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An environmental model predicting the relative recruitment success of blue crab, Callinectes sapidus (Rathbun), in Chesapeake Bay, Virginia

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AN ENVIRONMENTAL MODEL PREDICTING THE RELATIVE RECRUITMENT SUCCESS OF THE BLUE CRAB, *CALLINECTES SAPIDUS* (RATHBUN), IN CHESAPEAKE BAY, VIRGINIA

A Thesis

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Andrew J. Applegate

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APPROVAL SHEET

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ABSTRACT

The relationships between parental spawning stock size of *Callinectes sapidus* and environmental and meteorological features at the mouth of Chesapeake Bay, Va. can be used to predict winter dredge fishery catch. Estimates of recruitment and spawning stock size are obtained by application of the Leslie stock analysis method to catch rates observed in the winter dredge fishery. A stock recruitment model is employed to determine the degree of density dependent survival mechanisms. A survival index is developed from the stock recruitment model to test significant environmental relationships.

The blue crab stock recruitment model exhibits a "peaked-dome," characteristic of finfish with high fecundity who support heavy rates of exploitation. The survival index exhibits significant relationships with submerged aquatic vegetation acreage, Chesapeake Bay streamflow, incident sunshine, average atmospheric pressure, and prevalent wind conditions surrounding the time of spawning and larval development. Many of these relationships are explained on the basis of ontogenic behavioral response patterns impacting vertical distribution of larvae. This vertical distribution is important in determining the degree to which *C. sapidus* larvae are subject to estuarine salt-wedge circulation and normal circulation on the adjacent coastal shelf. Conditions creating favorable patterns of vertical distribution and circulation promote larval retention,

recruitment and survival and subsequent recruitment into the winter dredge fishery.

AN ENVIRONMENTAL MODEL PREDICTING THE RELATIVE RECRUITMENT SUCCESS OF THE BLUE CRAB, *CALLINECTES SAPIDUS* (RATHBUN)

INTRODUCTION

Fishery models, long term yield versus environmentally induced fluctuation.

Fishery management decisions are typically made on the basis of models which predict long-term, average yields. Consequently model output rarely approximates reality, a pragmatic problem for decision makers. From a biological standpoint, there is an intermediate level of exploitation that will support a sustainable maximum harvest over a period of time, hence maximum sustainable yield (MSY). MSY is usually calculated from one of two models, depending on the quality of information about a stock and its fishery.

The potential yield of a fishery may be calculated by either the surplus production model, or the yield per recruit model (Zuboy and Jones 1980). The production model derives its theoretical basis from the logistics "law" of population growth. That is, maximum production (reproduction and growth, less natural mortality) of a stock occurs at some intermediate population size. Controlled predation by man (fishing) can stimulate the stock to maintain this level, thus generating a maximum surplus production. The yield per recruit model seeks to maximize the yield (harvestable biomass) of a given year class before natural mortality removes biomass from the year class faster than growth can restore it. The yield per recruit can be maximized by controlling fishing effort.

These models require a number of assumptions be made, one of which being that environmental factors are constant (Zuboy and Jones 1980), or do not significantly affect potential yield. MSY is the largest average catch or yield that can continuously be taken from a stock under average environmental conditions (Ricker 1975). Regulations designed to avoid overfishing (i.e. quotas) based on MSY considerations would in fact, be disastrous if a series of years with poor recruitment due to unfavorable environmental conditions occur. When this occurs, the population size would be reduced to a point where reproductive capacity is insufficient to generate recovery to optimal stock size during favorable years. On the other hand, year classes with enhanced recruitment (favorable conditions) might be able to sustain greater fishing pressure than that dictated by MSY indications alone.

Secondarily, fishermen and processors can make more informed decisions with accurate estimates of yield. Fishermen would be able to change gear and fish for other species if predictions are low, and processors might be able to adjust processing capacities and market development based on relatively accurate predictions. Informed decisions based on accurate predictions might help to avoid overcapitalization and overfishing of a stock after yield decreases following a series of exceptional years.

Predicting stock abundance and catch from known environmental conditions is not a new concept, and has met with varying degrees of success. Walford (1938) attempted to explain the distribution of haddock eggs on Georges Bank by differential density structures of water masses. Sette (1943) predicted Atlantic mackerel year class strength based upon wind conditions during the larval stage. Walford (1946) correlated fluctuations in the abundance of the Pacific sardine (Sardinops caerulea) with sea surface salinity. Pearson (1948) found that blue crab catch seemed to be related to river discharge volume in Chesapeake Bay tributaries.

Often, these early attempts at environmental modelling eventually failed because the relationship studied did not reflect the true ecological interactions controlling survival. Use of proxy data (e.g. air temperature, precipitation, surface salinity) is tenuous, at best. For example, Walford (1946) found that sardine year-class strength was enhanced when sea surface salinities were high. But the true ecological relationship was based on upwelling which brought more nutrients to the surface, dispersing the proper concentrations of dinoflagellates and encouraging the bloom of diatoms (food for the larval anchovy). Sea surface salinity anomalies were only a manifestation of upwelling.

Nevertheless, Austin and Ingham (1979) recognize the importance and necessity of proxy data when developing environmental models, particularly when confronted by a lack of quality, primary data sets of long time series. Additionally, the use of proxy data, although not entirely valid if causal mechanisms are not known, may serve to direct future research and monitoring programs.

Yield models typically predict future catch levels much better for "density-dependent" stocks (where larval survival is more dependent on parental or larval abundance) than for "density-independent" stocks (where larval survival is dependent on tolerances of the physical environment, availability of suitable food, abundance of predators or competitors, etc.). Cushing and Harris (1973) found that an index of density dependence was related to the mean fecundity of a species. Specifically, the index of density dependence was proportional to the cube root of mean fecundity, despite fairly wide confidence intervals for a number of the indices. With a mean fecundity of approximately 1.5 million eggs per spawn (Van Engel 1958; Sulkin 1977) and females often spawning two or more times (Van Engel 1958), the Chesapeake Bay blue crab stock is expected to exhibit stock recruitment characteristics similar to cod and haddock (Gadidae), highly fecund species with 250,000 to one million eggs per spawn (Cushing 1971).

Blue crab life history - Estuarine adaptation

The blue crab, Callinectes sapidus (Rathbun), occurs from Massachusetts to Texas along the Atlantic and Gulf coasts of North America, and along the Atlantic coast of South America (Van Engel 1958). Its distribution during its life stages is described by Van Engel (1958) and Sulkin (1977). Female crabs copulate during their terminal molt, then migrate toward the Bay mouth before hibernating during winter. Larvae are hatched near the Bay mouth during the crab's third summer of life.

Hatching in near-oceanic salinities at the Bay mouth serves multiple purposes. Thermal and osmoregulatory environments tend to be more stable at the Bay mouth than within the interior of the Bay and within its tributaries. Thermal response times are much shorter in areas of shallow water, thereby increasing the degree of fluctuation in response to atmospheric temperatures. Additionally, salinities further into the estuary are more responsive to short-term changes in precipitation and runoff than at the Bay mouth.

After hatching during June and August, immature crabs go through several weeks (37 to 69 days when reared in the laboratory; Costlow and Bookhout 1959) in zoeal and megalopal (larval) stages near the Chesapeake Bay mouth (Van Engel 1958) or in near-shore shelf waters (Smyth 1979 and Sulkin 1981). It is during these larval stages that crabs are most susceptible to those physical and biological mechanisms producing year class fluctuations.

For example, passive drift mechanisms can affect larval retention or immigration into the Bay. Marsh detritus, pulverized by ice during severe winters, contributes to planktonic blooms and zooplankton reproductive capacity. Zooplankton blooms and their nauplii provide a food source for blue crab larvae survival at first-feeding (Costlow and Bookhout 1959). Ctenophores and chaetognaths act as both predator (feeding on crab larvae) and competitor (feeding on smaller zooplankton). Seasons when abundances of ctenophores and chaetognaths are below normal may be favorable to crab larvae survival.

Post-larval immature crabs drop to the bottom in autumn and begin to migrate up-estuary to nursery areas in the James, York, Rappahannock, and Potomac rivers on the western shore or Tangier and Pocomoke sounds on the eastern shore of the Bay. Van Engel and Joseph (1968) described a nursery area as a region which 1) is physiologically suitable in terms of chemical and physical features, 2) provides an abundant, suitable food supply with a minimum of competition at each trophic level, and 3) provides protection from predation. For example, nursery areas are either beneficiaries of or sites of high biological productivity, e.g. marsh zones or submerged vegetation beds. Secondarily, submerged vegetation and marshes provide protection from predators for molting blue crabs. The degree of predation in a given season may significantly alter the recruitment success of a year class.

Sulkin et al. (1980) and Sulkin (1981) have recently investigated several behavioral responses during the ontogeny of C. sapidus larvae. They deduced that the response patterns, when applied concurrently, produced a distinct vertical distribution agreeing with larval distributions observed in situ (Sandifer 1973, Goy 1976, and Smyth 1980). Early zoeal stages prevail in surface waters, while late larval stages are found in deeper waters.

Sulkin et al. (1980) and Sulkin (1981) found stage I zoeae to exhibit negative geotaxis (upward orientation), positive phototaxis, and increasing swimming rates as hydrostatic pressure and salinity increase. Each response pattern serves as a behavioral mechanism to promote upward migration and maintenance of larval distribution in surface waters. However, early stage larvae were rendered inactive or photo-neutral by a 5 ppt. reduction in salinity. They suggest that this effect and migration inhibition by sharp thermoclines or haloclines could serve to trap nascent larvae below strong pycnoclines.

By the terminal zoeal stage (VII), C. sapidus larvae exhibit positive geotaxis, negative phototaxis, and decreasing swimming rates upon acclimation to increasing hydrostatic pressure and salinity, and decreasing temperature. Each response pattern at this stage is indicative of larval distribution in the lower portion of the water column. Intermediate zoeal stages (IV) exhibit intermediate behavioral response patterns.

Blue crab environmental model - Recruitment based on life history and ontogenic behavioral response patterns

The ontogenic changes in behavioral response patterns of C. sapidus larvae, combined with adult female migration to the lower Chesapeake Bay before hatching and larval distribution observed by Sandifer (1973), Goy (1976) and Smyth (1980), suggest support for a larval retention and immigration model based on vertical distribution and passive transport mechanisms in a salt-wedge estuarine circulation system and in circulation on the adjacent coastal shelf. Conditions promoting larval retention and immigration under this system would be, 1) those inhibiting offshore surface transport of early stage zoeae in surface waters, 2) those promoting late stage zoeal and megalopal immigration back into the estuary through bottom drift, and 3) those affecting vertical larval distribution so they maintain favorable positions in relation to local circulation systems.

Salinity and river discharge have been found to be important factors regulating recruitment (entrance into the fishable stock) success of blue crabs. Pearson (1948) found that river discharge from the James and Potomac rivers (highest discharge rates of the four major rivers in the lower Bay) during the spawning season (May, June) was negatively correlated with the index of annual abundance of adult crabs of a given year class, thus indicating higher salinities during the spawning season enhance recruitment success to the fishable stock. More recently, Van Engel suggested that recruitment success was enhanced by high salinities and low runoff rates during the summer spawning season, and low salinities and high runoff rates during the subsequent autumn (Austin and Ingham 1979).

Larval survival is probably dependent upon a complex array of factors. Although larvae are susceptible to extremes in temperature and salinity, typically the ranges of temperature and salinity in the lower Bay do not exceed blue crab larval tolerances of 25-30°C and 20-31 ppt. (Costlow and Bookhout 1959). Nevertheless, temperature and salinity gradients may structure the water to enhance proper distribution of suitable food at first feeding, when the intake of food is so important to survival (Cushing 1972, Anger et al. 1981). The amounts of incident sunlight during a spawning season may also contribute to the abundance of suitable food. Decreased levels of sunlight due to cloud cover may delay and decrease planktonic bloom, and therefore browsing by zooplankton. Additionally, high winds may disrupt pycnocline stability, dispersing food but increasing the availability of dissolved oxygen near the bottom.

Furthermore, Penry (1982) suggested that submerged aquatic vegetation (SAV) was a significant winter nursery area offering predation protection (Tagatz 1968 and Lascara 1981) to juvenile C. sapidus. She found significant differences in juvenile abundance between seagrass beds and adjacent sandy (non-vegetated) and deep water areas in the lower York River and the adjacent Guinea Marsh area. Season, water depth, vegetation density and patchiness, and juvenile crab size were all important determinants of juvenile distribution and abundance. Blue crab juvenile densities ranged from 4 to 31 individuals per square meter (mean = 13). Significant reductions in the amount of SAV available to juvenile blue crabs since 1971 (Orth et al. 1982) would contribute to declining recruitment success if SAV beds were important nursery areas.

This study was designed to investigate fluctuations in stock size at the beginning of the winter dredge fishery and its relationship to parental stock size, environmental conditions at time of hatching, and the amount of submerged aquatic vegetation available to juvenile blue crabs for protection. Although designed to derive a functional predictive relationship, the model also serves to refine important environmental inputs, suggest mechanisms of interaction, and illuminate areas of future research needs.

METHODS

Data collection and analysis

Data sets used in this analysis were derived from a number of sources. Daily catch records by vessel, from December 1964 to March 1982, were collected by the author through a rigorous survey of blue crab wholesalers and packing houses in the Hampton Roads area. The records were obtained from catch logs and weekly receipts, fortunately retained by shore dealers. The data were checked for reasonableness and duplication, but stored by vessel-day anonymously. Prior daily catch records (1931 to 1946) were collected by the U.S. Fish and Wildlife Service. Catch records between 1944 and 1964 were collected by the Fisheries Department, Virginia Institute of Marine Science (VIMS).

The winter dredge fishery is a good estimator of spawning stock size for a number of reasons. Legal males (crabs larger than five inches) typically remain in the lower salinity reaches of the Bay and its tributaries, consequently the winter dredge fishery samples primarily from due-to-spawn females. Approximately 85 percent of the winter dredge catch is composed of adult females, the remaining 15 percent of adult males and immature crabs of both sexes (Van Engel 1962). Older, "ocean-run" females are not generally sought after because their iodoform odor makes them unmarketable (Van Engel 1958).

Hydrographic data sets, primarily temperature and salinity, were obtained from the Chesapeake Bay Institute. Documented sampling methods can be obtained from Karweit et al. (1976). Hydrographic conditions were averaged on a monthly basis at each station across the Bay mouth, from 1949 to 1978. Although the amount of available data were large, many months from 1951 to 1965 were not represented and data prior to 1951 were of dubious integrity and were not used.

Monthly mean streamflow at the mouth (section E) of Chesapeake Bay was collected and summarized by the U.S. Geological Survey (U.S. Department of the Interior 1951-1982). These data are currently available from the Fisheries Department, VIMS (Harris and Van Engel 1981).

Submerged aquatic vegetation (SAV) acreage for the lower (Virginia) portion of Chesapeake Bay, summarized by U.S. Geological Service topographic quadrangles, was obtained from Orth et al. (1982). Surveys were made in 1971, 1974, 1978, and 1981, but only quadrangle acreage on the western shore of the Bay was used in the analysis due to the lack of eastern shore survey data in 1971 and 1974. Linear interpolation was employed to estimate SAV acreage in each quadrangle for 1972, 1973, 1975, 1976, 1977, and 1979.

Average monthly percent of possible sunshine hours (number of hours of sunshine/sum of hours, sunrise to sunset) were collected and summarized by the National Climatic Center (U.S. Department of Commerce 1950-1981), and are maintained by the Fisheries Department, VIMS (Harris and Van Engel 1981).

Wind observations for Norfolk, Va. Municipal Airport (NMA) were obtained from the National Climatic Center, Asheville, N.C. through the Center for Environmental Assessment Services (EDIS/NOAA), Columbia, Mo. Hourly (sometimes on a 3 hour observation frequency) observations of wind speed and direction were resolved into north(+) - south(-), east(+) - west(-) components by the author and summarized on a monthly basis by the Fisheries Department, VIMS. Observations were obtainable from 1948 through 1979.

Data management and analysis was accomplished using a combination of Fortran 77, Advanced Graphics II (Tektronix), Statistical Package for the Social Sciences (SPSS) (Nie et al. 1970 and Hull and Nie 1981), and SPSS Graphics (Hull and Nie 1981) on the VIMS Prime 750 computer.

Leslie stock analysis (LSA)

Recruitment usually refers to the entry of a year class into the fishable portion of a stock. However, the blue crab fishery can be separated into two distinct portions. The summer fishery employs scrapes, pots, and trotlines to capture active adult crabs. The winter fishery employs dredges to dig hibernating crabs from the bottom. Recruitment, as usually defined occurs during the summer when adult crabs reach a legal minimum size of five inches. Nevertheless, recruitment will hereafter be used to connote the stock size, primarily females available at the beginning of the winter dredge fishery.

Female spawning stock and adult recruitment into the winter dredge fishery estimates were accomplished utilizing the methods of Leslie and Davis (1939). They involved plotting catch per unit effort, in this case catch per vessel-day, against cumulative catch over the winter dredge season, the functional relationship being:

$$C_t/E_t = qN_o - qK_t \qquad \text{(Eq. 1)}$$

where:

C_t/E_t = catch per vessel-day

q = catchability - the proportion of the stock taken by one unit of fishing effort

N_o = stock size at the beginning of the dredge season

K_t = cumulative catch of the dredge fishery from the start of a dredge-season day plus half the total catch on that day.

This relationship only holds when the measure of fishery effort recognizes any management-induced changes in true fishing effort due to catch restrictions or quotas. Since the late 1950's, daily catch quotas have been adjusted to between 20 and 30 barrels per vessel day, 2000 and 3000 lbs. (908 and 1362 kg.) respectively. When a legal catch limit was imposed, the Leslie stock analysis was adjusted to compensate. Each day during the dredge season was examined to determine when more than two-thirds of the vessels reached the legal quota. Days when this criterion was not met, catch per vessel-day was not entered into the regression but only contributed to the cumulative catch (K_t).

Additionally, cumulative catch was adjusted to reflect total catch by the fishery rather than only the portion sampled. This adjustment was accomplished by multiplying the cumulative daily catch observed by the total number of winter crab-dredge licenses issued (Virginia Marine Resources Commission 1980, Van Engel and Wojcik 1965) divided by the number of vessels sampled during the season.

Confidence limits for winter-dredge recruitment (N_o) were calculated at a 95% level of probability utilizing the formulae of DeLury (1951):

$$N^2 (q^2 - t_p^{\,2} S^2_{yx} C_{22}) - 2 (q^2 N_o - t_p^{\,2} S^2_{yx} C_{12}) + (q^2 N_o^{\,2} - t_p^{\,2} S^2_{yx} C_{11}) = 0 \qquad \text{(Eq. 2)}$$

where:

$C_{11} = \Sigma X^2 / n \Sigma x^2$

$C_{12} = \Sigma X / n \Sigma x^2$

$C_{22} = 1 / \Sigma x^2$

t_p = t value at P = 0.95 for N-2 degrees of freedom

n = number of vessel-days used in the relationship

S^2_{yx} = mean square for deviations from the regression

X = catch per vessel-day observation

Σx^2 = sum of squares of X

Solution for the confidence limits on N_o was accomplished by determining the quadratic roots of N.

Estimates for spawning stock size were obtained by removing total cumulative catch for the dredge season from the recruitment estimate (N_o-K_{t-max}). It obviously assumes that natural mortality does not remove potential spawners from the recruitment estimate between the beginning of the winter dredge season and the onset of spawning activity in early summer, and spring migration does not contribute to or remove from the spawning stock as estimated by catch rates during the winter dredge season.

Stock Recruitment Models

In order to examine environmentally induced changes in blue crab larval survival and subsequent recruitment into the winter dredge fishery, a density-independent index of survival was obtained. It was calculated as a ratio between the observed stock-recruit relationship and the expected stock-recruit relationship based upon density-dependent mortality.

Two stock recruitment models were employed to determine density-dependent mortality relationships, each abiding by criteria established by Ricker (1975). Essentially, the model must reflect density-dependent mortality reducing recruitment more than the reproductive potential increases recruitment when parental (spawning) stock is greater than some optimal level.

Ricker's (1954) first model can be described by the equation:

$$R = Se^{(S_r - S)/S_m} \quad \text{(Eq. 3)}$$

where: R = recruitment (= N_o)

S = parental stock size

e = base of natural logarithm

S_r = parental stock size when recruitment exactly replaces the parental stock

S_m = parental stock size when recruitment is at a maximum

The parameters of the model (S_r, S_m) were estimated through least squares linear regression of the functional form:

$$\log_e (R/S) = \frac{S_r}{S_m} - \frac{1}{S_m} \cdot S \qquad \text{(Eq. 4)}$$

When the above linear relationship is presented in its curvilinear form (Equation 3), the error term (E_{ij}) is no longer normally distributed with a mean of zero, but exhibits a skewed distribution. For this reason, a second stock recruitment model (Ricker 1958) was fitted by least squares approximation of a curvilinear fit utilizing simultaneous solution of normal equations describing the parameters A and B. The functional form of the model is:

$$R = AP \exp(-BP) \qquad \text{(Eq. 5)}$$

where:

R = recruited stock size (= N_o)

P = parental or spawning stock size (= S)

A,B = parameters describing the model

The algorithm deriving A and B, the error terms and estimates are described by Cushing and Harris (1973).

As employed by Nelson et al. (1977) when predicting year class strength of larval menhaden (Brevoortia tyrannus), a survival index was derived as the ratio of observed recruitment, estimated by the Leslie stock analysis at t + 2 years, to the expected recruitment based upon spawner stock size and the predicted stock recruitment relationship.

Environmental Analysis

A multiple regression model was developed to explain the variance in the stock recruit models and to predict an expected survival index based on environmental conditions at time of hatching:

$$SI = b + m_1X_1 + m_2X_2 + m_3X_3 + m_4X_4 + \ldots + m_mX_m \pm E_{ij} \qquad \text{(Eq. 6)}$$

where:

SI = survival index

b = intercept value

X_n = environmental quality index (e.g. temperature, wind conditions, water stability, etc.)

m_n = coefficient for X_n

E_{ij} = error term

A number of environmental features were examined for their influences on blue crab recruitment success as measured by the survival index. Each feature was summarized or averaged on a monthly basis, January through December, over the spawning year. After individual examination by least squares linear regression, environmental data sets without significance were not included in the final model. Data sets exhibiting significant relationships to the survival index were included in the linear multiple regression analysis for further distillation into the final environmental model.

Water conditions at hatching were examined from a data set of hydrographic observations on a transect across the Bay mouth. The transect was divided into halves, a southern sector and a northern sector. Sea surface temperatures and salinities were averaged for all observations in a given month and sector. Moreover, a water column stability index was developed to examine its relationship with the survival index. The stability index was derived by averaging the maximum sigma-t (see Sverdrup et al. 1942) difference between depth observations for each station across all stations along the Bay mouth transect.

Meterological conditions (i.e. atmospheric pressure, wind conditions and incident sunshine), obtained from observations of the U.S. National Weather Service, were summarized on a monthly basis across the spawning year.

Atmospheric pressure gradients at sea level, used as an indicator of wind-driven surface transport mechanisms, were expected to exclude some of the land/sea breeze phenomena exhibited by land-based observation of wind conditions and be more reflective of general long-term wind conditions. East-west and north-south atmospheric pressure gradients were calculated from the difference between the Norfolk - Roanoke Va. and Baltimore, Md - Cape Hatteras, N.C. monthly average sea level atmospheric pressure observations. When only ground-level atmospheric pressure observations were available, they were adjusted (Berry et al. 1942) to reflect sea level observation by:

$$\log_{10} p_o = \log_{10} p + h/221T \qquad \text{(Eq. 7)}$$

where:

p_o = mean sea level pressure, in millibars

p = observed pressure at station elevation, in millibars

h = station elevation, in ft.

T = mean station temperature, in °K

The atmospheric pressure gradient analysis was designed so that gradients representing easterly (from) and northerly (from) conditions were positive.

The components of hourly wind observations at NMA were averaged on a monthly basis and examined by least squares linear regression for significant relationships with the survival index. Additionally, the monthly average resultant magnitude was derived from the monthly average wind components in order to examine relationships between the wind magnitude and the survival index.

Other environmental features used in this analysis, were the monthly average atmospheric pressure at sea level and the percent possible sunshine for the month (the number of hours sunshine divided by the number of possible sunshine hours times 100). Both were observed at Norfolk Municipal Airport, Virginia (NMA). Chesapeake Bay section E streamflow was also examined on a monthly basis across the year of spawning. Estimates of submerged aquatic vegetation acreage by quadrangles were examined for significant relationships with the survival index.

Recruitment Prediction

Since, by definition:

$$R_p = R_{sr} \cdot SI \qquad \text{(Eq. 8)}$$

where:

R_p = predicted recruitment

R_{sr} = predicted recruitment based on stock recruitment model alone

SI = survival index

utilizing Ricker's (1958) second stock recruitment model (Equation 5) and the survival index predictive model (Equation 6), a final predictive model was developed of the form:

$$R_p = [AP \exp(-BP)][b + m_1X_1 + m_2X_2 + \ldots + m_nX_n \pm E_{ij}] \qquad \text{(Eq. 9)}$$

Only data from the spawning years 1950 through 1979 were used in the environmental analysis. By application of the spawning stock estimate (Equation 1) and significant environmental conditions for 1980, 1981, and 1982, recruitment into the winter dredge fishery was predicted for 1981-82, 1982-83, and 1983-84 respectively.

RESULTS AND DISCUSSION

Leslie stock analysis

The Leslie (Leslie and Davis 1939) stock analysis method was chosen to estimate blue crab recruitment into the winter dredge fishery because catch rates during the season (typically December 1st to March 31st) exhibited significant reductions as crabs were removed from the population by fishing. Moreover, it was chosen rather than the alternative DeLury (DeLury 1947) method because a better estimate of cumulative catch was available than of cumulative effort.

The conceptual basis for the Leslie method arises from the extrapolation of decreasing catch rates to the point when the fishery becomes completely exploited. Obviously, higher estimates of recruitment (N_0) have greater variances. Additionally, as the stock approaches complete exploitation, a unit of fishing effort produces less catch, hence less removal from the population and a decreased catch rate decline. As the stock approaches complete exploitation, catch rates approach zero as an asymptote rather than as a linear function. Despite its problems, blue crab recruitment estimates by the Leslie method have had reasonable fit and narrow confidence limits.

Least squares linear regression of daily catch by vessel-day on cumulative catch provided estimates of recruitment (N_0) and spawning stock size (N_o-K_{t-max}). For example, Figures 1-4 show the regressions for winter dredge seasons of 1950-51, 1957-58, 1967-68, and 1976-77, respectively. Total cumulative catch ranged from 1.21 million lbs. in 1943 to 26.34 million lbs. in 1966, while recruitment ranged from 2.90 million lbs. in 1941 to 48.79 million lbs. in 1966, if the aberrant values in 1948, 1969 and 1981 are ignored (Table 1).

The estimate of the fishery's total cumulative catch (K_{t-max}) sometimes exceeded total landings for the winter dredge fishery in Virginia. The variance between K_{t-max} and total landings occurs because only a portion of the fishery was sampled by the author, the U.S. Fish and Wildlife Service, and the Fisheries Department at VIMS. The adjustment of the sampled catch to reflect total cumulative catch for the fishery exacerbates the variance when the sampled portion is small (e.g. 1965 to 1974 in Table 1) and not representative of the average fishing effort. Inaccurate estimates of K_{t-max} contributed to a greater standard deviation on the estimates of recruitment (N_o) and spawning stock size (N_o-K_{t-max}) than that given by Equation 2.

The catchability coefficient (q) represents the expected decrease in catch (pounds) on a given day due to catches (pounds) made earlier in the season. For example, a catchability coefficient of 1.0×10^{-4} connotes an expected catch 1.0×10^{-4} pounds less for every pound of catch taken earlier in the season.

Nevertheless, certain conditions may exist to increase the catchability coefficient until it approaches or is less than zero (e.g. 1948, 1969, and 1981). Bad weather decreasing the amount of

Figure 1: Leslie stock analysis regression for December 1, 1950 to March 31, 1951.

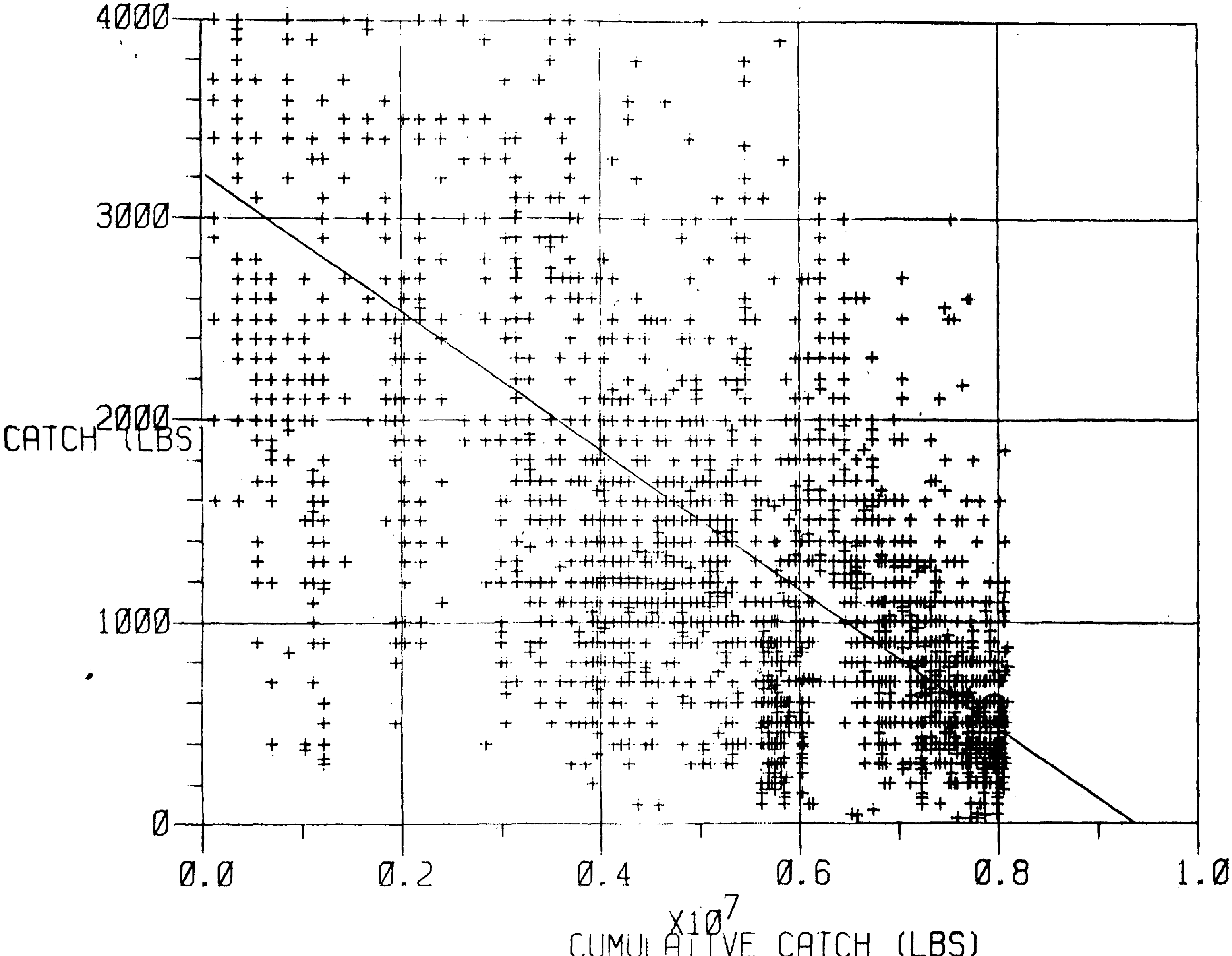

4000
3000
2000
1000
0
CATCH (LBS)
0.0
0.2
0.4
0.6
0.8
1.0
X10^7
CUMULATIVE CATCH (LBS)
CATCH.5

Figure 2: Leslie stock analysis regression for December 1, 1957 to March 31, 1958.

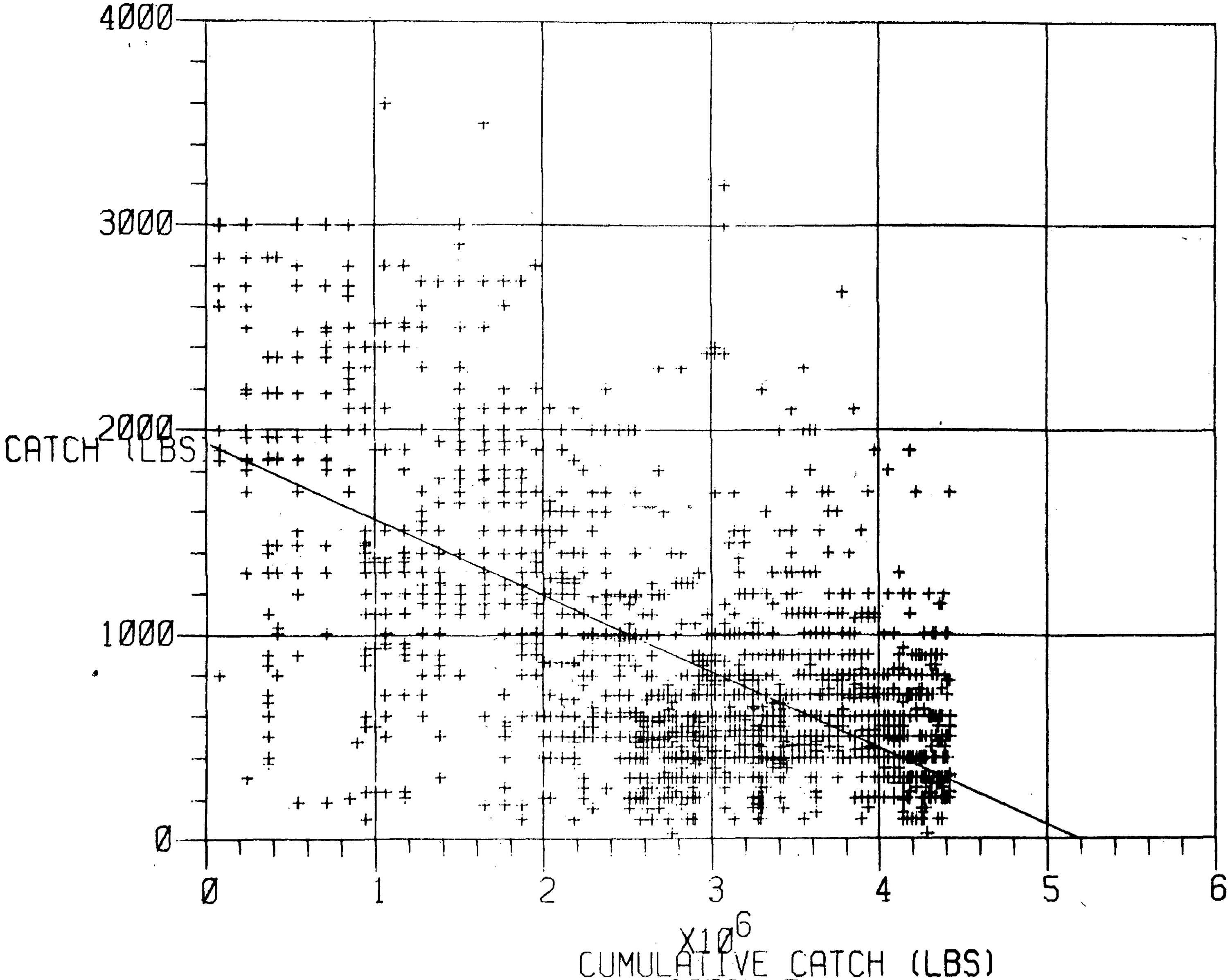

4000
3000
2000
1000
0
CATCH (LBS)
0
1
2
3
4
5
6
X10^6
CUMULATIVE CATCH (LBS)
CATCH.5

Figure 3: Leslie stock analysis regression for December 1, 1967 to March 31, 1968.

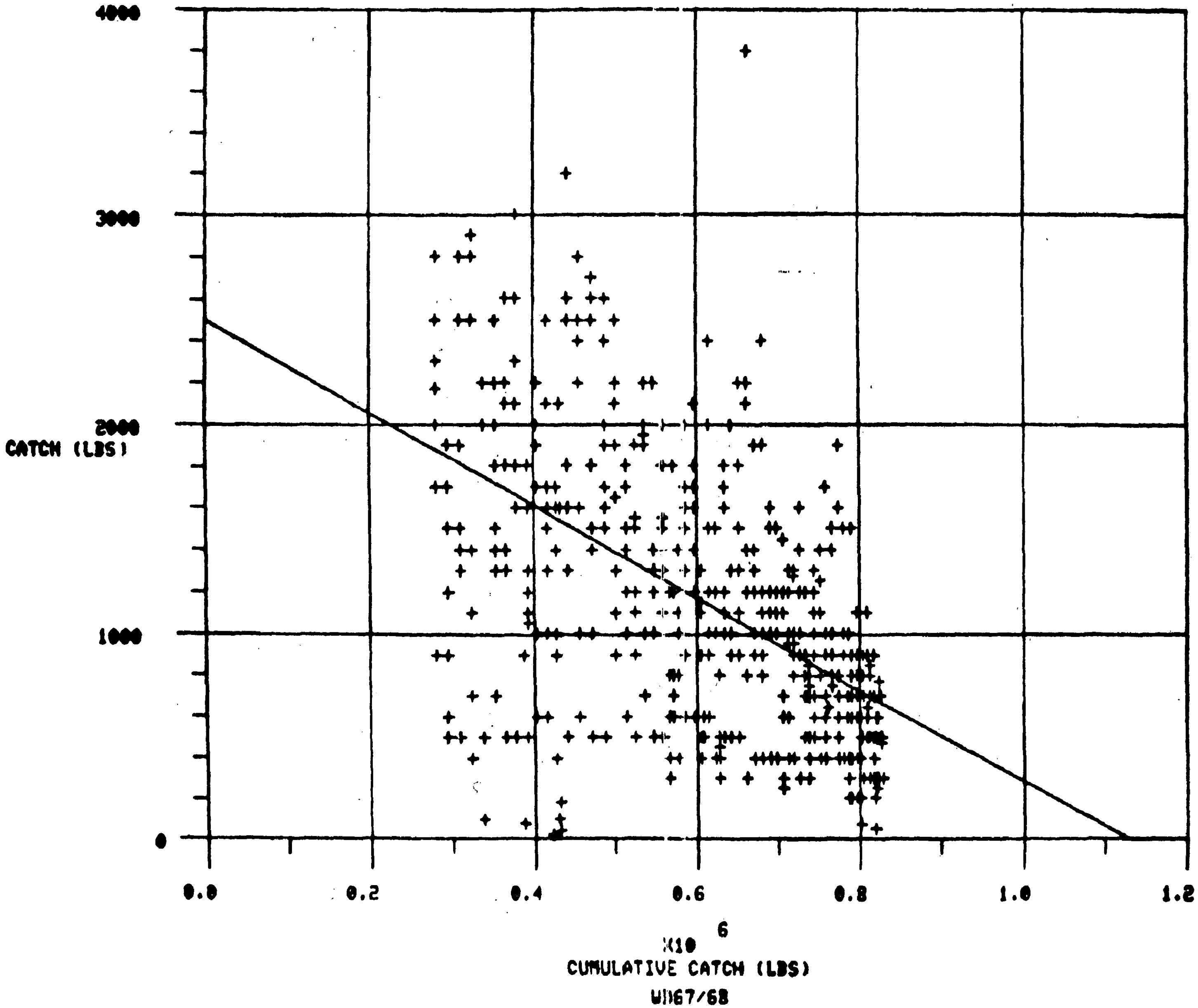
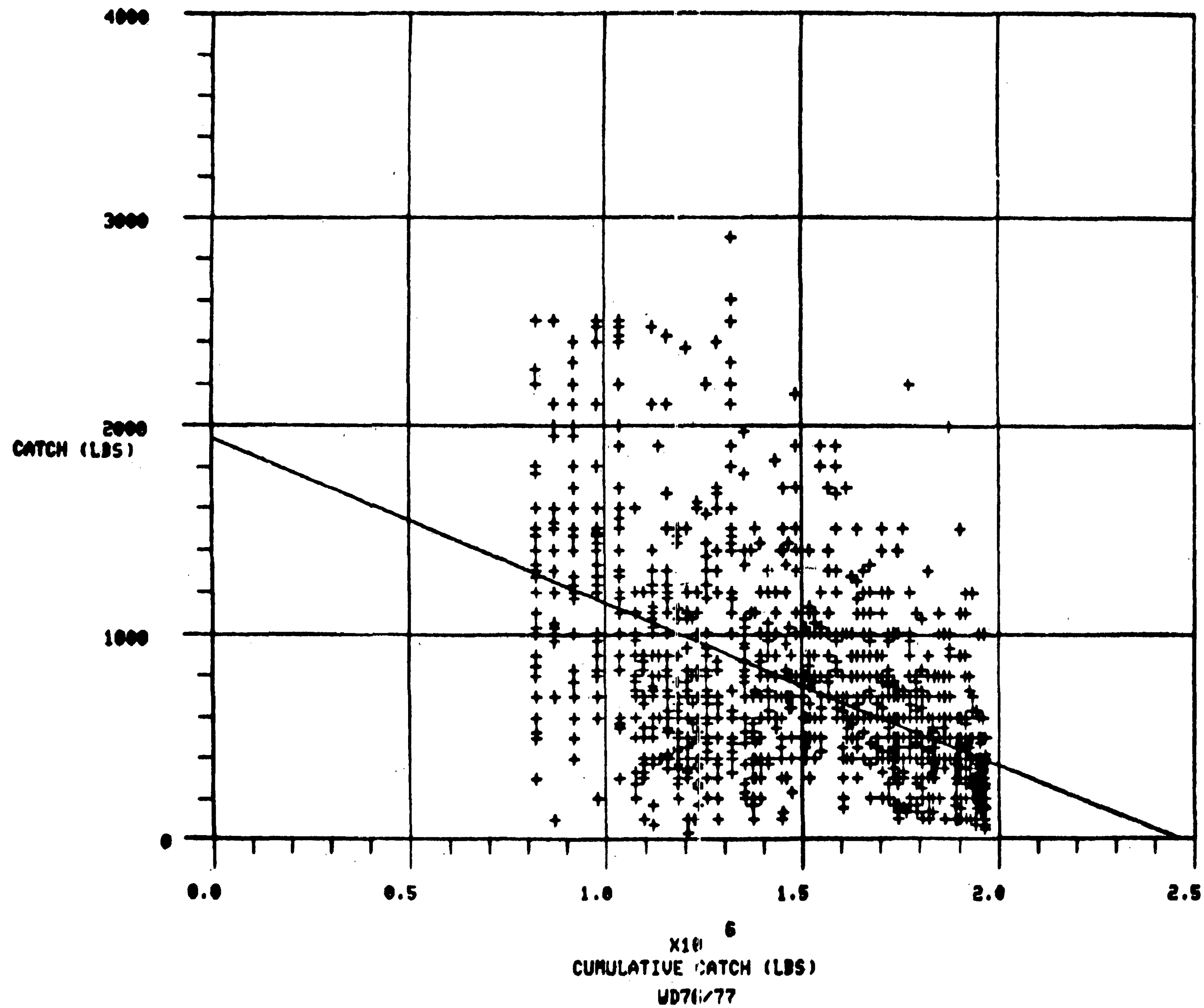

4000
3000
2000
CATCH (LBS)
1000
0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
X10 6
CUMULATIVE CATCH (LBS)
WN67/68

Figure 4: Leslie stock analysis regression for December 1, 1976 to March 31, 1977.



4000
3000
2000
CATCH (LBS)
1000
0
0.0
0.5
1.0
1.5
2.0
2.5
X10 6
CUMULATIVE CATCH (LBS)
WD76/77

TABLE 1. Leslie (Leslie and Davis 1939) stock analysis of winter dredge blue crab catch in Chesapeake Bay, December 1, 1931 to February 23, 1982.

(1) Winter Dredge Season beginning December 1	(2) Number of Licenses Issued	(3) Number of Vessels Sampled	(4) Number of Vessel-Days Used in Regression	(5) Total Cumulative Catch (K_t, million lbs.)	(6) Catchability Coefficient (q, x 10^{-4})
1931	61	3	257	11.68	1.38
1932	60	3	236	7.02	2.22
1933	54	4	254	3.47	3.70
1934	70	4	331	3.14	4.00
1935	92	6	335	4.72	3.15
1936	87	7	322	4.56	1.23
1937	105	8	441	4.23	1.66
1938	80	16	835	4.62	3.32
1939	79	14	896	4.93	3.44
1940	96	13	722	4.44	5.49
1941	70	12	752	1.99	2.62
1942	63	9	434	5.25	2.75
1943	54	12	584	1.21	0.79
1944	46	17	934	2.86	3.91
1945	70	32	1391	4.81	3.22
1946	77	39	2521	3.24	2.07
1947	78	66	3101	4.34	3.73
1948	99	50	2175	5.19	N/A
1949	107	50	2728	8.60	3.28
1950	94	51	3111	8.09	3.44
1951	122	40	2074	13.17	2.66
1952	128	49	2524	4.76	2.79
1953	150	54	2660	12.37	2.05
1954	85	45	2035	2.68	5.51
1955	107	34	2260	16.91	1.40
1956	110	46	1980	4.21	4.46
1957	109	47	1930	4.42	3.74
1958	104	37	1379	7.78	2.18
1959	109	16	613	6.14	3.17
1960	98	44	324	8.65	10.40
1961	144	45	2585	14.08	0.89
1962	115	55	1714	11.55	3.27

(1) Winter Dredge Season beginning December 1	(7) Recruitment (N_o, million lbs.)	(8) Recruitment Upper Limit (million lbs.)	(9) Recruitment Lower Limit (million lbs.)	(10) Spawning Stock (N_o-K_t, million lbs.)	(11) R^2
1931	22.82	29.96	18.93	11.14	0.142
1932	10.82	13.11	9.42	3.80	0.213
1933	4.80	5.55	4.30	1.33	0.267
1934	3.95	4.44	3.60	0.81	0.258
1935	5.85	6.43	5.41	1.13	0.325
1936	11.71	22.50	8.43	7.15	0.040
1937	6.84	7.95	6.08	2.61	0.185
1938	6.09	6.58	5.71	1.48	0.239
1939	5.94	6.22	5.70	1.01	0.387
1940	4.51	4.67	4.37	0.06	0.452
1941	2.90	3.21	2.67	0.91	0.198
1942	9.27	11.00	8.14	4.02	0.166
1943	6.47	35.96	3.80	5.26	0.009
1944	3.83	4.18	3.55	0.96	0.178
1945	7.70	8.37	7.16	2.88	0.168
1946	5.02	5.40	4.71	1.79	0.124
1947	5.79	5.99	5.61	1.45	0.286
1948	N/A	N/A	N/A	N/A	N/A
1949	10.14	10.37	9.92	1.54	0.433
1950	9.36	9.56	9.17	1.26	0.420
1951	16.07	16.54	15.65	2.91	0.415
1952	5.64	5.78	5.50	0.88	0.398
1953	15.83	16.24	15.44	3.45	0.415
1954	2.99	3.09	2.90	0.31	0.305
1955	26.90	28.23	25.74	9.99	0.257
1956	4.65	4.82	4.50	0.44	0.288
1957	5.18	5.34	5.04	0.76	0.393
1958	11.45	12.14	10.87	3.67	0.267
1959	7.53	8.03	7.15	1.39	0.254
1960	9.43	9.75	9.22	0.78	0.205
1961	24.49	26.03	23.19	10.40	0.157
1962	13.69	13.96	13.45	2.13	0.387

(1) Winter Dredge Season beginning December 1	(2) Number of Licenses Issued	(3) Number of Vessels Sampled	(4) Number of Vessel-Days Used in Regression	(5) Total Cumulative Catch (K_t, million lbs.)	(6) Catchability Coefficient (q, x 10^{-4})
1963	139	36	1654	13.97	1.03
1964	157	38	1683	13.97	1.02
1965	169	8	347	23.86	0.73
1966	186	8	399	26.34	5.24
1967	170	9	476	16.65	1.17
1968	178	11	488	9.28	0.92
1969	215	7	537	38.32	0.03
1970	198	8	432	17.17	0.77
1971	177	9	353	19.22	0.94
1972	162	8	506	16.80	1.00
1973	156	12	564	14.57	1.70
1974	181	13	575	14.99	1.16
1975	162	15	760	6.81	1.08
1976	143	48	1551	5.87	2.63
1977	140	15	732	10.99	0.54
1978	169	16	816	8.22	0.97
1979	180	21	1079	12.90	0.58
1980	207	36	1445	14.36	1.24
1981	N/A	45	1249	2.94	N/A

(1) Winter Dredge Season beginning December 1	(7) Recruitment (N_o, million lbs.)	(8) Recruitment Upper Limit (million lbs.)	(9) Recruitment Lower Limit (million lbs.)	(10) Spawning Stock (N_o-K_t, million lbs.)	(11) R^2
1963	21.22	22.50	20.17	7.25	0.191
1964	21.15	23.70	19.41	7.18	0.058
1965	40.03	47.09	35.74	16.17	0.155
1966	48.79	59.61	42.55	22.45	0.117
1967	21.32	23.16	19.94	5.67	0.263
1968	16.50	20.40	14.22	7.28	0.101
1969	692.07	6276.55	374.76	653.74	0.008
1970	26.44	29.80	24.12	9.27	0.205
1971	28.51	33.46	25.65	9.30	0.130
1972	23.54	26.01	21.77	6.74	0.213
1973	17.61	18.37	16.99	3.04	0.383
1974	19.46	20.77	18.47	4.46	0.237
1975	10.67	11.77	9.85	3.86	0.191
1976	7.34	7.61	7.10	1.47	0.271
1977	27.14	42.75	21.10	16.16	0.026
1978	14.24	16.35	12.76	6.03	0.129
1979	26.33	30.91	23.28	13.43	0.080
1980	19.42	20.30	18.68	5.06	0.254
1981	N/A	N/A	N/A	N/A	N/A

fishing effort represented by one "vessel-day", or conditions changing the accessibility of crabs to gear may yield a positive slope and negative catchability coefficient. Additionally, low levels of effort (few vessels) and high recruitment may create conditions such that fishing effort does not produce less catch per unit effort than that attributable to random variation. Because of the inability to calculate (1948, 1981) or uncertainty of its estimate (1969), these values for spawning stock size and recruitment into the winter dredge fishery were excluded from further analysis and consideration. However, if high recruitment contributed to the inability to estimate it by the Leslie method, the environmental analysis would be expected to predict high survival indices for 1947, 1968, and 1980.

Spawning stock estimates were derived by subtracting the cumulative catch (K_{t-max}) from the original winter dredge recruitment (N_o). This estimate of potential spawning stock is accurate if natural mortality is negligible between recruitment into the fishery and the onset of spawning activity the subsequent summer, and net migration does not contribute to or remove from the pool of potential spawners. The first condition is reasonably accurate when compared to high natural mortality during larval and immature stages (Penry 1982) and after spawning (Van Engel 1958). The second is without evidence or sufficient information to adjust the spawning stock size estimate.

Since recruitment estimates at t+2 were produced by the spawning stock at t, recruitment estimates were lagged two years to match to appropriate spawning stock estimate (compare Tables 1 and 4).

Furthermore, all estimates were advanced one year so that the corresponding year referenced the year of spawning rather than the preceeding winter dredge season. For example, recruitment into the 1933-34 dredge season was produced by the 1932 spawning stock as estimated from the 1931-32 dredge season.

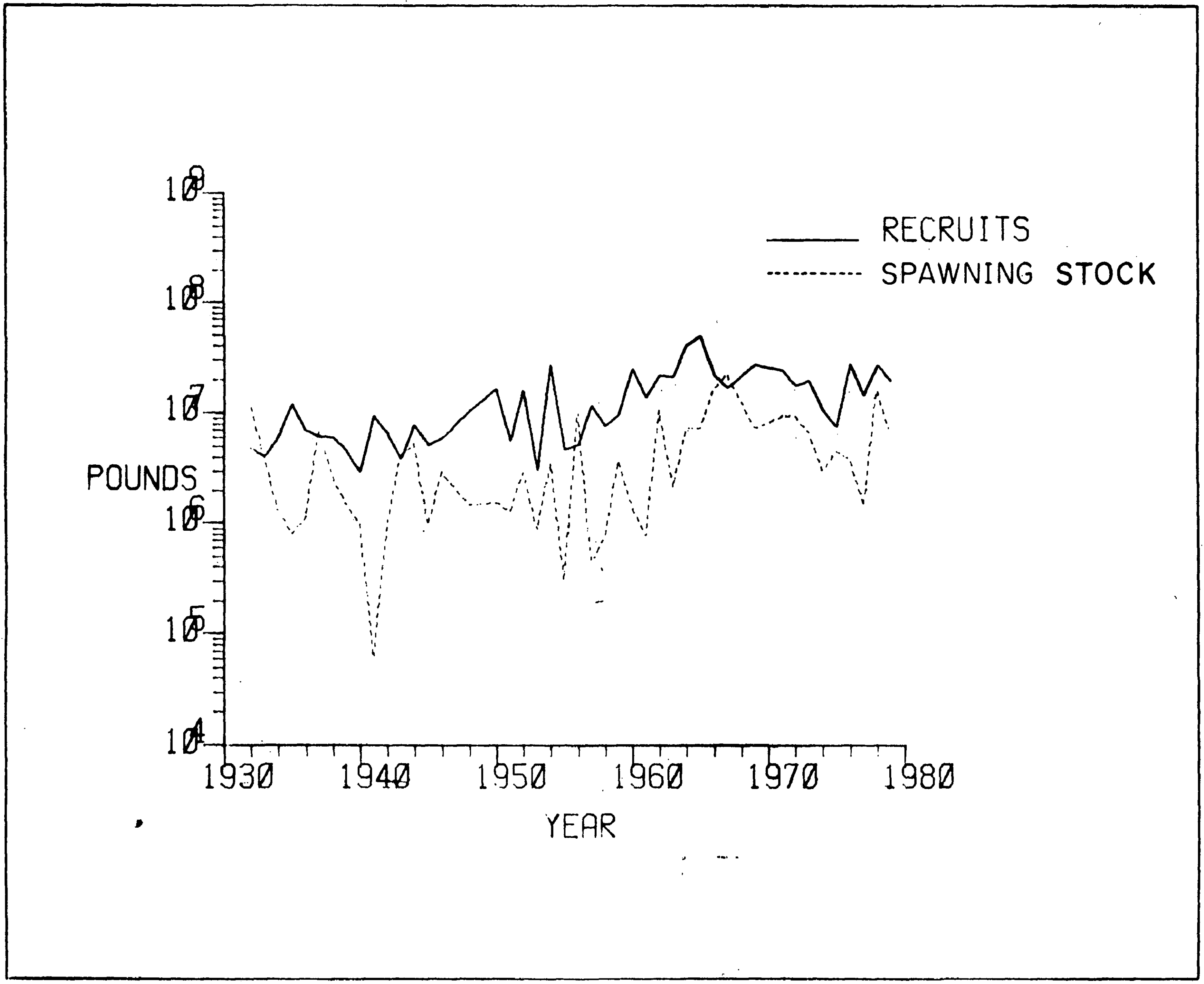
Plotting LSA recruitment estimates versus spawning stock estimates from 1932 to 1979 (Figure 5) reveals some interesting features. Only five years (1932, 1937, 1943, 1956 and 1967) exhibit conditions not producing recruitment at replacement level. A pattern is obvious between the recruitment and spawning stock estimates, especially when total cumulative catch exhibits mild interannual fluctuations. For example, a relationship exists between recruitment into the 1955-56 winter dredge season and the 1956 spawning stock estimate, the difference being the total cumulative catch (K_{t-max}) during the 1955-56 season.

Stock recruitment models

The stock recruitment models employed to isolate and estimate density-dependent mortality relationships reveal some interesting phenomena. Curvilinear functions and stock recruitment observations for Ricker's initial (1954) and second (1958) forms are found in Figures 6 and 7, respectively.

Least squares linear regression analysis of Ricker's (1954) initial model (Equation 4) yields a spawner-stock recruitment maximum (S_m) of 6.86 million pounds. This value represents an optimal level

Figure 5: Spawning stock and recruitment for spawning years (June to August) 1932 to 1979 estimated by the Leslie Stock Analysis method.



RECRUITS
SPAWNING STOCK
POUNDS
10^9
10^8
10^7
10^6
10^5
10^4
1930
1940
1950
1960
1970
1980
YEAR

Figure 6: Ricker's (1954) initial stock recruitment model for spawning years 1932 to 1979. Units for abscissa and ordinate are pounds x 10^7.

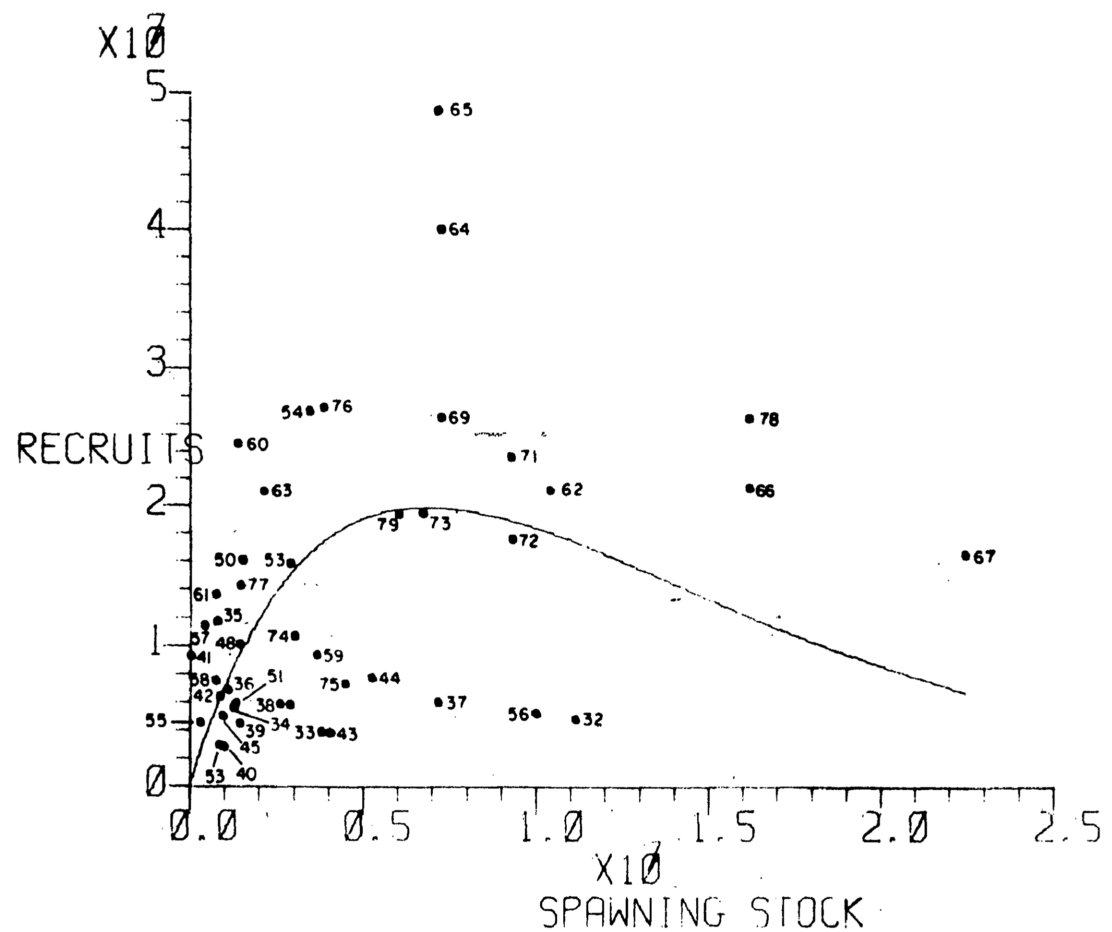
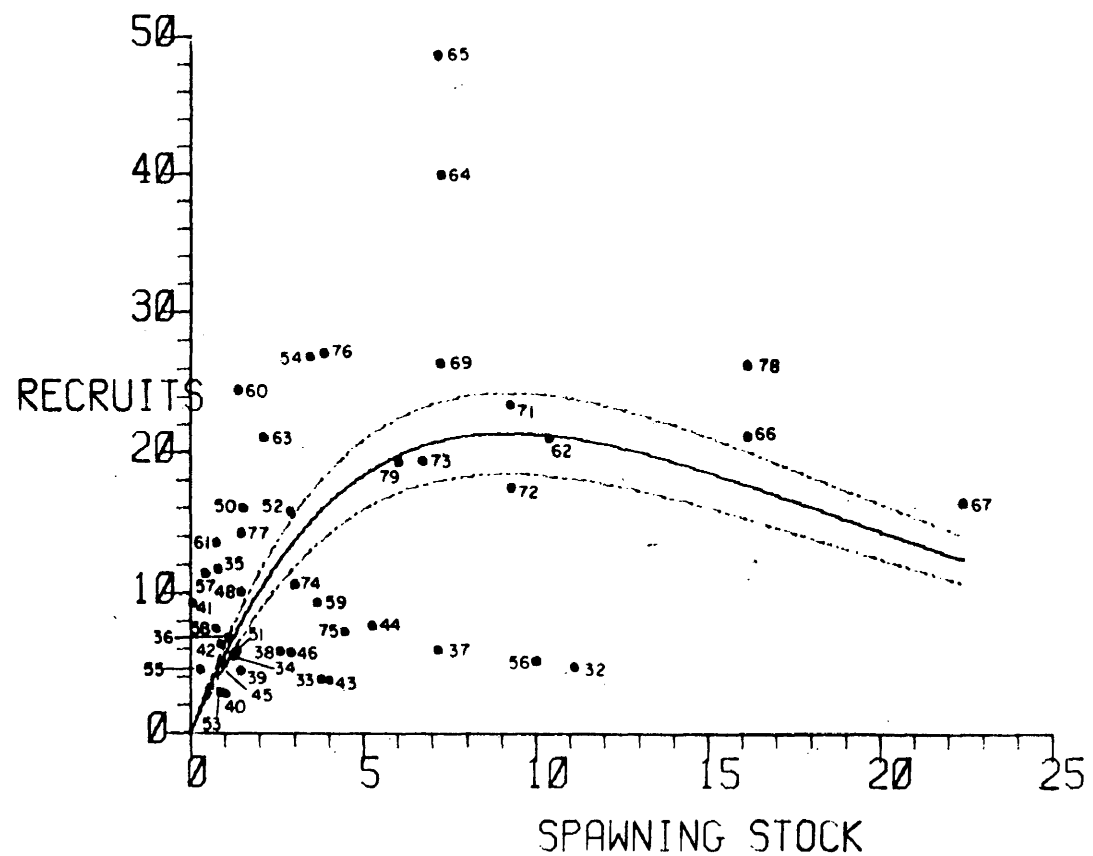

X10^7
RECRUITS
X10^7
SPAWNING STOCK

Figure 7: Ricker's (1958) second stock recruitment model for spawning year 1932 to 1979. Solid line is the model estimate. Dashed lines signify one standard deviation on the estimate of B. Units for the abscissa and ordinate are pounds x 10^6.


RECRUITS
SPAWNING STOCK
0
5
10
15
20
25
0
10
20
30
40
50

of spawning stock where reproductive potential due to spawning stock size less density-dependent larval mortality is maximized. Replacement spawning stock size (S_r), when predicted recruitment into the winter dredge fishery at t+2 exactly replaces the spawning stock at t, was 14.18 million pounds. Spawning stock size in excess of this value increases density-dependent mortality of the recruited stock to levels inhibiting replacement of the spawning stock.

The above regression model had an R^2 of 0.40, and was highly significant ($F_s = 27.99$, $F_{0.01[1,43]} = 7.26$); nevertheless, inspection of Figure 6 reveals poor fit of the curvilinear form (Equation 3) at high levels of spawning stock (1966, 1967 and 1978).

Ricker's (1958) second stock recruitment model was also employed. It was a derivation of Hoerl's (1954) general equation of the form:

$$y = ax^b e^c \qquad \text{(Eq. 10)}$$

when:

$b = 1$

$c < 0$

It maintains the same criteria and general form as Ricker's initial model, but density-dependent mortality is less effective at high spawner stock size. The second model is less dome-shaped and predicts higher recruitment at high spawning stock size than the initial model.

Least squares iterative estimation of the model's parameters, A and B (Equation 5), and solution of the normal equation matrix for a multiple regression with two independent variables where:

$$\log_e R = \log_e A + \log_e P - BP \qquad \text{(Eq. 11)}$$

gave 6.32 ± 0.85 and 0.108 ± 0.016, respectively. It had an R^2 of 0.441 and was highly significant ($F_s = 16.52$, $F_{0.01[2,42]} = 5.15$). The standard deviation of residuals was 9.55. The spawner-stock recruitment maximum (S_m) was 9.24 million pounds, 34% greater than that predicted by Ricker's initial model. Ricker's second stock recruitment model (Equation 5) appears to fit the observed blue crab spawning stock and recruitment data better than the initial model (Equation 3), primarily due to relatively high recruit survival at high spawning stock size.

Cushing (1971) and Cushing and Harris (1973) found the shape of the stock recruitment model to be related to the index of density independence ($-B\bar{P}$) and to the mean fecundity. Their indices of density dependence for finfish stocks are compared to the index for crabs in Table 2. Only stocks with good estimates of B, i.e. $SD_B/B < 40\%$, were used in their analysis. They found a trend of increasing density dependence from Atlantic herring through the gadoids.

Although a comparison of the index of density dependence for blue crabs ($-B\bar{P} = 0.508 \pm 0.541$; $SD_B/B = 21.7\%$) with that for finfish stocks may be inappropriate, many survival mechanisms operating on larval stages are the same. The index obtained for blue crabs is comparable to what Cushing and Harris (1973) found for Atlantic herring, a stock with low fecundity (Table 2) whose larval survival is least controlled by density dependent survival mechanisms. They also suggest that the index and its relationship to mean fecundity is underestimated at high levels of exploitation.

The ratio of the spawner stock recruitment maximum (S_m) to the replacement stock size (S_r) can be used to measure the shape of a stock recruitment curve. When comparing a family of stock recruitment curves, S_m approaches and then exceeds S_r as a curve becomes flattened. In the extreme cases, S_m approaches zero for "peaked-domes" and becomes infinite for those "flattish-domes" whose recruitment maximum becomes as asymptote. Therefore, the ratio (S_m/S_r) is small and less than unity for "peaked-domes" and approaches or exceeds unity for "flattish-domes."

Since their ratios (S_m/S_r) are similar (Table 2), blue crabs appear to exhibit a "peaked-dome" stock recruitment curve (Figure 7) similar to the gadoids. With the exception of Pacific herring, the ratio (S_m/S_r) for finfish stocks is inversely related ($R = -0.88$) to the index of density dependence ($-B\bar{P}$). Blue crabs and Pacific herring may deviate from this relationship possibly due to differences of exploitation rates.

Density dependent mortality and the associated high fecundity enable stocks with peaked stock recruitment curves to maintain considerable resilience in the face of heavy exploitation (Cushing 1981). Since the Chesapeake Bay blue crab stock exhibits a "peaked-dome" the stock should be able to support high exploitation levels. Additionally, estimates of spawning stock size from 1964 to 1979 have fluctuated around the optimal spawner stock recruitment

TABLE 2. Stock recruitment characteristics of blue crabs and finfish stocks. Data from the finfish stocks are from Cushing and Harris (1973).

(1) Stock	(2) Approximate Mean Fecundity	(3) Mean Index of Density Dependence ($-B\bar{P}$)	(4) Mean Stock Recruitment Ratio (S_m/S_r)
Blue crabs	1,500,000	0.51	0.54
Atlantic herring	170,000	0.54	0.75
Pink salmon	3,400	0.70	0.68
Red salmon	8,000	0.82	0.64
Flatfish	270,000	1.02	0.53
Pacific herring	45,000	1.16	1.20
Gadoids	700,000	1.75	0.50

maximum (S_m). At the present rate of exploitation, it appears that the Bay's blue crab stock is not being overfished by the winter dredge fishery.

Environmental Model

Survival indices for spawning years 1950 to 1979 were derived using Equation 8 from Ricker's second stock recruitment model (Equation 5). They ranged from 0.242 in 1956 to 4.274 in 1957 with a mean of 1.522 $\pm$ 0.899. Notable deviations occurred near the spawning stock recruitment maximum (S_m) for 1964 and 1965 (Figure 7), a series of years with drought conditions, and 1956, incident unknown.

Multiple regression analysis, of each environmental feature summarized on a monthly basis, revealed both significant relationships and environmental features with little or no influence on the survival index. All hydrographic conditions sampled at the Bay mouth, (including sea surface temperature, sea surface salinity, and a stability index derived from sigma-t gradients) were inadequate due to insufficient data. Chesapeake Bay Institute hydrographic data were available on a monthly basis only from 1966 to 1973. These limited data sets were insufficient to reveal strong relationships without extremely good fit to the survival indices. Multiple regression analysis of atmospheric pressure gradients of Baltimore, Md. to Cape Hatteras, N.C. and Norfolk, Va. to Roanoke, Va., and the east-west monthly average wind component at Norfolk, Va. Municipal Airport (NMA) gave no significant fits or interesting trends and were not considered further.

Other environmental features displayed significant relationships for some months and/or similar relationships for several months of duration. Monthly summaries of environmental variables with similar relationships to the survival indices were grouped for further analysis. Those variables displaying little or no relationships with the survival indices were not considered further. This elimination of meaningless variables and grouping of monthly summaries of environmental variables having similar relationships to the survival indices yielded nine independent variables to be considered further. Inclusion of these variables was based on significant relationships with the survival indices (significance of F less than or approximately equal to 0.100) or on suspected relationships between behavioral response patterns of crab larvae and the environmental features impacting survival through them. The nine independent variables were:

WARENECK - SAV acreage within the Ware Neck topographic quadrangle.

STFL - Cumulative Chesapeake Bay section E streamflow, July through November.

MAP - Sum of monthly average atmospheric pressure at NMA for July through October.

SUNE - Sum of percent possible sunshine at NMA for June and August.

SUNL - Sum of percent possible sunshine at NMA, September through November.

MAGMAY - Monthly average wind resultant magnitude at NMA for May.

MAGAUG - Monthly average wind resultant magnitude at NMA for August.

NSWAUG - Monthly average north-south wind component at NMA for August.

NSWOCT - Monthly average north-south wind compoennt at NMA for October.

Regressions of submerged aquatic vegetation (SAV) on the survival index exhibited some interesting relationships from a geographic viewpoint, but yielded a significant relationship (WARENECK in Table 3) only for the Ware Neck quadrangle (Figure 8). Only quadrangles including Mobjack Bay (Achilles, Ware Neck, and New Point Comfort) exhibited positive relationships to the survival index, with greater SAV promoting survival and subsequent recruitment. All other quadrangles exhibited negative, but not significant regressions. This finding is interesting in light of blue crab larval distribution around SAV beds investigated by Penry (1982). The survey region was adjacent to the Guinea Marsh area, north of the York River mouth and within the Achilles topographic quadrangle. Had the investigation occurred elsewhere, the distributional heterogeneity between vegetated and non-vegetated areas may not have been as distinct.

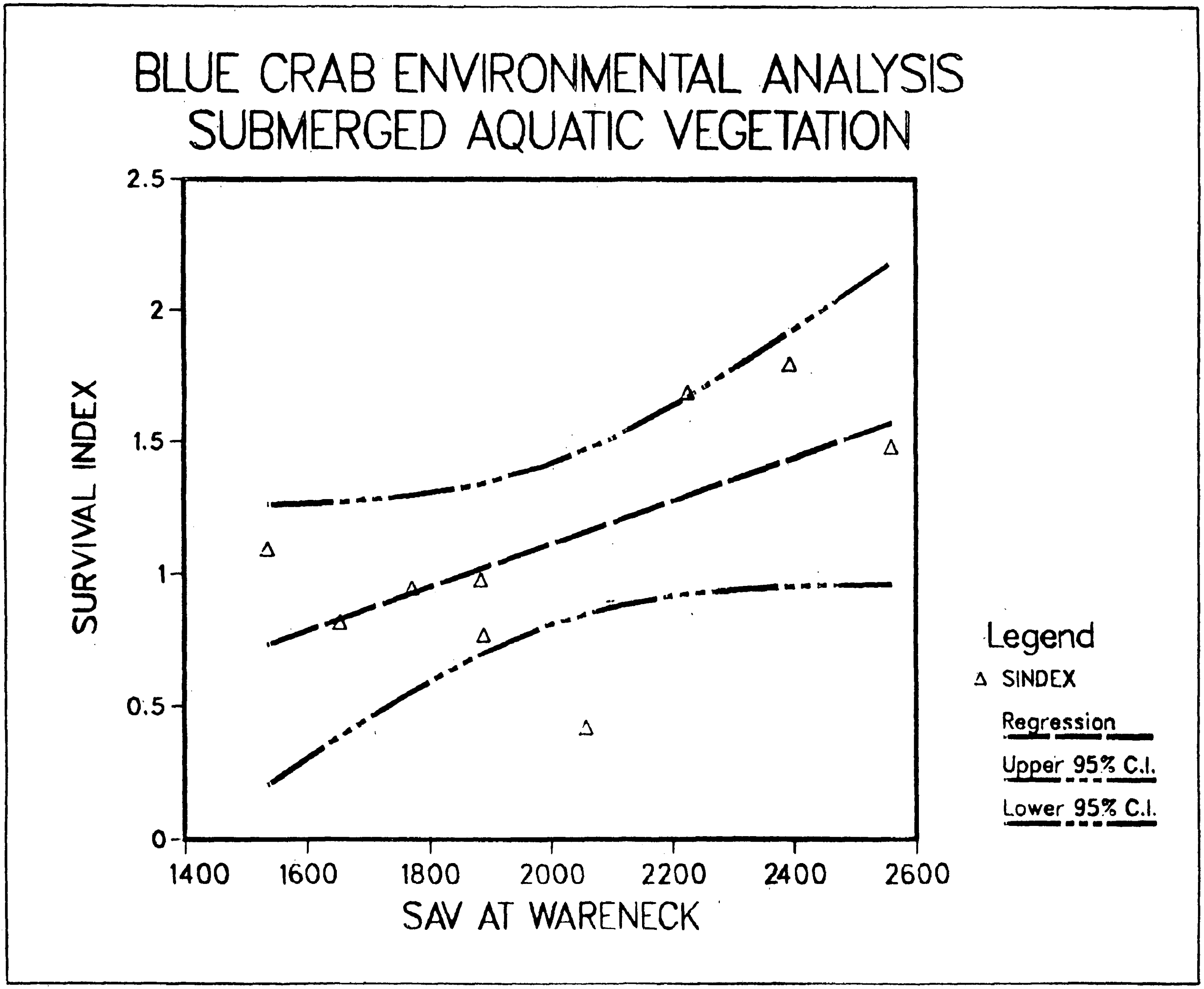
It would have been very informative if sufficient data were available to include SAV acreage for the Virginian Eastern Shore quadrangles in this analysis. Positive relationships with the

TABLE 3. Regression summary of grouped environmental features on the survival indices.

Environmental Feature	R^2	F-statistic	Significance of F[1]
WARENECK	0.377	4.236	0.079
STFL	0.104	2.902	0.101
MAP	0.050	0.895	0.357
SUNE	0.151	2.134	0.170
SUNL	0.080	1.043	0.327
MAGMAY	0.095	2.834	0.104
MAGAUG	0.019	0.523	0.476
NSWAUG	0.065	1.877	0.182
NSWOCT	0.134	4.178	0.051

[1]Significance of F equal to 0.100 indicates a confidence level of 0.900.

Figure 8: **Regression of survival index on submerged aquatic vegetation acreage within the Ware Neck topographic quadrangle.**

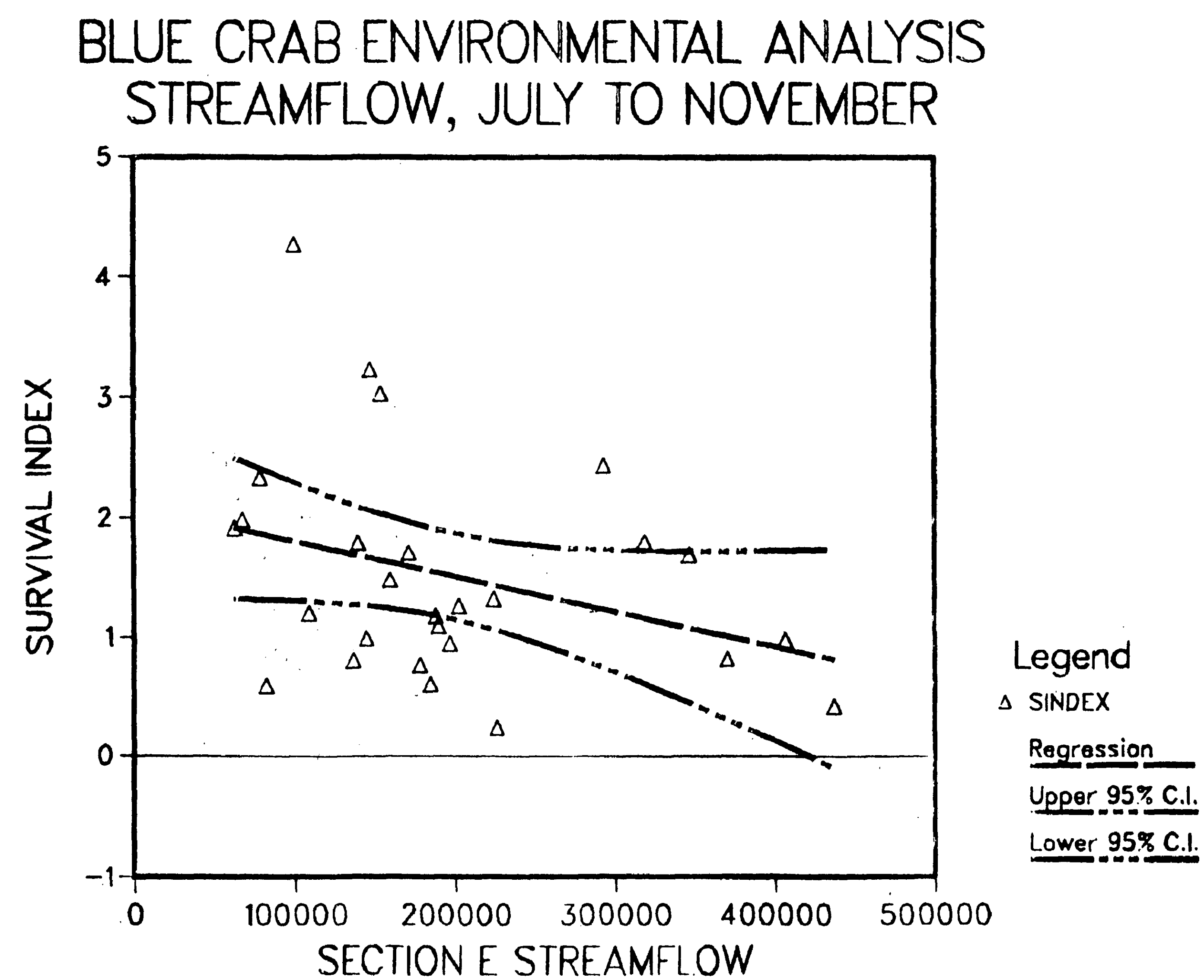


BLUE CRAB ENVIRONMENTAL ANALYSIS
SUBMERGED AQUATIC VEGETATION
SURVIVAL INDEX
2.5
2
1.5
1
0.5
0
1400
1600
1800
2000
2200
2400
2600
SAV AT WARENECK
Legend
SINDEX
Regression
Upper 95% C.I.
Lower 95% C.I.

survival indices would be expected based on the immature crab immigration timing differential into Maryland waters discovered by Sulkin (1977). He found that crab recruitment occurred somewhat earlier on the Eastern Shore than at the opposing mouth of the Potomac River. This timing differential is not unexpected in light of estuarine salt-wedge circulation features and ontogenic behavioral responses modifying vertical distribution of larvae, thus enhancing the survival value to crabs of SAV on the Eastern Shore between Cape Charles and Tangier Island, Va.

Analysis of Chesapeake Bay section E streamflow and the survival index reveals survival enhancement with low streamflow in all months except April. Notable relationships occurred for months between July and November (STFL in Table 3), all negative (Figure 9). This relationship is supported by Pearson's (1948) findings of an inverse relationship between James and Potomac River discharge for May and June, but contradicts the statement of Van Engel (Austin and Ingham 1979) of high runoff rates in autumn enhancing survival. In light of generous ranges of tolerable temperature and salinity for proper larval growth (Costlow and Bookhout 1959), Van Engel's comment is consistent with low discharge rates promoting larval retention within the estuary during early larval stages, and high discharge rates promoting larval or juvenile immigration into the estuary through salt-wedge circulation enhancement. Although it is fairly evident that low discharge rates during summer provide favorable survival conditions and promote larval retention, mechanisms resulting from

Figure 9: Regression of survival index on Chesapeake Bay cumulative section E streamflow, July to November. Streamflow is measured as monthly mean discharge in cubic feet per second.



BLUE CRAB ENVIRONMENTAL ANALYSIS
STREAMFLOW, JULY TO NOVEMBER
SURVIVAL INDEX
5
4
3
2
1
0
-1
0
100000
200000
300000
400000
500000
SECTION E STREAMFLOW
Legend
SINDEX
Regression
Upper 95% C.I.
Lower 95% C.I.

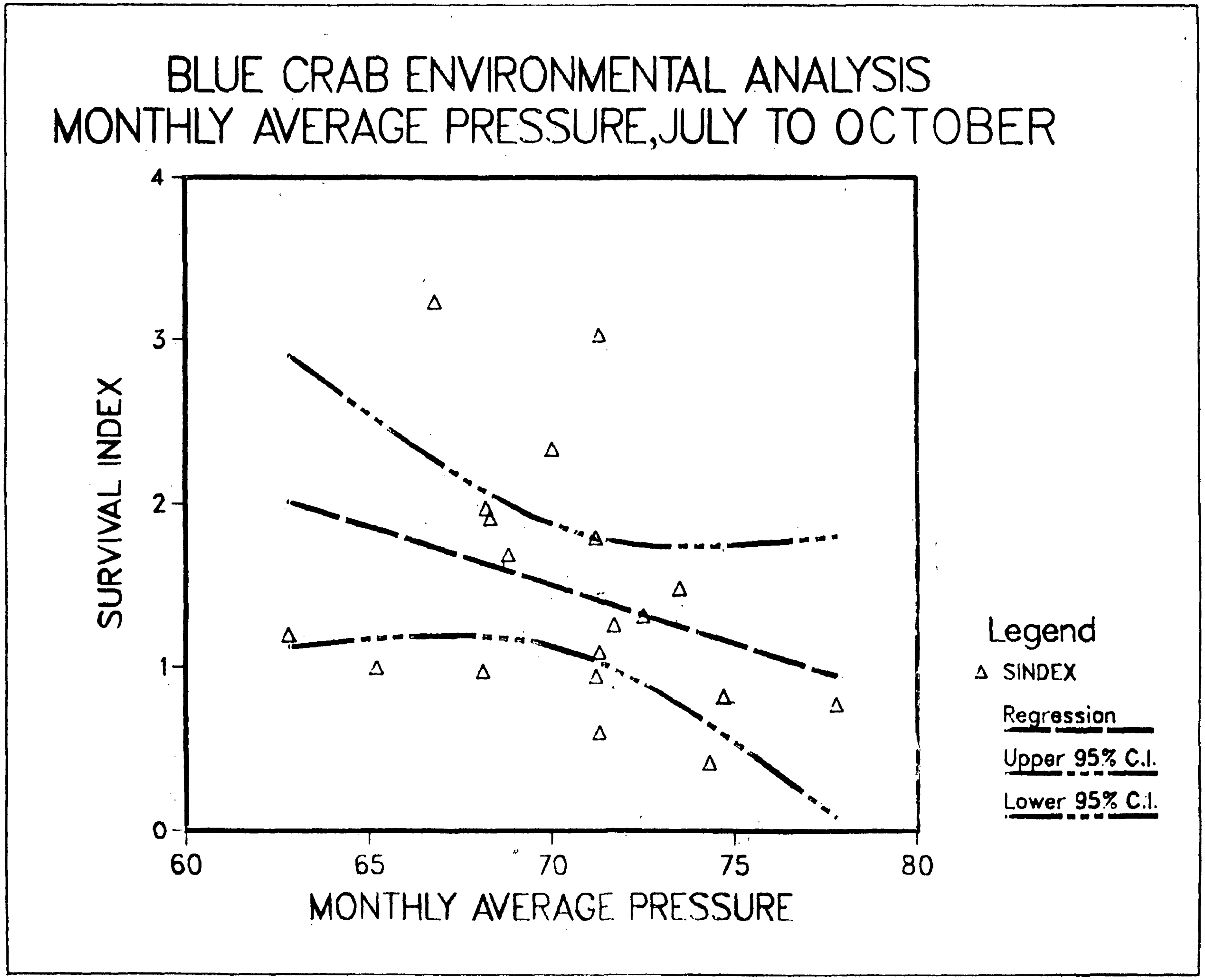
streamflow conditions in autumn which influence larval survival require further investigation.

The monthly average atmospheric pressure can be used to indicate the general meteorological conditions near the time of hatching. Low average pressure conditions are indicative of stormy weather having low amounts of incident sunshine and high amounts of precipitation.

Comparison of the monthly average atmospheric pressure at NMA for July to October (Figure 10, MAP in Table 3) revealed enhanced survival and recruitment into the dredge fishery when the average atmospheric pressure was low following hatching. Its relationship with the survival indices is curious when compared with optimal conditions of streamflow and percent possible sunshine to be discussed later in this section. Low pressure conditions promoting survival would be expected to accompany increased streamflow through increased precipitation and decreased sunshine. However, low streamflow promotes survival and subsequent recruitment. Nevertheless, the nebulous physical interaction between crab survival and the monthly average atmospheric pressure coupled with the low level of significance (Table 3) makes its inclusion in the final environmental model tenuous.

Less incident sunshine during summer (Figure 11, SUNE in Table 3) and more incident sunshine during autumn (Figure 12, SUNL in Table 3) are optimal conditions. Although the significance of F was rather high, the inclusion of incident sunshine during autumn in the environmental model was deemed necessary due to the behavioral response patterns observed by Sulkin et al. (1980) and Sulkin (1981).

Figure 10: Regression of survival index on monthly average pressure, July through October.



BLUE CRAB ENVIRONMENTAL ANALYSIS
MONTHLY AVERAGE PRESSURE, JULY TO OCTOBER
SURVIVAL INDEX
0
1
2
3
4
60
65
70
75
80
MONTHLY AVERAGE PRESSURE
Legend
SINDEX
Regression
Upper 95% C.I.
Lower 95% C.I.

Figure 11: Regression of survival index on sum of percent possible sunshine, June and August.

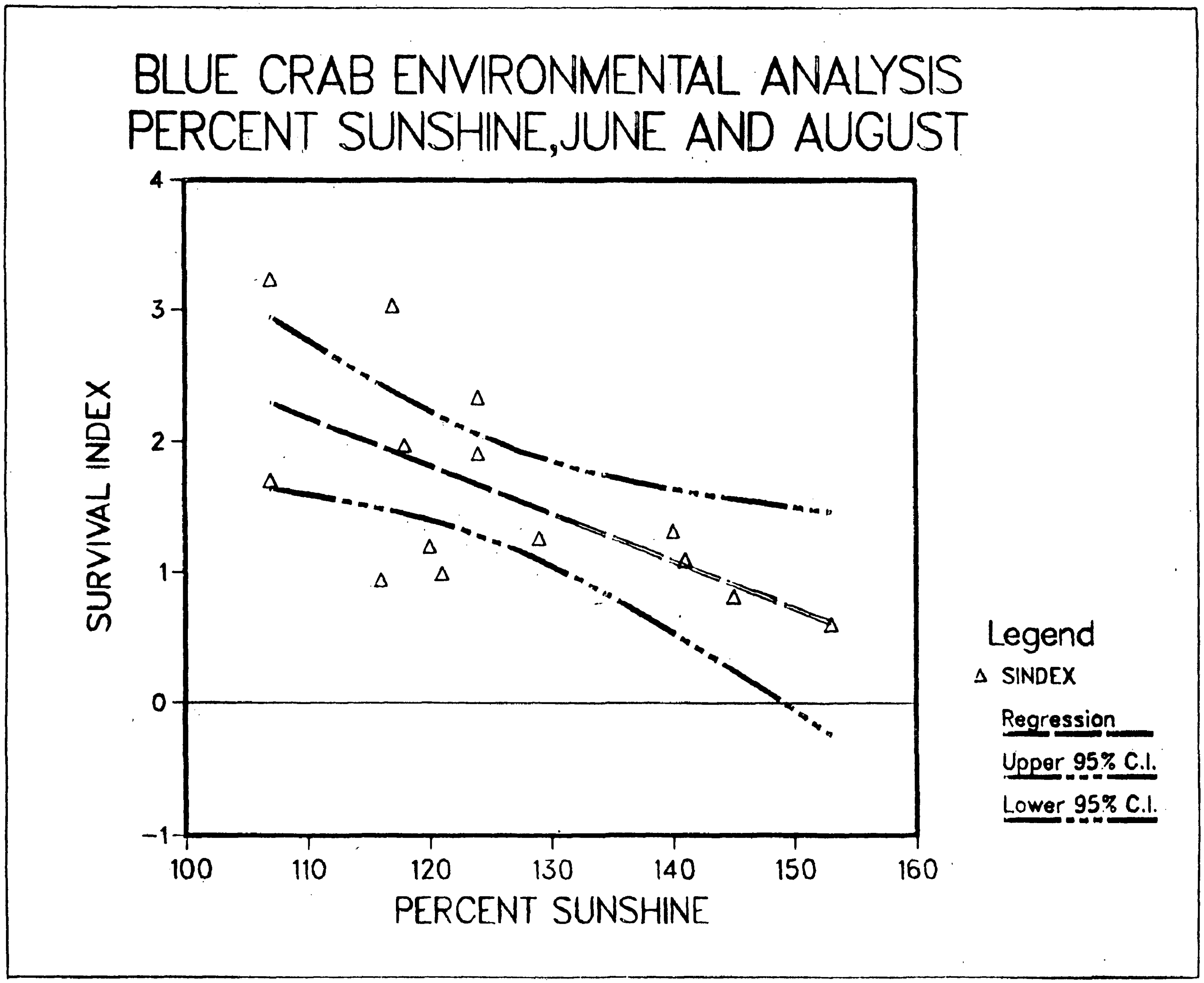
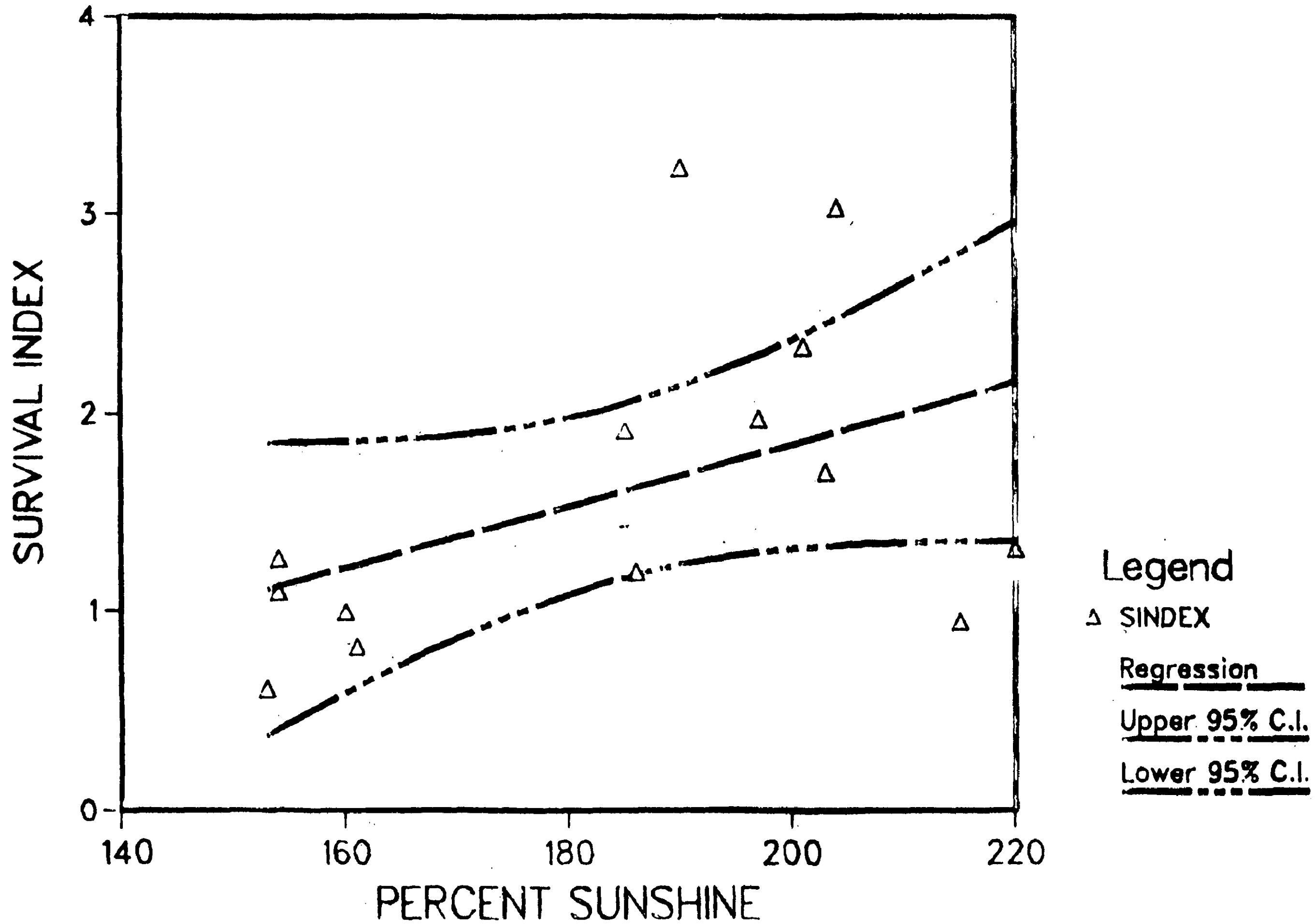

BLUE CRAB ENVIRONMENTAL ANALYSIS
PERCENT SUNSHINE, JUNE AND AUGUST
SURVIVAL INDEX
4
3
2
1
0
−1
100
110
120
130
140
150
160
PERCENT SUNSHINE
Legend
Δ SINDEX
Regression
Upper 95% C.I.
Lower 95% C.I.

Figure 12: Regression of survival index on sum of percent possible sunshine, September through November.

BLUE CRAB ENVIRONMENTAL ANALYSIS
PERCENT SUNSHINE, SEPTEMBER TO NOVEMBER



The survival mechanism for levels of incident sunshine is based on inhibition of positive phototaxis during peak hatching activity. Less sunshine reduces upward vertical migration and causes distribution of stage I zoeal larvae deeper in the water column. This location is less susceptible to offshore passive transport than in surface waters. Alternatively, high levels of incident sunshine during autumn activate negative phototaxis in late larval stages and in juveniles which then experience enhanced onshore passive bottom drift in the Bay and adjacent shelf area (Figure 17).

As with cumulative percent possible sunshine, wind conditions were found to have a contribution to survival, acting through passive transport mechanisms in the estuary and the adjacent coastal shelf. The monthly average resultant wind magnitude at NMA was found to exhibit a negative relationship for May (Figure 13, MAGMAY in Table 3) and a positive relationship for August (Figure 14, MAGAUG in Table 3) with the survival index. Low wind magnitudes in May allow pycnocline formation and effectively trap larvae hatched in June below the pycnocline or inhibit their surface migration through dampening of barokinesis at lower salinities (Sulkin 1981). Deeper larval distribution would promote retention by estuarine salt-wedge circulation. By late summer (August), high wind conditions (Figure 14) weaken pycnocline gradients and do not inhibit barokinesis, but allow vertical migration to bottom waters, favorable for immigration of larvae hatched in early summer. For this reason, the wind magnitude in August was included in the environmental model despite the high significance of F.

Figure 13: Regression of survival index on monthly average wind resultant magnitude for May. Units for the abscissa are in miles per hour.

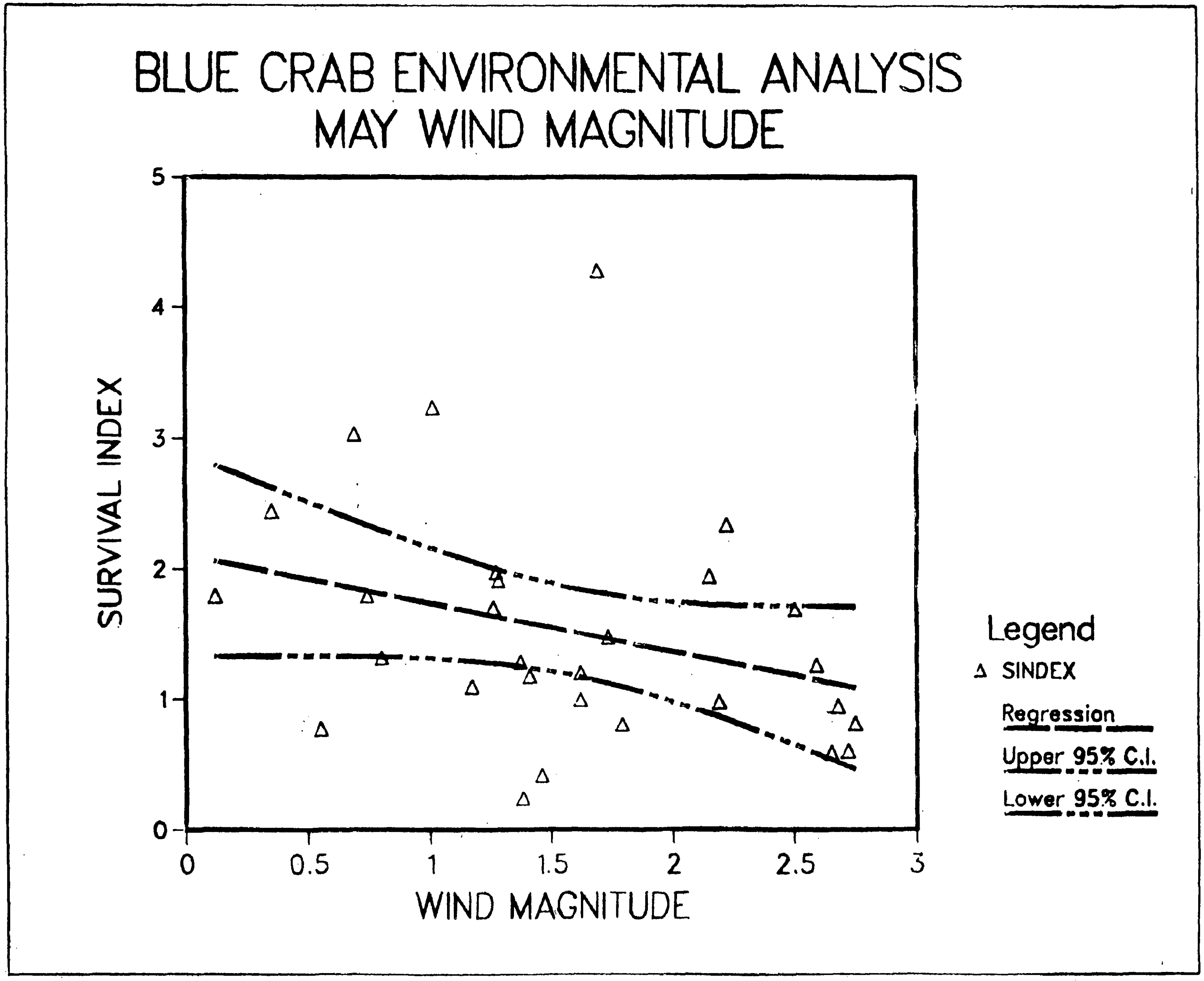
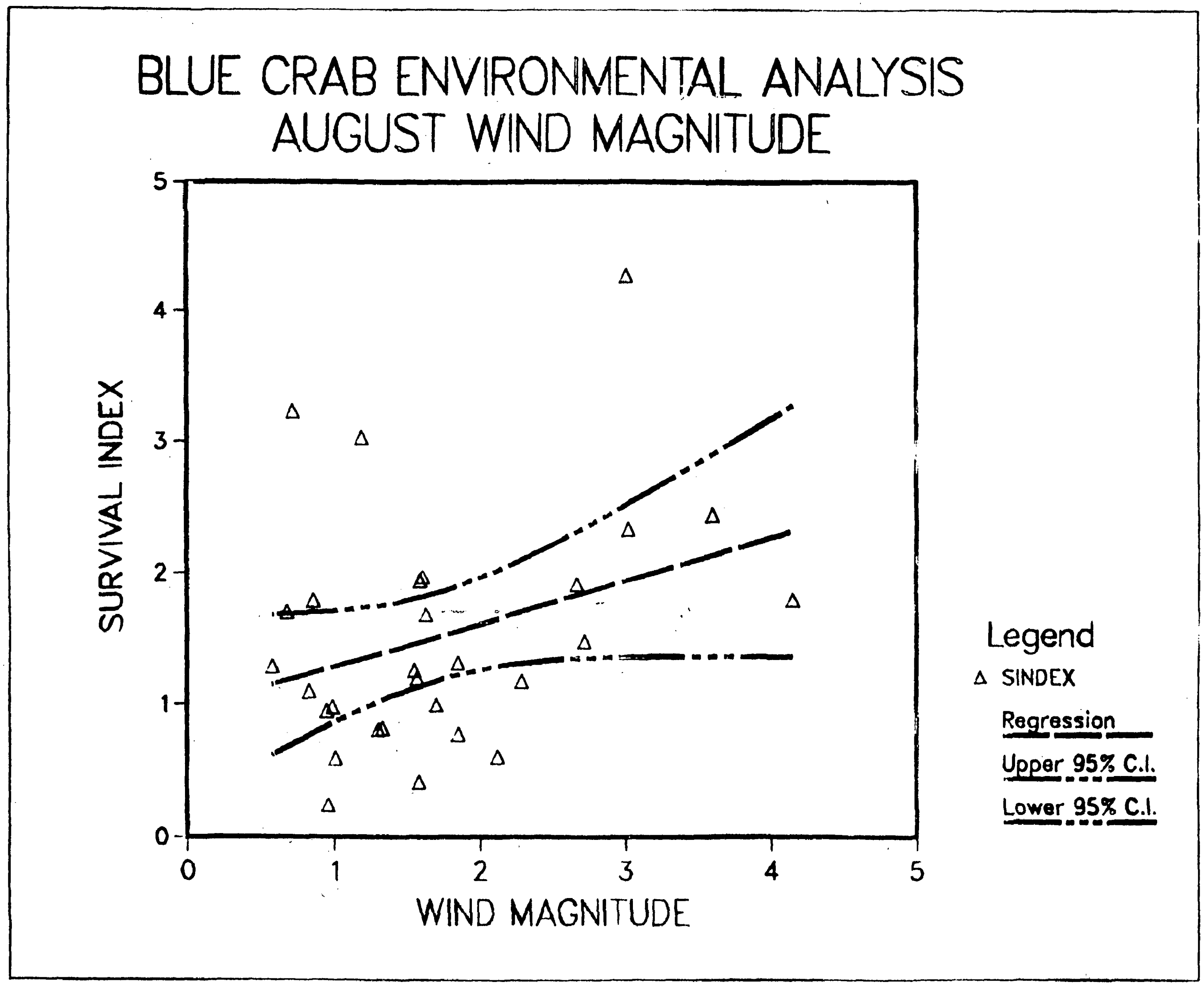

BLUE CRAB ENVIRONMENTAL ANALYSIS
MAY WIND MAGNITUDE
SURVIVAL INDEX
5
4
3
2
1
0
0
0.5
1
1.5
2
2.5
3
WIND MAGNITUDE
Legend
SINDEX
Regression
Upper 95% C.I.
Lower 95% C.I.

Figure 14: Regression of survival index on monthly average wind resultant magnitude for August. Units for the abscissa are in miles per hour.


BLUE CRAB ENVIRONMENTAL ANALYSIS
AUGUST WIND MAGNITUDE
SURVIVAL INDEX
WIND MAGNITUDE
0
1
2
3
4
5
Legend
SINDEX
Regression
Upper 95% C.I.
Lower 95% C.I.

Clear relationships were apparent between north-south monthly average wind components and the survival index. The mechanism acts through salt-wedge circulation enhancement via Ekman transport processes on the coastal shelf. During August, more northerly wind conditions act to enhance larval retention (Figure 15, NSWAUG in Table 3) through inhibitory effects on normal circulation patterns (northeastward surface drift, southwestward bottom drift) forced by onshore Ekman surface drift. During October, more southerly wind conditions act to promote larval immigration (Figure 16, NSWOCT in Table 3) through enhancement of onshore bottom circulation by offshore Ekman transport of surface waters. Because these relationships are contrary to the normal wind conditions prevalent during their respective seasons, it appears that a decrease or reversal of the normal north-south wind conditions promote larval retention, immigration, survival and subsequent recruitment to the winter dredge fishery.

Final Predictive Model

Elimination and grouping of environmental variables through multiple regression analysis yielded nine independent variables as suitable inputs to the final environmental model. Three of the nine variables had low confidence levels but were included due to suspected interactions between them and larval behavior and survival.

Analysis of the relationship between these independent variables and the survival indices derived from the stock recruitment model was accomplished through stepwise multiple regression (Hull and Nie 1981),

Figure 15: Regression of survival index on monthly average north-south wind component for August. Winds from the north are negative, from the south positive. Units for the abscissa are in miles per hour.

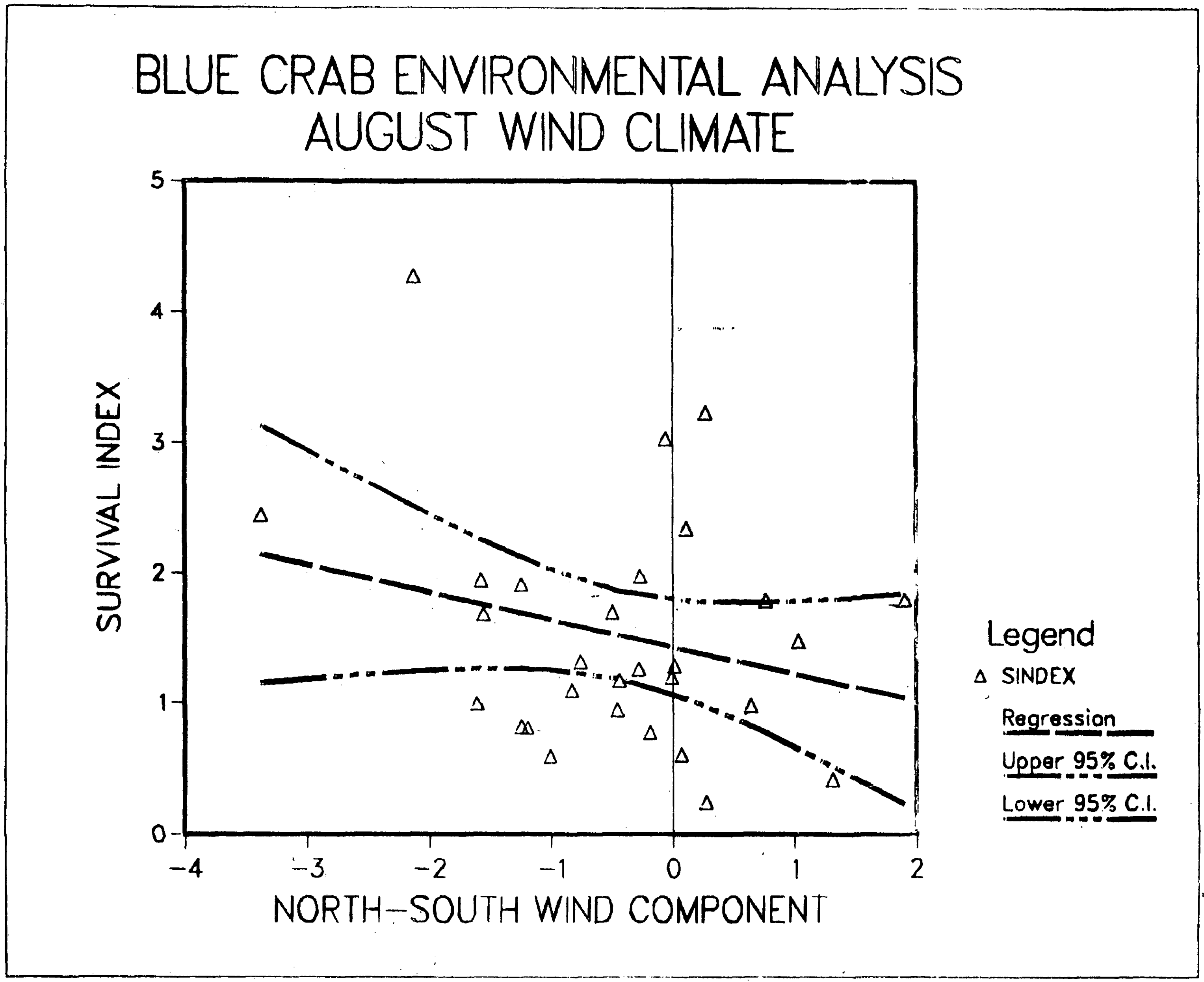
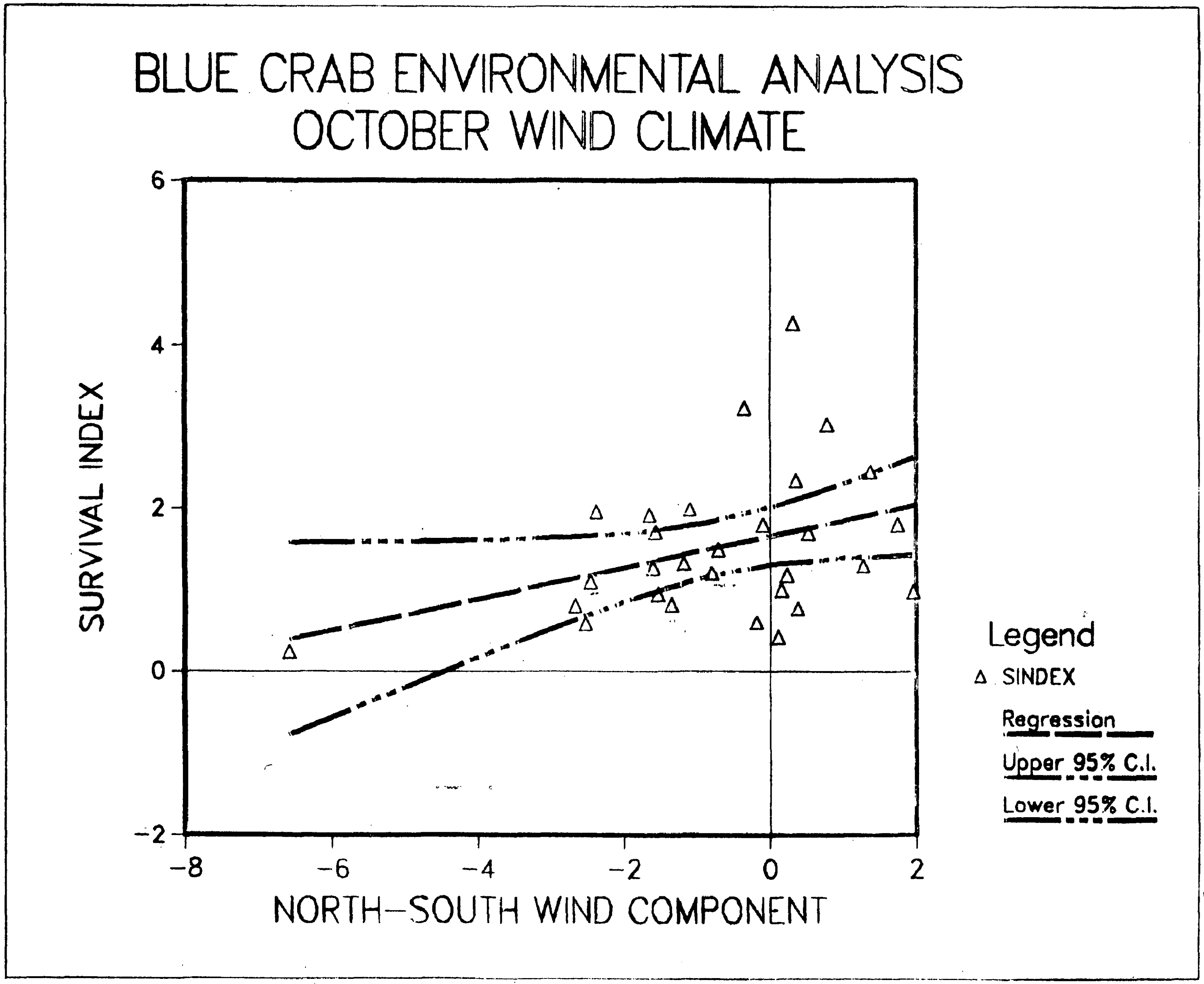
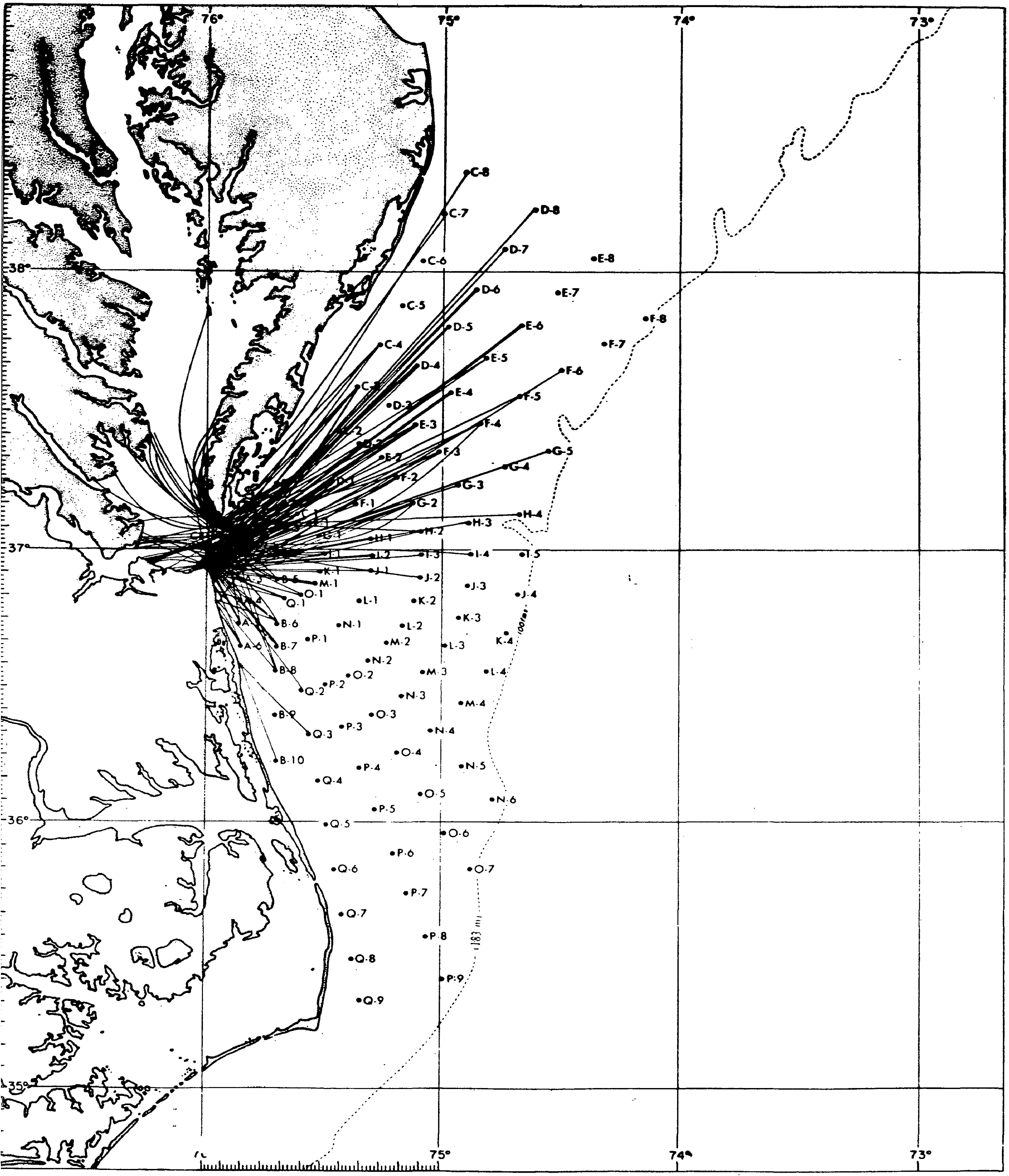

BLUE CRAB ENVIRONMENTAL ANALYSIS
AUGUST WIND CLIMATE
SURVIVAL INDEX
0
1
2
3
4
5
−4
−3
−2
−1
0
1
2
NORTH–SOUTH WIND COMPONENT
Legend
SINDEX
Regression
Upper 95% C.I.
Lower 95% C.I.

Figure 16: Regression of survival index on monthly average north-south wind components for October. Winds from the north are negative, from the south positive. Units for the abscissa are in miles per hour.



BLUE CRAB ENVIRONMENTAL ANALYSIS
OCTOBER WIND CLIMATE
SURVIVAL INDEX
6
4
2
0
-2
-8
-6
-4
-2
0
2
NORTH-SOUTH WIND COMPONENT
Legend
SINDEX
Regression
Upper 95% C.I.
Lower 95% C.I.

Figure 17: Plots of trajectories of seabed drifters released during November 1963 and May and June 1964 which drifted toward or penetrated Chesapeake Bay (from Norcross and Stanley 1967).



76°
75°
74°
73°
38°
37°
36°
35°
C-8
C-7
C-6
C-5
C-4
D-8
D-7
D-6
D-5
D-4
E-8
E-7
E-6
E-5
E-4
E-3
E-2
F-8
F-7
F-6
F-5
F-4
F-3
F-2
F-1
G-5
G-4
G-3
G-2
H-4
H-3
H-2
I-5
I-4
I-3
J-4
J-3
J-2
J-1
K-4
K-3
K-2
K-1
L-4
L-3
L-2
L-1
M-4
M-3
M-2
M-1
N-6
N-5
N-4
N-3
N-2
N-1
O-7
O-6
O-5
O-4
O-3
O-2
O-1
P-9
P-8
P-7
P-6
P-5
P-4
P-3
P-2
P-1
Q-9
Q-8
Q-7
Q-6
Q-5
Q-4
Q-3
Q-2
Q-1
B-10
B-9
B-8
B-7
B-6
A-6
183 m

substituting means of the environmental variables when data were missing. It produced a "best-fit" model utilizing five independent variables; STFL, SUNE, MAGAUG, NSWAUG and NSWOCT. Inclusion of the remaining independent variables WARENECK, MAP, SUNL and MAGMAY in the environmental model did not improve the fit, as measured by the F-statistic change as variables were entered, over that of the five variable model.

The form of and regression coefficients of the best environmental multiple regression model was:

$$\begin{aligned} SI = {} & \underset{(\pm 1.778)}{5.817} - \underset{(\pm 0.015)}{0.034}\,SUNE + \underset{(\pm 0.155)}{0.283}\,MAGAUG - \underset{(\pm 0.125)}{0.196}\,NSWAUG \\ & + \underset{(\pm 0.083)}{0.176}\,NSWOCT - \underset{(\pm 0.146 \times 10^{-5})}{0.228 \times 10^{-5}}\,STFL \end{aligned} \qquad \text{(Eq. 12)}$$

R-square = 0.499 F-statistic = 4.590

Significance of F = 0.0047

Although correlation between MAGAUG and NSWAUG might be expected, their correlation coefficient was -0.101 (Figure 18), a low value (significance of F = 0.602).

Combining the environmental model (Equation 12) with the results of Ricker's second stock recruitment model (Equation 5) gives:

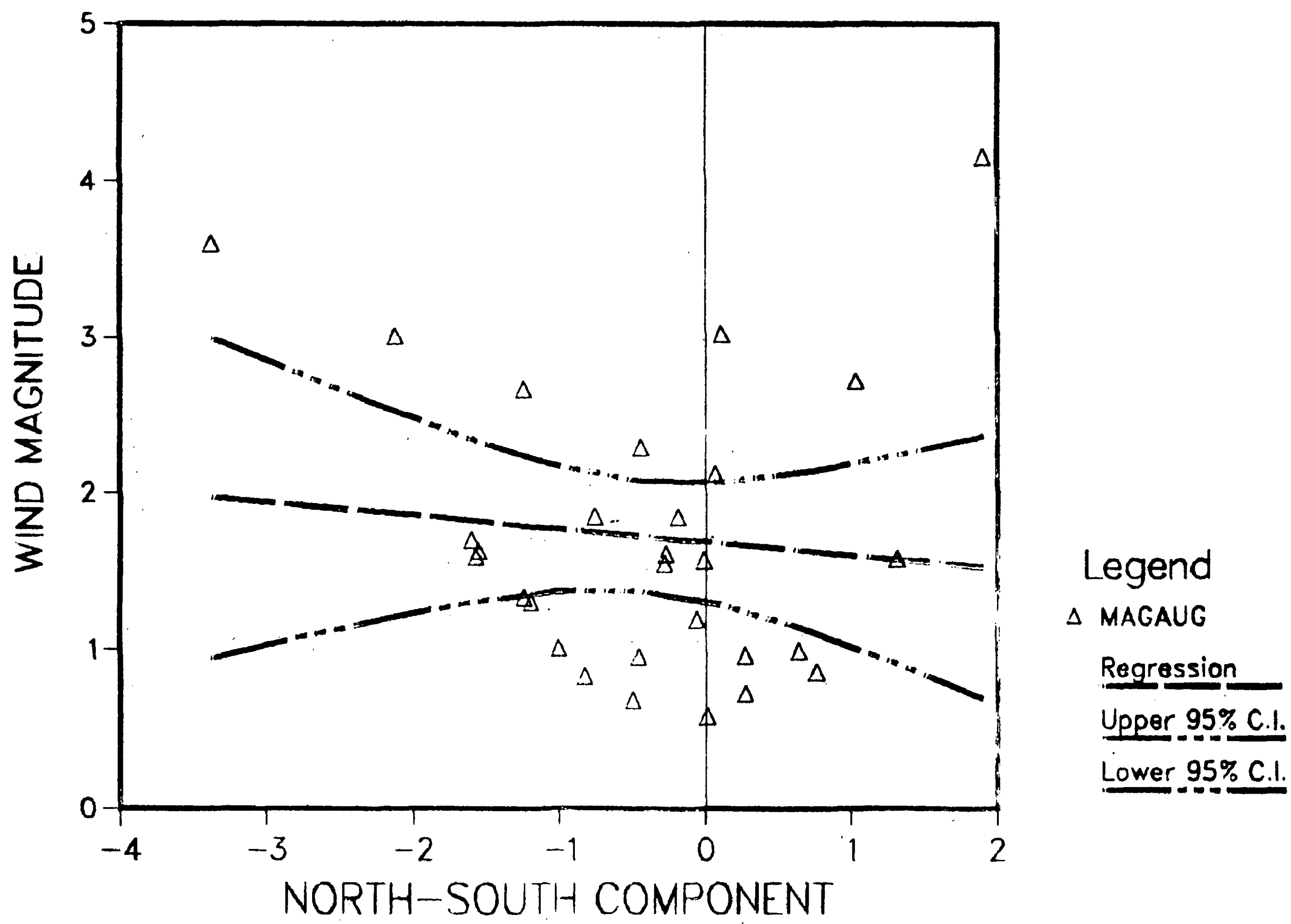
$$\hat{R} = [6.32\,Pe^{-0.108P}][5.817 - 0.034\,SUNE + 0.283\,MAGAUG - 0.196\,NSWAUG + 0.176\,NSWOCT - 0.228 \times 10^{-5}\,STFL] \qquad \text{(Eq. 13)}$$

where:

$\hat{R}$ = adjusted recruitment

Figure 18. Regression of monthly average wind resultant magnitude on north-south monthly average wind component, both for August. Units for the abscissa are miles per hour.

BLUE CRAB ENVIRONMENTAL ANALYSIS
AUGUST WIND CLIMATE



The results of Ricker's second stock recruitment model, the predicted survival index, and the adjusted recruitment from the environmental model (Equations 12 and 13) are in Table 4. A chi-square goodness-of-fit test for predicted recruitment (R_{sr}) and adjusted recruitment ($\hat{R}$), both on observed recruitment, gave chi-square statistics of 217.77 and 88.44, respectively. Both were significant at a 99% confidence level with 29 degrees of freedom, evidence that the values differ considerably from the observed recruitment. Nevertheless, the environmental model reduced the chi-square statistic by 59%. Moreover, reanalysis of Ricker's (1958) initial stock recruitment model was accomplished through division of observed recruitment by the predicted survival indices. It reduced the variance of residuals in the second stock recruitment model (Equation 5) from 91.14 to 58.27 (Figure 19), a decrease of 36%. The reanalysis is inclusive of unadjusted recruitment for 1932 to 1947.

Thus, the environmental model reduces deviations from the stock recruitment model by a substantial amount. Conditions of low streamflow from July through November, low incident sunshine levels for June and August, strong wind conditions in August, reduced southerly winds in August, and reduced northerly winds in October enhance larval retention, immigration, and survival. These conditions contribute to blue crab recruitment to the winter dredge fishery over that expected when density-dependent mortality acts on larval stages by itself.

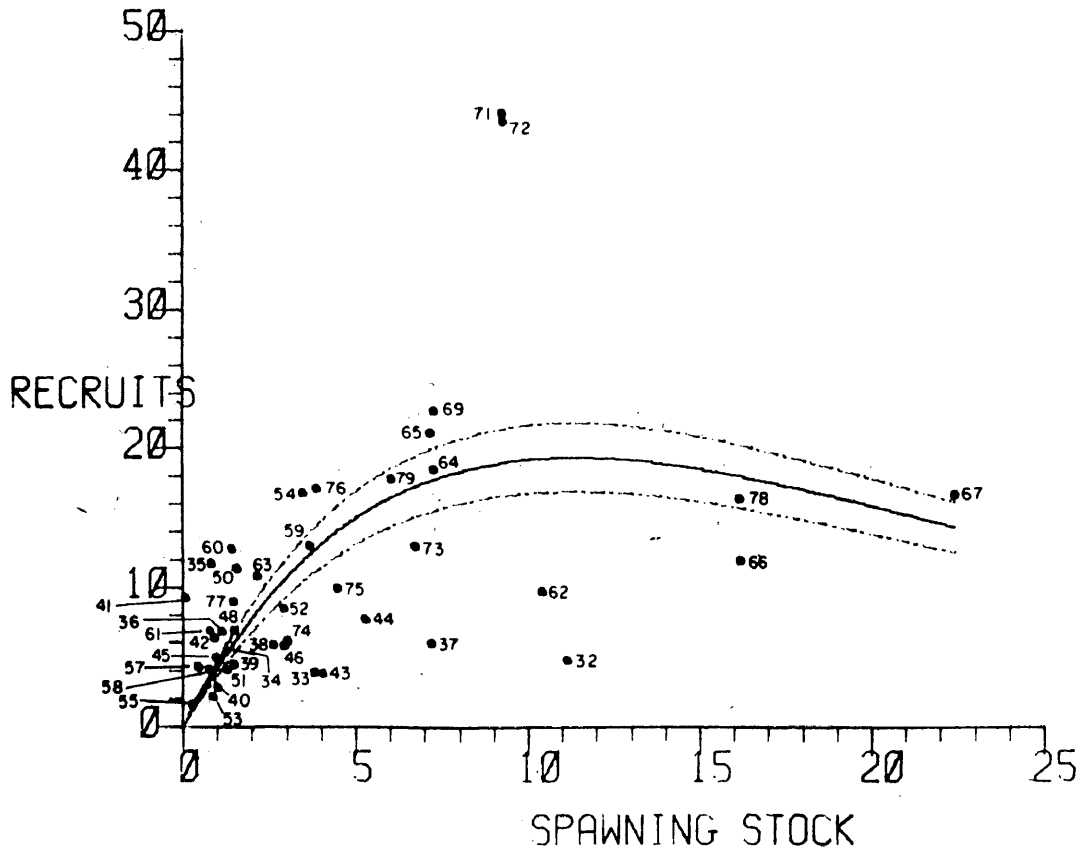
Table 5 contains the results of recruitment prediction from observed environmental conditions and spawning stock size for

TABLE 4. **Observed and predicted stock recruitment relationship** from Ricker's (1958) initial relationship as adjusted by environmental model.

(1) Year of Spawning (t)	(2) Spawning Stock Size (million lbs.)	(3) Observed Recruitment (million lbs.) (t+2)	(4) Predicted Recruitment (million lbs.)	(5) Predicted Survival Index	(6) Adjusted Recruitment (million lbs.)
1932	11.14	4.80	21.10		
1933	3.80	3.95	15.93		
1934	1.33	5.85	7.29		
1935	0.81	11.71	4.68		
1936	1.13	6.84	6.33		
1937	7.15	6.09	20.86		
1938	2.61	5.94	12.44		
1939	1.48	4.51	7.96		
1940	1.01	2.90	5.72		
1941	0.06	9.27	0.39		
1942	0.91	6.47	5.21		
1943	4.02	3.83	16.46		
1944	5.26	7.70	18.82		
1945	0.96	5.02	5.48		
1946	2.88	5.79	13.35		
1948	1.45	10.14	7.86	1.46	11.45
1950	1.54	16.07	8.24	1.41	11.66
1951	1.26	5.64	6.97	1.34	9.35
1952	2.91	15.83	13.43	1.87	25.06
1953	0.88	2.99	5.06	1.37	6.93
1954	3.45	26.90	15.02	1.60	24.07
1955	0.31	4.65	1.90	2.77	5.28

(1) Year of Spawning (t)	(2) Spawning Stock Size (million lbs.)	(3) Observed Recruitment (million lbs.) (t+2)	(4) Predicted Recruitment (million lbs.)	(5) Predicted Survival Index	(6) Adjusted Recruitment (million lbs.)
1956	9.99	5.18	21.43	0.06	1.35
1957	0.44	11.45	2.68	2.62	7.01
1958	0.76	7.53	4.42	1.79	7.89
1959	3.67	9.43	15.60	0.72	11.30
1960	1.39	24.49	7.58	1.92	14.52
1961	0.78	13.69	4.51	1.96	8.83
1962	10.40	21.22	21.34	2.18	46.49
1963	2.13	21.15	10.71	1.95	20.87
1964	7.25	40.03	20.92	2.15	44.97
1965	7.18	48.79	20.87	2.30	47.97
1966	16.17	21.32	17.77	1.78	31.56
1967	22.45	16.50	12.50	0.99	12.37
1969	7.28	26.44	20.93	1.16	24.32
1971	9.27	23.54	21.49	0.53	11.47
1972	9.30	17.61	21.49	0.41	8.71
1973	6.74	19.46	20.55	1.50	30.73
1974	3.04	10.67	13.82	1.74	24.04
1975	4.46	7.34	17.41	0.73	12.76
1976	3.86	27.14	16.07	1.59	25.51
1977	1.47	14.24	7.93	1.58	12.52
1978	16.16	26.33	17.77	1.60	28.41
1979	6.03	19.42	19.85	1.09	21.67

Figure 19. **Ricker's (1958) second stock recruitment model** for spawning years 1932 to 1979 as adjusted by the predicted survival index for 1948 to 1979. Solid line is the model estimate. Dashed lines signify one standard deviation on the estimate of B. Units for abscissa and ordinate are in pounds x 10^6.



RECRUITS
SPAWNING STOCK

TABLE 5. Predicted recruitment from stock recruitment model and environmental model for 1980 to 1982.

(1) Year of Spawning	Environmental Conditions[1] (2) STFL	(3) SUNE	(4) MAGAUG	(5) NSWAUG	(6) NSWOCT	(7) Predicted Survival Index	(8) Spawner Stock Size	(9) Predicted Recruitment	(10) Adjusted Recruitment
							million pounds		
(t)							(t)	(t+2)	(t+2)
1980	103000	128	2.0	-1.87	+0.90	2.32	13.43	19.85	46.07
1981	161000	133	1.9	+0.95	+3.25	1.85	5.06	18.50	34.25
1982	155000[2]	111	1.9	-1.79	-0.68[3]	2.46	14.21	17.15	42.17

[1] Units for environmental conditions:

(2) STFL - Sum of monthly mean discharge in cubic feet per second for July to November

(3) SUNE - Sum of percent of possible sunshine for June and August

(4) MAGAUG - Monthly average wind resultant in miles per hour for August

(5) NSWAUG - Monthly average north-south wind component for August

(6) NSWOCT - Monthly average north-south wind component for October

[2] Includes average streamflow for October and November

[3] Average condition for October

year classes resulting from spawning during 1980, 1981, and 1982. They correspond to recruitment to the winter dredge fishery for seasons of 1981-82, 1982-83, and 1983-84, respectively. Recruitment predicted by Ricker's second stock recruitment model (column 9) is somewhat less than the recruitment maximum, but is still near the peak of the curve (refer to Figure 7). Recruitment predicted by the full environmental model (column 10) is quite high and reminiscent of recruitment during spawning years 1964, 1965 and 1966. As in the summers of 1980 and 1981, the summers of 1964 and 1965 were considered to be "drought-years" and exhibited low runoff during late summer.

For the spawning years of 1962, 1971, and 1972, the estimated recruitment is close to that predicted by the stock recruitment model (Table 4). Upon reanalysis of the stock recruitment model using the adjusted recruitment, the deviations from the model increased for these years (Figure 19). In 1962, more northerly wind conditions in August contributed to 35 percent of the deviation from the average survival index. This condition contributed to the model's prediction of a high survival index and a low adjusted recruitment level. More northerly winds in October coupled with high levels of incident sunshine during hatching (accounting for 31 and 51 percent of the deviation from the average survival index) were the major causes of the low survival index prediction and of high adjusted recruitment for 1971 (Figure 19). In 1972, high streamflow after hatching and high incident sunshine at hatching contributed to 35 and 58 percent of the deviation from the average survival index, respectively. These conditions were the major cause of a low survival index prediction and of high adjusted recruitment. It appears that certain conditions existed to compensate for the survival impact predicted by the environmental model during these years.

Although estimated recruitment was not available to compare with the adjusted recruitment, the inability to compute estimated recruitment via LSA for the 1981-82 winter dredge season (refer to Table 1) may have been attributable to extremely high recruitment (adjusted recruitment at 46.07 million pounds). The high catch rates observed throughout the 1981-82 dredge season may have resulted from this high recruitment. The twenty-five barrel per vessel-day quota was often attained through February 1982, contributing to the cause of winter-dredge vessels striking for higher ex-vessel prices. If the predicted trends in recruitment are accurate, catch rates for the 1982-83 winter-dredge season are expected to be high, but not to the level observed in the 1981-82 dredge season. Catch rates for the 1983-84 winter-dredge season are expected to approximate those observed in the 1981-82 season.

Caution should be employed when using the predictions shown in Table 5. They only reflect predicted recruitment under known environmental conditions and estimated spawning stock size. Catch rates and total landings are not only determined by stock size, but also by changes in availability and effort. The predicted recruitment is not directly translatable into catch rates, but only suggest changes in the stock size at the beginning of the winter-dredge season. For example, warm temperatures during late autumn may keep crabs active. Under these conditions they do not burrow and are unavailable to the dredge boats. Therefore, decisions based on recruitment predictions should be tempered by other known influences on availability and potential effort.

Summary

A model derived from Ricker's (1958) second stock recruitment model and spawning stock estimates derived from the Leslie stock analysis (Leslie and Davis 1939) was formulated incorporating environmental variables. Climatological features of low streamflow in summer and autumn, low incident sunshine levels during summer hatching peaks, windy conditions in late summer, and reduction of normal patterns of north-south wind components were found to enhance larval retention, immigration, and survival and subsequent adult recruitment into the winter dredge fishery. More submerged aquatic vegetation acreage within Mobjack Bay, low monthly average atmospheric pressure in summer and autumn, and high levels of incident sunshine in autumn also contributed to the overall survival, but did not improve the fit of the final model. Many of these environmental features were explainable through changes in ontogenic behavioral response patterns (Sulkin et al. 1980 and Sulkin 1981), modulated by meteorological effects on estuarine salt-wedge circulation and circulation on the adjacent shelf.

Predictions of recruitment for the winter dredge seasons of 1981-82, 1982-83, and 1983-84 are relatively high. These predictions are comparable to those for the spawning years 1964 to 1966 when drought conditions were prevalent. Recruitment predictions for winters of 1982-83 and 1983-84 indicate moderate to high catch rates. Nevertheless, decisions based on recruitment predictions should be tempered by other known influences on availability.

CONCLUSIONS

1. Ricker's (1958) second stock recruitment model fits the observed spawning stock recruitment relationships better than the initial model of Ricker (1954). Despite having a low index of density dependence ($-B\bar{P}$) when compared to finfish, blue crabs appear to exhibit a "peaked-dome" similar to the Gadoids. The spawner stock recruitment characteristics of a "peaked-dome" suggest blue crabs maintain considerable resilience in the face of high exploitation levels.

2. Chesapeake Bay section E streamflow from July through November, incident sunshine levels at NMA in June and August, monthly average wind resultant magnitude at NMA in August, and the monthly average north-south wind components at NMA for August and October provide significant contributions to the final environmental model predicting the survival index.

3. Submerged aquatic vegetation acreage within the Ware Neck topographic quadrangle, monthly average atmospheric pressure at NMA from July through October, incident sunshine at NMA from September through November, and the monthly average wind resultant magnitude at NMA for May all exhibited meaningful relationships with the survival index, but did not contribute to an improved fit for the final environmental model.

4. Submerged aquatic vegetation (SAV) appears to enhance survival of immature blue crabs through physical interference with predators (Penry 1982). However, only SAV acreage within Mobjack Bay exhibits positive correlations with the survival index. Other areas on the Chesapeake's western shore have insignificant relationships. Since immature (sub-legal) crabs immigrate to the Maryland portion of the Bay somewhat earlier on the Eastern Shore than at the opposing Potomac River mouth (Sulkin et al. 1977) an investigation into the survival value of SAV presence on the Eastern Shore should be undertaken.

5. Reduced sunshine during peak hatching activity in June and August does not fully activate positive phototaxis of early stage larvae. This effect promotes larval retention since they remain deeper in the water column, away from surface waters subject to offshore drift via estuarine salt-wedge circulation and/or Ekman processes.

6. High levels of incident sunshine during autumn activate negative phototaxis displayed by late larval stages, placing them in a position to become entrapped in the onshore bottom drift in the Bay and adjacent shelf area, thus promoting estuarine immigration of late stage larvae.

7. Reduced winds in May allow stronger pycnocline formation and effectively trap June hatched larvae below the pycnocline or inhibit their surface migration through dampening of barokinesis when larvae encounter salinity gradients. Reduced winds,

therefore, promote larval retention in estuarine salt-wedge circulation.

8. Strong winds in August weaken pycnocline gradients and allow vertical migration to surface waters with favorable conditions to early stage larvae, and to bottom waters, favorable for larval immigration of those hatched in early summer.

9. Reduction of prevailing north-south wind conditions, southerly in summer and northerly in autumn, promotes larval retention and immigration, respectively, by reducing surface Ekman transport processes acting on the coastal shelf and on estuarine salt-wedge circulation.

10. Chesapeake Bay section E streamflow for July through November and monthly average atmospheric pressure for July through October exhibit negative correlations with the survival index. The survival mechanisms of these conditions are not known and require intensive investigation.

11. The full predictive recruitment model (Equation 13), inclusive of climatological adjustment, indicates relatively high recruitment to the 1981-82, 1982-83, and 1983-84 winter dredge seasons. The high recruitment predicted for the 1981-82 season may have contributed to the inability to estimate recruitment by the Leslie stock analysis and to strikes by the dredge boats for higher ex-vessel prices. Should influences on availability be known, effort and/or processing capacity and marketing activity

might be adjusted to take advantage of natural fluctuations in the blue crab stock.

12. It is curious that conditions reminiscent of those causing high recruitment predictions for spawning years 1980 to 1982 occurred in 1964 to 1966, a lapse of 17 years. Seventeen years prior to spawning years 1964 to 1966, or approximately 1947, recruitment estimated by the Leslie stock analysis was not obtainable. Moreover, recruitment for 1931-32, derived from the spawning stock of 1930 was high. Could blue crab recruitment be operating on a 17-year cycle? If so, what are the controlling mechanisms? Time series analysis of observed recruitment and an environmental analysis for periods surrounding 1930 and 1947 utilizing the environmental analysis developed here might bear this out.

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