AGE, GROWTH AND REPRODUCTION OF SPECKLED HIND, *EPINEPHELUS DRUMMONDHAYI*, OFF THE ATLANTIC COAST OF THE SOUTHEAST UNITED STATES

A thesis submitted in partial fulfillment of the requirement for the degree of

MASTER OF SCIENCE

in

MARINE BIOLOGY

by

GABRIEL LEE ZISKIN
APRIL 2008

at

THE GRADUATE SCHOOL OF THE COLLEGE OF CHARLESTON

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ABSTRACT

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This study provides life history and population data for speckled hind off the Atlantic coast of the southeast United States. A total of 1,365 speckled hind were sampled utilizing fishery-dependent and -independent sampling. The age of individuals was estimated by counting increments on sectioned sagittal otoliths. Sex and reproductive state were assessed by histological analysis of sectioned gonads. Data from two periods during the study (1977-93 and 2004-07) were compared to assess the effectiveness of a regulation put in place in 1994 by the South Atlantic Fishery Management Council. Speckled hind ranged in total length (TL) and age from 164 to 973 mm and 1 to 35 years. Marginal increment analysis indicated that annulus formation occurs between June and August. Mean TL, mean age and length at age of speckled hind have decreased since the 1977-1993 period. Von Bertalanffy growth parameters calculated for both periods indicated that the growth rate was slower during the 2004-07 period. Length and age at 50% maturity has increased since the 1977-93 period, but length and age at 50% transition has decreased. The male:female ratio in the speckled hind population from 1977-93 was 1:1.5 and from 2004-07 was 1:3.8. Spawning females were observed from May through October; however, none were sampled during the 2004-07 period. Catch curve analysis indicated that total mortality and fishing mortality have increased since 1977-1993. The results of the present study indicate that speckled hind continue to be over-exploited, despite the 1994 regulation, and may not be reproductively resilient enough to recover from depressed population levels. A new management strategy is necessary to improve the status of the population.

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INTRODUCTION

The speckled hind *Epinephelus drummondhayi* Goode & Bean, 1978, is a serranid (subfamily Epinephilinae) that inhabits deepwater reefs along the Atlantic coast of the southeast United States from the Florida Keys to Cape Hatteras, North Carolina, and around Bermuda, and in the Gulf of Mexico (Smith, 1971; Huntsman and Dixon, 1976; Roe, 1976; Heemstra and Randall, 1993). Speckled hind inhabit depths ranging from 25 to 183 m (Heemstra and Randall, 1993).

Commercial landings of speckled hind along the Atlantic coast of the southeastern United States prior to 1976 are thought to have been low and infrequent (Matheson and Huntsman, 1984). Commercial landings of speckled hind peaked in 1986 when 16.3 mt were landed (NMFS, 2005), and subsequently decreased steadily until 1993, when 9.2 mt were landed. In 1994, the South Atlantic Fishery Management Council (SAFMC) introduced a trip limit of one fish per vessel, and only 4.7 mt were landed commercially in 1994. From 1995 to 2006, commercial landings averaged less than 2 mt annually. A substantial amount of speckled hind were also captured by recreational fishermen participating in the headboat fishery. From 1972 to 1980, North Carolina and South Carolina headboats averaged approximately 12 mt of speckled hind annually (Matheson and Huntsman, 1984). During this period, headboat fishery landings declined substantially throughout the southeast region, from 28 mt in 1973 to approximately 3.0 mt in 1980 (Potts and Brennan, 2001). Landings remained at approximately 3.5 mt annually until 1990. Since 1990, less than 1 mt of speckled hind has been landed annually by the headboat fishery. In 1991, the SAFMC reported that it thought the speckled hind population off the Atlantic coast of the southeast United States was overfished and was undergoing overfishing (SAFMC, 1991).

Few life history studies have been completed on speckled hind. Matheson and Huntsman (1984) is the only published in-depth study on the age and growth of speckled hind along the Atlantic coast of the southeast United States. They reported a maximum size of 1,096 mm total length (TL), maximum age of at least 25 years and suggested that speckled hind is slow growing. Catch curves were used to determine instantaneous mortality rates. In the headboat fishery, fishing mortality (F) increased from 0.26 to 0.40 between 1972 and 1978. In the commercial fishery, F during 1977 and 1979 were 0.24 and 0.25, respectively. Yield per recruit (YPR) models from this study indicated that the headboat and commercial fisheries were harvesting 60-80% of the maximum available YPR (natural mortality (M) =0.20). Huntsman et al. (1999) reported that the total numerical population in 1990 was 10% of that in 1973. They further reported that the total population biomass decreased 95% and biomass of spawning-age speckled hind decreased 98% between 1973 and 1990. The spawning stock ratio (SPR) has decreased over time; from 12% in the 1990 fishing year (Huntsman et al., 1992), to 5% in the 1999 fishing year (assuming M = 0.15) (Potts, 2001).

There has only been one study published that examined aspects of the reproductive biology of speckled hind (Brulé et al., 2000); however, the sample size was small (n=47) and sampling occurred on the Campeche bank in the southern Gulf of Mexico. Histological examination of the gonads revealed that speckled hind is a protogynous hermaphrodite, but no data on size and age at maturity and at sex transition were reported.

Given the multi-species nature of the deepwater reef fishery and high release mortality due to barotraumas in deepwater species, it is important to assess the suitability of the current management regulations (Huntsman et al., 1999). The life history of this grouper and the history of this fishery suggest that it is necessary to determine if fishing pressure during the period of 1977 through 2007 has continued to affect the life history of speckled hind or if the one fish per vessel trip limit introduced in 1994 has allowed the population to recover from the status reported by Matheson and Huntsman (1984) and Huntsman et al. (1999). Data collected from 1977-93 and 2004-07 were compared to investigate the effect of the 1994 SAFMC regulation. My study provides the life history and population data on speckled hind essential for the proper management of this species. The data obtained from this study can assist in making ecosystem-based management decisions in the southeastern United States. These data can also be used for comparison to future studies on speckled hind.

METHODS

Sampling

Speckled hind were collected from May 1977 through April 2007. Fishery-independent sampling of speckled hind has occurred since 1977 during sampling by the Marine Resources Monitoring, Assessment and Prediction (MARMAP) program. MARMAP samples fishes in rocky reef habitats from Cape Hatteras, North Carolina, to Cape Canaveral, Florida, during daylight hours each year, usually between May and September. There are currently over 2,500 reef habitat sites in the MARMAP database, of which 300-600 are randomly sampled each year. In 1977 and 1978, samples were collected using mini Antillean s-traps and snapper reels. From 1979-87, samples were collected using blackfish traps, Florida traps, and hook and line gear. Traps baited with cut clupeids were released from the vessel and buoyed to the surface with a poly ball and high flyer. Traps were allowed to soak for 1-4 h and retrieved using a pot hauler. The hook and line gear consisted of snapper reels or rod-and-reel with 6/0 Penn Senator high-speed reels and Electramate electric motors. Snapper reels are commercial bottom-fishing hook and line, typically mounted to the vessel along the gunwale and powered by electricity or hydraulics. The terminal tackle on all of the hook and line gear was always three hooks baited with cut squid or scad (*Decapterus* sp.). In 1988, chevron traps were added to the sampling methods and soak time changed to approximately 90 min. In 1990, the use of blackfish and Florida traps was discontinued because chevron traps sampled a greater diversity of fish species (Collins, 1990). Vertical longlines were utilized in 1979 and 1987, but were first used regularly by MARMAP in 1996 to sample on rough bottom and rocky outcrops at depths greater than 80 m (Harris et al., 2004).

The vertical longline consists of 26 m of 6.4 mm solid braid dacron groundline dipped in green copper naphtenate with twenty hooks baited with squid attached every 1.2 m. One end of the groundline was brommeled to a length of poly warp; 11 kg weights were attached to both ends. The longline was buoyed to the surface with a poly ball and high flyer. The longline was soaked for 90 min and retrieved using a pot hauler.

Catch per unit effort (CPUE) for chevron traps and vertical longlines was calculated for each year they were utilized. CPUE was expressed as the number of speckled hind caught per trap per hour, or the number caught per hook per hour for vertical longlines.

Fishery-dependent samples were obtained from 1979-1981, 1983, 1993-94, 2001-2002 and 2004-2007, and supplied by commercial fishermen. Commercial fisherman typically caught speckled hind on snapper reels and rod-and-reel and stored whole specimens on ice. When available, depth and location of capture were recorded.

Whole speckled hind were weighed to the nearest gram (WW), and standard length (SL), fork length (FL), and total length (TL) were measured in mm. Sagittal otoliths and a section from the posterior portion of the gonad were removed from each fish. The otoliths were stored dry in a coin envelope and held for later processing. The section of the gonad removed from each fish was placed in a Tissue-Tek embedding capsule and preserved for histological analysis.

The length, weight, age and depth data were tested for normality and homogeneity of variances. Tests for normality included: Shapiro-Wilk’s test statistic, skewness, kurtosis, normal plots, and histograms. Tests for homogeneity of variances included: Levene’s test for equality of variances and residual vs. predicted value plots.

Non-parametric equivalents were used when assumptions of normality and homogeneity of variances were not met. A significance level (α) of 0.05 was selected for statistical tests; results of statistical tests were considered significant if the p-value was less than the α-level. All statistical tests, unless otherwise noted, were performed using SAS (SAS Institute, INC., 1990).

Age and growth

Otoliths were used to estimate the age of each fish. The left sagittal otolith of each fish was embedded in an epoxy resin, and thin sections (0.6 mm) were cut through the core in the dorsoventral plane using a low-speed saw with a diamond wafering blade. Sections were mounted on glass slides, covered with Accumount® mounting medium and viewed using a dissecting microscope and transmitted light. The microscope was linked to a personal computer equipped with Image Pro® image analysis software via a digital video camera.

Increments (one opaque and one translucent zone) were counted on otoliths from each specimen by two readers working independently, without any knowledge of specimen length or date of capture. The primary reader counted increments for each specimen a second time, after the first count of all specimens was completed. An edge type was assigned for each specimen by estimating the width of the translucent zone on the margin of the otolith (type 1: an opaque zone on the margin; type 2: a narrow translucent zone, width less than approximately 30% of the previous increment; type 3: a medium translucent zone, width approximately 30-60% of the previous increment; type 4: a wide translucent zone, width more than approximately 60% of the previous increment). The first increment counted was the innermost increment distinguished from the opaque core by a translucent zone. An exclusive axis of otolith radius was not chosen for increment counts because there was not a consistently legible axis. If the increment counts of the readers differed, then the otolith was examined simultaneously by both readers. If disagreement persisted, no count was assigned to the specimen, and it was discarded from analyses. Average percent error (APE) was calculated to estimate the precision of increment counts between the two readers, and between the two independent readings by the first reader (Beamish and Fournier, 1981).

The periodicity of increment formation was verified by marginal increment analysis using pooled fishery-dependent and -independent data of speckled hind age 4 and less. Only speckled hind age 4 and less were used in this analysis to minimize uncertainty due to difficulty discerning marginal increments in older fish. The proportion of edge type 1 otoliths was plotted as a function of month. A unimodal distribution was anticipated, and the month with the greatest proportion of edge type 1 was designated as the month of opaque zone formation.

Percent frequency distributions of TL and age were constructed for samples collected from 1977-2007, 1977-93 and 2004-07 and for fishery-dependent and -independent samples. Length- and age-frequency distributions from 1977-93 and 2004-07 were compared using a Kolmogorov Smirnov (KS) two-sample test. Length- and age-frequency distributions from fishery-dependent and -independent samples were compared using a KS test.

The relationships between TL and FL, TL and SL, FL and SL and WW and TL were determined using regression analysis. These length on length relationships were used to estimate TL for specimens lacking this measurement (n=9).

Mean TL and age were compared between fishery-dependent and -independent data by one way analysis of variance (ANOVA) tests or non-parametric Kruskal-Wallis (KW) tests. Mean TL and age were compared among snapper reels, vertical longlines, chevron traps, blackfish traps and Florida traps using a Tukey's Honestly Significant Difference (HSD) test. Mean lengths at age were calculated for fishery-dependent and -independent samples separately. Mean lengths at age for fishery-dependent and -independent samples were compared using one-way ANOVA to evaluate the appropriateness of pooling these data. Mean lengths at age for the five gear types listed above were also compared using ANOVA and a HSD test to further evaluate the appropriateness of pooling data from fishery-dependent and -independent sampling. Mean lengths at age for the two periods (1977-93 and 2004-07) were compared using ANOVA. Also, because 47% of the specimens in the 1977-93 period were collected by fishery-independent sampling and only 3% of the specimens in the 2004-07 period were collected by fishery-independent sampling, mean TL and age of specimens collected by each sampling source were compared for both periods to investigate the consequences of the disproportionate number of specimens collected by the two sampling sources during the two periods.

The relationships between TL and depth and age and depth were determined using least-squares linear regression.

A von Bertalanffy (VB) growth equation was fitted to length at age data by period using the NLIN procedure and Marquardt's algorithm (SAS institute Inc., 1990), using the equation:

$L_t=L_\infty(1-e^\wedge-k(t-t_0))$

where L_t is the TL at age t, L_∞ is the theoretical asymptotic TL, k is the VB growth coefficient and t_0 is the theoretical age at which TL equals zero (Bertalanffy, 1938).

Instantaneous rate of total mortality (Z) was estimated for both periods by catch curve analysis. Z is determined as the slope of the regression fitted to the descending limb of the natural logarithm of frequency of individuals by age class. The slope was measured from the first age class in which recruitment to the fishery could be considered complete, the modal age plus one, to the age class which included 98% of the speckled hind sampled from 1977-2007 (Ricker, 1975). M was estimated using Hoenig's (1983) equation based on the relationship between M and maximum age (t_{max}) observed:

$Ln(M)=1.44-0.982*Ln(t_{max})$

The age used for this calculation was 30, instead of the actual maximum observed age of 35, to adjust for the possibility of error in increment counts. Assuming this age is observed in an unfished population, this equation provides an estimation of M. This approach to estimate M, rather than the simpler approach of estimating M using the equation $M\approx3/T_{max}$, was selected based on arguments by Hewitt and Hoenig (2005). F was estimated by subtracting M from Z.

Beverton-Holt type YPR models were calculated for both periods using Microsoft Excel (Microsoft Excel, 2002, Microsoft Corporation, Seattle WA). The estimate of instantaneous natural mortality, M, was obtained by the previously described method for calculating M. Estimates of W_∞**,** k and t_0 were obtained from a von Bertalanffy growth equation fitted to observed weight at age data. The age at recruitment (t_r) was set at 1 year and was based on observation. The number of recruits selected for YPR calculations was 100,000. The maximum age was selected from observations. Since age of first capture (t_c) can be controlled by fisheries managers, multiple YPR models were constructed using varied ages at first capture.

Reproductive biology

Sections of gonad were stored in 11% seawater-formalin buffered with marble chips for two weeks, then transferred to 50% isopropanol for at least two weeks. Samples were then vacuum infiltrated, blocked in paraffin, and transverse sections were cut (7 µm) on a rotary microtome. Three sections were placed on a glass slide and stained with double-strength Gill's hematoxylin and eosin-y. The sections were viewed with a compound microscope at 40-400 X to determine sex and reproductive state.

Two readers viewed each section of reproductive tissue independently, without knowledge of length, age or date of capture of the specimen. If there was disagreement between readers, the section was re-examined simultaneously by both readers and omitted from further analyses if the disagreement was not resolved. A sex code (Table 1) was assigned following a revision of criteria described by Waltz et al. (1979). Fish with gonads that were developing, spawning, spent or regressed (Table 2) were be considered mature based on histological criteria published for red grouper *E. morio* (Burgos et al., 2007). Females with germinal vesicle migration, germinal vesicle break down, hydrated oocytes, or post-ovulatory follicles were considered in spawning condition. Males with predominance of spermatozoa in the lumen of lobules and ducts and relatively less spermatogenesis were considered in spawning condition. Percent frequency distributions of TL for immature, regressed, and definitely mature (developing, running ripe, or spent) females were compared to verify the correct assignment of immature and regressed stages. An overlap in distributions of resting and definitely mature females indicated that the maturity status of females was correctly assessed (Wyanski et al., 2000).

Length and age at 50% maturity and at 50% sexual transition were estimated and compared between periods using the PROBIT procedure (SAS Institute, Inc., 1990). The LOGISTIC procedure (SAS Institute, Inc., 1990) was used to identify which model best fit the data.

Sex ratios (number of males and transitionals per number of females) were estimated for all mature specimens sampled from 1977-2007 and the periods 1977-93 and 2004-07. Also, sex ratios were estimated for each age class and 50 mm TL interval.

Spawning season was determined by estimating the relative proportions of mature female reproductive categories by month. The spawning season was defined as the time between the dates of capture of the first and last specimens in spawning condition.

Spawning locations were determined by plotting the latitude and longitude of capture locations of females and males in spawning condition with ArcGIS version 9.2. The capture locations of non-spawning individuals were plotted on the same map in order to make comparisons between spawning and non-spawning locations.

RESULTS

Sampling

A total of 1,365 speckled hind were collected by MARMAP from May 1977 through April 2007. Samples were obtained every year except 1988 and 1995 (Figure 1) and during every month of the year throughout the course of the study (Figure 2). Specimens were collected from sites between 28°00’N/ 80°17’W and 34°13’N/ 76°6’W, in depths ranging from 28 to 183 m. Fishery-dependent sampling obtained 1,076 (79%) samples, with the majority obtained by snapper reel (n=1,064). Other specimens collected with fishery-dependent gear included: hook and line (n=6), roller trawl (n=3) and an unknown gear type (n=3). Fishery-independent sampling yielded 289 specimens, collected with hook and line (n=7), mini Antillean S-trap (n=10), snapper reel (n=51), blackfish trap (n=24), vertical longline (n=30), Florida trap (n=60), chevron trap (n=102), and an experimental trap (n=5). The frequency distributions of speckled hind by depth from fishery-dependent (33-183 m) and -independent sampling (28-114 m) were significantly different (D=0.45, n=1,108, $p<0.01$; Figure 3). The total number of speckled hind sampled during the 1977-1993 and 2004-2007 periods were 330 and 924, respectively. The frequency distributions of speckled hind by depth from 1977-93 (28-183 m) and 2004-07 (33-118 m) were significantly different (D=0.51, n=1,002, $p<0.01$; Figure 4).

The length of all speckled hind sampled ranged from 164 to 973 mm TL (mean=460 mm, SE=3.2, n=1,365; Figure 5). Length distributions of specimens collected via fishery-dependent and -independent sampling were significantly different (D=0.37, n =1,365, $p<0.01$; Figure 6). Fishery-dependent sampling (mean=480 mm TL, SE=3.3, n=1076) obtained significantly (F=179.29, n=1,365, p<0.01) larger fish than fishery-independent sampling (mean=384 mm TL, SE=6.4, n=289). Mean TL and length distributions of specimens collected from 1977-93 (mean=477 mm TL, SE=10.0, n=330) and 2004-07 (mean=462 mm TL, SE=2.7, n=924) were significantly different (F=4.10, n=1,254, p=0.04; D=0.26, n=1,254, p<0.01; Figure 7). Fishery-dependent sampling from 1977-93 (mean=579 mm TL, SE=13.1, n=174) obtained significantly (F=192.50, n=1067, p<0.01) larger fish than fishery-dependent sampling from 2004-07 (mean=462 mm TL, SE=2.7, n=893). Fishery-independent sampling from 1977-93 (mean=365 mm TL, SE=8.45, n=156) obtained significantly (F=25.30, n=187, p=0.30) smaller fish than fishery-independent sampling from 2004-07 (mean=469 mm TL, SE=19.0, n=31).

The mean lengths of specimens sampled by snapper reel and vertical longline were not significantly different (475 vs. 511 mm TL, p=0.71; Tables 3 and 4). Snapper reels collected significantly larger specimens than blackfish traps (475 vs. 312 mm TL, p<0.01), Florida traps (475 vs. 340 mm TL, p<0.01), and chevron traps (475 vs. 376 mm TL, p<0.01). Vertical longlines collected significantly larger specimens than blackfish traps (511 vs. 312 mm TL, p<0.01), Florida traps (511 vs. 340 mm TL, p<0.01), and chevron traps (511 vs. 376 mm TL, p<0.01). The mean length of specimens collected by chevron traps was not significantly different than blackfish traps (376 vs. 312 mm TL, p=0.18) or Florida traps (376 vs. 340 mm TL, p=0.51). The mean lengths of specimens collected by blackfish and Florida traps were not significantly different (312 vs. 340 mm TL, p=0.99).

The regression analyses of TL and FL, TL and SL, and FL and SL demonstrated strong linear relationships (Table 5). The regression analyses of TL and WW exhibited the expected exponential relationship (Figure 8).

CPUE for chevron traps ranged from 0 to 0.032 speckled hind per trap per hour (1988-2007; Figure 9). CPUE for vertical longlines ranged from 0 to 0.12 speckled hind per hook per hour (1979, 1987 and 1996-2007; Figure 9).

Age and growth

Increment counts and edge types were assigned to 1,197 of the 1,252 otoliths obtained, 55 were considered unreadable. The initial agreement in increment counts between the primary and secondary reader was 41.3 % (82.3% within one year, 91.3% within two years). The APE between the first and second reader was 9.09% (n=1,208). The APE between the two independent readings by the first reader was 4.59% (n=1,217).

Marginal increment analysis indicates that increments are formed annually and that increment formation occurs between June and August (Figure 10). June (0.58), July (0.54) and August (0.55) had similarly high proportions of edge type 1 otoliths, suggesting that the peak of opaque zone formation occurs during these months. Therefore, increment counts were adjusted based on a "birth date" of August 1st. Any specimen obtained after January 1st, but prior to August 1st which was assigned an edge type of 3 or 4 was thought to have not laid down an increment in that year; thus, their increment counts were increased by one to provide the age of the specimen. The age of specimens caught after August 1st or those collected after January 1st, but prior to August 1st, and assigned an edge type of 1 or 2 was equal to the increment counts.

The ages of sampled speckled hind ranged from 1 to 35 years (mean= 4.5 years, SE=0.07, n=1,197; Figure 11). Age distributions of specimens collected via fishery-dependent and -independent sampling were significantly different (D=0.56, n=1,197, p<0.0001; Figure 12). Fishery-dependent sampling (mean=4.8 years, SE=0.07, n=975) caught significantly (X^2 = 241.25, n=1,197, p<0.01) older fish than fishery-independent sampling (mean=3.1 years, n=222, SE=0.15). Mean age and age distributions of specimens sampled from 1977-93 (mean=4.9 years, SE=0.36, n=209) and 2004-07 (mean 4.5 years, SE=0.04, n=892) were significantly different (X^2 = 51.88, n=1,101, p<0.01; D=0.39, n=1,101, p<0.01; Figure 13). Fishery-dependent sampling from 1977-93 (mean=7.3 years, SE=0.7, n=101) obtained significantly (X^2=10.61, n=968, p<0.01) older fish than fishery-dependent sampling from 2004-07 (mean=4.5 years, SE=0.04, n=867). Fishery-independent sampling from 1977-93 (mean=2.8 years, SE=0.1, n=108) obtained significantly (X^2=41.03, n=133, p=<0.1) younger fish than fishery-independent sampling from 2004-07 (mean=4.6 years, SE=0.3, n=25).

The mean ages of specimens sampled by snapper reel and vertical longline were not significantly different (4.7 vs. 5.0 years, p=1.0; Tables 6 and 7). Snapper reels collected significantly older specimens than blackfish traps (4.7 vs. 2.3 years, p<0.01), Florida traps (4.7 vs. 2.5 years, p<0.01), and chevron traps (4.7 vs. 3.0 years, p<0.01). Vertical longlines collected significantly older specimens than blackfish traps (5.0 vs. 2.3 years, p<0.01), Florida traps (5.0 vs. 2.5 years, p<0.01), and chevron traps (5.0 vs. 3.0 years, p<0.01). The mean age of specimens collected by chevron traps was not significantly different than blackfish traps (3.0 vs. 2.3 years, p=0.83) or Florida traps (3.0

vs. 2.5 years, p=0.85). The mean lengths of specimens collected by blackfish and Florida traps were not significantly different (2.3 vs. 2.5 years, p=1.0).

Mean lengths at age for speckled hind obtained by fishery-dependent and -independent were not statistically different for age classes 1-5 and 7 (Figure 14). Sample sizes for age classes 8 and above were too small for statistical analysis. Mean lengths at age were similar among the five gear types compared (Tables 8 and 9). Samples sizes for age classes 6, 8 and above were too small for comparison. Despite the significant differences in mean length and mean age between sampling sources and some gear types, the data from both sources were pooled within period because there was not a significant difference in length at age between the two sources or gear types utilized by those sources.

Mean lengths at age for speckled hind obtained during 1977-93 and 2004-07 were not statistically different for age classes 1 through 3 and 7 through 9 (Figure 15). Mean lengths at age classes 4-6 for speckled hind obtained from 1977-93 were significantly larger than speckled hind obtained from 2004-07. Sample sizes from age classes above 9 were too small for statistical analysis.

There was a slightly positive trend in the relationship between depth and TL in speckled hind sampled from 1977-2007 ($p<0.01$, $r^2=0.11$, n=1,108; Figure 16). There was also a slightly positive trend in the relationship between depth and age for speckled hind sampled from 1977-2007 ($p<0.0001$, $r^2=0.05$, n=1,003; Figure 17).

Lengths at age were fitted using the VB growth equation for speckled hind collected from 1977-93 and 2004-07 (Table 10).

The percent frequency distributions of age for the 1977-93 and 2004-07 periods indicate that speckled hind were fully recruited to the fishery at ages 4 and 5, respectively (Figure 13). From 1977-93, Z was 0.64 (Figure 16). From 2004-07, Z was 1.27 (Figure 19). The estimated value of M was 0.15. This value of M was used for both periods, and assumes that natural mortality remained constant throughout the course of this study. From 1977-93 and 2004-07, F was 0.49 and 1.12, respectively.

YPR models estimating the potential yield of speckled hind were constructed for both periods of the study assuming M=0.15 and a maximum age of 30 years. During the 1977-93 period, YPR was maximized (=1.8 kg) if age at first capture was approximately 6 and fishing mortality approximately 0.5 (Figure 20). Given the observed age at first capture (t_c = 1) during this period, maximum YPR of 1.1 kg was obtained when F_{max} (or the F that produces maximum YPR) was 0.14 (Figure 21). At the estimated F (0.49) and the given age at first capture for this period, YPR was 60% of maximum YPR. At the estimated F for this period, YPR of 1.1 kg could have been produced if age at first capture was delayed until 2.4 years old.

During the 2004-2007 period, YPR was maximized (=1.0 kg) if age at first capture was between 8 and 9 years old and fishing mortality approximately 0.4 (Figure 22). Given the observed age at first capture (t_c = 1) during this period, maximum YPR of approximately 0.6 kg was obtained when F_{max} = 0.1 (Figure 23). At the estimated F (1.12) and the given age at first capture for this period, the YPR was 15% of maximum YPR. At the estimated F, YPR of 0.6 kg could have been produced if age at first capture was delayed until 4.5 years old.

Reproductive biology

Gonads from 1,209 speckled hind were collected and prepared for histological examination. Sex and reproductive state were assigned to 973 specimens. A reproductive state of unknown was assigned to 236 speckled hind because the samples were of inadequate quality. Overall sex ratios (male:female) from 1977-2007, 1977-93 and 2004-07 were 1:3.0 (n=238), 1:1.5 (n=47), and 1:3.8 (n=182), respectively. Sex ratios were male-biased for age classes 9 and above and TL intervals >651 mm (Tables 11 and 12).

The small degree of overlap in the percent frequency distributions of length for immature females with those of regressed and definitely mature females indicated that the criteria used to assess reproductive state adequately differentiated immature and regressed females (Figure 24). The smallest mature female observed from 1977-93 was 390 mm TL and from 2004-07 was 366 mm TL. The smallest male observed from 1977-93 was 500 mm and from 2004-07 was 605 mm TL. Length at 50% maturity from 1977-93 (Gompertz; 503 mm TL, CI=480-533; Figure 25) was smaller than that from 2004-07(Gompertz; 532 mm TL, CI=522-542; Figure 25), but the difference was not significant (X^2=2.69, n=725, p=0.10).

The youngest mature female observed from 1977-93 and 2004-07 was 3 years old and the youngest male observed from 1977-1993 was 8 years old and from 2004-07 was 4 years old. Age at 50% maturity from 1977-93 (Normal; 4.5 years, CI=4.0-5.3; Figure 26) was smaller than that from 2004-07 (Normal; 6.6 years, CI=6.1-7.6; Figure 26), but the difference was not significant (X^2=2.95, n=679, p=0.09).

Histological examination of speckled hind gonads verified that this species is a protogynous hermaphrodite. Transition from female to male gonads was identified by the presence of both female and male reproductive tissue in the gonad (Figure 27). Transitional status was assigned to 29 specimens. The size and age of transitional specimens ranged from 451-718 mm TL and 3-7 years. Transitional specimens were captured in all months of the year except November, but the majority were captured between February and April (n=16).

The smallest transitional individual observed from 1977-93 was 556 mm TL and from 2004-07 was 496 mm TL. Length at 50% transition from 1977-93 (Gompertz; 707 mm TL, CI=595-844; Figure 28) was larger than that from 2004-07(Gompertz; 627 mm TL, CI=610-651; Figure 28), but the difference was not significant (X^2=2.66, n=229, p=0.10).

The youngest transitional individual observed from 1977-93 was 5 years old and from 2004-07 was 4 years old. Age at 50% transition from 1977-93 (Logistic; 10.0 years, CI=7.4-17.2; Figure 29) was larger than age at 50% transition from 2004-07 (Logistic; 6.8 years, CI=6.3-7.9; Figure 29), but the difference was not significant (X^2=3.13, n=207, p=0.08).

From 1977-2007, female speckled hind in spawning condition were collected from May through August and in October, suggesting that spawning occurs during these months (Figure 30). However, from 2004-07, no females in spawning condition were collected. Running ripe males sampled from 1977-2007 were captured from June through August (n=8).

The location of capture was not available for every speckled hind in spawning condition. The available location of capture data indicated that spawning activity appears to occur at or near the shelf break, in depths greater than 44 m (Figure 31) where spawning females (n=1) and males (n=6) were captured. Spawning speckled hind were captured in locations near the capture of non-spawning individuals.

DISCUSSION

Sampling

The sample size obtained during the 2004-07 period represents the best sample of speckled hind collected off the Atlantic coast of the southeast United States to date. Although Matheson and Huntsman (1984) sampled 1,141 speckled hind, they only collected otoliths from 463 individuals and did not investigate the reproductive biology. Similarly, Brulé et al. (2000) reported on the histological examination of only 47 gonads. In contrast, during the 2004-07 period of this study, 893 speckled hind were assigned ages and 973 speckled hind gonads were histologically examined. Due to the small sample size obtained during the 1977-93 period, the results reported for the 1977-93 period and comparisons to these results should be interpreted with a degree of caution. However, the assessment of age, growth, and reproduction during 2004-07 is the most complete assessment of the speckled hind population in the southeast United States.

Fishery-dependent sampling collected larger and older speckled hind than fishery-independent sampling. However, mean length at age between sampling sources was not significantly different for age classes 1-5 and 7, suggesting that fishery-dependent and -independent schemes sampled different portions of the speckled hind population. Therefore, it was appropriate to pool data from these two sources so that the complete length and age range of speckled hind off the Atlantic coast of the southeast United States was included in the analysis. Fishery-dependent sampling obtained more specimens at greater depths than fishery-independent sampling, but the majority of speckled hind in age classes 1 and 2 were obtained by fishery-independent sampling. Fishery-independent sampling also obtained the majority of speckled hind less than 300 mm TL. The gear types utilized by commercial fishers do not target small speckled hind, thus it is necessary to utilize the gear types in fishery-independent sampling to sample the younger and smaller segment of the speckled hind population.

Only 7 specimens were obtained at depths greater than 120 m, and these were obtained from 1979 to 1981. Brulé et al. (2000) suggested that the size-depth distribution of speckled hind on the Campeche bank indicates an ontogenetic shift in habitat use similar to that of red grouper in which larger and older individuals move to deeper water. Although relationships between TL and depth and age and depth in this study indicate a tendency to find smaller and younger fish in shallower water, the relationships are weak. Additional efforts to obtain specimens at depths greater than 120 m will assist in determining the range of depth inhabited by speckled hind, potentially producing stronger positive relationships between TL, age and depth and identifying an ontogenetic shift in habitat use similar to that of red grouper, snowy grouper *E. niveatus,* gag *Mycteroperca microlepis,* scamp *M. phenax*, and yellowfin grouper *M. venenosa* (Moe, 1969; Low and Ulrich, 1983; Lindeman et al. 2000).

Age and growth

The timing of increment formation reported in the present study overlaps with the results reported by Matheson and Huntsman (1984), which indicated increments on otolith sections were annuli that formed between April and July. However, there were limitations to the marginal increment analysis by Matheson and Huntsman (1984); including small sample size (n=241) and inadequate samples from each month. The authors reported that most fish were caught between February and November, but did not report sample size by month. Disproportionate sampling by month could bias the result of marginal increment analysis. Therefore, I place more confidence in the results of the marginal increment analysis from the present study. Other groupers also form annuli during the same time of the year as speckled hind, including goliath grouper (May-August; Bullock et al., 1992), red grouper (July and August; Burgos et al., 2007) and gag (July and August; Harris and Collins, 2000).

I feel confident in the assessment of the age structure of the speckled hind population despite difficulties encountered while aging sections of otoliths. On some sections, groups of increments, rather than single increments, were observed. Groups consisted of a number of narrow translucent and opaque zones separated by a larger translucent zone. Because groups of narrow increments were separated by larger translucent zones, it was assumed that the narrow increments represented distinct growth events within a single year. Therefore, when groups of increments were encountered, they were counted as a single increment. The increments after the first few increments get increasingly narrow towards the margin, making it difficult to discern between increments. Opaque deformities observed in other groupers like red grouper and snowy grouper were also observed in speckled hind otoliths (Burgos, 2001; Wyanski et al., 2000; Figure 32). Opaque deformities often made it difficult to decide which increment to count as the first and which marginal increment to include or exclude. Increments on cross-sections of speckled hind otoliths were previously identified as annuli (Matheson and Huntsman, 1984). Since the result of the marginal increment analysis were similar to the results of Matheson and Huntsman (1984) and the APE between readers was at an acceptable level, I conclude that my technique for aging speckled hind otoliths was valid and the assessment of age was accurate.

Comparisons of mean TL and mean age between periods of the present study revealed changes in life history, presumably in response to fishing pressure, despite the 1994 SAFMC trip limit of one speckled hind per vessel. It is appropriate to conclude that mean length and mean age has decreased since the earlier period despite the discrepancy in the percentage of fishery-independent samples between periods. The higher percentage of fishery-independent samples during the earlier period likely caused the mean length and age from each period to appear to be less different then they would have been if the percentages of fishery-independent samples had been equal. Decreases in mean TL and mean age indicate that larger and older fish have been removed from the population.

Comparisons of length at age and VB growth coefficient between periods of the present study also revealed changes in life history, presumably in response to fishing pressure. The lower k during the later period indicates that during the later period speckled hind reached L_∞ more slowly than speckled hind during the earlier period. The decrease in length at age and growth rate between periods suggests that fast growing individuals have been and continue to be removed from the population. The loss of fast growing fish suggests that fishing mortality of speckled hind has remained stable or even increased between periods.

Blueline tilefish *Caulolatilus microps*, a long-lived, slow growing deepwater species, exhibited decreases in mean length, age, and length at age in response to sustained over-exploitation from 1983-1999 (Harris et al., 2004). Scamp exhibited decreases in median length and age over a period of exploitation from 1979-1999 (Harris et al., 2002). Snowy grouper, gag and red porgy *Pagrus pagrus* exhibited increased length at age in response to fishing pressure from 1979-1994, 1976-1995 and, 1972-1981, respectively (Harris and McGovern, 1997; Harris and Collins, 2000; Wyanski et al., 2000). This increase in length at age was a typical density-dependent response due to the increased availability of resources. After a decade of increasing fishing pressure, red porgy exhibited significantly smaller lengths at age. Sustained fishing pressure may have effectively reduced the number of individuals genetically predisposed to fast growth, allowing the slower growing individuals to proliferate. Speckled hind may be at, and possibly past, this point in the sequence of life history changes, with sustained fishing pressure having removed many of the faster growing individuals from the population.

Comparison of percent frequency distributions of age from the two periods indicates that age at recruitment to the fishery has increased by one age class. The increase in age at recruitment is likely the result of slower growth during the later period. The catch curves indicate that total mortality has increased over time. The estimates of Z from the present study are both higher than previously reported estimates of Z (Matheson and Huntsman, 1984). Because I assume natural mortality has been constant, fishing mortality must have increased over time.

Matheson and Huntsman (1984) reported a maximal YPR of 1.2 kg, which is less than the estimate from 1977-1993 (=1.8 kg) and greater than the estimate from 2004-07 (=1.0 kg). These results suggest that YPR had improved between 1972-79 and 1977-93, and then worsened between 1973-93 and 2004-07. However, Matheson and Huntsman (1984) calculated Ricker type YPR models using M=0.2, t_r=3.3 and t_{max}=25. Therefore, comparisons between the results of Matheson and Huntsman (1984) and the present study may not be sound. The range of YPR has decreased from 1977-93 to 2004-07, giving some indication of a decline in the status of the speckled hind population.

The fishing effort during the 1977-93 likely contributed to a decline in status of the speckled hind population off the Atlantic coast of the southeast United States because the estimated F was larger than F_{max}. During this time period, fishing effort removed more fish from the population than were recruited to the population. YPR could have been improved to 1.1 kg by decreasing fishing effort. However, YPR could have been improved to approximately 1.4, 1.6 and 1.8 kg at the observed fishing effort, if age of first capture was delayed until approximately 3 (390 mm TL), 4 (466 mm TL) and 6 (595 mm TL) years, respectively. Also, these YPRs could be obtained at even higher fishing efforts than that estimated for this period as long as first capture was delayed until the aforementioned ages. The status of the speckled hind population would have likely improved had F been below 0.14 or age at first capture above 6. The YPR analysis from this period should be interpreted with caution, as the analysis reflects data collected over a period of 16 years.

The YPR analysis from 2004-07 indicated that fishing effort during this period is not sustainable as the observed F was larger than F_{max}, indicating more fish were removed from the population than recruited to the population. The status of the speckled hind population will only improve at the observed age of first capture if F is reduced to 0.1, or at the estimated F if age at first capture is delayed at least until 10 (798 mm TL) years old. Ninety-nine percent of the speckled hind captured from 1977-2007 were 10 years old or younger. In order to delay the age of first capture until 10 years old, or reduce F to

0.1, the deepwater reef fishery would have to be closed. Since maximum YPR can not be achieved without closing the fishery, the status of the speckled hind population will not improve without closing the fishery. However, a series of marine protected areas (MPAs) closed to fishing is likely a suitable alternative to completely closing the deepwater reef fishery.

Fishing mortality of speckled hind increased despite the 1994 SAFMC one fish per vessel trip limit because most of this fishing mortality is actually release mortality. The SAFMC regulation did not reduce fishing mortality because speckled hind is caught in a multi-species fishery by fishermen targeting deepwater reef fish. However, all the speckled hind that are caught after the first have to be released. When fish from deepwater are rapidly brought to the surface, the decrease in ambient pressure causes the swim bladder to over-expand, damaging internal organs (Schmidt-Nielson, 1997). The symptoms associated with rapid ascent to the surface from deepwater are collectively termed catastrophic decompression syndrome (CDS) (Rummer and Bennet, 2005). Symptoms of CDS include: bulging eyes, external hemorrhaging, everted stomach, intestinal protrusions and loss of equilibrium (Harden-Jones, 1952; Gitschlag and Renaud, 1994). Some of the speckled hind captured during MARMAP fishery-independent sampling did suffer symptoms of CDS. The symptoms of CDS can be lethal themselves, but release mortality may occur because decompression results in positive buoyancy and equilibrium loss (Tytler and Blaxter, 1977; Rummer and Bennet, 2005). Released fish suffering from CDS may get trapped at the surface where they are susceptible to predators and unfavorable physical conditions (Keniry et al., 1996). Deepwater snappers and groupers caught at depths greater than 40-50 m experienced lower survival rates than individuals captured at shallower depths (Harden-Jones, 1953; Gitschlag and Renaud, 1994; Wilson and Burns, 1996). Although there have been no studies on speckled hind release survival, it is likely that speckled hind experience similar low release survival when captured at these depths. As long as speckled hind continue to be caught in the deepwater reef fishery, they will continue to experience high mortality related to fishing and will not exhibit changes in life history that indicate improvement in the status of the population.

Reproductive biology

Characteristics described as evidence of protogynous hermaphroditism by Sadovy and Shapiro (1987), including sperm sinuses within the ovarian wall and membrane-lined central cavities in the testes, were observed in 29 speckled hind sampled during this study. However, vitellogenic oocytes undergoing atresia, another characteristic described by Sadovy and Shapiro (1987) were not observed in these specimens; only primary growth oocytes were observed. A female-biased sex ratio also supports the theory of protogyny. These findings confirm the earlier report of protogyny in this species by Brulé et al. (2000). Protogynous hermaphroditism has been confirmed in a number of groupers of the southeast United States: red grouper (Burgos et al., 2007), gag (McGovern et al., 1998) and black grouper *M. bonaci* (Crabtree and Bullock, 1998).

Protogynous hermaphroditism poses a unique problem for fisheries managers. It has been suggested that protogynous fish populations are more susceptible to overfishing because a decline in males available to spawn results in limited sperm supply and reduced spawning potential (Bannerot et al., 1987). Also, a simulation of the impact of fishing on the reproductive biology of graysby *E. cruentatus*, a protogynous grouper, demonstrated that protogynous populations suffer a greater reduction in reproductive capacity, measured as fertilized egg production, as a result of fishing mortality than gonochoristic populations (Huntsman and Schaaf, 1994). Fishing pressure on a protogynous population such as speckled hind results in a reduction in reproductive capacity because the loss of males leads to sperm limitation and reduced fertilized egg production (Bannerot, 1987; Huntsman and Schaaf, 1994).

The observation of spawning females from May through August and in October was similar to the spawning season reported by Brulé et al. (2000) in the Gulf of Mexico. The absence of spawning females in the 2004-07 period is especially alarming because more speckled hind were sampled during this period than during any other study of reproduction in speckled hind.

Spawning females ranged in size from 557-720 mm TL and from 2004-07, 54 female speckled hind sampled were within this spawning size range (29 of these were captured during the estimated spawning season). This suggests that the lack of spawning females during the later period was due to an increase in length at maturity. Despite the small sample size (n=12), the size range of sexually active females (56-77 cm TL) reported by Brulé et al. (2000) was similar to the size range of spawning females collected during the present study. This too suggests that the lack of spawning females in the later period may be due an increase in length at maturity. Also of note is that the minimum length of immature and regressed females (33 cm TL) reported by Brulé et al. (2000) is noticeably larger than the minimum size of immature and regressed females (169 mm TL) from the present study; although this may only reflect the small sample size (n=19) of immature and regressed females reported by Brulé et al. (2000). They also reported that sexually active females, males and transitionals were caught at depths greater than 146 m. Since no samples from 2004-07 were collected from depths greater than 146 m, the findings of Brulé et al. (2000) suggest the absence of spawning females during the 2004-07 period may be due to lack of samples obtained from depths greater than 146 m. Also, many juveniles were collected during the later period, which is evidence of spawning events. Therefore, the absence of spawning females is likely due to a combination of the increase in length at maturity and inadequate sampling of adult habitat. If the absence of spawning females is indicative of a low frequency of spawning events, recruitment to the fished population will be impaired, and a further decline in the population can be expected.

The observed spawning locations and the observation of regressed females at inshore locations (depths between 33-37 m) suggest that spawning speckled hind probably make migrations between inshore habitats and deepwater spawning locations near the shelf break. However, with so few specimens observed in spawning condition, it is difficult to make conclusions about spawning behavior. Migrations from inshore locations to offshore spawning locations have been suggested for gag and red grouper (Coleman et al., 1996; Burgos et al., 2007). Scamp, snowy grouper, yellowedge grouper *E. flavolimbatus*, and yellowmouth grouper *M. interstitialis* also spawn at or near the shelf break (Sedberry et al., 2006).

The maturity schedules, transition schedules, and sex ratios determined for speckled hind suggest that the status of the population has not improved between the two sampling periods. Although the differences in length and age at 50% maturity and sexual transition between the two periods were not significant at α=0.05, if the α-level had been set at 0.10, these differences would have been significant. The typical response to fishing pressure seen in other protogynous fishes has been a decrease in length and age at maturity and at sexual transition and a shift to a more female biased sex ratio. Other fishes on the Atlantic coast of the southeast United States have experienced a decline in length and age at maturity and sexual transition and in the proportion of males coinciding with increased fishing pressure. Gag experienced decreases in length and age at 50% maturity, length at sexual transition and in the proportion of males (McGovern et al., 1998; Harris and Collins, 2000); scamp experienced decreases in length and age at 50% maturity (Harris et al., 2002); red porgy experienced a decrease in length at maturity, and length at sexual transition (Harris and McGovern, 1997); and snowy grouper experienced a decrease in the proportion of males in the population (Wyanski et al., 2000).

Although the typical response to fishing pressure is a decrease in length and age at maturity, speckled hind exhibited a non-significant increase in length and age at maturity. The changes in transition schedules and sex ratio are more consistent with changes assumed for an exploited protogynous hermaphrodite. The reduction in the proportion of males in the speckled hind population is compensated for by females transitioning at smaller sizes and younger ages. These changes in life history not only suggest continued exploitation of speckled hind, but also low reproductive resilience for this population due to diminished reproductive capacity. The combination of the reduced proportion of males and female speckled hind maturing late in life and transitioning shortly after maturation, likely results in lower recruitment due to reduced fertilized egg production.

Also, a reduction in males may lead to decreased genetic diversity in the population, as seen in gag (Chapman et al., 1999).

The non-significant increase in length and age at 50% maturity was an unexpected result. As previously noted, other protogynous species exhibited decreases in length and age at maturity. Snowy grouper experienced an increase in length and age at 50% maturity; however, this shift coincided with an increase in length at age attributed to a density-dependent response to a decrease in competition for resources (Wyanski et al., 2000). This explanation does not account for the changes observed in the speckled hind population, given the age and growth data from this study. The most likely explanations for this observation is the low sample size from 1977-1993 and inadequate sampling of the adult population from 2004-2007. Future studies of speckled hind should aim to explain why length and age at 50% maturity has increased, while mean length and age of the population has decreased.

It is also alarming that the ages at full recruitment to the fishery during both periods of this study were lower than the age at 50% maturity. Therefore, most speckled hind are available to the fishery before they are able to spawn. The mean age of speckled hind sampled from 2004-07 was consistent with the estimated age at full recruitment, and was more than two years younger than the age at 50% maturity.

Future studies need to focus on understanding reproductive behaviors of speckled hind. Sampling efforts should initially take place in areas where speckled hind in spawning condition have been collected to improve our understanding of the timing and location of spawning. Such studies may also reveal if speckled hind form spawning aggregations and the structure of any social hierarchy. The determination of a social hierarchy in speckled hind will allow scientists and managers determine how fishing pressure affects the reproductive potential of the speckled hind population.

The evidence presented in this study indicates that, under current management regulations, over-exploitation continues to occur and speckled hind are likely unable to recover from reduced population levels. The future of speckled hind management presents a dilemma. Current management is not working because speckled hind is a protogynous deepwater grouper that likely experiences high release mortality. Because speckled hind occur in a multi-species fishery, the only effective way to protect speckled hind is to close the entire fishery. Closure of this fishery may cause an undue economic burden on commercial fishermen targeting this fishery, which the Magnuson-Stevens Act attempts to avoid. Traditional methods such as catch limits and quotas will be ineffective because once the limits are met, fishing mortality of speckled hind will continue in the form of regulatory discards. Size limits will be ineffective because immature speckled hind recruit to the fishery well before they are sexually mature. Gear restrictions such as increased hook size may protect immature fish, but still promote the targeting of larger and older fish. The only suitable management techniques involve a closure of portions of the resource, in the form of MPAs.

MPAs are broadly defined as any area of the ocean protected from exploitive impact (Polunin, 2002). Although there can be different types of MPAs, MPAs from which no harvest is allowed offer a promising strategy for rebuilding and protecting the speckled hind population off the southeast United States. Reef fish scientists agree that MPAs may be the only realistic solution to the problem posed by combination of the multi-species nature of reef fisheries and the high bycatch mortality (Huntsman et al., 1999). In March of 2007, the SAFMC approved Amendment 14, which establishes eight deepwater marine protected areas along the Atlantic coast of the United States (SAFMC, 2007). Speckled hind have been captured in four of the proposed sites, including one site in which an individual in spawning condition was captured (Sedberry et al., 2006). Protected areas closed to fishing will eliminate fishing mortality of speckled hind, restore portions of the population, let immature individuals reach maturity and allow older fish to continue to contribute their gametes to the population. Protected areas established in spawning and recruitment habitats will also provide continual recruitment to the adult population. Closures of areas would thus allow speckled hind populations in these areas to re-establish characteristics of an unexploited population. Nassau grouper, graysby and black grouper populations exhibited increased abundance in protected areas compared to unprotected areas and may have provided recruits to areas open to fishing (Sedberry et al., 1996). Although further investigation into the effects of MPAs is needed, they will at least partly decrease fishing mortality in the speckled hind population and limit the economic burden on commercial fishermen. A management plan combining MPAs and traditional management strategies may be able to improve the status of the speckled hind population off the Atlantic coast of the southeastern United States.

Conclusion

Based on the findings of the present study, the outlook for speckled hind in the southeast United States is bleak without a change in the management strategy for deepwater reef fishes. The age and growth data are evidence that the current SAFMC regulation is not effective and speckled hind continue to be over-exploited. The reproductive data collected during 2004-07 represent a population that is not reproductively resilient to depressed population numbers. Indeed, the speckled hind population appears to be dramatically impacted by sustained over-exploitation and unable to recover under the current SAFMC trip limit of one speckled hind per vessel. Combining MPAs with traditional management strategies shows potential for improving the status of the speckled hind population off the Atlantic coast of the southeastern United States.

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Figure 1. Frequency of speckled hind captured by year from 1977-2007 during fishery-dependent and -independent sampling by MARMAP (n=1,365).

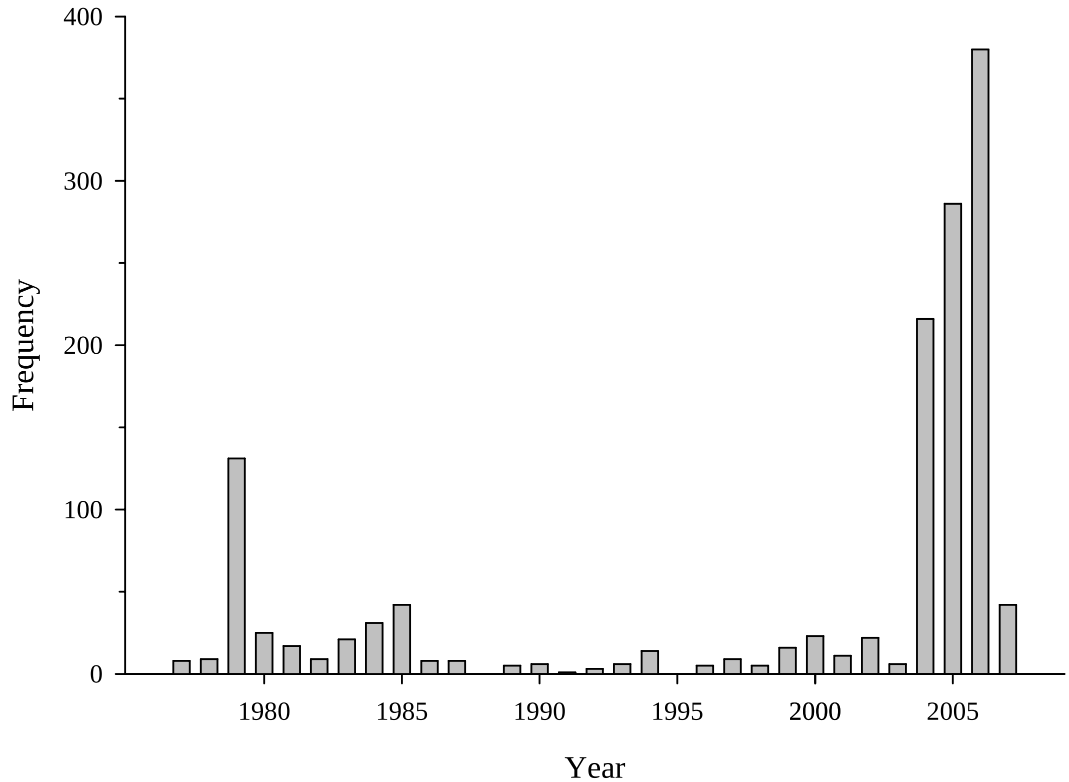
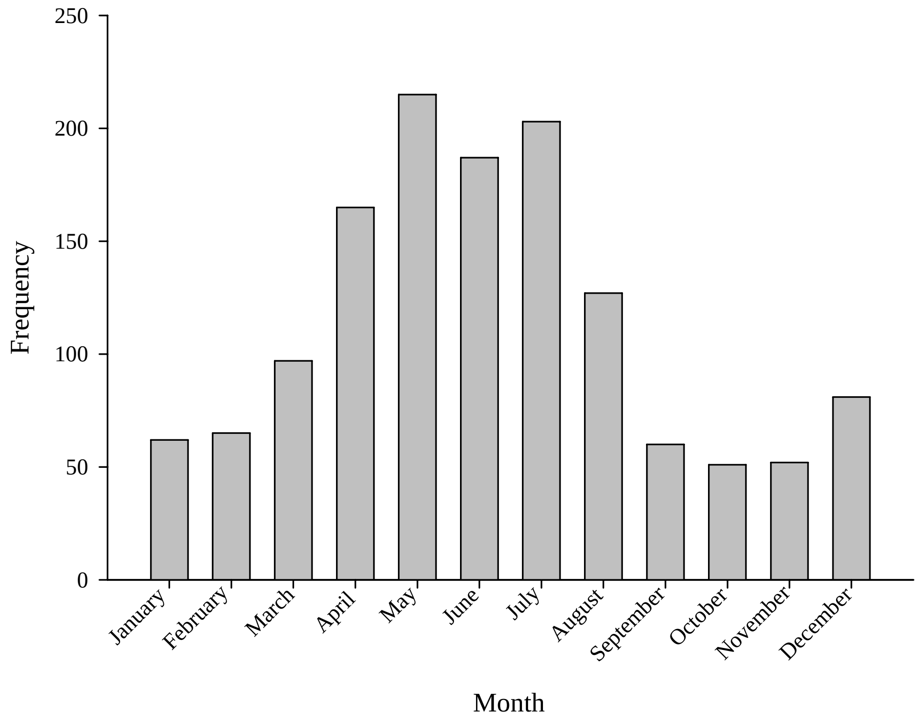
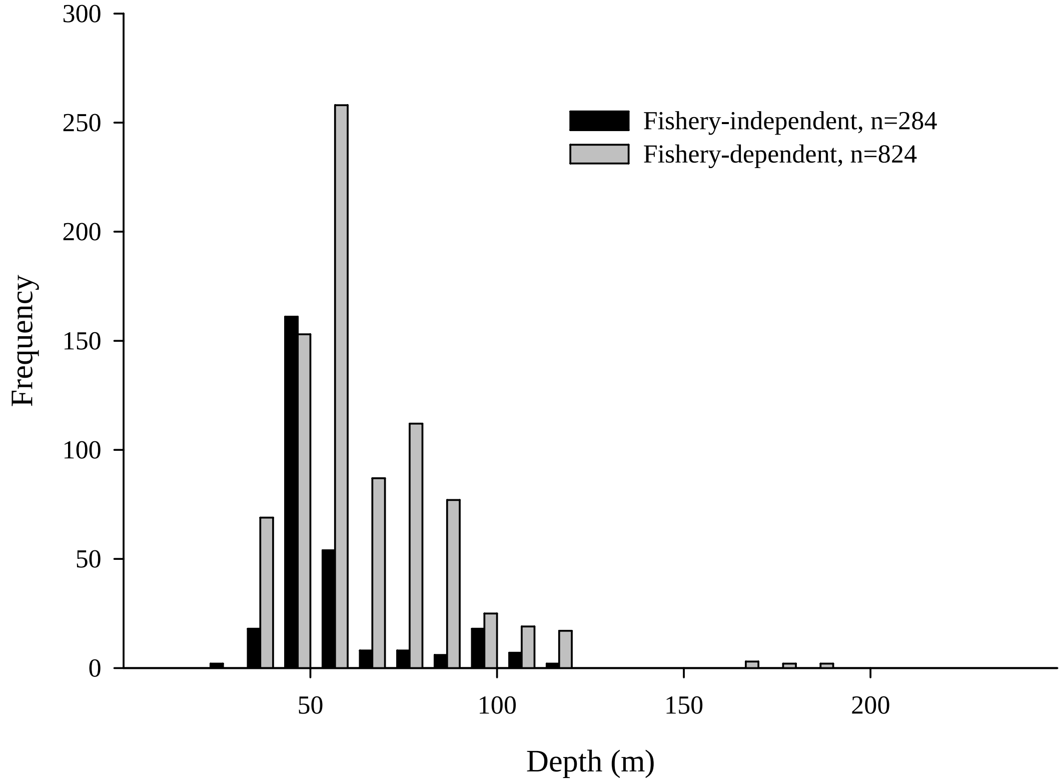

400
300
200
100
0
Frequency
1980
1985
1990
1995
2000
2005
Year

Figure 2. Frequency of speckled hind captured by month from 1977-2007 during fishery-dependent and -independent sampling by MARMAP (n=1,365).



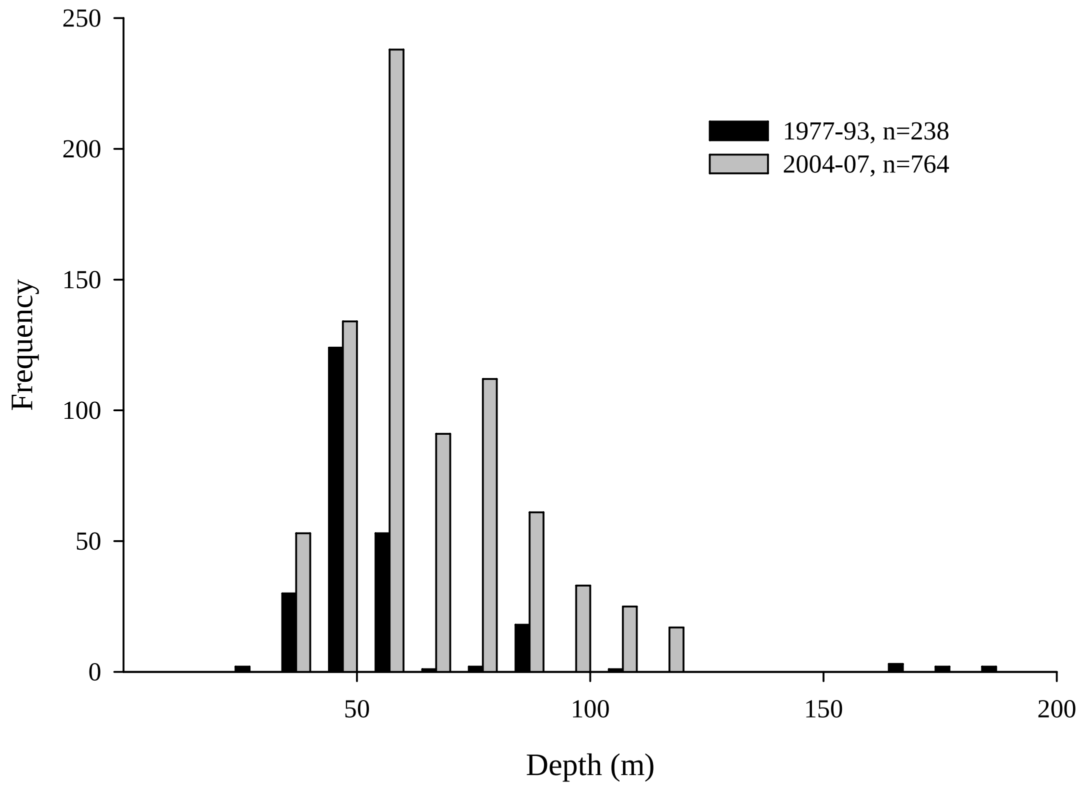
250
200
150
100
50
0
Frequency
January
February
March
April
May
June
July
August
September
October
November
December
Month

Figure 3. Comparison of frequencies of speckled hind by depth obtained during fishery-dependent and -independent sampling by MARMAP.



300
250
200
150
100
50
0
Frequency
Fishery-independent, n=284
Fishery-dependent, n=824
50
100
150
200
Depth (m)

Figure 4. Comparison of frequencies of speckled hind by depth obtained from 1977-93 and 2004-07 during fishery-dependent and -independent sampling by MARMAP.



250
200
150
100
50
0
Frequency
1977-93, n=238
2004-07, n=764
50
100
150
200
Depth (m)

Figure 5. Percent frequency of lengths for speckled hind collected from 1977-2007 during fishery-dependent and -independent sampling by MARMAP (n=1,365).

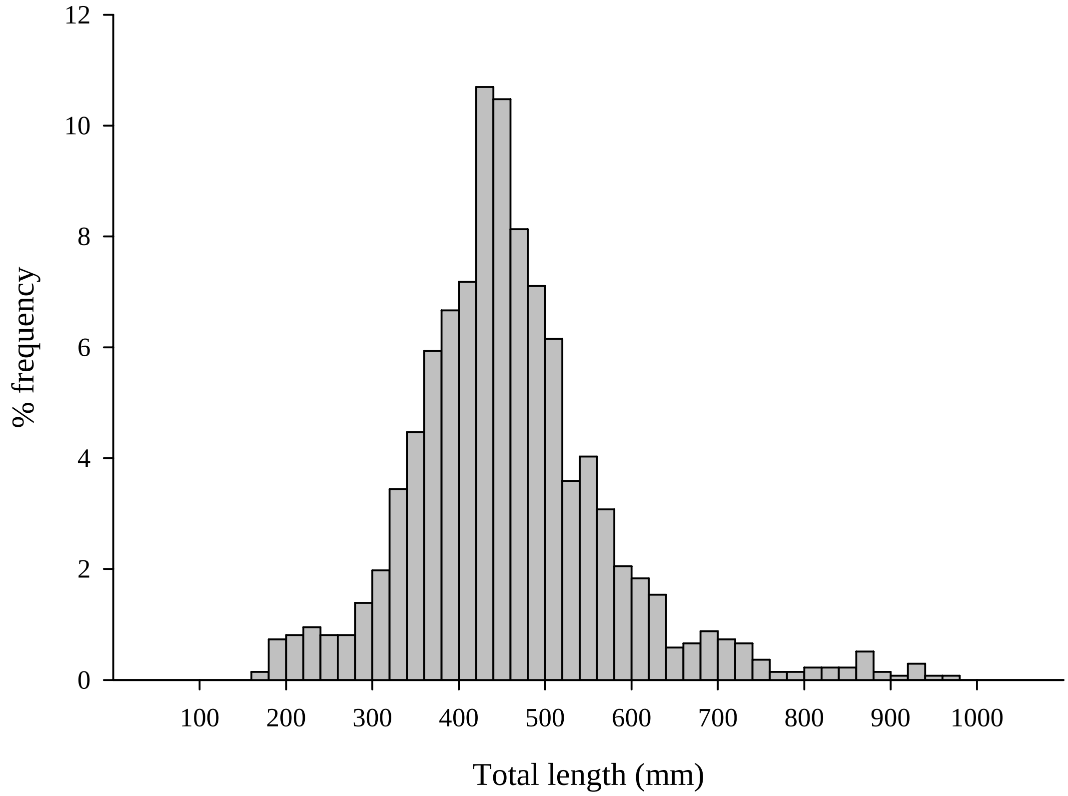

12
10
8
6
4
2
0
% frequency
100
200
300
400
500
600
700
800
900
1000
Total length (mm)

Figure 6. Comparison of percent frequencies of lengths for speckled hind collected from 1977-2007 during fishery-dependent and -independent sampling by MARMAP.

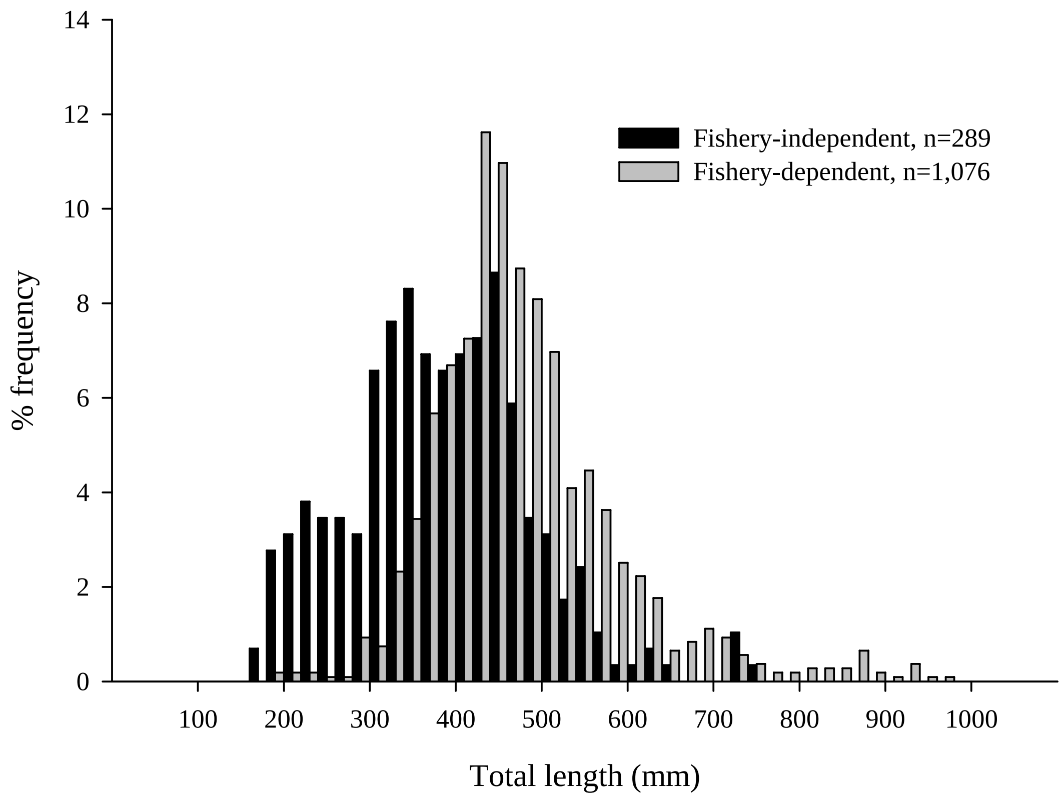
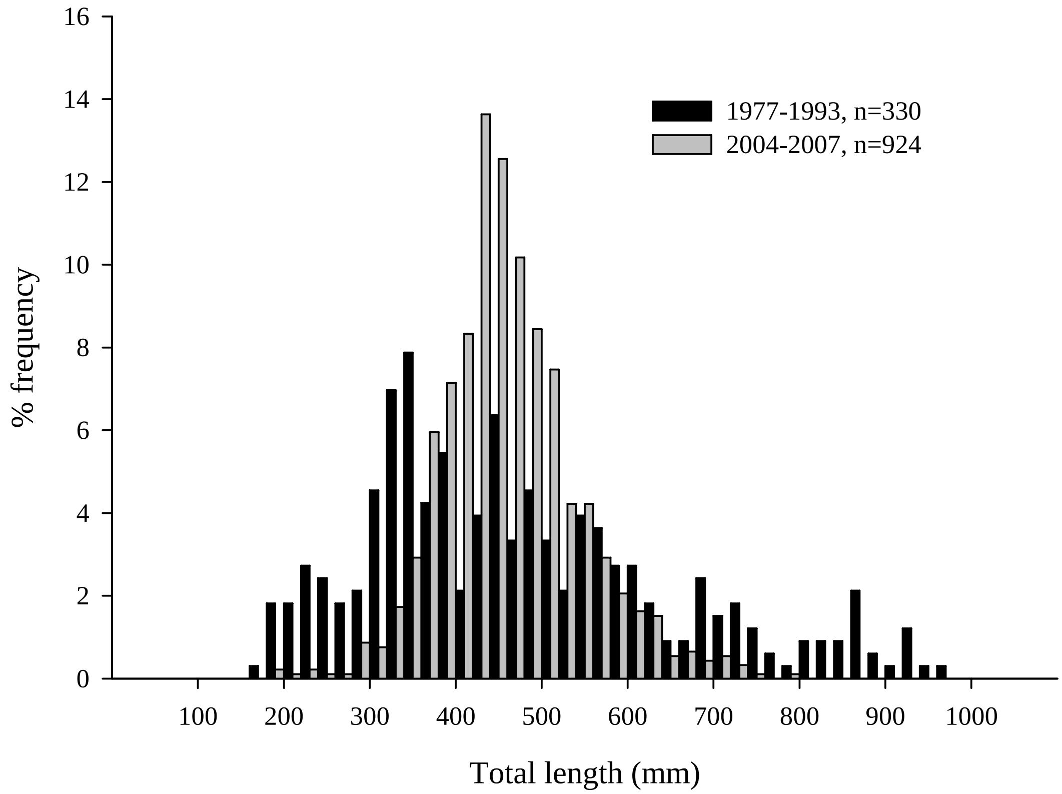
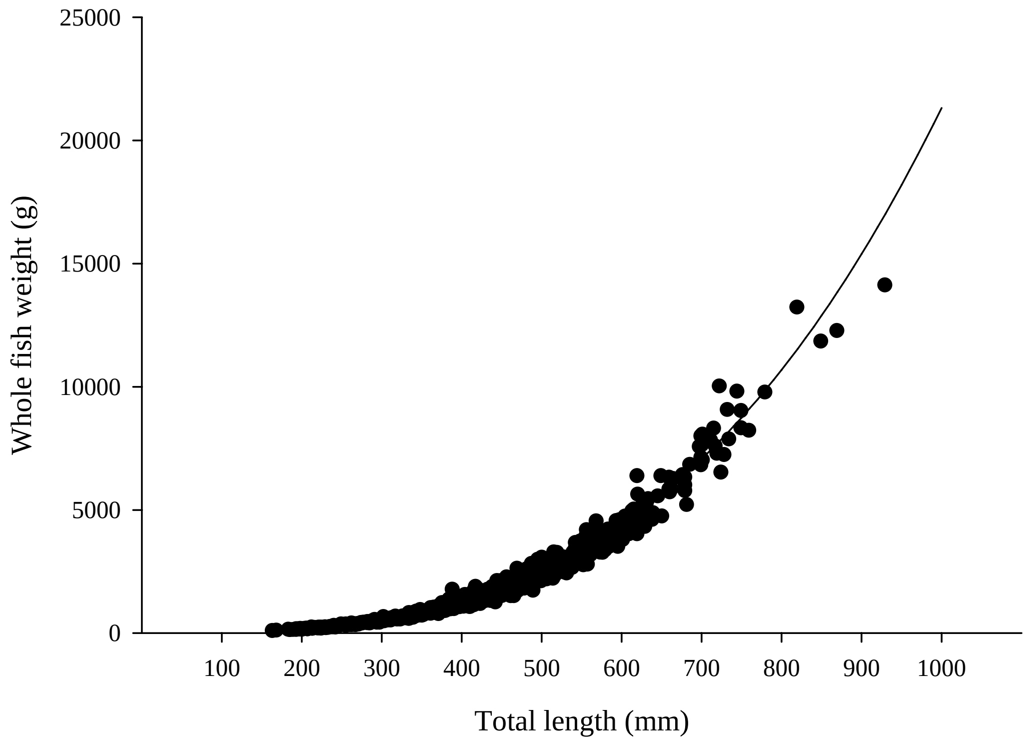

14
12
10
8
6
4
2
0
% frequency
Fishery-independent, n=289
Fishery-dependent, n=1,076
100
200
300
400
500
600
700
800
900
1000
Total length (mm)

Figure 7. Comparison of percent frequencies of lengths for speckled hind collected from 1977-93 and 2004-07 by the MARMAP fishery-dependent and -independent sampling program.



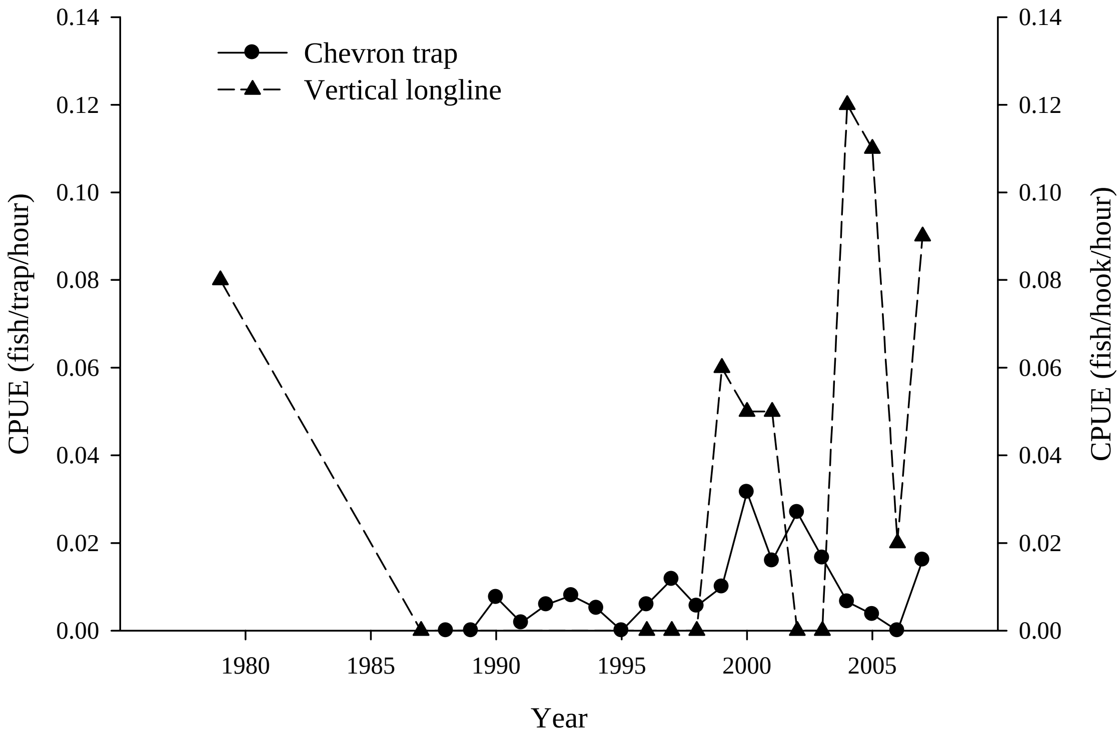
16
14
12
10
8
6
4
2
0
% frequency
1977-1993, n=330
2004-2007, n=924
100
200
300
400
500
600
700
800
900
1000
Total length (mm)

Figure 8. Relationship between total length and weight of speckled hind collected 1977-2007 during fishery-dependent and -independent sampling by MARMAP (n=1,220). Regression analysis yielded $WW = 1.1*10^{-5} *TL^{3.0958}$



25000
20000
15000
10000
5000
0
Whole fish weight (g)
100
200
300
400
500
600
700
800
900
1000
Total length (mm)

Figure 9. Catch-per-unit-effort by year for two gear types used during fishery-independent sampling of speckled hind by MARMAP.



Chevron trap
Vertical longline
CPUE (fish/trap/hour)
CPUE (fish/hook/hour)
Year
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
1980
1985
1990
1995
2000
2005

Figure 10. Proportion of edge type 1 by month in otoliths of speckled hind age 4 and less collected from 1977-2007 during fishery-dependent and -independent sampling by MARMAP.

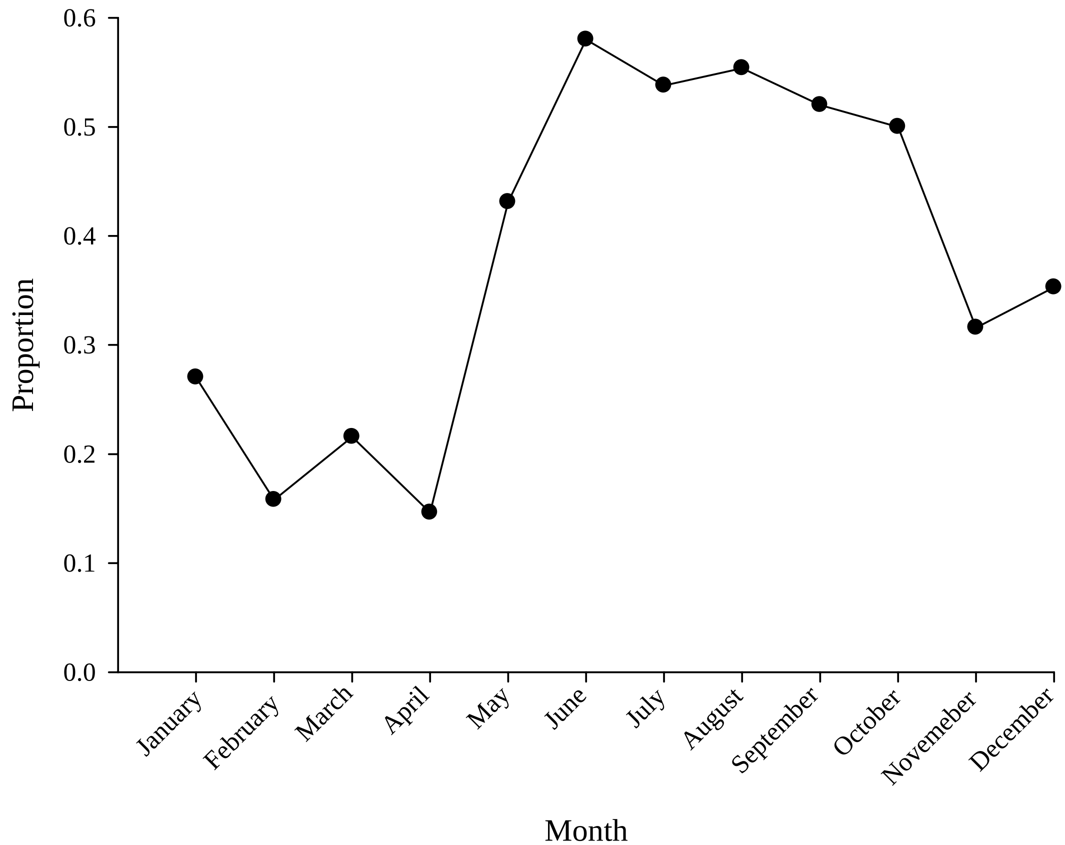
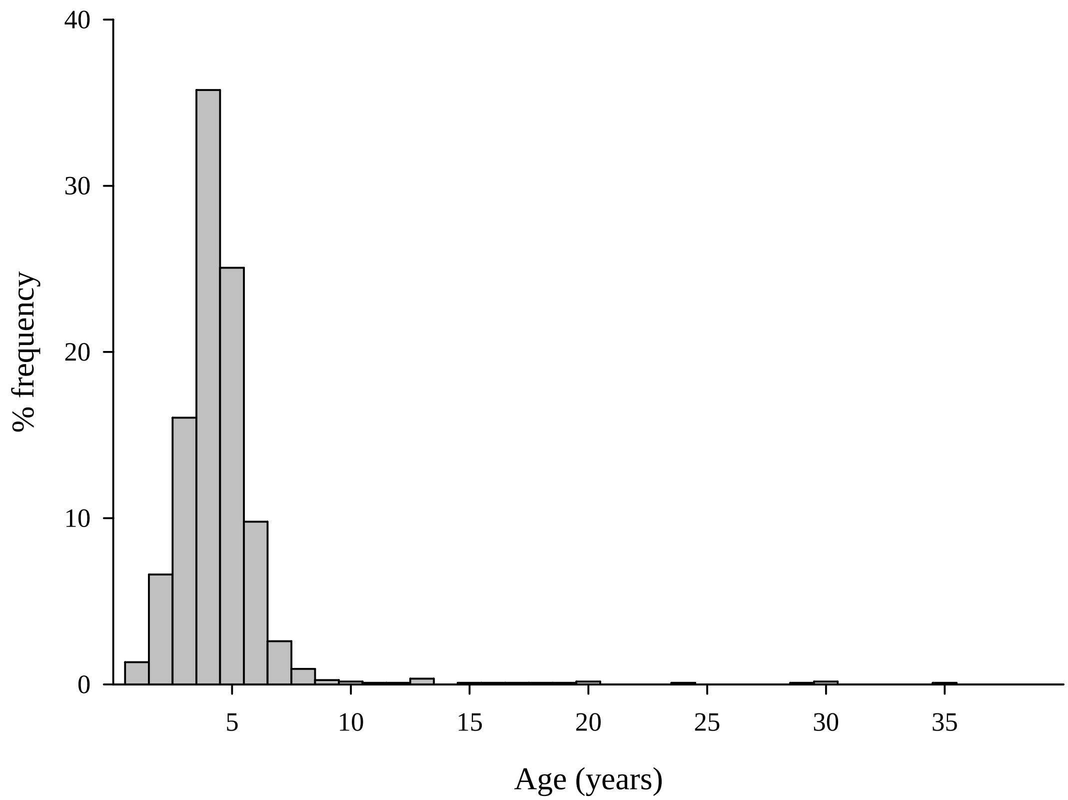
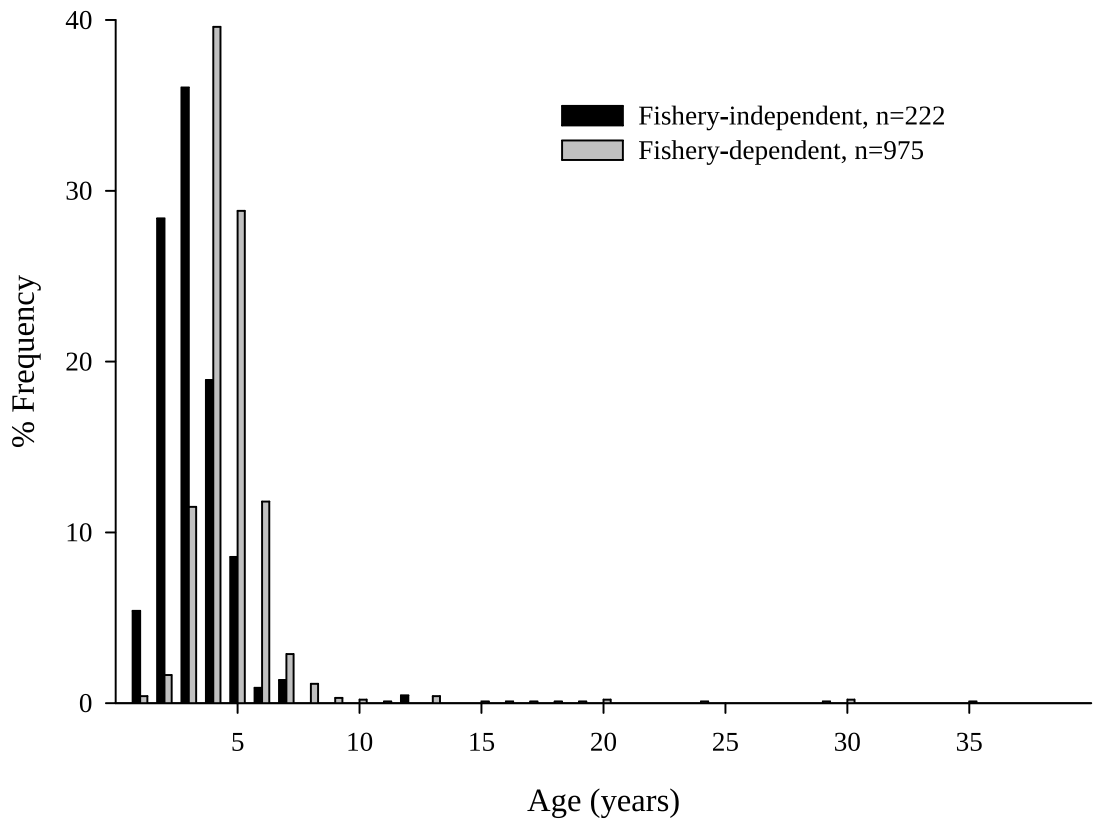

0.6
0.5
0.4
0.3
0.2
0.1
0.0
Proportion
January
February
March
April
May
June
July
August
September
October
Novemeber
December
Month

Figure 11. Percent frequency of ages for speckled hind collected from 1977-2007 during fishery-dependent and -independent sampling by MARMAP (n=1,197).



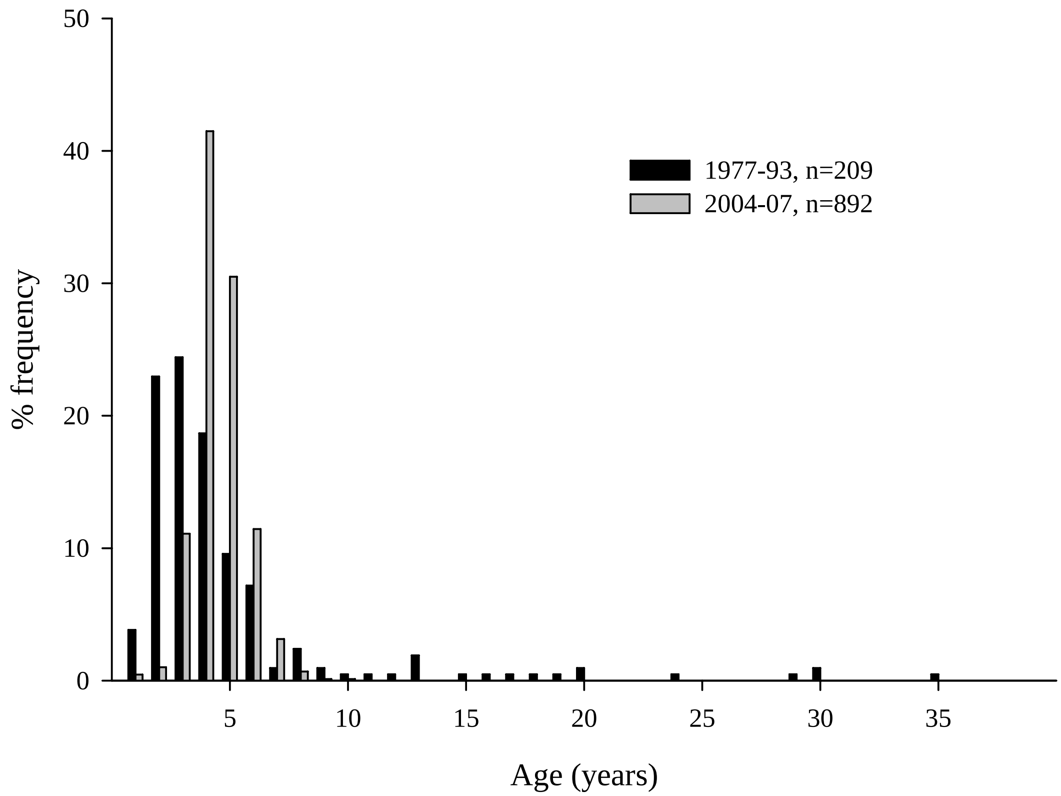
40
30
20
10
0
% frequency
5
10
15
20
25
30
35
Age (years)

Figure 12. Comparison of percent frequencies of ages for speckled hind obtained from 1977-2007 during fishery-dependent and -independent sampling by MARMAP.



Fishery-independent, n=222
Fishery-dependent, n=975
% Frequency
Age (years)
0
10
20
30
40
5
10
15
20
25
30
35

Figure 13. Comparison percent frequencies of ages for speckled hind obtained during the periods 1977-93 and 2004-07 during fishery-dependent and -independent sampling by MARMAP.



50
40
30
20
10
0
% frequency
1977-93, n=209
2004-07, n=892
5
10
15
20
25
30
35
Age (years)

Figure 14. Comparison of mean length at age for speckled hind collected during fishery-dependent sampling and independent sampling by MARMAP from 1977-2007.* indicates $p<0.05$.

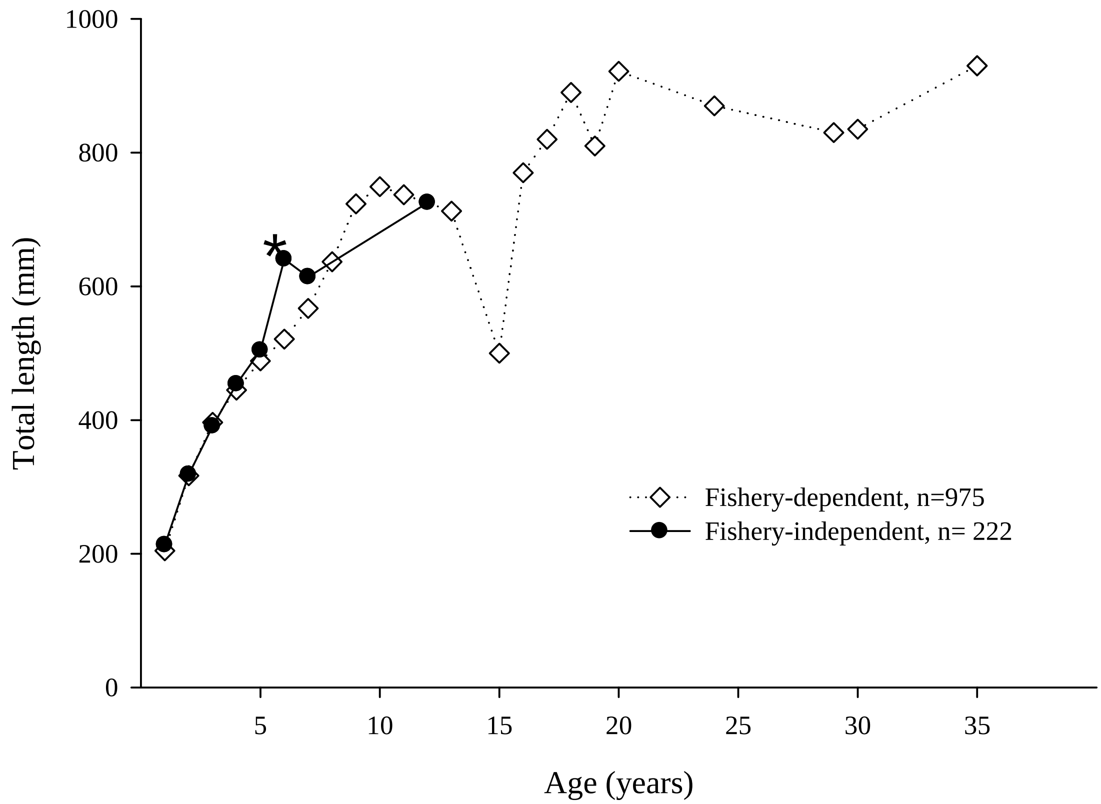

1000
800
600
400
200
0
Total length (mm)
*
Fishery-dependent, n=975
Fishery-independent, n= 222
5
10
15
20
25
30
35
Age (years)

Figure 15. Comparison of mean length at age for speckled hind collected during the periods 1977-93 and 2004-07 during fishery-dependent and -independent sampling by MARMAP. * indicates $p<0.05$.

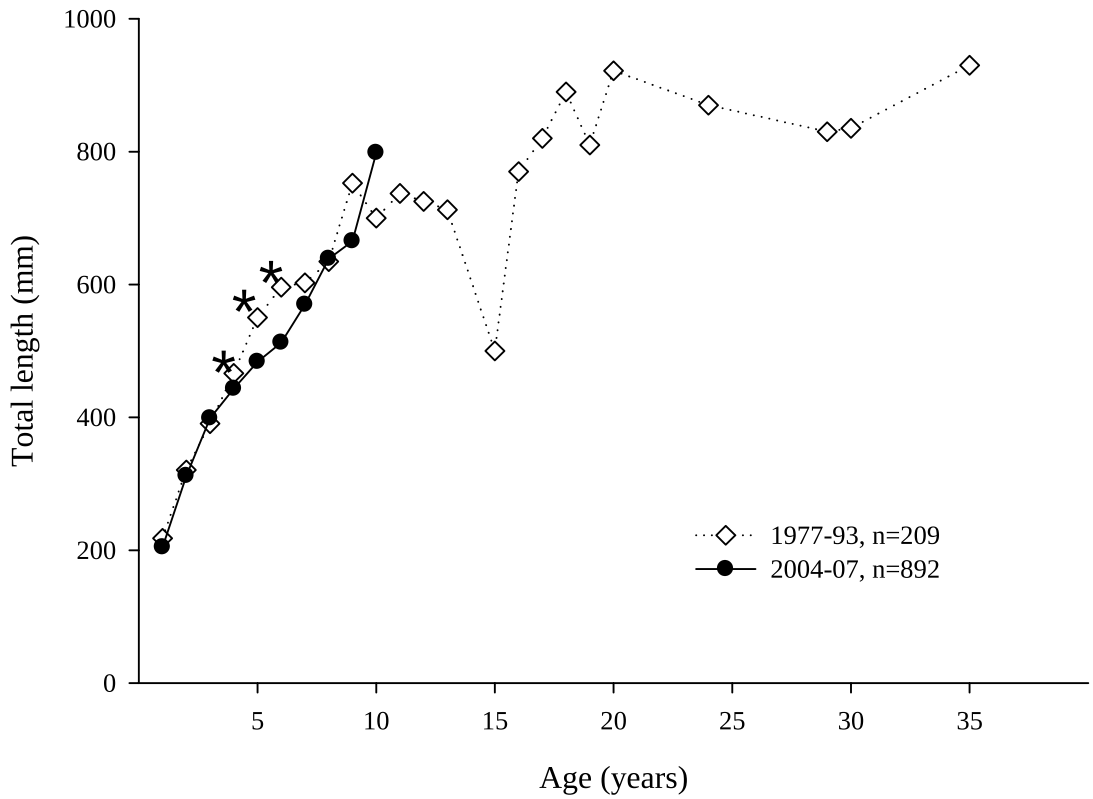

1000
800
600
400
200
0
Total length (mm)
5
10
15
20
25
30
35
Age (years)
1977-93, n=209
2004-07, n=892
*
*
*

Figure 16. Relationship between total length and depth for speckled hind collected from 1977-2007 during fishery-dependent and -independent sampling by MARMAP (n=1,108).

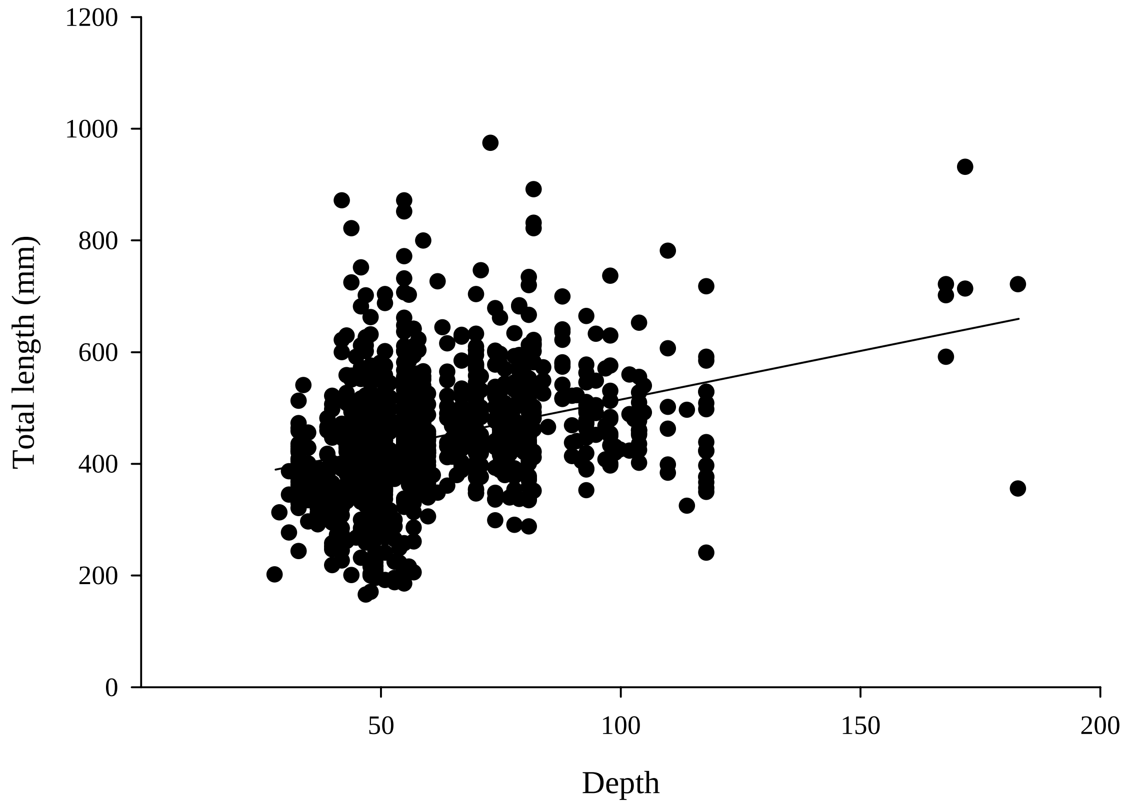
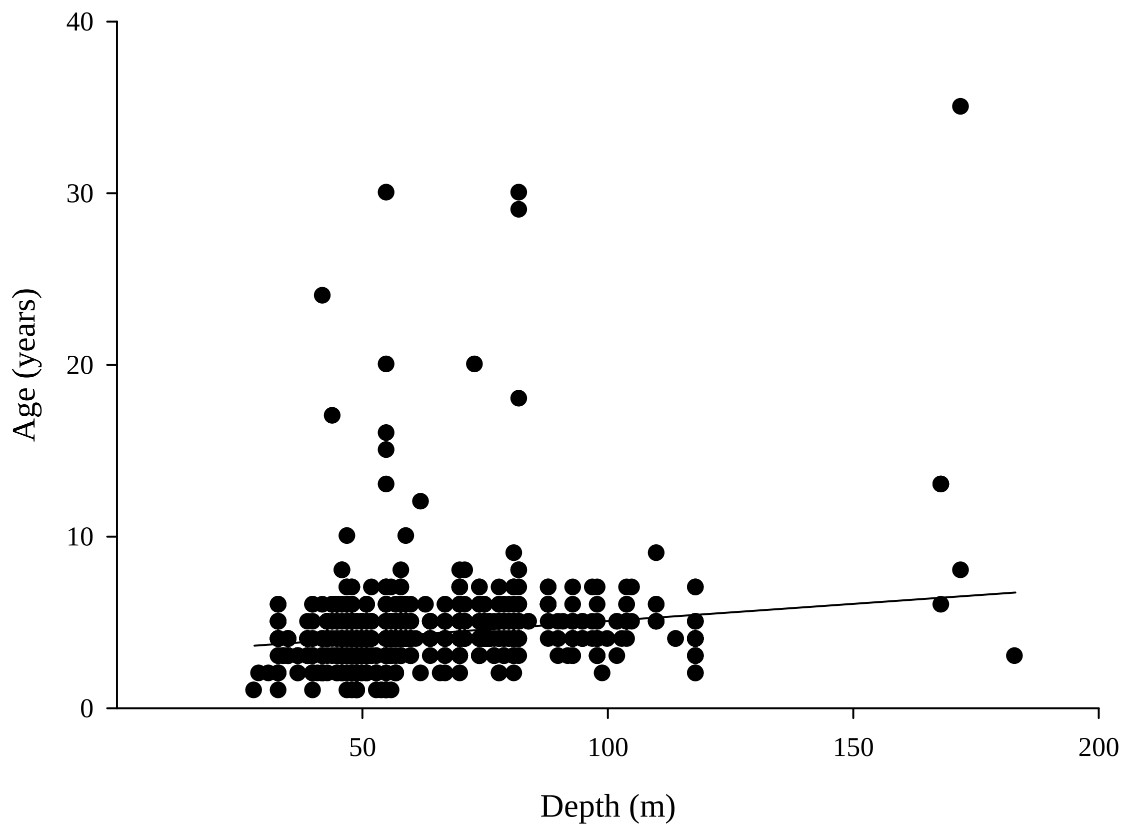
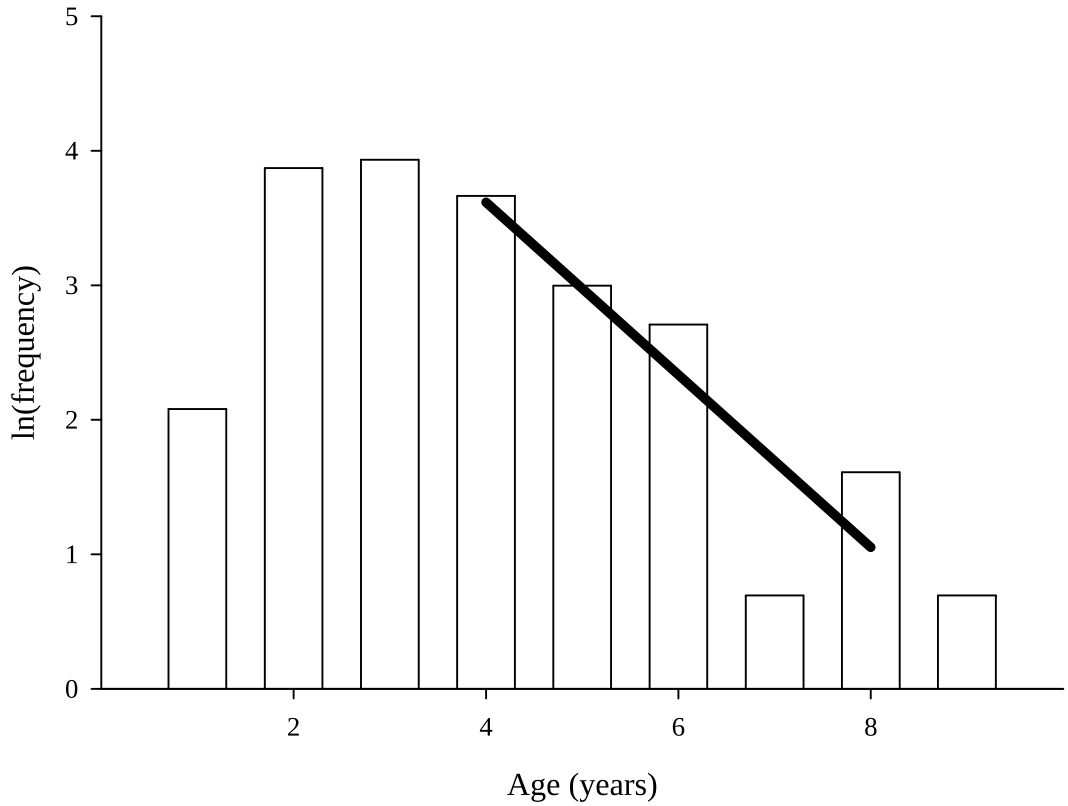

Total length (mm)
0
200
400
600
800
1000
1200
50
100
150
200
Depth

Figure 17. Relationship between age and depth for speckled hind collected from 1997-2007 during fishery-dependent and -independent sampling program by MARMAP (n=1,003).



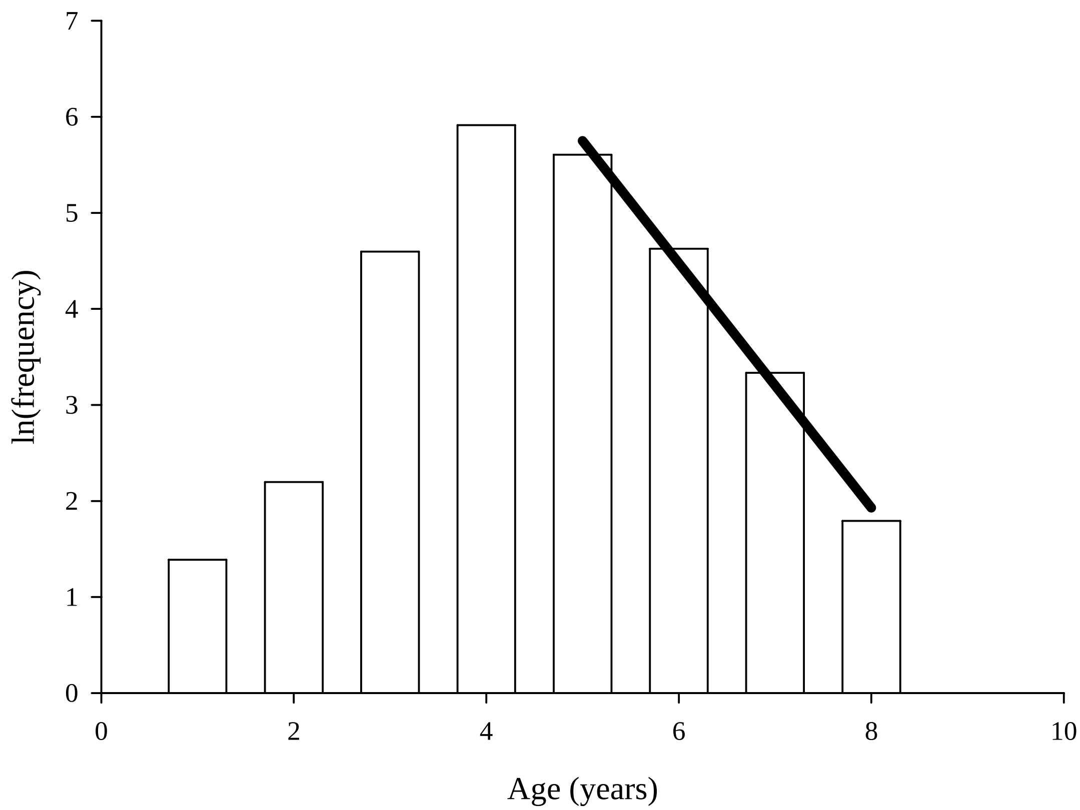
40
30
20
10
0
Age (years)
50
100
150
200
Depth (m)

Figure 18. Catch curve for speckled hind sampled from 1977-93 during fishery-dependent and -independent sampling by MARMAP (n=188).



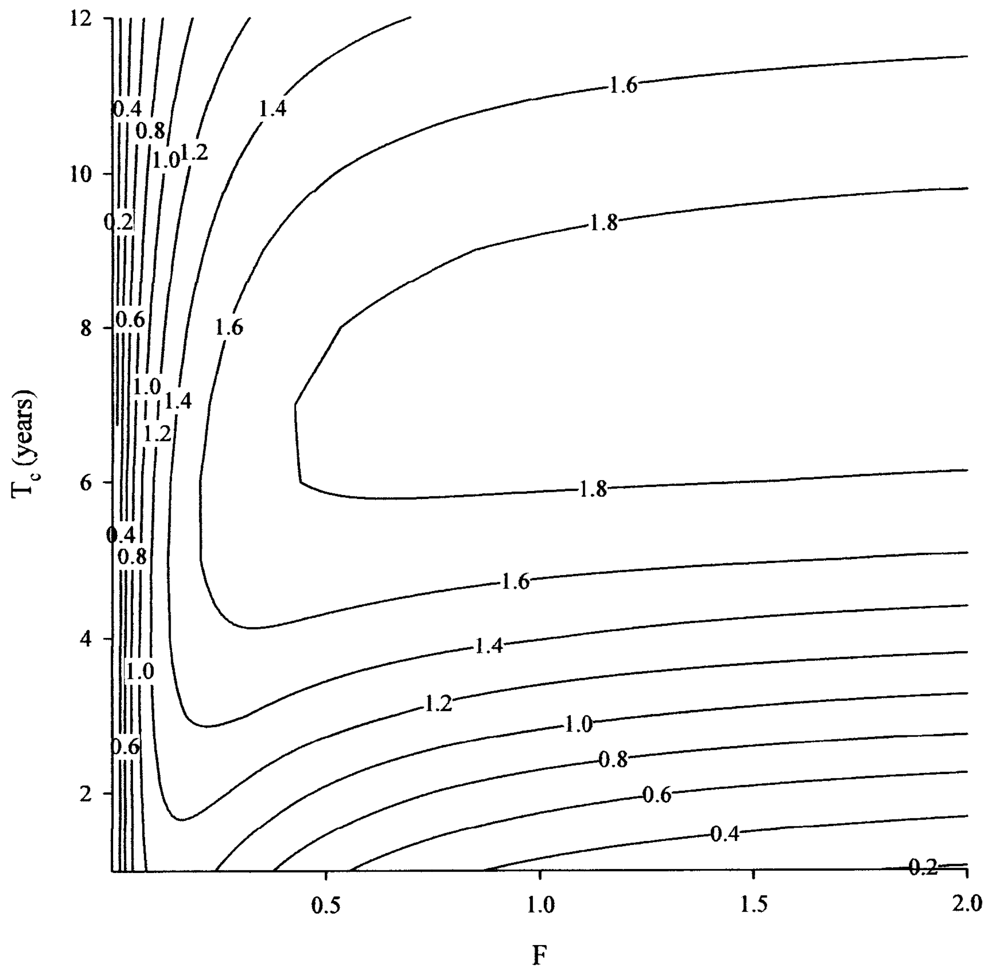
5
4
3
2
1
0
ln(frequency)
2
4
6
8
Age (years)

Figure 19. Catch curve for speckled hind sampled from 2004-07 during fishery-dependent and -independent sampling by MARMAP (n=890).



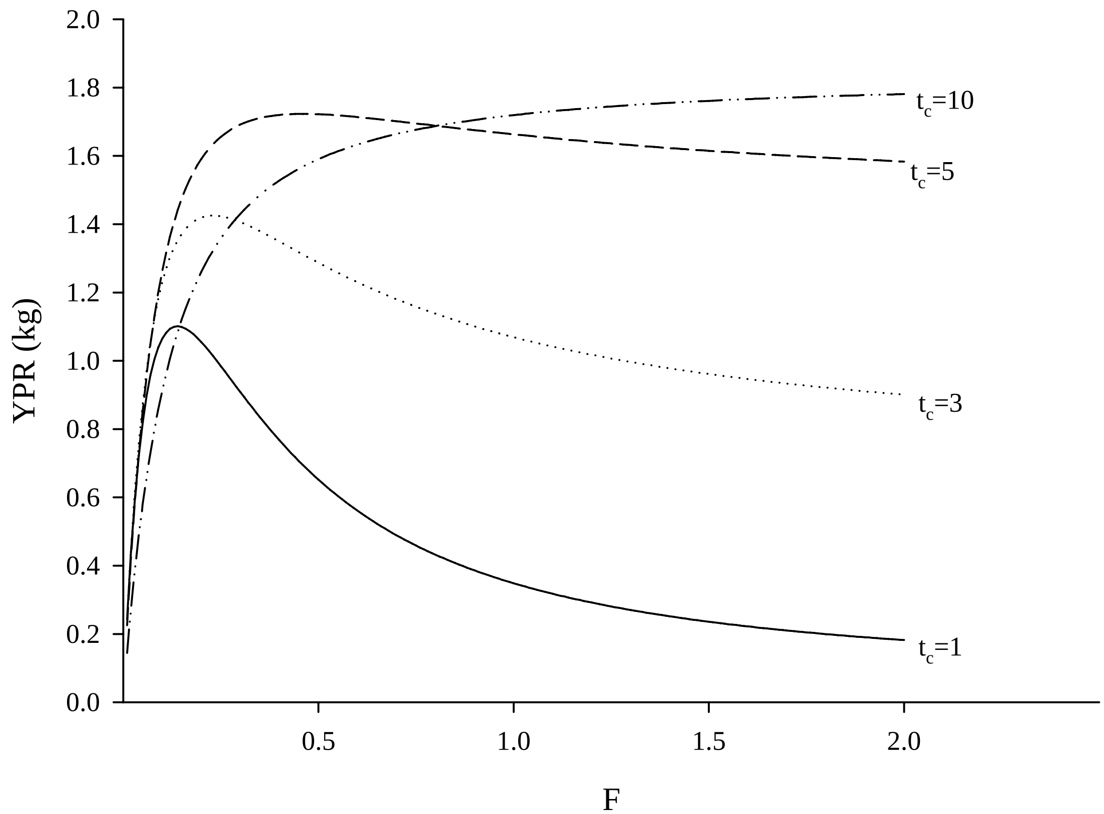
7
6
5
4
3
2
1
0
ln(frequency)
0
2
4
6
8
10
Age (years)

Figure 20. Yield per recruit (kg) for speckled hind sampled from 1977-93 during fishery-dependent and -independent sampling by MARMAP.



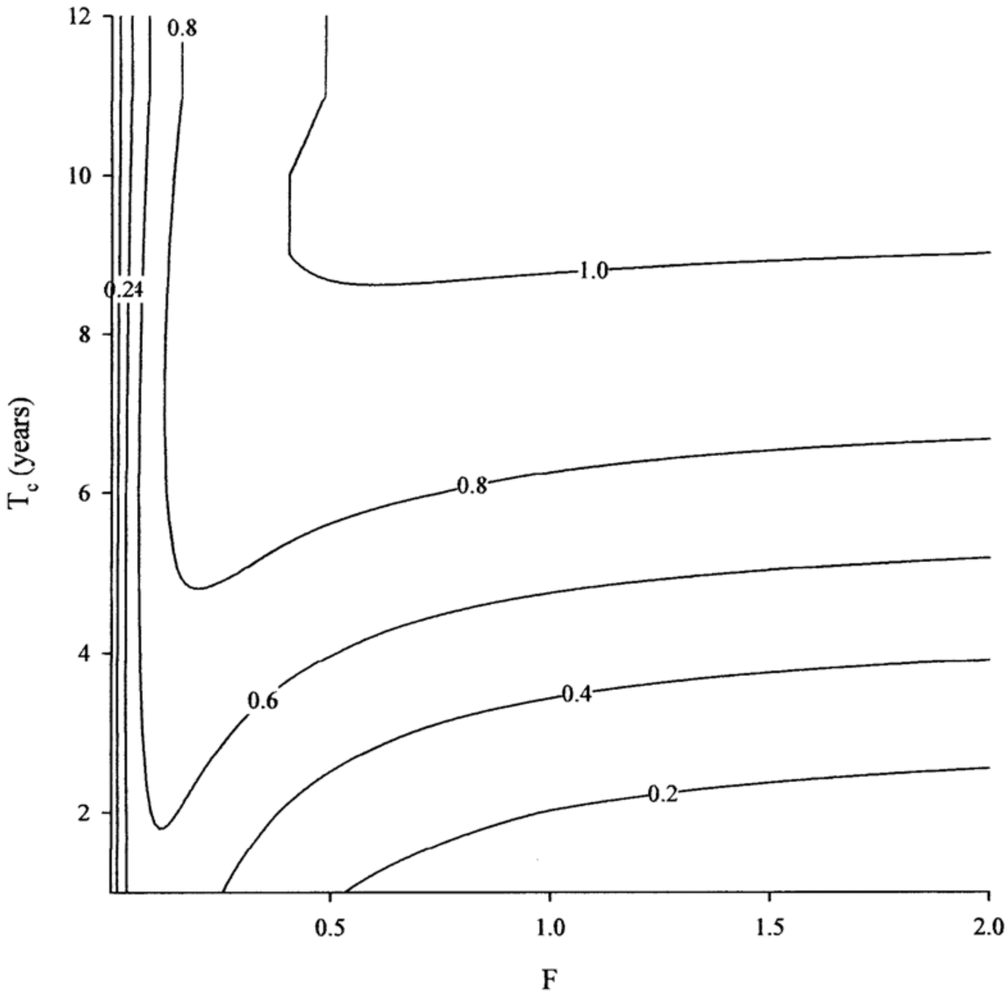
12
10
8
6
4
2
0.5
1.0
1.5
2.0
F
T_c (years)
0.4
0.8
1.0
1.2
1.4
0.2
0.6
1.6
1.8

Figure 21. Yield per recruit for speckled hind sampled from 1977-93 during fishery-dependent and -independent sampling by MARMAP.



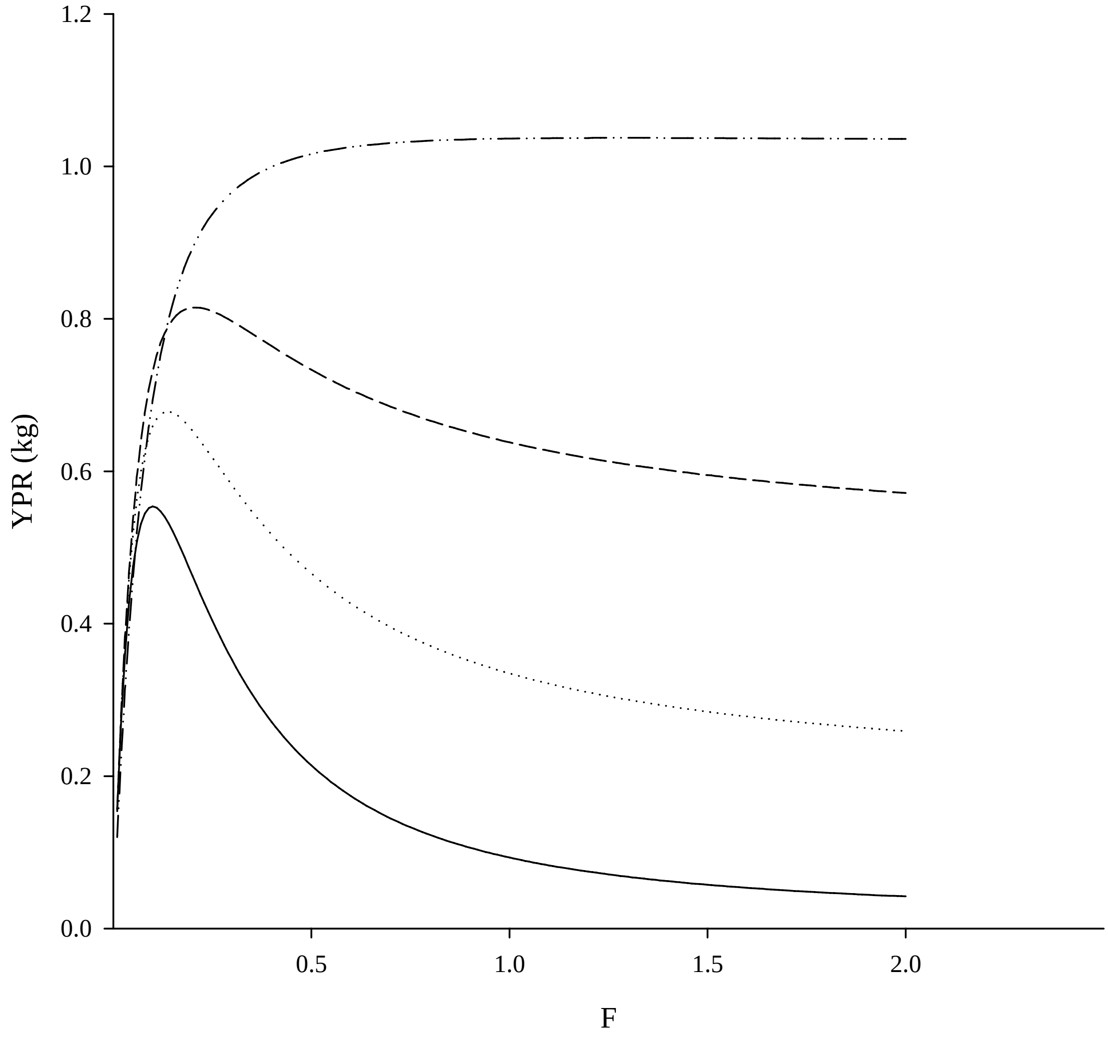
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
YPR (kg)
0.5
1.0
1.5
2.0
F
tc=10
tc=5
tc=3
tc=1

Figure 22. Yield per recruit (kg) for speckled hind sampled from 2004-07 during fishery-dependent and -independent sampling by MARMAP.



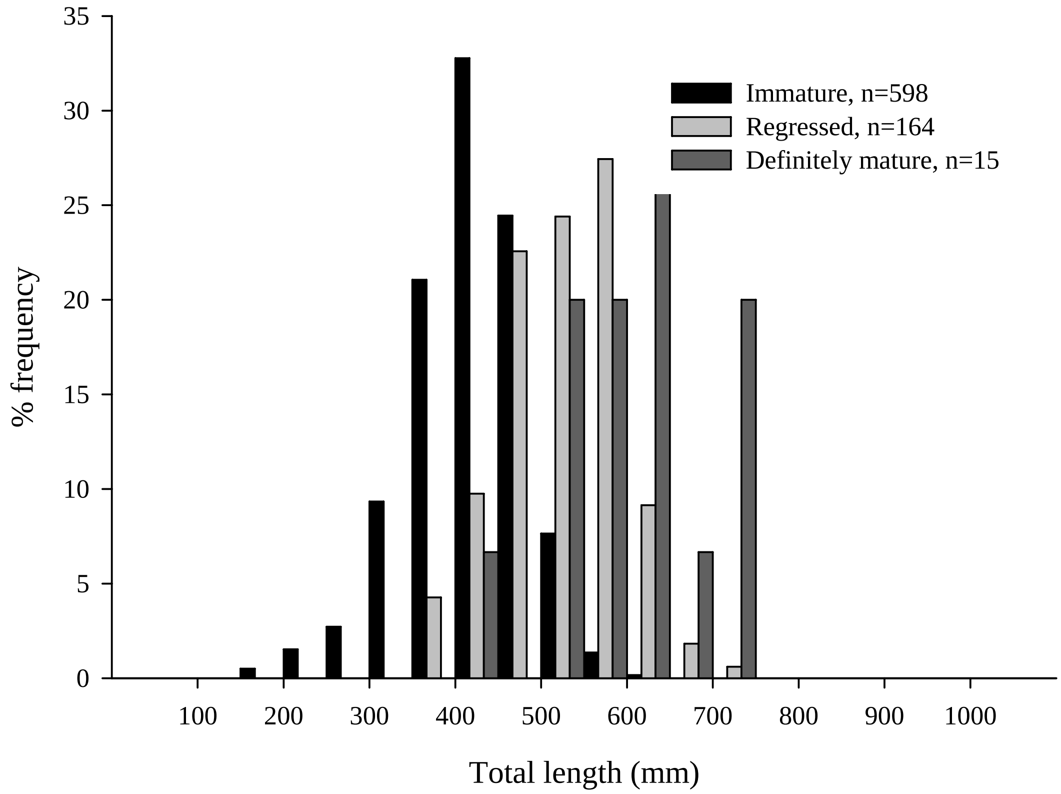
12
10
8
6
4
2
T_c (years)
0.8
0.24
1.0
0.8
0.6
0.4
0.2
0.5
1.0
1.5
2.0
F

Figure 23. Yield per recruit for speckled hind sampled from 2004-07 during fishery-dependent and -independent sampling by MARMAP.



1.2
1.0
0.8
0.6
0.4
0.2
0.0
YPR (kg)
0.5
1.0
1.5
2.0
F

Figure 24. Comparison of percent frequencies of lengths for immature, regressed and definitely mature female speckled hind collected from 1977-2007 during fishery-dependent and -independent sampling by MARMAP. Definitely mature females include developing, spawning and spent females.



35
30
25
20
15
10
5
0
% frequency
Immature, n=598
Regressed, n=164
Definitely mature, n=15
100
200
300
400
500
600
700
800
900
1000
Total length (mm)

Figure 25. Percentage of mature females by total length for speckled hind collected from 1977-93 and 2004-07 during fishery-dependent and -independent sampling by MARMAP.

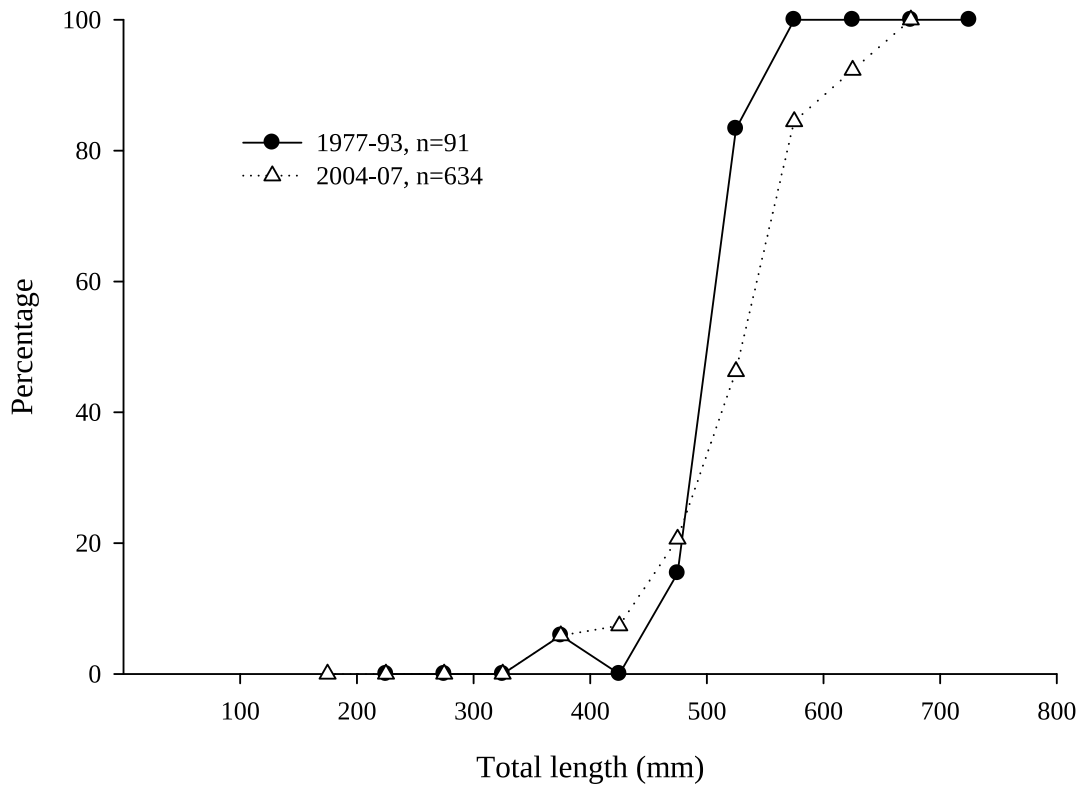
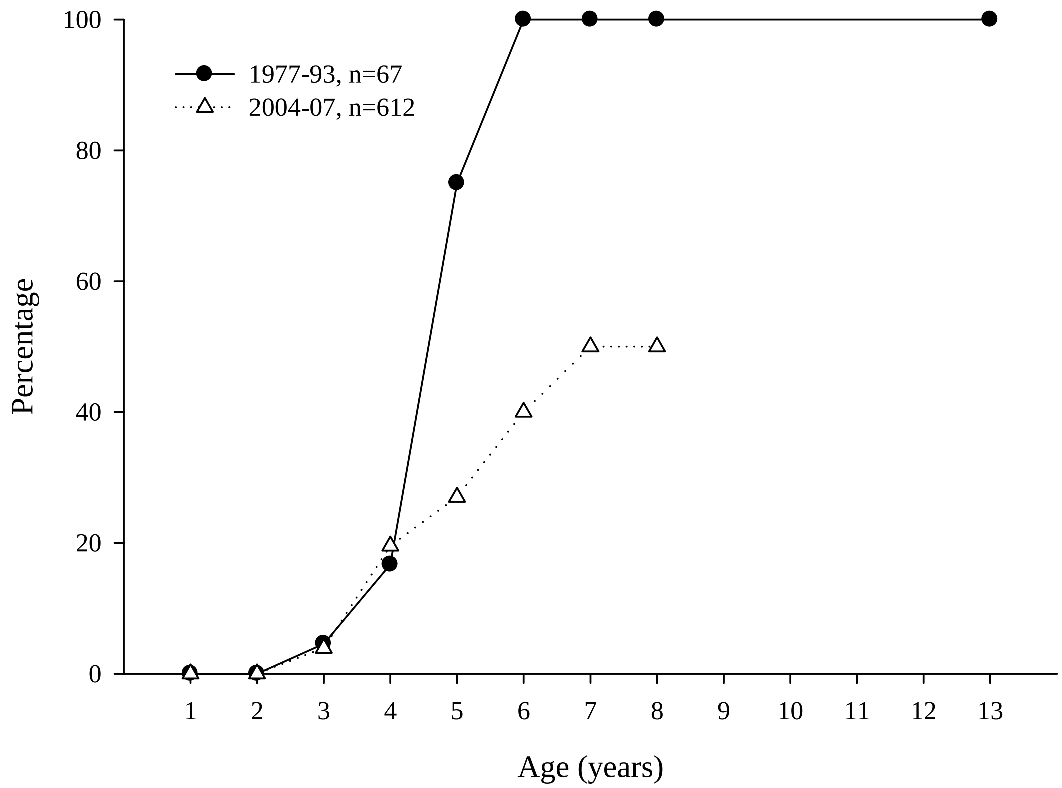

100
80
60
40
20
0
Percentage
1977-93, n=91
2004-07, n=634
100
200
300
400
500
600
700
800
Total length (mm)

Figure 26. Percentage of mature females by age for speckled hind collected from 1993-97 and 2004-07 during fishery-dependent and -independent sampling by MARMAP.



100
80
60
40
20
0
Percentage
1977-93, n=67
2004-07, n=612
1
2
3
4
5
6
7
8
9
10
11
12
13
Age (years)

Figure 27. Histological section of gonad tissue from of a transitioning speckled hind gonad showing pre-vitellogenic oocytes, cysts of spermatocytes and a sperm duct in the ovarian wall. Bar=100 µm. PO, primary growth oocytes; SPC, spermatocytes; SD, sperm duct.

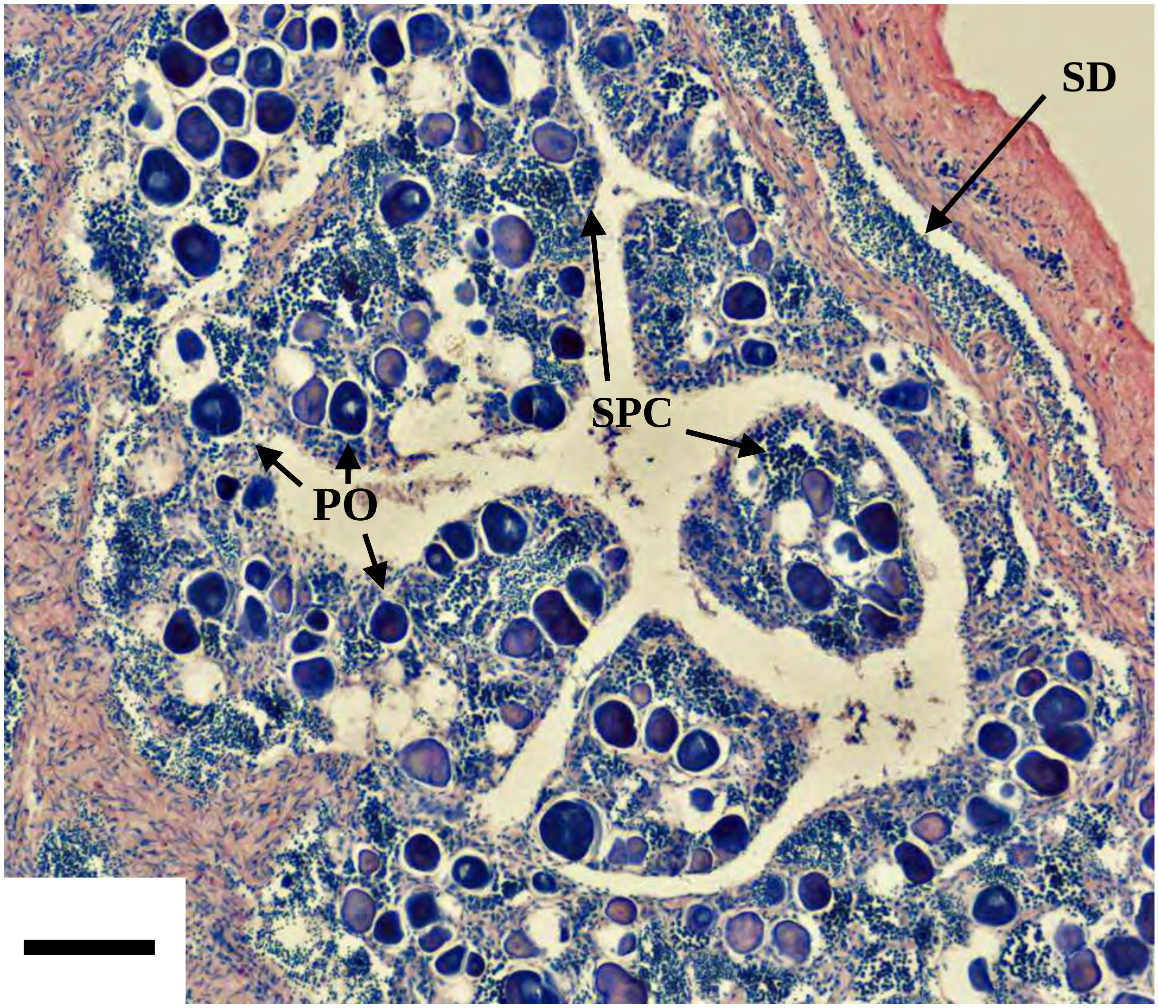
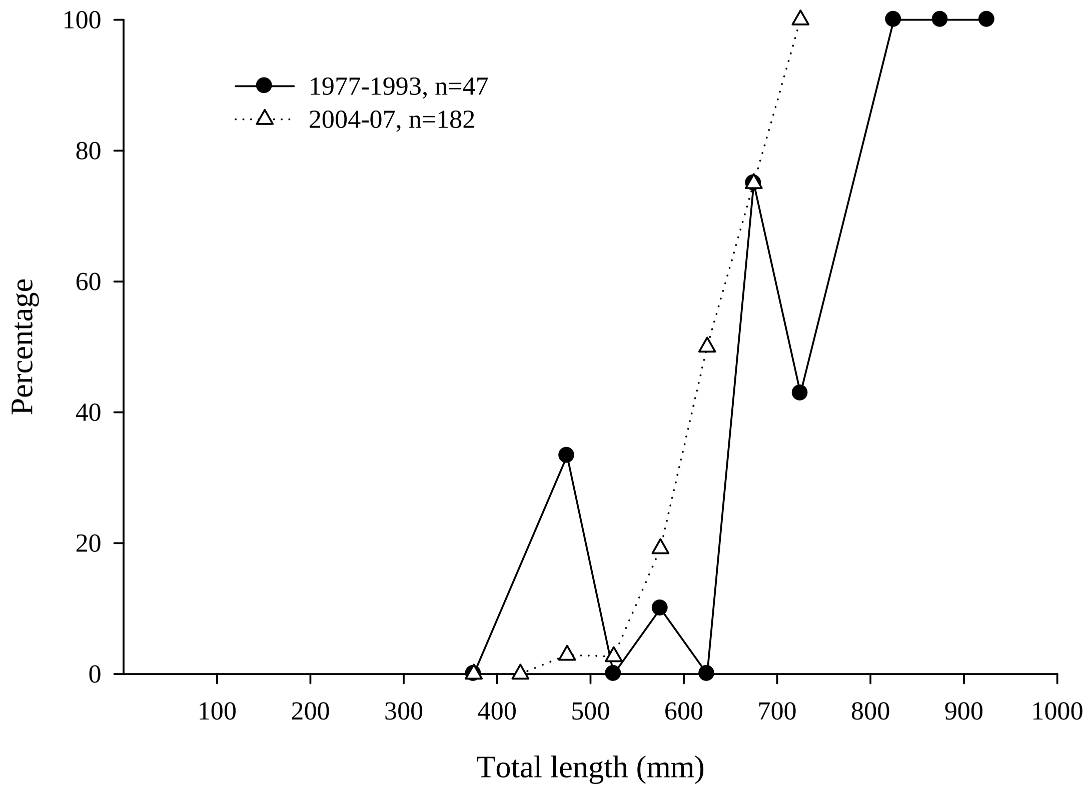
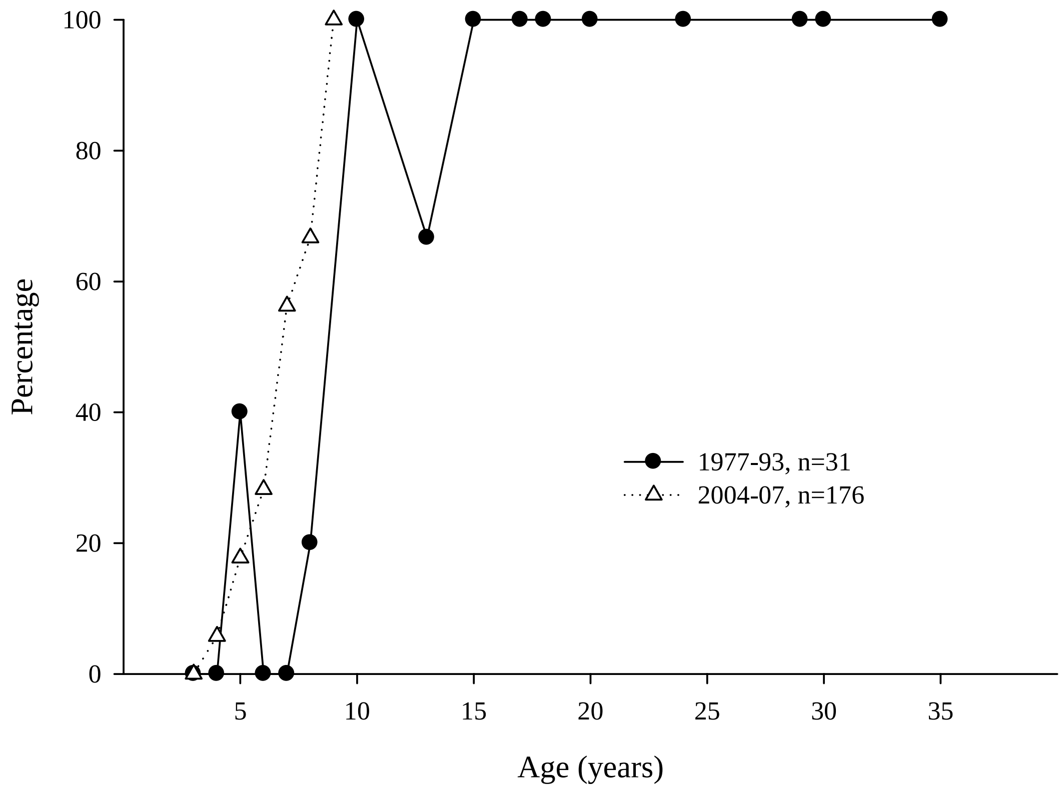

SD
SPC
PO

Figure 28. Percentage of males by total length for speckled hind collected from 1977-93 and 2004-07 during fishery-dependent and -independent sampling by MARMAP.



1977-1993, n=47
2004-07, n=182
Percentage
Total length (mm)
0
20
40
60
80
100
100
200
300
400
500
600
700
800
900
1000

Figure 29. Percentage of males by age for speckled hind collected from 1993-97 and 2004-07 during fishery-dependent and -independent sampling by MARMAP.



100
80
60
40
20
0
Percentage
5
10
15
20
25
30
35
Age (years)
1977-93, n=31
2004-07, n=176

Figure 30. Percentage composition of reproductive states by month of female speckled hind collected from 1977-2007 during fishery-dependent and -independent sampling by MARMAP. The number above each bar is the sample size of mature specimens.

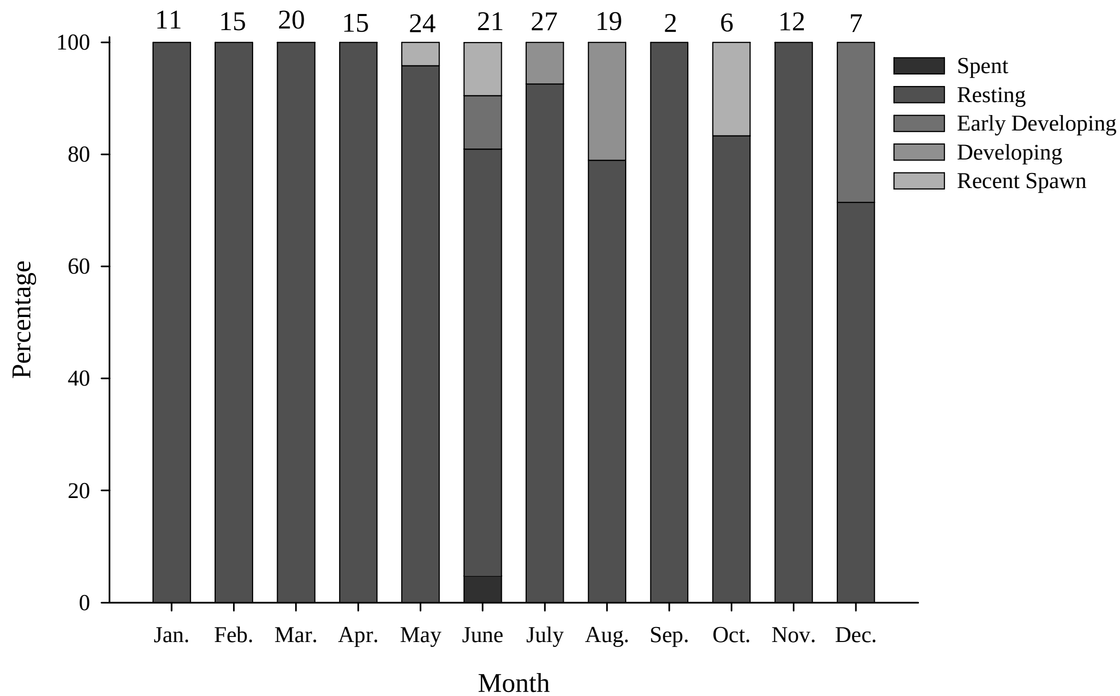
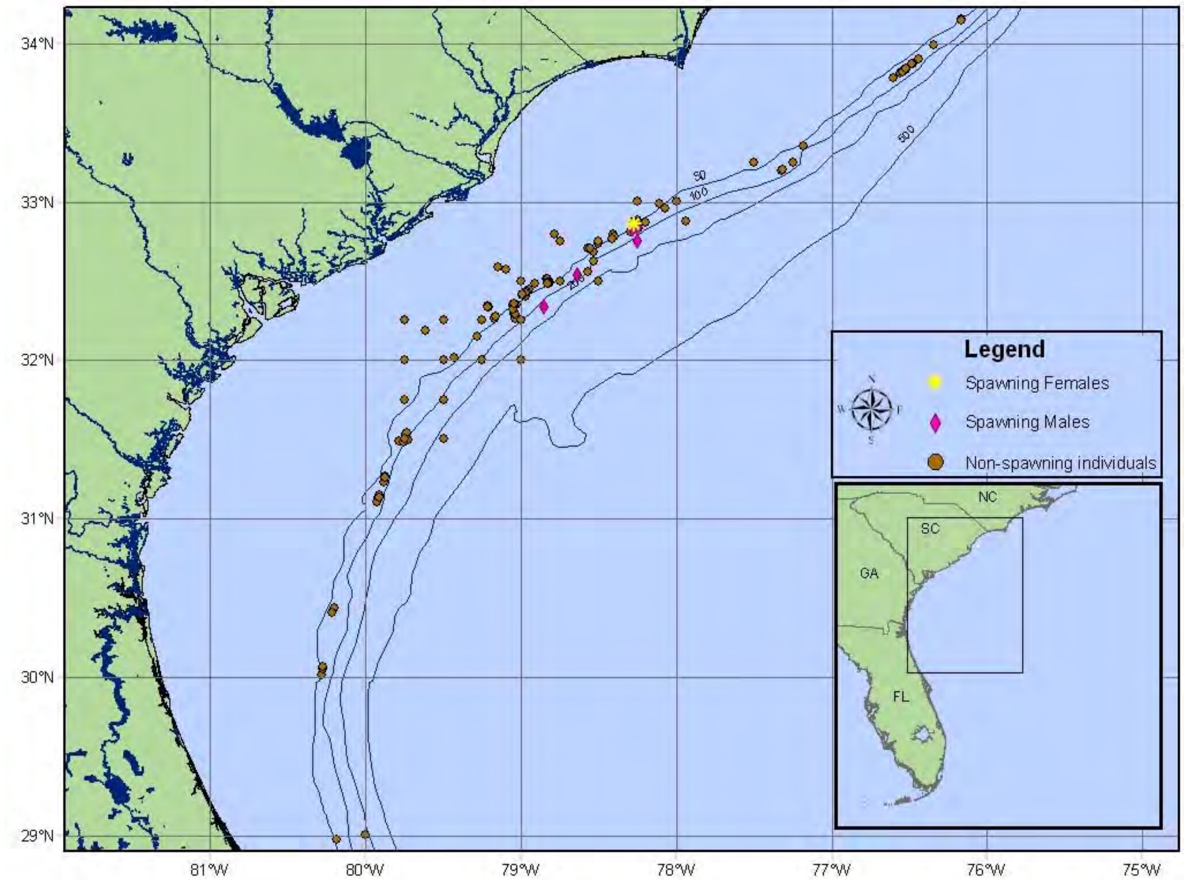

11
15
20
15
24
21
27
19
2
6
12
7
100
80
60
40
20
0
Percentage
Jan.
Feb.
Mar.
Apr.
May
June
July
Aug.
Sep.
Oct.
Nov.
Dec.
Month
Spent
Resting
Early Developing
Developing
Recent Spawn

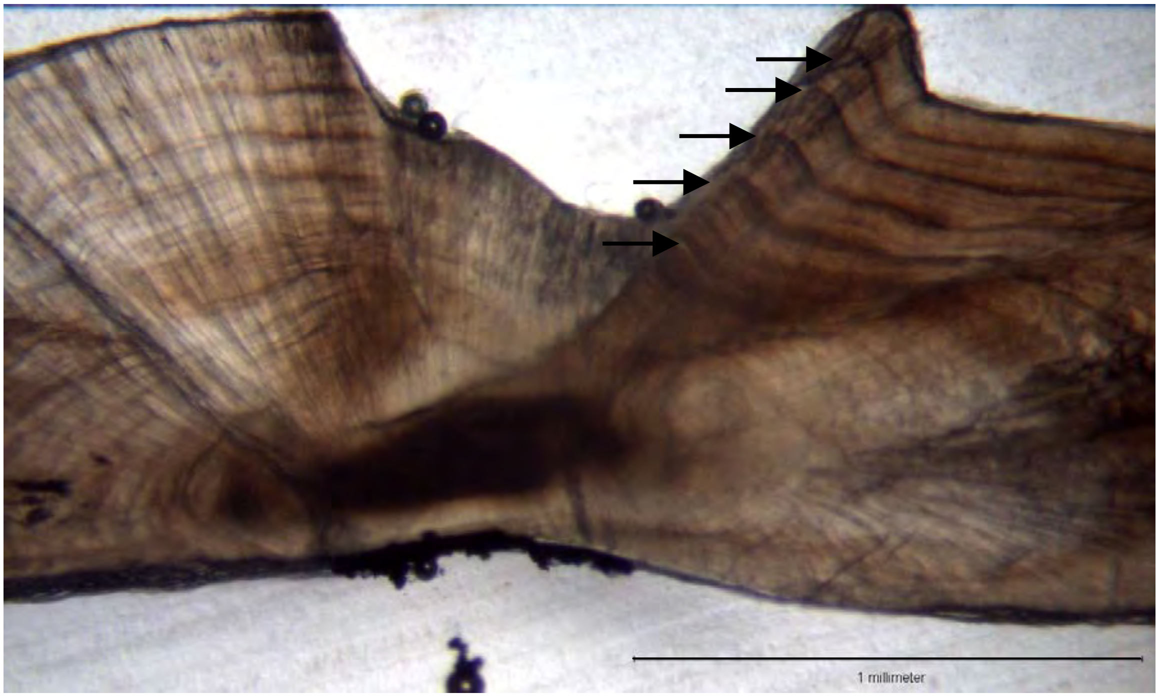
Figure 31. Locations where speckled hind in spawning condition were captured during fishery-dependent and -independent sampling by MARMAP from 1977-2007.



34°N
33°N
32°N
31°N
30°N
29°N
81°W
80°W
79°W
78°W
77°W
76°W
75°W
50
100
200
500
Legend
Spawning Females
Spawning Males
Non-spawning individuals
NC
SC
GA
FL

Figure 32. Transverse sections of speckled hind otoliths displaying (A) easily interpreted increments of an age-6 fish (only 5 increments marked, as age was adjusted upward owing to date of capture and width of translucent zone) and (B) opaque deformities in an age-17 fish.

A



B

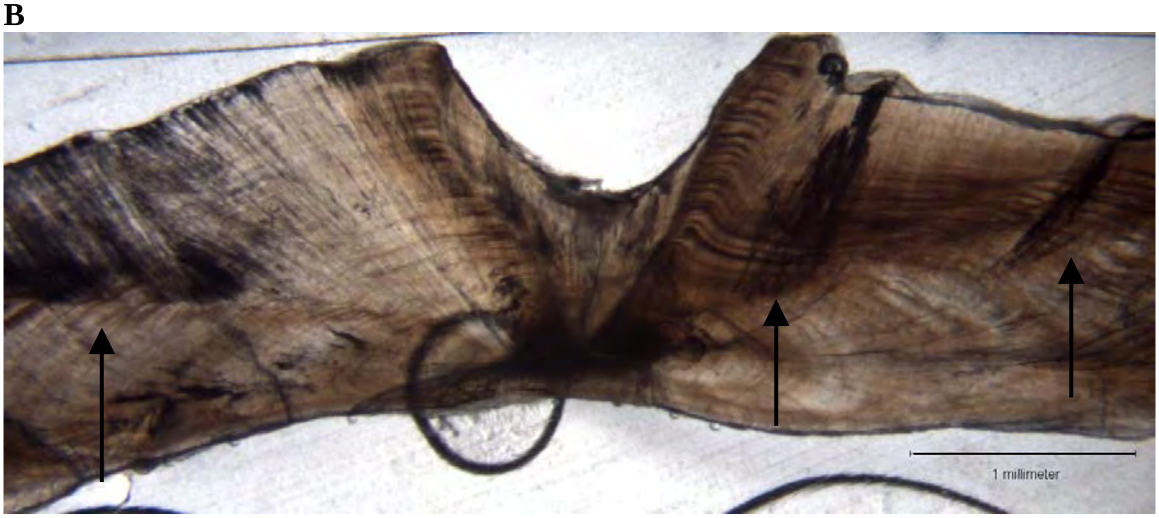


Table 1. Histological criteria used to assign sex codes for speckled hind (modification of Waltz et al., 1979).

Code	
0	Undifferentiated.
1	Gonad entirely testicular.
2	Gonad entirely ovarian.
4	Hermaphroditic male. Gonad functionally testicular with some traces of ovarian tissue
5	Hermaphroditic female. Gonad functionally ovarian with some traces of testicular tissue.
7	Testicular tissue, but insufficient quantity to determine presence or absence of ovarian tissue.
9	Unknown.

Table 2. Histological criteria used to assign maturity codes for speckled hind (Burgos et al., 2007).

Reproductive State	Male	Female
Uncertain maturity	Inactive testes; unable to assess maturity; state = 1 or 6.	Inactive ovaries with primary growth oocytes only; unable to assess maturity; state = 1 or 6.
Immature	No immature males observed.	Primary growth oocytes only, no evidence of atresia. In comparison to resting females, most primary growth oocytes < 50 um, areas of transverse section of ovary is smaller, lamellae lack muscle and connective tissue bundles and are not as elongate, oogonia abundant along margin of lamellae, ovary wall is thinner
Developing	Development of cysts containing primary and secondary spermatocytes through some accumulation of spermatozoa in lobular lumina and ducts.	2a. Early developing: Most-advanced oocytes in cortical-alveoli stage. 2b. Intermediate developing: Most-advanced oocytes in yolk-granule or yolk-globule stage. 2c. Late developing: Most-advanced oocytes in migratory-nucleus stage; partial coalescence of yolk globules possible.
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 radiate becomes thinner.
Developing, previous spawn		4.1 Vitellogenic oocytes and postovulatory follicles < 12 hrs old 4.2 Vitellogenic oocytes and postovulatory follicles 12-24 hrs old 4.3 Vitellogenic oocytes and postovulatory follicles > 24 hrs old

Table 2. (Continued)

Spent	No spermatogenesis; some residual spermatozoa in shrunken lobules and ducts.	More than 50% of vitellogenic oocytes with alpha or beta atresia.
Regressed	Little or no spermatocyte development; empty lobular lumina and ducts; some recrudescence (spermatogonia through primary spermatocytes) possible at end of state.	Primary growth oocytes only; traces of atresia. In comparison with immature females, most primary growth oocytes > 50 um, area of transverse section of ovary is larger, lamellae have muscle and connective tissue bundles, lamellae are more elongated and convoluted, oogonia less abundant along margin of lamellae, ovarian wall is thicker and exhibits varying degrees of expansion due to previous spawning, melano-macrophage centers and/or foci of inflammatory cells may be present.
Transitional	Protogyny: testicular proliferation (mitotic spermatogonial development and possibly limited spermatogenesis) within lamellae of spent or resting ovaries and development of peripheral sinuses in musculature of ovarian wall.	No protandry observed.
Mature specimen of unknown state	Mature, but inadequate quantity of tissue or postmortem histolysis prevents further assessment of reproductive state.	Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment of reproductive state.

Table 3. Mean length of speckled hind collected with various gear types from 1977-2007 during fishery-dependent and -independent sampling by MARMAP.

Gear type	Mean length (mm TL)	SE	n
Snapper reel	475	3.2	1,115
Vertical longline	511	19.3	30
Blackfish trap	312	21.6	24
Florida trap	340	13.7	60
Chevron trap	376	10.5	102

Table 4. Comparison of mean lengths of speckled hind collected with various gear types from 1977-2007 during fishery-dependent and -independent sampling by MARMAP using Tukey's Honestly Significant Difference test.

Gear type	Blackfish trap	Vertical longline	Florida trap	Chevron trap
Snapper reel	<0.01	0.71	<0.01	<0.01
Blackfish trap		<0.01	0.98	0.19
Vertical longline			<0.01	<0.01
Florida trap				0.51

Table 5. Relationships between TL, FL and SL (mm) for all speckled hind sampled from 1977-2007 during fishery-dependent and -independent sampling by MARMAP.

	Test statistics
TL=1.0482(FL)+3.51818	$p<0.01$ $r^2=1.0$, n=977
TL=1.17725(SL)+16.09795	$p<0.01$ $r^2=0.99$, n=1,258
FL=0.98193(TL)-1.88082	$p<0.01$ $r^2=1.0$, n=977
FL=1.15715(SL)+14.54437	$p<0.01$ $r^2=0.99$, n=976
SL=0.84121(TL)-9.98269	$p<0.01$ $r^2=0.99$, n=1,258
SL=0.85722(FL)-9.44758	$p<0.01$ $r^2=0.99$, n=976

Table 6. Comparison of mean ages of all speckled hind collected with various gear types from 1977-2007 by the MARMAP fishery-dependent and -independent sampling program.

Gear type	Mean age(years)	SE	n
Snapper reel	4.7	0.07	1003
Vertical longline	5.0	0.43	29
Blackfish trap	2.3	0.48	23
Florida trap	2.5	0.33	49
Chevron trap	3.0	0.26	79

Table 7. Comparison of mean ages of speckled hind collected with various gear types from 1977-2007 during fishery-dependent and -independent sampling by MARMAP using Tukey's Honestly Significant Difference test.

Gear type	Blackfish trap	Vertical longline	Florida trap	Chevron trap
Snapper reel	<0.01	0.99	<0.01	<0.01
Blackfish trap		<0.01	1.0	0.62
Vertical longline			<0.01	<0.01
Florida trap				0.63

Table 8. Mean length at age for speckled hind collected with various gear types during fishery-dependent and -independent sampling by MARMAP from 1977-2007.

Age	Snapper reel mm TL (SE, n)	Vertical longline mm TL (SE, n)	Blackfish trap mm TL (SE, n)	Florida trap mm TL (SE, n)	Chevron trap mm TL (SE, n)	Test statistic
1	203 (10.0, n=5)		246 (15.9, n=2)	210 (10.1, n=5)	204 (11.3, n=5)	See Table 9
2	311 (12.1, n=25)		297 (16.2 n=14)	330 (12.9, n=22)	322 (15.7, n=15)	See Table 9
3	395 (4.6, n=124)	422 (n=1)	349 (51.4, n=6)	417 (12.1, n=18)	387 (8.1, n=40)	See Table 9
4	445 (3.1, n=391)	471 (17.2, n=13)	445 (n=1)	422 (35.8, n=3)	433 (15.1, n=17)	See Table 9
5	489 (3.9, n=284)	509 (66.3, n=10)		470 (n=1)	453 (38.3, n=3)	See Table 9
6	521 (7.3, n=115)	651 (n=1)				
7	565 (18.6, n=27)	614 (55.8, n=3)				F=0.70, p=0.4081
8	637 (25.1, n=11)					
9	723 (48.1, n=3)					
10	700 (n=1)					
11	737 (n=1)					
12		725.0 (n=1)				
13	713 (15.0, n=4)					
15	500 (n=1)					
16	770 (n=1)					
17	820 (n=1)					
18	890 (n=1)					
19	810 (n=1)					
20	922 (58.9, n=2)					
24	870 (n=1)					
29	830 (n=1)					
30	835 (58.9, n=2)					
35	930 (n=1)					

Table 9. Comparison of length at age 1, 2, 3, 4, and 5 of speckled hind caught with various gear types from 1977-2007 during fishery-dependent and -independent sampling by MARMAP using Tukey's Honestly Significant Difference test.

Age 1

Gear type	Blackfish trap	Vertical longline	Florida trap	Chevron trap
Snapper reel	0.16		0.97	1.00
Blackfish trap			0.27	0.18
Vertical longline				
Florida trap				0.97

Age 2

Gear type	Blackfish trap	Vertical longline	Florida trap	Chevron trap
Snapper reel	0.98		0.90	1.00
Blackfish trap			0.62	0.89
Vertical longline				
Florida trap				1.00

Age 3

Gear type	Blackfish trap	Vertical longline	Florida trap	Chevron trap
Snapper reel	0.26	0.99	0.58	0.93
Blackfish trap		0.78	0.06	0.56
Vertical longline			1.00	0.98
Florida trap				0.31

Age 4

Gear type	Blackfish trap	Vertical longline	Florida trap	Chevron trap
Snapper reel	1.00	0.74	1.00	0.99
Blackfish trap		1.00	1.00	1.00
Vertical longline			0.88	0.64
Florida trap				1.00

Age 5

Gear type	Blackfish trap	Vertical longline	Florida trap	Chevron trap
Snapper reel		0.94	1.00	0.94
Blackfish trap				
Vertical longline			0.99	0.80
Florida trap				1.00

Table 10. Von Bertalanffy growth function parameters describing the growth of speckled hind collected by MARMAP during fishery-dependent and –independent sampling in 1977-93 and 2004-07.

Source	L_∞	k	t_0
1977-93	852	0.17	0.76
2004-07	945	0.09	2.76

Table 11. Frequency of sex category and sex ratio by age of speckled hind collected during fishery-dependent and -independent sampling by MARMAP.

Age (yr)	**Immature females (stage 1)**	**Females, uncertain maturity (stage 0)**	**Mature females (stages 2-6)**	**Transitionals**	**Males**	**Sex ratio (male: female)**
1	6	0	0	0	0	
2	39	0	1	0	0	
3	114	10	7	1	0	1:7.0
4	215	59	51	3	1	1:12.8
5	140	41	55	12	1	1:4.2
6	42	12	34	8	3	1:3.1
7	7	2	9	4	5	1:1.0
8	1	1	5	0	3	1:1.7
9	0	0	0	0	1	
10	0	0	0	0	1	
13	0	0	1	0	2	1:0.5
15	0	0	0	0	1	
17	0	0	0	0	1	
18	0	0	0	0	1	
20	0	0	0	0	1	
24	0	0	0	0	1	
29	0	0	0	0	1	
30	0	0	0	0	1	
35	0	0	0	0	1	
No age	34	9	16	1	5	1:2.7
Total	598	134	179	29	30	1:3.0

Table 12. Frequency of sex category and sex ratio by TL interval of speckled hind collected during fishery-dependent and -independent sampling by MARMAP

TL (mm)	**Immature females (stage 1)**	**Females, uncertain maturity (stage 0)**	**Mature females (stages 2-6)**	**Transitionals**	**Males**	**Sex ratio (male: female)**
151-200	3	0	0	0	0	
201-250	9	0	0	0	0	
251-300	16	0	0	0	0	
301-350	55	1	0	0	0	
351-400	124	11	7	0	0	
401-450	193	31	17	0	0	
451-500	144	43	37	2	1	1:12.3
501-550	45	34	43	2	0	1:21.5
551-600	8	13	48	10	0	1:4.8
601-650	1	1	19	9	3	1:1.6
651-700	0	0	4	4	8	1:0.3
701-750	0	0	4	2	7	1:0.4
751-800	0	0	0	0	0	
801-850	0	0	0	0	5	
851-900	0	0	0	0	5	
901-950	0	0	0	0	1	
Total	598	134	179	29	30	1:3.0