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Age, growth and reproduction of the barrelfish *Hyperoglyphe perciformis* (Mitchill) in the western North Atlantic

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Otoliths ($n = 847$) and gonads ($n = 817$) were collected from barrelfish *Hyperoglyphe perciformis* that were captured by commercial fishermen in the waters off South Carolina and Georgia in 1995, 1997 and 2001–2006. Of the otoliths collected, 97% were aged successfully, and specimens sampled ranged from 5 to 85 years, with a median age of 12 years. The von Bertalanffy growth parameters yielded the equation: $L_t = 857{\cdot}8\{1 - e^{-0{\cdot}0985[t-(-8{\cdot}95)]}\}$, where L_t is fork length (L_F) at time t. Through histological examination, 94% of the gonads assessed were assigned to a sex and reproductive class. Females spawned from September to May with a peak from November to January. Males spawned year round, but had a peak from September to April. The sex ratio (M:F) for this population was 1:1·34. The smallest mature female was 605 mm L_F and the youngest immature female was 697 mm L_F. Estimates of L_F and age at 50% maturity (L_{50} and A_{50}) for females were 660 mm L_F (95% CI = 633–667 mm L_F) and 6·08 years (95% CI = 3·50–7·27 years), respectively. The youngest mature male was 575 mm L_F and the oldest immature male was 762 mm L_F, and no estimates of L_{50} or A_{50} were made for males. It was determined that barrelfish exhibit the typical characteristics of long life span, slow growth and high age at maturity seen in other deepwater fishes, and that care should be taken to manage this species accordingly.

Key words: Blake Plateau; Centrolophidae; deepwater; intersex; maturity; spawning.

INTRODUCTION

Commercial and recreational fishermen in the south-eastern U.S.A. have traditionally focused their efforts on species of fishes in the continental shelf waters, which tend to be more available, abundant and faster growing than deep-sea fishes of continental slope waters; however, as shallow water stocks continued

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to decline in the 1980s, more commercial fishermen began to fish the deeper slope waters (Sedberry *et al.*, 1999). Fishes that occur there are slower growing, often larger species that tend to mature later than many of their shallow water counterparts, making them vulnerable to rapid declines in population size, caused by increasing fishing pressure, from which they cannot easily recover (Musick, 1999; Sedberry *et al.*, 1999; Wyanski *et al.*, 2000; Harris *et al.*, 2001).

The barrelfish *Hyperoglyphe perciformis* (Mitchill, 1818) is a deepwater species, found at depths >200 m, which occurs on both sides of the North Atlantic. In the western North Atlantic, barrelfish range from Nova Scotia to the Florida Keys, including Bermuda, and into the Gulf of Mexico (Springer, 1954; Liem & Scott, 1966; Martin & Drewry, 1978). In the eastern North Atlantic, small to moderately sized specimens [up to 410 mm fork length (L_F)] are occasionally found around the British Isles (Andrews, 1871; Holt & Byrne, 1903; Wheeler, 1969), with a single capture in Norway (Pethon, 1983). Additionally, a few specimens have been caught west of the Azores (Murray & Hjort, 1912) and in the western Mediterranean Sea (Karrer, 1986).

Barrelfish are landed in small numbers by a few commercial vessels in the Carolinas and on both coasts of Florida (J. McGovern, pers. comm.). Around the Miami Terrace (located at depths of 200–400 m in the Straits of Florida, between Boca Raton and South Miami), barrelfish are often landed as by-catch in fisheries for deepwater snappers (Lutjanidae), groupers (Serranidae) and other deep reef species. On the three vessels from these fisheries that have landed them most often, barrelfish made up almost 8% (almost 32 000 kg) of the total catch from 1999 to 2004 (J. McGovern, pers. comm.). Off South Carolina and Georgia, barrelfish are regularly caught as by-catch of the wreckfish *Polyprion americanus* (Bloch & Schneider, 1801) fishery around the Charleston Bump, a topographic feature located in the Gulf Stream at depths of 400–800 m between latitudes 31°N and 32°N. Wreckfish fishermen operating on the Charleston Bump have landed almost exclusively adult barrelfish, ranging from 614 mm total length (L_T) to 1043 mm L_T.

Pelagic juveniles, as large as 284 mm standard length (L_S), are often seen in New England waters during the summer and autumn months, from late June to October, in association with floating debris, such as barrels, boxes and *Sargassum* weed (Smith, 1898; Merriman, 1945; Haedrich, 1967). A few small specimens (179–310 mm L_T) were also noted in upper Chesapeake Bay associating with floating boxes (Schwartz, 1963). Holt & Byrne (1903) suggested that the juveniles may congregate around these floating objects to feed on the encrusted barnacles and also hypothesized that juveniles may cross the North Atlantic, drifting with floating logs and boxes to the British Isles. Juveniles found off the New England coastline double or triple in size during the summer months, and then disappear as winter approaches, possibly moving to deeper waters (Haedrich, 1967). Adults have been observed in association with the bottom during submersible surveys conducted on the Charleston Bump in 1989 (Popenoe & Manheim, 2001) and around the Miami Terrace during the winter of 2005 (Reed *et al.*, 2006).

Slow growth, long life span, and high age at maturity are common characteristics of deepwater species (Musick, 1999; Sedberry *et al.*, 1999), making them vulnerable to rapid overfishing, as was experienced by wreckfish in Bermuda

(Sedberry *et al.*, 1999). Depending on their recruitment success, barrelfish could be similarly threatened. As fishermen continue to face more restrictive regulations, including temporal and spatial closures of nearshore fisheries, their reliance on deepwater fish species will only increase. The implementation of management strategies that are more suited to these species will necessitate determining growth rates and reproductive schedules for deepwater species that stand to be targeted by fishermen in the near future. Barrelfish are already being landed from the Charleston Bump and Miami Terrace as by-catch, and occur on the menu of a local Charleston, SC, restaurant (pers. obs.). For these reasons, it is important to learn all that is possible about barrelfish to protect this population from overfishing. This study aimed to determine the age structure, growth rates, reproductive strategy and schedule, and size and age at maturity of the barrelfish population inhabiting the waters of the Charleston Bump.

MATERIALS AND METHODS

SAMPLE COLLECTION

Specimens of barrelfish were collected from commercial fishermen who landed them as by-catch of the wreckfish fishery around the Charleston Bump from January 2001 to November 2005, and in February 2006. Additional otoliths from 20 specimens, collected by port agents who sampled fishes landed by commercial vessels fishing around the Charleston Bump in 1995, 1997, 2004 and 2005 were obtained from the NOAA Fisheries Laboratory in Beaufort, NC. L_T, values of L_F, L_S (mm), total body mass (M_{TB}; g) and gonad mass (M_G; g) were recorded for each specimen. Sagittal otoliths were removed and stored dry in coin envelopes for age and growth determinations; gonad tissue was taken and preserved in 11% seawater-formalin buffered with marble chips for histological examination to investigate aspects of the reproductive biology.

AGE AND GROWTH

Methods for estimating age and growth data were adapted from Harris *et al.* (2002). The left sagittal otolith was weighed (g) and embedded in West System epoxy resin, and a thin (0·7 mm) transverse section through the core was cut, using a Buehler Isomet 1000 low-speed saw. Sections were mounted in Cytoseal mounting medium on glass slides. Otolith sections were examined using a dissecting microscope with both transmitted and reflected light. The microscope had either a Hitachi KP-D20BU digital camera and Flashpoint frame grabber or Scion CFW-1310C digital video camera, and otolith images were viewed on a personal computer with Optimas or ImagePro image analysis software. Otolith increments (one opaque and one translucent zone) were counted independently by two readers on the ventral side of the sulcus, with no prior knowledge of capture date or fish size, and counts between readers were compared. If any count discrepancies existed between readers, the readers examined the otolith together, and the otolith was omitted from analyses (including indices of average per cent error, I_{APE}; see below) if disagreements continued, for a total of 10 otoliths omitted (1·18%). The otoliths with >20 increments were generally the source of disagreement, with the difference in counts between the two readers reaching upwards of 15 increments or more. All otoliths were read twice by the first reader to determine within-reader variation. A subsample of 14 otoliths was read by a fourth reader who had previous experience with the otoliths of *Hyperoglyphe antarctica* (Carmichael) (Horn, 1988). Values of I_{APE} were calculated to compare the precision of ages obtained by the first reader with those of the second and third readers, and with a second reading by the first reader (Beamish & Fournier, 1981). The otoliths that had been removed from analyses were not included in the calculation of I_{APE}. Qualitative estimates of the edge type of each otolith were made by classifying edges into one of four categories: 1, opaque zone on edge; 2, narrow translucent zone, <30% of previous translucent zone; 3, medium translucent zone, *c*. 30–60% of previous; 4, wide translucent zone, >60% of previous. For otoliths with ≤14 increments, the proportion of otoliths with an opaque zone on the edge (category 1) was plotted by month to determine the periodicity of increment formation.

An additional nine samples were processed for radiocarbon analysis to aid in the validation of the age estimates. The right otolith of nine fish that had previously been aged using increment counts was embedded in West System epoxy resin and a 1 mm transverse section was taken through the core, using the Buehler Isomet 1000 low-speed saw. The otolith section was mounted on a small metal plate using tape, and the core was removed using a Dremel tool (Baker & Wilson, 2001). The core section was then rinsed for 15–30 s in 5% HCl, cleaned ultrasonically with distilled water, weighed, packaged and shipped to the accelerator mass spectrometry (AMS) laboratory of the National Ocean Service at the Woods Hole Oceanographic Institute in Massachusetts.

A $\Delta^{14}C$ value was provided for each otolith by the AMS laboratory as defined in Stuiver & Polach (1977) (see http://www.nosams.whoi.edu/clients/data.html for methods and analytical procedures employed). These $\Delta^{14}C$ values were then plotted against the hatch date (year) as determined by the earlier age estimates from increment counts. This plot was compared to published findings from radiocarbon analyses performed on red snapper *Lutjanus campechanus* (Poey, 1860) in the Gulf of Mexico (Baker & Wilson, 2001) and haddock, *Melanogrammus aeglefinus* (L., 1758), in the north-western Atlantic (Campana, 1997). If the hatch-dates obtained from increment counts and the $\Delta^{14}C$ values obtained corresponded to the curves of these standards used, then the increment count was assumed to be an accurate reflection of the age of the fish.

Mean length at age was calculated and a von Bertalanffy growth curve (von Bertalanffy, 1938) was fitted to the unweighted size at age data with SAS software (SAS Institute Inc., Cary, NC, U.S.A.). Length at age was compared between sexes to determine if any sexual dimorphism was present. Additionally, the relationship between otolith masses and the ages of the specimens was determined using a non-linear regression, and the relationships between L_T and L_F, L_S and L_F, and M_{TB} and L_F were assessed using a least-squares linear regression. All statistical analyses were performed using SAS software (SAS Institute Inc.), Microsoft Excel (Microsoft Corporation, Seattle, WA, U.S.A.) or R statistical computing software (R Foundation for Statistical Computing, Vienna, Austria).

REPRODUCTION

All methods for the preparation of gonads and determination of reproductive strategy were adapted from Harris *et al.* (2004). The posterior portion of each gonad of each specimen was excised and preserved in 11% seawater-formalin buffered with marble chips for 7–14 days, and then placed in 50% isopropanol for 7–14 days. Samples were processed and vacuum infiltrated in an ATP1 tissue processor and blocked in paraffin. Three sections (6–8 μm) were then taken from the embedded samples using a motorized rotary microtome, mounted on glass slides, stained with double-strength Gill's haematoxylin and counterstained with eosin-Y.

Sex and reproductive class of each specimen were determined microscopically by three independent readers, with no knowledge of length, age or date of capture of specimens, using histological criteria developed for another deepwater gonochorist, the blueline tilefish *Caulolatilus microps* Goode & Bean, 1878 (Harris *et al.*, 2004). If assessments of each reader differed, the sample was examined by all readers and omitted from analyses if the difference could not be resolved. Specimens considered to be sexually mature were those with developing, ripe, spent or resting gonads. For females, this definition included those with oocyte development at or beyond the cortical alveoli stage and specimens with beta, gamma or delta stages of atresia (Hunter & Macewicz, 1985). Spawning seasonality was determined by the presence of hydrated oocytes (HOs) and postovulatory follicles (POFs) and by calculating the gonado-somatic index (I_G), where $I_G = 100M_GM_{TB}^{-1}$ of mature females. The age of POFs was estimated according to criteria developed by Hunter & Goldberg (1980) for the northern anchovy *Engraulis mordax* Girard, 1854, since the temperature range of the waters around the Charleston Bump, in which barrelfish most likely spawn, is similar to that in which *E. mordax* spawns (Sedberry *et al.*, 1999, 2004). To ensure that the fish were assigned to immature and resting classes correctly, the length-frequency histogram of fish with certain evidence of maturity (developing, resting or spent classes) was compared to those for specimens placed in the resting and immature classes. Size (L_{50}) and age (A_{50}) at 50% maturity were estimated using the PROBIT procedure in SAS software (SAS Institute Inc.). Sex ratios were determined, and a χ^2 goodness of fit test with Yates correction was used, for each size class and for each month, to determine if the ratios differed from 1:1 (Sokal & Rohlf, 1995).

RESULTS

SAMPLE COLLECTION

A total of 827 barrelfish was collected from commercial fishermen fishing around the Charleston Bump, and otoliths from an additional 20 specimens were obtained from the NOAA Fisheries laboratory in Beaufort, NC. Due to an annual closure of the wreckfish fishing grounds from 15 January to 15 April, implemented in 1991 (SAFMC, 2006), sample sizes for those months were smaller, and no specimens were collected in March. More than 50 specimens were collected for each month in which sampling took place, except for February, during which 17 specimens were collected. Since lengths were not normally distributed (Shapiro–Wilk test, $n = 840$, $P = 0{\cdot}01$), median lengths are reported instead of mean lengths. The median L_F of all fish sampled was 755 mm ($n = 840$), with a minimum of 556 mm L_F and a maximum of 960 mm L_F. There was a strong linear relationship between L_T and L_F, L_S and L_F and L_F and M_{TB} (Table I).

AGE AND GROWTH

Ages were determined for 824 of the 847 barrelfish for which otoliths were collected (97%). The otoliths of the younger specimens had rather easily distinguished, widely spaced increments [Fig. 1(a)], while the increments that were

TABLE I. Least-square linear regressions relating total length (L_T; mm) to fork length (L_F; mm), standard length (L_S; mm) to L_F and total body mass (M_{TB}; g) to L_F, for barrelfish collected from commercial fishermen fishing around the Charleston Bump in 1995, 1997 and 2001–2006

	d.f.	r^2	P
$L_T = 1{\cdot}068(L_F) + 32{\cdot}415$	807	0·99	<0·001
$L_S = 0{\cdot}920(L_F) - 21{\cdot}372$	807	0·98	<0·001
$\text{Log}_{10}(M_{TB}) = 2{\cdot}833(\log_{10}(L_F)) - 4{\cdot}239$	812	0·91	<0·001

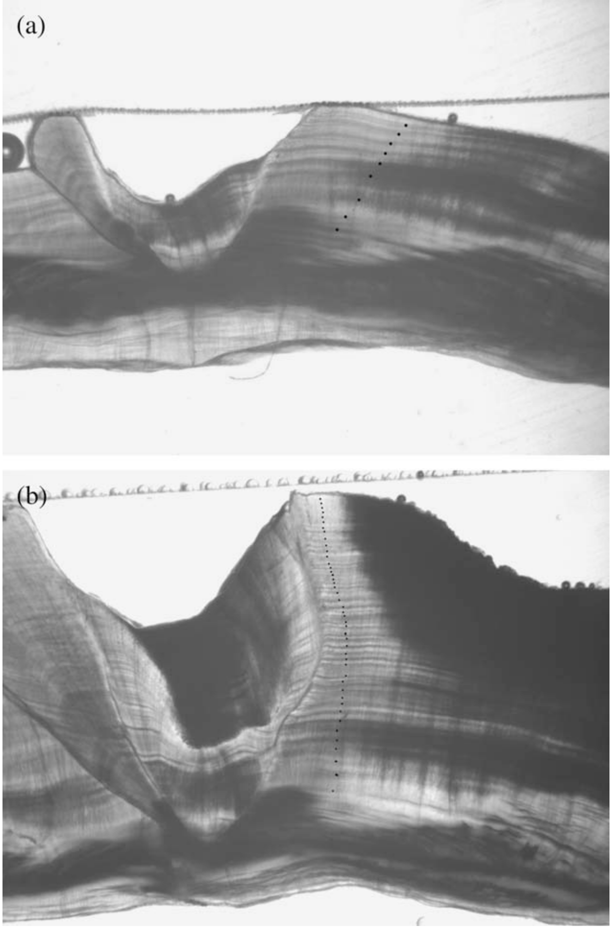

FIG. 1. Transverse sections of the sagittal otoliths of barrelfish: (a) 9 year-old specimen and (b) 45 year-old specimen. Counts were made along ventral side of the sulcus (●, one increment).

farther from the core in older specimens were very tightly spaced and more difficult to resolve [Fig. 1(b)]. Of the otoliths aged, only those with <15 increments ($n = 685$) were used for marginal increment analysis because of the tight spacing of the outer increments in the otoliths of older fish. Also, due to variation in within-otolith increment widths observed in the majority of otoliths examined, a qualitative assessment of marginal increments was performed by plotting the proportion of otoliths with an opaque zone on the edge in each month sampled (Fig. 2). This indicated annual increment formation, though the range of values obtained (0·16–0·40) was not large enough to be conclusive, emphasizing the difficultly of marginal increment analysis on a deepwater, long-lived species.

The results of the radiocarbon analysis suggested that one increment was formed per year when compared to the haddock reference chronology from Campana (1997), although there appeared to be a phase shift of between 7 and 8 years (Fig. 3). The specimens used for this analysis were chosen because

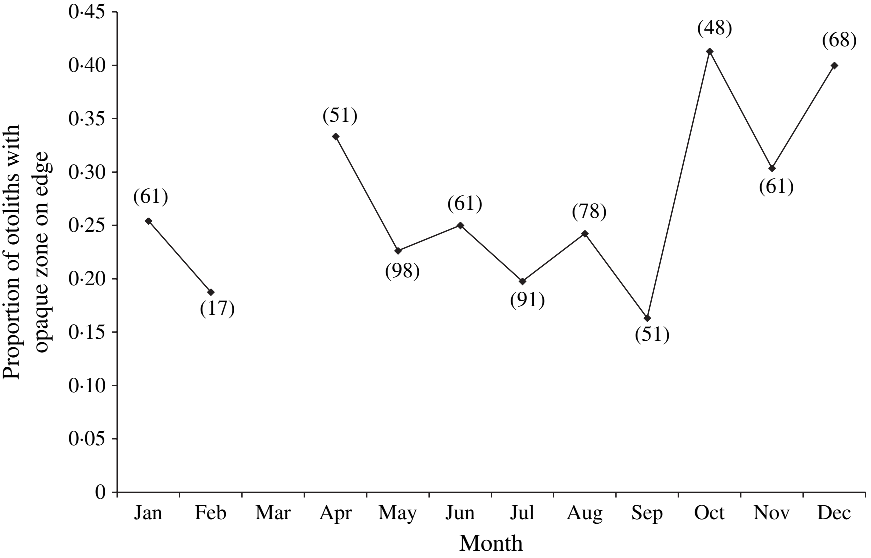

FIG. 2. Proportion of barrelfish otoliths with an opaque zone on the edge in each month. Numbers in parentheses are sample sizes. Barrelfish collected from commercial fishermen fishing around the Charleston Bump in 1995, 1997 and 2001–2006. Due to the spawning season closure of the wreckfish fishery, no specimens were collected in March.

their otolith-derived birth years, which ranged from 1962 to 1977, fell within the period of atmospheric testing of nuclear weapons. The radiocarbon analysis returned a minimum $\Delta^{14}C$ value of –94·9‰ for 1962 and a maximum value of 56·8‰ for 1974 (Table II). The two samples with otolith-derived birth dates

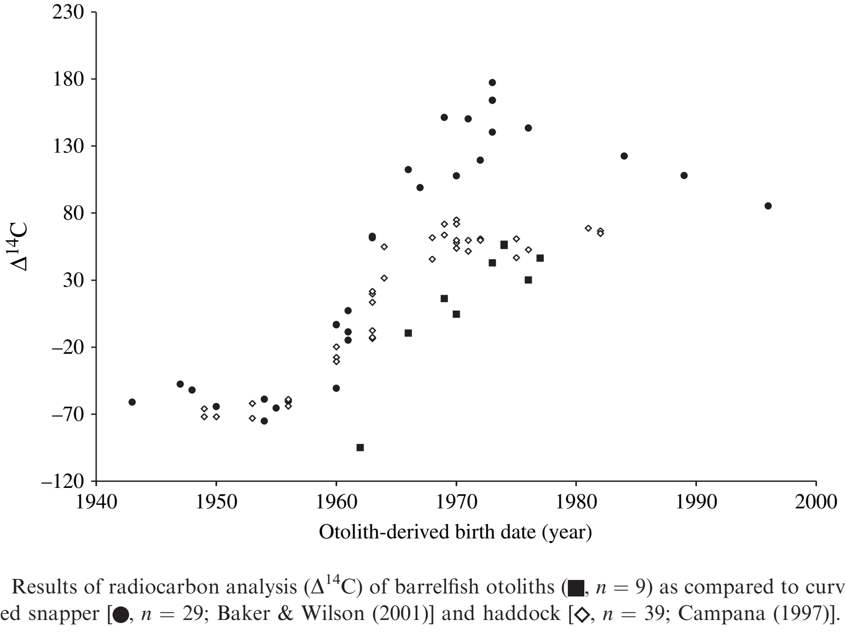

FIG. 3. Results of radiocarbon analysis ($\Delta^{14}C$) of barrelfish otoliths (■, $n = 9$) as compared to curves for red snapper [●, $n = 29$; Baker & Wilson (2001)] and haddock [◇, $n = 39$; Campana (1997)].

TABLE II. Data for otoliths used in radiocarbon ($\Delta^{14}C$) age validation from barrelfish collected from commercial fisherman fishing around the Charleston Bump

Birth year	Collection year	L_F (mm)	Core mass (mg)	Age	$\Delta^{14}C$ (‰)
1962	2003	811	6·04	41	−94·9
1966	2003	850	8·46	37	−9·4
1969	2003	868	5·84	34	16·2
1970	2005	877	9·80	35	4·7
1973	2004	826	10·87	31	42·9
1974	2004	870	9·26	30	55·8
1974	2004	858	6·79	30	56·8
1976	2003	879	6·22	27	30·1
1977	2003	828	7·50	26	46·4

L_F, fork length.

after 1974 were lower than in the samples from 1974, which may suggest a decrease in $\Delta^{14}C$ values that would be consistent with the peak of $\Delta^{14}C$ values in the world's oceans, but more samples would be necessary to validate this decrease. Samples from the pre-bomb era would also be ideal, but it was not possible to process more otolith cores.

Barrelfish ranged in age from 5 to 85 years, with a modal age of 12 years and a mean of 16·28 years (Fig. 4). Despite the difficulty encountered in interpreting barrelfish otoliths, all of the I_{APE} were similar to one another and were fairly precise. The two independent readings by the first reader had an I_{APE} value of 7·1% (n = 817). The I_{APE} between the readings of first and second reader was 9·6% (n = 833) and the I_{APE} between the readings of first and third reader was 7·8% (n = 14). The non-linear relationship between otolith mass and fish age was determined using a least-squares non-linear regression model

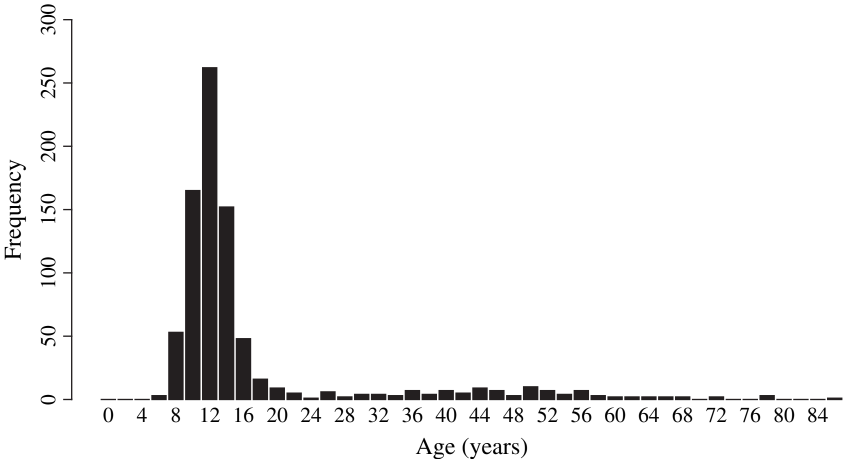

FIG. 4. Age frequency distribution of barrelfish sampled from the commercial fishery around the Charleston Bump in 1995, 1997 and 2001–2006 (n = 824).

and showed that age does have an effect on the otolith mass, with a relationship of: $y = -1e^{-4}x^2 + 0{\cdot}015x + 0{\cdot}214$ ($r^2 = 0{\cdot}78$, d.f. = 648, $P < 0{\cdot}001$).

Mean L_F of barrelfish increased steadily until age 16 years, after which time mean lengths varied more within ages. The sample size of fish in age class ≥17 years, however, was much smaller ($n = 137$) than the sample size for age class ≤16 years ($n = 679$). Although the largest fish were generally females, for all ages, no statistically significant sexual dimorphism was present (ANOVA, $P > 0{\cdot}05$), so a von Bertalanffy growth curve was fitted to combined unweighted length-at-age data with the resultant equation: $L_t = 857{\cdot}8\{1 - e^{-0{\cdot}0985[t-(-8{\cdot}95)]}\}$, where L_t is L_F at time t.

REPRODUCTION

All intact specimens collected were examined histologically for sex and reproductive class ($n = 817$). Sex and reproductive class were determined for 94% ($n = 767$) of all gonads obtained, and 99% ($n = 811$) were assigned to a sex class. A length-frequency histogram of immature, resting and definitely mature fish showed very little overlap between immature and mature specimens, and a high degree of overlap between the resting and the definitely mature specimens, indicating that all specimens were placed in the correct reproductive class (Fig. 5). The overall sex ratio of male to female barrelfish (1:1·34) was significantly different from 1:1 (χ^2, d.f. = 1, $P < 0{\cdot}01$). This deviation from 1:1 was only observed, however, in the larger size classes, as significantly more females than males were present in those size classes (>750 mm L_F; Table III). Additionally, females were only collected in significantly higher numbers than males in November, December and January, which were peak spawning months for females (Table IV).

The smallest mature female was 605 mm L_F (Table V) and the largest immature female was 697 mm L_F, with an L_{50} estimate of 660 mm L_F (Gompertz model; 95% CI = 633–667 mm L_F). The youngest mature female was 5 years old and the oldest immature female was 15 years old, with an A_{50} estimate of 6·08 years (logistic model; 95% CI = 3·50–7·27 years). The smallest mature male was 575 mm L_F and the largest immature male was 762 mm L_F; the youngest mature male was 7 years old and the oldest immature male was 12 years old. Due to the very small number of immature males in the samples collected ($n = 3$), the PROBIT procedure was not performed to estimate L_{50} or A_{50} for the males. Immature females were present in all size classes <701 mm L_F, and all females were not mature until after 15 years of age (Tables VI and VII). With the exception of one specimen, the immature males were in the two smallest size classes (<651 mm L_F), and all males were mature by age 13 (Tables VI and VII).

Based on the presence of HOs and POFs, female barrelfish were in spawning condition between the months of September and May, with a peak in activity between November and January [Fig. 6(a)]. The values of I_G ranged from 0·93 to 3·55, with a peak occurring in April (Fig. 7). While male barrelfish were found in spawning condition in all months sampled, they were present in the highest proportions during September to April [Fig. 6(b)].

An interesting feature that was encountered with the males is the fairly large proportion (9·8%) that contained primary growth oocytes in their testicular

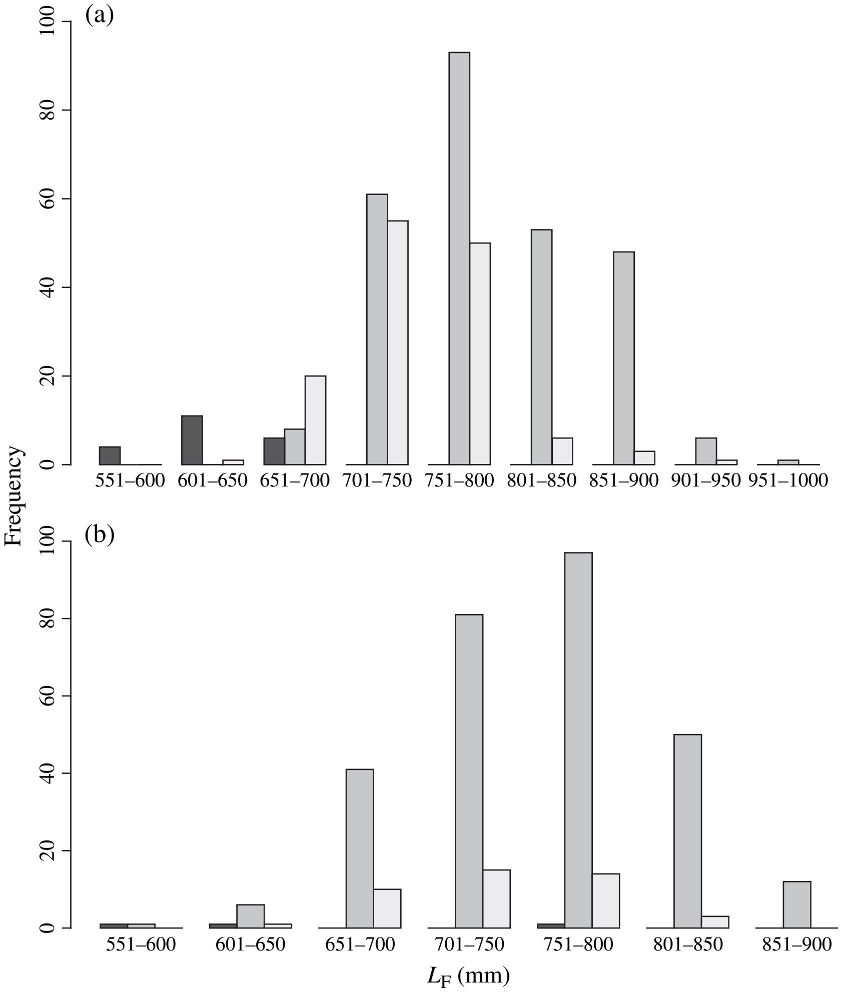

FIG. 5. Fork length (L_F)-frequency histogram of all (a) female and (b) male barrelfish defined as immature (■), resting (▨) and definitely mature (developing, spawning or spent; □). Specimens were collected from the commercial fishery around the Charleston Bump from 2001 to 2006.

tissue, a phenomenon known as intersex or ovotestis (Fig. 8). These males were found in all classes of the reproductive cycle, with the exception of immature specimens. This may be due, however, to the very low number of immature males (<1%) collected overall. Additionally, at least one male in the intersex condition was collected in each month, except in February and April. The 34 specimens exhibiting intersex ranged from 609 to 815 mm L_F, and had a median of 723 mm L_F.

In addition to intersex in a number of male barrelfish, two other atypical histological features were noted. The first is that the primary growth oocytes of resting females were often as small as the primary growth oocytes seen in the immature females. Typically, primary growth oocytes seen in immature females are smaller than those seen in resting females. The second feature is that

TABLE III. χ^2 analysis, with Yates' continuity correction, of sex ratios of barrelfish collected from commercial fishermen fishing around the Charleston Bump from 2001 to 2006, by fork length (L_F) (H_o = male to female ratio of 1:1)

L_F (mm)	Males	Females	Male:female	χ^2
551–600	3	4	—	—
601–650	9	17	1:1·89	1·88
651–700	56	49	1:0·88	0·34
701–750	100	127	1:1·27	2·98
751–800	113	146	1:1·29	3·95*
801–850	53	60	1:1·13	0·32
851–900	12	51	1:4·25	22·92†
901–950	0	7	—	—
951–1000	0	1	—	—
Total	346	462	1:1·34	16·65†

*$P < 0·05$, 1 d.f.
†$P < 0·01$, 1 d.f.

the majority of the male barrelfish examined were developing, actively spawning or spent, with only a small proportion in the resting class (12%).

DISCUSSION

The validation of the ages of deepwater fishes is a difficult task to accomplish (Horn, 2003; Harris *et al.*, 2004). The ages obtained for barrelfish in this study were probably very close to the actual ages of these specimens. Although the marginal increment analysis did not produce a range wide enough to fully

TABLE IV. χ^2 analysis, with Yates' continuity correction, of sex ratios of barrelfish collected from commercial fishermen fishing around the Charleston Bump from 2001 to 2006, by collection month (H_o = male to female ratio of 1:1)

Month	Males	Females	Male:female	χ^2
January	19	48	1:2·53	11·70†
February	4	13	1:3·25	3·76
April	19	28	1:1·47	1·36
May	53	53	1:1·00	0·01
June	33	48	1:1·45	2·42
July	56	53	1:0·95	0·04
August	52	42	1:0·81	0·86
September	30	35	1:1·17	0·25
October	28	42	1:1·50	2·41
November	26	46	1:1·77	5·01*
December	27	56	1:2·07	9·45†
Total	347	464	1:1·34	16·88†

*$P < 0·05$, 1 d.f.
†$P < 0·01$, 1 d.f.

TABLE V. The range, mean and modal fork lengths (L_F) of immature, mature (developing, ripe, spent or resting) and all male and female barrelfish collected from commercial fishermen fishing around the Charleston Bump from 2001 to 2006

	Male L_F (mm)				Females L_F (mm)			
	n	Range	Mean	Mode	*n*	Range	Mean	Mode
Immature	3	560–762	642·3	605	21	556–697	635·9	633
Mature	331	575–885	752·8	755	408	605–960	776·6	767
All	345	560–885	749·4	752	462	556–960	763·9	760

confirm that one increment is formed per year, the radiocarbon analysis was consistent with yearly increment formation. In the nine barrelfish otoliths examined, the curve of $\Delta^{14}C$ observed resembled the reference chronology obtained for haddock found in waters off the east coast of Canada (Campana, 1997) with an apparent phase shift of 7–8 years. Since juvenile barrelfish have been observed during the summer months inhabiting the waters around New England, close to the sampling sites for haddock, the $\Delta^{14}C$ values obtained may be similar. As water masses in which pelagic early life-history stages occur are not precisely known, this phase shift may represent the radiocarbon chronology of oceanic conditions that are different from those where haddock reside. Additionally, barrelfish that are spawned around the Charleston Bump are subject to upwelling that occurs in this area, so the otolith cores may have incorporated upwelled carbon from earlier times, which would contain a lower amount of ^{14}C compared to the haddock reference chronology, and which could impede the timing of increase of ^{14}C in barrelfish otoliths (Piner *et al.*, 2005).

It is also possible that ageing errors could have produced the phase shift seen in the barrelfish curve relative to the reference. The between-reader agreement

TABLE VI. Percentage of mature (developing, ripe, spent or resting) fish by fork length (L_F) for female and male barrelfish collected from commercial fishermen fishing around the Charleston Bump from 2001 to 2006, as determined by histological examination

L_F (mm)	Females % ($n = 431$)	Males % ($n = 335$)
551–600	0 (4)	50·0 (2)
601–650	8·3 (12)	87·5 (8)
651–700	82·4 (34)	100·0 (51)
701–750	100·0 (117)	100·0 (96)
751–800	100·0 (143)	99·1 (113)
801–850	100·0 (60)	100·0 (53)
851–900	100·0 (51)	
901–950	100·0 (7)	100·0 (12)
951–1000	100·0 (1)	
No L_F	100·0 (2)	

n, number of specimens.

TABLE VII. Percentage of mature (developing, ripe, spent or resting) fish by age for female and male barrelfish collected from commercial fishermen fishing around the Charleston Bump from 2001 to 2006, as determined by histological examination

Age (years)	Females % ($n = 423$)	Males % ($n = 325$)
5	50·0 (2)	
6	100·0 (1)	
7	100·0 (4)	100·0 (4)
8	66·7 (18)	90·0 (10)
9	79·4 (34)	96·4 (28)
10	97·6 (42)	100·0 (41)
11	98·3 (60)	100·0 (62)
12	98·5 (65)	98·1 (52)
13	98·3 (57)	100·0 (37)
14	100·0 (33)	100·0 (14)
15+	99·0 (102)	100·0 (75)

n, number of specimens.

for the nine otoliths examined was 11%, indicating that exact reproducibility of ages of the older specimens in this study was difficult to achieve. There was not a bias for underestimation of ages, however, such that ageing errors were random for these specimens and most likely would not account for underestimation of the ages by 7–8 years. A reference chronology of dissolved inorganic carbon from the area in which the barrelfish specimens resided as juveniles would be necessary to determine whether the observed phase shift was due to ageing error or some oceanographic feature (Piner *et al.*, 2005), but because of the uncertainty of where these specimens resided as juveniles, the two processes cannot be distinguished from one another.

The von Bertalanffy growth parameters obtained indicate that barrelfish experience a fast rate of growth during their first 5 years of life, as the two youngest fish collected were 5 years old, with L_F of 627 and 727 mm. Growth slows greatly after this initial phase, however, with moderately fast growth occurring up to *c*. 20 years of age, and very slow growth after that. Further insight into barrelfish growth cannot be gained from the von Bertalanffy parameters because of the lack of young fish collected.

One explanation for this slow growth rate in barrelfish could be dietary limitation. Barrelfish have been shown in previous studies to feed on a variety of organisms, such as small fishes, crustaceans, squid, barnacles and ctenophores (Haedrich, 1967; Bigelow & Schroeder, 2002). In an ongoing research project, the bulk of the organisms found in stomachs of the barrelfish specimens used in this age and growth study were colonial tunicates or salps (S. F. Goldman, unpubl. data). The energetic content of salps is less than that which could be derived from a diet comprised mostly of fishes and crustaceans (Bailey *et al.*, 1995; Bullard & Hay, 2002). Perhaps when juvenile barrelfish are living in productive surface waters, they are feeding on more nutrient rich organisms and are therefore able to grow at a faster rate. While these fish are pelagic, they feed on encrusting organisms attached to floating debris, and it has been suggested that they may follow these food-encrusted objects across the North

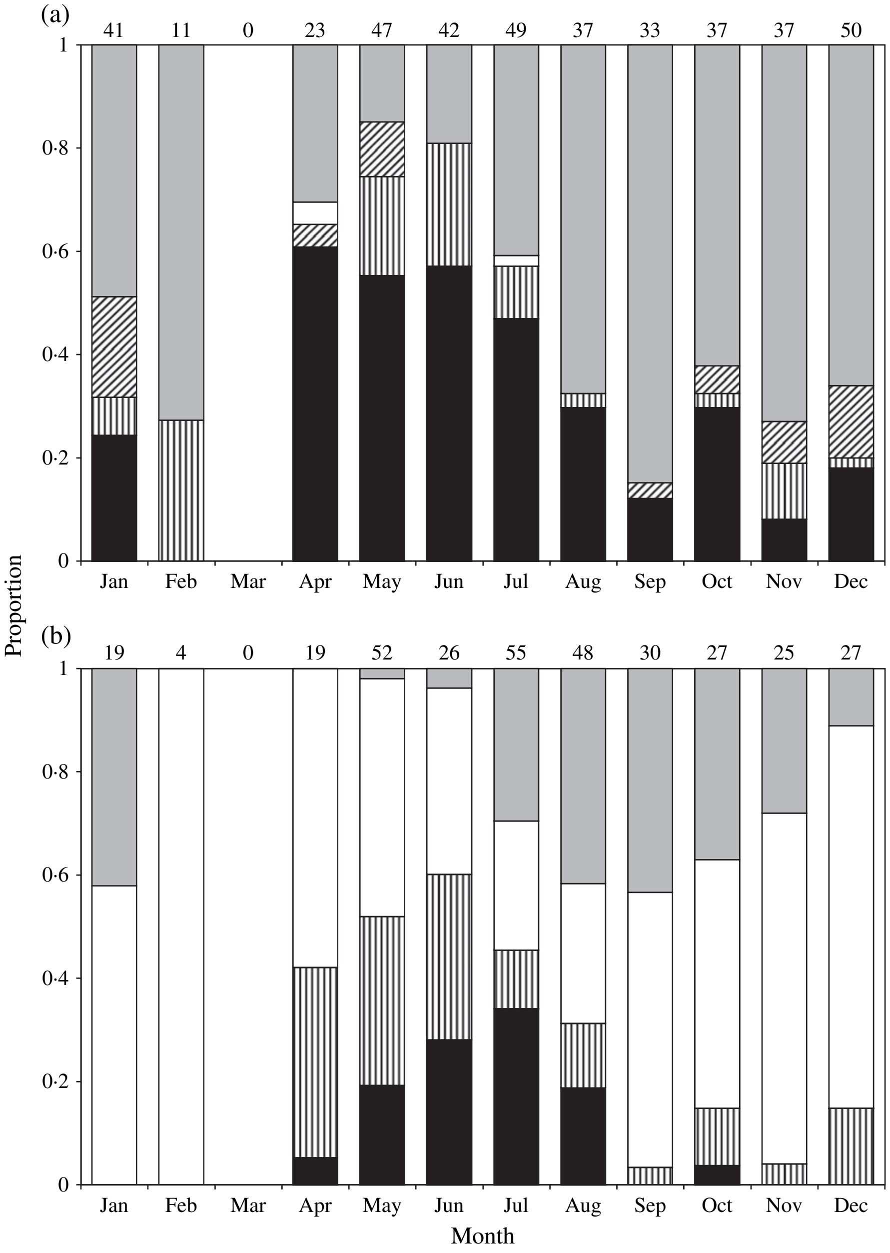

Fig. 6. Proportion of specimens in each reproductive class (■, developing; □, ripe; ▨, postovulatory follicle present; ▥, spent; ▒, resting). Number of specimens is located above the bars by month for (a) female and (b) male barrelfish sampled from the commercial fishery around the Charleston Bump from 2001 to 2006.

Atlantic (Holt & Byrne, 1903). When these fish make an ontogenetic shift to deeper waters, their diet may change to the less nutritious salps, thereby resulting in a very slow growth rate.

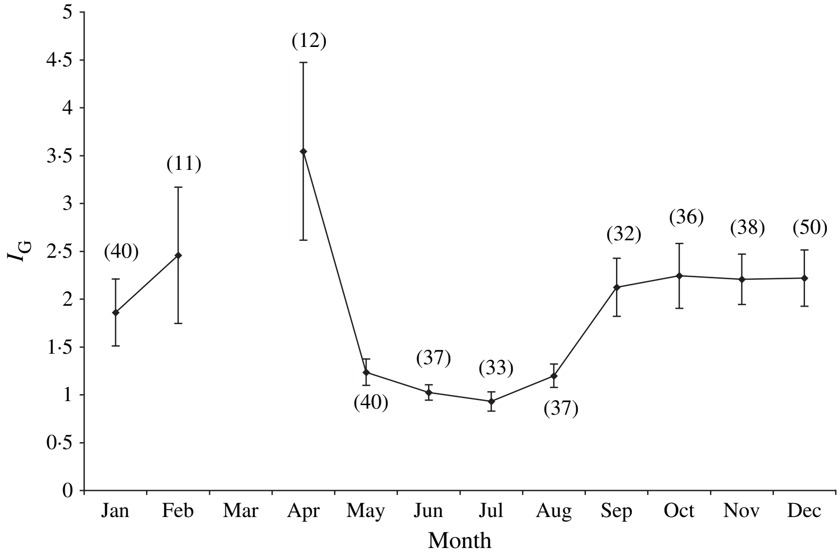

FIG. 7. Mean ± 1 S.E. gonado-somatic index (I_G) of female barrelfish sampled from the commercial fishery around the Charleston Bump from 2001 to 2006 ($n = 366$). Numbers in parentheses are sample sizes.

In addition to the extremely slow growth rate seen in barrelfish in this study, the size range for specimens of a given age was often quite wide, as evidenced by the high S.E. associated with mean length at age. For example, age 8 year barrelfish in this study ranged in L_F from 556 to 896 mm. This observation suggests that length is not a good predictor of age in barrelfish.

One of the obstacles encountered in interpreting barrelfish otoliths was identifying the first increment. A large dark area surrounded the core of the majority of the otoliths examined, and varied in size between otoliths. This entire structure was considered the first increment, although disagreement between ages obtained by separate readers often still existed, due to the differences in interpretation. Juvenile barrelfish grow very quickly during their time in the waters around New England (Haedrich, 1967), which may explain the presence of this dark area. Perhaps this high growth rate continues after their disappearance from the coastal waters in the autumn, as was suggested by the von Bertalanffy parameters and observed length-at-age data obtained in this study. This could cause the first few increments to be laid down in irregular and widely spaced intervals, as was observed in most of the otoliths examined. The latter increments were much closer together and more regularly spaced, which parallels the slower growth rate suggested by the von Bertalanffy parameters and length-at-age data obtained.

Barrelfish sampled for this study follow the trend exhibited in other deepwater fishes of older ages at maturity. For example, female *H. antarctica* mature at *c.* 11–12 years and males at 8–9 years, although these are preliminary estimates due to the difficulty in validating the ages in this species (Baelde, 1996). Male and female wreckfish collected in the western North Atlantic were shown to reach maturity around 8–10 years, and wreckfish sampled in the South Atlantic

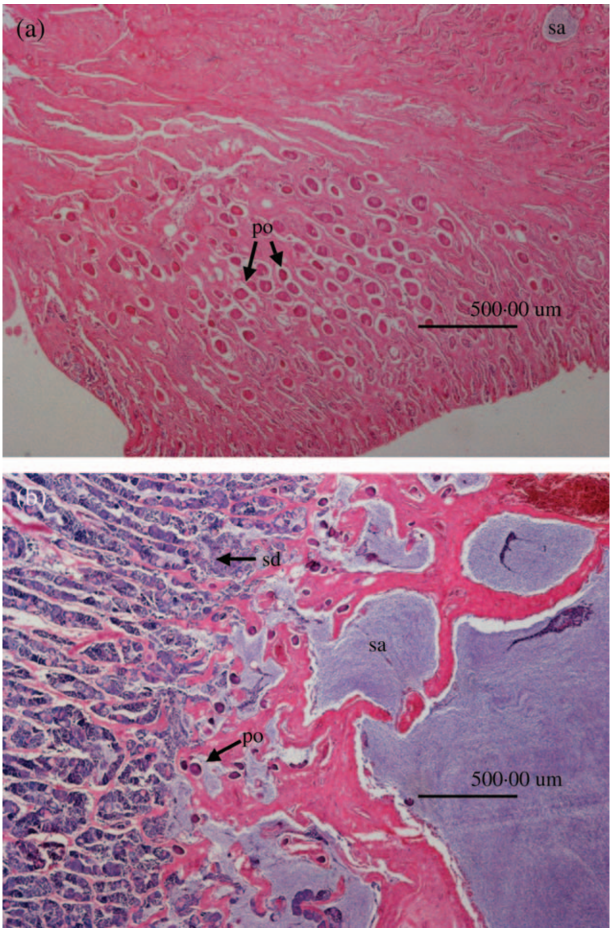

FIG. 8. Haematoxylin and eosin-stained transverse sections of gonads that were sampled around the Charleston Bump from (a) an 820 mm fork length (L_F) spent male captured in August and (b) a 726 mm L_F spawning male captured in January, both of which exhibited an ovotestis structure. sa, spermatozoa; sd, spermatid; po, primary growth oocyte.

had similar ages at maturity, with first maturity at 10·4 years for females and 9·0 years for males, and 100% maturity at 15·2 years for females and 10·9 years for males (Sedberry *et al.*, 1999; Peres & Klippel, 2003). The ages at maturity obtained for barrelfish (first maturity at 5 years for females and 7 years for males, and 100% maturity at 16 years for females and 13 years for males) fit within the ranges observed for the deepwater species above and indicate that care should be taken to develop a management plan that will allow these fish to spawn before being harvested. This will be a particularly difficult management goal because release mortality is probably 100% for deepwater fishes, due to embolisms when being brought up from the deep (Matheson & Huntsman, 1984), and minimum size regulations would afford no protection to juvenile fish. Additional research is needed to determine if there is differential habitat use by juveniles and adults, which could be used to enact area closures to protect juveniles. If pelagic juveniles are subject to by-catch in drift-net and other pelagic fisheries, as has been found for wreckfish (Sedberry *et al.*, 1999), restrictions on certain pelagic fisheries might be needed to protect barrelfish.

Female barrelfish mature later than males, but more samples are needed to verify this trend, due to the very small numbers of immature males collected ($n = 3$). Since only 0·86% of the males collected were immature, the argument that males mature earlier than females is strengthened, as it would be unlikely to collect such a small proportion of immature males if more were available to the fishery. Small immature males may not be vulnerable to the large hooks used in the wreckfish fishery (Sedberry *et al.*, 1994) or they may not be present in the areas fished.

As in many other marine fish species, such as scamp *Mycteroperca phenax* Jordan & Swain, 1884 (Harris *et al.*, 2002) and red snapper (White & Palmer, 2004), male barrelfish collected from the Charleston Bump were found in spawning condition for a more protracted time than were females. Their peak spawning time of September to April, however, coincided with the female spawning season.

Some unusual observations have arisen in the histological study of barrelfish gonads. For instance, in the females, the primary growth oocytes are often very small, which is generally an indicator of immaturity. These small oocytes, however, were frequently observed in mature females in the resting class. Because of this, it was concluded that the presence of small primary growth oocytes is not a reliable criterion for determining maturity of female barrelfish. Instead, more reliable criteria were used to determine maturity in resting female barrelfish, including the presence of muscle bundles throughout the lamellae, space between the lamellae, and a thick ovary wall, all results of previous spawning episodes. Also, it seems that male barrelfish often do not cease activity between spawning cycles. For example, only *c.* 12% of the males collected in this study were placed into the resting class, meaning that these males were mature, but not actively spawning or developing. The vast majority of the males collected were either developing spermatozoa for the next spawning cycle, actively spawning or spent after a recent spawning season. While it is not unusual for male marine teleosts in the region to be in spawning condition throughout the year (Harris *et al.*, 2002; White & Palmer, 2004), they typically do not go directly from the spent class to developing for another spawning season. This constant activity may also be a factor affecting the slow growth of adult barrelfish.

Another interesting feature observed in 9·8% of the males in the present study was the occurrence of intersex, which is the most common abnormality reported in marine fish gonadal development and is most often linked to exposure of fishes to endocrine disrupting substances like oestrogen (Matthiessen, 2003). Intersex has been described most often in freshwater fishes, but has recently been noted in many estuarine and a few continental shelf species. For example, studies in oestrogen-contaminated estuaries of the U.K. have documented that up to 15–20% of the males of the flounder *Platichthys flesus* (L., 1758) and the viviparous blenny *Zoarces viviparus* (L., 1758) exhibited intersex, with no occurrences noted in these same species from far less contaminated waters (Allen *et al.*, 1999*a*, *b*; Simpson *et al.*, 2000).

There have only been two documented cases of non-estuarine marine fishes in the intersex condition. One study showed the occurrence of intersex in the highly migratory Mediterranean swordfish *Xiphias gladius* L., 1758, with 25% of the males collected exhibiting primary growth oocytes in the testicular tissue, similar to those observed in male barrelfish (De Metrio *et al.*, 2003). Also, in the central North Sea, two of 14 males collected in a study of the continental shelf-dwelling dab *Limanda limanda* (L., 1758) exhibited intersex (Stentiford & Feist, 2005). In addition to these two open ocean species that have been documented in the intersex condition, juvenile male blueline tilefish have been documented with primary growth oocytes in the testicular tissue, although this phenomenon was attributed to protogynous sex reversal and not to intersex (Ross & Merriner, 1983).

As far as is known, this is the first documentation of a deepwater fish from continental slope waters with males in the intersex condition. The 9·8% of male barrelfish that did contain ovotestis were most likely mild cases, as the oocytes were spread throughout the testicular tissue, were often only a few in number (<50 per transverse section), and did not seem to disrupt the development of the testicular tissue. In laboratory studies on sheepshead minnow *Cyprinodon variegatus* Lacepède, 1803, researchers were able to induce intersex through the exposure of larvae to endocrine disrupting compounds but were unsuccessful in doing so in adult fish (Zillioux *et al.*, 2001). Barrelfish may therefore be exposed to endocrine disrupting compounds while in nearshore waters during their pelagic larval stage.

Other studies have noted the possibility of bioaccumulation of organochlorines by top predators in communities as a mechanism of causing intersex in a population (Matthiessen *et al.*, 2002). Some of this bioaccumulation in females may be offloaded to the oocytes, which would lead to the expression of intersex in males of the next generation. Closer monitoring of intersex in deepwater fishes may be needed, although the effects of endocrine disrupting compounds often vary greatly between species, and as such may be more or less pronounced in other fishes living in the deep waters of the North Atlantic (Matthiessen, 2003).

The youngest barrelfish obtained in this study was 5 years old, and the smallest specimen was 556 mm L_F, indicating that barrelfish do not recruit into the fishery around the Charleston Bump until about that age. No data suggest an age or size at which barrelfish transition from pelagic to benthic habitats, making it difficult to know where to find any younger specimens that may be living in the area. There are a few possibilities for why younger, smaller barrelfish were not observed in this study. These factors include habitat differences between juveniles and adults, either within the water column or throughout the ocean, sampling artefacts associated with fishery-dependent sampling, and differences in dietary preference that would preclude the smaller fish from taking the bait.

Barrelfish living around the Charleston Bump demonstrate the typical life-history characteristics of deepwater fishes that make them so vulnerable to overfishing, such as long life span, extremely slow growth rate and high age at maturity. Because of this, and because of the uncertainty about the size of the population, it is important to monitor barrelfish landings to determine the need for a management strategy for barrelfish. Fishermen have already moved into the deeper slope waters to target fishes such as wreckfish, deepwater groupers (Serranidae) and tilefishes (Malacanthidae) (Sedberry *et al.*, 1999), and barrelfish are already caught as by-catch of the wreckfish fishery around the Charleston Bump and as by-catch of other fisheries around the Miami Terrace and the Florida Keys (J. McGovern, pers. comm.).

Most of the management plans currently in place for demersal fisheries in the U.S.A. are modelled around the smaller, shallow water species of fishes and may not be appropriate for deepwater fishes. For example, size limits, an often-implemented management strategy, could not be utilized for most deepwater fishes, since they experience fatal embolisms when brought to the surface (Matheson & Huntsman, 1984). Some strategies, such as total allowable catch (TAC), individual transferable quotas (ITQ), gear restrictions and spawning season closures have proved beneficial to the population of one deepwater species, the wreckfish in the western North Atlantic (Sedberry *et al.*, 1999). As of yet, no management strategy has been put into place for barrelfish. Some of the management approaches used for the wreckfish fishery, however, may also prove beneficial for managing barrelfish.

The occurrence of different life stages of barrelfish in scattered parts of the North Atlantic seems to point to a circumnavigation of the basin during its life cycle, possibly following the subtropical anticyclonic gyre, a phenomenon proposed and genetically supported for wreckfish in the North Atlantic (Sedberry *et al.*, 1996; Ball *et al.*, 2000). If this truly occurs with barrelfish, then management strategies employed around the south-eastern U.S.A. would have to allow for fishing pressures exerted on this population in other parts of the world. The possibility of panmixia only enhances the need to know as much as possible about barrelfish, and indeed all deepwater fishes, before the fisheries for them expand.

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