Age, growth, and reproduction of greater amberjack, *Seriola dumerili*, off the Atlantic coast of the southeastern United States.

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Abstract

The greater amberjack, *Seriola dumerili*, is a widely distributed pelagic and epibenthic member of the family Carangidae. Life history samples from a total of 2,729 greater amberjack were collected between 2000-2004 by personnel of the Marine Resource Monitoring Assessment and Prediction (MARMAP) program and National Marine Fisheries Service port agents in commercial fish houses from Cape Lookout, NC to Key West, FL. Ages were assigned to 1,996 specimens using thin transverse otolith sections, and sex and reproductive state were assigned to 2,517 from histological preparations of gonadal tissues. Ages of greater amberjack sampled ranged from 1-13; these data were described with a von Bertalanffy growth equation fitted to all specimens aged $L_t=1{,}241.5(1-e^{-0.28(t+1.56)})$. Sexual dimorphism was evident, with females being larger at age than males. The size at 50% maturity was 644 mm FL for males, and 733 mm FL for females. Age at 50% maturity for females was 1.3 yr. Estimates of potential annual fecundity ranged from 18,271,400 to 59,032,800 oocytes for specimens 930-1,296 mm FL and from 25,472,100 to 47,194,300 oocytes for ages 3-7. Peak spawning occurred primarily off south Florida and the Florida Keys during April and May. Even though the growth and reproductive characteristics of amberjack – extremely fast growth, early maturation, very high fecundity, and wide distribution - suggest the population would be difficult to overexploit, a recent stock assessment of the Gulf of Mexico population shows the species is vulnerable to overexploitation, and that the species might need to be managed more conservatively than the life history parameters may imply.

Introduction

The greater amberjack, *Seriola dumerili*, is a pelagic and epibenthic member of the family Carangidae (Carpenter 2002). This large jack is occurs from Nova Scotia through the Caribbean to Brazil, in the Gulf of Mexico, and throughout the Pacific, Indian and Eastern Atlantic Oceans as well as the Mediterranean Sea (Manooch 1984; Shipp 1988; Manooch and Potts 1997a, 1997b; Thompson et al. 1999; Carpenter 2002). Greater amberjack are often found near reefs, rocky outcrops or wrecks in depths ranging from 18-72 m (Manooch and Potts 1997b; Carpenter 2002). Due to their association with reefs and similar habitats, greater amberjack off the Atlantic coast of southeastern United States are included in the snapper-grouper complex and are managed by the South Atlantic Fishery Management Council (SAFMC).

Recreational fishing for greater amberjack began in the early 1950s from New York to Texas (Manooch and Potts 1997a). There was not a targeted fishery until charter boat fishermen popularized this fish in the 1970s because of its aggressive fighting behavior when hooked (Manooch and Potts 1997a; Cummings and McClellan 1999). Commercial landings for Atlantic greater amberjack increased from 3 mt in 1962 to 1,013 mt in 1991 (Cummings and McClellan 1999). This increase in landings may have been due to hook and line fishermen shifting toward greater amberjack during the mid 1980s when human consumption of this fish increased (Cummings and McClellan 1999). In April 1991, the SAFMC established a minimum size limit of 36 inches fork length for commercially harvested greater amberjack and a recreational bag limit of 3 fish per person per day (SAFMC 1991). Commercial landings have declined steadily since 1991 (when regionwide species landings data for greater amberjack first became available) to a low of 195 mt in 2003 (Figure 1). Similarly, recreational landings have shown a steady decline, albeit with relatively large annual fluctuations, since a peak in landings in 1987 (Figure 1). In 1998, additional regulations were established for greater amberjack, including a reduced bag limit of 1 fish per person per day, a 1,000 pound daily commercial trip limit, prohibition of harvest and possession in excess of the recreational bag limit during April, fishing year beginning on May 1 and a quota of 63% of 1995 landings (SAFMC 1998). However, recreational and commercial landings continued to decrease. Nonetheless, spawning potential ratio (SPR) for greater amberjack off the Atlantic coast of the southeastern United States was reported to be 84% in 1993 and the stock is currently being managed using an SPR value of 40% (SAFMC, 1998), suggesting the stock is not experiencing overfishing and is not overfished.

Studies on greater amberjack along the southeastern coast of the United States are limited and focused primarily on age and growth. Burch (1979) aged greater amberjack primarily from the upper Florida Keys using scales, and Manooch and Potts (1997a) utilized sectioned otoliths to age 323 fish from North Carolina to Florida. Burch (1979) conducted a limited study on the reproductive biology of greater amberjack off the southeastern coast of Florida using macroscopic staging techniques.

Management of greater amberjack has been based on insufficient and incomplete life history data; therefore, the purpose of this study was to assess the age structure, growth, sex ratio, size and age at maturity, spawning season, and annual fecundity of this species along the Atlantic coast of the southeastern United States.

Materials and Methods

Sampling

Life history samples from greater amberjack were collected during 2000-2004 by personnel of the Marine Resource Monitoring Assessment and Prediction (MARMAP) program and National Marine Fisheries Service port agents in commercial fish houses from Cape Lookout, NC to Key West, FL. All fishermen from whom samples were collected utilized snapper reels (hook and line, see Wyanski et al. 2000). During 2000-2002, up to 150 specimens per month were collected during the open season (all months except April). Sub-legal fish were sampled from vessels based in South Carolina during this period. In 2003, a directed effort was made to sample greater amberjack during the spawning season. Sampling was conducted in the Florida Keys, a well-known spawning area, during March, April and May. A minimum of 100 specimens per month were sampled from four participating fishing vessels. This effort was continued in 2004, however, sampling was restricted to potentially fecund females (macroscopic evidence of final oocyte maturation), as sampling in 2003 identified very few females with hydrated oocytes. Only one vessel was utilized for specimen collection in 2004. Additional samples were collected during fishery-independent sampling by MARMAP using chevron traps, hook and line and bottom longline (see Harris and McGovern 1997 and Harris et al. 2004, for a complete description of MARMAP sampling).

Total length, fork length, standard length (TL, FL, SL; mm) and whole weight (WW; 10 g) were measured for each fish sampled. Left and right (when possible) sagittal otoliths were removed and temporarily stored in vials of ethanol. The entire gonad of each fish was removed, weighed (g) and a section from the posterior portion retained for histological processing. Selected ovaries were preserved for fecundity analyses.

Age Determination

In the laboratory, otoliths were rinsed clean and stored dry in vials. Several methods of otolith preparation were tested to determine which method produced a clearer view of the core and increments. Otoliths were mounted whole and polished to the core; transverse sections through the core were made and polished on one or both sides, and transverse sections (0.5 mm) were made and viewed unpolished but immersed in Cytoseal® mounting media. The last method produced the most consistent results, and was utilized as the protocol for preparation of all remaining amberjack otoliths (approximately 90%). Increments (one opaque and one translucent zone) were counted on all sections by two readers working independently using a dissecting microscope with transmitted and reflected light and without knowledge of the size, sex or date of capture of any specimen. Each reader counted increments for each fish once and quantified the edge type of each section aged (1=opaque zone, 2=narrow translucent zone, 3=medium translucent zone or 4=wide translucent zone). Otoliths were re-examined simultaneously by both readers if increment count and/or edge type assignments differed. Specimens which were deemed unreadable by either or both readers as well as specimens for which the difference between readers was 5 increments or greater, were discarded from the age analyses. Periodicity of increment formation was indirectly validated using the mean edge type value by month, and the month of opaque zone formation (when the mean edge type value approached one) was determined using these data. The ages assigned to specimens with a medium or wide translucent zone captured after January 1 of a given year, but before the month of opaque zone formation, were the increment counts plus one; the ages assigned to all other specimens reflected the increment count for each specimen.

Mean observed fork lengths, mean ages, and mean observed fork lengths at age were compared between sexes using Student's *t*-test. Von Bertalanffy growth curves were fitted to individual observed lengths at age for both sexes separately and for sexes combined.

Reproductive biology

The posterior portion of the gonads was fixed in 11% seawater- formalin solution buffered with marble chips for 7-14 days and transferred to 50% isopropanol for an additional 7-14 days. Reproductive tissue was processed in an automated (self-enclosed) tissue processor and blocked in paraffin. Three transverse sections (6-8 μm thickness) were cut from each sample with a rotary microtome, mounted on glass slides, stained with double-strength Gill hematoxylin, and counterstained with eosin-y.

Sections were viewed under a compound microscope, and sex and reproductive state were determined independently by two readers without knowledge of date of capture, specimen length, and specimen age; the second reader examined sections from one-third of the specimens. Reproductive state was assigned using histological criteria described in Harris et al. (2004) for blueline tilefish, *Caulolatilus microps*. Sections were re-examined simultaneously by both readers when assignments differed. Specimens with developing, ripe, spent, or resting gonads were considered sexually mature. For females, this definition of maturity included specimens with oocyte development at or beyond the cortical alveoli stage and specimens with beta, gamma, or delta stages of atresia (see Hunter and Macewicz 1985a). To ensure that females were correctly assigned to the immature and resting categories, the length-frequency histogram of females that were definitely mature (i.e., those that were developing, ripe, or spent) was compared with those of immature and resting females. Size and age at 50% maturity were estimated with the PROBIT procedure (SAS Institute, Inc. 1989). The LOGISTIC procedure was used to determine which cumulative distribution function (normal, logistic, Gompertz) to use in the PROBIT procedure.

Spawning season for female greater amberjack was estimated based on the presence of migratory-nucleus (MN) oocytes and postovulatory follicles (POFs); hydrated oocytes were observed in histological sections from only two specimens. Because the rate of POF degradation is a function of water temperature, POFs were assigned approximate ages according to the criteria developed by Hunter et al. (1986) for skipjack tuna *Katsuwonus pelamis*. Greater amberjack spawn in outer continental shelf and upper slope waters with spring bottom temperatures around 24 ^{o}C (Lee and Williams 1999; Sedberry et al. 2006), similar to the temperatures (23-24 ^{o}C) at which skipjack tuna spawn. A female gonadosomatic index (GSI; Nikolsky 1963) was calculated to quantify the reproductive cycle: GSI = (ovary weight/WW)(100). Sex ratios (male:female; mature specimens only) were examined for each size and age class with a chi-square goodness of fit test to determine if the ratios differed from the expected 1:1. A comparison was made only if the expected frequency was >5. All samples collected in 2004 and one collection from 2003 were excluded from in sex ratio calculations as they were specifically targeted toward sampling fecund females.

Fecundity

We used four fecundity terms that are defined in Hunter et al. (1992): (1) Total fecundity, (2) batch fecundity, (3) potential annual fecundity, and (4) indeterminate fecundity. To reduce the amount of formalin used, developing gonads from only 12 females were preserved whole in 10% seawater formalin. Fresh and preserved gonad weights were obtained for those ovaries and a regression equation (Preserved wt (g) =

fresh wt (g) * 0.966 - 15.531; adj. r^2=0.997, n = 12) was developed to convert fresh weight to preserved weight thereafter. This equation was also applied to specimens with MN oocytes, which have a composition similar to that of yolked oocytes in developing-state gonads. For subsequent specimens, a longitudinal strip of tissue (3 cm x 10 cm) from one ovarian lobe, representing the anterior through posterior portions was preserved. Oocyte stages referred to here as hydrated, MN, and yolked (stages 2 and 3, as defined by Hunter et al. (1992)) were identified and counted in all samples for the various aspects of this fecundity assessment. Oocyte size distribution in 15 specimens with developing gonads was assessed using Global Lab® image analysis software. The software calculated the average radius, which was then doubled to get diameter, of each oocyte in a subsample of 180-300 whole yolked oocytes per specimen. The size distributions from these measurements and the assessment of total fecundity were used to address whether or not greater amberjack exhibited indeterminate fecundity.

To determine whether the MN oocytes were randomly distributed within the ovary, samples from one lobe were taken at anterior, middle, and posterior locations, for a total of three 75-mg samples from each of nine fish undergoing final oocyte maturation. Samples were weighed with a Sartorius® digital balance (±0.00001 g) and all MN oocytes in the samples were counted. A two-way analysis of variance without interaction was used to test for the effects of location and individual fish on oocyte density (number of MN oocytes per g of ovary).

To estimate total fecundity in females with developing gonads, two 25-30 mg samples were taken from random locations and the number of stage-3 oocytes was counted. Total fecundity was calculated by multiplying the preserved ovary weight by oocyte density (number of stage-3 oocytes per g ovary). The relationship between total fecundity and FL was described for three months (March, April, and May) and the effect of each month on total fecundity was examined using ANCOVA.

Greater amberjack exhibited evidence of indeterminate fecundity; therefore, batch fecundity and spawning frequency in specimens from southeast Florida (24-25^{0} N) were estimated to calculate potential annual fecundity. The hydrated oocyte method (Hunter and Goldberg 1980; Hunter et al. 1985) was modified and used to determine batch fecundity. Two 75-mg samples were taken from random locations in ovaries undergoing final oocyte maturation and immersed in a 1-5% formalin solution to count the MN and hydrated oocytes. The effect of month on batch fecundity was examined using ANCOVA.

We obtained two estimates of spawning frequency based on histological criteria (presence of: 1) MN or hydrated oocytes, and 2) POFs $<$ 24 hr old) that indicate imminent or recent spawning (see Goldberg 1980; Hunter and Macewicz 1985b). Estimates of spawning frequency represented the proportion of specimens with each criterion among reproductively active females (i.e., vitellogenic oocytes present, developing and ripe reproductive states) collected during the spawning season, defined here as the first and last occurrence specimens with MN oocytes, hydrated oocytes, or POFs $<$ 24 hr old. The two estimates of spawning frequency were averaged (see Fitzhugh et al. 1993) and the average was multiplied by the number of days in the spawning season to determine the number of spawning events in that season. Potential annual fecundity was calculated by multiplying batch fecundity by the number of spawning events.

All statistical analyses were performed in SAS (SAS Institute, Inc. 1989), and the results were considered significant at $\alpha < 0.05$.

Results

Sampling

A total of 2,729 amberjack were sampled during the sampling period, from 24°N to 34°N, encompassing almost the entire range of greater amberjack off the southeastern United States (Figure 2), in depths ranging from 17 to 212 m, although 36% of specimens were caught between 50 – 60 m (n=982). The vast majority of the samples were obtained by fishery-dependent sampling (99%; n=2,702).

The mean fork length of all fish sampled was 950 mm FL (standard deviation (SD) 154 mm; range 233-1,445; n=2,700; Figure 3). Fork length was not recorded for 29 specimens. The mean length of males (918 mm FL (SD 128); range 267-1,311; n=1,107; Figure 3) was significantly smaller than that for females (969 mm FL (SD165); range 352-1,435; n=1,390; t=-8.37; df=2,495; P<0.0001). The length frequency distributions for the two sexes were significantly different (KSa=5.13; P< 0.001; Figure 3).

Age determination

Of the 2,335 otoliths collected, 1,985 were successfully aged (85%). Age data was unavailable for all specimens due to missing, broken, or unreadable otoliths. The average percent error (APE) was 10.3%, with an associated CV of 14.5 (Beamish and Fournier 1981). Opaque zone formation occurred once per year during June (Figure 4). Based on this result, the increment counts of specimens captured between January and May of any year, and with a medium or wide translucent zone on the edge of the section were advanced by one to provide a calendar age. The mean age of all fish aged was 4.2 years old (SD 1.63; range 1-13; Figure 5), while the mean age of males was 4.1 (SD 1.6; range 1-13, n=820) and females was 4.23 (SD 1.65; range 1-13; n=1,026; Figure 5).

There were no significant differences between the mean ages (*t*=-1.69, df=1,844, *P*=0.09), or the age frequency distributions of male and female amberjack (*KSa*=1.17; *P*=0.12).

Sexual dimorphism was evident in greater amberjack, with females being larger at age than males, although females were significantly larger than males only for ages 3, 4, 7 and 9 ($P<0.05$; Figure 6). A von Bertalanffy growth curve were fitted to all specimens aged generated the equation $L_t=1{,}241.5(1-e^{-0.28(t+1.56)})$. Curves were additionally fitted to sex specific age data and females showed the largest L_∞ and lowest k, while males had the smallest L_∞ and highest k (Table 1).

Reproductive Biology

A total of 2,537 gonad samples were obtained from the 2,729 fish sampled. Sex and reproductive state were assigned to 2,517 of these. The overall male:female sex ratio for greater amberjack was 1:1.11, significantly different from a 1:1 ratio (Table 2), although this might be a function of females dominating the larger size classes (> 1100 mm FL), where the sex ratio was significantly biased toward females. The sex ratio was significantly biased toward females for only two age classes, and no obvious trends were evident in these data (Table 2).

Immature specimens comprised 4.5% (n=115) of the specimens for which reproductive stage was established. Correct assignment of reproductive tissue to the immature and resting categories is indicated by the near or complete overlap in the left tail of length histograms for specimens that were definitely mature (i.e., developing, ripe, and spent) and specimens that were resting and by the minimal overlap in the histograms for immature and resting specimens (Figure 7). The smallest mature male was 464 mm

FL (Table 3) and the youngest was age 1 (Table 4); the size at 50% maturity was 644 mm FL (Probit; 95% CI = 610-666), and the largest immature male was 755 mm FL, and the oldest was age 5 . All males were mature at 751-800 mm FL and age 6. The smallest mature female was 514 mm FL (Table 3), and the youngest was age 1 (Table 4); the size at 50% maturity was 733 mm FL (Logit; 95% CI = 719-745), and the largest immature female was 826 mm FL, and the oldest was age 5. All females were mature by 851-900 mm FL and age 6. Age at 50% maturity for females was 1.3 yr (Gompit; 95% CI = 0.7-1.7).

Based on the occurrence of MN oocytes and (POFs), spawning occurred from January through June, with peak spawning in April and May (Figure 8). Mean GSI values also peaked in April and May (Figure 9). Although fish in spawning condition were captured from North Carolina through the Florida Keys (Figure 2), spawning appears to occur primarily off south Florida and the Florida Keys. Greater amberjack in spawning condition were sampled from a range of depths, although the bulk of samples were from the shelf break (Figure 2).

Fecundity

There was no significant difference in the density of MN oocytes among three selected locations in the ovaries of nine specimens (F=2.65; df=2; P=0.1016), which indicated that samples for estimating batch fecundity could be taken from any location without bias.

Total fecundity as a function of fork length was essentially constant throughout the spawning season and did not exhibit a declining trend over time (Figure 10). The interaction term in an ANCOVA showed that the slopes of the equations were not significantly different among months (*F* = 1.38; df=2; *P* = 0.2578); however, the intercept of the March equation was lower than that for April (*P*=0.0151) because oocyte development was at an earlier stage of vitellogenesis. No difference in intercepts was noted between April and May (*P*=0.0779).

Annual fecundity in greater amberjack is indeterminate because total fecundity did not decrease during the spawning season and no size gap between stage-3 and earlier stage oocytes developed at any time during the spawning season (Figure 11). Continuous production of oocytes was also evident, as the percentage of stage-3 yolked oocytes did not progressively decrease over time.

Spawning frequency and batch fecundity, necessary to estimate potential annual fecundity, were based on MN and hydrated oocytes, and spawning frequencies based on the occurrence of POFs were estimated for comparative purposes. Hydrated oocytes never represented more that 2% of the oocytes counted to estimate batch fecundity, as fishing generally occurred during morning hours, apparently several hours prior to the time of peak oocyte hydration. MN oocytes were predominant in the 31 specimens with oocytes sufficiently developed to clearly identify the batch to be released. The proportion of specimens with MN or hydrated oocytes among females with oocytes undergoing vitellogenesis was similar to the proportion with POFs < 24 hr old (0.213 vs. 0.241; Table 5). The average of the two proportions was 0.227, which corresponded to a spawning periodicity of approximately 5 days. With a spawning season of approximately 73 days off South Florida (27 February through 10 May; see Figure 9), an individual female could spawn approximately 14 times.

Statistically significant relationships were developed between batch fecundity and total length, fork length, and age (Table 6). Given the small sample sizes in late March

(19-28th) and early May (3rd) and the similarity of the data from all months, data were combined to estimate the relationship between batch fecundity and fork length (Figure 12). Multiplying the estimated number of spawning events (14) by batch fecundity (BF) estimates (BF = 7.955*FL – 6,093,049); Table 6 and Figure 12) for greater amberjack 930-1296 mm FL produced estimates of potential annual fecundity that ranged from 18,271,400 to 59,032,800 oocytes. Relative to age, estimates of potential annual fecundity ranged from 25,472,100 to 47,194,300 oocytes for ages 3-7.

Discussion

Our study of the age, growth and reproduction of greater amberjack is the most comprehensive conducted to date. Samples were collected from the Dry Tortugas off the Florida Keys to Cape Lookout in North Carolina, almost the entire range of greater amberjack off the southeastern United States, and the number of specimens sampled is the largest in any published study (Burch 1979; Manooch and Potts 1997a; 1997b; Thompson et al. 1999). Although greater amberjack were sampled over a period of four years for this study, the results presented should provide an accurate reflection of the current life history parameters of the greater amberjack population off the southeastern United States.

The otoliths of greater amberjack are very small (approximately 1 cm x 0.3 mm x 0.1 mm), making the production of consistent sections quite problematic. Furthermore, the sections were quite difficult to interpret, as has been documented in previous studies (Manooch and Potts 1997a; 1997b). Nonetheless, the ages appear accurate, as evidenced by the APE of 10%, and the ages generated should reflect the age structure of the population off the southeastern United States. We were able to indirectly validate the annual periodicity of increment formation using state of the increment at the otolith edge. We found that one increment formed per year in greater amberjack, which agreed with Manooch and Potts (1997a; 1997b). Furthermore, Thompson et al. (1999) used information from six otoliths marked with oxytetracycline to show the formation of one increment between November and March in 2-3 yr old specimens. Our results differed slightly with Manooch and Potts (1997b) regarding the timing of increment formation (June vs. April). While relatively small, a two-month difference in the timing of increment formation could affect the assignment of calendar age for some specimens. The number of specimens utilized for our estimate of when opaque zone formation is completed (n=1,985) might be more precise than that reported in Manooch and Potts (1997b, n≈155) for specimens in the Atlantic.

Greater amberjack are fast growing and relatively short-lived. Our study showed a larger size at age for ages 1 through 5 when compared to one study from the Gulf of Mexico (Thompson et al. 1999), after which the size at age of fish from our study where smaller than those from the Gulf (Figure 13). However, our results showed a greater size for almost all ages than two other studies – one from the Atlantic (Manooch and Potts 1997a) and one the Gulf of Mexico (Manooch and Potts 1997b) (Figure 13). The large sample size of our study might provide a better estimate of the age structure of greater amberjack off the Atlantic coast of the southeastern United States than previous studies.

Sexual dimorphism was previously documented by Burch (1979) and Thompson et al. (1999). Thompson et al. (1999) suggested this might due to females living longer than males. However, they compared the sums of squares of von Bertalanffy growth curves fitted to male and female amberjack and found no differences (Thompson et al

1999). Our study showed no difference in longevity between males and females. Furthermore, sex-specific growth curves are typically not utilized for stock assessments.

The sex ratio of greater amberjack reflects the sexual dimorphism observed, as females grow to dominate the larger size classes, while males dominated the smaller size classes. However, no trends were apparent in the age-based sex ratio, confirming that there is no difference in longevity between males and females. Greater amberjack is an extremely fecund species, producing from 18 to 59 million eggs per individual female in a single spawning season. Females might attain a larger size to maximize fecundity and increase their potential contribution to future generations.

In spite of sampling females along the entire Atlantic coast of the southeastern United States, we were unable to locate ovaries containing hydrated oocytes during the first two years of the study. Anecdotal information identified the Florida Keys as a primary spawning area, and that area was targeted for sampling during the spawning season in 2003. Our data confirm this as the area where most greater amberjack spawn, and demonstrate that the further north a female amberjack occurs in the Atlantic, the less likely it will be in spawning condition. The percentage of mature females with histological evidence of spawning during April and May ranged from 77% off southeast Florida (24-25^{o} N) to 10% off Georgia and the Carolinas (31-34^{o} N). It appears that although greater amberjack is a wide-ranging species, moving all along the southeastern Atlantic coast and into the Gulf of Mexico (MARMAP unpub. data), a primary spawning area might exist for Atlantic specimens. The extent to which spawning events in the Atlantic north of 25^{o}N contribute to recruitment is unknown, however, our data suggests the spawning occurring off the Florida Keys between late February and May might generate the bulk of recruitment. It is possible that the spawning season off the Florida

Keys does extend beyond May 10, as only four adult females, one of which had developing gonads, were collected during the remainder of May and June. Burch (1979) reported sampling fish off southeast Florida in spawning condition (based on macroscopic examination) from March through June, with a peak in April and May. It is not known if greater amberjack from the Gulf of Mexico utilize this spawning area off southeast Florida.

Although commercial landings of greater amberjack have decreased markedly over time, the most recent stock assessment (Legault and Turner 1999) and trends report (Potts and Brennan 2001) submitted to the SAFMC made no indication that greater amberjack is being overfished or experiencing overfishing in the Atlantic off the southeastern United States. However, there is little long-term data against which to compare current life history parameters for the purpose of identifying changes that may have occurred over time. Greater amberjack in the present study were larger at age when compared to the results of the only other age and growth study off the southeastern United States that utilized otoliths, perhaps suggesting an increase in fishing mortality as population numbers decrease, and more resources become available for fewer fish. Similarly, the smaller fish in older age classes seen in our study might reflect an increase in mortality, as the larger old individuals are removed from the population. However, increased growth rates could also simply reflect less interspecific competition, as more resources become available for greater amberjack as other pelagic and demersal species are increasingly exploited. Even though the growth and reproductive characteristics of amberjack – extremely fast growth, early maturation, very high fecundity, and wide distribution - suggest the population would be difficult to overexploit, a recent stock assessment of the Gulf of Mexico population (SEDAR09 2007) shows the species is vulnerable to overexploitation, and that the species might need to be managed more conservatively than the life history parameters may imply.

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Table 1. The parameters derived from the von Bertalanffy growth equations fitted to individual size at age data for greater amberjack sampled off the Atlantic coast of the southeastern United States, 2000-2004.

Sex	L_∞	k	t_0
Combined	1241.5	0.28	-1.56
Male	1105.6	0.36	-1.42
Female	1351.6	0.22	-1.83

Table 2. The sex ratio of mature greater amberjack sampled off the Atlantic coast of the southeastern United States during 2000-2003 for 100 mm length classes, and ages. Only collections during which amberjack were randomly sampled were used to derive sex ratio.

Length Class (mm FL)	Male	Female	Sex Ratio (male:female)	χ^2	*p*	H_0
401-500	1	0	1:0			
501-600	1	2	1:2			
601-700	15	3	1:0.2			
701-800	120	43	1:0.36	36.37	<0.0001	Reject
801-900	264	253	1:0.96	0.23	0.631	Accept
901-1000	347	276	1:0.79	8.09	0.004	Reject
1001-1100	255	289	1:1.14	2.13	0.145	Accept
1101-1200	38	206	1:5.4	115.7	<0.0001	Reject
1201-1300	3	72	1:24	63.41	<0.0001	Reject
1301-1400	2	15	1:7.5			
1401-1500	0	2	0:1			
Overall	**1,046**	**1,160**	**1:1.11**	**5.89**	**0.015**	**Reject**
Age class (year)						
1	4	1	1:0.25			
2	37	37	1:1	0	1	Accept
3	249	240	1:0.96	0.17	0.683	Accept
4	257	257	1:1	0	1	Accept
5	122	157	1:1.29	4.39	0.036	Reject
6	54	84	1:1.55	6.52	0.011	Reject
7	24	34	1:1.42	1.72	0.193	Accept
8	12	22	1:1.83	2.94	0.082	Accept
9	6	12	1:2	2	0.157	Accept
10	4	6	1:1.5			
11	4	4	1:1			
12	1	0	1:0			
13	3	2	1:0.66			

Table 3. Percentage of mature specimens by length interval for female and male greater amberjack collected during 2000-2004 off the Atlantic coast of the southeastern United States. Specimens in the developing, spawning, spent, or resting stages were considered mature. All specimens were examined histologically. *n* = number of specimens.

mm TL	Female *n* = 1,299		Male *n* =1,077	
	%	*n*	%	*n*
251-300	-	(0)	0.	(1)
301-350	-	(0)	0.	(1)
351-400	0.	(5)	0.	(3)
401-450	0.	(3)	0.	(1)
451-500	0.	(5)	50.0	(2)
501-550	33.3	(3)	33.3	(3)
551-600	0.	(7)	0.	(2)
601-650	25.0	(8)	11.1	(9)
651-700	3.7	(27)	63.6	(22)
701-750	31.3	(32)	97.3	(38)
751-800	76.2	(42)	98.8	(84)
801-850	99.1	(110)	100.0	(127)
851-900	100.0	(144)	100.0	(137)
901-950	100.0	(131)	100.0	(155)
951-1000	100.0	(156)	100.0	(192)
1001-1400	100.0	(626)	100.0	(300)

Table 4. Percentage of mature specimens by age interval for female and male greater amberjack collected during 2000-2004 off the Atlantic coast of the southeastern United States. Specimens in the developing, spawning, spent, or resting stages were considered mature. All specimens were examined histologically. *n* = number of specimens.

Age	Female *n* = 955		Male *n* = 796	
	%	*n*	%	*n*
1	14.3	(7)	66.7	(6)
2	62.7	(59)	78.7	(47)
3	90.4	(270)	99.2	(251)
4	99.3	(272)	99.2	(260)
5	99.4	(167)	99.2	(123)
6	100.0	(89)	100.0	(55)
7	100.0	(42)	100.0	(24)
8	100.0	(25)	100.0	(12)
9	100.0	(12)	100.0	(6)
10-11	100.0	(10)	100.0	(8)
12-13	100.0	(2)	100.0	(4)

Table 5. Number of female greater amberjack with migratory nucleus or hydrated oocytes (MN) oocytes, < 24 h old postovulatory follicles (POFs), and total number of mature females with oocytes undergoing vitellogenesis in samples collected by commercial fishers off the Florida Keys with snapper reels during February 27 through May 10 of 2001-2004. The proportions were averaged to estimate spawning frequency.

Date	No. with MN or hydrated oocytes	No. with < 24 h old POFs	Total mature females
February	-	1	3
March	9	6	53
April	45	46	195
May	15	25	73
Total	69	78	324
Proportion of total	0.213	0.241	

Table 6. Linear regression coefficients for the relationship between batch fecundity (BF; number of migratory nucleus and hydrated oocytes) and total length, fork length, and age in greater amberjack. Specimens were collected off the Florida Keys with snapper reels by commercial fishers during March through May of 2003-04. **P<0.0001 and *P<0.001.

Linear equation BF = a + bX

X	a	95%CI	b (x10^3)	95%CI (x10^3)	Adjusted r^2	F	N	Range
Total length (mm)	-7,807,063	±1,508,900	8.398	±1.245	0.6053	45.47**	30	1,075-1,425
Fork length (mm)	-6,093,049	±1,428,888	7.955	±1.339	0.5336	35.32**	31	930-1,296
Age (yr)	655,746	± 1,312,306	387.897	± 269.342	0.2609	8.77*	23	3-7

Figure Legends

Figure 1. Commercial and recreational landings of greater amberjack off the Atlantic coast of the southeastern United States.

Figure 2. Capture locations for greater amberjack 2000-2004. Fishery-dependent locations data may be approximate.

Figure 3. Length frequency of all greater amberjack sampled during 2000-2004 off the Atlantic coast of the southeastern United States.

Figure 4. The timing of opaque zone formation for greater amberjack based on the mean monthly appearance of the marginal increment. Codes used: 1=opaque zone on the otolith edge; 2=narrow width translucent zone on the edge; 3=medium width translucent zone; 4=wide width translucent zone. Error bars represent ± 1 standard error.

Figure 5. Age frequency of all greater amberjack sampled during 2000-2004 off the Atlantic coast of the southeastern United States.

Figure 6. The mean size at age for male and female greater amberjack, 2000-2004 off the Atlantic coast of the southeastern United States. The von Bertalanffy growth curve is that fitted to the combined data set. Error bars represent ± 1 standard error.

Figure 7. Comparison of length frequencies of female (A) and male (B) greater amberjack sampled along the Atlantic coast of the southeastern United States, 2000-2004 that were categorized as immature, definitely mature, or resting. Definitely mature specimens were developing, ripe, or spent.

Figure 8. Reproductive seasonality of female greater amberjack collected during 2000-2004 in three latitudinal zones along the Atlantic coast of the southeastern United States: **A**) 24-25^{o} N, **B**) 26-30^{o} N, and **C**) 31-34^{o} N. The number of specimens examined is above each bar. FOM = final oocyte maturation (mostly specimens with migratory-nucleus oocytes, as only two specimens were classified as "Ripe" – presence of hydrated oocytes), POF = postovulatory follicles.

Figure 9. Gonadosomatic index (GSI) and mean fork length by month for female greater amberjack collected off the Atlantic coast of the southeastern United States during 2000-2004. The GSI = 100 X gonad weight/whole body weight. Error bars represent one standard error; numbers in parentheses are the number of specimens examined.

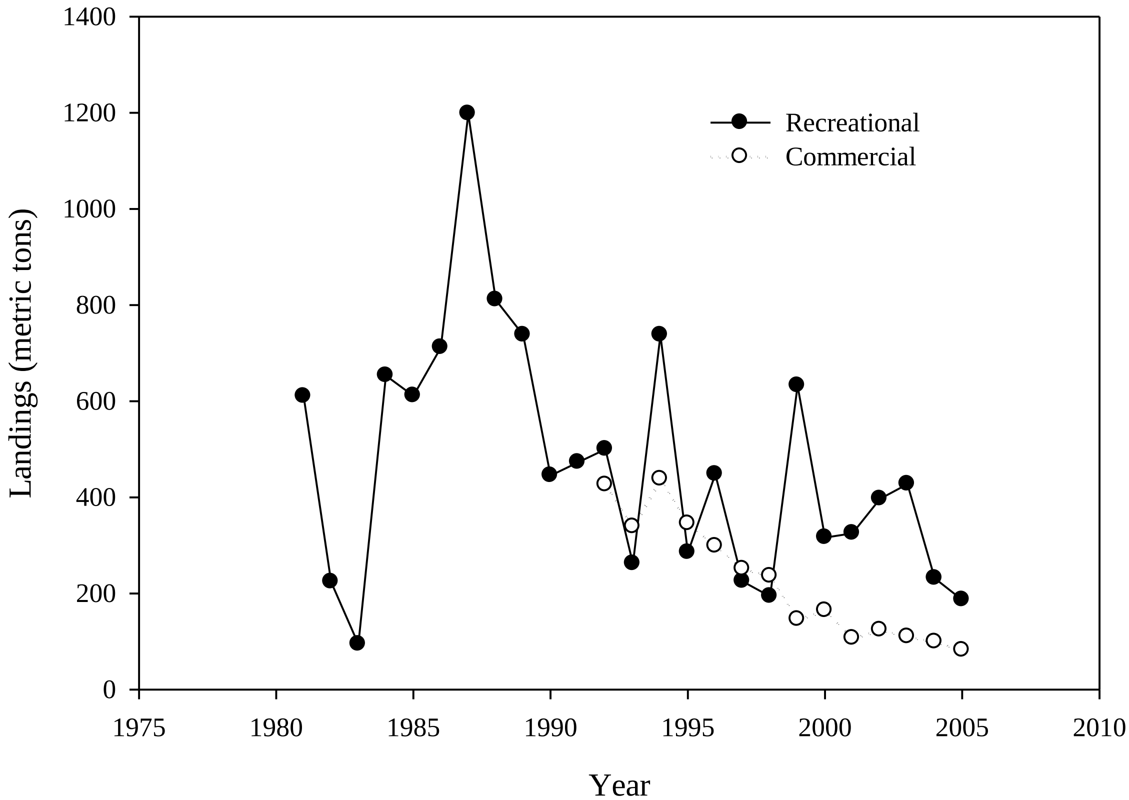
Figure 10. Estimates of total fecundity in greater amberjack relative to fork length during March, April and May. The specimens were captured along the Atlantic coast of the southeastern United States, 2000-2004.

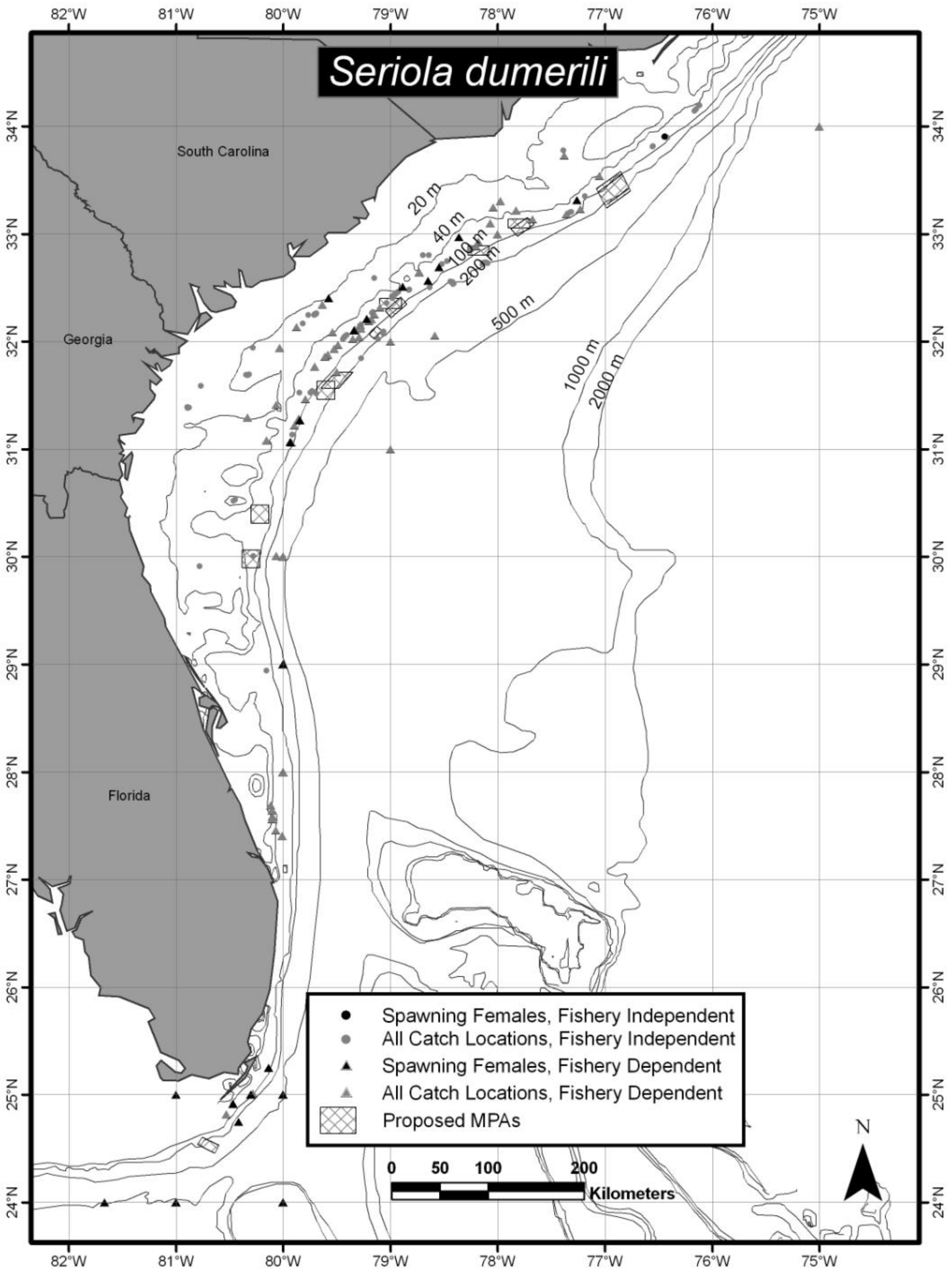
Figure 11. Percentage frequency by diameter for two stages of vitellogenic oocytes (see Hunter et al. 1992) in 15 greater amberjack (five specimens per month). Specimens were

collected off the Florida Keys with snapper reels by commercial fishers during March through May of 2001-2004.

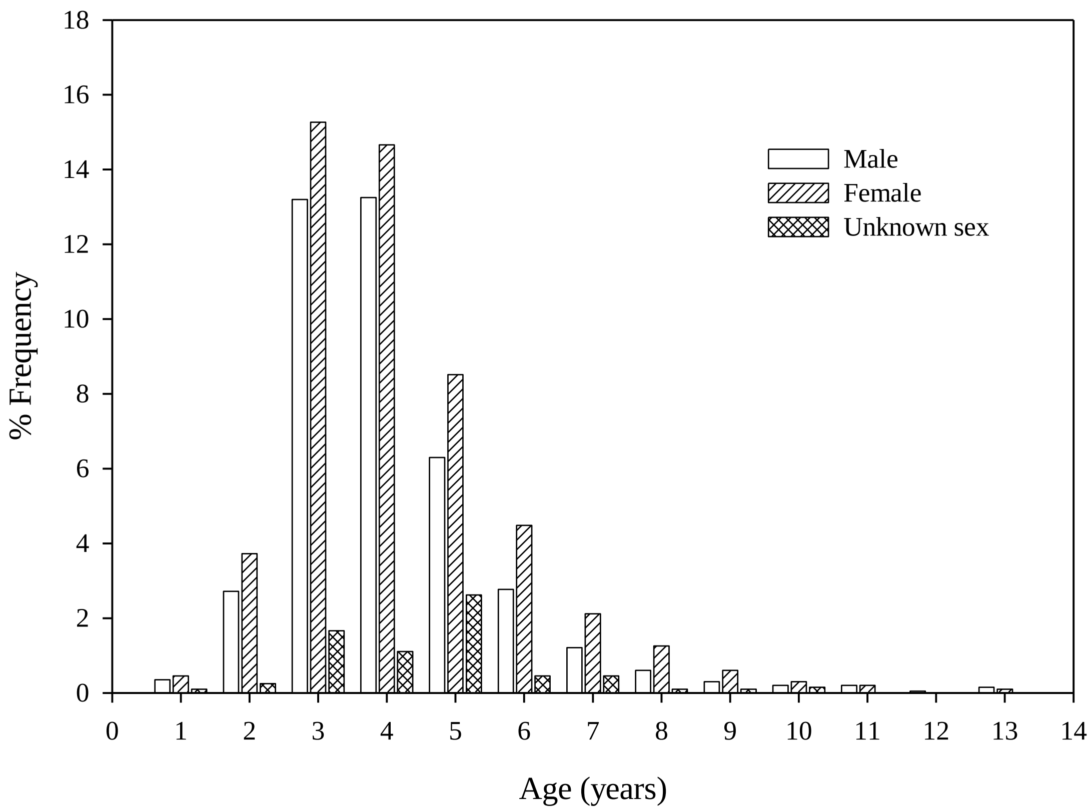
Figure 12. Estimates of batch fecundity in greater amberjack relative to fork length during late March through early May. Migratory-nucleus and hydrated oocytes were counted in 31 specimens that were captured off the Florida Keys with snapper reels in the commercial fishery during 2003-2004.

Figure 13. A comparison study of the mean size at age of greater amberjack from several studies in the Gulf of Mexico and Atlantic off the southeastern United States.

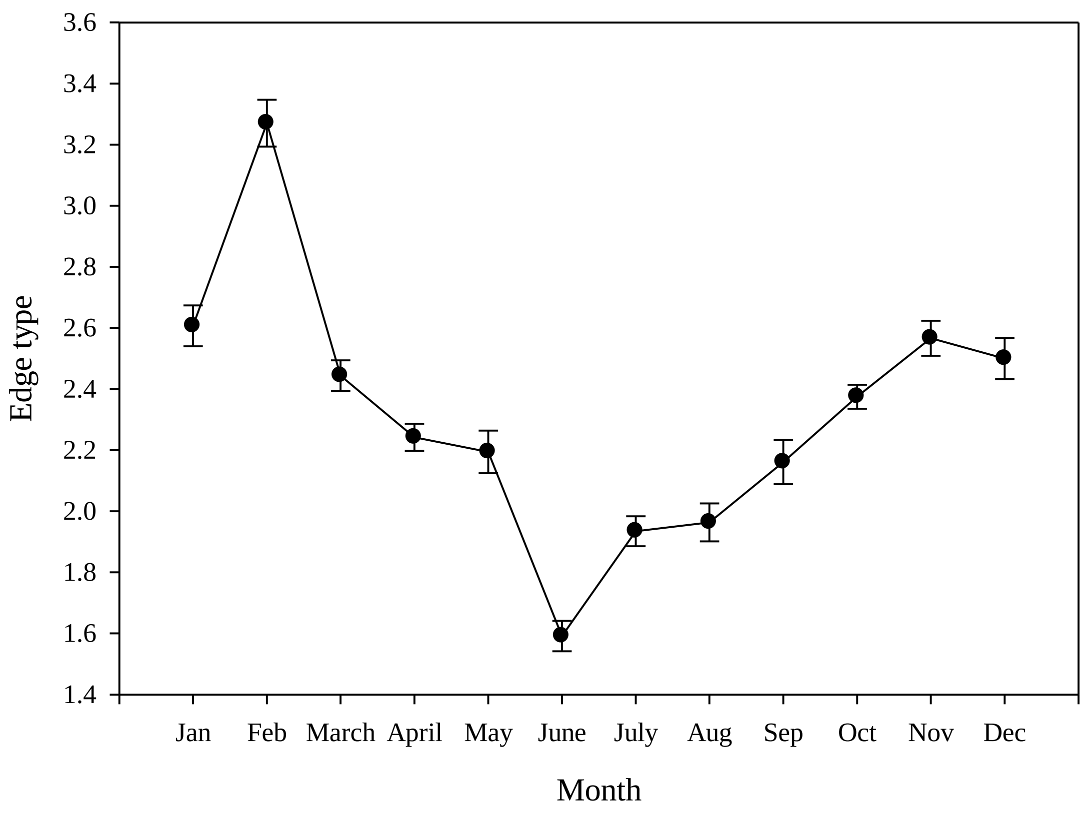

1400
1200
1000
800
600
400
200
0
1975
1980
1985
1990
1995
2000
2005
2010
Year
Landings (metric tons)
Recreational
Commercial

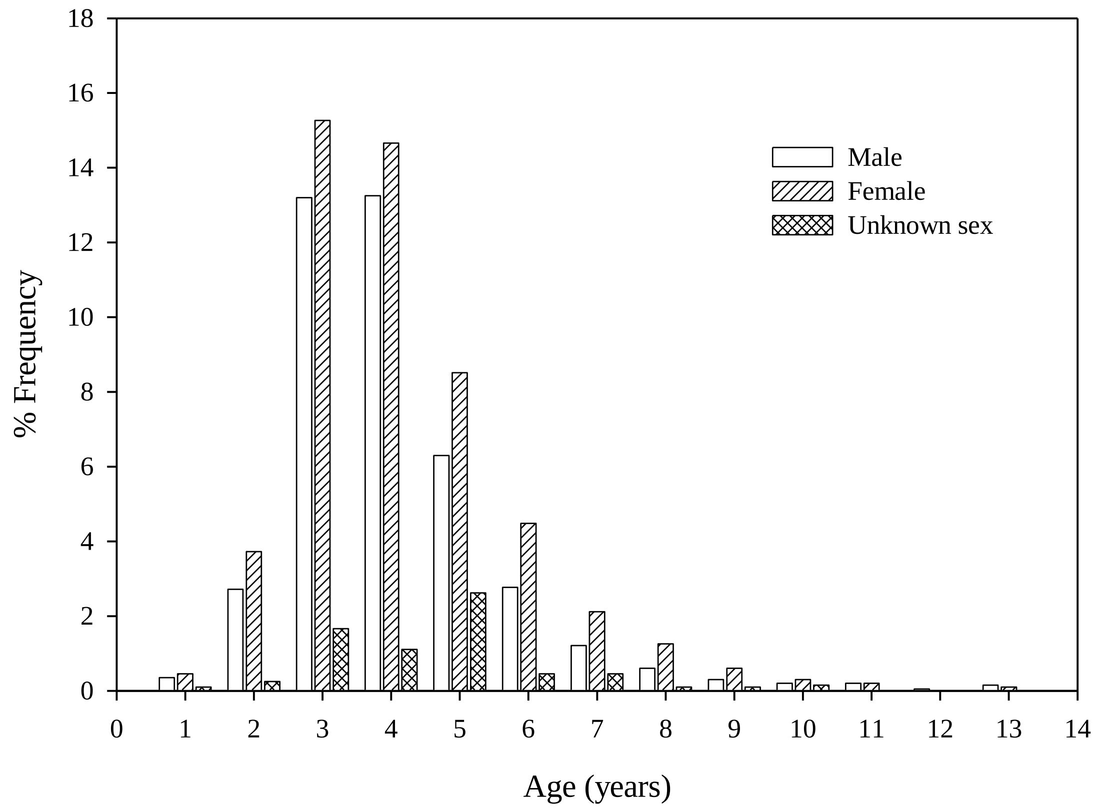


Seriola dumerili
South Carolina
Georgia
Florida
20 m
40 m
100 m
200 m
500 m
1000 m
2000 m
82°W
81°W
80°W
79°W
78°W
77°W
76°W
75°W
34°N
33°N
32°N
31°N
30°N
29°N
28°N
27°N
26°N
25°N
24°N
Spawning Females, Fishery Independent
All Catch Locations, Fishery Independent
Spawning Females, Fishery Dependent
All Catch Locations, Fishery Dependent
Proposed MPAs
0 50 100 200
Kilometers
N

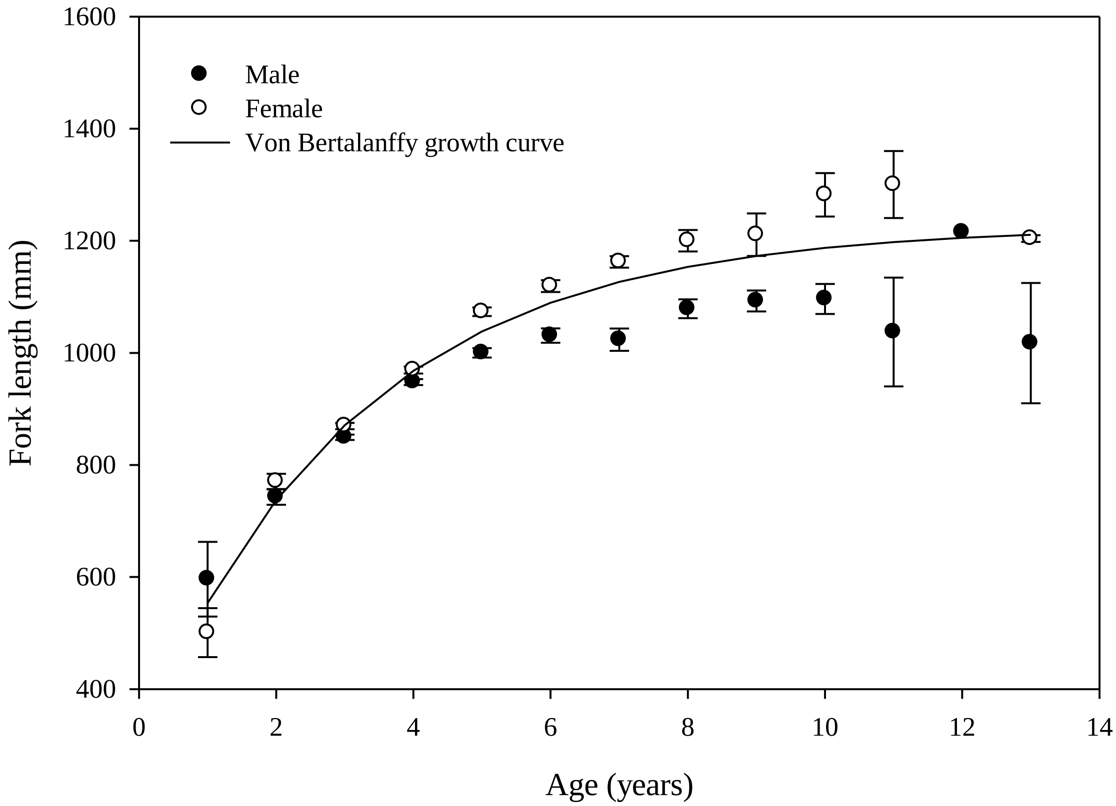


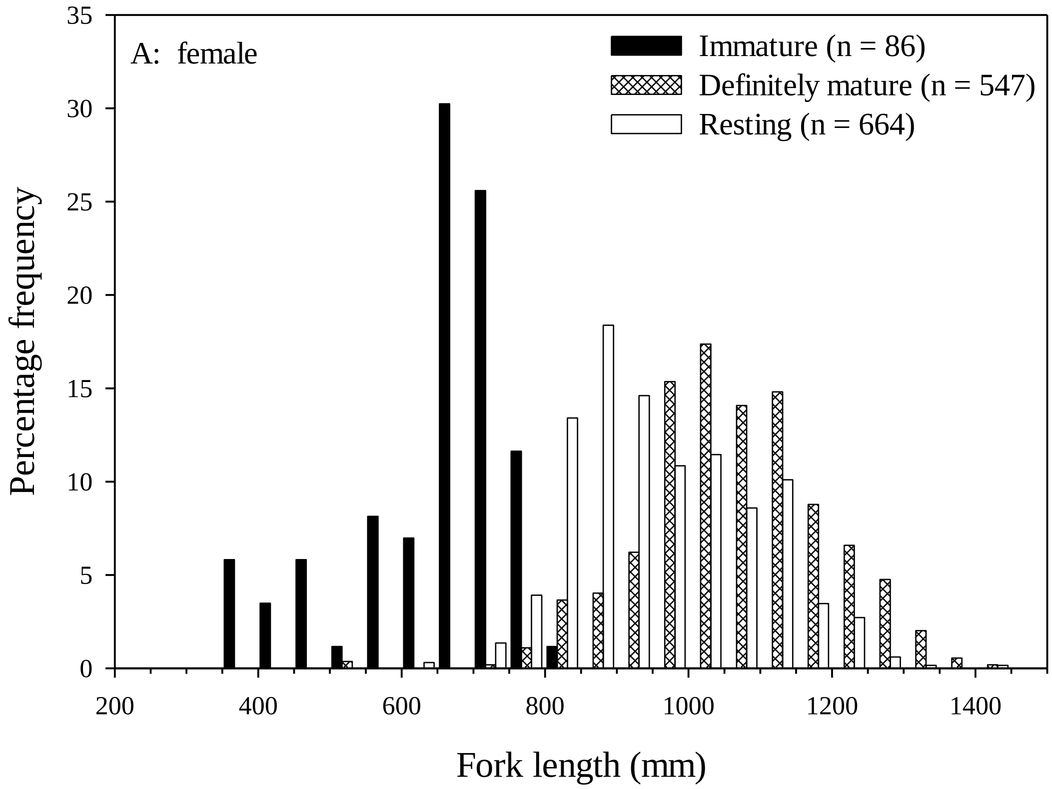
18
16
14
12
10
8
6
4
2
0
% Frequency
Male
Female
Unknown sex
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Age (years)

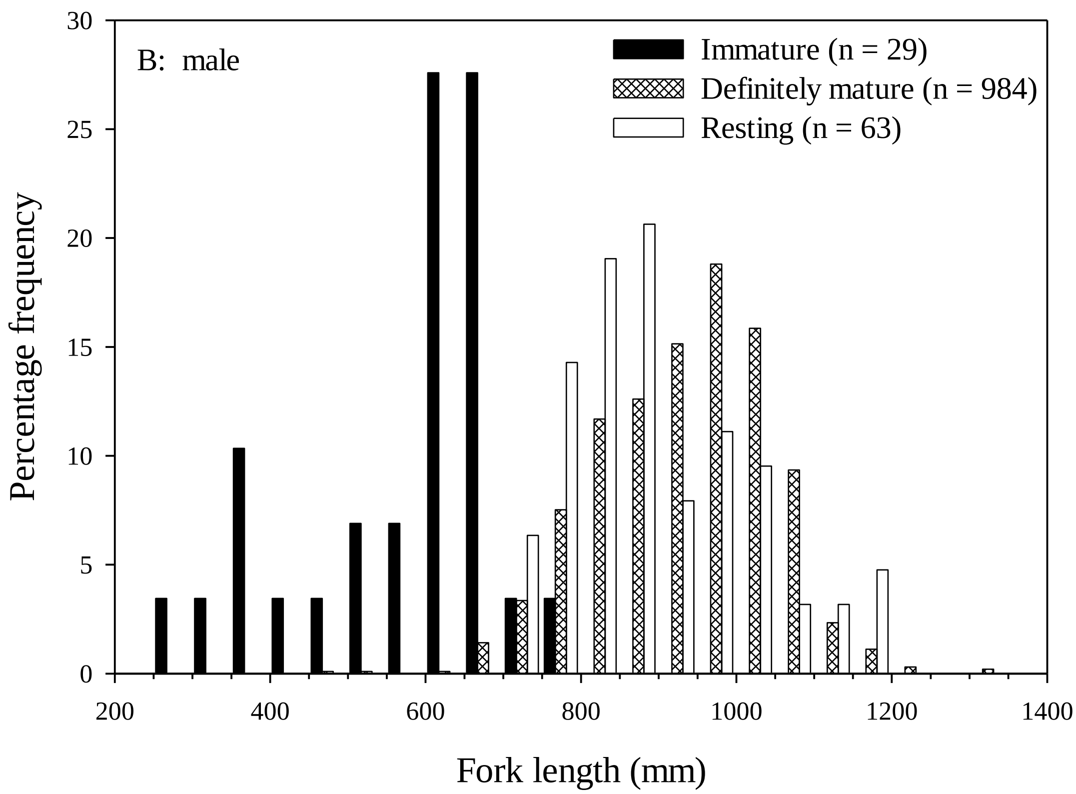

3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
Edge type
Jan
Feb
March
April
May
June
July
Aug
Sep
Oct
Nov
Dec
Month

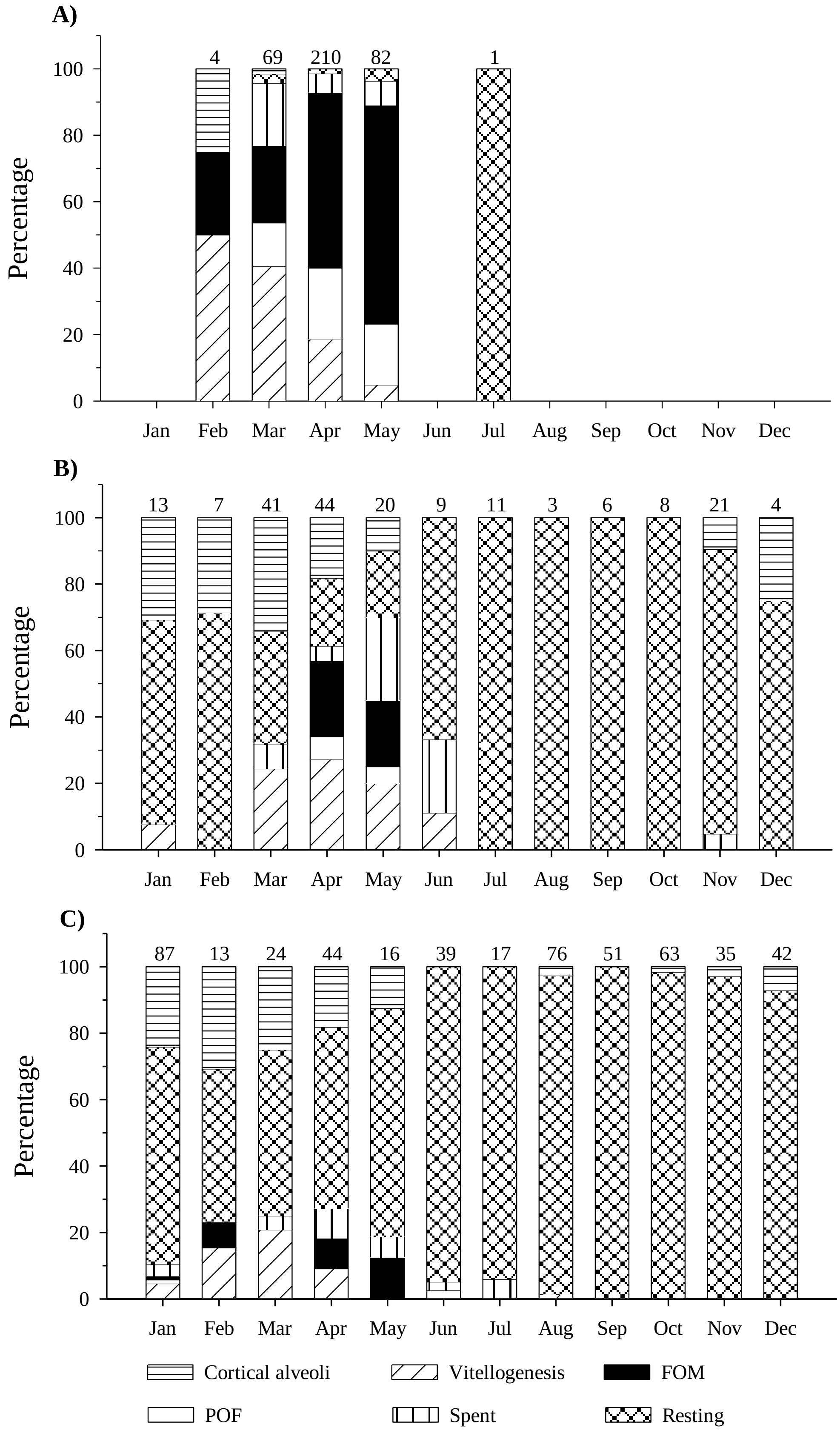


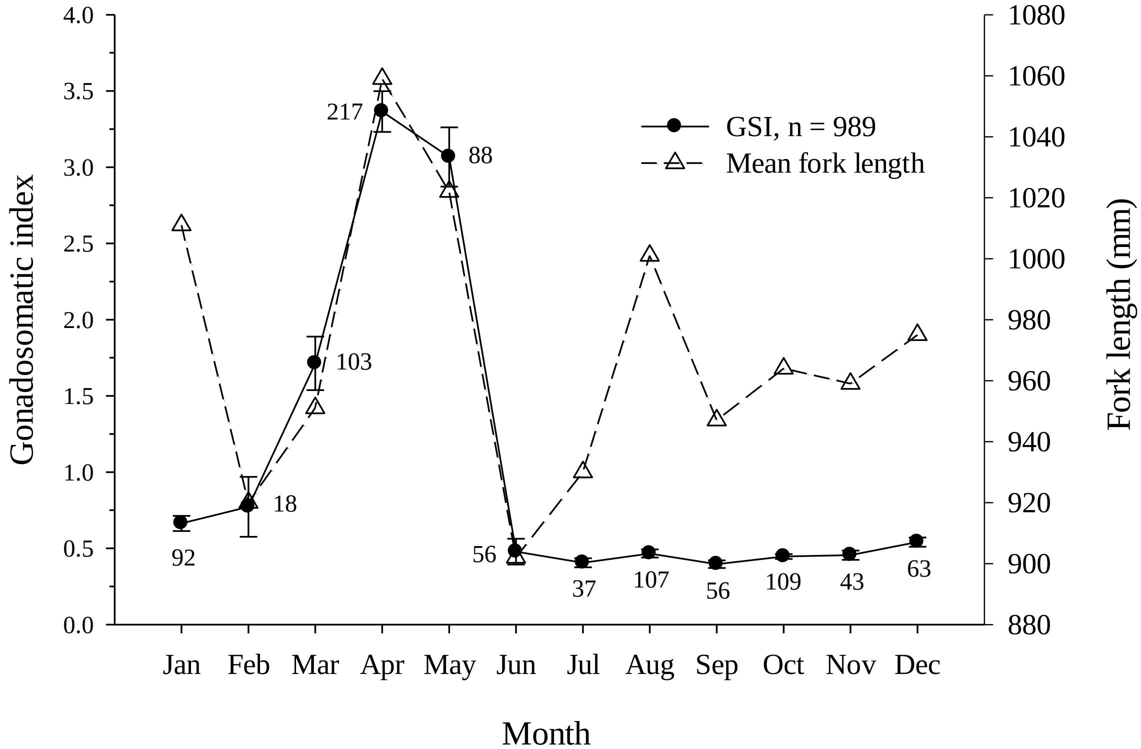
18
16
14
12
10
8
6
4
2
0
% Frequency
Male
Female
Unknown sex
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
Age (years)


Male
Female
Von Bertalanffy growth curve
Fork length (mm)
Age (years)
1600
1400
1200
1000
800
600
400
0
2
4
6
8
10
12
14

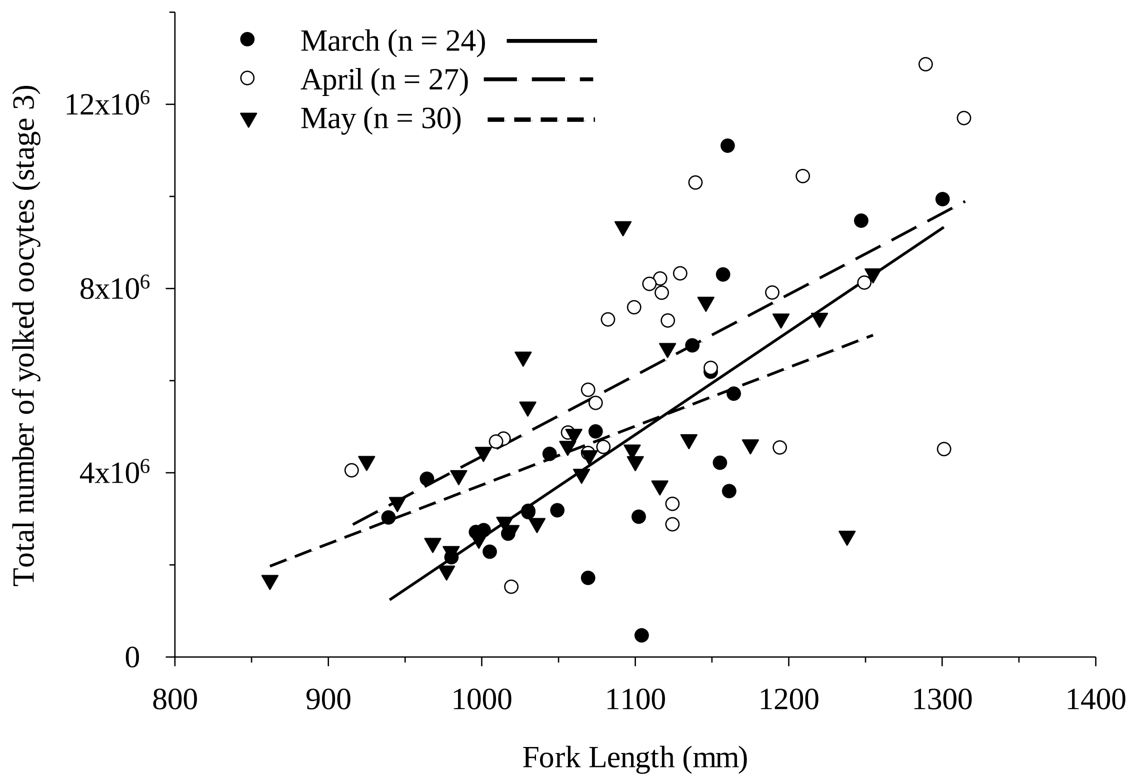

A: female
Immature (n = 86)
Definitely mature (n = 547)
Resting (n = 664)
Percentage frequency
0
5
10
15
20
25
30
35
200
400
600
800
1000
1200
1400
Fork length (mm)


B: male
Immature (n = 29)
Definitely mature (n = 984)
Resting (n = 63)
Percentage frequency
0
5
10
15
20
25
30
200
400
600
800
1000
1200
1400
Fork length (mm)

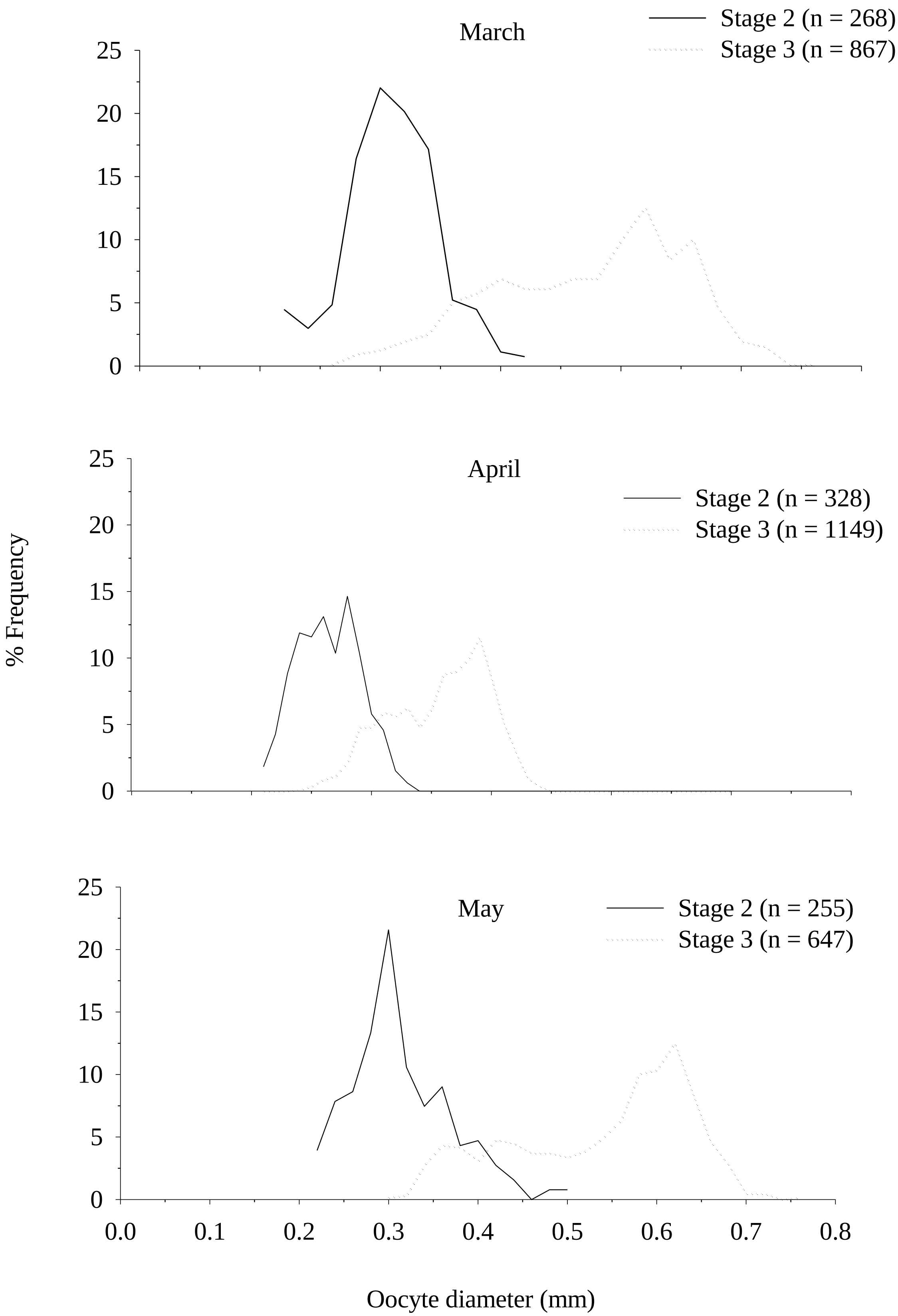

A)
Percentage
0
20
40
60
80
100
4
69
210
82
1
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
B)
Percentage
0
20
40
60
80
100
13
7
41
44
20
9
11
3
6
8
21
4
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
C)
Percentage
0
20
40
60
80
100
87
13
24
44
16
39
17
76
51
63
35
42
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Cortical alveoli
Vitellogenesis
FOM
POF
Spent
Resting



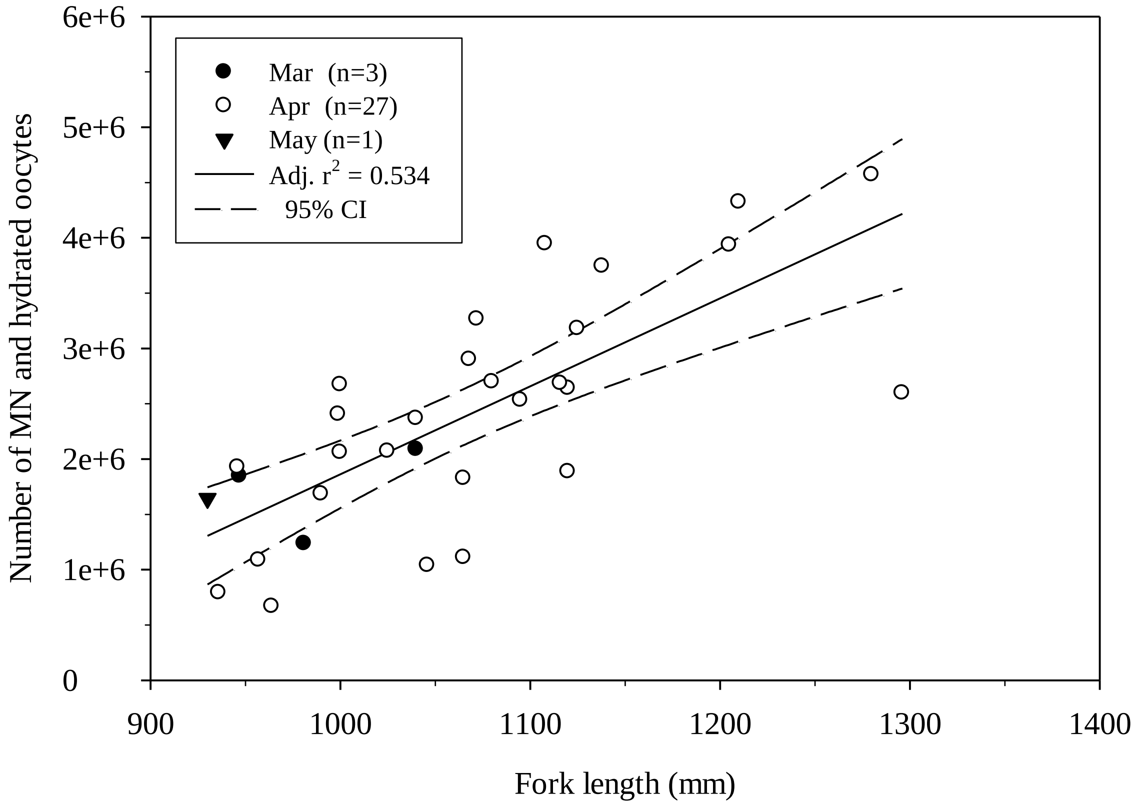
GSI, n = 989
Mean fork length
Gonadosomatic index
Fork length (mm)
Month
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
92 18 103 217 88 56 37 107 56 109 43 63
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
880 900 920 940 960 980 1000 1020 1040 1060 1080



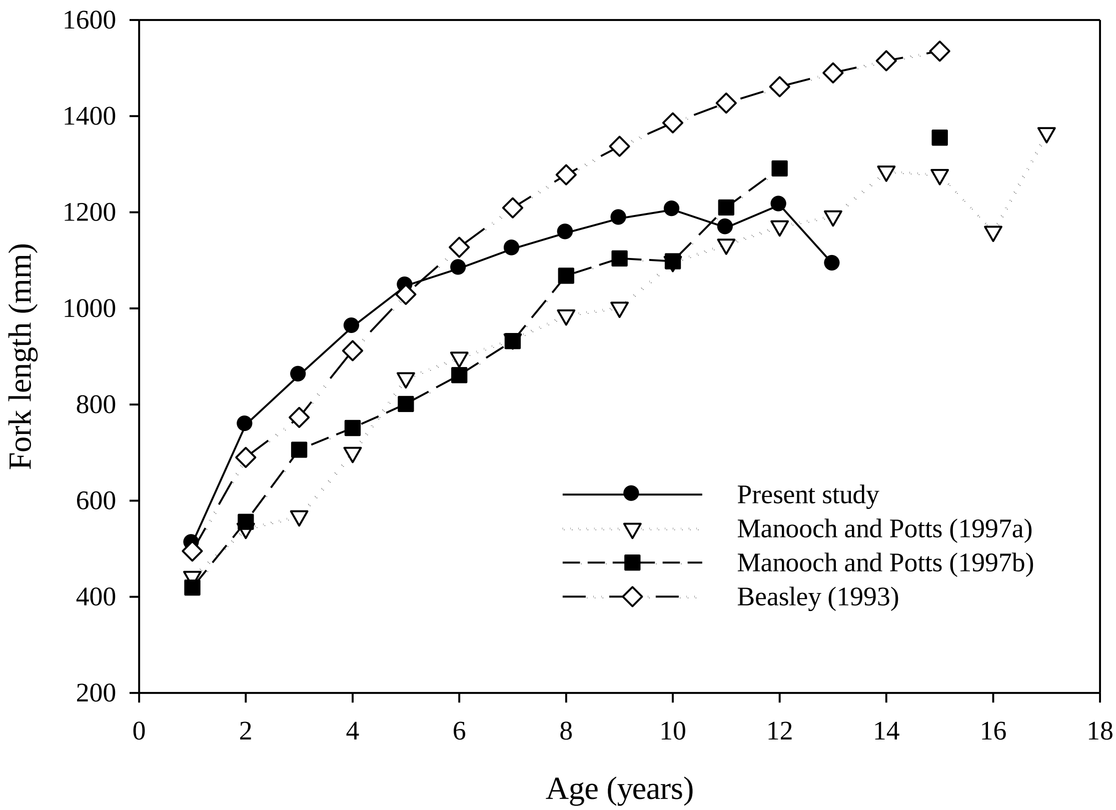
March (n = 24)
April (n = 27)
May (n = 30)
12x10^6
8x10^6
4x10^6
0
800
900
1000
1100
1200
1300
1400
Total number of yolked oocytes (stage 3)
Fork Length (mm)



March
Stage 2 (n = 268)
Stage 3 (n = 867)
April
Stage 2 (n = 328)
Stage 3 (n = 1149)
May
Stage 2 (n = 255)
Stage 3 (n = 647)
% Frequency
0
5
10
15
20
25
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Oocyte diameter (mm)



6e+6
5e+6
4e+6
3e+6
2e+6
1e+6
0
Number of MN and hydrated oocytes
Mar (n=3)
Apr (n=27)
May (n=1)
Adj. r^2 = 0.534
95% CI
900
1000
1100
1200
1300
1400
Fork length (mm)



Fork length (mm)
1600
1400
1200
1000
800
600
400
200
0
2
4
6
8
10
12
14
16
18
Age (years)
Present study
Manooch and Potts (1997a)
Manooch and Potts (1997b)
Beasley (1993)