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**Development of Age Determination Methods, Life History/  
Population Dynamics Information, and Yield-per-Recruit  
Simulation Modeling to Evaluate the Potential for Growth and  
Recruitment Overfishing of Atlantic Croaker, *Micropogonias  
undulatus*, in the Chesapeake Bay**

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STUDY OF IMPORTANT RECREATIONAL  
FISHES OF CHESAPEAKE BAY

Federal Aid in Sport Fish Restoration Act  
Project F-88-R-2

*Development of Age Determination Methods,  
Life History/Population Dynamics Information,  
and Yield-per-Recruit Simulation Modeling  
to Evaluate the Potential for Growth and Recruitment  
Overfishing of Atlantic Croaker, *Micropogonias undulatus*,  
in the Chesapeake Bay*

By

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Final Report on Atlantic Croaker Studies  
for the Period September 1988 - May 1994

August 1994

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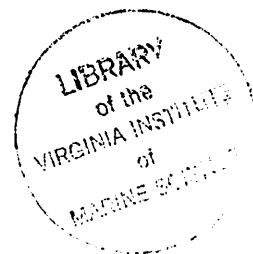
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TABLE OF CONTENTS

SECTION I. . . . . 2

    GENERAL ABSTRACT/SUMMARY . . . . . 2

    GENERAL INTRODUCTION . . . . . 14

SECTION II. LIFE HISTORY, POPULATION DYNAMICS,  
AND YIELD-PER-RECRUIT MODELING OF  
ATLANTIC CROAKER, MICROPOGONIAS  
UNDULATUS, IN THE CHESAPEAKE BAY AREA . . . . . 21

ACKNOWLEDGEMENTS . . . . . v

LIST OF TABLES . . . . . vi

LIST OF FIGURES . . . . . vii

ABSTRACT . . . . . ix

GENERAL INTRODUCTION . . . . . 2

CHAPTER 1. A COMPARISON OF HARD PARTS FOR AGE  
DETERMINATION OF ATLANTIC CROAKER . . . . . 8

    Introduction . . . . . 9

    Materials and Methods . . . . . 10

    Results . . . . . 13

    Discussion . . . . . 20

CHAPTER 2. AGE, GROWTH, AND MORTALITY . . . . . 23

    Introduction . . . . . 24

    Materials and Methods . . . . . 25

    Results . . . . . 30

    Discussion . . . . . 47

CHAPTER 3. REPRODUCTIVE BIOLOGY . . . . . 53

    Introduction . . . . . 54

    Materials and Methods . . . . . 56



Results . . . . .	62
Discussion . . . . .	79
CHAPTER 4. YIELD-PER-RECRUIT ANALYSIS . . . . .	92
Introduction . . . . .	93
Materials and Methods . . . . .	94
Results . . . . .	99
Discussion . . . . .	106
GENERAL DISCUSSION . . . . .	113
REFERENCES . . . . .	120
VITA . . . . .	140
<b>SECTION III. SIMULATIONS OF THE EFFECTS OF FISHING ON THE ATLANTIC CROAKER, MICROPOGONIAS UNDULATUS, IN THE CHESAPEAKE BAY REGION . . . . .</b>	<b>22</b>
ABSTRACT . . . . .	23
METHODS . . . . .	31
Beverton-Holt Model Yield- Per-Recruit Simulations . . . . .	31
Ricker Model Yield- Per-Recruit Simulations . . . . .	34
RESULTS . . . . .	36
Beverton-Holt Model Yield- Per-Recruit Simulations . . . . .	36
Ricker Model Yield- Per-Recruit Simulations . . . . .	50
DISCUSSION . . . . .	56
Responses to Variation in Model Parameters and Delineation of Biological Danger Zones . . . . .	56
Evaluation of the Current Fishery and Current Status of Atlantic Croaker Stocks . . . . .	58

Evaluation of Growth and Reproduction Dynamics, Their Implications for Wise Management, and Management Strategies . . . . .	64
Evaluation of Fluctuations in Abundance . . . . .	72
Eggs-Per-Recruit Model Simulations . . . . .	74
LITERATURE CITED . . . . .	75
<b>SECTION IV.</b> . . . . .	<b>77</b>
Accomplishments on Atlantic Croaker . . . . .	77
Journal Papers . . . . .	78
Theses . . . . .	79
Professional Society Presentations . . . . .	79
Major Management Agency Presentations . . . . .	80

## SECTION I.

### GENERAL ABSTRACT/SUMMARY

The Atlantic croaker, Micropogonias undulatus, supports large recreational fisheries in the Chesapeake Bay region, where it has historically shown large fluctuations in abundance. Although many studies have been conducted on this species in this region over the last 50 years or more, commencing at least as early as Wallace (1940), little or no information exists to support yield modeling and wise management. The present studies were undertaken to provide basic life history/population dynamics information and yield modeling needed to wisely manage this species in the Chesapeake Bay region, and to evaluate the role that fishing plays in their fluctuations. Accordingly, the basic objectives of the present studies were threefold:

- 1) To develop validated methods of age determination required to conduct basic life history/population dynamics studies,
- 2) To develop basic life history/population dynamics information required to conduct yield modeling, and
- 3) To conduct, as feasible, yield-per-recruit and eggs-per-recruit modeling needed to evaluate growth overfishing, recruitment potential, and to provide advice for wise management.

More detailed background, and objectives that flesh out the basic three above, are presented in Section III, General Introduction. We have successfully met these objectives in our six-year study, and the rest of this Abstract/Summary presents our results and

findings. The basic life history/population information and parameters presented are based on an important PhD dissertation supported by these studies (Barbieri 1993) and papers based on it (Barbieri et al. 1994; Barbieri et al. in press). The extensive yield model simulations and interpretations presented were based on that basic information.

Otoliths, scales, dorsal spines, and pectoral fin rays were compared for legibility of presumed annual marks and precision in repeated readings, to determine the best hard part for aging. Marks on transverse otolith sections were easiest to read, showed the best agreement between readings by far, and gave us the greatest confidence when making readings. Marks on other hard parts were much harder to interpret than those on otoliths, showed much poorer agreement between readings, and gave us much less confidence when making readings. Mark counts were often lower on other hard parts than on otoliths, a pattern often reported in fishes. Agreement in mark counts was usually low between hard parts. We concluded, therefore, that otoliths were the best structure and showed the most promise for aging. Criteria were developed and presented for identification of otolith annuli. Atlantic croaker collected from commercial catches in Chesapeake Bay and in Virginia and North Carolina coastal waters during 1988-1991 were then aged using otolith sections, and marginal increment analysis was then used to validate use of transverse otolith sections. Marginal increment analysis showed that, for each age in the range 1-7 yr, annuli



are formed once a year in the period April-May. Otolith age readings were very precise, with greater than 99% agreement within and between readers on nearly 2,000 fish. Ages 1-8 were found in our analyses, but eight-year-old fish were rare. Otolith-fish size regression relationships related to back-calculation were evaluated.

Age 1 and older Atlantic croaker occur in the Chesapeake Bay in the period April-October, though the new young-of the-year occur there over the winter. Observed lengths-at-age were highly variable and showed a rapid decrease in growth after the first year. No differences in observed growth were found between the sexes. Some 64% of the cumulative observed growth occurred in the first year, and 84% was completed at the end of the second year. As a result, our data showed clear evidence of an asymptote and criteria were met for valid fitting of the von Bertalanffy growth model. Observed lengths at ages 1-7 showed a good fit ( $r^2 = .99$ ;  $n = 753$ ) to the von Bertalanffy model for which related parameters were:  $L_{inf} = 312.4$  mm total length;  $W_{inf} = 409.9$  g;  $K = 0.36$ ; and  $t_0 = -3.20$  yr. Asymptotic 95% confidence limits for  $K$  were 0.20-0.53. Size and age compositions of commercial catches were described and mean age at recruitment to the fishery ( $t_c$ ) was estimated. Maximum lengths and ages were 408 mm total length and 8 yr, respectively, these being estimates of  $t_L$  and an  $l_L$ , respectively. For pooled data, 99% and 99.5% of the fish were less than or equal to 345 and 356 mm total length, respectively, these being additional estimates for  $l_L$  that are

less sensitive to extreme values of individual observations. The smallest fish retained in the foodfish catch was about 200 mm total length, regardless of gear. Age 2 was the first age fully recruited (age  $t_c$ ) to haul-seines, gill-nets, and trawls, but age 3 was the first age fully recruited (age  $t_c$ ) to pound nets. Age 1 fish, however, occur in the scrap catch of these fisheries. Estimates of  $t_c$  were supplemented with an estimate that  $t_r = 0$  based on general life history information. Total annual instantaneous mortality rates (Z) estimated from maximum age and from a linear regression catch curve of pooled Chesapeake Bay catches ranged from 0.55 to 0.63, the mean being about 0.60. Calculated 95% confidence limits for the point estimate (0.63) from the linear regression catch curve were 0.36-0.90. Rates of annual instantaneous natural mortality (M) and fishing mortality (F) were estimated as described below for yield modeling. Length-weight, length-length, and length-girth relationships were described. The latter relationship can be used, as necessary, to develop additional estimates of  $t_c$ .

Life history results above do not indicate the existence of a group of larger, older fish in the Chesapeake Bay region and suggest that the hypothesis of a different population dynamics pattern for Atlantic croaker north and south of North Carolina should be reevaluated.

Maturity stages, oocyte development, spawning pattern, and ovarian cycles were described, and parameters for reproduction were estimated. Atlantic croaker are multiple spawners with

asynchronous oocyte development and indeterminate fecundity. Mean length at first maturity was 182 and 173 mm total length for males and females, respectively. More than 85% of both sexes were mature by the end of their first year, and all were mature by the end of their second year. Spawning extends over a protracted period (July-December), but individual fish spawn for only 2-3 months. Spawning starts in Chesapeake Bay and continues offshore and south as Atlantic croaker migrate from the estuary. However, some individuals seem to complete spawning in estuarine waters. Seasonal fluctuations in sex ratios suggest that males start leaving the estuary earlier than females. A high incidence of atretic advanced yolked oocytes in spawning females (60-100% in spawning phase females; 95-100% in running ripe females) suggests that a surplus production of yolked oocytes may be part of Atlantic croaker reproductive strategy. Under that concept (Barbieri 1993 and Barbieri et al. in press), females would hydrate and spawn more or less of these yolked oocytes depending on environmental conditions. However, the high incidence of atresia in Atlantic croaker of the Chesapeake Bay region may also be a warning signal of some anthropogenic environmental stressor, because it, seemingly at first glance, may not make biological sense that such a large percentage of the females develop and resorb their yolked eggs. We take no position that some anthropogenic environmental stressor actually affects Atlantic croaker, only the position that prudent stewardship of the environment suggests that toxicology (?) studies may be desirable

to evaluate that possibility.

More detail on life history information and population dynamics parameters presented above is given in Section II.

We present yield-per-recruit simulations for Atlantic croaker in the Chesapeake Bay region using the Beverton-Holt model to generate curves of  $Y/R$  on  $F$  and  $Y/R$  on  $t_c$ , and the Ricker model to generate curves of standing stock biomass on age. We also generated Beverton-Holt model curves of  $Y/R$  on  $t_c$ , in addition to yield isopleths presented in Barbieri (1993), because curves of  $Y/R$  on  $t_c$  are a simpler, easier-to-understand graphic presentation than isopleths.

Point estimates for parameters needed in the Beverton-Holt model, given in Barbieri (1993) and Barbieri et al. (1994), along with some interval estimates, are:

- 1) for von Bertalanffy equation growth parameters:  $K = 0.36$ , with asymptotic 95% confidence limits being 0.20-0.53;  $L_{inf} = 312.4$  mm total length;  $W_{inf} = 409.9$  g; and  $t_0 = -3.26$  yr,
- 2) for time parameters:  $t_r = 0$  yr;  $t_c = 2$  yr, and
- 3) for mortality parameters:  $Z = 0.55-0.63$ , the latter value having 95% confidence limits of 0.36-0.90. We used for simulations a value of current  $Z$  ( $Z_{cur}$ ) = 0.60, about the mean of the individual point estimates, to estimate current  $F$  ( $F_{cur}$ ) from postulated values of  $M$  ( $M_{pos}$ ).  $F_{cur}$  was estimated from  $Z_{cur}$  and  $M_{pos}$  by solving for  $F_{cur}$  in the equation:  $Z_{cur} = M_{pos} + F_{cur}$ .

For best use of yield-per-recruit modeling,  $M$  must be known. It was estimated in Barbieri (1993) as 0.29, 0.31, and 0.36 using three methods based on maximum age in the unexploited state, that age being estimated as 15 yr based on Hales and Reitz' (1992) study of otolith age structure in Indian middens from 1600-1700



AD at St. Augustine, FL. Although  $M$  is not well known, we argue that the most likely range is 0.20-0.40, with a most likely point estimate being 0.30. We used the approaches described above to estimate  $M$  and  $F$ , because we felt the initially intended mark-recapture studies were not feasible due to a wide-spread spirit of "no cooperation" that appeared to exist in the various fisheries of the Chesapeake Bay region.

Mortality rates just described were also used in the Ricker model. Growth parameters ( $G$ ) needed for that model were calculated from mean weights-at-age. Weights were estimated using von Bertalanffy predictions of mean lengths-at-age converted to weights using the length-weight relationship, noted above, from Barbieri (1993) and Barbieri et al. (1994).

Finally in parameter estimation, we estimated values of  $F_{.10}$  and combined them with estimates in Barbieri (1993) to supplement Beverton-Holt and Ricker model simulations.

Major findings from simulations were:

- 1) Yields are inversely related to  $M$ , decreasing as  $M$  increases,
- 2) Yields are directly related to  $K$ , increasing as  $K$  increases,
- 3) Yields strongly depend on  $t_c$ , increasing with  $t_c$  to a peak, referred to as a "level of eumetric fishing", and then decreasing as  $t_c$  further increases,
- 4)  $F_{MAX}$  strongly depends on the magnitude of  $M$ ,  $K$ , and  $t_c$ , increasing with each of these parameters,
- 5) The shape of the curve of  $Y/R$  on  $F$  strongly depends on the magnitude of  $M$ ,  $K$ , and  $t_c$ , changing according to the following pattern: it usually rises to a peak at very low or low levels of  $M$ ,  $K$ , and  $t_c$ , becomes asymptotic at intermediate levels of these parameters,

and forms a rising curve at high levels. As a result, specific parameter combinations form response areas or zones in which there is little or no danger of biological overfishing and zones in which there is danger of biological overfishing,

- 6) Over much of the range of  $M$ ,  $K$ , and  $t_c$ , large fisheries and high  $F$  will not reduce yields, because  $Y/R$  rises to an asymptote, or keeps increasing, as  $F$  increases. This response area constitutes a zone in which there is little or no danger of biological overfishing, because there is little or no decrease in yield. It generally occurs (see details in Section III, Results) when  $M = 0.20$  or greater is combined with  $K = 0.20$  or greater and  $t_c = 1$  yr or greater. Because this response zone covers so broad a range of parameter combinations, Atlantic croaker in the Chesapeake Bay region have great capacity to resist biological overfishing,
- 7) At very low  $M$ , yields are sensitive to biological overfishing, because  $Y/R$  rises to a peak at  $F_{MAX}$  and then declines as  $F$  increases further. This response area constitutes a danger zone of biological overfishing. It generally occurs, though not always (see details in Section III, Results and Discussion), when very low  $M$  ( $M = 0.05$ ) is combined with low  $K$  ( $K = 0.20$ ) and low  $t_c$  ( $t_c = 1$  yr). Though yields decrease in this danger zone compared to those at  $F_{MAX}$ , they only decrease some 35% even at levels of  $F$  much higher than  $F_{MAX}$ , for example  $F = 2.00$ ,
- 8) Over much of the range of  $M$ , the current fishing mortality rate ( $F_{CUR}$ ) is below  $F_{MAX}$ , and current yield ( $Y_{CUR}$ ) is below  $Y_{MAX}$ . This situation generally occurs, though not always (see details in Section III, Results and Discussion), when  $M = 0.20$  or greater is combined with  $K = 0.20$  or greater and  $t_c = 1$  yr or greater,
- 9) At very low  $M$ ,  $F_{CUR}$  exceeds  $F_{MAX}$ . This generally occurs when very low  $M$  ( $M = 0.05$ ) is combined with low  $K$  ( $K = 0.20$ ) and low  $t_c$  ( $t_c = 1$  yr). We argue herein, however, that levels of  $M = 0.05$  are too low for Atlantic croaker in the Chesapeake Bay region, because that level of  $M$  is consistent with a life span of more than 90 yr in the unexploited state,
- 10) Assuming  $M = 0.30$ , which we feel is the most likely level, the current fishery is below  $F_{MAX}$ . That conclusion must be reached regardless of the level of  $K$  in the range 0.20 or greater and  $t_c$  in the range 1 yr or greater.  $F_{MAX}$  generally equals 2.00 or greater when

$M = 0.20$  or greater is combined with  $K = 0.20$  or greater and  $t_c = 1$  yr or greater,

- 11) Maximum yield at given  $F$  generally occurs when  $t_c = 1-2$  yr, because curves of  $Y/R$  on  $t_c$  generally rise to a peak in this  $t_c$  range and then decline. This pattern occurs when  $M = 0.20$  or greater is combined with  $K = 0.36-0.53$ , if not at low  $K$  ( $K = 0.20$ ). This  $t_c$  range represents levels of eumetric fishing in curves of  $Y/R$  on  $t_c$  and in yield isopleths given in Barbieri (1993). Based on this age, minimum size limits of 200-260 mm total length would provide a modicum of protection needed to resist biological overfishing, if some protection is judged necessary for management,
- 12) Levels of  $F_{.10}$  are much lower than  $F_{MAX}$ . The current fishery does not exceed  $F_{.10}$  if  $M = 0.30$  or greater. However, it does exceed  $F_{.10}$  if  $M = 0.20$  or lower. The current fishery is at  $F_{.10}$  if  $M = 0.25$ . Present data, however, do not permit confident choice among possible  $M$  levels in the range 0.20-0.30.
- 13) Total standing stock biomass and stock biomass at age is inversely proportional to  $F$ , being greatest when  $F = 0.00$ , eg -- when there is a virgin stock, and
- 14) Although biological overfishing is not now occurring according to Beverton-Holt model simulations, the current fishery has greatly juvenesced the stock, eg -- it has greatly reduced total standing stock biomass and stock biomass-at-age.

The above basic simulations are interpreted and discussed in detail in Section III, a section that, in general, presents very extensive discussion of the simulations and the important implications they have for management. Those discussions are organized under the basic headings of: 1) "Responses to Variation in Model Parameters and Delineation of Biological Danger Zones", 2) "Evaluation of the Current Fishery and Current Status of Atlantic Croaker Stocks", 3) "Evaluation of Growth and Reproduction Dynamics, Their Implications for Wise Management, and Management Strategies", and 4) "Evaluation of Fluctuations in

Abundance".

Although Atlantic croaker in the Chesapeake Bay region have great capacity to resist biological overfishing, two kinds of biological overfishing can be distinguished, growth overfishing and recruitment overfishing. Because of their basic assumptions, yield-per-recruit simulations presented herein primarily indicate this species has great capacity to resist growth overfishing. That capacity rests on their intense growth dynamics which are discussed extensively in Section III, along with the important implications they have for management. Atlantic croaker in the Chesapeake Bay region also have great capacity to resist recruitment overfishing. That capacity rests on their remarkable reproduction dynamics which are also discussed extensively in Section III, again along with the important implications they have for management. And finally, appropriate management strategies are discussed extensively in Section III.

All in all, Atlantic croaker seem to have evolved a remarkable life history strategy that is well-adapted to resist both growth and recruitment overfishing. That strategy is probably responsible for the great success this species shows throughout much of it's range -- it is one of the most abundant inshore and/or coastal fishes from the Chesapeake region south to Florida and across the northern Gulf of Mexico through Texas.

Atlantic croaker have historically shown great fluctuations in abundance in the Chesapeake Bay region. Our simulations indicate these fluctuations do not reflect growth overfishing,



because there is little or no decrease in yield over a broad range of parameter conditions, including what appear to be the most likely conditions. Even with the combination of very low  $M$  ( $M = 0.05$ ), low  $K$  ( $K = 0.20$ ), and low  $t_c$  ( $t_c = 1$  yr), the most sensitive set of parameters modeled,  $Y/R$  declines only some 35% in one year. Therefore, our simulations imply that fluctuations of Atlantic croaker in the Chesapeake Bay region largely reflect recruitment phenomena. Because they have great capacity to resist recruitment overfishing, natural causes and/or anthropogenic causes not due to fishing may largely determine population fluctuations. Convincing evidence exists, for example, indicating that low winter water temperatures in Chesapeake estuarine nurseries may result in large mortality, seemingly catastrophic in some years. And, that mortality follows, or co-occurs with, all the other natural perils of early life history stages.

The originally intended eggs-per-recruit studies have not yet proven feasible. Despite collecting and examining many thousands of fish, we have not been able to collect sufficient fish to usefully estimate batch fecundity, much less total annual fecundity. Though unforeseen from the literature on this species, as noted above, it has proven to be a multiple spawner with indeterminate fecundity, a pattern which makes much more difficult the estimation of fecundity. As a result, we could not perform eggs-per-recruit modeling. However, we were able to use yield-per-recruit modeling, as described above, to evaluate

whether population fluctuations were due to growth overfishing or recruitment problems. Furthermore, as described above, we were able to use life history/population dynamics information, as described above, to evaluate the capacity of this species to avoid recruitment overfishing.

## SECTION I, continued

### GENERAL INTRODUCTION

This report presents a Multi-year Final Report for studies conducted on Atlantic croaker, Microponias undulatus, in the period 1988-1994. These studies were conducted with support to the Principal Investigators, Mark E. Chittenden, Jr. and Cynthia M. Jones, from the Wallop/Breaux program of the U.S. Fish and Wildlife Service, from the Virginia Marine Resources Commission, from the College of William and Mary, Virginia Institute of Marine Science, and from the Old Dominion University, Applied Marine Research Laboratory.

The Atlantic croaker, the subject of the present studies, ranges in the western Atlantic from the Gulf of Maine to Argentina (White and Chittenden 1977). It ranges in U.S. waters primarily from Delaware Bay south to Florida and across the northern Gulf of Mexico through Texas. It is one of the most abundant inshore and estuarine fishes, and supports important recreational fisheries, over much of its primary U.S. range.

The Atlantic croaker supports large recreational fisheries in the Chesapeake Bay region, where it has historically shown large fluctuations in abundance (Joseph 1972). The present studies were undertaken to provide basic life history/population dynamics information and yield modeling needed to wisely manage this species in the Chesapeake Bay region, and to evaluate the

role that fishing plays in their stock fluctuations.

Accordingly, the basic objectives of the present studies were threefold:

- 1) To develop validated methods of age determination required to conduct basic life history/population dynamics studies,
- 2) To develop basic life history/population dynamics information required to conduct yield modeling, and
- 3) To conduct, as feasible, yield-per-recruit and eggs-per-recruit modeling needed to evaluate growth overfishing, recruitment potential, and to provide advice for wise management.

The above basic objectives were each fleshed out with more specific objectives as follows. For development and validation of age determination methods, specific objectives included:

- 1) comparison of several hard parts, e.g. scales, otoliths, and fin rays to determine and select the best method including:
  - a) development of criteria to recognize the "annulus",
  - b) analysis of marginal increments to validate the annulus at each age, as feasible, and determine when the annulus forms in the yearly cycle,
  - c) development of body-hard part regression relationships, and
  - d) estimation of precision via repeated readings, and
- 2) determination of how designated observed ages agree between hard parts, with an evaluation of agreement by age.

For development of basic life history/population dynamics information, specific objectives included:

- 1) estimation of time parameters and related sizes for:
  - a)  $t_c$  and  $l_c$ , the age and size at entry to the exploited phase of life, eg -- the fishery,



- b)  $t_L$  and  $l_L$ , the age and size at the end of the fishable life span, eg -- maximum size and age in the catch, and
  - c)  $t_r$ , the age at entry to the exploited area, and
- 2) estimation of growth parameters including:
- a) sizes-at-age from which exponential and von Bertalanffy growth models can be constructed,
  - b) estimates of growth model parameters such as  $G$ ,  $L_{inf}$ ,  $W_{inf}$ ,  $K$ , and  $t_0$ , and
- 3) estimation of mortality parameters including:
- a)  $S$ ,  $1-S$ , and  $Z$ , estimates of survivorship and total mortality, and
  - b) if tagging is feasible, to estimate  $u$ ,  $v$ ,  $M$ , and  $F$ , (expectations of death and instantaneous rates due to fishing and natural causes); if tagging is not feasible, to develop yield-per-recruit models based on selected values of  $M$  and  $F$ , and
- 4) estimation of parameters for reproduction including:
- a) sex ratios,
  - b) fecundity, and
  - c) age and size at maturity, and
- 5) development of ancillary modeling-related data including:
- a) spawning periodicity,
  - b) spatial/temporal movements and distribution,
  - c) age and size compositions of the sampled catch, and
  - d) length-weight, length-girth, and length-length relationships.

For modeling, specific objectives included:

- 1) development of yield-per-recruit assessments of potential growth overfishing and related management concerns in the form of:

- a) Beverton-Holt model curves of  $Y/R$  on  $F$  with simulations of their sensitivity to  $M$ ,  $K$ , and  $t_c$ ,
  - b) Beverton-Holt model yield isopleths with curves of eumetric fishing and  $MSY$ , as feasible, or curves of  $Y/R$  on  $t_c$  as an alternate to estimate eumetric fishing, and
  - c) Ricker model curves of relative biomass on age in relation to  $F$  to evaluate potential for stock juvenescence, and
- 2) development, as feasible, of curves of eggs-per-recruit on  $t_c$  for different values of  $F$  to evaluate how egg production and recruitment potential can be affected by management of  $F$ .

We have successfully met these objectives in our six-year study.

Prior to our studies, there existed little information useful for management of Atlantic croaker in the Chesapeake Bay region, or for evaluating how fishing affects this species there, although many studies had been conducted on this species in this region over the last 50 years or more, commencing at least as early as Wallace (1940). Much of the little life history/population dynamics information published for the Chesapeake region was historical, such as that of Wallace (1940). Much of the other published information on this species was from outside the Chesapeake region, information that may or may not apply well to that region. No modeling, moreover, had been published upon which to base sound management advice for that region. And finally, the age information on which the few available parameters were based from the Chesapeake region were not reliable, because methods of age determination had not even been developed and validated (Beamish and McFarlane 1983, 1987)

for Atlantic croaker in the Chesapeake region.

To meet our objectives, we developed a set of logically-planned, mutually interdependent, and supporting studies. We began by choosing models to be eventually used to evaluate the effects of fishing on Atlantic croaker. We then identified the parameters required in those models and other necessary supplemental information. And finally, we identified the basic information, e.g. validated methods of age determination, needed to successfully estimate model parameters. Accordingly, our studies were planned from the reverse sequence of objectives given above, then were accomplished in the direct 1, 2, 3 sequence. In this respect, our studies have been much different from other long-term studies which often collect data and, only in the final stages, try to figure out "what to do with it". The latter approach often ends up with data that has little or no value, or is not complete enough, for the modeling which is probably the most important result of work funded for management purposes.

Our studies supported, and their objectives formed the basis for, an important PhD dissertation on Atlantic croaker in the Chesapeake Bay region (Barbieri 1993). Accordingly, that dissertation makes up an important part of this Multi-year Final Report. We have cited that dissertation and papers based on it (Barbieri et al. 1994; Barbieri et al. in press) throughout this report. Materials in the dissertation and papers were fleshed out with a substantial concluding section herein that: 1)

presents model simulations over a broader set of parameter ranges to address uncertainty in the parameter values modeled in Barbieri (1993), 2) identifies ranges of parameters that constitute danger zones for biological overfishing and zones of little or no danger, and 3) evaluates the potential for stock juvenescence at fishing mortality rates below those that result in overfishing.

Finally, the format of our report consists of:

1) a Section I which includes:

a) an Abstract/Summary which briefly describes the background, our major objectives and our findings, and

b) a General Introduction which describes in more detail the background, objectives, and need for our work,

3) a Section II on Barbieri's (1993) dissertation which describes basic studies to develop validated methods of age determination, estimates life history/population dynamics information required to conduct yield modeling, and presents initial modeling over a narrow range of parameters,

4) a Section III which builds on the basic studies in Section II and describes the results of yield-per-recruit simulations over a broad range of parameter levels to address uncertainty, identifies response zones for which there is and is not danger of biological overfishing, evaluates the potential for stock juvenescence at fishing mortality rates below those that result in overfishing, and evaluates stock fluctuations, growth overfishing, and recruitment potential to provide a basis for wise management, and

5) a Section IV which describes Accomplishments of our studies to date in terms of journal papers, theses, presentations at national/international professional society meetings, and presentations to state, regional, and national management agencies.

Though it forms the second section of this report to maintain a smooth, logical flow that describes our work in relation to the numerical sequence of our three major objectives, we have presented the sequence of page numbers in Section II as 1-140. That is the sequence in Barbieri's (1993) dissertation, and such handling permits ready citation of the dissertation. Numbering of the remaining sections follows the sequence of 1-80, matching the combined total pages of the rest of the report.

SECTION II.

Life History, Population Dynamics, and Yield-per-Recruit Modeling  
of Atlantic Croaker, Micropogonias undulatus,  
in the Chesapeake Bay area

by

Luiz R. Barbieri

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

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

Life history, population dynamics and yield-per-recruit modeling  
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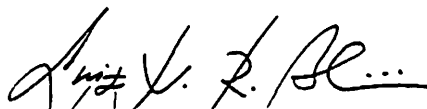
By

Luiz R. Barbieri

1993

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

Doctor of Philosophy



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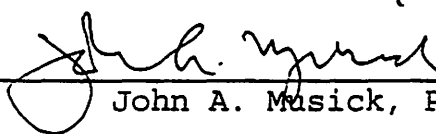
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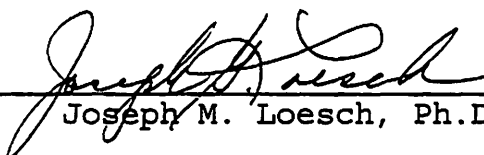
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Mark E. Chittenden, Jr., Ph.D.



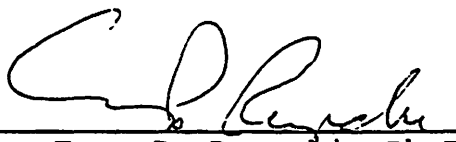
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## TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS.....	v
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
ABSTRACT.....	ix
GENERAL INTRODUCTION.....	2
CHAPTER 1. A COMPARISON OF HARD PARTS FOR AGE	
DETERMINATION OF ATLANTIC CROAKER.....	8
INTRODUCTION.....	9
MATERIALS AND METHODS.....	10
RESULTS.....	13
DISCUSSION.....	20
CHAPTER 2. AGE, GROWTH AND MORTALITY.....	23
INTRODUCTION.....	24
MATERIALS AND METHODS.....	25
RESULTS.....	30
DISCUSSION.....	47
CHAPTER 3. REPRODUCTIVE BIOLOGY.....	53
INTRODUCTION.....	54
MATERIALS AND METHODS.....	56
RESULTS.....	62
DISCUSSION.....	79
CHAPTER 4. YIELD-PER-RECRUIT ANALYSIS.....	92
INTRODUCTION.....	93

MATERIALS AND METHODS.....	94
RESULTS.....	99
DISCUSSION.....	106
GENERAL DISCUSSION.....	113
REFERENCES.....	120
VITA.....	140

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## LIST OF TABLES

Table	Page
1. Percent agreement between mark counts from hard parts of Atlantic croaker from Chesapeake Bay.....	17
2. Summary of ANCOVA to evaluate the effect of Atlantic croaker total length (TL) and age on otolith maximum thickness (OT), maximum length (OL), weight (OW), and radius (OR).....	37
3. Mean observed total lengths-at-age (mm) for male and female Atlantic croaker caught in September, 1988-1990, in the Chesapeake Bay region.....	40
4. Parameter estimates, standard errors, and 95% confidence intervals for the von Bertalanffy growth model for Atlantic croaker in the Chesapeake Bay region (1988-1990).....	41
5. Description of gonad maturity stages for female Atlantic croaker, in the Chesapeake Bay region.....	61
6. Number of males and females by month and Chi-square tests for the monthly sex ratios of Atlantic croaker in the Chesapeake Bay region, 1990-1991.....	70
7. Parameter estimates or range of values used in yield-per-recruit simulations for Atlantic croaker in Chesapeake Bay.....	96
8. Percent increase in yield-per-recruit of Atlantic croaker from $F_{0.75}$ to $F_{MAX}$ for $t_c=1-5$ and $M=0.25-0.40$ .....	102
9. Values of $F_{CUR}$ and $F_{0.1}$ for Atlantic croaker in Chesapeake Bay estimated for $M=0.25-0.40$ .....	105
10. State records of Atlantic croaker caught by recreational fishermen along the East coast of the U.S. ....	117

## LIST OF FIGURES

Figure	Page
1. Marks on hard parts of a 293 mm TL Atlantic croaker from Chesapeake Bay. (A) otolith section; (B) dorsal spine section; (c) pectoral ray section; (D) scale impression.....	14
2. Frequency of occurrence of the absolute difference in mark counts between repeated readings for Atlantic croaker hard parts.....	16
3. Comparison of scale and otolith mark counts for Atlantic croaker from Chesapeake Bay.....	18
4. Transverse otolith section of an 8-year-old Atlantic croaker caught in September 1988 in Chesapeake Bay.....	31
5. Mean monthly marginal increment for Atlantic croaker ages 1-8 from the Chesapeake Bay region, 1988-1991.....	32
6. Transverse otolith section of a young-of-the-year Atlantic croaker (114 mm TL) collected in June 1990 in Chesapeake Bay.....	34
7. Scatter plots and fitted regression lines of different otolith measurements versus Atlantic croaker total length.....	36
8. Observed lengths-at-age and fitted von Bertalanffy regression line for Atlantic croaker from the Chesapeake Bay region (September, 1988-1991).....	39
9. Age frequency (left panels) and length frequency (right panels) distributions by fishing gear for Atlantic croaker in the Chesapeake Bay region, 1988-1991.....	44
10. Catch curve for Atlantic croaker collected from pound-net, haul-seine and gill-net commercial catches in Chesapeake Bay, 1988-1991.....	46

11.	Map of the Chesapeake Bay region. Black dots in Chesapeake Bay indicate pound-net, haul-seine or gill-nets collection sites.....	57
12.	Percentage of mature male and female Atlantic croaker by 10 mm total length intervals, with a logistic function (continuous line) fitted to the data.....	63
13.	Percentage of gonad maturity stages by month for mature female Atlantic croaker in the Chesapeake Bay region.....	64
14.	Monthly mean gonadosomatic index for male and female Atlantic croaker in the Chesapeake Bay region, 1990-1991.....	66
15.	Monthly sex ratios for Atlantic croaker in the Chesapeake Bay region, 1990-1991.....	69
16.	Monthly oocyte diameter distributions during the spawning season of Atlantic croaker in the Chesapeake Bay region.....	71
17.	Appearance of advanced yolked oocytes of Atlantic croaker. (a) healthy (non-atretic) oocyte; (b) oocytes in early stage of $\alpha$ atresia; (c) oocyte in intermediate stage of $\alpha$ atresia; (d) oocytes in late stage of $\alpha$ atresia.....	75
18.	Comparison of the appearance of $\alpha$ -atretic advanced yolked oocytes of a fully-developed Atlantic croaker in a histology slide (a), and in a smear of fresh oocytes under a dissecting scope (b) and (c).....	76
19.	Diagrammatic representation of the ovarian cycle of Atlantic croaker.....	78
20.	Yield-isopleth diagrams estimated using different values of natural mortality ( $M$ ) for Atlantic croaker in Chesapeake Bay.....	100
21.	Curves of yield-per-recruit on $F$ for Atlantic croaker, estimated for $t_c=1-5$ and $M=0.25-0.40$ .....	103
22.	Number of citations of Atlantic croaker $\geq 1.82$ Kg (4 lbs) caught by recreational fishermen in Virginia and Delaware during 1960-1990.....	116

## ABSTRACT

Otoliths, scales, dorsal spines, and pectoral fin rays, of Atlantic croaker, Micropogonias undulatus, were compared for legibility of presumed annual marks and precision in repeated readings, to determine the best hard part for ageing. Marks on transverse otolith sections were easiest to read and showed the best agreement between readings. Atlantic croaker collected from commercial catches in Chesapeake Bay and in Virginia and North Carolina coastal waters during 1988-1991 were then aged using otolith sections. Ages 1-8 were recorded, but eight-year-old fish were rare. Marginal increment analysis showed that for ages 1-7 annuli are formed once a year during the period April-May. Otolith age readings were very precise, with percent agreement within and between readers greater than 99%. Observed lengths-at-age were highly variable and showed a rapid decrease in growth after the first year. Observed lengths for ages 1-7 showed a very good fit to the von Bertalanffy growth model ( $r^2=0.99$ ;  $n=753$ ). No differences were found between sexes. Total annual instantaneous mortality ( $Z$ ) estimated from maximum age and from a catch curve of combined Chesapeake Bay catches ranged from 0.55 to 0.63.

Atlantic croaker are multiple spawners with asynchronous oocyte development and indeterminate fecundity. Mean length at first maturity for males and females was 182 and 173 mm TL, respectively. More than 85% of both sexes were mature by the end of their first year and all were mature by age 2. Spawning extends over a protracted period (July-December), but individual fish spawn for only 2-3 months. Spawning starts in Chesapeake Bay and continues offshore and south as Atlantic croaker migrate from the estuary. However, some individuals seem to complete spawning in estuarine waters. Seasonal fluctuations in sex ratios suggest that males start leaving the estuary earlier than females. A high incidence of atretic advanced yolked oocytes in spawning females suggests that a surplus production of yolked oocytes is part of Atlantic croaker reproductive strategy. Females would hydrate and spawn more or less of these yolked oocytes depending on environmental conditions.

Yield-per-recruit modeling results indicated that, over a likely range of natural mortality values, present levels of harvest in Chesapeake Bay are below the maximum potential yield-per-recruit.

Results from this study do not indicate the existence of a group of larger, older fish in the Chesapeake Bay region and suggest that the hypothesis of a different population dynamics pattern for Atlantic croaker north and south of North Carolina, should be reevaluated.

Life history, population dynamics and yield-per-recruit modeling  
of Atlantic croaker, *Micropogonias undulatus*,  
in the Chesapeake Bay area



## GENERAL INTRODUCTION

The Atlantic croaker, Microponias undulatus (Linnaeus) ranges from Cape Cod, Massachusetts to the Bay of Campeche, Mexico (Welsh and Breder 1923, Chao 1978). Although not common north of New Jersey (Welsh and Breder 1923, McHugh 1981), it represents one of the most abundant inshore demersal species of the Atlantic and Gulf of Mexico coasts of the United States (Joseph 1972, Chittenden and McEachran 1976).

The Atlantic croaker is a seasonal migratory species. In the Middle Atlantic region adults move north into Chesapeake Bay waters in the spring, and offshore and south in the fall to overwinter along the coasts of Virginia and North Carolina (Pearson 1932, Wallace 1940, Haven 1959). However, details of these migratory patterns are still unknown. Spawning is reported to take place over the continental shelf (Colton et al. 1979, Morse 1980, Norcross and Austin 1988, Norcross 1991), over a large area that may include waters near the mouth of the Chesapeake Bay (Welsh and Breder 1923, Pearson 1941). Post-larvae and small juveniles recruit into the Chesapeake Bay and its major tributaries in the fall and stay until the following year,

when they leave as yearlings (Haven 1957, Chao and Musick 1977, Norcross 1983).

The geographic distribution of Atlantic croaker commercial and recreational catches has greatly changed during the past 40 years (Wilk 1981, Mercer 1987). Catches were primarily from the Chesapeake region during the 1940s, but most of the recent commercial and recreational landings have come from the Gulf of Mexico and South Atlantic. The Middle Atlantic area, for the most part, has not contributed significantly to the total catch (Wilk 1981, Mercer 1987). However, despite the recent low landings, Atlantic croaker still represents an important fishery resource along the Atlantic coast, particularly from Maryland to North Carolina (Norcross 1983, Mercer 1987). In the Chesapeake Bay area they are caught in pound-nets, haul-seines and gill-nets mainly during spring and fall migrations and to a lesser extent during the summer (Chittenden et al. 1990, Chittenden 1991). During winter Atlantic croaker are caught offshore in the otter trawl and gill-net fisheries.

Despite the importance of Atlantic croaker as a fishery resource, historic landings have fluctuated widely during the past 50 years. Landings exceeded 20,000 metric tons between 1937 and 1940 and dropped to less than 1,000 metric tons between 1967 and 1971 (McHugh and Conover 1986, Mercer 1987). The most recent peak in landings occurred in 1977

and 1978 at just over 13,000 metric tons annually (Mercer 1987). Recreational landings have also declined steadily since 1960 and have been below the 20-year average of 1,800 metric tons in the Chesapeake Bay area since 1965 (Rothschild et al. 1981).

Reasons for these long-term fluctuations are not well known. The main hypotheses in the literature include: (1) an increase in fishing pressure to a level detrimental to the population, especially due to the introduction in the 1920s of active fishing methods such as otter trawls and haul-seines to a fishery until then dominated by pound-nets (Perlmutter 1959), (2) a not clearly defined population response to long-term climatic changes, with periods of high landings apparently associated with warming trends and mild winters (Joseph 1972), and (3) a combination of environmentally defined fluctuations in year-class strength and fishing pressure (Norcross and Austin 1981, Norcross 1983). Recent low landings have been also attributed to: (1) habitat alteration within estuarine nursery grounds, (2) the incidental bycatch and discard mortality of small croaker in non-directed fisheries such as the southern shrimp fishery, and (3) the scrap/bait catch of small Atlantic croaker from the pound-net, haul-seine, and trawl fisheries (Mercer 1987).

The possible existence of two groups of Atlantic

croaker, exhibiting different life history/population dynamics attributes north and south of Cape Hatteras, North Carolina, has been extensively discussed in the literature (Chittenden 1977, White and Chittenden 1977, Morse 1980, Ross 1988). Although preliminary stock identification results suggest differences may not be genetically controlled (Sullivan 1986), published information describes the group ranging from North Carolina to the Gulf of Mexico as having high mortality, low longevity (1-2 years), early maturation and fall-winter spawning. Another group, ranging from North Carolina to about New Jersey is reported to have lower mortality, higher longevity (6-7 years), greater sizes-at-age, late summer-fall spawning, and often a greater age-at-maturity (White and Chittenden 1977, Ross 1988). Ross (1988) hypothesized that these groups may overlap and mix in North Carolina and stated that, if the Atlantic croaker designated in his study as "northern" were fish migrating south from the Chesapeake and Delaware Bay areas, their larger sizes (350-520 mm TL) and older ages (5-7 years, as aged by scales) would be consistent with the proposed northern group life history pattern. However, despite its significance for management, evaluation of this hypothesis is presently difficult because information on age and size compositions, growth, mortality, and reproduction of Atlantic croaker in the Chesapeake Bay and Mid-Atlantic

areas is either non-existent, incomplete or outdated.

This dissertation consists of four chapters. In the first chapter, otoliths, scales, dorsal spines, and pectoral fin rays are compared in terms of legibility of presumed annuli and precision in repeated readings to determine the best prospective hard part for ageing Atlantic croaker. In Chapter 2, I describe otolith-ageing criteria, validate the otolith method for fish ages 1-7 and, based on this method, provide information on age, growth, and mortality of Atlantic croaker in the Chesapeake Bay region. In Chapter 2 I also evaluate the relationship between otolith size and fish size and age, and discuss its implications in choosing otoliths as ageing structures for Atlantic croaker. Chapter 3 addresses the reproductive biology of Atlantic croaker in the Chesapeake Bay area. In this Chapter I test the assumption of determinate annual fecundity, and describe spawning periodicity and location, size- and age-at-maturity, sex ratios, ovarian cycle, and oocyte atresia for Atlantic croaker in this area. In Chapter 4, life history and population dynamics information, mainly from Chapter 2, is used to apply the Beverton-Holt yield-per-recruit model and evaluate the effects of fishing on Atlantic croaker. Implications of this analysis for management of Atlantic croaker stocks in the Chesapeake Bay region are also discussed. Finally, in the "General

Discussion" section information from these four chapters is integrated with information from the literature to evaluate the hypothesis of a basically different population dynamics pattern for Atlantic croaker north and south of Cape Hatteras, North Carolina.

**CHAPTER 1**

**A Comparison of Hard Parts for Age Determination  
of Atlantic Croaker**

## INTRODUCTION

Although studies on age and growth of Atlantic croaker have used a variety of ageing methods, e.g., length frequencies (Haven 1957); eye-lens weight (Mericas 1977); scales (White and Chittenden 1977, Music and Pafford 1984, Ross 1988); and sectioned otoliths (Music and Pafford 1984, Barger 1985, Hales and Reitz 1992), there is still disagreement on the best method of age determination for this species. Barger and Johnson (1980) evaluated scales, otoliths, and vertebrae of fish from the northern Gulf of Mexico and concluded that otoliths showed the most potential for age determination. Music and Pafford (1984) used scales and otoliths to age fish in Georgia and reported that, although both hard parts could be used for ageing, scales appeared to form two annulus-like marks per year, with the first one being indistinct and often undetectable. Despite these reports, Ross (1988) used a validated scale method to age Atlantic croaker in North Carolina. He described criteria to differentiate true and false marks, reported a low incidence of double marks, and disagreed with previous authors who found Atlantic croaker scale marks poorly defined (Barger and Johnson 1980), irregular in frequency



(Haven 1954), and difficult to distinguish (Roithmayr 1965, Joseph 1972, Mericas 1977). However, because Ross (1988) presented no information on percent agreement in repeated readings, it is difficult to evaluate the precision of his method and how it compares with methods using other hard parts. Beamish and McFarlane (1987) recommended that, even for a validated method, comparisons among structures should be a routine procedure for laboratories providing age estimates for management.

In this study, otoliths, scales, dorsal spines, and pectoral fin rays were compared in terms of legibility of presumed annuli and precision in repeated readings to determine the best prospective hard part for ageing Atlantic croaker.

#### MATERIALS AND METHODS

Forty-five fish ranging from 225 to 319 mm total length (TL) were randomly selected from two 22.7-kg (50 lb) boxes of small and large grade Atlantic croaker obtained in August 1988 from a commercial pound-net located in the lower Chesapeake Bay at Lynnhaven, Virginia. For each fish, both sagittal otoliths were removed, wiped clean, and stored dry. Scales were removed from an area near the tip of the left pectoral fin below the lateral line. The left pectoral fin

and the entire dorsal fin (spines and rays) were removed by cutting below the base of the rays. Scales and fin rays were stored in paper envelopes and kept frozen until processed.

Otoliths were attached to cardboard slips with thermoplastic cement and transversely sectioned through the nucleus with a thin diamond blade using a Buehler low-speed Isomet saw. Sections 350-500 $\mu$ m thick were then mounted on glass slides with Flo-texx clear mounting medium. Presumed annual opaque marks along the otolith sulcal groove were counted under a dissecting microscope (12-24 $\times$  magnification) with transmitted light and bright field.

Five scales from each fish were soaked in water and cleaned with a soft-bristled tooth brush to remove adhering epidermal tissue. Three unregenerated scales were then dried, taped to an acetate sheet, inserted between two other blank sheets, and pressed with a Carver laboratory scale press for two minutes at 2,724 kg of pressure and 71°C. Scale impressions were read under a dissecting microscope at 12-50 $\times$  with transmitted light and bright field. Presumed annual marks were identified by scale-ageing criteria described in Bagenal and Tesch (1978) and Ross (1988), and consistency among the three scales examined.

The third spine from the spiny dorsal fin, and the fifth ray from the left pectoral fin were selected for processing. These are the largest spine and ray from each

of the selected fins, making handling and processing easier. Fin rays and spines were cleaned of adhering tissue and cut transversely into two halves. The proximal halves were mounted with thermoplastic cement on cardboard slips and transversely sectioned with a thin diamond blade using a Buehler low-speed Isomet saw. At least three transverse serial sections, 300-500 $\mu$ m thick, were taken starting at the base. Sections were then mounted on microscope slides with Flo-texx clear mounting medium and read under a dissecting microscope using transmitted light with dark field at 12-24 $\times$  magnification. Presumed annual opaque marks were counted if they were not blurred or partially fused, and were consistent in the replicate sections.

To assess the precision of mark counts, all hard parts were read twice, with at least one week between the first and second readings and without knowledge of fish length. Reading sequence for each hard part and for individual fish were independently randomized before readings were done. Agreement in mark counts between readings and hard parts was evaluated by percent agreement.

## RESULTS

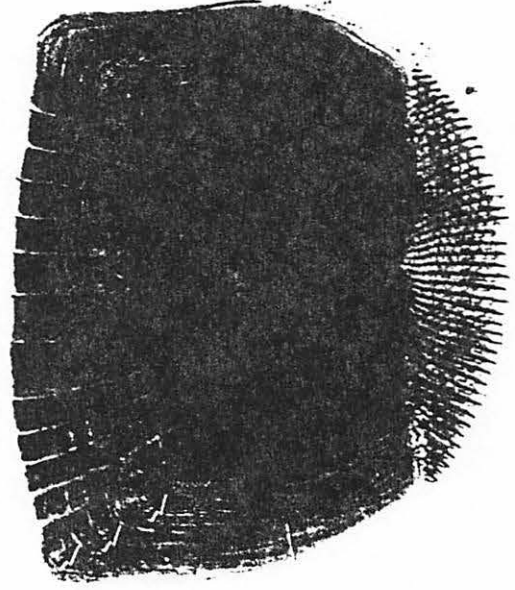
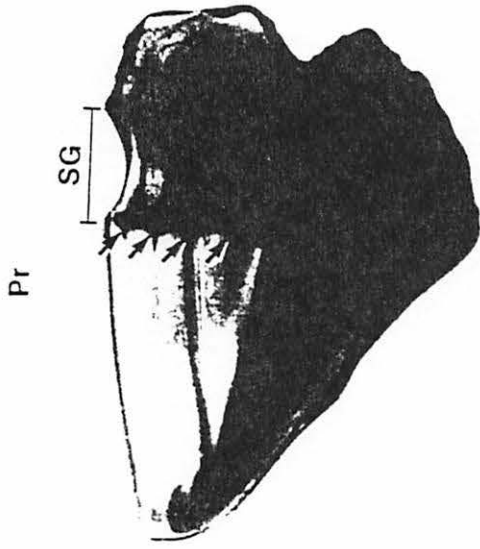
### *Legibility and appearance of marks*

All hard parts exhibited a pattern of regular, concentric marks that could represent annuli (Fig. 1). However, otoliths were the only hard part that showed clear, consistent marks for every fish.

Typical otolith sections showed an opaque nucleus surrounded by an opaque area composed of very fine circular opaque bands (Fig. 1a). Following the proximal margin of this opaque area a pattern of narrow opaque bands alternating with wide translucent bands can be clearly identified, especially along the ventral edge of the otolith sulcal groove mark. I interpreted the opaque area around the nucleus as representing the first mark. With the exception of this first mark, which was sometimes very close to the otolith core, otolith marks were very clear and easy to identify.

Marks on dorsal spines (Fig. 1b) were clear in some sections but usually incomplete or blurred. Pectoral ray sections, however, showed better defined marks (Fig. 1c), and seemed to have fewer incomplete or blurred marks than dorsal spines. Identifying the first mark was usually difficult on both dorsal spines and pectoral rays. Presumed

Fig. 1. Marks on hard parts of a 293 mm TL Atlantic croaker from Chesapeake Bay. (A) otolith section; (B) dorsal spine section; (c) pectoral ray section; (D) scale impression. Arrows indicate individual marks counted. The fish was four-years-old as aged by otoliths. SG=sulcal groove; Ve=ventral axis; Pr=proximal axis.



Ve

a

b

c

d

Pr

SG

annual marks on dorsal spines and pectoral rays appeared as wide opaque semicircular bands alternating with narrow translucent bands.

Scale marks were usually hard to identify using objective scale-ageing criteria. Although some kind of mark could almost always be distinguished (Fig. 1d), inconsistency between the three scales read and the occasional occurrence of double marks (checks) made scale readings more subjective compared to other structures. As a result, I usually had low confidence in assigning presumed annual marks to scales.

#### *Agreement between readings and hard parts*

Percent agreement results support my qualitative evaluation of mark legibility among hard parts. Otoliths showed by far the best precision of all hard parts, with 97.8% agreement between readings. Pectoral rays and dorsal spines were similar in precision, with 75.5 and 71.1% agreement, respectively. Scales showed the lowest precision, with 60.0% agreement.

The magnitude of differences in mark counts assigned in the first and second readings was often higher for scales than for other hard parts (Fig. 2). All hard parts had at least once a difference of one mark between readings, but only scales had differences of two or three marks between readings.

Fig. 2. Frequency of occurrence of the absolute difference  
in mark counts between repeated readings for  
Atlantic croaker hard parts.



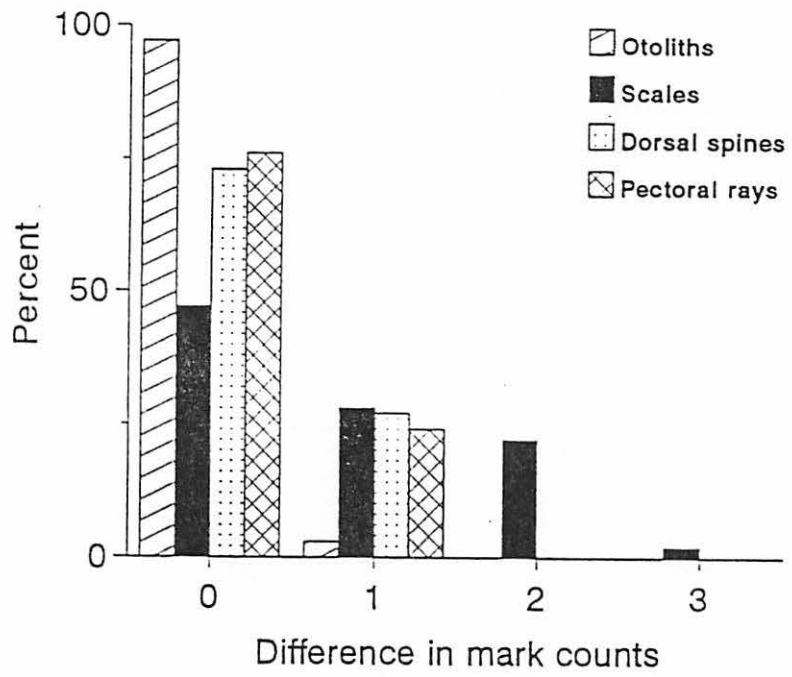
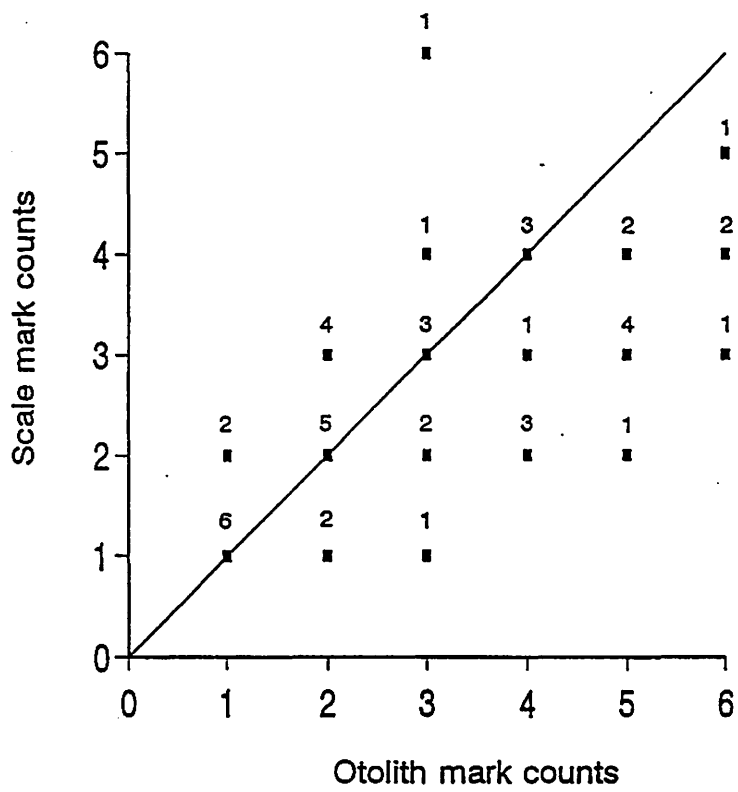


Table 1. Percent agreement between mark counts from hard parts of Atlantic croaker from Chesapeake Bay.

	Pectoral rays	Scales	Otoliths
Dorsal spines	17.7	26.7	22.2
Pectoral rays		24.4	20.0
Scales			37.8

Fig. 3. Comparison of scale and otolith mark counts for Atlantic croaker from Chesapeake Bay. Numbers on top of points indicate the number of fish in each point. The 45° line indicates agreement in mark counts assigned by each hard part.



Agreement in mark counts between hard parts was usually low (Table 1). Agreement was 37.8% between scales and otoliths, 17.7% between dorsal spines and pectoral rays, and ranged from 20.0 to 26.7% comparing dorsal spines and pectoral rays to scales and otoliths. Although mark counts from scales and otoliths showed an approximately linear relationship (Fig. 3), there was a large variation in the number of marks assigned with each hard part. Agreement between scales and otoliths was highest for fish with 1 and 2 otolith marks. Scale mark counts were consistently lower than otolith counts for fish with 5 and 6 otolith marks.

## DISCUSSION

My results confirm previous reports (Barger and Johnson 1980, Barger 1985) that marks on transverse sections of Atlantic croaker otoliths are clear and easy to identify, with very high precision in repeated readings. Although dorsal spines and pectoral rays also showed fairly clear marks that could be interpreted as annuli, they showed much lower precision than otoliths. Additionally, the low agreement of dorsal spines and pectoral rays with otoliths—a method that is very precise and has been validated for Atlantic croaker (see Chapter 2)—suggests marks on spines and rays may not represent true annuli.

Scales were usually difficult to read, had the lowest precision in repeated readings, and showed the highest discrepancies between the first and second readings. Despite Ross's (1988) success with the scale method for ageing Atlantic croaker in North Carolina, problems in interpreting scale annuli have been widely reported for this species. White and Chittenden (1977) working with fish up to age 2 in the northwestern Gulf of Mexico reported that scales appeared to form two marks each year, except that some formed no mark in the first year. The occurrence of

occasional double marks on Atlantic croaker scales has been also reported by Haven (1954), Music and Pafford (1984), and Ross (1988). Problems in interpreting scale marks may explain the differences of up to three marks I found in repeated scale readings and the large variation in mark counts between scales and otoliths. The tendency of scales to give lower counts than otoliths as the number of otolith marks increases suggests that scales may underestimate age in older fish.

Validation of the scale method for Atlantic croaker in the Gulf of Mexico (White and Chittenden 1977), Georgia (Music and Pafford 1984), and North Carolina (Ross 1988) indicates scale-ageing may be used with this species. However, my results, as well as previous reports of problems in using scales for ageing Atlantic croaker (Haven 1954, Roithmayr 1965, Joseph 1972, Mericas 1977, Barger and Johnson 1980) indicate that, for this species, scale-ageing is time-consuming and requires extensive experience due to the large degree of subjectivity in interpreting marks. The greatest advantage of the scale method is that, because it does not require killing the fish, it can be used in mark-recapture studies. However, modern otolith-marking techniques, such as fluorochrome labeling through oxytetracycline injection (Casselman 1983), have allowed researchers to overcome this problem and use the otolith method in mark-recapture studies (Beckman et al. 1988,

Murphy and Taylor 1990, 1991).

In conclusion, I believe, based on legibility of marks and precision in repeated readings, that otoliths are the best structure for ageing Atlantic croaker in Chesapeake Bay. Considering that Atlantic croaker have a maximum longevity of about 8 years (Barger 1985, Chapter 2), validation of otolith annuli for fish ages 1-7 and very high percent agreement within and between readers (>99%; Chapter 2), indicates that, besides being very precise, the otolith method represents a reliable, accurate method of age determination for this species.



## **CHAPTER 2**

### **Age, growth, and mortality**

## INTRODUCTION

Little is known about age, growth and mortality of Atlantic croaker in the Middle Atlantic and Chesapeake Bay regions. Studies based on length frequencies (Haven 1957, Chao and Musick 1977) require considerable subjective interpretation given the extended spawning period of Atlantic croaker (Morse 1980, Warlen 1982, Chapter 3) and the difficulty of distinguishing modal groups at older ages (White and Chittenden 1977, Jearld 1983). Although scale-ageing has also been used (Welsh and Breder 1923, Wallace 1940, Ross 1988), problems in applying this method to Atlantic croaker have been widely reported (Haven 1954, Roithmayr 1965, Joseph 1972, Mericas 1977, Barger and Johnson 1980, Chapter 1).

In Chapter 1, I evaluated different hard parts as prospective age determination methods for Atlantic croaker in Chesapeake Bay and concluded that, based on legibility of marks and precision in repeated readings, otoliths were the best hard part for ageing. In this chapter I describe otolith-ageing criteria, validate the otolith method for fish ages 1-7, and provide information on age, growth, and mortality of Atlantic croaker in the Chesapeake Bay region.

I also evaluate the relationship between otolith size and fish size and age, and discuss its implications in choosing otoliths as ageing structures for Atlantic croaker.

#### MATERIALS AND METHODS

Atlantic croaker were collected from June 1988 to June 1991, mainly from commercial pound-net, haul-seine, and gill-net fisheries which operate from early spring to early fall in Chesapeake Bay. Local fish processing houses and seafood dealers were contacted weekly or fortnightly, and one 22.7-Kg (50-lb) box of fish of each available market grade (small, medium, or large) was purchased for processing. Although boxes of fish were not randomly selected, Chittenden (1989a) found only minor among-box differences in Atlantic croaker length compositions in pound-net and haul-seine catches. Because nearly all variation in size compositions was captured by the within-box variation, box selection did not represent a problem.

Since Atlantic croaker migrate out of Chesapeake Bay in early fall to overwinter offshore (Haven 1959), samples for the period November-March were obtained from commercial trawlers which operate in Virginia and North Carolina shelf waters. Young-of-the-year (90-114 mm total length) used to

validate the first annulus on otoliths were obtained from the Virginia Institute of Marine Science juvenile bottom trawl survey. Details on sampling design and gear description can be found in Chittenden (1989b) and Geer et al. (1990).

Fish were measured for total length (TL) to the nearest millimeter, weighed for total weight (TW) to the nearest gram, and both sagittal otoliths were removed and stored dry. The left otolith was transversely sectioned through the core with a diamond blade using a Buehler low-speed Isomet saw. Sections 350-500  $\mu\text{m}$  thick were then mounted on glass slides with Flo-texx clear mounting medium and read under a dissecting microscope (6-12x) using transmitted light and bright field, with the exception of samples from the period April-May, when sections were also read with reflected light and dark field to help identify the last annulus. Ages were assigned based on annulus counts, assuming January first as an arbitrary average birthdate when fish from one age-class were assigned to the next oldest (Jearld 1983). Although the average spawning date, and thus average biological birthdate, of Atlantic croaker in the Chesapeake Bay region occurs in September (see Chapter 3), I chose, for ageing purposes, to use January first as the arbitrary average birthdate because annuli are formed during the period April-May (see *Age determination* below). To assess ageing precision, all otolith sections

(n=1,967) were read twice by two readers, and agreement between readings and readers evaluated by percent agreement. Disagreements were resolved by a third reading with both readers.

Annuli were validated by the marginal increment method (Bagenal and Tesch 1978). For each age the translucent margin outside the proximal end of the last annulus was measured along the ventral side of the otolith sulcal groove (Fig. 4). Measurements were taken with an ocular micrometer to the nearest 0.02 mm (one micrometer unit at 25x).

To evaluate growth, observed lengths-at-ages 1-7 were fit to the von Bertalanffy model (Ricker 1975) using nonlinear regression (Marquardt method). Model parameters are:  $L_{\infty}$ , the mean asymptotic length;  $K$ , the Brody growth coefficient; and  $t_0$ , the hypothetical age at which a fish would have zero length (Ricker 1975). Only data for September, were used for this growth analysis. September is when peak spawning occurs and thus is the average biological birthdate for the Chesapeake Bay region (see Chapter 2). As a result, sizes in September correspond best to sizes-at-age, and they in effect, correct for growth after the time of annulus formation.

To evaluate changes in otolith size relative to fish size and age, 30 randomly selected otoliths per age, for ages 1-7 (198-400 mm TL), were measured for maximum length and maximum thickness to the nearest 0.05 mm using a vernier

caliper, and weighed to the nearest 0.001 g using a top-load electronic balance. After sectioning, otoliths were also measured for otolith radius, the distance between the center of the core and the otolith outer edge along the ventral side of the sulcal groove (Fig. 4), to the nearest 0.02 mm using an ocular micrometer. Relationships between otolith measurements and fish total length were evaluated by regression analysis. The effect of fish age on these relationships was evaluated by analysis of covariance (ANCOVA).

Fish ranging from 152 to 400 mm (36.3 to 967.0 g TW) were used to determine total length-total weight, girth-total length, and standard length-total length relationships. Differences between sexes were tested by ANCOVA. The hypothesis of isometric growth (Ricker 1975) was tested by *t*-test.

Instantaneous total annual mortality rates, *Z*, were estimated from maximum age using Hoenig's pooled regression equation (Hoenig 1983), by calculating a theoretical total mortality for the entire lifespan following the reasoning of Royce (1972:238) as described in Chittenden and McEachran (1976), and by the regression method using a catch curve of combined pound-net, haul-seine, and gill-net data for all recruited ages having five or more fish (Chapman and Robson 1960). As recommended by Ricker (1975), to avoid unknown sampling bias associated with individual gears, I considered

the age frequency distribution obtained from data from combined gears as the best estimate of Atlantic croaker age composition in Chesapeake Bay. Commercial trawl collections were not used in this analysis because they showed a different length composition than the other gears and could be biased towards small fish. Because in catch curve analysis the age group representing the top of the dome may or may not be fully recruited to the gears (Everhart and Youngs 1981), mortality estimates were based on ages 3-7 only. Data from 1988-1991 were combined to minimize the effect of variation in year-class strength (Robson and Chapman 1961). The right limb of the catch curve (Ricker 1975) was tested for deviation from linearity by analysis of variance (ANOVA). Values of  $Z$  were converted to total annual mortality rates,  $A$ , using the relationship  $A = 1 - e^{-Z}$  (Ricker 1975).

All statistical analyses were performed using the Statistical Analysis System (SAS 1988).  $F$ -tests in ANCOVA were based on Type III sums of squares (Freund and Littell 1986). Assumptions of linear models were checked by residual plots as described in Draper and Smith (1981). Data analyzed by regression analysis or ANOVA were  $\log_{10}$ -transformed to correct for non-linearity or heterogeneous variances.

## RESULTS

### *Age determination*

Transverse otolith sections of Atlantic croaker show very clear, easily-identified marks that can be used for ageing. Typical sections show an opaque core surrounded by a blurred opaque band composed of fine opaque and translucent zones (Fig. 4). This band represents the first annulus. The width of this annulus varies among fish, from a very narrow band that is almost continuous with the core, to a wide, well-defined band clearly separated from the core. Because of this variation in width and proximity to the core the first annulus is sometimes difficult to identify. Subsequent annuli are represented by easily-identified, narrow opaque bands that alternate with wider translucent bands outside the proximal margin of the first annulus (Fig. 4).

Annuli are formed on otoliths once a year in the period April-May. For ages 1-7, mean monthly marginal increment plots show only one trough during the year, indicating that only one annulus is formed each year (Fig. 5). The trough starts abruptly in April, a period when there is generally maximum variation in the mean marginal increment. This



Fig. 4. Transverse otolith section of an 8-year-old Atlantic croaker caught in September 1988 in Chesapeake Bay. Arrows indicate the typically easily-identified individual annuli. The translucent zone beyond the last annulus represents additional growth after the annulus was formed during April May. SG=sulcal groove. a=artifact of preparation. Ventral and proximal indicate axes of orientation, respectively.

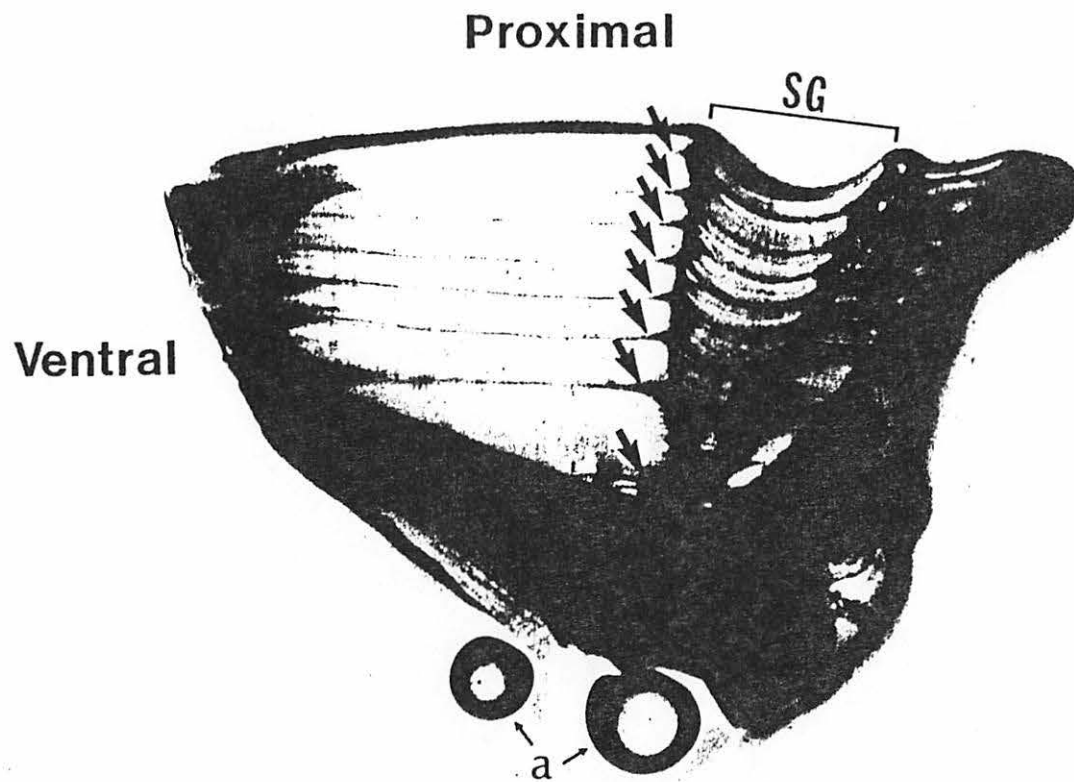
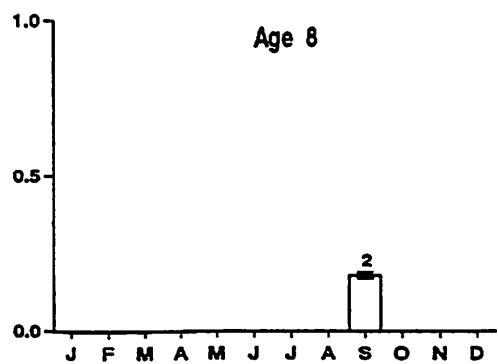
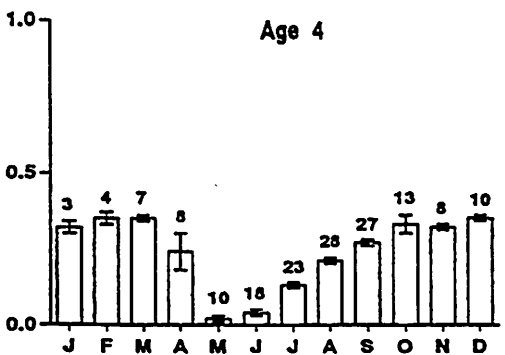
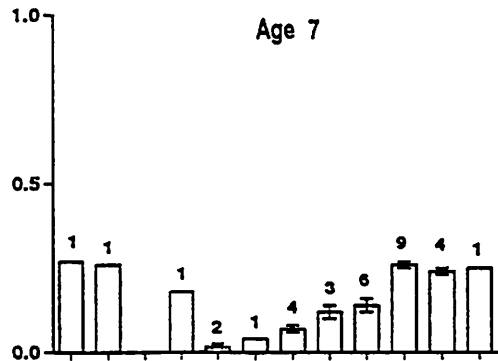
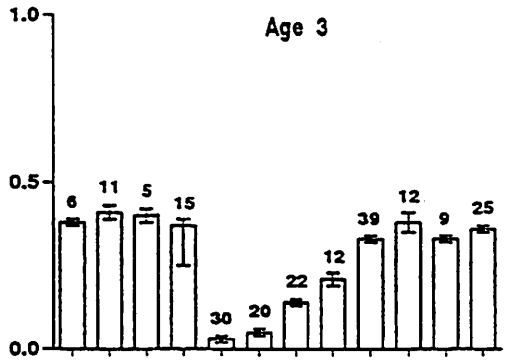
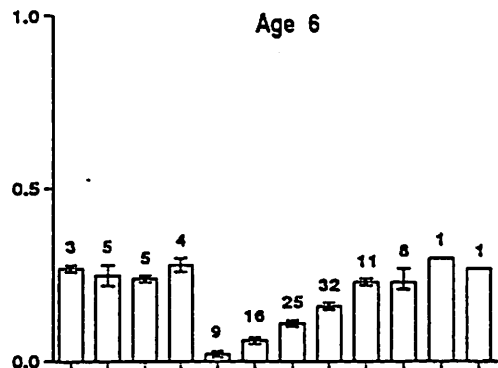
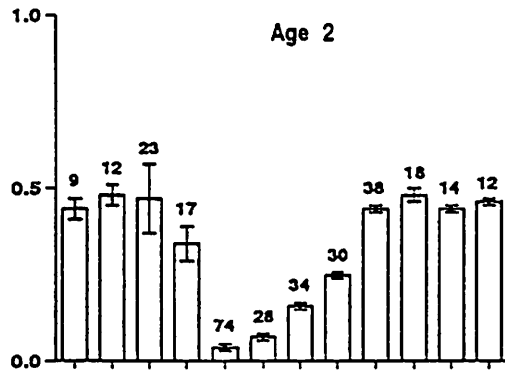
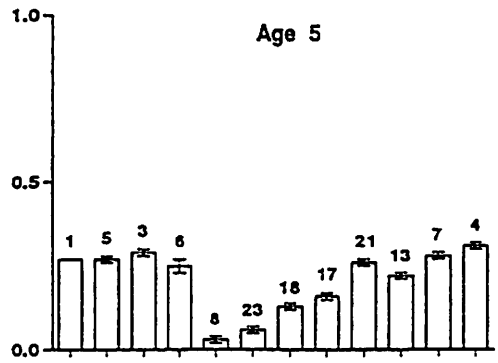
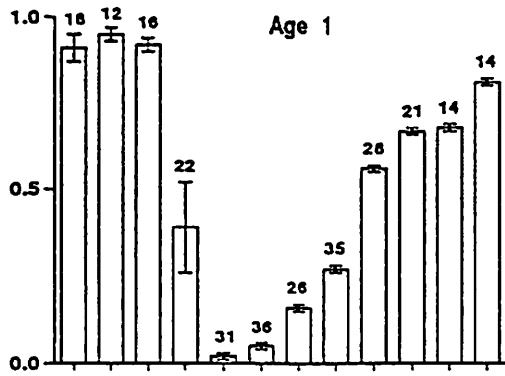


Fig. 5. Mean monthly marginal increment for Atlantic croaker ages 1-8 from the Chesapeake Bay region, 1988-1991. Vertical bars are  $\pm 1$  standard error. Numbers above the bars are sample sizes.

Marginal increment (mm)



Months

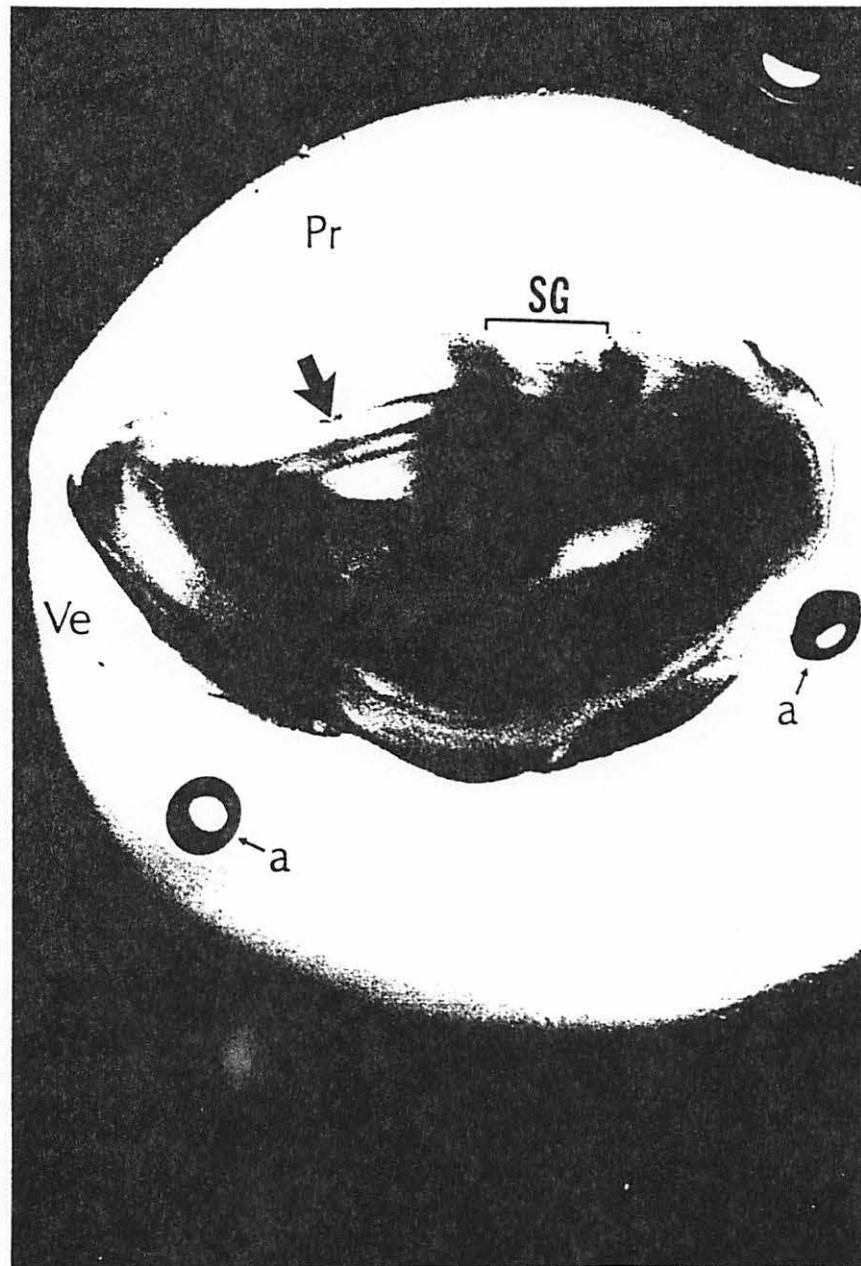
suggests that some fish have begun to form the annulus while others have not. Lowest marginal increment values occurred in May, indicating this as the most intensive period of annulus formation. Subsequently, marginal increment values progressively rise to a somewhat stable maximum from October through March or April, indicating a period of little or no otolith growth. Because only two age 8 fish were collected, it was not possible to validate annuli beyond age 7.

To confirm my interpretation that the blurred opaque band around the otolith core represents the first annulus, i.e., that fish hatched in the fall form a mark during their first spring, otolith sections of young-of-the-year (94-114 mm) collected during the period March-June were examined. All those collected in March-April were beginning to develop fine, opaque marks around the core, and all those in May-June had an opaque mark already formed (Fig. 6).

Otolith age readings were very precise, both within and between readers. Percent agreement was 99.5% for reader 1, 99.3% for reader 2, and 99.2 % between readers. In all cases of disagreement the difference never exceeded 1 year. Only one of the 1,967 otoliths sectioned was crystallized and could not be read. In that case, the right otolith was read.

Difficulty in ageing Atlantic croaker using otolith sections did not increase with increasing age. However, proper identification of the first annulus was very

Fig. 6. Transverse otolith section of a young-of-the-year Atlantic croaker (114 mm TL) collected in June 1990 in Chesapeake Bay. The arrow indicates the outer edge of the first annulus formed during the period April-May. SG=sulcal groove; Ve=ventral; Pr=proximal; a=artifact of preparation.



important. All disagreements, independent of age, were due to problems in identifying the first annulus.

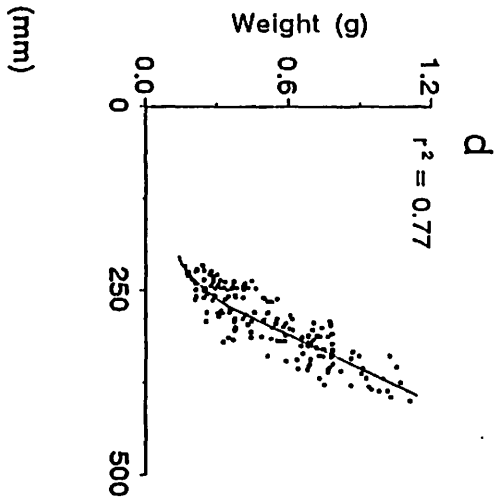
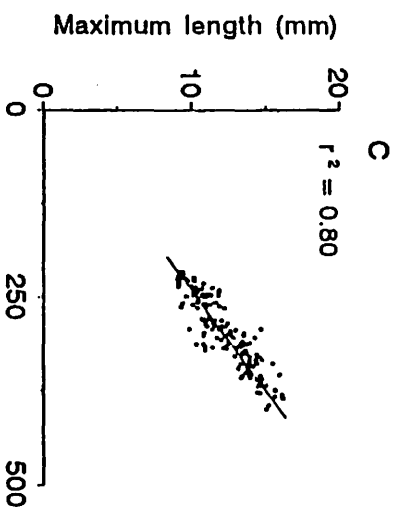
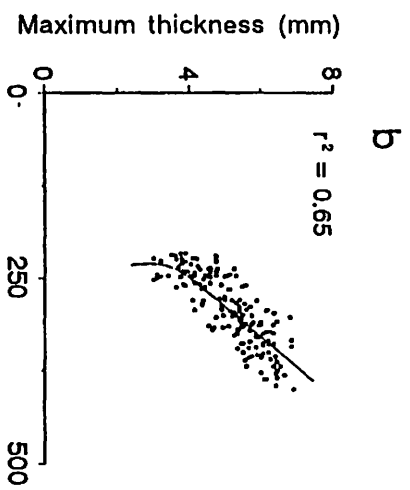
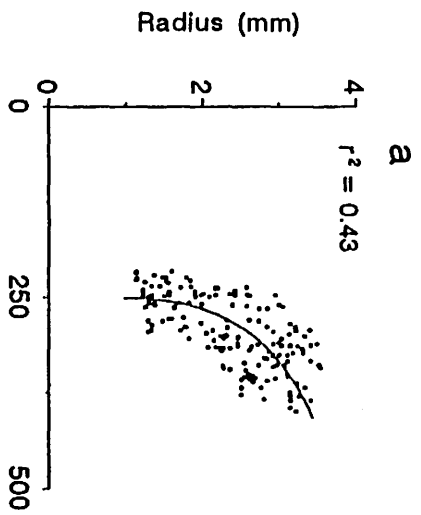
*Otolith size relative to fish size and age*

Changes in otolith size relative to fish size were not constant along all axes (Fig. 7). Otolith maximum length was the only axis that showed a linear, isometric increase with fish length. Otolith radius, the axis along which annuli were read in transverse sections, showed a non-linear relationship with fish length, and had the smallest coefficient of variation of all variables ( $r^2=0.43$  for a quadratic regression). The curvilinear, allometric relationship suggests that otolith growth relative to fish growth slows down along this axis as fish get bigger.

Despite its poor fit with fish length, otolith radius showed a very strong linear relationship with fish age. An ANCOVA model having length, age, and their interaction explained 97% of the variation in otolith radius (Table 2). All factors in the model were highly significant ( $P<0.01$ ). Similar models for otolith maximum length, maximum thickness, and weight were also highly significant and had high coefficients of determination ( $r^2\geq 0.85$ ). However, significance for these models was due to fish length only, neither age nor the interaction factor were significant.



Fig. 7. Scatter plots and fitted regression lines of different otolith measurements versus Atlantic croaker total length: (a) otolith radius; (b) otolith maximum thickness; (c) otolith maximum length; and (d) otolith weight. Sample size is 210 in each plot.



Total length (mm)

Table 2. Summary of ANCOVA to evaluate the effect of Atlantic croaker total length (TL) and age on otolith maximum thickness (OT), maximum length (OL), weight (OW), and radius (OR). n=210 for each analysis.  $\alpha=0.05$ .

Otolith relation	Source of variation	r <sup>2</sup>	P-value
OT	model	0.85	0.0001
	TL		0.0001
	age		0.3263
	TL x age		0.6214
OL	model	0.88	0.0001
	TL		0.0001
	age		0.9780
	TL x age		0.7907
OW	model	0.90	0.0001
	TL		0.0001
	age		0.0863
	TL x age		0.1402
OR	model	0.97	0.0001
	TL		0.0001
	age		0.0001
	TL x age		0.0008

### *Growth*

Observed lengths varied greatly within ages (Fig. 8). Atlantic croaker showed a rapid increase in size during the first year, but annual growth greatly decreased during the second year, remaining comparatively low thereafter (Fig. 8). On average, 64% of the cumulative total observed growth occurred in the first year and 84% was completed after two years. Mean observed lengths-at-age were always slightly larger for females (Table 3), but differences were not statistically significant (t-test at each age;  $P > 0.05$  for all ages). Mean observed total lengths for pooled sexes were 201, 263, 274, 285, 290, 307, 309, and 313 mm, for ages 1-8, respectively. Despite the high variability in sizes-at-age, observed lengths at ages 1-7 showed a very good fit to the von Bertalanffy growth model ( $r^2 = 0.99$ ;  $n = 753$ ). Estimated model parameters, asymptotic standard errors, and 95% confidence intervals are given in Table 4.

No difference in the total length-total weight relationship was found between sexes (ANCOVA;  $F = 2.46$ ;  $df = 3, 005$ ;  $P = 0.15$ ). The equation for pooled sexes was:

$$TW = 2.41 \times 10^{-6} TL^{3.30} \quad (r^2 = 0.97; n = 3,006; P < 0.01)$$

Fig. 8. Observed lengths-at-age and fitted von Bertalanffy regression line for Atlantic croaker from the Chesapeake Bay region (September, 1988-1991). Numbers above data points are sample sizes at each age.

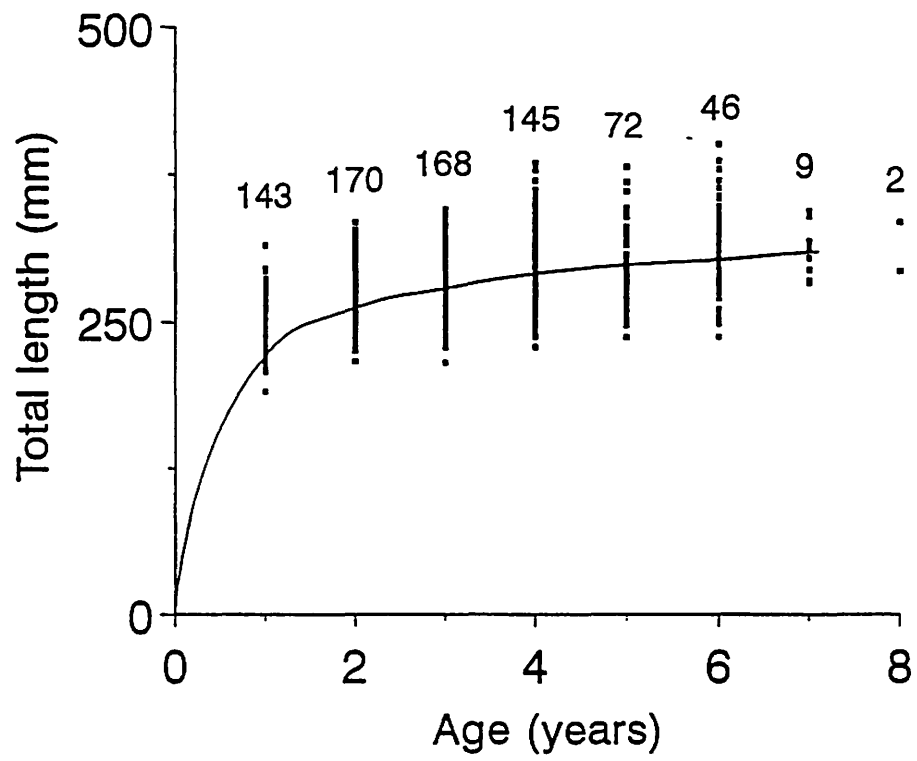


Table 3. Mean observed total lengths-at-age (mm) for male and female Atlantic croaker caught in September, 1988-1990, in the Chesapeake Bay region.  
SD=standard deviation; n=sample size.

Age	Males			Females		
	Mean	SD	n	Mean	SD	n
1	199	20.7	62	204	23.4	81
2	260	24.4	56	266	21.9	114
3	268	31.8	64	277	28.5	104
4	279	26.3	50	288	33.3	95
5	291	25.2	28	294	31.2	44
6	304	38.5	16	310	33.9	30
7	305	17.4	3	312	24.1	6
8	313	29.0	2	---	----	0

Table 4. Parameter estimates, standard errors, and 95% confidence intervals for the von Bertalanffy growth model for Atlantic croaker in the Chesapeake Bay region (1988-1990).

Parameter	Estimate	Standard Error	95% confidence intervals	
			Lower	Upper
$L_{\infty}$	312.43	7.44	297.82	327.04
K	0.36	0.08	0.20	0.52
$t_0$	-3.26	0.84	-4.91	-1.61



The slope of the regression line ( $b=3.30$ ) was significantly different from 3.00 ( $t$ -test;  $t=7.26$ ;  $P<0.01$ ), indicating allometric growth.

The girth (G) to total length (TL) relationship was:

$$G = -26.68 + 0.74 \text{ TL} \quad (r^2=0.91; n=1,537; P<0.01)$$

$$\text{TL} = 58.37 + 1.21 \text{ G} \quad (r^2=0.91; n=1,537; P<0.01)$$

No difference was found between sexes.

The total length (TL) to standard length (SL) relationship was:

$$\text{SL} = -9.46 + 0.85 \text{ TL} \quad (r^2=0.99; n=1,537; P<0.01)$$

$$\text{TL} = 14.69 + 1.15 \text{ SL} \quad (r^2=0.99; n=1,537; P<0.01)$$

No difference was found between sexes.

### *Size and age compositions*

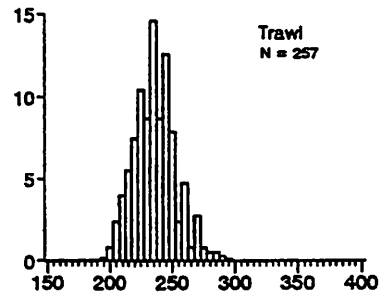
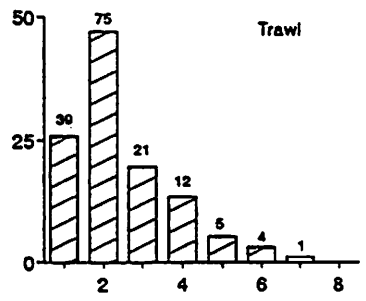
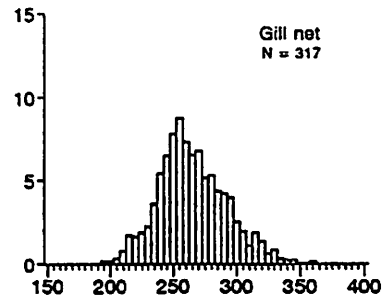
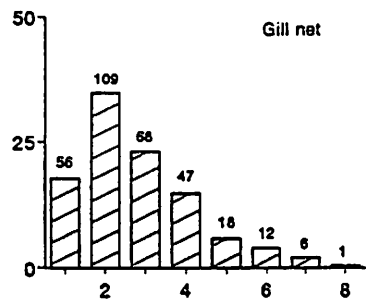
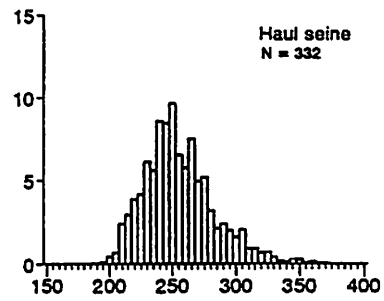
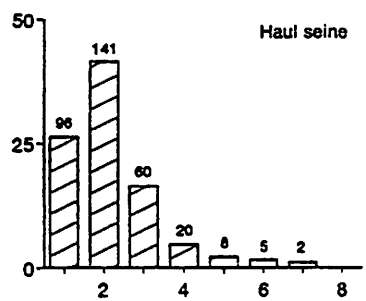
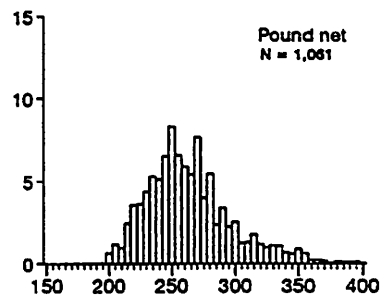
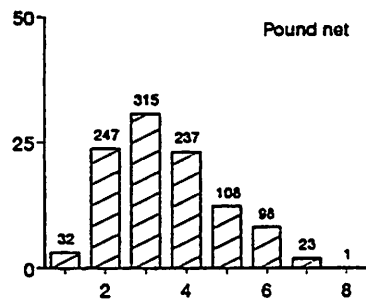
Length frequency distributions of Atlantic croaker samples obtained from different fishing gears were similar (Fig. 9), with the exception of commercial trawl data which was dominated by fish smaller than 275 mm. The smallest fish captured by each gear was approximately 200 mm, although these data represent only market foodfish grades (small, medium or large) and do not include smaller fish sold as scrap. The maximum length recorded was 400 mm, from a pound-net catch in 1988. However, for all gears 99.5% of the Atlantic croaker collected were  $\leq 356$  mm, 99% were  $\leq 345$  mm, and 90% were  $\leq 295$  mm.

Age compositions from different gears were not as

similar as length frequencies would suggest (Fig. 9). Haul-seines, gill-nets, and commercial trawls caught a larger proportion of fish at ages 1 and 2, and had age 2 as the first age fully recruited. Pound-nets showed a comparatively larger proportion of fish at ages 4-7, and had age 3 as the first age fully recruited. Age 1 fish were not fully recruited to any of the gears sampled, but this may reflect, in part, the exclusion of scrap fish from collections.

Fig. 9. Age frequency (left panels) and length frequency (right panels) distributions by fishing gear for Atlantic croaker in the Chesapeake Bay region, 1988-1991. Numbers above bars are sample sizes by age.

Frequency (%)



Age (years)

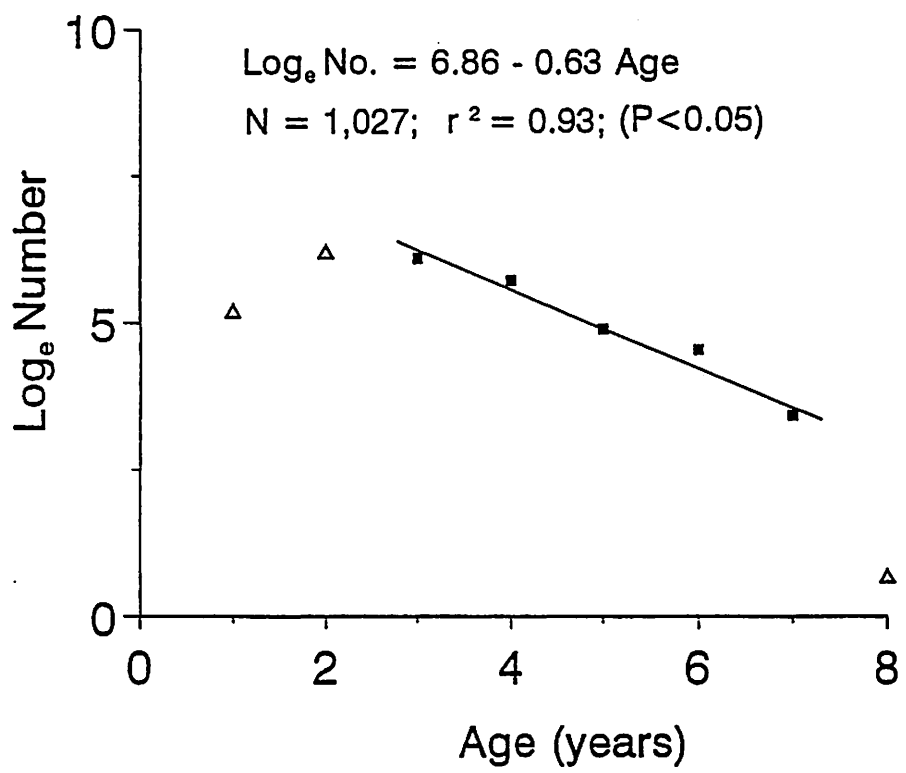
Total length (mm)

Atlantic croaker in the Chesapeake Bay area have a maximum longevity of approximately 8 years. Despite the large sample size and the variety of gears used only two eight-year-old fish were collected, one from a pound-net in September 1988 (334 mm) and one from a gill-net in September 1990 (293 mm).

### *Mortality*

Instantaneous total annual mortality rates ( $Z$ ) ranged from 0.55 to 0.63. Estimates obtained for a maximum age of 8 years were 0.55 ( $A=42\%$ ) using Hoenig's (1983) method, and 0.58 ( $A=43\%$ ) using Royce's (1972) method. A regression estimate obtained from the slope of the catch curve (Fig. 10) was 0.63 ( $A=47\%$ ), with confidence intervals being 0.36 ( $A=30\%$ ) and 0.90 ( $A=59\%$ ). Although data points at ages 3 and 7 are below the regression line suggesting a curvilinear relationship, the regression line did not deviate significantly from linearity (ANOVA;  $F=1.15$ ;  $P=0.40$ ).

Fig. 10. Catch curve for Atlantic croaker collected from pound-net, haul-seine and gill-net commercial catches in Chesapeake Bay, 1988-1991. Ages 1, 2 and 8 (triangles) were not used in calculating the regression line.



## DISCUSSION

### *Age determination*

My criteria for ageing Atlantic croaker using otolith sections differ from those of Barger (1985) in that I considered the first annulus to be the blurred opaque band surrounding the otolith core. However, evidence from both studies seems to support my interpretation. Barger (1985) reported 58% of the otoliths having marks that were too thin or discontinuous, and too close to the core to be considered annuli. By examining otoliths of young-of-the-year during the period of annulus formation I was able to validate this mark as the first annulus, formed during their first spring in the estuary. Because spawning of Atlantic croaker in the Chesapeake Bay area extends from late July to December (see Chapter 3) and the first annulus is formed during their first spring after hatching, fish forming the first annulus could range from 5 to 10 months of age. As marginal increment plots indicated, all subsequent annuli are formed at yearly intervals.

The observed variation in the width of the first annulus also seems to reflect the protracted spawning period of Atlantic croaker. Early hatched fish (July-August) would



probably be large enough by April or May to have this annulus close to, but not continuous with the otolith core. In contrast, late-hatched fish (November-December) would be small in the spring and probably show the first mark and the core virtually fused together. Since Atlantic croaker also spawn over a long period in the Gulf of Mexico (White and Chittenden 1977), this might explain why the first annulus was apparent in only a portion of Barger's (1985) fish.

My interpretation of the first annulus is also consistent with evidence from another ageing method. Ross (1988) reported that some Atlantic croaker from North Carolina showed an early, age-0 scale mark, apparently formed during their first winter. However, he did not count them as annuli because such marks were evident in only a few fish.

The high precision of repeated age readings and the fact that I was able to validate annuli almost to the maximum observed age indicate that otolith sections represent a very reliable method for ageing Atlantic croaker. Identifying the first annulus may require some practice, but all other annuli are extremely clear and easy to identify. Otolith sections do not have the problems scales reportedly do, such as the occurrence of double marks (Haven 1954, White and Chittenden 1977, Music and Pafford 1984, Ross 1988, Chapter 1), or marks that are poorly defined and difficult to distinguish (Joseph 1972, Mericas

1977, Barger and Johnson 1980, Chapter 1).

The pattern of otolith growth relative to fish growth also indicated the high reliability of transverse otolith sections for ageing Atlantic croaker. Although otolith radius, the axis I used to read annuli, showed a poor correlation with fish length, the strong linear relationship between otolith radius and age indicates that otolith growth along this axis is continuous with age, independent of fish growth. This supports previous suggestions (Mosegaard et al. 1988, Wright 1991) that a process other than somatic growth governs the rate of otolith accretion. Casselman (1990) pointed out that, because otoliths grow at a faster rate than the body during slow somatic growth, they are excellent structures for recording the seasonal cycle and age in slow-growing and old fish, especially those approaching asymptotic length. The high correlation I found between otolith radius and age for Atlantic croaker seems to confirm this pattern.

### *Growth and mortality*

The high variability of observed lengths-at-age indicates that size is a very poor predictor of age for Atlantic croaker, especially beyond ages 1 or 2. A 250 mm fish, for example, could be of any age from 2 to 8 years. This wide range in lengths-at-age can be attributed to a combination of two factors: (1) most of Atlantic croaker's

growth occurs during the first two years, becoming clearly asymptotic after age 2; and (2) the different growth rates of fish born at different times during the extended spawning season. Warlen (1982) reported that Atlantic croaker larvae from North Carolina offshore waters caught later in the spawning season (after January) had slower growth rates than those taken during peak spawning (September-November). While early-hatched larvae grow during warm summer and fall temperatures and have higher food availability, larvae born late in the season must survive winter in estuarine nursery areas where they are susceptible to rapid and unfavorable temperature changes. In Chesapeake Bay, unusually colder winters are reported to cause massive mortalities and poor recruitment of Atlantic croaker (Massmann and Pacheco 1960, Joseph 1972, Chao and Musick 1977, Setzler-Hamilton 1987). Increased mortality due to low water temperatures has been also hypothesized as the reason of a six-week period of low recruitment of larval Atlantic croaker in the Newport River estuary, North Carolina (Warlen and Burke 1991).

Growth parameter estimates reported here generally do not agree well with previous reports for Atlantic croaker. My estimate of  $L_{\infty}$  (312 mm) is smaller than the largest fish collected (400 mm), and well below the maximum size reported for this species (668 mm TL, Rivas and Roithmayr 1970). This is normal because  $L_{\infty}$  is a regression estimate, thus an average, that represents an average maximum length if fish

live and grow according to the von Bertalanffy equation. It seems to represent, moreover, a reasonable average maximum length for the Chesapeake Bay area, given the sharp decrease in growth I observed during the second year, and the leveling-off of sizes-at-age that I observed after age 2 as fish approach about 300 mm on average.

It is difficult to compare growth parameter estimates reported here with those in previous studies. Previous estimates were based on different ageing methods (White and Chittenden 1977, Ross 1988). As a result of different ageing techniques, the accuracy of age determinations, thus sizes-at-age, in previous studies may differ from mine. This may be especially so with scale-based age determination. In Chapter 1 I showed that age determination of Atlantic croaker was much more difficult with scales than otoliths, and that precision was much lower with scales than otoliths.

Methods used to estimate length-at-age data or to fit the von Bertalanffy model have also varied. Previous studies on Atlantic croaker growth generally used back-calculated rather than observed lengths-at-age, like I used. Although back-calculation has been widely used and represents standard methodology in age and growth studies (Bagenal and Tesch 1978, Jearld 1983), recent evidence indicates that it may generate biased results (Campana 1990, Ricker 1992).

Total mortality estimates presented here are the lowest ever reported for Atlantic croaker. However, the close agreement I found between estimates obtained from maximum age and from the catch curve indicates these values are probably realistic, at least for the Chesapeake Bay area.

**CHAPTER 3**

**Reproductive biology**

## INTRODUCTION

Despite the large number of studies describing spawning periodicity of Atlantic croaker in the Mid-Atlantic and Chesapeake regions (e.g., Hildebrand and Schroeder 1928, Wallace 1940, Johnson 1978, Colton et al. 1979, Morse 1980, Norcross and Austin 1988), studies on reproductive biology are rare and mostly incomplete. Information on sexual maturity, fecundity, and sex ratios has been reported (Hildebrand and Schroeder 1928, Wallace 1940, Morse 1980). However, speculation on whether or not Atlantic croaker spawn within Chesapeake Bay (Welsh and Breder 1923, Pearson 1941, Haven 1957) has not been verified; estimates of size-at-maturity (Wallace 1940, Morse 1980) do not agree; estimates of age-at-maturity (Welsh and Breder 1923, Wallace 1940) were based on poor methods of age determination, i.e., length frequencies and scales (Chapter 1); and available fecundity estimates (Morse 1980) cannot be used without an evaluation of Atlantic croaker's fecundity pattern, i.e., whether they have determinate or indeterminate annual fecundity.

Traditionally, estimates of fish fecundity have been based on the assumption that the total number of eggs

spawned by a female each year—annual fecundity—is fixed prior to the onset of spawning, a condition known as determinate fecundity (Hunter et al. 1992). However, recent evidence (Hunter and Goldberg 1980, Hunter and Macewicz 1985a, Hunter et al. 1985, Horwood and Greer Walker 1990) indicates that, in many temperate and tropical fish, annual fecundity cannot be estimated from the standing stock of advanced oocytes, because unyolked oocytes continue to be matured and spawned throughout the spawning season. This condition is called indeterminate fecundity (Hunter et al. 1992). The only way to estimate annual fecundity, then, is by estimating batch fecundity—the number of eggs released during each spawning—and multiplying it by spawning frequency—the number of times an average female spawns during the spawning season (Hunter and Macewicz 1985a, Hunter et al. 1985, 1992). Although the extended spawning season of Atlantic croaker (Wallace 1940, Colton et al. 1979, Warlen 1982) suggests it is a multiple spawner with indeterminate fecundity, no attempt has been made to evaluate its fecundity pattern.

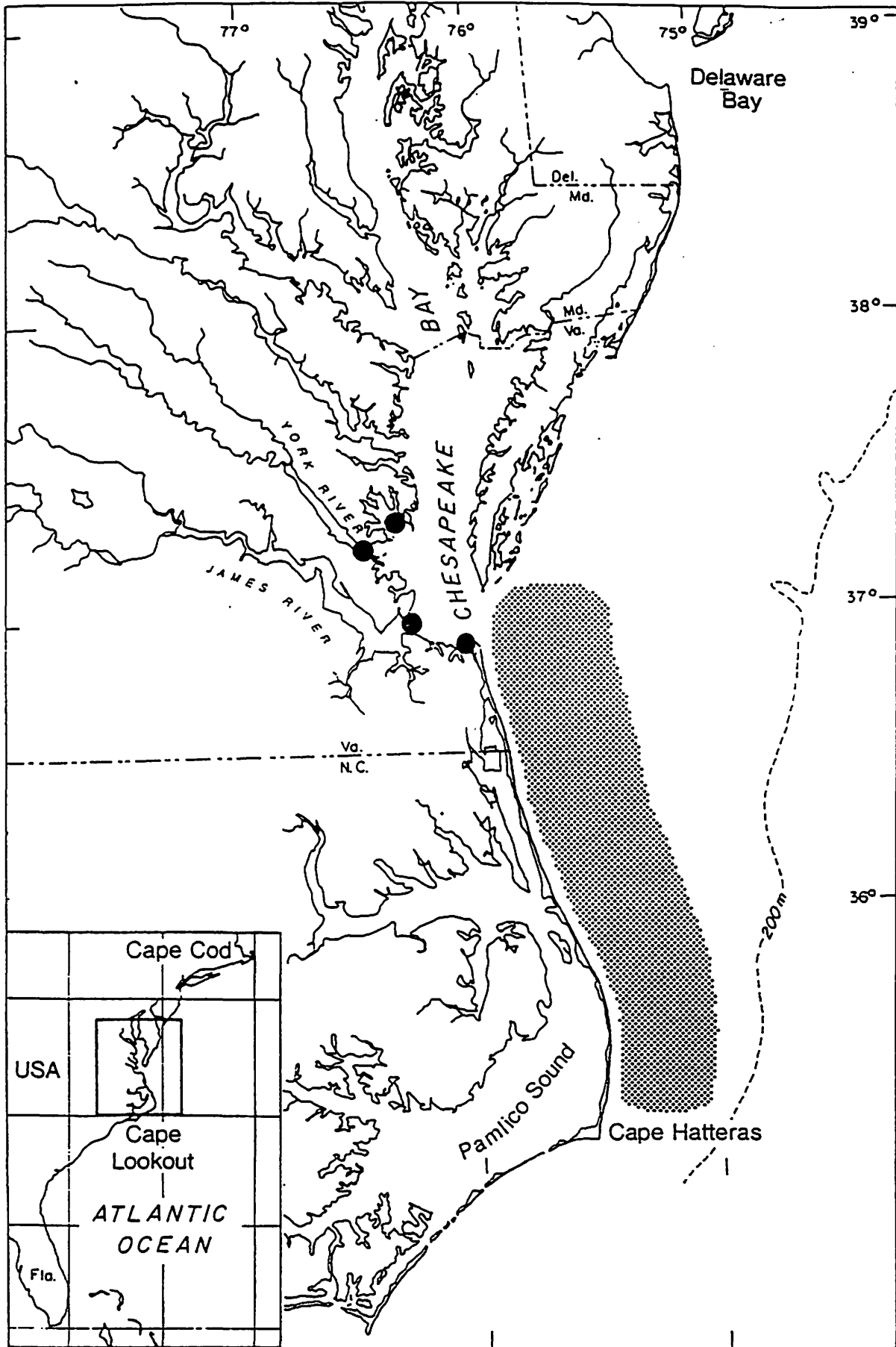
In this chapter, I test the assumption of determinate annual fecundity, and describe spawning periodicity and location, size- and age-at-maturity, sex ratios, ovarian cycle, and oocyte atresia for Atlantic croaker in the Chesapeake Bay region.



## MATERIALS AND METHODS

Four approaches were used to sample Atlantic croaker for this study. In 1990 and 1991 fish were collected mainly from commercial pound-net, haul-seine, and gill-net fisheries, which operate from late spring to early fall in the lower Chesapeake Bay (Fig. 11). Local fish processing houses and seafood dealers were contacted weekly, and one 22.7-Kg (50-lb) box of fish of each available market grade (small, medium or large) was purchased for processing. Since Atlantic croaker migrate out of Chesapeake Bay in mid-fall to overwinter offshore (Haven 1959), monthly samples in November-March 1990 and November-December 1991 were obtained from commercial trawlers operating in Virginia and North Carolina shelf waters. In addition to these collections, daily samples from a gill-net in the lower York River were obtained during the period August-October 1990 and July-October 1991, except on weekends. In 1991 the net was emptied twice a day: in the early morning (6:00-8:00 am) and in the evening (5:00-7:00 pm). Time of death was recorded for fish alive at the time the net was emptied. Daily gill-net samples were used to monitor small-scale (less than weekly) changes in Atlantic croaker reproductive

Fig. 11. Map of the Chesapeake Bay region. Black dots in Chesapeake Bay indicate pound-net, haul-seine or gill-nets collection sites. Hatched area off Virginia and North Carolina indicates where otter trawl collections were obtained.



condition, and as an attempt to collect hydrated or recently-spawned females for estimates of batch fecundity and spawning frequency. Finally, collections from the commercial fisheries were supplemented by fish obtained from the Virginia Institute of Marine Science (VIMS) juvenile bottom trawl survey. The VIMS trawl survey uses a monthly stratified random sampling program in the lower Chesapeake Bay and monthly fixed mid-channel stations in the York, James, and Rappahannock rivers. Details on sampling design and gear are described in Chittenden (1989b) and Geer et al. (1990).

Fish were measured for total length (TL) to the nearest millimeter, weighed for total weight (TW) and gonad weight (GW) to the nearest gram, sexed, and both sagittal otoliths were removed and stored dry. The left otolith was sectioned through the core and aged under a dissecting microscope (6-12x) using criteria described in Chapter 2. The gonadosomatic index, GSI, was calculated for individual fish as  $(GW/(TW-GW)*100)$ . Females were assigned a macroscopic gonad maturity stage (Table 5). Males were classified only as sexually mature or immature, because more detailed gonad staging was considered subjective and imprecise. Female macroscopic stages were verified microscopically by inspecting fresh oocyte samples and histology slides of a randomly selected sub-sample of ovaries in each maturity stage. Fresh oocytes were removed from one ovary, spread on

a microscope slide, and examined under a dissecting microscope (12-50 $\times$ ). Color photographs were used to permanently record the appearance of fresh oocyte samples. This allowed fresh oocytes to be later compared with histology slides in assessing gonad maturity stage and the occurrence and intensity of oocyte atresia. For histological preparation, tissue samples were fixed in 10% neutrally-buffered formalin for 24 hours, then soaked in water another 24 hours, and stored in 70% ethanol. Samples were embedded in paraffin, sectioned to 5-6 $\mu\text{m}$  thickness and stained with Harris' Hematoxylin and Eosin Y. Histological classification of ovaries (Table 5) was based on the occurrence and relative abundance of five stages of oocyte development (primary growth; cortical alveoli; partially yolked; advanced yolked; and hydrated), and on the occurrence and intensity of Alpha ( $\alpha$ ) atresia. Terminology for stages of oocyte development and ovarian atresia follows Wallace and Selman (1981), Hunter and Macewicz (1985b) and Hunter et al. (1992).

To estimate mean length at first maturity ( $L_{50}$ ) for males and females, the fraction of mature fish per 10 mm length intervals was fit to the logistic function by nonlinear regression (Marquardt method), using FISHPARM (Saila et al. 1988).  $L_{50}$  was defined as the smallest length interval in which 50% of the individuals were sexually mature. Females were considered sexually mature if they

were in gonad stages 2 (developing) or higher (Table 5). To avoid classifying resting (reproductively inactive) fish as immature, and thus getting biased estimates of  $L_{50}$ , only fish collected in September, when no resting stages occurred, were used for this analysis.

Fecundity pattern was evaluated through oocyte size-frequency distributions of fully-developed (gonad stage 3) females collected throughout the spawning season. Before measurements were taken oocytes were hydraulically separated from each other and from the ovarian membrane and preserved in 2% formalin using the method of Lowerre-Barbieri and Barbieri (1993). Oocyte measurements were taken after a preservation period of at least 24 hours. Samples were stirred before oocytes were removed, to reduce bias due to settling differences caused by oocyte size or density. Oocytes  $\geq 0.1$  mm were measured to the nearest 0.02 mm (one micrometer unit at 50 $\times$ ) with an ocular micrometer in a dissecting microscope. Measurements were taken along the median axis of the oocyte parallel to the horizontal micrometer gradations (Macer 1974, DeMartini and Fountain 1981).

Table 5. Description of gonad maturity stages for female Atlantic croaker, Micropogonias undulatus, in the Chesapeake Bay region. Macroscopic appearance refers to fresh ovaries. Females in gonad stages 3, 4, and 5 are in spawning phase (see Fig. 19).

Stage	Macroscopic appearance	Microscopic appearance
(1) Immature	Ovaries very small, light pink in color; translucent.	Only primary growth oocytes present; no atresia; ovarian membrane thin.
(2) Developing	Ovaries ranging from small to medium ( $\leq 25\%$ of body cavity); yellow to light orange in color; some opaque oocytes present, but most oocytes are not opaque.	Only primary growth, cortical alveoli and a few partially yolked oocytes present; no major atresia.
(3) Fully-developed	Ovaries ranging from large (25-50% of body cavity) to very large (taking almost all space available in body cavity); creamy yellow to light orange in color; opaque oocytes present; if partially spent may have some left-over hydrated oocytes at the posterior end of the ovarian lumen.	Primary growth to advanced yolked oocytes present; may have some left-over hydrated oocytes from previous spawning; there may be major atresia of advanced yolked oocytes, but no major atresia of other oocytes.
(4) Gravid	Ovaries ranging from large (25-50% of body cavity) to very large (taking almost all space available in body cavity); creamy yellow to light orange in color; hydrated oocytes intermixed with opaque oocytes and not collected in the ovarian lumen (unovulated).	Primary growth to hydrated oocytes present; there may be major atresia of advanced yolked oocytes, but no major atresia of other oocytes; hydrated oocytes still in follicles (unovulated).
(5) Running-ripe	Ovaries ranging from large (25-50% of body cavity) to very large (taking almost all space available in body cavity); creamy yellow to light orange in color; most hydrated oocytes are collected in the ovarian lumen (ovulated), but some may be still intermixed with opaque oocytes.	Primary growth to hydrated oocytes present; there may be major atresia of advanced yolked oocytes, but no major atresia of other oocytes; hydrated oocytes not in follicles (ovulated).
(6) Regressing	Ovaries ranging from small to medium ( $\leq 25\%$ of body cavity); creamy yellow to light orange in color; more flaccid and watery than previous stages; opaque oocytes present.	Primary growth to advanced yolked oocytes present, but the number of yolked oocytes relative to unyolked oocytes is now much smaller; major atresia of cortical alveoli, partially yolked and advanced yolked oocytes.
(7) Resting	Ovaries very small; dark orange to reddish in color; no opaque oocytes present;	The majority ( $> 90\%$ ) of oocytes are primary growth; may have other oocytes in late stages of atresia; ovarian membrane thicker than immature fish.

## RESULTS

### *Size- and age-at-maturity*

Atlantic croaker in the Chesapeake Bay region mature at a small size and early age. Males and females started to mature at 170 and 150 mm, respectively, after which the percentage of mature fish increased very rapidly (Fig. 12). Estimated mean length at first maturity ( $L_{50}$ ) was 182 mm for males (S.E.=1.46), and 173 mm for females (S.E.=1.33). For both sexes all individuals were mature by 250-260 mm.

The percentage of mature fish by age showed a similar pattern of early maturation. More than 85% of both males and females were sexually mature by the end of their first year and all were mature by the end of their second.

### *Spawning*

Spawning of Atlantic croaker in the Chesapeake Bay region extends over a protracted period. Females in spawning phase (gonad stages: fully-developed, gravid, or running-ripe; Table 5) were collected from July through December (Fig. 13). However, the occurrence of developing



Fig. 12. Percentage of mature male and female Atlantic croaker by 10 mm total length intervals, with a logistic function (continuous line) fitted to the data. Arrows indicate mean length at first maturity ( $L_{50}$ ). n=sample size.

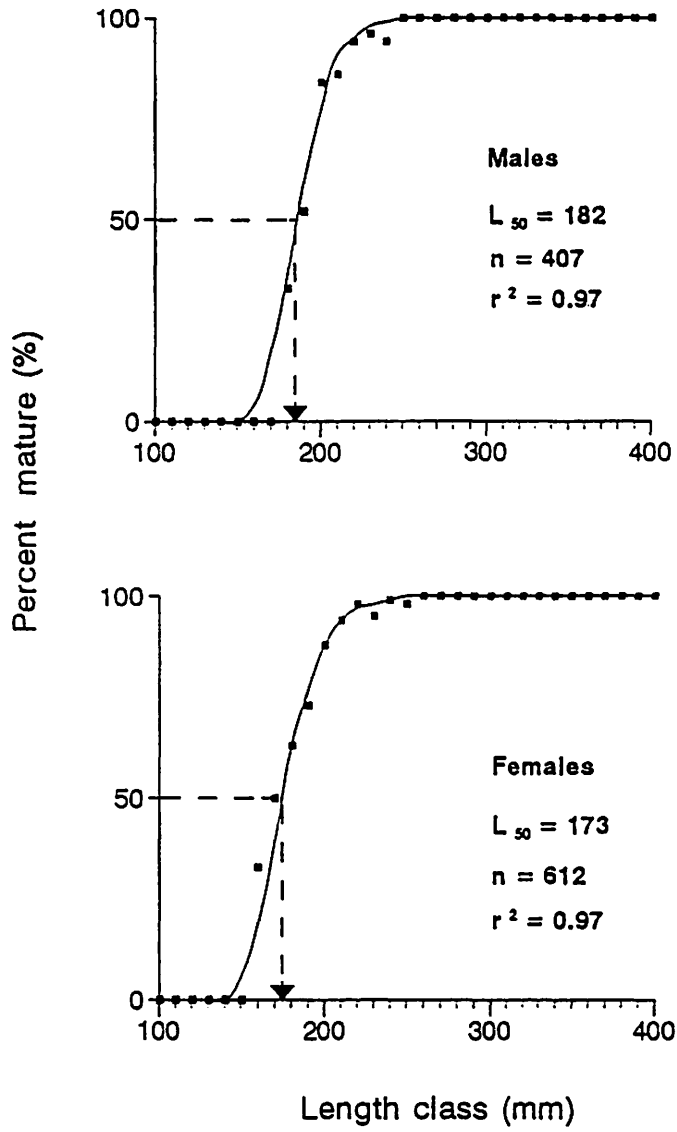
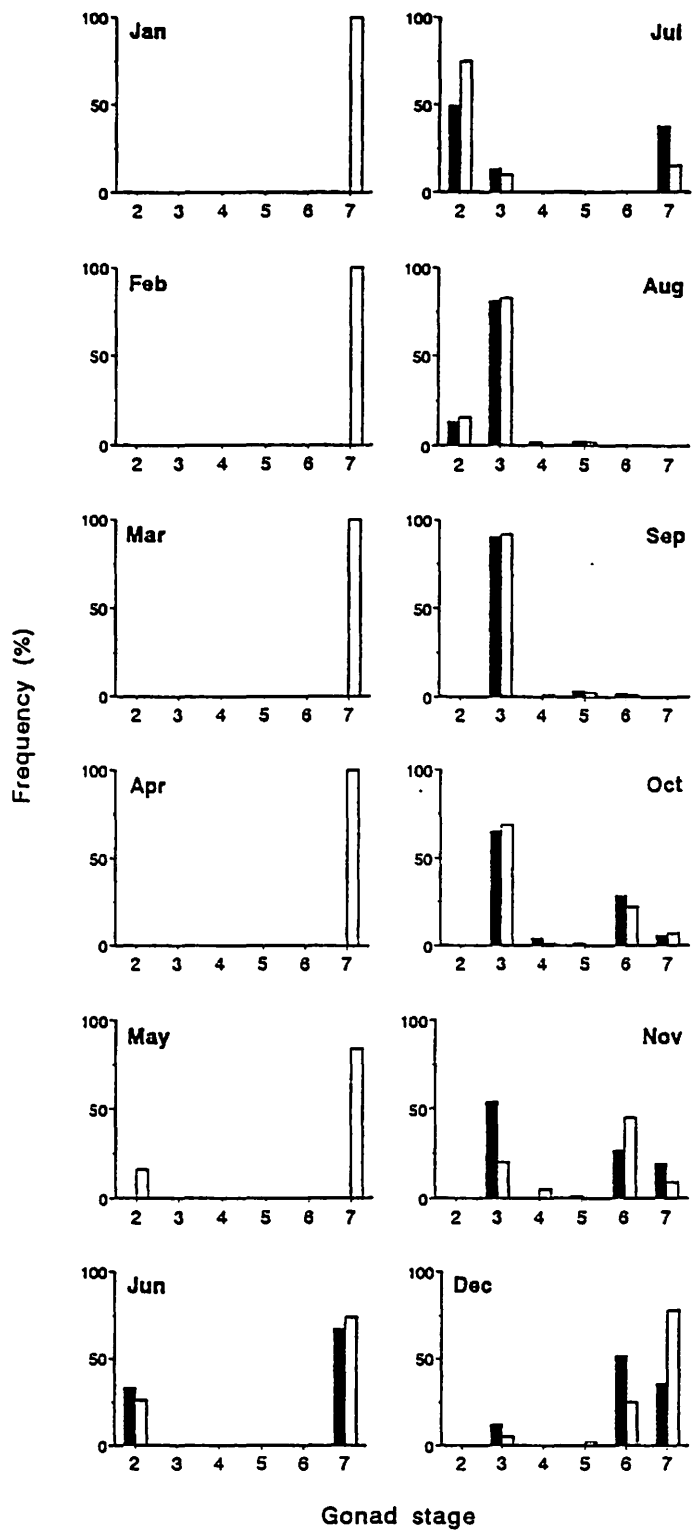


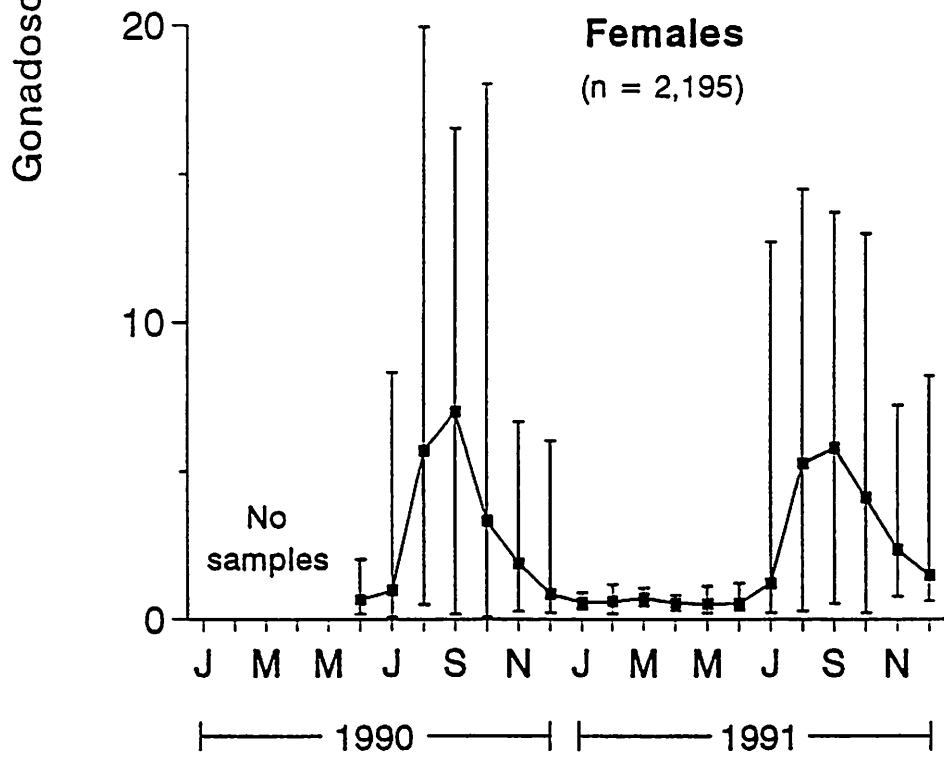
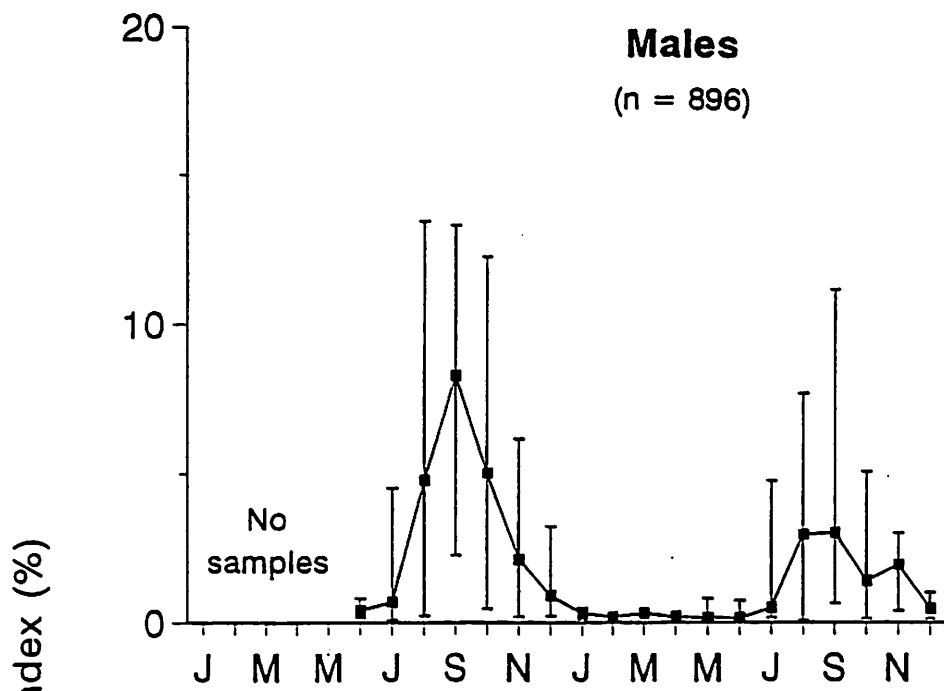
Fig. 13. Percentage of gonad maturity stages by month for mature female Atlantic croaker in the Chesapeake Bay region. Black bars = 1990 data; open bars = 1991 data. Gonad stages are: (2) developing; (3) fully-developed; (4) gravid; (5) running-ripe; (6) regressing; and (7) resting. Monthly sample sizes are in Table 6.



females from May through August, and regressing females from September through December indicates that gonad maturation was not synchronous among individuals. Although, at the population level, spawning occurred over a six-month period (July-December), individual fish apparently spawned for only two to three months, with some beginning as early as July and some finishing as late as December. The pattern of gonad development in males agrees well with results from females and provides further evidence of an extended spawning season. Mean and maximum GSI values increased sharply during July and August, and remained relatively high until November or December, depending on the year (Fig. 14). In addition, during August-September males with very large testes and free-running milt were common in collections from all locations and sampling gears, indicating intense male spawning during this period.

Spawning of Atlantic croaker occurred in the estuary as well as in coastal oceanic waters. Spawning fish—females with hydrated oocytes and males with free-running milt—were collected in the lower Chesapeake Bay, the lower York and James rivers, and from coastal waters off Virginia and North Carolina. Collections of spawning fish in Chesapeake Bay during the period July-October, and from offshore waters during November-December indicate that, at the population level, spawning starts in Chesapeake Bay and continues offshore and south as Atlantic croaker migrate out of the

Fig. 14. Monthly mean gonadosomatic index for male and female Atlantic croaker in the Chesapeake Bay region, 1990-1991. Vertical bars are ranges. n=sample size.



estuary. However, the occurrence during the fall of some regressing and resting females in Chesapeake Bay (Fig. 13) indicates that at least some individuals complete their spawning in estuarine waters.

Although gravid and running-ripe females were collected during almost the entire spawning season (Fig. 13), they occurred in very low numbers. During both years of sampling only 7 gravid and 8 running-ripe females were collected. In Chesapeake Bay, despite the large number of pound-net and haul-seine collections (1,422 mature females processed), gravid or running-ripe females were obtained only from gill-nets, and mainly from collections from the lower James River (6 gravid and 4 running-ripe females). Daily gill-net collections obtained during the period August-October 1990 and July-October 1991 (456 mature females processed) showed only one running-ripe and one partially spent female, i.e., a fully-developed female which had fresh left-over hydrated oocytes in the ovarian lumen indicating recent spawning but still had a large number of advanced yolked oocytes and could potentially spawn again. Offshore collections during November-December of 1990 and 1991 also showed a small number of gravid and running-ripe females (Fig. 13).

### *Sex Ratios*

Atlantic croaker in the Chesapeake Bay region showed



wide temporal fluctuations in sex ratio. During both years, the frequency of males started decreasing in June-July, at the beginning of the spawning season, reached a minimum in the period September-October and started increasing again during November-December (Fig. 15). Chi-square test results (Table 6) showed highly significant differences ( $P < 0.01$ ) in sex ratios during July-October 1990 and June-October 1991.

### *Oocyte development and spawning pattern*

Atlantic croaker are multiple spawners with indeterminate fecundity. Monthly oocyte diameter distributions of fully-developed females collected throughout the spawning season showed three main groups of oocytes (Fig. 16). However, oocyte development appears to be asynchronous, with a large degree of overlap and no clearly defined limits between modal groups. Histological analysis showed that the first group, ranging approximately from 0.06 to 0.24 mm diameter, is composed mainly of primary growth and cortical alveolus oocytes, but may include a few partially yolked oocytes in the beginning stages of yolk deposition (0.22-0.24 mm diameter). The second group, ranging approximately from 0.26 to 0.38 mm diameter, is composed of partially yolked oocytes in several stages of yolk deposition. The third group, ranging approximately from 0.40 to 0.60 mm diameter, is formed by advanced yolked

Fig. 15. Monthly sex ratios for Atlantic croaker in the Chesapeake Bay region, 1990-1991.

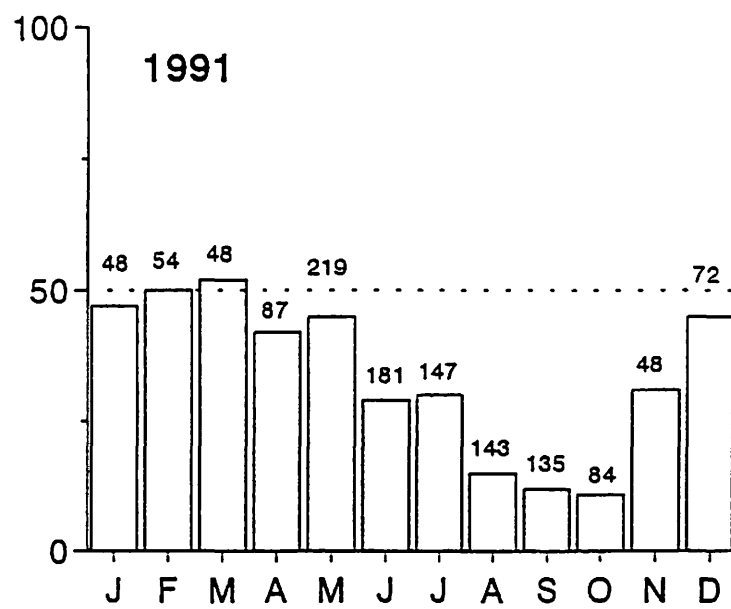
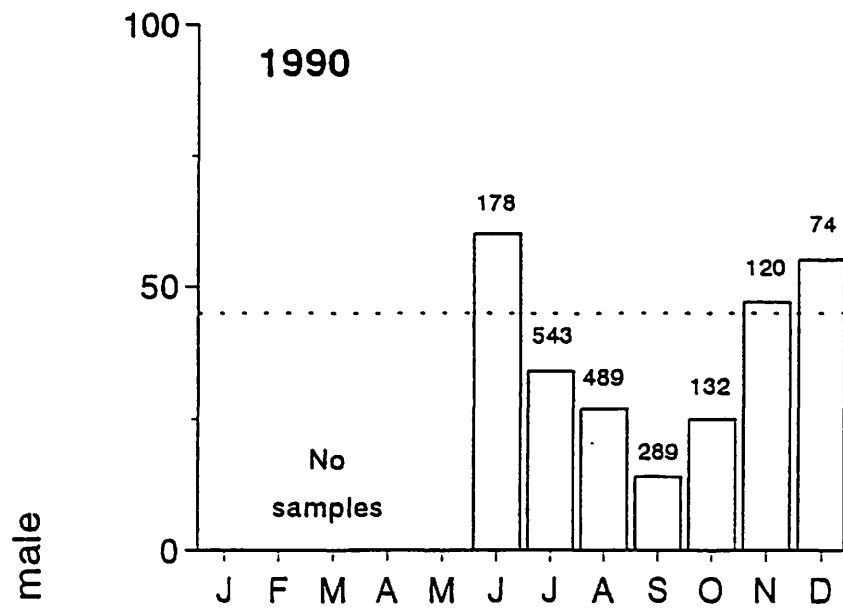
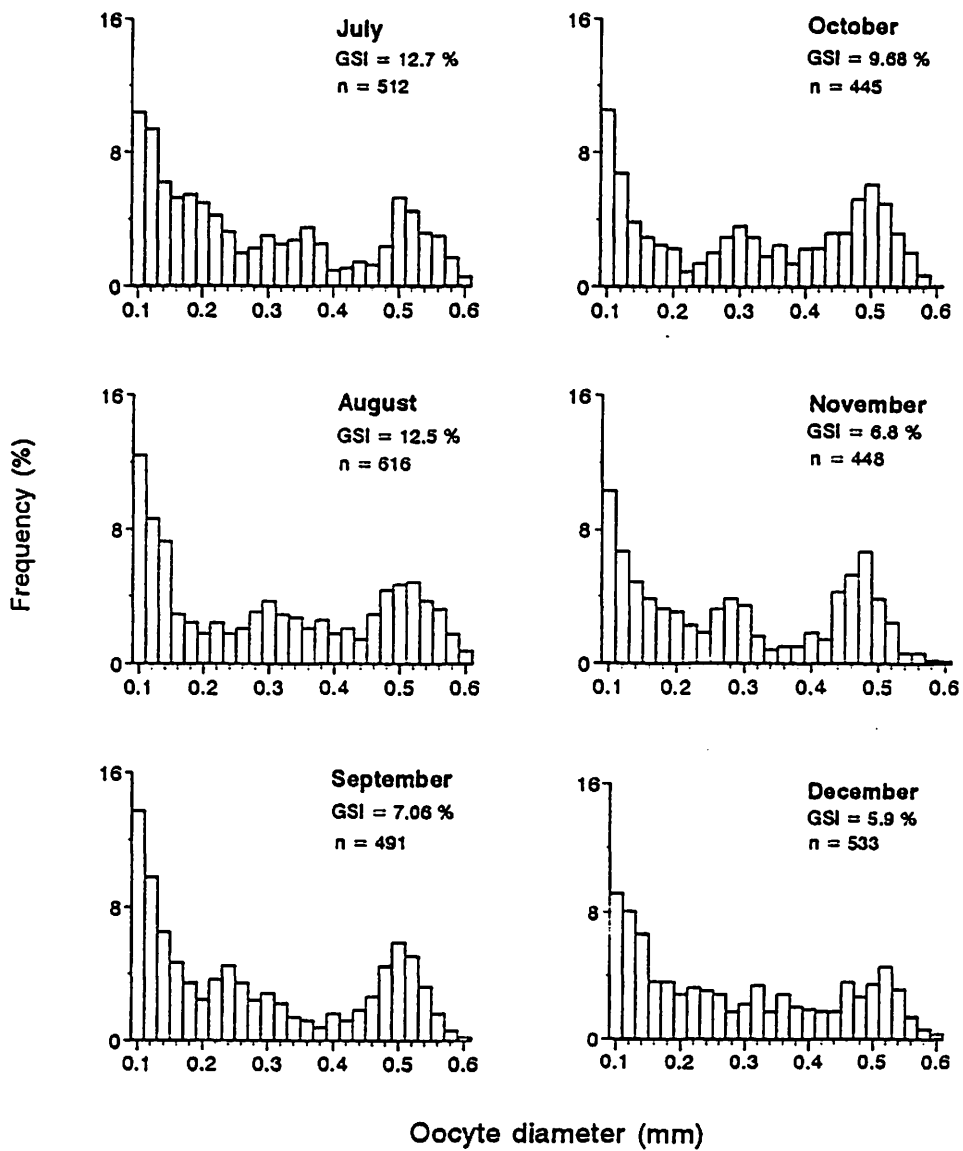


Table 6. Number of males and females by month and Chi-square tests for the monthly sex ratios of Atlantic croaker, Microponogonias undulatus, in the Chesapeake Bay region, 1990-1991. \*\* =  $P < 0.01$ .

Year	Month	Number of		Chi-square
		males	females	
1990	Jun	107	71	3.64
	Jul	185	358	27.80 **
	Aug	132	357	51.74 **
	Sep	40	249	74.91 **
	Oct	33	99	16.50 **
	Nov	56	64	0.22
	Dec	41	33	0.37
1991	Jan	22	26	0.04
	Feb	27	27	-----
	Mar	25	23	0.04
	Apr	36	51	1.29
	May	98	121	1.10
	Jun	52	129	15.96 **
	Jul	44	103	11.84 **
	Aug	21	122	34.96 **
	Sep	16	119	38.99 **
	Oct	9	75	25.61 **
	Nov	15	33	3.37
	Dec	32	40	0.44

Fig. 16. Monthly oocyte diameter distributions during the spawning season of Atlantic croaker in the Chesapeake Bay region. Each panel represents one female in the fully-developed gonad stage. GSI=gonadosomatic index; n=number of oocytes measured.



oocytes and represents the group from which individual spawning batches will be formed.

Although Atlantic croaker showed a clear pattern of multiple spawning and indeterminate fecundity, postovulatory follicles (POFs) were identified only in recently-ovulated, running-ripe females. No POFs were found in fully-developed females, even those with left-over hydrated oocytes in the posterior end of the ovarian lumen. As a result, it was usually impossible to distinguish fully-developed females spawning for the first time from those which had spawned at least once before.

#### *Atresia of advanced yolked oocytes*

Spawning-phase Atlantic croaker females (Table 5) showed a high incidence of  $\alpha$  atresia of advanced yolked oocytes throughout the spawning season (July-December). Although a small percentage (< 1%) of atretic cortical alveoli and partially yolked oocytes were also occasionally found, most atresia in spawning-phase females was limited to advanced yolked oocytes. High levels of atresia of cortical alveoli and partially yolked oocytes were found only in regressing females (Table 5).

In general, 60-100% of advanced yolked oocytes in spawning-phase females were in some stage of  $\alpha$  atresia (from early to late stages), with higher percentages of atretic

oocytes in running-ripe females (95-100%), indicating only a portion of the advanced yolked oocytes were actually spawned. However, in most females the exact proportion of atretic oocytes could not be determined because of the difficulty in identifying oocytes in very early stages of atresia. Some females showed healthy advanced yolked oocytes, atretic advanced yolked oocytes in different stages of degeneration, as well as atretic follicles ( $\beta$ -,  $\gamma$ -, and  $\delta$ -stage atresia) in the same ovary. Less than 1% of spawning females showed no atretic advanced yolked oocytes.

The high incidence of atresia of advanced yolked oocytes in Atlantic croaker does not seem to be caused by conditions in any particular area. Spawning females collected in Chesapeake Bay, in the lower York and James rivers, and in coastal waters off Virginia and North Carolina showed a high frequency of atretic advanced yolked oocytes.

Compared to healthy oocytes (Fig. 17a), early phases of  $\alpha$  atresia of advanced yolked oocytes in Atlantic croaker are characterized by the disintegration of the nucleus, which loses its integrity, becoming amorphous and slightly basophilic, and by the disintegration of yolk globules, which begin to dissolve, forming a continuous, amorphous mass, especially around the nucleus (Fig. 17b). At this stage, the majority of yolk granules at the periphery of the cytoplasm still maintain their structural integrity,



spherical shape and strong acidophilic staining. At intermediate stages, disintegration of yolk globules progresses towards the peripheral cytoplasm, which by now may have a band of dark, basophilic material (Fig. 17c), and the zona radiata begins to deteriorate. At late stages of  $\alpha$  atresia (Fig. 17d), the nucleus has completely disappeared, the zona radiata has lost its structural integrity, and the cytoplasm has been invaded by phagocytizing granulosa cells. Only portions of dissolved yolk and a few yolk globules remain at this stage. However, atresia will continue until the oocyte is completely resorbed, leaving only the remaining follicle. After this phase,  $\alpha$ -stage atresia has been completed and follicular atresia begins with the resorption of the remaining granulosa and thecal cells.

Comparisons of fresh oocyte samples and histology slides confirmed the high incidence of  $\alpha$  atresia of advanced yolked oocytes in Atlantic croaker. Although the histological method appeared more sensitive in detecting earlier stages of atresia (Fig. 18a), the use of fresh oocytes was indispensable. Fresh oocytes provided an easy, fast way to assess gonad condition, to identify oocyte atresia. A large proportion of atretic advanced yolked oocytes could be easily identified by clumping and darkening of the yolk granules, formation of a clear zone in the peripheral cytoplasm (Fig. 18b), and at later stages, formation of several light yellow vacuoles (Fig. 18c).

Fig. 17. Appearance of advanced yolked oocytes of Atlantic croaker. (a) healthy (non-atretic) oocyte; (b) oocytes in early stage of  $\alpha$  atresia; (c) oocyte in intermediate stage of  $\alpha$  atresia; (d) oocytes in late stage of  $\alpha$  atresia. N=nucleus; Zr=zona radiata; Pc=peripheral cytoplasm; La=late stage of  $\alpha$  atresia. Bars = 0.1 mm.

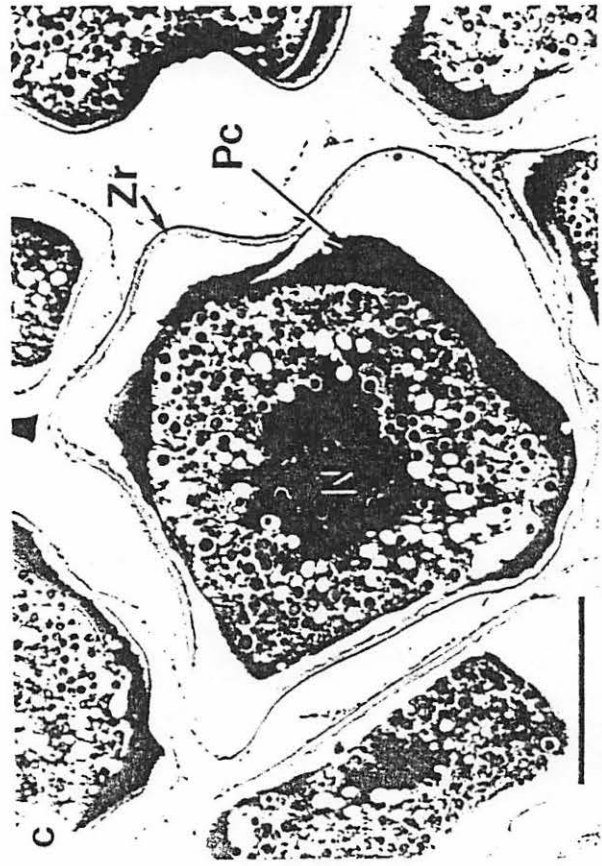
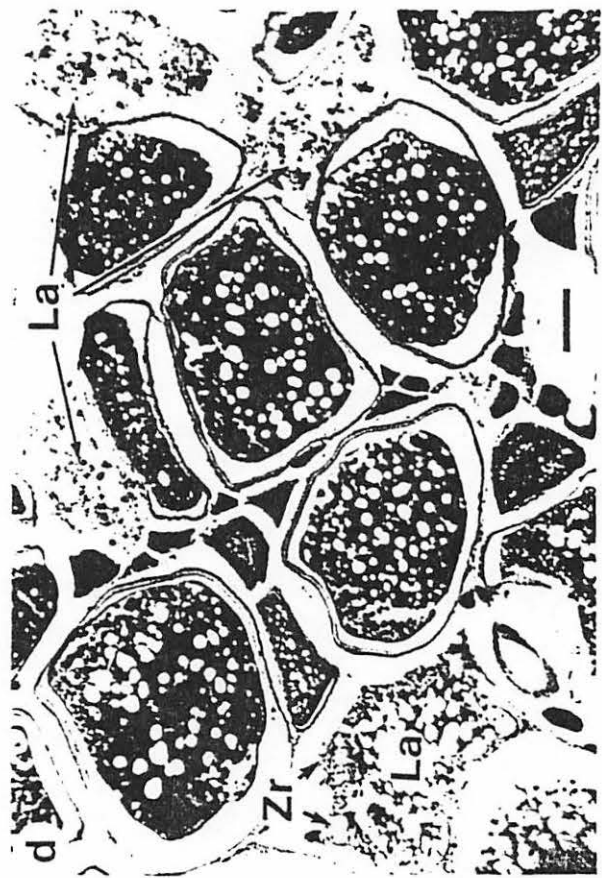
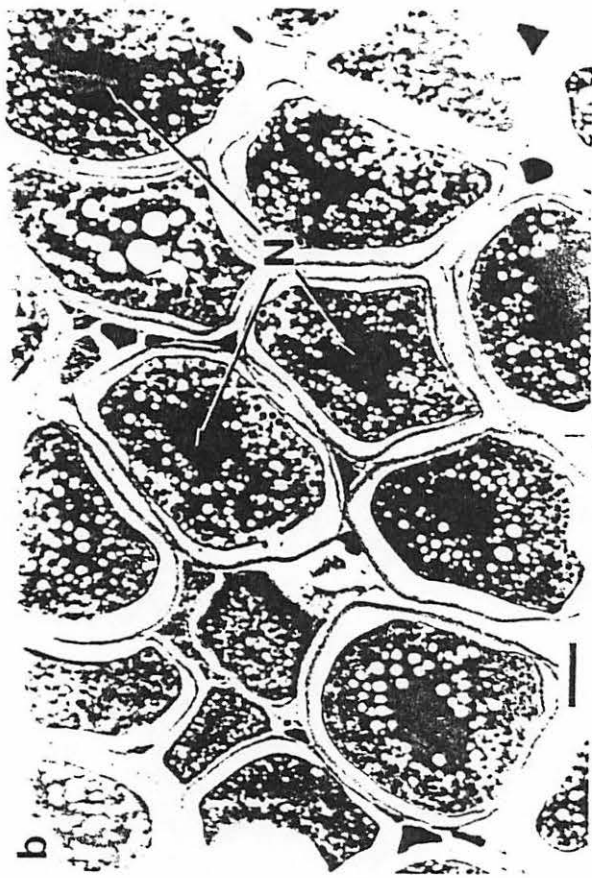
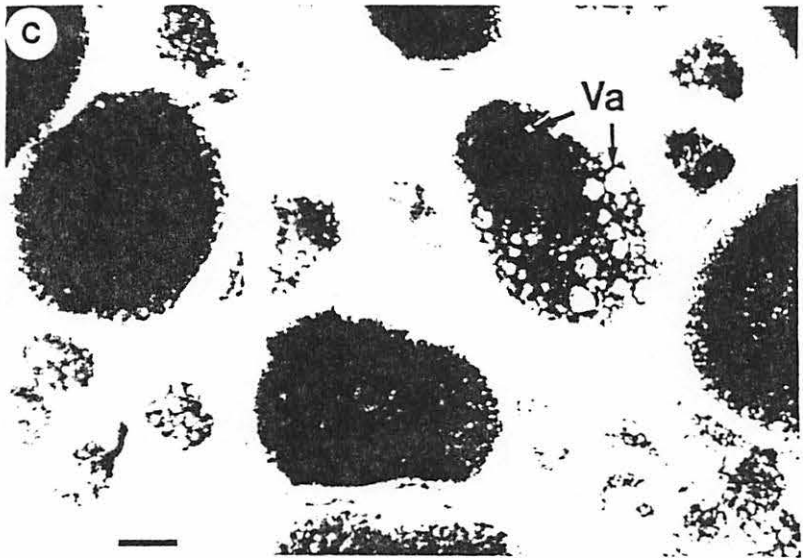
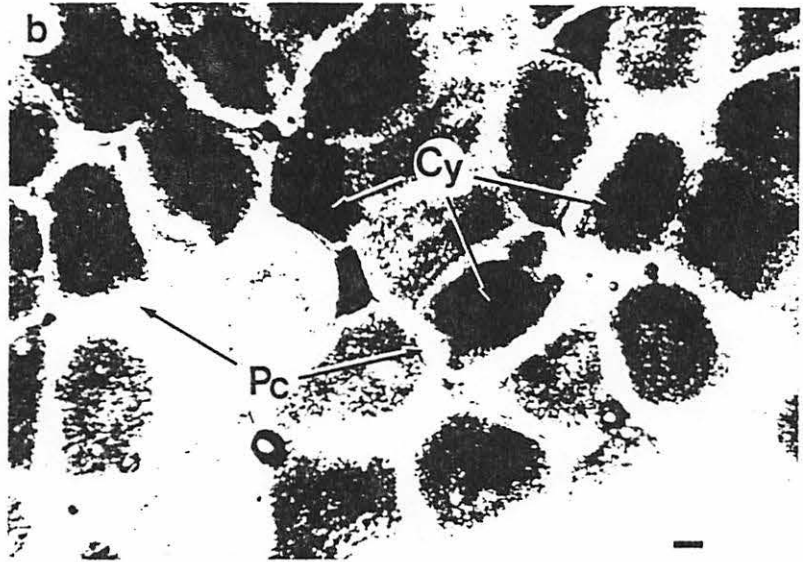
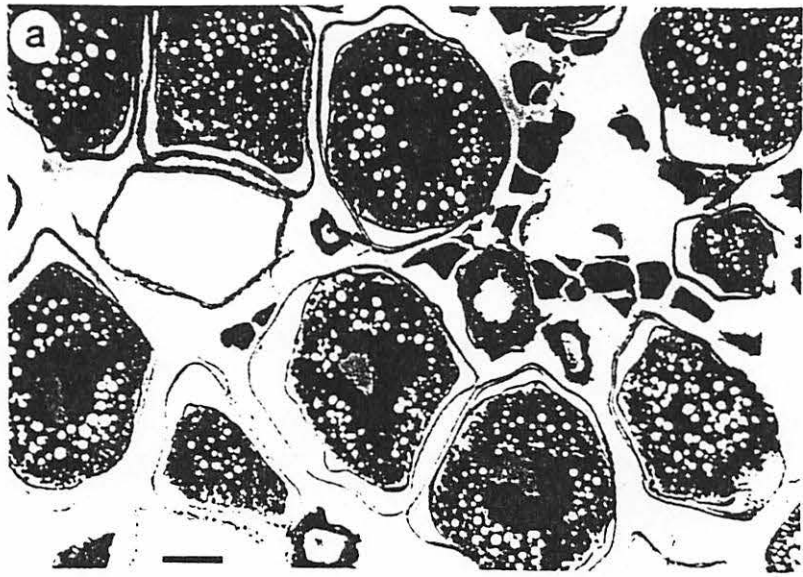


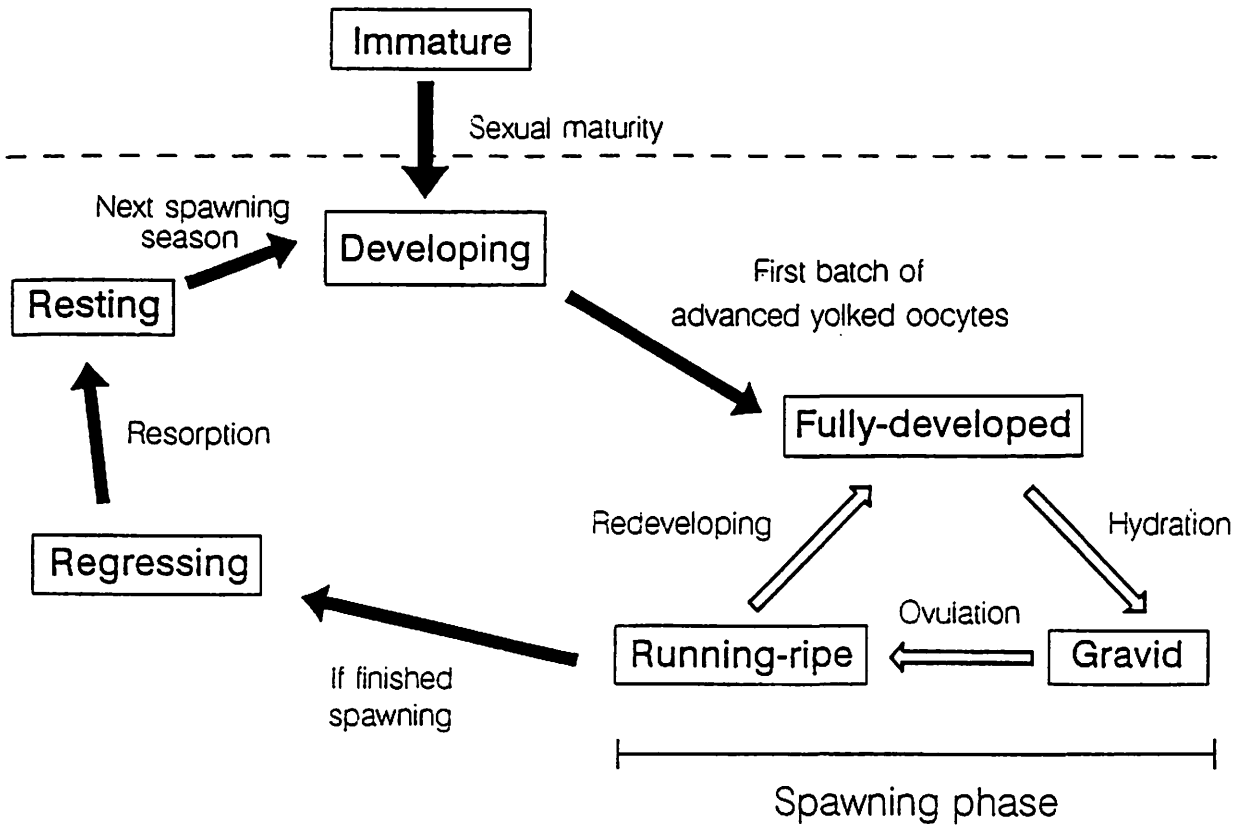
Fig. 18. Comparison of the appearance of  $\alpha$ -atretic advanced yolked oocytes of a fully-developed Atlantic croaker in a histology slide (a), and in a smear of fresh oocytes under a dissecting scope (b) and (c). Cy=clumping of yolk globules; Pc=peripheral cytoplasm; Va=vacuoles. Bars=0.1 mm.



### *Description of the ovarian cycle*

A diagrammatic representation of the Atlantic croaker ovarian cycle, based on the temporal distribution of maturity stages and the pattern of oocyte development is presented in Figure 19. The cycle can start either with immature females, which enter the cycle for the first time by reaching sexual maturity, or with adult resting females, which restart the cycle by entering the developing stage at the beginning of each spawning season. After the first batch of advanced yolked oocytes is completed, females, now in the fully-developed stage, go through a smaller cycle (spawning phase) which characterizes Atlantic croaker's pattern of multiple spawning and indeterminate fecundity. During this phase, fully-developed females cycle through the gravid and running-ripe stages by undergoing the processes of hydration, ovulation, and spawning. If spawning has not been completed, left-over advanced yolked oocytes are resorbed, a new batch of advanced yolked oocytes is recruited from the group of partially yolked oocytes (redeveloping process), and females are ready to go through the cycle again. If spawning is completed, females will then move to the regressing stage, where, through the process of oocyte atresia, left-over oocytes (cortical alveoli to advanced yolked stage) will be resorbed, after which ovaries return to the resting stage.

Fig. 19. Diagrammatic representation of the ovarian cycle of Atlantic croaker (see text for details).





## DISCUSSION

### *Spawning periodicity and location*

My results on spawning periodicity of Atlantic croaker agree well with previous reports for the Chesapeake Bay and Mid-Atlantic regions. Prior studies (Welsh and Breder 1923, Wallace 1940, Johnson 1978, Colton et al. 1979, Morse 1980) describe a protracted spawning season, extending from July/August through November/December, with peak spawning during September/October. However, reports of spawning from September/October through March/April along the South-Atlantic Bight (Hildebrand and Cable 1930, Bearden 1964, Warlen 1982, Lewis and Judy 1983), indicate that south of Cape Hatteras, North Carolina, spawning seems to start a little later and continue through early spring, perhaps as a result of the southward late summer-early fall migration of Atlantic croaker (Hildebrand and Schroeder 1928, Wallace 1940, Haven 1959). Norcross and Austin (1988) hypothesized that the match-mismatch of the timing of cessation of the summer wind regime and Atlantic croaker migration out of estuaries is likely to be significant in determining where they spawn along the Mid-Atlantic Bight. If the wind

cessation occurs prior to their fall migration, spawning would occur in northern and middle sections of the Mid-Atlantic Bight. Prolonged summer winds would keep nearshore waters cool and force Atlantic croaker to migrate further southward to spawn.

Occurrence of small juveniles (<20 mm TL) in the York River from August/September through May/June has prompted suggestions that north of Cape Hatteras spawning of Atlantic croaker may also continue through spring (Haven 1957, Chao and Musick 1977). However, results presented here confirm previous reports (Wallace 1940, Colton et al. 1979, Morse 1980) that in the Chesapeake Bay and Mid-Atlantic regions spawning is essentially completed by the end of December. Instead of reflecting a continuation of spawning through spring, the occurrence of small juveniles in Chesapeake Bay until April/May (Chao and Musick 1977, Geer et al. 1990, Bonzek et al. 1991), probably reflects a combination of: (1) slow winter growth of fish spawned late in the season (Warlen 1982), and (2) late recruitment of post-larvae and small juveniles from areas further south, where spawning reportedly continues through early spring (Weinstein 1981). The almost year-round occurrence of small young-of-the-year of whitemouth croaker, Micropogonias furnieri and mullet, Mugil platanus in the estuary of Lagoa dos Patos, Brazil, has also been attributed to one or both of these factors (Chao et al. 1985, Barbieri 1986, Vieira 1991), suggesting

this pattern may not be uncommon in species that recruit into estuarine nursery grounds but spawn over a large area and have a long spawning season.

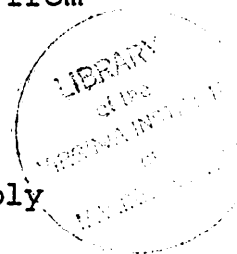
Despite Welsh and Breder's (1923) statement that spawning takes place in large estuaries such as Delaware and Chesapeake bays, this study represents the first documented report of estuarine spawning for Atlantic croaker. Previous studies (Pearson 1929, Hildebrand and Cable 1930, Wallace 1940, Haven 1957, Warlen 1982, Lewis and Judy 1983, Setzler-Hamilton 1987) have consistently described Atlantic croaker as strict marine spawners whose larval and juvenile stages migrate into estuarine nursery areas. However, the fact that during both years I found spawning-phase females in Chesapeake Bay from July through October, and that regressing and resting females—which probably had completed spawning for the season—were collected in the estuary before moving offshore indicate that the role of estuaries as additional spawning areas for Atlantic croaker is probably more important than previously thought. Whether significant spawning occurs in smaller estuaries and coastal lagoons elsewhere or whether the close oceanographic interaction between Chesapeake Bay and the continental shelf is responsible for the observed estuarine spawning of Atlantic croaker there requires further investigation. Other sciaenids which were believed to be strict marine spawners have also been reported to occasionally spawn in estuaries.

Although most spawning of the whitemouth croaker, Micropogonias furnieri, occurs in coastal waters off southern Brazil, spawning may also occur in deep channels of the estuary of Lagoa dos Patos during periods of strong saltwater intrusion (Castello 1985). A high salinity regime and the presence of deep dredged areas have also been hypothesized as the main factors responsible for spawning of red drum, Sciaenops ocellatus, in Mosquito Lagoon, east-central Florida (Johnson and Funicelli 1991).

Haven (1957) stated that spawning of Atlantic croaker within Chesapeake Bay was unlikely because fish less than 10 mm TL had never been collected there. However, although no larvae have been collected in surface samples and oblique plankton tows (Olney 1983), larvae and postlarvae 1.5-15 mm TL have been caught in subsurface and bottom plankton tows at the Chesapeake Bay mouth (Pearson 1941, Norcross 1991), and large numbers of early larvae 5-10 mm TL have been collected in juvenile bottom trawls at the York River mouth (Donald Seaver, Virginia Institute of Marine Science, Gloucester Point, VA 23062, unpublished data). Although recruitment from offshore spawning grounds and upstream transport of postlarval and juvenile Atlantic croaker have been frequently reported in Chesapeake Bay (Wallace 1940, Haven 1957, Chao and Musick 1977, Norcross 1991), the presence of early larvae (5-10 mm TL) as far up in the estuary as the York River suggests these fish were probably

spawned within the Bay.

Failure of previous studies to identify spawning of Atlantic croaker in Chesapeake Bay can be attributed, at least in part, to their pattern of multiple spawning and indeterminate fecundity. Haven (1957) did not believe spawning of significant magnitude occurred within Chesapeake Bay because, after examining thousands of adult females from the commercial catch, he found no running-ripe or recently-spent fish. However, because the processes of hydration, ovulation and spawning are very rapid, probably occurring within a matter of hours, the probability of collecting gravid or running-ripe females is much lower compared to other maturity stages. This explains why, despite the large number of mature females examined and the fact that my collections included fish from estuarine as well as coastal waters, hydrated and recently-spent females occurred in such small numbers. Additionally, contrary to what happens with total spawners, partially-spent ovaries contain oocytes ranging from primary growth to advanced yolked stage making the macroscopic identification of partially-spent fish very difficult (Hunter and Macewicz 1985a). In most cases I was not able to macroscopically distinguish between fully-developed and partially-spent ovaries, and it is likely that in previous studies fully-developed females were incorrectly classified as some kind of "developing" stage not yet capable of spawning



(e.g., Wallace 1940, Haven 1954).

Diel periodicity of spawning could also influence the occurrence of hydrated females in samples from different gears. The thousands of adult Atlantic croaker examined by Haven (1957) and Wallace (1940) were collected primarily from Chesapeake Bay commercial pound-nets and haul-seines, which are usually fished in the pre-dawn or early morning hours (Reid 1955, Chittenden 1991). During the rest of the day and through most of the night fish remain alive in the pound-head or in the seine-bag until the nets can be fished (emptied), usually during slack water, and between 4:00 and 9:00 am. I hypothesize that during this period Atlantic croaker spawn within the nets at their usual spawning time of dusk (Holt et al. 1985). Females collected from these nets the following morning would probably show little or no signs of spawning and be identified as "developing" (Wallace 1940, Haven 1954) or fully-developed (this study). However, contrary to what happens with pound-nets and haul-seines, gill-nets usually kill the fish within a short time after capture. Females undergoing hydration or ovulation, especially those caught a few hours before dusk, would die before they finished spawning and the presence of hydrated oocytes in the ovaries could be recorded. This explains why we observed hydrated or recently-spent females only in gill-net collections. A similar pattern has also been observed for weakfish, Cynoscion regalis, which, like

Atlantic croaker, spawn primarily between 6:00 and 9:00 pm (Susan Lowerre-Barbieri, personal communication).

### *Size- and age-at-maturity*

Estimates of size- and age-at-maturity reported here are generally below values previously reported for Atlantic croaker in the Chesapeake Bay and Mid-Atlantic regions. Disagreement with previous reports can be attributed to three main factors. First, failure of at least some studies (Wallace 1940, Morse 1980) to sample small, young fish from fishery-independent sampling programs. Second, the inclusion of samples collected from a period when resting (reproductively inactive) fish occurred to estimate the proportion of mature fish by size or age. Because of the difficulty in distinguishing resting and immature gonads, estimates based on samples pooled over the entire spawning season or during a period when resting fish occurred (e.g., Wallace 1940, Morse 1980) are probably biased towards larger sizes or older ages. Hunter et al. (1992) found that estimates of  $L_{50}$  for Dover sole were higher when females were taken during the spawning season than when they were sampled before spawning began. They suggested that estimates of length or age at first maturity should always be based on samples collected prior to the onset of spawning, when post-spawning females with highly regressed

ovaries are rare. However, for species like Atlantic croaker, which show individually asynchronous gonadal maturation, sampling before the onset of spawning will not prevent the occurrence of pre-spawning, resting fish. To avoid this problem I used only fish collected in September, when no resting or developing stages occurred, to estimate size and age at first maturity.

Finally, disagreement with previous estimates of age-at-maturity probably reflect problems with age determination methods previously used for Atlantic croaker. The use of length frequencies (Welsh and Breder 1923) require considerable subjective interpretation given their extended spawning season, the generally asymptotic growth after age 1 or 2, and the great overlap in observed sizes-at-age (Chapter 2). Although Welsh and Breder (1923) and Wallace (1940) have also used scales, problems in applying this method to Atlantic croaker have also been reported (Barger and Johnson 1980, Chapter 1).

### *Sex ratios*

My results on temporal fluctuations in Atlantic croaker sex ratios agree well with previous reports for the Chesapeake Bay and Mid-Atlantic regions (Welsh and Breder 1923, Wallace 1940). The predominance of females during the first 3-4 months of spawning may indicate that either males



start leaving the estuary earlier than females as fish migrate out of Chesapeake Bay to complete spawning offshore or that spawning-phase females are more susceptible to the fishing gears used in Chesapeake Bay (pound-nets, haul-seines, and gill-nets). During both years, the frequency of males decreased during the first two months of spawning and started increasing again in October/November when the first offshore trawl collections were obtained. Mark-recapture studies are necessary to better evaluate the migratory patterns of Atlantic croaker in Chesapeake Bay and the Mid-Atlantic region.

#### *Atresia of advanced yolked oocytes*

In most multiple spawning fishes high levels of atresia are typically used to identify regressing ovaries and represent a key histological marker for the cessation of spawning (Hunter and Macewicz 1985a, 1985b, Hunter et al. 1986). Hunter and Macewicz (1985b) described four stages of ovarian atresia for the northern anchovy, Engraulis mordax, and showed that the occurrence of females in atretic stage 2 ( $\geq 50\%$  of yolked oocytes undergoing  $\alpha$  atresia) could be used to forecast the end of the spawning season. This criterion has also been used to indicate the end of the spawning season in skipjack tuna, Katsuwonus pelamis (Hunter et al. 1986), and to identify reproductively active females of the

Dover sole, Microstomus pacificus (Hunter et al. 1992).

However, my results with Atlantic croaker indicate that high levels of atresia do not necessarily imply the end of spawning. Although I found significant atresia of cortical alveoli and partially yolked oocytes only in regressing ovaries, indicating it could in fact be used to mark the end of spawning, major atresia of advanced yolked oocytes was observed in actively spawning females throughout the spawning season.

Instead of indicating the end of spawning, major atresia of advanced yolked oocytes in Atlantic croaker may represent a normal part of their reproductive biology. The fact that hydrated females—which were either actively spawning or just about to spawn—showed 95-100% of advanced yolked oocytes undergoing atresia indicates that a portion of these oocytes are never matured and spawned. In other words, it appears that a surplus production of advanced yolked oocytes is part of Atlantic croaker's reproductive strategy. Fully-developed females would hydrate and spawn more or less of these oocytes depending, for example, on environmental conditions (including stimuli induced by the occurrence of males, courtship, etc.). Under unfavorable conditions a larger proportion of advanced yolked oocytes would fail to mature, become atretic and batch fecundity would be small. However, maternal investment in yolk production would not be wasted since at least part of the

energy invested is being recovered by the resorption of excess oocytes.

Small numbers of vitellogenic oocytes which fail to be ovulated prior to a spawning, or an entire batch of oocytes can become atretic when environmental conditions become unfavorable (DeVlaming 1983). By maintaining a standing stock of advanced yolked oocytes ready throughout the spawning season, fully-developed Atlantic croaker females could take advantage of rapid changes in environmental conditions, thus enhancing spawning success. However, the dynamics of production and resorption of advanced yolked oocytes and its link to environmental stimuli is still unclear. The process of maintaining a batch of these oocytes ready throughout the spawning season may involve either groups (batches) of oocytes being produced and eventually spawned or resorbed in a group-synchronous way, or an asynchronous, continuous process of oocyte recruitment and resorption.

Evidence from laboratory studies seems to support the hypothesis that a surplus production of advanced yolked oocytes is part of Atlantic croaker's reproductive strategy. Middaugh and Yoakum (1974) used chorionic gonadotropin to induce laboratory spawning of Atlantic croaker. They found that although the abdomen of females became extremely distended, and sometimes even ruptured as a result of oocyte hydration, only 500-2,000 eggs could be stripped from fish

on each successful attempt. More recently, Trant and Thomas (1988) and Patiño and Thomas (1990) evaluated in vitro germinal vesicle breakdown (GVBD, an index of final oocyte maturation) in laboratory-spawned Atlantic croaker. They reported that in this species there is always a residual number of "advanced oocytes" which fail to complete GVBD or even enter the morphological maturation process, suggesting they were unhealthy and would not be spawned.

#### *Estimates of batch fecundity and spawning frequency*

The small number of gravid females collected and identification of POFs only in recently-ovulated, running-ripe females prevented batch fecundity and spawning frequency from being estimated. Hunter et al. (1985) suggested using the oocyte size-frequency method (McGregor 1957) if the number of females with hydrated oocytes is insufficient to estimate batch fecundity. In this method, the most advanced mode of yolked oocytes of spawning-phase, non-hydrated females is considered the spawning batch. However, the method is inappropriate for Atlantic croaker because of the high levels of atresia found in advanced yolked oocytes. Unless the proportion of atretic advanced yolked oocytes in spawning-phase females is accurately estimated, batch fecundities based on these oocytes would be biased. Future studies on the reproductive biology of

Atlantic croaker in the Chesapeake Bay region should concentrate on offshore—preferably fishery-independent—trawl collections to obtain gravid females for batch fecundity estimates using the hydrated oocyte method (Hunter et al. 1985).

My failure to identify POFs in post-spawning, fully-developed females may indicate high rates of POF deterioration and resorption in Atlantic croaker. In the dragonet, Callionymus enneactis, POFs cannot be identified 15 h after spawning and are clearly distinguishable only within 3 h after spawning (Takita et al. 1983). Similarly, in the bay anchovy, Anchoa mitchilli, they are identifiable within 21 h after spawning, but are clearly detectable only up to 8 h after spawning (Luo and Musick 1991). Rates of deterioration and resorption of POFs must be evaluated in laboratory-spawned Atlantic croaker to determine if the postovulatory follicle method (Hunter and Macewicz 1985a) can be used to estimate spawning frequency for this species.

## **CHAPTER 4**

### **Yield-per-recruit analysis**

## INTRODUCTION

Yield-per-recruit models are often used in fish population dynamics (Beverton and Holt 1957, Ricker 1975, Gulland 1983) to define routine fisheries management measures such as minimum size limits, minimum mesh sizes, catch and effort quotas, etc. (Gulland 1983, Deriso 1987). These models use cohort growth and survival to evaluate the effect of different fishing mortality and age at first capture schedules on biomass yields.

Although a management plan for Atlantic croaker has been recently issued by the Atlantic States Marine Fisheries Commission (Mercer 1987), the major problem addressed in the plan is the lack of stock assessment data needed for effective management. The only published application of yield-per-recruit models to simulate the effects of fishing on Atlantic croaker (Chittenden 1977) is specific for the warm-temperate waters of the Carolinian Province, and points out that results may not apply to more northern areas.

In this chapter I use the Beverton-Holt yield-per-recruit model (Beverton and Holt 1957) to assess the effect of different fishing mortality and age at first capture schedules on Atlantic croaker yield.

## MATERIALS AND METHODS

### *Yield-per-recruit computations*

The Beverton-Holt model (Beverton and Holt 1957) was used for yield-per-recruit analysis.

$$Y/R = F e^{-M(t_c - t_r)} W_\infty \sum_{n=0}^3 \frac{U_n e^{-nK(t_c - t_0)}}{F + M + nK} \quad (1)$$

$Y/R$  = yield-per-recruit;

$F$  = instantaneous fishing mortality coefficient;

$M$  = instantaneous natural mortality coefficient;

$W_\infty$  = asymptotic weight from the von Bertalanffy growth equation;

$U_n$  = summation parameter  $U_0 = 1$ ,  $U_1 = -3$ ,

$U_2 = 3$ ,  $U_3 = -1$ ;

$t_c$  = age at first capture;

$t_r$  = age at recruitment to the fishing area;

$t_0$  = a von Bertalanffy growth parameter;

$K$  = the Brody growth coefficient.

Calculations were performed using the computer program



B-H3, available in the Basic Fisheries Science Programs package (Saila et al. 1988).

### *Parameter estimates*

Parameter values used in simulations are summarized in Table 7. Growth parameters ( $L_{\infty}$ ,  $K$ , and  $t_0$ ) were estimated using the von Bertalanffy equation (Chapter 2).  $L_{\infty}$  was converted to asymptotic weight,  $W_{\infty}$ , using the length-weight relationship in Chapter 2.

The instantaneous rate of natural mortality,  $M$ , was estimated in two ways. First, by obtaining a regression estimate using the relationship of growth parameters ( $K$  and  $L_{\infty}$ ) and mean water temperature to  $M$  developed by Pauly (1980). In doing so, I used values of  $K$  and  $L_{\infty}$  and annual mean water temperature for Chesapeake Bay ( $15.5^{\circ}\text{C}$ ) obtained from the Virginia Institute of Marine Science juvenile trawl survey (Chris Bonzek, personal communication). Second, by estimating the instantaneous rate of total mortality,  $Z$ , from maximum age ( $t_{\text{MAX}}$ ), using a value of  $t_{\text{MAX}}$  reported for a period before significant fisheries developed for Atlantic croaker. Under these conditions,  $F$  was probably very small, thus  $Z \approx M$ . In doing so, I used the methods of Hoenig (1983) and Royce (1972:238) to estimate  $Z$  and an estimate of  $t_{\text{MAX}}=15$  years based on Hales and Reitz (1992) report of finding otoliths of 15-year-old Atlantic croaker in Indian

Table 7. Parameter estimates or range of values used in yield-per-recruit simulations for Atlantic croaker in Chesapeake Bay.

Parameter	Estimate	Method	Value or range used in simulations
$K$	0.36	growth curve <sup>1</sup>	0.36
$W_{\infty}$	409.90	converted from $L_{\infty}$ <sup>1</sup>	409.90
$t_0$	-3.26	growth curve <sup>1</sup>	-3.26
$t_r$	0	life history information <sup>2</sup>	0
$t_c$	2	age composition of catches <sup>1</sup>	1 - 5
$F$	-----	-----	0 - 2
	0.29	longevity <sup>3</sup>	
$M$	{ 0.31	longevity <sup>4</sup>	} 0.25 - 0.40
	0.36	regression estimate <sup>5</sup>	

<sup>1</sup>Chapter 2; <sup>2</sup>Haven (1957), Chao and Musick (1977) and Norcross (1991); <sup>3</sup>Hoenig (1983);

<sup>4</sup>Royce (1972); <sup>5</sup>Pauly (1980)

middens from the period 1600-1700 A.D. at St. Augustine, FL.

Estimates of the instantaneous total annual mortality rate,  $Z$ , for Atlantic croaker in Chesapeake Bay range from 0.55 to 0.63 (see Chapter 2), with a mean value of 0.59. For practical purposes, I used  $Z=0.60$  to estimate current levels of fishing mortality ( $F_{CUR}$ ) for different values of  $M$ , as:

$$F_{CUR} = Z - M \quad (2)$$

I estimated  $t_r$ , the age at recruitment to the fishing area, as  $t_r=0$  based on reports that Atlantic croaker recruit to Chesapeake Bay as larvae or young juveniles (Haven 1957, Chao and Musick 1977, Norcross 1991). The estimate of current  $t_c$ , the average age at first capture, was based on Atlantic croaker age compositions in the Chesapeake Bay pound-net, haul-seine and gill-net catches for the period 1988-1991 (see Chapter 2). I found that fish begin to recruit to the Chesapeake Bay fishery at age 1 as part of the scrap catch, and that age 2 or 3 was the first age at which they were fully recruited depending on the gear.

To evaluate the proportion of the potential growth span remaining when Atlantic croaker enter the exploited phase of life—e.g., the fishery—(Beverton and Holt 1957), I used the quantity  $(1 - L_c/L_\infty)$  (Beverton 1963), where  $L_\infty$ , the asymptotic length, was obtained from the von Bertalanffy equation (Chapter 2), and  $L_c$ , the average length at first capture, was obtained by converting postulated ages at first

capture ( $t_c$ ) using that (Chapter 2).

An alternative to the concept of maximum sustainable yield that has gained much recent acceptance in management is  $F_{0.1}$ , the level of  $F$  for which the marginal increase in yield-per-recruit due to a small increase in  $F$  is 10% of the marginal yield-per-recruit in a lightly exploited fishery (Gulland and Boerema 1973, Anthony 1982). I estimated  $F_{0.1}$  for Atlantic croaker in the Chesapeake Bay region using  $t_c=2$  and  $F=0.01$ .

The maximum possible yield for a given year-class may be taken at a critical age,  $t_{CRITIC}$ , the age where cohort biomass is maximum in the absence of fishing (Alverson and Carney 1975, Deriso 1987). I estimated  $t_{CRITIC}$  for Atlantic croaker following Alverson and Carney (1975) and Deriso (1987) as:

$$t_{CRITIC} = t_0 + \frac{1}{K} \ln(3K/M+1) \quad (3)$$

where  $t_0$ ,  $K$  and  $M$  are defined as in equation the Beverton-Holt equation. Parameter estimates used in calculations are listed in Table 7.

## RESULTS

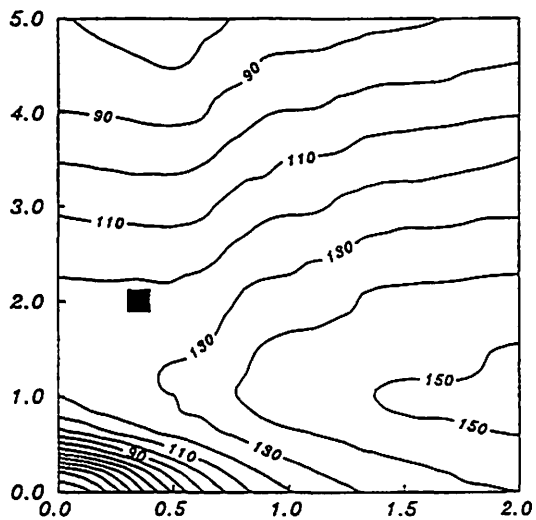
### *Yield-isopleth analysis*

Although the magnitudes of yield isopleths and maximum yield-per-recruit values were dependent on the level of  $M$  used, relative changes in Atlantic croaker yield as a function of  $F$  and  $t_c$  were very similar, regardless of  $M$  (Fig. 20). At all levels of  $M$ , yield values increased rapidly in the range of  $t_c$  between 0 and 1 and  $F$  between 0 and 0.50-0.75, and started decreasing slowly with  $t_c$  greater than 2.0, regardless of  $F$ . For all levels of  $t_c$  (1-5), yield values increased continuously with  $F$ . However, they seemed to reach a plateau in the range of  $F$  between 0.50 and 0.75, increasing very slowly thereafter. Maximum yield values were consistently associated with the highest level of fishing mortality and the lowest age at first capture used in simulations ( $F=2.0$  and  $t_c=1$ ). For the range of  $M$  used herein (0.25-0.40) current estimates of fishing mortality ( $F_{CUR}$ ) and  $t_c$  for Atlantic croaker in Chesapeake Bay (Fig. 20) indicate that present levels of harvest are below the maximum potential yield-per-recruit.

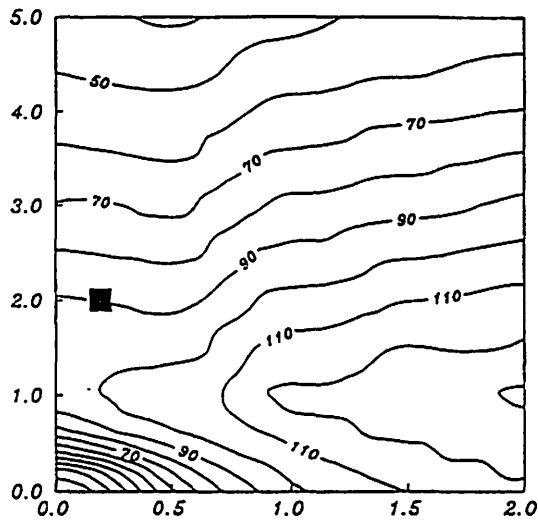
Fig. 20. Yield-isopleth diagrams estimated using different values of natural mortality ( $M$ ) for Atlantic croaker in Chesapeake Bay. Isopleths represent yield-per-recruit in grams. The black boxes in each panel indicate the estimated current position of the fishery.

$t_c$

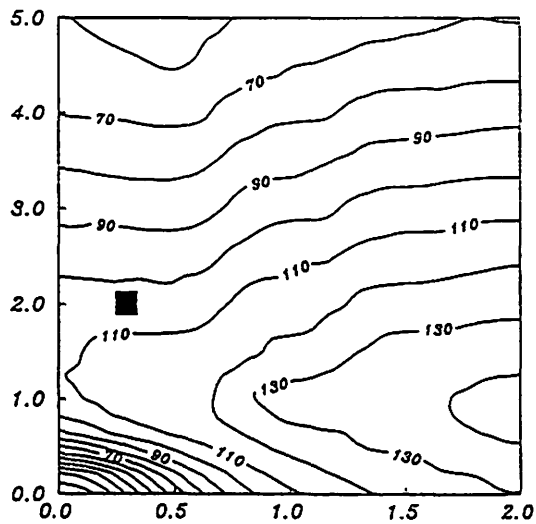
$M = 0.25$



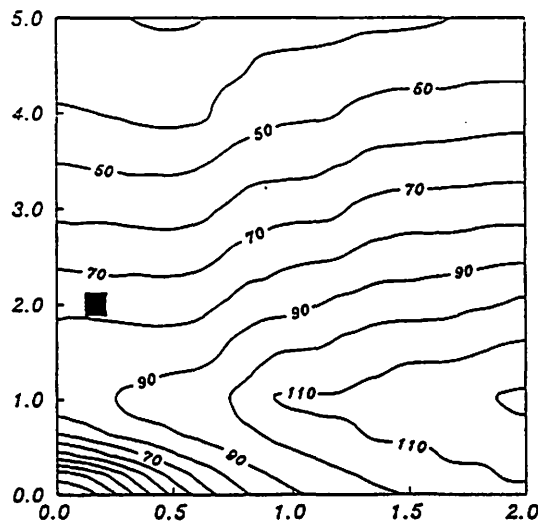
$M = 0.35$



$M = 0.30$



$M = 0.40$



F

### *Yield-Fishing mortality curves*

Curves of yield-per-recruit on  $F$  for different levels of  $M$  and  $t_c$  (Fig. 21) showed no clearly defined peaks. Yield curves increased rapidly in the range of  $F$  between 0 and 0.75, and remained relatively flat thereafter, regardless of  $t_c$ . Although yield increased continuously with  $F$ —maximum yield-per-recruit always occurred at the highest level of  $F$  ( $F_{MAX}$ )—marginal increases in yield beyond  $F=0.50-0.75$  were negligible. Increases in yield from  $F=0.75$  to  $F_{MAX}$ , for instance, ranged from 6.4 to 19.8%, depending on the level of  $M$  and  $t_c$  used (Table 8). However, in terms of  $F$  this relatively small gain in yield represents an increase of 166.7%.

Curves of yield-per-recruit on  $F$  (Fig. 21) also clearly show that independent of the level of  $M$  or  $F$  used in simulations, yield values decreased consistently with increases in  $t_c$ . Differences in yield resulting from differences in  $t_c$  were larger at higher levels of  $M$ . At  $F=0.75$ , for instance, decreases in yield between  $t_c=1$  and  $t_c=2$  were 8.0% at  $M=0.25$ , 12.7% at  $M=0.30$ , 16.7% at  $M=0.35$  and 20.6% at  $M=0.40$ .

Values of  $F_{0.1}$  estimated for Atlantic croaker using  $t_c=2$  and  $M=0.25-0.40$  ranged from 0.35 to 0.64 (Fig. 21, Table 9). At  $M=0.25$ , both  $F_{CUR}$  and  $F_{0.1}$  equal 0.35, indicating that although below the maximum potential yield-per-recruit,

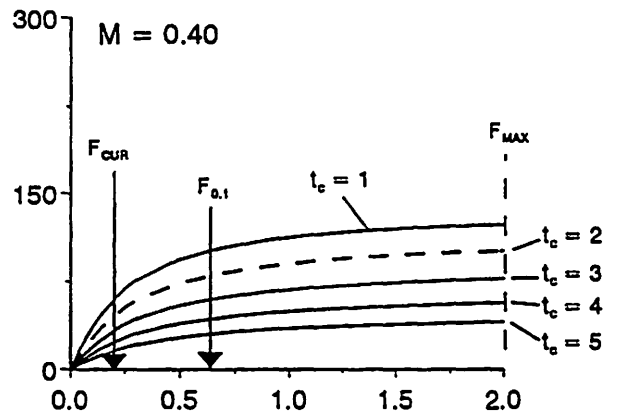
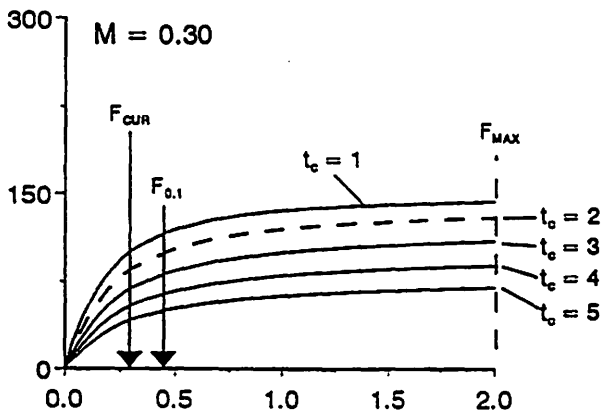
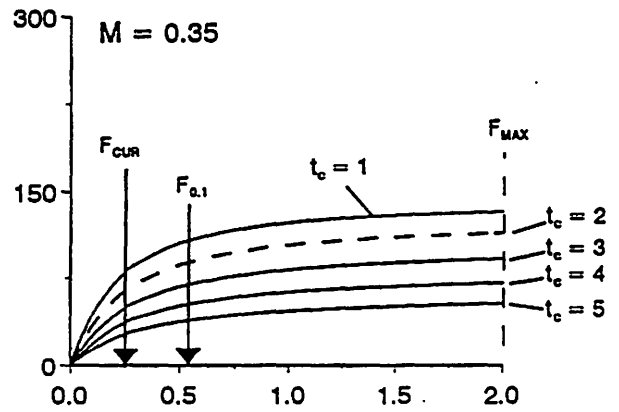
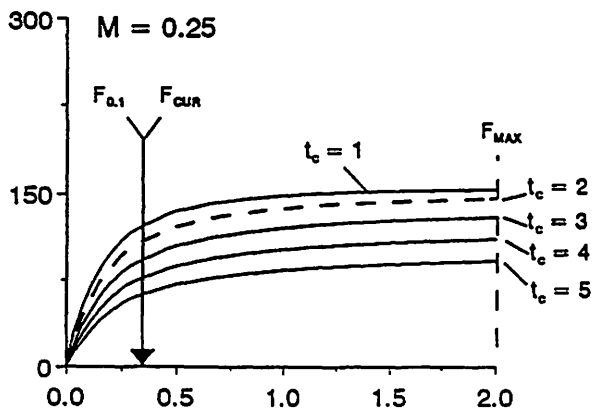


Table 8. Percent increase in yield-per-recruit of Atlantic croaker in the Chesapeake Bay region, from  $F=0.75$  to  $F_{MAX}$ , for  $t_c=1-5$  and  $M=0.25-0.40$ .

Yield-per-recruit (g)				
$M$	$t_c$	$F_{0.75}$	$F_{MAX}$	% increase
0.25	1	143.7	153.5	6.4
	2	131.6	145.8	9.7
	3	114.3	129.5	11.7
	4	95.8	110.3	13.1
	5	78.5	91.2	13.9
0.30	1	129.2	142.5	9.3
	2	112.8	128.9	12.5
	3	93.4	109.0	14.3
	4	74.6	88.2	15.4
	5	58.2	69.4	16.1
0.35	1	116.5	132.4	12.0
	2	97.0	114.0	14.9
	3	76.5	91.7	16.6
	4	58.1	70.7	17.8
	5	43.1	52.9	18.5
0.40	1	105.3	123.1	14.5
	2	83.6	100.9	17.1
	3	62.8	77.2	18.6
	4	45.6	56.6	19.4
	5	32.3	40.3	19.8

Fig. 21. Curves of yield-per-recruit on  $F$  for Atlantic croaker, estimated for  $t_c=1-5$  and  $M=0.25-0.40$ . Refer to text for definitions of  $F_{0.1}$ ,  $F_{CUR}$  and  $F_{MAX}$ . The segmented line in each panel ( $t_c=2$ ) represents the estimated current level of  $t_c$  for Atlantic croaker in Chesapeake Bay.

Yield-per-recruit (g)



F

estimated current levels of harvest probably correspond to the most efficient level of  $F$ . In contrast, if  $M$  ranges from 0.30 to 0.40,  $F_{0.1}$  is always higher than  $F_{CUR}$  (Table 9), indicating there would still be room to efficiently increase yield-per-recruit by increases in  $F$ . However, at the higher levels of  $M$ , increases in  $F$  to the desired  $F_{0.1}$  level may be still unrealistically high. For  $M$  equal to 0.30, 0.35 and 0.40, increases in  $F$  to bring  $F_{CUR}$  to the level of  $F_{0.1}$  would be equal to 50, 108 and 220%, respectively (Table 9).

#### *Cohort biomass and time of harvest*

Values of  $t_{CRITIC}$  estimated using different values of  $M$ , were relatively low. For  $M$  equal to 0.25, 0.30, 0.35 and 0.40, values of  $t_{CRITIC}$  were 1.4, 1.0, 0.6 and 0.4 years, respectively. This indicates that, for the range of  $M$  considered herein, maximum theoretical cohort biomass for Atlantic croaker in Chesapeake Bay is achieved before fish reach age 2.

The proportion of the potential growth span remaining when fish enter the exploited phase can be evaluated by the quantity  $(1 - L_c/L_\infty)$ . For Atlantic croaker in Chesapeake Bay, for  $L_\infty=312$  mm total length, and  $L_c=265$  mm total length (for  $t_c=2$ ),  $(1 - L_c/L_\infty) = 0.15$ , i.e., on the average, only 15% of their potential growth is still remaining when fish enter the exploited phase at age 2. For alternative values

Table 9. Values of  $F_{\text{CUR}}$  and  $F_{0.1}$  of Atlantic croaker in Chesapeake Bay estimated for  $M=0.25-0.40$ .

$M$	$F_{\text{CUR}}$	$F_{0.1}$
0.25	0.35	0.35
0.30	0.30	0.45
0.35	0.25	0.52
0.40	0.20	0.64

of  $t_c$  equal to 1, 3, 4 and 5, values of the potential growth span would be equal to 0.21, 0.10, 0.07 and 0.05, respectively.

## DISCUSSION

Simulation results indicated that, over a likely range of natural mortality values, yield-per-recruit of Atlantic croaker in Chesapeake Bay can be maximized by management strategies that incorporate early age at first capture ( $t_c=1$ ) and high rates of fishing mortality ( $1.5 < F \leq 2.0$ ). However, the analysis also showed that, because of the essentially asymptotic relationship between yield-per-recruit and  $F$ , harvesting at or near the maximum potential yield requires a disproportionate increase in fishing mortality—and consequently fishing effort—making it an economically inefficient management option. Furthermore, given the multi-species nature of the fisheries in Chesapeake Bay (Austin 1987, Chittenden 1991), raising current levels of  $F$  to a level at or near the estimated  $F_{MAX}$  for Atlantic croaker would be impractical because it would greatly increase rates of exploitation and probably interfere with management of other species.

Instead of concentrating on harvesting at the level of maximum yield, a more efficient management strategy may be

obtained by targeting a fishing mortality rate at  $F_{0.1}$  (Gulland and Boerema 1973, Anthony 1982, Deriso 1987). Because economic incentives to increase harvest beyond the level given by  $F_{0.1}$  are usually negligible,  $F_{0.1}$  has received recent wide application in fisheries management (e.g., Anthony 1982, Doubleday et al. 1984, Deriso 1987). Additionally, because it usually represents a significant reduction in fishing mortality from the level given at  $F_{MAX}$ ,  $F_{0.1}$  constitutes a conservative management approach that provides added protection against recruitment and growth overfishing (Anthony 1982, Deriso 1987). For Atlantic croaker, however, management by  $F_{0.1}$  may be still impractical if  $M > 0.30$ . If  $M = 0.35 - 0.40$ , to bring  $F_{CUR}$  to the level of  $F_{0.1}$ , fishing mortality rates would have to be increased by 2-3 times the current levels. Although these increases would be relatively small when compared to the levels required to reach  $F_{MAX}$ , they might still be prohibitively high, especially considering the multi-species nature of the fisheries in this area.

Even if  $M < 0.30$ ,  $F_{0.1}$  may still not be a realistic management option for Atlantic croaker in Chesapeake Bay because information on the relationship between  $F$  and fishing effort,  $f$ , is presently not available for the main fisheries in this area (Mercer 1987). Until a long series of concurrent effort and mortality estimates is obtained and the relationship between  $F$  and  $f$  for the pound-net,

haul-seine, gill-net, and offshore trawl fisheries in the Chesapeake Bay area is established, management of Atlantic croaker by  $F_{0.1}$  or by any other management strategy that involves regulating fishing mortality, would be extremely difficult, if not impossible.

A more practical approach may be obtained by considering management measures that regulate the age, and consequently the size at entry to the fisheries. Because of the relationship between fish size and age, the magnitude of  $t_c$  usually can be defined by mesh size of the gear and its selection property (Chittenden 1977). Therefore, even if detailed information on  $F$ —or its relationship to  $f$ —is not available, relatively high values of yield-per-recruit can be obtained by adjusting mesh sizes so as to catch fish which, on the average, are in the best range of  $t_c$ . For Atlantic croaker, this approach seems logical because curves of yield-per-recruit on  $F$  clearly showed that the effect of varying  $F$  was of secondary importance when compared to  $t_c$ . Independent of the values of  $M$  or  $F$  used, yield-per-recruit was always maximized at  $t_c=1$  (245 mm total length), rather than at the current estimated level of  $t_c=2$  (265 mm total length), or alternative values of  $t_c$  varying from 3 to 5 (279-296 mm total length). However, given the large overlap of sizes-at-age reported for Atlantic croaker (White and Chittenden 1977, Barger 1985, Ross 1988, Chapter 2), it is unclear at this point how effective mesh size regulations



would be in determining a specific, knife-edge level of  $t_c$  for this species.

Adjusting current levels of  $t_c$  for Atlantic croaker may be also complicated by other factors. Although modeling results indicated that, from a theoretical point of view, yield-per-recruit could be maximized by measures aimed at reducing the current level of  $t_c$ , it seems unlikely this would be beneficial to the fishery. First, for the range of  $M$  considered in simulations, changes in yield-per-recruit from  $t_c=2$  to  $t_c=1$  were relatively small, with a maximum increase of only about 20% if  $M=0.40$ . Second, because the magnitude of the scrap catch by the pound-net, haul-seine and trawl fisheries in the Chesapeake Bay area is presently unknown, it is possible, and in fact likely, that Atlantic croaker are already entering the exploited phase at age 1 or younger (Mercer 1987). The current estimate of  $t_c=2$  (Chapter 2) is probably biased because it is based on arbitrarily defined commercial market grades instead of the overall catches. In other words, because the market only accepts fish above a certain size, a reduction in mesh sizes to attempt to increase the proportion of age 1 Atlantic croaker in the catches would probably only increase the number of fish sold as scrap and have little or not effect on commercial market grades.

Despite these problems, regulatory measures do not seem to represent a critical issue for Atlantic croaker in

Chesapeake Bay. First, yield-per-recruit modeling results and estimated values of  $F_{CUR}$  indicated that, over a likely range of  $M$ , current levels of harvest ( $E=33-58\%$ ) are below the levels at  $F_{MAX}$  and, under most scenarios, even below the levels at  $F_{0.1}$ . Second, curves of yield-per-recruit on  $F$  showed that although marginal yield increased very slowly after  $F=0.50-0.75$ , it showed no signs of decrease at high levels of  $F$ , even if  $M$  is as low as 0.25. This pattern suggests that stocks of Atlantic croaker in the Chesapeake Bay area seem to have the same great biological capacity to resist growth overfishing reported for stocks in the Gulf of Mexico (Chittenden 1977). The low values of  $t_{CRITIC}$  and of the quantity  $(1 - L_c/L_\infty)$  indicated that: (1) for a reported maximum longevity of about 8 years (Gutherz 1977, Barger 1985, Ross 1988, Chapter 2), maximum theoretical biomass is achieved very early in life, before fish reach age 2; and (2) very little of the potential growth span is still remaining when fish enter the exploited phase at age 2. In other words, because most of Atlantic croaker's growth occur during their first year (White and Chittenden 1977, Barger 1985, Ross 1988, Chapter 2), and  $M$  is relatively high compared to  $K$ , fish should be harvested at a young age before they die of natural causes.

The specific value of  $M$  used in simulations presented here had no effect on the levels of  $F$  or  $t_c$  giving the maximum yield-per-recruit and would not change the

conclusion that Atlantic croaker in Chesapeake Bay are not being growth-overfished. However, this conclusion is still critically dependent on how realistic is the range of  $M$  used in these simulations. Methods currently used to estimate  $M$  in fish populations have strong limitations and disadvantages (Vetter 1988), and the methods I used here are no exception. I feel comfortable with the range of  $M$  used in simulations, however, because: (1) the close agreement between estimates obtained using different methods suggest that  $M$  probably ranges from 0.30 to 0.35; and (2) these values are reasonable when we consider estimates of  $Z$  reported for Atlantic croaker in the Chesapeake Bay area (Chapter 2).

Yield-per-recruit analysis is only part of a rational fishery management strategy (Beverton and Holt 1957, Gulland 1983, Deriso 1987). If applied in conjunction with eggs-per-recruit models (Campbell 1985, Prager et al. 1987), however, they allow managers to examine the effects of different policies on both reproduction (egg production) and biomass yield. Although modeling results presented here do not consider the potential effects of fishing on Atlantic croaker reproductive potential, their pattern of early maturation, multiple spawning, long spawning season, and indeterminate fecundity (Chapter 3), suggests that reproduction would be compromised only at extremely high levels of fishing. Additional information on the

reproductive biology of Atlantic croaker (e.g., batch fecundity, spawning frequency, total annual fecundity, etc.) is still necessary until this issue can be better evaluated.

## GENERAL DISCUSSION

The possible existence of two groups of Atlantic croaker, exhibiting different life history/population dynamics attributes north and south of Cape Hatteras, North Carolina, has been extensively discussed in the literature (Chittenden 1977, White and Chittenden 1977, Ross 1988). Ross (1988) hypothesized that these groups may overlap and mix in North Carolina and stated that, if the Atlantic croaker designated in his study as "northern" were fish migrating south from the Chesapeake and Delaware Bay areas, their larger sizes (350-520 mm TL) and older ages (5-7 years, as aged by scales) would be consistent with the proposed northern group life history pattern. However, my results do not support the hypothesis of a group of larger, older Atlantic croaker in Chesapeake Bay, at least in recent years. Maximum length and size ranges reported here are consistent with recent data from North Carolina, both for inshore waters (Ross and Moye 1989) as well as for the offshore trawl fishery (Ross et al. 1990, Ross 1991). Similarly, although I collected fish up to age 8, most were age 5 or younger.

Instead of reflecting a different population dynamics

pattern, the group of larger Atlantic croaker designated by Ross (1988) as "northern" probably reflects the occurrence of unusually large individuals from a few dominant year-classes that seem to have disappeared after 1982. Since 1982, Atlantic croaker trawl catches in North Carolina have been dominated by unmarketable (<225 mm TL) and small (225-275 mm TL) fish. Fish larger than 300 mm TL and older than 3 years have represented less than 1% of the recent catches (Ross et al. 1990, Ross 1991). Although records of large fish do exist, Atlantic croaker as large as those reported by Ross (1988) have never been common in commercial catches from the Chesapeake Bay region. Even in the early 1930s, when the winter trawl fishery had just been established off the coasts of Virginia and North Carolina and catches of Atlantic croaker were dominated by large fish, most were 260-360 mm TL (Pearson 1932). Length frequencies of Atlantic croaker sampled from commercial pound-nets in the lower Chesapeake Bay in 1922 (Hildebrand and Schroeder 1928) and during 1950-1958 (Haven 1954, Massmann and Pacheco 1960), as well as from pound-nets and haul-seines in Pamlico and Core sounds, North Carolina (Higgins and Pearson 1928), show the same pattern. Fish larger than 400 mm TL represented less than 2% of these catches, with most being 250-300 mm TL.

Recreational catch records also indicate that the large Atlantic croaker reported by Ross (1988) have not been

common in the Chesapeake and Delaware Bay areas. Between 1960 and 1970 the minimum citation weight for Atlantic croaker in the Virginia Saltwater Fishing Tournament ranged from 0.91 to 1.36 Kg (2-3 lbs) (Claude M. Bain, III, personal communication<sup>1</sup>). Although 741 citations were issued during this period, only 14 (1.9%) were for Atlantic croaker  $\geq 1.82$  Kg (4 lbs). Between 1971 and 1976, due to few entries in the late 1960s, Atlantic croaker was dropped from the citation program. Between 1977 and 1982, however, although the minimum citation weight was raised to 1.82 Kg (4 lbs), 599 citations were issued, including 47 entries for Atlantic croaker  $\geq 2.27$  Kg (5 lbs) and ranging from 483 to 610 mm TL (19-24 inches). The largest number of citations occurred in 1979 and 1980 (Fig. 22), coinciding with Ross's (1988) sampling period in North Carolina. In contrast, since 1983 only five citations have been issued for Atlantic croaker in Virginia, two in 1986 and three in 1988. As a result, in 1990 the citation weight was again decreased to 1.36 Kg (3 lbs). Records from the Delaware State Fishing Tournament show the same pattern as Virginia (Jessie Anglin, personal communication<sup>2</sup>). The number of citations was very

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<sup>2</sup> Jessie Anglin, Delaware Department of Natural Resources & Environmental Control, Division of Fish and Wildlife, P.O. Box 1401, Dover, Delaware 19901

Fig. 22. Number of citations of Atlantic croaker  $\geq 1.82$  Kg (4 lbs) caught by recreational fishermen in Virginia and Delaware during 1960-1990. The absence of data for Virginia during 1971-1976 reflects a period when Atlantic croaker was dropped from the citation program.



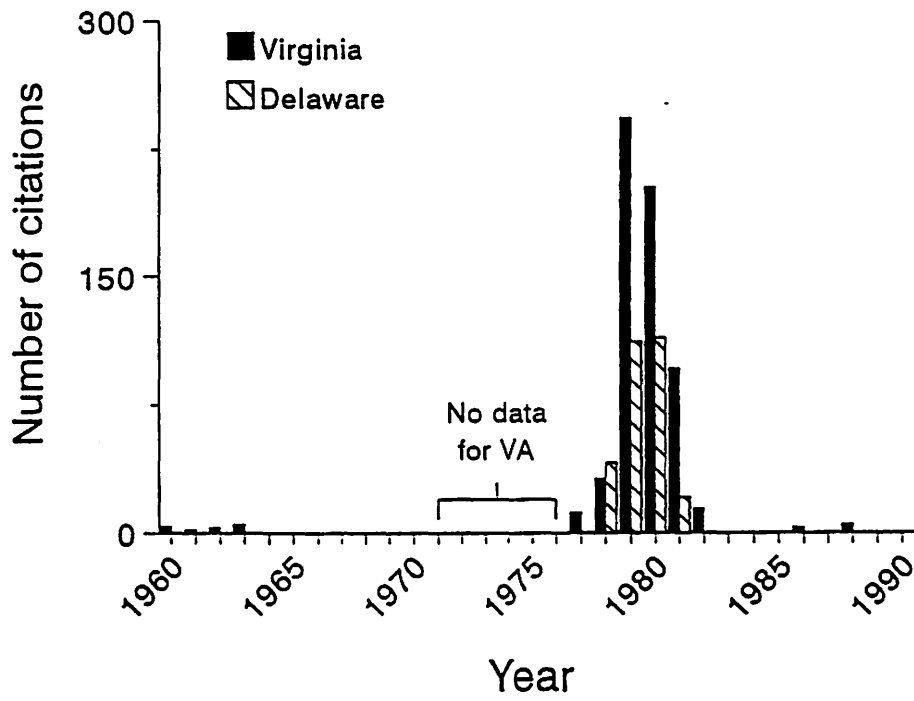


Table 10. State records of Atlantic croaker caught by recreational fishermen along the East coast of the U.S.

State	Weight		Year
	kg	Lbs	
New Jersey	2.49	5.50	1981
Delaware	2.37	5.25	1980
Virginia	2.64	5.81	1982
North Carolina	2.27	5.00	1981
South Carolina	2.07	4.56	1979
Georgia	2.61	5.75	1977

small during the early 1970s, reached a peak in 1980, and decreased rapidly thereafter. The period 1978-1981 was the only period in the last 30 years when there were citations of Atlantic croaker larger than 1.82 kg (4 lbs) in Delaware (Fig. 22). Although complete information covering their entire range is not available, state records of Atlantic croaker along the East coast of the U.S. show the same pattern. Records in six states were broken during the period 1977-1982 (Table 10), indicating that: (1) unusually large fish occurred during this period and have not occurred since; and (2) their occurrence was not limited to areas north of North Carolina.

In conclusion, recent size and age composition data do not indicate the existence of a group of larger, older Atlantic croaker in the Chesapeake Bay region compared to more southern waters. Historic information (Higgins and Pearson 1928, Hildebrand and Schroeder 1928, Pearson 1932, Haven 1954, Massmann and Pacheco 1960), agrees well with these results and indicates that, at least for the last 60 or 70 years, fish >400 mm TL have not represented a large proportion of Atlantic croaker in this area. The abundance of unusually large fish during the period 1977-1982 apparently constituted an unusual event, and may reflect passage through the fishery of a few strong year-classes, that seemingly disappeared after 1982. Similar episodes—the occurrence of larger fish for a few years—have been

previously reported for Atlantic croaker in Chesapeake Bay (Hildebrand and Schroeder 1928, Haven 1954, Massmann and Pacheco 1960), suggesting the phenomenon happens periodically. An increase in survivorship of early-spawned fish (July-August), which have been shown to have higher growth rates (Warlen 1982), combined with higher mortality of late-spawned fish (November-December) as a result of unusually low winter temperatures in estuarine nursery areas (Massmann and Pacheco 1960, Joseph 1972, Chao and Musick 1977, Warlen and Burke 1991) could account for an increase in the proportion of larger fish in certain years and explain the episodic occurrence of large Atlantic croaker in this area.

My results for Chesapeake Bay, together with records of large fish south of North Carolina during 1977-1982, and other accounts of large or old individuals in the Gulf of Mexico and South Atlantic (e.g., Rivas and Roithmayr 1970, Gutherz 1977, Music and Pafford 1984, Barger 1985), suggest that the hypothesis of a basically different life history/population dynamics pattern for Atlantic croaker north and south of Cape Hatteras, North Carolina, should be reevaluated. However, sampling programs over time describing size and age compositions of Atlantic croaker throughout their range are still necessary to fully evaluate this question.

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SECTION III.

Simulations of the Effects of Fishing on Atlantic croaker,  
Micropogonias undulatus, in the Chesapeake Bay Region

by

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## ABSTRACT

We present yield-per-recruit simulations for Atlantic croaker in the Chesapeake Bay region using the Beverton-Holt model to generate curves of Y/R on F and Y/R on  $t_c$ , and the Ricker model to generate curves of standing stock biomass on age. We also generated Beverton-Holt model curves of Y/R on  $t_c$ , in addition to yield isopleths presented in Barbieri (1993), because curves of Y/R on  $t_c$  are a simpler, easier-to-understand graphic presentation than isopleths.

Point estimates for parameters needed in the Beverton-Holt model, given in Barbieri (1993) and Barbieri et al. (1994), along with some interval estimates, are:

- 1) for von Bertalanffy equation growth parameters:  $K = 0.36$ , with asymptotic 95% confidence limits being 0.20-0.53;  $L_{inf} = 312.4$  mm total length;  $W_{inf} = 409.9$  g; and  $t_0 = -3.26$  yr,
- 2) for time parameters:  $t_r = 0$  yr;  $t_c = 2$  yr, and
- 3) for mortality parameters:  $Z = 0.55-0.63$ , the latter value having 95% confidence limits of 0.36-0.90. We used for simulations a value of current  $Z$  ( $Z_{cur}$ ) = 0.60, about the mean of the individual point estimates, to estimate current  $F$  ( $F_{cur}$ ) from postulated values of  $M$  ( $M_{pos}$ ).  $F_{cur}$  was estimated from  $Z_{cur}$  and  $M_{pos}$  by solving for  $F_{cur}$  in the equation:  $Z_{cur} = M_{pos} + F_{cur}$ .

For best use of yield-per-recruit modeling,  $M$  must be known. It was estimated in Barbieri (1993) as 0.29, 0.31, and 0.36 using three methods based on maximum age in the unexploited state, that age being estimated as 15 yr based on Hales and Reitz' (1992) study of otolith age structure in Indian middens from 1600-1700

AD at St. Augustine, FL. Although M is not well known, we argue that the most likely range is 0.20-0.40, with a most likely point estimate being 0.30. We used the approaches described above to estimate M and F, because we felt the initially intended mark-recapture studies were not feasible.

Mortality rates just described were also used in the Ricker model. Growth parameters (G) needed for that model were calculated from mean weights-at-age. Weights were estimated using von Bertalanffy predictions of mean lengths-at-age converted to weights using the length-weight relationship, noted above, from Barbieri (1993) and Barbieri et al. (1994).

Finally in parameter estimation, we estimated values of  $F_{.10}$  and combined them with estimates in Barbieri (1993) to supplement Beverton-Holt and Ricker model simulations.

Major findings from simulations were:

- 1) Yields are inversely related to M, decreasing as M increases,
- 2) Yields are directly related to K, increasing as K increases,
- 3) Yields strongly depend on  $t_c$ , increasing with  $t_c$  to a peak, referred to as a "level of eumetric fishing", and then decreasing as  $t_c$  further increases,
- 4)  $F_{MAX}$  strongly depends on the magnitude of M, K, and  $t_c$ , increasing with each of these parameters,
- 5) The shape of the curve of Y/R on F strongly depends on the magnitude of M, K, and  $t_c$ , changing according to the following pattern: it usually rises to a peak at very low or low levels of M, K, and  $t_c$ , becomes asymptotic at intermediate levels of these parameters, and forms a rising curve at high levels. As a result, specific parameter combinations form response areas or zones in which there is little or no danger of biological overfishing and zones in which there is

danger of biological overfishing,

- 6) Over much of the range of  $M$ ,  $K$ , and  $t_c$ , large fisheries and high  $F$  will not reduce yields, because  $Y/R$  rises to an asymptote, or keeps increasing, as  $F$  increases. This response area constitutes a zone in which there is little or no danger of biological overfishing, because there is little or no decrease in yield. It generally occurs when  $M = 0.20$  or greater is combined with  $K = 0.20$  or greater and  $t_c = 1$  yr or greater. Because this response zone covers so broad a range of parameter combinations, Atlantic croaker in the Chesapeake Bay region have great capacity to resist biological overfishing,
- 7) At very low  $M$ , yields are sensitive to biological overfishing, because  $Y/R$  rises to a peak at  $F_{MAX}$  and then declines as  $F$  increases further. This response area constitutes a danger zone of biological overfishing. It generally occurs, though not always, when very low  $M$  ( $M = 0.05$ ) is combined with low  $K$  ( $K = 0.20$ ) and low  $t_c$  ( $t_c = 1$  yr). Though yields decrease in this danger zone compared to those at  $F_{MAX}$ , they only decrease some 35% even at levels of  $F$  much higher than  $F_{MAX}$ , for example  $F = 2.00$ ,
- 8) Over much of the range of  $M$ , the current fishing mortality rate ( $F_{CUR}$ ) is below  $F_{MAX}$ , and current yield ( $Y_{CUR}$ ) is below  $Y_{MAX}$ . This situation generally occurs, though not always, when  $M = 0.20$  or greater is combined with  $K = 0.20$  or greater and  $t_c = 1$  yr or greater,
- 9) At very low  $M$ ,  $F_{CUR}$  exceeds  $F_{MAX}$ . This generally occurs when very low  $M$  ( $M = 0.05$ ) is combined with low  $K$  ( $K = 0.20$ ) and low  $t_c$  ( $t_c = 1$  yr). We argue herein, however, that levels of  $M = 0.05$  are too low for Atlantic croaker in the Chesapeake Bay region, because that level of  $M$  is consistent with a life span of more than 90 yr in the unexploited state,
- 10) Assuming  $M = 0.30$ , which we feel is the most likely level, the current fishery is below  $F_{MAX}$ . That conclusion must be reached regardless of the level of  $K$  in the range 0.20 or greater and  $t_c$  in the range 1 yr or greater.  $F_{MAX}$  generally equals 2.00 or greater when  $M = 0.20$  or greater is combined with  $K = 0.20$  or greater and  $t_c = 1$  yr or greater,
- 11) Maximum yield at given  $F$  generally occurs when  $t_c = 1-2$  yr, because curves of  $Y/R$  on  $t_c$  generally rise to a peak in this  $t_c$  range and then decline. This pattern

occurs when  $M = 0.20$  or greater is combined with  $K = 0.36-0.53$ , if not at low  $K$  ( $K = 0.20$ ). This  $t_c$  range represents levels of eumetric fishing in curves of  $Y/R$  on  $t_c$  and in yield isopleths given in Barbieri (1993). Based on this age, minimum size limits of 200-260 mm total length would provide the modicum of protection needed to resist biological overfishing, if some protection is judged necessary for management,

- 12) Levels of  $F_{.10}$  are much lower than  $F_{MAX}$ . The current fishery does not exceed  $F_{.10}$  if  $M = 0.30$  or greater. However, it does exceed  $F_{.10}$  if  $M = 0.20$  or lower. The current fishery is at  $F_{.10}$  if  $M = 0.25$ . Present data, however, do not permit confident choice among possible  $M$  levels in the range 0.20-0.30.
- 13) Total standing stock biomass and stock biomass at age is inversely proportional to  $F$ , being greatest when  $F = 0.00$ , eg -- when there is a virgin stock, and
- 14) Although biological overfishing is not now occurring according to Beverton-Holt model simulations, the current fishery has greatly juvenesced the stock, eg -- it has greatly reduced total standing stock biomass and stock biomass-at-age.

The above basic simulations are interpreted and discussed in detail in this Section, a section that, in general, presents very extensive discussion of the simulations and the important implications they have for management. Those discussions are organized under the basic headings of: 1) "Responses to Variation in Model Parameters and Delineation of Biological Danger Zones", 2) "Evaluation of the Current Fishery and Current Status of Atlantic Croaker Stocks", 3) "Evaluation of Growth and Reproduction Dynamics, Their Implications for Wise Management, and Management Strategies", and 4) "Evaluation of Fluctuations in Abundance".

Although Atlantic croaker in the Chesapeake Bay region have great capacity to resist biological overfishing, two kinds of

biological overfishing can be distinguished, growth overfishing and recruitment overfishing. Because of their basic assumptions, yield-per-recruit simulations presented herein primarily indicate this species has great capacity to resist growth overfishing. That capacity rests on their intense growth dynamics which are discussed in detail, along with their important implications for management. Atlantic croaker in the Chesapeake Bay region also have great capacity to resist recruitment overfishing. That capacity rests on their remarkable reproduction dynamics which are also discussed in detail, along with their important implications for management. Appropriate management strategies are also discussed in detail. All in all, this species seems to have evolved a remarkable life history strategy that is well-adapted to resist both growth and recruitment overfishing. That strategy is probably responsible for the great success this species shows throughout much of its range -- it is one of the most abundant inshore and/or coastal fishes from the Chesapeake region south to Florida and across the northern Gulf of Mexico through Texas.

Atlantic croaker have historically shown great fluctuations in abundance in the Chesapeake Bay region. Our simulations indicate these fluctuations do not reflect growth overfishing, because there is little or no decrease in yield over a broad range of parameter conditions, including what appear to be the most likely conditions. Even with the combination of very low  $M$  ( $M = 0.05$ ), low  $K$  ( $K = 0.20$ ), and low  $t_c$  ( $t_c = 1$  yr), the most



sensitive set of parameters modeled, Y/R declines only some 35% in one year. Therefore, our simulations imply that fluctuations of Atlantic croaker in the Chesapeake Bay region largely reflect recruitment phenomena. Because they have great capacity to resist recruitment overfishing, natural causes and/or anthropogenic causes not due to fishing may largely determine population fluctuations. Convincing evidence exists, for example, indicating that low winter water temperatures in Chesapeake estuarine nurseries may result in large mortality there, seemingly catastrophic in some years. And, that mortality follows, or co-occurs with, all the other natural perils of early life history stages.

The originally intended eggs-per-recruit studies have not yet proven feasible. Despite collecting and examining many thousands of fish, we have not been able to collect sufficient fish to usefully estimate batch fecundity, much less total annual fecundity. Though unforeseen from the literature on this species, as noted above, it has proven to be a multiple spawner with indeterminate fecundity, a pattern which makes much more difficult the estimation of fecundity. As a result, we could not perform eggs-per-recruit modeling. However, we were able to use yield-per-recruit modeling, as described above, to evaluate whether population fluctuations were due to growth overfishing or recruitment problems. And, we were able to use life history and population dynamics information, as described above, to evaluate the capacity of this species to avoid recruitment overfishing.

## INTRODUCTION

The Atlantic croaker, Micropogonias undulatus, ranges in the western Atlantic from the Gulf of Maine to Argentina (Chao and Musick 1977; White and Chittenden 1977). Its primary range in the northern hemisphere is in U.S. waters, from Delaware Bay on the north, south to Florida, and across the northern Gulf of Mexico through Texas. It is one of the most abundant inshore and estuarine fishes over much of its primary range. It supports important recreational and commercial fisheries on the Atlantic seaboard and in the Gulf of Mexico.

The Atlantic croaker has supported large fisheries in the Chesapeake Bay region where it has historically shown large fluctuations in abundance (Joseph 1972; Mercer 1987). Though many studies have attempted to explain these fluctuations (Joseph 1972; Norcross and Austin 1988), the role of fishing has never been adequately addressed. As a result, it is still not known whether or not overfishing has occurred, and causes of the fluctuations are still not clear.

Much work has been done on Atlantic croaker in the Chesapeake region. Despite the abundance of this species in that region, the important fisheries there, and the large amount of previous work there, little or no life history/population dynamics information has existed until recently on which modeling can be based to properly evaluate the effects of fishing.

Indeed, reliable methods of age determination had not even been developed and validated for the Chesapeake region, though that is required to properly estimate life history/population dynamics parameters.

The recent work of Barbieri (1993), Barbieri et al. (1994), and Barbieri et al. (in press), arising from the present project, has provided for the Chesapeake region validated methods of age determination and estimates of life history/population dynamics parameters needed for modeling. Barbieri (1993) also presented Beverton-Holt (1957) yield-per-recruit modeling. Other than modeling intended for the Carolinian Province (Chittenden 1977), that is the only published modeling for Atlantic croaker. However, it targets only a narrow, most-likely set of parameter ranges in mortality, e.g. --  $M = 0.25-0.40$ , and point estimates for parameters of the von Bertalanffy growth equation. It does not broadly simulate uncertainty in ranges of the parameters  $M$  and  $K$ , nor identify parameter ranges that constitute danger zones of biological overfishing. Finally, it also does not address the potential for juvenescence of the stock prior to overfishing.

The present studies use life history/population dynamics parameters in Barbieri (1993), Barbieri et al. (1994), and Barbieri et al. (in press) to simulate, using the Beverton-Holt yield-per-recruit model, uncertainty over a broad set of parameter ranges in  $K$  and  $M$ , and to identify danger zones of biological overfishing. We also use the Ricker yield-per-recruit model to evaluate the potential for stock juvenescence. In

addition, we assemble life history/population dynamics information to describe life history strategy in Atlantic croaker and present implications of their growth and reproduction dynamics for their capacity to resist growth and recruitment overfishing. Finally, we evaluate their population fluctuations based on the implications of their capacity to resist growth and recruitment overfishing.

## METHODS

### Beverton-Holt Model Yield-per-Recruit Simulations:

We used the Beverton-Holt (1957) yield-per-recruit model, described in Ricker (1975) and Gulland (1983) and programmed in Saila et al. (1988), to generate curves of Y/R on F and Y/R on  $t_c$ . These curves let us assess the effects of harvesting Atlantic croaker over broad ranges of the rate parameters for mortality (Z, F, M) and growth (K). Point estimates and interval estimates of the Z and K parameters, and point estimates for the other Beverton-Holt model parameters, are given in Barbieri (1993) and Barbieri et al. (1994). We summarize them below.

Growth parameters used in the Beverton-Holt model come from the von Bertalanffy equation (Ricker 1975; Gulland 1983): K,  $L_{inf}$ ,  $W_{inf}$ , and  $t_0$ . Calculated point estimates for these parameters were used in the basic simulations: K = 0.36,  $L_{inf}$  = 312.4 mm,  $W_{inf}$  = 409.9 g, and  $t_0$  = -3.26 yr. Asymptotic 95% confidence limits

of  $K$  were 0.20-0.53. We used point and interval estimates for  $K$  in our broad-range simulations:  $K = 0.20, 0.36, \text{ and } 0.53$ . We note that 84% of the cumulative growth of Chesapeake Bay Atlantic croaker was completed after two years and that data for the von Bertalanffy equation "heeled-over" sharply after age 1 (Barbieri et al. 1994), both points giving clear evidence of an asymptote. As a result, our data meet criteria for an appropriate fitting of the von Bertalanffy equation (Knight 1968; Gallucci and Quinn 1979).

Time parameters needed in the Beverton-Holt model include  $t_r$  and  $t_c$ . The value of  $t_r$  was taken as 0 yr, because young Atlantic croaker begin to recruit to Chesapeake Bay in the larval stages and many overwinter there. We used one-year increments of  $t_c$  values in our simulations, varying  $t_c$  from 1-5 yr. A  $t_c$  level of 5 yr is only a little less than the oldest fish observed in the Chesapeake region: 8 yr (Barbieri et al. 1994). Our best estimate of current  $t_c$  was 2 yr. That was the age at full recruitment to gillnet and haul-seine fisheries (Barbieri et al. 1994), though recruitment to pound-net fisheries was not complete until age 3.

Mortality parameters needed in the Beverton-Holt model include  $Z$ ,  $F$ , and  $M$ . Point and interval estimates for  $Z$  are given in Barbieri et al. (1994). They include a point estimate of  $Z = 0.63$  derived from a linear regression catch curve, with 95% confidence limits being 0.36-0.90. Additional point estimates of  $Z$ , derived from a maximum age of 8 yr, were 0.55

using Hoenig's (1983) method and 0.58 using Royce's (1972) method, both methods being based on maximum age. To estimate the current  $F$  ( $F_{cur}$ ), which is needed to choose current positions on curves of  $Y/R$  on  $F$  and  $Y/R$  on  $t_c$  to judge whether or not the current fishery exceeds  $F_{MAX}$ , we followed Chittenden (1977) and used the relationships:

$$Z_{cur} = M_{pos} + F_{cur} \quad (1)$$

and

$$F_{cur} = Z_{cur} - M_{pos} \quad (2)$$

where:

$M_{pos}$  = postulated values of  $M$  varied over the range  $M = 0.05-1.00$  for modeling, and

$Z_{cur} = 0.60$ . This value of  $Z_{cur}$  was a convenient value, about the mean of the three actual point estimates of  $Z_{cur}$  given above.

In practice, we varied  $F$  over the range  $F = 0.00-2.00$  to generate curves of  $Y/R$  on  $F$  and  $Y/R$  on  $t_c$ .

We estimated  $F_{.10}$  (Pauly 1984) at  $M = 0.20$  using the following parameter values as input:  $K = 0.36$ ;  $t_c = 2$  years; and  $F = 0.01$ . This estimate was combined with  $F_{.10}$  values from Barbieri (1993) to tabulate values of  $F_{.10}$ ,  $F_{MAX}$ , and  $F_{CUR}$  over what we considered the most-likely range of  $M$  ( $M = 0.20-0.40$ ).

Justification for using these parameter values to estimate  $F_{.10}$  includes: 1) values of  $K$  and  $t_c$  were our best estimates of current values of these parameters, being derived from the von Bertalanffy equation and age compositions of the commercial

foodfish catch (Barbieri et al. 1994), respectively; 2) the value of  $F = 0.01$  is a standard value used to estimate  $F_{.10}$ , the yield-per-unit-effort between  $F = 0.00$  and  $F = 0.01$  being used as the baseline for a light fishery, and  $F_{.10}$  being the value of  $F$  when the yield-per-unit-effort is 10% of the baseline (Pauly 1984), and 3) the  $M$  range of 0.20-0.40 was meant to bracket our best estimates of  $M$ , values of 0.29, 0.31, and 0.36 given in Barbieri (1993).

Finally on Beverton-Holt model parameter estimation methodology, we used the approaches described above to estimate  $M$  and  $F$ , because we felt the initially intended mark-recapture studies, in principle probably the best approach, were not feasible and probably would not provide reliable tag returns and estimates at this time. Our reason for that feeling was the wide-spread spirit of "no cooperation" that appeared to exist in the various recreational and commercial fisheries of the Chesapeake Bay region.

#### Ricker Model Yield-per-Recruit Simulations:

We used the Ricker yield-per-recruit model, described in Ricker (1975) and programmed in Saila et al. (1988), to generate curves of stock biomass on age. These curves let us assess the potential for juvenescence of Atlantic croaker stocks, a classical effect of fishing (Ricker 1975), which begins even before overfishing occurs. The Ricker yield-per-recruit model

uses as parameter estimates weights-at-age, from which a growth rate parameter  $G$  is calculated for each age, and estimates of mortality-at-age ( $Z$ ,  $M$ , and  $F$ ). To estimate weights-at-age, we used the von Bertalanffy equation in Barbieri et al. (1994) to predict average lengths-at-age and converted lengths to average weights-at-age using the length-weight equation in Barbieri et al. (1994). To estimate total mortality ( $Z$ ), we followed methods given above for Beverton-Holt model simulations. Briefly, we used the three point and/or interval estimates of  $Z$  given in Barbieri et al. (1994) to estimate current  $Z$ . We again chose the value  $Z_{\text{CUR}} = 0.60$  as a convenient value from which to estimate  $F_{\text{CUR}}$  from eq. (1, 2) above. Similarly, we again postulated values of  $M$  ( $M_{\text{pos}}$ ) from which to estimate  $F_{\text{CUR}}$  given  $Z_{\text{CUR}}$ .

We generated curves of stock biomass on age for several values of  $M$ : 0.05, 0.20, 0.40, 0.60, 0.80, and 1.00. The latter two  $M$  values exceed our estimate of  $Z_{\text{CUR}}$  but were included for completeness to approximate and slightly exceed the upper 95% confidence limit for  $Z$  (0.90). Simulations were done at each of four levels of  $t_c$  ( $t_c = 1, 2, 3, \text{ and } 4 \text{ yr}$ ) and four levels of  $F$  ( $F = 0.00, 0.20, 0.40, \text{ and } 0.60$ ). The highest level of  $F$  simulated in this model (0.60) has the same value as our best estimate of current  $Z$ .



## RESULTS

### Beverton-Holt Model Yield-per-Recruit Simulations:

Yields that can be taken from Atlantic croaker in the Chesapeake Bay region are inversely related to the magnitude of  $M$ . Given  $K = 0.36$ , our point estimate for  $K$ , maximum values of  $Y/R$  ( $Y/R_{MAX}$ ) range from less than 75 g/R to greater than 200 g/R, and they are inversely related to the magnitude of  $M$  at any  $t_c$  level (Fig. 1). Similar patterns occur at all  $K$  levels in the broad range 0.20-0.53 (Figs. 2,3), the 95% asymptotic confidence limits for  $K$ .

Yields that can be taken from Atlantic croaker in the Chesapeake Bay region are directly related to the magnitude of  $K$ . At given  $M$ , for any  $t_c$  level,  $Y/R$  increases with increase in  $K$  (Figs. 1-3). For example,  $Y/R$  at  $M = 0.40$ ,  $t_c = 1$  yr, and  $F = 2.00$  is less than 75 g/R at  $K = 0.20$ , about 120 g/R at  $K = 0.36$ , and exceeds 150 g/R at  $K = 0.53$ .

Yields that can be taken from Atlantic croaker in the Chesapeake Bay region strongly depend on the magnitude of  $t_c$ . At given levels of  $F$ ,  $Y/R$  generally increases with  $t_c$  to a point, then decreases with further increase in  $t_c$  (Figs. 4-6). The point at which  $Y/R$  is a maximum in curves of  $Y/R$  on  $t_c$  is referred to (Beverton and Holt 1957) as a "level of eumetric fishing". A level of eumetric fishing represents the largest yield that can be taken at a given level of  $F$ . It is not the

Figure 1. Beverton-Holt model curves of Y/R on F for  $K = 0.36$  and given levels of  $M$  and  $t_c$ . The vertical black box indicates  $F_{CUR}$  at given  $M$ . Because  $Z_{CUR} = 0.60$ ,  $F_{CUR}$  would equal zero at  $M = 0.60, 0.80,$  and  $1.00$ , though  $F_{CUR} = 0.00$  is not realistic.

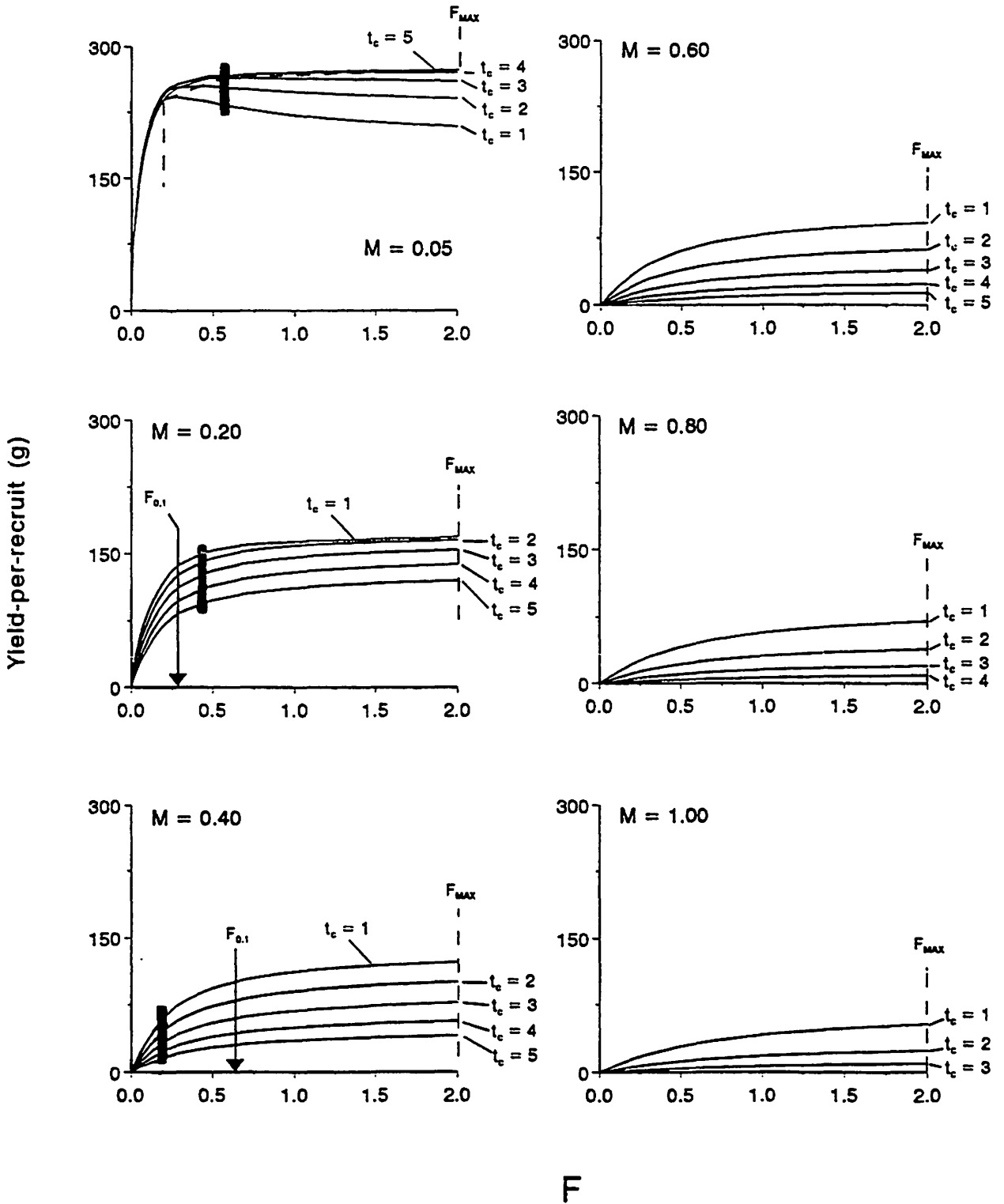


Figure 2. Beverton-Holt model curves of  $Y/R$  on  $F$  for  $K = 0.53$  and given levels of  $M$  and  $t_c$ . The vertical black box indicates  $F_{CUR}$  at given  $M$ . Because  $Z_{CUR} = 0.60$ ,  $F_{CUR}$  would equal zero at  $M = 0.60, 0.80,$  and  $1.00$ , though  $F_{CUR} = 0.00$  is not realistic.

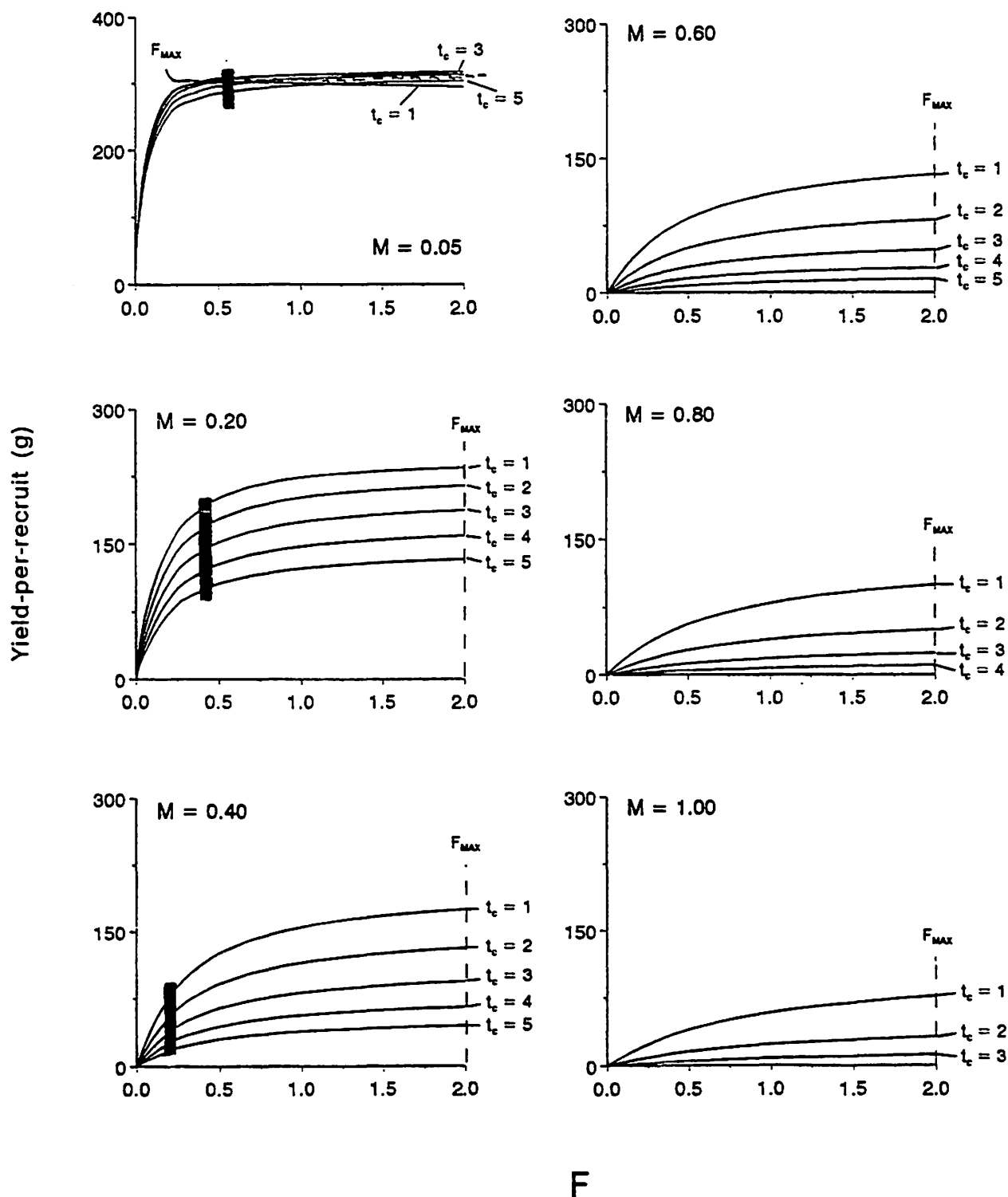


Figure 3. Beverton-Holt model curves of Y/R on F for  $K = 0.20$  and given levels of  $M$  and  $t_c$ . The vertical black box indicates  $F_{CUR}$  at given  $M$ . Because  $Z_{CUR} = 0.60$ ,  $F_{CUR}$  would equal zero at  $M = 0.60, 0.80, \text{ and } 1.00$ , though  $F_{CUR} = 0.00$  is not realistic.

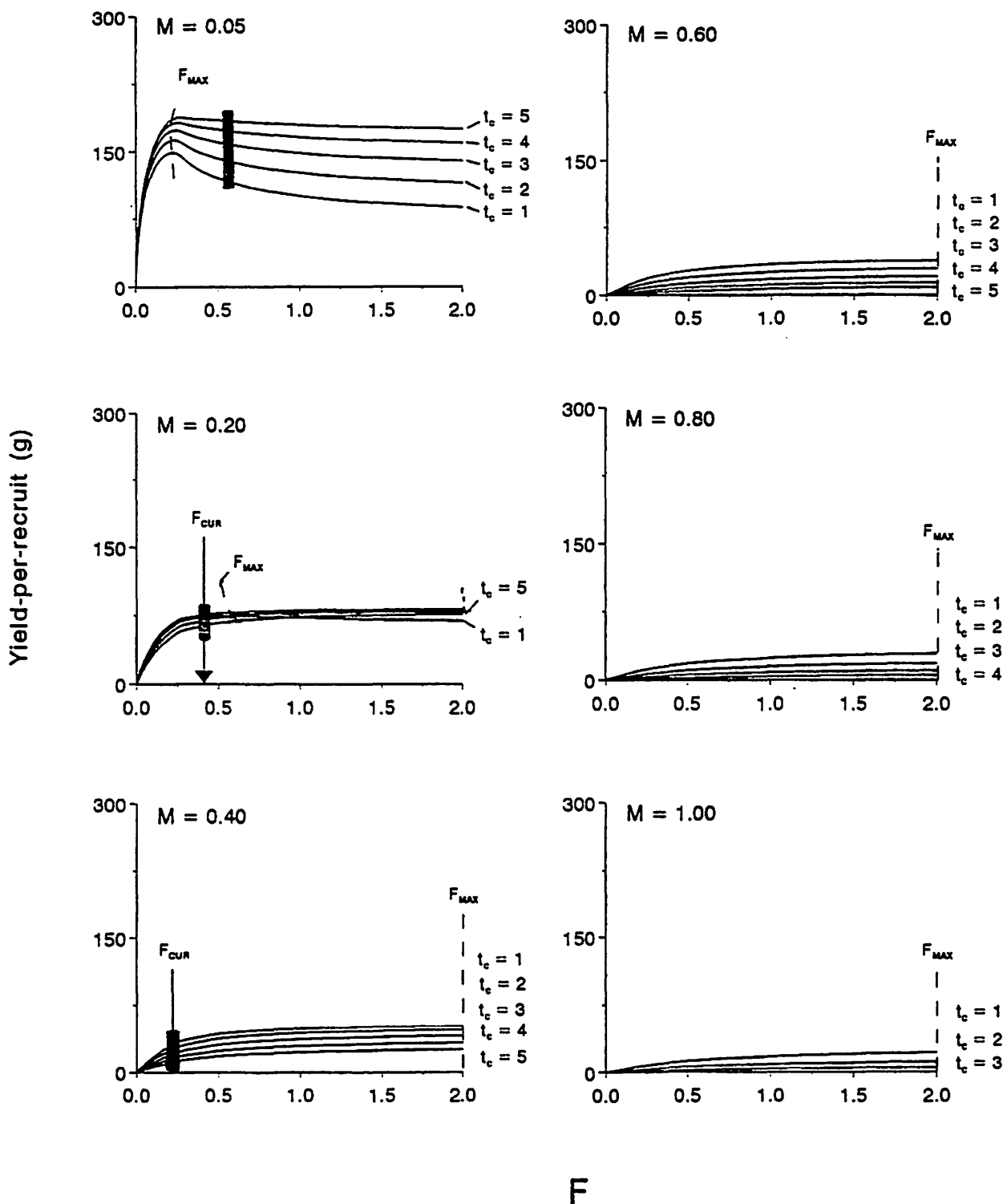


Figure 4. Beverton-Holt model curves of Y/R on  $t_c$  for  $K = 0.36$  and given levels of  $M$  and  $F$ . EUM indicates eumetric fishing conditions.

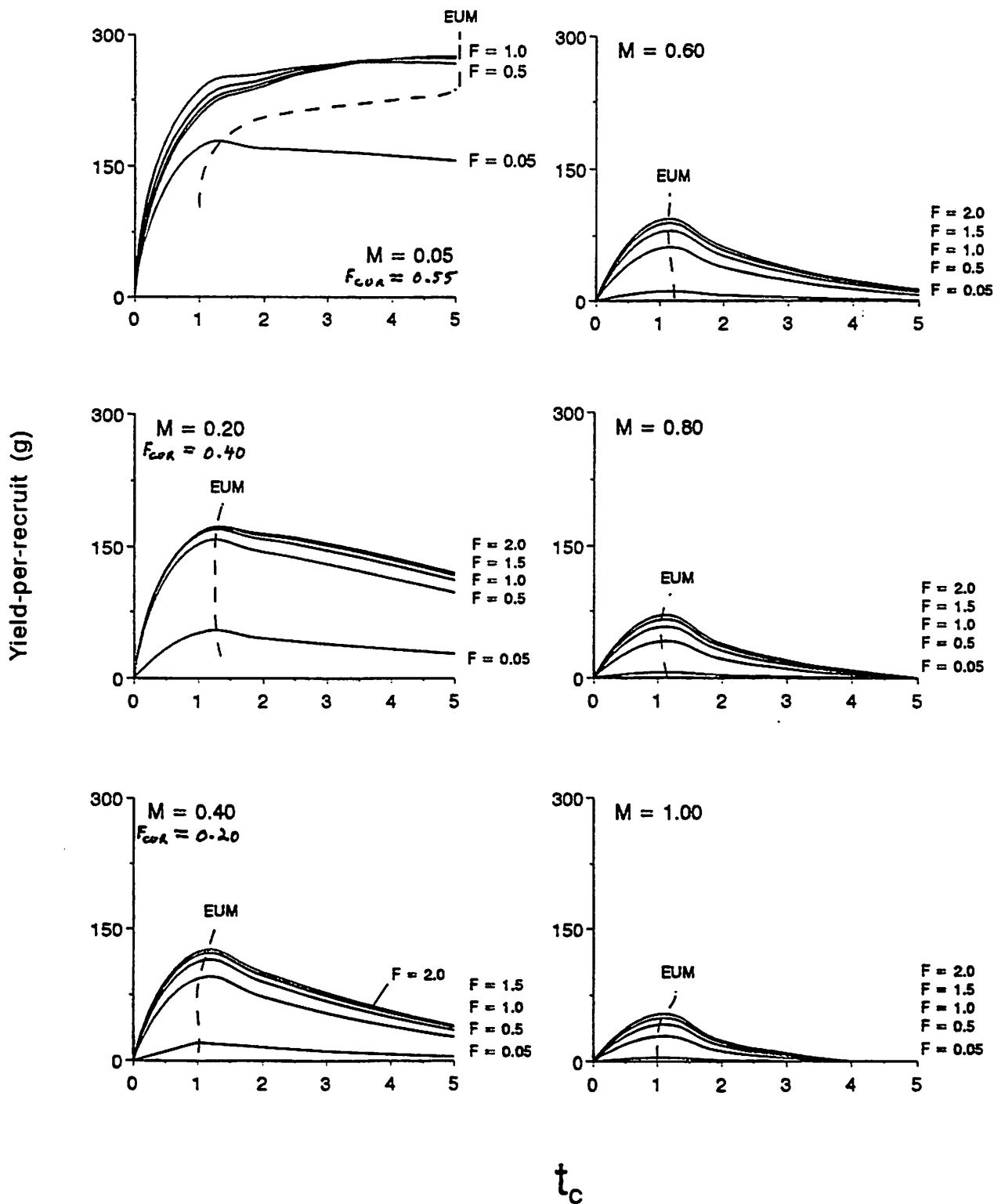


Figure 5. Beverton-Holt model curves of  $Y/R$  on  $t_c$  for  $K = 0.53$  and given levels of  $M$  and  $F$ . EUM indicates eumetric fishing conditions.

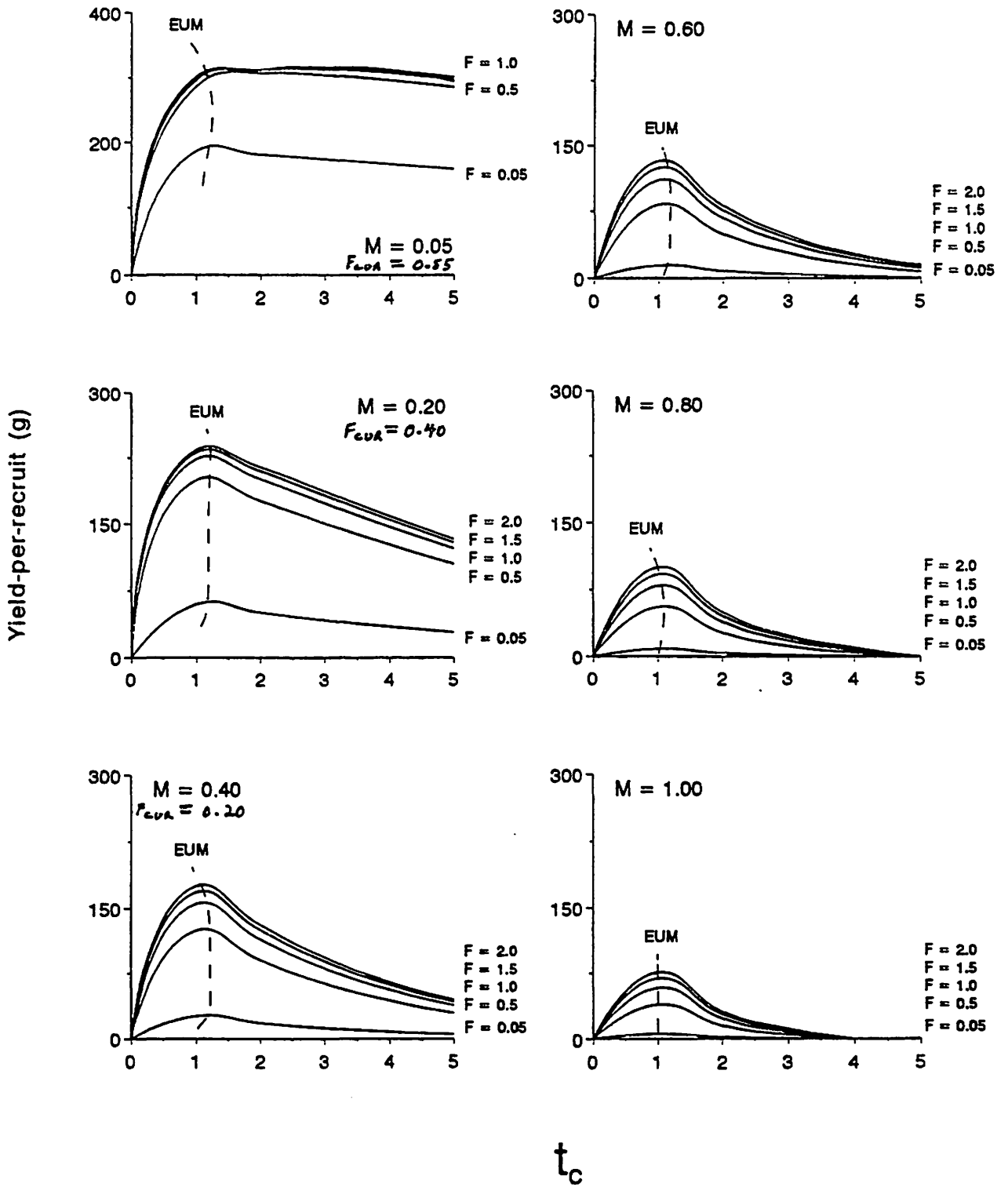
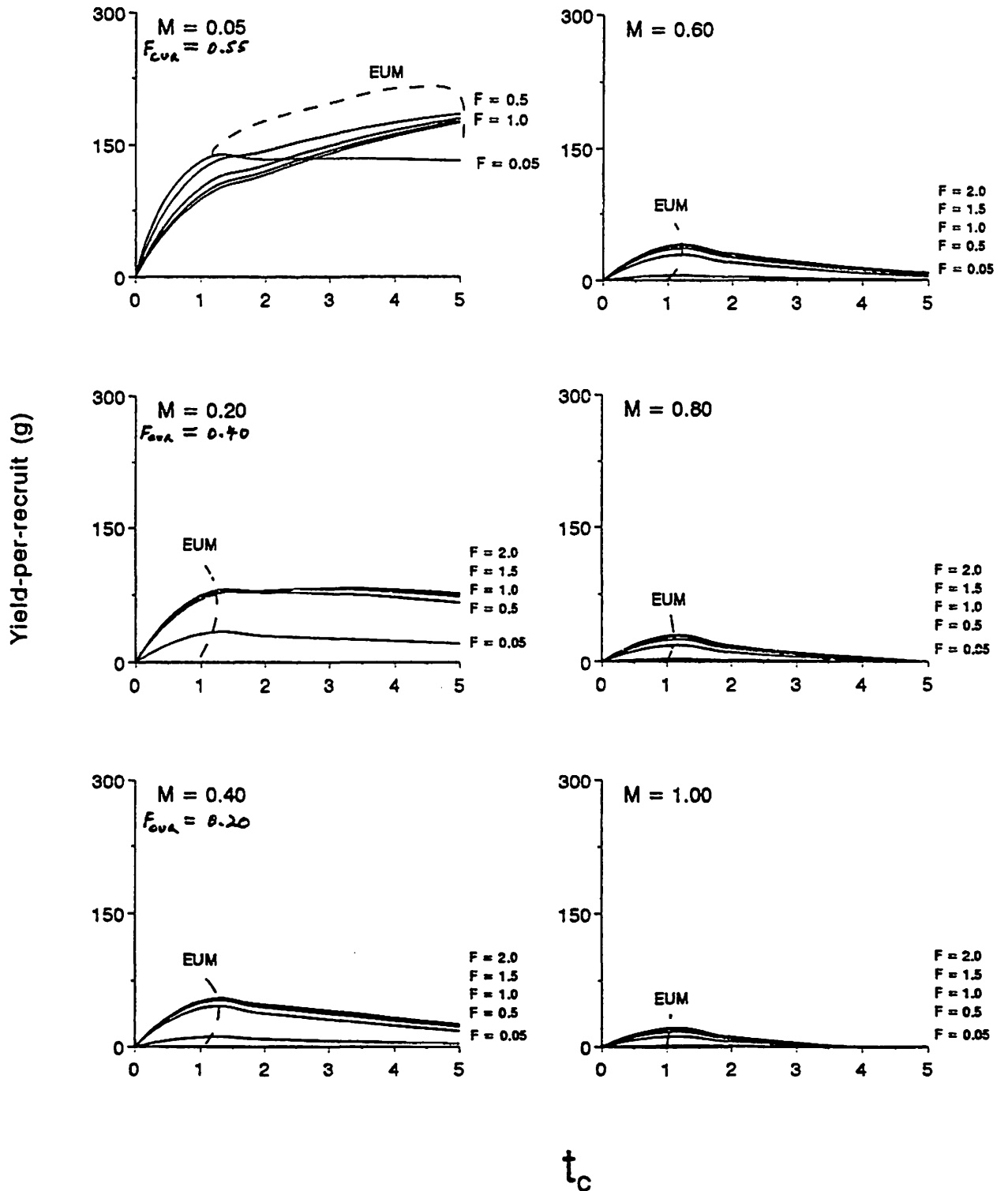


Figure 6. Beverton-Holt model curves of Y/R on  $t_c$  for  $K = 0.20$  and given levels of  $M$  and  $F$ . EUM indicates eumetric fishing conditions.



same as  $Y/R_{MAX}$ , the maximum in curves of  $Y/R$  on  $F$ . Rather, yield at eumetric fishing is generally a little lower than  $Y/R_{MAX}$ , and levels of eumetric fishing are generally thought of as a surrogate for some economic "optimum".

The level of fishing mortality ( $F_{MAX}$ ) at which yields are a maximum ( $Y_{MAX}$ ) is directly related to the magnitude of  $M$  in Atlantic croaker of the Chesapeake Bay region.  $F_{MAX}$  values in curves of  $Y/R$  on  $F$  increase as  $M$  increases, so the curve of  $F_{MAX}$  shifts to the right with increasing  $M$ . This response is seen best in graphs for low  $K$  levels ( $K = 0.20$ ), because, at higher  $K$  levels,  $F_{MAX}$  generally occurs at the highest  $F$  simulated ( $F = 2.00$ ). Given  $K = 0.20$ ,  $F_{MAX}$  is only about 0.25 when  $M = 0.05$ , regardless of  $t_c$  (Fig. 3).  $F_{MAX}$  becomes 0.55-2.00 when  $M = 0.20$ , depending on  $t_c$ , and  $F_{MAX}$  is 2.00 or greater at  $M = 0.40$  and higher.

The level of fishing mortality at which yields are a maximum is directly related to the magnitude of  $K$  in Atlantic croaker of the Chesapeake Bay region.  $F_{MAX}$  values in curves of  $Y/R$  on  $F$  increase as  $K$  increases, so the curve of  $F_{MAX}$  shifts to the right with increasing  $K$ . This response is seen best in graphs for low  $M$  values ( $M = 0.05$ ), again because, at higher  $M$  levels,  $F_{MAX}$  generally occurs at the highest  $F$  simulated ( $F = 2.00$ ). Given  $M = 0.05$ ,  $F_{MAX}$  is only about 0.25 when  $K = 0.20$ , regardless of  $t_c$  (Fig. 3).  $F_{MAX}$  becomes about 0.25-2.00 when  $K = 0.36$ , depending on  $t_c$  (Fig. 1), and  $F_{MAX}$  becomes about 0.40-2.00 when  $K = 0.53$ , again depending on  $t_c$  (Fig. 2).



The level of fishing mortality at which yields are a maximum is directly related to the magnitude of  $t_c$  in Atlantic croaker of the Chesapeake Bay region.  $F_{MAX}$  values in curves of Y/R on F increase as  $t_c$  increases, so the curve of  $F_{MAX}$  shifts to the right with increasing  $t_c$ . This response is seen best when very low M (0.05) is combined with  $K = 0.36$  (Fig. 1), once more because, at higher  $t_c$  levels,  $F_{MAX}$  generally occurs at the highest F simulated ( $F = 2.00$ ). Under the conditions just specified,  $F_{MAX}$  is slightly less than 0.25 at  $t_c = 1$  yr and rapidly increases to 2.00 at  $t_c = 4-5$  yr.

Shapes of the curve describing the response of yield to fishing mortality strongly depend on magnitudes of M, K, and  $t_c$  in Atlantic croaker of the Chesapeake Bay region. Curves of Y/R on F rise to a distinct peak as F increases and then decrease with further increase in F only when: 1) M is very low; for examples, see curves of Y/R on F given  $M = 0.05$  and  $K = 0.20-0.36$  (Figs. 1,3), 2) K is low; for examples, see curves of Y/R on F given  $M = 0.05$  and  $K = 0.20$  vs  $K = 0.53$  (Figs. 2,3), and 3)  $t_c$  is low; for example, see curves of Y/R on F for  $t_c = 1$  yr vs  $t_c = 5$  yr when  $M = 0.05$  and  $K = 0.20$  (Fig. 3). In contrast, curves rise to an asymptote, or keep rising, when M, K, and  $t_c$  are not low or very low. For examples of the latter phenomena, see curves of Y/R on F for all values of M, K, and  $t_c$  other than those just cited. The shape of the curve of Y/R on F, in summary, generally changes according to the following pattern: it usually rises to a distinct peak at "low" levels of M, K, and  $t_c$ , becomes asymptotic

at "intermediate" levels of these parameters, and becomes a rising curve at "high" levels.

Over much of the range of  $M$ , large fisheries and high rates of  $F$  will not reduce yields of Atlantic croaker in the Chesapeake Bay region. Over much of the range of  $M$ ,  $Y/R$  rises to an asymptote with increasing  $F$ , or keeps increasing with  $F$ . At all levels of  $M$  in the range  $M = 0.20-1.00$ , given  $K = 0.36$ ,  $Y/R$  rises to an asymptote or keeps increasing with  $F$  (Fig. 1). This pattern occurs at all  $t_c$  levels in the range 1-5 yr. Similar patterns in  $Y/R$  with  $M = 0.20-1.00$  generally occur at all  $K$  levels over the broad range 0.20-0.53 (Figs. 2,3). As with  $K = 0.36$ , these patterns generally occur at all  $t_c$  levels in the range 1-5 yr. The exception to this is that  $Y/R$  decreases slightly with high  $F$  when low  $M$  ( $M = 0.20$ ) is combined with low  $K$  ( $K = 0.20$ ) and low  $t_c$  ( $t_c = 1$  yr). Even at very low  $M$  ( $M = 0.05$ ),  $Y/R$  rises to an asymptote when  $t_c$  levels are high ( $t_c = 4-5$  yr, if not always  $t_c = 3$  yr) and  $K = 0.36-0.53$ .

At very low  $M$ , yields of Atlantic croaker in the Chesapeake Bay region are sensitive to overfishing. At very low  $M$  ( $M = 0.05$ ), given  $K = 0.36$ ,  $Y/R$  often rises to a peak and then declines with increasing  $F$ . This pattern occurs, however, only at low  $t_c$  levels (Fig. 1), eg -- at  $t_c = 1-2$  yr and, less noticeably, 3 yr. At modeled  $M$  levels only a little higher ( $M = 0.20$ ), there is no decline in  $Y/R$  even at  $t_c$  levels as low as 1 yr. At higher  $K$  levels ( $K = 0.53$ , Fig. 2),  $Y/R$  rises to a peak with  $F$  and declines with further increase in  $F$  only when low  $t_c$

( $t_c = 1$  yr) is combined with very low  $M$  ( $M = 0.05$ ). Even in this case, however, there is little decline in  $Y/R$ . In contrast, at low  $K$  ( $K = 0.20$ , Fig. 3),  $Y/R$  noticeably rises to a peak with  $F$  and then declines at all levels of  $t_c$  when  $M = 0.05$ . Even in this latter case, however, there is little decline in  $Y/R$  with high  $t_c$  ( $t_c = 5$  yr, or so).

Over much of the range of  $M$ , the current level of fishing mortality ( $F_{cur}$ ) on Atlantic croaker of the Chesapeake Bay region would be below  $F_{MAX}$ , usually well below it, and current yield would be below  $Y_{MAX}$ . Given  $K = 0.36$ ,  $F_{MAX}$  and  $Y/R_{MAX}$  generally occur at the highest values of  $F$  simulated ( $F = 2.00$ , Fig. 1). This pattern occurs at all  $t_c$  levels in the range 1-5 yr when  $M = 0.20-1.00$ , and the pattern even occurs at very low  $M$  ( $M = 0.05$ ) as long as  $t_c$  is 4-5 yr or so. Similar patterns in  $F_{MAX}$  generally occur at all  $K$  values in the broad range 0.20-0.53 when  $M = 0.20-1.00$  (Figs. 2,3). As with  $K = 0.36$ , these patterns in  $F_{MAX}$  generally occur at all  $t_c$  levels in the range 1-5 yr, though  $F_{MAX}$  is only about 0.65 if low  $t_c$  ( $t_c = 1$  yr) is combined with low  $M$  ( $M = 0.20$ ) and low  $K$  ( $K = 0.20$ ).

At very low  $M$ , the current level of fishing mortality on Atlantic croaker in the Chesapeake Bay region would often exceed  $F_{MAX}$ . Given  $K = 0.36$ ,  $F_{cur}$  exceeds  $F_{MAX}$  in some cases (Fig. 1). These cases, however, include only the combination of very low  $M$  ( $M = 0.05$ ) with low  $t_c$  levels, eg --  $t_c = 1-2$  yr and, less noticeably, 3 yr. At low  $K$  ( $K = 0.20$ ),  $F_{cur}$  exceeds  $F_{MAX}$  at all  $t_c$  levels when  $M = 0.05$ . At high  $K$  ( $K = 0.53$ ), however,  $F_{cur}$  exceeds

$F_{MAX}$  only when  $t_c = 1$  yr and  $M = 0.05$  (Fig. 2).

Given stable values of  $t_c$  and  $K$ , yields generally show little or no decrease even at high levels of  $F$  on Atlantic croaker in the Chesapeake Bay region. Because curves of  $Y/R$  on  $F$  are generally asymptotic or rising, yields generally do not decrease at high  $F$ . Rather, they remain stable or keep increasing with  $F$ . This pattern occurs at all levels of  $K$  in the range 0.20-0.53 when  $M = 0.20-1.00$  (Figs. 1-3). Decreases in  $Y/R$  with increasing  $F$  generally occur only when very low  $M$  ( $M = 0.05$ ) is combined with low and/or the current  $K$  ( $K = 0.20$  and  $0.36$ , respectively). Decrease in  $Y/R$  is accentuated by low  $t_c$  levels, depending on  $K$ . It is quite pronounced at  $t_c = 1-4$  yr for  $K = 0.20$  and at  $t_c = 1-2$  yr for  $K = 0.36$ . It is not pronounced, even at  $t_c = 1$  yr, for  $K = 0.53$ . However, even the most pronounced declines in  $Y/R$ , which occur with  $K = 0.20$ ,  $M = 0.05$ , and  $t_c = 1$  yr, are not great. With the latter set of parameter combinations,  $Y/R$  declines from about 140 g/R at  $F_{MAX}$  to about 90 g/R at  $F = 2.00$ , a decrease of only some 35%.

Over much of the range of  $M$ , yields of Atlantic croaker in the Chesapeake Bay region rise to a distinct peak with increasing  $t_c$  and then decline. Given  $K = 0.36$ ,  $Y/R$  rises to a distinct peak with  $t_c$  and then declines when  $M = 0.20-1.00$  (Fig. 4). This pattern occurs at all  $F$  levels in the range 0.05-2.00. However,  $Y/R$  curves form more pronounced peaks as  $F$  increases, less pronounced peaks as  $F$  decreases. For example, at  $M = 0.40$ , the curve shows a pronounced peak at  $F = 2.00$ , but it is much flatter

at  $F = 0.05$ . With few exceptions, the pattern of an increase in  $Y/R$  to a peak and then a decrease with increasing  $t_c$  occurs at all  $K$  levels in the broad range 0.20-0.53 (Figs. 5,6) when  $M = 0.20-1.00$ . The chief exception is that  $Y/R$  more or less rises to an asymptote with increase in  $t_c$  when low  $K$  ( $K = 0.20$ ) is combined with low  $M$  ( $M = 0.20$ , Fig. 6).

At very low  $M$ , yields of Atlantic croaker in the Chesapeake Bay region rise to an asymptote, or keep increasing, with increasing  $t_c$ . At higher  $K$  levels ( $K = 0.36$  and  $0.53$ ) and very low  $M$  ( $M = 0.05$ ),  $Y/R$  rises to a more or less stable asymptote with  $t_c$  at all  $F$  levels modeled (Figs. 4,5). At low  $K$  ( $K = 0.20$ ) and very low  $M$  ( $M = 0.05$ ), however,  $Y/R$  generally keeps increasing with  $t_c$  at  $F = 0.50$  and higher (Fig. 6). At low  $K$  ( $K = 0.20$ ), moreover, this pattern occurs even at  $M$  as high as 0.20.

Maximum yield is generally taken from Atlantic croaker in the Chesapeake Bay region at  $t_c$  levels in the range 1-2 yr, regardless of  $F$ . Given  $K = 0.36$ , maximum  $Y/R$  is taken at  $t_c = 1-2$  yr when  $M = 0.20-1.00$  (Fig. 4). This pattern occurs at all  $F$  levels in the range 0.05-2.00. A similar pattern generally occurs at other  $K$  levels in the broad range 0.20-0.53 (Figs. 5,6). It occurs at all  $M$  levels in the range  $M = 0.05-1.00$  for  $K = 0.53$ , and at all  $M$  levels in the range 0.20-1.00 for  $K = 0.20$ .

Levels of  $F_{.10}$  for Atlantic croaker in the Chesapeake Bay region are much lower than levels of  $F_{MAX}$ . Our estimates of  $F_{.10}$  (Table 1) are 0.27 at  $M_{pos} = 0.20$ , 0.35 at  $M_{pos} = 0.25$ , 0.45 at  $M_{pos} = 0.30$ , 0.52 at  $M_{pos} = 0.35$ , and 0.64 at  $M_{pos} = 0.40$ . These values

Table 1. Summary of estimates of  $F_{MAX}$ ,  $F_{0.1}$ , and  $F_{CUR}$  at listed values of postulated  $M$  ( $M_{POS}$ ). Values for  $M_{POS} = 0.25, 0.30, 0.35,$  and  $0.40$  are taken from Barbieri (1993). See text for details of estimation procedures.

$M_{POS}$	$F_{CUR}$	$F_{MAX}$	$F_{0.1}$
0.20	0.40	>2.0	0.27
0.25	0.35	>2.0	0.35
0.30	0.30	>2.0	0.45
0.35	0.25	>2.0	0.52
0.40	0.20	>2.0	0.64=

of  $F_{.10}$  are much lower than our estimates of  $F_{MAX}$ , all of which equal or exceed  $F = 2.00$  using the same parameter combinations used to estimate  $F_{.10}$ .

Whether or not the current fishery exceeds  $F_{.10}$  for Atlantic croaker in the Chesapeake Bay region depends on the level of  $M$ . The current fishery does not exceed  $F_{.10}$  if  $M = 0.30$  and higher. However, the current fishery is at  $F_{.10}$  if  $M = 0.25$ . The current fishery exceeds  $F_{.10}$  if  $M = 0.20$  and lower.

#### Ricker Model Yield-per-Recruit Simulations:

Total standing stock biomass of Atlantic croaker in the Chesapeake Bay region, and stock biomass at any age, is inversely proportional to  $F$ , being greatest when  $F = 0.00$ , eg -- when there is a virgin stock. At all values of  $M$  and at all levels of  $t_c$ , standing stock biomass is highest at any age when  $F = 0.00$  (Figs. 7-10). Similarly, area under the curve is greatest at  $F = 0.00$ , indicating that total standing stock biomass is also highest in a virgin stock. Total standing stock and stock biomass at any age both become progressively lower as  $F$  increases past  $F = 0.00$ .

Although overfishing is not now occurring, unless  $M$  is very low, the current fishery has greatly reduced standing stock biomass of Atlantic croaker in the Chesapeake Bay region. As described above, Beverton-Holt model simulations indicate that current  $F$  would not exceed  $F_{MAX}$ , unless  $M$  is very low ( $M = 0.05$ ) and  $t_c$  is also low ( $t_c = 1-2$  yr, or, less noticeably, 3 yr).

Figure 7. Ricker model curves of standing stock biomass on age for  $t_e = 1$  yr and given levels of  $M$  and  $F$ . At  $M = 0.60-1.00$ , curves are for  $F$  values in the same descending order as in the left panels.

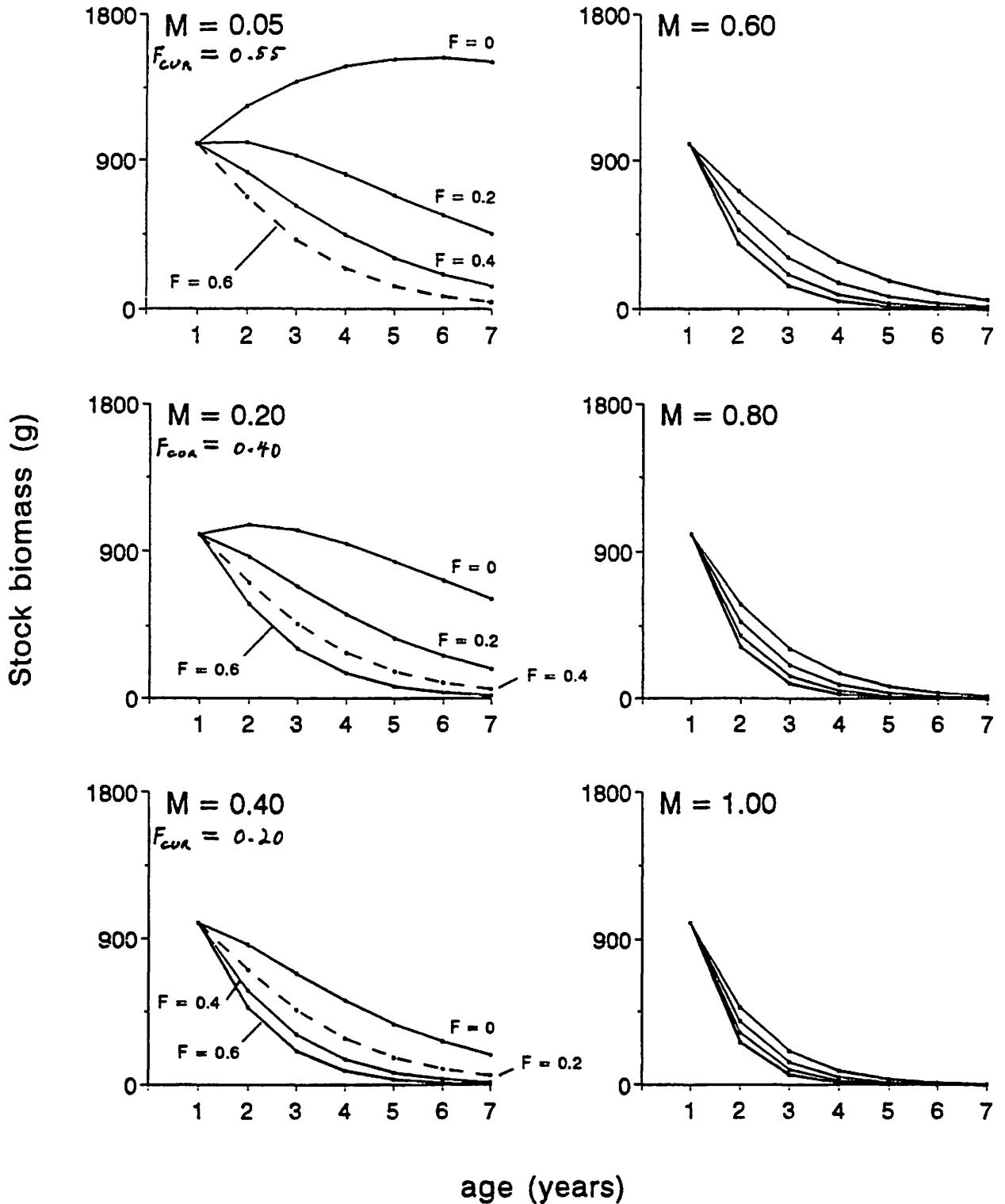




Figure 8. Ricker model curves of standing stock biomass on age for  $t_c = 2$  yr and given levels of  $M$  and  $F$ . At  $M = 0.60-1.00$ , curves are for  $F$  values in the same descending order as in the left panels.

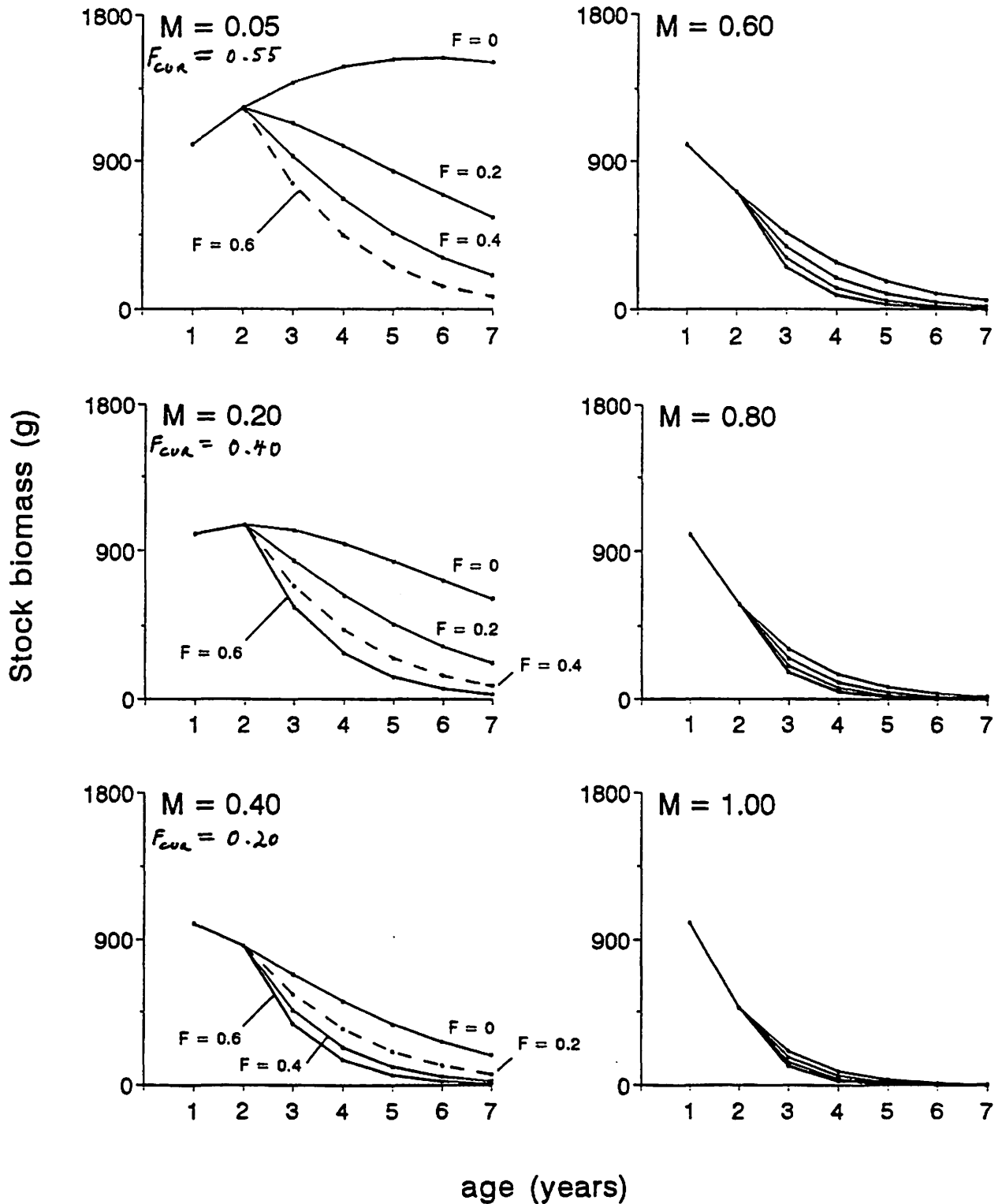


Figure 9. Ricker model curves of standing stock biomass on age for  $t_c = 3$  yr and given levels of  $M$  and  $F$ . At  $M = 0.60-1.00$ , curves are for  $F$  values in the same descending order as in the left panels.

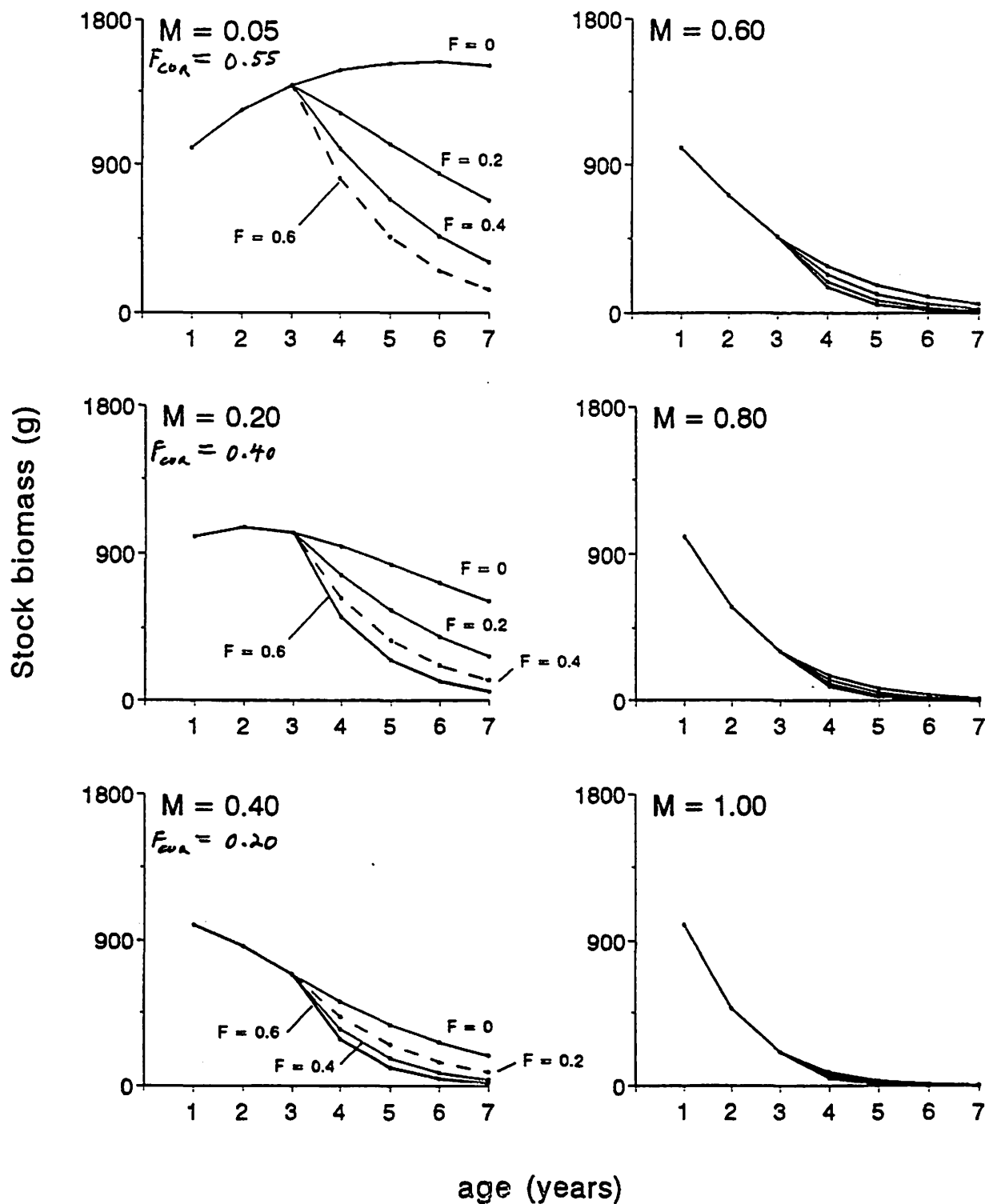
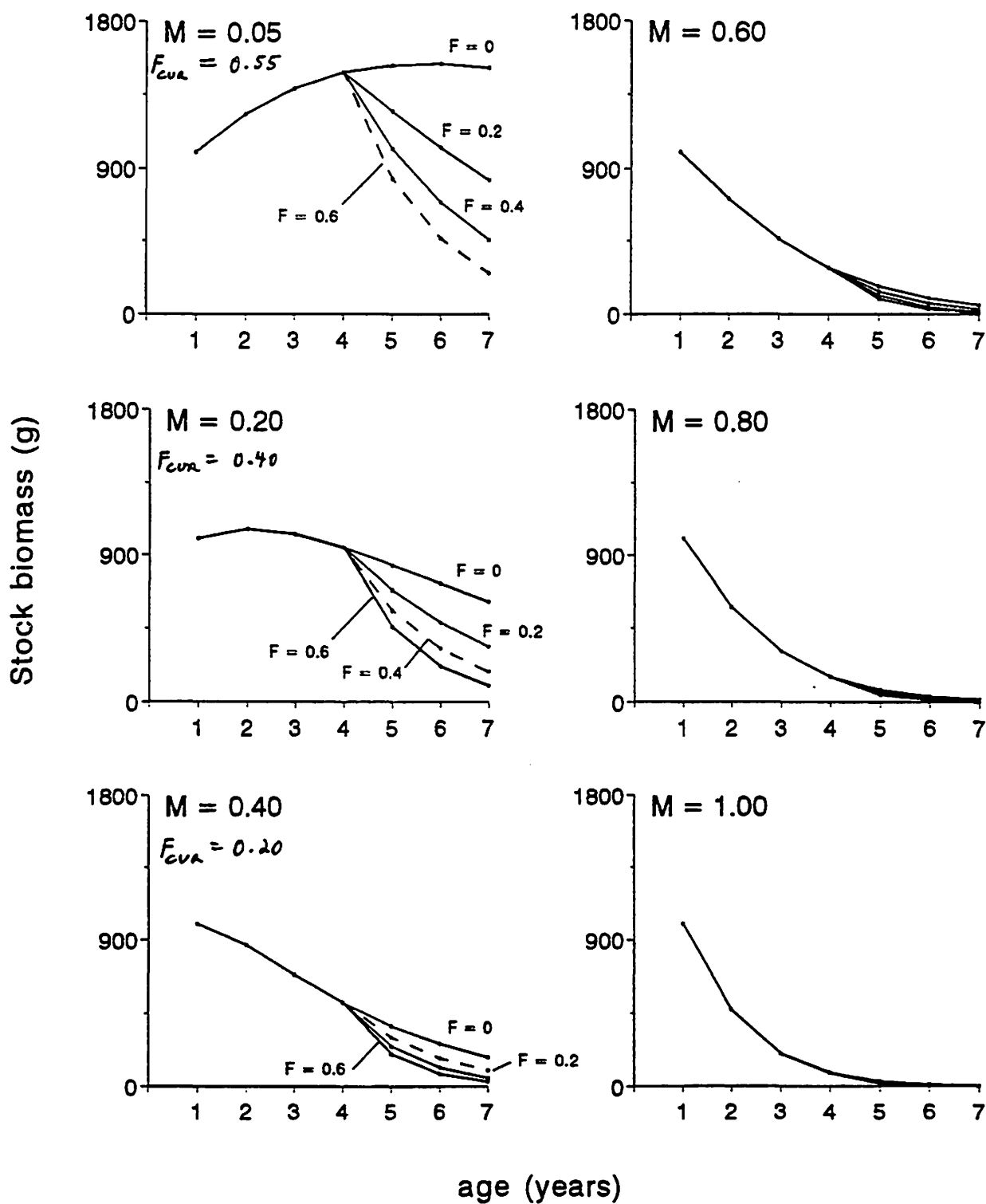


Figure 10. Ricker model curves of standing stock biomass on age for  $t_c = 4$  yr and given levels of  $M$  and  $F$ . At  $M = 0.60-1.00$ , curves are for  $F$  values in the same descending order as in the left panels.



However, at each level of  $M$  simulated using the Ricker model ( $M = 0.05-0.40$ ), area under the curve is greatly reduced at  $F_{CUR}$ , and with any increase in  $F$  past  $F = 0.00$  (Figs. 7-10). For examples, if  $M = 0.20$ ,  $F_{CUR} = 0.40$ , and total standing stock biomass is reduced roughly 60-70%. Similarly, if  $M = 0.40$ ,  $F_{CUR} = 0.20$ , and total standing stock is reduced roughly 25%.

Concurrent with reduction in total standing stock biomass, the current fishery has greatly reduced stock biomass-at-age in Atlantic croaker of the Chesapeake Bay region. At each value of  $M$ , the height of the curve at any age, which expresses stock biomass-at-age, has been greatly reduced at  $F_{CUR}$ , and it is progressively reduced with any increase in  $F$  past  $F = 0.00$  (Figs. 7-10). This reduction becomes relatively greater at older ages, because a given annual level of  $F$  has been exerted more times on older ages. For example, at  $M = 0.20$  and  $t_c = 1$  yr, age 7 fish make up a large fraction of the total standing stock biomass in the virgin stock, as indicated by the height of the curve at  $F = 0.00$  and age 7. In contrast, at  $F_{CUR} = 0.40$ , age 7 fish make up a negligible fraction of the total standing stock. The reduction in age 7 fish is less marked at  $M = 0.40$  and  $F_{CUR} = 0.20$ , but it still exceeds 50% of their level in a virgin stock. As a result of this process, total standing stock biomass is progressively made up of relatively more and more younger fish as  $F$  increases, a phenomenon referred to as "juvenescence of the stock" (Ricker 1975).

## DISCUSSION

### Responses to Variation in Model Parameters and Delineation of Biological Danger Zones:

Our simulations describe basic responses of Atlantic croaker yields in the Chesapeake Bay region to variation in model parameters. We have shown that potential yields,  $F_{MAX}$ , and shapes of the curve of Y/R on F strongly depend on the magnitude of M, K, and  $t_c$ . Yields decrease as M increases, increase as K increases, and increase with increase in  $t_c$  to a point beyond which they decrease with further increase in  $t_c$ .  $F_{MAX}$  increases as M, K and  $t_c$  each increase, and curves of  $F_{MAX}$  shift to the right as a result. Shapes of the curve of Y/R on F, therefore, rise to a distinct peak and then decline at "low" levels of M, K, and  $t_c$ , become asymptotic at "intermediate" levels of these parameters, and become rising curves at "high" levels. In agreement with our findings, Chittenden (1977) and Barbieri (1993) reported similar responses of yields to variation in M and  $t_c$ , though they did not describe responses to variation in K. Graphs of Y/R on F in Chittenden (1977) also show that curves of  $F_{MAX}$  shift to the right as M and  $t_c$  each increase. This latter pattern is not shown in Barbieri's (1993) graphs, because he modeled only a narrow range of M for which  $F_{MAX}$  was at the highest levels of F modeled.

Patterns given above reflect the basic balancing of growth against mortality in yield-per-recruit models. As M increases,

natural mortality "takes biomass away" more rapidly in relation to growth. As a result, it is often worthwhile, in principle, to harvest at high levels of  $F$  and/or early age when  $M$  is high, and, conversely, to harvest at low levels when  $M$  is low. As  $K$  increases, however, growth produces more biomass in relation to  $M$ , which permits higher  $F$ , in principle, and may make it worthwhile to wait and harvest at older age. Waiting to harvest at age older than two years makes little sense in Atlantic croaker, however, because most of the potential growth is completed by the end of their second year (Barbieri et al. (1994)).

Our simulations show that, over a broad range of  $M$ ,  $K$ , and  $t_c$  levels, yields of Atlantic croaker in the Chesapeake Bay region rise to an asymptote, or keep rising, with increase in  $F$ . This response area represents a broad set of parameter conditions in which overfishing would not occur in the sense of exceeding an  $F_{MAX}$ . As a result, it is a zone in which there is little or no danger of biological overfishing, regardless of  $F$ . Little danger of biological overfishing occurs when  $M$  is 0.20 or greater as long as: 1)  $K$  is 0.20 or greater, a value well below the current  $K = 0.36$  described by the von Bertalanffy equation in Barbieri et al. (1994), and 2)  $t_c$  is 1 yr or greater, a value below the current estimate of  $t_c$  in Barbieri et al (1994). Even at very low  $M$  ( $M = 0.05$ ), there is little danger of biological overfishing when  $K$  in the range 0.36-0.53 is combined with  $t_c = 4-5$  yr, or, less so, 3 yr.

Although there is little or no danger of biological overfishing over a broad range of  $M$ ,  $K$ , and  $t_c$  levels in Atlantic croaker of the Chesapeake Bay region, our simulations also show a distinct danger zone in which fishing would exceed an  $F_{MAX}$ . This generally occurs when very low  $M$  ( $M = 0.05$ ) is combined with: 1) high  $K$  ( $K = 0.53$ ) and low  $t_c$  ( $t_c = 1$  yr), 2) current  $K$  ( $K = 0.36$ ) and low  $t_c$  ( $t_c = 1-2$  yr, or, less so, 3 yr), or 3) low  $K$  ( $K = 0.20$ ) and  $t_c = 1-4$  yr, or so. We have not made simulations for  $M$  in the range 0.05-0.20, so it is not clear where the danger zone actually begins. However, it would be difficult to confidently choose among such values of  $M$ , given the present state of knowledge on  $M$  (see below).

#### Evaluation of the Current Fishery and Current Status of Atlantic Croaker Stocks:

Simulations presented herein provide an informed basis for wise management of Atlantic croaker in the Chesapeake Bay region. For best usage, however, parameter combinations of the current fishery and stock must be known to choose appropriate figures, panels, curves, and points on the curves from among the alternatives in Figures 1-3. The key parameters of the Beverton-Holt model that must be known are  $M$ ,  $K$ , and  $t_c$ , because they determine the shape of the curve of  $Y/R$  on  $F$ . Other model parameters which we did not vary in simulations, such as  $W_{inf}$ ,  $t_r$ , and  $t_o$ , only scale the y-axis (eg, yields) and do not have to be known well to manage on a yield-per-recruit basis, because they

do not determine the shape of the curve.

We feel that point (0.36) and interval estimates (0.20-0.53) of current  $K$ , presented for the von Bertalanffy equation in Barbieri et al. (1994) are strong, because most Atlantic croaker growth occurs in the first year or two of life, and the data underlying the curve sharply "heel over" and evidence an asymptote. As a result, our data are appropriate for a von Bertalanffy fit. Moreover, the  $r^2$  value (0.99) was high (Barbieri et al. 1994), indicating a good fit to that model.

We feel, also, that point estimates of current  $t_c$  ( $t_c = 2$  yr) presented in Barbieri et al. (1994) are realistic, being based on age and size compositions of the commercial foodfish catch in the Chesapeake Bay region. If there is error, our estimate of current  $t_c$  may be too high (eg, too old), because the scrap catch in the Chesapeake Bay pound net, haul seine, and gill net fisheries includes young-of-the-year. In addition, we note: 1) size/age compositions of the recreational fishery are not known, though responses of yields to  $t_c$  in our simulations indicate this potential error would be serious only if  $t_c$  for the recreational fishery was lower than that for the commercial fisheries, and 2) the effects of fishing outside the Chesapeake region are not known if Chesapeake region Atlantic croaker are produced in part elsewhere, or mix with other stocks outside the Chesapeake region.

Though our estimates of  $K$  and  $t_c$  appear reasonable, we have less confidence in estimates of  $M$  presented in Barbieri (1993).



Those estimates are largely based on estimates of  $Z$  (0.55-0.58) from maximum age in the unexploited state given in Barbieri (1993) and Barbieri et al. (1994). We feel, with those authors, that those estimates of  $Z$  are realistic, because they agree with their estimates of  $Z$  (0.63) from a linear regression catch curve. Therefore, we feel that the convenient estimate of  $Z_{\text{CUR}}$  (0.60) we used to estimate  $F_{\text{CUR}}$  from  $M_{\text{POS}}$  is realistic. In agreement with Barbieri (1993), moreover, we feel that the most likely range of current  $M$  is about 0.20-0.40, though he suggested 0.25-0.40, and we feel that the best estimate is about 0.30. The latter value is very close to estimates of  $Z$  (Barbieri et al. 1994) derived using Hoenig's (1983;  $M = Z = 0.29$ ) and Royce's (1972;  $M = Z = 0.31$ ) methods, both of which are based on maximum age in the unexploited or lightly-fished state. Our estimate of maximum age in the unexploited state (15 yr), presented in Barbieri et al. (1994), was based on Hales and Reitz' (1992) study of ages in Indian middens from the period 1600-1700 AD at St. Augustine, FL. That is the only evidence of maximum age in the unexploited state based on otolith age determination, a method validated by Barbieri et al. (1994) for the Chesapeake Bay region. Barbieri (1993) also estimated  $M = 0.36$  using Pauly's (1980) method, a "quick and dirty" method. Though this  $M$  is similar to our other estimates, we have reservations about applying Pauly's method to the family Sciaenidae in the Chesapeake region, an area for which no other strong estimate of  $M$  exists for this family. Pauly's method largely relies on a purported, but significant, multiple

regression relationship between M and K, and with mean water temperatures in areas the fish inhabit. Some workers (Gulland 1969; 1983), however, report the M/K ratio varies between families of fishes, suggested ratios being 1:1 in clupeoids and 2 or 3:1 in gadiforms. If these simple ratios apply to Atlantic croaker in the Chesapeake region, M would be 0.36- 1.08, suggesting, with Pauly's method, that our estimate of  $M = 0.30$  might be low. That our estimate of  $M = 0.30$  might be low is also suggested by an inadvertent error in Barbieri's (1993) application of Pauly's method. Barbieri used for the temperature variable a value of 15.5 C, the annual mean in Chesapeake Bay. However, that value may be a good bit lower than values in areas adult Atlantic croaker actually inhabit. Age 1 and older fish abandon Chesapeake Bay for much of the period November-March, spending those cold winter months in the ocean towards Cape Hatteras, N.C., where minimum temperatures would be higher than those in Chesapeake Bay. Regardless of our reservations about Pauly's method, however, little solid data exists to estimate M in Atlantic croaker of the Chesapeake Bay region, and the value of  $M = 0.30$  should be accepted with that understanding.

Assuming  $M = 0.30$ , it appears that  $F_{CUR}$  is now below  $F_{MAX}$ , and that Atlantic croaker are currently not biologically overfished in the Chesapeake Bay region. Barbieri (1993) reached the same conclusion based on modeling in a narrow range of M ( $M = 0.25-0.40$ ), and without simulating uncertainty in K. Our simulations using a broad range of parameter levels to address uncertainty

force us into this conclusion, given current  $K = 0.36$  and current  $t_c = 2$  yr, which we argue above are reasonable estimates. With these parameter combinations, the current fishery is well within the zone described above for which there is little danger of biological overfishing. Indeed, if we accept  $M = 0.30$ , that conclusion must be reached regardless of the levels of  $K$  in the range of our interval estimates for  $K$  (0.20-0.53) and  $t_c$  in the range 1-5 yr. And, it must be reached as long as  $M$  equals or exceeds 0.20, given the same set of  $K$  and  $t_c$  levels. That there is little danger of biological overfishing even at  $t_c = 1$  yr is an important finding, because it alleviates concern (see above) that  $t_c$  may be lower than 2 yr given that: 1) young-of-the-year appear in scrap catches of the various Chesapeake Bay commercial fisheries, and 2)  $t_c$  for the recreational fishery is not known. The current fishery, therefore, is in a biological danger zone only if  $M$  is less than 0.20, a level consistent with a maximum age of 23 yr in the unexploited state, an age considerably higher than our estimate of 15 yr. We feel that levels of  $M = 0.05$ , which generally place the current fishery in a biological danger zone, are much too low for Atlantic croaker in the Chesapeake Bay region. Our reason for that feeling is that a level of  $M = 0.05$  is consistent with a maximum age of more than 90 yr in the unexploited state, an age that seems absurdly high for this small species. Although solid data on  $M$  does not exist, all lines of evidence suggest current  $M$  is most likely about 0.30, and quite possibly higher. A level of  $M$  higher than 0.30 would not be a

problem, however, because our simulations indicate the possibility of biological overfishing decreases as  $M$  increases.

Though the current fishery apparently does not exceed  $F_{Max}$  for Atlantic croaker in the Chesapeake Bay region, it is close to  $F_{.10}$  if  $M$  is about 0.30. The combination of  $F_{.10}$  values described in the present study and in Barbieri (1993) indicate the current fishery is at  $F_{.10}$  if  $M = 0.25$ , a conclusion Barbieri reached. The fishery exceeds  $F_{.10}$  if  $M = 0.20$  and lower, however, an  $M$  level that Barbieri did not include in his calculations. As a final finding on  $F_{.10}$ , the fishery does not exceed  $F_{.10}$  if  $M = 0.30$  and higher. Present data, though, do not permit confident choice among possible  $M$  levels in the range 0.20-0.30.

Our simulations indicate, that, compared to the virgin stock, the current fishery probably has now greatly reduced total standing stock biomass and strongly juvenesced Atlantic croaker stocks in the Chesapeake Bay region. This is a classical response of stocks to fishing (Ricker 1975). Assuming  $M = 0.20-0.40$ ,  $F_{CUR}$  must be 0.40-0.20, and total standing stock biomass has been reduced about 60-70% and 25% under these respective conditions. Similarly, strong juvenescence has occurred. At  $M = 0.20$  and  $F_{CUR} = 0.40$ , age 7 fish make up a negligible fraction of the total standing stock, though they would be abundant in a virgin stock where  $F = 0.00$ . And, at  $M = 0.40$  and  $F_{CUR} = 0.20$ , age 7 fish are reduced to less than half their level in the virgin stock. The reduction of stock biomass-at-age due to the juvenescence process is relatively greater at older ages, because

a given annual level of F is cumulative and has been exerted more times on older ages.

Evaluation of Growth and Reproduction Dynamics, Their Implications for Wise Management, and Management Strategies:

Our simulations indicate Atlantic croaker in the Chesapeake Bay region have great biological capacity to resist overfishing. This great capacity reflects the asymptotic, or rising, nature we have shown for curves of Y/R on F over a broad range of parameter levels. Although this species has great capacity to resist biological overfishing, Chittenden (1977) pointed out that two kinds of biological overfishing can be distinguished, following Cushing (1976): 1) growth overfishing in which fish are harvested at too small a size and maximum cohort biomass is not permitted to develop, and 2) recruitment overfishing in which parent stocks are so reduced that progeny stocks, and sustainable yields, also decline. Yield-per-recruit models employed herein assume no parent-progeny relationship exists over the range of stock sizes fished. Therefore, our simulations indicate primarily a great capacity to resist growth overfishing. This great capacity rests on the basic growth dynamics of this species described in Barbieri et al. (1994). Atlantic croaker grow rapidly in their first two years of life, so rapidly that 64 and 84% of their total growth is completed by the end of ages 1 and 2, respectively. Comparatively little growth remains after age

2, and mean sizes-at-age increase slowly thereafter. There is, moreover, great variability in size among individual fish, so a 250 mm total length fish could be any age from 2-8 yr. This growth pattern is supplemented by their age structure pattern. Relatively many age groups occur in Atlantic croaker stocks (up to 8, or so, given that maximum age is 8 yr), and they have a relatively long life span. Because biomass is spread out over relatively many years, such an age structure helps dampen effects on total standing stock biomass due to fluctuations in year class strength.

The patterns of growth dynamics described above for Atlantic croaker in the Chesapeake Bay region have important implications for management, ones beyond the great capacity to resist growth overfishing. They imply, as our simulations show, that, though reduction in  $F$  (via, for examples, bag and other catch limits) and increase in  $t_c$  (via, for example, minimum size limits) would reverse the juvenescence process and increase the number of older fish by reducing the cumulative total mortality they experience at age, this would not necessarily translate into many larger fish or trophy fish. The reason for that is that Atlantic croaker grow little when past age 2, vary greatly in size, and are much the same size at ages 2-8. Though our simulations show that management restrictions would result in greater numbers, thus greater catch-per-unit-effort, more older fish, and increased stock biomass-at-age, management would not be as successful in producing larger fish, or trophy fish.

Of the two classical management strategies to reduce juvenescence and/or growth overfishing (Gulland 1974) -- reduction in  $F$  and increase in  $t_c$  -- in principle at least, the more successful one in the long run is reduction in  $F$ . The reason for that is that it "puts a cork" on the fundamental problem of heavy fishing -- too much effort. Increase in  $t_c$  is less successful over the long run for the paradoxical reason that it may be successful in the short term. The reversed juvenescence and increased standing stocks that increase in  $t_c$  may bring about are, unfortunately, often short-lived, because they tend to then attract more effort and, thereby, depress the stock back towards it's previous state. The problem is that increase in  $t_c$  does not "put a cork" on the amount of effort. Reduction in  $F$ , therefore, is, in principle, the most fundamentally successful tool for management. It's effects are often successfully supplemented with increase in  $t_c$ .

Whether or not Atlantic croaker in the Chesapeake Bay region now need active management depends on their current status, and anthropomorphic reaction to it. From our simulations, it appears that this species is not now growth overfished and has great capacity to resist that, though total standing stocks have been considerably reduced in comparison to the virgin stock and though there has been considerable juvenescence. Stocks, moreover, now appear to be fished near some economic "optimum" given that effort now approximates levels of eumetric fishing and  $F_{.10}$ . And, the growth pattern of this species -- they reach a roughly

asymptotic size by the end of their first or second year -- implies that management would have little success in producing larger, or trophy, fish, even though they would reach older age. If managers decide that a modicum of protection is desirable to help protect against growth overfishing, a minimum size limit might be considered. Our simulations for M levels of 0.20 and greater, the most likely minimum range, indicate that maximum yields, and eumetric fishing, would be achieved with a minimum  $t_c$  of 1-2 yr. That translates into a minimum size of 200-260 mm total length, using the von Bertalanffy growth model in Barbieri et al. (1994).

A modicum of protection against growth overfishing might also be provided in management for other species. The Chesapeake Bay pound-net, gill-net, and haul seine fisheries are multiple species fisheries which also catch weakfish, bluefish and many other fishes. Initial evidence from our studies on weakfish, described in Lowerre-Barbieri (1994), suggest weakfish, unlike Atlantic croaker, have long life spans, continue to grow rapidly for some eight years, and, as a result, would be more sensitive to growth overfishing than Atlantic croaker. Weakfish management, therefore, may eventually provide protection beyond what a 200-260 mm minimum size limit on Atlantic croaker might do.

Besides their great capacity to resist growth overfishing, Atlantic croaker in the Chesapeake Bay region also seem to have great capacity to resist recruitment overfishing. This latter



capacity rests on the remarkable reproduction dynamics of this species described in Barbieri et al. (in press). Atlantic croaker are asynchronous multiple spawners with indeterminate fecundity, a pattern that implies they can adjust their egg production and rapidly adapt -- within each spawning season -- to favorable or unfavorable conditions. Through this pattern, adjustment of egg production can be mediated in two dynamic ways: 1) through adjustment in time and space for batch fecundity, basically the number of eggs spawned in a given short (eg, daily, weekly etc) spawning session, and 2) through adjustment in time and space of spawning frequency, basically the number of short spawning sessions in an overall spawning season. This species, moreover, largely (85%) matures to first spawn at twelve months of age (age 1), an attribute that maximizes their reproductive life span, and lifetime fecundity, given any maximum age parameter value. Indeed, they have a relatively long reproductive life span, as much as 7-8 yr, or so, given the maximum age of eight years that Barbieri et al. (1994) reported. Atlantic croaker apparently also have high fecundity, though we have not yet been able to estimate it. Hansen (1969) reported high fecundity in fish from Florida waters. His estimate, however, was made before the multiple spawning pattern became widely known and appreciated in fishes, an unfortunate circumstance, because such early estimates have often proven too low. In addition, this species spawns over a broad period (July-December), and a broad range of habitat conditions, eg -- from

estuarine to coastal waters. That pattern would increase chances that adults encounter favorable conditions for egg production and spawning, and that early life stages encounter favorable transport and other conditions important to their survival. Finally, Atlantic croaker in the Chesapeake Bay region have a spawning stock made up of at least eight age groups, another important character. As Ricker (1954) showed, multiple age groups in the spawning stock provide buffering against population fluctuations.

The above patterns of reproduction dynamics in Atlantic croaker of the Chesapeake Bay region have important implications for management. Many of the implications occur in concert with those for growth dynamics discussed above, and management for growth dynamics would generally benefit reproduction dynamics. As noted above, reduction of  $F$  (via, for examples, bag and other catch limits) and increase in  $t_c$  (via, for example, minimum size limits) would tend to reverse the juvenescence process and improve the capacity of both growth and reproduction dynamics to resist growth and recruitment overfishing, respectively. By reducing the cumulative total mortality they experience at age, reduction of  $F$  and increase in  $t_c$ , through their effects on growth dynamics, would increase the total number of fish, number of older fish (if not larger ones), and the number of spawning age groups. That response has important implications for reproduction dynamics. Both population fecundity and individual fecundity would be increased, in principle, because population

fecundity tends to increase with number of fish, and individual fecundity tends to increase with size (which changes only a little in adult Atlantic croaker) and age. Reduction of the cumulative total mortality would also increase individual lifetime fecundity, in principle, because ages in the spawning stock would increase and so would, in principle, the reproductive life span. Similarly, reduction in the cumulative total mortality would, in principle, increase the number of spawning age groups and help buffer against population fluctuations. The existence of the multiple spawning pattern with indeterminate fecundity also has important implications for management, because it implies a stronger degree of density dependence in Atlantic croaker than in fishes that are total spawners with determinate fecundity. In principle, high stock size might tend to create relatively unfavorable density conditions in this species and depress expression of the multiple spawning pattern and, thereby, individual fecundity. In contrast, low stock size might tend to create favorable density conditions and encourage expression of the multiple spawning pattern and, thereby, individual fecundity. The current young age at maturity they show, moreover, may reflect a density dependent response to population size change, because age at maturity in animals often tends to become younger in response to low stock size. Such density dependent responses probably play an important role in the great capacity of this species to resist recruitment overfishing.

All in all, it appears that Atlantic croaker in the Chesapeake Bay region have evolved a remarkable life history strategy that gives them great capacity to rapidly respond to favorable opportunities and resist both growth and recruitment overfishing. This species is among the most abundant species of inshore and/or estuarine waters throughout its range in warm temperate waters of the Carolinian Province, eg -- from about Cape Hatteras, N.C. south to Florida, and across the northern Gulf of Mexico. It is also one of the most abundant species in the Chesapeake region, though that region is really on the northern fringe of their range. This successful performance probably reflects their remarkable life history strategy. It is difficult to see what more this species could readily do to improve it's capacity to resist recruitment overfishing: they now mature at very early age and, presumably, cannot mature much earlier and still retain their synchrony with intra-year environmental cues, they spawn over a broad range of conditions in time and space, they apparently have high fecundity, they have a remarkably flexible, adaptive multiple spawning pattern and indeterminate fecundity which makes adjustments possible in both batch fecundity and spawning frequency, their young age at maturity gives them a relatively long reproductive life span, and they have many ages in the spawning stock. Similarly, it is also difficult for them to do more to resist growth overfishing: they now grow rapidly and reach a roughly asymptotic size by the end

of their first or second year, yet they have a relatively low mortality rate and relatively long life span. The latter attribute tends to dampen effects on stock biomass due to fluctuations in year class strength. All in all, it is difficult to escape the conclusion that, biologically, Atlantic croaker have done their part to help management avoid both growth and recruitment overfishing.

#### Evaluation of Fluctuations in Abundance:

Atlantic croaker have historically shown great fluctuations in the Chesapeake Bay region. Our simulations indicate these fluctuations do not reflect growth overfishing, because there is little or no decrease in yields over a broad range of parameter conditions, even at high  $F$ . This occurs because curves of  $Y/R$  on  $F$  are generally asymptotic or rising over a broad set of parameter levels. Even when very low  $M$  (0.05), low  $K$  (0.20), and low  $t_c$  (1 yr) co-occur, the most sensitive set of parameters modeled, yields decrease only some 35% in one year at  $F$  levels much higher than  $F_{MAX}$ . Such apparent stability of growth/mortality dynamics suggests that fluctuations of Atlantic croaker in the Chesapeake Bay region reflect recruitment -- unless  $M$ ,  $K$ , and  $t_c$  levels fluctuate greatly, something not easily detectable in our short three-year period to collect biological data. Because this species has great capacity to resist both growth and recruitment overfishing, it seems quite

probable that natural causes and/or anthropogenic causes not due to fishing largely determine their population fluctuations. Convincing evidence exists, for example, indicating that low winter water temperatures in Chesapeake nurseries may result in large mortality of the new young-of-the-year and larvae, seemingly catastrophic mortality at times (Massmann and Pacheco 1960). And that mortality follows, or co-occurs with, all the other normal perils in the early life history stages. In addition, long-term fluctuations related to climatic warming and cooling trends have been suggested (Joseph 1972), an apparent cause and effect relationship not readily affected by management. Finally, besides nagging concerns about habitat loss, some warning signals exist that anthropogenic toxicological (?) environmental stressors might affect Atlantic croaker stocks in the Chesapeake Bay region. Barbieri (1993) and Barbieri et al. (in press) reported a high incidence of atretic advanced yolked oocytes in spawning females (60-100% in spawning phase females; 95-100% in running ripe females. They suggested that a surplus production of yolked oocytes may be part of the reproductive strategy, females hydrating and spawning more or less of these yolked oocytes depending on environmental conditions. However, the high incidence of atresia may also be a warning signal of some anthropogenic environmental stressor, because it, seemingly at first glance, may not make biological sense that such a large percentage of the females develop and resorb their yolked eggs. We take no position that some anthropogenic environmental

stressor actually affects Atlantic croaker, only the position that prudent stewardship of the environment suggests that toxicology (?) studies may be desirable to evaluate that possibility.

#### Eggs-per-Recruit Model Simulations:

To this point in this Section we have not mentioned the eggs-per-recruit studies we had intended. Unfortunately, these have not yet proven feasible. Despite collecting and examining many thousands of fish, we have not been able to collect sufficient fish to usefully estimate batch fecundity, much less total annual fecundity. Though unforeseen from the literature on this species, as noted above, it has proven to be a multiple spawner with indeterminate fecundity, a pattern which makes much more difficult the estimation of fecundity. As a result, we could not perform eggs-per-recruit modeling. However, we were able to use yield-per-recruit modeling, as described above, to evaluate whether population fluctuations were due to growth overfishing or recruitment problems. In addition, we were able to use life history/population dynamics information, as described above, to evaluate the capacity of this species to avoid recruitment overfishing.

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## SECTION IV.

### ACCOMPLISHMENTS ON ATLANTIC CROAKER

This section summarizes important accomplishments of our studies to date in terms of journal papers, theses, presentations at national/international professional society meetings, and the major presentations we have made to state, regional, and national management agencies as our initial final results began to become clear in the period 1993-1994. Presentations to management agencies have been in the form of 1-2 hour verbal presentations describing our initial overall results integrating: 1) studies to develop validated methods of age determination, 2) studies of age, growth, mortality, and reproductive biology from which model parameters were estimated, and 3) results of yield-per recruit model simulations to evaluate the effects of fishing on Atlantic croaker of the Chesapeake Bay region. We have also communicated interim results, not described below, to the U.S. Fish and Wildlife Service and the Virginia Marine Resources Commission in the form of annual performance summaries.

These studies were conducted, and accomplishments made, with support to the Principal Investigators, Mark E. Chittenden, Jr. and Cynthia M. Jones, from the Wallop/Breaux program of the U.S. Fish and Wildlife Service, from the Virginia Marine Resources Commission, from the College of William and Mary, Virginia Institute of Marine Science, and from the Old Dominion University, Applied Marine Research Laboratory.

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#### MAJOR MANAGEMENT AGENCY PRESENTATIONS:

Chittenden, M.E., Jr. and C.M. Jones. Development of age determination methods, studies of age, growth, mortality, and reproductive biology, and initial yield-per-recruit model simulations of the effects of fishing on Atlantic croaker in the Chesapeake Bay region. Presented to:

- 1) Virginia Marine Resources Commission, March 1993,
- 2) U.S. Fish and Wildlife Service, June 1993,
- 3) Atlantic States Marine Fisheries Commission,  
December 1993
- 4) Virginia Marine Resources Commission, June, 1994.