AGE, GROWTH AND REPRODUCTION OF TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS*, ALONG THE SOUTHEAST ATLANTIC COAST OF THE UNITED STATES, 1980-87 AND 1996-98

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ABSTRACT

Increases in fishing effort over the last three decades may have resulted in changes in life history patterns of tilefishes. The purpose of this study was to test this hypothesis by assessing the life history from two periods (1980-87 and 1996-98). Tilefish were collected from the southeastern United States for life history analysis using bottom-longline gear deployed by commercial fishermen and during research cruises. Sagittae from a total of 2,484 tilefish were aged successfully. Observed length at age data indicated that male and female tilefish were significantly smaller at most ages during 1996-98 than during 1980-87. Most fish examined (99%) were sexually mature. Up to and during the period of heavy exploitation of tilefish (1980-87), the overall sex ratio was not significantly different from 1:1, however during 1996-98 the sex ratio was significantly different (1:1.35, male: female). Male and female tilefish spawn from March through November with a spawning peak occurring between April and June. Spawning frequency was estimated to be once every four days or 34 times per year. Estimates of batch fecundity and spawning frequency resulted in the following equation for annual fecundity: $AF = -9.539 \times 10^5 + 3209.4(TL)$. Tilefish off the southeastern coast of the United States show many symptoms of severe overfishing including reduced landings and decreased length at age.

INTRODUCTION

The tilefish, *Lopholatilus chamaeleonticeps*, is a long-lived, slow-growing deepwater demersal member of the fish family Malacanthidae distributed along the outer continental shelf of North America from Nova Scotia to Key West, Florida; in the Gulf of Mexico from the northern shoreline to Campeche Bank and off South America from Venezuela to Surinam (Dooley, 1978; Grimes et al., 1982; Turner et al., 1983; Grimes et al., 1988; Hightower and Grossman, 1988). Tilefish move little as adults and occupy burrows within clay bottoms or scour depressions around boulders or rubble piles in depths of 100-400 m and water temperatures of about 9 -14 C (Grimes et al., 1982; Low and Ulrich, 1983; Erickson et al., 1985; Grimes et al., 1986; Grimes et al., 1988; Hightower and Grossman, 1988).

A commercial bottom-longline fishery for tilefish developed in the South Atlantic Bight (SAB) from Cape Hatteras, NC, to Cape Canaveral, FL, in the early 1980s (Low and Ulrich, 1983). In the early 1980's, tilefish were initially an incidental catch of the deepwater grouper fishery by a few handline fishermen, but were soon targeted by an expanded bottom-longline fishing fleet. This fleet consisted of boats from Georgia and Florida, many of which transported their catches back to their home port (Low et al., 1987). Commercial landings for tilefish peaked in 1982 at 1,560 t, but by 1985 landings had dropped drastically (200 t) due to a major decrease in the bottom-longline production of tilefish (Low et al., 1987). In 1997, only 84.7 t of tilefish were landed (NMFS Fish Statistics and Economic Division, pers. comm.; Fig. 1). Spawning potential ratio (SPR) for tilefish off the southeast Atlantic coast was reported to be 22% in 1997, well below the overfished threshold value of 30% (SAFMC, 1997). A total allowable catch (TAC) of 700 t and a trip limit of 2.5 t were introduced in 1993 by the SAFMC to prevent the further depletion of the stock (SAFMC, 1993).

Recent studies have suggested that increases in fishing effort over the last three decades have resulted in changes in life history patterns of deepwater reef fishes (Harris and McGovern, 1997; Wyanski et al., 2000). The purpose of this study was to determine if similar changes have occurred for tilefish by assessing the age structure, growth rates, sex ratio, size and age at maturity, and spawning season of the tilefish population from two periods (1980-87 and 1996-98), and determining annual fecundity from 1996-98.

MATERIALS AND METHODS

Sampling

Tilefish were collected during 1980-87 and 1996-98 with fishery-independent gear by the Marine Resources Monitoring, Assessment and Prediction program (MARMAP). To supplement MARMAP collections, 50-100 whole unsorted tilefish were sampled each month from commercial bottom-longline catches off North Carolina and South Carolina during 1980-87 and 1996-98.

Tilefish habitat was identified during MARMAP research cruises in 1980 and 1981 with electric snapper reels; bottom-longline gear (hereafter referred to as longline gear) and bottom grab samples. Since known tilefish grounds occur within a limited depth range (100-400 m), an area along the 200 m (100 fathom) curve between 3120N, 7940W and 3310N, 7720W was divided into blocks where sampling was concentrated during 1980-87 and 1996-98 (Low et al., 1983; Barans and Stender, 1993). In 1982-87, Kali poles (an off-bottom longline; Russell et al., 1988) and longline gear were used to sample tilefish. Twenty kali poles (5 hooks/pole) were set over a bottom of rocky outcrops and soaked for approximately 90 minutes. Longlines consisting of 100 tuna circle hooks (#5 and #7), baited with squid, that were tied to gangions and placed at 3.7 m intervals on 366 m of 6.4 mm solid braid dacron were set over mud and sand bottom when bottom temperatures were above 9C. During 1996-98, a longline of 1,219 m of galvanized cable groundline was baited with one hundred gangions of squid. Gangions were placed every 12 m and each longline was buoyed to the surface with 457 m of cable. Each 100-hook set was soaked for approximately 90 minutes.

Observers onboard commercial vessels collected 1980-87 samples, and 1996-98 samples were collected from commercial fish houses. Total lengths (TL, mm) of all tilefish caught during 1980-87

were recorded, and otoliths and gonads were removed from a random subsample of the catch. Tilefish sampled during 1996-98 were intercepted prior to sorting at the fish house. When possible, the entire catch of the vessel was sampled; otherwise 50-100 fish off the vessel were randomly sampled.

Total, fork, standard lengths (TL, FL, and SL, mm) and total body weight (TBW, g) were measured for each tilefish sampled from 1996-98. Sagittae were removed (only the left sagitta from commercial samples) and a posterior section of each gonad (if available in commercial samples) was taken for histological analysis and preserved in 10% buffered seawater formalin. Whole ovaries for fecundity analysis were collected during sampling from 1996-98. Ovaries were weighed to the nearest gram and preserved in 10% buffered seawater formalin.

Age and growth

Excised sagittae were stored dry in coin envelopes and the left sagitta was used in age determination. Sagittae were marked through the core along the dorsoventral axis and embedded in epoxy resin. A transverse section (0.7-1.0 mm thickness) was made through the core using a Buehler Isomet low speed saw. Sections were mounted on glass slides with Accumount mounting medium and viewed at 30 X under reflected light using an image analysis system consisting of a dissecting microscope linked to a video camera and personal computer with a frame grabber and Optimas software. Increments (one translucent and one opaque zone) were counted independently by two readers without knowledge of specimen length or date of capture (Fig. 2). If counts differed, otoliths were reread by both readers simultaneously and discarded from analyses if disagreement persisted. Based on previous studies, we assumed that increment formation was annual (one per year) (Turner et al., 1983; Harris and Grossman, 1985), and ages used reflect biological age, not calendar age.

Mean observed lengths at age were calculated for tilefish sampled from each period. Differences in lengths at age between tilefish sampled from 1980-87 and 1996-98 were examined using analysis of variance (ANOVA). Von Bertalanffy growth curves (von Bertalanffy, 1938) were fitted to the observed length at age for both periods. All statistical analyses were performed using SAS (SAS Institute, Inc., 1990) and hypotheses tested at = 0.05.

Reproduction

Reproductive tissues were processed in a Modular Vacuum Processor, vacuum infiltrated, blocked in paraffin, and sectioned (7 m thickness) on a rotary microtome. Three sections from each sample were placed on a glass slide, stained in double-strength Gill hematoxylin and counter-stained with eosin-y.

Sections were viewed under a compound microscope at 40-400 X to determine sex and maturity stages. Maturity stages were assigned using criteria modified from Schmidt et al. (1993) (Table 1). Two readers independently assigned sex and maturity stages, and if a difference in maturity assignment occurred, the slide was reread simultaneously by both readers. The sample was excluded from data analyses if the disagreement persisted. To establish that resting and immature stages were assigned correctly, the number of immature, mature, and resting stages was plotted against total length for each sex. Developing, spawning, and spent individuals were considered mature.

Spawning season for female tilefish was based on the presence of hydrated oocytes and/or postovulatory follicles (POFs). Post-ovulatory follicles were assigned approximate ages according to the criteria of Hunter and Goldberg (1980) (Table 1). A gonadosomatic index (GSI) calculated as gonad weight (GW)x100 divided by total body weight (TBW) was used to determine reproductive seasonality (Nikolsky, 1963). The chi-square goodness of fit test was used to determine if the sex ratios differed from the expected 1:1 for each period and size class.

Fecundity

A sample of ovarian tissue was removed from whole fixed ovaries and weighed with a Sartorius digital scale (0.00001 g). The following definitions (modified from Hunter et al., 1992) were used for this

study:

Total Fecundity (TF)	Standing stock of yolked oocytes - stages 2 and 3.
Annual Fecundity (AF)	Total number of eggs spawned by a female per year.
Batch Fecundity (BF)	Number of hydrated oocytes released in one spawning; determined by counting the number of hydrated oocytes in the ovary.
Determinate Fecundity	Annual fecundity is determinate when the potential annual fecundity becomes fixed prior to the onset of spawning.
Indeterminate Fecundity	Annual fecundity is indeterminate when the potential annual fecundity of a female is not fixed prior to the onset of spawning and unyolked oocytes continue to be matured andspawned during the spawning season.

The following criteria (see Hunter et al., 1992) were used to determine if tilefish was a determinate spawner: a hiatus developed between early yolked oocytes and advanced yolked oocytes; mean oocyte diameter of advanced yolked oocytes increased during the spawning season, and total fecundity declined over the spawning season.

Random distribution of oocyte stages within the ovary was determined by obtaining samples from each lobe. Samples were taken arbitrarily from the anterior, middle, and posterior positions for a total of six samples from ten fish. A two-way ANOVA without interaction was used to test for the effects of location and individual fish on oocyte density. Six oocyte stages as defined by Hunter et al. 1992 were identified: stages 1-3, hydrated (HO), migratory-nucleus (MNO), and atretic (AO). All stages were counted except for stage-1 oocytes (nonvitellogenic).

To estimate total fecundity (TF), two randomly selected samples (28-30 mg) were taken from each of 76 ovaries. Sample weight was 30 mg when hydrated oocytes were present in order to obtain samples with similar oocyte counts. Total fecundity was calculated using the equation
*TF = POW * OD*
where POW = preserved ovary weight (g) and OD = oocyte density. Oocyte density was calculated by dividing the sample weight (g) into the number of stage 2 and stage 3 oocytes. Monthly regression equations were computed to examine the relationship between total fecundity and fish length. An ANCOVA was performed to determine the effect of month and fish length on total fecundity.

For an indeterminate spawner, annual fecundity is computed using estimates of batch fecundity and spawning frequency. Batch fecundity (BF) was estimated using the following equation:
*BF = HO / sample weight (g) * POW*
To determine spawning frequency, the fraction of females with hydrated oocytes to total mature females and the fraction of Day-1 spawning females (females with Day-1 POFs) to total mature females were averaged (Fitzhugh et al., 1993). Only females containing vitellogenic oocytes were used in calculating spawning frequency. Spawning season was defined as the first date when hydrated oocytes or Day-0 POFs were histologically evident up to the first date when major atresia of advanced yolked oocytes occurred. GLOBAL LAB image analysis software was used to measure yolked oocytes (all stages except stage-1 and atretic) from approximately 25 samples (5 samples/month). A gap would develop between early yolked oocytes and the more advanced yolked oocytes when maturation of early yolked oocytes does not continue in indeterminate spawners (Hunter et al., 1992).

RESULTS

Age and growth

Fourfold more fish were collected for age and growth by fishery-dependent sampling than fishery-independent sampling and approximately 80% of all samples were aged (Table 2). Initial agreement between readers was very low (19%) with 25% of the disagreement occurring in assignment of the first increment. The length frequencies of tilefish sampled in each period showed marked differences. Larger fish, male and female, were not as frequently encountered during 1996-98 as compared to 1980-87 (Fig. 3), and the mean lengths of males and females were significantly smaller during 1996-98 (ANOVA; $P<0.005$, df=1) (Table 3). The length frequencies of aged tilefish were very similar to the length frequency sampled for both sexes and time periods (Fig. 3). Females sampled during 1980-87 ranged in age from 2-40 (380-1092 mm TL) and males ranged from 2-27 (361-1110 mm TL) (Fig. 4). Ages for females collected from 1996-98 ranged from 3-32 (327-1075 mm TL) whereas males ranged from 2-32 (383-1155 mm TL) (Fig. 4). The mean age of males (ANOVA: $P=0.68$, df=1) and females did not change significantly between time periods (ANOVA; $P=0.07$,df=1).

Lengths at age were significantly larger for fish collected from 1980-87 than those from 1996-98 (ANOVA; $P<0.05$, df=1) (sexes combined, Fig. 5). There were significant differences in lengths at age between males and females, with males being larger, regardless of time period (ANOVA; $P<0.05$, df=1) (Fig. 6A and B). Lengths at age for both male and female tilefish indicated that fish from 1996-98 were smaller at most ages than fish from 1980-87 (Fig. 7A and B). Males were significantly smaller in 1996-98 for ages 3-15, excluding age-9, and females were significantly smaller for ages 5-19 than tilefish sampled in 1980-87 (ANOVA, $P<0.05$).

The von Bertalanffy growth curves derived from observed lengths at age were markedly different for each sex between the two periods (Fig. 7A and B). Theoretical mean maximum total length (L_∞) further demonstrated that tilefish from 1980-87 reached larger lengths than those from 1996-98 (Table 4). The theoretical growth parameter, K, showed that females from 1980-87 were approaching L_∞ faster than males (Table 4). The L_∞ and K were higher for males from 1996-98 than females (Table 4).

Reproduction

As with age/growth samples, many more fish were obtained by fishery-dependent sampling compared to fishery-independent sampling (Table 2). Only 16 immature males and four immature females were collected between 1980-87, ranging from 361-775 mm TL (ages 3, 4, and 6) and from 390-540 mm TL (ages 3 and 6), respectively. No immature females and only one immature male (406 mm TL, age 7) were collected during 1996-98. As few immature fish were collected, neither size nor age at maturity could be determined. There was very little overlap of resting and immature individuals and there was a substantial overlap of resting and definitely mature individuals indicating that maturity stage was assigned correctly (Fig. 8A and B).

The overall sex ratio was not significantly different from a 1:1 for samples collected in 1980-87; however, during 1996-98 the overall sex ratio was 1:1.35 males: females (Tables 5 and 6). Significantly more males were found in the larger size classes (> 900 mm TL) regardless of time period (Tables 5 and 6). There was no significant difference in the expected 1:1 sex ratio among the different age classes regardless of time period.

Histological examination of the gonads revealed that tilefish are gonochorists and female tilefish spawn from March through November with a spawning peak occurring between April and June (Fig. 9). The GSI for female tilefish from 1996-98 ranged from a high in April to a low in July (Fig. 10) and the large decrease in the GSI between April and June indicated the period of peak spawning. Male tilefish were also in spawning condition from March through November, however, most spawning activity occurred from April through June (Fig. 11). Evidence of previtellogenic oocytes was found in 15 adult males.

Fecundity

Samples taken from different locations within the ovary indicated that advanced yolked oocytes were randomly distributed and therefore samples could be taken from any location or lobe without bias (Table 7).

Monthly mean TF estimates of tilefish increased from 1,091,153 oocytes in February (*n*=14, TL range 551-757 mm) to 1,146,114 oocytes in May (*n*=16, TL range 468-833 mm) and then decreased to 626,050 oocytes in June (*n*=14, TL range 515-735 mm) (Fig. 12). Analysis of covariance of monthly regression equations of TF and TL indicated that the slopes of these equations were significantly different (P<0.001, df=3). In the 152 samples used to estimate fecundity, atresia (oocyte resorption) was observed in 83% with an average portion of 0.006 (number of atretic oocytes/number of total oocytes).

Mean monthly oocyte diameters and the relative amounts of early yolked oocytes (stage 2) and more advanced yolked oocytes (Stage 3, MNOs, and HOs) appeared to remain constant throughout the spawning season suggesting that oocytes continued to mature and develop during the spawning season (Fig. 13). This is further supported by the diameter distributions of early yolked ooytes and advanced yolked oocytes broadly overlapping with no gap or hiatus between stages. The larger number of stage 2 and stage 3 oocytes present in February is probably due to the small size of these oocytes. These samples were collected prior to the onset of spawning during early development of the oocytes.

Annual fecundity was estimated as the product of batch fecundity and spawning frequency (Fig. 14). ANCOVA revealed that there was no significant difference in the slopes of the mean monthly equations of TL and BF (P=0.828, df=3). A test of elevations indicated that BF increased with increasing TL, however batch size was not significantly different between months (ANCOVA, P=0.111, df=3). The variation in batch fecundity was high (4,337-88,173), however, there was no significant difference in BF between months (ANOVA, P=0.328, df=3). The number of Day-1 spawning females (82) was much higher than the number of females with hydrated oocytes (31; n=202 mature females). An average proportion of 0.278 was calculated, corresponding to a spawning frequency of approximately every four days or 38 times in a spawning season of 135 days. Estimates of BF and spawning frequency resulted in the following equation for annual fecundity (Fig. 14): $AF = -9.539 \times 10^5 + 3209.402$ (TL). Estimates of total fecundity and annual fecundity were very similar (Figures 12 and 14).

DISCUSSION

Anal fin ray sections have been used to age tilefish off Georgia (Harris and Grossman, 1985) and sectioned sagittae were used as the aging structure for tilefish in the Middle Atlantic-Southern New England region (Turner et al., 1983) but sectioned sagittae had not previously been utilized as an aging structure for tilefish taken off the southeastern United States. Compared with some species occurring at shallower depths, tilefish otoliths were difficult to interpret. Establishing the location of the core prior to sectioning proved difficult due to the thickness of the otoliths. This difficulty resulted in some sections that were off the core thus making assignment of the first increment arduous. Similar to Turner et al. (1983), we found that older fish had a tendency to change their growth axis from the ventral to the medial face of the otolith. As the point at which the growth axis changed was inconsistent between otoliths, it was impossible to measure otolith radius in a consistent and repeatable manner in different otoliths. The difficulties in precisely locating the core and the change in growth axis made the development of a valid fish length/otolith radius regression virtually impossible. As a result, back-calculation of fish length at age could not be performed. Furthermore, we frequently observed a ‘group’ of increments with very narrow translucent and opaque zones, which were separated from the next group by a larger translucent zone, particularly in the first few increments of older fish. We counted each group of increments as a single increment. This increment grouping, and tightly packed increments at the otolith edge of older fish, precluded any validation of the periodicity of increment formation based on the analysis of the marginal increment. We therefore assumed that one increment

was formed per year, as described by Turner et al. (1983) for sectioned otoliths.

Size composition of tilefish caught in the longline fishery has changed significantly since the 1980s. Tilefish over 900 mm TL composed almost 11% of the samples collected from 1980-87 whereas only 2.5% of the tilefish sampled from 1996-98 were over 900 mm TL. The mean TL of males and females also decreased. A decrease in the size of commercially caught tilefish was noted as early as 1983 by Low and Ulrich (1983). Barans and Stender (1993) reported that mean total length of tilefish from commercial catches off South Carolina and Georgia decreased 28 cm from 1977 to 1985. A reduction in mean length is usually attributed to a 'fishing up' effect, as the larger individuals are typically the first to be harvested by a developing fishery or when fishing mortality increases (Ricker 1977). However, the decline in size at age for almost all age classes as seen in 1996-98 suggests that the population may be undergoing fishery induced selection for slower growing, smaller fish in the population (Harris and McGovern, 1997; Conover and Munch, 2002). The decrease in growth rates between time periods (regardless of sex) was further demonstrated by the decline of L_{∞}, demonstrating the effect of fishing pressure on the population. Sustained removal of larger fish from the population will depress the growth rate of individuals within the population over many generations (Harris and McGovern, 1997; Zhao et al., 1997; Cardinale and Arrhenius, 2000; Conover and Munch, 2002).

Sexual dimorphism was readily apparent during both time periods for tilefish sampled off the Carolinas, and is a common occurrence in most malacanthids (Ross and Huntsman, 1982; Turner et al., 1983; Harris and Grossman, 1985; Grimes et al., 1988) with males attaining larger lengths at age. However, a decrease in the age of onset of sexual dimorphism between males and females (from age 10 in 1980-87 to age 7 in 1996-98) has been described for this population (see Harris et al, 2000). Sexual dimorphism is thought to occur when sexually mature but previously inactive females, first begin reproducing. An effect of the decrease in age at first reproduction in females is the mean size of first reproduction has decreased from 730 mm TL (age 10, 1980-87) to 582 mm TL (age 6, 1996-98).

Since tilefish are space limited (Grimes et al., 1986; Grimes and Turner, 1999), spawning and mate selection may be strongly density-dependent. Harris et al. (2000) suggested there might be a population of sexually mature, non-spawning, satellite females in addition to the satellite males described by Grimes et al. (1988). As fishing pressure increased and larger males and females were removed, smaller satellite males and females may have occupied the now vacant habitat and begun reproducing. The gear used to harvest specimens had the same or similar hook sizes during both time periods, and fishing occurred in the same habitat, therefore it is unlikely that these changes were due to gear selectivity or differences in habitat. Similarly, Harris and McGovern (1997) noted no trends in mean summer bottom temperature of the continental shelf between 1987 and 1994, suggesting that these differences were not due to changes in ambient bottom temperature in the habitat of tilefish.

Sex ratio changed over time. During 1980-87, prior to and during heavy exploitation, the sex ratio was not significantly different from 1:1. In 1996-98 after a collapse of the population, the overall sex ratio was significantly different from 1:1 in favor of females. This change in the sex ratio appears to be due to the absence of larger fish, predominantly males, which have presumably been removed from the population by the commercial fishery. However, a decrease in the female size was also reflected in the sex ratio, as females outnumbered males from 400-900 mm Tl. By 1996-98, females were predominant only from 400-700 mm TL. Erickson and Grossman (1986) and Turner et al. (1983) also found disproportionately larger numbers of females at smaller lengths and males at larger lengths and concluded that differential mortality or growth rates, or differential catchability, may have been responsible for the observed skewed sex ratios. We feel the sex ratios observed in our study, and those reported by Erickson and Grossman (1986) and Turner et al. (1983) are accurate representations of the sex ratio in the population, resulting from the differential growth rates of males and females.

Tilefish along the southeastern United States are asynchronous multiple spawners with a protracted spawning season of eight months from March through November with peak spawning between April

and June. A gonadosomatic index indicated a similar spawning pattern with the highest GSI values occurring in April and decreasing in May and June. Our results differ from Erickson et al. (1985) who reported a much shorter spawning season for tilefish off Georgia. These specimens were collected from May 1982 to December 1983. They found that female tilefish were in spawning condition for only four months from March through June with a peak in April. Small sample sizes for later months (July-Nov) could account for the short spawning season reported by Erickson et al. (1985). The spawning season of tilefish from our study is comparable to the spawning season of tilefish from the Mid-Atlantic–southern New England area. Grimes et al. (1988) found that tilefish in this area spawn from March through November with a peak occurring from May to September. Like Erickson and Grossman (1986) and Grimes et al. (1988), histological examination of male gonads from this study revealed that a few (15) adult males had evidence of previtellogenic oocytes, however, no observations of transitional ovotestes were noted.

Our study suggests that tilefish are indeterminate spawners due to the uninterrupted production of vitellogenic oocytes throughout the spawning season, the absence of a hiatus between oocyte stages, and a protracted spawning season (nine months). Hunter and Macewicz (1985) stated that the traditional evidence of a determinant spawner is the presence of a major gap in oocyte maturity stages and the absence of a discontinuity in stages is evidence for indeterminate fecundity. The most conservative assumption for multiple spawning fishes in tropical and temperate climates is that fecundity is indeterminate (Hunter and Macewicz, 1985). Differences in fecundity estimation methods between our study and Grimes et al. (1988) and Erickson and Grossman (1986) made comparisons difficult. Both studies determined advanced yolked oocytes based on oocyte diameters (> 0.15 mm).

Our estimates of batch size are small (4,[illegible]7 to 8,172 oocytes) compared to other similar studies. Because tilefish are pair spawners and not aggregate spawners, small batch sizes are not unusual. Another explanation for small batch size is that some oocytes may have already ovulated resulting in an underestimation of batch fecundity. We examined ovaries both macroscopically and histologically to minimize this possibility.

Tilefish off the southeastern coast of the United States show many symptoms of severe overfishing, including reduced landings, decreased length at age, and a possible decrease in size at first reproduction. The loss of a large portion of the population during the late 1970s and early 1980s most probably have caused the changes seen in the life history of tilefish, in spite of the short amount of time that has passed since a targeted fishery first began. These changes may only reflect the loss of larger, faster growing individuals and not a genetic shift towards the smaller, slower growing individuals. If, however, fishing pressure continues unabated a resultant genetic change may occur as the larger, faster growing individuals are eliminated from the spawning population.

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FIGURE LEGENDS

Figure 1. Commercial landings (metric tons) of tilefish from North Carolina, South Carolina, Georgia and Florida during 1970-2001. Fishing effort consisted of handlines in the 1970s and predominantly bottom-longlines in the 1980s and 1990s. Landings peaked in 1982 at 1,560 tons.

Figure 2. Transverse section of a tilefish sagitta. This is an age-7 fish. Asterisks represent increment counts.

Figure 3. Length frequency histograms for male tilefish sampled and aged from 1980-87 (A) and 1996-98 (B), and females sampled and aged from 1980-87 (C) and 1996-98 (D). Mean lengths of males and females were significantly smaller in 1996-98 ($p<0.05$) compared to 1980-87.

Figure 4. Age frequency histograms for male and female tilefish from 1980-87 and 1996-98. No significant differences in age were found between time periods (P=0.09).

Figure 5. Mean observed length at age data (SE) for tilefish collected from 1980-87 and 1996-98, sexes combined. Tilefish sampled from 1980-87 were significantly larger than those from 1996-98 ($P<0.05$). Figure includes individuals that were not assigned a sex.

Figure 6. Mean observed length at age and fitted von Bertalanffy growth curves (SE) for male and female tilefish from 1980-87 (A) and male and female tilefish from 1996-98 (B).

Figure 7. Mean observed length at age (± SE) fitted with von Bertalanffy growth curves derived for male (A) and female (B) tilefish collected between 1980-87 and 1996-98.

Figure 8. Length frequency histogram comparing immature, mature and resting male tilefish (A), and immature, mature and resting female tilefish (B), time periods combined. Mature individuals were developing, ripe or spent.

Figure 9. Percent composition (based on histological examination) of maturity stages by month for female tilefish (all data combined). Number of specimens examined is above each bar. POFs = postovulatory follicles (12-48 hours old).

Figure 10. Mean gonadosomatic index (GSI) values (SE) by month for female tilefish that were collected from 1996-98. Sample size is in parentheses. GSI=(gonad wt/total body wt)*100.

Figure 11. Percent composition (based on histological examination) of maturity stages by month for male tilefish (all data combined). Number of specimens examined is above each bar.

Figure 12. Mean total fecundity estimates for tilefish by month collected during 1996-1998. An ANCOVA revealed that the slope of monthly equations of TF and TL were significantly different (P=0.0001).

Figure 13. Mean oocyte diameters by month of stages 2,3, migratory nucleus (MNO) and hydrated oocytes (HO) for tilefish collected during 1996-98.

Figure 14. Plot of annual fecundity and TL by month for individual fish collected during 1996-98. A linear regression of annual fecundity (AF) on total length (mm) for tilefish demonstrates the high variability observed in fecundity samples. Annual fecundity was estimated as the product of batch fecundity and spawning frequency (34 times per year).

Table 1. Histological criteria used to assess maturity stage in male and female tilefish, modified from Schmidt et al. (1993).

Reproductive state	Male	Female
Immature	Small cross-section compared to resting male; little or no spermatocyte development	Small cross-section in comparison to resting female; primary growth oocytes (<60 μm in diameter); lamellae are not elongated; thin gonad wall; no evidence of atresia
Developing	Development of cysts containing primary and secondary spermatocytes through some accumulation of spermatozoa in lobular lumina and ducts	See below
Running ripe	Predominance of spermatozoa in lobules and ducts; little or no occurrence of spermatogenesis	Completion of yolk coalescence and hydration in most advanced oocytes; zona radiata becomes thin
Spent	No spermatogenesis; some residual spermatozoa in lobules and ducts	>50% of vitellogenic oocytes undergoing alpha or beta atresia
Resting	Lobules, efferent ducts and main duct empty; early spermatogenesis (spermatogonia through primary spermatocytes) may be evident along the extreme periphery of the testis	Primary growth oocytes > 60 μm in diameter; traces of atresia, cross-section larger in comparison to immature female; lamellae more elongate and gonad wall is thicker; bundles of connective and muscle tissue present
Developing, recent spawn		Vitellogenic oocytes predominant and POFs (postovulatory follicles) <24 hours old (sensu Hunter and Goldberg, 1980)
Developing, recent spawn		Vitellogenic oocytes predominant and POFs ≥24 h but <48 h (sensu Hunter and Goldberg, 1980)
Developing, recent spawn		Vitellogenic oocytes predominant and POFs >48 hours old (sensu Hunter and Goldberg, 1980)
Early developing, cortical alveoli		Most advanced oocytes in cortical-alveoli stage
Developing, vitellogenesis		Most advanced oocytes in yolk-globule stage
Final oocyte maturation		Most advanced oocytes in migratory-nucleus stage or early yolk-coalescence stage

Table 2. Source and number of tilefish sampled during 1980-87 and 1996-98. The term staged refers to those fish that were assigned a maturity stage. Fishery-dependent refers to samples collected from the commercial fishery. Fishery-independent refers to those samples collected by MARMAP. TL = total length.

	Fishery-dependent					Fishery-independent				
	Sampled	TL	Aged	Sexed	Staged	Sampled	TL	Aged	Sexed	Staged
								d		
1980-87	1,302	1,242	849	931	742	464	437	355	430	398
1996-98	1,403	1,401	1,119	966	933	176	176	162	142	134
Total	2,705	2,643	1,968	1,897	1,675	640	613	517	572	532

Table 3. The mean lengths and ages of tilefish sampled during 1980-87. Standard errors are in parentheses. An asterix denotes a significant difference between periods at $P < 0.05$.

	Males		Females		Combined	
	Age (years)	TL (mm)	Age (years)	TL (mm)	Age (years)	TL (mm)
1980-87	8.3 (± 0.14)	*740 (± 6.3)	8.9 (± 0.22)	*683 (± 4.5)	8.7 (± 0.12)	*714 (± 3.6)
1996-98	8.4 (± 0.16)	671 (± 6.6)	8.4 (± 0.15)	593 (± 3.4)	8.4 (± 0.09)	625 (± 3.1)

Table 4. Parameters of the von Bertalanffy growth curves fitted to mean observed total lengths for males and females from 1980-87 and 1996-98.

	Males		Females	
von Bertalanffy parameters	1980-87	1996-98	1980-87	1996-98
L_∞	1222.2	966.9	867.1	777.4
K	0.09	0.14	0.15	0.10
t_0	-1.84	-0.44	-2.09	-5.72

Table 5. Chi-square (χ^2) analysis of sex ratios for tilefish, *Lopholatilus chamaeleonticeps*, from 1980-87. Sex ratios based on mature individuals. H_o (null hypothesis) = Male to female ratio is 1:1.

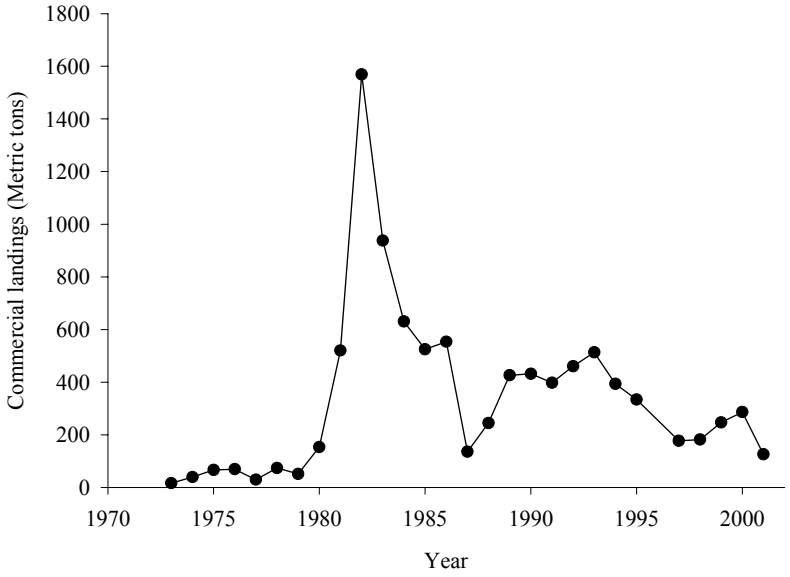
Total length (mm)	Males	Females	Male:Female	χ^2	Prob.	H_o
301-400	5	3	1:0.60	0.62	0.50>P>0.25	Accept
401-500	37	44	1:1.19	0.62	0.50>P>0.25	Accept
501-600	85	108	1:1.27	2.74	0.10>P>0.05	Accept
601-700	167	188	1:1.12	1.24	0.50>P>0.25	Accept
701-800	153	212	1:1.38	9.54	0.005>P>0.001	Reject
801-900	80	95	1:1.19	1.29	0.50>P>0.25	Accept
901-1000	77	4	1:0.05			
1001-1100	59	1	1:0.02			
1101-1200	1	0				
Total	664	655	1:0.99	0.06	0.90>P>0.75	Accept

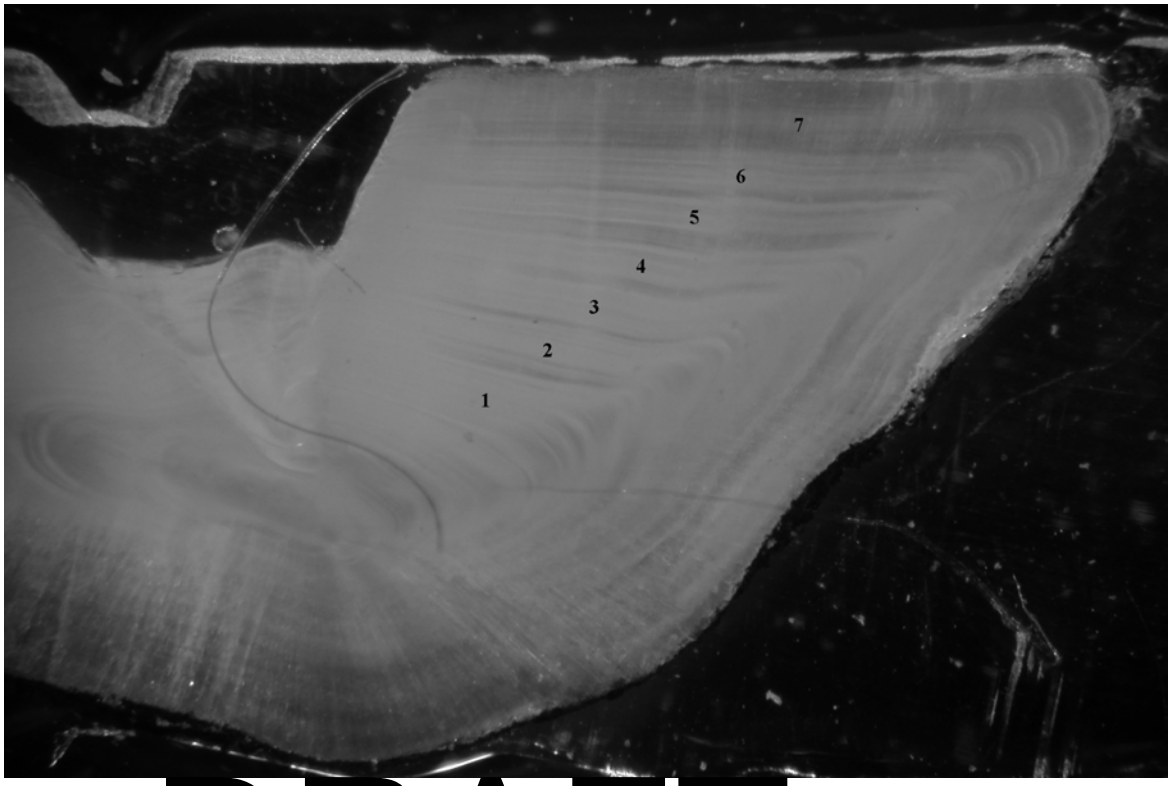
Table 6. Chi-square (χ^2) analysis of sex ratios for tilefish, *Lopholatilus chamaeleonticeps*, from 1996-98. Sex ratios based on mature individuals. H_o (null hypothesis) = Male to female ratio is 1:1.

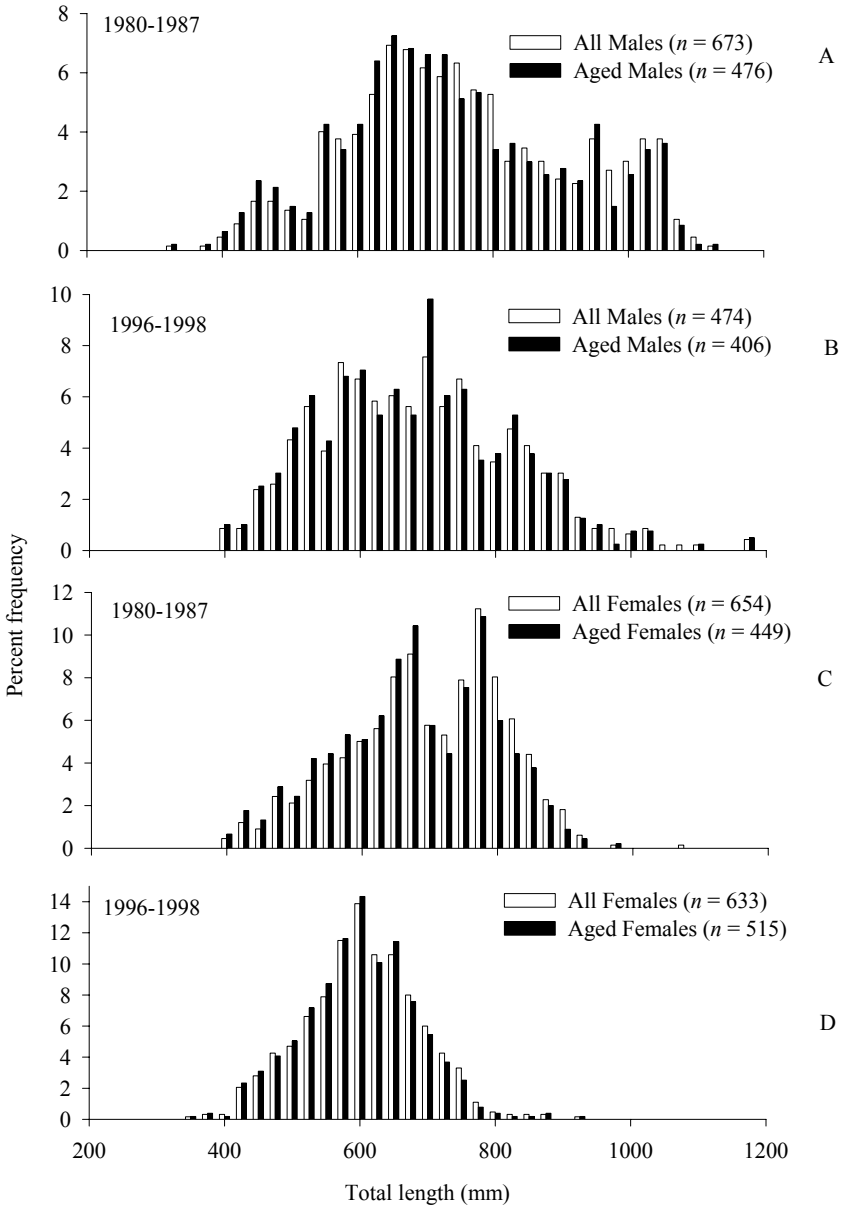
Total length (mm)	Males	Females	Male:Female	χ^2	Prob.	H_o
301-400	4	4	1:1	0.13	0.75>P>0.50	Accept
401-500	49	87	1:1.77	10.62	0.005>P>0.001	Reject
501-600	109	254	1:2.33	57.92	0.001>P	Reject
601-700	118	221	1:1.87	31.29	0.001>P	Reject
701-800	94	60	1:1.56	7.52	0.01>P>0.005	Reject
801-900	69	6	1:0.09	52.94	0.001>P	Reject
901-1000	17	1	1:0.06			
1001-1100	7	0				
1101-1200	2	0				
Total	469	633	1:1.35	24.40	0.001>P	Reject

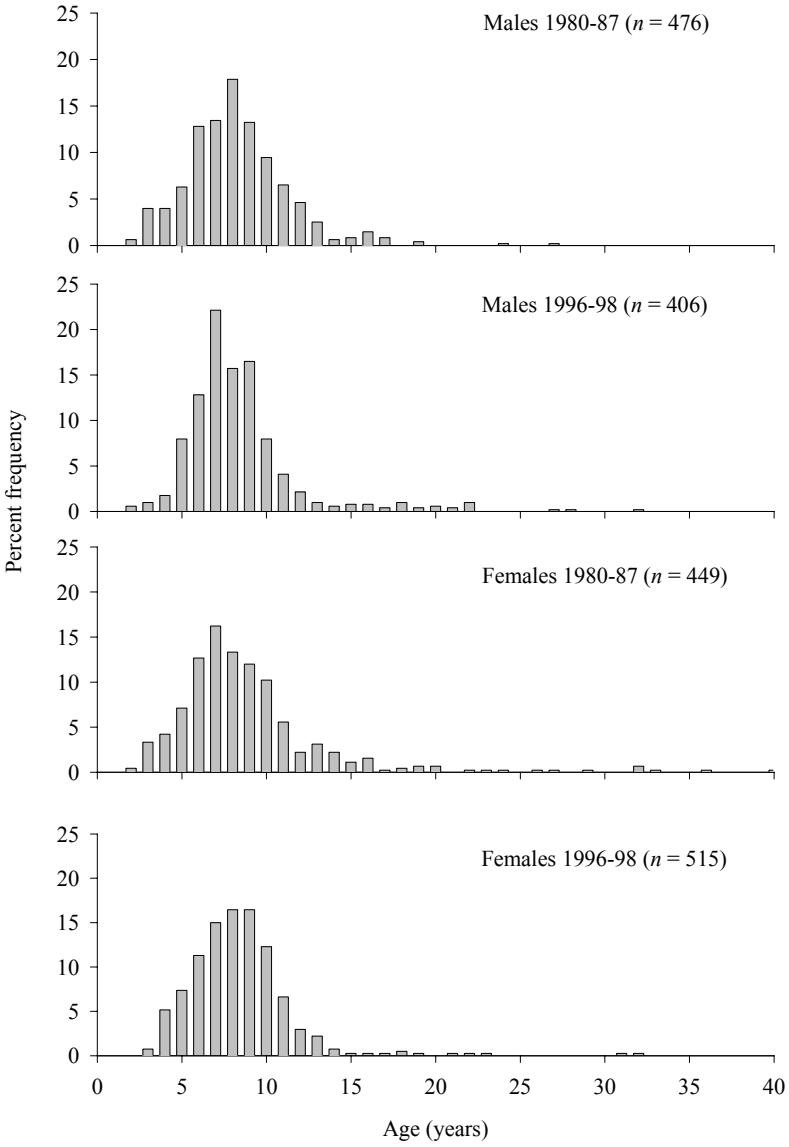
Table 7. Effect of location of tissue samples within the ovary on oocyte density (number of advanced oocytes per unit sample weight) for tilefish. Mean, standard deviation (SD), and two-way analysis of variance results are given.

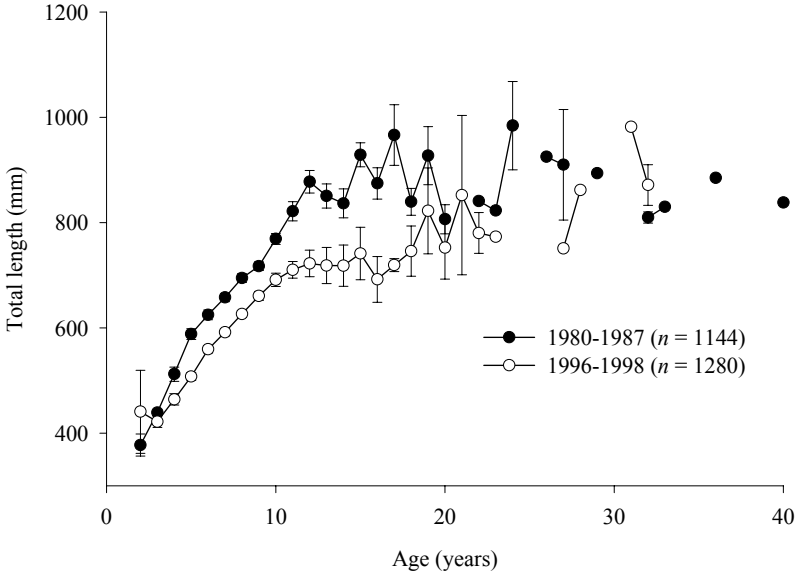
Location of sample			Oocyte density		
Position no.	Lobe	Long. plane	*n*	Mean	SD
1	Left	Anterior	10	508.9	141.35
2	Left	Middle	10	546.9	182.92
3	Left	Posterior	10	551.6	134.55
4	Right	Anterior	10	500.2	107.14
5	Right	Middle	10	518.5	111.34
6	Right	Posterior	10	515.5	163.18

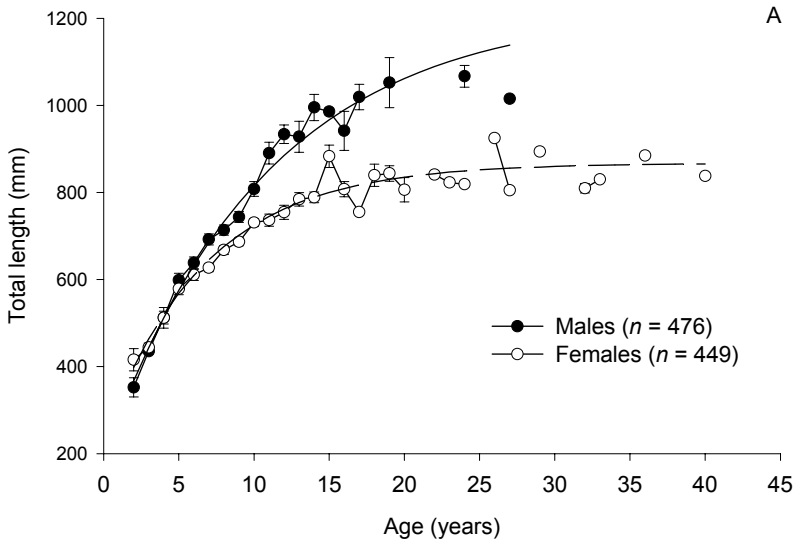

Commercial landings (Metric tons)
1800
1600
1400
1200
1000
800
600
400
200
0
1970
1975
1980
1985
1990
1995
2000
Year

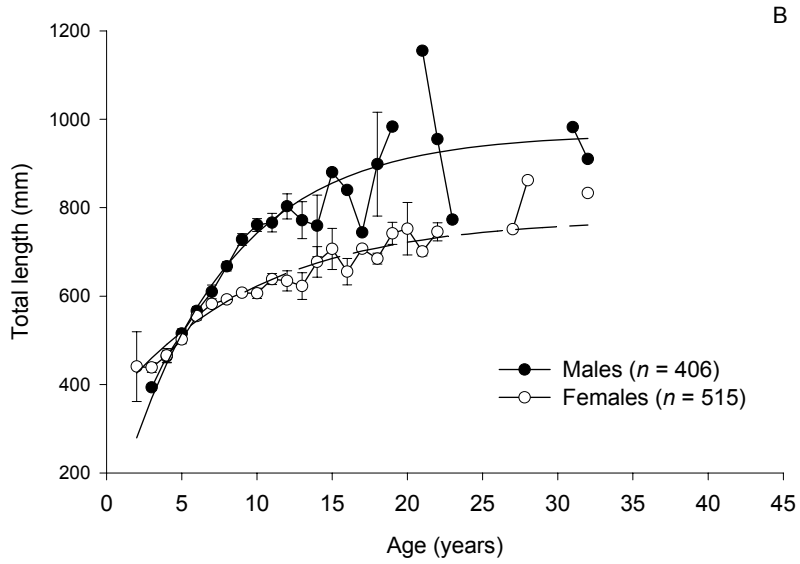


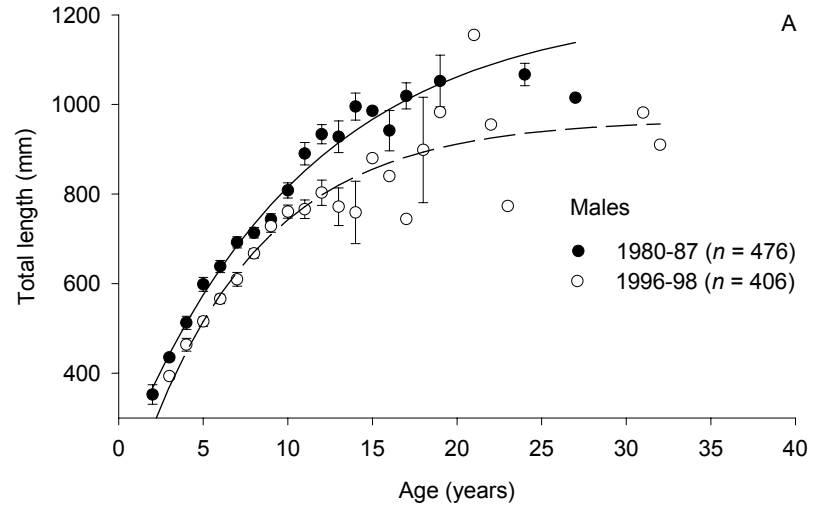

1980-1987
All Males (n = 673)
Aged Males (n = 476)
A
1996-1998
All Males (n = 474)
Aged Males (n = 406)
B
1980-1987
All Females (n = 654)
Aged Females (n = 449)
C
1996-1998
All Females (n = 633)
Aged Females (n = 515)
D
Percent frequency
Total length (mm)
0
2
4
6
8
10
12
14
200
400
600
800
1000
1200

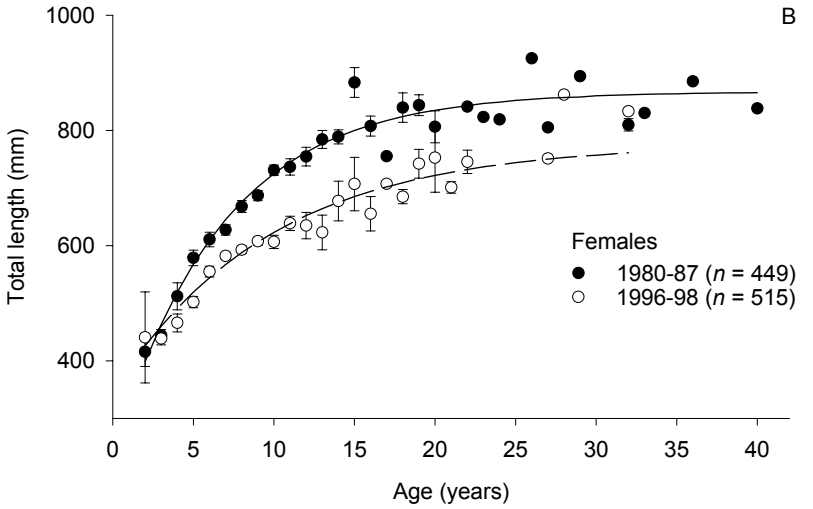

Males 1980-87 (n = 476)
Males 1996-98 (n = 406)
Females 1980-87 (n = 449)
Females 1996-98 (n = 515)
Percent frequency
Age (years)
0
5
10
15
20
25
30
35
40

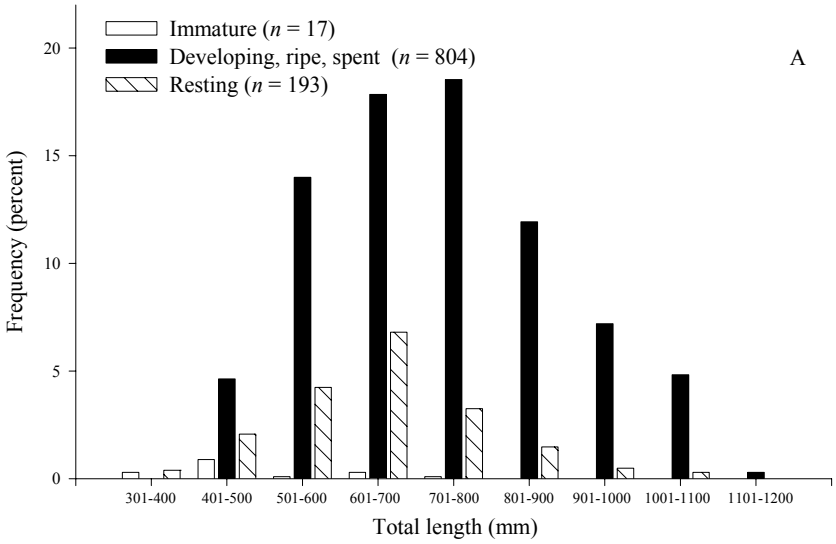

1200
1000
800
600
400
Total length (mm)
0
10
20
30
40
Age (years)
1980-1987 (n = 1144)
1996-1998 (n = 1280)

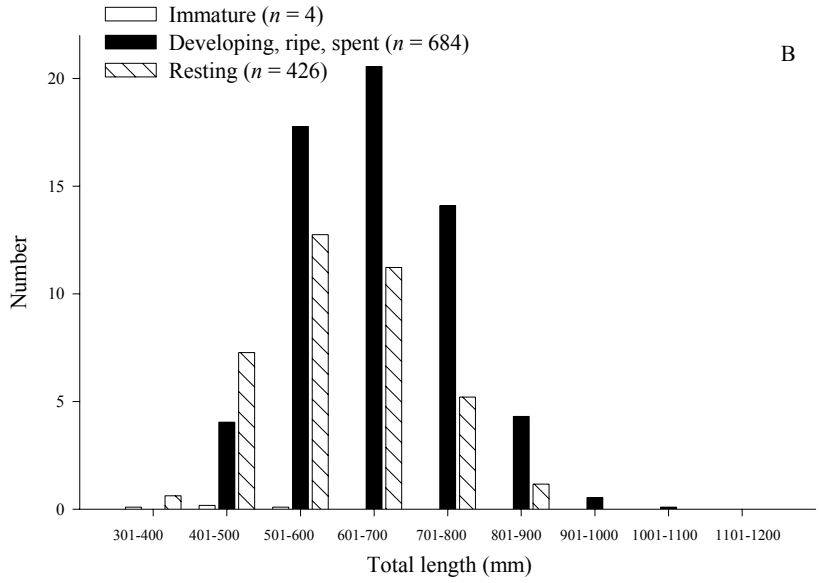

A
Total length (mm)
1200
1000
800
600
400
200
0
5
10
15
20
25
30
35
40
45
Age (years)
Males (n = 476)
Females (n = 449)

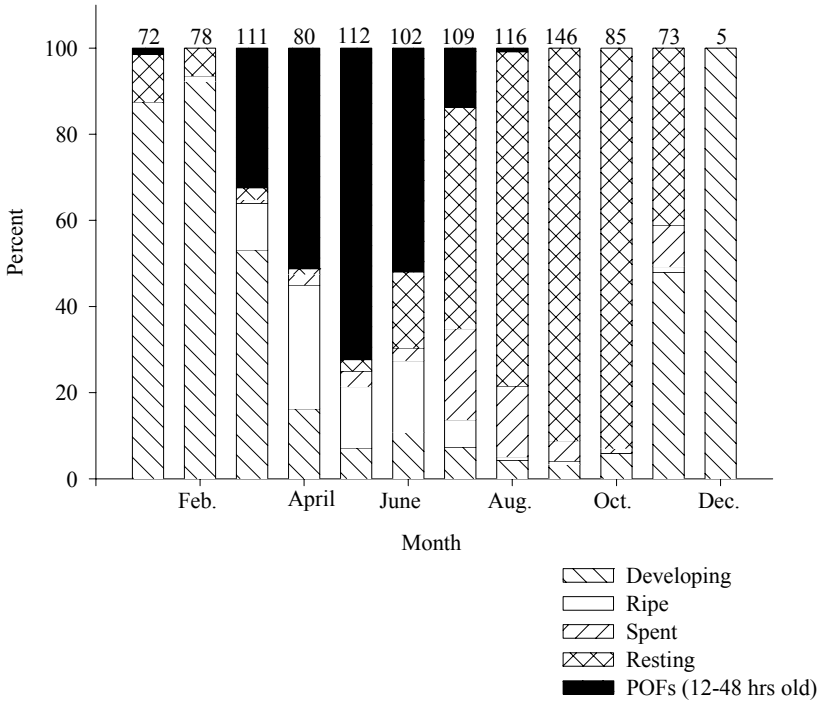

B
Total length (mm)
1200
1000
800
600
400
200
0
5
10
15
20
25
30
35
40
45
Age (years)
Males (n = 406)
Females (n = 515)

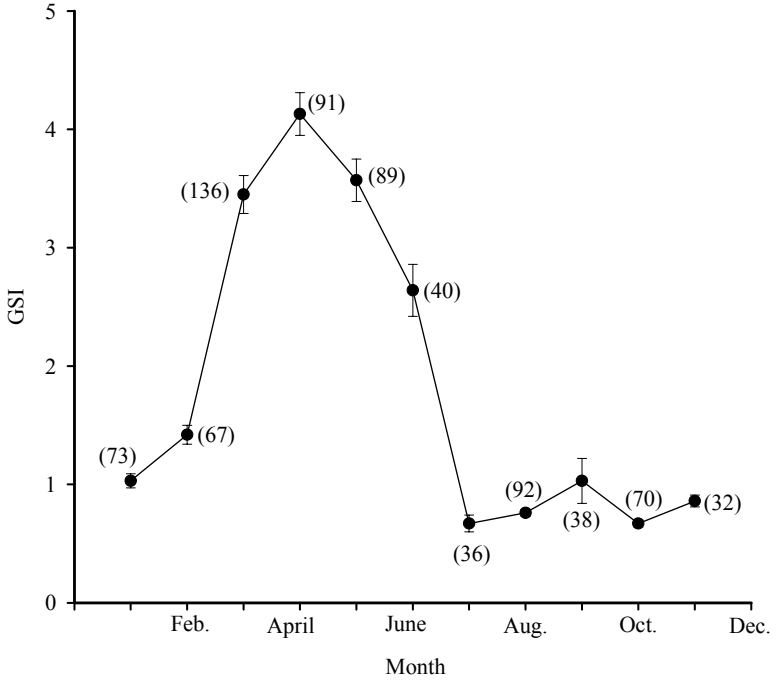

A
Total length (mm)
1200
1000
800
600
400
0
5
10
15
20
25
30
35
40
Age (years)
Males
1980-87 (n = 476)
1996-98 (n = 406)

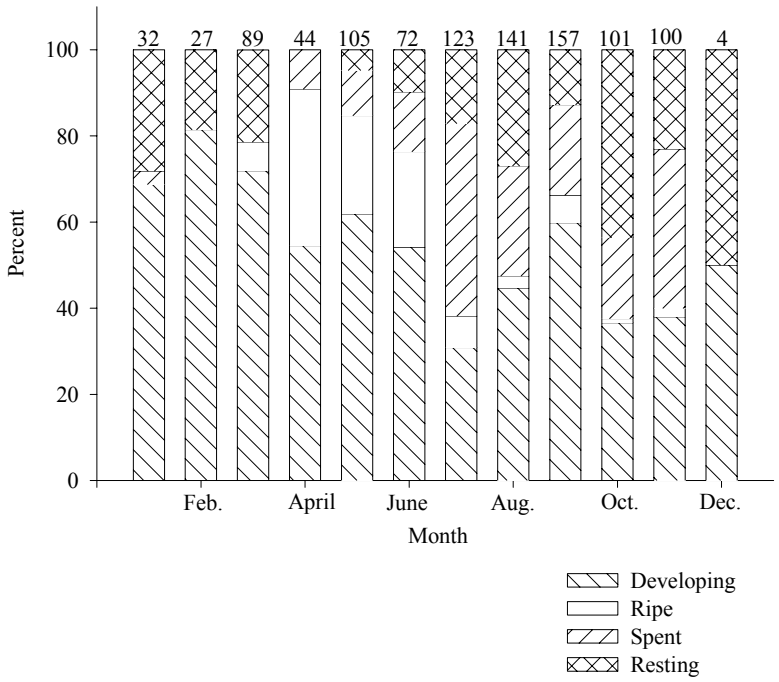

B
Total length (mm)
1000
800
600
400
0
5
10
15
20
25
30
35
40
Age (years)
Females
1980-87 (n = 449)
1996-98 (n = 515)

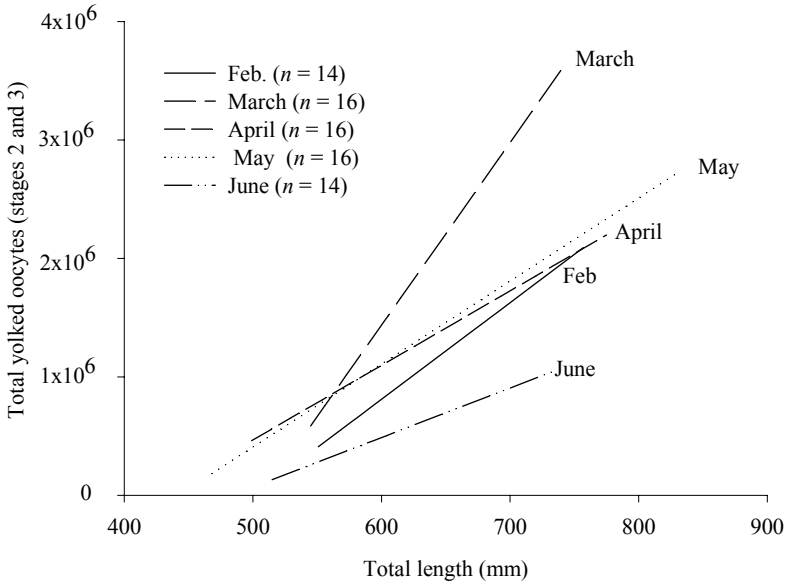

Immature (n = 17)
Developing, ripe, spent (n = 804)
Resting (n = 193)
A
Frequency (percent)
0
5
10
15
20
301-400
401-500
501-600
601-700
701-800
801-900
901-1000
1001-1100
1101-1200
Total length (mm)

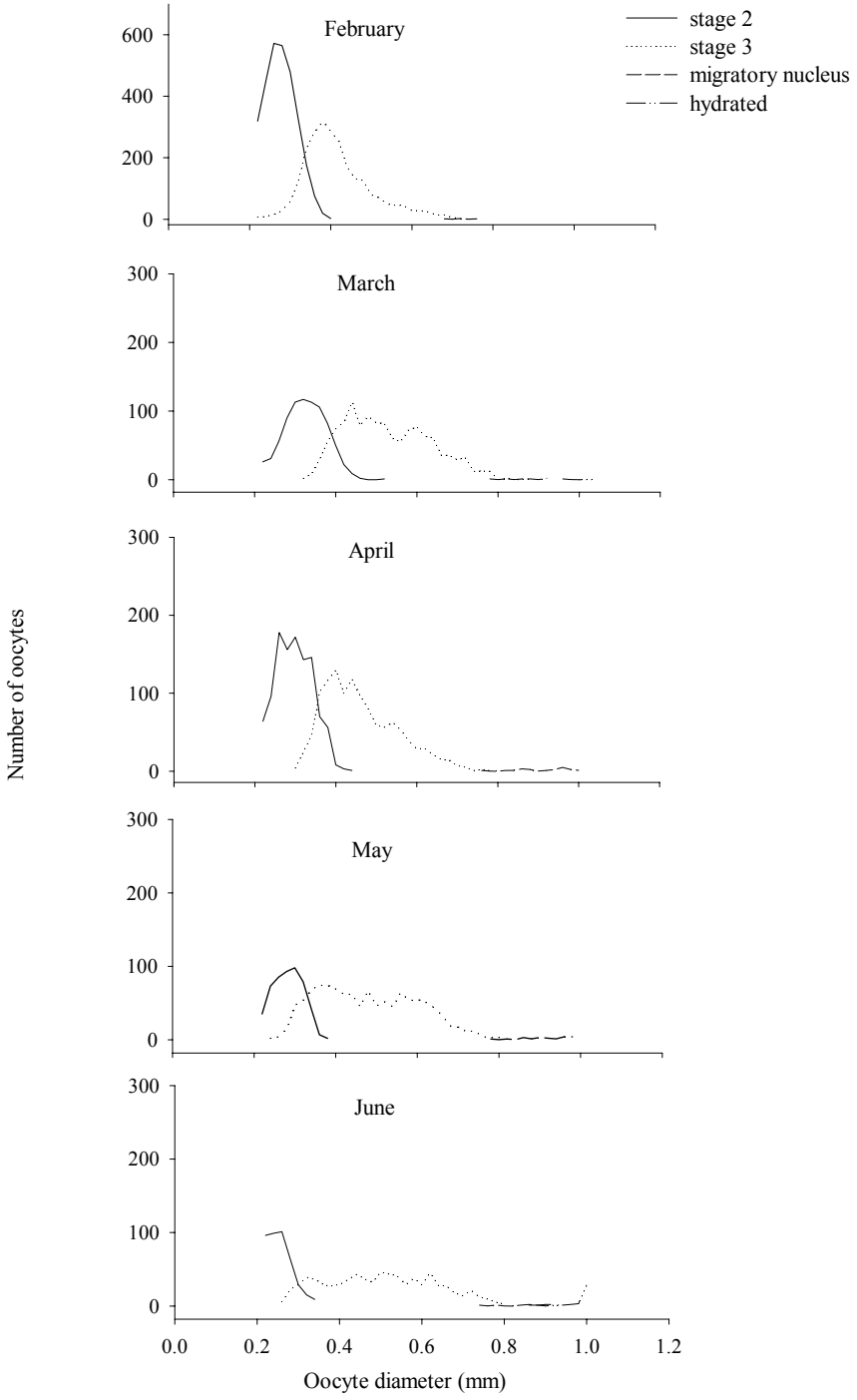

Immature (n = 4)
Developing, ripe, spent (n = 684)
Resting (n = 426)
B
Number
0
5
10
15
20
301-400
401-500
501-600
601-700
701-800
801-900
901-1000
1001-1100
1101-1200
Total length (mm)

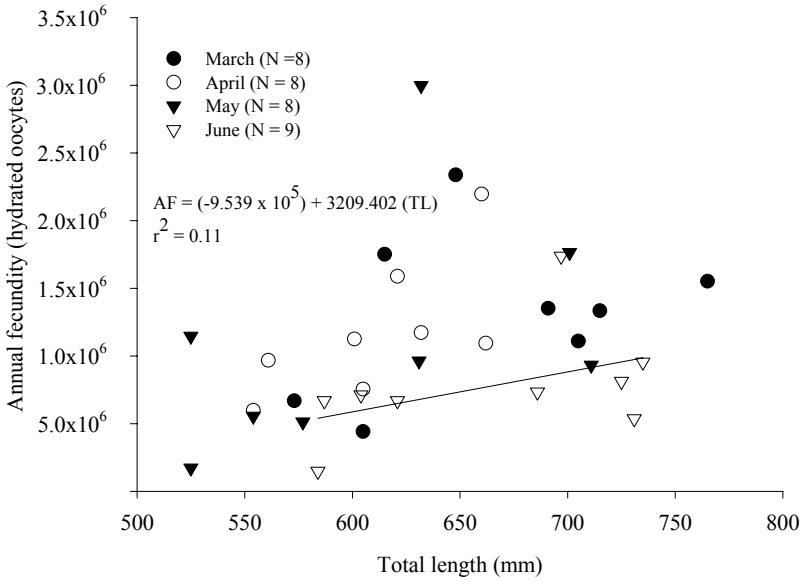

72
78
111
80
112
102
109
116
146
85
73
5
100
80
60
40
20
0
Percent
Feb.
April
June
Aug.
Oct.
Dec.
Month
Developing
Ripe
Spent
Resting
POFs (12-48 hrs old)


5
4
3
2
1
0
GSI
(73)
(67)
(136)
(91)
(89)
(40)
(36)
(92)
(38)
(70)
(32)
Feb.
April
June
Aug.
Oct.
Dec.
Month


32
27
89
44
105
72
123
141
157
101
100
4
100
80
60
40
20
0
Percent
Feb.
April
June
Aug.
Oct.
Dec.
Month
Developing
Ripe
Spent
Resting


4x10^6
3x10^6
2x10^6
1x10^6
0
Total yolked oocytes (stages 2 and 3)
Feb. (n = 14)
March (n = 16)
April (n = 16)
May (n = 16)
June (n = 14)
March
May
April
Feb
June
400
500
600
700
800
900
Total length (mm)


stage 2
stage 3
migratory nucleus
hydrated
February
March
April
May
June
Number of oocytes
Oocyte diameter (mm)
0
100
200
300
400
600
0.0
0.2
0.4
0.6
0.8
1.0
1.2


3.5x10^6
3.0x10^6
2.5x10^6
2.0x10^6
1.5x10^6
1.0x10^6
5.0x10^6
Annual fecundity (hydrated oocytes)
March (N =8)
April (N = 8)
May (N = 8)
June (N = 9)
AF = (-9.539 x 10^5) + 3209.402 (TL)
r^2 = 0.11
500
550
600
650
700
750
800
Total length (mm)