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A MODEL OF THE POPULATION DYNAMICS OF THE BLUE CRAB IN CHESAPEAKE BAY

by

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Approved by:

Donald R. Johnson (Director)

ABSTRACT

A MODEL OF THE POPULATION DYNAMICS OF THE BLUE CRAB IN CHESAPEAKE BAY

Betty Springer Hester
Old Dominion University, 1983
Director: Dr. Donald R. Johnson

This study has particular application to the blue crab fisheries in Chesapeake Bay, an economically important industry whose successful management has been hindered by relatively poor understanding of the population dynamics. Recent biological studies have indicated a systematic spawning behavior which seems designed for ejection of larvae seaward from the bay entrance where they spend their pre-metamorphosis stages in the neuston. A physical mechanism for retention of the larvae in sufficient proximity to the bay entrance for their return at the proper time which involves the action of wind stress in shallow waters is proposed. Since the supply of blue crabs in the bay may be dependent upon this action, the abundance of crabs is related to the variability of the wind stress. The consequences of a simple mathematical model of the population dynamics are described. Cohorts must originate on time intervals which are no longer than approximately one month because longer time intervals obscure critical aspects of the life cycle. Different instantaneous rates of mortality must be applied to the cohorts in order to reach numerical equilibrium. Relative abundance at equilibrium and the age structure of the population depend on whether the terminal molt hypothesis or the maximum fishable life span hypothesis is used to calculate post-recruitment total mortalities. The application of wind stress as a driving force in the life history model produced a decrease in harvest. Current levels of information about the population dynamics of this commercially important species are too poor to permit the formulation of rational harvest control regulations in Chesapeake Bay.

ACKNOWLEDGEMENTS

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I would like to thank my committee for their help and guidance: Dr. Phillip R. Mundy, Dr. McConaugha, Dr. William M. Dunstan, and especially Dr. Johnson, my chairman, for allowing me to become an "honorary" physical oceanographer. I would also like to thank Susan Cooke, Deborah Miller-Carson, Yvonne Wilson, and Richard Kemp for their assistance with the illustrations. Thanks to my cronies for all the moral support through my many trials and tribulations.

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CHAPTER I

INTRODUCTION

Successful management of the blue crab fishery in Chesapeake Bay, Virginia, has been hindered by a poor understanding of the population dynamics of this commercially important species. Information dealing with life history, biology, and fisheries has been compiled by Cronin et al. (1957), Tagatz and Hall (1971), and Rhodes and Van Engel (1978). The mechanics of spawning, mating, and the reproductive biology in Chesapeake Bay have been investigated by Hay (1905), Churchill (1919), Van Engel (1958, 1962), and Hartnoll (1969). Other recent work has involved studies on energetics, physiological responses to toxic substances and pollutants, and histology. Although various aspects of the biology of the blue crab have been studied extensively, the population dynamics of this species as a whole have been somewhat overlooked. The most complete and widely accepted account of the life history information was presented by Van Engel (1958).

Recent evidence on offshore larval development has greatly improved our understanding of blue crab population dynamics. Previously, blue crab larvae were thought to be found in the lower bay with the later stages found at depth facilitating retention by inflowing lower layer water (Sandifer, 1975; Goy, 1976). However, recent studies concerning larval distribution have shown that the larvae are found seaward of the bay entrance and remain in the neuston during development to metamorphosis (Sulkin et al., 1982; McConaugha et al., 1983; Provenzano et al., 1983). Female crabs migrate to the entrance of the bay to release their larvae; first stages and megalopae are found in the entrance, while intermediate stages are found seaward of the entrance (McConaugha et al., 1981; McConaugha et al., 1983; Provenzano et al., 1983) with more than seventy five percent of the larvae, all stages, remaining in the neuston while offshore. Consequently the spawning behavior of Callinectes seems designed for ejection of the larvae seaward where they come under the influence of surface currents. Laboratory studies on growth under various salinity conditions suggest that a higher salinity requirement is not the specific cause of migration. Therefore, the systematic behavior of the blue crab in ejecting larvae seaward is probably related to some life history strategy which relies upon the relatively consistent environmental conditions in shelf waters which effectively aid in return of the megalopal stage to the bay.

A poleward pressure gradient along the Mid-Atlantic Bight gives rise to an equatorward drift. During July and August (peak spawning months), the wind stress is consistently toward the northeast quadrant; in September, it is westward. Away from the near-field dynamics of the bay mouth, it seems likely that in July and August a corridor of poleward flowing water exists between the shoreline and the midshelf flow (pressure gradient-forced) which is dominated by wind stress.

During July and August larvae are probably advected from the bay in the southeast direction with the outflowing surface water. When the outflow intensity is diffused, the effect of the corridor becomes dominant, and the larvae are carried poleward. In the absence of the poleward corridor, larvae would be carried toward Cape Hatteras and lost to the Chesapeake Bay system. The existence of this corridor permits the larvae to be retained in the area with access to the bay at the proper time for re-entry.

If the recruitment of megalopae to the bay is dependent on the corridor, the supply of adult blue crabs in the fisheries of Chesapeake Bay would also be dependent upon the presence of the corridor. The objective of this research is to develop a model that describes the population dynamics of the blue crab in the bay in terms of the recent advances in knowledge in relation to its geographic distribution.

This model can be described as exponential depletion of the cohorts of a population with replacement through reproduction. Wind stress is incorporated as a mechanism influencing larval recruitment and the subsequent strength of the cohort in the harvest. The importance of this approach is that a clear physical hypothesis is used to describe the effect of the environment on larval distribution which can then be related to commercial exploitation.

The model predicting the existence of the nearshore poleward flow caused by wind stress effects is presented in Chapter II. The basic model of the population dynamics of the blue crab is developed in Chapter III. The fourth chapter deals with the influence of the wind on the simulated harvest and further examination of the historical wind record. A general discussion and summary are included in the last chapters. A brief history of the crab fishery in Chesapeake Bay follows.

History of the Blue Crab Fishery

Early history of the industry has been compiled by Van Engel (1962). The importance of the century-old blue crab industry to the economy of Chesapeake Bay increased due to the development of the hard crab fishery. In the early 1960's it ranked second or third among Virginia and Maryland fisheries, exceeded in landings only by menhaden and in value by oysters and menhaden. At that time total bay hard crab catch equalled the total catch of all other Atlantic and Gulf Coast states.

Limited transportation and refrigeration facilities prevented early expansion of the fishery. The first interstate shipment occurred in 1873 when soft shell crabs were shipped from Crisfield, Maryland, to Philadelphia. In 1878 a summer trotline fishery was started to furnish crabs for James McMenamin and Company of Hampton, Virginia, the first producer of cooked crab meat in hermetically sealed cans. Fresh-cooked crab meat in iced, unsealed cans became available in 1883.

Prior to 1900 the average annual catches in Virginia and Maryland were less than ten million pounds. Seventy five percent of the value was attributed to soft and peeler crabs. Landings from 1946 to 1960 averaged 60 million pounds with about 80% of the value derived from hard crabs. More than 85% of the total Atlantic and Gulf Coast catch of blue crabs came from Chesapeake Bay between 1929 and 1932. From 1933 to 1953, the average Chesapeake landings were about 60% of the United States total, declining to about 47% of that total from 1953 to 1962. The largest catch to date exceeded 90 million pounds (1966).

Many types of gear have been tried over the years, but pots, trotlines and dredges continue to be the most effective equipment. Trotlines with various modifications were used for catching hard crabs during the summer in the early fishery. Crab pots, patented in 1938, gradually replaced the trotline. In the early 1960's pots were responsible for two thirds of the Virginia and half of the Maryland hard crab catch. First used in 1900, the dredge is still the primary winter gear in Virginia.

Harvesting of blue crabs occurs year-round in Virginia although various restrictions apply during various seasons in different locations. The pot, trotline and dipnet season lasts from April to November. Dredging is restricted to use during the winter from 1 December to 31 March. All forms of crabbing are restricted in the lower bay from Hampton Roads Bridge Tunnel eastward from 1 June to 15 September. This restriction applies to the spawning grounds and represents one effort made to conserve future stocks. The harvesting season in Maryland lasts from April through December. Maryland does not support a winter dredge fishery so catch is virtually zero during January, February, and March.

Today the hard blue crab fishery in Virginia is still of great economic importance. In 1980 landings were exceeded in quantity only by menhaden, while only menhaden, sea scallops, surf clams, and oysters exceeded blue crabs in landed value. Commercial landings in Chesapeake Bay by Maryland and Virginia comprised more than 40% of the total United States landings by weight. Virginia's catch alone provided 23% of the United States total. Economic trends in the fishery are characterized by increased demand for crab meat, higher product prices, recent innovations in processing, variable supply, and competition from the king, snow and tanner crab industries. Increased demand has stimulated interest in crab picking machines and, consequently, the efforts of watermen to provide adequate supplies to processors. Labor and fuel costs have also pushed retail prices upward. Increased demand in conjunction with fluctuating supply are currently causes for concern in the industry.

According to Van Engel (1962), records of types of hard crab gear have been available since 1921 from unpublished license records of the Virginia Commission of Fisheries (now Marine Resources Commission), these included ordinary crabbers, potters and dredge boats. Maryland hard crab licenses have been available from 1916 for crabbers, potters, and dredge boats from the Maryland Conservation Department and the Department of Natural Resources. Maryland and Virginia trotline boat records have been maintained by the United States Bureau of Fisheries and the United States Fish and Wildlife Service.

Along with the annual catch statistics for Chesapeake Bay's blue crab fisheries, the National Marine Fisheries Service (1952-1980) has supplied comments concerning the harvesting conditions and the industry for several years. These comments appear to be the only available record (excluding popular accounts) of the crab fisheries in the bay and as such are included here. Catches during 1963, 1964, 1972, and 1973 were not as high as expected. These low values were attributed to cold springs that retard pot catches. In 1966 landings were low early in the pot and trotline season as a result of cool, wet weather. A peak harvest from July through September aided in making 1966 a record year, even though the dredging season was poor.

The early season in 1967 surpassed that of the previous year, but landings during the rest of the year were smaller. A bait shortage hampered fishermen during the entire season. Dredge crabs were scarce in the spring since unusually warm weather brought the crabs out of the mud earlier than usual. In December during the first week of the season, fishermen went on strike asking six dollars per barrel (100 pounds), while packers were offering five dollars. Greatly reduced landings in 1968 revived a long-standing dispute between Maryland and Virginia fishermen in which Marylanders claimed that the winter dredge fishery, which takes egg-bearing females, is depleting stocks of crabs in the bay. Fishermen attributed the decline to overfishing of the brood stocks. Landings in 1968 were also thought to be poor as a result of high mortality among crabs hatched the previous year.

The crab harvest during the first half of 1969 went down sharply because the fishery depended on the 1967 year class which had a poor survival rate during the winter of 1967-1968. The 1969 year class, which would primarily supply the catches during the first half of 1971, was depleted by high mortalities during the winter of 1969-1970. When the 1970 year class entered the fishery, the landings increased somewhat, but an unusually warm fall was blamed for a poor December dredging season.

Hurricane Agnes in June, 1972, destroyed pots compounding problems caused by a bait shortage and a cool spring. Agnes apparently caused little damage to the blue crab stocks in the bay (Andersen et al., 1973). Most crabs avoided the unfavorable environmental changes brought by the storm, although silt, low dissolved oxygen levels, and red tide toxins were responsible for unspecified adult mortality (Andersen et al., 1973). Reproduction was assumed to have been successful even though the storm coincided with the early summer hatch. Perhaps the effects of Agnes on the 1972 year class contributed to the low catch of 1973. Fuel was also at a premium and rationed during the fall of the year when this country suffered severe fuel shortages.

The decline in catch in the early to mid-seventies has been attributed to the loss of the juvenile crab habitat supplied by the submerged aquatic vegetation known as eel grass. The catches of the later seventies were undoubtedly affected by the extremely cold winters. In 1976 and 1977 the lower bay was frozen, and the fishing fleet was iced in at the dock. The year 1980 marked the last time that the National Marine Fisheries Service was responsible for compiling harvest statistics.

Van Engel and Wojcik (1965, 1969) have compiled catch and value data pertinent to the industries of Virginia and Maryland from 1880 to 1966. These annual data were compiled to aid in an effort to evaluate their usefulness as indices of historical abundance; unfortunately, no attempt was made to assess their value. Some recent data are also available. Monthly catch statistics from 1960 to 1980 for Maryland and Virginia have been compiled by Robert E. Harriss, Virginia Institute of Marine Science, Gloucester Point, Virginia (included in Appendix A). The National Marine Fisheries Service has computerized catch data along with value, gear type, and location by water body for 1967 to 1980. Unfortunately, reliable effort data needed for calculations of catch per unit effort are virtually non-existent from any source.

CHAPTER II

THE ACTION OF WIND STRESS IN SHALLOW WATERS AND ITS RELATION TO BLUE CRAB ABUNDANCE

INTRODUCTION

Recent biological studies have indicated that the spawning behavior of the blue crab seems designed for the ejection of larvae seaward from the Bay entrance. Provenzano et al. (1983) investigated the diurnal vertical distribution of first stage larvae in the Bay mouth and found that the larvae are hatched synchronously just prior to maximum ebb tide. Immediately rising to the neuston, these larvae are transported offshore in the ebb flow.

McConaugha et al. (1983) and Johnson (1982) examined the horizontal distribution of blue crab larvae in the Chesapeake Bay entrance and surrounding shelf waters. Early stages together with postlarvae (megalopae) were found in the Bay mouth, while intermediate stages were collected at offshore stations. Maximum abundances of all stages were found in the upper meter of the water column where wind forcing is optimum. The offshore dispersal mechanism is probably related to the relatively consistent environmental conditions in shelf waters which aid in return of megalopae to the Bay.

Hatches of blue crab larvae occur at the mouth of Chesapeake Bay during late spring and summer, with a peak hatch in late July-early August (McConaugha et al., 1983). For the next 30 to 40 days, they continue to develop offshore until they reach the megalopal stage and subsequent metamorphosis. At this point they are ready to re-enter the bay to mature. A physical mechanism for the retention of the larvae within sufficient proximity to the bay entrance is suggested for their return at the appropriate time. A model involving the action of wind stress in shallow water has been proposed by Johnson et al. (1983).

The classical estuarine circulation of Chesapeake Bay consists of a two layer flow: the upper layer discharges low salinity water onto the continental shelf, while the lower layer moves more saline water into the bay (Pritchard, 1955). Data from drift-bottle and seabed drifter experiments by Bumpus (1973) suggested that the inflow to the bay occurs as a slow, widely dispersed flow from the north and east. Boicourt (1973) showed that the source of incoming water depends on wind direction. The inflow is confined to Chesapeake Channel, near Cape Henry, while the outflow turns to the south as a quasigeostrophic jet along the Virginia and North Carolina coasts.

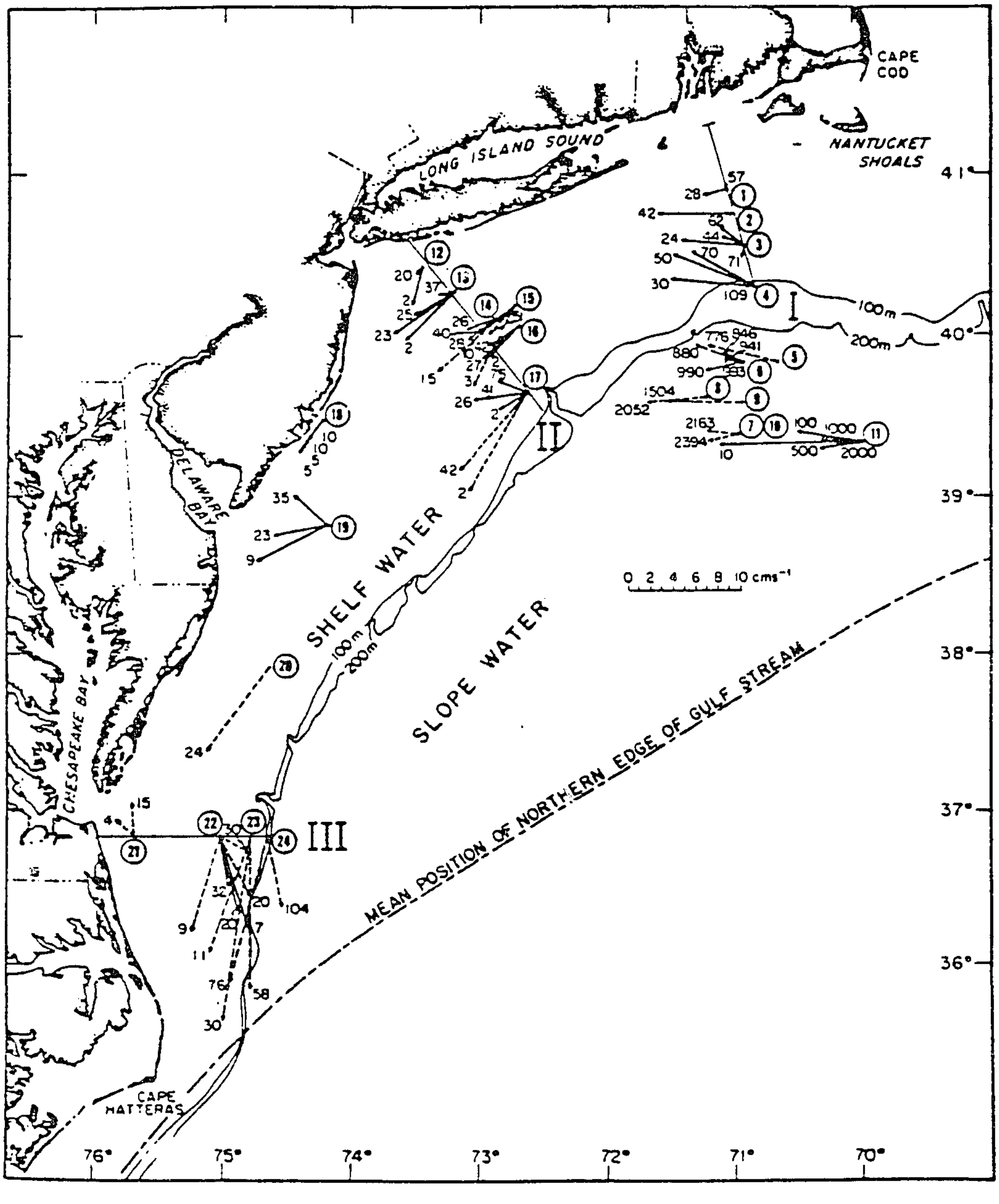
The exchange between the bay and the adjacent continental shelf waters does not necessarily occur as a steady, two layer outflow and inflow. Boicourt (1973) found that wind can dominate this exchange, such that a northwest wind in November, 1971, could drive an outflow surge that discharged 10% of the mean volume of the bay in a two day period. Wang (1979) found that on time scales of two to three days large transport could be induced in the lower bay by local longitudinal wind. On longer time scales Wang and Elliott (1978) found evidence of large coastal wind-induced transport. Over a short period strong winds can drive outflow surges, but over longer periods (five to 10 days) the water level in the bay can be controlled by set-up and set-down on the shelf, a process that may counteract the level changes produced on the shorter time scale (Boicourt, 1981).

Mean flow on the continental shelf of the Middle Atlantic Bight is southward. The concept that the inner shelf, away from the mouths of estuaries, is dominated by wind forcing is supported by two observations: 1) the mean longshore flow from Cape Cod to Cape Hatteras decreases shoreward from a maximum near the shelf break, and 2) the inner shelf is shallow and prone to wind driving (Johnson et al., 1983). The shoreward decrease in the southward mean flow is apparently the result of the increased influence of bottom friction as depth decreases. Recent long term measurements suggest more variability about this mean in the waters off Chesapeake Bay than in northern shelf waters (Boicourt and Beardsley, 1980).

Boicourt (1981) cited an example of dominant wind-driven motion over the mean flow for the inner shelf region off Virginia Beach. The wind stress record from Norfolk was positively correlated with the current record at an inner shelf station which indicated the wind to be the primary driving force. Offshore the wind-driven motion appeared to modulate the southward flow. The prevailing southerly winds reversed the mean flow in the inner shelf. Data collected in recent moored array experiments (Beardsley et al., 1976) showed that the mean currents generally increased in magnitude offshore and decreased with depth (Fig. 1). Referring to Figure 1, note the net northward flow at station 21 near the bay mouth, which is Boicourt's example of the dominance of wind-driven motion over the southward flow.

A winter study was carried out during January and February, 1979, with vertical arrays of current meters and temperature-salinity

Figure 1. Mean current velocities along the Middle Atlantic Bight. The currents are plotted as vectors with the magnitudes equal to the average speed. Dashed vectors indicate summer measurements, while solid vectors mark winter measurements. Numbers at the ends of the vectors indicate depth of measurement. Circled numbers indicate station locations. From Beardsley et al., 1976.


CAPE COD
NANTUCKET SHOALS
LONG ISLAND SOUND
DELAWARE BAY
CHESAPEAKE BAY
SHELF WATER
SLOPE WATER
MEAN POSITION OF NORTHERN EDGE OF GULF STREAM
CAPE HATTERAS
100m
200m
I
II
III
0 2 4 6 8 10 cms⁻¹
41°
40°
39°
38°
37°
36°
76°
75°
74°
73°
72°
71°
70°
①
②
③
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㉒
㉓
㉔
57
28
42
24
50
30
109
2052
2163
2394
1504
100
1000
500
2000
35
23
9
104

recorders moored in the bay entrance and the adjacent inner shelf (Boicourt, 1981). The outflow from the bay occurred as a jet along the Virginian coast, with greatest thickness near the shore and the halocline shoaling to a lateral front eight to 15 km offshore. The southward mean flow resulted from both the outflow and the component driven by the northerly winds.

In the summer substantial changes in both estuarine and continental shelf waters are seen. Stratification is increased in the estuary and on the shelf by spring runoff and by spring warming respectively. The winds also switch from prevailing northwesterly in winter to prevailing southwesterly. Johnson et al. (1983) suggests that during the summer months the increased stratification allows greater independence of the the upper and lower layer flows, and the prevailing southerly winds will drive northward flow on the inner shelf. Data from the 1980 Superflux experiments included mean velocities for a 38 day interval beginning 23 June 1980, in the mouth of the bay and adjacent shelf waters. These upper layer flow measurements support the hypothesis that the shelf currents are ordered in a series of bands parallel to the coast in the Middle Atlantic Bight. The mean flow of the outer shelf is southward, while the inner shelf is subject to wind-driven motion, such that the summer flow is typically north.

THE EFFECTS OF WIND STRESS IN SHALLOW WATER

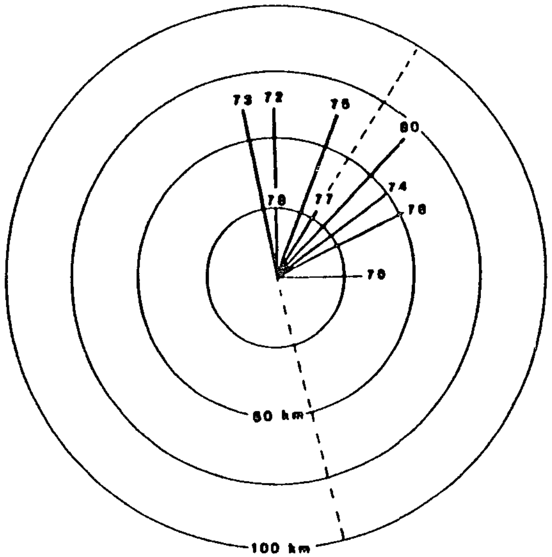
A theoretical model that describes the effects of onshore winds on the surface circulation patterns near the entrance to Chesapeake Bay has been proposed by Johnson et al., (1983). The study provides a theoretical basis for the existence of a corridor of poleward flowing water near the shoreline in the Mid-Atlantic Bight during summer.

During the period of offshore larval development, local wind stress is typically northward. The effect of wind stress alone on the surface waters of an infinite ocean shows the directions and distances larvae could have been carried by surface drift currents during the months of July, August and September from 1972 to 1980 (Fig. 2). In July and August the larvae would typically be moved to the northeast. In September the drift currents could move move the larvae shoreward.

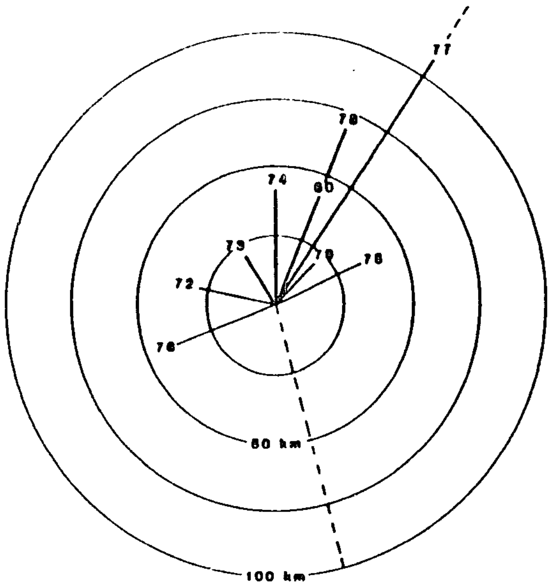
The suggestion is that during July and August, larvae are probably advected from the bay in the southeast direction with the outflowing surface waters. During this period when the larvae are offshore, local wind stress is typically northward, but relatively weak at 0.1 dyne cm^{-2}. Wind stress may then counteract the southward drift. A strong pycnocline develops during summer which tends to decouple the wind-driven surface layer from the lower layer that is subject to bottom frictional loss. This enhances the effect of wind stress transport on the surface water and, therefore, on the larvae. When the outflow intensity is diffused, the effect of the poleward bearing corridor dominates the larval drift. In the absence of the poleward corridor, the larvae would be carried toward Cape Hatteras to be lost to the Chesapeake Bay system. The poleward corridor facillitates larval retention in the area with access to the bay at the proper time.

Johnson et al. (1983) investigated a local Ekman model of wind-driven currents on the shelf with vertical decoupling at the pycnocline. Additional driving forces included an alongshore sea

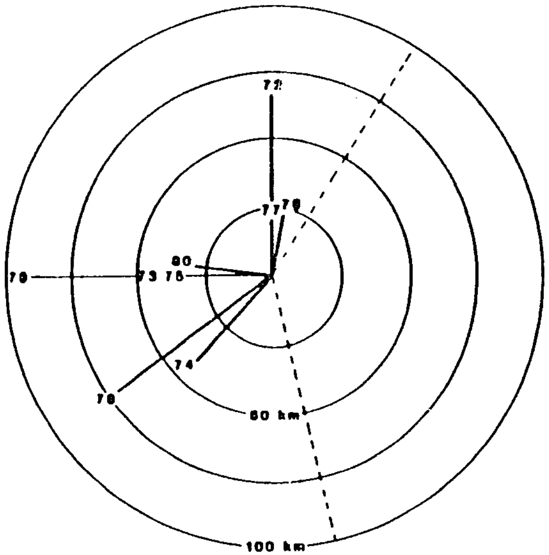
Figure 2. Wind rosettes for July, August and September, 1972-1980. The vectors (labelled by year) represent distance travelled by larvae carried by surface drift currents. The center of each rosette represents the point of release, the center of the bay mouth. The concentric rings mark distance travelled in 25 km increments. The dashed lines indicated the shoreline, north and south from the Capes.



JULY



AUGUST



SEPTEMBER

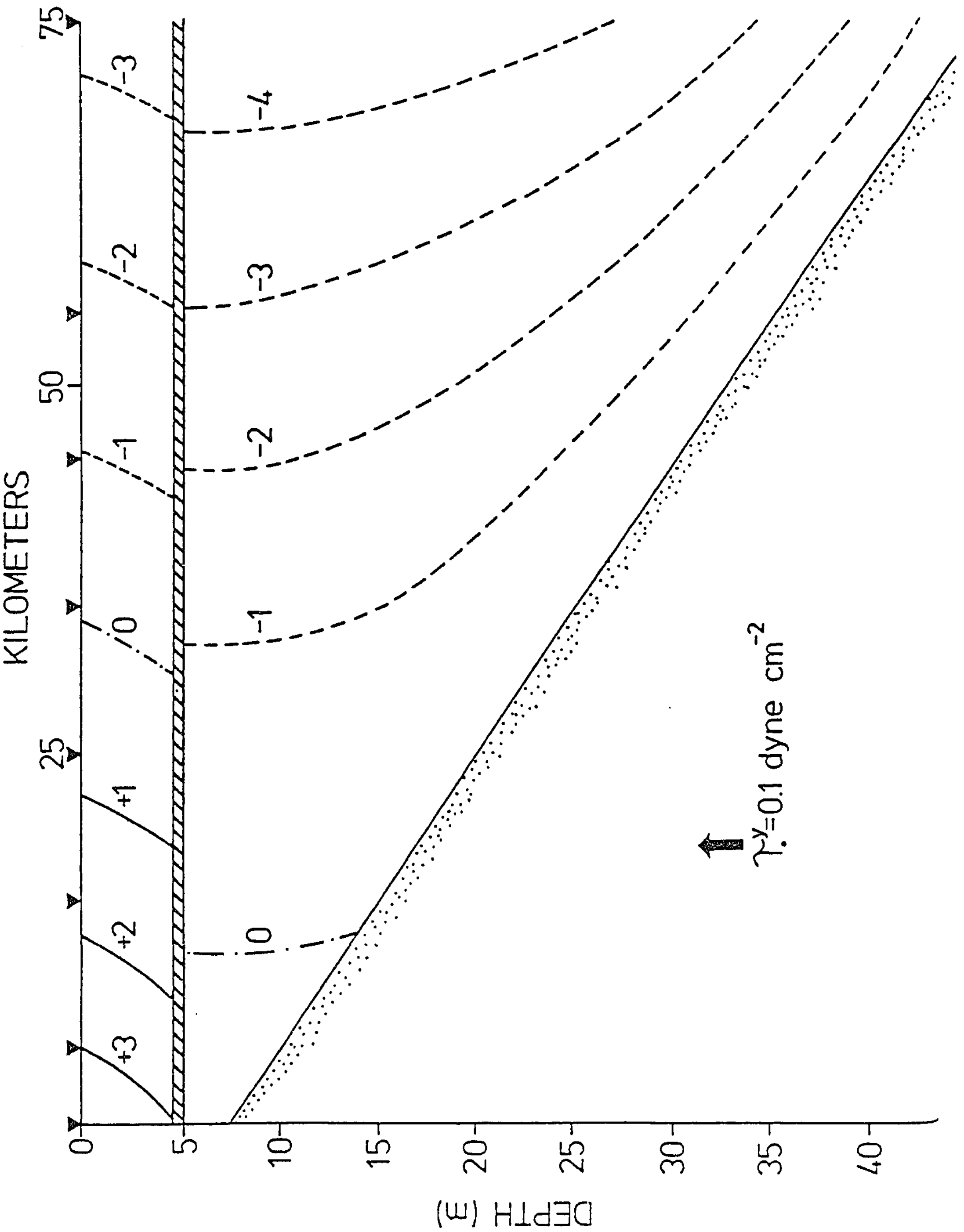
surface slope and horizontal pressure gradients. In an area of shallow depth with a summer thermocline, the surface currents were found to be nearly parallel to the direction of wind stress, not 45° to the right of the wind stress as predicted by Ekman dynamics. The typically light wind stress has been found sufficient to drive a light northward flow.

The model system is a two-layered nearshore system with the thermocline located at a depth of five meters in which the surface currents move in the direction of the wind stress (Fig. 3). When the wind stress is to the north, as it is in June through August, the inner shelf flow is northward above the thermocline to about 25 km offshore. Current velocities are positive (northward flow) above the the thermocline in the nearshore region, shifting to negative (southward flow) about 45 km offshore (Fig. 3). When the wind stress is southward as it is in September, there is pronounced onshore flow in the upper layer.

THE RELATION BETWEEN WIND AND BLUE CRAB ABUNDANCE

The characteristically light, but northward wind stress during the critical summer months has been shown to be sufficient to prevent the larvae from being advected away to be lost from Chesapeake Bay (Johnson et al., 1983). Since this northward corridor exists as a result of winds, there should be some sort of predictable relation between wind stress and the abundance of blue crabs a few years later. The preceding information on the biology of the blue crab and the physical oceanography of the region near the mouth of Chesapeake Bay have led to

Figure 3. Two layer nearshore system with thermocline at 5 km. The horizontal axis is distance offshore, the vertical axis is depth. The positive values represent velocities of northward flowing currents, the negative values indicate southward flow. Wind stress, τ, equals 0.1 dyne cm^{-2}.


KILOMETERS
0
25
50
75
DEPTH (m)
0
5
10
15
20
25
30
35
40
+3
+2
+1
0
-1
-2
-3
0
-1
-2
-3
-4
τ^{y}_{*}=0.1 dyne cm^{-2}

the hypothesis: Recruitment of blue crabs to the fishery is directly proportional to the wind stress experienced by the recruits during larval drift as neuston on the continental shelf.

An index of the effect of wind stress has been developed from wind records taken at Norfolk International Airport, Norfolk, Virginia. Hourly wind speeds and directions from 1952 to 1982 (obtained from the National Climatic Center in Asheville, North Carolina) were used to calculate the average distance blue crab larvae could have been moved by surface drift currents.

The velocity (u_i) of wind-induced drift currents, calculated from Wu (1975), incorporated the linear form of the drag coefficient (C_D) discussed by Garratt (1977).

$$u_i = 0.55(C_D)^{1/2}(S_i) \qquad (1)$$

where: u_i = surface current speed

C_D = drag coefficient

S_i = wind speed in msec^{-1}

i = hour of observation

$$C_D = (0.75 + 0.067S_i) \times 10^{-3} \qquad (2)$$

The current velocity was then computed in a component along the Eastern Shore in order to approximate the location of the larvae. The wind directions were converted to the same coordinate system as the currents by subtracting 180°, and were rotated 30° in approximate alignment with the Eastern Shore.

$$\underline{u}_i = u_i\cos(D_i - 180^o - 30^o) \qquad (3)$$

where: $\underline{u}_i$ = current velocity toward Eastern Shore in msec^{-1}

D_i = wind direction

The average distance the larvae would have been transported was calculated as

$$R_i = \int_{i=1}^{t} \underline{u}_i \, dt \qquad (4)$$

$$R_i = \Delta t \sum_{i=1}^{t} \underline{u}_i \qquad (5)$$

where: R_i = distance in m

Δt = seconds per time interval

Various forms of the wind index were compared to historical catch records for the Chesapeake Bay, the only available data possibly indicative of the abundance of the blue crab population. The impact of the wind is felt when crabs reach recruitment to the fishery at sexual maturity; therefore, the wind index is offset from the catch data by one or two years (Figs. 4-7). The extremely high yield in 1966 was thought to have been caused by the addition of year old crabs that entered the fishery late in the summer (National Marine Fisheries Service, 1952-1980) so initially the data were lagged by a year. Since the

Figure 4. Catch and wind index. The annual catch in millions of pounds is plotted as a dashed curve. The index represents distance travelled along a component along the Eastern Shore from July to September as a solid line. The index is offset one year.

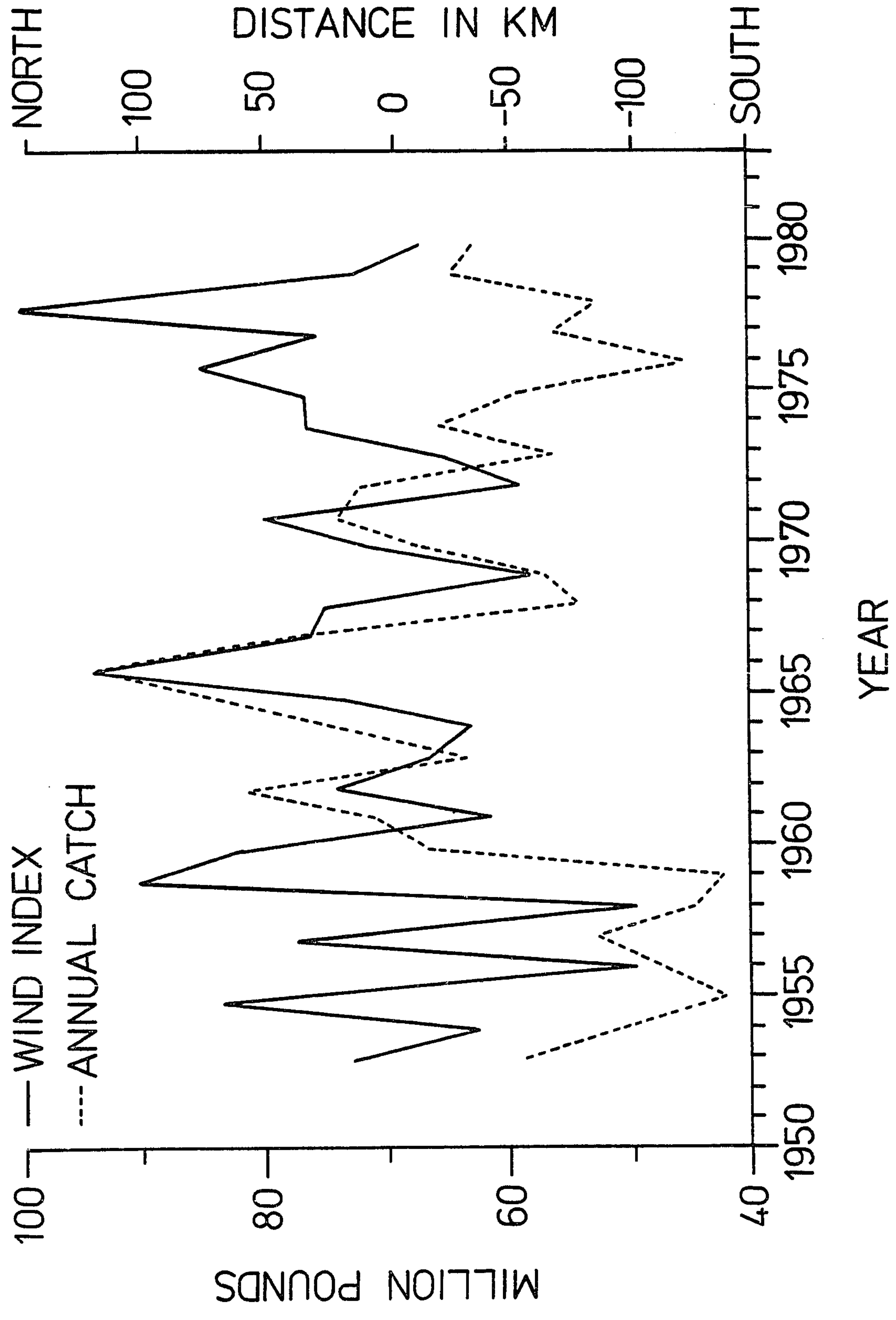

WIND INDEX
ANNUAL CATCH
DISTANCE IN KM
NORTH
100
50
0
-50
-100
SOUTH
MILLION POUNDS
100
80
60
40
YEAR
1950
1955
1960
1965
1970
1975
1980

Figure 5. Catch and wind index. The annual catch in millions of pounds is plotted as a dashed curve. The index represents number of days wind stress was northward along a component along the Eastern Shore from July to September as a solid line. The index is offset two years. Coriolis forces are included in calculations.

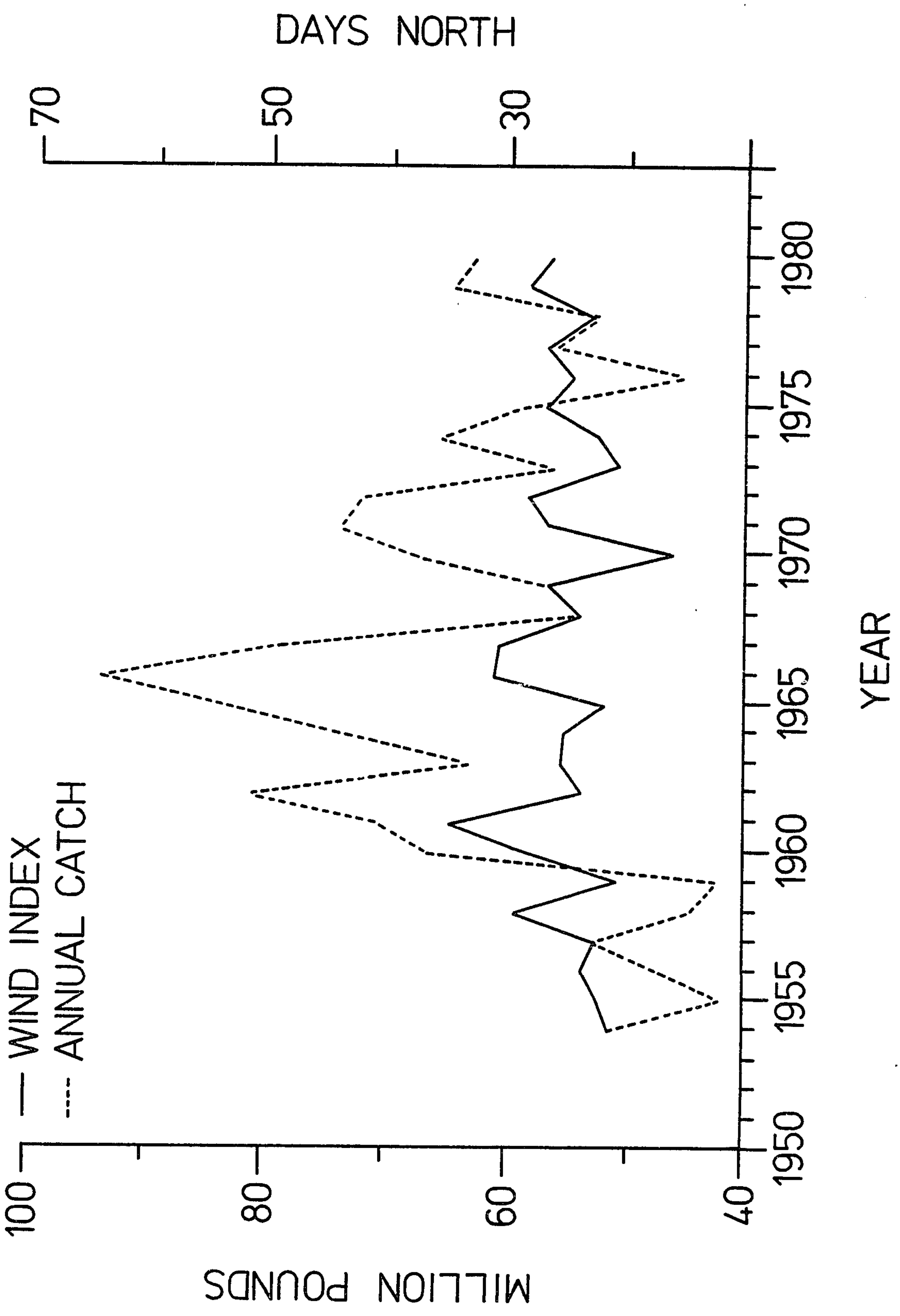

— WIND INDEX
--- ANNUAL CATCH
DAYS NORTH
70
50
30
MILLION POUNDS
100
80
60
40
YEAR
1950
1955
1960
1965
1970
1975
1980

Figure 6. Catch and wind index. The annual catch in millions of pounds is plotted as a dashed curve. The index represents number of days wind stress was northward along a component along the Eastern Shore with a minimum distance travelled of 0.5 km per day from June to September (solid line). The index is offset two years. Coriolis forces are included in calculations.

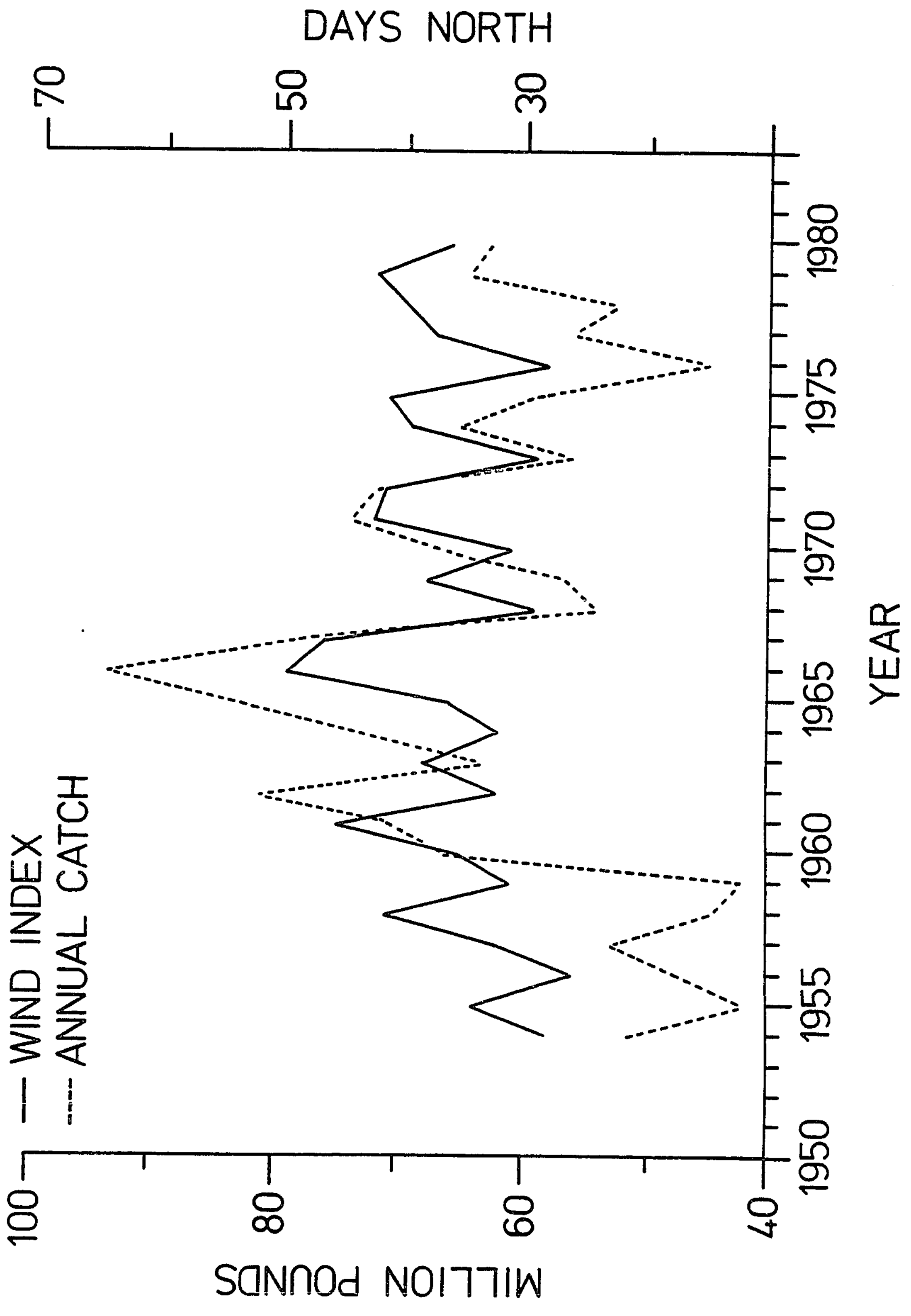
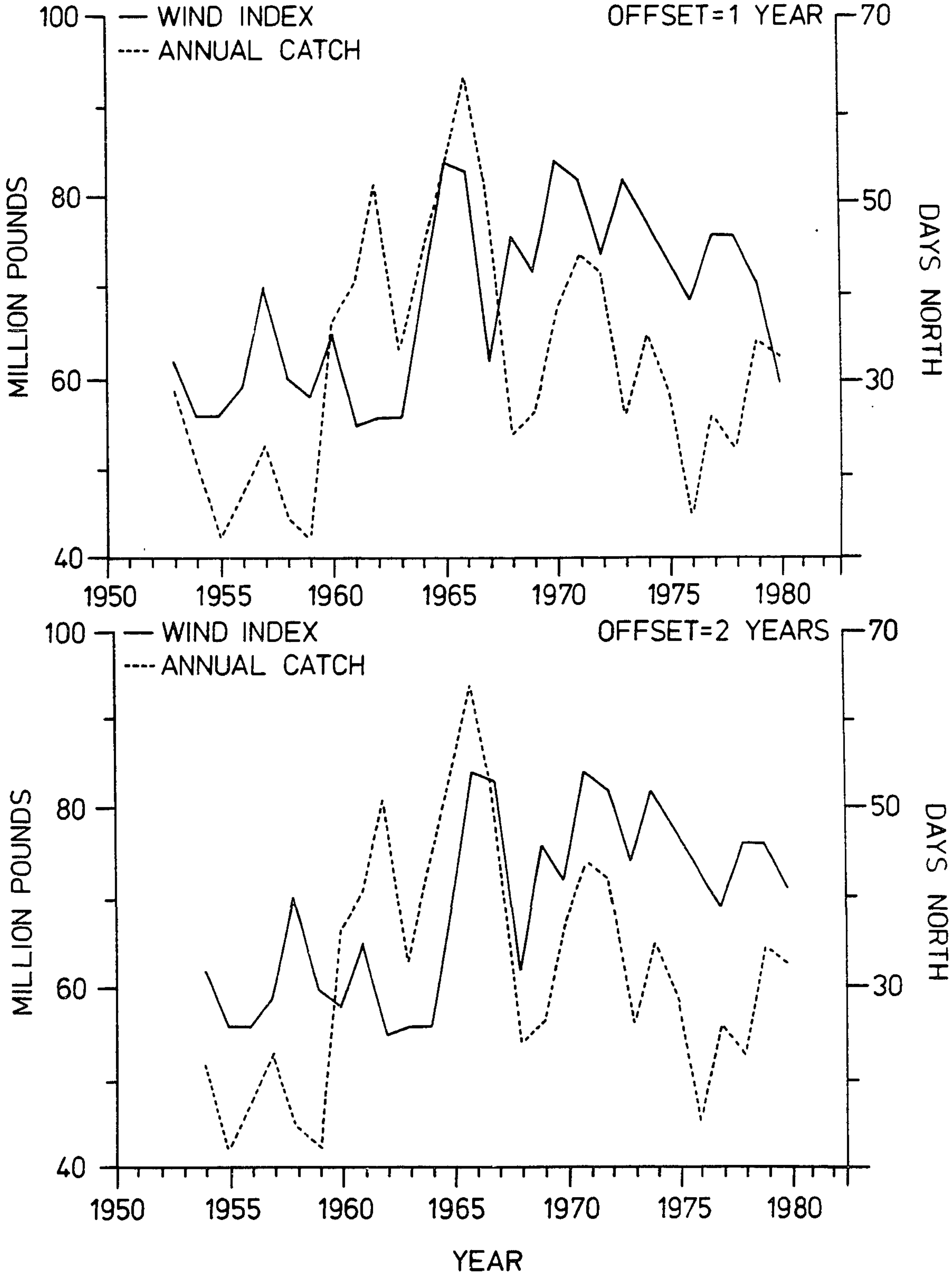

WIND INDEX
ANNUAL CATCH
DAYS NORTH
70
50
30
MILLION POUNDS
100
80
60
40
YEAR
1950
1955
1960
1965
1970
1975
1980

Figure 7. Catch and wind index. The annual catch in millions of pounds is plotted as a dashed curve. The index represents number of days wind stress was northward into the octant 345° to 030° with a minimum distance travelled of 0.5 km per day from July to September (solid line). The index is offset two years. Coriolis forces are included in calculations.



— WIND INDEX
---- ANNUAL CATCH
OFFSET=1 YEAR
MILLION POUNDS
DAYS NORTH
100
80
60
40
70
50
30
1950
1955
1960
1965
1970
1975
1980
— WIND INDEX
---- ANNUAL CATCH
OFFSET=2 YEARS
MILLION POUNDS
DAYS NORTH
100
80
60
40
70
50
30
1950
1955
1960
1965
1970
1975
1980
YEAR

curves are measures of different quantities, million of pounds of crabs and days north, only the relative peaks and valleys are significant.

Initially the magnitude of the wind stress was thought to be of greatest importance in retaining the larvae near the bay mouth. Therefore, the average distance travelled during the summer months of July, August and September was selected as the index. When the wind curve is offset one year, so that the 1952 average distance for the summer is plotted with the catch for 1953, the peaks and valleys match fairly well for the middle years of the series, 1961-1971, but the remaining year shows little agreement (Fig. 4).

Since the averaged effect of the wind's magnitude could be biased by extremely high wind speeds or obscured by equivalent speeds in opposing directions, the frequency of occurrence was thought to be more indicative of the relation between annual catch and larval drift. Therefore, the number of days the wind stress is northward during the summer would be a more significant determinant of catch than the distance travelled. The coordinate system was also rotated 45^o to the right to compensate for the effects of Coriolis forces. With an offset of larval drift to catch of two years, the middle sixties again show some correspondence between catch and the wind index (Fig. 5). A lag time of one year would be more appropriate for the early years, while the last decade of data is not well correlated.

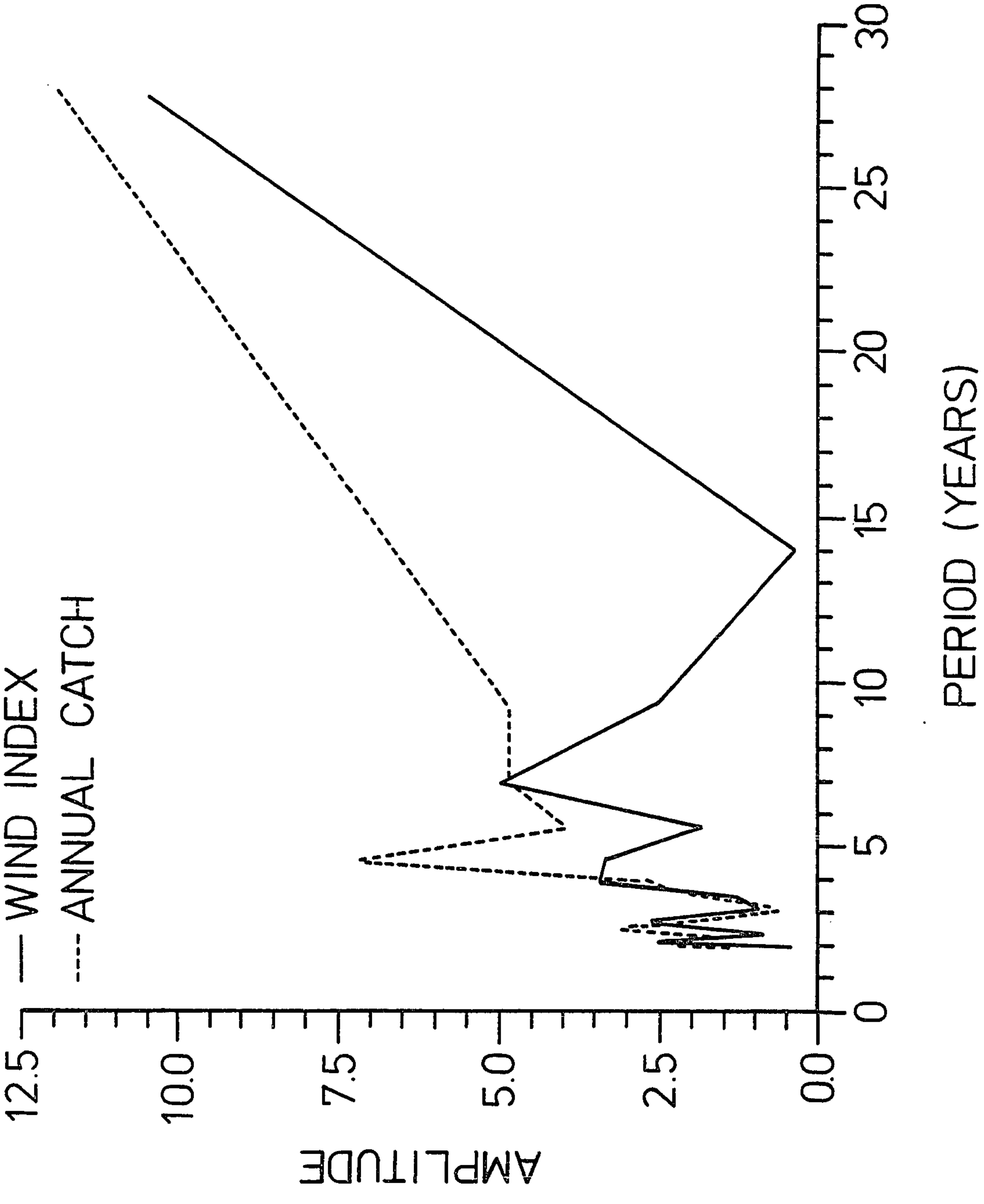
In order to produce better agreement between the index and the catch data, another modification was made to the index. Days of very light wind stress would produce little or no larval movement so a threshold value of 0.5 km travelled per day was used in this form of the index. The offset of larval drift to catch is two years; the index represents a summer average for June through September; and the coordinate system is again rotated 45° to include the effects of Coriolis forces. The last 15 years show significant correlation, again data from the early years seem to need a different time lag (Fig. 6).

In the preceding analysis a wind index was computed such that the distance travelled was along a component northward. Since the larvae must be retained in an area outside to the bay mouth for re-entry, an index was generated that encompassed an octant northward where the covariate was the average number of days the distance travelled exceeded 0.5 km into the octant from 345° to 030° (Fig. 7). The offset of larval drift to catch is one year (upper curves) and two years (lower curves). Although the first few years show better agreement with a year offset, the peaks and valleys of the remainder of the curves are significantly matched when offset two years.

A correlation of these two curves would obscure the relation between harvest and wind stress. The appropriate technique for statistically evaluating this relation is in cross covariance and cross power spectral analysis of the two time series. However, the number of data points is two few to permit successful analysis. Therefore, in order to approximate the significance of the relation between the catch data and the effect of wind stress, Fourier analysis of the two separate time series was performed. [Fourier analysis is described in Appendix B.] The Fourier Transform of annual catch data from 1952 to 1980 shows periods of five and seven years that correspond to the five and seven year periods seen in the most favorable index of wind stress.

Wind stress is by no means the only factor controlling abundance; however, the above relationship can be drawn between historical data of

Figure 8. Amplitudes of blue crab catch (dashed curve) and wind index (solid curve) versus period in years computed by Fourier transform of the curves shown in Figure 7.


— WIND INDEX
--- ANNUAL CATCH
AMPLITUDE
12.5
10.0
7.5
5.0
2.5
0.0
0
5
10
15
20
25
30
PERIOD (YEARS)

wind stress and harvest. Catch data may be a poor indicator of population size and are subject to the vagaries of economics and the fishing industry. Variations in harvest have been attributed to bait shortages, strikes among fishermen and processing plants, fuel shortages, loss of juvenile habitats, and environmental conditions which are responsible for increased mortality and reduced catch. The proper offset of the indices to the catch data remains undetermined. Before the effects of wind or other environmental factors may be evaluated, the age composition of the population must be determined. The following chapter includes a model of the current knowledge of the population dynamics of the blue crab in Chesapeake Bay. An attempt is made to determine which age classes dominate the harvest.

CHAPTER III

A MODEL OF AVAILABLE LIFE HISTORY INFORMATION ON THE BLUE CRAB IN CHESAPEAKE BAY[1]

INTRODUCTION

In an effort to investigate the environmental pathway taken by the larval stages during dispersal from Chesapeake Bay and in subsequent return as postlarvae, records of sea surface wind stress were analyzed for the critical period during which the larvae are in shelf waters. Time histories of a wind index, representing forces which act to produce a nearshore drift current (Johnson et al., 1983) which counterbalances the measured midshelf southward flow (Beardsley et al., 1976), showed a surprisingly good relationship to the harvest of blue crabs in subsequent years. However, uncertainty of lag time between the effect of the wind index and later harvest indicated a need to study the life history of the blue crab and, particularly, the age structure of the catch. The relation between index and catch must be understood within the context of the average age of the catch.

Information dealing with the blue crab life history, biology, and fishery has been compiled by Cronin et al. (1957), Tagatz and Hall

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[1] This chapter was presented as "Impediments to Rational Regulation of Harvest for the Blue Crab on Chesapeake Bay" by B. S. Hester and P. R. Mundy at a workshop on blue crab stock dynamics in Chesapeake Bay, December 13-15,1982, Chesapeake Biological Laboratory, Solomons, Maryland.

(1971), and Rhodes and Van Engel (1978). Investigations on the mechanics of spawning, mating, and the reproductive biology of this crab in Chesapeake Bay have been conducted by Hay (1905), Churchill (1919), and Van Engel (1958, 1962). The generally accepted description of blue crab biology in the bay was presented by Van Engel (1958).

A mathematical description has been developed as a vehicle to evaluate the consistency of current information concerning the population dynamics of the blue crab. A brief narrative of the life history compiled from the above authors sets the stage for model development.

Life History of the Blue Crab, Current Knowledge

Mating occurs from early May to October, reaching a peak in late August and early September. Sperm may be retained in the female receptacles for at least a year and may be used as often as the female lays eggs. After one mating, the females migrate to the higher salinity waters near the bay entrance.

If mating occurs as early as May, the first egg mass may be laid in August. In most females, those mating in August and September, the eggs develop to completion during the fall, but egg laying is delayed until the following May or June. Peak sponge production occurs the last week of May and the first two weeks of June, a second smaller peak occurs in August. The number of spawning females decreases rapidly, and none can be found by mid-September. The rapid decrease in sponge crabs is accompanied by the disappearance of females which have spawned.

Post-spawning crabs are thought to move to deeper waters of the bay, or to the ocean, where they die or join an ocean going population that may return to the bay as "ocean" crabs the following year. Crabs which mate in August produce their first sponge the following May or June and a second sponge later in August.

A two week period of embryological development occurs between egg laying and hatching. The number of eggs per sponge ranges from 7×10^5 to 2×10^6. One egg in a million (1×10^{-6}) survives to maturity. [Development includes eight zoeal stages and a megalopa, and metamorphosis is reached within 40 days of hatching (Costlow and Bookhout, 1959).] The "first crabs" begin migrating from the lower bay and the ocean adjacent to the Capes into the rivers and the upper bay where they mature to adulthood.

Growth is rapid; those larvae hatched in late May become adults in August of the following year. Those hatched in August reach maturity in May of the third summer. Crabs live at least a year past reaching adulthood, and the maximum age may be three to three and a half years.

Adult male crabs remain in brackish waters and mate with females that are moving toward the spawning grounds at the bay mouth. A fall peak migration in October/November following mating results in females concentrating in the lower bay. A smaller migration of females occurs in May and consists of recently mated females and those which mated the previous fall but were forced to overwinter en route to the lower bay. "Ocean" crabs which appear in late July or early August in Lynnhaven Roads may add significantly to the commercial catch.

METHODS

A self-generating model traces groups of females born in the same month as they grow to maturity, enter the fishery, reproduce, and die as a result of fishing and natural causes. The model contains exponential depletion (Tyler and Gallucci, 1980) with replacement through reproduction, with no adult emigration. The abundance of females is assumed proportional to the total abundance. Notation follows Ricker (1975). All mortality rates are instantaneous unless otherwise noted.

Individuals are added to the population through the following relation:

$$N_o = \alpha S + f(\underline{x}) \qquad (6)$$

where: N_o = initial number of females in a cohort

α = average number of eggs per female

S = number of spawning females

$\underline{x}$ = environmental factors

The initial number in a cohort, N_o, which is proportional to the number of female spawners, S, is influenced by some function of environmental factors that may regulate population abundance, $f(\underline{x})$. For simplicity, both environmental and density-dependent factors are ignored here in order to illustrate the fundamental dynamics; $f(\underline{x})=0$. The constant of proportionality, α, is 1.35×10^6, the midpoint of a range of fecundities given by Van Engel (1958). All eggs are assumed to hatch as first stage zoeae.

A cohort is depleted over time by a constant percentage which is specified by a constant instantaneous mortality rate. Total mortality (Z) is attributed to two sources: mortality due to fishing (F) and natural mortality (M). Fishing pressure is not applied to the population until adulthood is reached; therefore, Z = M during larval and juvenile stages. When the crabs reach maturity, they are subject to both commercial fishing pressure and post-recruitment natural mortality, M'; M' $\neq$ M.

Recruitment to the fishery is defined as

$$R = N_0 e^{-Mt_R} \tag{7}$$

$$R = \alpha S e^{-Mt_R} \tag{8}$$

where: R = number of recruits to the catchable stock
M = natural mortality prior to recruitment
t_R = age in months at recruitment

After recruitment, abundance is determined as follows:

$$N_t = Re^{-(F + M')t} \tag{9}$$

where: N_t = abundance in month t
F = fishing mortality
M' = post-recruitment natural mortality

Let Z' = F + M', total mortality after recruitment.

After determining the number of fully recruited crabs, annual catch is calculated by Baranov's catch equation (Ricker, 1975), where catch is F times the average population, $C = F\bar{N}$, and

$$\bar{N}_{a,b} = [R \int_a^b e^{-Z't} dt]/(b-a) \qquad (10)$$

$$\bar{N}_t = R[(e^{-Z'a} - e^{-Z'b})/Z']/(b-a) \qquad (11)$$

where: $\bar{N}_{a,b}$ = average abundance during a given time interval

a,b = limits of a time interval

$\bar{N}_t$ = average abundance during month t

$$C_t = F\bar{N}_t \qquad (12)$$

where: C_t = catch in month t and,

$$C. = \sum_{t=1}^{12} C_t \qquad (13)$$

where: C. = annual catch

We define two annual cohorts, those animals hatched at the end of May and those animals hatched in August. The number of animals born at other times is assumed negligible. The two groups undergo depletion throughout their life cycles by natural and/or fishing mortality. Each group is replenished through reproduction, and the new generation is then depleted accordingly. Annual catch is also calculated for the two groups as each generation is depleted.

Although hatching occurs continuously during the summer months, peaks of production apparently occur early and late in the summer season (Van Engel, 1958). The life history information suggests two production schedules: 1) those females originally hatched in late May-early June (MAY crabs) reach maturity in 15 months, by August of the following year, spawn twice at ages 24 months and 27 months, and die at age 33 months; 2) those crabs initially hatched in August (AUGUST crabs) reach maturity in 21 months, by May of the third summer, spawn at age 24 months, and remain in the population until age 39 months. Maturity is defined as the onset of sexual maturity, in this case the time of mating, and as the time of recruitment to the fishery. Since the crabs are presumed to live at least a year past the onset of maturity, and since the crabs may reach ages of three to three and a half years, adulthood is assumed to be 18 months, $t_f = 18$. A three month delay in spawning becomes a nine month delay in recruitment to the fishery, since those crabs hatched in May are subject to commercial fishing pressures for a period of nine months before those hatched in August reach maturity and recruitment.

Equations (6)-(13) are modified to define the two cohort system where subscript 'm' denotes MAY, and subscript 'a' denotes AUGUST. The following equations (14-23) describe the life history of each cohort. Subscript 'j' denotes a given generation, and it is used as an index to catalog, and subsequently retrieve, total abundance and catch values produced by the model. The initial abundance of each cohort is calculated as

$$N_{m_j}(0) = \alpha S_{m_{j-1}} \qquad j>1 \qquad (14)$$

$$N_{a_j}(0) = \alpha S_{a_{j-1}} \qquad j>1 \qquad (15)$$

where: $N_{m_j}(0)$ = initial number of females hatched in May

$S_{m_{j-1}}$ = number of females spawning in May

$$= N_{m_{j-1}}(24) \qquad (15A)$$

$N_{a_j}(0)$ = initial number of females hatched in August

$S_{a_{j-1}}$ = number of females spawning in August

$$= N_{m_{j-1}}(27) + N_{a_{j-1}}(24) \qquad (15B)$$

Note that only members of the MAY cohort spawn in May (15A) while both the MAY and AUGUST cohorts spawn in August (15B). The number of recruits to the fishery from each group is determined by

$$R_{m_j} = \alpha S_{m_{j-1}} e^{-M_m t_{R_m}} \qquad (16)$$

$$R_{a_j} = \alpha S_{a_{j-1}} e^{-M_a t_{R_a}} \qquad (17)$$

where: R_{m_j} = recruits to stock hatched in May of the jth generation

M_m = natural mortality for animals hatched in May

t_{R_m} = age in months at recruitment for crabs born in May = 15 months

R_{a_j} = recruits to stock hatched in August of the jth generation

M_a = natural mortality for animals hatched in August

t_{R_a} = age in months at recruitment for crabs born in August = 21 months

Abundance during adulthood is calculated by the following equations. Note that $t > t_R$ and that $Z'_m = F_m + M'_m$ and $Z'_a = F_a + M'_a$.

$$N_{m_j}(t) = R_{m_j} e^{-(F_m + M'_m)t} \tag{18}$$

$$N_{a_j}(t) = R_{a_j} e^{-(F_a + M'_a)t} \tag{19}$$

where: $N_{m_j}(t)$ = number of crabs of generation j at time t which were originally hatched in May

F_m = fishing mortality for crabs born in May

M'_m = post-recruitment natural mortality for crabs born in May

$N_{a_j}(t)$ = number of crabs of generation j at time t which were originally hatched in August

F_a = fishing mortality for crabs born in August

M'_a = post-recruitment natural mortality for crabs born in August

Catch per month is then predicted for each cohort, and the predictions are used to calculate annual catch:

$$C_{m_j}(t) = F_m \bar{N}_{m_j}(t) \tag{20}$$

$$C_{a_j}(t) = F_a \bar{N}_{a_j}(t) \tag{21}$$

$$C_{\cdot m_j} = \sum_{t=1}^{12} C_{m_j}(t) \tag{22}$$

$$C_{\cdot a_j} = \sum_{t=1}^{12} C_{a_j}(t) \tag{23}$$

where: $C_{m_j}(t)$ = catch in month t of crabs born in May

$\bar{N}_{m_j}(t)$ = average abundance in month t of crabs born in May

$C_{a_j}(t)$ = catch in month t of crabs born in August

$\bar{N}_{a_j}(t)$ = average abundance in month t of crabs born in August

$C_{\cdot m_j}$ = annual catch of crabs born in May

$C_{\cdot a_j}$ = annual catch of crabs born in August

Assuming that the mortality rates and time sequences from arguments presented by Van Engel (1958) are appropriate, the percentages of the catch produced by each group of recruits can be adjusted by varying the respective mortality rates until the summation (total catch) approximates the historical pattern of total annual catch.

Regardless of the hatch date, mature females produce the first spawn at age 24 months. To produce new hatches each year, the above system of equations (14-23) must be initiated in two consecutive years. The abundances calculated in the first year and the successive generations are cataloged as occurring in odd years, those initiated in the second year and successive generations are cataloged as occurring in even years. The total abundance of adult crabs at any point in time may be calculated as a summation of the numbers present in each cohort initialized in both odd and even years as follows in equations (24), (25), and (25A).

The abundances each month, $N_{m_j}(t)$ and $N_{a_j}(t)$, were defined in equations (18) and (19). The values are cataloged as double subscripted arrays: the first subscript is 'j', the generation number; the second defines 't', age of the cohort in months. The number of the generation is directly related to the year of harvest: the model simulates the crab fisheries with output in terms of annual catch in numbers of crabs. In odd years, the year of harvest is twice the generation number plus one ($Year_D = 2j+1$); in even years, the year of harvest is twice the generation number plus two ($Year_E = 2j+2$).

Total abundance during month i in an odd year is calculated in equation (24):

$$\begin{aligned} TN_D(i) &= N_{m_D}(j,i+19) + N_{m_E}(j-1,i+31) \\ &\quad N_{a_D}(j,i+16) + N_{a_E}(j-1,i+28) \end{aligned} \tag{24}$$

when $1 \leq i \leq 4$, $N_{a_D}(j,i+16) = 0.0$, not recruited

$3 \leq i \leq 7$, $N_{m_E}(j-1,i+31) = 0.0$, senescent

$i \geq 8$, $N_{m_E}(j-1,i+31) = N_{m_E}(j,i+7)$

$i=12$, $N_{a_E}(j-1,i+28) = 0.0$, senescent

where: TN_D = total abundance during month i, odd year

i = month in a calendar year, i=1,2,...,12

j = generation number, j=1,2,...

N_{m_D} = abundance in a given month for MAY cohort hatched in an odd year

N_{m_E} = abundance in a given month for MAY cohort hatched in an even year, see Eqn. (18)

N_{a_D} = abundance in a given month for AUGUST cohort hatched in an odd year

N_{a_E} = abundance in a given month for AUGUST cohort hatched in an even year, see Eqn. (19)

Total abundance during month i in an even year is calculated in equation (25):

$$TN_E(i) = N_{m_D}(j,i+31) + N_{m_E}(j,i+19) + N_{a_D}(j,i+28) + N_{a_E}(j,i+16) \qquad (25)$$

when $1 \leq i \leq 4$, $N_{a_E}(j,i+16) = 0.0$, not recruited

$3 \leq i \leq 7$, $N_{m_D}(j,i+31) = 0.0$, senescent

$i \geq 8$, $N_{m_D}(j,i+31) = N_{m_D}(j+1,i+7)$

$i=12$, $N_{a_D}(j,i+28) = 0.0$, senescent

where: TN_E = total abundance during month i, even year

For example, the number of crabs available for harvest in May of the 35th year is calculated as follows: i = 5; j = $(\text{Year}_D - 1)/2 = (35-1)/2 = 17$; therefore, the total abundance is

$$TN_D(5) = N_{m_D}(17,24) + N_{a_D}(17,21) + N_{a_E}(16,33) \qquad (25A)$$

In July of the 80th year, the total abundance is $N_{m_E}(39,26) + N_{a_D}(39,25) + N_{a_E}(39,23)$.

The average age of the population at any point in time is defined as the arithmetic mean of the age frequency distribution. The mean ages of the population during month i in odd and even years are calculated in equations (26) and (27) respectively and are subject to the same restrictions that apply in equations (24) and (25) respectively.

$$\bar{t}_D(i) = [1/TN_D(i)][(i+19)(N_{m_D}(j,i+19)) + (i+31)(N_{m_E}(j-1,i+31)) + (i+16)(N_{a_D}(j,i+16)) + (i+28)(N_{a_E}(j-1,i+28))] \qquad (26)$$

$$\bar{t}_E(i) = [1/TN_E(i)][(i+31)(N_{m_D}(j,i+31)) + (i+19)(N_{m_E}(j,i+19)) + (i+28)(N_{a_D}(j,i+28)) + (i+16)(N_{a_E}(j,i+16))] \qquad (27)$$

where: $\bar{t}_D$ = mean age of population during month i, odd year

$\bar{t}_E$ = mean age of population during month i, even year

The mean age of the population for harvest in May of the 35th year is calculated below. The total abundance, $TN_D(5)$, was computed in equation (25A).

$$\bar{t}_D(5) = [1/TN_D(5)][24 \cdot N_{m_D}(17,24) + 21 \cdot N_{A_D}(17,21) + 33 \cdot N_{A_E}(6,33)] \qquad (27A)$$

Instantaneous mortality rates were calculated by solving for Z:

$$N_t = N_o e^{-Zt} \qquad (28)$$

$$\ln(N_t/N_o) = -Zt \qquad (29)$$

$$Z = (-1/t)[\ln(N_t/N_o)] \quad (30)$$

One millionth (1×10^{-6}) of the eggs produced are presumed to survive to maturity, $N_{t_R}/N_o = 1 \times 10^{-6}$ (Van Engel, 1958). Natural mortality, M, during the subadult stages is calculated by the same method to produce different pre-recruitment mortalities for each of the two annual cohorts: $t_{R_m} = 15$, $M_m = 0.9210$; and $t_{R_a} = 21$, $M_a = 0.6579$.

The model simulates conditions when crabs remain available to the fishery after the spawning season (Case I), and the model simulates conditions when crabs are removed from the fishery by death immediately after the spawning season (Case II). Within Case I the total mortality rate, Z', applies to both cohorts, and this constant post-recruitment mortality rate is partitioned such that 95% of total mortality results from fishing pressure. $F = (0.95)Z'$. Starting with $N_{t_f}/R = 0.001 = e^{-Z}$, $Z' = 0.3838$ ($F = 0.3646$, $M = 0.0192$), it is obvious that total mortality is too high to be realistic (Fig. 9). An equilibrium abundance with respect to the AUGUST cohort is sought by decreasing Z' to 0.1000 (Fig. 10). Decreasing Z' further to 0.0333, an equilibrium abundance with respect to MAY is attempted (Fig. 11). The same values of Z' are repeated for Case II (Figs. 12-14).

When exact replacement of each cohort of crabs occurs, the total mortality rates must change with age and cohort. Z_1' depletes the population such that the number of spawning individuals remains constant for each generation, and Z_2' removes 99.9% of the remaining crabs by the end of the life cycle (when t = 18 months). For crabs born in May, $N_{m_j}(24)$ must equal $S_{m_{j-1}}$ (spawners of the previous generation) to replace the group. Total mortality, Z_{m_1}', is chosen so that $N_{m_j}(24) =$

Figure 9. Harvest in numbers of crabs caught yearly for a half century of model output. Crabs remain in the fishery for 18 months. $M_m = 0.9210$, $M_a = 0.6579$; $Z'_m = Z'_a = 0.3838$, $F = 0.3646$. (Case I)

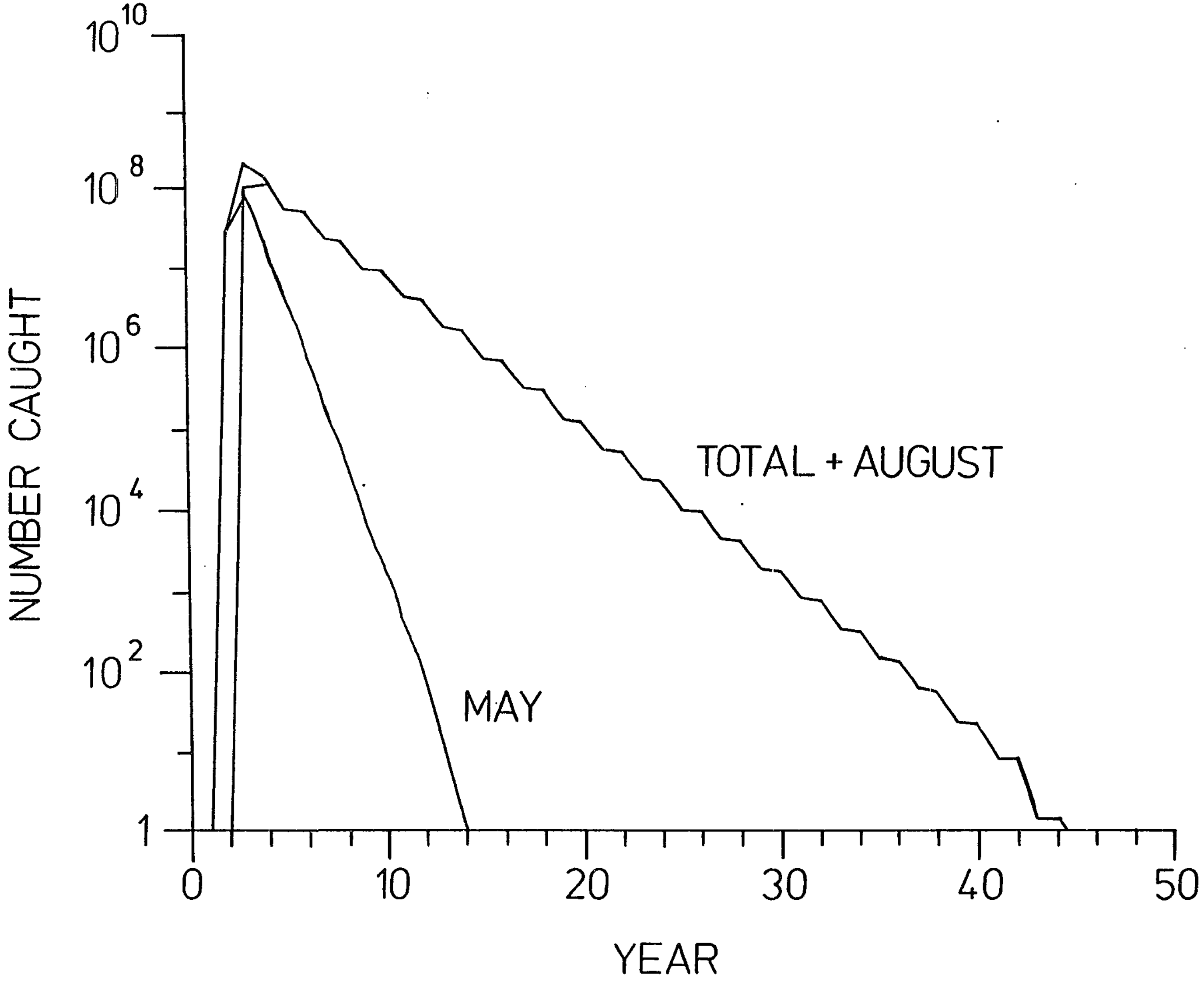

10^{10}
10^{8}
10^{6}
10^{4}
10^{2}
1
NUMBER CAUGHT
TOTAL + AUGUST
MAY
0
10
20
30
40
50
YEAR

Figure 10. Harvest in numbers of crabs caught yearly for a century of model output. Crabs remain in the fishery for 18 months. $M_m = 0.9210$, $M_a = 0.6579$; $Z_m' = Z_a' = 0.1000$, $F = 0.0950$. (Case I)

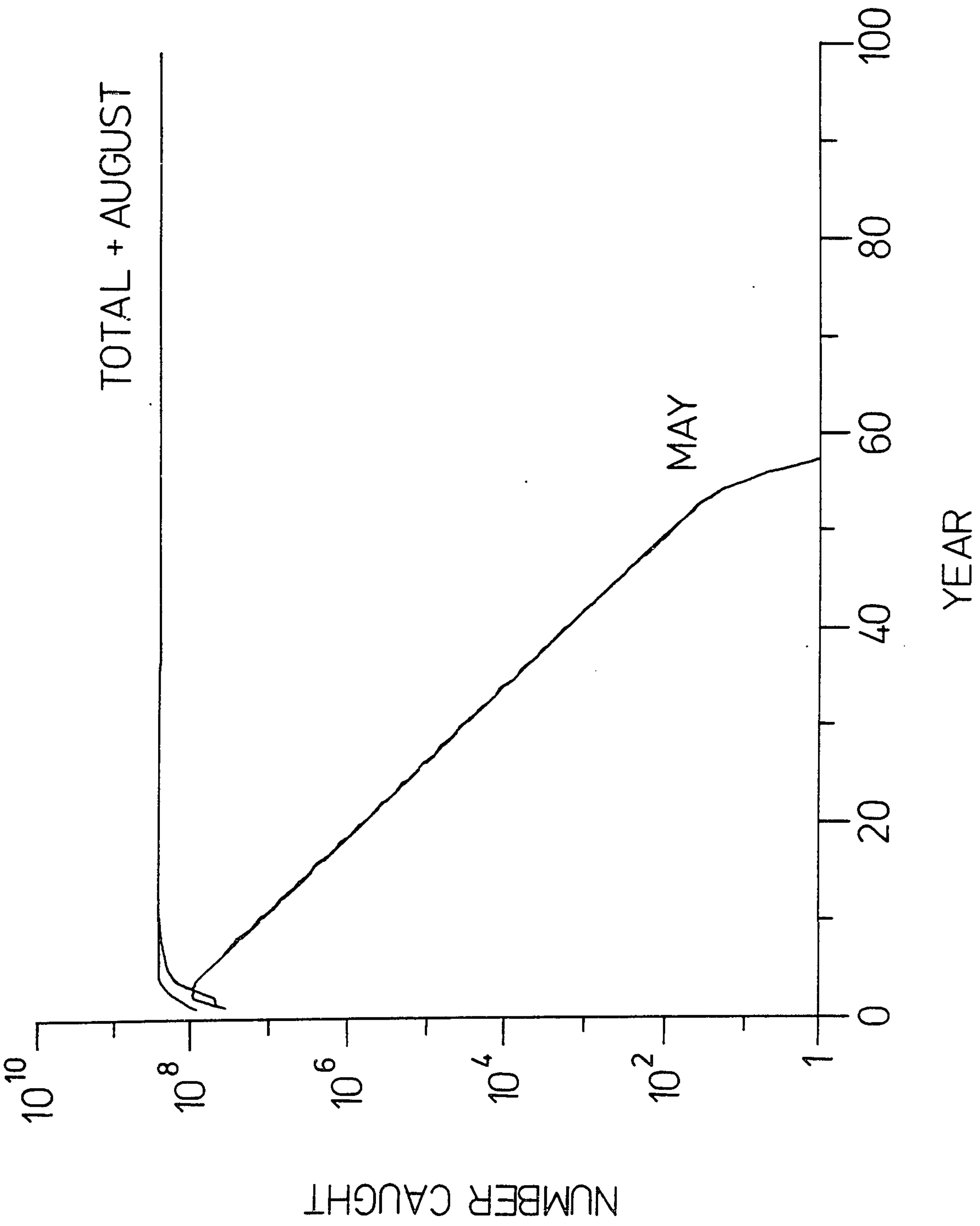
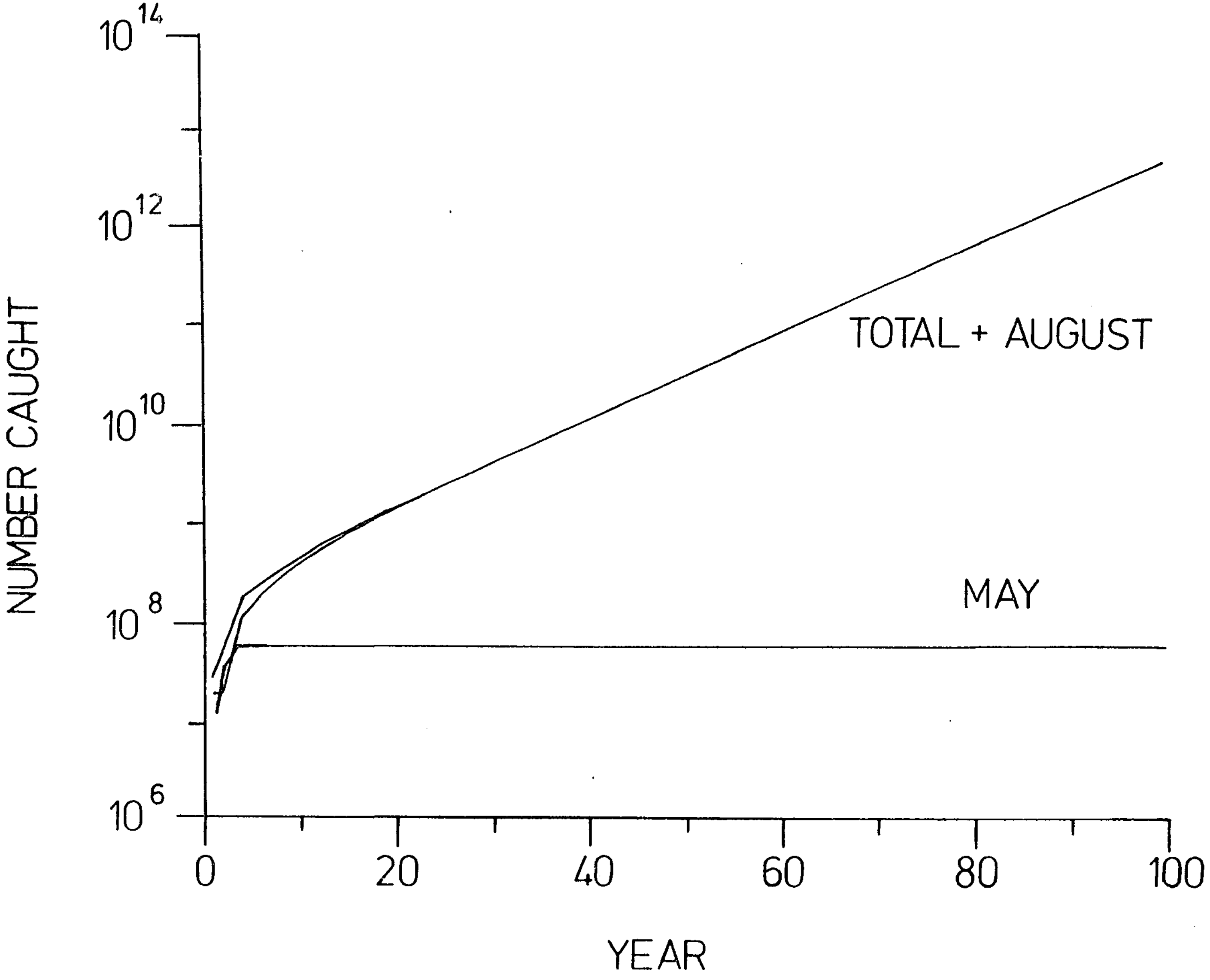

NUMBER CAUGHT
10^{10}
10^{8}
10^{6}
10^{4}
10^{2}
1
YEAR
0
20
40
60
80
100
TOTAL + AUGUST
MAY

Figure 11. Harvest in numbers of crabs caught yearly for a century of model output. Crabs remain in the fishery for 18 months. $M_m = 0.9210$, $M_a = 0.6579$; $Z'_m = Z'_a = 0.0333$, $F = 0.0316$. (Case I)



NUMBER CAUGHT
10^{14}
10^{12}
10^{10}
10^{8}
10^{6}
0
20
40
60
80
100
YEAR
TOTAL + AUGUST
MAY

Figure 12. Harvest in numbers of crabs caught yearly for a half century of model output. Crabs die at the end of the spawning season. $M_m = 0.9210$, $M_a = 0.6579$; $Z'_m = Z'_a = 0.3838$, $F = 0.3646$. (Case II)

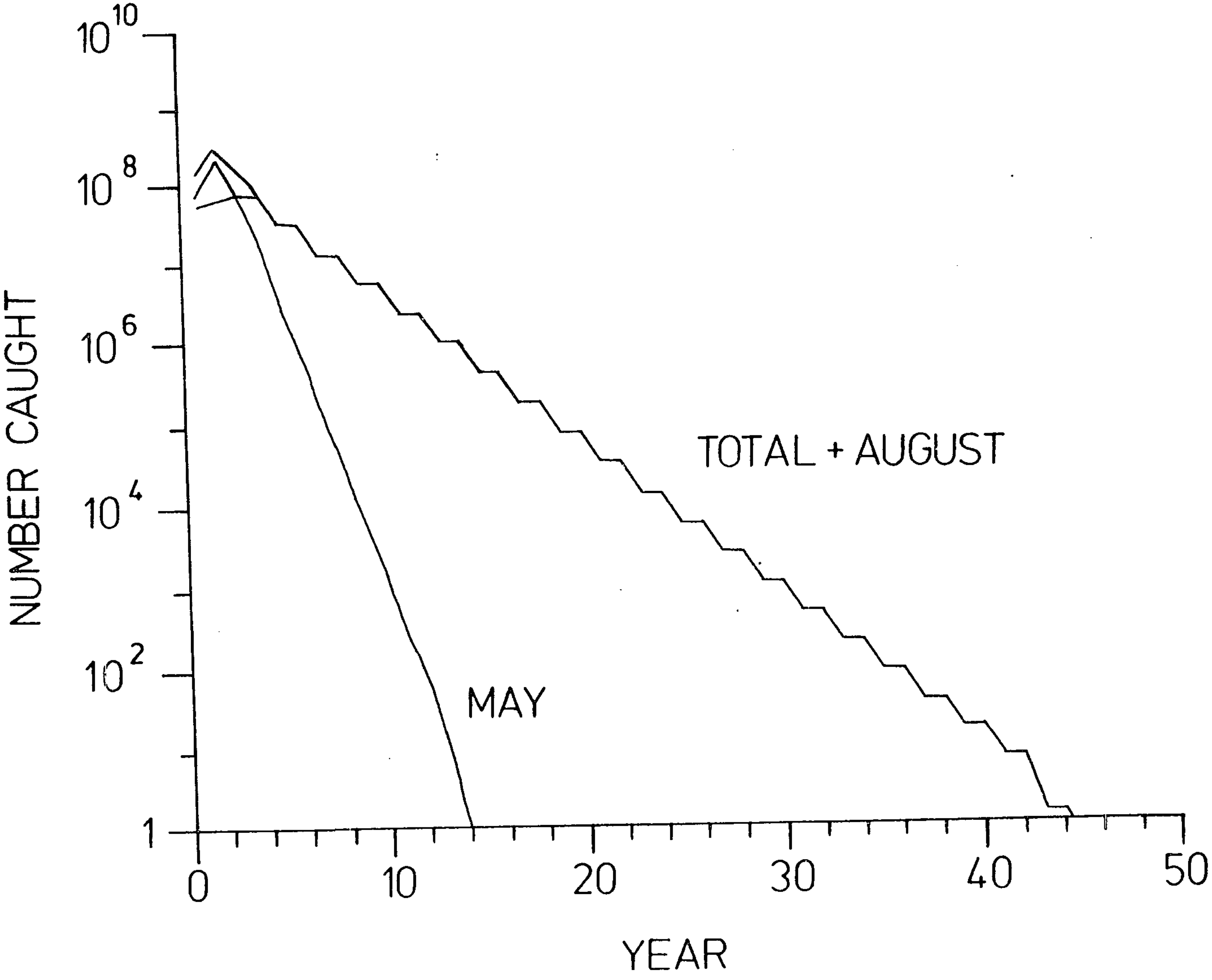

10^10
10^8
10^6
10^4
10^2
1
NUMBER CAUGHT
TOTAL + AUGUST
MAY
0
10
20
30
40
50
YEAR

Figure 13. Harvest in numbers of crabs caught yearly for a century of model output. Crabs die at the end of the spawning season. $M_m = 0.9210$, $M_a = 0.6579$; $Z'_m = Z'_a = 0.1000$, $F = 0.0950$. (Case II)

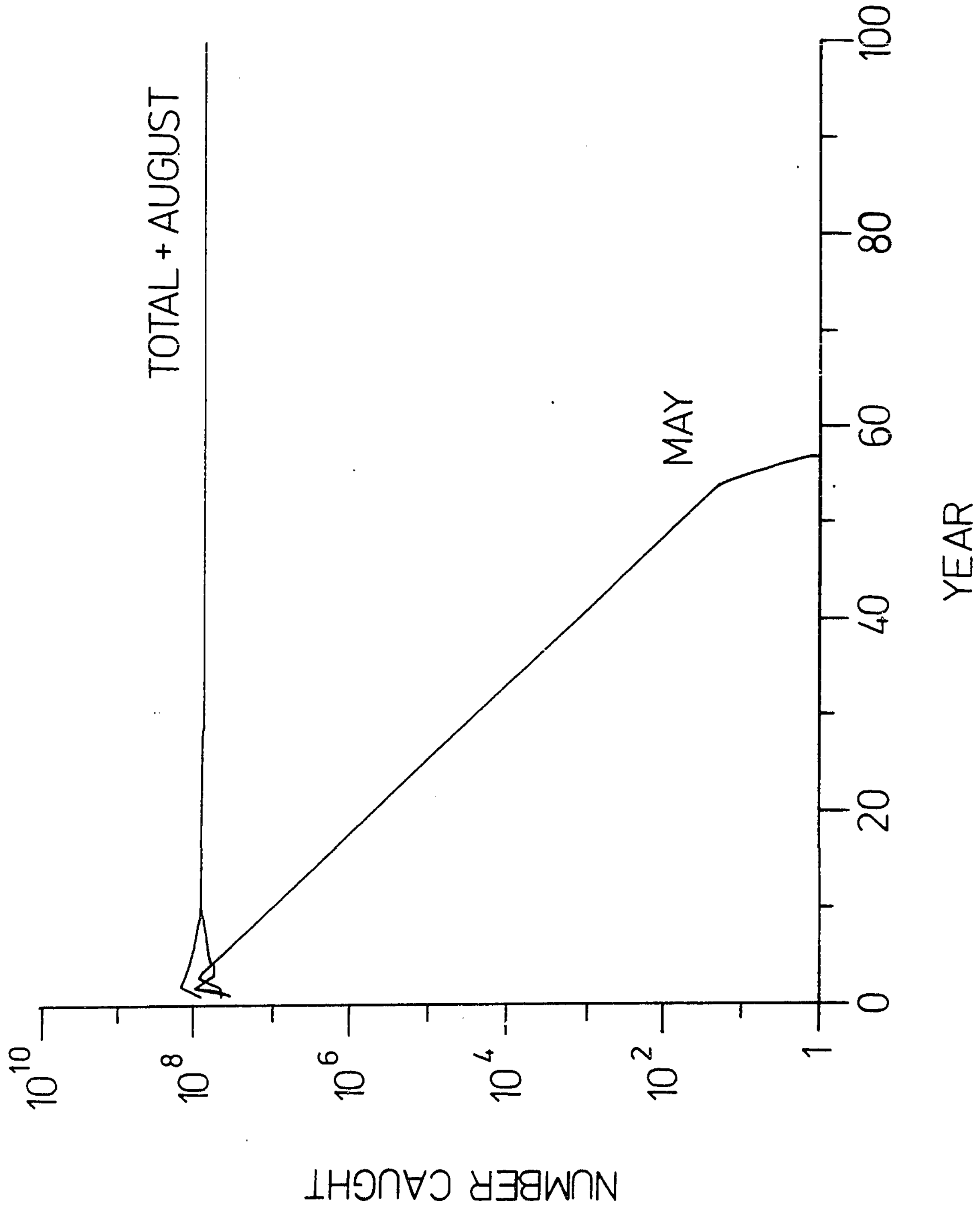
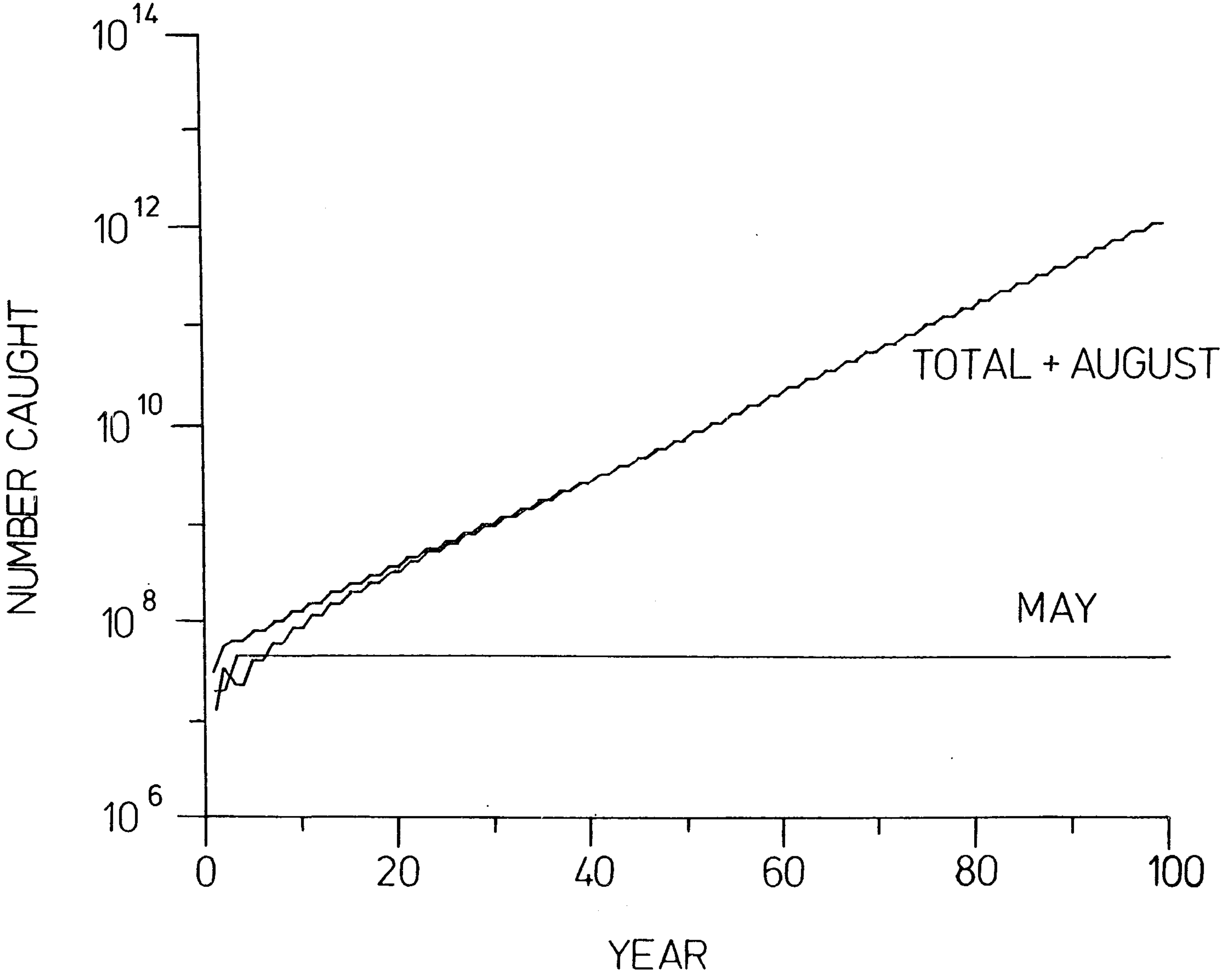

NUMBER CAUGHT
10^{10}
10^{8}
10^{6}
10^{4}
10^{2}
1
0
20
40
60
80
100
YEAR
TOTAL + AUGUST
MAY

Figure 14. Harvest in numbers of crabs caught yearly for a century of model output. Crabs die at the end of the spawning season. $M_m = 0.9210$, $M_a = 0.6579$; $Z'_m = Z'_a = 0.0333$, $F = 0.0316$. (Case II)


10^14
10^12
10^10
10^8
10^6
NUMBER CAUGHT
0
20
40
60
80
100
YEAR
TOTAL + AUGUST
MAY

$S_{m_{j-1}}$ when $N_{m_j}(24) = R_{m_j}e^{-Z'_{m_1}t}$ where t = 9 months since MAY crabs are fished nine months before they spawn. Therefore, $Z'_{m_1} = 0.0333$; $Z'_{m_2} = 0.7675$ for removal of 99.9% of the population in the remaining nine months of life.

For crabs born in August, all crabs spawning in August must equal the number of spawners from the previous generation: $N_{a_j}(24) + N_{m_j}(27) = S_{a_{j-1}}$ such that $N_a(0)$ is maintained each generation. Total mortality for August, Z'_{a_1} is calculated when $N_{a_j}(24) = R_{a_j}e^{-Z'_{a_1}t}$ where t = 3 months since August crabs are fished for three months before spawning, $Z'_{a_1} = 0.1352$. $Z'_{a_2} = 0.4605$ for removal of 99.9% of the population during the remaining 15 months of life.

Fishing mortality is again assumed to account for 95% of the total post-recruitment mortality: $F_{m_1} = 0.0316$, $F_{m_2} = 0.7291$, $F_{a_1} = 0.1284$, and $F_{a_2} = 0.4375$. These differential post-recruitment mortality values insure exact replacement of both groups of crabs. The premise is classic steady-state population dynamics: at least one egg must survive to maturity to replace its parent and, therefore, maintain the population. Fluctuations in the total annual abundance are assumed to be the result of environmental perturbations.

Mortality rates are summarized in Table 1.

RESULTS

The mortality rates for the MAY and AUGUST cohorts are presented for comparison in Table 2. Differential pre-recruitment natural mortality is coupled with constant post-recruitment total mortality in

TABLE 1. Instantaneous rates of total, natural and fishing mortality applied in the model.

Mortality Rate	Definition	Value
M_m	pre-recruitment natural mortality for MAY	0.9210
M_a	pre-recruitment natural mortality for AUGUST	0.6579
$Z'_m = Z'_a$	post-recruitment total mortality for MAY and AUGUST	0.3838
$F_m = F_a$	fishing mortality for MAY and AUGUST	0.3646
$M'_m = M'_a$	post-recruitment natural mortality for MAY and AUGUST	0.0192
Z'_{m_1}	post-recruitment total mortality before spawning occurs for MAY	0.0333
Z'_{m_2}	post-recruitment total mortality after spawning occurs for MAY	0.7675
Z'_{a_1}	post-recruitment total mortality before spawning occurs for AUGUST	0.1352
Z'_{a_2}	post-recruitment total mortality after spawning occurs for AUGUST	0.4605
F_{m_1}	fishing mortality before spawning occurs for MAY	0.0316
F_{m_2}	fishing mortality after spawning occurs for May	0.7291

F_{a_1}	fishing mortality before spawning occurs for AUGUST	0.1284
F_{a_2}	fishing mortality after spawning occurs for AUGUST	0.4375
M'_{m_1}	post-recruitment natural mortality before spawning occurs for MAY	0.0017
M'_{m_2}	post-recruitment natural mortality after spawning occurs for MAY	0.0383
M'_{a_1}	post-recruitment natural mortality before spawning occurs for AUGUST	0.0068
M'_{a_2}	post-recruitment natural mortality after spawning occurs for AUGUST	0.0230

TABLE 2. Comparison of Mortality Rates for MAY and AUGUST cohorts. See Table 1 for definitions of mortality rates.

MAY Cohort		AUGUST Cohort	
Mortality Rate	Value	Value	Mortality Rate
M_m	0.9210	0.6579	M_a
Z'_m	0.3838	0.3838	Z'_a
F_m	0.3646	0.3646	F_a
M'_m	0.0192	0.0192	M'_a
Z'_{m_1}	0.0333	0.1352	Z'_{a_1}
Z'_{m_2}	0.7675	0.4605	Z'_{a_2}
F_{m_1}	0.0316	0.1284	F_{a_1}
F_{m_2}	0.7291	0.4375	F_{a_2}
M'_{m_1}	0.0017	0.0068	M'_{a_1}
M'_{m_2}	0.0383	0.0230	M'_{a_2}

an effort to describe the life history absent environmental limitations. Natural mortality for the MAY cohort (M_m = 0.9210) is substantially higher than that for the AUGUST cohort (M_a = 0.6579). Most (99.9%) of the adult population is depleted throughout adulthood at a constant rate. In order to reach equilibrium in both cohorts, these pre-recruitment natural mortalities must be applied in conjunction with differential post-recruitment natural mortality rates. These mortality rates are calculated specifically to replace each cohort each generation. The MAY cohort must be depleted slowly during its first winter in the fishery to permit replacement (Z'_{m_1} = 0.0333). The AUGUST cohort must be depleted much more quickly since fishing pressure occurs only three months before spawning takes place (Z'_{a_1} = 0.1352). The post-recruitment total mortalities after spawning for both cohorts are necessarily much higher in order to deplete the population in the allotted time frames.

When depletion throughout adulthood is controlled by one total mortality rate, it is impossible to achieve equilibrium in both cohorts simultaneously (Fig. 9). MAY crabs cease contributing to the harvest within 13 years. The AUGUST catch approaches extinction in the 42nd year at $Z'_m = Z'_a = 0.3838$. Adjusting the initial ratio of MAY to AUGUST crabs has little effect on the annual harvest statistics, influencing only the rate of decline.

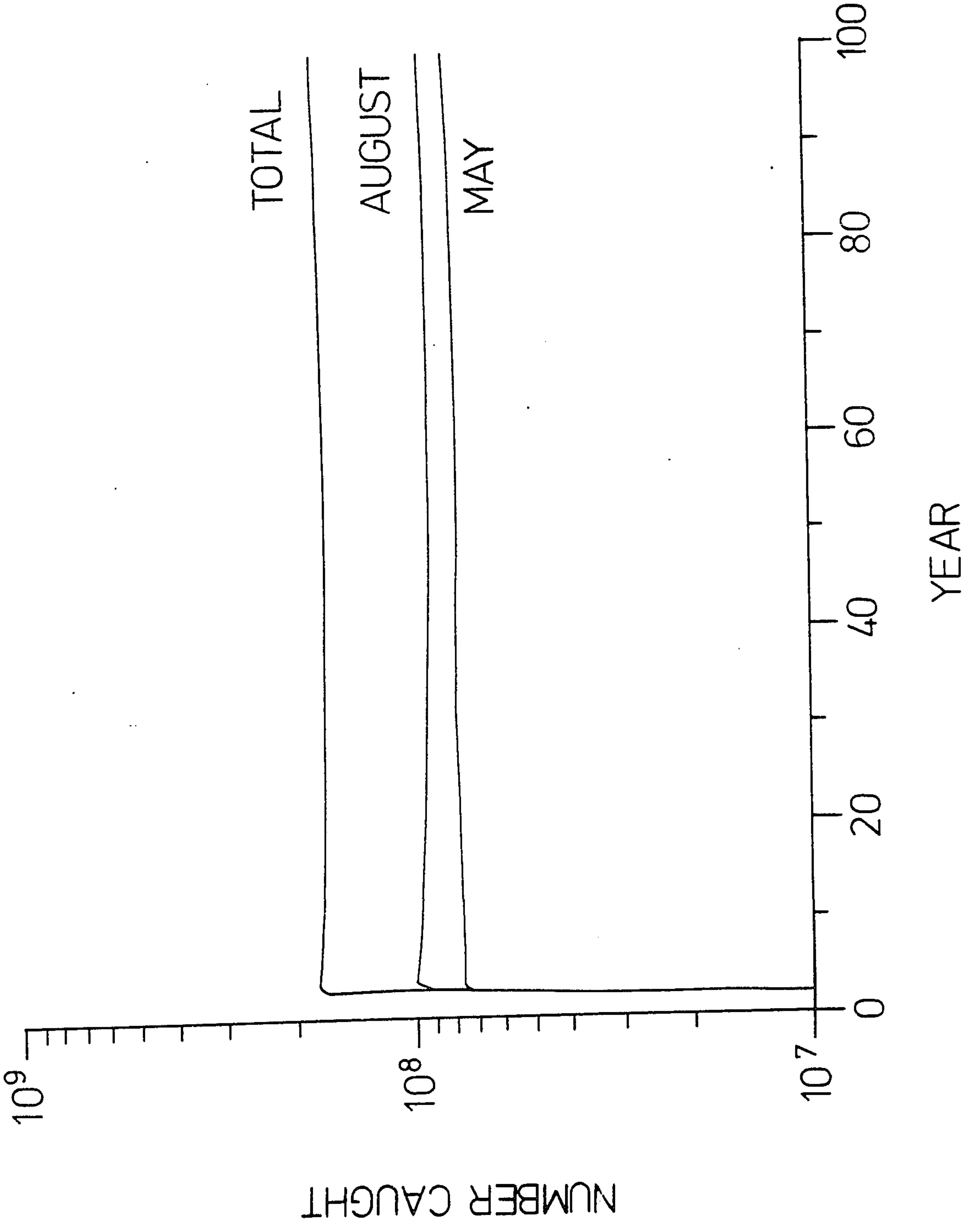
The life history information states that females that have spawned may disappear by the end of September (Van Engel, 1958). The results are quite similar when all crabs die at the end of the spawning season (Fig. 12). MAY crabs are fished for 12 months, while AUGUST crabs are fished only three months. Initially the MAY catch surpasses that of

AUGUST, but by the fifth year, the AUGUST cohort has begun to dominate the catch. The MAY catch declines rapidly and is non-existent by the 13th year. By the end of the 44th year the AUGUST catch fades out. Adjusting the initial ratio of MAY to AUGUST spawners affects the catch values, but relative abundances remain the same; there is no harvest within 45 years.

It is possible to reach equilibrium conditions for the AUGUST cohort by reducing the value of Z' to 0.1000, however the MAY catch approaches zero in the 57th year (Fig. 10). As Z' is decreased further, both catch curves begin to increase. When Z' = 0.0333, the MAY catch reaches steady-state, while the abundance of the AUGUST cohort catch increases toward infinity so rapidly that the contribution of MAY crabs to the catch (Fig. 11) is essentially negated. Results are similar when all crabs die at the end of the spawning season when Z' = 0.1000 (Fig. 13) and when Z' = 0.0333 (Fig. 14).

When total mortality rates are calculated for exact replacement of the population, the catch curves reach equilibrium relatively quickly (Fig. 15). Varying the initial number of spawners produces changes in absolute abundances, but the MAY to AUGUST ratios at the end of a century are equal. When equivalent numbers of spawning females are input for each cohort, when the initial number of MAY spawners is half that of AUGUST spawners, or when the initial input of MAY spawners is an order of magnitude above that of the AUGUST spawners, the MAY to AUGUST ratio at the end of a century is 0.86. In all of these simulations, those crabs hatched in MAY are responsible for approximately 46% of the total annual catch. The initial relative abundance of MAY and AUGUST spawners determines the time to equilibrium but does not alter it.

Figure 15. Harvest in numbers of crabs caught yearly for a century of model output. Crabs remain in the fishery for 18 months. $M_m = 0.9210$, $M_a = 0.6579$; $Z'_{m_1} = 0.0333$, $Z'_{m_2} = 0.7675$; $Z'_{a_1} = 0.1352$, $Z'_{a_2} = 0.4605$. $F_{m_1} = 0.0316$, $F_{m_2} = 0.7291$; $F_{a_1} = 0.1284$, $F_{a_2} = 0.4375$. (Case I)


NUMBER CAUGHT
10^9
10^8
10^7
YEAR
0
20
40
60
80
100
TOTAL
AUGUST
MAY

Immediate removal of post-spawning crabs in conjunction with exact replacement of the population also produces equilibrium conditions (Fig. 16). The MAY catch dominates the harvest statistics. Adjusting the initial numbers in each spawning group has little effect on relative abundances. The MAY catches, being twice that of the AUGUST catches, are responsible for 65% of the total catch.

Constant pre-recruitment mortality rates are coupled with both constant and differential post-recruitment mortality rates in order to evaluate all different production strategies. When the pre-recruitment mortality rate for MAY is held constant ($M_m = M_a = 0.9210$) and used in conjunction with one post-recruitment total mortality ($Z'_m = Z'_a = 0.3838$), both cohorts approach extinction within 15 years (Fig. 17). However, when the AUGUST pre-recruitment mortality rate is employed such that $M_m = M_a = 0.6579$, the abundances of both cohorts increase rapidly (Fig. 18).

When differential post-recruitment mortalities ($Z'_{m_1} = 0.0333$; $Z'_{m_2} = 0.7675$; $Z'_{a_1} = 0.1352$; $Z'_{a_2} = 0.4605$) are applied concurrently with $M_m = M_a = 0.6579$, catch for each cohort increases exponentially with curves quite similar to those seen in Figure 18. Although the rate of increase and absolute harvest values vary, the trend toward rapid increase is maintained (Fig. 19). Selecting the constant pre-recruitment mortality rate of the MAY cohort ($M_m = M_a = 0.9210$) in conjunction with differential post-recruitment rates produces equilibrium catch (Fig. 20). However, when harvested, the MAY catch exceeds that of the AUGUST cohort by three orders of magnitude, effectively negating the influence of the late summer cohort.

Figure 16. Harvest in numbers of crabs caught yearly for a century of model output. Crabs die at the end of the spawning season. $M_m = 0.9210$, $M_a = 0.6579$; $Z'_{m_1} = 0.0333$, $Z'_{m_2} = 0.7675$; $Z'_{a_1} = 0.1352$, $Z'_{a_2} = 0.4605$. $F_{m_1} = 0.0316$, $F_{m_2} = 0.7291$; $F_{a_1} = 0.1284$, $F_{a_2} = 0.4375$. (Case II)

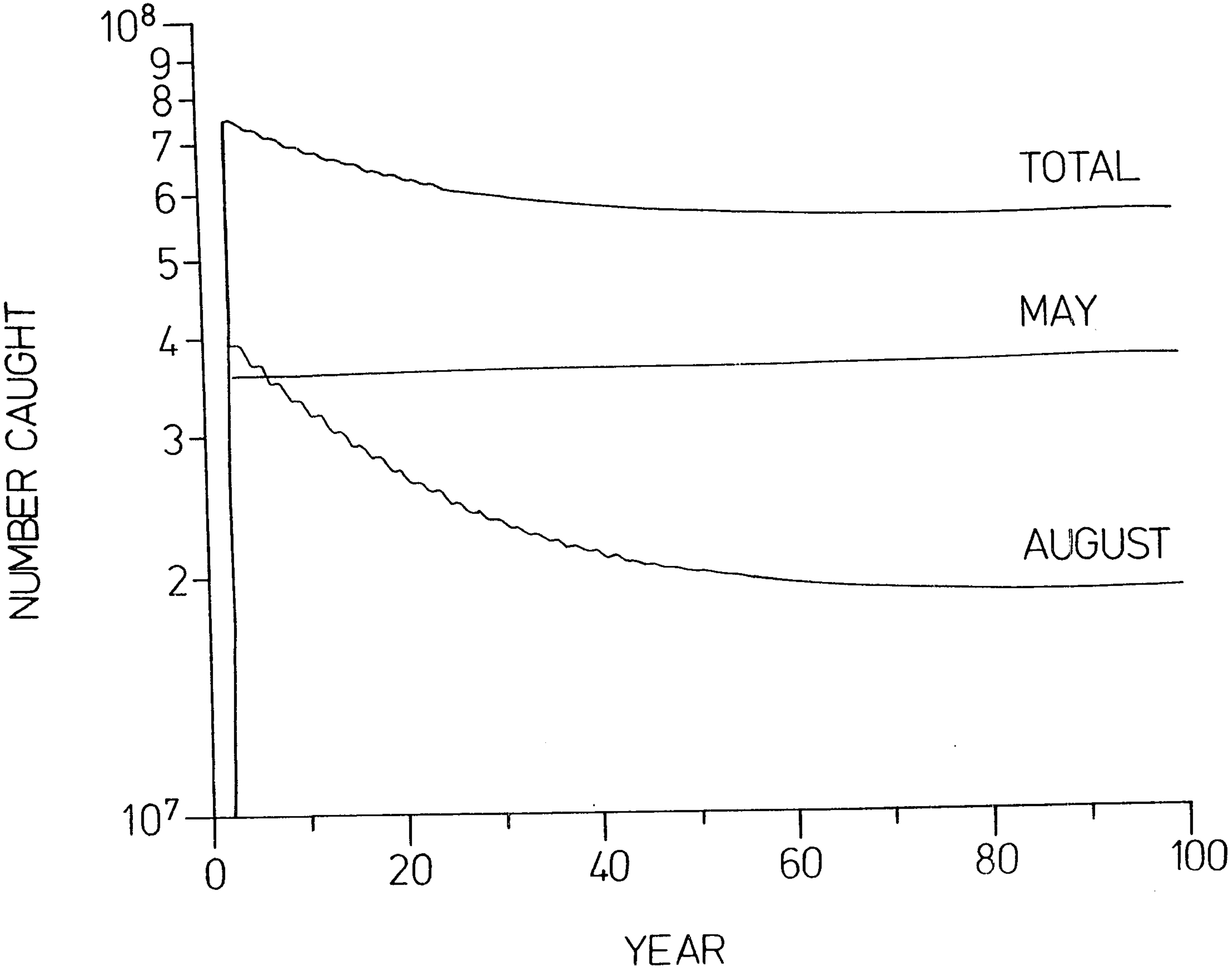

10^8
9
8
7
6
5
4
3
2
10^7
NUMBER CAUGHT
TOTAL
MAY
AUGUST
0
20
40
60
80
100
YEAR

Figure 17. Harvest in numbers of crabs caught yearly for a half century of model output. Crabs remain in the fishery for 18 months. $M_m = M_a = 0.9210$; $Z'_m = Z'_a = 0.3838$; $F_m = F_a = 0.3646$. (Case I)

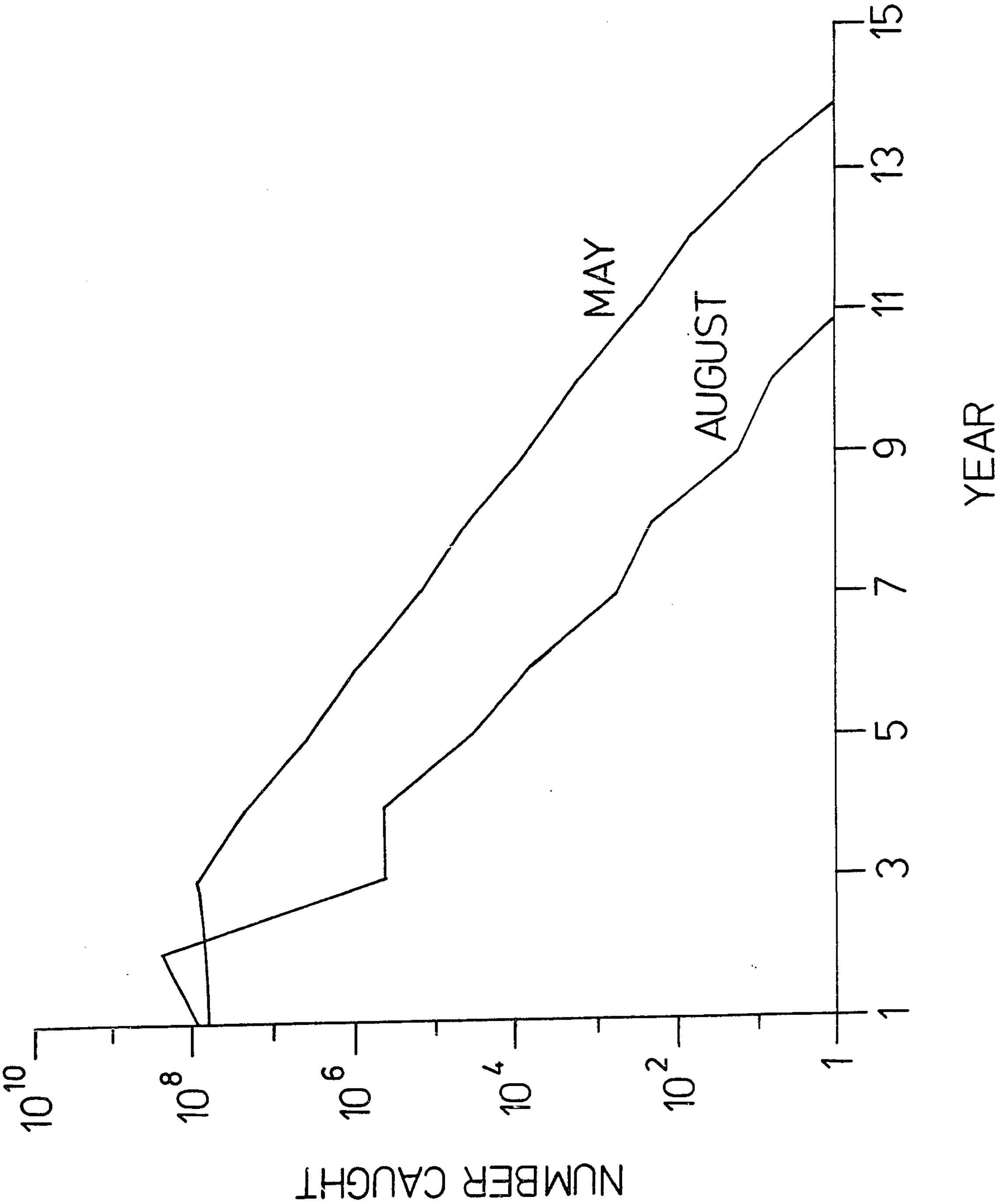

NUMBER CAUGHT
10^10
10^8
10^6
10^4
10^2
1
YEAR
1
3
5
7
9
11
13
15
MAY
AUGUST

Figure 18. Harvest in numbers of crabs caught yearly for a half century of model output. Crabs remain in the fishery for 18 months. $M_m = M_a = 0.6579$; $Z_m^! = Z_a^! = 0.3838$; $F_m = F_a = 0.3646$. (Case I)

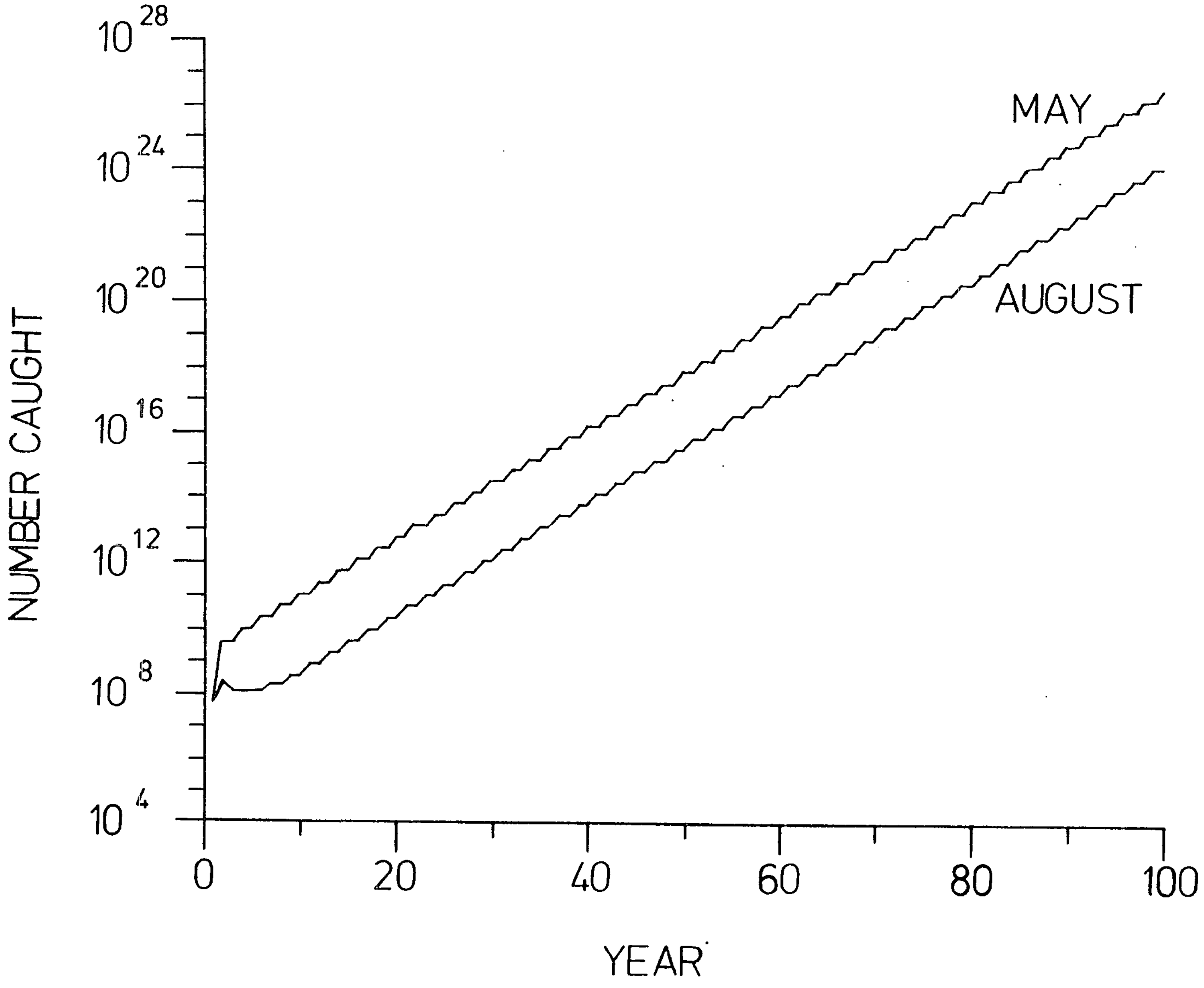
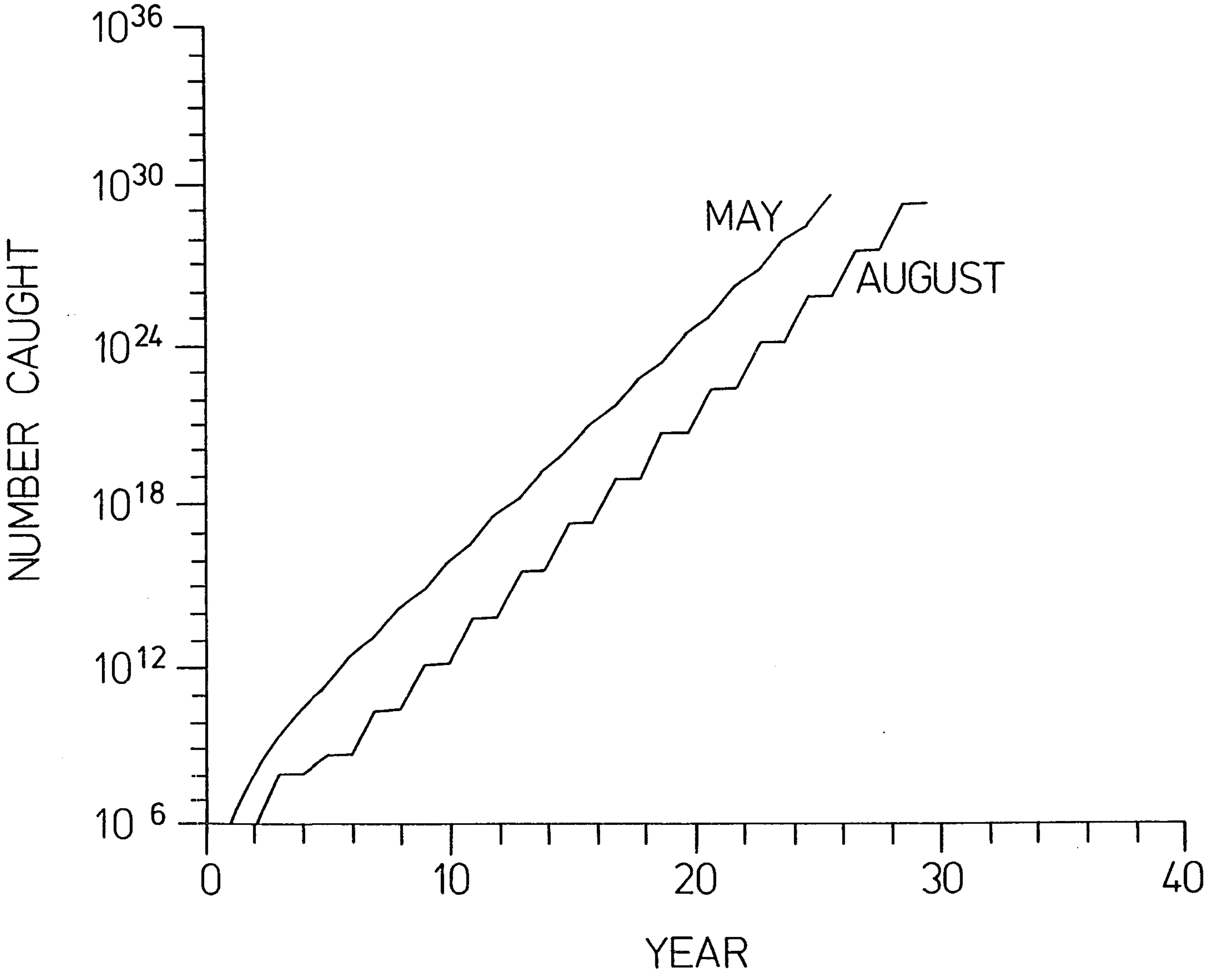
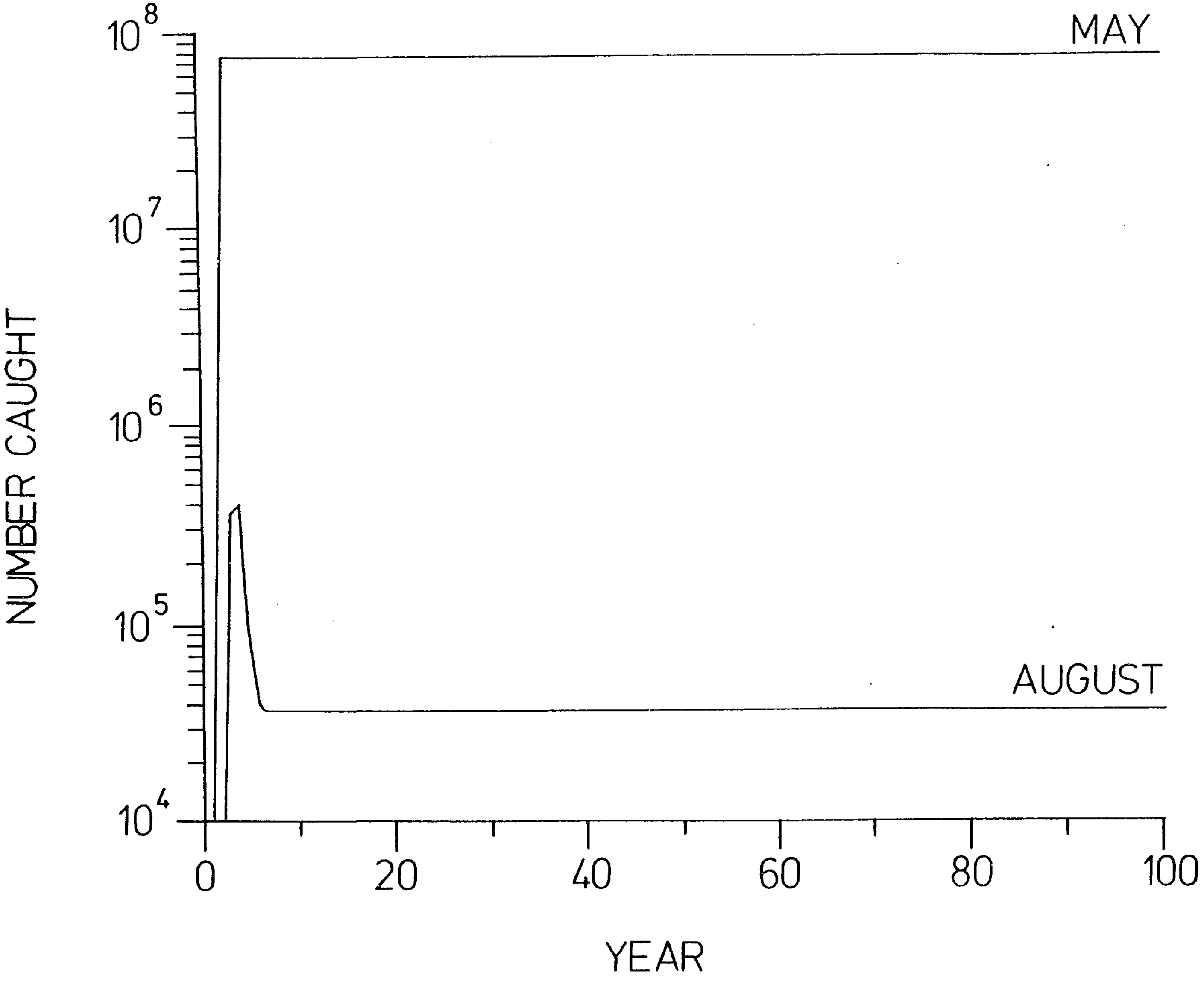

MAY
AUGUST
NUMBER CAUGHT
10^{28}
10^{24}
10^{20}
10^{16}
10^{12}
10^{8}
10^{4}
0
20
40
60
80
100
YEAR

Figure 19. Harvest in numbers of crabs caught yearly for a half century of model output. Crabs remain in the fishery for 18 months. $M_m = M_a = 0.6579$; $Z'_{m_1} = 0.0333$, $Z'_{m_2} = 0.7675$; $Z'_{a_1} = 0.1352$, $Z'_{a_2} = 0.4605$. $F_{m_1} = 0.0316$, $F_{m_2} = 0.7291$; $F_{a_1} = 0.1284$, $F_{a_2} = 0.4375$. (Case I)



MAY
AUGUST
NUMBER CAUGHT
10^{36}
10^{30}
10^{24}
10^{18}
10^{12}
10^{6}
0
10
20
30
40
YEAR

Figure 20. Harvest in numbers of crabs caught yearly for a half century of model output. Crabs remain in the fishery for 18 months. $M_m = M_a = 0.9210$; $Z'_{m_1} = 0.0333$, $Z'_{m_2} = 0.7675$; $Z'_{a_1} = 0.1352$, $Z'_{a_2} = 0.4605$. $F_{m_1} = 0.0316$, $F_{m_2} = 0.7291$; $F_{a_1} = 0.1284$, $F_{a_2} = 0.4375$. (Case I)


NUMBER CAUGHT
10^8
10^7
10^6
10^5
10^4
MAY
AUGUST
0
20
40
60
80
100
YEAR

The application of Case II, death immediately after the spawning season, has little effect when constant pre-recruitment mortalities are combined with both constant and differential post-recruitment mortality rates. Absolute catch values vary, but the trends are equivalent to those seen in Figures 17-20. When $M_m = M_a = 0.9210$ is coupled with one post-recruitment total mortality rate ($Z'_m = Z'_a = 0.3838$), both cohorts become extinct in a decade. When $M_m = M_a = 0.6579$ is applied with this same post-recruitment mortality ($Z' = 0.3838$), the catch increases rapidly for both cohorts. The application of $M_m = M_a = 0.6579$ with differential post-recruitment total mortalities ($Z'_{m_1} = 0.0333$; $Z'_{m_2} = 0.7675$; $Z'_{a_1} = 0.1352$; $Z'_{a_2} = 0.4605$) also produces exponential increase in both cohorts. When $M_m = M_a = 0.9210$ and these same differential post-recruitment total mortality rates are used simultaneously, equilibrium harvest is produced. Again the MAY catch exceeds that of the AUGUST cohort by several orders of magnitude. The major effect of this terminal molt hypothesis is the augmentation of the MAY cohort and its effect on the average of the catch.

DISCUSSION

Although hatching occurs continuously during the summer months, identifying the cohorts with respect to month of spawning is a necessary result of the analysis which is also supported by biological evidence. The presence of several spawning groups is well documented. Van Engel (1958) reported two peaks of sponge production in Chesapeake Bay, in late May-early June and in August. More (1969) found evidence of spring, summer, and fall periods of spawning in the blue crab in the Texas fishery. Adkins (1972) noted a winter group of spawning females, in addition to the spring, summer, and fall spawning groups in the offshore waters of Louisiana. Perry (1975) collected blue crab zoeae in spring, summer, and fall and noted that the seasonal pattern of zoeal abundance coincided with the appearance of berried females in Mississippi's Gulf and coastal waters. Stuck and Perry (1981) collected blue crab megalopae in Mississippi coastal waters monthly over a five year period. They found two peaks in abundance: the first in late spring-early summer and a second larger peak in late summer-early fall.

Various combinations of the mortality rates are employed to simulate crab production. The use of a constant pre-recruitment mortality rate in conjunction with constant and differential post-recruitment rates produces several results. The application of M = 0.9210 to both cohorts generates immediate decline of the population when $Z_m' = Z_a'$. With differential adult mortality rates, M = 0.9210 produces an equilibrium of predominantly MAY crabs. Rapid increase of both cohorts results from the use of M = 0.6579 for both cohorts over a wide range of post-recruitment mortality rates. The terminal molt hypothesis alters the age composition of the catch but has no effect on the ultimate equilibrium state.

In these simulations the survival rates of the larvae (Eqn. 29) seems too diverse to be realistic. When $M_m = M_a = 0.9210$, the rate of survival is 1×10^{-6}, for the MAY cohort, but 3.9×10^{-9} for the AUGUST cohort. The AUGUST cohort is depleted too quickly to replace itself (Fig. 17) or it is maintained at a very low level (Fig. 20). When $M_m = M_a = 0.6579$, the AUGUST cohort survives at a rate of 1×10^{-6}, while the

MAY cohort experiences a higher survival of 5.2×10^{-5}. The increased MAY survival rate is reflected in the rapidly increasing catch. The MAY cohort is able to support itself and contribute to the AUGUST cohort at this rate. This variability in survivorship is a result of adjustments made in the mortality rates in order to examine several possible production schemes and serves to point out the paucity of information concerning blue crab mortality.

Differential pre-recruitment mortality rates are also coupled with constant and differential post-recruitment total mortality rates. In these simulations, the mortality rates are selected in an effort to describe the life history. Differential juvenile mortality rates are matched with constant post-recruitment mortality rates to provide a general description of the known life history information. The differential post-recruitment mortality rates are used to produce numerical equilibrium.

Considering the mortality schedules under which the AUGUST cohort dominates the population, the differential natural mortality rates for the subadult populations appear to be reversed at first glance; however, they do not seem inappropriate on further examination. The values for M_m and M_a represent the same survivability, one millionth of the eggs produced reach maturity; however, the time frames are different. Survival to adulthood occurs over a 15 month period for the MAY cohort but over a 21 month period for the AUGUST cohort. Although the time frames differ, periods of growth are also equivalent for the two cohorts: both mature through two summer seasons. The values of the natural mortality rates are a function of the application of the different time frames in the calculations.

The relative magnitudes of these rates do have some biological basis. Larvae released early in the season are subject to fluctuating environmental parameters: low or oscillating temperatures tend to prevent production of food organisms, while retarding growth of larvae. MAY larvae are part of the early summer zooplankton bloom, becoming prey for larger organisms. First crabs, and the smaller juveniles, are also subject to removal from the system until they outgrow their predators. The two groups have different growth rates: in the first four months of life, the larvae hatched in May have grown to a juvenile size of two to two and a half inches; the August hatches grow to a size of one half inch in the two months before cold temperatures force dormancy (Van Engel, 1958).

The values of the differential post-recruitment mortality rates are also a function of the varying time frames over which the mortality schedules operate. To produce exact replacement of the population and, consequently, equilibrium, a quarter of the MAY cohort and a third of the AUGUST cohort must be depleted before spawning occurs in both cohorts. The MAY cohort is fished nine months before the first spawning occurs. The AUGUST cohort is fished only three months before spawning occurs; therefore, this total mortality rate is much higher ($Z'_{a1} > Z'_{m1}$). After spawning, the total mortality rates reverse in magnitude ($Z'_{m1} > Z'_{a1}$). The remaining population must be removed by the end of the life span: 75% in nine months for the MAY cohort, and 67% in 15 months for the AUGUST cohort.

The conclusion derived by applying one constant post-recruitment total mortality is that crabs hatched late in the season (in August) must dominate the population structure, to the exclusion of crabs hatched earlier. This result is unrealistic when the life history information is considered because crabs do spawn in May, however it serves to emphasize the inescapable conclusion that the MAY crabs contribute to their own replenishment and to that of the AUGUST cohort. There is no AUGUST input to the MAY cohort. Different fishing pressures must be applied to the two groups in order for May spawning to occur. The MAY crabs are fished nine months before they first spawn, while the AUGUST crabs are fished for three months before spawning. Fishing pressure is depleting the MAY line at a critical time before reproduction occurs. The preceding is also true in the case of differential post-recruitment total mortalities.

One necessary result of a population dominated by AUGUST crabs is that all females are two years old before they can be harvested. Eighty five percent of the dredge catch (December through March) are adult females, the remaining 15% are males and immature crabs of both sexes (Van Engel, 1962). If females die after spawning, the only females available to the winter harvest are those crabs hatched early in the summer. These MAY crabs mate at age 15 months, overwinter, and spawn at ages 24 and 27 months: these are the only crabs available to support a winter dredge fishery.

Death at the end of the spawning season is a generally accepted theory in life history studies on the blue crab. When the model uses a uniform adult mortality value to predict the harvest of a population that dies immediately after spawning, the resulting catch population is predominantly composed of crabs hatched in August (Figs. 12-14). Equilibrium mortality rates require the catch to be dominated by MAY crabs. In both cases MAY crabs are fished twelve months before removal from the system, while AUGUST crabs are fished only three months before death occurs. Crabs are thought to survive at least a year past the onset of maturity; therefore, both cohorts should be available for harvest for a similar period of time. Since AUGUST females would be allowed to survive only a few months past the onset of maturity, an extremely high natural mortality must be applied in order to explain the demise of this group. Such a wide disparity in natural mortalities among members of the same species within the same geographic area seems unlikely.

The alternate concept is an adulthood of a year or longer, or a maximum fishable life span. Van Engel (1958) reported that females either died after their spawning season or moved out to sea to overwinter and returned to the bay the following July or August as "sea-run" crabs. In the summer of 1954, these "ocean" crabs migrated into the James River where they added substantially to the commercial catch.

According to the literature no provision is made for replacement of the MAY cohort. These ocean crabs could possibly use retained sperm to produce another sponge; however, sperm are thought to be viable for only a year. Whether from MAY or AUGUST, these crabs mated at least 16 months earlier. MAY crabs actually mated 24 months earlier. If the sperm did remain viable, these crabs would release larvae in August and increase the tendency toward an AUGUST population. Another possibilty is that crabs hatched in August may also produce two sponges, the second spawn would necessarily occur in May of their third summer at age 33 months. A sufficient percentage of sperm would have to remain viable for fertilization since these crabs mated a year earlier at age 21 months.

Replacement of the MAY population is needed to stabilize the system. The results of the model in conjunction with the literature suggest two alternate hypotheses to accomplish the replacement. Sperm must be viable for more than a year, at least long enough to insure that a significant portion of the August crabs remain fertile and spawn in May of their second summer as adults. The other possibility is that the ocean crabs return to the bay, move inshore and mate before overwintering. Crabs mating in August produce sponges the following May.

In summary, it is apparent that the reproductive biology of the blue crab is too poorly known to permit a rational fisheries approach on Chesapeake Bay. Date of birth determines the schedule of mortality experienced by an individual throughout its life. Time intervals no longer than a month are required since longer intervals obscure critical aspects of the life cycle. The age structure of the population is a function of the hypothesis chosen to describe adulthood, the maximum fishable life span of the terminal molt hypothesis. The selection and application of mortality rates will determine the model's output. However, at the present time selection of mortality rates is problematic. Depending on the choice of mortality rates, crabs hatched later in the summer dominate the population, or MAY and AUGUST crabs contribute similar amounts to the harvest, or MAY dominates the catch when females die immediately after spawning. Whatever the case, no provision is made to replace the May hatches and these early summer crabs are differentially removed by fishing pressure at a critical point in their life history. Two alternate hypotheses were advanced whose action would stabilize the system: 1) sperm viability must be longer that previously thought and 2) crabs mate at least twice to replenish the original stock.

CHAPTER IV

THE EFFECTS OF WIND STRESS ON THE MODEL POPULATION

INTRODUCTION

The blue crab model was designed to produce the classic steady-state population in order to examine the effects of wind stress on the population and, ultimately, the harvest. In Eqn. (6), the initial number in a cohort, N_0 , is proportional to the number of spawners, S, and is influenced by some function of environmental factors that may regulate the abundance of the population, f($\underline{x}$). Since wind stress has been proposed as an important factor influencing retention of larvae in proximity of the bay mouth for reinvasion, f($\underline{x}$) will be defined in terms of the wind index that produced the most significant relationship with catch (Fig. 7).

In order to examine the behavior of the crab model in response to a driving force, a simulated wind index was used initially. A sine curve with a four year period was applied to the system as follows. The curve oscillated around a mean of one with an amplitude of 0.5, which produced fluctutations similar to those seen in the annual catch statistics.

$$W_* = 1.0 + 0.5\sin(2\pi t_y/T) \qquad (31)$$

where: W_* = yearly wind index

t_y = time in years

T = period = 4 years

The initial abundance of the cohort becomes

$$N_o = \alpha S W_* \qquad (32)$$

$$N_o = \alpha S(1.0 + 0.5\sin(2\pi t_y/T)) \qquad (33)$$

Equation (6) is now defined as

$$N_o = \alpha S + (0.5\sin(2\pi t_y/T))\alpha S \qquad (34)$$

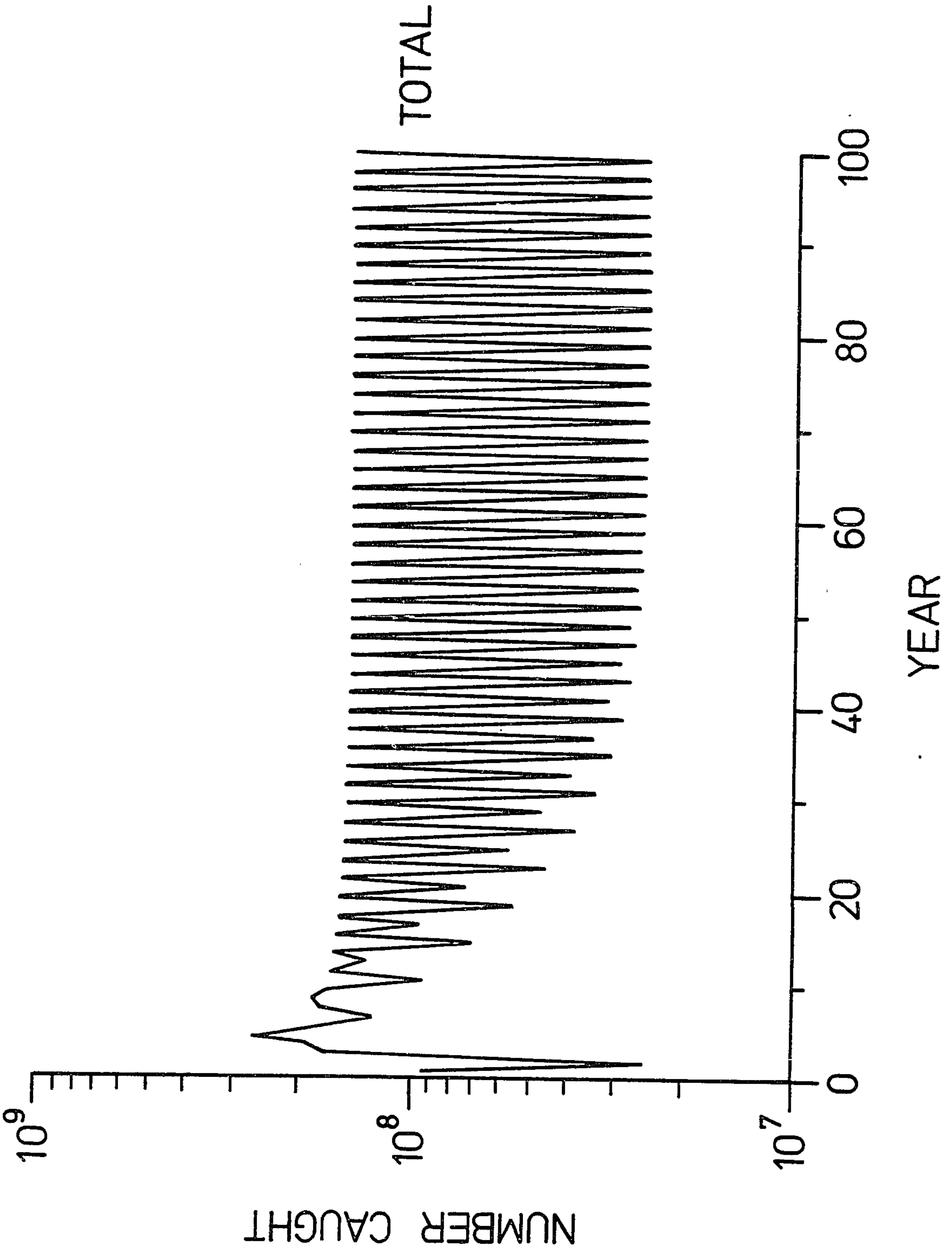
and

$$f(\underline{x}) = (0.5\sin(2\pi t_y/T))\alpha S \qquad (35)$$

RESULTS

Figure 21 shows the total harvest when the above sinusoidal environmental factor is used to drive the system. The oscillation in abundance corresponds to a 40 million pound variation in catch, a reasonable value in view of the historical catch data. The wind index is applied to both cohorts in the maximum fishable life span system. The oscillation in catch remains stable over a millenium of model output. The four year periodicity is obscured by the end of year 50. When the terminal molt hypothesis is applied, the shape of the output is

Figure 21. Total harvest influenced by a predetermined sinusoidal wind index. The sine function has a four year period and is applied to both cohorts. (Case I)


TOTAL
NUMBER CAUGHT
10^9
10^8
10^7
YEAR
0
20
40
60
80
100

quite similar initially; however, the AUGUST cohort oscillates wildly, is eventually destroyed, and the MAY cohort reaches a new level of stable oscillation.

When this index is applied to the AUGUST cohort alone, the total harvest retains the four year periodicity. Harvest by cohort under the maximum fishable life span hypothesis serves to re-emphasize the lack of AUGUST input into the MAY cohort (Fig. 22). The MAY harvest remains at equilibrium while the AUGUST cohort oscillates about some lower mean. The AUGUST cohort seems to crash every four years; however, the effect of the MAY cohort's input is enough to prevent total loss of the cohort. The application of wind to the AUGUST cohort alone seems to demonstrate the stabilizing influence of the dual cohort population structure.

Sine functions of different periods can also be used to simulate the wind effect. When a four year periodicity is applied to MAY and a twelve year periodicity is applied to AUGUST, high frequency oscillations dominate the system, and the trend in output is toward decrease (Fig. 23).

Since the model seemed to respond in a consistent manner to the simulated wind index, the actual wind data were then computed in the form of the driving function. The number of days northward in June becomes $f(\underline{x})$ for the MAY cohort, the number of days northward in September becomes the factor for the AUGUST cohort. The monthly values for the 31 year time series are averaged, and the standard deviation is calculated. The environmental factor oscillates about a mean of one and is scaled so that 68% of the values fall between 0.75 and 1.25. The values for June and September are computed as Z scores to give equal weight to both indices.

Figure 22. Total, MAY and AUGUST harvests influenced by a predetermined sinusoidal wind index. The sine function has a four year period and is applied to the AUGUST cohort only. (Case I)

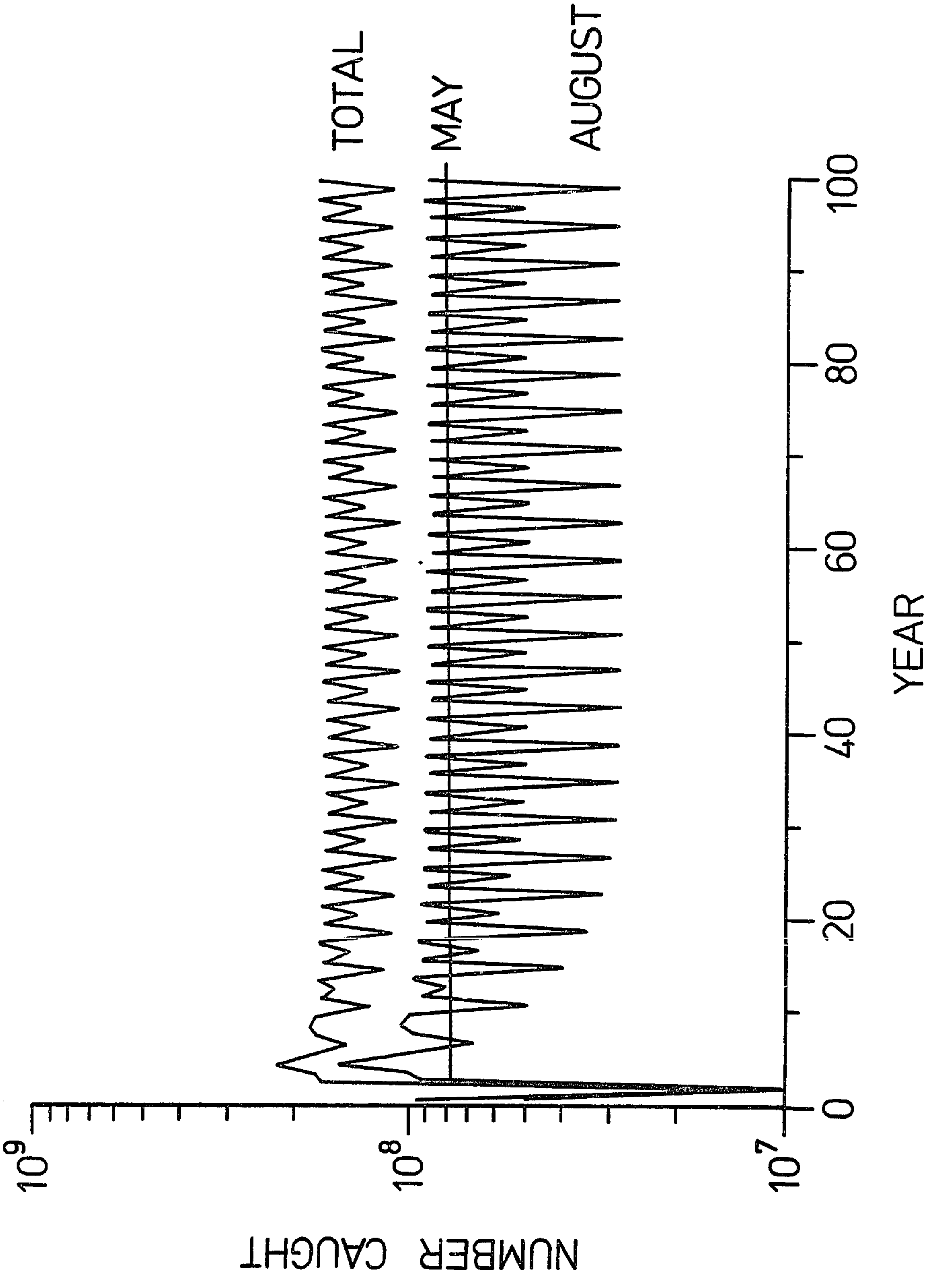
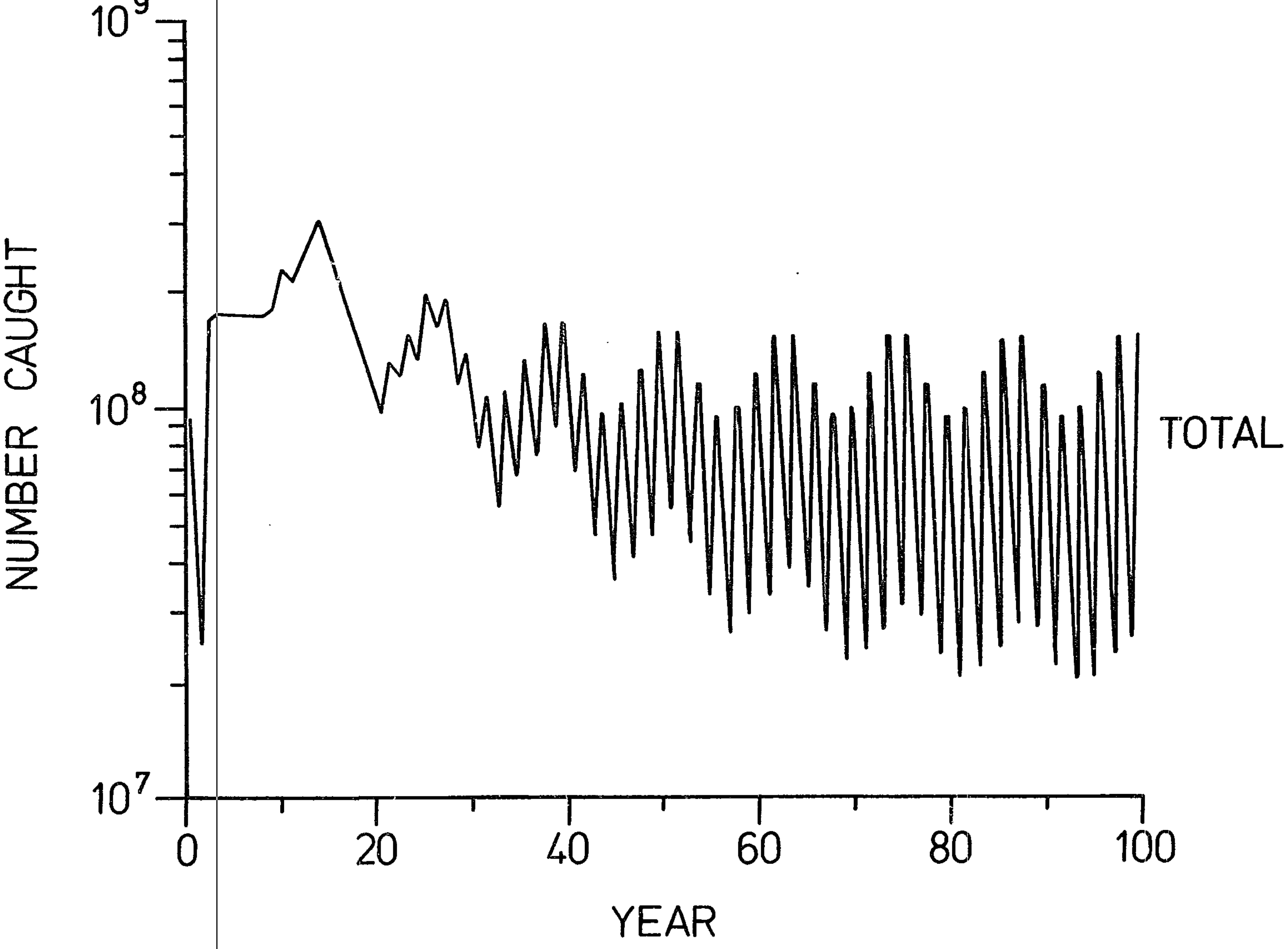

NUMBER CAUGHT
10^9
10^8
10^7
0
20
40
60
80
100
YEAR
TOTAL
MAY
AUGUST

Figure 23. Total harvest influenced by a predetermined sinusoidal wind index. A sine function with a four year period is applied to the MAY cohort, a twelve year period to the AUGUST cohort. (Case I)


NUMBER CAUGHT
10^9
10^8
10^7
TOTAL
0
20
40
60
80
100
YEAR

$$W_{*_M} = 1.0 + (W_J - \overline{W})/4\sigma_W \tag{36}$$

$$W_{*_A} = 1.0 + (W_S - \overline{W})/4\sigma_W \tag{37}$$

where: W_{*_M} = wind factor for MAY cohort

W_J = number of days north in June of a given year

W_{*_A} = wind factor for AUGUST cohort

W_S = number of days north in September of a given year

$\overline{W}$ = average monthly number of days north for time series

σ_W = standard deviation of days north for time series

For the May cohort the initial abundance is

$$N_m(0) = \alpha S_{m_{j-1}} + \alpha S_{m_{j-1}}((W_J - \overline{W})/4\sigma_W \tag{38}$$

for the AUGUST cohort:

$$N_a(0) = \alpha S_{a_{j-1}} + \alpha S_{a_{j-1}}((W_S - \overline{W})/4\sigma_W \tag{39}$$

When the preceding environmental factors are applied to their respective cohorts under the maximum fishable life span scenario, the catch decreases drastically for some years before the system recovers

(Fig. 24). Eventually the catch settles into a two year oscillation about some mean. Quite similar results are obtained when the terminal molt hypothesis is used (Fig. 25). The total catch has decreased, and the MAY cohort dominates the harvest. Note the severe crash in the AUGUST cohort. The total catch curve is primarily an image of the MAY catch, the AUGUST cohort seems to have little effect.

In order to use a continuous time series for wind input, reconstituted Fourier series were derived for both wind factors. [Appendix C contains a discussion of this application of Fourier analysis.] The harvest decreased exponentially over a millenium. Figure 26 shows this decrease over a period of 500 years.

DISCUSSION

Many more varieties of the wind index were applied to the system than were reported here, but the above examples represent the typical outcome. When the actual wind data are used as the environmental factor driving the system, the model loses stability and tends toward extinction. The original expectation was that the entered oscillation would be output as a form similar to the harvest. The simulated harvest could then be compared to the historical record to make inferences about the mechanisms of population dynamics.

The first ten years of the wind index are below the mean so that some proportion of the initial number in the cohort that produces equilibrium is applied for those years. The effect is to increase the downward trend. The next 20 years of the index are above the mean and

Figure 24. Total, MAY, and AUGUST harvests influenced by actual wind indices applied to the respective cohorts. (Case I)

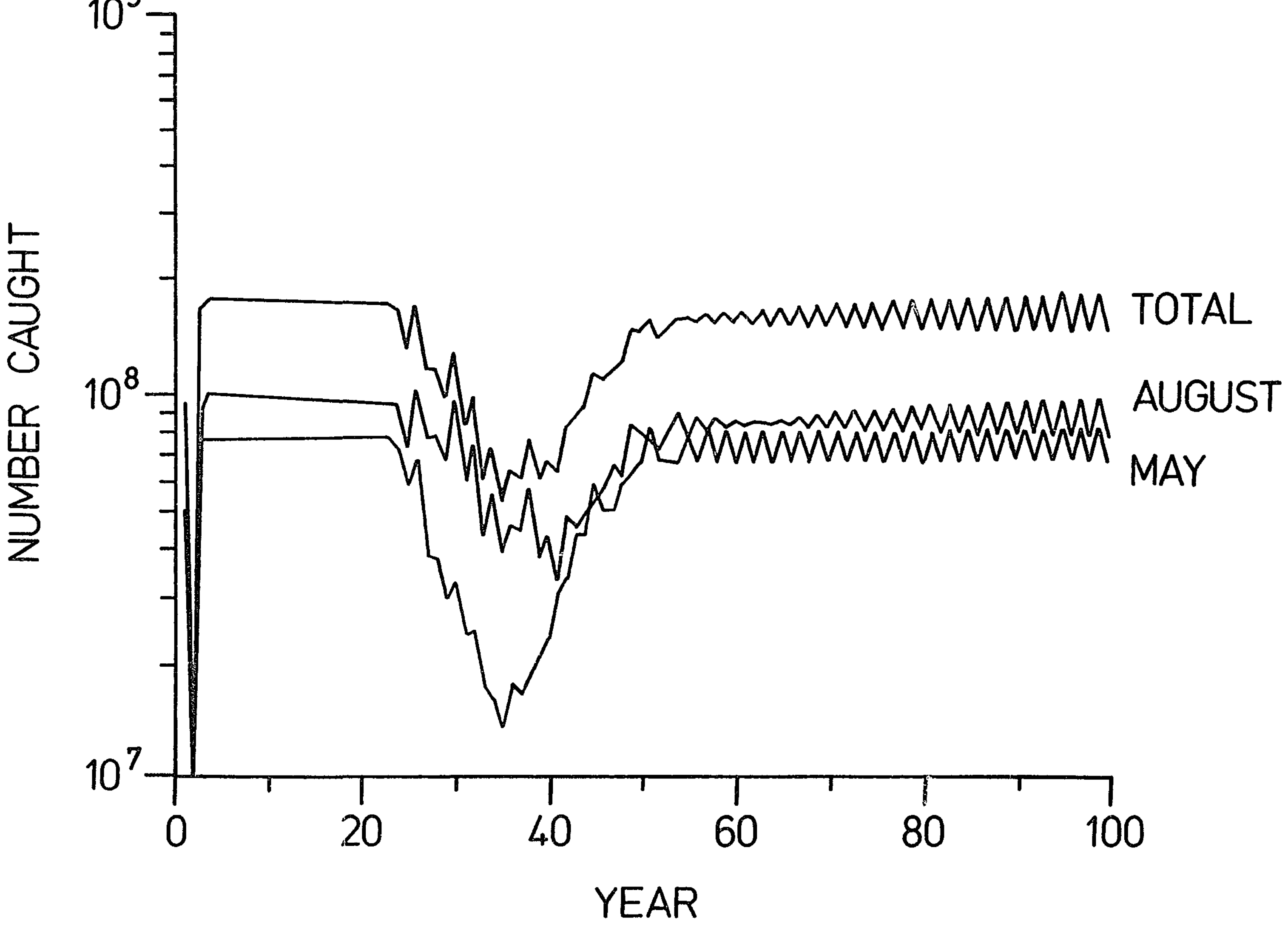

10^9
10^8
10^7
NUMBER CAUGHT
0
20
40
60
80
100
YEAR
TOTAL
AUGUST
MAY

Figure 25. Total, MAY, and AUGUST harvests influenced by actual wind indices applied to the respective cohorts. (Case II)

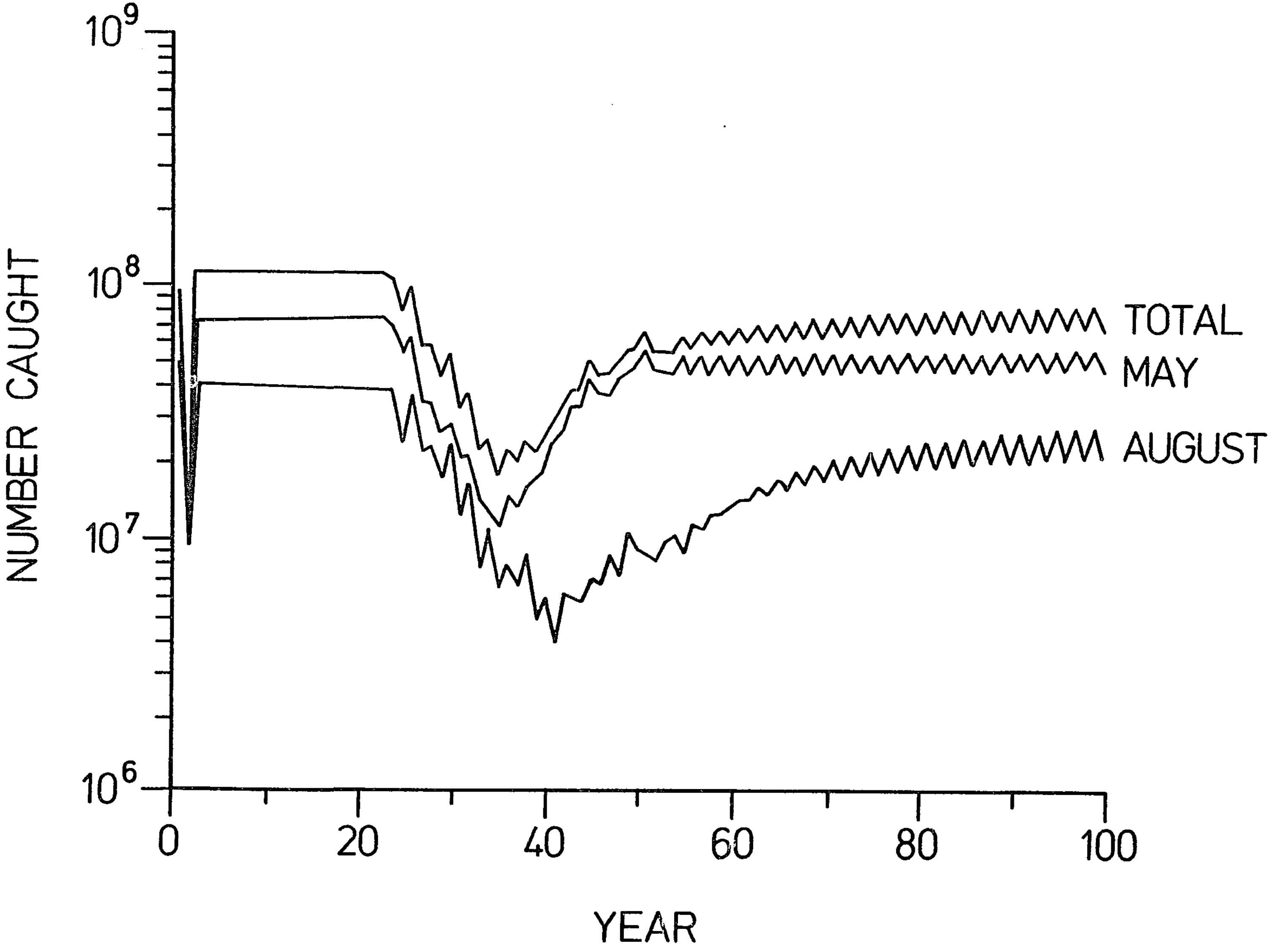
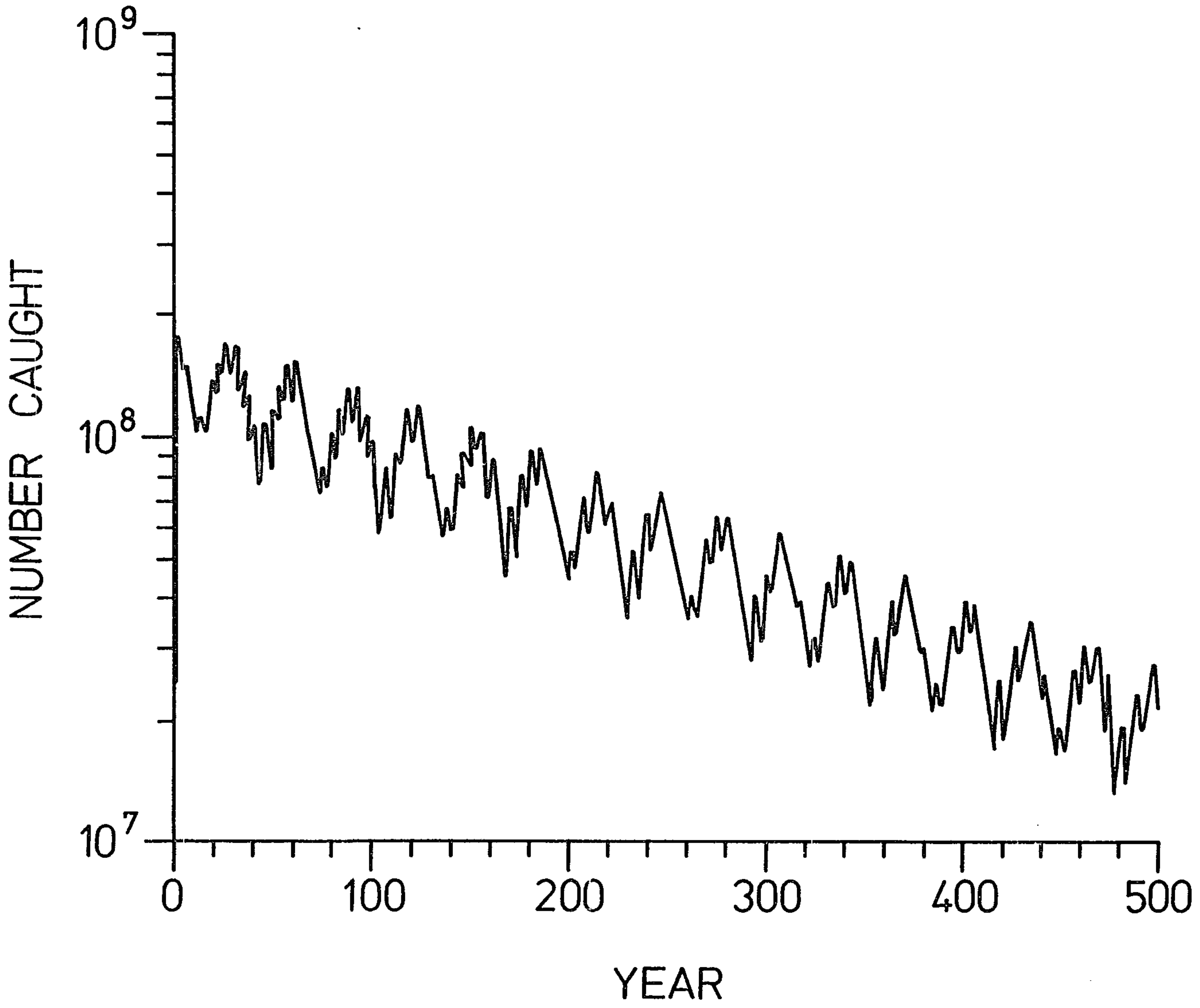

10^9
10^8
10^7
10^6
NUMBER CAUGHT
0
20
40
60
80
100
YEAR
TOTAL
MAY
AUGUST

Figure 26. Total harvest influenced by continuous series of wind data for 500 years of output. (Case I)


NUMBER CAUGHT
10^9
10^8
10^7
0
100
200
300
400
500
YEAR

slowly force the system back toward equilibrium. When a single time series of wind stress is applied, the system gradually returns to some sort of oscillatory equilibrium at a level lower than steady-state in the unperturbed model. When a continuous series of the wind index is applied, the model responds as above for each 31 year increment. The system finds a new, lower equilibrium with each increment, thus producing the downward trend.

High frequency oscillations obscure the curve. Initially the higher frequencies were expected to approximate the wind index and, consequently, the historical catch curve. Unfortunately, these oscillations are erratic, and the curve appears to be dominated by the low frequencies. The test index composed of two different period sine waves also showed a downward trend. The lower frequencies and the ten year period of below average winds may act in conjunction to produce the decrease.

The wind effect on the initial number in a cohort, N_0, is quite complex. The primary effect of the wind is to restrict or augment the number of larvae that survive. A secondary effect also operates on this cohort: the number of spawners that gave rise to this cohort is limited by previous winds. A tertiary effect may also be affecting N_0, the effect of wind on the the grandparents whose offspring are the spawners responsible for the current generation. This last effect is probably minimal but may be important in response to catastrophic events from which the system must recover. The wind's effect on the catch is also multifold. Five cohorts contribute to the catch each year; therefore, five different wind factors are being applied to produce yield in any given year. The catch from each cohort is also subject to the three effects of the wind factor. The annual catch is influenced by many overlapping wind-produced oscillations.

A small oscillation in one parameter of a model equation usually causes a similar small population fluctuation of the same frequency. The input of the sine functions suggests that the model adapts to consistent input, that "stable" behavior is achieved with "stable" input. If the imposed oscillation is of large amplitude or if the undriven system is limit cycling, then nonlinear effects may cause qualitative changes in the behavior of the population (Nisbet and Gurney, 1982). The overlapping wind factors in the model may result in the production of subharmonic resonance and/or synchronization. Subharmonic resonance occurs if a deterministically stable population oscillates at a frequency equal to a subharmonic of the driving frequency, when driven by a large oscillation in an environmental parameter (see Fig. 24). When a non-replicated series (length = 31 years) of the wind factor is applied, the system recovers but is subject to oscillations with a two year period. Synchronization occurs when a population exhibits oscillations at the frequency of the driving perturbation. The importance of this effect is that periodic change of climate tends to impose its period upon oscillations of internal origin, or to cause such oscillations to have a harmonic relation to periodic climatic change (Nisbet and Gurney, 1982).

Under the assumption that the population has the ability to respond to environmental stress, the wind factor should change the shape of the cohort curves. However, in the current configuration of the model the curves are actually raised or lowered in response to the wind since the mortality rates remain constant. A change of ±0.002 in the MAY post-recruitment total mortality rate (M'_{m1}) can destroy equilibrium, while the AUGUST cohort is more tolerant; a ±0.05 deviation in M'_{a1} is required to produce havoc. Since the mortality rates for MAY are more sensitive, the MAY cohort seems to be the more likely candidate to be subject to density dependent effects which may act as a stabilizing force. In reality the sensitive mortality rates may change very slightly in response to environmental factors and impart a stabilizing influence to the system. The decline of the model population under wind stress (Fig. 26) may result from density dependent effects which are not incorporated in the system.

The major result of the wind model relative to the population dynamics developed in Chapter III is a definitive assessment of important questions governing the reproductive biology of the bay's blue crab population.

1. The mortality rates are best estimates based on weak support from the literature and may not be realistic.
2. The time scale of events is uncertain.
3. The application of two distinct cohorts is artificial.
4. Population fluctuations depend on a multitude of factors. Hatching success, larval mortality and juvenile growth are affected by environmental conditions. Mortality and sublethal effects may be experienced by juveniles in nursery grounds. Recruitment rates, harvesting rates and adult mortality also influence population levels. Unusual environmental stresses can also affect population abundance.
5. The use of wind stress alone in the model to affect larval mortality in order to produce fluctuations in the population is an oversimplification of the natural system. However, the effects of wind

stress, as an important mechanism influencing larval retention, and ultimately the abundance of the population, cannot be ignored.

Various suggestions can be made to improve the model. The most important of these is to incorporate the proper biological data and upgrade the model as new information is collected.

1. The model directs research by pointing out deficiencies in biological knowledge. The wind factor was applied to the two cohorts described by Van Engel (1958). Evidence supplied by McConaugha (personal communication) suggests that peaks of megalopae occur in mid-July to mid-August. The times of spawning should be changed somewhat so that the August peak would be influenced by the more northerly August winds in an attempt to alleviate some of the problems associated with the downward trend during the first ten years of wind data.
2. A more realistic approach would be to incorporate the spawning season as a continuous distribution, perhaps normal or bimodal. Currently hatching occurs as one of two point sources. During this season perhaps a daily time scale would be more appropriate for describing the survival of the larvae to metamorphosis.
3. Rather than entering the wind index as a factor affecting N_0, the wind might be applied as a mortality rate that affects larval survival during that critical period in the neuston.
4. Density dependent influences of the size of the population should also be examined.
5. The stability of the model should be examined with attention paid to the influences of subharmonic resonance and synchronization.

CHAPTER V

GENERAL DISCUSSION

The blue crab is exploited from New England to the Gulf of Mexico. Many areas have made attempts to determine population abundances from catch, effort and other data. Fischler (1965) has examined catch-effort, catch-sampling, and tagging data in order to estimate the size of the blue crab population in the Neuse River, North Carolina. More (1969) stated that fluctuations in Texas populations appeared to be independent of the actions of the fishery. McKenzie (1970) investigated fluctuations in abundance and factors affecting mortalities in South Carolina's crab industry. Pullen and Trent (1970) developed a size-weight relationship for crabs from Galveston Bay.

Adkins (1972) produced an in depth study of the crab fishery in Louisiana and included larval and juvenile catch per unit effort data. Perry (1975) analyzed the blue crab fishery in Mississippi. She presented data on the distribution and abundance of crabs in Mississippi Sound and noted that rise in catch per unit effort followed the migration of females into the Sound. Although commercial landings in Chesapeake Bay have represented more than 40% of the total United States landings, a laissez faire attitude toward the fishery and data collection has produced little useful information. Recent work on the bay's crab fishery has included economic analysis, spectral analysis of catch and environmental data, development of a new survey technique, discussions on the need for reliable statistics, and a model of the winter dredge fishery.

A Fourier transform of annual catches from 1922 to 1976 in Chesapeake Bay produced periodicities of 18.0, 10.7, and 8.6 years (Hurt et al., 1976). Transforms of various environmental parameters showed similar periods. Agreement of periods of minimum rainfall and average annual temperature in Philadelphia, crab catch in the bay, and tidal forces were explained as follows: nutrients are washed into the surface waters of the bay, minimum rainfall allows the surface waters to become more saline, and higher temperatures promote crab growth. Temperature variation and rainfall also agreed with sunspot periodicity which supports the premise that minute variations in the sun's radiation influences climate conditions on the earth's surface. Blue crab production was predicted to reach a new peak between 1980 and 1990.

Shabman and Vance (1982) examined the potential returns to public sector management of the number of vessels in the Virginia crab pot fishery. They developed a production function for the fishery, relating levels of effort and abundance to productivity of the fishing crafts. In the 1960's Virginia seemingly had no need for management in the pot fishery in spite of open-access to the resource. However, by the early 1970's the fishery seemed to move into a period of excess effort and reduced net income, typical of open-access fisheries. The authors suggested that this change resulted from steadily rising ex-vessel prices which produced a loss of sensitivity to harvest fluctuations and increased investment in larger vessels. The collapse of the oyster fishery in the early sixties may have contributed to the increased fishing pressure when oystermen switched to full-time crabbing.

Management of the fishery must be based on certain necessary information including predictions of harvest costs, prices, and a stock variable (Shabman and Vance, 1982). Their stock variable was the total annual hard crab landings for Virginia. Effort data were the number of vessels annually licensed for the hard crab fishery. The classic life history information was also discussed. Shabman and Vance proposed that management strategies could be developed on price and cost predictions rather than on stock predictions.

Studies by members of Maryland's Department of Natural Resources have shown that the usual procedure of mail questionnaires for fishery census is probably invalid (Summers et al., 1983). Watermen tended to underreport their catches or did not report at all. Landings appraised aboard ship by a third party accounted for 55% of the total landings for a given area. In some instances the observed landings were an order of magnitude above the reported census. Random sample surveys were implemented to estimate the 1981 blue crab harvest, thereby reducing mailing costs and data processing efforts.

The results of the new technique were rather interesting. The 1979 census assumed that potters accounted for most of the annual catch. Potters did account for 30% of the annual harvest with 7% of the licenses, but commercial trotliners produced 60% of the annual catch. Recreational crabbers did contribute significantly to the total catch but had been ignored prior to 1980. Harvest estimates projected by the sample surveys were more precise than previous harvest evaluations. The 1981 survey showed a total annual harvest of more than 50 million pounds, more than twice the annual average for the last two decades

(Summers et al., 1983).

A companion paper discussed application of the random sample survey design to Maryland's blue crab fishery (Summers et al., 1983). Sample sizes used in 1981 were reassessed; for example, the total sample size was reduced by 17% for the commercial trotline survey and by 26% for the potters survey. In both 1981 and 1982, the National Marine Fisheries Service estimates were 55% of the survey estimates. Over the next several years, comparison of historical records with the new survey estimates will produce a correction factor that would permit use of the early data in conjunction with the estimates generated by the new survey.

The most recent research has suggested that the relationships between spawning stock size and environmental and meterological features at the bay mouth can be used to predict catch for the winter dredge fishery (Applegate, 1983). Survival indices for spawning years 1950 to 1979 were derived from Ricker's stock recruitment model. Multiple regression analysis revealed significant relationships between environmental features and the survival index. Predictions for recruitment under known environmental conditions are not directly translatable into catch rates but suggest changes in stock sizes at the beginning of the winter dredge season. Total landings are determined by stock size, availability, effort, economics, et cetera.

The life history data used in Applegate's model was derived from Van Engel (1958). This author's work has hopefully pointed out some of the discrepancies in our current knowledge of the life history of the blue crab as related to population dynamics. Several of Applegate's conclusion about the effects of environment on larval retention are based on the precept that late stage larvae and megalopae are found near the bottom where they are entrapped in onshore drift. He suggests that reduced winds promote larval retention in estuarine salt-wedge circulation.

Recent field studies have found 85% of all larval stages in the upper meter of the water column (Sulkin et al., 1982; Provenzano et al., 1983; McConaugha et al., 1983). The mechanism for larval retention proposed by Johnson et al. (1983) in Chapter II has been adapted as the model of larval recruitment for the blue crab in Mid-Atlantic Bight estuaries proposed by a tri-state Sea Grant program researching the population dynamics of the crab in Chesapeake and Delaware Bays (Sulkin et al., 1982). Ongoing research at Old Dominion University suggests that blue crab larvae are retained outside the bay mouth by wind-driven circulation patterns.

All of these efforts have pointed out the overwhelming need for valid information about the blue crab population of the bay (Cronin, 1982). Before management of the fishery can proceed, the most basic information about the stock must be collected. Stock assessments of juveniles including abundance, distribution, size, age, sex, and food habits should be valuable in estimating recruitment. The distribution and abundance of reproducing adults by size, sex, instar and age composition should be determined. Mortality and growth rates need to be determined for the different life history stages.

Does a three month delay in hatching cause a nine month delay in recruitment to the fishery?

What is the maximum fishable life span of the blue crab?

Is the terminal molt of females fact or fiction?

How many times do females spawn in a season, what is the egg content of an average sponge, and what causes the egg content to vary?

What proportion of the eggs give rise to first stage zoeae?

How many larvae survive through metamorphosis in the field?

What are the effects of competition and predation on the abundance of the early instars?

Variations in year-class size and recruitment must be determined. Valid estimates of total commercial and recreational catch must be made. In view of Maryland's random sample survey, are Virginia's catch statistics of any value? Catch per unit effort is needed by at least gear type and area. Effort data should incorporate labor numbers, gear numbers, time spent fishing, and skill of captain and crew. Weight, size, sex, and age composition of the catch should be determined on a small enough time scale to produce useful information. This work has suggested that annual data are insufficient for valid analysis and that monthly data are more realistic. The question of the proper time scale for estimating the stock abundance of the blue crab fishery of Chesapeake Bay remains open.

CHAPTER VI

SUMMARY

A model was developed to describe the population dynamics of the blue crab in Chesapeake Bay. Part of this objective was met by understanding the physical processes which control the nearsurface outflow of the bay and its subsequent trajectory on the continental shelf. Thus, a physical mechanism could be used to explain the retention of larvae in sufficient proximity to the bay entrance for re-entry.

1. Northward wind stress during June, July and August is strong enough to maintain a corridor of poleward flowing water during the critical time of larval development in the nearshore waters.

2. The variability of this corridor was quantified as number of days or distance northward and compared to annual harvest statistics for the years 1952-1980. An index of days northward when distances travelled exceeded 0.5 km produced the most significant match when compared to the catch data. Since recruitment to the fishery ultimately depends on larval survival, there must be some relation between wind stress and abundance of crabs. The extent of this relation remains to be elucidated and is another subject for future investigation.

3. The available life history data was modelled in an attempt to understand the basic population dynamics of the blue crab. Cohorts were found to originate on time intervals no longer than a month. Longer

time intervals obscured the critical aspects of the life cycle. Numerical equilibrium was reached by application of different mortality rates to the cohorts. Relative abundance of cohorts in the catch depended on whether crabs died at the end of the spawning season or remained in the fishery. The post-recruitment mortality experienced by a cohort at equilibrium was a function of month of birth. The age structure of the population depended on whether the terminal molt or maximum fishable life span hypothesis was selected.

4. The incorporation of wind stress as a driving force in the life history model produced a decrease in harvest over a millenium, although simulated wind data in the form of sine functions produced consistent output. The form and application of the wind index need further investigation. Addition of more reliable life history information would also improve the model's response to environmental factors. The stability of the system prior to and after the introduction of wind stress needs to be examined.

5. In summary, the current levels of information about the population dynamics of this commercially important species are too poor to permit selection and application of mortality rates in the model. At this point the formulation of rational harvest control regulations in Chesapeake Bay is not feasible. A number of fundamental questions must be answered before objective regulations can be produced.

LITERATURE CITED

Adkins, G. 1972. A study of the blue crab fishery in Louisiana. Louisiana Wildlife and Fisheries Commission Technical Bulletin 3:1-57.

Andersen, A. V., W. J. Davis, M. P. Lynch, and J. R. Schubel. editors. 1973. Effects of Hurricane Agnes on the environment and organisms of Chesapeake Bay, early findings and recommendations. Virginia Institute of Marine Science, Gloucester Point, Virginia. Special Report in Marine Science and Ocean Engineering 29:1-172.

Applegate, A. J. 1983. An environmental model predicting the relative recruitment success of the blue crab Callinectes sapidus (Rathbun) in Chesapeake Bay, Virginia. Master's Thesis, School of Marine Science, The College of William and Mary, Williamsburg, Virginia. 73pp.

Beardsley, R. C. and W. C. Boicourt. 1980. On estuarine and continental shelf circulation in the Middle Atlantic Bight. In: B. A. Warren and Wunsch, editors. Massachusettes Institute of Technology Press, Cambridge, Massachusettes. 623pp.

Beardsley, R. C., W. C. Boicourt, and D. V. Hansen. 1976. Physical oceanography of the Middle Atlantic Bight. American Society of Limnology and Oceanography, Special Symposium 2:20-34.

Boicourt, W. C. 1973. The circulation of water on the continental shelf from Chesapeake Bay to Cape Hatteras. Doctoral Thesis, The Johns Hopkins University, Baltimore, Maryland. 183pp.

Boicourt, W. C. 1981. Circulation in the Chesapeake Bay entrance region: Estuary-shelf interaction. In: J. W. Campbell and J. P. Thomas, editors. Chesapeake Bay Plume Study: Superflux, 1980. NASA Conference Publication 2188, NOAA/NEMP III 81 ABCDFG 0042. pages 61-78.

Bumpus, D. F. 1973. A description of the circulation on the continental shelf of the east coast of the United States. Progress in Oceanography 6:111-157.

Churchill, E. P. 1919. Life history of the blue crab. Bulletin of United States Bureau of Fisheries 36(870):95-128.

Cronin, L. E. editor. 1982. Report of workshop on Chesapeake Bay fisheries statistics. Held in Fredericksburg, Virginia, July

12-13, 1982. Chesapeake Biological Laboratory, Chesapeake Research Consortium, Maryland Department of Natural Resources, Virginia Marine Resources Commission. 111pp.

Cronin, L. E., W. A. Van Engel, D. G. Cargo, and F. J. Wojcik. 1957. A partial bibliography on the genus Callinectes. Virginia Fisheries Laboratory, Gloucester Point, Virginia. Special Scientific Report 8:1-21.

Fischler, K. J. 1965. The use of catch-effort, catch-sampling and tagging data to estimate a population of blue crabs. Transactions of the American Fisheries Society 94(4):287-310.

Garratt, J. R. 1977. Review of drag coefficients over oceans and continents. Monthly Weather Review 105:915-929.

Goy, J. W. 1976. Seasonal distribution and retention of some decapod crustacean larvae within the Chesapeake Bay, Virginia. Master's Thesis, Old Dominion University, Norfolk, Virginia. 334pp.

Hartnoll, R. G. 1969. Mating in the Brachyura. Crustaceana 16(2):161-181.

Hay, W. P. 1905. The life history of the blue crab (Callinectes sapidus). Report of United States Bureau of Fisheries, 1904. pages 395-413.

Hurt, P. R., L. M. Libby, L. J. Pandolfi, L. H. Levine, and W A. Van Engel. 1979. Periodicities in the blue crab population of Chesapeake Bay. Climatic Change 2:75-78.

Johnson, D. F. 1982. A comparison of recruitment strategies among brachyuran crustacean megalopae of the York River, lower Chesapeake Bay and adjacent shelf waters. Doctoral dissertation. Old Dominion University, Norfolk, Virginia.

Johnson, D. R. , B. S. Hester, and J. R. McConaugha. 1983. An environmental mechanism influencing the recruitment of blue crabs to Chesapeake Bay. In preparation.

Marine Resources Commission. 1982. Eighty-third and eighty-fourth annual reports of the Marine Resources Commission for the fiscal years ending June 30, 1981 and June 30, 1982. Marine Resources Commission, Commonwealth of Virginia, Newport News, Virginia. 65pp.

McConaugha, J. R., D. F. Johnson, A. J. Provenzano, and R. C. Maris. 1983. The seasonal distribution of larvae of Callinectes sapidus in the waters adjacent to the Chesapeake Bay. Journal of Crustacean Biology 3(4):000-000. In press.

McConaugha, J. R., A. J. Provenzano, D. F. Johnson, J. Clark, and P. Sadler. 1981. Offshore displacement and reinvasion of Callinectes sapidus larvae in Chesapeake Bay. Estuaries 4:277.

McKenzie, M. D. 1970. Fluctuations in abundance of the blue crab and factors affecting mortalities. South Carolina Wildlife Resources Department, Charleston, S.C. Technical Report 1:1-45.

More, W. R. 1969. A contribution to the biology of the blue crab (Callinectes sapidus Rathbun) in Texas, with a description of the fishery. Texas Parks and Wildlife Department. Technical Series 1:1-31.

National Marine Fisheries Service. 1952-1980. Current fisheries statistics, annual summaries, for Chesapeake, Maryland, and Virginia landings. National Marine Fisheries Service, National Oceanic and Atmospheric Administration, United States Department of Commerce, Washington, D.C.

Nisbet, R. M. and W. S. C. Gurney. 1982. Modelling fluctuating populations. John Wiley and Sons, Chichester, England. 379pp.

Perry, H. M. 1975. The blue crab fishery in Mississippi. Gulf Research Reports 5(1):39-57.

Pritchard, D. W. 1955. Estuarine circulation patterns. Proceedings of the American Society of Civil Engineers 81:Separate No. 717. 11pp.

Provenzano, A. J., J. R. McConaugha, K. B. Philips, D. F. Johnson, and J. E. Clark. 1983. Vertical distribution of first stage larvae of the blue crab, Callinectes sapidus, at the mouth of the Chesapeake Bay. Estuarine Coastal and Shelf Sciences 16:000-000. In press.

Pullen, E.J. and W. L. Trent. 1970. Carapace width-total weight relation of blue crabs from Galveston Bay, Texas. Transactions of the American Fisheries Society 4:795-798.

Rhodes, R. J. and W. A. Van Engel. 1978. Report of the national blue crab industry workshop. Special Report in Applied Marine Science and Ocean Engineering no. 185. Virginia Institute of Marine Science, Gloucester Point, Virginia.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191:1-182.

Sandifer, P. A. 1975. The role of pelagic larvae in recruitment of adult decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay. Estuarine and Coastal Marine Science 3:269-279.

Shabman, L. and T. Vance. 1982. Influence of effort and stock variability on Virginia's crab pot fishery. Department of Agricultural Economics, Virginia Polytechnical Institute, Blacksburg, Virginia. 113pp.

Stuck, K. C. and H. M. Perry. 1981. Observations on the distribution and seasonality of portunid megalopae in Mississippi coastal waters. Gulf Research Reports 7(1):93-95.

Sulkin, S. D., C. F. Epifanio, and A. J. Provenzano. 1982. The blue crab in Mid-Atlantic Bight estuaries: A proposed recruitment model. Maryland Sea Grant Program Technical Report, Publication Number UM-SG-TS-82-04, University of Maryland Sea Grant Program, College Park, Maryland.

Summers, J. K., H. W. Hoffman and W. A. Richkus. 1983. Randomized sample surveys to estimate annual blue crab harvests by a multi-gear fishery in the Maryland waters of Chesapeake Bay. North American Journal of Fisheries Management 3:9-20.

Summers, J. K., W. A. Rickhus, H. W. Hoffman, C. Bonzek, H. H. King, and M. Burch. 1983. Application of random sample survey designs to estimate the commercial blue crab harvest in Maryland. North American Journal of Fisheries Management 3:21-25.

Tagatz, M. E. and A. B. Hall. 1971. Annotated bibliography on the fishing industry and biology of the blue crab, Callinectes sapidus. National Oceanic and Atmospheric Administration Technical Report. National Marine Fisheries Service, Special Scientific Report--Fisheries NMFS-SSRF 640:1-94.

Tyler, A. V. and V. F. Gallucci 1980. Dynamics of fished stocks. In: R. T. Lackey and L .A. Nielsen, editors. Fisheries management. John Wiley and Sons, New York. pages 111-147.

Van Engel, W. A. 1958. The blue crab and its fishery in Chesapeake Bay. Part I: Reproduction, early development, growth, and migration. Commercial Fisheries Review 20:6-17.

Van Engel, W. A. 1962. The blue crab and its fishery in Chesapeake Bay. Part II: Types of gear for hard crab fishing. Commercial Fisheries Review 24:1-10.

Van Engel, W. A. and J. Wojcik. 1965. Catch and value of the Chesapeake Bay blue crab, 1880-1960. Virginia Institute of Marine Science, Gloucester Point, Virginia. Data Report 2:1-39.

Van Engel, W. A. and J. Wojcik. 1965. Catch and value of the Chesapeake Bay blue crab, 1880-1966. Virginia Institute of Marine Science, Gloucester Point, Virginia. Supplement and Amendments to Data Report 2. 38pp.

Wang, D. P. 1979. Subtidal sea level variations in the Chesapeake Bay and relations to atmospheric forcing. Journal of Physical Oceanography 9:564-572.

Wang, D. P. and A. J. Elliott. 1978. The effects of meterological forcing on the Chesapeake Bay: The coupling between an estuarine system and its adjacent coastal waters. In: J. C. J. Nihoul. editor. Hydrodynamics of Estuaries and Fjords. Elsevier, Amsterdam. pages 127-145.

Wu, J. 1975. Wind-induced drift currents. Journal of Fluid Mechanics 68(1):49-70.

APPENDIX A

MONTHLY CATCH DATA, 1960-1980

Obtained from Robert E. Harriss
Virginia Institute of Marine Science
Gloucester Point, Virginia

TABLE A1. Virginia Hard Crab Catch, 1960-1980. Monthly Landings in Millions of Pounds.

YEAR	JAN	FEB	MAR	APR	MAY	JUN
1960	0.840	0.875	0.664	1.082	2.245	2.508
1961	2.627	2.896	2.478	2.951	2.898	5.127
1962	3.007	2.757	2.360	4.628	5.169	6.368
1963	6.150	2.405	0.864	1.360	2.260	2.340
1964	4.233	4.258	1.237	2.020	5.257	4.382
1965	2.444	1.555	0.960	2.884	5.218	6.338
1966	3.738	3.464	2.044	4.785	5.571	6.388
1967	4.209	2.167	2.493	4.044	5.513	7.146
1968	3.116	2.130	1.312	1.536	3.105	4.523
1969	2.164	1.107	0.683	0.909	1.076	2.369
1970	1.737	2.307	2.136	1.545	4.076	4.235
1971	1.444	2.376	1.369	2.400	5.281	4.859
1972	2.694	2.239	2.166	3.662	4.202	5.107
1973	2.579	2.033	1.157	2.190	2.230	3.629
1974	2.533	1.178	1.020	3.502	4.485	4.978
1975	1.414	0.724	0.514	2.175	3.856	5.771
1976	1.970	0.953	1.508	1.372	1.095	3.170
1977	0.649	0.815	0.187	0.459	1.615	3.543
1978	1.994	1.364	0.755	0.816	2.264	3.928
1979	1.014	0.969	1.058	1.630	3.653	5.693
1980	1.963	2.038	1.319	3.018	2.650	3.976

YEAR	JUL	AUG	SEP	OCT	NOV	DEC
1960	4.338	5.128	6.277	3.716	2.067	4.448
1961	6.118	5.236	4.437	4.498	1.823	4.464
1962	5.531	6.522	4.524	5.330	0.978	4.626
1963	4.531	6.859	6.140	6.760	1.461	4.969
1964	6.742	5.543	5.043	5.383	2.727	4.746
1965	6.735	4.323	5.693	5.826	3.197	5.387
1966	6.963	7.724	7.480	6.233	3.316	6.028
1967	7.921	7.212	5.219	4.083	1.146	3.650
1968	5.890	6.394	6.274	5.171	1.930	3.358
1969	2.258	3.901	4.893	6.808	3.689	3.878
1970	4.542	5.981	4.311	5.018	2.759	3.769
1971	5.530	5.705	4.965	4.560	3.262	6.056
1972	4.800	6.825	4.740	4.419	3.363	4.338
1973	4.573	5.259	4.636	3.935	1.225	3.301
1974	5.044	4.815	4.265	3.805	1.643	3.580
1975	5.285	4.008	4.164	3.160	1.861	1.885
1976	3.975	2.941	2.739	2.673	0.341	3.023
1977	6.060	6.861	5.453	4.595	2.855	4.085
1978	5.217	5.890	4.900	3.887	2.530	2.510
1979	6.011	5.718	3.496	4.019	2.413	4.161
1980	4.709	5.335	4.230	3.273	1.000	4.186

TABLE A2. Maryland Hard Crab Catch, 1960-1980. Monthly Landings in Millions of Pounds.

YEAR	JAN	FEB	MAR	APR	MAY	JUN
1960	0.010	0.077	0.037	0.482	0.736	2.048
1961	0.000	0.000	0.000	0.294	0.540	2.582
1962	0.000	0.005	0.000	0.371	1.588	5.500
1963	0.000	0.000	0.000	0.009	0.501	1.198
1964	0.020	0.004	0.000	0.186	1.253	3.304
1965	0.000	0.005	0.000	0.219	1.687	5.057
1966	0.000	0.000	0.000	0.060	1.539	4.238
1967	0.000	0.000	0.000	0.383	2.365	4.125
1968	0.000	0.000	0.000	0.013	0.241	1.728
1969	0.109	0.087	0.114	0.196	0.729	0.630
1970	0.000	0.000	0.000	0.259	3.320	3.439
1971	0.000	0.000	0.000	0.445	1.425	4.077
1972	0.000	0.000	0.000	0.546	1.630	2.726
1973	0.000	0.000	0.000	0.539	0.770	2.815
1974	0.000	0.000	0.025	1.935	1.145	3.379
1975	0.000	0.000	0.000	0.865	1.280	3.244
1976	0.000	0.000	0.000	0.398	0.286	2.994
1977	0.000	0.000	0.000	0.017	0.242	2.430
1978	0.000	0.000	0.000	0.064	0.312	1.042
1979	0.000	0.000	0.000	0.678	0.849	2.978
1980	0.000	0.000	0.000	0.867	0.868	3.730

YEAR	JUL	AUG	SEP	OCT	NOV	DEC
1960	5.465	5.036	5.747	5.640	1.720	0.004
1961	6.669	4.438	6.908	2.944	2.283	0.000
1962	5.618	4.825	3.992	5.285	0.447	0.000
1963	3.379	4.336	4.359	2.653	0.469	0.030
1964	2.866	4.532	6.763	2.286	0.388	0.000
1965	6.147	8.118	5.890	3.641	1.213	0.018
1966	8.206	5.457	4.049	4.521	2.199	0.101
1967	6.419	6.149	2.306	2.464	0.365	0.012
1968	2.778	2.428	1.397	0.527	0.200	0.033
1969	4.092	6.187	4.345	4.055	1.902	0.523
1970	5.623	4.572	4.083	2.710	0.805	0.124
1971	5.677	5.615	4.514	2.824	1.269	0.201
1972	5.070	7.253	3.239	1.979	0.856	0.182
1973	4.168	4.616	3.063	2.464	0.551	0.231
1974	5.648	4.950	4.017	2.803	0.553	0.205
1975	6.133	5.858	3.567	3.532	0.450	0.104
1976	5.103	4.462	3.751	2.235	0.200	0.001
1977	4.769	5.366	3.885	2.998	0.229	0.007
1978	3.126	3.852	4.529	3.207	0.410	0.049
1979	5.014	5.801	4.714	3.540	1.153	0.093
1980	5.494	4.700	3.976	4.614	1.022	0.032

TABLE A3. Chesapeake Bay Hard Crab Catch, 1960-1980. Monthly Landings in Millions of Pounds.

YEAR	JAN	FEB	MAR	APR	MAY	JUN
1960	0.850	0.950	0.700	1.560	2.980	4.550
1961	2.627	2.896	2.478	3.245	3.438	7.709
1962	3.007	2.762	2.360	4.999	6.757	11.868
1963	6.150	2.405	0.864	1.369	2.761	3.538
1964	4.253	4.262	1.237	2.206	6.489	7.686
1965	2.444	1.560	0.960	3.103	6.905	11.395
1966	3.738	3.464	2.044	4.845	7.110	10.626
1967	4.209	2.167	2.493	4.427	7.878	11.271
1968	3.116	2.130	1.312	1.549	3.346	6.251
1969	2.273	1.194	0.797	1.105	2.377	2.999
1970	1.737	2.307	2.136	1.804	7.396	7.674
1971	1.444	2.376	1.369	2.845	6.733	8.936
1972	2.694	2.239	2.166	4.208	5.832	7.833
1973	2.579	2.033	1.157	2.729	3.000	6.444
1974	2.533	1.178	1.045	5.437	5.630	8.357
1975	1.414	0.724	0.514	3.043	5.136	9.015
1976	1.970	0.953	1.508	1.770	1.381	6.164
1977	0.649	0.815	0.187	0.476	1.857	5.973
1978	1.994	1.364	0.755	0.880	2.576	4.970
1979	1.014	0.969	1.058	2.308	4.502	8.671
1980	1.963	2.038	1.319	3.885	3.518	7.706

YEAR	JUL	AUG	SEP	OCT	NOV	DEC
1960	9.800	10.160	12.020	9.350	3.780	4.450
1961	12.787	9.674	11.345	7.442	4.106	4.464
1962	11.149	11.347	8.513	10.615	1.455	4.626
1963	7.910	11.195	10.499	9.413	1.930	4.999
1964	9.608	10.075	11.806	7.669	3.115	4.746
1965	12.882	12.441	11.583	9.467	4.410	5.407
1966	15.169	13.181	11.529	10.754	5.515	6.129
1967	14.340	13.361	7.525	6.547	1.511	3.662
1968	8.668	8.822	7.671	5.698	2.130	3.391
1969	6.350	10.088	9.238	10.863	5.591	4.401
1970	10.165	10.553	8.394	7.728	3.564	3.893
1971	11.207	11.320	9.479	7.384	4.531	6.257
1972	9.870	14.078	7.979	6.398	4.219	4.520
1973	8.741	9.875	7.699	6.399	1.776	3.532
1974	10.692	9.765	8.282	6.608	2.196	3.785
1975	11.418	9.093	7.731	6.692	2.311	1.989
1976	9.078	7.403	6.490	4.908	0.541	3.024
1977	10.829	12.227	9.338	7.593	3.084	4.092
1978	8.343	9.742	9.429	7.094	2.940	2.559
1979	11.025	11.519	8.210	7.559	3.566	4.254
1980	10.203	10.035	8.206	7.887	2.022	4.218

APPENDIX B

FOURIER ANALYSIS

FOURIER ANALYSIS

Fourier analysis can be used to estimate deterministic signals that are contaminated by random signals (noise). The time series should be both 1) stochastic, with similar statistical behavior between various series from the same process and 2) stationary, with little fluctuation in statistical parameters. A Fourier series is a representation of a periodic function as a linear combination of those cosine and sine functions that form the time series.

$$X(t) = \sum_{i=1}^{\infty} A_i \cos \sigma_i t + B_i \sin \sigma_i t \qquad (1)$$

with amplitude = $(A^2 + B^2)^{1/2}$ and phase = arctan(B/A)

where: A = amplitude of cosine component

B = amplitude of sine component

σ = radial frequency = $2\pi f$

f = frequency = $1/T$, T = period

t = time

i = time index

To describe the time series, one must select the frequency, amplitude and phase for the best fit. A Fourier transform of the time series computes the Fourier coefficients (A_i, B_i) of a series that best describes it.

The time series of n data points can be written in terms of the time index (i) and the frequency index, (j):

$$X_i = \sum_{j=0}^{n/2} A_j \cos 2\pi ij/n + B_j \sin 2\pi ij/n \qquad (2)$$

The coefficients, A_j and B_j, can be calculated as follows.

$$A_0 = 1/n \sum_{i=0}^{n-1} X_i \qquad (3)$$

$$A_j = 2/n \sum_{i=0}^{n-1} X_i \cos 2\pi ij/n \qquad j=1,\ldots,{}^{n}/_{2}-1 \qquad (4)$$

$$B_j = 2/n \sum_{i=0}^{n-1} X_i \sin 2\pi ij/n \qquad j=1,\ldots,{}^{n}/_{2}-1 \qquad (5)$$

To determine the energy peaks (signals) in the series, the amplitude is plotted against the period or frequency. Peaks indicate dominant periodic or cyclic behavior in the series.

In Chapter IV the 31 year wind index was expanded to predict a continuous series. The Fourier coefficients of the wind index were determined by Eqns. (3-6). These amplitudes were then substituted into Eqn. (2) to generate the wind index over a period of 1000 years.

APPENDIX C

PROGRAM LIST

ONEZ.FOR, constant total mortality rate for adulthood
MULTIZ.FOR, differential total mortality rates for adulthood

```
C       * * * * * ONEZ.FOR * * * * *
C
C       THIS VERSION IS THE BASIC MODEL WITH COMMENTS.
C       THIS FORM PERMITS CRABS TO LIVE 18 MONTHS AS
C       ADULTS (MAX. FISH. LIFE SPAN) OR TO DIE AFTER
C       SPAWNING SEASON (TERMINAL MOLT THEORY).
C       CATCH IS CALCULATED AS BARANOV'S CATCH EQUATION:
C       C=NFA/Z.  ONE Z IS APPLIED FOR ALL ADULTS, FOR
C       18 MONTHS.  CATCH IS CALCULATED AND RECORDED FOR
C       THE FIRST 3 YEARS, THOUGH NOT ALL COHORTS CONTRIBUTE
C       UNTIL YEAR 5.
C       TWO ALPHAS ARE APPLIED TO THE MAY POPULATION FOR
C       SPAWNING AT 2:1 RATIO (ACCORDING TO GENE CRONIN).
C
C
C       ARRAYS NEEDED FOR CALCULATIONS ARE RESERVED IN MEMORY.
C
        DIMENSION RNT(18),AUG1(55,40),AUG2(55,40),AUGH1(55)
        DIMENSION AUGH2(55),CM(10),CA(20),RNTA(20)
        DIMENSION CAUG1(55,40),CAUG2(55,40),CMAY1(55,40)
        DIMENSION CMAY2(55,40)
        DIMENSION TOTCAT(55),TCMAY(55),TCAUG(55),TCAT2(55)
        DIMENSION TCMAY2(55),TCAUG2(55)
        REAL MAY1(55,40),MAY2(55,40),MAY
        COMMON ALPHA,ZMAYM,ZAUGM,ZFMMAY,ZFMAUG,F
        COMMON ALPHA1,ALPHA2,NOMOLT
C
C       NAMES OF OUTPUT FILES FOR RESULTS ARE SELECTED.
C
        TYPE 110
        OPEN(UNIT=21,ACCESS='SEQOUT',MODE='ASCII',DIALOG)
        TYPE 120
        OPEN(UNIT=22,ACCESS='SEQOUT',MODE='ASCII',DIALOG)
C
C       DATA ARE INPUT:
C          MAY=INITIAL NUMBER OF CRABS FOR MAY (RECRUITS)
C          AUG=INITIAL NUMBER OF CRABS FOR AUGUST (RECRUITS)
C          ZMAYM=M, NATURAL MORTALITY FOR LARVAE HATCHED IN MAY
C          ZAUGM=M, NATURAL MORTALITY FOR LARVAE HATCHED IN AUGUST
C          ZFMMAY=Z', TOTAL MORTALITY FOR ADULTS--NATURAL AND
C            FISHING--FOR MAY
C          ZFMAUG=Z', TOTAL MORTALITY FOR ADULTS--NATURAL AND
C            FISHING--FOR AUGUST
C          F=FISHING MORTALITY FOR ADULTS
C          NUMYRS=LENGTH OF RUN IN YEARS (MAX=100)
C          ALPHA1=NUMBER OF EGGS PER FEMALE--FIRST MAY SPAWN
C          ALPHA2=NUMBER OF EGGS PER FEMALE--SECOND MAY SPAWN
C          ALPHA=NUMBER OF EGGS PER FEMALE--AUGUST SPAWN
C          NOMOLT=1--TERMINAL MOLT, =2--MAX. FISH. LIFE SPAN
C
        TYPE 100
        ACCEPT *,MAY,AUG
        TYPE 130
        ACCEPT *,ZMAYM,ZAUGM,ZFMMAY,ZFMAUG,F
```

```
      TYPE 140
      ACCEPT *,NUMYRS
C
C     ITIME=GENERATION NUMBER, NEW GENERATION IS
C     FORMED EVERY 24 MONTHS.
C
      ITIME=(NUMYRS-2)/2
      TYPE 150
      ACCEPT *,ALPHA1,ALPHA2, ALPHA
      TYPE 50
      ACCEPT *,NOMOLT
C
C     WRITE SELECTED DATA IN OUTPUT FILES
C
      WRITE(21,60)
      WRITE(21,160)ZMAYM,ZAUGM,ZFMMAY,ZFMAUG,F
      WRITE(21,170)NUMYRS
      WRITE(21,70)ALPHA1,ALPHA2,ALPHA
C
C     CALCULATE RNOM1,RNA,RNOA1
C     RNOM1=N(0) FOR MAY FOR LINE 1
C          =NUMBER OF ADULTS IN MAY X NUMBER OF EGGS/CRAB
C       RNA=PARTIAL N(0) FOR AUGUST FOR LINE 1
C          =NUMBER OF ADULTS ENTERED FOR AUGUST X □EGGS/CRAB
C     RNOA1=N(0) FOR AUGUST FOR LINE 1
C     [AUGUST LARVAE ARE DERIVED FROM CRABS ENTERED TO
C     INITIALIZE AUGUST RUN AND FROM THOSE LEFT AFTER FISHING
C     THE MAY POPULATION FOR 3 MONTHS.]
C
      RNOM1=MAY*ALPHA1
      RNA=AUG*ALPHA
C
C     CALCULATE CATCH DURING THE FIRST FOUR YEARS.
C     NOTE:  NOT ALL COHORTS CONTRIBUTE TO THE POPULATION
C            UNTIL THE FIFTH AND SIXTH YEARS.
C     FAZM=BARANOV'S CONSTANT--FA/Z FOR MAY.  MULTIPLY
C          BY N(T) TO GET CATCH FOR MAY.
C     CM(I)=MAY CATCH FOR MONTH T
C     FAZA=BARANOV'S CONSTANT--FA/Z FOR AUGUST.  MULTIPLY
C          BY N(T) TO GET CATCH FOR AUGUST.
C     CA(I)=AUGUST CATCH FOR MONTH T
C     RNT(I)=N(T) FOR MAY COHORT, RNT(3)=CRABS THAT SPAWN
C            AUGUST.
C     RNTA(I)=N(T) FOR AUGUST COHORT
C
      FAZM=(F*(1.-EXP(-ZFMMAY)))/ZFMMAY
      FAZA=(F*(1.-EXP(-ZFMAUG)))/ZFMAUG
      DO 20 I=1,15
      T=I
      IF(I.GT.9)GO TO 10
      RNT(I)=MAY/EXP(ZFMMAY*T)
      CM(I)=RNT(I)*FAZM
10    RNTA(I)=AUG/EXP(ZFMAUG*T)
      CA(I)=RNTA(I)*FAZA
```

```
20     CONTINUE
C
C     CALCULATE ACTUAL NUMBER OF CRABS THAT SPAWN IN AUGUST.
C     BEGAUG=NUMBER ENTERED FOR AUGUST (AUG) + NUMBER LEFT
C      AFTER FISHING MAY CRABS FOR 3 MONTHS (RNT(3))
C     WRITE IN OUPUT FILE.
C
      BEGAUG=AUG+RNT(3)
      WRITE(21,180)MAY,AUG,BEGAUG
      IF(NOMOLT.EQ.1)WRITE(21,80)
      IF(NOMOLT.EQ.2)WRITE(21,90)
      WRITE(21,190)
      RNOA1=RNT(3)*ALPHA2+RNA
C
C     USE SUBROUTINE HATCH TO GENERATE ABUNDANCES AFTER
C     EXPONENTIAL DEPLETION BY Z (=F+M) AND HARVEST
C     HAVE OCCURRED DURING THE LIFE CYCLE FOR EACH LINE.
C     EX. MAY1(1,25) OR MAY2(1,25)
C       THIS ARRAY CONTAINS ABUNDANCES AFTER TOTAL
C       MORTALITY HAS BEEN APPLIED.  [PROPERLY
C       CALLED INSTANTANEOUS RATES THEREOF!]
C       MAY1=CRABS HATCHED IN MAY OF THE FIRST YEAR, LINE 1
C       MAY2=CRABS HATCHED IN MAY OF THE SECOND YEAR, LINE 2
C       (1,25)=1=HATCH NUMBER, I.E., HATCH □1
C          25=AGE OF THAT HATCH IN MONTHS
C
C     EX. CMAY1(1,25)
C       THIS ARRAY CONTAINS CATCH AFTER BARANOV.
C       THE SUBSCRIPTS ARE THE SAME AS ABOVE.
C
      CALL HATCH(MAY1,RNOM1,AUG1,RNOA1,ITIME,AUGH1,CMAY1,CAUG1)
C
C     SUBROUTINE HATCH IS USED TO GENERATE VALUES FOR THE
C     SECOND LINE OF CRABS, I.E., THOSE HATCHED IN YEAR TWO.
C     RNOM2, RNOA2=RECRUITS FOR MAY AND AUGUST,LINE 2,
C     RESPECTIVELY.
C
      RNOM2=MAY*ALPHA1
      RNOA2=RNT(3)*ALPHA2+RNA
      CALL HATCH(MAY2,RNOM2,AUG2,RNOA2,ITIME,AUGH2,CMAY2,CAUG2)
C
C     YEAR 1--CRABS HARVESTED
C     WRITE OUT YEAR, TOTAL CATCH, CATCH FROM MAY COHORT,
C     AND CATCH FROM AUGUST COHORT.
C     TCM1=FIRST YEAR CATCH FROM MAY COHORT
C     TCA1=FIRST YEAR CATCH FROM AUGUST COHORT
C     TC1=TOTAL CATCH
C
      IYR=1
      TCM1=CM(1)+CM(2)+CM(3)+CM(4)+CM(5)+CM(6)+CM(7)
      TCA1=CA(1)+CA(2)+CA(3)+CA(4)
      TC1=TCM1+TCA1
      WRITE(21,*)IYR,TC1,TCM1,TCA1
C
```

```
C        THE RANGE M□□ TO N□□ INDICATES THE MONTHS DURING
C        WHICH CRABS ARE FISHED (CATCH CALCULATED) FOR A
C        CHOSEN HATCH FOR A CHOSEN YEAR.
C
         M16=16
         N19=19
         M22=22
         N28=28
         M20=20
         N31=31
         M29=29
         N39=39
         M32=32
         N33=33
C
C        SUBROUTINE CATCH GENERATES NUMBERS OF CRABS
C        CAUGHT MONTHLY IN EACH LINE AND PRODUCES A YEARLY TOTAL.
C        EX.  SMAY1=SUM OF ALL CRABS CMAYHT FROM
C             THE MAY1 LINE IN A GIVEN YEAR.
C
         CALL CATCH(CMAY1,SMAY1,IYR,M16,N19)
C
C        YEAR 2--CALCULATE CATCH AND WRITE IN OUTPUT FILE.
C
         IYR=IYR+1
         TCM2=SMAY1+CM(8)+CM(9)
         TCA2=CA(5)+CA(6)+CA(7)+CA(8)+CA(9)+CA(10)+CA(11)
         TCA2=TCA2+CA(12)+CA(13)+CA(14)+CA(15)
         TC2=TCM2+TCA2
         WRITE(21,*)IYR,TC2,TCM2,TCA2
C
C        CALCULATE CATCH USING SUBROUTINE CATCH.
C        THIS DO LOOP CALCULATES CATCH FOR ODD
C        NUMBERED YEARS, THEN EVEN NUMBERED
C        YEARS.
C
         DO 30 K=1,ITIME
         KK=K
         CALL CATCH(CAUG1,SAUG1,KK,M22,N28)
         CALL CATCH(CMAY1,SMAY1,KK,M20,N31)
         CALL CATCH(CMAY2,SMAY2,KK,M16,N19)
         N=K-1
         CALL CATCH(CAUG2,SAUG2,N,M29,N39)
         CALL CATCH(CMAY2,SMAY2N,N,M32,N33)
C
C        CALCULATE YEARLY CATCH BY ADDING UP
C        CATCH FROM DIFFERENT LINES.
C        TOTCAT(K)=TOTAL FOR YEAR
C        TCMAY(K)=TOTAL MAY CATCH FOR THE YEAR
C        TCAUG(K)=TOTAL AUGUST CATCH FOR THE YEAR
C        WRITE CATCH FOR THE YEAR IN OUTPUT FILE.
C
         TOTCAT(K)=SAUG1+SMAY1+SMAY2+SAUG2+SMAY2N
         TCMAY(K)=SMAY1+SMAY2+SMAY2N
```

```
        TCAUG(K)=SAUG1+SAUG2
        IYR=IYR+1
        WRITE(21,*)IYR,TOTCAT(K),TCMAY(K),TCAUG(K)
C
C       CALCULATE CATCH FOR EVEN NUMBERED YEARS.
C       WRITE CATCH FOR THE YEAR IN OUTPUT FILE.
C
        CALL CATCH(CMAY1,S2MAY1,KK,M32,N33)
        CALL CATCH(CAUG1,S2AUG1,KK,M29,N39)
        CALL CATCH(CMAY2,S2MAY2,KK,M20,N31)
        CALL CATCH(CAUG2,S2AUG2,KK,M22,N28)
        K1=K+1
        CALL CATCH(CMAY1,SMAY1K,K1,M16,N19)
        TCAT2(K)=S2MAY1+S2AUG1+S2MAY2+S2AUG2+SMAY1K
        TCMAY2(K)=SMAY1K+S2MAY1+S2MAY2
        TCAUG2(K)=S2AUG2+S2AUG1
        IYR=IYR+1
        WRITE(21,*)IYR,TCAT2(K),TCMAY2(K),TCAUG2(K)
30        CONTINUE
C
C       WRITE CATCH FOR EACH DECADE IN SECOND OUTPUT FILE.
C
        IYEAR=10
        WRITE(22,60)
        WRITE(22,160)ZMAYM,ZAUGM,ZFMMAY,ZFMAUG,F
        WRITE(22,170)NUMYRS
        WRITE(22,70)ALPHA1,ALPHA2,ALPHA
        WRITE(22,180)MAY,AUG,BEGAUG
        IF(NOMOLT.EQ.1)WRITE(22,80)
        IF(NOMOLT.EQ.2)WRITE(22,90)
        WRITE(22,190)
        DO 40 I=4,ITIME,5
        WRITE(22,*)IYEAR,TCAT2(I),TCMAY2(I),TCAUG2(I)
        IYEAR=IYEAR+10
40        CONTINUE
        STOP
C
C       FORMAT STATEMENTS
C
50      FORMAT(/5X,'ENTER TYPE OF ADULTHOOD EXPERIENCED:',
        1  /10X,'1=TERMINAL MOLT HYPOTHESIS',/10X,'2=MAXIMUM',
        2  ' FISHABLE LIFE SPAN HYPOTHESIS')
60      FORMAT(' ***** ONEZ.FOR OUTPUT *****')
70      FORMAT(1H ,'ALPHAS: MAY1=',E10.3,'  MAY2=',E10.3,'  AUG=',E10.3)
80      FORMAT(1H ,'TERMINAL MOLT HYPOTHESIS')
90      FORMAT(1H ,'MAXIMUM FISHABLE LIFE SPAN HYPOTHESIS')
100     FORMAT(/5X,'ENTER NUMBER OF CRABS:  MAY, AUGUST')
110     FORMAT(/5X,'ENTER OUTPUT FILE NAME FOR YEARLY VALUES')
120     FORMAT(/5X,'ENTER OUTPUT FILE NAME FOR DECADE VALUES')
130     FORMAT(/5X,'ENTER MORTALITY RATES: M(MAY), M(AUG),',
        1     ' Z(MAY), Z(AUG), F')
140     FORMAT(/5X,'ENTER LENGTH OF RUN IN YEARS (MAX=100)')
150     FORMAT(/5X,'ENTER ALPHAS:  MAY1, MAY2, AUGUST')
160     FORMAT(1H ,'M(MAY)=',F5.4,2X,'M(AUG)=',F5.4,2X,
```

```
        1    'Z(MAY)=',F5.4,2X,'Z(AUG)='F5.4,2X,'F=',F5.4)
170     FORMAT(1H ,'LENGTH OF RUN =',I4,' YEARS')
180     FORMAT(1H ,'INITIAL NUMBER OF MAY CRABS (ENTERED) =',E10.3,
        1  /1H ,'NUMBER OF AUGUST CRABS ENTERED =',E10.3,
        2  /1H ,'INITIAL NUMBER OF AUGUST CRABS (TOTAL) =',E10.3)
190     FORMAT(/1H ,'YEAR    TOTAL        MAY         AUGUST')
        END
C
C       END OF MAIN PROGRAM
C
C
C
C       SUBROUTINE HATCH
C
C
        SUBROUTINE HATCH (MAY,RNOM,AUG,RNOA,IT,AUGH,CMAY,CAUG)
        DIMENSION AUG(55,40),AUGH(55),CMAY(55,40),CAUG(55,40)
        REAL MAY(55,40)
        COMMON ALPHA,ZMAYM,ZAUGM,ZFMMAY,ZFMAUG,F
        COMMON ALPHA1,ALPHA2,NOMOLT
C
C       CALCULATE A FOR MAY AND AUGUST FOR
C       CATCH CALCULATIONS--AMAY, AAUG.
C
        AMAY=1.0-EXP(-ZFMMAY)
        AAUG=1.0-EXP(-ZFMAUG)
        IT1=IT+1
C
C       L=HATCH NUMBER
C       SINCE A HATCH OCCURS EVERY 24 MONTHS, L CORRESPONDS TO
C       TWO YEARS O CALENDAR TIME.  IT REFERS TO ITIME, THE
C       LENGTH OF RUN/2.
C
        DO 50 L=1,IT1
C
C       THE MAY HATCH TAKES 15 MONTHS TO REACH MATURITY.
C       DEPLETION BY M ALONE.
C       RNOM=N(0) FOR MAY COHORT
C
        DO 10 I=1,15
        T=I
        MAY(L,I)=RNOM/EXP(ZMAYM*T)
10        CONTINUE
C
C       RNM=RECRUITS TO FISHERY FROM MAY COHORT
C       MAY(L,K)=ABUNDANCE IN A GIVEN MONTH
C       IF MAY(L,K)<1, CONSIDER ABUNDANCE = 0.0
C       CMAY(L,K)=CATCH IN A GIVEN MONTH
C           UPMAY=N X F X A
C       IF SELECT TERMINAL MOLT, CATCH =0.0 AFTER SPAWN
        RNM=MAY(L,15)
        DO 20 I=1,18
        T=I
        K=I+15
```

```
        MAY(L,K)=RNM/EXP(ZFMMAY*T)
        IF(MAY(L,K).LT.1.)MAY(L,K)=0.0
        UPMAY=MAY(L,K)*F*AMAY
        CMAY(L,K)=UPMAY/ZFMMAY
        IF(NOMOLT.EQ.1.AND.K.GT.27)CMAY(L,K)=0.0
20        CONTINUE
        RNOM=MAY(L,24)*ALPHA1
C
C       AUGUST HATCH TAKES 21 MONTHS TO REACH MATURITY.
C       DEPLETION BY M ALONE, 18 MONTH ADULTHOOD.
C       VARIABLES ANALOGOUS TO THOSE FOR MAY COHORT--
C       DENOTED BY 'A':  RNOA, RNAUG, AUG(L,K), CAUG(L,K)
C
        DO 30 J=1,21
        T=J
        AUG(L,J)=RNOA/EXP(ZAUGM*T)
30        CONTINUE
        RNAU=AUG(L,21)
        DO 40 J=1,18
        T=J
        K=J+21
        AUG(L,K)=RNAU/EXP(ZFMAUG*T)
        IF(AUG(L,K).LT.1.)AUG(L,K)=0.0
        UPAUG=AUG(L,K)*F*AAUG
        CAUG(L,K)=UPAUG/ZFMAUG
        IF(NOMOLT.EQ.1.AND.K.GT.24)CAUG(L,K)=0.0
40        CONTINUE
        RNOA=(AUG(L,24)*ALPHA)+(MAY(L,27)*ALPHA2)
50        CONTINUE
        RETURN
        END
C
C
C       SUBROUTINE CATCH
C
C
        SUBROUTINE CATCH (CATCH,SUMCAT,L,M,N)
        DIMENSION CATCH(55,40)
        SUMCAT=0.
C
C       SUMCAT=TOTAL CATCH FOR EACH LINE FOR EACH YEAR
C       M,N=MONTHS DURING A YEAR THAT CRABS ARE FISHED
C       CATCH(L,I)=CATCH DURING THAT MONTH, I
C       IF MONTHLY CATCH IS LESS THAN 1, CONSIDER IT ZERO.
C
        DO 10 I=M,N
        IF(CATCH(L,I).LT.1.0)CATCH(L,1)=0.0
        SUMCAT=SUMCAT+CATCH(L,I)
10        CONTINUE
        RETURN
        END
```

```
C      * * * * * MULTIZ.FOR * * * * *
C
C      THIS VERSION IS THE BASIC MODEL WITHOUT COMMENTS.
C      THIS FORM PERMITS CRABS TO LIVE 18 MONTHS AS
C      ADULTS (MAX. FISH. LIFE SPAN) OR TO DIE AFTER
C      SPAWNING SEASON (TERMINAL MOLT THEORY).
C      CATCH IS CALCULATED AS BARANOV'S CATCH EQUATION:
C      C=(NFA)/Z.  EXACT REPLACEMENT OF THE POPULATION IS
C      SELECTED.  TWO Z'S ARE USED TO DESCRIBE ADULTHOOD:
C      Z1 FOR REPLACEMENT OF INITIAL NUMBER, AND Z2 FOR
C      DEATH OF 99.9% OF THE POPULATION BY END OF LIFE
C      SPAN.  FISHING ACCOUNTS FOR SOME PERCENTAGE OF
C      Z SO TWO F'S ARE NEEDED, FISHING BEFORE
C      SPAWNING AND F2, POST-SPAWN FISHING MORTALITY.
C      TWO ALPHAS ARE APPLIED TO THE MAY POPULATION FOR
C      SPAWNING AT 2:1 RATIO (ACCORDING TO GENE CRONIN).
C      CATCH IS CALCULATED FOR FIRST 3 YEARS, THOUGH NOT ALL
C      COHORTS CONTRIBUTE UNTIL YEARS 5 AND 6.
C
C      ALL VARIABLES ARE EQUIVALENT TO THOSE DEFINED IN
C      THE COMMENTS IN ONEZ.FOR.
C      DIFFERENCES:
C          ZM1, ETC. REPLACE THE Z'S IN ONEZ.FOR AT THE
C            APPROPRIATE TIMES.
C          F=X% OF Z AND IS CALCULATED IN THE PROGRAM:
C            FM1,FM2,FA1,FA2
C
       DIMENSION RNT(18),AUG1(55,40),AUG2(55,40),AUGH1(55)
       DIMENSION AUGH2(55),CM(10),CA(20),RNTA(20)
       DIMENSION CAUG1(55,40),CAUG2(55,40),CMAY1(55,40)
       DIMENSION CMAY2(55,40)
       DIMENSION TOTCAT(55),TCMAY(55),TCAUG(55),TCAT2(55)
       DIMENSION TCMAY2(55),TCAUG2(55)
       REAL MAY1(55,40),MAY2(55,40),MAY
       COMMON ALPHA,ZMAYM,ZAUGM,ZFMM1,ZFMA1
       COMMON ZFMM2,ZFMA2,FA1,FA2,FM1,FM2
       COMMON ALPHA1,ALPHA2,NOMOLT
       TYPE 110
       OPEN(UNIT=21,ACCESS='SEQOUT',MODE='ASCII',DIALOG)
       TYPE 120
       OPEN(UNIT=22,ACCESS='SEQOUT',MODE='ASCII',DIALOG)
       TYPE 100
       ACCEPT *,MAY,AUG
       TYPE 130
       ACCEPT *,ZMAYM,ZAUGM,ZFMM1,ZFMM2,ZFMA1,ZFMA2,PERCNT
       TYPE 140
       ACCEPT *,NUMYRS
       ITIME=(NUMYRS-2)/2
       TYPE 150
       ACCEPT *,ALPHA1,ALPHA2,ALPHA
       TYPE 50
       ACCEPT *,NOMOLT
       PC=PERCNT/100.0
       FM1=PC*ZFMM1
```

```
      FM2=PC*ZFMM2
      FA1=PC*ZFMA1
      FA2=PC*ZFMA2
      WRITE(21,60)
      WRITE(21,160)ZMAYM,ZAUGM,ZFMM1,ZFMM2,ZFMA1,ZFMA2,
     1 FM1,FM2,FA1,FA2
      WRITE(21,180)NUMYRS
      WRITE(21,70)ALPHA1,ALPHA2,ALPHA
      RNOM1=MAY*ALPHA1
      RNA=AUG*ALPHA
      FAZM2=(FM2*(1.-EXP(-ZFMM2)))/ZFMM2
      FAZA2=(FA2*(1.-EXP(-ZFMA2)))/ZFMA2
      DO 20 I=1,15
      T=I
      IF(I.GT.9)GO TO 10
      RNT(I)=MAY/EXP(ZFMM2*T)
      CM(I)=RNT(I)*FAZM2
10    RNTA(I)=AUG/EXP(ZFMA2*T)
      CA(I)=RNTA(I)*FAZA2
20      CONTINUE
      BEGAUG=AUG+RNT(3)
      WRITE(21,190)MAY,AUG,BEGAUG
      IF(NOMOLT.EQ.1)WRITE(21,80)
      IF(NOMOLT.EQ.2)WRITE(21,90)
      WRITE(21,200)
      RNOA1=RNT(3)*ALPHA2+RNA
      CALL HATCH(MAY1,RNOM1,AUG1,RNOA1,ITIME,AUGH1,CMAY1,CAUG1)
      RNOM2=MAY*ALPHA1
      RNOA2=RNT(3)*ALPHA2+RNA
      CALL HATCH(MAY2,RNOM2,AUG2,RNOA2,ITIME,AUGH2,CMAY2,CAUG2)
      IYR=1
      TCM1=CM(1)+CM(2)+CM(3)+CM(4)+CM(5)+CM(6)+CM(7)
      TCA1=CA(1)+CA(2)+CA(3)+CA(4)
      TC1=TCM1+TCA1
      WRITE(21,*)IYR,TC1,TCM1,TCA1
      M16=16
      N19=19
      CALL CATCH(CMAY1,SMAY1,IYR,M16,N19)
      IYR=IYR+1
      TCM2=SMAY1+CM(8)+CM(9)
      TCA2=CA(5)+CA(6)+CA(7)+CA(8)+CA(9)+CA(10)+CA(11)
      TCA2=TCA2+CA(12)+CA(13)+CA(14)+CA(15)
      TC2=TCM2+TCA2
      WRITE(21,*)IYR,TC2,TCM2,TCA2
      DO 30 K=1,ITIME
      KK=K
      M22=22
      N28=28
      CALL CATCH(CAUG1,SAUG1,KK,M22,N28)
      M20=20
      N31=31
      CALL CATCH(CMAY1,SMAY1,KK,M20,N31)
      M16=16
      N19=19
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      CALL CATCH(CMAY2,SMAY2,KK,M16,N19)
      N=K-1
      M29=29
      N39=39
      CALL CATCH(CAUG2,SAUG2,N,M29,N39)
      M32=32
      N33=33
      CALL CATCH(CMAY2,SMAY2N,N,M32,N33)
      TOTCAT(K)=SAUG1+SMAY1+SMAY2+SAUG2+SMAY2N
      TCMAY(K)=SMAY1+SMAY2+SMAY2N
      TCAUG(K)=SAUG1+SAUG2
      IYR=IYR+1
      WRITE(21,*)IYR,TOTCAT(K),TCMAY(K),TCAUG(K)
      CALL CATCH(CMAY1,S2MAY1,KK,M32,N33)
      CALL CATCH(CAUG1,S2AUG1,KK,M29,N39)
      CALL CATCH(CMAY2,S2MAY2,KK,M20,N31)
      CALL CATCH(CAUG2,S2AUG2,KK$,M22,N28)
      K1=K+1
      CALL CATCH(CMAY1,SMAY1K,K1,M16,N19)
      TCAT2(K)=S2MAY1+S2AUG1+S2MAY2+S2AUG2+SMAY1K
      TCMAY2(K)=SMAY1K+S2MAY1+S2MAY2
      TCAUG2(K)=S2AUG2+S2AUG1
      IYR=IYR+1
      WRITE(21,*)IYR,TCAT2(K),TCMAY2(K),TCAUG2(K)
30      CONTINUE
      IYEAR=10
      WRITE(22,60)
      WRITE(22,160)ZMAYM,ZAUGM,ZFMM1,ZFMM2,ZFMA1,ZFMA2,
     1 FM1,FM2,FA1,FA2
      WRITE(22,180)NUMYRS
      WRITE(22,70)ALPHA1,ALPHA2,ALPHA
      WRITE(22,190)MAY,AUG,BEGAUG
      IF(NOMOLT.EQ.1)WRITE(22,80)
      IF(NOMOLT.EQ.2)WRITE(22,90)
      WRITE(22,200)
      DO 40 I=4,ITIME,5
      WRITE(22,*)IYEAR,TCAT2(I),TCMAY2(I),TCAUG2(I)
      IYEAR=IYEAR+10
40      CONTINUE
      STOP
50    FORMAT(/5X,'ENTER TYPE OF ADULTHOOD EXPERIENCED:',
      1  /10X,'1=TERMINAL MOLT HYPOTHESIS',/10X,'2=MAXIMUM',
      2  ' FISHABLE LIFE SPAN HYPOTHESIS')
60    FORMAT(' ***** MULTIZ.FOR OUTPUT *****'/)
70    FORMAT(1H ,'ALPHAS: MAY1=',E10.3,'  MAY2=',E10.3,'  AUG=',E10.3)
80    FORMAT(1H ,'TERMINAL MOLT HYPOTHESIS')
90    FORMAT(1H ,'MAXIMUM FISHABLE LIFE SPAN HYPOTHESIS')
100   FORMAT(/5X,'ENTER NUMBER OF CRABS:  MAY, AUGUST')
110   FORMAT(/5X,'ENTER OUTPUT FILE NAME FOR YEARLY VALUES')
120   FORMAT(/5X,'ENTER OUTPUT FILE NAME FOR DECADE VALUES')
130   FORMAT(/5X,'ENTER MORTALITY RATES: M(MAY), M(AUG),',
      1    /10X,'Z1(MAY), Z2(MAY), Z1(AUG), Z2(AUG),',
      2    /10X,'PERCENT FISHING (F=X% OF Z)')
140   FORMAT(/5X,'ENTER LENGTH OF RUN IN YEARS (MAX=100)')
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```
150     FORMAT(/5X,'ENTER ALPHAS:  MAY1, MAY2, AUGUST')
160     FORMAT(1H ,'M(MAY)=',F5.4,2X,'M(AUG)=',F5.4,2X,
        1    'Z1(MAY)=',F5.4,2X,'Z2(MAY)=',F5.4,/,
        2    ' Z1(AUG)=',F5.4,2X,'Z2(AUG)=',F5.4,2X,'FM1=',F5.4,
        3    2X,'FM2=',F5.4,/,' FA1=',F5.4,2X,'FA2=',F5.4)
170     FORMAT(1H ,'ALPHA =',E10.3,5X,'LENGTH OF RUN =',I4,' YEARS')
180     FORMAT(1H ,'LENGTH OF RUN =',I4,' YEARS')
190     FORMAT(1H ,'INITIAL NUMBER OF MAY CRABS (ENTERED) =',E10.3,
        1  /1H ,'NUMBER OF AUGUST CRABS ENTERED =',E10.3,
        2  /1H ,'INITIAL NUMBER OF AUGUST CRABS (TOTAL) =',E10.3)
200     FORMAT(/1H ,'YEAR    TOTAL          MAY          AUGUST')
        END
        SUBROUTINE HATCH (MAY,RNOM,AUG,RNOA,IT,AUGH,CMAY,CAUG)
        DIMENSION AUG(55,40),CMAY(55,40),CAUG(55,40)
        REAL MAY(55,40)
        COMMON ALPHA,ZMAYM,ZAUGM,ZFMM1,ZFMA1
        COMMON ZFMM2,ZFMA2,FA1,FA2,FM1,FM2
        COMMON ALPHA1,ALPHA2,NOMOLT
        AMAY1=1.0-EXP(-ZFMM1)
        AMAY2=1.0-EXP(-ZFMM2)
        AAUG1=1.0-EXP(-ZFMA1)
        AAUG2=1.0-EXP(-ZFMA2)
        IT1=IT+1
        DO 70 L=1,IT1
        DO 10 I=1,15
        T=I
        MAY(L,I)=RNOM/EXP(ZMAYM*T)
10        CONTINUE
        RNM=MAY(L,15)
        DO 20 I=1,9
        T=I
        K=I+15
        MAY(L,K)=RNM/EXP(ZFMM1*T)
        IF(MAY(L,K).LT.1.)MAY(L,K)=0.0
        UPMAY1=MAY(L,K)*FM1*AMAY1
        CMAY(L,K)=UPMAY1/ZFMM1
20        CONTINUE
        DO 30 I=1,9
        T=I
        K=I+24
        MAY(L,K)=MAY(L,24)/EXP(ZFMM2*T)
        IF(MAY(L,K).LT.1.)MAY(L,K)=0.0
        UPMAY2=MAY(L,K)*FM2*AMAY2
        CMAY(L,K)=UPMAY2/ZFMM2
        IF(NOMOLT.EQ.1.AND.K.GT.27)CMAY(L,K)=0.0
30        CONTINUE
        RNOM=MAY(L,24)*ALPHA1
        DO 40 J=1,21
        T=J
        AUG(L,J)=RNOA/EXP(ZAUGM*T)
40        CONTINUE
        RNAU=AUG(L,21)
        DO 50 J=1,3
        T=J
```

```
      K=J+21
      AUG(L,K)=RNAU/EXP(ZFMA1*T)
      IF(AUG(L,K).LT.1.)AUG(L,K)=0.0
      UPAUG1=AUG(L,K)*FA1*AAUG1
      CAUG(L,K)=UPAUG1/ZFMA1
50      CONTINUE
      DO 60 J=1,15
      T=J
      K=J+24
      AUG(L,K)=AUG(L,24)/EXP(ZFMA2*T)
      IF(AUG(L,K).LT.1.)AUG(L,K)=0.0
      UPAUG2=AUG(L,K)*FA2*AAUG2
      CAUG(L,K)=UPAUG2/ZFMA2
      IF(NOMOLT.EQ.1.AND.K.GT.24)CAUG(L,K)=0.0
60      CONTINUE
      RNOA=(AUG(L,24)*ALPHA)+(MAY(L,27)*ALPHA2)
70      CONTINUE
      RETURN
      END
      SUBROUTINE CATCH (CATCH,SUMCAT,L,M,N)
      DIMENSION CATCH(55,40)
      SUMCAT=0.
      DO 10 I=M,N
      IF(CATCH(L,I).LT.1.0)CATCH(L,I)=0.0
      SUMCAT=SUMCAT+CATCH(L,I)
10      CONTINUE
      RETURN
      END
```

VITA

Betty Springer Hester was born in Kingsport, Tennessee, on December 31, 1951. She received a Bachelor of Science in Biology from Guilford College, Greensboro, North Carolina, in 1973 and a Master of Science in Marine Science from the College of Charleston, Charleston, South Carolina in 1976. She has held research assistantships at the College of Charleston and Old Dominion University and has worked primarily on the Sea Grant Chesapeake Bay Blue Crab Project at Old Dominion University for the last three years. She has published the following:

1) Davis, W. P., B. S. Hester, R. L. Yoakum, and R. G. Domey. 1977. Marine ecosystem testing units: Design for assessment of benthic organism responses to low level pollutants. Helgolander wiss. Meeresunters. 30:673-681.

2) Calder, D. R. and B. S. Hester. 1980. Phylum Cnidaria. <u>In</u>: R. G. Zingmark, ed. An annotated checklist of the biota of the coastal zone of South Carolina. University of South Carolina Press, Columbia, South Carolina. pages 87-93.

<u>Honors and Awards</u>:

1) University Fellowship, 1976, Old Dominion University
2) Best Student Paper Award, 1982, Spring meeting of the Atlantic Estuarine Research Society, Baltimore, Maryland

<u>Membership in Professional Societies</u>

1) Sigma Xi Scientific Research Society
2) American Society of Limnology and Oceanography
3) The Crustacean Society
4) Atlantic Estuarine Research Society