WILLIAM & MARY
CHARTERED 1693

W&M ScholarWorks

Dissertations, Theses, and Masters Projects   Theses, Dissertations, & Master Projects

1993

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

Luiz R. Barbieri
College of William and Mary - Virginia Institute of Marine Science

Follow this and additional works at: https://scholarworks.wm.edu/etd

Part of the Ecology and Evolutionary Biology Commons, Fresh Water Studies Commons, Marine Biology Commons, Oceanography Commons, and the Zoology Commons

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

U·M·I

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

Barbieri, Luiz Roberto, Ph.D.

The College of William and Mary, 1993

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

of Atlantic croaker, *Micropogonias undulatus*,

in the Chesapeake Bay area

———————————

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

———————————
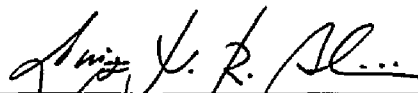
By

Luiz R. Barbieri
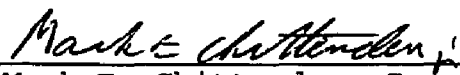
1993
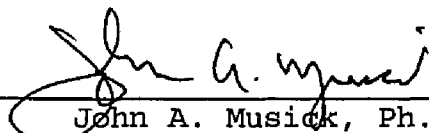
This dissertation is submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

_____
Luiz R. Barbieri

Approved, August 1993

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

_____
John A. Musick, Ph.D.

_____
Joseph M. Loesch, Ph.D.

_____
Evon P. Ruzecki, Ph.D.

_____
Cynthia M. Jones, Ph.D.
Applied Marine Research Laboratory
Old Dominion University
Norfolk, VA

ii

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

LIST OF TABLES

LIST OF FIGURES

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 re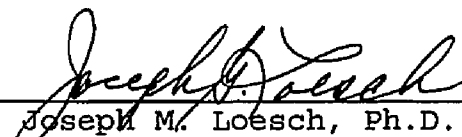corded, but eight-year-old fish were rare. Marginal increment analysis showed that for ages 1-7 annuli are formed once a year during the period April-May. Otolith age readings were very precise, with percent agreement within and between readers greater than 99%. Observed lengths-at-age were highly variable 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, <u>Micropogonias</u> <u>undulatus</u>
(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,

2

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

9

(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 350-500μm 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 (12-24x 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 12-50x 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, 300-500μm 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 12-24x
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

13

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.

Pr

SG

Ve.

a

b

c

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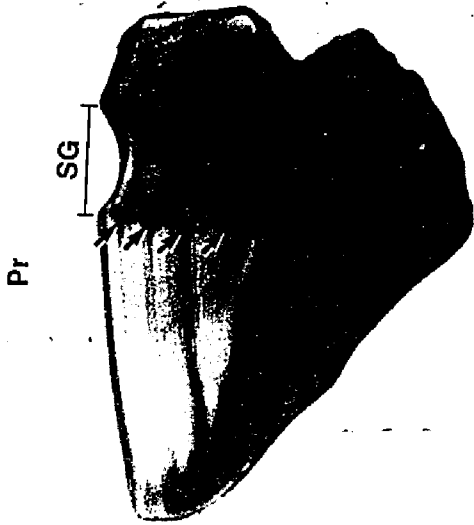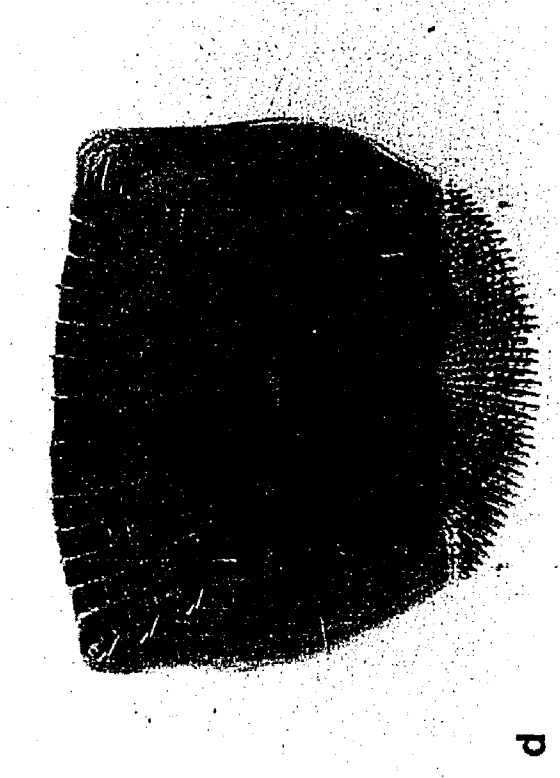
annual marks on dorsal spines and pectoral rays appeared as wide opaque semicircular bands alternating with narrow translucent bands.

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.

Legend:
- Otoliths
- Scales
- Dorsal spines
- Pectoral rays

Percent

100

50

0

0   1   2   3

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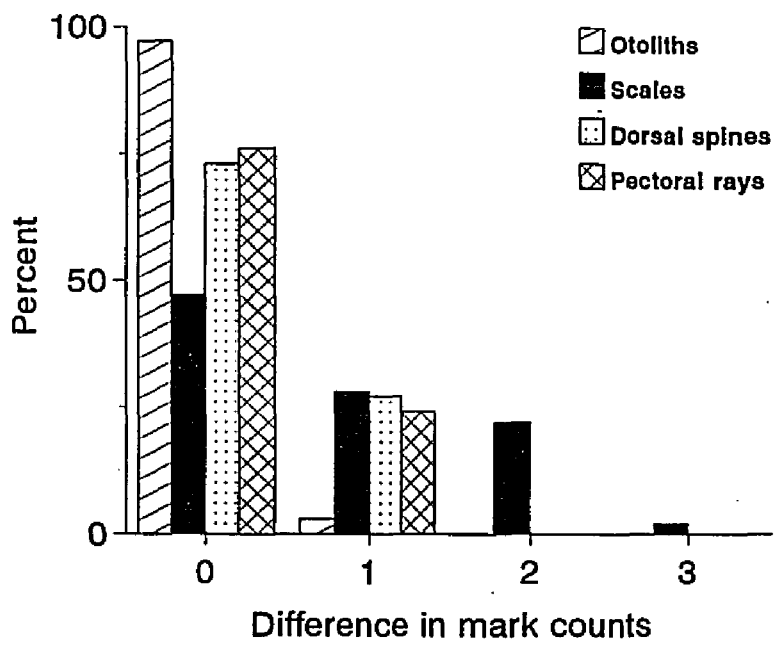
Table 1. Percent agreement between mark counts from hard
parts of Atlantic croaker from Chesapeake Bay.

	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.
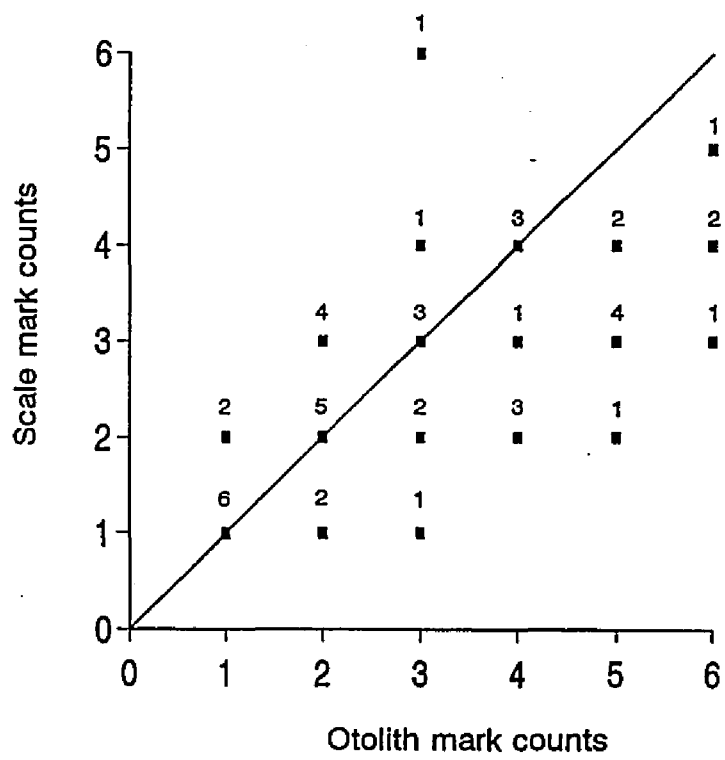
Agreement in mark counts between hard parts was usually low (Table 1). Agreement was 37.8% between scales and otoliths, 17.7% between dorsal spines and pectoral rays, and ranged from 20.0 to 26.7% comparing dorsal spines and pectoral rays to scales and otoliths. Although mark counts from scales and otoliths 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.

24

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 μm 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_∞, 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

30

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.

Proximal

SG

Ventral

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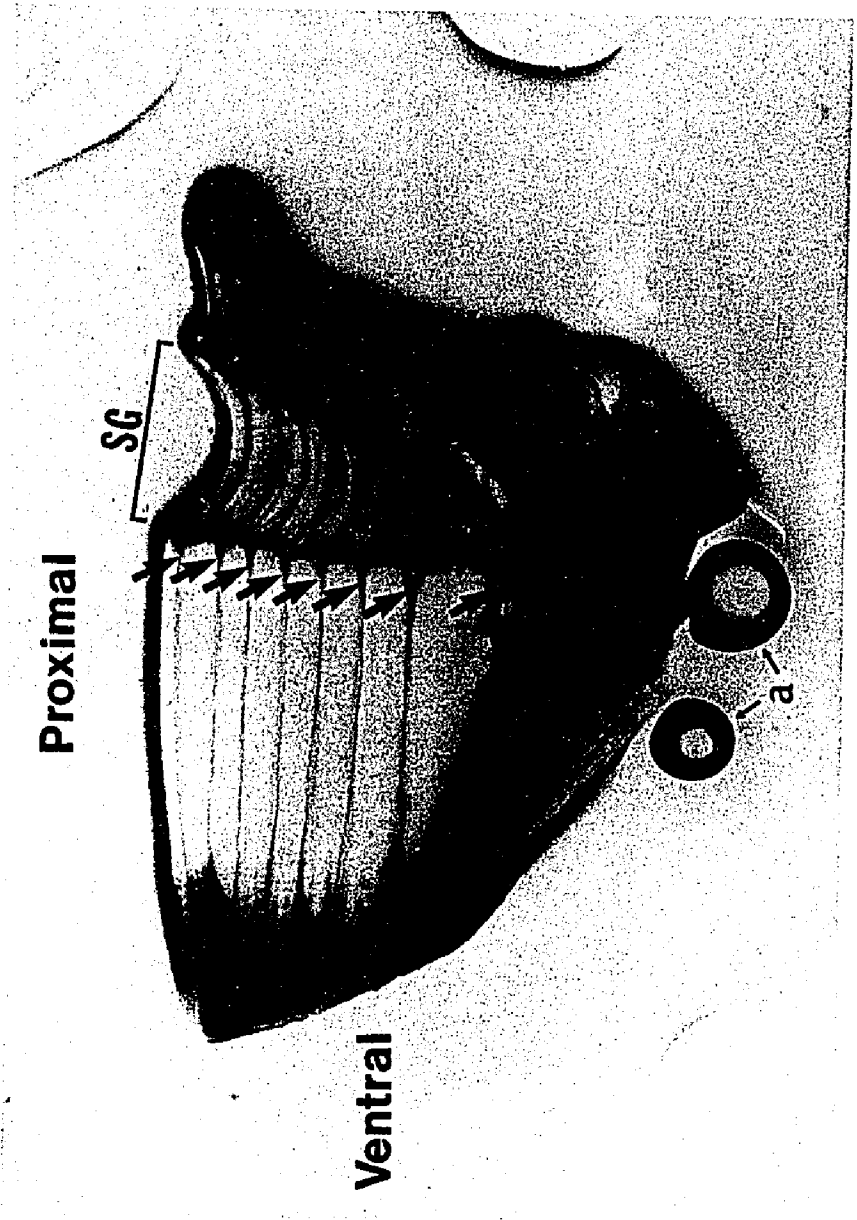
Fig. 5. Mean monthly marginal increment for Atlantic
croaker ages 1-8 from the Chesapeake Bay region,
1988-1991. Vertical bars are ±1 standard error.
Numbers above the bars are sample sizes.

Marginal increment (mm)
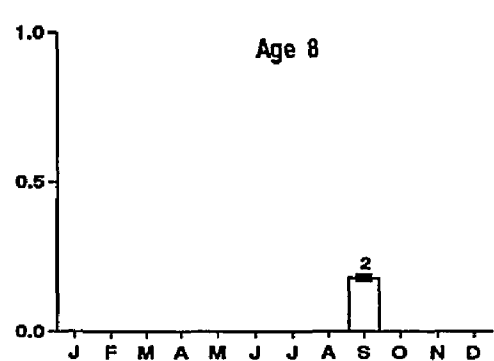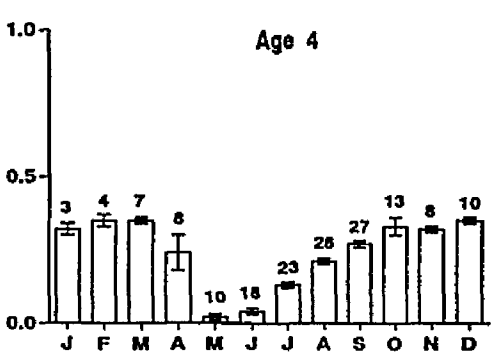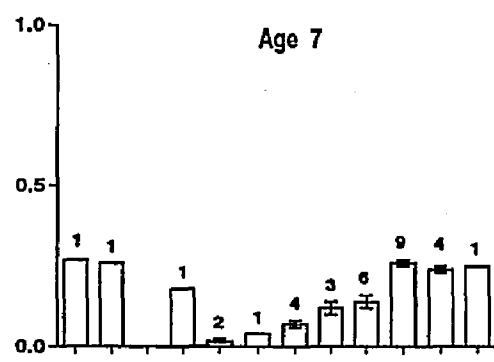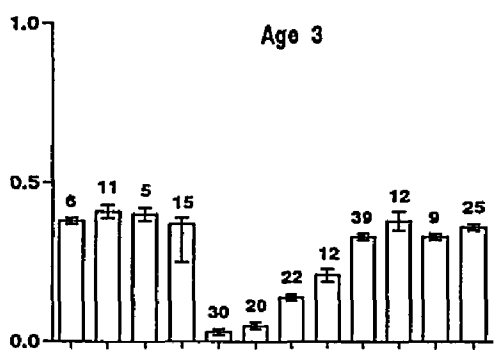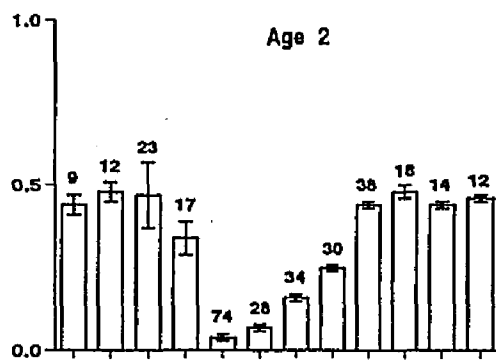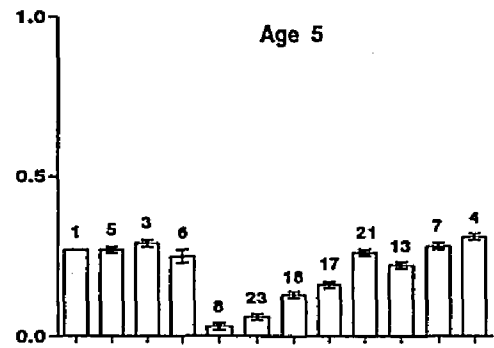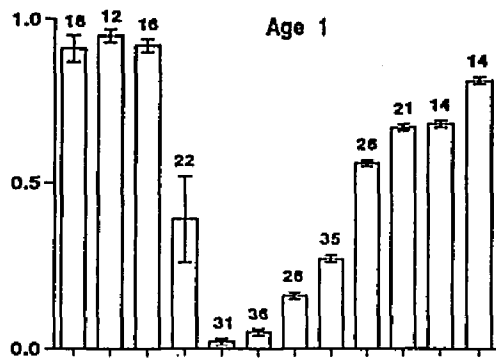
Months

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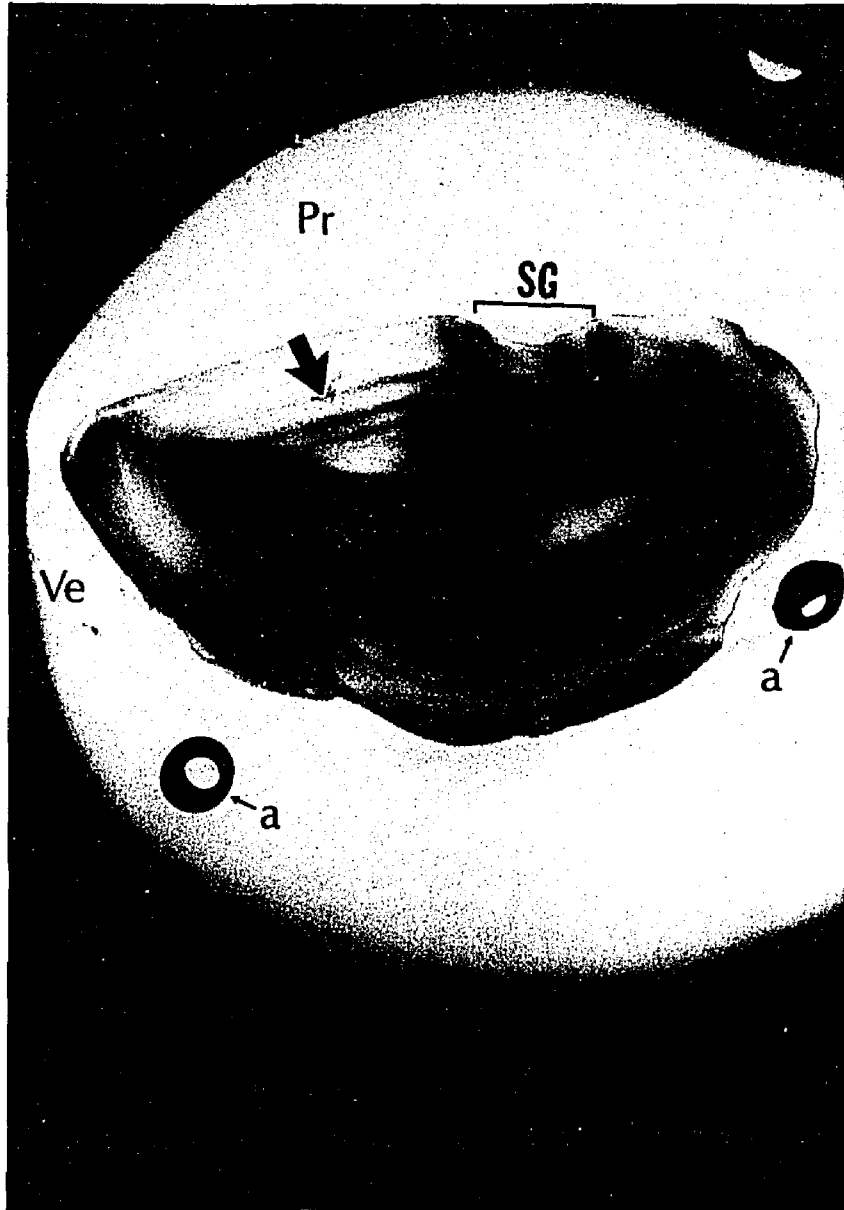
important. All disagreements, independent of age, were due
to problems in identifying the first annulus.

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≥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.

a
$r^2 = 0.43$
Radius (mm)

b
$r^2 = 0.65$
Maximum thickness (mm)

c
$r^2 = 0.80$
Maximum length (mm)

d
$r^2 = 0.77$
Weight (g)
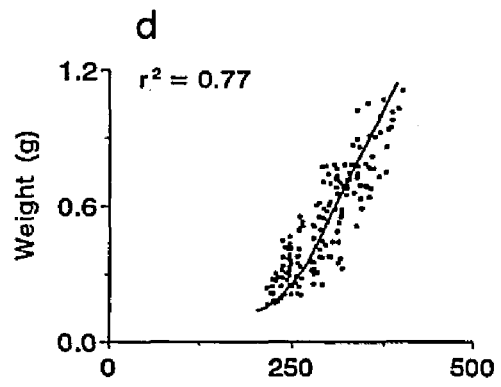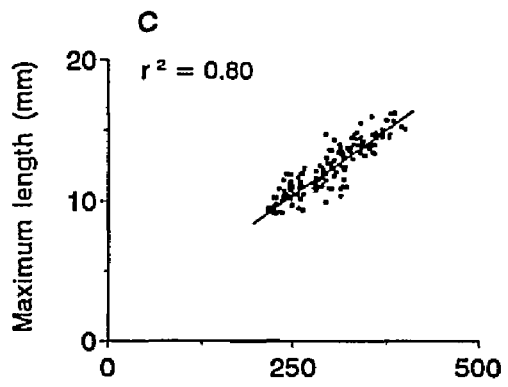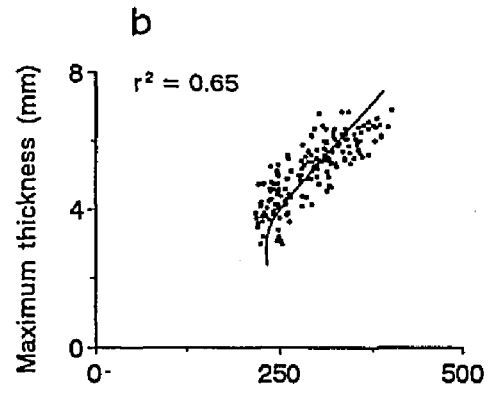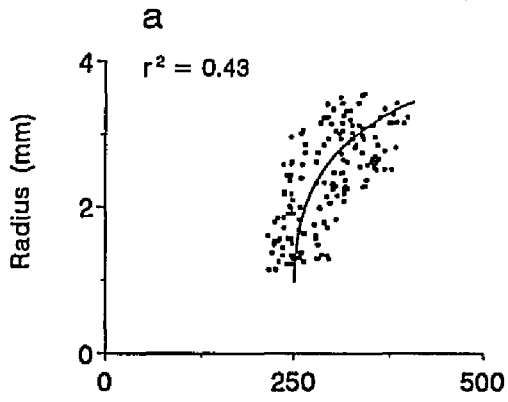
Total length (mm)

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. α=0.05.

Otolith relation	Source of variation	r^2	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.
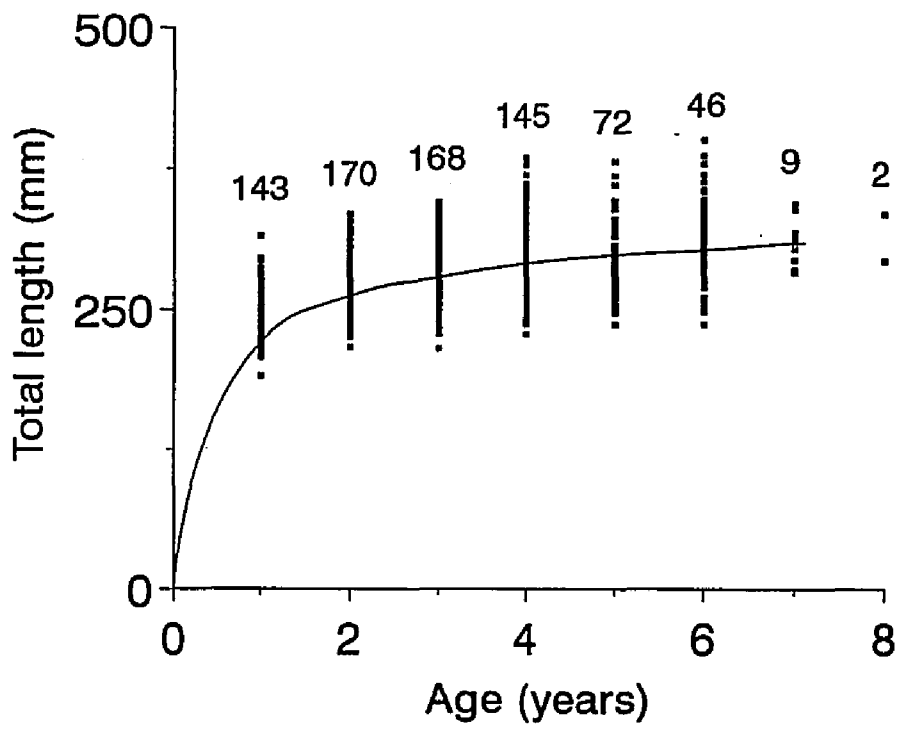
Table 3. Mean observed total lengths-at-age (mm) for male
and female Atlantic croaker caught in September,
1988-1990, in the Chesapeake Bay region.
SD=standard deviation; n=sample size.

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_∞	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 TL $\quad$ (r^2=0.91; n=1,537; P<0.01)

TL = 58.37 + 1.21 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:

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

TL = 14.69 + 1.15 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 ≤356 mm, 99% were ≤345 mm, and 90% were ≤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.
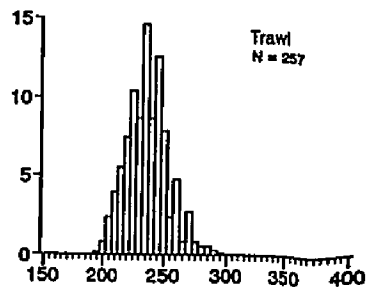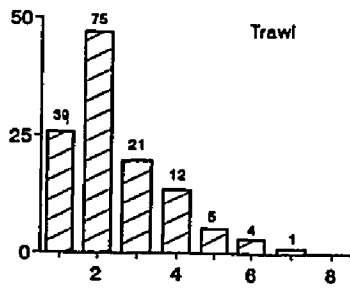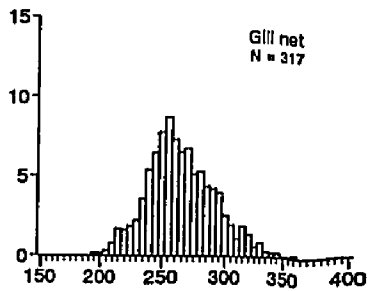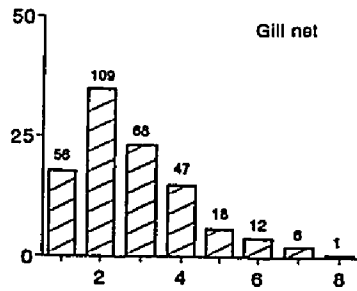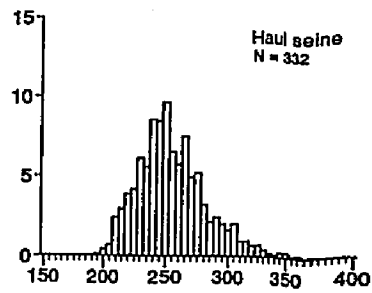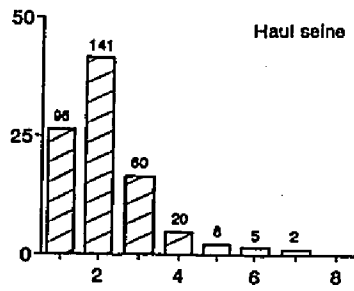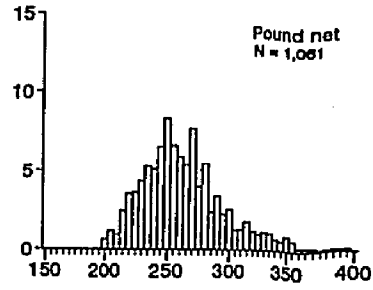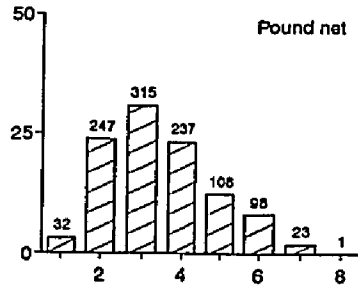
Atlantic croaker in the Chesapeake Bay area have a maximum longevity of approximately 8 years. Despite the large sample size and the variety of gears used only two eight-year-old fish were collected, one from a pound-net in September 1988 (334 mm) and one from a gill-net in September 1990 (293 mm).

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.

$$\text{Log}_e \text{ No.} = 6.86 - 0.63 \text{ Age}$$

$$N = 1{,}027; \quad r^2 = 0.93; \quad (P < 0.05)$$
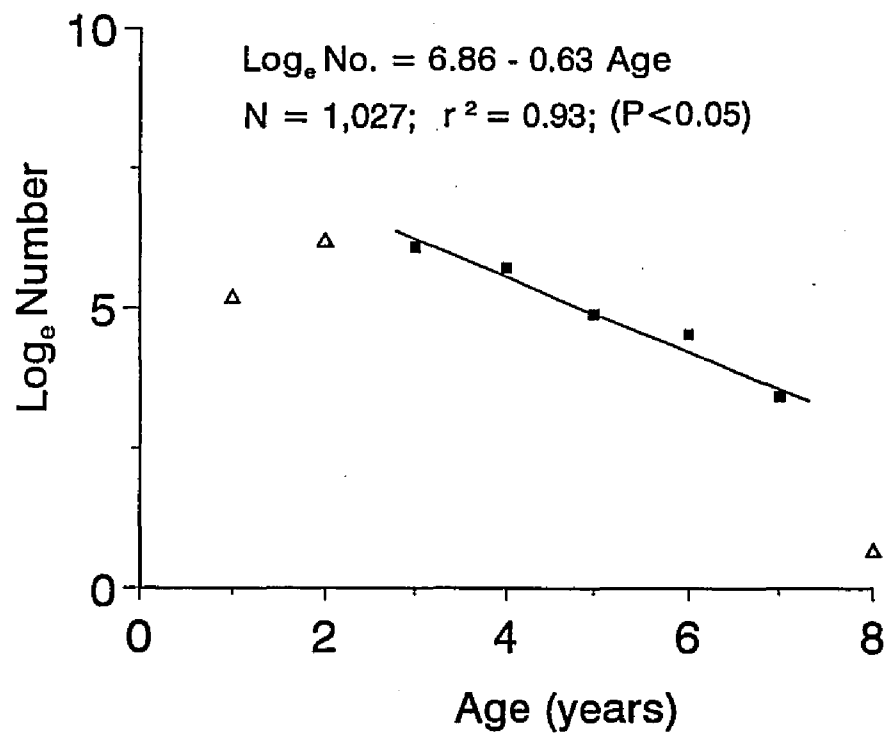
DISCUSSION

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

47

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_∞ (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_∞ 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

56

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.
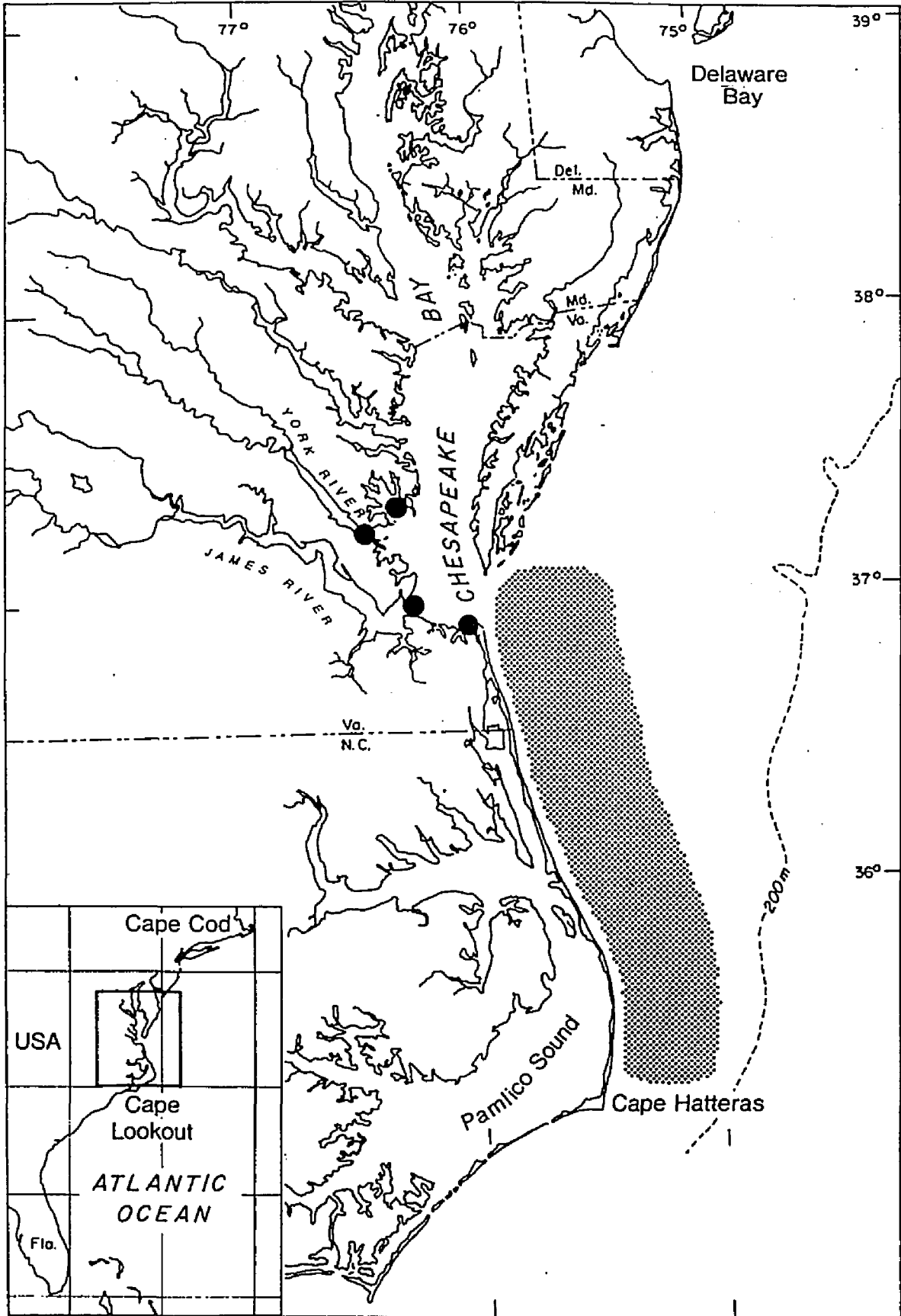
condition, and as an attempt to collect hydrated or recently-spawned females for estimates of batch fecundity and spawning frequency. Finally, collections from the commercial fisheries were supplemented by fish obtained from the Virginia Institute of Marine Science (VIMS) juvenile bottom trawl survey. 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 (12-50x). 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 5-6μm 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 (α) 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 ≥ 0.1 mm were measured to the nearest 0.02 mm (one micrometer unit at 50x) 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 (≤ 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 (≤ 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.
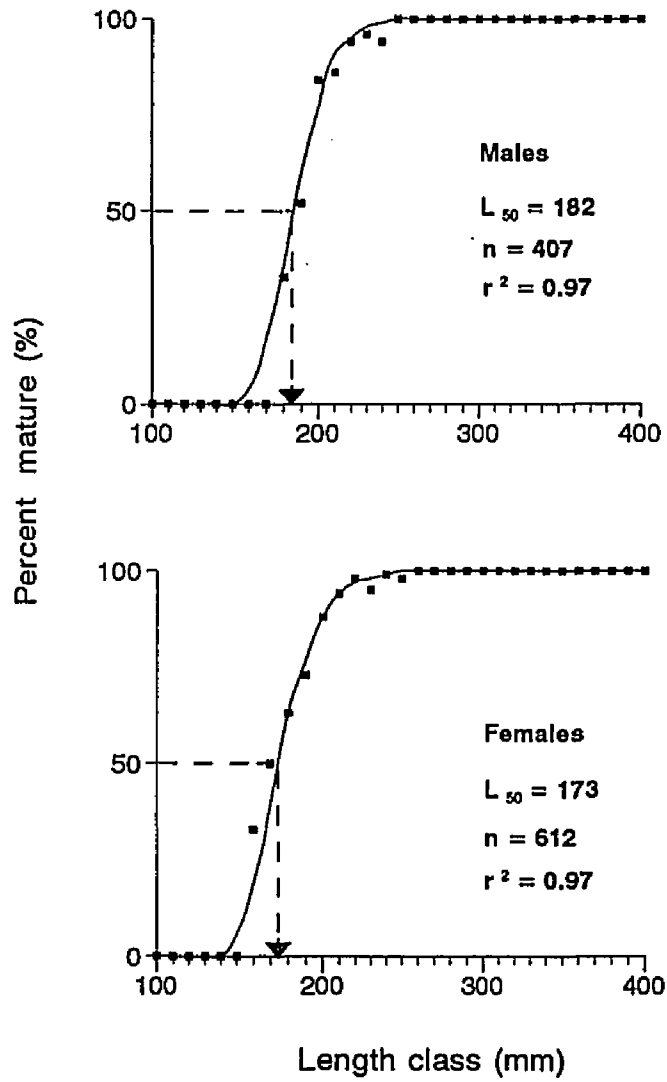
Fig. 13. Percentage of gonad maturity stages by month for mature female Atlantic croaker in the Chesapeake Bay region. Black bars = 1990 data; open bars = 1991 data. Gonad stages are: (2) developing; (3) fully-developed; (4) gravid; (5) running-ripe; (6) regressing; and (7) resting. Monthly sample sizes are in Table 6.

Frequency (%)

Gonad stage
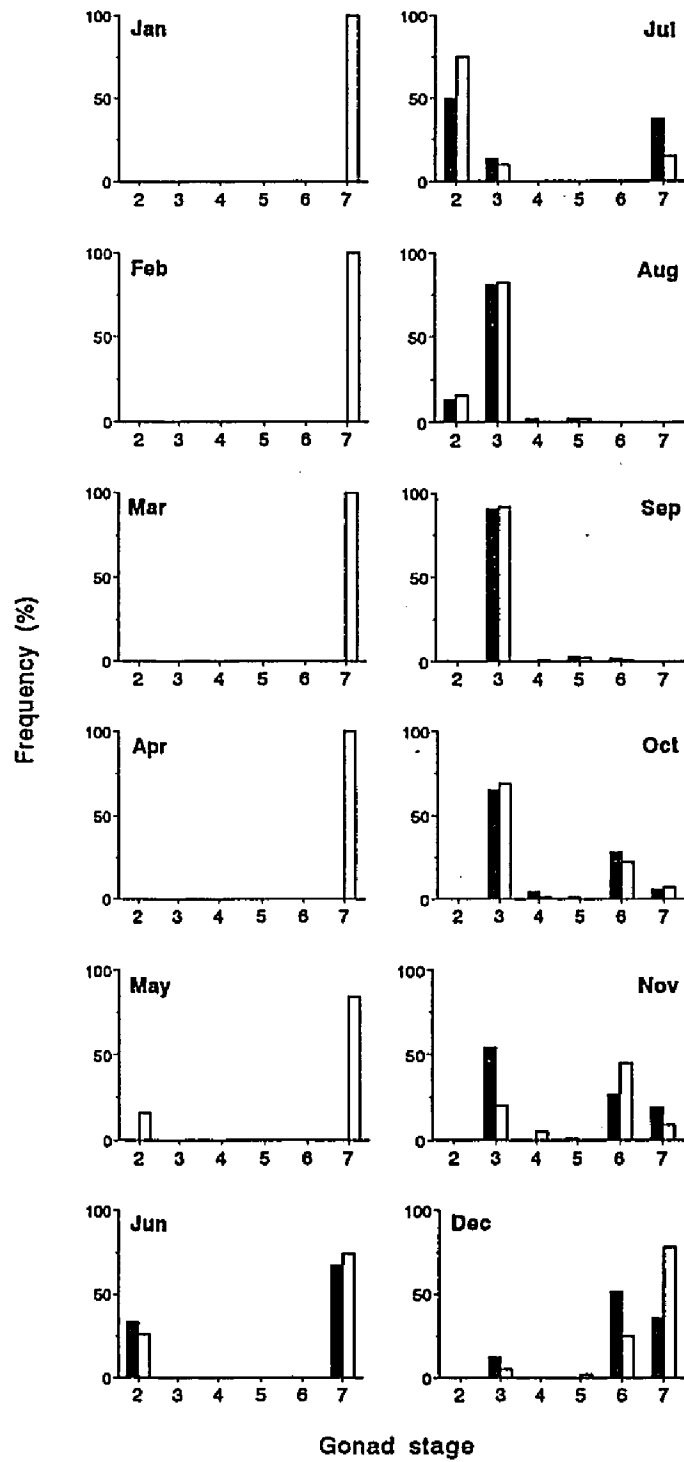
females from May through August, and regressing females from September through December indicates that gonad maturation was not synchronous among individuals. Although, at the population level, spawning occurred over a six-month period (July-December), individual fish apparently spawned for only two 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.

Males
(n = 896)

Females
(n = 2,195)

No samples

No samples

Gonadosomatic index (%)

J M M J S N J M M J S N

├─── 1990 ───┤ ├─── 1991 ───┤
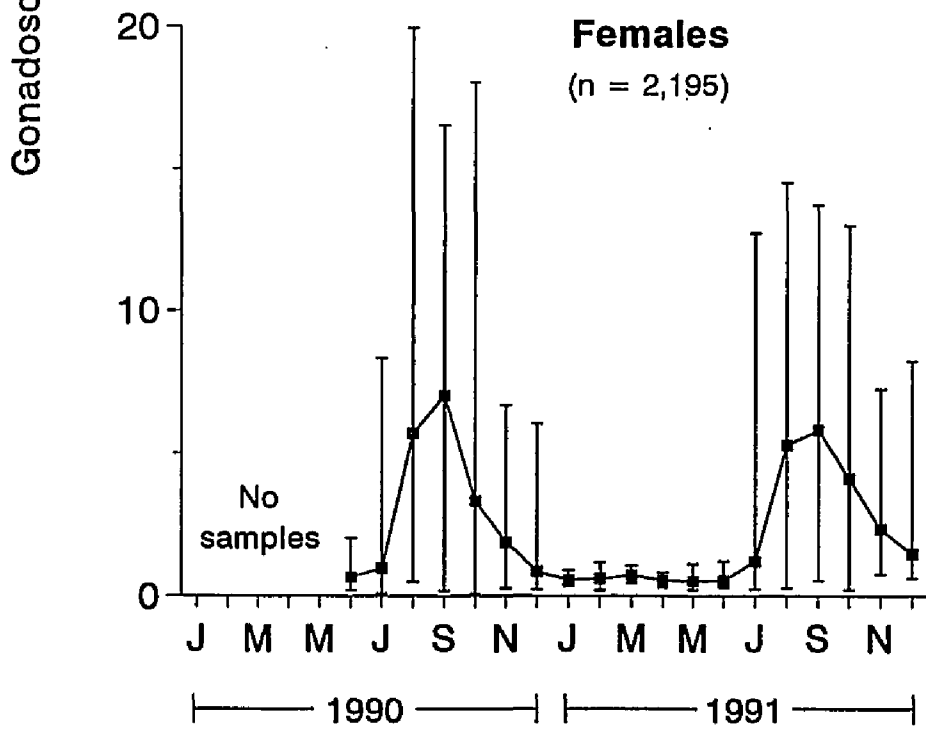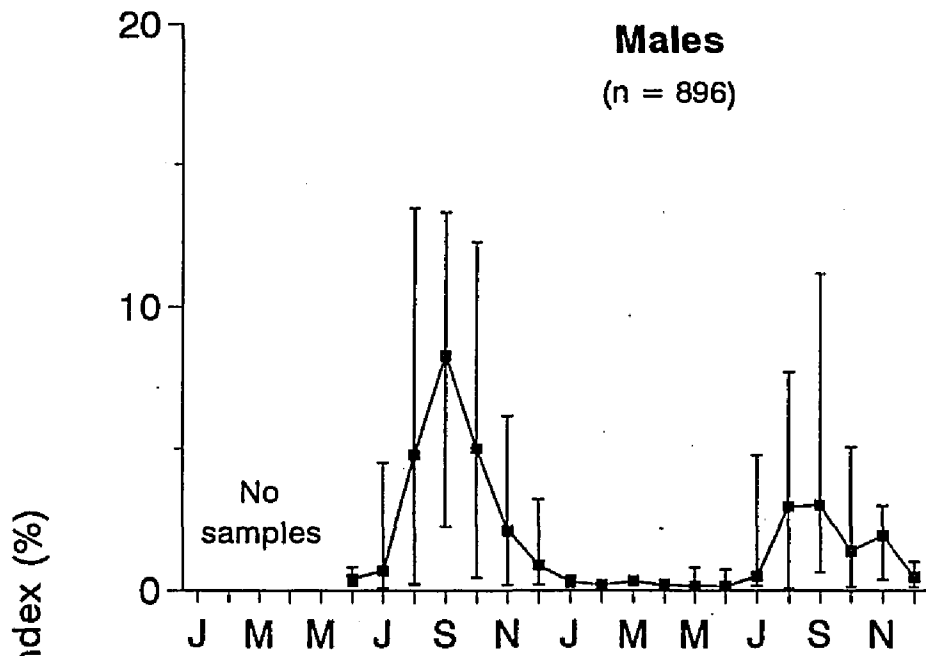
estuary. However, the occurrence during the fall of some regressing and resting females in Chesapeake Bay (Fig. 13) indicates that at least some individuals complete their spawning in estuarine waters.

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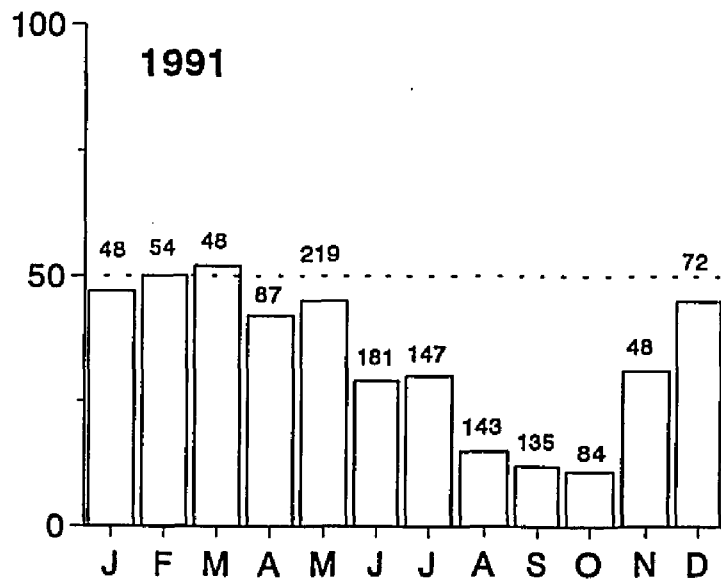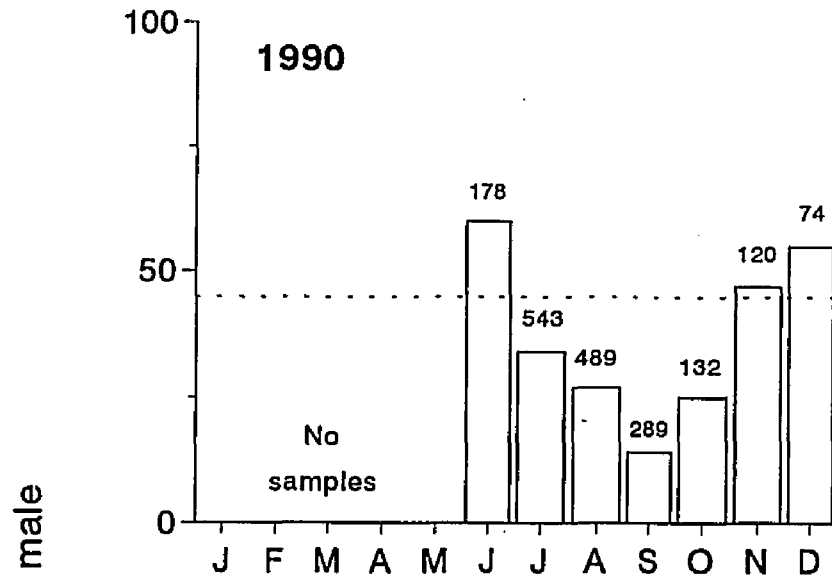
Table 6. Number of males and females by month and Chi-square
tests for the monthly sex ratios of Atlantic
croaker, Micropogonias undulatus, in the Chesapeake
Bay region, 1990-1991. ** = P<0.01.

Year	Month	Number of males	females	Chi-square
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.

July
GSI = 12.7 %
n = 512

October
GSI = 9.68 %
n = 445

August
GSI = 12.5 %
n = 616

November
GSI = 6.8 %
n = 448

September
GSI = 7.06 %
n = 491

December
GSI = 5.9 %
n = 533

Frequency (%)

Oocyte diameter (mm)
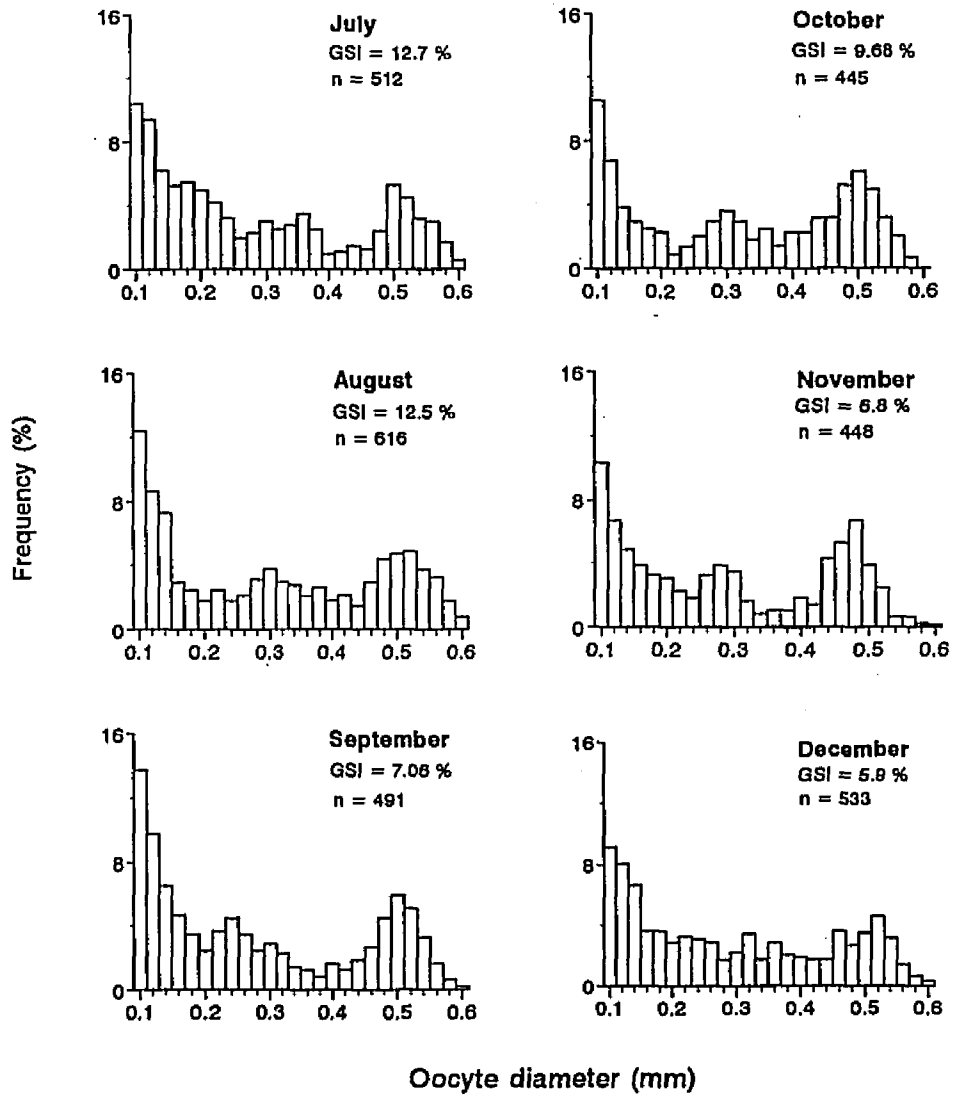
oocytes and represents the group from which individual spawning batches will be formed.

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 α 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 α 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 (β-, γ-, and δ-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 α atresia of advanced yolked oocytes in Atlantic croaker are characterized by the disintegration of the nucleus, which looses 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 α 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, α-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 α 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 α atresia; (c) oocyte in

intermediate stage of α atresia; (d) oocytes in

late stage of α atresia. N=nucleus; Zr=zona

radiata; Pc=peripheral cytoplasm; La=late stage of

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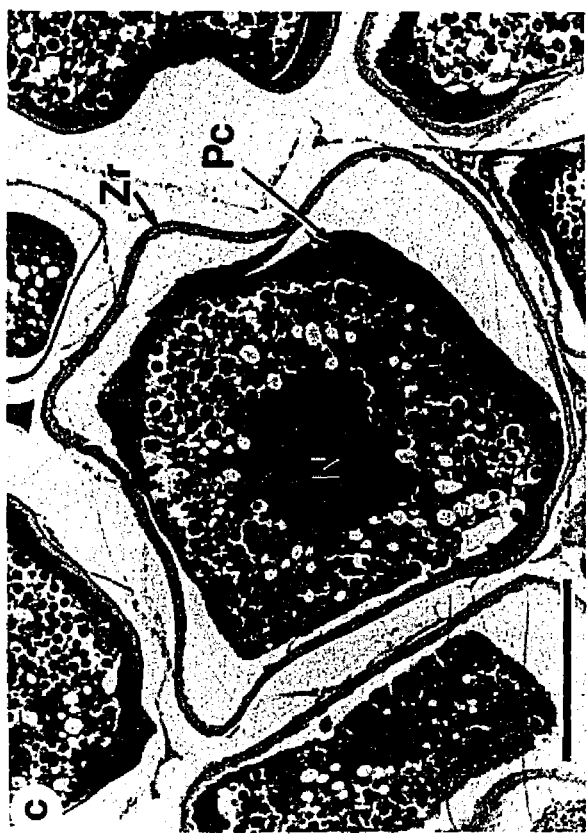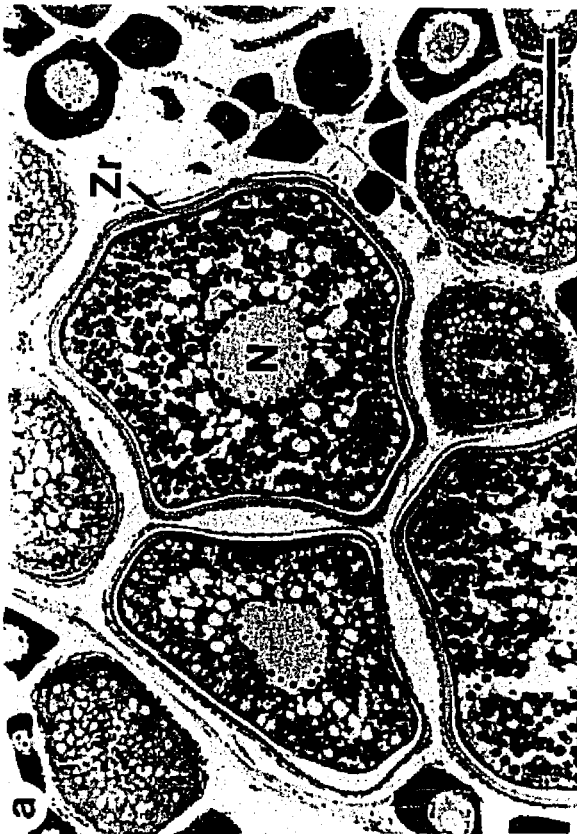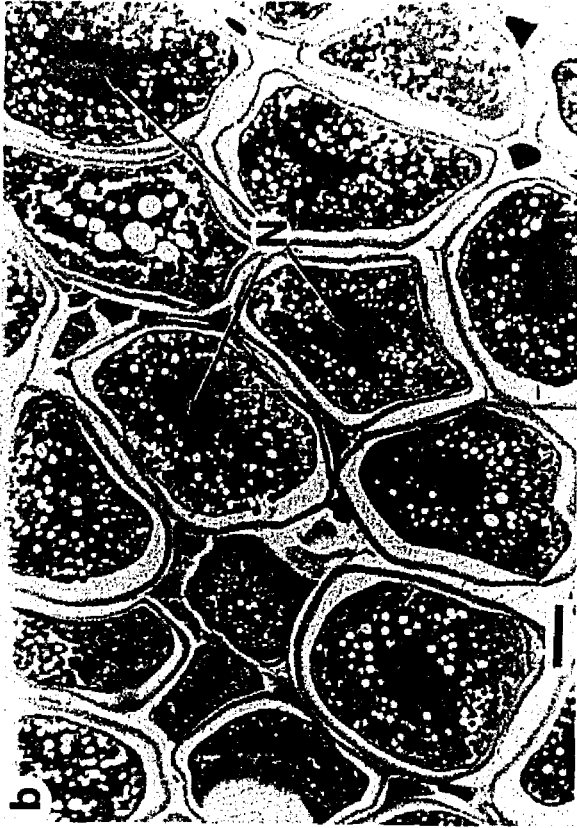
Fig. 18. Comparison of the appearance of α-atretic advanced
yolked oocytes of a fully-developed Atlantic
croaker in a histology slide (a), and in a smear of
fresh oocytes under a dissecting scope (b) and (c).
Cy=clumping of yolk globules; Pc=peripheral
cytoplasm; Va=vacuoles. Bars=0.1 mm.

Figure a, b, c showing cellular structures labelled Cy, Pc, and Va.
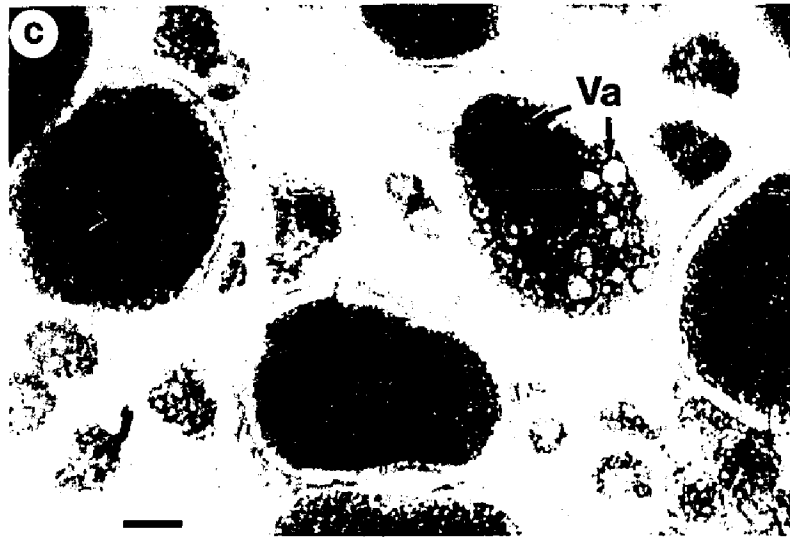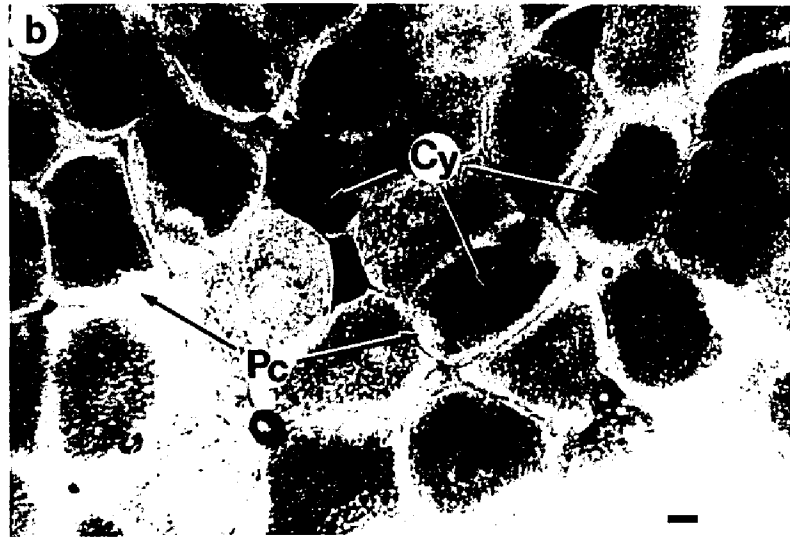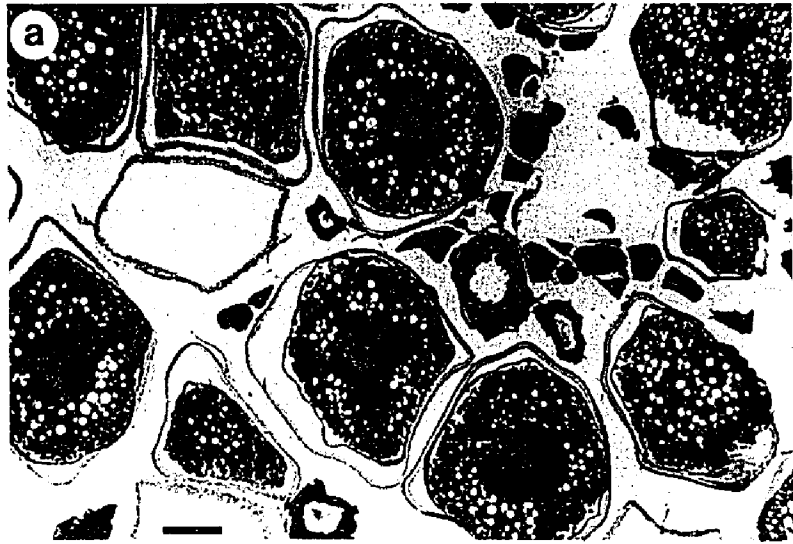
Description of the ovarian cycle

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).
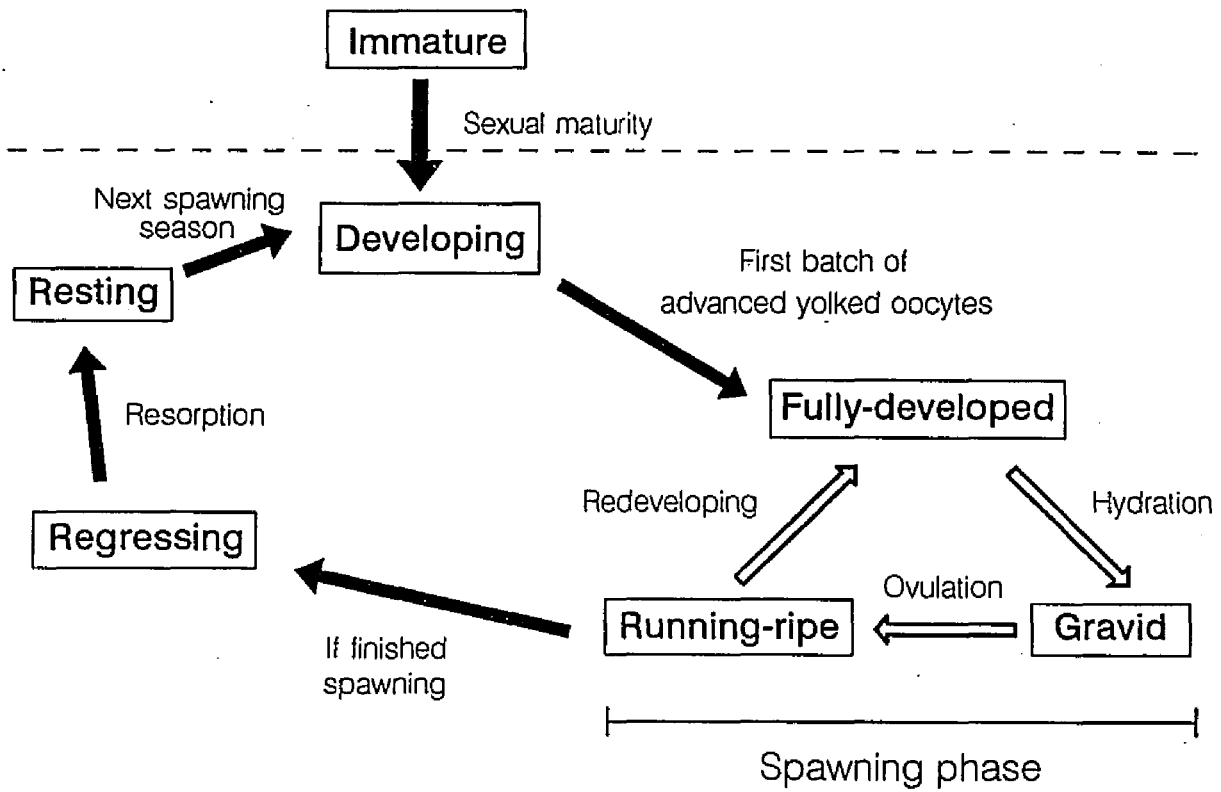
DISCUSSION

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, <u>Cynoscion regalis</u>, 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 α 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.

93

MATERIALS AND METHODS

Yield-per-recruit computations

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

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

Y/R = yield-per-recruit;

F = instantaneous fishing mortality coefficient;

M = instantaneous natural mortality coefficient;

W_∞ = 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

94

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_∞, K, and t_0) were estimated
using the von Bertalanffy equation (Chapter 2). L_∞ was
converted to asymptotic weight, W_∞, 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_∞) and mean water temperature to M developed by Pauly
(1980). In doing so, I used values of K and L_∞ and annual
mean water temperature for Chesapeake Bay (15.5°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_{MAX}), using a value of t_{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_{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[1]	0.36
W_∞	409.90	converted from L_∞[1]	409.90
t_0	-3.26	growth curve[1]	-3.26
t_r	0	life history information[2]	0
t_c	2	age composition of catches[1]	1 - 5
F	------	----------	0 - 2
M	0.29	longevity[3]	
	0.31	longevity[4]	0.25 - 0.40
	0.36	regression estimate[5]	

[1]Chapter 2; [2]Haven (1957), Chao and Musick (1977) and Norcross (1991); [3]Hoenig (1983);
[4]Royce (1972); [5]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:

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

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_∞, 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:

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

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.
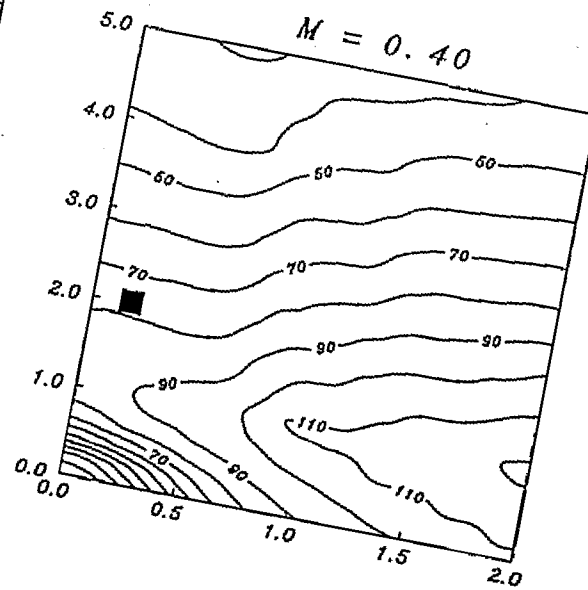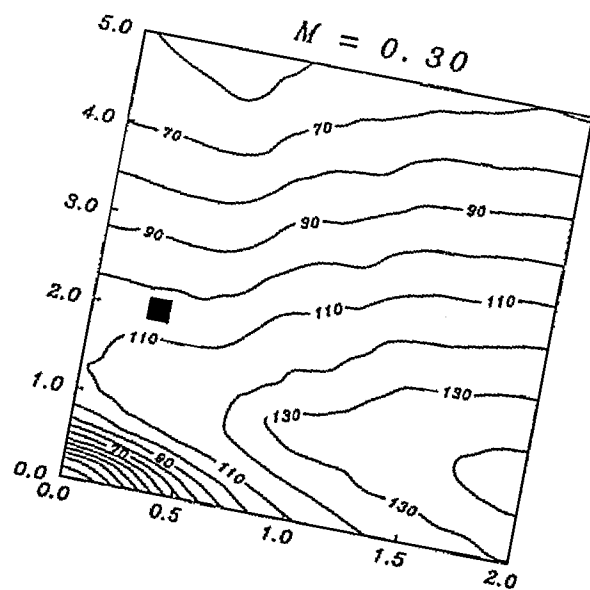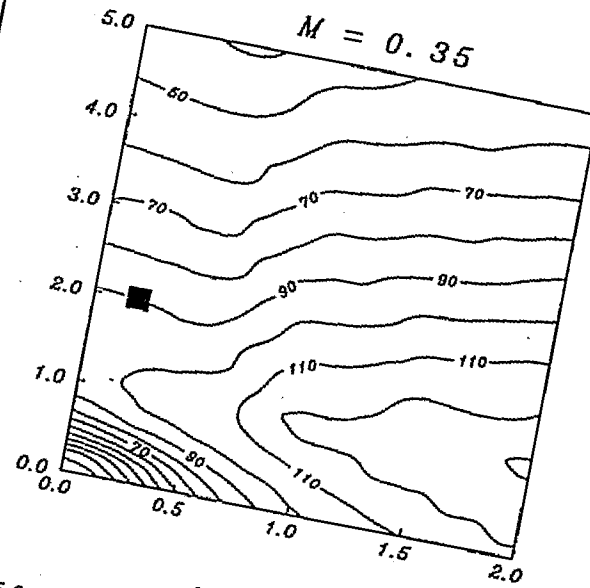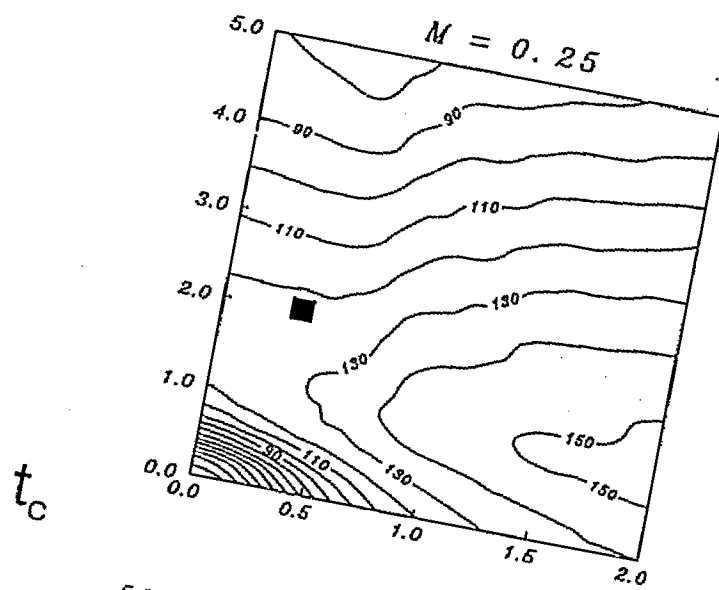
Yield-Fishing mortality curves

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.

M	t_c	Yield-per-recruit (g)		% increase
		$F_{0.75}$	F_{MAX}	
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 $t_c=1\text{-}5$ and $M=0.25\text{-}0.40$. 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.
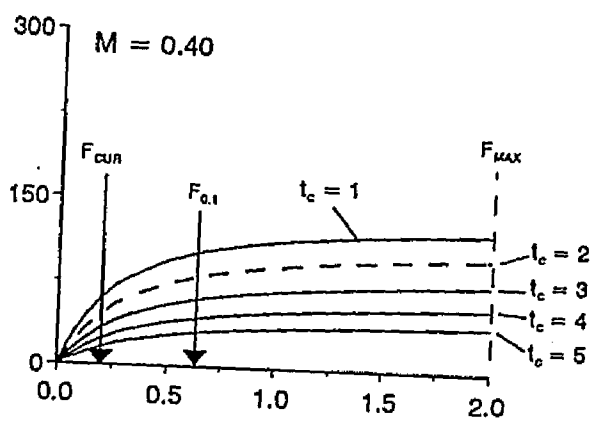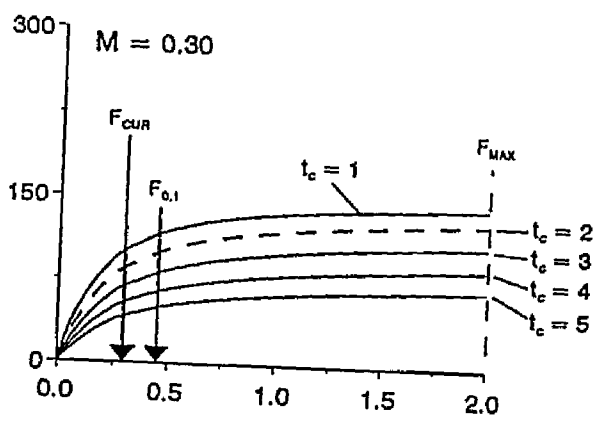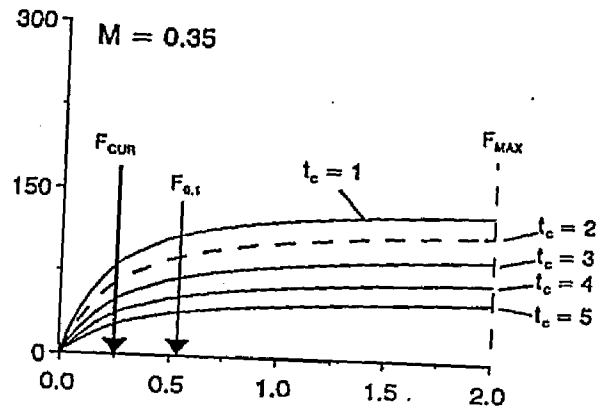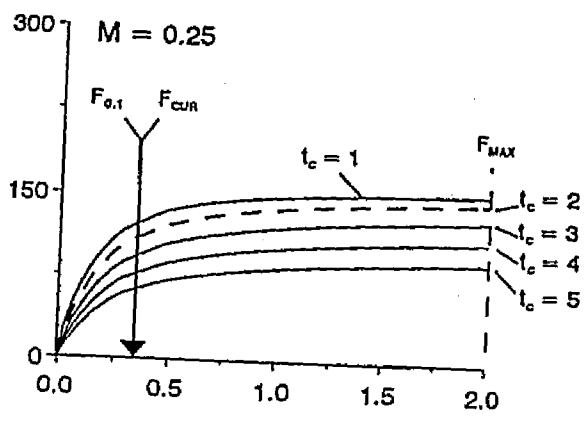
estimated current levels of harvest probably correspond to
the most efficient level of F. In contrast, if M ranges
from 0.30 to 0.40, $F_{0.1}$ is always higher than F_{CUR} (Table 9),
indicating there would still be room to efficiently increase
yield-per-recruit by increases in F. However, at the higher
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_∞=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_{CUR} and $F_{0.1}$ of Atlantic croaker in

Chesapeake Bay estimated for M=0.25-0.40.

M	F_{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 ($1.5<F\leq2.0$). 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[1]). Although 741 citations were
issued during this period, only 14 (1.9%) were for Atlantic
croaker ≥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 ≥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[2]). The number of citations was very

---

[1] Claude M. Bain, III, Virginia Saltwater Fishing Tournament,
968 South Oriole Drive, Suite 102, Virginia Beach,
Virginia, 23451

[2] 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 ≥ 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.
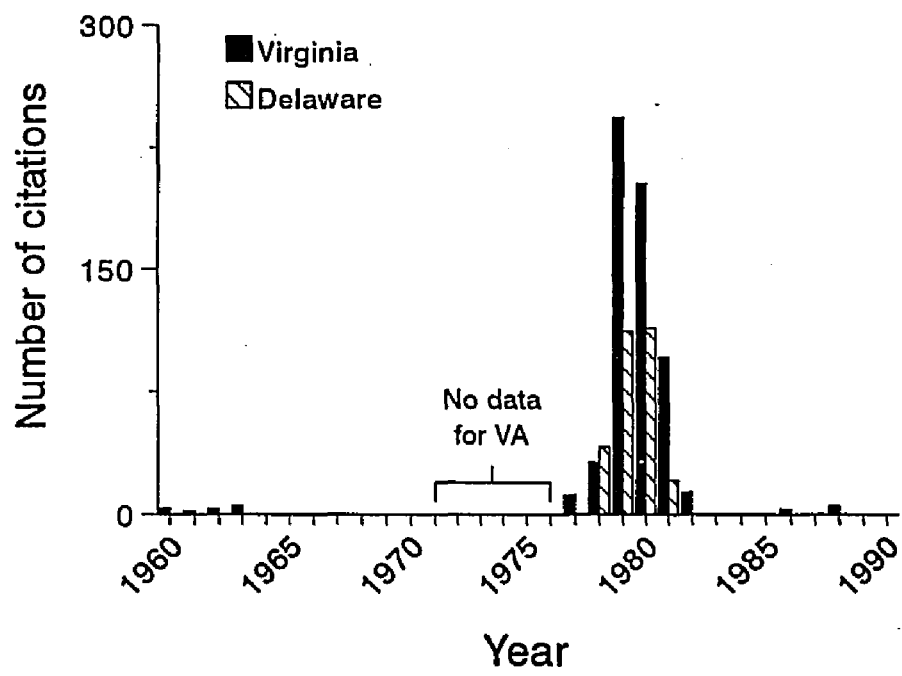
Table 10. State records of Atlantic croaker caught by
recreational fishermen along the East coast of the
U.S.

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.

REFERENCES

Alverson, D.L., and M.J. Carney. 1975. A graphic review of
    the growth and decay of population cohorts. J. Cons.
    Int. Explor. Mer 36:133-143.

Anthony, V.C. 1982. The calculation of $F_{0.1}$: a plea for
    standardization. NAFO SCR Doc. 82/VI/64 Ser. No.
    N557:15 p.

Austin, H. 1987. Chesapeake Bay fisheries: an overview. In
    Majumdar, S.K., L.W. Hall, and H.M. Austin, (eds.),
    Contaminant problems and management of living
    Chesapeake Bay resources, p. 33-53. The Pennsylvania
    Academy of Science, Philadelphia, Pennsylvania.

Bagenal, T.B. 1978. Aspects of fish fecundity. In S.D.
    Gerking (ed.), Ecology of freshwater fish production,
    p. 75-101. Oxford, Blackwell.

Bagenal, T.B., and F.W. Tesch. 1978. Age and growth. In
    Bagenal, T.B. (ed.), Methods for assessment of fish
    production in fresh waters, p. 101-136. 3rd edition,

Blackwell Scientific Publications, Oxford.

Barbieri, L.R. 1986. Distribuição espacial e temporal de sciaenídeos juvenis no estuário da Lagoa dos Patos, RS, Brasil. M.Sc. Thesis. Universidade do Rio Grande, Rio Grande, Brasil, 98 p.

Barger, L.E. 1985. Age and growth of Atlantic croakers in the northern Gulf of Mexico, based on otolith sections. Trans. Am. Fish. Soc. 114:847-850.

Barger, L.E., and A.G. Johnson. 1980. An evaluation of marks on hardparts for age determination of Atlantic croaker, spot, sand seatrout, and silver seatrout. NOAA Technical Memorandum, NMFS, SEFC-22, 5 p.

Beamish, R.J., and G.A. McFarlane. 1987. Current trends in age determination methodology. In R.C. Summerfelt, R.C., and G.E. Hall, (eds.), Age and growth of fish, p. 15-42. Iowa State University Press, Ames.

Bearden, C.M. 1964. Distribution and abundance of Atlantic croaker, Micropogon undulatus, in South Carolina. Contrib. Bears Bluff Lab., South Carolina 40:1-23.

Beckman, D.W., G.R. Fitzhugh, and C.A. Wilson. 1988. Growth

and validation of age estimates of red drum, *Sciaenops ocellatus*, in a Louisiana salt marsh impoundment. Contr. Mar. Sci. 30:93-98.

Beverton, R.J.H. 1963. Maturation, growth, and mortality of clupeid and engraulid stocks in relation to fishing. Rapp. Reun. P.-V. Cons. Int. Explor. Mer 154:44-67.

Beverton, R.J.H., and S.J. Holt. 1957. On the dynamics of exploited fish populations. U.K. Min. Agric. Fish. Food., Fish. Invest. (Ser. 2) 19:1-533.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. 47:2219-2227.

Campbell, A. 1985. Application of a yield and egg-per-recruit model to the lobster fishery in the Bay of Fundy. North Amer. J. of Fish. Managem. 5:91-104.

Casselman, J.M. 1983. Age and growth assessment of fish from their calcified structures—techniques and tools. NOAA Tech. Rep. NMFS 8:1-17.

Casselman, J.M. 1990. Growth and relative size of calcified structures of fish. Trans. Am. Fish. Soc. 119:673-688.

Castello, J.P. 1985. The ecology of consumers from dos Patos
    Lagoon estuary, Brazil. In A. Yáñez-Arancibia (ed.)
    Fish community ecology in estuaries and coastal
    lagoons: towards an ecosystem integration, chapter 17,
    p. 383-406. DR(R) UNAM Press, Mexico.

Chao, L.N. 1978. Family:Sciaenidae. Micropogonias undulatus
    In W. Fischer (ed.), FAO species identification sheets
    for fishery purposes, western central Atlantic: fishing
    area 31, volume 4 [unpaged]. FAO, Rome.

Chao, L.N., and J.A. Musick. 1977. Life history, feeding
    habits, and functional morphology of juvenile sciaenid
    fishes in the York River estuary, Virginia. Fish.
    Bull., U.S. 75:657-702.

Chao, L.N., L.E. Pereira, and J.P. Vieira. 1985. Estuarine
    fish community of dos Patos Lagoon, Brazil: a
    baseline study. In A. Yáñez-Arancibia (ed.) Fish
    community ecology in estuaries and coastal lagoons:
    towards an ecosystem integration, chapter 20, p.
    429-450. DR(R) UNAM Press, Mexico.

Chapman, D.G., and D.S. Robson. 1960. The analysis of a
    catch curve. Biometrics 16:354-368.

Chittenden, M.E., Jr. 1977. Simulations of the effects of fishing on the Atlantic croaker, _Micropogon undulatus_. Proc. Gulf Carib. Fish. Inst. 29:68-86.

Chittenden, M.E., Jr. 1989a. Sources of variation in Chesapeake Bay pound-net and haul-seine catch compositions. N. Amer. J. Fish. Mgmt. 5:86-90.

Chittenden, M.E., Jr. 1989b. Final report on "Initiation of trawl surveys for a cooperative research/assessment program in the Chesapeake Bay", CBSAC III. College of William and Mary, VIMS, Gloucester Point, 123 p.

Chittenden, M.E., Jr. 1991. Operational procedures and sampling in the Chesapeake Bay pound-net fishery. Fisheries (Bethesda) 16:22-27.

Chittenden, M.E., Jr., and J.D. McEachran. 1976. Composition, ecology, and dynamics of demersal fish communities on the northwestern Gulf of Mexico continental shelf, with a similar synopsis for the entire Gulf. Texas A&M University, TAMU-SG-76-208, 104 p.

Chittenden, M.E., Jr., L.R. Barbieri, C.M. Jones, S.J. Bobko, and D.E. Kline. 1990. Initial information on

the Atlantic croaker, a final report on 'Development of age determination methods, life history-population dynamics information and evaluation of growth overfishing potential for important recreational fishes', VMRC I. College of William and Mary, VIMS, Gloucester Point, Va, 88 p.

Colton, J.B., Jr., W.G. Smith, A.W. Kendall Jr., P.L. Berrien, and M.P. Fahay. 1979. Principal spawning areas and times of marine fishes, Cape Sable to Cape Hatteras. Fish. Bull., U.S. 76:911-915.

DeMartini, E.E., and R.K. Fountain. 1981. Ovarian cycling frequency and batch fecundity in the queenfish, Seriphus politus: attributes representative of serial spawning fishes. Fish. Bull., U.S. 79:547-560.

Deriso, R.B. 1987. Optimal $F_{0.1}$ criteria and their relationship to maximum sustainable yield. Can. J. Fish. Aquat. Sci. 44(Suppl. 2):339-348.

DeVlaming, V. 1983. Oocyte development patterns and hormonal involvements in teleosts. In J.C. Rankin, T.J. Pitcher, and R.T. Duggan (eds.), Control processes in fish physiology, p. 176-199. Wiley & Sons, N.Y.

Doubleday, W.G., D. Rivard, and W.D. Mckone. 1984.
    Estimation of partial recruitment and yield per recruit
    for an otter trawl fishery for deepwater redfish. N.
    Am. J. Fish. Manage. 4:15-31.

Draper, N.R., and H. Smith. 1981. Applied regression
    analysis. 2nd edition, John Wiley & Sons, N.Y.,
    709 p.

Everhart, W.H., and W.D. Youngs. 1981. Principles of fishery
    science. 2nd edition, Cornell University Press, Ithaca,
    349 p.

Freund, R.J., and R. Littell. 1986. SAS system for linear
    models. 1986 edition, SAS Institute Incorporated, Cary.

Geer, P.J., C.F. Bonzek, J.A. Colvocoresses, and R.E.
    Harris, Jr. 1990. Juvenile finfish and blue crab stock
    assessment program bottom trawl survey annual report
    series, Volume 1989. VIMS Spec. Sci. Rep. No. 124,
    211 p.

Gulland, J.A. 1983. Fish stock assessment. John Wiley &
    Sons. New York, N.Y. 223 p.

Gulland, J.A., and L.K. Boerema. 1973. Scientific advice on

catch levels. Fish. Bull., U.S. 71:325-335.

Gutherz, E.J. 1977. The northern Gulf of Mexico groundfish
fishery, including a brief life history of the croaker
(Micropogon undulatus). Proc. Gulf Carib. Fish. Inst.
29:87-101.

Hales, L. S., Jr., and E.J. Reitz. 1992. Historical changes
in age and growth of Atlantic croaker, Micropogonias
undulatus (Perciformes: Sciaenidae). J. Archaeol. Sci.
19:73-99.

Haven, D.S. 1954. Croakers. In Virginia Commission of
Fisheries, 54th and 55th annual report 1952-1953, p.
49-53. Richmond.

Haven, D.S. 1957. Distribution, growth, and availability
of juvenile croaker, Micropogon undulatus, in Virginia.
Ecology 38:88-97.

Haven, D.S. 1959. Migration of the croaker, Micropogon
undulatus. Copeia 1959:25-30.

Higgins, E., and J.C. Pearson. 1928. Examination of the
summer fisheries of Pamlico and Core sounds, N.C., with
special reference to the destruction of undersized fish

and the protection of the gray trout, _Cynoscion regalis_. Rep. U.S. Comm. Fish. 2:29-65.

Hildebrand, S.F., and W.C. Schroeder. 1928. The fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43:1-388.

Hildebrand, S.F., and L.E. Cable. 1930. Development and life history of fourteen teleostean fishes at Beaufort, N.C. Bull. U.S. Bur. Fish. 46:383-488.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull., U.S. 82:898-902.

Holt, G.J., S.A. Holt, and C.R. Arnold. 1985. Diel periodicity of spawning in sciaenids. Mar. Ecol. Prog. Ser. 27:1-7.

Horwood, J.W., and M. Greer Walker. 1990. Determinacy of fecundity in sole (_Solea solea_) from the Bristol Channel. J. Mar. Biol. Assoc. U.K. 70:803-813.

Hunter, J.R., B.J. Macewicz, and J.R. Sibert. 1986. The spawning frequency of skipjack tuna, _Katsuwonus pelamis_, from the South Pacific. Fish. Bull., U.S. 84:895-903.

Hunter, J.R., and B.J. Macewicz. 1985a. Measurement of
    spawning frequency in multiple spawning fishes. In R.
    Lasker (ed.), An egg production method for estimating
    spawning biomass of pelagic fish: application to the
    northern anchovy, Engraulis mordax, p. 79-94. NOAA
    Tech. Rep. NMFS 36.

Hunter, J.R., and B.J. Macewicz. 1985b. Rates of atresia in
    the ovary of captive and wild northern anchovy,
    Engraulis mordax. Fish. Bull., U.S. 83:119-136.

Hunter, J.R., N.C.H. Lo, and R.J.H. Leong. 1985. Batch
    fecundity in multiple spawning fishes. In R. Lasker
    (ed.), An egg production method for estimating spawning
    biomass of pelagic fishes: application to the northern
    anchovy, Engraulis mordax, p. 67-77. NOAA Tech. Rep.
    NMFS 36.

Hunter, J.R., B.J. Macewicz, N.C. Lo, and C.A. Kimbrell.
    1992. Fecundity, spawning, and maturity of female Dover
    sole Microstomus pacificus, with an evaluation of
    assumptions and precision. Fish. Bull., U.S.
    90:101-128.

Jearld, A., Jr. 1983. Age determination. In Nielsen, L.A.,
    and D.L. Johnson, (eds.), Fisheries techniques,

p.301-324. Am. Fish. Soc., Bethesda.

Johnson, G.D. 1978. Micropogonias undulatus (Linnaeus),
    Atlantic croaker. U.S. Fish and Wildl. Serv.
    FWS/OBS-78/12:227-233.

Johnson, D.R., and N.A. Funicelli. 1991. Spawning of the red
    drum in Mosquito Lagoon, East-central Florida.
    Estuaries 14:74-79.

Joseph, E.B. 1972. The status of the sciaenid stocks of the
    middle Atlantic coast. Chesapeake Sci. 13:87-100.

Lewis, R.M., and M.H. Judy. 1983. The occurrence of spot,
    Leiostomus xanthurus, and Atlantic croaker,
    Micropogonias undulatus, larvae in Oslow Bay and
    Newport River estuary, North Carolina. Fish. Bull.,
    U.S. 81:405-412.

Lowerre-Barbieri, S.K., and L.R. Barbieri. 1993. A new
    method of oocyte separation and preservation for fish
    reproduction studies. Fish. Bull., U.S. 91:167-170.

Luo, J., and J.A. Musick. 1991. Reproductive biology of the
    bay anchovy in Chesapeake Bay. Trans. Am. Fish. Soc.
    120:701-710.

Macer, C.T. 1974. The reproductive biology of horsemackerel, Trachurus (L.), in the North Sea and English Channel. J. Fish Biol. 6:415-438.

Massmann, W.H., and A.L. Pacheco. 1960. Disappearance of young Atlantic croakers from the York River, Virginia. Trans. Am. Fish. Soc., 89:154-159.

Massmann, W.H., E.B. Joseph, and J.J. Norcross. 1962. Fishes and fish larvae collected from Atlantic plankton cruises of R/V Pathfinder, March 1961-March 1962. VIMS Spec. Sci. Rep. No. 33, 20 p.

McGregor, J.S. 1957. Fecundity of the Pacific sardine (Sardinops caerulea). Fish. Bull., U.S. 57:427-449.

McHugh, J.L. 1981. Marine fisheries of Delaware. Fish. Bull., U.S. 79:575-599.

McHugh, J.L., and D. Conover. 1986. History and condition of food finfisheries in the Middle Atlantic region compared with other sections of the coast. Fisheries 11:8-13.

Mercer, L.P. 1987. Fishery management plan for Atlantic croaker (Micropogonias undulatus). North Carolina

Dept. Nat. Res. Comm. Dev., Div. Mar. Fish., Spec. Sci. Rep. No. 48, 90 p.

Mericas, C.E. 1977. The eye lens weight technique in aging of the Atlantic croaker, *Micropogon undulatus*. Gulf Res. Rep. 6:71-73.

Morse, W.W. 1980. Maturity, spawning and fecundity of Atlantic croaker, *Micropogonias undulatus* occurring north of Cape Hatteras, North Carolina. Fish. Bull., U.S. 78:190-195.

Mosegaard, H., H. Svendang, and K. Taberman. 1988. Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Can. J. Fish. Aquat. Sci. 45:1514-1524.

Murphy, M.D., and R.G. Taylor. 1990. Reproduction, growth, and mortality of red drum, *Sciaenops ocellatus*, in Florida. Fish. Bull., U.S. 88:531-542.

Murphy, M.D., and R.G. Taylor. 1991. Direct validation of ages determined for adult red drums from otolith sections. Trans. Am. Fish. Soc. 120:267-269.

Music, J.L., Jr., and J.M. Pafford. 1984. Population dynamics and life history aspects of major marine sportfishes in Georgia's coastal waters. Georgia Dept. Nat. Res., Coast. Res. Div., Contr. Ser. No. 38, Brunswick, 382 p.

Norcross, B.L. 1983. Climate scale environmental factors affecting year-class fluctuations of Atlantic Croaker (_Micropogonias undulatus_) in the Chesapeake Bay, Virginia. Ph.D. Thesis, School of Marine Science, College of William and Mary, 388 p.

Norcross, B.L. 1991. Estuarine recruitment mechanisms of larval Atlantic croakers. Trans. Am. Fish. Soc. 120:673-683.

Norcross, B.L., and H.M. Austin. 1981. Climate environmental factors affecting year class fluctuations of Chesapeake Bay croaker _Micropogonias undulatus_. Va. Inst. Mar. Sci. Spec. Sci. Rep. No. 110, 78 p.

Norcross, B.L., and H.M. Austin. 1988. Middle Atlantic Bight meridional wind component effect on bottom water temperatures and spawning distribution of Atlantic croaker. Cont. Shelf Res. 8:69-88.

Olney, J.E. 1983. Eggs and larvae of the bay anchovy, Anchoa
     mitchilli, and the weakfish, Cynoscion regalis, in
     lower Chesapeake Bay with notes on associated
     ichthyoplankton. Estuaries, 6:20-35.

Patiño, R., and P. Thomas. 1990. Induction of maturation of
     Atlantic croaker oocytes by 17α,20β,21-trihydroxy-4-
     pregnen-3-one in vitro: consideration of some
     biological and experimental variables. J. Exp. Zool.
     255:97-109.

Pauly, D. 1980. On the interrelationships between natural
     mortality, growth parameters, and mean environmental
     temperatures in 175 fish stocks. J. Cons. Int. Explor.
     Mer 39:195-212.

Pearson, J.C. 1932. Winter trawl fishery off the Virginia
     and North Carolina coasts. U.S. Bur. Fish., Invest.
     Rep. No. 10, Washington, 31 p.

Pearson, J.C. 1941. The young of some marine fishes taken in
     lower Chesapeake Bay, Virginia, with special reference
     to the grey seatrout Cynoscion regalis (Bloch). Bull.
     U.S. Fish. Wildl. Serv. 50:79-102.

Perlmutter, A. 1959. Changes in the populations of fishes

and in their fisheries in the middle Atlantic and
Chesapeake regions, 1930 to 1955. Trans., N.Y. Acad.
Sci., Ser. II 21:484-496.

Prager, M.H., J.F. O'Brien, and S.B. Saila. 1987. Using
lifetime fecundity to compare management strategies: a
case history for striped bass. North Amer. J. of Fish.
Managem. 7:403-409.

Reid, G.K., Jr. 1955. The pound-net fishery in Virginia.
Part 1. History, gear description, and catch. Comm.
Fish. Rev. 17(5):1-15.

Ricker, W.E. 1975. Computation and interpretation of
biological statistics of fish populations. Bull. Fish.
Res. Board Can. 191, 382 p.

Ricker, W.E. 1992. Back-calculation of fish lengths based on
proportionality between scale and length increments.
Can. J. Fish. Aquat. Sci. 49:1018-1026.

Rivas,L.R., and C.M. Roithmayr. 1970. An unusually large
Atlantic croaker, _Micropogon undulatus_, from the
northern Gulf of Mexico. Copeia 1970:771-772.

Robson, D.S., and D.G. Chapman. 1961. Catch curves and

mortality rates. Trans. Am. Fish. Soc. 90:181-189.

Roithmayr, C.M. 1965. Review of industrial bottomfish
fishery in northern Gulf of Mexico, 1959-62. Comm.
Fish. Rev., U.S. 27:1-6.

Ross, J.L., J.H. Hawkins, and D.A. DeVries. 1990. Assessment
of the North Carolina winter trawl fishery, September
1982-April 1985. North Carolina Dep. Environ. Health
Nat. Res., Div. Mar. Fish., Spec. Sci. Rep. No. 53,
97 p.

Ross, J.L., and D.W. Moye. 1989. Assessment of North
Carolina commercial finfisheries, 1985-1987 fishing
seasons. North Carolina Dep. Environ. Health Nat. Res.,
Div. Mar. Fish., Compl. Rep., Project 2-419-R, 279 p.

Ross, J.L. 1991. Assessment of the North Carolina winter
trawl fishery, September 1985-April 1988. North
Carolina Dep. Environ. Health Nat. Res., Div. Mar.
Fish., Spec. Sci. Rep. No. 54, 80 p.

Ross, S.W. 1988. Age, growth, and mortality of Atlantic
croaker in North Carolina, with comments on population
dynamics. Trans. Am. Fish. Soc. 117:461-473.

Rothschild, B.J., P.W. Jones, and J.S. Wilson. 1981. Trends in Chesapeake Bay fisheries. Trans. 46th N. Am. Wildl. Nat. Resour. Conf. :284-298.

Royce, W.F. 1972. Introduction to the fisheries sciences. Academic Press, N.Y., 351 p.

Saila, S.B., C.W. Recksieck, and M.H. Prager. 1988. Basic fisheries science programs. Elsevier. New York. 230 p.

SAS. 1988. SAS/STAT user's guide. Release 6.03 edition, SAS Institute Inc., Cary, 1028 p.

Schauss, R.P., Jr. 1977. Seasonal occurrence of some larval and juvenile fishes in Lynnhaven Bay, Virginia. Am. Midl. Nat. 98:275-282.

Setzler-Hamilton, E.M. 1987. Utilization of Chesapeake Bay by early life history stages of fishes. In Majumdar, S.K., L.W. Hall, and H.M. Austin, (eds.), Contaminant problems and management of living Chesapeake Bay resourses, p. 63-93. The Pennsylvania Academy of Science.

Snyder, D.E. 1983. Fish eggs and larvae. In Nielsen, L.A. and D.L. Johnson (eds.), Fisheries techniques, p.

165-197. American Fisheries Society, Bethesda, Maryland.

Sullivan, J.B. 1986. Stock identification of Atlantic croaker, Micropogonias undulatus, and bluefish, Pomatomus saltratrix, using biochemical methods. In J.L. Ross, D.A. DeVries, J.H. Hawkins III, and J.B. Sullivan. assessment of North Carolina commercial finfisheries. N C Dep. Nat. Resour. Community Dev. Div. Mar. Fish., Completion Report, Project 2-386-R, Morehead City.

Takita, T., T. Iwamoto, S. Kai, and I. Sogabe. 1983. Maturation and spawning of the dragnet, Callionymus enneactis, in an aquarium. Jap. J. Ichthyol. 30:221-226.

Trant, J.M., and P. Thomas. 1988. Structure-activity relationships of steroids in inducing germinal vesicle breakdown of Atlantic croaker oocytes in vitro. Gen. Comp. Endocrinol. 71:307-317.

Vetter, E.F. 1988. Estimation of natural mortality in fish stocks: a review. Fish. Bull., U.S. 86:25-43.

Vieira, J.P. 1991. Juvenile mullets (Pisces:Mugilidae) in

the estuary of Lagoa dos Patos, RS, Brazil. Copeia 1991:409-418.

Wallace, R.A., and K. Selman. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. Amer. Zool. 21:325-343.

Wallace, D.H. 1940. Sexual development of the croaker, Micropogon undulatus, and distribution of the early stages in Chesapeake Bay. Trans. Am. Fish. Soc. 70:475-482.

Warlen, S.M., and J.S. Burke. 1991. Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. Estuaries 13:453-461.

Warlen, S.M. 1982. Age and growth of larvae and spawning time of Atlantic croaker in North Carolina. Proc. Annu. Conf., S.E. Assoc. Fish Wildl. Agencies 34:204-214.

Weinstein, M.P. 1981. Biology of adult sciaenids. In Clepper, H. (ed.) Proceedings of the 6th annual marine recreational fisheries symposium, p. 125-138. Sport Fish. Inst., Washington.

Welsh, W.W., and C.M. Breder. 1923. Contributions to life

histories of Sciaenidae of the eastern United States
coast. Bull. U.S. Bur. Fish. 39:141-201.

White, M.L., and M.E. Chittenden, Jr. 1977. Age
determination, reproduction, and population dynamics
of the Atlantic croaker, _Micropogonias undulatus_.
Fish. Bull., U.S. 75:109-123.

Wilk, S.J. 1981. The fisheries for Atlantic croaker, spot,
and weakfish. _In_ Clepper, H. (ed.) Proceedings of the
6th annual marine recreational fisheries symposium, p.
15-27. Sport Fish. Inst., Washington.

Wright, P.J. 1991. The influence of metabolic rate on
otolith increment width in Atlantic salmon parr, _Salmo
salar_ L. J. Fish Biol. 38:929-933.

VITA

Luiz Roberto Barbieri

Born in Rio de Janeiro, Brazil, 02 June 1958. Entered Santa Úrsula Univerity, Rio de Janeiro, Brazil in 1977. Earned B.S. in Biological Sciences in 1981, and worked as a high school biology teacher and as a fisheries research technician from 1981 to 1983. Entered masters program at the University of Rio Grande, Rio Grande do Sul, Brazil, in 1984. Earned a M.Sc. in Biological Oceanography in 1986. Came to the U.S. and entered the Ph.D. program in Marine Science at the College of William and Mary, School of Marine Science, Virginia Institute of Marine Science in August 1986. Defended his dissertation on 23 June 1993.