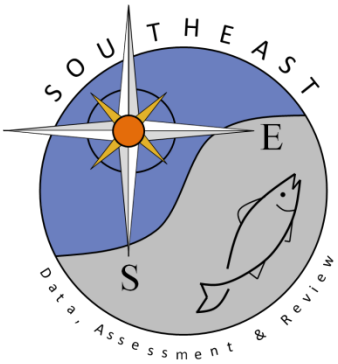
Age, growth, and reproduction of dolphinfish (*Coryphaena hippurus*) caught off the coast of North Carolina

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Abstract—Age, growth, and reproductive data were obtained from dolphinfish (*Coryphaena hippurus*, size range: 89 to 1451 mm fork length [FL]) collected between May 2002 and May 2004 off North Carolina. Annual increments from scales (n=541) and daily increments from sagittal otoliths (n=107) were examined; estimated von Bertalanffy parameters were L_∞ (asymptotic length)=1299 mm FL and k (growth coefficient)=1.08/yr. Daily growth increments reduced much of the residual error in length-at-age estimates for age-0 dolphinfish; the estimated average growth rate was 3.78 mm/day during the first six months. Size at 50% maturity was slightly smaller for female (460 mm FL) than male (475 mm FL) dolphinfish. Based on monthly length-adjusted gonad weights, peak spawning occurs from April through July off North Carolina; back-calculated hatching dates from age-0 dolphinfish and prior reproductive studies on the east coast of Florida indicate that dolphinfish spawning occurs year round off the U.S. east coast and highest levels range from January through June. No major changes in length-at-age or size-at-maturity have occurred since the early 1960s, even after substantial increases in fishery landings.

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The dolphinfish (*Coryphaena hippurus*) is a highly migratory oceanic pelagic fish found worldwide in tropical and subtropical waters. The distribution range for dolphinfish in the western Atlantic Ocean is from Nova Scotia (Vladykov and McKenzie, 1935; Tibbo, 1962) to Brazil (Shcherbachev, 1973). However, this species is most common from North Carolina, throughout the Gulf of Mexico and Caribbean, to the northeastern coast of Brazil where it is seasonally abundant (Oxenford, 1999). Dolphinfish support economically important recreational and commercial fisheries in the United States, Caribbean, and Brazil, and is thus a shared resource among multiple countries. Previous reviews of the scientific literature on dolphinfish biology in the western Atlantic were completed by Palko et al. (1982) and Oxenford (1999).

Landings of dolphinfish from the Atlantic, Caribbean, and Gulf of Mexico have increased. According to the National Marine Fisheries Service landings statistics, recreational landings in the Atlantic Ocean have increased gradually, whereas commercial landings in the Atlantic have increased dramatically from approximately 20 metric tons (t) in the 1980s to over 620 t in the 1990s. Although dolphinfish are fast growing and mature early, concern has been raised about this trend in landings and the potential for localized depletion of stocks. Intense harvesting may select for traits such as slow growth (Conover and Munch, 2002) or early maturity (Trippel, 1995); it is important to update growth and reproductive data to test for changes in these data and to provide current information for stock assessments. Unfortunately, the most recent estimates of these parameters for dolphinfish in the southeast United States were based on data from the 1960s (Beardsley, 1967; Rose and Hassler, 1968).

Here, we update the age and growth relationship and collect reproductive data on dolphinfish captured in North Carolina from recreational and commercial sources and fishery-independent collections. Our specific objectives were 1) to determine daily ages of age-0 dolphinfish and determine age-0 dolphinfish growth rates, 2) to identify the best method of aging >age-0 dolphinfish (either by otolith or scale annual marks) and, with the method determined to be the best, to determine the annual ages of >age-0 dolphinfish, 3) to validate annual marks, and 4) to estimate time of spawning and size-at-maturity.

Materials and methods

Collections

Dolphinfish from recreational fishery sources were obtained every month between May 2002 and May 2004 (except December 2002 and 2003, January 2003, and February 2004) from fishing ports in North Carolina. Recreational anglers typically fished for dolphinfish in waters associated with the western wall of the Gulf Stream. In the summers of 2002–03, samples of large fish were provided through various sportfishing tournaments held in these same areas. To supplement length-at-maturity data once peak spawning was identified, maturity staging was conducted on male and female dolphinfish from April 2005 through July 2005.

Sampling of commercial dolphinfish catches was done in addition to recreational dolphinfish sampling and was primarily conducted in the winter months to increase the sample sizes available for this time period. Small dolphinfish were not readily available through recreational and commercial sampling; therefore sample sizes were augmented by two different methods. First, a total of four fishery-independent trips were made in August 2003 and July 2004. During these trips, the distance traveled offshore averaged 20 km, and small lures were trolled, as opposed to large dead bait or large lures as is done in the recreational and commercial fishery. Second, small and intact dolphinfish were obtained from stomachs of larger dolphinfish and yellowfin tuna (*Thunnus albacares*) caught by anglers from recreational charter boats.

Dolphinfish were measured to the nearest mm for fork length (FL) and total length (TL), sex was determined (through macroscopic examination of the gonads), and the fish were weighed (to the nearest 0.1 kg) and tagged. Date and location of port sampled were recorded for each dolphinfish. Scale samples were collected before the fish were filleted according to methods established by Beardsley (1967). In some instances, filleted dolphinfish carcasses were only available; therefore scale samples were not obtained on all sampled fish. All tagged carcasses were brought to the laboratory for extraction of otoliths and gonads.

Age and growth

To determine if daily rings were present on sagittal otoliths of age-0 dolphinfish, the otoliths were removed, cleaned, and stored dry until mounted in epoxy resin. To avoid interotolith variability, only the left otolith was used for reading. Otoliths were prepared for reading following methods described for transverse sections in Secor et al. (1992). Reading was done with a light microscope equipped with a digital camera. The image from the camera was transmitted to a computer and examined by using Image-Pro Plus software (Image-Pro, vers. 4.5, Media Cybernetics, Silver Spring, MD). Growth increments were counted from the core, beginning at the first clearly defined mark that encircled the primordium (Massutí et al., 1999), towards either the dorsal or ventral edge, depending on ease of counting. To determine the precision of the readings of juvenile dolphinfish ages, blind readings of daily growth increments were conducted twice by the same investigator. Error greater than 10% in reading precision for an individual otolith caused that otolith to be rejected. If error in reading precision was less than or equal to 10%, then the average between the first and second readings was taken as the final age.

The deposition of increments in dolphinfish otoliths begins on the hatching date, and rings are laid down daily (Uchiyama et al., 1986; Massutí et al., 1999). Thus, no adjustment was required to estimate age from incremental counts of sagittae, and it was assumed that rings were formed daily. Previous studies on the microstructure of sagittal otoliths of dolphinfish from the western Mediterranean Sea had found that the daily ages from larger dolphinfish (>650 mm FL) appeared to be underestimated (Massutí et al., 1999). Furthermore, daily ages of dolphinfish have been validated to a size of 554 mm FL (Uchiyama et al., 1986). Therefore, our analysis was restricted to dolphinfish less than or equal to 650 mm FL. To determine individual dolphinfish growth rates, the fork length at capture was divided by the daily age.

The annual age of dolphinfish was estimated with scales. Eight to ten scales were mounted, sculptured side down, on sheets of cellulose acetate 0.5 mm thick, and then placed on a scale press to make impressions. Scale impressions were examined with a microfiche reader at 32× magnification to permit detection of circuli, annual marks, and other features of the scale. Age groups were classified according to the number of annual marks present (see Beardsley, 1967, for a figure of an annual mark on a dolphinfish scale).

To determine the precision of dolphinfish age estimates, blind readings of annual marks on scales were conducted twice by the same investigator. If agreement between the first and second reading was not 100%, then a scale was reread a third time and was only used in the analyses if the third reading agreed with either the first or second reading. Additionally, blind readings of a subsample (n=50) of dolphinfish scales were conducted by an independent reader who was trained to identify annual marks on dolphinfish scales.

To validate annual marks in dolphinfish scales, an indirect validation based on marginal increment analysis was used. Marginal increment widths were determined by measuring the distance from the outer edge of the scale to the closest annual mark. Marginal increment width was measured only on dolphinfish with one annual mark in order to standardize the method, and because the majority of dolphinfish aged with annual marks were age-1. Measurements (mm) were taken from the magnified (32×) scale image on a microfiche reader along a straight line from the lateral edge of the scale to the outermost annual mark by using a digital caliper. Marginal increment widths were analyzed by analysis of variance (ANOVA) to test for an effect of month.

Marginal increment widths were only analyzed for the months of March through November because of the low sample sizes of dolphinfish scales from the winter months (December through February). To differentiate between changes in the marginal increment width attributed to potentially sampling different cohorts of age-1 dolphinfish, we calculated the monthly mean fork length of all age-1 dolphinfish whose scales were measured for a marginal increment width.

A subsample (n=50) of dolphinfish that was determined to be >age-0 by using scales was further examined for the presence of annual marks by using otoliths. We prepared transverse cross sections of sagittal otoliths using methods described above. These sections were viewed under the light microscope (first at 100×, then 400×) to determine if annual marks could be detected in these structures.

The von Bertalanffy growth curve was fitted to two dolphinfish age-length data sets: 1) daily ages from age-0 dolphinfish with a fork length less than 650 mm and annual marks on scales from >age-0 dolphinfish by using absolute ages, and 2) daily ages from age-0 dolphinfish with a fork length less than 650 mm and relative scale ages. Relative scale ages were assigned by adding the number of days after the fixed birth date of 15 April (middle of estimated southeastern U.S. spawning season) when the dolphinfish was caught to the absolute annual age determined from scales. The 15 April birth date was chosen according to the trends in gonadosomatic indices in Florida and North Carolina and back-calculated hatching dates (Beardsley, 1967; this study).

The von Bertalanffy growth parameters were estimated separately by nonlinear regression for male and female dolphinfish and were compared by using the likelihood-ratio test (Kimura, 1980; Cerrato, 1990; Haddon, 2001). To detect if any significant changes in growth had occurred since the last dolphinfish aging study in North Carolina, the mean size-at-age values from Rose and Hassler (1968) were plotted with the von Bertalanffy growth curve fit (relative age data set) and compared qualitatively. Additionally, von Bertalanffy growth functions estimated from past studies within different regions were plotted together for comparison.

Reproduction

Gonadosomatic indices and back-calculated hatching dates were used to determine timing of spawning, and maturity staging was used to determine length-at-maturity. When available, intact gonads were removed, weighed to the nearest 0.1 g, and assigned a maturity stage determined by gross examination of the gonads. Maturity stages for both male and female dolphinfish have been described (Beardsley, 1967; Oxenford, 1985). Female dolphinfish were considered mature or immature on the basis of the criteria developed by Beardsley (1967). Male dolphinfish were classified as mature on the basis of the presence or absence of milt in their gonads.

A gonadosomatic index (GSI) was calculated as *gonad weight*/(*body weight* – *gonad weight*) separately for male and female dolphinfish pooled for 2002–04. Because dolphinfish body weight and length are correlated with GSI values (Chatterji and Ansari, 1982) and dolphinfish size differed significantly by month (see below), ANCOVA was used to compare *ln* (*gonad weight*) by month with *ln* (*fork length*) as the covariate for males and females separately. Log transformations were used to meet assumptions of ANCOVA. To determine which months had significantly different gonad weights, the length-adjusted mean *ln* (*gonad weight*) value was compared among months for both male and female dolphinfish by using ANCOVA univariate test of significance for planned comparisons. Significance levels were adjusted by the standard Bonferroni technique to account for multiple comparisons.

Hatching dates were determined by subtracting age in days (determined from age-0 otoliths) from the catch date. Because the daily deposition of increments in dolphinfish sagittal otoliths begins on the hatching date (Uchiyama et al., 1986; Massutí et al., 1999), and because ripe eggs hatch within 50–60 hours after fertilization (Palko et al., 1982), back-calculated hatching dates provide an estimate of spawning dates for surviving offspring.

The length at which 50% of the fish had become mature was determined for both sexes by using a logistic model. The model was fitted by using nonlinear regression analysis based on the following equation:

$$\%\ Maturity = 1/(1 + e^{(-Q \times (L - L_{50}))}),$$

where Q = model parameter;
L = fork length (mm); and
L_{50} = fork length (mm) at 50% maturity.

Results

Collections

Dolphinfish were collected mostly from the recreational charter fishery (n=611, 76%), but also from the commercial fishery (n=45, 6%), sportfishing tournaments (n=130, 16%), and from four fishery-independent trips (n=16, 3%). There was a seasonal trend in the total amount (number) of dolphinfish collected by month, with nearly half (n=364, 45%) of all dolphinfish collected in the months of June, July, and August. Only 17 fish (2%) were obtained in the months of November, December, and January (Table 1). The majority of the dolphinfish were sampled from catches in Morehead City, NC (n=676, 84%).

The size range for the pooled sample of dolphinfish was 89 to 1451 mm FL (mean=736 mm FL, standard error (SE)=9.3). Males (n=257) ranged in length from 310 to 1451 mm FL (mean length and weight of all males sampled was 855 mm FL [SE=16.0] and 6.44 kg [SE=0.4]) and females (n=422) ranged in length

Table 1

Monthly mean (±SE) fork length (FL; mm), FL range, and sample size (n) for male and female dolphinfish (*Coryphaena hippurus*) collected from May 2002 through May 2004. Sex was unable to be determined for six dolphinfish and their size information is not shown here. No dolphinfish were caught in December. SE=standard error.

	Male			Female		
	Mean FL (SE)	FL range	n	Mean FL (SE)	FL range	n
January	682 (81.1)	559–835	3	708 (70.3)	575–966	5
February	—	—	0	699 (62.4)	545–850	4
March	709 (61.3)	453–915	6	730 (17.9)	560–889	20
April	820 (26.1)	550–1130	24	773 (12.1)	608–1020	50
May	935 (17.4)	582–1315	92	765 (14.2)	485–1275	101
June	1123 (25.4)	552–1395	72	688 (31.8)	295–1145	43
July	705 (50.9)	395–1451	31	607 (25.5)	205–980	48
August	805 (41.5)	310–1333	46	650 (24.1)	295–1205	101
September	689 (51.0)	462–1280	16	510 (19.8)	278–800	40
October	594 (25.6)	432–798	17	556 (26.1)	410–1435	41
November	570 (50.0)	520–620	2	628 (60.7)	460–905	7

from 205 to 1435 mm (mean length and weight of all females sampled was 655 mm FL [SE=9.0] and 3.13 kg [SE=0.2]; Table 1). There were significant differences in male dolphinfish mean weight (Kruskal-Wallis ANOVA: χ^2=80.6, df=9, P<0.001) and fork length (χ^2=98.9, df=9, P<0.001) by month (pooled over 2002–04). There were also significant differences in the mean weight of female dolphinfish (Kruskal-Wallis ANOVA: χ^2=85.1, df=9, P<0.001) and fork length (χ^2=140.0, df=10, P<0.001) by month (pooled over 2002–04).

Age and growth

Because of the small size and complex structure of dolphinfish sagittae, counts were typically made on the dorsal side of the otolith as that region was the easiest to follow a clear increment sequence (Massutí et al., 1999). Alternating light and dark bands, assumed to be daily increments (see Methods section), varied in width; tightly packed increments were located more toward the core and outer edge of the sagittae, and wider increments were located more in the center of the dorsal wing (see Massutí et al., 1999, for a picture of growth increments).

A total of 181 dolphinfish otoliths were examined (n=131 age-0 otoliths, n=50 >age-0 otoliths). Annual marks could not be detected in transverse cross-sections of sagittal otoliths of >age-0 dolphinfish. Daily increment counts were possible for a total of 107 (82%) otoliths from age-0 dolphinfish (designated age-0 because of a lack of annual marks on scales [see below]). Of these, 62 were from female dolphinfish (mean FL=509; range: 278–650 mm) and 39 were from males (mean FL=538; range: 310–650 mm). Sex could not be determined for five of the smallest dolphinfish whose sagittae were examined (mean FL=152; range: 89–285 mm) and was not recorded for one of the larger dolphinfish aged from daily growth increments (FL=575 mm); however, these dolphinfish were still used in the von Bertalanffy analyses. Four of the 131 otoliths from age-0 dolphinfish were rejected because percent agreement between the first and second count exceeded 10%, and 20 age-0 otoliths were unreadable because of problems with cross-sectioning or polishing. Minimum and maximum age estimates ranged from 31 to 204 days. Average growth rates based on daily ring counts were 3.78 mm FL/day for all age-0 fish less than 650 mm FL.

Scales were collected from 560 fish; 14 of the resulting scale impressions were unreadable and five more were discarded because of uncertainty in the determination of age (i.e., the three counts did not agree with each other). A total of 234 scales were classified as age-1 or older (84 females, 150 males) and the remaining scales (n=307) were estimated to be age-0. The >age-0 dolphinfish were classified as follows: 175 age-1 dolphinfish ranging from 575 to 1435 mm FL (mean=938 mm, SE=9.8), 46 age-2 dolphinfish ranging from 925 to 1451 mm FL (mean=1197 mm, SE=17.3), and 13 age-3 dolphinfish ranging from 1095 to 1334 mm FL (mean=1249 mm, SE=17.9). Final agreement between readings by the same investigator was 99%; an independent reader who was trained to identify annual marks on dolphinfish scales examined a subsample of 50 >age-0 dolphinfish scales, and agreement between the independent reader's reading and the first reader's final age was 69% (Schwenke, 2004).

Marginal increment widths from age-1 dolphinfish (n=182) were greatest in May, June, and July, dropped slightly in August, then dropped considerably during

Table 2

Von Bertalanffy growth parameters calculated for male, female, and combined sexes (including individuals whose sex could not be determined) of dolphinfish (*Coryphaena hippurus*) from nonlinear regression model fits. Data are presented for (**A**) daily ages of otoliths (from dolphinfish <650 mm) along with annual ages of >age-0 dolphinfish presented as absolute ages, and (**B**) daily aged otoliths (from dolphinfish <650 mm) along with annual ages of >age-0 dolphinfish presented as relative ages, assuming a 15 April hatching date. The standard errors of each parameter are shown in parentheses. n=sample size, L_∞=asymptotic length, k=growth coefficient, and t_0=theoretical age at zero length.

Method	n	$L_{\infty\,(\mathrm{mm})}$	k (1/yr)	$t_{0\,(\mathrm{yr})}$
A Otoliths (<650 mm) aged daily and scales aged yearly (absolute ages)				
Males	189	1286 (29.10)	1.33 (0.12)	−0.016 (0.04)
Females	146	1250 (109.60)	1.24 (0.28)	−0.059 (0.05)
Combined sexes	341	1289 (25.95)	1.27 (0.08)	−0.026 (0.02)
B Otoliths (<650 mm) aged daily and scales aged yearly (in relation to a 15 April hatching date)				
Males	188	1299 (30.80)	1.12 (0.11)	−0.089 (0.05)
Females	145	1237 (92.14)	1.10 (0.23)	−0.116 (0.06)
Combined sexes	339	1299 (26.31)	1.08 (0.07)	−0.086 (0.03)

the fall, and stayed low during winter months (Fig. 1). There was a significant difference in marginal increment width per month (ANOVA: P=<0.001) for the period of March through November. Mean marginal increment width in May was significantly higher than in April (Tukey HSD: P=0.03) and October (P=0.03), whereas in June, it was significantly higher than in April (P<0.001), September (P=0.04), and October (P<0.001). All other comparisons were nonsignificant.

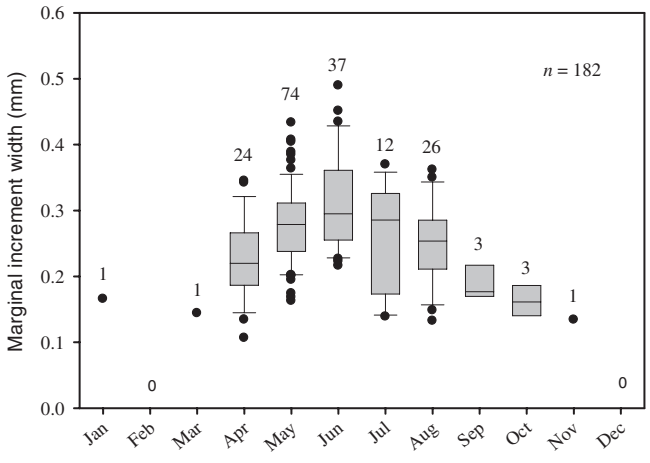


Figure 1

Box plot of the marginal increment width (mm) for age-1 dolphinfish (*Coryphaena hippurus*) (sampled from May 2002 through May 2004) pooled by month (January–December). The 25th percentile of the marginal increment width data is represented by the boundary of the box closest to zero, relative to the y-axis, and the 75th percentile is represented by the boundary of the box farthest from zero. The line within each box is the median value. Whiskers (error bars) above and below the boxes indicate the 90th and 10th percentiles, respectively. Outlying values for both upper and lower ranges are represented by closed circles. Sample sizes are given above the box for each month.

Growth rates of dolphinfish are extremely fast during their first year and their maximum longevity is only three years (Fig. 2A). Female dolphinfish appeared to have a slower growth and shorter longevity than male dolphinfish; only three female dolphinfish reached age 2. However, there was no significant difference between the male and female von Bertalanffy growth models (likelihood ratio tests: χ^2=6.52, df=3, P=0.08).

The growth model fitted the relative age data well (under the assumption of a biological hatching date of 15 April) for >age-0 dolphinfish. However, the sizes of age-0 dolphinfish (where age was estimated by using annual marks on scales) at their relative age (Fig. 2B) did not show good agreement with size-at-age based on daily ages determined from otoliths. Thus, a combination of otolith-based daily ages for age-0 dolphinfish and scale-based relative ages for >age-0 dolphinfish were used when fitting a second von Bertalanffy growth model. The second von Bertalanffy growth function showed that males grow faster and reach a larger maximum size than females (likelihood ratio test: χ^2=10.14, df=3, P=0.02) (Fig. 2C; Table 2). By using a biological hatching date, the combined sexes model fit was improved from an r^2 of 0.67 to an r^2 of 0.73. The mean length-at-age values for dolphinfish collected in June, July, and August

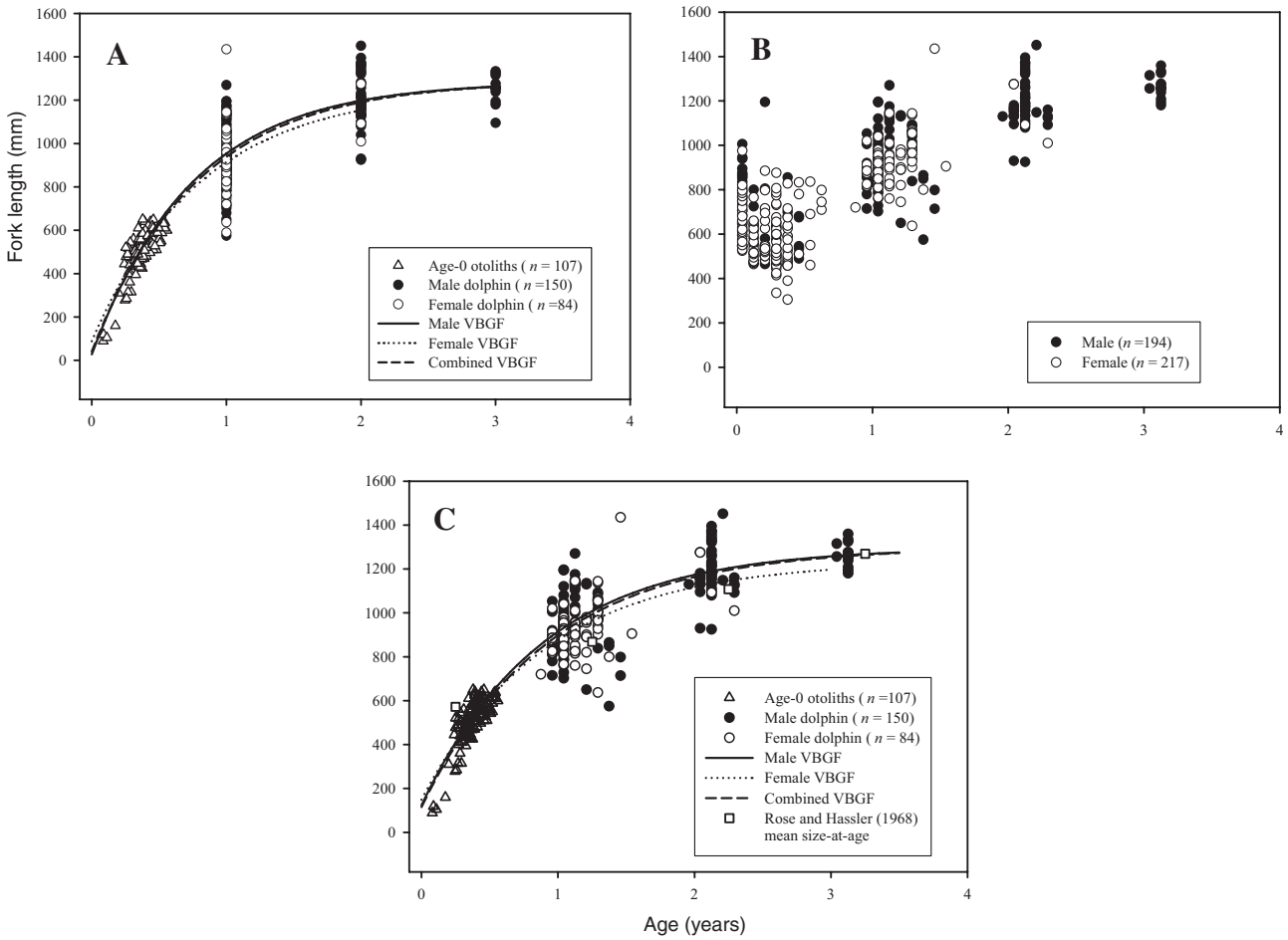


Figure 2

Length-at-age data for male (filled circles) and female (open circles) dolphinfish (*Coryphaena hippurus*) from (**A**) annual marks on scales from >age-0 dolphinfish, (**B**) annual marks on scales from age-0 and >age-0 dolphinfish (with the assumption of a 15 April hatching date, and (**C**) annual marks on scales from >age-0 dolphinfish (with the assumption of a 15 April hatching date). Length-at-age data (A and C) from daily otolith increments for age-0 dolphinfish with fork length <650 mm (male, female, and sex undetermined; open triangles) are presented. Functions A and C are presented for von Bertalanffy model fits to male (solid line), female (gray dashed line), and combined sexes (dark dashed line) length-at-age data (otolith and scale data combined for model fitting). Mean size-at-age data for dolphinfish from Rose and Hassler (1968) are plotted (C; open squares) for comparison with 2002–04 length-at-age values; values from Rose and Hassler (1968) were not used in fitting the von Bertalanffy growth function. VBGF=von Bertalanffy growth function.

1961–62 are shown in Figure 2C (where a mean capture date of 15 July was assumed for all plots; Rose and Hassler, 1968), and are similar to length-at-age values from the present study.

Length-at-age data for dolphinfish from past studies from different regions show an apparent trend in regional groupings (Fig. 3). The von Bertalanffy growth functions calculated for the Gulf of Mexico and Caribbean all display faster growth rates than those for Florida, North Carolina, and the Mediterranean, and an average longevity of less than one year. Dolphinfish collected from Florida, North Carolina, and the Mediterranean Sea all displayed similar first-year growth rates and a maximum age of 3 or 4 years (Fig. 3). However, Mediterranean dolphinfish have a slightly smaller size at age 2 and 3 compared to size for these ages of Florida and North Carolina dolphinfish.

Reproduction

Males reached 50% maturity at 476 mm FL and 100% maturity was reached at 645 mm FL (Table 3). Females reached 50% maturity at a slightly smaller size than males, although confidence limits for this parameter overlapped with those of males. At 458 mm FL, 50% of female dolphinfish were mature, and 100% were mature at about 560 mm FL.

Table 3

Length at 50% maturity for male and female dolphinfish (*Coryphaena hippurus*). Lengths were estimated by fitting a logistic model (see text) with nonlinear regression analysis. The standard errors (SE) of each parameter are shown in parentheses. n = sample size, Q = model parameter, L_{50} = fork length (mm) at 50% maturity, and CI = 95% confidence interval for L_{50}.

Sex	n	Q (SE)	L_{50} (SE)	CI
Males	74	0.05 (0.02)	476.13 (6.24)	460.9–494.7
Females	154	0.08 (0.02)	457.58 (2.54)	453.1–462.5

The highest median GSI values occurred in May for both male (Fig. 4A) and female (Fig. 4B) dolphinfish; however, these values were not corrected for differences in body size. Length-adjusted mean gonad weights were significantly different by month (ANCOVA: $P<0.001$) for both male and female dolphinfish (Fig. 4C). Length-adjusted mean gonad weights were highest in the late spring and summer and then decreased from midsummer into the fall. Gonad weights from November to February were not included because of the low sample size ($n=9$). September gonad weights were significantly lower than May and June gonad weights in males (Fig. 4C); all other male comparisons were nonsignificant. There were significant differences in the length-adjusted gonad weights of females between almost every month, but most differences were found for October, when gonad weights were significantly lower than in May, June, July, and August ($P<0.001$ for all) (Fig. 4C).

For both 2002 and 2003, hatching dates of dolphinfish occurred for all months, but the bulk occurred from January to June (Fig. 5). In 2002, the majority of age-0 dolphinfish sampled (83%) had back-calculated hatching dates in the months of January through June. Similarly, in 2003, 76% of age-0 dolphinfish had back-calculated hatching dates for this same period.

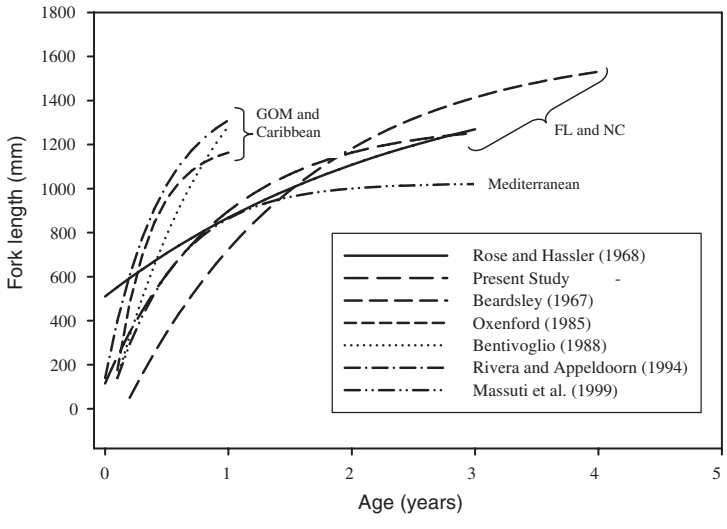


Figure 3

Calculated von Bertalanffy growth functions (VBGFs) for dolphinfish (*Coryphaena hippurus*) from various locations in the North Atlantic. GOM = Gulf of Mexico, FL = Florida, NC = North Carolina.

Discussion

Age and growth

This study is the first to use transverse cross-sections of sagittal otoliths to determine daily ages of dolphinfish; whole otoliths (Oxenford and Hunte, 1983; Uchiyama et al., 1986; Rivera and Appledoorn, 2000) or exposed sagittal planes (Massutí et al., 1999; Morales-Nin et al., 1999) were used in prior studies. Our estimated birth dates are in good agreement with known spawning dates (Beardsley, 1967; this study); a similar independent comparison indirectly validated daily age data for dolphinfish in the Mediterranean Sea (Massutí et al., 1999; Morales-Nin et al., 1999). Future work is needed to compare the multiple techniques that have been used to prepare age-0 dolphinfish otoliths in order to determine which technique is most efficient.

The daily growth rates for dolphinfish are faster than those of many species, but are a common characteristic of pelagic piscivores (Brothers et al., 1983; La Mesa et al., 2005). Our estimate of daily growth rate (3.78 mm FL/day) is similar to that of 550–1325 mm FL dolphinfish from Puerto Rico (3.59 mm/day; Rivera and Appledoorn, 2000) and 200–600 mm FL dolphinfish from the western Mediterranean Sea (~3.50 mm/day; Massutí et al., 1999). In Barbados, the average growth rate of dolphinfish of 174–1100 mm SL is estimated at 4.71 mm standard length per day (Oxenford and Hunte, 1983). Based on daily growth increments in sagittal otoliths of dolphinfish from the Gulf of Mexico, average first-year growth rate is 4.15 mm FL/day for fish in the size range of 250–1200 mm SL (Bentivoglio, 1988).

Annual marks are not detectable on sagittal otoliths of >age-0 dolphinfish with

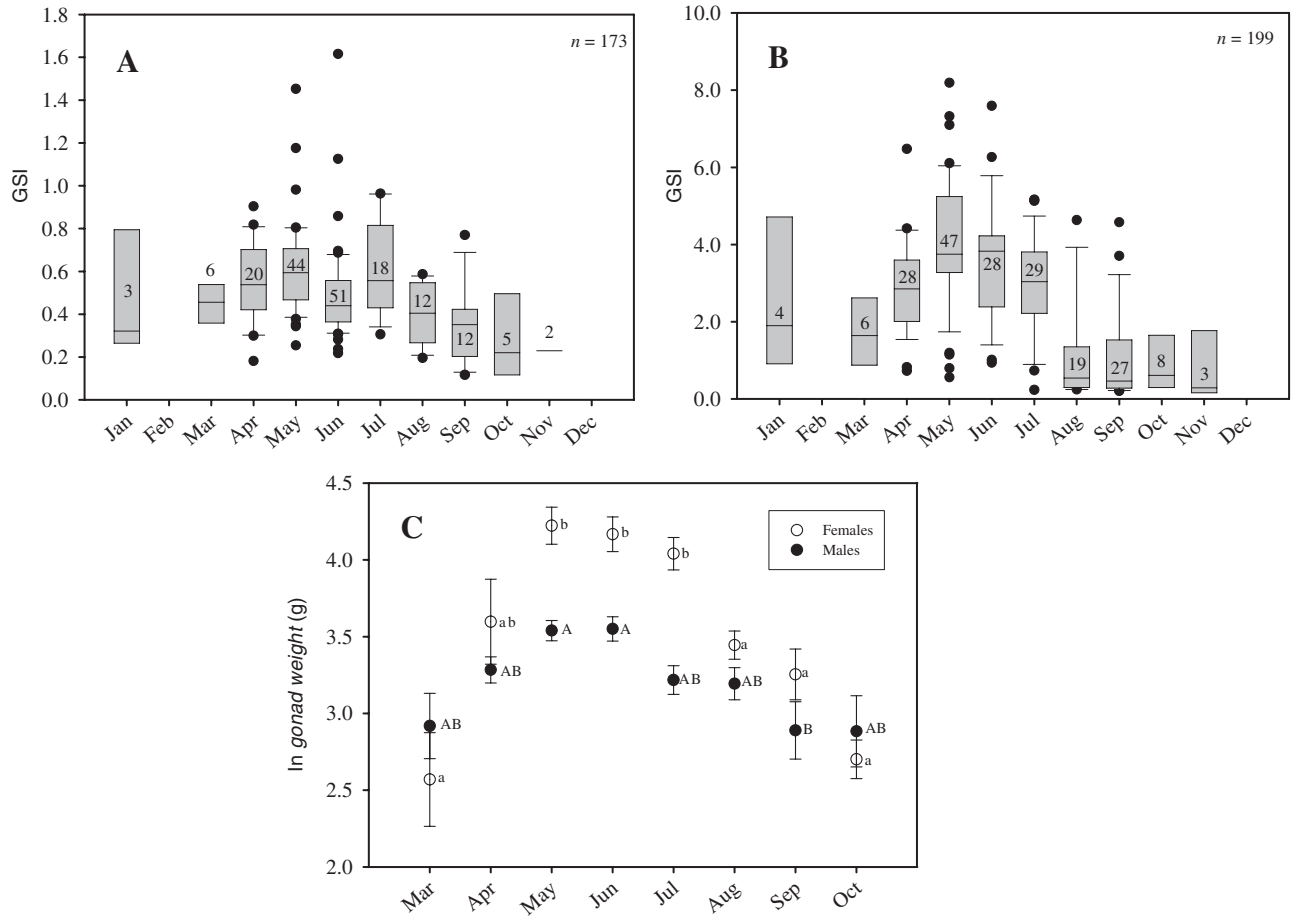


Figure 4

Box plots of gonadosomatic indices (GSI) for (**A**) males and (**B**) female dolphinfish (*Coryphaena hippurus*) collected from January 2002 through December 2004, and (**C**) mean (±SE) ln (*gonad weight*) of male (closed circles) and female (open circle) dolphinfish adjusted to a common length for March through October of 2002–04. Like letters for each sex in C indicate no significant difference between months as determined with ANCOVA. The 25th percentile of the GSI data is represented by the boundary of the box closest to zero, in relation to the *y*-axis, and the 75th percentile is represented by the boundary of the box farthest from zero. The line within the box is the median value. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles, respectively. Outlying values for both upper and lower ranges are represented by closed circles (in A and B). SE=standard error. Sample sizes are given inside the boxes (in A and B).

methods used to date. Massutí et al. (1999) using sagittal plane sections did not observe annual marks on dolphinfish otoliths from the Mediterranean Sea, although the authors speculated that detection of annual marks on the outer edges of adult otoliths may have been hindered by otolith preparation. A transverse cross-section approach was used in our study in an attempt to obtain a view of the outer edges, but the technique used in otolith preparation or the complex structure of >age-0 dolphinfish otoliths may have prevented detection of any annual marks. Alternatively, annual marks may not exist on sagittal otoliths of dolphinfish.

Validation of scale annuli has been attempted in only a few studies of dolphinfish. Although the annual marks on scales of >age-0 dolphinfish were relatively easy to interpret and within-laboratory agreement of age assignments was good in our study, these features do not establish that the ages are correct. In general, the monthly pattern in marginal increment widths in our study was similar to prior work in Florida (Beardsley, 1967). After measuring the distance between the last annulus and the margin of the scale for all dolphinfish with one or more year marks, Beardsley (1967) considered November to be the period of annulus formation because of an abrupt decrease in width of the increments from October to November. The smallest mean marginal increment in our study occurred during winter; this finding supports the hypothesis that dolphinfish lay a new annulus in winter as a result of decreased water temperature. The temperature of the

Gulf Stream and associated waters off the North Carolina coast is variable enough to cause a decrease in growth rates during the winter (Rose, 1966); the same conclusion was reached for Florida dolphinfish (Beardsley, 1967). It is unknown what proportion of the dolphinfish population inhabits these regions during winter and whether some dolphinfish are not exposed to environmental conditions that lead to annulus formation.

It is surprising that the mean marginal increment width dropped during late summer and fall in our study. The age-1 dolphinfish sampled in the late summer and early fall were smaller than those collected in the spring and early summer months of the same year, and for that reason perhaps a different cohort was sampled (Schwenke, 2004). Sampling from different cohorts is likely given the highly migratory nature of dolphinfish. Marginal increment width is correlated with dolphinfish body size (Schwenke, 2004); therefore, monthly differences in the mean fork length can affect the monthly marginal increment width. Wide variation in marginal growth in any given month was also noted by Beardsley (1967).

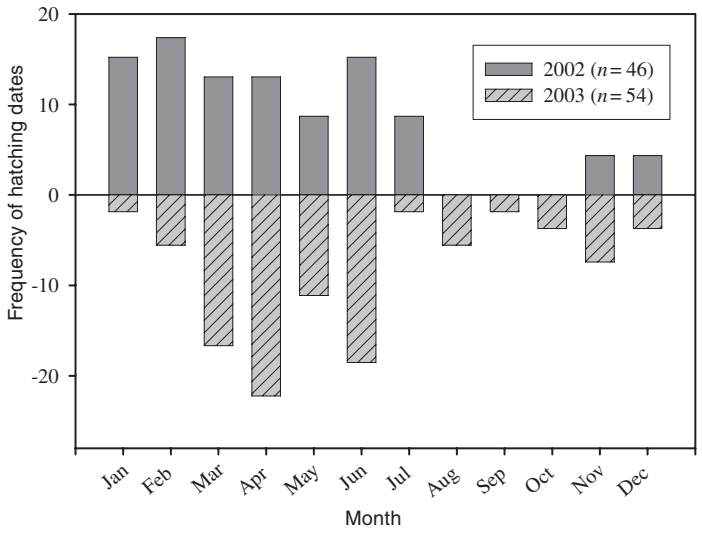


Figure 5

Frequency distribution of back-calculated hatching dates estimated from daily otolith increments for age-0 dolphinfish (*Coryphaena hippurus*) collected off North Carolina. The hatching dates were pooled by month for both 2002 (solid bars) and 2003 (hatched bars).

The assumption of a winter-formed annulus was supported by evidence of deposition of a winter-formed annulus in scales from a dolphinfish that had previously been tagged. The dolphinfish was tagged 18 October 2003 off Hudson Canyon (Mid-Atlantic Bight) at a fork length of 660 mm through the Dolphin Tagging Program run by Cooperative Science Services, Charleston, SC. The dolphinfish was recaptured on 16 May 2004 off Morehead City, NC, at a fork length of 864 mm and was estimated to be a one year old with a clearly defined annulus. This finding supports the assumption that dolphinfish lay down a new annulus in the winter. The likelihood that this dolphinfish had already laid down an annulus when tagged is not great, because 98% of the fish that were age-1 in our study had a fork length greater than 660 mm.

To date, scales seem to be the most appropriate hard part to use to determine annual ages of dolphinfish because findings are comparable between studies where this structure was used. With scales used for age determination, the maximum age of dolphinfish from Straits of Florida is four years (n=511; Beardsley, 1967), three years off North Carolina (n=738, Rose and Hassler, 1968; n=339, this study), and three years in the Mediterranean Sea (n=150, Massutí et al., 1999). Longevity and first-year growth for dolphinfish in Florida (Beardsley, 1967) and North Carolina (Rose and Hassler, 1968; this study) have greater similarity to longevity and first-year growth of western Mediterranean Sea dolphinfish (Massutí et al., 1999) than to longevity and first-year growth of dolphinfish in other regions (Fig. 3). First-year growth of dolphinfish in the Gulf of Mexico (Bentivoglio, 1988) and the Caribbean (Oxenford, 1985; Rivera and Appeldoorn, 2000) is faster and maximum age is younger than corresponding measures for other regions (Fig. 3). Differences in estimated growth between regions can be due to different laboratory methods, genetics, or environmental conditions (i.e., water temperature, food availability, exploitation levels). For example, the aging of dolphinfish solely with otoliths is found to underestimate the age of older, larger fish (Massutí et al., 1999). Alternatively, regional differences may represent different genetic stocks (reviewed by Oxenford, 1999). One of the first ways to make progress in identifying the factors responsible for this inter-region variability in growth would be to standardize age and growth methods.

Lengths of age-0 dolphinfish are highly variable and age-0 dolphinfish comprised the majority of the sampled population in this study. The large age-0 dolphinfish that were caught near the time of the theoretical hatching date may have represented fall-spawned dolphinfish whose annual marks would not be discernible on scales. Previous age and growth studies on the U.S. east coast have relied solely on annual marks on scales for their age estimates, and for these studies all samples were obtained through fishery-dependent sources. Because dolphinfish do not become fully recruited to the fishery until ~400 mm FL, past length-at-age-0 curves may be biased because smaller dolphinfish were not represented. In our study, small dolphinfish obtained through fishery-independent sampling allowed for daily aging of dolphinfish, and thus reduced the variability associated with length-at-age of age-0 dolphinfish and provided an estimate of first-year growth rates.

Reproduction

Peak spawning in dolphinfish off the southeastern United States extends from January through July (Beardsley, 1967; this study). Previous reviews of the reproductive characteristics of dolphinfish revealed that young dolphinfish are throughout the year in the Florida current and their presence may indicate year round spawning there (Oxenford, 1999). However, there are regional peaks in spawning activity off the southeastern U.S. coast. Peaks occur from January to March in Florida (Beardsley, 1967) and from May and June (Schuck, 1951) or June and July (Rose, 1966) in North Carolina. Unfortunately, sampling in North Carolina was limited to May and June in the former study (Schuck, 1951) and June, July, and August in the latter study (Rose, 1966). Based on our nearly year round collections of gonad weights, peak spawning in dolphinfish occurs from May to July off the coast of North Carolina; interestingly, peak spawning (determined from GSI values) occurs from May to June in Barbados (Oxenford, 1985).

Back-calculated hatching dates of age-0 fish collected in North Carolina confirm a spawning period from January through July off the southeastern United States; hatching dates do occur in other months, but at lower levels. Similarly, there is good correspondence between dolphinfish spawning and back-calculated hatching dates for the Mediterranean Sea (Morales-Nin et al., 1999). There is interannual variation in the hatching-date distribution of dolphinfish (Massutí et al., 1999; this study); this may be due to changes in the spawning peak or to differential mortality (Massutí et al., 1999). Given the lack of information on dolphinfish mortality, corrections for mortality in hatching-date distributions were not made.

The assignment of a 15 April biological hatching date to all >age-0 dolphinfish in this study reduces much of the variability associated with length-at-age seen in the von Bertalanffy growth curve where a biological hatching date is not used. Some variability in length-at-age still exists, however, and may be a result of other environmental factors experienced by an individual dolphinfish (i.e., water temperature, differences in prey consumption and prey quality). However, the protracted spawning season is likely the most important factor responsible for variability in length-at-age.

Overall, there has been little evidence of changes in size-at-maturity in dolphinfish off the U.S. east coast from the 1960s to the time of our study. Males first begin to mature at a fork length of about 435 mm, which is in agreement with Beardsley's (1967) observation of first maturity in males at a fork length of 427 mm. A previous estimate of the length at 50% maturity for female dolphinfish caught off Florida in the 1960s (Beardsley, 1967) is nearly identical to our estimate (450 [Beardsley, 1967] vs. 457 mm FL [our study]); however, Beardsley (1967) found earlier first maturity in females (~350 mm FL) compared to our study (~430 mm FL).

Summary and implications

Age, growth, and reproduction data for dolphinfish caught off the coast of North Carolina are provided. Using scale annual marks and daily growth increments from otoliths, we determined an updated age-length function. Furthermore, comprehensive seasonal estimates of gonad weights and marginal increment widths, as well as back-calculated hatching dates and daily growth-rate estimates, are the first for dolphinfish in North Carolina waters. Because this species is highly migratory, a much broader study encompassing the U.S. east coast or western North Atlantic may be needed in order to truly characterize dolphinfish reproduction and marginal increment widths. Direct validation through mark and recapture studies could also confirm annual marks on scales and provide good estimates of growth rates for tagged dolphinfish that remain at large through suspected periods of annulus deposition.

Intense positive size-selective mortality can lead to changes in life history parameters (Pitcher and Hart, 1982; Conover and Munch, 2002). However, there have been no changes in size-at-age or size-at-maturity of dolphinfish; therefore, the increased harvests in the 1980s and 1990s have not influenced these life history parameters to date. Because of their fast growth rates and small size-at-maturity, dolphinfish appear an ideal fishery resource species capable of withstanding high rates of fishing mortality.

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