Climate scale environmental factors affecting year-class fluctuations of Atlantic croaker (micropogonias undulatus) in the Chesapeake Bay (Maryland, Virginia)

Brenda L. Norcross

College of William and Mary - Virginia Institute of Marine Science

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CLIMATE SCALE ENVIRONMENTAL FACTORS AFFECTING YEAR-CLASS FLUCTUATIONS OF ATLANTIC CROAKER (MICROPOGONIAS UNDULATUS) IN THE CHESAPEAKE BAY

The College of William and Mary in Virginia

Ph.D. 1983

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CLIMATE SCALE ENVIRONMENTAL FACTORS AFFECTING
YEAR-CLASS FLUCTUATIONS OF ATLANTIC CROAKER
(Micropogonias undulatus) IN THE CHESAPEAKE BAY

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

by
Brenda L. Norcross
December 1983
APPROVAL SHEET

This dissertation is submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

Brenda L. Norcross
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ABSTRACT

A conceptual life history of the Atlantic croaker (Micropogonias undulatus) identifies the effects of the environment on juvenile recruitment. In a multi-disciplinary approach to modelling, the major effects are investigated, quantified and presented in a flow chart. The model is divided into three sub models, each representing a major component which affects juvenile recruitment.

North/south spawning location in the Mid-Atlantic Bight is affected by the bottom water temperature as influenced by the cessation of the summer winds in relation to timing of croaker migration. The pelagic phase is the most critical time in the life history of a larval croaker as they are subjected to wind-induced transport which may cause direct loss off the shelf and entrainment in the Gulf Stream, or indirect loss by prolonging time in transit to the nursery area. The magnitude of this wind-included effect is a function of the direction, strength, duration and time relative to spawning and is incorporated in an equation to predict year-class strength of croaker.

The juvenile croaker overwinter in the Chesapeake Bay system. Winter temperature is shown to be the predominant variable affecting year-class survival to the following summer in very cold years. However, in very warm years, the predictive capabilities of the model are improved when a measure of fall recruitment, i.e. wind-induced transport, is incorporated.

Croaker is basically a density-independent stock as, juvenile recruitment is erratic and dependent upon these environmental parameters. The effect of spawning stock size is only apparent after accounting for density-independent effects, and slightly improves the explained variance of the statistical relationship.

Year-class strength and fishing pressure cause interannual variability in commercial catch. Overfishing a weak year class reduce spawning potential, and several poor year classes in a row magnify this.

The model, tested for the 1982-82 data, predicts a strong year class.
Climate Scale Environmental Factors Affecting Year-class Fluctuations of Atlantic Croaker (Micropogonias undulatus) in the Chesapeake Bay
CHAPTER 1

Introduction

Contemporary fisheries assessment (yield and quotas) is dependent upon environmentally static yield models (Austin and Ingham 1978) which often produce large residuals due to environmental fluctuations acting on recruitment or availability. Fishery yield models do not usually consider effects on fluctuating environments (Sissenwine, Brown and Brennan-Hoskins 1978). There is some recognition among biologists that high recruitment and variable yields may be caused by environmental fluctuations. It is necessary to separate trends due to alteration in climate from effects due to fishing to understand the processes controlling stock abundance (Natl. Res. Coun. 1980). Future efforts to predict abundance and distribution of stocks must consider the influence of abiotic factors (Austin and Ingham 1978).

Fish stock fluctuations are generally due to density-dependent factors, fishing pressure, predation, environmental insult (pollution), and natural environmental variations. Each factor is responsible for a percentage of the interannual variations in stock abundance or distribution. Fisheries science presently is capable of measuring fishing pressure with reasonable accuracy. Environmental insult is causing increasing concern, but as yet, in most cases there is no method of accurate estimation of the chronic effects. Natural variation in the
environment also accounts for large interannual fluctuations in abundance, distribution and recruitment.

Two types of "recruitment" need to be recognized—to the stock as eggs and larvae and to the fishery as adults. Significant relationships have been demonstrated between environmental effects and larval recruitment (Cushing and Dickson 1976, Hunter 1976, Nelson, Ingham and Schaal 1977, Lasker 1978, Lough, Bolz, Grosslein and Potter 1979, Applegate 1983), thus affecting recruitment to the fishery. The current practice is to integrate processes of available catch data (stock size) with juvenile assessment data (recruitment) and, by means of stock-recruitment functions, to develop catch curves. These functions may provide poor fits especially on the juvenile stage, due to unaccounted for environmental effects (Sissenwine et al. 1978).


Investigation and quantification of the environmental factors controlling a specific fish, the Atlantic croaker (Micropogonias undulatus), is the purpose of this dissertation (Figure 1.1). Interannual fluctuations in the physical environment of lower Chesapeake Bay and its tributaries and continental shelf seaward of the Bay entrance is hypothesized to cause concurrent fluctuations in abundance of young-of-the-year croaker in the Chesapeake Bay. The annual "signal to noise" ratio is poor and only becomes discernible when data are examined over long time periods (decades or longer). Time series analyses allow cause and effect relationships to be identified empirically, quantified statistically, and modelled conceptually.
Figure 1.1

Overview of model developed in this dissertation to predict croaker recruitment. Chapter numbers indicate where each portion of the model is developed.
Biological factors must be considered so that a relationship is not assumed to be environmentally caused when it really has a biological basis. The dynamics of bio-environmental links must be understood, allowing one to begin with a conceptual model and a priori knowledge on which to base a search for relationships (Austin and Ingham 1978). Such an a priori model is developed in Chapter 3, Conceptual Life History of Atlantic Croaker. This chapter reviews the literature on croaker and outlines significant physical factors which are the bio-environmental bases of the modelling process in this dissertation. It also discusses other factors not included in this study (Figure 1.1).

The Atlantic croaker has been chosen for this study for a variety of reasons: 1) commercial importance, 2) documented environmentally induced abundance fluctuations (Hildebrand and Schroeder 1927, Richards 1965, Schwartz 1964, Joseph 1972, Wojcik 1978), 3) susceptibility of young-of-the-year to the bottom trawl gear used in surveys in the deep channels of the rivers, 4) their completeness in the 29-year survey, and 5) concurrent physical data. Because of the rarity of two matching data sets existing in the same locality and covering the same time span, there is often a need for proxy data (Austin and Ingham 1978). The VIMS bottom trawl survey was used as the main biological data base. Other data are used in various aspects of this research, including Norfolk Airport wind, VIMS pier temperatures, and bottom temperatures, and adult and larval abundance and distribution from MARMAP surveys (Appendix 1.1 - Table).

Fish migrate in complicated yet integrated environmental systems, often making it difficult to identify and quantify their fluctuations. Consequently, bio-environmental modelling of fish would
provide an efficient management tool. Here, each bio-environmental relationship is analyzed individually and referred to as a Sub Model. These relationships are used to identify the percent of the year to year variability attributable to natural fluctuations. Identifying factors influencing year-class strength will aid in a more complete understanding of the population as a whole.

Croaker spawn in the fall on the shelf and the larvae are transported into the Bay where they overwinter as juveniles. Exploratory analyses of historic data and publications of the croaker and environmental parameters affecting them revealed the necessity of critical investigations of the spawning and larval stages. Chapter 4.1 establishes a Relationship Between the Meridional Wind Component and Fall Bottom Temperatures in the Mid-Atlantic Bight. Based on the seasonal wind shift and bottom temperature relationship demonstrated in Chapter 4.1, Chapter 4.2 investigates Spawning Times and Locations of Atlantic Croaker in the Mid-Atlantic Bight. These two parts of Chapter 4 comprise Part 1 of Sub Model I (Figure 1.1).

The ideas and techniques from the Sub Models are incorporated into a model which integrates croaker abundance and environmental fluctuation (Figure 1.1). This type of study would not be possible without the 29-year VIMS York River bottom trawl survey to serve as the primary base of the model. The length and completeness of the survey data (1953-82) is unique on the east coast. VIMS bottom trawl data have been used for numerous studies (Massmann and Pacheco 1960, Pacheco 1962, Massmann 1962, Joseph 1966, Grant and Joseph 1968, Joseph 1972, Markle 1976) but never as a unit time series to evaluate a single species. Chapter 5, Juvenile Atlantic Croaker, describes this data base and the
derivation of the fall and summer juvenile indices on which the model is based (Figure 1.1).

Significant environmental forcing may occur on the shelf (e.g. Gulf Stream position, Ekman transport, forage). The effects of Transport of Larval Croaker Into the Chesapeake Bay are investigated in Chapter 6. This comprises Part 2 of Sub Model I. The output from Sub Model I, which predicts fall juvenile croaker abundance in the Chesapeake Bay, is input to Sub Model II (Figure 1.1).

The effects of winter temperatures on young-of-the-year croakers and the resultant effect on the fishery two years later have been shown (Wojcik 1978). Warm winters (1976) yield good catches two years later and cold winters (1918, 1958, 1977), poor catches. Similar effects have been noted in the Chesapeake Bay for other sciaenids, i.e., weakfish (Cynoscion regalis) and spot (Leiostomus xanthurus) (Hildebrand and Schroeder 1928). Chapter 7, Effects of Winter Temperature on Survival of Juvenile Croaker, quantifies this as Sub Model II (Figure 1.1). It then incorporates the relationship established in Sub Model I to calculate year-class strength of juvenile croaker at age 0+.

Chapter 8, The Atlantic Croaker Fishery, examines the history of the fishery in light of the previously defined environmental relationships. In analyzing this data for potential bio-environmental interactions, the degree of density-independence must also be established (Parrish and MacCall 1978). Therefore, Chapter 9, Spawner-Recruit Relationship: Density-Dependence versus Density-Independence, investigates this. Both Chapters 8 and 9 recognize that stock size is strongly controlled by environmental effects on year-class strength; this comprises Sub Model III (Figure
1.1). Fishing pressure, the necessity of maintaining a spawning population, and management recommendations are discussed.

This study provides statistical and conceptual relationships between larval and juvenile croaker and their shelf and river environment and develops a model to reflect the effect of environmental factors on the various life stages of the croaker population. Results from all the Chapters are used to determine the environmental parameters which affect the population. The type of relationship considered is defined conceptually from knowledge of response of croaker to its environment. Incorporation of the time lag between environmental events and measured biological effect have been inferred and supported by the research. The physically and biologically significant relationships and parameters are used to statistically develop a model to forecast the croaker population. This is tested in Chapter 10, Application of the Model, by predicting the 1982-83 year class of croaker in the Chesapeake Bay.

The ultimate goal of this research is to identify and quantify the interrelationship of the Atlantic croaker and its environment in such a manner as to incorporate this knowledge into stock assessment and yield prediction models. This work investigates the life history of the Atlantic croaker over time and space, and identifies significant factors acting on different crucial life history stages. The significant findings of this dissertation are listed in Chapter 11, Model Summary.
CHAPTER 2

Environmental Variables in Marine Fishery Models

Why? When? How?

INTRODUCTION

This is a review chapter. Its' purpose is not to present new insight into the use of environmental variables in marine fishery models, nor to reiterate what can be found in several comprehensive reviews (Cushing and Dickson 1976; Pella 1979; Bardach and Santerre 1981). The purpose is provide a background of this aspect of fisheries.

Recruitment fluctuation depends on interannual physical environmental variability. This dependency is attributed by Cushing (1975) to Russell's (1930) match-mismatch concept between the spring bloom and spawning. This observation has served to start a long line of observations and/or research attempting to pinpoint the larval stage as the most susceptible to environmental perturbations. The NMFS/EDIS sponsored Climate and Fisheries Workshop in 1976 proposed several simplistic recommendations. The 1978 Climate and Fisheries Workshop then detailed a number of requirements necessary to follow the recommended modelling plans through. This latter workshop expressed the consensus that it would be "easier to develop climate/fisheries models for those species which need favorable circulation patterns to control
larval survival than for species whose survival is geared to a match/mismatch of either food or predators."

DISCUSSION

Need and Recognition

To be addressed here are the "Why?", "When?" and "How?" that have emerged from decisions to incorporate environmental variables into fisheries recruitment and yield models. The "Why?" and "When?" are relatively straight-forward. It's the "How?" which is complicated and may be difficult to quantify or implement.

"Why"—because Cushing (1975), Lasker (1978) and others have demonstrated relationships between physical forcing factors, larval forage, and recruitment. The goal of the Joint IOC/FAO Meeting of Experts on Ocean Sciences in Relation to Living Resources (OSLR), was to identify research requirements concentrating on questions of recruitment and predation (Bakun, Beyer, Pauly, Pope and Sharp 1982). A schematic life cycle of fishes depicting the life cycle as a circle was divided into quadrants representing the major stages: (1) eggs and larvae, (2) juveniles, (3) nonreproducing adults, and (4) spawning adults. Vulnerable periods in the life history were related to environmental factors. The concept was advanced of combining density-dependent (e.g. predation, growth rate, starvation) and density-independent (e.g. transport, temperature) relationships by mathematically incorporating environmental factors into standard population dynamics equations.
The passage of the Magnuson Fishery Conservation and Management Act of 1976 has emphasized the need for greater understanding of factors that determine the variability in fish production and distribution. Federal and state management plans cannot tolerate ±50% predictions that have been generated by environmentally static fishery yield models. Biologists are beginning to acknowledge that highly fluctuating yields may be caused by natural environmental variability, making it necessary to separate trends due to alteration in climate from effects due to fishing.

**Time Scales**

"When?" read as when should this approach be implemented, can be answered simply with "as soon as possible."

"When", in terms of the time scales of analyses, is complicated because frames of reference and needs vary depending upon the system or stock. Changes in fish populations over long time scales (decades to centuries) may be related to climatic scale warming and cooling trends in the earth’s heat budget. There was a 65-year warming trend from 1880 to 1945 which caused distributional changes, penetration of higher latitudes by "southern" species (e.g., the cod off western Greenland) and increased year-class strengths in the northeast Atlantic (Cushing and Dickson 1976). There are large fluctuations in surface temperature and salinity on a time scale of 1 to 10 years. During the 1956 to 1959 warm period on the Pacific coast, water temperature was positively correlated with increased northward catch of subtropical species along the California coast (Radovich 1976).
The time scale of an El Nino event is 1 to 2 years. During that time, anomalies of temperature and salinity result in geographic changes of centers of anchoveta abundance and availability which adversely affect the fishery (Figure 2.1). Seasonal cycles on a scale of weeks or months, may impact primary production, be magnified up the food chain and affect year-class strength. On a shorter time scale, storms can cause a disruption of food supply (Lasker 1978) and can effect recruitment if they happen during time of first feeding (e.g., Hurricane Agnes). Individual fish larvae survive in a microscale of time and space, but year-class strength is probably governed by mesoscale events (such as wind strength, duration and direction) which alter the micro-scale habitat.

Fishery hydrography is the study of interrelationships of oceanography, maritime meteorology, aquatic ecology and practical problems in fisheries. These are related to productivity of oceans, fishery resources, behavior, availability of fish, and effects of oceanographic and meteorological conditions on the conduct of fishery (Hela and Laevastu 1961). An extension of this recognition of the connections between biological and physical systems is a new hybrid science of "fishery climatology". Its goal is the application of this combined knowledge to remove some of the uncertainties associated with variations in fish distribution or abundance. This may be descriptively referred to as "fishery oceanography with time-series data" (Ingham 1981). This advances the complicated question of "How?" How does one approach a modelling effort of a fishery which incorporates environmental factors?
Figure 2.1

Life History

Before quantitative analyses can begin, the crucial life stages and physical forcing factors must be identified in time and space. In many cases this identification may require basic research to fill the gaps in the life history. Specific parameters such as spawning place and time, larval forage needs, growth rates, and migration habits are often unknown or poorly understood for many species. Empirical correlations between biological and physical data may give initial clues to the establishment of relationships when field and laboratory studies are not feasible.

These empirical or statistical relationships must be treated with extreme care, as cause and effect may be totally lacking. Further, the popular application of a multiple regression statistical treatment must be functionally based as it can lead to false conclusions if independent variables are autocorrelated (e.g., salinity and river discharge). These relationships must be identified and formulated into a conceptual model before a quantitative model can be attempted. In such a multifaceted area, investigation may reveal possible relationships and new hypotheses may be continuously developed and tested.

Data Bases

Inherently everyone knows there are a lot of data around; but data are like fish stocks, abundance does not reflect availability. Thus, the three big problems with data bases are: (1) location, (2) acquisition, and (3) manipulation.
The impetus for most projects is generally a specific fishery management problem. A species is given priority and research begins with whatever data are or can be made available. The initial effort is to discover what data may exist in national archives, public and private institutions or consulting firms conducting research. Next, these data must be identified with proximity in time and space. Despite the reliance on existing data, appropriate data are not always available; therefore, ancillary or proxy data must be used. Proxy data must first be identified and acquired. A mathematical relationship or statistical correlation may then be developed for the desired time or place to insure its validity for later application in the model.

It is necessary to understand the errors and deficiencies of available data and to glean from them whatever is significant. Historic data often come with inherent problems, many of which are not recognized, or seem insignificant until computations are attempted. The risk of using data that one did not personally collect should not outweigh the benefits of the data that would be otherwise unavailable to a single investigator. However, this use of somewhat unsatisfactory data often means missing data, insufficient documentation, non-standardized methodology and many initially unrecognized problems. It is usually necessary to seek additional sources of data as one set is seldom inclusive enough for a fishery climatology approach.

The ultimate goal is generally to predict adult stock size as reflected by commercial catch. Herein lie some of the biggest difficulties with the data bases from which a predictive model of catch will be developed. Most often commercial catch data are inappropriately collected for a modeller's needs. These data are usually expressed as
ex-vessel (dockside) pounds, often neglecting effort, time, and area fished. For each species caught, the catch is usually comprised of multiple year class contributions, unknown age-composition, and biological year differing from the calendar year. Further, several stocks from disparate geographic locations may be landed concurrently at one port.

The use of juvenile (prerecruit) survey data bypasses the need for information on the vulnerable, poorly understood larval stage, has fewer sampling problems, and has progressed further in the life-history (i.e., closer to the commercial catch that one wishes to predict).

The Models

The term "model" connotes many different things to different people, dependent upon their frame of reference. Here, it is a numerical representation that quantifies relationships. The model basis may be biological-environmental or biological-biological. The relationships are based on past observed occurrences in a manner that provides predictive capabilities. That is, given measured or estimated values of a forcing function (biological and/or physical), the "model" can be applied to yield an estimate of future stock abundance.

Various techniques are available with which to develop models. Formerly, models were developed from basic statistical techniques that biologists had at hand and could comprehend, principally linear regression. Biological systems, however, are non-linear. Therefore, modelling efforts, particularly time-series, must consider more sophisticated non-linear and autoregressive statistical treatments.
Although these techniques are not as widely used, the concept of relating the environment to year-class strength is not new.

Pertinent at this time is a discussion of the historical attempts at environment-stock modelling. Carruthers (1938) recognized a link between winds, larval drift and year-class strength of herring and haddock. Sette (1943) cited unfavorable winds as a reason for high larval mortality in the Atlantic mackerel. Walford (1946) correlated the size of a year class of sardines with average daily summer surface salinities from 1934 to 1941, using salinity as an index of upwelling. Chase (1955) also related winds and larval drift, but improved the correlations by adding temperature as an estimator of spawning time. Lower water temperatures produce slower larval development. Ketchen (1956) linked longer pelagic drift and thus less critical feeding conditions, with strong year classes in lemon sole.

Ottestad (1942) related mechanisms of climatic change with fisheries yield. Taylor, Bigelow and Graham (1957) discussed the warming trend from 1900-1940 of Boothbay Harbor waters in relationship to landing statistics. Radovich (1961, 1976) related the 1957-1959 warming of Northwest Pacific waters to range extensions and later to commercial catch of barracuda, tuna, and yellowtail. Parrish and MacCall (1978) have developed a recruit model which includes environmental factors linked with the degree of density-dependence for the Pacific mackerel. Nelson, Ingham and Schaaf (1977) developed a spawner-recruit model which incorporated a "survival index" based on Ekman transport. Pauly (1980) has calculated coefficients of natural mortality for 175 stocks of fish by modifying the von Bertalanffy growth formula with mean annual water temperatures.
Non-population dynamics spectral analyses have been used by some researchers as an approach to modelling. Van Winkle, Kirk and Rust (1979) used Fourier analysis to remove periodicities in fluctuations of striped bass abundance considered to be caused by density-independent environmental factors. Jensen (1976) developed a Box-Jenkins model to forecast yield of menhaden. His model only included historical catch data and did not include fluctuations due to effort. Therefore, it is only reliable as long as there is no change in effort. Hunt, Carroll, Chincilli and Frankenburg (1980) developed a model which predicts brown shrimp harvest in Pamlico Sound, North Carolina. The model uses April-May temperatures and salinities. They found growth rates decrease and mortality rates increase when salinities are below 10 °/oo and temperature below 20°C.

Botsford and Methot (1981) used a technique of time-lagged correlation functions as an analytical tool to uncover actual mechanisms responsible for the relationship between environment and populations. They attempt to explain fluctuations in California dungeness crab catch on the basis of upwelling and temperature. Relating causal links on several time scales and the use of multivariate analysis makes the process more complex.

Tyler (1981) used an array of techniques to reach the simulation model stage. He analyzed the Dover sole population using cohort-analysis and catch-per-unit-effort. Hayman and Tyler (1980) investigated the relationship between cohort strength and oceanographic factors using a multiple regression treatment. A correlation model incorporating upwelling in early summer and offshore divergence the next winter explained 65% of the cohort strength variation. It is important
to note, that these mathematical relationships have biological foundations. Upwelling is likely to influence cohort strength by affecting food availability. Winter convergence prevents inshore transport of larvae during settling time. The cohort strength of the English sole is determined by oceanographic factors different from those which act as forcing functions on the Dover sole. However, both the relationships are equally justifiable biologically.

In fisheries model development the oceanic environment is measured, not modelled (Bledsoe 1981). The effect it has on fish and fisheries is what is to be modelled. Improvements in explained variance may be a measure of effectiveness of including environmental information in a model. Thus, testing hypotheses concerning environmental influences can be performed on historical fisheries. Environmental variables as predictors could be incorporated into established population dynamics models, thus interweaving density-dependent and density-independent effects.

CONCLUSIONS

As relationships are established and modelling efforts increase, more meteorologic/oceanographic factors are being incorporated. Examination of these relationships, especially in an effort to avoid autocorrelated variables, increasingly reveals meteorologic parameters to be factors driving the measured oceanographic conditions. Sette (1959) said:
"...the events affecting the fisheries as originating in the atmospheric circulation, operating through their direct effects on the properties of sea water and indirectly by modifying the oceanic circulation, and these, in turn, affecting our marine animal populations, both directly and indirectly through the chain of plant populations."
CHAPTER 3

Conceptual Life History of Atlantic Croaker

INTRODUCTION

The Atlantic croaker (*Micropogonias undulatus*) is basically a southern species which is prominent in the Gulf of Mexico and South Atlantic Bight, although it has a wide geographic range from the New England States to South America (Chao and Musick 1977). It is an important commercial and recreational species from Maryland through North Carolina. During climatically warmer periods, such as the 1930's and 1940's, the croaker extended its range north and it was fished commercially in New York. Now Virginia, Maryland and Delaware are considered to be the northern range of the species. The Atlantic croaker spawns in coastal marine waters and uses estuaries as nursery and feeding grounds (Diaz 1982).

The conceptual life history would have to be developed from Atlantic and Gulf research combined if based solely on the literature available. However, this is inappropriate. Research on the Atlantic stock reveals dramatic differences compared to the Gulf stock (White and Chittenden 1977, Morse 1980). Based on this, I believe that life history must be dealt with independently, Atlantic and Gulf. This research is concerned with distribution and migration of croaker north of and around Cape Hatteras, generally disregarding the South Atlantic
Bight and Gulf of Mexico except when references are appropriate, or more likely, the only ones available.

This study was originally designed to develop a predictive model of adult croaker based on fluctuations in juvenile abundance in the York River. Gaps in the life history of the croaker have revealed needed areas of investigation and possible sources of inadequacy in the predictive capability of such a model. To enable the pursuit of a comprehensive predictive model, a conceptual model of the life history of the Atlantic croaker was developed.

The following discussion of the conceptual life history of the Atlantic croaker attempts to include most of the factors important in determining year-class strength and/or commercial catch. While this conceptual life history forms the framework for the model developed in this dissertation, it also includes discussion of factors considered but not ultimately included in the final model.

The joint IOC/FAO Meeting of experts on Ocean Sciences in Relation to Living Resources (OSLR) produced a schematized life cycle of fishes (Figure 3.1) (Bakun, Beyer, Pauly, Pope and Sharp 1982):

**Stage I** comprises entry of the egg into the environment, fertilization and subsequent pre-hatch embryo development, hatching of the larvae and subsequent development up through metamorphosis (to be loosely defined here as where scales form or where dominant respiration switches to the gills).

**Stage II** includes the metamorphosis of juvenile stages which precede recruitment of the fish into fishery operations. This is the least understood stage in the life history cycle of many fish
Figure 3.1

Schematized life cycle of fishes (from IOC 1980).
because there is no appropriate gear to sample them during this stage.

**Stage III** includes the period from initial entry of the fish into fishery or sampling operations, of fishery susceptible adult fishes before they mature.

**Stage IV** is defined as that period from the onset of gamete differentiation and fabrication to the end of the reproductive period of the individual. This may be seasonal, annual or continuing over varying time scales, depending upon the species. Also, egg maturation and subsequent spawning may happen once or several times in a lifetime, i.e. iterative within any year or annual.

An amended scheme of the OSLR life stage designations provides a conceptual model of Atlantic croaker life history including environmental factors (Figure 3.2). The model starts with the spawning adult in quadrant I as opposed to the OSLR designation of IV (Figure 3.1). It is believed to be the first step, rather than last, to be considered in a croaker model.

**DISCUSSION**

**Stage I - Spawning Adults**

Croaker migrate out of bays and rivers, their summer habitat, in the fall and spawn in the ocean, possibly near the mouth of the Chesapeake Bay, probably very nearshore (Hildebrand and Cable 1930, Pearson 1941, Bearden 1964, Nelson 1969, Chao and Musick 1977). The north-south range of croaker spawning in relation to the mouth of the
Figure 3.2

Conceptual model of Atlantic croaker life history, including environmental factors, based on the OSLR model in Figure 3.1.
Chesapeake Bay is considered to be density and temperature dependent. Initial inspection of Atlantic shelf ichthyoplankton (P. Berrien, NOAA/NMFS/NEFC/Sandy Hook Lab pers. comm.) and fecundity data (Morse 1980) from Cape May, New Jersey to Cape Hatteras, North Carolina indicated the position of the croaker on the shelf during spawning to be closely related to bottom temperature. In the "cold" years of the 1960's, when the commercial catch of croaker in Virginia hit an all time low (6200 pounds, 1968), croaker larvae were found near or south of Cape Hatteras. Inference of surface isotherms indicated that the larvae south of the Cape were being advected offshore to the Gulf Stream, and thus lost to potential recruitment as juveniles into the Chesapeake Bay. In the warmer years of the 1970s, ripe croaker and ichthyoplankton were collected north of Cape Hatteras, and in some cases, even north of the Chesapeake Bay. The commercial catch of croaker increased during this time to 8,600,191 pounds in 1977, near what it had been in the late 1950s. Unpublished NMFS plankton and temperature data (P. Berrien pers. comm.) and R/V DOLPHIN cruise data (Clark, Smith, Kendall and Fahay 1969 and 1970, Berrien, Fahay, Kendall and Smith 1978) were analyzed. My analyses of these data indicate shelf water temperature and wind-induced upwelling (Figure 3.2) to be important factors determining where and when croaker spawn. Laboratory experiments indicated that croaker spawn at 16°- 24°C (W. Hettler, NOAA/NMFS/SEFC/Beaufort Lab pers. comm.). This information was used when making assumptions regarding croaker spawning times and areas investigated in Chapter 4.
Stage II - Larvae

Stage II (OSLR Stage I) covers the time from the entrance of the egg into the environment through larval metamorphosis. For the croaker, this means movement from some site of spawning in shelf waters to the Chesapeake Bay. OSLR (Bakun et al. 1982) recognizes this as a time of extreme vulnerability and high rates of mortality that is most critical to eventual recruitment.

Figure 3.3 is a schematic representation of Stages I, II and III of the croaker life cycle. Adult croaker spawn on the shelf. Eggs and larvae are pelagic at hatching. At some undocumented point in their development, larval croaker become demersal and move into estuaries. Mechanisms of larval transport into the estuarine nursery grounds are undocumented and are probably a combination of both passive transport by currents and active swimming (Pearson 1929, Weinstein, Weiss, Hodson and Gerry 1980, Norcross and Austin 1981, Diaz 1982).

Successful first feeding may be the single most important determinant of larval success, despite its brief duration. Second to this is predation (Bakun et al. 1982). Many larval studies have been done on first feeding success (Lasker 1975 and 1981a) and starvation (Theilacker 1978, O'Connell 1981), size selective predation (Christensen, Christensen and Beyer 1980), food consumption modelling (Beyer and Christensen 1980), effects of prey kind and density on growth and survival (Lasker 1975, Beyer and Laurence 1981), turbidity (Beyer and Christensen), and water column stability (Lasker 1981b, Sharp 1980). However, though copepods (calanoid and harpacticoid) are thought to be the major dietary component for larval and juvenile croaker (Diaz 1982), no direct observations or species-specific studies have been made for
Figure 3.3

Schematic representation of movement of croaker life stages I, II and III in relation to Chesapeake Bay circulation.
croaker. This type of research, is quite necessary, but not within the scope of the research based on environmental factors outlined here.

The environment may affect larval feeding through turbulent conditions which destroy food aggregations and dilute potential food organisms below threshold concentrations. Strong upwelling in 1975 and storms in 1978 limited food for first-feeding anchovies (Lasker 1981a). Physical dispersion of larvae and their food could be caused by wave-induced turbulence, wind-induced shear, upwelling, tidal currents, and eddies of various time and space scales (Hunter 1976). Wind disperses patches of food and larvae so that they no longer come together in "windows" of space and time (Russell 1930, Bakun et al. 1982). Feeding and starvation, though considered by some to be the major cause of larval mortality (Hunter 1976, Lasker 1981b), is not included in this model. It was originally thought that Cushing's (1975) match/mismatch hypothesis may be used to infer a biologically applicable explanation for a similar situation between shelf wind-stress and juvenile croaker abundance. However, the lack of zooplankton collections, larval condition indices and laboratory observations make this inference untenable for croaker.

Similarly, though recognized as having an extremely important effect on larval mortality, relatively little work has been done on larval croaker predation. Predators, co-occurrence with croaker eggs and larvae, abundance in time and space, feeding strategies and ability to capture different life stages need to be determined (Hunter 1976). Predation on larvae, specifically on croaker larvae on the Atlantic shelf, is not known. Preliminary results of studies on the role of jellyfish and chaetognaths as planktonic predators of marine fish larvae
show that they prey on larval fish, but the significance of their predation under natural conditions with patch plankton masses is unclear (Coston-Clements 1980, Ferraro 1980).

Another factor which must be considered during this stage of development is growth rate. Larval growth can be characterized as a moderate increase in length immediately following hatch, followed by a period of minimal growth, with mean size increasing rapidly at onset of feeding (Zweifel and Lasker 1976). This has been found valid for croaker larvae, which are 1.6-2.0 mm at hatching, begin feeding at about five days and reach 3.1 mm at age thirteen days (Warlen 1980). Through daily aging of otoliths of croaker larvae, a Laird-Gompertz growth model has been constructed which estimates an age of 62 days for a standard length up to 13.4 mm (Warlen 1980). Croaker larvae collected after mid-January have slower growth rates which may be due to colder ocean temperatures and less than optimal food supplies (Warlen 1980). Growth rates for croaker are more variable with low than with high water temperatures (Lewis and Judy 1983). Time from fertilization to hatching of *Menidia menidia* varies inversely with temperature (Austin, Sosnow and Hickey 1975). Also, although no significant direct correlations between limited-range temperatures and northern anchovy (*Engraulis mordax*) growth rates have been found (Methot and Kramer 1979), they have been found for the dungeness crab (*Cancer magister*) (Wild 1980). For the purpose of discussion, it will be assumed that growth slows as temperatures decrease.

Larvae collected in the ocean off North Carolina appear as distinct cohorts each month and are continually transported to inshore nursery areas (Warlen 1980). Conceptually, if the larvae are found
north of the Chesapeake Bay offing, the environmental forcing factor becomes the wind. Timing of spawning may be most important in relation to the seasonal fall wind change. "Summer" winds are less favorable for larval recruitment, because they blow out of the southwest, carrying pelagic croaker eggs and larvae offshore and away from the Chesapeake Bay. After the seasonal wind shift to the "winter" pattern, the mean wind direction is northwest, with a southerly and onshore component of drift (Lettau, Brower and Quayle 1976). The farther north of the Chesapeake Bay larvae are, the better chance they have of withstanding periods of unfavorable winds and reaching the Chesapeake Bay mouth.

Data for winds, temperature, and probable spawning site as determined from ichthyoplankton and spawning data are used to test the hypotheses regarding larval transport and subsequent recruitment in Chapter 6. Such investigations are expanded by using the juvenile length data from the VIMS bottom trawl survey. Warlen's growth curve (1980) allows back extrapolation of the juvenile croaker data to determine time of spawning. Identification of spawning time was then used to investigate the relationship of the shelf environment to larval recruitment. Explanations of wind-induced larval transport with details of croaker are found in Chapter 6.

Stage III - Juveniles

Larvae (8-15 mm) move up-estuary to fresh or brackish water (Bearden 1964) by means of salt wedge transport (Weinstein et al. 1980). Distribution of small juveniles from the VIMS trawl surveys shows their greatest abundance to coincide with the upstream location of the salt wedge (Haven 1957). Transition to juveniles occurs between 15 and 25 mm
(Diaz 1982), but for the purpose of this model, any young croaker within the estuary will be referred to as a juvenile, irrespective of size. On the east coast, juvenile croaker prefer the deep channels and tidal creeks in the estuaries as nursery grounds (Weinstein 1979). In the winter, when the bottom waters in the channels are warmer than the shallows, this may enhance juvenile survival. When dissolved oxygen drops during the summer, croakers will leave the deep areas and go to the shallows (Chao and Musick 1977). Juvenile croaker may also expand into shallow habitats in years when they are particularly abundant.

Deep channels with unconsolidated sediments or areas of soft mud bottoms with high organic detritus content are considered optimal habitats for juvenile croaker. Croaker is an opportunistic bottom feeder whose diet may include: mysids, decapods, amphipods, copepods, polychaetes, mollusks, finfish and detritus (Chao and Musick 1977, Kobylninski and Sheridan 1979, Diaz 1982). It seems certain however, that no one factor is completely responsible for croaker distribution within the estuary. Food, substrate, salinity, protection from predation and temperature interact. Distinguishing which is more important is difficult (Diaz 1982).

Little is known about predation on juvenile croaker. Fish that overwinter in estuaries may be avoiding predation by adult demersal fish, as there are few adults in the rivers in the winter (J. Miller, North Carolina State University pers. comm.). The hypothesis of predation on juvenile croaker by striped bass (McHugh 1967, Dovel 1968) should be analyzed. Correlations lagging Maryland DNR young-of-the-year striped bass survey data one year with respect to the croaker (0+) the next year could be used to test this hypothesis. Similar correlations
using the VIMS trawl survey data (1954-1982) for striped bass and croaker should be examined. Care should be taken however, if strong statistical coherence is found. It is likely that there is no predator-prey relationship, but that the juveniles react in opposite ways to the same environmental parameter, i.e., cold winters are bad for croaker (Wojcik 1978) but are good for striped bass (Kohlenstein 1980).

Juveniles, though more cold-tolerant than adults (Hildebrand and Cable 1930, Johnson 1978), are vulnerable to extremely cold winter temperatures. Low temperatures have been documented to be lethal to juvenile croaker (Joseph 1972, Wojcik 1978). Preliminary laboratory studies showed that feeding activities of juveniles could be regulated by altering the temperature. At 5°C or less, feeding activity ceased. Distress was noted at 1.5°C, and 0.5°-1.0°C produced death with 24 hours (Joseph 1972). A temperature of 4°C for an indefinite period of time is generally accepted as critical (F. Wojcik, VIMS pers. comm.). This aspect is included in the model in detail in Chapter 7.

Down-estuary movement may be stimulated by seasonality and growth. Small juveniles are found in lower salinity waters with size increasing down-estuary (Haven 1957). I originally intended to try to quantify this movement, but data management problems prevented this. It most likely would not have been a significant input to the model, unless I could have shown that juvenile croaker move down-estuary in response to a winter temperature decrease. Juvenile croaker were observed outside the mouth of the Bay in January 1982 (J. Sypek, VIMS pers. comm.). Joseph (1972) revealed that, as the water temperature lowers, the juvenile croaker move downstream and aggregate near the mouth of the Chesapeake Bay where it is warmer. It is not known if they are reacting
to a temperature change or if they are being passively carried downriver as they become moribund. I have hypothesized that a sudden temperature decrease over a short period of time causes the observed stunned condition, while a gradual decrease may cause croaker to move out of the Bay to warmer water. This aspect is not developed here because it requires analysis of the distribution of croaker within the Bay in relation to bottom temperatures. These data are not available. Additional laboratory experiments are needed of specific size and age juvenile croaker responses to time-dependent decreasing temperatures.

**Stage IV - Adults**

The juvenile croaker leave the Bay as 0+ fish in fall and migrate onto the shelf (Merriner, Kriete and Grant 1976). There has been no quantification of those factors affecting survival and abundance of juvenile croaker either during the next summer when they are back in the Bay (I+) or until they are caught commercially. Parasite populations in croaker have been studied but a negative effect on croaker survival was not suggested by Benner (1980).

Dead yearling (I+) 100 mm to 200 mm inch croaker had been found recently in Pamlico Sound, North Carolina (Austin 1981). This phenomenon has been previously recorded (Hildebrand and Cable 1930) and is not considered unusual by fisheries personnel in North Carolina (Austin 1981). North Carolina data on these fish kills have been obtained (J. Hawkins, NCDNR/DMF/Washington, NC pers. comm.) but are insufficient to determine if North Carolina winter temperatures killed one-year old croaker that overwinter in Pamlico Sound. If I+ croaker are subject to winter kill in Pamlico Sound, N.C., two cold winters in a
row, e.g., 1977-78 and 1978-79, would be especially deleterious, affecting first $0^+$ fish and remaining $I^+$ fish the next year. Such conditions have apparently affected commercial croaker catch in the Chesapeake Bay.

Environmental factors which may affect distribution and abundance of Stage IV adults, those recruited to the fishery but not in spawning condition, have not been identified and probably exert a lesser impact. It is known that juvenile croaker make up a major component of the shrimp by-catch in North Carolina (Keiser 1976) and are recruited commercially as early as age $I^+$ in the Chesapeake Bay (Massman and Pacheco 1960). The significance of this is that when stock size is small, young fish are actively pursued commercially and harvested before spawning. This is addressed in detail in Chapter 8 (Commercial Catch). Croaker leave the estuary at age II and move onto the shelf to spawn, completing the circle. The adult fish is then in Stage IV for the rest of its existence.

CONCLUSIONS

The conceptual croaker life history identified the necessity for investigating spawning time and position, larval distribution and transport in relation to environmental factors on the shelf, and the effect on juveniles of winter temperatures within the Chesapeake Bay. Stages in which recruitment may be affected by environmental factors are targeted in a primary model of croaker life history shown in Figure 3.4.

Sub Model I, larval recruitment, combines conceptual OSLR-based stages I and II. Fall overturn on the shelf as a result of
cooling and the seasonal shift in wind direction and speed (summer: southwest; winter: northwest) is a significant factor in determining the extent of "warm" bottom waters available to the spawning croaker. This stage will be quantified by analyzing adult, larval and physical data collected on NMFS MARMAP surveys (Appendix 3.1 - Table). Larval movement and wind-driven transport are modelled by correlating larval size and abundance on the shelf with larval size and abundance over time in relation to daily larval growth rates, wind direction and strength. The hypothesis of into- and within-the-Bay transport of larval/post-larval croaker by entrainment in the bottom waters is also be examined. Unexplained fall recruitment success or failure may be dependent upon first feeding success, water column stability, predation, or stock size.

Sub Model II, juvenile survival, is OSLR stage III. Although many factors may affect juvenile survival during this stage, temperature is the only one which will be assessed. Output from Sub Model I provides input for sub Model II. Physical data on the shelf can be directly correlated with Chesapeake Bay juvenile data for years when no biological data exist. Therefore by using data as available to establish, test and quantify relationships, the VIMS trawl survey data base (Chapter 5) is used to form a consistent base.

Sub Model III, commercial catch, is OSLR stage IV with feedback through spawning stock size (OSLR stage I) to Sub Model I. Year-class strength indices as derived from Sub Models I and II provide input
Figure 3.4

Basic model of croaker life history stages in which recruitment potential may be affected.
SPAWNING STOCK SIZE

LARVAL RECRUITMENT

JUVENILE RECRUITMENT (Survival)

COMMERCIAL CATCH

SUB MODEL I

SUB MODEL II

SUB MODEL III
to Sub Model III. These, together with the age composition of the commercial catch are used in order to utilize appropriate lag times from juvenile to commercial catch. Thus, spawning stock size can be assessed. This study provides an insight into the overall life history of the Atlantic croaker and quantifies aspects of the croaker's relationship with environmental forcing factors, resulting in a predictive model.
INTRODUCTION

The "cold pool", first reported by Bigelow (1933), is a continuous subsurface water type located on the bottom of the continental shelf between Georges Bank and Cape Hatteras (Ingham 1982b). Although it warms and diminishes in volume as the summer progresses, the cold pool persists in the Mid-Atlantic Bight into the fall (Houghton, Schlitz, Beardsley, Butman, and Chamberlin 1982) (Figure 4.1.1). The summer wind regime in the Mid-Atlantic Bight is south-southwest (Saunders 1977, Ingham 1982a). This pattern generates an offshore component in the surface Ekman layer as a "two-cell" coastal upwelling system and brings the cold pool closer to the beach (Hicks and Miller 1980, Johnson 1982). This upwelling is a phenomenon due to the seasonal movement of the Polar Front created by two distinctly different wind regimes (Godshall, Williams, Bishop, Everdale and Fehler 1980), summer, May-August, (southerly) and winter, October-March, which has northwest or west winds (Ingham 1982a). The purpose of this part of the chapter is to show the link between the cessation of the southerly (summer) meridonal wind component and the relaxation of the upwelling in the Mid-Atlantic Bight. The result of this relaxation is that the cold
Figure 4.1.1

The Mid-Atlantic Bight, indicating Stations 1 through 7 which refer to the temperature section in Figure 4.1.6.
pool slides offshore allowing the areal extent of "warm" bottom waters to increase.

MATERIALS and METHODS

Bottom isotherms for fall 1967-1981 NMFS MARMAP cruises were obtained from Davis (1979), Nickerson and Wright (1980), charts (S. Nickerson, NOAA/NMFS/Woods Hole Lab pers. comm.) and unprocessed data provided by the Sandy Hook and Woods Hole NMFS Laboratories. To equate locations, only data south of 39°N latitude, north of 35°S latitude, west of the 200 m isobath and east of the smoothed coastline were considered. Not all cruises sampled as far north as 39°N nor as far south as 35°N, necessitating extrapolation of isotherms. Bottom water temperature data were contoured using 16°C as an index of warm water. This isotherm was chosen because it was the highest bottom temperature reliably present on the shelf from July to November, the period considered here. The areal extent in square nautical miles (nmi)² inshore of the contour was determined using hand and digital planimeters (Welch 1948). Twenty-six sets of isotherms spanning fifteen years were used. The time periods were standardized using numerical assignments for each third of a month, as follows: July - 1, 2, 3; August - 4, 5, 6; September - 7, 8, 9; October - 10, 11, 12; November - 13, 14, 15. Thirds of months were used because ten days was the average time needed to collect bottom temperature data across the whole Bight. In the months with more than 30 days, the last third contained eleven days.
Time series plots (1977-1981) of bottom temperatures at the mouth of the Chesapeake Bay utilized these same MARMAP data. Transect location and station designations (Figure 4.1.1) corresponded to those used by the 1965-66 R/V DOLPHIN cruises (Berrien, Fahay, Kendall and Smith 1978).

Hourly and/or three-hourly wind observations from Norfolk airport, Virginia were obtained through the National Climatic Data Center (NCDC), Asheville, N.C. Norfolk airport, 36°51' N, 76°12' W, is 9.1 m above sea level, 6.4 km to the nearest water, and 17.8 km to the open coast (Raynor and Hayes 1981). These data were validated for use offshore by Frederic Godshall (NOAA/National Environmental Satellite and Data Information Service (NESDIS)/Marine Environmental Assessment Division (MEAD) pers.comm.). His analyses compared the average monthly climatological range of 1947-1980 Norfolk winds with 1906-1980 marine observations in blocks of one degree latitude and one-half degree longitude. The resulting shift in direction offshore compared to Norfolk was from 0 to 4 degrees to the right with the speed adjusted by a factor of 1.0 to 1.4 (Appendix 4.1.1 - Figures). Since Godshall felt these factors were minimal, Norfolk airport data were not adjusted (Appendix 4.1.2 - Text).

Upwelling caused by longshore winds is long-lived, whereas that due to an offshore wind is ephemeral (Csandy 1981a). Therefore meridional components were averaged weekly and plotted as two-week moving averages by the VIMS Prime 850 computer, using oceanographic convention for currents, i.e., indicating the direction toward which the water, in this case air, is moving. Meteorologic convention is direction from which the wind is blowing. The temperature contours indicated that the
warm water was present on the shelf prior to the onset of strong winds blowing from the north in the fall. Thus, the time of cessation of the prolonged southerly winds (meteorologic convention) was designated as the end of the summer regime, even though no northerly component was yet present. This relaxation of the southerly wind component was assigned a value 1 – 15 corresponding to the time scale by thirds of month described for temperature collections.

Each explained variance ($R^2$) was adjusted for small sample size based upon degrees of freedom in each particular relationship. Linear and parabolic regression equations were determined using Business Graphics software on an Apple IIe computer.

RESULTS

The shaded areas above the line in Figure 4.1.2 indicate southerly winds, i.e. summer winds which blow towards the north and cause upwelling. Numbered rectangles indicate time of assigned cessation of the summer winds. The average time of the cessation for 15 years was 6.6, the end of August to the beginning of September. Some years had a clear-cut shift from a predominantly southerly to a predominately northerly regime (1968, 1970, 1972, 1977). Other years were not as abrupt (1971, 1975, 1976). For this reason, the cessation time was designated based on the following criteria using meteorologic convention: 1) the first crossing of the axis from southerly to northerly; 2) the cessation of the strong southerly component; 3) the commencement of the strong northerly component.
Figure 4.1.2

Meridional wind component for Norfolk airport, Virginia, 1967-1981. Shaded areas above the axis indicate the summer wind regime which blows from the south and causes upwelling. Numbered rectangles designate time of cessation of summer wind by thirds of months past 1 July.
The contours of the 16°C bottom isotherms were examined at the assigned times of wind cessation. Figure 4.1.3 shows contours of 16°C at 26 sampling times. When sampled at the end of September the areal extent of 16°C water show the effects of progressively later times of wind cessation: mid-August, 1981; beginning of September, 1974; mid-September, 1979; end of September, 1980; and beginning of October, 1977. There is a noticeable difference in position of the contour offshore in 1981, the year of early wind cessation, as compared to inshore with the late cessation in 1977.

The trend is from large areal extent of bottom waters of 16°C or greater temperature and early summer wind cessation to small areal extent and late summer wind cessation. This is especially apparent at the extremes. However, there is no significant statistical correlation \( R^2 = 0.11, n=26 \) (Appendix 4.1.3 - Figure) because of many mid-range, "average" years. The time of data collection is significantly related to the areal extent of warm water \( R^2 = 0.61, n=26 \) (Appendix 4.1.4 - Figure). To adjust for this additional effect, I calculated a wind-cruise interval by subtracting the time of the collection from that of the wind cessation. These are plotted on the abscissa in Figure 4.1.4 versus the area \( (\text{nmi})^2 \) of warm water plotted on the ordinate \( R^2 = 0.78, n=26 \). This relationship shows that 78% of the variation in the areal extent of warm water on the shelf observed by the fall NMFS cruises was explained by the time intervening between the cessation of the summer winds and the observation of bottom temperatures. Using this relationship to correct for the collection time, the areal extent of bottom water greater than or equal to 16°C \( (\text{nmi})^2 \) can be adjusted to a specific collection time. A linear relationship exists between the time
Figure 4.1.3

Location of the 16°C isotherm in the Mid-Atlantic Bight at 26 sampling times over 15 years.
Figure 4.1.4

Relationship between the time of collection of bottom temperature data minus the time of cessation of the summer wind regime (wind-cruise interval = x) and the area of (nmi)$^2$ of bottom water greater than or equal to $16^\circ$C (x): $y = 6231 + (897\times x) - (62\times x^2)$,

$(R^2 = 0.78, n=26)$.
of the wind cessation and the areal extent of warm bottom waters (Figure 4.1.5) (Appendix 4.1.5 - Figures). The slope is steeper and the fit is better earlier in the season because those warm waters affected at this time are likely to have been caused by the cessation of upwelling. Later in the fall, there is more variation in data due to mixing and fall overturn.

DISCUSSION

Forming, in part, as Gulf of Maine Intermediate Water in the winter, the cold pool is advected southward along mid-shelf in the Mid-Atlantic Bight (MAB) (Shaw 1982). Transport time of the cold pool from the New York Bight (NYB) to the Chesapeake Bay offing is about 150 days (Beardsley, Boicourt and Hansen 1976). Thus, the February-April NYB cold pool waters are in the southern Mid-Atlantic Bight (MAB) in July-September (Appendix 4.1.6 - Text). The cold pool has been documented off Chesapeake Bay (Whitcomb 1970) and its spatial structure illustrated using 1979 MARMAP bottom temperature charts (Houghton et al. 1982). Maximum shelf bottom temperatures off the Chesapeake Bay are delayed until September, October, or as late as November though maximum surface temperatures occur in the MAB in August. This is due to the seasonal wind shift, relaxation of upwelling, and subsequent movement of warmer waters into the area as the cold pool moves offshore, as explained below.

Onshore-offshore flows in the upper Ekman layer are compensated by opposite flows in the lower layer (Beardsley et al. 1976). Surface waters flow away from shore when a wind is blowing with
Figure 4.1.5

The predicted area \((\text{nmi})^2\) of water greater than or equal to \(16^\circ\text{C}\) that would be on the shelf at designated times:

3 VIII - end of August, 1 IX - beginning of September,
2 IX - middle of September, 3 IX - end of September.

Based on the time of the summer wind cessation and calculated from the relationship established in Figure 4.1.4.
the coast on its left in the northern hemisphere. This creates a divergence, and deep waters are upwelled along the coast (Cushman-Roisin, O'Brien, and Smith 1983). Upwelling of dense waters along the east coast of the U.S. also has been documented (E. Ruzek, VIMS pers. comm.). Offshore surface Ekman transport responds to the local winds within a few hours, but upwelling requires a few days of persistent winds (Johnson 1982). A model of time-dependent quasi-geostrophic upwelling shows that initially, the onshore flow in the water column balances the offshore top Ekman volume flux. As time progresses, the bottom Ekman layer supplies increasingly more of the required onshore flux and the onshore flow in the interior of the water column decreases (Janowitz and Pietrafessa 1980). This model was favorably compared with data collected in Onslow Bay, N.C.

Movement of bottom waters can result from persistent weak winds from the south (Hicks and Miller 1980), as well as episodes of strong southerly winds. The duration of the local winds seems to be the determining factor (Johnson 1982). Depression of surface water temperatures has been observed off North Carolina following southerly winds in July and August (Wells and Gray 1960). Two days of strong southerly winds cause upwelling of the cold pool and are documented as responsible for dropping the surf temperature at Long Branch, N.J. from 18.3° C to 9.0° C in mid-July 1976 (Hicks and Miller 1980). Similar occurrences were also reported for August and September 1973 (Hicks and Miller 1980). During periods of prevailing southerly winds, upwelling should occur along the New Jersey-Virginia coast (Ingham 1982b). Upwelling wind components correlated well with a concurrent change in shallow bottom water temperatures of
Atlantic City, N.J. in June-August 1981, indicating that summer time upwelling occurs in that portion of the Mid-Atlantic Bight also (M. Ingham, NOAA/NMFS/Atlantic Environmental Group (AEG) pers. comm.).

The climatological (1941-72) mean directional shift (summer-fall) of the meridional wind component occurs at the end of August (Saunders 1977). A mixed wind pattern is average for September then northwest winds for October (Bishop 1980a). Wind data for the fall of 1963 and 1964 (Harrison, Norcross, Stanley and Pore 1967) show that this wind shift occurred between the end of August and the end of September both years. The results shown here are consistent with these earlier observations. Observations of bottom temperatures in the fall (August-November) 1975, 1976, and 1977 (Welch and Ruzecki 1979) substantiate the effect of the time of summer wind cessation and position of the cold pool. The presence/absence and onset of warm bottom waters that they documented compared favorably to the time of the summer wind cessation analyzed here: first in 1976 (mid-July), next in 1975 (end of September), and last in 1977 (begin of October).

Figure 4.1.6 shows the seasonal and interannual spatial variation of bottom temperatures on the shelf at the mouth of the Chesapeake Bay extending from nearshore (Station 1) to offshore (Station 7). The offshore persistence of the 8°C cold pool water in 1979 noted by Houghton et al. (1982) is seen here. Cold pool waters can be seen at the edge of the shelf in other years also, although extent and persistence appears to vary year to year.

Comparison of the distribution of bottom water isotherms (Figure 4.1.6) to the meridional wind component (Figure 4.1.2) provides insight into the seasonal scale of response of bottom water to wind
Figure 4.1.6

Bottom temperatures (1977-1981) at a transect off the mouth of the Chesapeake Bay. Station 1 is inshore, Station 7 is at the edge of the shelf. See Figure 4.1.1 for station locations.
forcing. A late (early October) cessation of the southerly component in 1977 resulted in 16°-18°C water primarily in September and October. The 16°C isotherm extends out just past Station 5. Another late cessation (end of September) in 1980 shows 16°C water extending seaward approximately the same distance. However, weak summer winds and lack of onset of strong winter (northerly) winds produced a different pattern. The 16°C water lasted longer (July – December) in 1980 than it did in 1977.

A slightly earlier (mid-September) shift in 1979 allowed the 16°C isotherm to extend seaward to Station 6. Weak summer and winter winds allowed 16°C water to be present nearshore from June through November. The shoreward dips in the 16°, 12°, 10° and 8°C isotherms are responses to the August-September strengthening of the southerly component following a period of weak winds which allowed these warmer waters to extend offshore during July and August.

Early cessation of summer winds (mid-August) in 1978 and 1981 aided the extension of warm water offshore to Station 7. The sudden shift in the predominance of the wind direction in 1981 pushed the 20°C isotherm farther offshore than in any other year. Seaward movement of 16°C water in July 1978 appears to be a response to a temporary reduction of the southerly component. The abrupt cessation of the southerly wind component can be seen in the 16° and 18°C isotherms that year as warm waters quickly go offshore at the beginning of September.

As the winds begin to relax, the near-bottom layer responds first with down slope flow (Johnson 1977). Response in the upper layers is relatively slow, persisting a few days beyond the cessation of the causative winds (Johnson 1977, Lewis 1981). With the seasonal fall
shift from a southwest wind regime, upwelling ceases, and the cold pool returns offshore.

CONCLUSIONS

Relaxation of these winds causes readjustment of the water column and a redistribution of the biota (Johnson 1977). Just as bottom fishes can be trapped close to the beach by upwelling (Hicks and Miller 1980), its relaxation can result in an expansion of the area of warm bottom waters available to fishes. This could stimulate fish migration that is cued by temperature. The relationships established here, based on the cessation of the southerly wind component (Figure 4.1.5), can be used to predict the amount of warm water that will be available on the bottom of the Mid-Atlantic Bight at specific time periods of the fall. These can be applied to predict affect on fish migration through time of onshore/offshore constraints.

This concept is directly applicable to the Atlantic croaker (*Micropogonias undulatus*), a fall spawner on the MAB continental shelf. This southern demersal species, whose migration is cued by temperature, requires warm water to spawn (Bearden 1964). Therefore, the expansion and contraction of warm bottom waters would directly affect the size of the spawning ground of the croaker. The physical constraints of the northward and offshore limits of the spawning ground of the croaker and other species with similar life histories, has implications for recruitment of larvae and juveniles to the Chesapeake Bay. This is investigated in Chapter 4.2.
CHAPTER 4.2

Spawning Times and Locations of Atlantic Croaker
(Micropogonias undulatus) in the Mid-Atlantic Bight

INTRODUCTION

The Atlantic croaker, Micropogonias undulatus, has historically been an important commercial species along the Atlantic coast of the United States, especially in the Chesapeake Bay region (Figure 4.2.1). Interest in its spawning season and location was expressed as early as 1923 (Welsh and Breder 1923). The common belief has been that croaker, a demersal species, spawn offshore in the fall and early winter. The historical basis of this stems from larval/post-larval collections of croaker in the Chesapeake Bay (Welsh and Breder 1923, Hildebrand and Schroeder 1928, Wallace 1940, Pearson 1941, Raney and Massman 1953), in Beaufort Inlet, South Carolina (Bearden 1964), and in the passes along the Texas coast (Pearson 1929, Gunter 1945, Suttkus 1955), and from very limited observations of gonadal conditions (Welsh and Breder 1923, Hildebrand and Schroeder 1928). Several authors have succinctly reviewed the literature available on croaker spawning both in the Atlantic and the Gulf of Mexico (Haven 1957, Powles and Stender 1978, Thomas 1978).
Figure 4.2.1

The Mid-Atlantic Bight study area. Stations 1 through 5, indicated at the Chesapeake Bay mouth and Cape Hatteras, are referred to in Figure 4.2.7. Station 5 at Cape Hatteras, not shown here, is at the 200 m contour, slightly south of 35°N.
There is a southward progression, from the Chesapeake Bay through North Carolina, of commencement and cessation of croaker spawning activity (Hildebrand and Cable 1930). North of Cape Hatteras, spawning takes place from August or early September through December (Johnson 1978, Colton, Smith, Kendall, Berrien and Fahay 1979, Morse 1980), although spring spawning has also been suggested (Haven 1957, Chao and Musick 1977). South of Cape Hatteras spawning occurs from September or October through January–March (Pearson 1929, Hildebrand and Cable 1930, Bearden 1964, Warlen 1980) with the peak late September to November (Warlen 1980). It has been hypothesized that these differences are the result of separate spawning stocks north and south of Cape Hatteras (White and Chittenden 1977, Morse 1980).

Time and location of peak Atlantic croaker spawning may vary year to year as suggested by the above reports, even though croaker are protracted spawners. The croaker is thought to migrate out of east coast estuaries to spawn, stimulated by photoperiod and 18° to 25°C shelf waters (Warlen 1980). Water temperature has a direct effect on croaker migration (Bearden 1964, Johnson 1977), thus it is likely to affect spawning timing and location. Croaker tagged off Maryland–Virginia in the fall migrate southward to North Carolina waters (Haven 1959). One objective of this chapter is to describe the spawning time and distribution of Atlantic croaker in the Mid-Atlantic Bight and around Cape Hatteras and to show that they are linked to bottom temperatures on the continental shelf.

The summer southwesterly winds cause bottom temperatures of the Mid-Atlantic Bight to be cold due to upwelling (Hicks and Miller
Cessation of the summer wind regime results in warming of bottom waters. The time of cessation is not the same every year, therefore bottom temperature patterns vary interannually as discussed in Chapter 4.1. Therefore, another objective of this chapter is to show that the time of cessation of summer winds affects croaker migration and maturity and, with it, spawning time and location.

METHODS

All adult abundance, maturity (1973-1976), and bottom temperature data were collected during the National Marine Fisheries Service (NMFS) Marine Resources Monitoring, Assessment, and Prediction (MARMAP) bottom trawl surveys (1971, 1973-81) with the exception of those for 1967 which were collected by the Virginia Institute of Marine Science (VIMS) (Musick, Colvoecaresses and Foell 1979). These collections were chosen because both inshore and offshore areas were surveyed and simultaneous bottom temperatures were recorded. MARMAP cruise listing, sampling methods and gear, survey design and data handling are described by Grosslein (1969a, 1969b), Clark (1979) and Flescher (1980). The data were provided courtesy of National Oceanic and Atmospheric Administration (NOAA)/NMFS/Northeast Fisheries Center (NEFC)/Resource Assessment Division. Adult abundance are presented as number caught per standard 30 minute tow. No attempt was made to compensate for gear and effort differences since the necessary information is not available.

Morse (1980) investigated maturity, spawning and fecundity of the Atlantic croaker north of Cape Hatteras, and provided his maturity
stage analyses and distribution information (W. Morse, NOAA/NMFS/NEFC/Sandy Hook Lab pers. comm.). The percentage of each maturity stage (1-6) determined for subsamples at each station was used to estimate the maturity stages of the entire croaker catch at that station. These total maturity stage estimates were used for distributional analyses from which the maturity calculations presented for 1973 through 1976 were prepared. Numbers of each stage at each station were totaled for the entire cruise and used as an index of croaker maturity at the time of the cruise.

In September 1981, croaker were collected on the NMFS MARMAP cruise aboard the R/V DELAWARE II. Croaker were subsampled for length, sex, maturity stage, and gonad displacement volume. In accordance with the methods of Wallace (1940) and Morse (1980), stage of maturity was assigned based on the morphological criteria for field use shown in Table 4.2.1. Estimates of 1981 maturity stages were calculated as described for 1973-1976. For analyses, stages 3 and 4 were combined as they were often difficult to differentiate.

To equate locations, only data south of 39°N latitude, north of 35°N latitude, west of the 200 m isobath and east of the smoothed coastline were considered (Figure 4.2.1). However, it should be noted that all cruises did not sample as far north as 39°N nor as far south as 35°N. Data were contoured for values of >0, 50, 100, 500, 1000 and 5000 adult croaker per tow and 16°, 18°, 20°, 22°, and 24°C bottom water temperatures. These temperatures were chosen to examine the hypothesis that croaker spawn in warm water and to check the 16°C index of warm water used by in Chapter 4.1. The areal extent of croaker and warm water distribution in square nautical miles (nmi)^2 of each contour was


<table>
<thead>
<tr>
<th>Stage</th>
<th>Color</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Immature</td>
<td>Pale, light to dark pink</td>
<td>Sex may be indistinguishable, no development or differentiation, very small in size, usually rounded.</td>
</tr>
<tr>
<td>2. Developing</td>
<td>Ovaries pale to dark pink. Testes pale to light pink</td>
<td>Sex distinguishable, obviously larger than immature, no visible eggs, first time spawners.</td>
</tr>
<tr>
<td>3. Ripening</td>
<td>Ovaries pink. Testes milky-white.</td>
<td>Distended gonads. When gonad opened, individual eggs visible to naked eye.</td>
</tr>
<tr>
<td>4. Running Ripe</td>
<td>Ovaries pink-orange. Testes pink or orange around edges</td>
<td>&quot;Very&quot; distended gonads, fish extrudes eggs or milt with slight pressure. Ovaries may have some clear eggs.</td>
</tr>
<tr>
<td>5. Spent or partially spent</td>
<td>Both ovaries and testes have red-orange areas.</td>
<td>Blood vessels very enlarged, loose eggs visible, may appear to have only spawned one end of gonad, especially in younger fish.</td>
</tr>
<tr>
<td>6. Resting</td>
<td>Ovaries and testes grey-white, light to dark pink.</td>
<td>Very much like Stage 2, except the fish is larger, not a first-time spawner. Eggs usually not visible to naked eyes, may be seen microscopically. No milt, testes often flat.</td>
</tr>
</tbody>
</table>
determined using a digital planimeter (Welch 1948). Abundance of adult croaker was obtained by multiplying the area (nmi)$^2$ of each contour interval by the value of that contour (Saville and Schnack 1981).

Since collection times varied, time indices were assigned according to those designated in Chapter 4.1 for each third of month, beginning, middle and end, as follows: July - 1, 2, 3; August - 4, 5, 6; September - 7, 8, 9; October - 10, 11, 12; November - 13, 14, 15. These time periods were chosen because a sampling cruise across the Mid-Atlantic Bight lasted about ten days and to agree with those used in Chapter 4.1.

Time plots presented here of bottom temperatures at the mouth of Chesapeake Bay and at Cape Hatteras utilized these same MARMAP data supplemented by additional bottom temperature data collected and supplied by NMFS (S. Nickerson, NOAA/NMFS/NEFC pers. comm.). Transect location and station designations (Figure 4.2.1) correspond to those used by 1965-66 R/V DOLPHIN cruises (Berrien, Fahay, Kendall and Smith 1978).

The data presented for larval croaker concentration by two-month intervals 1973-1981 were collected by NMFS ichthyoplankton surveys in the Mid-Atlantic Bight and provided by the NOAA/NMFS/NEFC/Sandy Hook Laboratory. The sample areas, methods and treatments are the same as those described by Berrien, Naplin and Pennington (1981). A detailed description of the bongo samplers has been presented by Posgay and Marak (1980). Larval densities (#/1000 m$^3$) were calculated by dividing the number per oblique tow by water volume filtered and multiplying by 1000, because croaker larvae are not assumed to be confined to a narrow depth stratum (Judkins, Wirick and Esais 1980).
Each explained variance ($R^2$) was adjusted for small sample size based upon degrees of freedom in each particular relationship. Linear and parabolic regression equations were determined using Business Graphics software on an Apple IIe computer.

RESULTS

The areas ($\text{nmi}^2$) inside the 0-contours in Figure 4.2.2 were the full ranges occupied by adult croaker on the shelf in the Mid-Atlantic Bight at the time of fall collections. Isopleths show the concentration of abundance within that distribution. Bottom temperatures were plotted for these same collections (Figure 4.2.3). The area ($\text{nmi}^2$) inside the $16^\circ\text{C}$ isotherm is an index on warm water on the shelf as described in Chapter 4.1. The areal extent occupied by croaker ($\text{nmi}^2$) inside the 0-contour was found to be directly related to the areal extent of warm bottom waters ($\text{nmi}^2$) inside $16^\circ\text{C}$ ($R^2 = 0.78$, $n=11$) (Figure 4.2.4).

The areal extent of warm bottom waters varies with the time of the cessation of the summer winds as shown in Chapter 4.1. Therefore, its areal extent available to adult croaker should also be related to this time of cessation. Reduced offshore distribution of adult croaker (Figure 4.2.2) and warm bottom waters (Figure 4.2.3) resulted from progressively later wind cessation. This change in extent was apparent for the three years when samples were collected at the end of September. In 1981 with an early (mid-August) cessation, croaker extended seaward to or beyond $75^\circ\text{W}$ from $38^\circ\text{N}$ to $36^\circ\text{N}$ and at Cape Hatteras. This extent was somewhat reduced in 1974 which had an average, beginning of
Figure 4.2.2

Figure 4.2.3

Contours of bottom temperatures (°C) in the Mid-Atlantic Bight concurrent with the collections of croaker shown in Figure 4.2.2.
Figure 4.2.4

Linear relationship of the areal extent (nmi)$^2$ occupied by adult croaker (x) based on the area of bottom water greater than or equal to 16°C (y): $y = 807 + (0.63 \times x)$, ($R^2 = 0.78$, n=11).
September, cessation. Croaker extented seaward beyond 75°W at 38°N, 36°N and at Cape Hatteras, but not at 37°N. The 1980 late (end of September) cessation confined the croaker inshore at 37°N and 36°N, with extent seaward to 75°W restricted to 38°N and Cape Hatteras only.

A relationship between the time of collection and areal extent of warm water was discussed in Chapter 4.1. A similar relationship exists here between time of collection and areal extent of adult croaker ($R^2 = 0.55$, n=11) (Appendix 4.2.1 - Figure). To adjust for the dual effect of time of wind cessation and time of data collection on the observed areal extent of croaker, a wind-cruise interval was calculated in Chapter 4.1 by subtracting the index of collection time from that of wind cessation. Based on this relationship between the wind-cruise interval and the areal distribution of adult croaker ($R^2 = 0.66$, n=11) (Appendix 4.2.2 - Figure), a linear relationship was revealed between the time of the cessation of the summer wind and the areal extent of adult croaker when they would be migrating out of the Chesapeake Bay (Figure 4.2.5, Appendix 4.2.3 - Figures).

Additional investigations supported the evidence that the time of the summer wind cessation affected adult croaker. Croaker length at 50% maturity for both males and females was greater in 1974 and 1975 than in 1973 and 1976 (Morose 1980). Therefore, lengths of croaker at 50% and 100% maturity given by Morose (1980) were regressed on the time of summer wind cessation. Earlier cessation of summer wind causes earlier warming of bottom waters as shown in Chapter 4.1. Gonad maturation appeared to be stimulated by these warm bottom waters. This is indicated by linear relationships between time of wind cessation and length of croaker at 50% maturity ($R^2 = 0.75$, n=8) and 100% maturity ($R^2 = 0.76$, n=10) (Figure 4.2.6).
Figure 4.2.5

The predicted areal extent (nmi)$^2$ available to adult croaker that would be on the shelf at designated times:
3 VIII - end of August, 1 IX - beginning of September, 2 IX - middle of September, 3 IX - end of September. Based on the time of the summer wind cessation.
DISCUSSION

Maturation

Croaker spawn in the fall at a time of decreasing photoperiod and surface temperatures (Killebrew 1973), two factors known to influence reproductive cycles (Aronson 1965, Brett 1970). Spawning is better in warm water than in cold water (Killebrew 1973) and takes place in a laboratory at temperatures greater than 19.0°C (Middaugh and Yoakum 1974) with 22°- 24°C being optimum (W. Hettler, NOAA/NMFS/Southeast Fisheries Center (SEFC)/Beaufort Lab pers. comm.). Gonad maturation, which is variable in croaker (Middaugh and Yoakum 1974), may be temperature controlled (Laevestu and Hela 1970, Kruse and Tyler 1983).

The summer wind regime in the Mid-Atlantic Bight causes upwelling of cold bottom waters as cold pool waters are drawn onshore. Gonad maturation in Atlantic croaker may be inhibited by prolonged fall upwelling as in the English sole (*Parophrys vetulus*) (Hayman and Tyler 1980, Kruse and Tyler 1983). Therefore the time of cessation of this southerly wind component should affect the rate of croaker gonad maturation as the linear relationship found in this study indicates (Figure 4.2.6). Croaker are shorter, and thus younger, at size of 50% and 100% maturity in years of early summer wind cessation (e.g. 1976) as compared to late wind cessation (e.g. 1975). According to this, time of onset of spawning is not the same year to year as evidenced by the variations in reported spawning times (Welsh and Breder 1923, Hildebrand and Schroeder 1928, Wallace 1940, White and Chittenden 1976, Morse 1980).
Figure 4.2.6

Male and female croaker lengths at maturity regressed on time of wind cessation:

at 100% maturity—$y = 229 + (6.2x)$, ($R^2 = 0.76$, $n=10$);

at 50% maturity—$y = 170 + (6.6x)$, ($R^2 = 0.75$, $n=8$).
Since onset of maturity changes yearly with time of summer wind cessation and warm bottom temperatures, this could also explain the size of croaker at maturity being reported as 190 mm to 275 mm (Wallace 1940, White and Chittenden 1976, Powles and Stender 1978, Morse 1980). The largest average length at 50% maturity in this study was 233 mm in 1975 (Morse 1980) while for 1938-1940 it was 275 mm (Wallace 1940). This 1938-40 value is significantly larger than those used here to correlate with time of wind cessation (Figure 4.2.6). Although no wind data are available for that time with which to hindcast the relationship, this size at first maturity is unlikely. Ripe females in the 1938-40 samples were all three years old, with no two year old being ripe (Wallace 1940). Those July-August collections may have sampled only older fish and not young, first-time spawners, since in protracted spawners, older fish are among the first to spawn (Cushing 1981). Therefore, there may not have been a significant long-term change in the length at 50% maturity between the 1930's and 1970's as suggested by Morse (1980).

I used 16°C here as an index of warm bottom temperatures though recent laboratory observations indicate 22°- 24°C to be the optimum spawning temperature for Atlantic croaker. Choice of this temperature was based on the relationship found between distribution of the 16°C isotherm and time of cessation of the summer wind regime as discussed in Chapter 4.1. An excellent linear relationship was found between the areal extent (nmi)^2 of water greater than or equal to 16°C and that of adult croaker (Figure 4.2.4). The extent of 22° and 24°C bottom waters on the shelf is very limited (Figure 4.2.3) and does not suggest these very warm temperatures to be controlling initiation of
spawning north of Cape Hatteras. This may indicate 1) croaker react differently to conditions for spawning in the field and laboratory, 2) there are two croaker stocks north and south of Cape Hatteras which are kept separate by keying on different temperatures to initiate spawning activity, or 3) the temperature sampling employed a spatial-temporal frequency which was too large. Although the correlation with a water temperature which is lower than indicated in the laboratory may not represent a physiological cause-and-effect, it can be used as an oceanographic indicator (Smith, Eber and Zweifel 1981) of a relationship between abundance of spawning adult croaker and warm bottom water.

Migration

Sexually mature individuals leave the estuary as early as July, but mainly during August or September (Wallace 1940) cued by decreasing photoperiod and temperature (Warlen 1980). However, the area of warm water encountered upon out-Bay migration onto the shelf determines spawning distribution. Offshore dispersal of croaker at the time of fall spawning (Figure 4.2.2) is limited by offshore extent of warm bottom waters (Figure 4.2.3). Note that the adult croaker in 1978 appear to be bisected by cold bottom waters encroaching nearshore. The meridional wind component used in Chapter 4.1 does not explain this event. It may have been caused by local wind conditions at the time of collection or it may be an artifact of the data collections. The croaker on the shelf in mid-July 1971, prior to the wind cessation in mid-August, were restricted very close inshore by the water temperature. The mid-September wind cessation in 1979, which coincided with the
collection of croaker, resulted in the fish being confined inside the 16°C isotherm.

There are also latitudinal differences in the extent of warm bottom waters as evidenced by time plots of bottom temperatures at Chesapeake Bay mouth and Cape Hatteras (Figure 4.2.1) which show seasonal and interannual variations (Figure 4.2.7). While the isotherm pattern each year is dependent upon characteristics and interactions of the cold pool, winds and air temperatures, the seasonal difference in availability of warm waters off Chesapeake Bay compared to Cape Hatteras is apparent in Figure 4.2.7. Warm waters (unshaded) are restricted to the late summer and fall at the northern transect. However, at the southern transect, these warm waters are present all year except for a short period in late winter and early spring. This southerly persistence of warm waters is a result of a convergence zone which causes a dramatic increase in bottom water temperature near Cape Hatteras (Bumpus 1973). Packed isotherms which can be seen near Cape Hatteras in 1967, 1973, 1975, 1978 and 1979 (Figure 4.2.3) are indicative of this zone.

Croaker migration southward in the Mid-Atlantic Bight (Haven 1959) is directly affected by water temperature (Bearden 1964). Distribution patterns of croaker and bottom temperatures are related as shown by the linear regression in Figure 4.2.4. Time of migration together with time of warming of bottom waters, as indicated by cessation of summer winds, influence the resulting distribution pattern of adult croaker on the shelf. Distribution charts for 1974, 1977, 1978 and 1980 (Figure 4.2.2) show aggregations of croaker migrating southward from the Delaware and Chesapeake Bays respectively. This dual origin of
Figure 4.2.7

Time plots of bottom temperatures at transects off the mouth of the Chesapeake Bay and a transect off Cape Hatteras. Station 1 is inshore, Station 5 is on the middle of the shelf off the Chesapeake Bay and at the edge of the shelf off Hatteras. See Figure 4.2.1 for station locations.
spawning (stages 3-6) croaker on the shelf in relation to the time of the summer wind cessation is seen in Figure 4.2.8. The northerly aggregation is interpreted as being from Delaware Bay and the southerly one as from Chesapeake Bay. This dual pattern is not as distinct in non-spawning (stages 1-2) croaker (Figure 4.2.8) which have no reproductive requirement for warm water.

There is an apparent linear relationship between latitude of concentration of mature croaker and time of summer wind cessation although the number of observations is too small for statistical quantification (Figure 4.2.8, Appendix 4.2.4 - Figure). Croaker appear to be concentrated northward upon early wind cessation and southward as wind cessation occurs later. With early cessation, bottom waters are warm when croaker migrate onto the shelf. Northern bottom waters may not yet be warm enough for croaker spawning when the cessation is late, thus prompting a southward migration. An early cessation (2, mid-July) in 1976 produced a concentration of spawning croaker near the Chesapeake Bay mouth, while a late cessation (9, end of September) in 1975 concentrated the spawning croaker south of Oregon Inlet, North Carolina (Figure 4.2.8). The concentration of adult croaker south of Chesapeake Bay off Oregon Inlet in 1980 indicates that southward migration had begun prior to the late wind cessation and simultaneous bottom trawl survey collection in late September that year.

Croaker migrating southward in the Mid-Atlantic Bight prior to wind-induced warming of northern bottom waters will encounter temperatures suitable for spawning at the Cape Hatteras convergence zone. This temperature-salinlity barrier separates the Virginian and Carolinian faunal provinces, though it is frequently breached by
Figure 4.2.8

Latitudinal distribution of croaker concentrations in relation to time of summer wind cessation (2 = mid-July, 5 = mid-August, 7 = beginning of September, 9 = end of September). Concentrations (#/tow) are average abundance at each latitude from contours such as those in Figure 4.2.2. Mature (on left) croaker - stages 3 through 6 inclusive. Immature (on right) croaker - stages 1 and 2.
MATURE (Stages 3-6) vs IMMATURE (Stages 1-2)

Cessation of Summer Wind (month/3)

- Delaware Bay 39°N
- Chesapeake Bay 37°N
- Oregon Inlet 36°N
- Cape Hatteras 35°N

# Croaker/Tow

- >0
- 5
- 100
- 500
- 1000
northern species moving into Raleigh Bay (Bumpus 1973) and possibly by southern species, such as croaker, moving northward in the spring and returning in the fall. It appears that the later the cessation of the southerly wind component, the farther south croaker migrate to spawn in warm bottom waters.

The area of warm water available to spawning croaker is severely limited to essentially nearshore when the wind cessation is late, inducing a migration southward. Croaker, as a species, are protracted spawners as is common in sub-tropical waters (Cushing 1981). There is also evidence that individuals may be protracted or serial spawners or that unspawned eggs past optimal spawning diameter atrophy while still in the ovary (Middaugh and Yoakum 1974) as suggested by observations of stage 5 gonads (Table 4.2.1) in 1981. Spawning may begin in these restricted inshore waters as migration continues southward, thus, some larvae would be available for recruitment into the Chesapeake Bay. However the general pattern of surface circulation in the MAB is south-southeasterly, culminating in a seaward exit between Chesapeake Bay and Cape Hatteras (Bumpus 1973). Consequently, a major spawn south of the Bay mouth would be more beneficial for recruitment to Pamlico Sound, North Carolina through Oregon Inlet, than to Chesapeake Bay. Not only is the potential recruitment to Chesapeake Bay lowered when the bottom waters warm late and croaker spawn southward, but the total potential Virginia-North Carolina recruitment is reduced because of proximity to the Gulf Stream and potential offshore loss of larvae. Data from the R/V DOLPHIN (Berrien et al. 1978) indicate that croaker larvae can become entrained in the Gulf Stream. The result of this physical situation is the reverse of that found for English sole off
Oregon in which delayed spawning due to prolonged upwelling produced stronger cohorts (Hayman and Tyler 1980, Kruse and Tyler 1983).

**Spawning Time**

Mid-Atlantic Bight species that spawn primarily in late summer and fall commence spawning in the northern part of the Bight, and move south with the season (Kendall 1975). Croaker spawning moves southward in the MAB in response to bottom water temperatures until warm bottom waters are encountered at Cape Hatteras (Figure 4.2.7) making further southward migration unnecessary. The almost continual presence of warm bottom waters from Cape Hatteras southward makes shelf temperature an unlikely initiator of croaker spawning south of Hatteras. Spawning can continue south of Hatteras into February (Warlen 1980), but probably ceases north of Cape Hatteras by November (Wallace 1940). Temperature, which can influence the onset of spawning, can also affect duration of the spawning season (Hunter 1976). Cessation of spawning appears to be linked to time of onset of cold (shaded) bottom water temperatures (Figure 4.2.7). This may be caused by a temperature-regulating factor, i.e., a minimum temperature below which spawning cannot take place (Brett 1970). Croaker gonad maturation begins in the warm waters of the Chesapeake Bay (Wallace 1940, Benner 1980) as I observed when sampling within-the-Bay commercial catches. Trends of initiation and cessation of spawning in relation to bottom water temperatures show that even if gonad maturation is complete, English sole cannot spawn below about 8°C (Kruse and Tyler 1983). Therefore, it is likely that the 16°C temperature chosen here could be interpreted as a minimum temperature-regulating factor and that croaker cannot spawn below this temperature.
The period of peak larval concentration for croaker in the Mid-Atlantic Bight is September-October as shown by Table 4.2.2. Occasionally larvae are found earlier or later, but no larvae were taken from January through April 1973-81. Although small croaker have been reported in Chesapeake Bay in the spring (Chao and Musick 1977), abundance of larval croaker collected May through August does not suggest any spring spawning of Atlantic croaker in the Mid-Atlantic Bight. These occurrences may then be explained as misidentified larvae, early spawning close to shore of a few individuals, extremely slow winter growth (Chao and Musick 1977) or spawning south of Hatteras, possibly by a separate stock, with transport into the Mid-Atlantic Bight area (Kendall 1975, Cox and Wiebe 1979, Olney and Markle 1979). Croaker spawning occurring in May, June or July is likely to be an insignificant contribution to the stock north of Hatteras. In 1962, no croaker larvae were collected on the shelf during a 28 June - 11 July sampling period (Massman, Joseph and Norcross 1963). This concurs with the conclusion reached here based on bottom temperatures and that of Morse (1980) based on maturity; this sampling time was prior to croaker spawning. Additionally, few were collected during similar plankton sampling 26 September - 10 October, 1962 (Massman, Joseph and Norcross 1963). Since the summer winds ceased at the end of July that year, the peak spawn of croaker had passed. A spring spawning peak does not occur in the Atlantic croaker population north of Cape Hatteras because spawning time in this area is linked to warm bottom temperatures which do not occur until fall.

This does not prove or disprove the hypothesis of separate croaker stocks north and south of Cape Hatteras (White and Chittenden
**TABLE 4.2.2**

Total Number of Larval Croaker per 1000 m³ Taken in the Mid-Atlantic Bight NMFS/MARMAP Samples, Cape Hatteras to Long Island, 1973-1981.

<table>
<thead>
<tr>
<th>Year</th>
<th>Jan-Feb</th>
<th>Mar-Apr</th>
<th>May-Jun</th>
<th>Jul-Aug</th>
<th>Sep-Oct</th>
<th>Nov-Dec</th>
</tr>
</thead>
<tbody>
<tr>
<td>1973</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>2250 (115)</td>
<td>—</td>
</tr>
<tr>
<td>1974</td>
<td>*0 X</td>
<td>—</td>
<td>*0 X</td>
<td>*26 X</td>
<td>25739 (157)</td>
<td>*0 X</td>
</tr>
<tr>
<td>1975</td>
<td>*0 X</td>
<td>0 X</td>
<td>*0 X</td>
<td>*0 X</td>
<td>2197 (173)</td>
<td>—</td>
</tr>
<tr>
<td>1976</td>
<td>*0 X</td>
<td>*0</td>
<td>*0 X</td>
<td>—</td>
<td>10530 (159)</td>
<td>*25 (43)</td>
</tr>
<tr>
<td>1977</td>
<td>*0 X</td>
<td>0 X</td>
<td>9 X</td>
<td>192 (21)</td>
<td>4209 (64)</td>
<td>*9 X</td>
</tr>
<tr>
<td>1978</td>
<td>0 X</td>
<td>0 X</td>
<td>381 X</td>
<td>197 (72)</td>
<td>*7 (43)</td>
<td>—</td>
</tr>
<tr>
<td>1979</td>
<td>0 X</td>
<td>0 X</td>
<td>695 (73)</td>
<td>48 (69)</td>
<td>10723 (66)</td>
<td>*6 (10)</td>
</tr>
<tr>
<td>1980</td>
<td>0 X</td>
<td>0 X</td>
<td>22 X</td>
<td>0 (70)</td>
<td>7840 (70)</td>
<td>1524 (70)</td>
</tr>
<tr>
<td>1981</td>
<td>*0 (47)</td>
<td>0 (62)</td>
<td>—</td>
<td>*0 (62)</td>
<td>489 (62)</td>
<td>—</td>
</tr>
</tbody>
</table>

*: Sampled north of Chesapeake Bay mouth only.

-: No samples taken.

( ): Maximum number of hauls given as an estimate of CPUE.

X: No value indicates information unavailable to me.
1977, Morse 1980) as Cape Hatteras has not been shown to be an effective barrier to croaker. Field collections in 1981 revealed many age 1+ croaker with developing gonads (stage 2). It is unknown whether these fish may readsoorb their spawning products or contribute to the later spawn south of Cape Hatteras. Additionally, since adults migrating out of North Carolina estuaries begin to spawn in the fall, the question is raised whether the late spawn is all young fish, or caused by separation of spawning stocks in time as opposed to the proposed physical barrier of Cape Hatteras. Answers to these questions, as well as direct effect of water temperature on the croaker reproductive cycle, require controlled laboratory experiments.

CONCLUSIONS

Atlantic croaker (Micropogonias undulatus) spawn in the Mid-Atlantic Bight from Cape May, N.J. to Cape Hatteras, N.C., with greatest concentrations in the middle and southern parts of this range. The time of cessation of the summer wind regime in the Mid-Atlantic Bight influences spawning migration and location and time of spawn. Sub Model I - Part 1 (Figure 4.2.9) depicts the interactions of wind, water and croaker in a flow chart. Distribution of adult croaker on the shelf in the fall is directly related to distribution of warm bottom waters greater than or equal to 16°C. Analyses of gonad stage development reveal that croaker begin to spawn earlier in years when the wind cessation is early than in years when it is later in the fall. When the wind cessation occurs earlier, the bottom waters warm earlier, and croaker can spawn farther north. Additionally, because water
Figure 4.2.9

Sub Model I - Part 1: A flow chart of the effects of summer wind cessation on croaker spawning and larvae available to be recruited into the Chesapeake Bay.
SUB MODEL I — PART 1

INCREASED AREA WARM WATER

INCREASED AREAL EXTENT OF CROAKER

INCREASED NORTHERLY DISTRIBUTION OF CROAKER

SPAWNING FARTHER NORTH

RESULTANT LARVAL DISTRIBUTION

SPAWNING FARTHER SOUTH

DECREASED AREAL EXTENT OF CROAKER

DECREASED NORTHERLY DISTRIBUTION OF CROAKER

REDUCED AREA WARM WATER

TIME CESSION SUMMER WINDS

"AVERAGE"
temperatures affect the fall migration, croaker appear to spawn farther south in the years when the wind cessation is late. If cessation does not take place before the out-Bay migration, only a narrow, inshore band of warm water exists, prompting croaker to migrate south to find appropriate conditions for spawning. This match/mis-match of the timing of cessation of the summer wind regime and croaker migration out of the Chesapeake Bay is significant in determining where croaker spawn. This results in enhanced or reduced recruitment of juveniles to the Chesapeake Bay.
CHAPTER 5
Juvenile Atlantic Croaker

INTRODUCTION

A index of juvenile croaker recruitment was developed to test proposed relationships between juveniles and environmental factors. The VIMS trawl survey data base is unique on the east coast because of its duration and continuity. No other data set exists that samples the same species in the same locality with concurrent physical data over a long period of time. Austin and Ingham (1978) have noted that time series analyses of biological data sets are often difficult due to their poor quality and short duration. These data however are reliable and consistent for croaker because it is a demersal fish found in the deep channels of the river, where the gear samples most efficiently. It is especially fortuitous that this survey encompassed the period of the disappearance, absence and resurgence of the Atlantic croaker in the Chesapeake region.

METHODS

A croaker biological year was designated as October through September. This designation was assigned because October is the peak of spawning, and, as such, is considered the spawning date when aging
croaker (White and Chittenden 1977). Abundance values were standardized to croaker per ten minute tow as a measure of effort. These were averaged by month over all collections for the entire York River system including the Pamunkey and Mattaponi. A single index was calculated to represent the juvenile croaker abundance each biological year ($Y_{yr}$).

The VIMS trawl survey data (1955-82) for all Virginia rivers, James, York, Rappahannock, Potomac in the Chesapeake Bay system, including the Bay itself, were analyzed using SIR (Scientific Information Retrieval) (Robinson, Anderson, Cohen, Gazdzik, Karpel, Miller and Stein 1980) on a Prime 850 computer (Appendix 5.1 - Figure) (see Norcross and Shaw 1983). Croaker were not analyzed according to position within the river for this study, but only according to river in which collected. Use of all rivers combined increased the sample sizes, number of samples and number of months sampled. Average croaker abundance per month was calculated from the total number of croaker captured per month divided by the total number of tows per month 

$$\text{AVG} = \frac{\text{Total \# Croaker/Month}}{\text{Total \# Tows/Month}}$$

While in the field participating in the VIMS trawl surveys, I discovered that the croaker captured by this survey were not just young-of-the-year. Therefore, I obtained the croaker length data from all the VIMS trawl surveys. SPSS (Statistical Package for the Social Sciences) (Hull and Nie 1981) was used on a Prime 850 to produce one graph for each month data were available. Two sets of graphs were made, one for all the rivers combined and one for just the York River system. Though the data from all the Virginia rivers in the Chesapeake Bay system were utilized, the York River data were also analyzed. When divisions between year classes for the Bay-wide data were obscure, such as in 1976
(Figures 5.1), the York River data were used to help interpret break-points (Figure 5.2).

The time of cessation of the summer wind, as discussed in Chapter 4, was used to interpret the incoming year class, i.e. it was assumed that spawning began about the time of cessation, and that new young-of-the-year appeared soon after that. Table 5.1 shows results of the analysis of the time of cessation for the entire time series of Norfolk airport data, 1948-1981. The assessment of first appearance of each year class was made based on the lengths when available. When there were no lengths, the apparent increase in abundance of croaker was interpreted as the incoming year class. While this latter technique represents the time of the majority of the year class entering the Bay, it not necessarily comparable to years when a few juveniles were detected earlier than the major influx. Size range and modal size of the croaker in the first month of appearance is shown in Table 5.1.

There was some trouble interpreting the difference between "slow" growing previous year classes and "new" year classes. Chao and Musick (1977) discuss modal year-class sizes and interpret small croaker in the spring as "new" recruits. However, based on the analysis of spawning place and time in Chapter 4, I did not agree that these came from a spring spawn in the Mid-Atlantic Bight. To analyze this, July was chosen as representative because lengths for more collections existed for that month. Modal lengths and ranges were plotted against the average January-February-March VIMS pier temperature (Figure 5.3). This plot showed that when the average temperature was cold, the modal size was smaller than with a warm temperature. Growth is expected to be slower with colder temperatures (Warlen 1980). The variation in modal
Figure 5.1

Length/frequency for croaker taken by the VIMS trawl survey within the whole Chesapeake Bay system, July 1976.
Figure 5.2

Length/frequency for croaker taken by the VIMS trawl survey within the York River system only, July 1976.
Length Frequency for Croaker July, 1976
York River
N = 169

0.0

500

200

300

400

Length

Percent
## TABLE 5.1

Juvenile Croaker Recruitment: Physical and Biological Data

<table>
<thead>
<tr>
<th>Year</th>
<th>Cessation of Summer Wind (Index - Month/3)</th>
<th>New Yearclass First Appearance (size mm)</th>
<th>Juvenile Indices</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>J&lt;sub&gt;FALL&lt;/sub&gt;</td>
</tr>
<tr>
<td>1948</td>
<td>Begin August 4</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1949</td>
<td>Begin August 4</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1950</td>
<td>Mid August 5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1951</td>
<td>Mid September 8</td>
<td>December</td>
<td>-</td>
</tr>
<tr>
<td>1952</td>
<td>Mid August 5</td>
<td>October (20, 30, 90)</td>
<td>-</td>
</tr>
<tr>
<td>1953</td>
<td>End September 9</td>
<td>September (20, 60)</td>
<td>57.99</td>
</tr>
<tr>
<td>1954</td>
<td>Mid October 11</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1955</td>
<td>Mid August 5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1956</td>
<td>End July 3</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1957</td>
<td>End July 3</td>
<td>August (20, 50, 60)</td>
<td>10.22</td>
</tr>
<tr>
<td>1958</td>
<td>Mid August 5</td>
<td>-</td>
<td>5.62</td>
</tr>
<tr>
<td>1959</td>
<td>End August 6</td>
<td>-</td>
<td>9.09</td>
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<td>1960</td>
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<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1961</td>
<td>End August 6</td>
<td>-</td>
<td>1.08</td>
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<tr>
<td>1962</td>
<td>End July 3</td>
<td>September (70)</td>
<td>0.73</td>
</tr>
<tr>
<td>1963</td>
<td>End August 6</td>
<td>November</td>
<td>3.22</td>
</tr>
<tr>
<td>1964</td>
<td>End August 6</td>
<td>August (30)</td>
<td>11.43</td>
</tr>
<tr>
<td>1965</td>
<td>Mid October 11</td>
<td>October (60, 70)</td>
<td>18.83</td>
</tr>
<tr>
<td>1966</td>
<td>End August 6</td>
<td>October (40, 50, 90)</td>
<td>7.74</td>
</tr>
<tr>
<td>1967</td>
<td>Begin September 7</td>
<td>December (20, 60)</td>
<td>0.01</td>
</tr>
<tr>
<td>1968</td>
<td>Mid August 5</td>
<td>October (30)</td>
<td>11.39</td>
</tr>
<tr>
<td>1969</td>
<td>Mid August 5</td>
<td>September (10, 30, 40)</td>
<td>41.14</td>
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<tr>
<td>Year</td>
<td>Cessation of Summer Wind (Index - Month/3)</td>
<td>New Yearclass First Appearance (size mm)</td>
<td>Juvenile Indices</td>
</tr>
<tr>
<td>---------</td>
<td>--------------------------------------------</td>
<td>----------------------------------------</td>
<td>-----------------</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>J_FALL</td>
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<tr>
<td></td>
<td></td>
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<td>J_SUM*</td>
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<tr>
<td>1970</td>
<td>Begin October 10</td>
<td>October (20,40,70)</td>
<td>21.15</td>
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<tr>
<td></td>
<td></td>
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<td>0.33</td>
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<td>22.89</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>14.52</td>
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<tr>
<td>1972</td>
<td>End August 6</td>
<td>July (40)</td>
<td>16.51</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>6.80</td>
</tr>
<tr>
<td>1973</td>
<td>Mid August 5</td>
<td>August (30,40)</td>
<td>30.20</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>113.72</td>
</tr>
<tr>
<td>1974</td>
<td>Begin September 7</td>
<td>October -</td>
<td>10.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>43.02</td>
</tr>
<tr>
<td>1975</td>
<td>End September 9</td>
<td>August (10,20,60)</td>
<td>106.12</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>51.13</td>
</tr>
<tr>
<td>1976</td>
<td>Mid July 2</td>
<td>July (20,40,50)</td>
<td>136.94</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3.43</td>
</tr>
<tr>
<td>1977</td>
<td>Begin October 10</td>
<td>October -</td>
<td>62.66</td>
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<td></td>
<td></td>
<td></td>
<td>2.04</td>
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<tr>
<td>1978</td>
<td>Mid August 5</td>
<td>September -</td>
<td>83.48</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>10.48</td>
</tr>
<tr>
<td>1979</td>
<td>Mid September 8</td>
<td>September (10,20,40)</td>
<td>42.27</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>13.20</td>
</tr>
<tr>
<td>1980</td>
<td>End September 9</td>
<td>September (10,80,100)</td>
<td>70.68</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.98</td>
</tr>
<tr>
<td>1981</td>
<td>Mid August 5</td>
<td>October (1,20,80)</td>
<td>38.72</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>5.72</td>
</tr>
</tbody>
</table>
Figure 5.3

Modal lengths and ranges for croaker in July versus the average January-February-March VIMS pier temperature.
size appeared to be the greatest between 4.5°C and 5.0°C. Additionally, as would be expected, the range appeared to be related to the sample size, i.e., the range was greater with a large sample size. Young croaker, 20–30 mm, previously have been reported in the York River in the spring (Raney and Massman 1953, Massman 1954). Generally, with a large sample size, the lower limit of the range was extended, e.g., 1975, 1976 and 1977. However, while in some years this extension appeared as a continuum over the size range (e.g., 1975, Figure 5.4), in other years there was clearly a bimodal distribution in 0+ fish (e.g., 1973, Figure 5.5). What may appear to be an absence of growth, may be because of the continuous removal of young-of-the-year, due to migration, predation or natural mortality, from the area sampled (Fortier and Legget 1982). Secondary modes at a smaller size are indicated (Figure 5.3). Simultaneous introduction of a "new" year class with these patterns further complicates age/class interpretation. Thus this July investigation of age at size, as well as time of wind cessation and York River length distributions, were used to interpret the other months.

Length data were not available for all collections in all years. Lengths published by Massman and Pacheco (1960) were used for 1956, 1957 and 1958. It should be noted however, that their data did not include croaker less than 50 mm. This is because their gear was a 30 foot trawl with one-inch mesh and three-quarters inch cod end, thus not sampling smaller fish. A comparison of the two months, August and September 1957, for which both Massman and Pacheco’s (1960) and VIMS’s trawl survey lengths are available, shows that the incoming year class was represented in VIMS trawl survey but not in the published data. This may misrepresent the data for the other years also. For
Figure 5.4

Length/frequency for croaker in July 1975. Note the extended size range of $0^+$ fish.
Figure 5.5

Length/frequency for croaker in July 1973. Note the bimodal size range of $0^+$ fish.
N = 3396
Chesapeake Bay System
Length Frequency for Croaker July 1973
this reason, because of the time of summer wind cessation, and because of the relationship between modal size and winter temperature, 1958 data were reinterpreted to reflect young-of-the-year recruitment in the summer.

No length data were collected for the 1973-78 Crustaceology cruises that were used to augment the survey data (Norcross and Shaw 1983). Length/frequencies for 1974-1976 from Chao and Musick (1977) were used to interpret year-class strength when trawl survey lengths were not available. Interpretation of July 1975, which included a large size range of young-of-the-year, was aided by data from Stillpond Neck in Maryland (Kaufman, Otto and Miller 1980). In these collections, young-of-the-year croaker with a modal length of 30 mm did not appear in the upper Bay until October. Therefore, the small croaker in July were considered to be slow growers from the previous year's recruitment.

To verify these analyses, modal larval, post-larval, and juvenile lengths from several sources were used: MARMAP cruises on the shelf; VIMS neuston cruises at the Chesapeake Bay mouth; VIMS SAV (Submerged Aquatic Vegetation) project on the Virginia eastern shore (Brooks, Merriner, Meyers, Olney, Boehlert, Lascara, Estes and Munroe 1981); VIMS entrainment and impingement collections and trawl and seine data (White 1976) at the WEPCO Surry Nuclear Power Plant on the James River; and Benedict Estuarine Laboratory collections (J. Hixson pers. comm) at Calvert Cliffs Nuclear Power Plant, Maryland, in mid Chesapeake Bay. Figure 5.6 shows modal sizes below 60 mm at these locations in the Mid-Atlantic Bight and Chesapeake Bay, 1973-1980. Time of wind cessation is indicated by vertical hashmarks on the time scale at the bottom of the figure. Interpretation of year-class separations are
Figure 5.6

Time series (1973-1980) of modal sizes of croaker in the Chesapeake Bay and nearshore region. Year classes are separated by curved vertical lines. Average January-February-March temperatures (°C) are designated between these separations. Cessation of summer wind is indicated by hashmarks in the time scale at the bottom.
depicted by vertical curved lines. This division is based on spring size of croaker and time of beginning of spawning the next fall. The space separating the year classes is larger in cold years and smaller in warm years. Average January-February-March temperatures (°C) are shown in the space between year classes. In the warmer years, there are smaller croaker in the spring; while in colder years, there are no croaker in the spring.

Length/frequency charts for each month of juvenile data available 1952-82, divided by year class, can be found in Norcross and Shaw (1983). The percent of each year class was multiplied by the total index \( J_{\text{AVG}} \) (average number per 10-minute tow) that had been calculated for that month. For each year class, a monthly index was calculated \( J_{\text{MON}} \) when data were available. The index is often zero for the older (II and III) year classes. These are the indices \( J_{\text{MON}} \) that were used for the interpretation of year-class strength in the remainder of this dissertation. The details are found in Norcross and Shaw (1983).

RESULTS and DISCUSSION

Indices of year-class strength were generated by combining months of data. The data could not be added to produce a sum because there were months when no collections were made. Thus, the fall index \( J_{\text{FALL}} \) (October-December) was the result of totaling croaker (per 10-minute tow) caught for all fall months sampled, divided by the number of months sampled. The summer (April-September) index \( J_{\text{SUM}} \) was calculated in a similar manner. These indices (Table 5.1) are be used
to correlate with transport and survival indices in Chapters 6 and 7 and to empirically establish causal relationships.

The possibility that differences in gear may have caused variations in the abundance results was examined. During preliminary analyses, gear comparisons were made on croaker data from 1971-1977 York River collections. Only one gear, an unlined 30 foot otter trawl, was used from 1955 through 1970. Five different gear types were used from 1971 through 1977, with the unlined 16 foot otter trawl and unlined 30 foot semi-balloon trawl, used only in 1972 and 1973, respectively. Table 5.2 shows, by year and gear, the number of tows taken, number of croaker caught per tow, percent of croaker per tow captured by each gear within a year and chi-square value of this percent.

While there is no statistically significant difference among gears used in 1971, 1972, and 1976, the chi-square values for 1973 ($X^2 = 25.0$), 1975 ($X^2 = 36.0$) and 1977 ($X^2 = 46.3$) indicate a significant difference ($p = 0.0005$). The unlined 16 foot otter trawl in 1972 and unlined 30 foot semi-balloon trawl in 1973 appear to have caught less croaker, but the results are contradictory for the lined 16 foot otter trawl and the lined and unlined 30 foot otter trawls. These tests were inconclusive. For example, the unlined 30 foot and lined 16 foot otter trawls appear to have equal catch rates in 1971 and 1972. However, comparisons of lined and unlined 16 and 30 foot trawls show their catch rates to be about equal in 1976, the 30 foot trawl better in 1975, and the 16 foot trawl better in 1977.

Investigation of the absolute values of these monthly indices ($J_{MON}$) reveals variation may be due to gear differences, however, the values could not be corrected. Table 5.1 shows fall and summer indices.
### TABLE 5.2


<table>
<thead>
<tr>
<th>Year</th>
<th>Gear</th>
<th># Tows</th>
<th># Croaker/Tow</th>
<th>% C/T by Gear/year</th>
<th>$\chi^2$</th>
<th>df</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>71</td>
<td>Unlined 16 foot otter trawl</td>
<td>112</td>
<td>12.43</td>
<td>54%</td>
<td>0.32</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lined 16 foot otter trawl</td>
<td>264</td>
<td>10.38</td>
<td>46%</td>
<td>0.32</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td><strong>376</strong></td>
<td><strong>22.81</strong></td>
<td><strong>100%</strong></td>
<td><strong>0.64</strong></td>
<td>1</td>
<td><strong>NS</strong></td>
</tr>
<tr>
<td>72</td>
<td>Unlined 16 foot otter trawl*</td>
<td>8</td>
<td>20.25</td>
<td>20%</td>
<td>5.31</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Unlined 30 foot otter trawl</td>
<td>82</td>
<td>41.65</td>
<td>41%</td>
<td>1.78</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lined 16 foot otter trawl</td>
<td>373</td>
<td>39.54</td>
<td>39%</td>
<td>0.98</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td><strong>463</strong></td>
<td><strong>101.44</strong></td>
<td><strong>100%</strong></td>
<td><strong>8.07</strong></td>
<td>2</td>
<td><strong>NS</strong></td>
</tr>
<tr>
<td>73</td>
<td>Lined 16 foot otter trawl</td>
<td>600</td>
<td>28.08</td>
<td>75%</td>
<td>12.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Unlined 30 foot semi-balloon trawl*</td>
<td>16</td>
<td>9.25</td>
<td>25%</td>
<td>12.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td><strong>616</strong></td>
<td><strong>37.33</strong></td>
<td><strong>100%</strong></td>
<td><strong>25.0</strong></td>
<td>1</td>
<td><strong>&lt;0.0005</strong></td>
</tr>
<tr>
<td>74</td>
<td>Lined 16 foot otter trawl</td>
<td>-</td>
<td><strong>100%</strong></td>
<td>-</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>75</td>
<td>Lined 16 foot otter trawl</td>
<td>79</td>
<td>73.14</td>
<td>20%</td>
<td>18.0</td>
<td></td>
<td><strong>&lt;0.0005</strong></td>
</tr>
<tr>
<td></td>
<td>Lined 30 foot otter trawl</td>
<td>94</td>
<td>301.51</td>
<td>80%</td>
<td>18.0</td>
<td></td>
<td><strong>&lt;0.0005</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td><strong>173</strong></td>
<td><strong>374.65</strong></td>
<td><strong>100%</strong></td>
<td><strong>36.0</strong></td>
<td>1</td>
<td><strong>&lt;0.0005</strong></td>
</tr>
<tr>
<td>76</td>
<td>Lined 16 foot otter trawl</td>
<td>98</td>
<td>59.88</td>
<td>52%</td>
<td>0.08</td>
<td></td>
<td><strong>NS</strong></td>
</tr>
<tr>
<td></td>
<td>Lined 30 foot otter trawl</td>
<td>25</td>
<td>55.49</td>
<td>48%</td>
<td>0.06</td>
<td></td>
<td><strong>NS</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td><strong>123</strong></td>
<td><strong>115.37</strong></td>
<td><strong>100%</strong></td>
<td><strong>0.16</strong></td>
<td>1</td>
<td><strong>NS</strong></td>
</tr>
<tr>
<td>77</td>
<td>Lined 16 foot otter trawl</td>
<td>95</td>
<td>4.29</td>
<td>84%</td>
<td>23.12</td>
<td></td>
<td><strong>&lt;0.0005</strong></td>
</tr>
<tr>
<td></td>
<td>Lined 30 foot otter trawl</td>
<td>76</td>
<td>0.82</td>
<td>16%</td>
<td>23.12</td>
<td></td>
<td><strong>&lt;0.0005</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td><strong>171</strong></td>
<td><strong>5.11</strong></td>
<td><strong>100%</strong></td>
<td><strong>46.24</strong></td>
<td>1</td>
<td><strong>&lt;0.0005</strong></td>
</tr>
</tbody>
</table>

* Indicates gear used during one year only.
An abrupt increase in fall values is seen in 1969, the year before the lined trawl was used. No such increase is apparent in the summer indices. The data also could not be numerically adjusted for gear since no VIMS gear comparison studies are currently available, but are being planned for 1983-84, (R. Dias, VIMS pers. comm.). No adjustment was made for vessel, since that is a difficult parameter to quantify and no data are available. Trawling effort was standardized in number per ten minute tow only.

All indices for 1955 through 1979 are probably underestimated. From 1955 to 1970, the unlined half-inch mesh 30 foot trawls that were used did not adequately sample the very small young-of-the-year croaker thus underestimating the indices (J\textsubscript{MON}). This is verified by the decrease in fall modal size and fall size range in later years (Norcross and Shaw 1983). The values for 1970-79, while higher, do still not directly correspond to the 1980-82 samples. In the most recent samples, a lined 30 foot trawl was used. A lined trawl in the earlier years was often only 16 feet, which should catch fewer croaker than the larger trawl all seasons, not just during the fall like the unlined trawls. This, together with the fact that the supplementary 1973-78 crab tows were made with an unlined 30 foot trawl (R. Harris, VIMS pers. comm.), underestimated those values from 1970-1979. All the gear used in the York River in 1971, 1972, and 1973 were less efficient than the 30 foot lined trawl, but the lined 30 foot trawl began to be used earlier in rivers other than the York (Norcross and Shaw 1983). However a 16 foot trawl was still used extensively from 1974 through 1978, and somewhat in 1979 in all rivers.
Autoregressive tendencies allow predictions of abundance to be made based on present or some defined past abundance. The VIMS trawl survey data for croaker were tested for these tendencies, but results were not significant ($t = 2.189$, $p = 0.0378$). Only the first value for the previous year was slightly significant ($t = -2.978$), which indicates a tendency for each year's abundance to be lower than it was the previous year. There is no biological basis for this as it is an artifact of the data manifested by an overall decreasing trend in abundance during the time period of the data. Thus, future abundance of juvenile croaker can not be predicted based on present abundance. This indicates the necessity for predictor variables to be identified and tested in the predictive model.

Prior to using lengths to divide year classes, the biological year (October-September) index developed from the VIMS York River trawl survey (1955-77) was tested as a predictor for commercial catch in later years. Correlations were run using this index and the yearly commercial landings in Virginia. Knowledge of the life history of the croaker, age of commercial catch (from Massman and Pacheco 1960) and apparent relationships between juveniles and commercial catch (Figure 5.7) suggested that croaker are fished at ages II to IV. Commercial catch was correlated with the total yearly index ($Y_{yr}$) lagged 0 to 5 years (variables: YOY, YOY1, YOY2, YOY3, YOY4, YOY5) (Table 5.3). Nonparametric statistics results were more significant than parametric results, indicating, perhaps, a nonlinear relationship. Lags of 2, 3, 4 and 5 years correlated relatively well ($p = 0.01$ to 0.04), however, no single yearly juvenile index ($Y_{yr}$) produced a fit to predict commercial catch. These results indicated that no single yearly index of York
Figure 5.7

Overlay of Virginia commercial landings of croaker (pounds) and yearly index ($Y_{YR}$) from the VIMS trawl survey in the York River three years previously.
VIRGINIA CROAKER DATA
COMMERCIAL CATCH AND JUVENILE TRAWL SURVEY
SUMMER JUVENILES THREE YEARS PRECEDING

NMFS AND VIMS DATA (1951-1979)
STANDARDIZED SCALE
POUNDS OF COMMERCIAL CROAKER—SOLID LINE
JUVENILE CROAKER PER 10 MINUTE TRAWL—DASHED
TABLE 5.3
Correlations of Commercial Catch vs. All Young-of-the-Year Croaker
(Simultaneously and 1-5 Years Previously)

<table>
<thead>
<tr>
<th></th>
<th>YOY</th>
<th>YOY1</th>
<th>YOY2</th>
<th>YOY3</th>
<th>YOY4</th>
<th>YOY5</th>
</tr>
</thead>
<tbody>
<tr>
<td>R</td>
<td>-0.099</td>
<td>0.104</td>
<td>0.267</td>
<td>0.327</td>
<td>0.390</td>
<td>0.291</td>
</tr>
<tr>
<td>p</td>
<td>0.62</td>
<td>0.61</td>
<td>0.18</td>
<td>0.10</td>
<td>0.05</td>
<td>0.17</td>
</tr>
<tr>
<td>n</td>
<td>27</td>
<td>27</td>
<td>27</td>
<td>26</td>
<td>25</td>
<td>24</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spearman Corr. Coef. (Non-Parametric)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>0.319</td>
<td>0.407</td>
<td>0.398</td>
<td>0.441</td>
<td>0.539</td>
<td></td>
</tr>
<tr>
<td>p</td>
<td>0.11</td>
<td>0.04</td>
<td>0.04</td>
<td>0.03</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>27</td>
<td>27</td>
<td>26</td>
<td>25</td>
<td>24</td>
<td></td>
</tr>
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<td></td>
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</tr>
<tr>
<td></td>
<td>2-3</td>
<td>3-4</td>
<td>4-5</td>
<td>2-3-4</td>
<td>3-4-5</td>
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<td>Multiple Regression</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>1.46</td>
<td>2.17</td>
<td>2.49</td>
<td>1.40</td>
<td>1.67</td>
<td></td>
</tr>
<tr>
<td>p,</td>
<td>0.25</td>
<td>0.14</td>
<td>0.11</td>
<td>0.27</td>
<td>0.21</td>
<td></td>
</tr>
<tr>
<td>R²</td>
<td>0.113</td>
<td>0.165</td>
<td>0.192</td>
<td>0.167</td>
<td>0.201</td>
<td></td>
</tr>
<tr>
<td>t-2</td>
<td>0.382</td>
<td>0.569</td>
<td>0.354</td>
<td>0.470</td>
<td></td>
<td></td>
</tr>
<tr>
<td>t-3</td>
<td>1.023</td>
<td>1.1795</td>
<td>1.670</td>
<td>1.126</td>
<td>0.167</td>
<td></td>
</tr>
<tr>
<td>t-4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.117</td>
<td></td>
</tr>
<tr>
<td>t-5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Stepwise Regression</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>F</td>
<td>2.87</td>
<td>4.14</td>
<td>5.20</td>
<td>4.14</td>
<td>5.20</td>
<td>5.20</td>
</tr>
<tr>
<td>p,</td>
<td>0.10</td>
<td>0.05</td>
<td>0.03</td>
<td>0.05</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td>R²</td>
<td>0.106</td>
<td>0.152</td>
<td>0.191</td>
<td>0.152</td>
<td>0.191</td>
<td>0.191</td>
</tr>
<tr>
<td>Selected Variables</td>
<td>YOY2</td>
<td>YOY4</td>
<td>YOY4</td>
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<td>Only</td>
<td>Only</td>
<td>Only</td>
<td>Only</td>
<td>Only</td>
<td>Only</td>
</tr>
</tbody>
</table>
River croaker abundance was a significant predictor of the commercial croaker catch in Virginia. These results did not rule out one year olds contributing substantially, although less significantly than the older fish, to the statewide commercial catch during years of abundance. Conversely, commercial catch the same year, as an index of spawning stock size, did not correlate well with the yearly York River index (Y_YR) of recruitment.

SUMMARY AND CONCLUSIONS

Monthly croaker indices were generated from the VIMS trawl survey data base (1952-82) by year class (J_MON). Preliminary analyses show that the juvenile indices cannot be predicted autoregressively. Also, no direct correlation between these indices and commercial catch was found. These findings suggest that environmental factors need to be incorporated in the predictive model of croaker abundance between juvenile and adult stages.

The juvenile indices derived from this survey data are not directly comparable but will be used in subsequent analysis of year-class strength. The annually increasing indices, which correspond to increased recruitment, also correspond to the increasing gear efficiency. Therefore, discrepancies which may result in the model, may be explained by these errors in the data due to gear.
CHAPTER 6
Transport of Larval Croaker into the Chesapeake Bay

INTRODUCTION

Like most members of the family Sciaenidae, Atlantic croaker (Micropogonias undulatus) eggs and pref lexion larvae are buoyant and occur in the surface waters (Lewis and Judy 1983). Laboratory spawning and hatching indicate that these eggs probably hatch within 36-48 hours at 22°C (J. Govoni, NMFS/SEFC/Beaufort Lab pers. comm.). Very little is known, however, about the morphology, abundance, or distribution of croaker eggs. In fact, the positive identification of field samples remains uncertain (Lippson and Moran 1974).

The length of the pelagic larval period is not documented. If it is similar to spot (Leiostomus xanthurus), then it is within a 30-60 days range at 22°C (J. Govoni, pers. comm.). Croaker larvae (yolk-sac through post-larvae) 2-11 mm have been reported from oblique tows in the Mid-Atlantic Bight (MAB) (Berrien, Fahay, Kendall and Smith 1978). Larval and juvenile croaker, 3-15 mm, have been caught off the bottom of Beaufort Inlet, North Carolina (Hildebrand and Cable 1930), 1.5-15 mm croaker have been taken at the mouth of the Chesapeake Bay (Pearson 1941), and croaker, 9-10 mm, have been found on the bottom of York River at Gloucester Point, Virginia (D. Haven/VIMS pers. comm.). A daily growth rate regression equation for larval croaker has been developed by
Warlen (1980). Larvae probably become demersal during the flexion and post-flexion stages (Lewis and Judy 1983). Correlation of this assumption to records of size and catch depth in the water column should allow an estimate of the size and age at which the croaker leave the pelagic life stage and become demersal. No pelagic larvae have been caught in oblique tows within the Bay (Olney 1978). Accordingly, it is assumed that the larvae are demersal before entering the Chesapeake Bay and are carried into the Bay and up the rivers in the near-bottom salt wedge (Pearson 1929, Wallace 1940, Weinstein, Weiss, Hodson and Gerry 1980) to areas of low salinity (Haven 1957, Weinstein 1979).

Coastal water movement at the mouth of the Chesapeake Bay may affect the entrainment of pelagic croaker into the Bay and may alter year-class strength as a result. Coastal circulation has an offshore component at the surface and an onshore component at the bottom (Bumpus 1973) (Figure 6.1). The average water column transport in the lower Mid-Atlantic Bight is dominated by south-southwesterly currents on the outershelf (Boicourt 1980). This general southerly flow in the MAB is not directly related to the surface winds and doesn't fit the Ekman transport mechanism (Ruzecki, Welch, Usry and Wallace 1976). However, the wind-driven effect increases significantly over the inner shelf and particularly the southern section of the MAB where the nearshore subtidal current is dominated by meteorological forcing (Beardsley, Boicourt and Hansen 1976). A net onshore southward current predominates at the bottom throughout the MAB except at the Chesapeake Bay mouth which is mainly onshore (Norcross, Massman and Joseph 1962, Bumpus 1973) (Figure 6.1). In the Bight from Virginia to North Carolina the flow is southward and is affected by estuarine circulation and winds, as
Figure 6.1

The area of study, Mid-Atlantic Bight from 39°N to 35°N, with mean surface and bottom flow indicated by arrows. Outline of area at the mouth of the Chesapeake Bay refers to the inserts. Bottom currents are into the Bay mouth with calm, northerly and southerly winds (after Boicourt 1981).
evidenced in surface temperature and salinity contours (Chase 1969). Bottom flow compensates for the onshore-offshore upper Ekman layer flow. Average currents increase in velocity offshore and decrease near bottom. The mean current veers toward shore with increasing depth (Beardsley, et al. 1976). Surface runoff may be enhancing bottom water transport shoreward in response to a coastal slope current. This two-layer flow of the estuarine salt-wedge transport system has been demonstrated at the mouth of the Chesapeake Bay (Harrison, Norcross, Stanley and Pore 1967, Kuo, Ruzecki and Fang 1975, Bumpus 1973, Boicourt 1981).

Croaker larvae in the pelagic stage are subject to wind-driven transport which can enhance or inhibit recruitment into Chesapeake Bay. Winds blowing offshore at this time could cause transport of larvae away from suitable estuarine nursery grounds (Cushing 1975). Demersal stage larvae at the Bay mouth are entrained in the salt-wedge transport system and carried into the Chesapeake Bay. This sequence from spawning through the subsequent transport of larvae into or away from the Chesapeake Bay is schematically depicted in Figure 6.2. As discussed in Chapter 4.2, croaker is a southern demersal species, requiring warm water to spawn. The planktonic larvae are subject to transport mechanisms within the water column until they become demersal (Lewis and Judy 1983). If larvae are near the Bay mouth at time of descent, they are entrained by the inward-flowing bottom waters and successfully recruited as juveniles to the Chesapeake Bay. Therefore, variations in the strength, duration and direction of wind-driven transport potentially affect croaker year-class strength.
Figure 6.2

Schematic diagram of spawning, transport and recruitment of larval/juvenile croakers in relation to Chesapeake Bay two-layer circulation.
METHODS

Wind-Induced Transport

Wind speed (kts) and direction (15° intervals) data from the airport at Norfolk, Virginia were obtained from the National Climatic Data Center (NCDC), Asheville, North Carolina. These data were validated as applicable for use offshore by F. Godshall (NOAA/NESDIS/MEAD pers. comm.) as discussed in Chapter 4.1. According to these analyses (Appendices 4.1.1 and 4.1.2), the angle of the offshore wind is no greater than 4° to the right of Norfolk wind and usually of the same magnitude in August, September and October, when croaker larvae are present in the Mid-Atlantic Bight. Because these differences were minimal, the wind data from Norfolk airport were not adjusted to approximate offshore conditions.

Winds were averaged for 10-day time periods (thirds-of-month) which approximated the length of a sampling cruise across the Mid-Atlantic Bight. Since collection times varied, time indices were assigned according to those designated in Chapter 4.1 for each third of month, beginning, middle and end, as follows: July - 1, 2, 3; August - 4, 5, 6; September - 7, 8, 9; October - 10, 11, 12; November - 13, 14, 15.

Preliminary analysis of neustonic and discrete depth (1, 3, 6 meters and bottom) plankton tows revealed that croaker larvae were not neustonic. Therefore, it was not appropriate to use the compromise surface drift model, which assumes transport is 15° to the right of the wind direction and 3% of the wind speed (Murray, LeDuc and Ingham 1983). There is not an analogous model for subsurface, although there are
theoretical formulas (Ekman 1905, Neumann and Pierson 1966). To develop an analogue, I sought measurements of the current to compare with the Norfolk wind.

Current meters were deployed on a transect off the mouth of Chesapeake Bay in July and August 1974, for which 4-hourly vectors are published (Beardsley and Boicourt 1981). The mid-shelf location closest to the Bay mouth, Mooring 408A (Appendix 6.1 - Figure), most closely approximated the area of interest for larval croaker transport. The depth at Mooring 408A was only 18 m, thus the 16 m reading was disregarded because of the strong influence of bottom topography (Csandy 1981a). Analysis of discreet depth plankton tows (Figure 6.3) showed the 10 m reading to be appropriate for larval croaker movement within the water column.

The 23 July to 16 August 1974 time frame employed by Beardsley and Boicourt (1981) was used as test data. Current meter vectors were low-pass filtered to remove tidal and high frequency components above 0.7 cpd (Figure 6.4). Norfolk wind stress vectors which had been low-pass filtered (Beardsley and Boicourt 1981) were compared to wind stress vectors from the test data which had been subjected to a 9-point (27 hour) equally-weighted moving average. The raw 3-hourly Norfolk airport wind data were then smoothed using a 9-point (27 hour) equally-weighted moving average. The magnitudes and angles of the smoothed raw wind vectors were compared to the current meter vectors to infer water movement from wind data (W. Boicourt, UMCEES (University of Maryland Center for Environmental Estuarine Studies)/Horn Point Lab pers. comm.). While a lag in the response of the water to the wind is observed, the current is most accurately approximated by wind during periods of prolonged strong winds from a consistent direction, as seen in the test
Figure 6.3

Length/frequency distribution of larval croaker taken from discreet depth (surface, 1 m, 3 m, 6 m, and bottom) plankton tows at the Chesapeake Bay mouth, August and September 1980. Plankton collections provided by the Department of Oceanography, Old Dominion University, Norfolk, Virginia.
Figure 6.4

Norfolk airport, Virginia three-hourly and smoothed winds, and current meter readings from Mooring 408A, near the Chesapeake Bay mouth, 23 July - 16 August 1974. Calculated water movement was based on comparison of wind and water vectors.
data 1-5 and 9-12 August. To estimate the water movement, the direction was determined to be 20° to the right of the smoothed wind direction and the movement estimated to be 5% of the smoothed wind velocity. This calculated water movement is shown at the bottom of Figure 6.4. It was considered to provide a reasonable estimate of observed water movement. Water movement was computed for fall winds and plotted to scale on a Prime 850 computer.

**Distribution and Transport of Larval Croaker**

Analyses of larval distribution are based on data from ichthyo plankton surveys conducted by the National Marine Fisheries Service (NMFS) in the Mid-Atlantic Bight and provided by the Northeast Fisheries Center (NEFC)/Sandy Hook Laboratory. The sample area, methods and treatments have been described for the Marine Resources Monitoring, Assessment, and Prediction (MARP MAP) cruises (Smith, Wells and McMillan 1979, Berrien, Naplin and Pennington 1981). A detailed description of the MARMAP bongo samplers used on the 1973-81 cruises is given by Pospay and Marak (1980). Data obtained from the Sandy Hook Lab had been recorded as number per standard 30 minute tow, number per 10 m² surface area, or number per 1000 m³ (P. Berrien, NMFS/Sandy Hook Lab pers. comm.). Since croaker larvae are not assumed to be confined to a narrow depth stratum (Judkin, Wirick and Esaís 1980), larval densities (#/1000 m³) were calculated by dividing the number per oblique tow by water volume filtered and multiplying by 1000.

Adult abundance, distribution and bottom temperature data from MARMAP trawl surveys (1971, 1973-81) were obtained. MARMAP cruise listing, sampling methods and gear, survey design and data handling are
described by Grosslein (1969a, 1969b), Clark (1979) and Fleischer (1980). The data were provided courtesy of NMFS/NEFC/Resource Assessment Division. Adult abundances are presented as number caught per standard 30 minute tow.

Most, but not all, cruises sampled at least as far north as $39^\circ$N and as far south as $35^\circ$N. To make all sample locations equal, only data between $35^\circ$N and $39^\circ$N latitude, west of the 200 m isobath and east of the smoothed coastline were considered (Figure 6.1). Contours for values of $\geq 0$, 50, 100, 500, 1000 and 5000 larvae ($#/1000m^3$) and adult ($#/tow$) croaker were determined.

Plankton samples from 21 stations at the Chesapeake Bay mouth (Appendix 6.2 - Figure) were taken at 2 week intervals, 13 August to 28 September 1980, and provided by the Department of Oceanography, Old Dominion University, Norfolk, Virginia. The samples consisted of neuston, 1, 3 and 6 meter, and epibenthic collections. Gear efficiencies were calculated to be: neuston net - 100%, 12 inch Clark-Bumpus Opening-Closing Plankton Sampler - 85%, and epibenthic sled - 65% (J. McConougha, ODU pers. comm.). A detailed description of sampling and preserving procedures and development of gear is provided by Johnson (1982). All croaker larvae were measured to the nearest 0.01 mm but grouped in 0.05 mm increments for analysis. Since the purpose was to analyze vertical distribution, as opposed to horizontal distribution, all station data were combined by depth. The resulting total numbers were then adjusted for gear efficiency.

Described larval croaker specimens are 1.7-10.5 mm (Fruge and Truesdale 1978) with no information known about yolk-sac larvae (Johnson 1978). The term "larvae" is used in this study to mean larval and post-
larval croaker caught with plankton sampling gear, usually in this size range, but occasionally reported as larger than 10.0 mm. Croaker larvae were identified using Hildebrand and Schroeder (1928), Scotton, Smith, Smith, Price and de Sylva (1973), Fruge and Truesdale (1978), Johnson (1978), and Powles and Stender (1978). A reference collection of laboratory spawned specimens was provided by W. Hettler (NMFS/Southeast Fisheries Center (SEFC)/Beaufort Lab). Questionable larvae were sent for verification to J. Govoni and W. Hettler (NMFS/Beaufort Lab), P. Berrien (NMFS/Sandy Hook Lab), and B. Stender (South Carolina Marine Resources Research Center (SCMRRC)/Charleston,S.C.) (Appendix 6.3 - Table). Those larvae which could not be positively identified as Micropogonias undulatus were discarded.

Small croaker were captured inside the Chesapeake Bay in the fall by the VIMS trawl surveys. Those croaker caught within the Bay with non-plankton gear are referred to as juveniles. Only data from 1971 onward were used for transport analysis, because that is when most collections employed a lined trawl. The unlined trawl, discussed in Chapter 5, underestimates fall collections of newly recruited croaker.

The September through December 1974-78 collections were part of the supplemental data from VIMS Crustaceology Department surveys for juvenile blue crabs. These collections primarily used unlined 30 foot trawls with an occasional lined 16 foot trawl. There are no comparisons of lined and unlined 30 foot trawls, but both are compared to a lined 16 foot trawl.

Unlined 16 and 30 foot trawls appear to be about as efficient as lined 16 foot trawls (Table 5.2). This may be deceptive because it means that the lined 16 foot trawl is effective for smaller fish, but
the abundance is too low, while the unlined 30 foot trawl is effective for larger fish but the abundance should be higher. Comparisons between lined 16 foot and lined 30 foot trawls in 1975, 1976, and 1977 show the catch rate of 30 foot trawls to be between 1/2 and 5 times that of lined 16 foot trawls. Because of the discrepancies in these results, it was subjectively assumed (since the opening of the a lined 30 foot trawl is twice that of the 16 foot trawl), that the larger trawl would generally catch twice as many fish. The lined 30 foot trawl was assigned an catchability of twice that of 16 foot trawls and unlined 30 foot trawls.

This catchability factor was applied to fall juvenile monthly collections \( J_{\text{MON}} \) to adjust the monthly index \( J_{\text{ADJ}} \) in an upward direction and make the eleven years more comparable. Since lined 30 foot trawls were not used in the fall of the year 1971-78, September-December indices for those years were doubled, except for December 1978. December 1978 and September-December 1979 were equated with 1980, 1981 and 1982, in which 100% of the collections were made with lined 30 foot trawls (see Norcross and Shaw 1983). These data adjustments were made as follows:

\[
100\% \text{ Tows} = \%30' + \%0G
\]

\[
J_{\text{MON}} = (\%30' \times J_{\text{MON}}) + (\%0G \times J_{\text{MON}})
\]

\[
J_{\text{ADJ}} = (\%30' \times J_{\text{MON}}) + 2(\%0G \times J_{\text{MON}})
\]

where:

\( \%30' \) = \% Tows with lined 30 foot trawls

\( \%0G \) = \% Tows with gear other than 30 foot lined trawls

\( J_{\text{MON}} \) = Juvenile Monthly Index

\( J_{\text{ADJ}} \) = Adjusted Juvenile Monthly Index

Adjusted monthly indices and averages are shown in Table 6.1.
### Table 6.1

Monthly Juvenile Croaker Indices ($J_{\text{MON}}$)

<table>
<thead>
<tr>
<th>Year</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
<th>Sep-Dec</th>
<th>Oct-Dec</th>
</tr>
</thead>
<tbody>
<tr>
<td>71</td>
<td>0.30</td>
<td>4.72</td>
<td>37.58</td>
<td>94.68</td>
<td>34.32</td>
<td>45.66</td>
</tr>
<tr>
<td>72</td>
<td>9.20</td>
<td>16.06</td>
<td>45.42*</td>
<td>37.60</td>
<td>27.07</td>
<td>33.03</td>
</tr>
<tr>
<td>73</td>
<td>45.26</td>
<td>166.64*</td>
<td>10.56</td>
<td>4.00</td>
<td>56.62</td>
<td>60.40</td>
</tr>
<tr>
<td>74</td>
<td>-</td>
<td>20.82*</td>
<td>19.36</td>
<td>-</td>
<td>15.59</td>
<td>15.59</td>
</tr>
<tr>
<td>75</td>
<td>2.52</td>
<td>-</td>
<td>212.24*</td>
<td>-</td>
<td>107.38</td>
<td>212.24</td>
</tr>
<tr>
<td>76</td>
<td>5.76</td>
<td>200.06</td>
<td>347.70*</td>
<td>-</td>
<td>184.51</td>
<td>273.88</td>
</tr>
<tr>
<td>77</td>
<td>-</td>
<td>38.62</td>
<td>212.00*</td>
<td>-</td>
<td>125.31</td>
<td>125.31</td>
</tr>
<tr>
<td>78</td>
<td>23.42</td>
<td>37.34</td>
<td>174.16</td>
<td>201.12*</td>
<td>109.01</td>
<td>137.54</td>
</tr>
<tr>
<td>79</td>
<td>3.62</td>
<td>17.14</td>
<td>54.21</td>
<td>72.12*</td>
<td>36.78</td>
<td>47.82</td>
</tr>
<tr>
<td>80</td>
<td>1.41</td>
<td>8.46</td>
<td>137.38*</td>
<td>66.20</td>
<td>53.63</td>
<td>70.68</td>
</tr>
<tr>
<td>81</td>
<td>0.00</td>
<td>7.49</td>
<td>79.26*</td>
<td>29.40</td>
<td>29.04</td>
<td>38.72</td>
</tr>
</tbody>
</table>

* = $J_{\text{MAX}}$
Vector additions of computed water movement over 10-day periods, July to December, revealed that July, November, and December have almost no onshore transport. Therefore, the time span from 1 August through 10 November was evaluated for each year. The time of best onshore transport varied year to year, and while in proximity to the time of the wind cessation (as discussed in Chapter 4), there was no predictable pattern. Thus, analysis of a standard time subsample within a uniform time frame every year would be biased toward those years which were "average".

Since, the maximum length of continuous onshore transport was about 40 days, this time length was chosen for analysis. Each year was investigated and the "best" 40-day time frame, in third-of-month increments, was used. To determine what was "best", 40-day vectors for time spans of 4 continuous third-of-month increments were computed. Criteria considered for "best" transport were: 1) direction, i.e., most onshore; 2) speed, i.e. higher is better; and 3) time relative to wind cessation, i.e., transport after cessation is better than before cessation. The result was one composite 40-day vector per year, with known direction, magnitude and time frame. Not all years showed good transport for the same length of time. Therefore, the analysis was weighted more heavily for those years with a longer period of favorable transport.

Instead of using absolute direction and speed, an index was assigned to each value. Directly onshore transport, i.e., 270° ±5° was considered the best direction and given a value (D) of 10. Deviation
from 270°, in ±5° increments, was assigned a decreasingly lower value (D) i.e., ±6°-10° = 9 through ±41°-45° = 2, with ±> 46° = 1. Velocity (nmi/40 days) was similarly evaluated and assigned an index value (S). However, as wind velocity was not as important as direction, its values were somewhat lower: 0-49 = 1, 50-90 = 2, 100-149 = 3, 150-199 = 4, 200-249 = 5 and ≥ 250 nmi/40 day = 6. The only method available for evaluating spawning time was the time of the summer wind cessation, as discussed in Chapter 4. The time index for the cessation of the summer winds was subtracted from the time index for the start of the best 40-day transport period. The result was a time lag value (T).

These three parameters of the wind were converted into a single wind transport index (WINDEX=W).

\[ W = D + S - T \]

where:

- \( W \) = wind transport index (WINDEX)
- \( D \) = direction index
- \( S \) = speed index
- \( T \) = time lag

The results of this analysis for 1971-81 are shown in Table 6.2.

The discrete depth plankton tows confirmed the preliminary analysis that croaker larvae are pelagic though not neustonic. Descent of croaker larvae in the water column does not appear to be triggered at a specific size, larval size and abundance generally increase with depth (Figure 6.3). This vertical distribution agrees with the calculated water movement at 10 m.

The abundance of croaker larvae increased dramatically from 13 August (n=1) and 29 August (n=1), through 14 September (n=375) to
<table>
<thead>
<tr>
<th>YEAR</th>
<th>DIRECTION (degrees)</th>
<th>SPEED (mi/40da)</th>
<th>TIME (month/3)</th>
<th>WIND CESSION (month/3)</th>
<th>WINDEX</th>
</tr>
</thead>
<tbody>
<tr>
<td>71</td>
<td>284</td>
<td>8</td>
<td>4</td>
<td>5-8</td>
<td>11</td>
</tr>
<tr>
<td>72</td>
<td>233</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>-2</td>
</tr>
<tr>
<td>73</td>
<td>287</td>
<td>6</td>
<td>2</td>
<td>7</td>
<td>12</td>
</tr>
<tr>
<td>74</td>
<td>388</td>
<td>0</td>
<td>7</td>
<td>7</td>
<td>12</td>
</tr>
<tr>
<td>75</td>
<td>268</td>
<td>7</td>
<td>2</td>
<td>5</td>
<td>15</td>
</tr>
<tr>
<td>76</td>
<td>271</td>
<td>1</td>
<td>3</td>
<td>10</td>
<td>8</td>
</tr>
<tr>
<td>77</td>
<td>238</td>
<td>10</td>
<td>4</td>
<td>4</td>
<td>15</td>
</tr>
<tr>
<td>78</td>
<td>265</td>
<td>10</td>
<td>4</td>
<td>6-9</td>
<td>7</td>
</tr>
<tr>
<td>79</td>
<td>306</td>
<td>8</td>
<td>2</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td>80</td>
<td>283</td>
<td>8</td>
<td>2</td>
<td>7-10</td>
<td>5-8</td>
</tr>
<tr>
<td>81</td>
<td>242</td>
<td>5</td>
<td>3</td>
<td>8</td>
<td>0</td>
</tr>
</tbody>
</table>
The cessation of the summer wind was at the end of September in 1980, the collection time of highest abundance in this study. This supports the estimation of spawning time based on cessation of summer winds, as discussed in Chapter 4.2. It is unfortunate that larval collections were not available for later dates to allow establishment of peak spawning and transport time.

Distributions of adult and larval croaker on the shelf in the fall are shown in Figures 6.5 through 6.13. Also shown are the 10-day moving average vectors for August through November as well as the 40-day composite "best" transport vector. Qualitatively, the distribution of larvae on the shelf appears to be related to the distribution of adults and wind vectors (Figures 6.5 - 6.13). This concept is supported by the fall juvenile indices (Table 6.1).

Quantification of this wind/croaker link required identification of key parameters of water transport, i.e. wind direction, speed, duration and timing. Each parameter was evaluated for relative importance. Examination of the juvenile indices ($J_{\text{adj}}$) revealed the value of the largest index ($J_{\text{MAX}}$), September through December, to be the most reliable indicator of transport success. $J_{\text{MAX}}$ is more accurate than average September-December or October-December index because the average values may be underestimated when the time of spawning or best transport is late, or when the collection was early in the month. In such years it would be appropriate to incorporate the winter month values. This would not be an acceptable parameter for all years however, because of the negative effect of winter temperatures on juvenile croaker survival (Chapter 7). The accuracy of $J_{\text{MAX}}$ is unknown in years such as 1975 when collections were not made every month.
Simultaneous distribution of number of adult, number of larvae, and larval lengths for 1973. Ten day moving average water vectors are plotted to the same scale as the distribution charts. "Best" 40-day vector is shown in bold, above time line. Triangle indicates time of cessation of the summer wind.
Figure 6.6

Sequential distribution of number of larvae, larval lengths and number of adults for 1974. Ten day moving average water vectors are plotted to the same scale as the distribution charts. "Best" 40-day vector is shown in bold, above time line. Triangle indicates time of cessation of the summer wind.
Figure 6.7

Simultaneous distribution of number of adults, number of larvae and larval lengths for 1975. Ten day moving average water vectors are plotted to the same scale as the distribution charts. "Best" 40-day vector is shown in bold, above time line. Triangle indicates time of cessation of the summer wind.
Figure 6.8

Simultaneous distribution of number of adults, number of larvae and larval lengths for 1976. Ten day moving average water vectors are plotted to the same scale as the distribution charts. "Best" 40-day vector is shown in bold, above time line. Triangle indicates time of cessation of the summer wind.
Figure 6.9

Sequential distribution of number of adults, number of larvae and larval lengths for 1977. Ten day moving average water vectors are plotted to the same scale as the distribution charts. "Best" 40-day vector is shown in bold, above time line. Triangle indicates time of cessation of the summer wind.
ADULTS (#/tow)  LARVAE (#/1000m³)  LARVAL LENGTH (mm)

1977 BEG OCT  1977 END OCT

[Map of distribution with symbols and lines indicating adult and larval presence and lengths]

Symbols:
- 0
- 50
- 100
- 500
- 1000
- 5000

Units:
- N. MILES / 10 DAYS
- AUG  SEP  OCT  NOV
Sequential distribution of number of larvae, larval lengths and number of adults for 1978. Ten day moving average water vectors are plotted to the same scale as the distribution charts. "Best" 40-day vector is shown in bold, above time line. Triangle indicates time of cessation of the summer wind.
Figure 6.11

Sequential distribution of number of adults, number of larvae and larval lengths for 1979. Ten day moving average water vectors are plotted to the same scale as the distribution charts. "Best" 40-day vector is shown in bold, above time line. Triangle indicates time of cessation of the summer wind.
Figure 6.12

Sequential distribution of number of adults, number of larvae and larval lengths for 1980. This is the only year in which two larval collections were available. Ten day moving average water vectors are plotted to the same scale as the distribution charts. "Best" 40-day vector is shown in bold, above time line. Triangle indicates time of cessation of the summer wind.
Figure 6.13

Simultaneous distribution of number of adults, number of larvae and larval lengths for 1981. Ten day moving average water vectors are plotted to the same scale as the distribution charts. "Best" 40-day vector is shown in bold, above time line. Triangle indicates time of cessation of the summer wind.
The maximum fall juvenile index ($J_{\text{MAX}}$) was correlated with the wind transport index ($W$). The resulting correlation ($R^2 = 0.62$, $n=11$) confirms the hypothesis that there is increased abundance of juvenile croaker inside the bay when good wind-driven transport occurs, and low abundance with poor transport (Figure 6.14). This curve is represented as: $J_{\text{MAX}} = 18.11 + (3.90*W) + (0.86*W^2)$.

DISCUSSION

Wind-Induced Transport of Larval Croaker

Circulation in the Mid-Atlantic Bight is strongly affected by local wind forcing, duration of alongshore winds, non-locally generated alongshore baroclinic effects, water density, stratification and (Chuang, Wang and Boicourt 1979). Surface circulation models incorporate not only the effect of classical wind-driven Ekman currents, but also tidal currents, baroclinic currents (Bishop 1980b, Bush and Kupperman 1980), and Stokes drift derived from surface wave motion (Haung 1979, Kirwan, McNally, Pazan and Wert 1979). However, modelling the circulation of the Mid-Atlantic Bight also requires a 3-dimensional perspective in addition to time dependency and density stratification (Chuang et al. 1979).

Wind stress is a significant component in determining the flow in the Mid-Atlantic Bight (Bishop 1980b). The effect is greatest on the innershelf within 30 km of shore, supporting the boundary layer theory of shelf circulation (Csandy 1981b). There is a strong correlation between wind stress and current meter readings at depth in this region, with the correlation being best in the alongshelf direction (Hunter,
Maximum fall index ($J_{\text{MAX}}$) regressed against the wind transport index ($\text{WIND EX}$):

$$J_{\text{MAX}} = 18.11 + (3.90W)(0.86W^2).$$

The resulting equation and curve represent the extent to which croaker recruitment to the Chesapeake Bay is determined by wind-induced transport. ($R^2 = 0.62$, $n=11$)
Boicourt and Hacker 1977). The synoptic scale alongshelf current fluctuations are generally coherent with the alongshelf wind stress, up to 235 km. The weaker cross-shelf current component has a smaller alongshelf coherence of 50 km or less but is coherent in the cross-shelf plane (Beardsley and Boicourt 1981).

The inner MAB shelf, away from the mouth of estuaries, is dominated by wind forcing (Beardsley and Boicourt 1981). This mean flow from Cape Cod to Cape Hatteras decreases between the shelf break and the coast. Because the inner shelf is shallow, this area is prone to wind forcing (Boicourt 1981). Current meter data show that offshore the wind-driven motion is a modulation of the mean southerly flow. However, there is a strong correlation of the wind stress record from Norfolk with the 10 m current record at the inner shelf station 408A, the one used here, indicating clearly that the wind is the primary driving force in this region (Boicourt 1981).

Comparison of current meter data from Mooring 408A (Beardsley and Boicourt 1981) and Norfolk winds, as described in the Methods section, provided an approximation of wind-induced water movement at 20° to the right of the wind. This correlates very well with observed directional change in the Gulf of Bothnia, between 0 and 20 m depth, of 19° to the right, which is in close agreement with Ekman's theory (DeFant 1961). However, the estimate of velocity used here, 5% of the wind speed, is higher than expected, when compared to the surface model value of 3%. DeFant (1961) also found the velocity at depth to be higher than theory dictates. He could only explain this as related to stratification, i.e. the layer above the thermocline moves faster. In the evaluations here, no data regarding the depth of the thermocline are available,
though as surface waters continue to warm, the thermocline deepens and increases in intensity. The intensity of the thermocline increases and reaches a maximum in mid-August to early September (Ingham 1982b). Therefore, it is likely that the thermocline was quite deep and that 10 m was above the thermocline, therefore moving faster.

It is known that differences in speed exist between onshore and offshore winds. The velocity of Norfolk winds were not increased for this study based on climatological average comparison with offshore data (F. Godshall pers. comm.) (see Chapter 4.1). However, yearly comparisons with Chesapeake Light Ship winds show the offshore winds to be stronger than Norfolk winds (Chuang et al. 1979). A study relating sea bouys to land stations reveals the strength of the wind at sea to be an average of 1.6 times greater than observed on land (Hsu 1981). In this investigation, fall water movement is estimated. In the fall, surface currents more readily penetrate to the bottom in coastal MAB (Ludwick 1978). Though local winds may not always be the dominant driving mechanism for surface drift, they might be useful as predictors of drift by virtue of the winds being sufficiently correlated with the dominant drift mechanisms (Harrison et al. 1967). Therefore, although the application of the local Ekman model is probably restricted with regard to the Mid-Atlantic Bight (Chuang et al. 1979), water movement on the shelf is approximated here as wind-induced transport.

Prevailing currents and wind-induced transport affect movement of larvae from spawning grounds to nursery areas, thus influencing recruitment and subsequent year-class success. Larval transport has been demonstrated by several early authors (Carruthers 1938, Walford 1938, Sette 1943, Bishai 1960) and recently reviewed by Norcross
and Shaw (In press, Appendix 6.4 - Text). Intuitively, wind-induced transport in the MAB should affect recruitment of larval croaker from the ocean spawning site to the estuarine nursery area, specifically, the Chesapeake Bay.

This concept is upheld by investigation of croaker larval length distributions and larval and adult abundance distributions. Vectors depicting 10-day water movement, plotted to the same scale as these distribution charts (Figures 6.5 - 6.13), add additional support. Larval distribution is seen to be closely related to wind direction. Offshore larval movement results from winds blowing offshore. This is verified by the patch of 5 mm larval surrounded by smaller, younger larvae in the beginning of October 1979. Similarly, southward winds with a seaward component carried some larvae past the shelfbreak at the end of October 1977. The farther from the coast, the more the offshore component intensifies (Bumpus 1973, Ruzecki et al. 1976). Investigation of plots of larval croaker distribution, from the R/V DOLPHIN (Clark, Smith, Kendall and Fahay 1969, Berrien, Fahay, Kendall and Smith 1978) and from unpublished data in Onslow Bay (S. Warlen, NMFS/Beaufort Lab pers. comm.), in relation to temperature and salinity isobaths indicate entrainment of croaker larvae in the Gulf Stream, resulting in recruitment loss. Field observations that I made aboard the R/V JOHN DE WOLFE II in December 1979 substantiate this. Of the croaker taken on a cross-shelf transect south of Cape Lookout, N.C., the largest number were found at the Gulf Stream station (>100 fathoms). This cruise followed four days of gale-force northwest winds. Since offshore Ekman transport has been linked to low year-class strength in other species (Nelson, Ingham and Schaaf 1977, Bailey 1981, Bolz, Lough and Potter
1981, Parrish, Nelson, and Bakun 1981), transport directed away from juvenile nursery grounds is hypothesized to cause poor recruitment of croaker to the Chesapeake Bay.

Strength does not appear to be as important as direction of the wind (Murray, LeDuc and Ingham 1983). Low magnitude winds in September and October 1976 and 1980 concentrated larvae at or north of the Bay mouth as compared with strong winds at the same time in 1974 which transported larvae south, bypassing the Chesapeake Bay. Adult distribution changes as southward migration continues. Larval distributions are farther north than those of adults in 1973 and 1980. Wind vectors do not indicate northward movement of larvae, therefore, it is probably a southward movement of adults.

Although qualitatively there was an apparent relationship between larvae and wind, variability in time and absolute measures of direction and speed made the wind-induced transport difficult to quantify. The "best" 40-day vector for each year is shown in bold in Figures 6.5 through 6.13. The time of this vector is indicated under each vector, above the time scale. While there were 40 continuous days of good transport in 1973 and 1976, there were not 40 "good" days in 1974 and 1977. Thus, this time choice incorporates a factor for duration of good transport. According to daily growth analysis of larvae, 40 day old croaker are between 9 and 10 mm (Figure 6.15) (Warlen 1980). This encompasses the sizes of larvae on the shelf (Figures 6.5-6.13) and at the Chesapeake Bay mouth (Figure 6.3), and also is consistent with the largest larvae found on the shelf, 11 mm in 1975 (Figure 6.7). This size is historically reported within the Bay, as well as the Newport River estuary, North Carolina (Lewis and Judy 1983).
Figure 6.15

Age in days compared to standard length (mm) of croaker
(after Warlen 1980).
This is the same size at which the VIMS juvenile trawl survey first begins to capture young croaker (Norcross and Shaw 1983). Therefore, 40 days are considered a sufficient length of time from which to devise a wind transport index (WINDEX).

Analyses of the east/west components of the Norfolk winds provide a good first-cut choice of time for the 40-day vectors. The times used, 1973 through 1981, are indicated in boxes in Figure 6.16. Though there is variability in these times, the average is consistent with the strongest westerly wind stress, which has a climatological mean in September (Saunders 1977). Discrepancies in this first-cut analysis require closer investigation of the 10-day moving average vectors based on the criteria of direction, speed and time discussed in the Results section of this chapter. For example, compared to the first-cut analysis, the times used for 1978 and 1980 appear to be too early and too late, respectively. However, the 10-day moving averages reveal that in 1978 (Figure 6.10), the vector had a strong component toward the south and was not actually onshore. Conversely, in 1980 (Figure 6.12), the component toward the north was quite strong since it was before the cessation of the summer winds. The result was the same. The direction of the wind was not onshore. Additionally the timespans used for both 1978 and 1980 were closer to the time of the summer wind cessation, and thus closer to spawning than those indicated by the east-west component analysis.

Absolute measures of direction and speed were not considered good indices of transport because they assume precision of measurement, are biased because of the 360° directional base, and attribute too much accuracy to the computed magnitude. The "best" 40-day vector for each
Figure 6.16

East/west components of Norfolk airport winds, 1973–1981, used as indicators of onshore transport. Boxed areas depict time of "best" 40-day transport.
year (Figures 6.5 - 6.13) was used to calculate a wind transport index (WINDEX), which was described in the Results section (Table 6.2). Note that the strong northwest vector for 1979 (Figure 6.11) had only half the WINDEX value (W=7) of the weaker onshore vector in 1976 (W=15) (Figure 6.8). Compared to 1976 (S=3), the wind was stronger in 1979 (S=6), but the 1979 direction was not directly onshore (D=3), and the period of good transport began prior to cessation of the summer winds (T=-2). The vectors for 1975 (Figure 6.7) and 1978 (Figure 6.10) are almost identical, but 1975 has a lower WINDEX (W=12) than 1978 (W=15) because the period of good transport began prior to the cessation of the summer winds. Thus, this index incorporates the key components of wind-induced water transport, direction, speed and time, and weights them with regard to onshore movement of croaker larvae and subsequent recruitment into the Chesapeake Bay.

**Estuarine Transport of Larval/Juvenile Croaker**

Classical estuarine circulation of the Chesapeake Bay is twolayered, with low salinity water flowing out at the surface and high salinity water flowing in at the bottom (Pritchard 1967). A mean bottom inflow prevails at the Chesapeake Bay mouth (Norcross, Massman and Joseph 1962, Harrison et al. 1967, Bumpus 1973). Estuarine inflow can affect this lower layer as far seaward as the 20 m isobath (Boicourt 1981).

Ekman flux is consistent with wind-induced transport at the Chesapeake Bay mouth at periods of 10 days or greater (Wang and Elliott 1978). Between the Chesapeake Bay and coastal ocean, a wind-driven/density-induced circulation interaction is atmospherically
coupled. The mean bottom flow is into the Bay mouth (Figure 6.1), though typically restricted to the deep channel by "summer" (southerly) winds as shown for June-July 1980 in Figure 6.17. "Winter" wind patterns (northwest) increase the net downstream estuarine flow and, in turn, strengthen the net return bottom flow (Harrison et al. 1967). Thus, the lessening of winds coupled with reduced freshwater outflow results in more bottom water inflow in the fall. By September 1980, the inflow was not restricted to just the deep channels. The flow below 3 m was consistently into the Bay, with the surface layer fluctuating with the tides (W. Boicourt pers. comm.) (Figure 6.17). In 1980 and 1981, a severe drought may have reduced surface freshwater flow from the Bay and enhanced inflow of saline bottom waters (Ingham 1982b).

Discreet depth larval collections at this time reveal most of the croaker to be at or below 3 m (Figure 6.3). Though a few were found in the tidally influenced 1 m layer, the majority were being transported into the Bay. This is consistent with previous observations that post-larval/juvenile croaker are commonly found on the bottom when entering the Chesapeake Bay (Haven 1957), North Carolina estuaries (Hildebrand and Cable 1930), and Gulf coast passes (Hoese 1965). Thus they use deep estuarine currents to move upbay (Powles and Stender 1978). Croaker larvae have been observed settling to the bottom 72 hours after hatching in the laboratory. However, the exact triggering mechanism and timing of larval descent in the water column from their original pelagic state is not known.

Miller et al. (In press) suggest an active response by larval croaker to vertical temperature gradients. For Onslow Bay, N.C., they show that croaker larvae remain in warmer waters, thus moving onshore at
Figure 6.17

Vertical section at the Chesapeake Bay mouth depicting inward and outward flow, June-July 1980 (after Boicourt 1981), and September 1980 (W. Boicourt pers. comm.).
the surface in the fall and at mid-depth in the winter. They felt that observed age distributional differences in the water column must have been generated as an active response. In Figure 6.3, larval lengths increase with depth on 14 September, but do not exhibit this pattern on 30 September. Temperatures were collected simultaneously with the larval collections at the Chesapeake Bay mouth and provided by J. McConougha (ODU pers. comm.). On 14 September 1980, a slight thermocline (3°- 4°C) was still present at the stations outside the Bay mouth (Appendix 6.2 - Figure). However, conditions were isothermal by 28 September. Thus, there appears to be size related vertical response to the temperature gradient (25.5°- 21.5°C) which was present at the time of the early collection, but absent (23.5°- 22.5°C) at the later collection. Though larvae less than 4 mm were found at all temperatures within these ranges, those croaker larvae 4 mm or greater were never found at temperatures greater than 23.5°C.

Temperature recognition and preference increase with the number of days post hatching in larval grunion, *Leuresthes tenuis* (Ehrlich and Muszynski 1982). The larvae are sensitive to a narrow range of temperatures. Although growth efficiency is maximum between 18°C and 23°C, yolk-sac larvae prefer temperatures about 25°C. This higher temperature has been found to increase growth rate, minimize the yolk-sac stage and probably decrease invertebrate predation for both grunion (Ehrlich and Muszynski 1982) and Pacific hake, *Merluccius productus* (Bailey 1981).

Larval sciaenids respond similarly to temperature. Time spent in the yolk-sac stage has been shown to increase from 40 hours at 30°C to 85 hours at 20°C for red drum, *Sciaenops ocellata* (Holt, Godbout and
Arnold 1981). The optimum temperature for hatching is 25°C for red drum (Holt et al. 1981), and 22°C for spot (J. Govoni pers. comm.). Since croaker is a fall spawner like red drum, its optimum temperature may be closer to 25°C. However, the temperatures observed in conjunction with this study span the range of both these sciaenids.

Once past the yolk-sac stage, hake larvae are found in deeper water when sea surface temperatures are warm (Bailey 1981). Grunion larvae on the other hand, seek cooler temperatures to conserve energy when not feeding (Ehrlich and Muszynski 1982). A vertical response to temperature would work to insure onshore transport of croaker larvae in the Mid-Atlantic Bight as it does in Onslow Bay (Miller et al. In press). The young larvae would be nearer the surface, and more subject to wind-induced onshore transport. Pronounced thermal stratification on the shelf disappears around September (Harrison et al. 1967). Larvae tend to be closer to the surface when the water column is less stratified (Ahlstrom 1959, Bailey 1981). This was exhibited by croaker larvae at isothermal conditions 28 September (Figure 6.3). As the larvae get near the Chesapeake Bay mouth, and the thermocline starts to break down in the fall, the numbers collected at 6 m, as opposed to 1 m and 3 m, indicate that they descend vertically which reduces offshore transport at the surface. However, since most of the flow at the Bay mouth is inward at this time of year, a large scale vertical response is not necessary.

The hypothesis that croaker larvae/post-larvae come in along the bottom of the Bay and are carried upstream in the salt-wedge transport system had been accepted (Wallace 1940) but not substantiated by physical measurements or field collections. Newly hatched croaker
larvae are neutrally buoyant. Observations in the laboratory reveal that yolk-sac larvae appear to expend energy fighting to descend (W. Nettler pers. comm.). Weinstein et al. (1980) have shown that post-larval croaker maintain a bottom orientation, and exhibit behavioral responses to photoperiod and tide, which would help post-larvae accumulate in upstream nurseries by utilizing net non-tidal flows in the lower layer (Appendix 6.5 - Figure). While such a tidal response may be particularly important in well-mixed estuaries such as Pamlico Sound, N.C., it is not likely to be as important in the two-layer flow of the Chesapeake Bay. In a two-layer system, bottom orientation may be the only behavioral response necessary for juvenile fish to successfully enter the estuary (Miller et al. In press).

Croakers most likely move upriver using salt wedge transport, since they accumulate, in many systems, where deposition is greatest (Weinstein 1979). Just as an increase in larval size from offshore spawning to inshore nursery areas is apparent (Warlen 1980, Lewis and Judy 1983, Miller et al. In press), an increase in size from offshore through the Chesapeake Bay and upriver is demonstrated by 1973-1980 composite monthly length/frequencies (Figure 6.18). Continuation of upbay movement, protracted spawning and growth are evidenced here.

CONCLUSIONS

Part 2 of Sub Model I (Figure 6.19) represents the effect of transport on larval croaker recruitment to the Chesapeake Bay. To successfully enter the Bay, croaker must avoid the outflowing surface layers. If the larvae can descend in the water column in proximity to
Figure 6.18

Average (1973-1980) monthly, August through January, length/frequencies of croaker showing increase in size and number over time and distance inshore.
Figure 6.19

Sub Model I - Part 2: The effect of transport on larval croaker recruitment into the Chesapeake Bay.
SUB MODEL I - PART 2

SURFACE TRANSPORT

ONSHORE

BROUGHT NEAR BAY MOUTH

VERTICAL TRANSITION

BOTTOM TRANSPORT

ONSHORE

RECRUITED TO CHESAPEAKE BAY

CARRIED AWAY FROM BAY MOUTH

LOST (GULF STREAM)

CARRIED AWAY FROM BAY MOUTH

LOST
the mean inward bottom flow, they will get into the Chesapeake Bay by a combination of active swimming and passive transport (Lewis and Judy 1983). The potential loss of larvae is greatly reduced once they have reached this stage. Though the surface drift is not always favorable, the bottom drift provides a consistent transport toward inshore nursery areas (Harrison et al. 1967). However, away from the Chesapeake Bay mouth, the current turns offshore with increasing depth (Chuang et al. 1979). Thus, it is important that the croaker are first brought near the mouth of the Bay.

Therefore, the most critical time in the life history of a larval croaker is during the pelagic stage. During this period, it is subject to wind-induced transport which may cause direct loss off the shelf and entrainment in the Gulf Stream. Offshore transport prolongs the time during which the larvae are vulnerable to predators, nutritional deficiencies, and adverse temperature changes. The magnitude of this wind-induced effect is a function of the direction, strength, duration and time relative to spawning, as has been suggested for mackerel, *Scomber scombrus*, (Carruthers 1938, Murray et al. 1983). Fall juvenile recruitment is determined by the effect of the wind due to transport combined with its effect on spawning location and time, as demonstrated in Chapter 4. Together, these form Sub Model I (Figure 6.20).

Quantification of transport effects on recruitment is based on that vulnerable wind-driven period rather than the more stable bottom stage (Figure 6.14). This hypothesized relationship needs to be field tested with concurrent biological and physical samples. An intense sampling regime of discreet depth plankton tows is needed during the
Figure 6.20

Sub Model I: The effect of wind on larval croaker recruitment into the Chesapeake Bay.
OFFSHORE WINDS (adjusted Norfolk)

CESSATION SUMMER WINDS

SURFACE TRANSPORT

OFFSHORE

ONSHORE

FALL JUVENILE ABUNDANCE [VIMS Trawl Surv]

FALL JUVENILE RECRUITMENT

LATE

RECRUITMENT (Physical)

RECRUITMENT (Physical)

SUB MODEL I
croaker spawning season not only near the Chesapeake Bay mouth, but also over the middle and southern areas of Mid-Atlantic Bight. When wind-induced transport is not conducive to Chesapeake Bay recruitment, as in 1974 (Figure 6.6), surface and bottom drift patterns (Figure 6.1) indicate that recruitment to Pamlico Sound may be enhanced through Oregon Inlet. Field sampling should include this area. Additional laboratory experiments also are needed to investigate active and passive mechanisms of larval vertical migration, optimum temperature range, critical period (May 1974), and predator/prey relationships. Until these goals can be accomplished, the relationship between the index of wind-induced transport (WINDEX) and the measure of juvenile recruitment within the Chesapeake Bay ($J_{\text{MAX}}$) can be used empirically and can form the basis for additional research.
CHAPTER 7

Effect of Winter Temperature on Survival of Juvenile
Atlantic Croaker in the Chesapeake Bay

INTRODUCTION

Croaker are more cold tolerant than most semi-tropical fish species. As such, they are seldom included in lists of fish killed by cold waters in Florida (Storey and Gudger 1936, Storey 1937, Miller 1940, Snelson and Bradley 1978). However, winter kills have been reported (Hildebrand and Cable 1930, Gunter and Hildebrand 1951). Juvenile croaker are known to be vulnerable to severe cold winter temperatures (Massman and Pacheco 1960), but are less sensitive to the cold than larger fish (Hilderbrand and Cable 1930, Gunter 1938). Temperature-induced mortalities of juvenile Atlantic croaker (Micropogonias undulatus) have been observed in the field (Van Engel and Joseph 1968, Joseph 1972, Wojcik 1978) and in the laboratory (Schwartz 1964, Joseph 1972).

In the Mid-Atlantic Bight, juvenile croaker are recruited to the Chesapeake Bay in the fall and spend their first winter within that estuary and its tributaries (Figure 7.1). Thus, they are susceptible to the severe winter temperatures that may be experienced in that region. The winter of 1958 was exceptionally cold, with January and February temperatures five or six degrees [F] colder than average
Figure 7.1

The Chesapeake Bay and its tributaries. The location of the Virginia Institute of Marine science (VIMS), on the York River, is the site at which the water temperatures were obtained.
The water temperatures not only were colder than any year since 1950, but remained colder for a continuous eight day period. A good croaker year class seemed to be indicated by juvenile catches in the fall of 1957, but young croaker completely disappeared by mid-winter 1958 (Massman and Pacheco 1960). That year class was conspicuously absent from the commercial catch in 1960 (Van Engel and Joseph 1968) and never contributed to future catches (Joseph 1972).

As "cold" winters are known to kill croaker, the purposes of this chapter are to define "cold" winter temperature and to empirically quantify its effect on juvenile croaker (0+) survival to the following summer. This effect is investigated in relation to other environmental factors known to affect young-of-the-year croaker recruitment, as discussed in Chapters 4.2 and 6. The result is a statistical predictive model of croaker year-class (0+) strength in the Chesapeake Bay.

METHODS

Winter sea water temperatures from the York River, Virginia were available 1954 through 1976 (Hsieh 1979). They were recorded at the pier at the Virginia Institute of Marine Science (VIMS), Gloucester Point (Figure 7.1) from a depth of about 2 m below mean low water. These temperatures have been shown to correlate well with observations taken by the VIMS trawl surveys (Massman and Pacheco 1960). Maximum and minimum daily temperatures, taken from a continuous recorder, were averaged. These daily values were then averaged to yield an average temperature for each month. I used this same method (Hsieh 1979) to calculate monthly average temperature from 1977 through 1982. When
daily data were unavailable due to equipment failure, estimates of temperature were derived from weekly maxima and minima.

As an estimate of yearly winter temperatures, January, February and March average temperatures were averaged. Although the year's lowest water temperatures usually occur in January or February, they have been recorded in March (e.g. 1967). The resulting average January-February-March temperature (JFM) was used in the analyses (Table 7.1).

The VIMS trawl survey, as described in Chapter 5, provided monthly indices ($J_{\text{MON}}$) of young-of-the-year croaker in the Chesapeake Bay, 1954-1982. An index of juvenile ($0^+$) survival through the winter to the first summer ($J_{\text{SUM}}$) was obtained from an average of the monthly ($J_{\text{MON}}$) values from April through September (Table 7.1). These juvenile indices were correlated with the January-February-March temperatures to determine empirically the effect of winter temperature on young-of-the-year croaker survival.

The calendar year that is used when referring to a specific year class of croaker is that in which the juveniles are age $0^+$ in the summer. This is not the same as the assignment of year class in Chapter 6 which only dealt with the fall. The fall value is lagged by a year when correlated with the summer indices resulting from that spawn. For example, the 1957 year class was spawned in the fall of 1956, spent the winter (January-March) of 1957 in the Chesapeake Bay, and survived to age $0^+$ in the summer of 1957 ($J_{\text{SUM}}$). Since the purpose is to assess and predict year-class strength ($0^+$) following the first winter, the year class is designated by the year of its first summer.
TABLE 7.1

Temperature and Juvenile Indices

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*From the previous fall, i.e., lagged one year
Statistical calculations and graphical presentations were accomplished using SPSS (1975, 1981) on a Prime 850 computer and Business Graphics (1982) on an Apple IIe. Multiple regression statistics were developed using SPSS. The explained variance ($R^2$) has been reduced to account for the number of explanatory variables and sample size in each case.

RESULTS AND DISCUSSION

Relationship Between Winter Temperature and Summer Juvenile Survival

The April-September summer index of juvenile croaker ($J_{SUM} = y$) was regressed on the average January-February-March temperature ($JFM = x$), 1954 through 1982. A quadratic relationship $[y = ax + bx^2]$ was initially indicated by a plot of the data and regression analyses. However, the following linear transformations were also examined: $[\ln y = \ln a + bx]$; $[y = a + b(\ln x)]$; $[\ln y = \ln a + b(\ln x)]$; $[1/y = (a + be^{-x})]$; and $[\ln y = \ln a + b(\ln x) + cx]$ (Daniel and Wood 1971). The fitted quadratic form is not physically reasonable at temperatures below $4.0^\circ C$ since it begins to curve upward. This falsely indicates that as temperature continues to decrease below $4^\circ C$, the summer survival increases. The quadratic equation with a linear term $[y = ax + bx^2 + cx]$ provided the best fit (Figure 7.2) between January-February-March ($JFM$) average VIMS pier temperatures and juvenile croaker abundance the following summer:

$$J_{SUM} = 118.07 - (53.02*JFM) + (5.99*JFM^2)$$
April-September croaker survival index ($J_{SUM}$) regressed on winter temperature (JFM), 1954-1982:

$$J_{SUM} = 118.07 - (53.02 \times JFM) + (5.99 \times JFM^2),$$

($R^2 = 0.78$, $n=29$).
The regression was highly significant ($R^2 = 0.78$, $n=29$, $F = 51.26$, $p < 0.0001$) as shown in Table 7.2.

The $R^2$ of 0.78 indicates that 78% of the variability in the summer survival index ($J_{\text{SUM}}$) can be explained by winter temperature (JFM). The relationship is particularly good in the lower temperature ranges (Figure 7.2), which agrees with the the conceptual life history proposed in Chapter 3. Most of the data are at temperatures less than 5.0°C where $J_{\text{SUM}}$ varies only slightly from zero. Although there are fewer data points at warmer temperatures, they have more variability and are significant as they potentially produce the dominant year classes. The best fit is still approximated by a quadratic equation. A linear regression provides a poor fit since it is neither asymptotic to zero at very low temperatures, nor approximates an exponential at temperatures greater than 8.5°C (Appendix 7.1 - Figure).

Other measures of temperature and juvenile summer survival also were investigated. December through March individual monthly temperatures, all combinations of these, and minimum monthly temperatures were tested. In addition, March-September and May-September summer juvenile indices were examined. The indices used, January-February-March average temperatures and April-September average young-of-the-year croaker, provided the best statistical fit. However with all indices tested, the best functional form proved to be a quadratic equation with the linear term included.

The quadratic equation was used to hindcast summer juvenile indices 1954-1982. Figure 7.3 shows the close agreement between the actual and hindcast (JFM) values when the summer index was low due to cold winter temperatures. As discussed above, the deviations from the
### TABLE 7.2
Multiple Regression Analysis

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>J_SUM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variable(s) Entered on Step Number</td>
<td>1. JFM 2. SQJFM</td>
</tr>
</tbody>
</table>

| MULTIPLE R | 0.89314 |
| R SQUARE | 0.79770 |
| ADJUSTED R SQUARE | 0.78213 |
| STANDARD ERROR | 11.21264 |

**Analysis of Variance**

<table>
<thead>
<tr>
<th>Source</th>
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<th>Sum of Squares</th>
<th>Mean Square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regression</td>
<td>2</td>
<td>12889.04057</td>
<td>6444.52029</td>
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<tr>
<td>Residual</td>
<td>26</td>
<td>3268.80800</td>
<td>125.72338</td>
</tr>
<tr>
<td><strong>F</strong></td>
<td></td>
<td><strong>51.25952</strong></td>
<td><strong>0.0000</strong></td>
</tr>
</tbody>
</table>

**Variables in the Equation**

<table>
<thead>
<tr>
<th>Variable</th>
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<th>SE B</th>
<th>Beta</th>
<th>T</th>
<th>SIG T</th>
</tr>
</thead>
<tbody>
<tr>
<td>JFM</td>
<td>-53.01877</td>
<td>13.66293</td>
<td>-2.60740</td>
<td>-3.880</td>
<td>0.0006</td>
</tr>
<tr>
<td>SQJFM</td>
<td>5.98886</td>
<td>1.18016</td>
<td>3.40977</td>
<td>5.075</td>
<td>0.0000</td>
</tr>
<tr>
<td>(CONSTANT)</td>
<td>118.07226</td>
<td>38.17541</td>
<td>3.093</td>
<td>0.0047</td>
<td></td>
</tr>
</tbody>
</table>
actual values were larger when the temperatures were greater than 5.0°C. The lowest daily and lowest weekly temperatures over the season were inspected, but did not account for this variability. This wide range of summer indices \( I_{\text{SUM}} \) indicates that factors other than temperature influence summer survival when winter temperatures are warm. This had also been the conclusion of preliminary analyses (Norcross and Austin 1981).

**Relationship Between Fall Juvenile Recruitment.**

**Winter Temperature and Summer Survival**

The number of juvenile croaker that are recruited to the Chesapeake Bay in the fall should affect the year-class strength the following summer. Therefore, the monthly indices \( I_{\text{MON}} \) for the individual fall months of the VIMS trawl surveys, as discussed in Chapter 5, were examined. Because newly recruited croaker may begin entering the Chesapeake Bay as early as July, combinations of months, July through December, were averaged. Since all months were not sampled, the average indices were calculated by totaling the monthly indices and dividing by the number of months sampled.

When entered in a multiple regression with the January-February-March temperature, none of these fall indices explained as much of the variance as temperature alone. Thus, when winter temperatures are very low, they mask the influence of other factors such that temperature appears to be the sole variable determining juvenile survival. For January-February-March temperatures less than 4.5°C \((n=7, \text{ Appendix 7.2 - Figure})\), the fall indices were set to 0.00 so not to influence the statistical relationships \((\text{Appendix 7.3 - Figure})\).
The October juvenile index \( (J_{\text{OCT}}) \) alone does not correlate well with the summer index when the coldest years are included (Appendix 7.4 - Figure) or excluded (Appendix 7.5 - Figure). However, it was a significant predictor of summer juvenile croaker survival when entered in a multiple regression with JFM temperature (Table 7.3). With the inclusion of \( J_{\text{OCT}} \), the explained variance was increased (to \( R^2 = 0.84 \) from \( R^2 = 0.78 \)). The number of years was decreased to 25 from 29 however, because data were not collected in October 1954, 1955, 1960 and 1975. The summer indices corresponding to the three early years ('55, '56 and '61) were low, as were the majority years, and could not be estimated because the surrounding months were also missing. The \( J_{\text{SUM}} \) for 1976 was one of the highest. When \( J_{\text{OCT}} \) was estimated from September and November 1975 indices, the change in the equation was insignificant. The following which resulted with these 4 years eliminated:

\[
J_{\text{SUM}} = 92.64 - (40.87*JFM) + (4.48*JFM^2) + (0.49*J_{\text{OCT}})
\]

This is graphically depicted in Figure 7.4.

The multiple regression equation was used to hindcast the summer juvenile indices 1954-1982 (Figure 7.5). These calculated values were closer to the actual indices than those based on winter temperature alone (Figure 7.3). Inadequate sampling of larger croaker in the summer of 1954 (Haven 1957), the only year in which an 8 foot trawl was used (see Chapter 5), may account for the overestimate of the \( J_{\text{SUM}} \) value in 1954.

All hindcast values are within 12 of \( J_{\text{SUM}} \) except 1957. The actual value for 1957 (\( J_{\text{SUM}} = 45.4 \)) is higher than its calculated value (\( J_{\text{SUM,OCT}} = 10.5 \)). Multiple regression analyses were performed for \( J_{\text{SUM}} \) with \( J_{\text{OCT}} \) and JFM as independent variables, excluding 1957 values. The
Figure 7.3


Hindcast values (JFM) are calculated solely from winter temperatures ($R^2 = 0.78$, n=29).
Summer Young-of-the-Year Croaker

Legend
△ Actual
× Hindcast (JFM)
TABLE 7.3
Multiple Regression Analysis

<table>
<thead>
<tr>
<th>VARIABLE(S) ENTERED ON STEP NUMBER</th>
<th>JFM</th>
<th>OCT</th>
<th>SQJFM</th>
</tr>
</thead>
<tbody>
<tr>
<td>MULTIPLE R</td>
<td>0.92658</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R SQUARE</td>
<td>0.85856</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ADJUSTED R SQUARE</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>STANDARD ERROR</td>
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<td></td>
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**ANALYSIS OF VARIANCE**

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<th>DF</th>
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<th>MEAN SQUARE</th>
</tr>
</thead>
<tbody>
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<td>12266.88264</td>
<td>4088.96088</td>
</tr>
<tr>
<td>RESIDUAL</td>
<td>21</td>
<td>2020.90653</td>
<td>96.23364</td>
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\[ F = 42.48993 \quad \text{SIGNIF } F = 0.0000 \]

**VARIABLES IN THE EQUATION**

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<th>SE B</th>
<th>BETA</th>
<th>T</th>
<th>SIG T</th>
</tr>
</thead>
<tbody>
<tr>
<td>JFM</td>
<td>-40.86535</td>
<td>12.73348</td>
<td>-2.03851</td>
<td>-3.209</td>
<td>0.0042</td>
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<td>OCT</td>
<td>0.48998</td>
<td>0.14315</td>
<td>0.37908</td>
<td>3.423</td>
<td>0.0026</td>
</tr>
<tr>
<td>SQJFM</td>
<td>4.48198</td>
<td>1.13824</td>
<td>2.58777</td>
<td>3.938</td>
<td>0.0008</td>
</tr>
<tr>
<td>(CONSTANT)</td>
<td>92.64366</td>
<td>34.92422</td>
<td>2.653</td>
<td>0.0149</td>
<td></td>
</tr>
</tbody>
</table>
Figure 7.4

Linear form of the April-September croaker survival index ($J_{SUM}$) regressed on the result of the multiple regression equation incorporating winter temperature (JFM) and the October juvenile index ($J_{OCT}$):

$$J_{SUM} = 92.64 - (40.87*JFM) + (4.48*JFM^2) + (0.49*J_{OCT}),$$

($R^2 = 0.84$, $n=25$).
Summer Young-of-the-Year Croaker

Legend
△ Actual
× Hindcast (OCI)

\[ J_{sum} = 92.64 - (40.87 \cdot JFM) - (4.48 \cdot Sq JFM) - (0.49 \cdot OCI) \]
Figure 7.5


Hindcast values (OCT) are calculated from October juvenile indices and winter temperatures ($R^2 = 0.89$, $n=11$).
correlation was significantly improved ($R^2 = 0.94$, n=24) and variances between hindcast and actual values were reduced (Appendices 7.6 - Table, 7.7 - Figure and 7.8 - Figure). This improved relationship with the removal of one year's data indicates a need to examine that year. The deviation in the actual and calculated 1957 values may be explained partially by the underestimation of all juvenile indices from 1955 to 1979 as discussed in Chapters 5 and 6. A higher 1956 October index ($J_{OCT}$) or a higher JFM temperature is needed to explain the high 1957 summer index ($J_{SUM} = 45.44$). The time of the summer wind cessation in 1956 was the end of July (as discussed in Chapters 4.1 and 4.2). This means that if transport into the Bay was good, a large number of new recruits should have been present that fall. Massman and Pacheco (1960) noted that this year class was abundant and that substantial numbers of young croaker were taken in the fall of 1956 and throughout the winter of 1957. They include croaker data, but no measure of effort.

Although the data presented by Massman and Pacheco (1960) were from the VIMS juvenile trawl survey, the numbers of croaker do not correspond to those used here (see Norcross and Shaw 1983). I attempted to examine the original data to verify the fall monthly juvenile indices for 1956 and the summer juvenile index for 1957; however, these data are only available in part on microfische. The catch values recorded on microfische did not contain collection numbers. Thus, it was impossible to compare the original and the computerized data.

These difficulties indicate that the relationship should be examined using other estimates of fall recruitment. Use of the October index may be biased in favor of those years in which maximum recruitment
is early because fall juvenile recruitment does not begin at the same
time each year. (The reasons for this have been discussed in Chapters
4, 5 and 6). However, for the conditions used above, the fall maximum
monthly index \( J_{\text{MAX}} \) did not show as strong a relationship as October
\( J_{\text{OCT}} \). A different approach was used to reexamine this variable
\( J_{\text{MAX}} \).

A subset of the data, 1972–82, (Table 7.1) was examined using
\( J_{\text{MAX}} \) as a predictor in place of \( J_{\text{OCT}} \). These years were chosen
because of the quality of the trawl data. They include the time in
which the VIMS trawl survey began initial use of a lined trawl. More
samples were collected. Original data were available for verification.
The residuals \( R_{\text{JFM}} \) from the JFM–\( J_{\text{SUM}} \) quadratic equation for these
years (Table 7.1) were regressed on the maximum fall recruitment \( J_{\text{MAX}} \).
Since the residuals are the unexplained variance, i.e. the difference
between the actual and predicted values, it was hypothesized that fall
recruitment should account for part of this variance. A linear
relationship below \( J_{\text{MAX}} \) of about 100 is apparent (Figure 7.6). After
that point there is no relationship.

All years with no apparent relationship (1977, 1978, 1979, and
1981) had JFM temperatures less than 5.0°C (see Table 7.1). Previously,
eight October values were disregarded because of cold temperatures.
When JFM temperatures were 4.5°–5.0°C, summer indices never exceeded
11.0 but were not been eliminated since 15 of 29 years had temperatures
less than 5.0°C. The fact that croaker cease feeding at 5.0°C (Joseph
1972) provides a physiologic reason to discount fall juvenile indices
when JFM temperatures are below this. In 1956 (JFM = 4.90°C) the winter
temperature was in this intermediate range (4.5°–5.0°C). A special
Figure 7.6

Residuals from the JFM-J$\text{SUM}$ quadratic regression ($R_{JFM}$) regressed on the fall maximum juvenile index ($J_{\text{MAX}}$), 1972-1982. Data for years when winter temperatures were below 5.0 °C have been eliminated:

$R_{JFM} = (0.47*J_{\text{MAX}}) - 29.42$, ($R^2 = 0.67$, n=6).
survey was conducted with a smaller trawl, but no croaker were caught in either April or May 1956 (Massman and Whitcomb 1956). The summer index reflects this (J_{SUM} = 0.33). The minimum water temperature in January 1956, 0.56°C (Massman and Pacheco 1960) was obscured when averaged with February and March. Similarly, the 1966 winter temperature was in this intermediate range (JFM = 4.87). New recruits were documented as strong in December 1965 and January 1966 (Van Engel and Joseph 1968). However, after a two-week cold snap lowered temperatures below 1.0°C in the York River, only dead croaker were found and few were collected in the spring and summer of 1966 (Joseph 1972). The 1966 summer index (J_{SUM} = 0.01) is the lowest in this time series.

It may be only very warm years that are not temperature limited, as opposed to the prior supposition that only very cold years are temperature limited. A regression is estimated to fit over the entire range of values; it may not be as accurate over the entire range, however. Temperature residuals ($R_{JFM}$) were regressed on fall maximum indices ($J_{MAX}$) for the six years in this subset, 1972-1982, with temperatures greater than 5.0°C (1972, 1973, 1974, 1975, 1976 and 1980). A good linear relationship resulted (Figure 7.6). The explained variation has been adjusted down based on sample size ($R^2 = 0.67$, n=6). A multiple regression using winter temperature (JFM) and $J_{MAX}$ as predictors of $J_{SUM}$ was calculated (Table 7.4). The resulting explained variance was greater than it had been with temperature alone or with temperature and the October index ($R^2 = 0.89$, n=11). The equation is:

$$J_{SUM} = 222.36 - (86.99 \times JFM) + (8.28 \times JFM^2) + (0.33 \times J_{MAX})$$
### TABLE 7.4
Multiple Regression Analysis

<table>
<thead>
<tr>
<th>DEPENDENT VARIABLE</th>
<th>(J_{\text{SUM}})</th>
</tr>
</thead>
</table>

**VARIABLE(S) ENTERED ON STEP NUMBER**
1. JFM
2. MAX
3. SQJFM

<table>
<thead>
<tr>
<th><strong>MULTIPLE R</strong></th>
<th>0.96006</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>R SQUARE</strong></td>
<td>0.92171</td>
</tr>
<tr>
<td><strong>ADJUSTED R SQUARE</strong></td>
<td>0.88816</td>
</tr>
<tr>
<td><strong>STANDARD ERROR</strong></td>
<td>11.39087</td>
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</tbody>
</table>

**ANALYSIS OF VARIANCE**

<table>
<thead>
<tr>
<th></th>
<th>DF</th>
<th>SUM OF SQUARES</th>
<th>MEAN SQUARE</th>
</tr>
</thead>
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<td>REGRESSION</td>
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<td>10693.69761</td>
<td>3564.56587</td>
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<td>RESIDUAL</td>
<td>7</td>
<td>908.26320</td>
<td>129.75189</td>
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\[F = 27.47217\] \(\text{SIGNIF } F = 0.0003\)

**---------------------------- VARIABLES IN THE EQUATION ---------------------------**

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<th>BETA</th>
<th>T</th>
<th>SIG T</th>
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</thead>
<tbody>
<tr>
<td>JFM</td>
<td>-86.99071</td>
<td>22.94550</td>
<td>-3.92720</td>
<td>-3.791</td>
<td>0.0068</td>
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<tr>
<td>MAX</td>
<td>0.33213</td>
<td>0.12287</td>
<td>0.38045</td>
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<td>0.0305</td>
</tr>
<tr>
<td>SQJFM</td>
<td>8.27973</td>
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<tr>
<td>(CONSTANT)</td>
<td>222.36409</td>
<td>66.55340</td>
<td></td>
<td>3.341</td>
<td>0.0124</td>
</tr>
</tbody>
</table>
The summer juvenile indices were hindcast for the 1972-1982 subset and plotted in Figure 7.7. This fit is better in years of high juvenile abundance than in low years. The curvilinear relationship produced an oscillation that calculated negative values of $J_{\text{SUM}}$ which were plotted as zero. This type of relationship, using $J_{\text{MAX}}$ when JFM was $5.0^\circ C$ or greater, was examined for the 1954-1982 period of collection. The explained variation for the whole time series was not as high as for the subset ($R^2 = 0.80, n=26$), and negative values were still produced. However, negative values were closer to zero and coefficients had smaller magnitudes than those calculated on the 11 year subset. The coefficients were closer to the coefficients estimated using JFM alone and $J_{\text{OCT}}$ as predictors (Appendix 7.9 - Table). As expected, the results were similar when $J_{\text{MAX}}$ indices were adjusted for gear as discussed in Chapter 6 (Appendix 7.10 - Table).

**Relationship Between Wind-Induced Transport, Winter Temperature and Summer Survival**

The inherent difficulties in the juvenile indices discussed above typifies those common to biological data (Austin and Ingham 1978). Therefore, it is desirable to develop a relationship in which physical data are independent variables with a known or understood biological effect, and variables which are readily available and of high quality. Chapter 6 has explained and quantified the relationship between wind-induced transport and juvenile croaker recruitment to the Chesapeake Bay in the fall. The result was a quadratic model which predicts $J_{\text{MAX}}$ based on WINDEX ($W = \text{wind-induced transport index}$):

$$J_{\text{MAX}} = 18.11 + (3.90*W) + (0.86*W^2)$$
Figure 7.7

Actual and hindcast summer juvenile indices, 1972-1982.

Hindcast values (MAX) are calculated from maximum fall juvenile indices and winter temperatures,

$(R^2 = 0.89, n=11)$. 
Summer Young-of-the-Year Croaker

Legend

△ Actual
× Hindcast (MAX)
Therefore, WINDEX was used instead of $J_{\text{MAX}}$ in a multiple regression with winter temperature as a predictor of the summer survival index ($J_{\text{SUM}}$).

Previously, the linear form of the fall index was included in multiple regression equation along with the quadratic and linear of JFM. Thus, the linear form of WINDEX was included in a multiple regression model with the winter temperature parameters (JFM and JFM$^2$) for the 1972-1982 subset. This regression included all the observations, even when JFM temperatures were less than 5.0°C. The explained variance was the same as that for $J_{\text{MAX}}$ ($R^2 = 0.89$, n=11). Negative values still resulted from the fitted regression equation, but the coefficients were of a smaller magnitude (Table 7.5).

However, since $J_{\text{MAX}}$ was fitted as a linear and quadratic function of WINDEX, $J_{\text{SUM}}$ was fitted as a function of JFM and WINDEX to derive the following:

$$J_{\text{SUM}} = 127.75 - (70.84 \times \text{JFM}) + (7.64 \times \text{JFM}^2) + (6.28 \times W) - (0.23 \times W^2)$$

The relationship was highly significant ($F = 27.99$, $p = 0.0005$). It explains 92% of the variation ($R^2 = 0.92$, n=11) in the summer juvenile index as a result of wind-induced transport affecting fall recruitment to the Chesapeake Bay and winter temperatures affecting survival (Table 7.6). The coefficients are in the range of the other relationships, i.e., with smaller magnitudes than with $J_{\text{MAX}}$, and the hindcast negative values for 1981 and 1982 are closer to zero than calculated by previous relationships. The hindcast values and actual values for the subset are shown in Figure 7.8. This is a large number of parameters (5) for the small sample size (11). The relationship may be changed somewhat, as with $J_{\text{MAX}}$, by incorporating the WINDEX from the entire time series with...
**TABLE 7.5**  
Multiple Regression Analysis

<table>
<thead>
<tr>
<th>VARIABLE(S) ENTERED ON STEP NUMBER</th>
<th>JFM</th>
<th>WINDEX</th>
<th>SQJFM</th>
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</thead>
<tbody>
<tr>
<td>MULTIPLE R</td>
<td>0.96235</td>
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<tr>
<td>R SQUARE</td>
<td>0.92613</td>
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<td>ADJUSTED R SQUARE</td>
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**ANALYSIS OF VARIANCE**

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<tr>
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<th>DF</th>
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<th>MEAN SQUARE</th>
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<tbody>
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<td>REGRESSION</td>
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<td>3581.62863</td>
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<td>RESIDUAL</td>
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\[ F = 29.25229 \]  
\[ \text{SIGNIF } F = 0.0002 \]

**------------------ VARIABLES IN THE EQUATION ------------------**

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<th>BETA</th>
<th>T</th>
<th>SIG T</th>
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</thead>
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<tr>
<td>JFM</td>
<td>-63.12727</td>
<td>21.54748</td>
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<td>SQJFM</td>
<td>6.92871</td>
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<td>3.78323</td>
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<td>(CONSTANT)</td>
<td>119.86595</td>
<td>63.90750</td>
<td></td>
<td>1.876</td>
<td>0.1028</td>
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</table>
### TABLE 7.6

**Multiple Regression Analysis**

**DEPENDENT VARIABLE:** $J_{SUM}$

**VARIABLE(S) ENTERED ON STEP NUMBER**

1. JFM  
2. SQWIND  
3. WINDEX  
4. SQJFM  

**MULTIPLE R**  \(0.97424\)

**R SQUARE**  \(0.94913\)

**ADJUSTED R SQUARE**  \(0.91522\)

**STANDARD ERROR**  \(9.91754\)

**ANALYSIS OF VARIANCE**

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<th>DF</th>
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<th>MEAN SQUARE</th>
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</thead>
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**F = 27.98926**  \(\text{SIGNIF F = 0.0005}\)

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<th><strong>BETA</strong></th>
<th><strong>T</strong></th>
<th><strong>SIG T</strong></th>
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</thead>
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<tr>
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<td>0.14152</td>
<td>-0.50742</td>
<td>-1.647</td>
<td>0.1506</td>
</tr>
<tr>
<td>WINDEX</td>
<td>6.27850</td>
<td>2.45449</td>
<td>0.80038</td>
<td>2.558</td>
<td>0.0430</td>
</tr>
<tr>
<td>SQJFM</td>
<td>7.63643</td>
<td>1.64857</td>
<td>4.16966</td>
<td>4.632</td>
<td>0.0036</td>
</tr>
<tr>
<td>(CONSTANT)</td>
<td>127.74867</td>
<td>57.47850</td>
<td></td>
<td>2.223</td>
<td>0.0680</td>
</tr>
</tbody>
</table>
Figure 7.8

Actual and hindcast summer juvenile indices, 1972-1982.

Hindcast values (WIND) are calculated from indices of fall wind-induced transport and winter temperatures ($R^2 = 0.92$, $n=11$).
the JFM temperature. This should be done, however, these values are not presently available.

CONCLUSIONS

Susceptibility of croaker to low temperatures is a widely known fact. The effect has not been previously quantified for croaker, although temperature has been correlated with year-class strength for other species (Dow 1977, Loucks and Sutcliffe 1978, Ulanowitz, Ali, Vivian, Heinle, Richkus and Summers 1982). Hettler and Chester (1982) explained 82% of the variance in pink shrimp populations based on winter temperatures, but did not include a measure of fall recruitment because previous studies had shown no direct relationship between fall and summer abundance.

The research presented here shows that, for croaker, winter temperature is the predominant variable in very cold years, but not in very warm years, and additionally combines an index of fall recruitment with temperature. This improves the explained variation by accounting for the years when year-class strength is not solely dependent upon temperature (Figure 7.9). The relationship established here also shows that, although the temperature is often the major factor determining survival, the magnitude of its effect is related to the initial strength of year-class recruitment. For example, there would be more survivors from an initially large year class that experiences high mortality than from a year class in which initial recruitment was weak but subsequent mortality was high.
Figure 7.9

Sub Model II: Summer juvenile recruitment is the result of fall juvenile recruitment, as determined in Sub Model I, and winter water temperatures.
Potential Reduction

Mechanism

Input

Fall Juvenile Recruitment

Water Temperature

Cold

Survival (Physical)

Summer Juvenile Recruitment

Winter Temperature

Warm

Fall Juvenile Abundance (VIMS Trawl Survey)

Summer Juvenile Abundance (VIMS Trawl Survey)
This study is unique in that it calculates a biological entity from physical factors and identifies biological reasons for the observed results. The basis of the model was a conceptual hypothesis of interactions among wind-induced transport, winter temperature, and young-of-the-year croaker survival. Statistical techniques were used to quantify the interactions. The inputs to Sub Model II (Figure 7.9), temperature and wind, through fall juvenile recruitment, predict year-class strength of $0^+$ croaker.

This model empirically quantifies these relationships, however the physiological mechanism of croaker response to temperature is unknown. Duration and intensity of temperature are incorporated in the averaging processes of this model. Reported collections and observations of juvenile croaker cover a wide range of "cold" temperatures, $7.0^\circ$C (Bearden 1964) to $0.6^\circ$C (Schwartz 1964). Laboratory observations show that a gradual decrease in temperature does not produce distress until $1.5^\circ$C (Joseph 1972). Small croaker are thought to concentrate in deeper, warmer waters as temperatures begin to decline (Wallace 1940, Nelson 1969, Merriner, Kriete and Grant 1976). Juvenile croaker were caught at the Chesapeake Bay mouth during the very cold winters of 1977 and 1978 (Wojcik 1978) and just outside the Bay following a cold period in December 1981 (J. Sypek, VIMS pers. comm.). Collections of dead juveniles have been reported with temperatures below $1.0^\circ - 1.5^\circ$C (Joseph 1972, Wojcik 1978). Other unreported winter kills of croaker may have occurred, but since croaker sink when they die of cold, this could be easily overlooked (Schwartz 1964).

The effect of temperature may be linked to size dependency. Some croaker have been reported moving out of the cold waters, but
perhaps they have to reach a specific size before they are large enough to move, or have to be below a certain size in order to remain and tolerate the cold. Though laboratory experiments have been conducted (Schwartz 1964, Joseph 1972), these questions have not been addressed. Laboratory experiments are needed to test the timing of the response in relation to size, change in temperature, and length of time over which the temperature changes. This type of specific knowledge could be used to refine and establish the relationships presented here.
CHAPTER 8
The Atlantic Croaker Fishery

INTRODUCTION

Atlantic croaker (*Micropogonias undulatus*) is reported on the Atlantic coast from the Gulf of Maine southward (Chao and Musick 1977) but is principally a southern species which extends north of the Chesapeake Bay only under conditions of favorable climate and population size (McHugh 1981). Croaker are extremely variable in abundance, with greatest fluctuations at extremes of their geographic range (McHugh 1977a). Stock fluctuations may be influenced by two types of changes in climate: (1) long term trends in periodicity and (2) interannual variations (Cushing 1975). Biologically influenced density-dependence and fishing pressure also influence variability. Stocks respond to climatic change by increasing in numbers during amelioration and decreasing during climatic deterioration (Cushing 1975). The geographic distribution of croaker landings has shifted noticeably (Wilk 1981) through time; often accompanied by large fluctuation in reported catches (Hildebrand and Schroeder 1928, Haven 1957 and 1959, Massman and Pacheco 1960, Joseph 1972, McHugh 1977a and 1981), which appears to be related to variations in climate and fishing pressure.

In the past when croaker were very abundant, they were commonly thought to be two years old or older when caught commercially.
However, this is not documented in the literature. The purpose of this chapter is to analyze the historic fluctuations of the commercial catch in light of preceding analyses of environmental effects on juvenile croaker survival. Additionally, this analyzes the age structure of the commercial catch and to investigate possible relationships among commercial catch, spawning stock and juvenile recruitment.

Data Sources and Methods


Early references to historic croaker catch records were obtained from the following publications: Higgins and Pearson (1927); Hildebrand and Cable (1930); McHugh (1977a, 1977b); and McHugh and Ginter (1978). Recent (1976–82) data by year and by gear were provided by the Virginia Marine Resource Commission (VMRC) (L. Pritchard pers.
comm.) and North Carolina Department of Natural Resources, Division of Marine Fisheries (NCDNR/DMF) (S. Ross pers. comm.). The total landing statistics include catch from all gears. Trawl landing for both states include only those croaker reported as being taken by otter trawls after 1963. After that time trawler landings (shrimp, finfish) were differentiated in North Carolina. Lengths of croaker caught by specific gears were obtained from the literature and unpublished data (Table 8.1). The principal gears used to catch croaker have been described: pound nets (Higgins and Pearson 1927, Rothchild, Jones and Wilson 1981); gill nets (Rothchild et al. 1981); long haul seines (Higgins and Pearson 1927, DeVries 1980); haul seines (Rothchild et al. 1981); and otter trawls (Pearson 1932). Indices of effort for Chesapeake Bay fisheries have been presented by Rothchild et al. (1981). Croaker catch-per-unit-effort (CPUE) in Virginia (1930-77) was calculated for the main gears, based on number of licenses issued (W. Hoagman pers. comm.) but is not available for other states or other times. A sub-sample consisting of eastern shore Virginia recreational croaker CPUE from 1955 to 1963 was presented by Richards (1965).

Year classes were assigned to length/frequency distributions based on naturally occurring groupings of the data; biology of the croaker as discussed in Chapter 5; and interpretations of data of other authors when available. These length/frequency analyses were not interpreted as absolute and year-to-year variations in growth were considered. Westrheim and Ricker (1978) however have suggested that age-length keys computed from one year's data cannot be applied to reliably another year or to a different population. I believe these data are comparable for my objective, to examine patterns and changes
## TABLE 8.1

**Virginia - North Carolina Commercial Croaker**

<table>
<thead>
<tr>
<th>N</th>
<th>YEAR</th>
<th>GEAR*(ST)</th>
<th>MO.'s SAMP.</th>
<th>MIN. SIZE</th>
<th>MONTH</th>
<th>COM. SIZE</th>
<th># YR CL/MO.</th>
<th>MAX. SIZE</th>
<th>SOURCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>942</td>
<td>1925</td>
<td>P.N.(NC)</td>
<td>6-10</td>
<td>130</td>
<td>OCT</td>
<td>150</td>
<td>2-3</td>
<td>400</td>
<td>Higgins &amp; Pearson (1928)</td>
</tr>
<tr>
<td>1303</td>
<td>1925</td>
<td>L.H.S.(NC)</td>
<td>7-10</td>
<td>150</td>
<td>OCT</td>
<td>190</td>
<td>1-2</td>
<td>420</td>
<td>Higgins &amp; Pearson (1928)</td>
</tr>
<tr>
<td>1946</td>
<td>1930</td>
<td>O.T.(NC)</td>
<td>11-12</td>
<td>200</td>
<td>NOV</td>
<td>240</td>
<td>2</td>
<td>470</td>
<td>Pearson (1932)</td>
</tr>
<tr>
<td>1337</td>
<td>1931</td>
<td>O.T.(NC)</td>
<td>1-4</td>
<td>200</td>
<td>JAN</td>
<td>240</td>
<td>2</td>
<td>480</td>
<td>Pearson (1932)</td>
</tr>
<tr>
<td>678</td>
<td>1949</td>
<td>P.N.(VA)</td>
<td>8-9</td>
<td>170</td>
<td>SEP</td>
<td>200</td>
<td>2</td>
<td>520</td>
<td>Haven(unpub.data)</td>
</tr>
<tr>
<td>289</td>
<td>1949</td>
<td>H.S.(VA)</td>
<td>8-9</td>
<td>160</td>
<td>AUG</td>
<td>180</td>
<td>2-3</td>
<td>470</td>
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<tr>
<td>522</td>
<td>1949</td>
<td>O.T.(VA)</td>
<td>9-10</td>
<td>180</td>
<td>SEP</td>
<td>190</td>
<td>1</td>
<td>480</td>
<td>Haven(unpub.data)</td>
</tr>
<tr>
<td>2572</td>
<td>1950</td>
<td>P.N.(VA)</td>
<td>4-10</td>
<td>120</td>
<td>JUL</td>
<td>160</td>
<td>2-3</td>
<td>480</td>
<td>Haven(unpub.data)</td>
</tr>
<tr>
<td>214</td>
<td>1950</td>
<td>H.S.(VA)</td>
<td>7,9</td>
<td>170</td>
<td>SEP</td>
<td>170</td>
<td>1</td>
<td>300</td>
<td>Haven(unpub.data)</td>
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<td>1728</td>
<td>1950</td>
<td>O.T.(VA)</td>
<td>1,3-4,10</td>
<td>170</td>
<td>JAN</td>
<td>190</td>
<td>1-2</td>
<td>480</td>
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</tr>
<tr>
<td>1885</td>
<td>1951</td>
<td>P.N.(VA)</td>
<td>5-10</td>
<td>120</td>
<td>JUL</td>
<td>160</td>
<td>1-2</td>
<td>460</td>
<td>Haven(unpub.data)</td>
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<tr>
<td>183</td>
<td>1951</td>
<td>H.S.(VA)</td>
<td>6,8</td>
<td>200</td>
<td>JUN</td>
<td>200</td>
<td>1-2</td>
<td>270</td>
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<td>275</td>
<td>1951</td>
<td>O.T.(VA)</td>
<td>10-12</td>
<td>180</td>
<td>NOV</td>
<td>190</td>
<td>1</td>
<td>430</td>
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<td>2536</td>
<td>1952</td>
<td>P.N.(VA)</td>
<td>4-10</td>
<td>150</td>
<td>APR</td>
<td>150</td>
<td>1</td>
<td>470</td>
<td>Haven(unpub.data)</td>
</tr>
<tr>
<td>670</td>
<td>1952</td>
<td>H.S.(VA)</td>
<td>5-8</td>
<td>160</td>
<td>MAY</td>
<td>170</td>
<td>1-2</td>
<td>230</td>
<td>Haven(unpub.data)</td>
</tr>
<tr>
<td>3556</td>
<td>1953</td>
<td>P.N.(VA)</td>
<td>410</td>
<td>150</td>
<td>AUG</td>
<td>170</td>
<td>1-2</td>
<td>480</td>
<td>Haven(unpub.data)</td>
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<tr>
<td>4</td>
<td>1953</td>
<td>P.N.(VA)</td>
<td>7</td>
<td>200</td>
<td>JUL</td>
<td>200</td>
<td>1</td>
<td>280</td>
<td>Reid (1955)</td>
</tr>
<tr>
<td>1271</td>
<td>1953</td>
<td>H.S.(VA)</td>
<td>6-9</td>
<td>160</td>
<td>AUG</td>
<td>180</td>
<td>1-2</td>
<td>430</td>
<td>Haven(unpub.data)</td>
</tr>
<tr>
<td>26</td>
<td>1953</td>
<td>G.N.(VA)</td>
<td>6</td>
<td>230</td>
<td>JUN</td>
<td>230</td>
<td>1</td>
<td>290</td>
<td>Haven(unpub.data)</td>
</tr>
<tr>
<td>5145</td>
<td>1954</td>
<td>P.N.(VA)</td>
<td>410</td>
<td>140</td>
<td>JUL</td>
<td>170</td>
<td>1-2</td>
<td>420</td>
<td>Haven(unpub.data)</td>
</tr>
<tr>
<td>1025</td>
<td>1954</td>
<td>H.S.(VA)</td>
<td>6-8</td>
<td>120</td>
<td>JUN</td>
<td>180</td>
<td>1</td>
<td>340</td>
<td>Haven(unpub.data)</td>
</tr>
<tr>
<td>14</td>
<td>1954</td>
<td>G.N.(VA)</td>
<td>6</td>
<td>200</td>
<td>JUN</td>
<td>250</td>
<td>1</td>
<td>330</td>
<td>Haven(unpub.data)</td>
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<tr>
<td>377</td>
<td>1955</td>
<td>P.N./H.S.(VA)</td>
<td>6-9</td>
<td>140</td>
<td>JUN</td>
<td>190</td>
<td>1-2</td>
<td>350</td>
<td>Haven(unpub.data)</td>
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</table>
### TABLE 8.1 (Continued)

<table>
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<th>N</th>
<th>YEAR</th>
<th>GEAR* (ST)</th>
<th>MO.'s SAMP.</th>
<th>MIN. SIZE</th>
<th>MONTH</th>
<th>COM. SIZE</th>
<th># YR CL/MO.</th>
<th>MAX. SIZE</th>
<th>SOURCE</th>
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<td>2629</td>
<td>1956</td>
<td>P.N. (VA)</td>
<td>5-9</td>
<td>130</td>
<td>JUN</td>
<td>170</td>
<td>1-2</td>
<td>460</td>
<td>Pacheco (1957), Massman &amp; Pacheco (1960)</td>
</tr>
<tr>
<td>?</td>
<td>1957</td>
<td>P.N. (VA)</td>
<td>4-9</td>
<td>170</td>
<td>JUN</td>
<td>200</td>
<td>1-2</td>
<td>410</td>
<td>Massman &amp; Pacheco (1960)</td>
</tr>
<tr>
<td>?</td>
<td>1958</td>
<td>P.N. (VA)</td>
<td>4-9</td>
<td>170</td>
<td>JUN</td>
<td>200</td>
<td>1-2</td>
<td>500</td>
<td>Massman &amp; Pacheco (1960)</td>
</tr>
<tr>
<td>2230</td>
<td>1978</td>
<td>P.N./L.H.S. (NC)</td>
<td>4-10</td>
<td>140</td>
<td>AUG</td>
<td>170</td>
<td>1-2</td>
<td>430</td>
<td>Scholar (1979)</td>
</tr>
<tr>
<td>102</td>
<td>1978</td>
<td>L.H.S. (NC)</td>
<td>10</td>
<td>110</td>
<td>OCT</td>
<td>10c</td>
<td>1</td>
<td>380</td>
<td>Norcross</td>
</tr>
<tr>
<td>5581</td>
<td>1979</td>
<td>L.H.S. (NC)</td>
<td>4-10</td>
<td>100</td>
<td>JUL</td>
<td>150</td>
<td>1-2</td>
<td>420</td>
<td>DeVries (1982)</td>
</tr>
<tr>
<td>16</td>
<td>1981</td>
<td>L.H.S. (NC)</td>
<td>5</td>
<td>230</td>
<td>JUN</td>
<td>230c</td>
<td>2</td>
<td>320</td>
<td>Norcross</td>
</tr>
<tr>
<td>30</td>
<td>1981</td>
<td>P.N. (VA)</td>
<td>5-6</td>
<td>220</td>
<td>MAY</td>
<td>220c</td>
<td>1</td>
<td>300</td>
<td>Norcross</td>
</tr>
<tr>
<td>313</td>
<td>1982</td>
<td>P.N. (VA)</td>
<td>9</td>
<td>170</td>
<td>SEP</td>
<td>170</td>
<td>2</td>
<td>310</td>
<td>Norcross</td>
</tr>
</tbody>
</table>

*GEAR:  

P.N. = Pound Net  

L.H.S. = Long Haul Sieve  

O.T. = Otter Trawl  

G.N. = Gill Net

\(c\) = Sampled commercially, may be biased upward to market size
over time. I assigned a spawning date of October. White and Chittenden (1977) discussed this and chose 15 October as the mid-point of the croaker spawning season and the assigned birth date. The monthly data used October as the month when year class designations are changed.

Length/frequency intervals were calculated in 10 mm intervals, 0–9 mm, 10–19 mm, 20–29 mm, etc. Composite length/frequencies show both commercial catch length distributions and research juvenile length distributions. The latter facilitates the interpretation of the commercial data and the identification of year classes within the commercial data by providing continuity where commercial data are sparse. In order to use the juvenile length data presented by Hildebrand and Cable (1930), I recalculated all composite length/frequencies according to their methods. Numbers of croaker at designated length intervals were totaled for the months January through December and not weighted by total catch numbers nor by number of months sampled. Though not as accurate as comparison of individual years, this method has advantages in that it allows data about which little information is available to be used. This increases the sample size yielding smoother, more easily interpretable curves. Since my intention is to make comparisons over 55 years, and not year-to-year, no compensation for gear was considered necessary or appropriate. The sources of the data for the composite length/frequencies are detailed in Table 8.2.

Long range and interannual temperature trends and anomalies were examined from the longest appropriate time series of data available. Providence, Rhode Island annual air temperatures were used as an index of long-term trends in this century, a time scale comparable
### TABLE 8.2

Data For Composite Length/Frequencies of Croaker

<table>
<thead>
<tr>
<th>Sample</th>
<th>Dates</th>
<th>Area</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pound nets and long haul seines</td>
<td>June-October 1925</td>
<td>Pamlico Sound, N.C.</td>
<td>Higgins and Pearson (1927)</td>
</tr>
<tr>
<td>Juveniles</td>
<td>Spring 1926 to March 1930</td>
<td>Beaufort Harbor, N.C. including Beaufort Inlet, Atlantic Ocean outside the Inlet, Bogue and Core Sounds.</td>
<td>Hildebrand and Cable (1930)</td>
</tr>
<tr>
<td>Otter trawls</td>
<td>September-April 1949-1951</td>
<td>Atlantic Ocean off VA and N.C.</td>
<td>Haven (unpub. data)</td>
</tr>
<tr>
<td>Pound nets, haul seines and gill nets</td>
<td>April-October 1949-1955</td>
<td>York River and Lower Chesapeake Bay, VA</td>
<td>Haven (unpub. data)</td>
</tr>
<tr>
<td>Juveniles</td>
<td>March 1952 to May 1954</td>
<td>York River, VA</td>
<td>Haven (1957)</td>
</tr>
</tbody>
</table>
to that of commercial croaker data. Likewise, Baltimore Harbor winter
water temperatures (Harris and Van Engel 1981) were used as an indicator
of year-to-year variability over a similar span of time. Annual
Norfolk, Virginia air temperatures were used to represent long and
short term changes over time in the southern Mid Atlantic Bight. Annual
temperatures were obtained from NCDC Climatological Data Summaries.

Correlations were determined and graphs were plotted using
Business Graphics (1982) software on an Apple IIe computer, and SPSS
(Statistical Package for the Social Sciences) (Hall and Nie 1981) on a
Prime 850.

RESULTS AND DISCUSSION

Analysis of Historic Catch

A graph of commercial catch of croaker from Massachusetts to
Florida (Figure 8.1) reveals that historically this sub-tropical species
has been primarily landed in Virginia. The long-range pattern of
increasing croaker catch the first half of this century seems to follow
the warming trend seen in the annual temperature at Providence, R.I.
(Figure 8.2) for the same time period. Although total landings by state
are not available yearly prior to 1929, the few years that are available
are plotted and points connected linearly (Figure 8.1). It is clear
that the commercial catch of croaker increased dramatically during this
time (Welsh and Breder 1923), but may be overestimated between 1908 and
1920. The Buchanan Brothers fishery in the Chesapeake Bay showed an
upward trend from 1908 to 1916 with a decline after that (Hildebrand and
Schroeder 1928) following the coldest winters on record, 1917-1918
Figure 8.1

Total commercial catch of croaker, 1889 to 1982, on the U. S. Atlantic coast from Massachusetts to Florida by state or group of states reporting landings.
Figure 8.2

Annual air temperatures (°F), 1905-1980, at Providence, Rhode Island airport indicate long-term climatic changes on the east coast of the U.S.A. Smooth line is 7-point moving average.
Chapter 7 documents the effect of cold winter temperatures on juvenile croaker recruitment. The Buchanan Brothers data further show the fishery starting to increase again in 1920, so the linear approximation between 1920 and 1925 may be reasonably accurate. Values for North Carolina in 1923 (Higgins and Pearson 1927) and 1927 and New Jersey in 1926 (Hildebrand and Cable 1930) were plotted based on these estimates. The decrease in catch from 1925 to 1929 appears to agree with the long range temperature trend of the cold winters of the mid-twenties, especially 1926 (Figure 8.3). The poor recruitment caused by these temperatures, together with the economic depression which caused a sharp decline in prices (McHugh 1977b), probably caused the decreased croaker catch at the beginning of the thirties. The warmest winter on record at Baltimore Harbor, 1932, coupled with an upward trend in long-range temperatures (Figures 8.2 and 8.4) resulted in a 300% increase in total landings from 1931 to 1938. This increase persisted despite the winters of 1934, 1935 and 1936, which had average January-February temperatures less than 2.5°C at Baltimore Harbor. Why this three year period, which should have, but did not, produce reduced catch, is unknown.

A climatic fluctuation induces relocation of a marine community away from its normal geographic range towards the more environmentally appropriate one (Walsh 1978). The climatic warming trend of the first half of the 20th century (Balling and Lawson 1982) appears to be linked to the northward range extension of adult croaker. The warm period during the thirties and forties (Cushing 1975), shown by the deviations from global mean surface air temperatures (Figure 8.4), supported a fishery for cod (Gadus morhua) off Greenland (Cushing and
Figure 8.3

Baltimore Harbor, Maryland (January-February average) water temperatures (°C), 1917-1978, indicate year-to-year variation in the Chesapeake Bay-Mid Atlantic Bight region over a long time period. Smooth line is 7-point moving average.
BALTIMORE HARBOR WATER TEMPERATURE
Figure 8.4

Deviations from the global mean surface air temperature, 1880 and 1969, indicate world-wide long-term temperature trends (from Cushing and Dickson 1976).
N. Hemisphere only

Yrs.

0.50

0.40

0.30

0.20

0.10

0.00

1870 80 90 1900 10 20 30 40 50 60 70

Years
Dickson 1976). Croaker are not mentioned as a commercially important species in New York or New Jersey in the 1880's (Earll 1887 and Mather 1887 as cited by McHugh 1977a). By the 1930's, adult and juvenile croaker were considered irregularly common in New York waters in the summer and fall (Nichols and Breder 1934). Croaker landings were first reported as far north as Delaware in 1880 (McHugh 1981), New Jersey in 1900 (McHugh and Ginter 1978) and New York in 1920 (McHugh 1977a). Recent commercial landings in Connecticut in 1935 show croaker landed there.

A cold winter in 1940 lowered recruitment as World War II decreased fishing effort by trawlers. These may have caused the decline in croaker landings seen from 1942-44 which was followed, in 1945, by the largest total landings of croaker in history, 68 million pounds. The absence of croaker landings since 1940 in Massachusetts and since 1945 in New York does not appear to have been a result of stock range contraction due to unfavorable conditions. The most pronounced long-term temperature increase was in the 1940's, as was the highest record catch. This increase in temperature, stock, and range may even have supported spawning as far north as Delaware Bay, as discussed in Chapter 4. Though this was undoubtedly a period of unusual abundance, it was also one of heavy exploitation (Perlmutter 1959, McHugh 1977a). The year of the greatest catch was not the year of greatest abundance (Joseph 1972), shown by the CPUE of pound nets and haul seines (Figure 8.5). This decline in northern commercial catch is paralleled by Virginia; but while the croaker fishery in Virginia recovered ten years later, it did not come back in the northern states. It is most likely that fishing pressure decreased the stock well below that indicated
Figure 8.5

Catch per unit effort for: Virginia eastern shore recreational catch (after Richards 1965), and Virginia commercial pound nets, haul seines and anchor gill nets.
by increased landings and removed Massachusetts and New York from the fishery at a time of apparent peak climatic and stock conditions.

This increased fishing pressure on adults was reducing the stock as the cold winters, as discussed in Chapter 7, of 1943, '45 and '48 were reducing recruits. Warm winters in 1947, '49, '50 and '53, aided rapid rebuilding of the stock to a total catch of 19 million pounds in 1958. The cold winters of 1958 and 1959, tapered somewhat by a warm winter in 1957, caused a further decline.

Recreational catches on the eastern shore of Virginia fluctuated similarly during this time with 7640 croakers caught in 1956, but only 112 landed from 1959-1962 (Richards 1965). Figure 8.5 shows the peak CPUE's by gear for both anglers and commercial gear. The combination of increased effort, sharp downward climatic trend and a series of cold winters, with no average January-February temperature at Baltimore Harbor greater than 4°C from 1958 to 1971 (Figure 8.3), held the total Atlantic catch at less than 5 million pounds from 1961 through 1974.

New Jersey and Delaware had been catching small numbers of croaker until this time, but they dropped out of the fishery in the early sixties. It is likely that the decline of the stock together with the climatic deterioration limited the range of the croaker to south of Delaware. Although Wilk (1981) shows a shift in croaker landings from the Chesapeake to the South Atlantic Bight, a southern progression did not follow this contraction of range towards the south. Combined South Carolina, Georgia and Florida landings are so low that, compared with the rest of the east coast, they appear only as a slightly thicker line on the graph above the North Carolina values (Figure 8.1). The largest
catch for these three states was 337,000 pounds in 1966, 12% of the total east coast landings. This is the only deviation from the superimposed line which represents these states. The next highest year of combined landings, 1955, was only 1.6% of the total catch. Florida landings ranged from less than 500 pounds in 1940 to 331,000 pounds in 1966, averaging about 100,000 pounds annually. The combined South Carolina and Georgia catch is even less, ranging from zero in 1968 to 112,000 in 1945, 0.18% of the record total landings that year. Therefore, the shift from the Chesapeake to the South Atlantic almost entirely represents increases in North Carolina landings since 1957 as shown in Figure 8.1.

In the 1970's there was a resurgence in commercial landings of croaker (Figure 8.1). Although not in the same quantity as in the 1940's, croaker were again landed in New Jersey starting in 1970 and in Delaware in 1974. A small number were even landed in New York in 1973. In citing fishes uncommon to the New Jersey coast, Milstein and Thomas (1976) purposely left croaker out because, though absent in 1972, croaker was quite common in 1973. Young-of-the-year were found once again successfully overwintering in Maryland waters in the mid-1970's (B. Florence, Maryland Department of Natural Resources (MDDNR) pers. comm.). Juveniles were reported in Delaware (S. Beck, Ichthyological Associates pers. comm., F. Hughes, Delmarva Power and Light pers. comm.) and New Jersey (P. Himchack, New Jersey Department of Environmental Protection pers. comm.) estuaries. The combination of warm winters and an interannual increase in temperature (Figures 8.2 and 8.3) in the 1970's resulted in successful year classes and subsequently in commercial catch. Large croaker from the successful 1974 year class
were caught as late as 1980, setting a Maryland Sport Fishing Tournament citation record (Boon 1981). At the same time that the croaker was once again expanding northward, catches in North Carolina were increasing well beyond what was previously recorded for that state. The result was that North Carolina usurped Virginia's place in croaker dominance. The short-lived warming trend and accompanying increased fishing effort, were followed by a fall in landings at the end of the 1970's. North Carolina still predominates, however.

The Geographic Center of the Fishery

Most of the Mid-Atlantic Bight croaker landings come from the Chesapeake Bay (McHugh and Ginter 1978) and discussion of that fishery usually considers Virginia and Maryland together (McHugh 1977b, Wilk 1981, Rothchild et al. 1981). Croaker ranked second in pounds (13,039,795) and dollars ($361,479) of finfish taken in the Chesapeake Bay, Virginia in 1920 (Hildebrand and Schroeder 1928) compared to a 1977 rank of first (7,044,189 pounds, $697,803) (Zaborski 1979). Although detailed effort data are not available for the Chesapeake Bay, time series of relative fluctuation of effort since 1934 are presented for the Bay as a whole (Figure 8.6).

An analysis of the percentage of combined Virginia-Maryland-North Carolina catch, by state, reveals that Maryland's highest contribution was 23% in 1951 and has been below 10% since 1956 (Figure 8.7). The Maryland catch contribution was less than both Virginia and North Carolina in all years except 1950 when it approximately equalled the catch of North Carolina. Though there are no quantitative recreational statistics, it has been shown that Maryland's recreational
Figure 8.6
Relative fluctuation of effort for four principal gears used within the Chesapeake Bay (from Rothchild et al. 1981).
Figure 8.7

Total Virginia, North Carolina and Maryland croaker catch, 1934, 1936-40, 1945, and 1950-79, divided by percent landed in each state.
croaker catch was 12 times its commercial catch in 1979 (Williams, Spier, Early and Smith 1982). Since the 1974 New Jersey to North Carolina recreational catch was four times the comparable commercial catch (McHugh 1977a), it is likely that Virginia and North Carolina recreational catches are also significantly larger than their commercial catches. The difference between the Virginia and Maryland commercial landings may be primarily due to large croaker catches at the Bay mouth in Virginia as the croaker concentrate to migrate inward in the spring and outward in the fall. Also, Maryland is further north and colder, thus in the years of reduced range and stock size, croaker are not as likely to migrate into Maryland waters.

Figure 8.7 emphasizes the recent dramatic shift in croaker landings from Virginia to North Carolina. This representation, together with the overall catch statistics shown in Figure 8.1 and the fact that 82% of the Atlantic coast recreational landings are in these two states (Wilk 1981), points out that the croaker is basically a Virginia-North Carolina stock. The overall croaker catch is dominated by Virginia’s landings, with total fluctuations paralleling those of the Virginia catch (Figure 8.1) until the record low catches in the 1960’s. At that time the pattern shifted to one of North Carolina catch predominance. The Virginia and North Carolina croaker fisheries are detailed in Appendix 8.1 - Text

To investigate croaker distribution trends and causes I assumed that fish caught north of Cape Hatteras were landed in Virginia, and south, in North Carolina. As noted above, the contraction of the croaker range is related to temperature trends. The annual Norfolk, Virginia temperature is shown in Figure 8.8. In Figure 8.9, it is
Figure 8.8

Annual air temperatures (°F), 1931-1982, at Norfolk, Virginia airport, indicate long-term climate fluctuations in the Mid-Atlantic Bight. Smooth line is 7-point moving average.
Figure 8.9

Annual air temperature at Norfolk, Virginia correlated with the percent landed in VNRXNINO AU BEORWB Virginia-North Carolina otter trawl landings, ($r = 0.61$, $n=33$).
NORFOLK ANNUAL AIR TEMP - DEG F
correlated with the percent of the combined Virginia-North Carolina croaker catch that was landed in Virginia. The positive correlation ($r = 0.61$) shown here indicates that croaker are farther north in warm years, and south in cool years. Subtropical species were reported as far north as New England in 1949 (Arnold 1951), an exceptionally warm year (Figures 8.2, 8.3 and 8.4). Note that the 1950's were the years of highest landings in Virginia and are represented by the points above the line. Boreal influence increased in the early 1960's, as indicated by a southerly distribution of mackerel (*Scomber scombrus*) in the 1960's and 1970's (Coombs and Mitchell 1981). Temperatures were warmer in the 1950's (McHugh 1976) than in the 1960's (Colton 1972). However, these landings also rose because it was prior to Wanchese, N.C. being fully exploited as landing area for commercial trawlers in the 1970's (S. Ross pers. comm.), resulting in disproportionately large numbers of trawlers were landing in Hampton (J. Davis, SCMRRC pers. comm.).

In the 1960's, with the historic low abundance of croaker, fewer large croaker. The cold temperatures during that period contracted the croaker range southward. The result was that fewer trawlers from Virginia fished for croaker. Apparently renewed interest in offshore fisheries, which increased the number of trawlers landing in Virginia by 160% from 1970 to 1978 (Zaborski 1979), is attributable to increased abundance as well as the warm years of the mid-1970's expanding the range of croaker. The trouble keeping Oregon Inlet open to trawlers for the last two to three years has forced more landings in Hampton, Virginia (M. Oesterling, VIMS pers. comm.), but has not significantly raised the percent of croaker landed in Virginia in 1980-1982 compared to the combined Virginia-North Carolina catch (Figure 8.9)
supporting the correlation between croaker landing place and temperature. These landings are for calendar years and therefore include the spring migration one year together with the fall migration the next year. Because of multiple assumptions due to lack of exact data, this correlation can only be interpreted as an indicator of croaker distribution on an interannual time scale.

**Age Composition**

To evaluate the impact of fishing on the croaker stock, composition as well as abundance of catch must be considered. A breakdown of catch by gear for individual years, from published sources and collections D. Haven (unpub. data.) and I have made, is shown in Table 8.1. Both size at first entry and common size when first recruited to the fishery seem to be a factor of gear type. With few exceptions, there is a progressive increase in size at entry from long haul seine through pound net, haul seine, otter trawl to gill net. The 1949 through 1953 total Virginia gill net catch of croaker was only 4% of the 1944 catch. This indicates a lack of older fish, since size caught by gill nets is generally larger (Table 8.1). As the croaker abundance decreased at this time, the percent caught by otter trawls and haul seines rose while the percent caught by pound nets, which normally catch smaller fish, declined (Perlmutter 1959), indicating weak recruitment. In recent years the upper limit of the catch has been markedly decreased as fewer larger fish are now available. Only 1 or 2 year classes now make up the majority of the catches.

To investigate long range trends which may be masked by interannual variability and to investigate catch composition in more
detail, 3 to 6 year composite catches of juvenile (research) and adult (commercial) length/frequencies at approximately 25-year intervals are plotted (Figures 8.10, 8.11 and 8.12). Sources and gear are detailed for each in the Methods sections, but in general, research samples were from bottom trawls, summer commercial samples were from pound nets, long and common haul seines and/or gill nets, while winter commercial samples were from otter trawls. Data shown for 1925-31 and 1978-80 were collected in and around Pamlico Sound, North Carolina and 1949-55 in the York River, Virginia.

Though the research and commercial gear differed over time, the susceptibility is demonstrated by size ranges collected. These data are comparable for the purpose of showing trends in age class composition due to gear efficiency and applicability. Protracted croaker spawning results in continuous recruitment and overlapping age/size classes. Probable age classes have been designated.

Both similarities and differences are found when comparing these three sets of length/frequencies. Research collections of juveniles in the 1920's (Figure 8.10) show little apparent monthly increase in size, which is indicative of continuous recruitment. The collections in the 1950's (Figure 8.11) and 1970's (Figure 8.12) had larger juvenile modal sizes and increased growth, with the catches in Virginia being slightly larger than those in North Carolina. These may be real differences attributed to earlier movement into the Bay or faster growth rates in Virginia, or may be a result of the sampling. The 1920's data collected at Beaufort Inlet is expected to have smaller juveniles moving inward than either the 1970's samples within Pamlico Sound and its tributaries or the 1950's samples, still farther from the
Figure 8.10

Composite length/frequencies from research and commercial samples 1925-31 (after Higgins and Pearson 1927, Hildebrand and Cable 1930, Pearson 1932).
Figure 8.11

Composite length/frequencies from research and commercial samples 1949-55 (Haven unpub. data).
Figure 8.12

ocean, in the York River, Virginia. The inshore, upbay, down-bay, out-bay pattern (Haven 1957), discussed in Chapters 3 and 6 also explains the decreased catches in Virginia in August and September as one year class moves out of the rivers before another comes in to replace it.

There are no I+ croaker caught in research trawls inside the Chesapeake Bay in the winter in Virginia 1949-55 (Figure 8.11) as compared with the North Carolina catches 1925-31 (Figure 8.10) and 1978-80 (Figure 8.12) though that size is susceptible to the gear. This may be a result of croaker adapting to the colder Virginia winters by migrating out of the Chesapeake Bay. Juvenile length/frequency analysis in Chapter 5 reveals no I+ croaker remain within the Chesapeake Bay over the winter except during exceptionally warm years such as 1974. The out-Bay migration of I+ fish continues through December in the Chesapeake, and possibly later in North Carolina as indicated by the apparent decrease in modal size of year class I, December to January in the 1930's and October to November in the 1970's. However, most of the I+ fish leave in the fall, as evidenced by the closure of the North Carolina long-haul fishery in October.

Comparisons and contrasts are also apparent among the commercial catches at these times. Though the same age classes were being fished at all three periods, the periods differed in proportions of abundance, especially of larger fish. Few fish larger than 350 mm were taken in the 1970's, but it was not uncommon to catch fish greater than 400 mm in the 1950's and 1930's. However, there was a distinct reduction in percentage of III+ fish taken by the winter trawl fishery from 1925-31 (Figure 8.10) to 1949-55 (Figure 8.11). This could be partially attributable to the possible sampling bias toward larger fish.
as noted by Pearson (1932). During all time periods, in the summer the fisheries essentially fish two year classes, $I^+$ and $II^+$. As the summer progresses, reduction in catch of larger fish is found due to fishing pressure and out-bay migration.

One year class ($II$) primarily was fished in the 1920's, younger fish ($I$) were recruited to the fishery during the 1950's and comprised a significant portion of the October catch during the 1970's. Size at first entry into the commercial catch appeared to decrease over time (for gear specific sizes see Table 8.1). The 1920's and 1950's entry size averaged about 150 mm, though being slightly smaller in June and slightly larger for the winter trawl of the earlier period. Fish 120 mm were routinely recruited to the fishery in the 1930's from July through October as larger fish were no longer available.

Significant changes in the fishery have occurred over 55 years. One has been the reduced size at recruitment and the increased percentage of catch that has not yet reached sexual maturity. Croaker are thought to mature at age $II$ as they first migrate onto the shelf to spawn (Diaz 1982). Thus all croaker within the bays and sounds age $I^+$ or less have probably never spawned. In the 1920's (Figure 8.10) immature $I^+$ and $II$ (October) croaker were taken in the sound, though they only comprised a substantial portion of the catch in June and October. The winter trawl fishery appeared to fish few that were immature. A larger proportion of the croaker were immature at capture in the 1950's (Figure 8.11), with $0^+$ fish recruited to the fishery in September and immature $I$ and $II$ contributing the majority of the October catch. Though the winter trawl fishery caught many mature two-year ($II^+$) olds, it also took many immature one-year olds ($I^+$), unlike the
1920's. In the 1970's (Figure 8.12), few mature fish were caught. Age II+ predominated in April only, though contributed a significant proportion of the May catch. However, in 1980, the two-year old spring component was absent from these catches (Ross and Carpenter 1983b).

From June through August the majority of the fish caught were immature I+ (DeVries 1980). Recruitment of 0+ croaker began in July, contributing the bulk of the catch by September and October. No winter trawl data are available for this time to allow comparison, but it is assumed, based on the 1950's commercial data and research data (S. Wilk, NOAA/NMFS/Sandy Hook Lab unpub. data) that the trawl fishery is presently fishing the immature I+ and mature II+ and older croaker on the shelf. Sholar (1979) presents preliminary aging data from 444 croaker taken by the 1978 long haul seine and pound net fisheries. His results show age/percent distributions as follows: 0+, 1.4%; I+, 60%; II+, 34.2%; III+, 4.3%. These results depict the fish as older than I have described. Since he did not specify date of collection and assignment of birthday, and he concluded better aging techniques are needed, my interpretations may not be inconsistent with his results.

Size at maturity varies, but, in the fall, mean size at 100% maturity is 260 mm. Because of varying spawning times and growth rates, this size is difficult to apply. While the size of the individual fish cannot decrease as it appears to in the winter (Figures 8.10, 8.11 and 8.12), the modal size of the cohort decreases as its larger members are fished out. Thus it is difficult to separate the smaller mature II+ and the larger immature I+ fish by these lengths. I assigned 260 mm, the length of 100% maturity when the summer winds cease in mid to late August, as the division between immature and mature. This length at
100% maturity was chosen because the catches were all inside the bays and sounds, previous to the out-bay migration to spawn. Even though some of these fish are old enough or large enough to spawn for the first time, since they were caught in the Bay, they had not yet had the opportunity to spawn. The percent of the commercial catch that was immature, i.e., less than 260 mm (10.2 inches) was calculated June through October. The percent of immature croaker caught commercially within-the-bay rose from 61.0% in the 1920's, to 69.2% in the 1950's, and increased to 85.7% in the 1970's (Figures 8.10, 8.11 and 8.12). The result is that few croaker survive to migrate out onto the shelf to spawn and that a small percentage of the biomass reported as commercial catch actually contributes to the spawning stock.

CONCLUSIONS

Climatic change has shifted the distribution of the croaker. This affects the croaker by reducing the area available to it and also affects the fishermen by making the croaker less accessible to them, i.e., with the southward movement, croaker are less available to Virginia gear. The cold winter temperatures in the Chesapeake Bay since 1977 have severely reduced juvenile recruitment resulting in both North Carolina and Virginia relying on recruitment from North Carolina. North Carolina has changed its method of reporting landings by including landings of croaker from trawlers other than fish trawls. These fish were caught previously, but not reported, thus appearing to increase North Carolina landings in recent years. Additionally, since the record low catches of the late 1960's and early 1970's, effort has increased in
North Carolina. From 1971 to 1975, both catch and effort of long haul seine crews increased substantially (DeVries 1980). Since the dramatic rise in croaker landings began in North Carolina in 1973, an average of 46% of each year’s landings have been caught in haul seines (DeVries and Ross 1983). Besides increasing landings in North Carolina, this increased effort also decreased numbers of fish surviving to migrate to the Chesapeake the following summer, and reduced those surviving to spawning age.

Since fishing decreases the number of age classes present, one or two bad reproductive years has greater effect on the size of a fished population than an unfished populations (Botsford 1981). Because of the environmental vulnerability of larvae on the shelf (Chapters 4 and 6) and juveniles in the estuaries (Chapter 7), year-class strength fluctuates markedly in croaker. It is these fluctuations, together with fishing pressure, that caused the historic variability in croaker catch. Since populations being harvested for sustained yield take longer to recover from environmentally imposed disturbances (Beddington and May 1977), croaker should be managed according to the success of each year class.

Sub Model III (Figure 8.13) concisely represents the importance of year-class strength in croaker. Overfishing a weak year class will potentially reduce spawning, referred to as growth overfishing (when fishing mortality takes small fish, never giving them a chance to mature). This is represented in the first part of Sub Model III. Several weak year classes in succession increases the fishing pressure on each individual year class, shown in the second part of Sub Model III (Figure 8.13), further reducing spawning potential.
Figure 8.13

Sub Model III: Croaker commercial catch is dependent upon individual year-class strength and age composition of adult stock.
Conversely, fishing prespawners, $0^+$ and $1^+$, is acceptable when year classes are strong. A flexible management plan could contend with this.

It may be that year-class strength within the Chesapeake Bay makes the difference between an inadequate and a flourishing fishery for croaker. Successful recruitment in the Bay is dependent upon time of the summer wind cessation and climate conditions governing spawning area over a period of years, successful transport of larvae into the Bay, and warm winter temperatures. Recruitment is not stable. However, there are fewer environmental perturbations affecting North Carolina recruits, hence it is more consistent. North Carolina recruits probably migrate north and contribute to the summer croaker fishery in the Chesapeake Bay. Therefore, in years of poor recruitment in the Bay, the croaker from North Carolina may be the sole source for the fishery.

There is no size limit for croaker in North Carolina. The limit in Virginia is 8 inches (200 mm). According to the investigation of length at maturity in Chapter 4.1, 50% of the 200 mm croaker will be mature in years of early summer wind cessation (Figure 4.2.6). The percent drops as the wind cessation is delayed. Also, according to the length/frequency analysis here based on size at 100% maturity within the Bay (260 mm), approximately 85% of the fish caught inside the estuaries have never spawned (Figure 8.14). Overfishing is shown to be an important factor affecting stock size when recruitment has been poor, Sub Model III (Figure 8.13). Therefore, I propose that the year-class strength of croaker be assessed yearly and that the restrictions of croaker be adjusted according to those findings. When the year-class strength, as I have determined it in Chapter 7 is less than 1.00, croaker should not be legally caught unless they are 10 inches (260 mm).
Figure 8.14

Length of croaker at 50% and 100% maturity in relation to time of summer wind cessation, 8 and 10 inch size limits indicated.
If the index is between 1.00 and 20.00, they could be fished according to the present law, at 8 inches (200 mm). If the year strength is greater than 20.00, there is no need for restrictions.

This is not as indulgent as it first appears when one considers North Carolina is presently fishing under the last suggestion and that croaker under 8 inches are marketed in Virginia. The objective is to manage the stock so that it will not be decreased below a size such that if an unfavorable environmental incident were to occur, the stock would be negatively affected. The stock should be managed so that a crash will not result.
CHAPTER 9

Spawner-Recruit Relationship:
Density-Dependence versus Density-Independence

INTRODUCTION

Is there a relationship between spawning stock size and recruitment? Over the history of fisheries biology, this has been investigated and debated as exemplified by Clark and Marr's (1955) oft-quoted paper on the California sardine fishery. Parent stock size must have an effect, though it may be masked, even when recruitment is heavily dependent on environmental factors (Parrish and MacCall 1978). The search for relationships between stock size and recruitment, a major research directive for years, has ignored other factors (Sharp 1980) such as density-independent effects of the physical environment.

Density-dependence, though generally presumed, can be difficult to demonstrate (MacCall 1980). Two kinds of density-dependence are theorized: adult-larval interactions and larval-larval interactions (Hunter 1982). Larval mortality by predation manifests as cannibalism or as an increase in predators in relation to an increase in larval density. Density-dependent larval mortality may also be caused by starvation through intra- or interspecific competition for food or through expansion of a large stock for spawning in less than optimal
areas where larval forage is low (Hunter 1982). Large geographic areas with adequate food sources, require stability of food concentrations for successful larval recruitment; limited, relatively stable areas need a suitable and consistent source of food (Hunter 1976).

Recruitment is not dependent upon spawning stock size in all species. There appears to always be enough herring larvae produced on Georges Bank for a strong year class if conditions are favorable, but recruitment success is not constant (Lough, Bolz, Grosslein, and Potter 1981). High year-to-year variability results from the compounded effect of variation in environment and in parent stock size (Garrod and Colebrook 1978).

In a stock recruitment curve, the effect of the environment is shown in the variability of recruitment, e.g. blue crab, Callinectes sapidus (Applegate 1983), and the effect of fishing is shown in the state of the stock, e.g. cod, Gadus morhua (Cushing and Harris 1973). Shorter-lived, density-independent species are subject to rapid fluctuations in abundance as compared to more stable, long-lived, density-dependent species (Cushing 1971). The latter type are thus less vulnerable to climatic change (Cushing and Harris 1973). Therefore less fecund, less stable populations are easily damaged by overfishing, as shown for clupeoids (Cushing 1971). In a population comprised of few year classes like croaker, poor larval or juvenile survival due to environmental effects decreases the reproductive potential. Since fishing decreases, the number of age classes present, poor recruitment has a greater effect on a fished population than on an unfished one. Thus fishing increases the effect of the random environment on population (Botsford 1981).
METHODS AND RESULTS

Density-Dependence

The logarithm of recruitment is plotted against the logarithm of stock and gives a slope (b) that is an index of density-dependence but does not estimate density-dependent mortality (Cushing 1971). If \( b = 1.0 \) to \( 0.5 \), the relationship is proportionally density-dependent. If \( b = 0 \), recruitment is independent of the stock. If \( b = -0.5 \) to \( -1.0 \), recruitment is also density-dependent, though inversely proportional to stock size (Cushing and Harris 1973). The value of this slope is related to the position on stock-recruitment curve.

Logarithms of larval and adult abundances of croaker collected simultaneously on NMFS/MARMAP cruises (see Methods, Chapters 4.2 and 6) were used as indices of recruitment and stock size respectively. The slope of the regression line (\( b = 0.463, n=7 \)), is the index of density-dependence (Figure 9.1). There is not a strong density-dependent relationship. This relationship was not significantly improved when the sample size was reduced to five and adults were adjusted for percent maturity as discussed in Chapter 4.2. This density-dependence index assumes the environment has had no effect. However, in reality, such an instantaneous measurement of stock and recruitment is usually impossible.

This relationship also was tested after croaker recruited into the Chesapeake Bay, i.e., after the effects wind-induced transport, as discussed in Chapter 6, were considered. The October young-of-the-year VIMS trawl survey value was used as an index of recruitment into the estuary in the fall. The total yearly Virginia-North Carolina croaker
Figure 9.1

The relationship between the log of adult and log of larval abundances of croaker collected simultaneously on MARMAP cruises. The slope of the regression line, $b = 0.463$, is the index of density-dependence.
Test of Crocker Density-Dependence
landings were used as an index of stock size. The logarithm of the index of recruitment (ordinate) was regressed on the logarithm of the index of stock size (abscissa) in Figure 9.2. The slope of this fit, and therefore the resulting index of density-dependence is 0.800. The slope \( b = 0.800 \) appears to be a horizontal line in Figure 9.2 because the ordinal scale is logarithmic, ranging from 0.1 to 1000.

The index of density-dependence was calculated again using the April-September young-of-the-year index of juvenile recruitment. Use of the summer index measures the effect of stock size on recruitment after winter temperature has affected survival, as discussed in Chapter 7. The slope, \( b = 0.388 \) (Figure 9.3), is less than that of the previous indices. Thus, initial recruitment is very weakly density-dependent, but year-class strength is primarily density-independent.

**Spawner-Recruit Relationship**

Length/frequencies from the MARMAP collections (detailed in the Methods section of Chapter 4.2) were evaluated each year by time of wind cessation to determine length of 50% maturity (Appendix 9.1 - Figures). The adult abundance (1968-1981) was then adjusted for percent mature croaker. There was not a strong relationship with either the larval croaker abundance on the shelf or with the fall juvenile index in the Chesapeake Bay. This indicated other factors to be involved. An index of abundance of mature croaker per area occupied by croaker showed much scatter when correlated with the fall juvenile index \( (r = 0.43, n=14) \) (Appendix 9.2 - Figure).

It is those croaker spawning north of Cape Hatteras that potentially contribute to Chesapeake Bay recruitment. Since, in
Figure 9.2

The relationship between the log of the stock (total Virginia-North Carolina landings) and the log of Chesapeake Bay October recruitment. The slope of the regression line, $b = 0.800$, is the index of density-dependence.
Test of Croaker Density—Dependence

Legend
- OCTOBER

Regression
Upper 95% C.I.
Lower 95% C.I.

Total Virginia—North Carolina Landings

October Juvenile Index

10,000,000
10,000,000
100,000,000
1,000,000,000
10,000,000,000

10
1
0.1

100
10
1
Figure 9.3

The relationship between the log of the stock (total Virginia-North Carolina landings) and the log of Chesapeake Bay April-September recruitment. The slope of the regression line, $b = 0.388$, is the index of density-dependence.
Test of Croaker Density—Dependence

Legend
- SUMMER
- Regression
- Upper 95% C.I.
- Lower 95% C.I.

Total Virginia—North Carolina Landings

Summer Juvenile Index

1,000

100

10

1

0.1

1000000

10000000

100000000
Chapter 8, I assumed trawl landings in Virginia were from north of Hatteras, I used Virginia trawl landings as an index of stock size. These landings are by calendar year, with January-March indicative of the stock one year and October-December representative of the stock the next spawning season. The commercial landings correlated well with MARMAP croaker abundance \((r = 0.84, n=9, \text{Appendix 9.3 - Figure})\). Therefore I used MARMAP data to determine percent maturity and adjusted the otter trawl landings. This index of maturity was then divided by the area of bottom water greater than or equal to \(16^\circ\text{C}\), to incorporate the density of the stock \((\#\text{ mature individuals}/(\text{nm}^2))\), and correlated it to the fall index of recruitment in the Chesapeake Bay. There is a correlation \((r = 0.65, n=14, \text{Figure 9.4})\), but it is not significant enough to be used predictively. Further, this correlation reveals much scatter when the stock size is low, but high recruitment when the stock size is high.

I investigated Chesapeake Bay and Pamlico Sound summer catches as indices of spawning stock size because the calendar year data do not overlap spawning seasons. Most of Virginia's within-the-bay catches are made by pound and gill nets, while most of North Carolina's are made with long haul seines. These gears were chosen as representative. The correlation was slightly higher here than using otter trawl data \((r = 0.70, n=28)\) (Figure 9.5), but the same pattern can be seen, diverse recruitment at low stock sizes, with consistently high recruitment at high stock sizes. The percent of commercial catch that was mature was estimated as 30% of the pound net, 50% of the gill net, and 15% of the long haul seine catches (See Chapter 8, Table 8.1 and Figures 8.11 and 8.12). The correlation was not improved \((r = 0.59, n=28, \text{Appendix 9.4 -})\)
Correlation between the fall juveniles in the Chesapeake Bay as an index of recruitment and commercial trawl landings of croaker an index of spawning stock. The croaker landed by otter trawls in Virginia are adjusted by percent maturity and divided by the area (nmi)$^2$ of water greater than or equal to 16°C, ($r = 0.54$, n=14).
Figure 9.5

Correlation between the fall juveniles in the Chesapeake Bay as an index of recruitment and bay-sound landings as an index of spawning stock. The combined catches (pounds) of Virginia pound nets and gill nets and North Carolina long haul seines were used, \( r = 0.70, n=27 \).
Figure). Therefore, not only does croaker not appear to be a density-dependent species, but also its recruitment does not appear to be closely related to the stock size.

DISCUSSION

Conventional techniques of measuring stock size rely on commercial CPUE statistics or fishery-independent data collections. The estimation of parental stock products (Saville and Schnack 1981) or recruitment from spawning stock size (Lough et al. 1981) is dependent upon the existence of a very close relationship between spawning stock size and egg or larval abundance. Some have found this relationship (Saville 1981) while others have not (Conand 1981). The absence of the relationship may be due to multiple spawning periods of unequal importance (Conand 1981) or a number of, as yet unidentified, complex factors operating on the early life history of each species (Lough et al. 1981).

However, whether or not non-parent stock density-dependent control of fish populations exists is still hypothetical (Shepherd and Cushing 1981). The possible variations in any population may be because density-dependence is weak or because stochastic effects occur during or after the density-dependent process. Also, a stock which is highly density-dependent in a virgin state, may be driven by exploitation to a state where the degree of density-dependence has been reduced (Shepherd and Cushing 1981). Figure 9.6 shows a schematic of typical stock/recruitment curves. Recruitment, measured as year-class strength, may asymptote, continue to increase or form a dome-shaped curve on stock.
Figure 9.6

Stock-recruitment functions as interpreted by Ricker
\[ R = a P e^{-bP} \] (1954, 1975), Beverton and Holt
\[ R = P/(a + bP) \] (1957), and Cushing \[ R = aP^{-b} \] (1971).

R = recruitment, P = parent stock size, a = density-independent coefficient, b = density-dependent coefficient.

At point "a", with a low stock, a high year class will tend to return the stock to its stabilization point where the curve cuts the bisector, but a very low year class, below the bisector, will tend to reduce the stock considerably. The high stock condition is shown at point "b" (after Cushing 1978 and Bakun and Parrish 1980).
The stabilization point about which an unexploited stock varies is where recruitment cuts the 45° bisector. At a low stock size ("a" in Figure 9.6) a year class above the curve tends to return the stock strongly upward towards its stabilization point. A stock size below the bisector shifts it downward. At high stock sizes ("b" in Figure 9.6), year classes below the curve tend to strongly return the stock downward to the stabilization point, but one above the bisector shifts the stock only slightly upward (Cushing 1978).

This stock/recruitment relationship has been represented even more concisely by the National Research Council (1980) (Figure 9.7). For many species, the mean recruitment level is almost constant over a large intermediate domain of variation of the parental stock (Sharp 1980). Variability at moderate and high stock sizes is shown for density-dependent stocks (Beverton and Holt type) by "A" in Figure 9.7. Simultaneously, this form depicts a stock size "B", below which the stock cannot be maintained. Parrish and MacCall (1978) have incorporated density-independent effects into a spawner-recruit curve for Pacific mackerel (Scomber japonicus). To incorporate their results, which are applicable to density-independent species, I have amended Figure 9.7 by expanding the area of "A" and "B" to include "A" and "B". The variability within "A" is due to density-independent factors (Cushing type), i.e. recruitment can be exceptionally high or only moderate. "B" depicts recruitment results with low stock which can range from moderate with exceptional environmental conditions, to critically low with poor density-independent conditions. The dome-shaped (Ricker type) density-dependent form is not represented here.
Figure 9.7

Schematic representation of the stock/recruitment relationship illustrates "A", great variability normally found in yearly number of recruits for different stock sizes and "B", decrease in numbers of recruits observed at low stock levels when populations may be in danger, for density-dependent stocks. A' and B' indicate greater fluctuations possible in density-independent stocks, (after National Research Council 1980).
Classic reproduction curves (Figure 9.6) are represented by models proposed by Ricker (1954, 1975), Beverton and Holt (1957) and Cushing (1971). All three include an intrinsic rate of increase as a density-independent (a) term and a density-dependent (b) term which reduces the rate of increase of recruitment as the stock size increases (Bakun and Parrish 1980). Ricker's logistic model \[ R = a e^{-bP} \] implies that at high stock sizes, recruitment is low. This dome shaped curve hold true for cannibalism, but the potential shape is quite variable, i.e., if \( b > 1 \), the density-dependency processes are so strong that they over-compensate for changes in biomass, so that increased stock size leads to decreased recruitment. Beverton and Holt's asymptotic model \[ R = P/(a + bP) \] implies that at high stock sizes, recruitment reaches an asymptotic maximum. The ceiling of abundance is imposed by available food or habitat, i.e., if \( b = 1 \), at large stock sizes, density-dependent effects compensate exactly for increase in biomass, leading to asymptotically constant recruitment. Cushing's allometric model \[ R = aP^{-b} \] implies that recruitment increases with stock size, but at a continuously decreasing rate, i.e., if \( b < 1 \), recruitment continues to increase indefinitely as biomass increases (Shepherd 1982).

Cushing (1971) used new recruits to the fishery (average, IV+) as an index of recruitment. He found that stock recruitment curves for salmon- and herring-like fishes are slightly convex, flatfish resemble asymptotic curves, and gadoids and tunas have marked domes. Croaker never exhibit the dome shaped pattern that reduces recruitment as stock size becomes larger due to cannibalism. Therefore, the density-dependent index \( b = 0.388 \) of juvenile summer croaker is most similar to the herring-like fishes, which have density-dependent indices of
0.441 and 0.448 (Cushing 1971). The herring-like fishes are subject to large fluctuations as demonstrated by croaker. These fluctuations are due not only to fishing effort, but also to environmental effects. Two quantities relate to stock size, recruitment, i.e. absolute numbers of young fish produced, and survival, number of young fish surviving per million eggs (Gulland 1969). The density-dependent index is inversely correlated with the cube root of fecundity indicating that, for stocks of the same size, the distance between larvae plays an important part in the determination of density-dependence (Cushing 1971). Fecundity of croaker ranges from 100,000 eggs for a 196 mm female to 1,742,000 eggs for a 390 mm female (Morse 1980). The correlation with density-dependency relies on fecundity at mean weight, which is about 300,000 eggs for croaker (Morse 1980). The density-dependence index (b) of Cushing’s data (1971) is regressed on the cube root of fecundity. Croaker fecundity is between flatfish and gadoids (Point A, Figure 9.8). Stocks with the greatest fecundity are the most density-dependent. However, a serial spawner has a lower relative fecundity making the fecundity of croaker and its relative density-dependence actually lower. The majority of spawning croaker are young (II+), as shown in Chapter 8. Therefore the average fecundity is quite low, possibly near its lowest measured value of 100,000 (Point B, Figure 9.8).

With greater density-dependence, the stability of the stock size is greater under varying environmental conditions. If populations are to remain stable under different conditions, one of the vital parameters, mortality, growth or reproduction, must change (Gulland 1965). Growth can decrease with an increase of abundance. Populations which have declined to low levels following heavy exploitation, have
Figure 9.8

Croaker values superimposed on Cushing's (1971) relationship between the index of density-dependence, b, and the cube root of the mean fecundity for several stocks of fish. Point A is an estimate of mean croaker fecundity. Point B is the lowest estimate of croaker fecundity (after Cushing 1971).
been characterized by an increase in individual growth rates which could contribute to the maintenance of a smaller population through growth overfishing (Botsford 1981). However, this does not seem to be applicable to croaker. As shown in Chapter 8 (Figures 8.10, 8.11 and 8.12), modal size did not change significantly from the period of high croaker abundance in 1925-31, through the beginning of the first decline, 1949-55, to its present high level in North Carolina and low level in Virginia. In 1949-55, the mean size of age I seems to be larger, but grades into age II with no definitive separation. This is probably due to the incorporation of gill net landings which selectively catch larger fish. It may also be an artifact of the multiyear average, as some years have larger modal cohort sizes as discussed in Chapter 5.

The hypothesis that growth rate per individual fish is inversely related to the density of the fish was tested. The modal size of age II Chesapeake Bay stock striped bass from Long Island decreases as the year-class strength increases (Austin and Hickey 1978). Since an increase in individual growth rate at specific size is more commonly observed in the juvenile rates than adult stage (Botsford 1981), I plotted the young-of-the-year July modal size (see Chapter 5) on the April-September juvenile index (J_{SUM}) in a method similar to that of Austin and Hickey (1978). There is no correlation between modal size and strength (r = 0.20, Appendix 9.7 - Figure) nor between modal size and Virginia-North Carolina landings the preceding year (r = 0.11, Appendix 9.8 - Figure). These results further support the claim that croaker is principally a density-independent species, because in a density-independent stock growth should not change with density (Cushing 1981).
CONCLUSIONS

All finfish fall somewhere along a continuum from density-dependent to density-independent, with no species exactly at either extreme (Richkus, Summers, Polgar, Holland, Ross, Johnson and Souza 1980b). Further, the degree of density-dependence can change as stock size fluctuates. Major finfish stocks of Maryland are placed into one to three categories, relatively density-dependent, relatively density-independent, or recruitment pattern unknown. Atlantic croaker is classed as unknown because previously very little has been known about its recruitment patterns (Richkus et al. 1980b). However, several questions used in this classification have been answered in this dissertation. The age structure of a stock with a totally density-dependent recruitment is stable through time, so the behavior of the stock can be shown by following a single year class through its life. In totally density-independent recruitment, the age structure is unstable and dominated by particular year classes (Richkus et al. 1980b). This dominant year class pattern is more characteristic of croaker than is the stable population pattern.

A population with many age classes of more or less equal effect on the young-of-the-year mortality is more stable than a population with only one or two age classes (Botsford 1981) such as croaker. In a density-independent stock, year-to-year variability in mean CPUE is primarily affected by particular year classes as discussed in Chapter 8. In a density-dependent stock, the contributions of year classes are relatively constant year to year (Richkus et al. 1980b). Additionally, in a density-dependent stock, juvenile abundance varies predictably
through time (Richkus et al. 1980), but I have shown, in Chapters 4, 5, 6 and 7, that most juvenile recruitment in croaker is erratic and dependent upon specific environmental parameters.

This finding of density-independence should be interpreted with caution. The stock-recruit relationship may be masked statistically due to poor measures of spawning stock size (Walters and Ludwig 1981). Murray, LeDuc and Ingham (1983) found that fishing mortality is linked to recruitment in Atlantic mackerel (Scomber scombrus) through reductions in spawning stock size. This contribution, however, is minimal compared to the fluctuations observed in recruitment. Recruitment of sea herring (Clupea harengus) seems not to be dependent upon spawning stock size, but the effect of heavy fishing on a low stock cannot be ruled out since the collapse of the Georges Bank fishery in 1976 (Lough et al. 1981).

Alternatively, the effect of spawning stock size may only become apparent after accounting for the effects of density-independent variables. Inclusion of spawning stock size improves the predictability of a 400-year simulation model (Goodyear and Christensen In press). These effects of year to year variation in stock size are small compared to the effects of environmental variation. Therefore, I incorporated an index of stock size into the model as developed in Chapter 7. The Virginia-North Carolina within-the-bay catch (Figure 9.5) produced the best, albeit weak, correlation of those tested here. It was included in a multiple regression with the quadratic and linear forms of January-February-March temperature (JFM) and wind-induced transport (WINDEX). The explained variance was increased (to $R^2 = 0.96$ from $R^2 = 0.92$, n=11).
The relationship was significant ($F = 47.27, p = 0.0003$), and the $R^2$ has been adjusted to reflect addition of another variable as this is a large number of parameters (6) for the sample size (n=11) (Table 9.1). With the addition of the Virginia-North Carolina index of stock size (VN) in thousands of pounds, the equation becomes:

$$J_{\text{SUM}} = 82.69 - 63.24*JFM + (7.29*JFM^2) + 6.54*W - (0.25*W^2) + 0.0015*VN$$

The hindcast values from this relationship are shown in Figure 9.9.

Density-independent stocks in general, and croaker in particular, can only be managed by individual year classes and not as a whole stock (Richkus et al. 1980). Therefore, the model presented in this dissertation (Figure 1.1) includes spawning stock because lack of a strong observable relationship between spawners and recruits should not be interpreted an absolute independence (Goodyear and Christensen In press). This feedback which connects the output, through the effect of spawning stock size, to the input, is shown in Figure 9.10. Management schemes that preserve at least some minimum spawning stock should be employed whenever the dynamics of the population are not completely understood (Goodyear and Christensen In press).
### TABLE 9.1

Multiple Regression Analysis

<table>
<thead>
<tr>
<th>DEPENDENT VARIABLE</th>
<th>J&lt;sub&gt;SUM&lt;/sub&gt;</th>
</tr>
</thead>
</table>

**VARIABLE(S) ENTERED ON STEP NUMBER**

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<tr>
<th>Step</th>
<th>Variable</th>
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<td>SQWIND</td>
<td></td>
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<tr>
<td>3</td>
<td>VN</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>WINDEX</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>SQJFM</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**MULTIPLE R** 0.98959  
**R SQUARE** 0.97928  
**ADJUSTED R SQUARE** 0.95857  
**STANDARD ERROR** 6.93319

**ANALYSIS OF VARIANCE**

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<thead>
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<th>DF</th>
<th>SUM OF SQUARES</th>
<th>MEAN SQUARE</th>
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</thead>
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<td>REGRESSION</td>
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<td>11361.61522</td>
<td>2272.32304</td>
</tr>
<tr>
<td>RESIDUAL</td>
<td>5</td>
<td>240.34559</td>
<td>48.06912</td>
</tr>
</tbody>
</table>

**F = 47.27199**  
**SIGNIFICANT P = 0.0003**

---------- VARIABLES IN THE EQUATION ----------

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<thead>
<tr>
<th>VARIABLE</th>
<th>B</th>
<th>SE B</th>
<th>BETA</th>
<th>T</th>
<th>SIG T</th>
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<tr>
<td>JFM</td>
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<td>14.17549</td>
<td>-2.85479</td>
<td>-4.461</td>
<td>0.0066</td>
</tr>
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<td>SQWIND</td>
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<td>0.09914</td>
<td>-0.54429</td>
<td>-2.523</td>
<td>0.0530</td>
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<tr>
<td>VN</td>
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<td>0.5453E-03</td>
<td>0.23254</td>
<td>2.698</td>
<td>0.0429</td>
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<tr>
<td>WINDEX</td>
<td>6.53266</td>
<td>1.71848</td>
<td>0.83278</td>
<td>3.801</td>
<td>0.0126</td>
</tr>
<tr>
<td>SQJFM</td>
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<td>1.15971</td>
<td>3.97930</td>
<td>6.284</td>
<td>0.0015</td>
</tr>
<tr>
<td>(CONSTANT)</td>
<td>82.68627</td>
<td>43.51623</td>
<td>1.900</td>
<td>0.1158</td>
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</tr>
</tbody>
</table>
Figure 9.9

Actual and hindcast summer juvenile indices, 1972-1982. Hindcast values (VN) are calculated from indices of fall wind-induced transport, winter temperatures, and spawning stock size ($r^2 = 0.96$, $n=11$).
Summer Young-of-the-Year Croaker

Legend

△ Actual
× Hindcast (VN)
Figure 9.10

Effect of spawning stock size connects model output back to input.
CHAPTER 10
Model Applications

INTRODUCTION

One purpose of a model is to predict and/or to guide the analytical processes (Probert 1981). The process should be started with the collection of data which are repeatedly examined for the purposes of evaluating and modifying the model. First data should be plotted and qualitatively evaluated. Partitioning of the overall system into submodels, allows components to be modelled independently. The interaction and interdependence between the subsystems can then be studied conceptually and modelled (Gold 1977). There should be iterative interplay between hypothesis formulation and modelling. A continual reexamination of results of earlier steps and modification in response to insight is required. Models should be used to test hypotheses and establish relationships between those things which can be measured as well as to make inferences about those which cannot (Gold 1977).

Semantics, however, may be a problem. One could differentiate between "modelling", as attempting to answer all interlocking questions simultaneously, and "investigating", as answering a unit question (Fielou 1981). Correlative, or empirical, models are a form of investigating which describe and summarize relationships so that they
may be verified and used as a basis for prediction and control. If statistical agreement is not close enough in a correlative model, an alternative form may be tested (Gold 1977). The original goal of ecosystem modelling was to explain fluctuating populations, i.e. investigating, as opposed to using a mathematical model to impose constraints on the real world (Pielou 1981). Strictly speaking, explanatory, or rational, models begin with a preconceived mathematical statement to explain and reflect the concept of the causal mechanism underlying a relationship. However, because of the causal base, the equation of the underlying physical principle cannot be changed (Gold 1977). This can lead to futility of striving for an exact match between models and reality (Pielou 1981).

However, in an iterative process, it is not necessary for the two types of models to be mutually exclusive (Figure 10.1). A relationship should be hypothesized and investigated, then stated in a mathematical form. The model can be used to suggest further study and to refine the hypothesized relationship (McKelvey, Hankin, Yanosko and Snygg 1980). The simplest mathematical expression that gives sufficient agreement with the data should be used (Gold 1977). It is not necessary to include the complexity of the whole system as long as the model predicts successfully. The complexity depends on the purpose of the model (Probert 1981). The responsiveness of the model should be studied and the knowledge continually applied to the iterative process.

A correlative modelling, or investigating, approach was employed in this study. The conceptual model was the first step in the iterative process of formulating hypotheses. The flow chart model (Figure 10.2) of juvenile croaker recruitment was based on this
Figure 10.1

Representation of the model-building process. Note that "test" arrows carry one back to the data at every opportunity (from Gold 1977).
With wider latitude under change of physical situation cautious extrapolation.

Inferences about related situations which are difficult or impossible to directly observe.
Figure 10.2

Flow chart diagram of Sub Models I, II and III, including interconnections and feedback.
INPUT

- CATCH STATISTICS (VMRC)
- OFFSHORE WINDS (adjusted Norfolk)
- FALL JUVENILE ABUNDANCE (VIMS Trawl Sum)
- WINTER TEMPERATURE (VIMS Pier)
- SUMMER JUVENILE ABUNDANCE (VIMS Trawl Sum)
- ADULT LENGTH FREQUENCIES (Pub.VIMS)

MECHANISM

- SPAWNING STOCK SIZE
- CESSATION SUMMER WINDS
- SURFACE TRANSPORT
- FALL JUVENILE RECRUITMENT
- WATER TEMPERATURE
- SUMMER JUVENILE RECRUITMENT
- YEARCLASS STRENGTH
- AGE COMPOSITION OF ADULT STOCK
- COMMERIAL CATCH

POTENTIAL REDUCTION

- SMALL
- LARGE
- LATE
- RECRUITMENT (Biological)
- RECRUITMENT (Physical)
- SURVIVAL (Physical)
- SPawning (Overfished)
- FISHING PRESSURE (Per Year)

OTHER FACTORS NOT INCLUDED

- Separate Stock
- Larval Starvation
- Larval and Juvenile Predation
- Larval and Juvenile Growth
- Parasites and Diseases
- Fishing Pressure
- Effect of Shrimp By-Catch

ADJUSTED FOR % SPawning AGE
conceptual life history. The functional form of the relationships at each step has been derived. This model empirically quantifies these relationships. While hypothesized, the causal mechanisms are not investigated here, i.e. the underlying physical principals do not define the form of the equations. The relationships that have been quantified statistically are based on determinations of empirical biological-physical links in the conceptual model.

The resulting statistical fit of the model was good \( R^2 = 0.96, n = 11 \) and the hindcast estimates from the model were close to the actual values (Figure 9.9). The statistical correlations were not derived randomly, but were based on hypotheses of vulnerable life history stages and environmental effects. They are used here to predict the 1982-83 year class of croaker in Chesapeake Bay. The applicability and appropriateness of the model are discussed in relation to other types of models. Eventual prediction of commercial catch of croaker is also discussed.

METHODS AND RESULTS

To test the predictability of the model developed in this dissertation, the daily wind direction and speed at Norfolk airport, Virginia for the summer and fall of 1982 were obtained from Local Climatological Data Records (NCDC). The north-south components were analyzed for time of summer wind cessation according to methods described previously (Chapter 4.1). The average time of cessation during this period of study was the beginning of September (7). Ten-day vectors and the "best" 40-day transport, from the beginning of September
through the beginning of October, were calculated and plotted (Figure 10.3). The calculated WINDEX ($W=14$) was one of the best in the period examined. Fall juvenile recruitment actual maximum ($J_{\text{MAX}} = 344.17$) value and the maximum predicted from the WINDEX ($J_{\text{MAX}} = 241.27$) are plotted in Figure 10.4 versus WINDEX. Sub Model I predicted a very good fall recruitment, and the actual recruitment was second only to the record 1976-77 year class.

The winter of 1982-83 was very mild, the warmest in six years. The average temperature ($JFM = 6.40$) was approximately equal to those of 1972 and 1973, but less than those of 1974, 1975 and 1976. Therefore, based on the relationship between January-February-March temperature and year-class survival, the summer of 1983 year class ($J_{\text{SUM}} = 24.09$) falls in the range of greatest variability (Figure 10.5). Sub Model II predicts a good year class (Appendix 10.1), but not an outstanding one, as indicated by the maximum fall recruitment in Sub Model I.

I have shown in Chapter 7 that an index of fall recruitment is necessary for a more accurate estimate of year-class size. When the index of wind-induced transport (WINDEX) is incorporated with winter temperature, the predicted summer ($0^+$) year class for 1983 ($J_{\text{SUM}} = 30.12$) is larger than the estimate from JFM alone (Appendix 10.2). This value is a much lower estimate than the one calculated using the maximum fall recruitment ($J_{\text{SUM}} = 118.29$) instead of the WINDEX (Appendix 10.3).

Though the croaker stock has been down in Virginia recently, the catch has been fairly good in North Carolina (Figure 8.1). An index of spawning stock size (8164 thousand pounds), as derived in Chapter 9, was incorporated in the predictive equation. This predicted year-class
Figure 10.3

Adult and larval distribution data are not used for 1982 since the wind-induced transport is used to predict juvenile recruitment to the Chesapeake Bay in the fall. Ten day moving average water vectors are plotted to the same scale as the charts. "Best" 40-day vector is shown in bold, above the time line. Triangle indicates time of cessation of the summer wind.
Figure 10.4

On the curve is 1982 maximum fall recruitment predicted from WINDEX ($J_{\text{MAX}} = 241.27$). Actual 1982 maximum fall recruitment ($J_{\text{MAX}} = 344.17$) is plotted above the curve.
Summer 1983 year class of croaker ($J_{\text{SUM}} = 24.09$) predicted from 1983 January-February-March temperature ($JFM = 6.4^\circ C$).
strength ($J_{\text{SUM}} = 31.36$) is only slightly higher than that predicted by temperature and wind-induced transport (Figure 10.6).

DISCUSSION

Interpretation of this multi-dimensional model is not simple, in part because of the large number of parameters identified which determine the results. The model will be interpreted for a few years, including feedback through spawning stock size. The first is the year class of 1974. In the fall of 1973, there was a small spawning stock size, early wind cessation (Sub Model I - Part 1) and good transport (Sub Model I - Part 2) resulting in good juvenile recruitment into the Chesapeake Bay in the fall. The winter of 1974 was the warmest of the time series (Sub Model II), and an excellent year class was produced in the summer of 1974.

The year class of 1975 was good. There was an average stock size in the fall of 1974, average time of summer wind cessation, poor transport and poor fall recruitment. However the winter temperature was warm and a good summer year class was produced in 1975. The 1976 year class was also good. Stock size in 1975 was average, increased somewhat by the favorable year class two years earlier. The wind cessation was late, but transport was good as was fall recruitment. The winter temperature was warm and a good 1976 summer year class resulted. The 1977 year class was poor despite the earliest summer wind cessation of those examined and the best transport index in fall of 1976. Several recent strong year classes had improved the stock size (Sub Model III)
Figure 10.6

and fall recruitment was excellent. However, a weak year class resulted after a record-cold winter.

The year-class strength predicted is the summer juvenile survival of croaker to age $0^+$. This index ($J_{\text{SUM}}$) was based on monthly young-of-the-year indices of croaker taken by the VIMS trawl survey, averaged April through September. Unfortunately, as of this writing, December 1983, the 1983 data are not available on computer, making it impossible to test the predicted value against the actual value. However, it is known that there were "a lot" of young croaker around in the summer of 1983. There have been reports of pinhead (young-of-the-year) croaker from both research sampling and fishermen. There were even young-of-the-year croaker, which have been uncommon since 1976, in the Maryland waters of the Chesapeake Bay in 1983.

The resulting model is a mathematical description of the contribution and variability of mechanisms producing interannual year-class fluctuations in recruitment. These have been characterized as the most critical considerations in fish population dynamics (Cushing 1973, McKelvey et al. 1980). Development of this type of model is significant since recruitment process models are thought to offer the largest potential improvement in predictive capability (Turgeon 1983). Complex multistage recruitment processes are more adequately described through statistical analyses than by simple stock-recruitment theory. In stock-recruitment theory only one observation is made annually, thus relating not only to parent stock but also to the fluctuating environmental conditions, although only a measure of the stock is included. This simple theory may not always be biologically appropriate and more complex seasonal multi-dimensional models of numerical population
dynamics may be required for biological realism and for meaningful data analysis (Hankin 1980).

The multistage recruitment process is ignored by most routinely used methods of calculating stock size. One of these, catch-per-unit-effort (CPUE), is based on the often invalid assumptions that CPUE is proportional to abundance and that effort is standardized (Kimura 1981). Stock production models for long-term forecasts predict next year's CPUE based on this year's CPUE. Autoregressive time series methods may be just as useful (Stocker and Hilborn 1981). In a comparisons with Dover (Microstomus pacificus) and English sole (Parophrys vetulus), the another method, Virtual Population Analysis (VPA), was found to be a better determinant of year-class strength change than CPUE. However, in either model, the variance from the central trend of the model is probably due to environmental factors (Hayman, Tyler and Demory 1980).

VPA, or cohort analysis, gained popularity because of the need for effort-independent data. However, VPA analysis requires information about the stock, including: estimates of past and present age composition of the stock, numbers-at-age of fish in the stock in the current year and for the oldest fish in all years, an estimate of recruitment to the fishery, weight of the stock, growth rates, and fishing mortality (Pierce and Hughes 1979, Cook 1981). VPA calculations do not provide forecasts, however, as estimates of the most recent year or two are subject to great error (Cook 1981, Turgeon 1983).

The conceptual links between the predictable summer recruitment of croaker, year-class strength and commercial catch have been developed as depicted in Sub Model III (Figure 10.2). However,
very little appropriate data exist for Atlantic croaker. The analysis of the fishery in Chapter 8 reveals that age composition of the stock (catch) is not accurately sampled. Thus, age composition of the stock cannot be estimated for use in a model. An index of fishing pressure, and its changes with year-class strength are needed to quantify the remainder of the model. Therefore, though juvenile year-class strength of age 0+ croaker in the Chesapeake Bay can be predicted with this model, lack of necessary commercial catch data prevents extension of the model to predicting commercial catch. Additionally, stock size was found to have a only slight effect in determining recruitment when included with the appropriate environmental factors. Better estimates of spawning stock size, via improved commercial catch data, may change this relationship, particularly during years of either very large or very poor spawning stock.

CONCLUSIONS

The modelling approach employed here is multi-disciplinary. Since there must be a starting place from which to begin modelling, logically this should include early life history stages of individual species and direct relations with ambient processes (Sharp 1980). The process used here begins with identification of a physical system such that its deviations from normal could affect larval survival, and biological systems (species) which are likely to be affected by these anomalies. The empirical relationships are used as tools to identify the mechanisms driving the recruitment success or failure. Such mechanistic models are more realistic in that they represent an actual course of events (Pielou 1981). The purpose is to identify the major
factors which result in anomalous year-class strengths. The result is a complicated, multistage process as described in this dissertation, because each factor does not contribute equally, nor is its significance the same each year.

Gulland (1965) pointed out that though many correlations between year-class strength and environmental factors have been suggested, few have stood the test of time. The purpose of beginning with a lengthy time series is to enable identification of trends, patterns and anomalies. A longer data set is more likely to include more variability. Long time series of both biological and physical data are now becoming available to accommodate this type of modelling. Models should be used as hypothesis-generating tools (Fielou 1981). The apparent failure of any model should be viewed as an extension of the iterative process of the modelling effort. Parameters may have been measured too imprecisely, the wrong parameters may have been measured, multi-species and/or life-stage interactions may have been dominant (Zweifel 1980), or conditions may have changed such that a factor originally unimportant became dominant.

A management biologist must choose the best method for short-term forecasts. Relatively good forecasts exist that do not imply a fundamental understanding of the system (Stocker and Hilborn 1981). Therefore, models that are empirically based should not be discarded because of lack of explanatory components. Such models can be used functionally if they provide the best available forecast. They also provide insight into needed experimental design, identification, and verification of mechanisms.

The empirical model of juvenile croaker recruitment presented here provides the best estimate of recruitment currently available.
Richkus, Summers, Polgar and Holland (1980a) have examined possibilities of modelling croaker in the Chesapeake Bay. They determined the following: that croaker have a nondeterministic stock-recruitment relationship; that total yield data do not exist; that a surplus production model could not be used; that insufficient data exist for a yield-per-recruit model; and that a statistical or a simulation model of environmental factors affecting croaker was the most likely to be successful. This model has identified the significant factors which affected croaker recruitment during the time series which was studied. The conceptual model and flow diagram have identified vulnerable periods of the croaker life history and indicate laboratory and field studies which are needed to verify this model.
CHAPTER 11
Model Summary

1. A conceptual life history of Atlantic croaker (Micropogonias undulatus) was developed to identify the effects of the environment on recruitment (Figure 3.1). Adult spawning and larval distribution on the shelf, and juvenile overwintering within the Chesapeake Bay were identified as key periods of environmental vulnerability.

2. Sub Model I - Part 1 (Figure 11.1) encompasses the interactions of the time of cessation of the summer wind regime in the Mid-Atlantic Bight, distribution of warm bottom waters (≥16°C), and croaker spawning time, location, and migration. When the seasonal wind cessation occurs earlier, the bottom waters warm earlier and a larger area of warm (≥16°C) exist, croaker mature earlier and can spawn farther north. This results in enhanced recruitment of juvenile croaker to the Chesapeake Bay.

3. Sub Model I - Part 2 (Figure 11.1) represents the effect of wind-induced transport of larval croaker on recruitment to the Chesapeake Bay. The pelagic phase is the most critical time in the life history of a larval croaker as they are subjected to wind-induced transport which may cause direct loss off the shelf and entrainment in the Gulf Stream, or indirect loss by prolonging time in transit to the nursery area. Larval descent in the water column proximal to the mean
Figure 11.1

Model summary, including equations determined for each Sub Model.
INPUT MECHANISM

- SPawning STOCK SIZE
  - SMALL RECRUITMENT (Biological)
  - LARGE

- CESSATION SUMMER WINDS
  - LATE RECRUITMENT (Physical)
  - EARLY

- OFFSHORE WINDS
  - SUMMER WINDS
  - EARLY
  - LATE RECRUITMENT (Physiological)

- SURFACE TRANSPORT
  - OFFSHORE RECRUITMENT (Physical)
  - ONSHORE

- FALL JUVENILE ABUNDANCE
  - VIMS Trawl Surveys

- WATER TEMPERATURE
  - COLD SURVIVAL (Physical)

- SUMMER JUVENILE RECRUITMENT

- YEARCLASS STRENGTH
  - WEAK SPAWNING (Overfished)
  - STRONG

- ADULT LENGTH FREQUENCIES
  - MULTl-YEAR FISHING PRESSURE
  - SINGLE YEAR

- ADJUSTED FOR % SPawning AGE

SUB MODEL I
- SEparate Stock
- Larval Starvation
- Larval and Juvenile Predation
- Larval and Juvenile Growth Rates
- Processes and Diseases

SUB MODEL II
- Fall Juvenile Abundance (VIMS Trawl Surveys)
- Fall Juvenile Recruitment

SUB MODEL III
- Fishing Pressure
- Effect of Shrimp By-Catch

J_{spaw} = 82.69 - (0.24 * JFM) + (7.29 * JFM^2) + (6.54 * W) - (0.23 * W^2) + (0.0015 * VN)
inward bottom flow, will transport the croaker into the Chesapeake Bay. The potential loss of larvae is greatly reduced once they have reached this stage. The magnitude of this wind-induced effect is a function of the direction, strength, duration and time relative to spawning, which is incorporated into a single variable (WINDEX=W). The maximum number of fall recruits is quantified as \( R^2 = 0.65, n=11 \):

\[
J_{\text{MAX}} = 18.11 + (3.90*W) + (0.86*W^2)
\]

4. Sub Model II (Figure 11.1) quantifies the effect of low temperatures on subsequent summer recruitment of juvenile croaker in the Chesapeake Bay. Winter temperature is shown in this study as the predominant variable in very cold years, but not in very warm years \( R^2 = 0.78, n=29 \):

\[
J_{\text{SUM}} = 118.07 - (53.02*JFM) + (5.99*JFM^2)
\]

5. This study additionally combines an index of the success of fall recruitment from Sub Model I with Sub Model II. This improves the explained variation by accounting for the years when year class strength is not solely dependent upon temperature (Figure 11.1). The relationship established here also shows that, though the temperature is often the major factor determining winter survival, the magnitude of its effect is related to the initial strength of year-class recruitment. Year-class strength of \( 0^+ \) croaker is quantified as \( R^2 = 0.92, n=11 \):

\[
J_{\text{SUM}} = 127.75 - (70.84*JFM) + (6.28*W) - (0.23*W^2)
\]

6. Croaker are shown to be basically a density-independent stock; and juvenile recruitment is erratic and dependent upon specific environmental parameters. The effect of spawning stock size may only
become apparent after accounting for the effects of density-independent variables. In the model, this is the feedback from commercial catch through spawning stock and back to the recruitment processes. Therefore, the Virginia-North Carolina within-the-bay landings, as an index of stock size, were incorporated into the model. It was included in a multiple regression with the quadratic and linear forms of January-February-March temperature (JFM) and wind-induced transport (WINDEX). The addition of the Virginia-North Carolina index of stock size (VN) in thousands of pounds, produces the following equation \( R^2 = 0.96, n=11 \):

\[
J_{\text{SUM}} = 82.69 - 63.24 \times \text{JFM} + (7.29 \times \text{JFM}^2) + 6.54 \times \text{W} - (0.25 \times \text{W}^2) + 0.0015 \times \text{VN}
\]

7. Sub Model III (Figure 11.1) represents the importance of year-class strength to the commercial catch of croaker. Because of this density-independence and environmental vulnerability of larvae on the shelf and juveniles in the estuaries, year-class strength fluctuates markedly in croaker. Fishing pressure in addition to these fluctuations caused the interannual variability in croaker catch. Overfishing a weak year class reduce spawning potential. Several weak year classes in succession (e.g. 1977-1979) increase the fishing pressure on each individual year class, further reducing spawning potential. Fishing pre-spawners, 0+ and 1+, is acceptable only when year classes are strong.

8. The model, tested for 1982-83 data, predicts a strong year class. The VIMS trawl survey data are not currently (December 1983) available with which to verify the prediction. Catch data are of too poor a resolution to use as input to the model, thus prohibiting output of predicted size of commercial catch.
### APPENDIX 1.1
Data Bases Used In Model

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<thead>
<tr>
<th>Data Base</th>
<th>Time Period</th>
<th>Content</th>
<th>Use/Comments</th>
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<td>1981(Norcross)</td>
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<td></td>
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<tr>
<td>VIMS Neuston Survey</td>
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<td>Larval abundance and lengths of all species caught in collections at mouth of Chesapeake Bay.</td>
<td>Interpret yearclasses. See Chapter 5.</td>
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APPENDIX 1.1 (Continued)

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<th>Use/Comments</th>
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<td>1929-1982</td>
<td>Annual landings of croaker (pounds) for Connecticut, Delaware, Florida,</td>
<td>Historic analysis of commercial catch and spawning</td>
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<td></td>
<td></td>
<td>Georgia, Maryland, Massachusetts, New Jersey, New York, North Carolina,</td>
<td>stock size. See Chapters 8 &amp; 9.</td>
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<tr>
<td></td>
<td></td>
<td>South Carolina and Virginia.</td>
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APPENDIX 3.1

Mid-Atlantic Bight and South Atlantic Bight Croaker Collections from MARMAP Cruises

Legend: X - Have data
0 - Have data. No croaker in collection
Blank - No data available

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<th>Cruise</th>
<th>Months</th>
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APPENDIX 3.1 (Continued)

Legend: X - Have data
0 - Have data. No croaker in collection
Blank - No data available

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<td></td>
<td></td>
<td></td>
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<td>N. of Bay mouth</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>S. of Hatteras</td>
</tr>
<tr>
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## APPENDIX 3.1 (Continued)

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0 - Have data. No croaker in collection  
Blank - No data available

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<td>Surface</td>
<td>Bottom Salinity</td>
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- **DOL6925** Sep-Oct  
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  - Adult: X  
  - Physical: X  

- **ALB6911** Oct-Nov  
  - Larval: X  
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- **DOL6929** Oct-Nov  
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- **EKL6911** Oct-Nov  
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- **1970** ALB7003 Mar-Apr  
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- **DOL7016** Jul  
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  - Maturity: X  
  - Adult: X  

- **DOL7011** Jul  
  - Larval: X  
  - Maturity: X  
  - Adult: X  

- **DOL7019** Aug  
  - Larval: X  
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  - Adult: X  

- **DEL7007** Sep  
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  - Maturity: X  
  - Adult: X  

- **ALB7006** Sep-Nov  
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  - Maturity: X  
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- **1971** DOL7103 Mar-Apr  
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- **ALB7101** Mar-May  
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- **DOL7111** Jul  
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- **ALB7106** Sep-Nov  
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- **DEL7103** Nov  
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- **ALB7202** Mar-Apr  
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- **DEL7215** May  
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268
### APPENDIX 3.1 (Continued)

#### Legend:
- **X** - Have data
- **0** - Have data, no croaker in collection
- **Blank** - No data available

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### APPENDIX 3.1 (Continued)

Legend: X - Have data  
0 - Have data. No croaker in collection  
Blank - No data available

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Appendix 4.1.1 - Figures

Comparison of offshore climatological mean monthly winds to winds at Norfolk airport. The upper number is the directional adjustment (degrees of the right) for that area and the lower number is the factor by which the speed should be multiplied.
APPENDIX 4.1.2

Analysis of Climatologic Comparison of Norfolk and Offshore Winds *

*Provided by Frederic Godshall (NOAA/NESDIS/MEAD pers. comm.)

Comparisons were made of Norfolk airport winds and winds observed at sea between 39°N and 35°N and 76°W and 74°W. In general, the winter season adjustments are with respect to direction and the summer are with respect to speed. The monthly wind direction and speed adjustment factors are slight.

The winter season is a time of greater air-sea temperature differences which promote offshore instability of the boundary layer and exchange of momentum with increased height above the surface. From the theoretical considerations of the atmospheric Ekman spiral, the wind should veer with increased height through the boundary layer. Hence, the downward momentum exchange would promote surface wind veering from coastal observations. Therefore, the results of these comparisons, which indicate slight adjustment to the Norfolk wind, are in line with theoretical considerations, i.e., anticyclonic turning of wind in offshore areas during winter.

The speed adjustment, being larger in the summer, seems to reflect the climatological speed differences common to coastal areas.
It is frequently calm onshore while offshore, speed increases are commonly expected.

In application of the wind adjustments, the factors are so small that the adjustments are practically in the noise level. However, knowledge of the magnitude of the shore-sea differences may be helpful for the purpose of establishing limits of data application.
Appendix 4.1.3 - Figure

Comparison of the time of cessation of the summer wind and the area (nmi)$^2$ of water $16^\circ C$ and warmer, unadjusted for collection time, 1967-1981:

$y = 10643 - (535x)$, ($R^2 = 0.11$, $n=27$)
Appendix 4.1.4 - Figure

Comparison of the time of data collection and the area $(\text{nm}i)^2$ of water $16^\circ C$ and warmer, unadjusted for time of wind cessation, 1967-1981:

$y = (827x) - 476, \ (R^2 = 0.61, \ n=26)$
Appendix 4.1.5 - Figures

The area (nmi)$^2$ of water 16°C and warmer (y) at specified time periods. Calculated from wind-cruise interval relationship (Figure 4.1.4) and based on time of summer wind cessation (x).

Predicted at the end of August:

$y = 12242 - (1031x)$, ($R^2 = 0.74$, n=26).

Predicted at the beginning of September:

$y = 11542 - (768x)$, ($R^2 = 0.59$, n=26).

Predicted at the middle of September:

$y = 11279 - (658x)$, ($R^2 = 0.58$, n=26).

Predicted at the end of September:

$y = 12189 - (665x)$, ($R^2 = 0.58$, n=26).
MIDDLE OF SEPTEMBER

CEASE SUMMER WIND (MONTH/3)
END OF SEPTEMBER

CEASE SUMMER WIND (MONTH/3)
APPENDIX 4.1.6

Cold Pool Movement

The cold pool results from winter cooling of mixed shelf water and the formation of the summer thermocline over that water (Houghton et al. 1982). However, the core or minimum temperature within the cold pool is not a conservative feature and is not uniform along the shelf. Along-shelf heating rates vary from 0.5°C per month in the New York Bight (NYB) north of Hudson Canyon, through 1°C per month off New England during the summer to 2°C per month south of Cape May, N. J. in March and April (Houghton et al. 1982). According to Beardsley, Boicourt and Hansen (1976), the mean southward cold pool current is about 5 cms, equalling or exceeding the current velocity of the surrounding warmer water. Ou and Houghton (1982) have shown that both the initial cold water source and spatial non-uniform heating rates are important in explaining the differential alongshore flow rates measured by Houghton et al. (1982). Nantucket Shoal (NSFE79), 5.0 cms; New York Bight (SW16), <2 cms; shelf off southern New Jersey (USCG/B), 5.6 cms. Thus, because a large volume of winter-cooled water resides for a longer time in the New York Bight north of Hudson Canyon, the greatest persistence of cold pool water with the minimum temperature is found there in early spring.
Appendix 4.2.1 - Figure

Comparison of the time of data collection and the areal extent $(nmi)^2$ of adult croaker, unadjusted for time of wind cessation: $y = 1011 + (499*x)$, ($R^2 = 0.55$, $n=11$).
Appendix 4.2.2 - Figure

Relationship between the time of collection of bottom temperature data minus the time of cessation of the summer wind regime (wind-cruise interval) and the areal extent (nmi$^2$) of adult croaker:

$$y = 4985 + (709x) - (68x^2), \quad (R^2 = 0.66, \, n=11).$$
Appendix 4.2.3 - Figures

The areal extent \((\text{nmi})^2\) of adult croaker \((y)\) at specified time periods when migrating out of the Bay, calculated from wind-cruise interval (Figure 4.1.4) and based on time of summer wind cessation \((s)\).

Predicted at the end of August:
\[ y = 8645 - (683x), (R^2 = 0.54, n=11). \]

Predicted at the beginning of September:
\[ y = 8761 - (557x), (R^2 = 0.54, n=11). \]

Predicted at the middle of September:
\[ y = 8554 - (557x), (R^2 = 0.52, n=11). \]

Predicted at the end of September:
\[ y = 7889 - (300x), (R^2 = 0.36, n=11). \]
MIDDLE OF SEPTEMBER

Cease summer wind (month/3)

Adult

Reprod

Area

1000

2000

3000

4000

5000

6000

7000

8000
Appendix 4.2.4 - Figure

Linear relationship between the time of the wind cessation and the latitude of croaker concentration:
from Delaware Bay, $y = 39 - (0.1x)$, ($R^2 = 0.56$, $n=3$), and
from Chesapeake Bay, $y = 37 - (0.15x)$, ($R^2 = 0.52$, $n=4$).
This is the source of the lines in Figure 4.2.8.
FROM DELAWARE BAY

FROM CHESAPEAKE BAY

CEASE SUMMER WIND (MONTH/3)
Appendix 5.1 - Figure

Configuration of SIR schema for data base management of VIMS trawl survey croaker data. See Norcross and Shaw (1983) for details.
CASE:  

| YEAR |

RECORD TYPE 1:  

| YEAR | RIVER | MONTH | COLLNUM | DAY | TEMP | SALT | LAT | LONG |

RECORD TYPE 2:  

| YEAR | RIVER | MONTH | COLLNUM | SPECIES | TOTALN | TOTALWT | AVGWT |

RECORD TYPE 3:  

| YEAR | COLLNUM | SPECIES | SIZEID | SIZE |
Appendix 6.1 - Figure

Map of the Mid Atlantic Bight showing the 200 m depth contour (dashed) and the wind, sea level and current meter stations. Mooring 408A is located near the Chesapeake Bay mouth (from Beardsley and Boicourt 1981). Current meter data from this site was used for comparison with Norfolk winds.
Appendix 6.2 - Figure

Location of 14 stations at the Chesapeake Bay mouth at which the discreet depth plankton samples were collected (J. McConougha, ODU pers. comm.).
APPENDIX 6.3

Larval Croaker (*Micropogonias undulatus*)
Specimens and Photographs

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</tbody>
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*Length calculated from ratio of size measured on slide.

*Photographed by Dennis Thoney, 13 April 1983
Appendix 6.4 - Text


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Oceanic and Estuarine Transport of Fish Eggs
and Larvae: A Review

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Abstract

Oceanic or coastal spawning grounds of fish are often distant from nursery areas. Fish larvae require appropriate currents and sufficient and suitable food during transit to reach the nursery area at the proper time, size, and condition. Meteorologic and oceanographic factors influence food availability and transport direction and time. Annual variation in these controlling factors could affect recruitment success. Certain generalizations can be made which apply to marine and estuarine systems.

Reproduction occurs in a selected portion of the total species range. Spawning often takes place close to gyral, upwelling, or other directional circulations which frequently are associated with major current systems. The coupling of spawning to natural oceanographic transport systems for eggs and larvae is advantageous to a species as long as those systems operate "normally". The details of such coupling, and the consequences for eggs and larvae of deviations from usual transport mechanisms, remain poorly understood. Investigation of year-class success requires a clearer understanding of the natural variability and periodicity inherent in these physical processes. Further research is needed to determine of these details, environmental cues to reproductive behavior, relative importance of passive and behaviorally-mediated transport, and to statistically analyze atmospheric and oceanographic cycles, and quantify transport mechanisms for spawner-recruit models and predictions of year-class success.
Introduction

The distribution of larval fish is controlled by both active behavior and passive transport mechanisms. These mechanisms result from a combination of biotic and abiotic factors. Biotic factors include seasonal abundance of adults and larvae, environmental preferences, availability of suitable food, potential predators, and behavior of larvae. Physical factors include the oceanography or hydrography and climatology of the area, specifically, temperature, salinity, stratification, turbidity, riverine discharges, and water and weather flow patterns, rates, directions, and anomalies.

As recently as 1979, transport of fish eggs and larvae was neglected in an overview of distribution and abundance from a major international symposium on early life history (Saville and Schnack 1981). Transport and its implications for recruitment have been subjects of recent studies, however. The purposes of this review are to (1) identify the importance of and briefly discuss mechanisms influencing distribution, transport, and survival of eggs and larvae; (2) provide case history examples of these influences; and (3) identify areas of expanding interdisciplinary research on the dynamics of ichthyoplankton transport and the resulting effects on recruitment and year-class success.

Oceanographic research has begun to isolate factors involved in the high recruitment variability characteristic of marine organisms. Research of causal relationships between environmental trends or perturbations and biomass fluctuations has obvious practical and
predictive applications. This research is also important to the fundamental understanding of reproductive patterns, spawning-stock isolations, community stability, and energy flow through the ecosystem.

Physical Processes

Oceans

When wind blows across a body of water, the current it generates moves to the right of the wind in the northern hemisphere and to the left in the southern hemisphere. The angle between the wind and surface current is usually less than 45°, and can be very small in shallow coastal areas. The angle between the wind and current movement increases with descent in the water column and the direction of net transport approaches 90°. Ekman (1905) first presented a mathematical theory to explain this phenomenon known as the Ekman spiral. The strength and direction of Ekman transport are important because the flow carries the eggs and larvae of nearshore and offshore spawners towards or away from appropriate nursery grounds.

In areas where wind-induced Ekman transport is offshore, inshore surface waters are replaced by upwelling of cold, nutrient-rich bottom waters. The most vigorous examples of upwelling occur along eastern boundary currents, western continental margins, but upwelling also takes place on a smaller scale along western sides of ocean basins, eastern coasts (Hofmann et al. 1981; Chew 1981). In North America then, upwelling is induced by northerly winds along the Pacific coast and southerly winds along the Atlantic coast. The consequences for
fish larvae are apparent: larvae needing shallow nursery areas will benefit from onshore Ekman transport; pelagic larvae will benefit from increased productivity associated with upwelling; and both types of larvae will perish if entrained by the "wrong" current.

Spawning may also be associated with semipermanent gyres occurring seasonally on a mesoscale in relatively shallow water, such as over a continental shelf, or in proximity to a coast. These gyres may be geostrophic, wind-driven, or driven by residual tidal flows (nonlinear interactions of bottom topography and local tidal characteristics) and are dependent upon the dynamics of each locale.

**Estuaries**

The dominant sources of circulation variability in estuaries are tide, river flow, wind, nontidal forcing from the coastal ocean, and topographically induced circulation (Wiseman 1980). Tidal, riverine, and some wind influences were the first to be recognized as important and therefore the first to be scrutinized by biologists. For example, correlations between observed current variation and wind stress within estuaries led to an increased awareness of the role of local wind forcing (Graham 1972; Wang 1979a, 1979b). Recently the concept of simple two-layered estuarine circulation and the importance of secondary estuarine circulations (residual flow variability) has been evaluated (Kjerfve et al. 1978; Carter et al. 1979). Physical oceanographers are now recognizing the significance of nonlocal forcing of nontidal variations in sea level and circulation. Coastal Ekman convergence (downwelling) can directly affect estuarine current
fluctuations (Smith 1978). More indirectly, Ekman convergence or divergence can alter the water column density structure along a coast which then can change the gravitational circulation within the estuary (Wiseman 1980). Fluctuations in estuarine circulation can be induced by short-term meteorological events like storm surges, by neap-spring tidal cycle variability, and by river flow changes between flood and drought conditions. In addition, several of the world's coastlines have significant seasonal, nontidal changes in sea level (Patullo et al. 1955). These can result in net (residual) current flows in estuaries (Smith 1978).

The interaction of coastal and basin topography and tidal variations, historically useful in classification of circulation patterns in estuaries (Bowden 1967; Pritchard 1967), is the subject of recent research (Carter et al. 1979). Topography can cause cross channel variations in tidal currents. The significance of these latter concepts has yet to be translated into biological terms. Their obvious applications for transport and retention by opportunistic larval fishes suggests further investigation.

Estuarine circulation and its physical properties have been reviewed elsewhere (Dyer 1973; Kjerfve 1978; Wiseman 1980). A typical exchange pattern for a positive estuary (one in which river discharge and precipitation is greater than evaporation) is a net nontidal downstream movement of fresh water at the surface level-of-no-net-motion at the mid-depth range, and a residual upstream countercurrent movement of saltwater at the bottom (Emery and
Stevenson 1957). This situation allows for the passive upstream transport of planktonic organisms as particles in the estuary's lower water layers, even though downstream losses will occur (Pritchard 1953; Ketchum 1954). Planktonic transport then depends on which water layer the organism occupies (Emery and Stevenson 1957).

Oceanic Transport

Water currents play an important ecological role for the majority of fish, egg and adult alike, and invoke a wide range of behavioral responses (Arnold 1974). Currents furnish a transport mechanism as well as directional information and are important in moving fish eggs and larvae to or from areas conducive to survival (Schmidt 1925; Carruthers 1938; Walford 1938; Sette 1943; Bishai 1960). Therefore, currents directly influence recruitment and subsequent year-class success.

During the early 1900's, pioneer research correlating water currents and distribution of fish spawning products centered around the British Isles and seas of northern Europe (Walford 1938). Some of the earliest U.S.A. work relating plankton distributions to circulation patterns was done in the Gulf of Maine (Bigelow 1926, 1927). This ground work led to the analysis of 1931-32 distributional data for haddock (*Melanogrammus aeglefinus*) eggs and larvae on Georges Bank. Along with simultaneous surface drift bottle data, the distribution of larvae indicated retention in a residual anticyclonic (clockwise in the northern hemisphere) gyre in 1931 (Walford 1938). The normal cyclonic circulation pattern returned in 1932 and caused
the loss of eggs and larvae to the deep water off Georges Bank (Walford 1938). Residual near-surface currents on Georges Bank are generally southerly and offshore, except for short periods in the summer (Colton and Temple 1961). This is most pronounced with strong southerly Ekman transport in late October and November. Transport off the Bank can result in mortality due to removal from feeding areas, changes in temperature and salinity, and transport to depths too great from larval settlement (Bolz et al. 1981). However, if the larvae are distributed throughout the water column, or at least below 10-20 m, they may recirculate around the shallower part of George's Bank since the mean currents at depth are more closely aligned with bank topography (Butman et al. 1982). Those spawning products which are transported in the southwestward flow along the southern flank of Georges Bank may contribute to Middle Atlantic Bight stocks since Georges Bank appears to be the source of much of that water (Butman et al. 1982).

In 1976, winds from the southwest pushed Georges Bank surface waters opposite of their normal southwest flow and resulted in increased densities of sand lance (Ammodytes sp.) larvae on the Bank (Smith et al. 1981). Though the abundance of sand lance larvae remained high in 1977, 1978, and 1979, the center of the abundance shifted back to the south after the return of strong prevailing northwesterly winds. Satellite imagery analysis of water mass distributions is being employed to determine the significance of wind-driven currents to the transport and survival of larvae on Georges Bank. The physical data seem to support the hypothesis that
pelagic fish eggs and larvae normally would be removed from the Bank which would adversely affect year-class success. Ichthyoplankton data, however, are insufficient to support this (Colton and Frisella In Press).

Spawning of walleye pollock (Theragra chalcogramma) in the Gulf of Alaska occurs mainly in Shelikof Strait, an offshoot of a cyclonic (counter-clockwise in the northern hemisphere) gyre, and eggs drift in a fast-flowing southwesterly current along the Alaska peninsula. During a two-week incubation period, and a larval period of several weeks, the fish are carried along the peninsula before they enter the fjords where they spend their first summer. An abundant food source within this current system increases larval survival during transit. In the Bering Sea, several oceanographic fronts that separate characteristic water masses have been identified. These water masses support different zooplankton communities that have varying food value for larval walleye pollock. Recruitment is likely to be affected by oceanographic features that influence the distribution and concentration of both walleye pollock spawning products and their food supply (A. Kendall, NOAA/NMFS/NWAF, pers. comm.).

Off Baja California, a cyclonic gyre develops in the fall-winter period and ends in the spring with the onset of wind-induced upwelling. Spawning times of the area's commercially important finfish species coincide with the development of the gyre (Parrish et al. 1981). Thus, dispersal of larvae is restricted. The presence of these semipermanent cyclonic eddies in the Southern California Bight
plays a role in retention and recruitment of pelagic larvae to adult populations.

Many species of fish consistently spawn on fixed grounds. This characteristic is important since it not only fixes the initial position of larval drift but also fixes the position of the nursery area given a regular (relatively predictable) current system. Therefore a given stock may be contained within, or be determined by the constancy of, a migratory circuit. The drift pattern of the young combined with the return to the parental spawning grounds would then form the stock's geographic base (Cushing 1976). The number of genetically distinct North Atlantic herring (Clupea harengus) stocks may be determined by the number of geographic retention areas of the larvae, which are physically separated by oceanographic conditions (Sinclair and Iles 1981; Iles and Sinclair 1982). Overwintering distributions of the larvae in the western and eastern North Atlantic indicate a low degree of stock mixing during the larval stage. Hydrographic features correspond to distribution patterns of the larvae and are generally associated with the same geographic areas year to year. Tidally-induced cyclonic gyres provide the physical mechanism for retaining the young of the individual stocks.

Examples of the separation of fish populations by current systems which restrict dispersal of larvae, can be found in other oceans of the world. The existence of a faunistic boundary along the northwest African coast may result from the prevailing regional hydrographic conditions. The Mauritanian upwelling prevents the northward
transport of epipelagic fish larvae (Hamann et al. 1981). Off southwest Africa, three distinct areas of ichthyoplankton distribution have been identified which also appear to be the result of local oceanographic processes (Badenhurst and Boyd 1980).

Currents generated by wind-induced upwelling of nutrient-rich bottom waters, produce some of the world's most productive fishing areas, as exemplified by the four major eastern boundary current systems, the California, Peru, Canary, and Benguela. These boundary currents appear to have similar environmental dynamics and are dominated, in terms of exploitable biomass, by very similar assemblages of pelagic fish species (Bakun and Parrish 1982).

Along the Pacific coast of the U.S.A., life histories are sometimes constrained by the California Current system and vigorous upwelling off Washington, Oregon, and northern California. Spawning is primarily: demersal (herring, cottids, lingcods), live-bearing (rockfish, embiotocids), anadromous (salmonids), deep-water (pleuronectids, sabelfish), and migrant (herrings) (Parrish et al. 1981). For example, the English sole (Parophrys vetulus) has a nearshore spawning pattern which negates the effects of offshore Ekman transport. Conversely, Dover sole (Microstomus pacificus) larvae are kept in suitable offshore waters by fronts associated with winter convergence (Hayman and Tyler 1980). This is not to imply that all the ichthyoplankton in this area are dependent on upwelling patterns. The summer distribution of northern anchovy (Engraulis mordax) larvae off Oregon is closely tied to another hydrographic feature, the
Columbia River discharge plume, a major source of nutrients and fresh water (Richardson 1981). In these examples, survival of larvae is mediated by the prevailing current systems.

The Southern California Bight is the spawning ground for the numerically dominant species of the California current system: northern anchovy, Pacific sardine (*Sardinops sagax*), Pacific hake (*Merluccius productus*), jack mackerel (*Trachurus symmetricus*), Pacific mackerel (*Scomber japonicus*), and Pacific bonito (*Sarda chilensis*). Larvae of some of the inshore spawners develop rapidly enough to maintain their position in the nearshore zone despite a persistent upwelling feature. Larvae with a longer planktonic life adjust their vertical position. They are initially carried offshore at the surface and later transported onshore by subsurface currents (Gruber et al. 1982). In the same region however, a study involving a galatheid crab, which spawns coastally and has a long larval pelagic life, failed to show a retention mechanism (Longhurst 1968). The crab larvae were transported into oceanic regions with little chance of immediate return to the coastal region to settle.

The apparent dependence of pelagic spawning success and recruitment upon drift conditions at the surface, as well as at depth (Rothlisberg 1982), suggests that anomalies in drift patterns or movement of spawning grounds could be a major source of the widespread variation in recruitment success. When population habitat boundaries shift, there is generally an effective change in potential habitat available to larvae, which can influence reproductive success (Sharp
Intensive fishing pressure increases a stock's sensitivity to environmental conditions (Bailey 1980). For example, the spawning migration of Pacific hake off California has been characterized by smaller, younger fish spawning earlier and in the north, while the older, larger fish produce the major spawn later in the season and further south. Smith (1975) suggests that as a result of fishing pressure reducing the numbers of larger fish, the principal hake spawning grounds shifted northward leading to the abandonment of the optimum southern habitat for larvae. This perturbation is compounded by the stronger Ekman transport in the north, which distributes the hake larvae farther offshore, decreasing survival and the resulting year-class success (Bailey 1980, 1981). Heavy fishing activity may have also reduced North Sea herring stocks and their capacity to fully exploit available nursery areas (Sinclair and Iles 1981).

Nelson et al. (1977) quantified the effects of Ekman transport on year-class strength of Atlantic menhaden (*Brevoortia tyrannus*). They hypothesized that a physical mechanism was necessary to transport the larvae from their offshore spawning ground to inshore nursery areas. The spawning peak appears to coincide with a period of shoreward surface transport. They employed a 16-year time series to develop a survival index based on the relationship between theoretical Ekman transport and survival of the young. This density-independent index was incorporated into a density-dependent spawner-recruit model to predict menhaden year-class strength. Similarly, Parrish and MacCall's (1978) density and environmental-dependent spawner-recruit
model incorporates upwelling indices as a measure of primary productivity and surface transport of larvae.

Another mechanism is responsible for the transport of the South African anchovy (Engraulis capensis) from its spawning ground to its nursery area 250 km to the north (Shelton and Hutching 1982). A strong shelf-edge frontal jet is a typical summer feature carrying larvae from the Cape to Lambert's Bay. However, strong northwest winds can cause this jet to deteriorate. The result is poor recruitment due to starvation of larvae remaining on spawning grounds or loss of larvae carried eastward by the wind-induced current reversal (Shelton and Hutching 1982).

Winds can also lead to the exchange or replacement of water masses which can result in local conditions being more favorable for the survival of larvae. An example of this occurs along coastal Newfoundland when onshore winds exchange a water mass rich in predators for one having fewer predators and more prey for larval fish. This exchange initiates the emergence of larval capelin (Mallotus villosus) from intertidal demersal eggs (Frank and Leggett 1982). Thus, capelin larvae begin their drift and first feeding in a wind-induced "safe-site". The timing of hatching may be positively reinforced by such a water mass transport which enhances survival of the young. Hypothetically, similar "safe sites" exist elsewhere. However, it is difficult to document the physical processes producing them and to quantify their role in larval survival (Frank and Leggett 1982). Ongoing research suggests that the larval drift of other
demersal spawners may be synchronized with that of capelin in this wind-induced "safe-site". Selective advantages to the less abundant species drifting with the numerically dominant species in this water mass include: reduced predator abundance, increased food availability and growth rates, and reduced predation rate (Frank and Leggett 1983).

Recently there has been an increase in the number of studies dealing with the consequences of Gulf Stream transport and migration (Boyd et al. 1978; Cox and Wiebe 1979; Taylor and Stephens 1980; The Ring Group 1981). Larval bluefish (Pomatomus saltatrix) spawned in the South Atlantic Bight may drift north of Cape Hatteras in the Florida current before moving shoreward (Kendall and Walford 1979; Powles 1981). This type of transport mechanism has also been demonstrated for the American eel, Anguilla rostrata, (Kleckner and McCleave 1982) and a number of other taxa (Olney and Markle 1979). Fisheries biologists have speculated that Gulf Stream rings might influence larval fish recruitment by removing eggs and larvae from the shelf. The transport of sand lance larvae was linked to entrainment of shelf water moved off-shelf by a warm core ring, an anticyclonic offshoot of the Gulf Stream (Friedlander and Smith 1983). This type of entrainment of larval fish has only recently been observed and there is a controversy as to the significance of these rings to long term recruitment. Recent work, employing a simplified mathematical model which incorporates historical Atlantic cod (Gadus morhua) and haddock ichthyoplankton data from Georges Bank, indicated that warm core rings could have a considerable impact on the distribution and
survival of cod and haddock larvae on the Bank (Flierl and Wroblewski, In press).

Estuarine Transport and Retention

One cannot always consider current transport systems in oceans apart from estuaries. Continental shelf and estuarine waters are physically coupled by circulation, sediment, and nutrient interactions (Turner et al. 1979). This coupling affects distribution of fish eggs, larvae, and juveniles through a variety of factors such as outwelling, and flushing from and transport into estuaries. For example, turbidity, as linked to predation pressure and food supply, can be an important factor influencing the young fish entering certain estuaries (Blaber and Blaber 1980).

Arnold (1974) reviewed the literature on fishes orienting within currents (rhetropoism), passively drifting with them, or modifying their horizontal drift by diel or seasonal vertical migrations. One type of this modified drift involves tidal transport and retention mechanisms. In such cases a marine organism undergoes horizontal displacement by tidal currents in a direction advantageous for survival. This dispersal may be behaviorally passive or active, in a landward or seaward direction, in an estuary or in the open sea, or in any combination of these. An organism may experience both seaward and landward displacements during different stages of its pelagic existence.
Vertical migration is influenced by the interaction of larvae with both physical and biological factors in the ocean, e.g. oceanic currents, stratification, light, oxygen, species-specific temperature preference, phototaxis, and predator or prey distributions. Strong salinity discontinuities can inhibit positive phototactic responses and diel vertical migrations of zooplankton (Grindley 1964) or the resulting density discontinuity may aggregate zooplankton (Harder 1968). Recently a relationship between vertical distribution of yolk-sac California grunion (Leuresthes tenuis) and water temperature has been demonstrated (Ehrlich and Muszynski 1982).

Diel vertical movements can be adaptive in that a migrator may move into water masses with different speeds and directions, thereby greatly enhancing its horizontal displacement capacity (Hardy 1953, 1956; Waterman 1958; Bainbridge 1961). Tidal currents can provide a vertical velocity gradient. The combination of tidal and riverine input in an estuary can provide a vertical gradient in net directional displacement. Estuarine tidal currents influence vertical migration, especially where plankters have to maintain a critical density in areas subject to strong dispersive tidal flows (Grindley 1964; Woodmansee 1966). The idea of synchrony between selective swimming and tidal cycles was first proposed by Nelson (1912, 1917) for oyster larvae, which ascend during flood tide and descend during ebb. A behavioral selection mechanism was also demonstrated for the migration of a penaid shrimp (Hughes 1969a, 1969b, 1972). Most of the early work on estuarine tidal transport or retention involved invertebrate studies (Prytherch 1928; Nelson and Perkins 1930; Nelson 1931, 1954;
Rughley 1933; Rogers 1940; Carriker 1951; Manning and Whaley 1954; Bousfield 1955; Kunkle 1957; Woodmansee 1966). Continuous measurements of spontaneous activity or metabolic rate of crustaceans revealed rhythmic components of both diel and tidal frequencies (Brown 1961). These early studies formed the basis for the present relatively advanced state of crustacean estuarine transport investigation (see Kennedy 1982 for collection of papers on physical export and reentry, behavior, reproductive strategies, and genetic selection). These mechanistic principles provide a basis for larval fish transport investigations.

Studies involving North Sea flatfish spawning migrations have demonstrated that adult sole (Solea solea) and plaice (Pleuronectes platessas) select tidal currents in favorable directions before vertically ascending (de Veen 1967; Greer Walker et al. 1978). This selective tidal transport results in a demonstrable energy savings (Weihs 1978). Energy conservation has also been shown to result from daily vertical migrations in northern anchovy up to 11 mm SL (Theilacker and Dorsey 1980). Similarly, the migratory behavior of larval fishes in estuaries is manifested mostly in the vertical rather than horizontal plane. Such behavior, in order to maximize the benefits of retention or transport, should be selective, although random vertical movement may be better than none at all. In fact, the retention of larvae in estuaries can sometimes be explained by totally mechanical processes (i.e. buoyance, tidal current variability, turbulence, etc.) which eliminate the need for behavioral suppositions such as the necessity of larval phototaxis or tidally
stimulated swimming behavior (DeWolf 1973). A study of the ichthyoplankton distribution and ecology in Connecticut's Mystic River, which has a well defined two-layered circulation system, indicated that demersal eggs may be an effective mechanism to ensure spawning success and nursery area retention (Pearcy and Richards 1962). The resulting larval densities were significantly greater in the landward-moving bottom layer than at the surface.

Rogers (1940) was the first to study the interaction of tidal currents and diurnal vertical migration in larval fish. He reported that larval rainbow smelt (Osmerus mordax) in the Miramichi River, New Brunswick were not flushed out of the estuary because of diurnal vertical migration, since the older larvae were negatively phototropic. An average of 15 hours of daylight during their larval season, June and July, ensured that the larvae had a longer residence time in the deeper landward-moving water layer. Such results have led some authors to conclude that the influence of diel migration on the distribution and survival of larval fish has been ignored too often (Smith et al. 1978).

Selective tidal transport can also be independent of the influences of diurnal vertical migration, as demonstrated for the spring inshore migration of Anguilla vulgaris elvers from the Dutch Wadden Sea and the Marsdiep tidal inlet (Creutzberg 1961). Later evidence was found for selective tidal transport by plaice larvae in the same area (Creutzberg et al. 1978). Estuarine selective tidal transport has also been demonstrated for the American eel (Shaw 1981;
McCleave and Kleckner 1982). This type of transport may be responsible for the discontinuous seaward migration of pink salmon (Oncorhynchus gorbuscha) fry (Healey 1967). Tidally phased activity rhythm has also been shown for the hogchoker, Trinectes maculatus, (O'Connell 1972) and for young plaice (Gibson 1973).

The triggering of active vertical migration by tidal currents in a two-layered estuarine circulation system leads to flushing, transport, or retention of larvae (Graham and Davis 1971; Graham 1972; Shaw 1981; Fortier and Leggett 1982). In the two-layered Cape Fear River, North Carolina, the larvae of spot (Leiostomus xanthurus), Atlantic croaker (Micropogonias undulatus), and flounders (Paralichthys sp.) displayed behavioral responses, primarily to tide and photoperiod, which aided their transport and retention within the estuary (Weinstein et al. 1980). This expands an earlier hypothesis (Wallace 1940; Haven 1957) that, in the Chesapeake Bay, larval croaker exhibit passive up-channel transport after actively seeking the bottom layer. A similar transport method is utilized by another offshore fall spawner, the hogchoker (Dovel et al. 1969).

In the upper reaches of the St. Lawrence River estuary, physical responses to estuarine circulation are shown by the surface downstream flushing of capelin, bottom upstream movement of Atlantic herring, and retention of rainbow smelt (Fortier and Leggett 1982). Life histories of fishes and associated plankton distributions in the lower reaches of this estuary also appear to be adapted to the circulation patterns (DeLaFontaine et al. 1981). The timing and spatial occurrence of
spawning tends to take advantage of periods and areas of high productivity, special predator-prey relationships, and conditions affecting transport, all of which will further the survival of the young. Fortier and Leggett (1982) have reviewed these interconnected cause and effect relationships which historically have been labelled critical period (Fabre-Domerge and Bietrix 1897; Hjort 1926; May 1974), environmental match/mismatch (Cushing 1972), and circulation-survival (Turner and Chadwick 1972).

Discussion and Conclusions

The ICES Report of the Working Group on the Distribution of Larval Fish (1979), an excellent international review of larval programs, includes the subject of transport. This working group developed a conceptual model (Figure 1) of the major elements of fisheries ecology. Included are physical factors affecting the distribution and transportation of larvae: stratification, advection, weather, and climate. Identification and quantification of these factors affecting larval transport, in relationship to recruitment, have been targeted as key issues in recent fisheries ecology meetings (Ad Hoc Group 1980; WHOI/NMFS 1981; Bakun et al. 1982; Rothchild and Rooth 1982).

Reproduction occurs only within a relatively small portion of, or at selected sites within the total species range. Reproductive aggregations of migratory species generally are concentrated in geographic areas which have historically provided conditions for reproductive success, i.e. areas of relative long-term hydrographic
stability but not necessarily consistent year-to-year stability (Cushing and Dickson 1976; Sharp 1981). Fish with pelagic eggs often reproduce in gyres and fronts (Loeb 1980; Frank and Leggett 1983), thus making areas of upwelling and boundary currents among the most productive (Garrod and Knights 1979). The genetic divergence of stocks, in some cases, is probably enhanced by prevailing gyral or upwelling conditions. Environmental variation, however, is always a factor, necessitating adaptable life history characteristics (Garrod and Knights 1979). Most coastal species have increased their reproductive potential with high fecundities, protracted spawning seasons, or multiple spawning sites to counteract the mortalities associated with "unpredictable" environments. Yet, certain species additionally maximize larval survival by taking advantage of "normal" oceanographic conditions. There are relatively few kinds of current systems, and these influence transport of young in predictable ways. Successful recruitment of larvae may be enhanced by "safe sites" in which physical processes usually insure that biological conditions are favorable for survival. Recruitment success for larvae of many species is linked to retention within, or appropriately timed transport into or out of estuaries. Therefore, displacement of spawning grounds or spawning products can have an adverse effect on recruitment. Anomalous physical and biological conditions can enhance or inhibit survival. Ultimate reproductive success for some species is dependent upon a match/mismatch of the most influential physical and biological factors.
Species and site-specific ichthyoplankton studies can help to understand the influence of several larval fish transport mechanisms such as: major ocean currents, oceanic fronts, upwelling regimes, coastal currents, estuarine/coastal coupling, river plumes, and two-layered estuarine circulation. Knowledge of current patterns, prevailing wind conditions, and periodicity of atmospheric frontal passages should be considered in planning studies and quantifying and predicting planktonic drift patterns. Since these interactions have an adaptive value to increase spawning success, future investigations should consider patterns of planktonic transport and dispersal since present day spawning areas and times have been reinforced by, and may owe their continued existence to the dominant physical conditions.

Initially, the investigation of marine transport mechanisms was approached descriptively. Early studies involved the documentation of seasonal, spatial, and vertical distributions with or without observations of the physical environment. Today's approach is more comprehensive and process oriented, involving empirical analyses of the factors driving transport. Regression and time-series analysis approaches, which involve spawning and transport success and year-class strength (along the lines of spawner-recruit environment-survivor models), would allow incorporation of these effects on larval survival into a predictive model. Research is needed to determine the environmental cues and behavioral responses involved in the directional selection of larvae actively migrating. Areas of estuarine research which show promise include continued biological studies on the effects of wind, and pioneer work on the
effects of nontidal forcing from the coastal ocean and the effects of
topography on transverse circulation in estuaries. Ideally the study
of ichthyoplankton dynamics, survival, and subsequent recruitment
success should include, the determination of physical and chemical
processes, as well as biological interactions that affect the natural
variability at both the macro- and microscales in time and space. We
must broaden our research approaches especially in light of the
expanding oceanographic data on the importance of long-term cycles;
the coupling of climatology, hydrography, productivity, and the
ecosystem; and the significance of the offshore-coastal-estuarine
linkage. A basic understanding of these linkages is an integral part
of developing, evaluating, and refining future spawner-recruit
environment-survival relationships and models. This understanding is
also important to the fundamental understanding of reproductive
patterns, genetic divergence, community stability, and ecosystem
energy flux. "The larval transport and retention problem will require
interdisciplinary communication for resolution...the problem stands at
the state of the art in both physical and biological fields" (Boicourt
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FIGURE LEGENDS

Figure 1. Schematic representation of the major elements of a fisheries ecology investigation designed to provide population information for resource management purposes. Environmental influences on the populations including gradients, currents, weather and climate, are subjected to correlative and cause-effect analyses. Analyses of energy linkages and transfer efficiencies provide a unifying matrix for the studies.

(After ICES 1979)
MESOSCALE MICROSCALE

STRATIFICATION ADVECTION WEATHER CLIMATOLOGY

GROWTH/FEEDING & MIGRATIONS/FEEDING

MESOSCALE

PREDATION / COMPETITION LARVAL SURVIVAL TROPHODYNAMICS

ADULTS JUVENILES

SPAWNING BIOMASS

FORECASTS OF RECRUITS

PREDATION/COMPETITION BENTHOS PLANKTON NEKTION

ENERGY FLOW ANALYSES

RESOURCE INFORMATION FOR PREDICTION & MANAGEMENT
Appendix 6.5 - Figure

Model depicting behavioral response of post-larval croaker to tide and photoperiod (from Weinstein et al. 1980).
A - TIDAL RESPONSE (MOVEMENT TOWARD BOTTOM ON EBB)
A' - TIDAL RESPONSE (MOVEMENT TOWARD SURFACE ON FLOOD)
B - PHOTOPERIOD RESPONSE (BOTTOM ORIENTATION DURING DAY)
B' - PHOTOPERIOD RESPONSE (SURFACE ORIENTATION AT NIGHT)
APPENDIX 7
Appendix 7.1 - Figure

Linear regression of the April-September summer survival index ($J_{SUM}$) on the January-February-March average temperature (JFM), 1954-1982, ($R^2 = 0.61$, $n=29$).
Appendix 7.2 - Figure

Quadratic relationship between the summer survival index \( (J_{\text{SUM}}) \) and the winter temperature \( (JFM) \). The seven coldest years in which the temperature is the predominant factor are labelled.
Appendix 7.3 – Figure

Quadratic relationship, with each point labelled by year, between the summer survival index and the winter temperature when it is greater than 4.5°C, 1954–1982.
Appendix 7.4 - Figure

Linear regression of the April-September summer survival index ($J_{SUM}$) on the October juvenile index ($J_{OCT}$), 1954-82. ($R^2 = 0.62$, n=25).
Appendix 7.5 - Figure

Linear regression of the April-September summer survival index ($J_{\text{SUN}}$) on the October juvenile index excluding the seven years when the January-February-March temperature was less than $4.5^\circ\text{C}$, 1954-1982, ($R^2 = 0.57$, $n=18$).
APPENDIX 7.6

Multiple Regression Analysis
Data for 1957 are Excluded

DEPENDENT VARIABLE..  J_{SUM}

VARIABLE(S) ENTERED ON STEP NUMBER 1..  JFM
2..  OCT
3..  SQJFM

MULTIPLE R  0.97552
R SQUARE  0.95165
ADJUSTED R SQUARE  0.94439
STANDARD ERROR  5.63766

ANALYSIS OF VARIANCE

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Appendix 7.7 - Figure

Linear form of the April-September croaker survival index $(J_{SUH})$ regressed on the result of the multiple regression equation incorporating winter temperature (JFM) and the October juvenile index, with 1957 data excluded:
Appendix 7.8 - Figure

Actual and hindcast summer juvenile indices, 1954-1982. Hindcast values (OCT) are calculated from October juvenile indices and winter temperatures with 1957 data excluded ($R^2=0.94, n=24$).
Summer Young-of-the-Year Croaker

Legend

△ Actual
× Hindcast (OC)
APPENDIX 7.9

Multiple Regression Analysis
Above 5.0°C, 1954-1982

DEPENDENT VARIABLE: J Sum

VARIABLE(S) ENTERED ON STEP NUMBER 1.. JFM
2.. MAX
3.. SQJFM

MULTIPLE R 0.90610
R SQUARE 0.82101
ADJUSTED R SQUARE 0.79660
STANDARD ERROR 11.31455

ANALYSIS OF VARIANCE

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APPENDIX 7.10

Multiple Regression Analysis
Adjusted and Above 5.0°C, 1954-1982

DEPENDENT VARIABLE: J Sum

VARIABLE(S) ENTERED ON STEP NUMBER
1.. JFM
2.. MAX
3.. SQJFM

MULTIPLE R 0.90676
R SQUARE 0.82222
ADJUSTED R SQUARE 0.79797
STANDARD ERROR 11.27635

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<td>MAX</td>
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<td>0.09337</td>
<td>0.23123</td>
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<td>40.54987</td>
<td>3.346</td>
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APPENDIX 8.1
Details of the Virginia and North Carolina Croaker Fisheries

North Carolina's coastal and sound fishery, like that of Virginia, is a "summer time" (April-October) fishery. However, the North Carolina fishery is largely comprised of long haul seine landings in Pamlico Sound, a fishery unique to that state since the early 1900's (DeVries 1980). Additional captures are made by common haul seines, pounds nets and gill nets. Pound net and long haul seine fisheries, the major sound gear for croaker, have been described by Higgins and Pearson (1927) and, the latter, more recently by DeVries 1980. No clear relationship between total capture and numbers of crews, an index of effort, is apparent for the long haul seine fishery, though increasing effort from 1971 through 1975 seems to parallel increased catches, primarily of croaker, which increased 45-fold from 1971 to 1979 (Devries 1980).

The Mid-Atlantic Bight 1930 maximum landings of foodfish came shortly after a winter trawl fishery was instituted on the shelf to increase the geographic and time spans for fishing (McHugh 1977b). The winter otter trawl fishery, which began about 1920 on a small scale in New Jersey, pursued estuarine species, specifically croaker, to their winter grounds as far south as Cape Hatteras by 1928-29 (Pearson 1932). The early expansion of this fishery, including composition, gear type and effort has been thoroughly described by Pearson (1932). This is
still used as a reliable source and there has been no recent study to replace it. NCDNR/DMF initiated a study of the trawl fishery in 1979, but since that time, the landings have been inadequate for analysis (S. Ross pers. comm.).

As the trawling fleet knows, and confirmed by tagging studies (Pearson 1932, Pacheco 1958, Haven 1959), fish leaving the inshore waters from Chesapeake Bay and northward migrate south toward Cape Hatteras. Catch composition north and south of Cape Hatteras differs, separated by a marked gradient in water temperature (Pearson 1932) indicative of the thermal convergence here (Bumpus 1973), making the area south of Cape Hatteras attractive to southern species (Pearson 1932). The development of the winter trawl fishery increased pressure on summer fisheries that may have already been at their sustained peak, and Pearson (1932) perceived that the future of fisheries at that time seemed dependent on the ability of stocks to withstand further pressure.

The catches in the early years were mainly marketed in Phoebus, Hampton and Norfolk, Virginia, although some were landed in New Jersey (Pearson 1932). This may have contributed to the higher landings of croaker north of Virginia in the 1930's discussed earlier. Detailed statistics are not available, so it is difficult to assess when significant trawler landings began to occur in North Carolina. This coastal fishery extends from the Virginia Capes south of Cape Hatteras. Port of landing does not necessarily indicate area where croaker were caught, as landing site is usually determined by the home port of the vessel.

The otter trawl fishery is supported by croaker migrating from the bays to offshore warmer water (Wallace 1940). Croaker gradually
leave bay/sound waters from July to November (Wallace 1940), but a mass exodus is noticed when water temperatures begin to fall (Bearden 1964). Another North Carolina fishery which takes advantage of this fall spawning out-bay migration is the sinking gill net (S. Ross pers. comm.). It takes place at the same time, in winter and early spring, and the same place, concentrating on spawning aggregations around Cape Lookout up to Cape Hatteras, as the trawl fishery. There has been no literature documentation nor analysis of this fishery.

The croaker available on the in the fall shelf are I+ and II+, immature or first-time spawners. Research trawl catch size frequencies range from 100 mm upward because of different gear which catches smaller fish than commercial trawls which catch fish 200 mm to 450 mm. The September and October 1950 commercial catches were chiefly age II. There are no recent studies to show length/age composition of this trawl fishery so it may be inferred that the fish now captured are as least as small as the 1950 size and possibly as small as those taken in the research gear. Pearson (1932) says that fish under 250 mm were too small to market, so croaker taken by the early trawlers were at least II years old. Pearson's study only consisted of marketable croaker with no measure of shipboard discards. The fact that 46% of the trips yielded marketable croakers (Pearson 1932) indicates that they were being actively fished, were relatively numerous and were likely to have been caught at smaller sizes than shown. A 2 1/2 inch stretch mesh was used in 1930 (Pearson 1932), allowing primarily larger fish to be taken. This resulted in reduced catches when the stock size was down and few large fish were available. Pearson (1932) mentions improvement of techniques and both local and out-of-state increases of fishing
pressure, and although he says the fishery was expanding, gave no measure of effort.

Waste in this fishery has long been a problem. Pound nets were introduced in 1870 (Reid 1955). By 1883 pound nets were accused of catching fish too small to use and by 1909 were charged with destroying more than marketed (Higgins and Pearson 1927). During the early, increasing years of the fishery, 1910-15, croaker were taken in such large quantities in the spring that they were unmarketable (Hildebrand and Cable 1930) and protective legislation was discussed in Virginia (McHugh and Bailey 1957). Wastage of croaker and other species was so constant in the 1920's North Carolina pound net fishery, and probably paralleled in that of the Chesapeake Bay, that Higgins and Pearson (1927) concluded that the "supply of fish in North Carolina does not equal the demand." The large quantity of croaker in 1956 glutted the market so that the price fell to two cents per pound and could not be sold (McHugh and Bailey 1957). Croaker less than 240mm (9.5 inches) are classed as discards in North Carolina and in 1978 made up 69% of the pound net catch in July, 86% in August, 33% in September and 12% in October (Sholar 1979). These are the months when 0+ fish are heavily exploited.

Long haul seines, presently greatly improved over the earlier gear, are very effective and capable of catching practically all demersal fish in its path (DeVries 1980). They were touted as worse than pound nets by a fish dealer in 1912 (Higgins and Pearson 1927). In 1978 the discard croaker from long haul seines comprised 33% of the catch in April, 42% in May, 58% in June, 45% in July, 87% in August and 31% in September (Sholar 1979). DeVries 1980 says these are too small
to sell but Sholar (1979) says most are sold as crab bait. Declining croaker populations have also been attributed to stock reduction through young-of-the-year incidental catches by the North Carolina shrimp fishery (Haven 1959, McHugh 1978). Atlantic croaker is one of the major components by weight of the shrimp by-catch in the South Atlantic Bight, comprising 24.2% in North Carolina, 8.8% in South Carolina and 20.9% in Georgia percent by weight discard (Keiser 1976). Forty-nine percent of croaker in the scrap fishery are age $0^+$; the rest $1^+$ (Wolff 1972). Only a fraction of this catch is landed. Most is discarded at sea. Although Keiser (1976) found no evidence to substantiate the concern that this practice is depleting commercial finfish stocks, no matter what the gear, catches of immature croaker potentially reduce the size of the spawning stock.
Appendix 9.1 - Figure

Length/frequencies of croaker on the shelf in fall months taken by MARMAP cruises, 1968-81. Length at 100% maturity, based on time of cessation of summer winds, and percent of catch that is 100% mature is indicated on each.
Length Frequency for Croaker October, 1969
Mid-Atlantic Bight
N = 48
Length Frequency for Croaker October, 1971
Mid-Atlantic Bight
N = 3
Length Frequency for Croaker, November, 1972

Mid-Atlantic Bight

N = 2623

Percent

25.9%
Length Frequency for Croaker November, 1975
Mid-Atlantic Bight
N = 51550

14.7%

Percent

Length
Length Frequency for Croaker August, 1977
Mid-Atlantic Bight
N = 4768

Percent

Length

67.6 %
Length Frequency for Croaker September, 1977
Mid-Atlantic Bight
N = 856

Percent

Length

51.5%
Length Frequency for Croaker October, 1977
Mid-Atlantic Bight
N = 9080

95.2%
Length Frequency for Croaker October, 1979
Mid-Atlantic Bight
N = 10

Percent

0 10 20 30 40

Length

0 100 200 300 400 500

100%
Appendix 9.2 - Figure

Correlation between the fall recruitment index in the Chesapeake Bay and the mature croaker taken by fall MARMAP cruises divided by area (nmi)$^2$ occupied by croaker during those collections ($r = 0.43$, $n=14$).
Appendix 9.3 - Figure

Correlation between MARMAP croaker abundance and otter trawl landings in Virginia, \((r = 0.84, n=9)\).
Appendix 9.4 - Figure

Correlation between Chesapeake Bay fall recruitment index and the combined Virginia pound net and gill net landings and North Carolina long haul seine landings adjusted for percent maturity ($r = 0.59$, $n=28$). This is the same relationship as Figure 9.5, but the maturity of the commercial catch has been estimated.
Appendix 9.5 - Figure

Correlation between young-of-the year July modal size and
the April-September index of year-class strength,
(r = 0.20, n=25).
Test of Crocker Density Dependence

Legend

Regression

△ JULY SIZE

Summer Juvenile Index

June Model Size
Appendix 9.6 - Figure

Correlation between young-of-the-year July modal size and the total Virginia-North Carolina commercial catch of croaker the preceding year, \( r = 0.11, n=25 \).
Appendix 10.1 - Figure

Summer 1983 year class of croaker ($J_{SUM, JFM} = 24.09$)
predicted from 1983 January-February-March temperature.
Summer Young-of-the-Year Croaker

Legend
- Actual
- Hindcast (JFM)
Appendix 10.2 - Figure

Summer 1983 year class of croaker ($J_{SUM,W} = 30.12$) predicted from 1982 fall wind-induced transport and 1983 January-February-March temperature.
Summer Young-of-the-Year Croaker
Appendix 10.3 - Figure

Summer 1983 year class of croaker ($J_{\text{SUM},\text{MAX}} = 118.29$) predicted from 1982 fall maximum recruitment and 1983 January-February-March temperature.
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