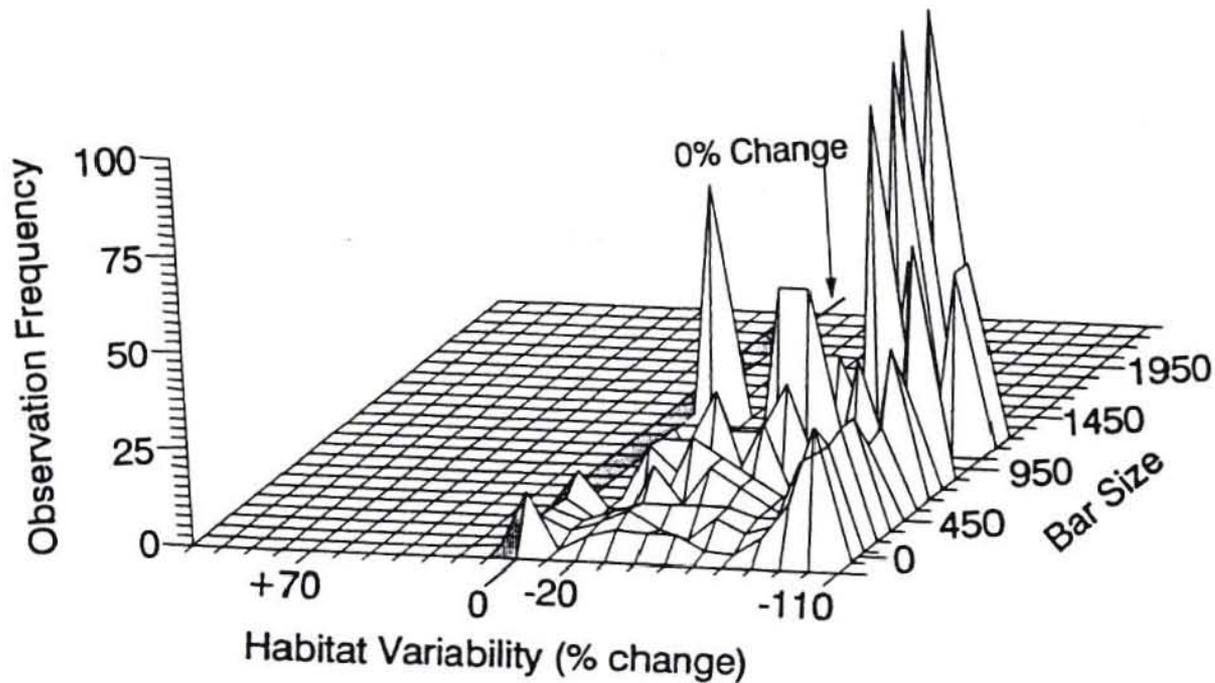


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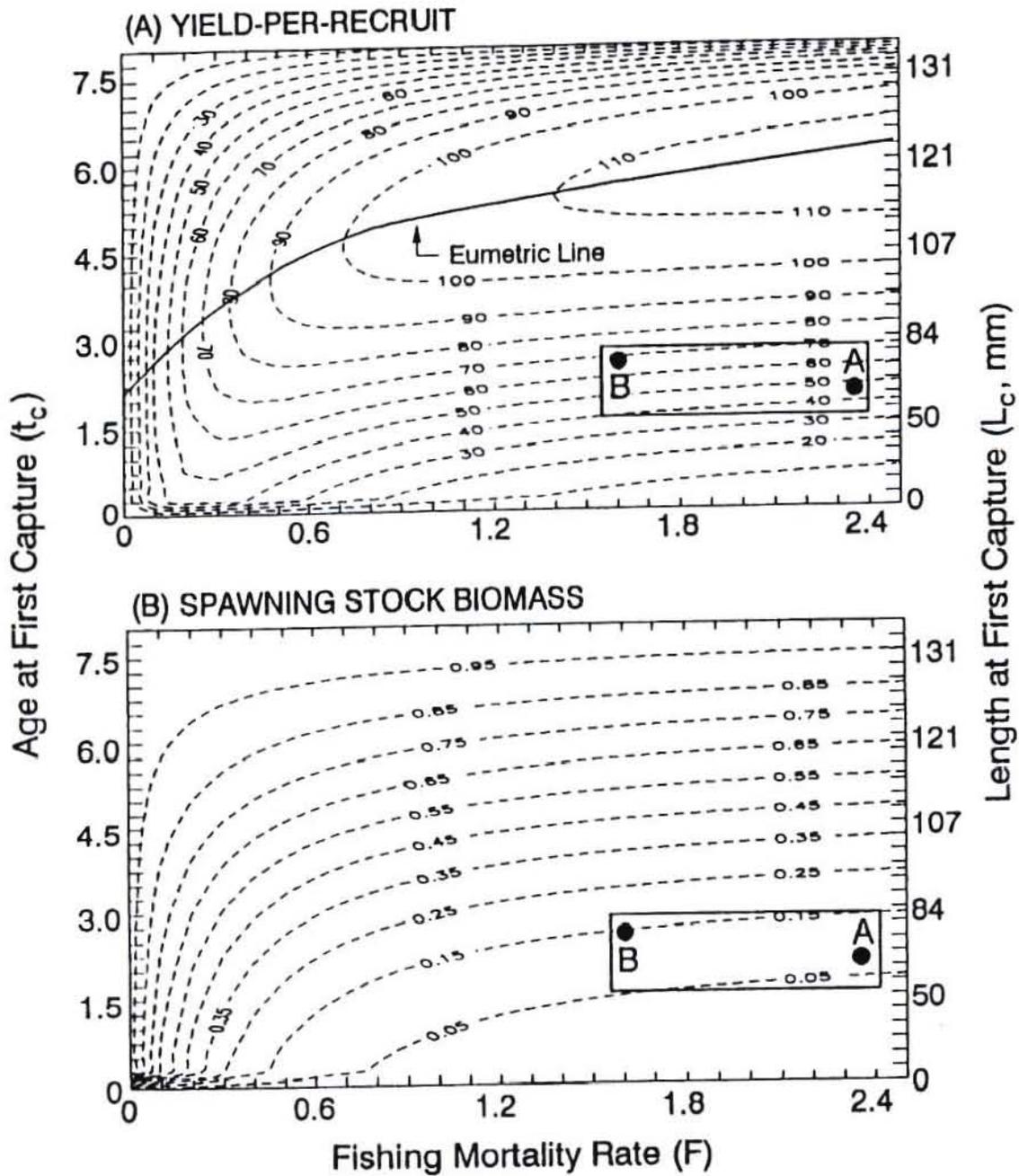


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