Age, growth, and mortality of bonefish, *Albula vulpes*, from the waters of the Florida Keys

Roy E. Crabtree
Christopher W. Harnden
Derke Snodgrass
Connie Stevens
Florida Marine Research Institute, Department of Environmental Protection,
100 Eighth Avenue SE, St. Petersburg, Florida 33701-5095

Abstract.—We examined 528 bonefish ranging from 21 to 702 mm FL collected in South Florida waters from 1989 to 1995. Ages of 451 bonefish ranging from 228 to 702 mm FL were estimated from thin-sectioned otoliths (sagittae). Examination of OTC-marked otoliths from five fish held in a pond in the Florida Keys for periods ranging from 14 to 29 months suggested that a single annulus was formed each year. Marginal-increment analysis also showed that a single annulus was formed each year during March–June. Bonefish reach a maximum age of at least 19 years. Growth of the bonefish in our study was rapid until an age of about six years and then slowed considerably. The von Bertalanffy growth equation for females was FL=680.9(1–$e^{(-0.279(Age+0.934))}$) and for males was FL=670.7(1-$e^{(-0.242(Age+1.318))}$). The overall growth models for males and females were significantly different, but estimates of individual growth parameters L_∞, K, and t_0 were not. Predicted lengths of females were greater than those of males for all ages greater than 1 year. Catch-curve estimates of instantaneous rates of total mortality (Z) were 0.21 (95% confidence interval 0.167–0.303) for females and 0.25 (95% confidence interval 0.098–0.406) for males. Empirically derived estimates of natural mortality were similar to total mortality estimates, suggesting that fishing mortality is low.

Bonefish, *Albula vulpes*, are moderate-size elopomorph fish that frequent coastal and inshore waters of tropical seas worldwide. In the western Atlantic, bonefish regularly occur in the Florida Keys, the Bahama Islands, and throughout the Caribbean Sea (Hildebrand, 1963). In many areas of the species' range, including the waters off the Florida Keys, bonefish are the basis of economically important recreational fisheries. Bonefish are renowned by anglers for their wariness and fighting abilities and are often caught in water as shallow as 0.3 m. In the Florida Keys, fishing for bonefish is a year-round activity and provides an important source of income for professional fishing guides. The commercial sale of bonefish in Florida is prohibited; the limits placed upon the recreational fishery for bonefish are a bag limit of one fish per angler per day and a minimum fish size of 457 mm total length. Bonefish are not considered a food fish in Florida, and most bonefish caught are released.

Bonefish life history has not been adequately described. Bruger (1974) described the age and growth of bonefish from an examination of scales of 205 bonefish from South Florida waters. He estimated the age of the oldest bonefish in his study to be 12 years and suggested that greater ages may be attained. His attempt to validate annulus formation on scales using the marginal-increment technique was inconclusive, perhaps because annulus formation in scales often occurs over a prolonged period and because annuli are often closely spaced in older fish, making validation of scale-derived ages by the marginal-increment technique difficult (Lowerre-Barbieri et al., 1994). In addition, Bruger's sample sizes for many months were small.

Since Bruger's work, studies on a variety of species have shown that scales are not reliable for ageing long-lived fishes and that scale-derived age estimates are typically lower than validated estimates derived from sectioned otoliths (Beamish and McFarlane, 1983; Casselman, 1983; Lowerre-Barbieri et al., 1994). Ageing of bonefish with a validated method is needed to assess Bruger's estimates of longevity. In addition, sex-specific differences in growth rates have not been evaluated and growth-model parameters have not been estimated for Florida bonefish. The only published growth-model parameters for bonefish are those by Morales-Nin (1994), who used length-frequency analyses to estimate von Bertalanffy growth parameters for a small sample of bonefish from Mexico's Pacific coast. In this article, we describe the age and

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growth of bonefish from the waters off the Florida Keys and estimate mortality rates from a sample of fish whose ages were determined from an examination of sectioned otoliths.

Methods

We examined 528 bonefish collected from South Florida waters from February 1989 to April 1995. Most of these bonefish were caught with hook-and-line gear either by biologists or by a single professional bonefish guide and his anglers from waters off the Florida Keys and in Florida and Biscayne Bays. Five bonefish caught with hook-and-line gear were obtained from taxidermists in Fort Lauderdale and five others from tournaments in waters off the Keys. Supplemental collections of small bonefish (<425 mm) were made with various-size seines and gill nets in waters off the Keys. We collected young-of-the-year (YOY) bonefish using 21.4-m seines constructed with 6.35-mm mesh. These collections were made from shallow (<1 m) sand- and grass-bottom areas on the ocean (Florida Straits) side of Key West, Bahia Honda Key, and Lower Matecumbe Key and from the Indian River Lagoon on Florida's Atlantic coast.

Standard length (SL), fork length (FL), and total length (TL) were measured to the nearest millimeter (mm) and fish were weighed to the nearest gram. All lengths reported are fork lengths. Otoliths (sagittae) were removed, cleaned with bleach (5.25% sodium hypochlorite), and rinsed first in water and then in 95% ethanol. Otoliths were stored dry until sectioned. Sex of all fish, except that of YOY (age 0), was recorded and confirmed histologically.

The left sagitta was usually used for age estimation; however, in cases where the left otolith was broken, lost, or damaged during processing, the right otolith was substituted. We prepared most otoliths by cutting three or four thin sections approximately 0.5 mm thick, one of which was through the otolith core, using a Buehler Isomet low-speed saw with a diamond blade. Sections were then mounted on a microscope slide with Histomount. Initially, we prepared some otoliths for age estimation by embedding them in Spurr, a high-density plastic medium (Secor et al., 1992). A 1- to 2-mm thick transverse section containing the otolith core was cut. The section was mounted on a microscope slide with thermoplastic glue (CrystalBond 509 adhesive) and polished with wet/dry sandpaper (grit sizes ranging from 220 to 2,000 grits per sheet) until annuli were visible. Sections were then polished on a Buehler polishing cloth with 0.05-µ gamma alumina powder to remove scratches. There was no consistent difference in the quality of either preparation technique. Mounting the sections in Histomount took less time than embedding them in Spurr; therefore, this technique was adopted as our standard protocol.

Annuli were counted three times by each of two independent readers who used a dissection microscope equipped with reflected light at magnifications of 8–25×. After the readers completed counting annuli on all the otoliths, we re-examined the otoliths for which different counts had been given. Most disagreements in counts concerned the presence or absence of an annulus on the otolith's margin. We were usually able to reconcile these disagreements and to assign an age to the otolith. A few otoliths had irregular and poorly defined annuli (n=20, 4.2%); these were discarded from the analysis.

Measurements for marginal-increment analysis were made with a digital image-processing system along an axis extending from the otolith's core to the ventral proximal margin of the section (Fig. 1). We expressed the distance from the final annulus to the otolith's edge (marginal increment) as a percentage of the distance between the last two annuli formed on the otolith. For all bonefish, the distance between the otolith core and the first annulus (r_1) was typically much greater than the distance between the first and second annuli ($r_2 - r_1$). For this reason, we divided the distance between the first and second annuli by the distance between the otolith's core and the first annulus for each otolith measured and then calculated the mean of this number for the entire sample,

$$\frac{\sum_{i=1}^{n}\left((r_2 - r_1)/r_1\right)_i}{n} = 0.406 \qquad (\mathrm{SE} = 0.0081).$$

We then estimated the expected distance between the first and second annulus for each age-1 bonefish otolith as a function of the distance between the otolith's core and the first annulus. The percent marginal increment for age-1 fish was then calculated as $(MI/(0.406 \times r_1))\cdot 100$, where MI = the marginal increment. We then plotted the median percent marginal increment as a function of capture month for the 36-month period during which we made regular monthly bonefish collections. We also plotted marginal increments for individual age classes 4–9 for all study years pooled. Our monthly sample sizes for other individual age classes were insufficient for marginal-increment analysis.

Bonefish were captured with hook-and-line gear from the waters off the Florida Keys for age-valida-

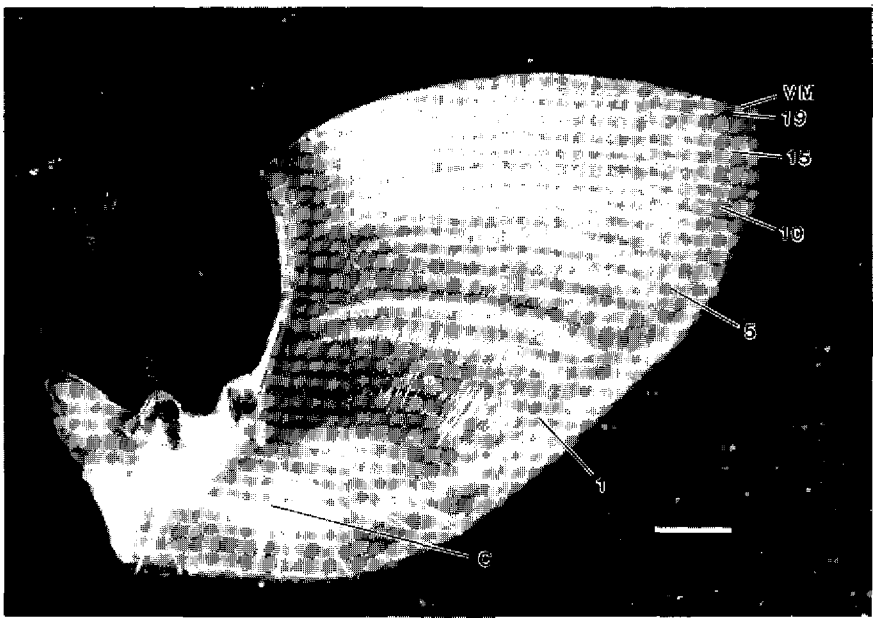

Figure 1

Transverse section from a 19-year-old (641-mm-FL) bonefish, *Albula vulpes*, otolith viewed with reflected light showing the annuli counted for age estimation. Measurements for marginal-increment analysis were made along an axis extending from the otolith core (c) to the ventral margin (vm) of the section. Scale bar = 1 mm.

tion experiments (Table 1). After capture, fish were measured for fork length and tagged with dart-type tags. Bonefish were then injected with Liquamycin LA-200 (200-mg oxytetracycline [OTC]/mL) in the dorsal musculature at a dosage of 100-mg OTC per kg fish weight. Fish weight was estimated with a length-weight regression. Bonefish were then transported to a 33.5-m by 5.5-m by 0.75-m deep pond at the Keys Marine Laboratory in Long Key, where they were held for 14 to 29 months. Water at ambient temperatures was pumped continuously from Florida Bay through the pond. Fish were fed at least three times a week with as much frozen fish or shrimp as they would consume. Sections from OTC-marked otoliths were examined with a compound microscope (40–100×) equipped with ultraviolet light so that the fluorescent OTC marks could be detected.

The von Bertalanffy (1957) growth equation $FL_t = L_\infty(1-e^{-K(t-t_0)})$ was fitted to observed age-length data with nonlinear regression procedures. Likelihood-

Table 1

Data for oxytetracycline (OTC)-injected bonefish, *Albula vulpes*. Otolith measurements were made along an axis extending from the otolith core to the OTC mark, annuli, and ventral margin of the section (Fig. 1). Measurements were made to the annulus at or just before the OTC mark and all subsequent annuli.

Injected		Sacrificed				Distance from core (mm)				
Date	Fork length (mm)	Date	Fork length (mm)	Months held	Age (years)	OTC mark	Annulus	Annulus	Annulus	Otolith edge
Nov 91	546	Oct 93	583	24	5	4.85	4.89	5.44		5.81
April 92	660	Nov 93	661	20	18	7.61	7.57	7.73		7.94
Oct 92	465	Nov 93	511	14	4	5.34	5.39			5.98
Oct 92	360	March 94	465	18	4	4.82	4.84	5.68		5.77
Dec 91	—	April 94	645	29	15	6.83	6.84	7.10	7.28	7.31

ratio tests were used to compare parameter estimates for males and females (Kimura, 1980; Cerrato, 1990). We used the outlier detection methods described by Sokal and Rohlf (1995) to test the significance of two perceived outliers from the age-length and otolith weight-age relations. Dixon's test statistic for outliers was used for sample sizes ≤ 25, and Grubb's test statistic for outliers was used for larger sample sizes. Outliers were considered significant at the $P<0.05$ significance level. Because we could not sex YOY bonefish, they were not included in growth models, but they were included in length-length regressions and pooled length-weight regressions. Sex-specific length-weight regressions were calculated by linear regression of $\log_{10}$-transformed data, and we compared the slopes and elevations using a *t*-test (Zar, 1984).

We used a catch curve to estimate the instantaneous total mortality rate (*Z*) from age-frequency data (Robson and Chapman, 1961). The age of full recruitment to the fishery for the catch-curve analysis was assumed to be 5 years, and year classes represented by fewer than five individuals were eliminated from the analysis. We estimated the instantaneous rate of natural mortality (*M*) using Pauly's (1980) formula $\ln M = -0.0152 - 0.0279 \ln L_\infty + 0.6543 \ln K + 0.463 \ln T$, where L_∞ and K are parameters from the von Bertalanffy growth equation, and T is the average annual surface temperature. An average annual temperature of 25.9°C (SD=0.13) was calculated from daily temperature measurements made from 1992 to 1994 at the Keys Marine Laboratory's water intake pump in Florida Bay. Pauly (1983) suggested that for schooling species, such as bonefish, the estimate of natural mortality derived from the above equation should be reduced by 20%. We used Pauly's formula and the 20% correction to suggest a possible range of values for natural mortality.

Undamaged otoliths were weighed to the nearest 0.01 mg in order to evaluate the use of otolith weight as a predictor of age. If both left and right otolith weights were available for an individual fish, the mean of the two weights was calculated. Sex-specific linear regressions were fitted to $\log_{10}$-transformed otolith weight and age data, and we compared the slopes and elevations of the regressions using a *t*-test (Zar, 1984).

Results

The 528 bonefish we examined ranged from 21 to 702 mm in length; 56 (10.6%) of these fish were YOY (21–116 mm). Fish caught on hook-and-line gear ranged in length from 228 to 702 mm (median=591 mm, interquartile range=111 mm, n=452) and most (80%) were from 500 to 700 mm (Fig. 2). Among all bonefish that we sexed, females ranged from 228 to 702 mm in length (median=601 mm, interquartile range=110 mm, n=274) and males ranged from 290 to 700 mm (median=566 mm, interquartile range= 146 mm, n=192). The size-frequency distributions of males and females were significantly different (Kolmogorov-Smirnov two-sample test, D=0.231, $P<0.001$); females were significantly larger than males (Mann-Whitney U-test, $P<0.001$). Females were also more abundant than males. In our sample there were 192 males and 274 females, and the sex ratio was significantly different from 1:1 (χ^2=14.43, df=1, $P<0.001$).

Neither slopes (*t*-test, df=453, t=0.474, P=0.318) nor elevations (*t*-test, df=454, t=0.084, P=0.467) of the length-weight regressions for male and female bonefish were significantly different. The pooled length-weight equation for sexed and unsexed fish and the relations between SL, FL, and TL are presented in Table 2.

Bonefish otoliths when viewed with reflected light have clear and easily counted narrow, opaque (bright) annuli that alternate with broad translucent (dark) zones (Fig. 1). Proceeding from the otolith's core towards the otolith's proximal margin, these translucent zones become increasingly opaque in appearance as the otolith grows. In the portion of the otolith

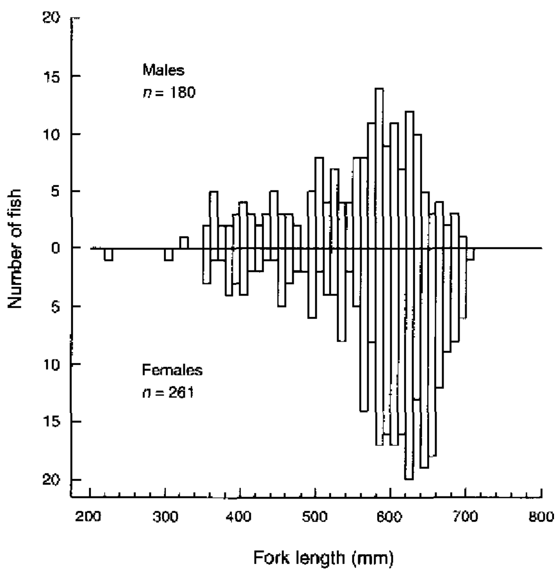

Figure 2

Length-frequency distributions for Florida Keys bonefish, *Albula vulpes*, caught with hook-and-line gear.

Table 2

Length-length, length-weight, and otolith weight-age regressions for bonefish, *Albula vulpes*, from the waters of the Florida Keys. TL = total length (mm), FL = fork length (mm), SL = standard length (mm), WT = weight (g), OWT = otolith weight (g), and AGE = age in years. Sample fork-length range for all length-length and length-weight regressions was 21–702 mm. Age range for the otolith weight-age regression was 1–19 years. Values in parentheses are standard errors.

			$Y = a+bX$		
Y	X	n	a (1 SE)	b (1SE)	r^2
FL	SL	521	4.5538 (1.0819)	1.0284 (0.0021)	0.998
FL	TL	516	–5.3384 (1.0297)	0.8652 (0.0017)	0.998
SL	FL	521	–3.3737 (1.0584)	0.9703 (0.0020)	0.998
SL	TL	516	–8.5152 (1.4894)	0.8394 (0.0024)	0.996
TL	FL	516	7.2580 (1.1770)	1.1537 (0.0022)	0.998
TL	SL	516	12.5401 (1.7404)	1.1864 (0.0034)	0.996
$\log_{10}$WT	$\log_{10}$FL	518	–5.3240 (0.0142)	3.1871 (0.0054)	0.999
$\log_{10}$OWT	$\log_{10}$AGE	427	–0.7161 (0.0107)	0.6489 (0.0133)	0.849

formed after about age 4, the dark translucent zones are narrow and only apparent in the region immediately adjacent to the annuli. The broad opaque zones in the outer portions of the otolith section are separate and distinct from the narrow opaque annuli, which are still visible at higher magnifications (30–50×) within the translucent zones in older fish, especially along the ventral ridge of the sulcus acusticus and the ventral margin of the otolith section.

We examined OTC-marked otoliths from five bonefish ranging from 465 to 661 mm in length and from 4 to 18 years in age (Table 1). All otoliths showed the expected pattern of otolith growth; one annulus had been formed per year. Marginal-increment analysis of otoliths also suggested that one annulus had been formed during March–June each year (Fig. 3). Median marginal increments had a consistent seasonal minimum during April–June and a maximum in October–February from 1992 to 1994. When median marginal increments were plotted for individual age classes 4–9, a similar pattern was seen (Fig. 4).

Of 471 otoliths processed for age estimation, only 20 (4.2%) were rejected because of disagreements among readings. The length-frequency distribution of fish whose otoliths were rejected because they were unsuitable for age estimation was not significantly different from that of all fish whose otoliths were examined (Kolmogorov-Smirnov two-sample test, D=0.234, P=0.22). The oldest bonefish examined were a 650-mm female estimated to be 19 years old and a 641-mm male also estimated to be 19 years old (Table 3). Bonefish growth was rapid until an age of about 6 years and then slowed considerably (Fig. 5). Results of likelihood-ratio tests showed a significant difference in the overall von Bertalanffy growth models for males and females (χ^2=26.15, df=3, P<0.001, Table 4). Estimates of L_∞(χ^2=0.406, df=1, P=0.52), K (χ^2=1.54, df=1, P=0.21), and t_0 (χ^2=1.28, df=1, P=0.26) were not significantly different between sexes. Lengths at age predicted by the von Bertalanffy equation agreed with the observed lengths of both female and male bonefish (Fig. 5). Predicted lengths at age of females were greater than those of males for all ages greater than 1 year, and observed lengths at age of females were greater than those of males for all ages except 1 and 18 (Table 3). The age-frequency distributions of males and females were significantly different (Kolmogorov-Smirnov two-sample test, D=0.265, P<0.001); females (median age=7 yr, interquartile range=4 yr, n=262) in our sample were significantly older than males (median age=6 yr, interquartile range=4 yr, n=181; Mann-Whitney U-test,

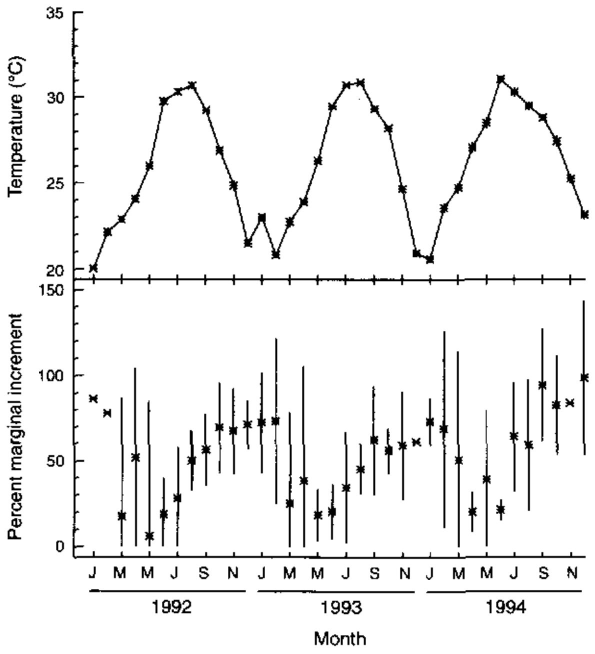

Figure 3

Mean monthly water temperatures (°C) calculated from daily temperature measurements at the water intake pump in Florida Bay adjacent to the Keys Marine Laboratory, and monthly median percent marginal increment and interquartile range for bonefish, *Albula vulpes*, otoliths.

P=0.012). Most bonefish (86%) in our sample that were caught with hook-and-line gear were from 3 to 10 years old (Fig. 6). On the basis of visual inspection of the age-frequency distributions, bonefish were not fully recruited to the fishery until an age of about 5 years.

The instantaneous rate of total mortality (Z) estimated by our catch-curve analysis was 0.25 (95% confidence interval 0.098–0.406, r^2=0.805, n=7, P<0.001) for males and 0.21 (95% confidence interval 0.167–0.303, r^2=0.922, n=9, P<0.001) for females. The instantaneous rate of natural mortality (M) estimated with Pauly's formula was 0.29 for males and 0.31 for females. The 20% reduction of this estimate recommended by Pauly (1983) for schooling species suggests a range of 0.2–0.3 for natural mortality.

Otolith weight was significantly related to age (Fig. 7). The slopes (t-test, df=417, t=1.34, P=0.09) and intercepts (t-test, df=418, t=0.49, P=0.31) of the otolith weight-age equations for males and females were not significantly different (Table 2).

Two of the bonefish that we aged were exceptionally small for their estimated ages and the weights of their otoliths were exceptionally light. One was a 351-mm female that was 7 years old and the other was a 458-mm female that was 18 years old. These two fish were statistically significant outliers, and we excluded them from growth models, age-frequency distributions, and otolith weight-age regressions. Both fish were caught with hook-and-line gear on the ocean (Florida Straits) side of North Key Largo, and they were the smallest females examined with active vitellogenic ovaries.

Discussion

We obtained bonefish from a variety of fishery-dependent and fishery-independent sources, but all fish larger than 405 mm that we examined were caught with hook-and-line gear. The size-frequency distribution of the hook-and-line-caught fish in our sample is probably similar to that of the fish caught in the fishery. Most of the hook-and-line-caught fish we examined were killed without regard to size, but a few fish included in our analysis were received from private anglers, tournaments, and taxidermists, sources that were presumably biased towards larger fish. Bonefish were not fully recruited to the hook-and-line gear until they reached a length of 550–600 mm and an age of about 5 years. We assume that our sample was representative of the Keys bonefish population beyond this size and age, but it is possible that hook-and-line gear introduced unknown biases that affected our mortality rates and growth-parameter estimates. We have no basis to evaluate the extent of these potential biases.

Age-validation experiments with OTC-marked otoliths supported our hypothesis that bonefish otoliths formed annual marks, and marginal-increment analysis suggested that annuli formed during March–June. Although sample sizes were insufficient to reveal trends for some individual age classes, age classes 4–9 showed marginal-increment patterns consistent with our hypothesis that annuli formed during March–June. Annulus formation appears to take place shortly after the season of minimal water temperatures in the Keys (Fig. 3). Monthly mean temperatures in Florida Bay at the Keys Marine Laboratory's water intake pump varied seasonally from a low of about 21°C during mid-December–February to a high of about 31°C during June–September (Fig. 3). These temperatures were probably similar to those of typical Keys bonefish habitat, and indeed on several occasions we collected bonefish on the flats adjacent to the pump. It is possible that holding fish under captive conditions and an artificial feeding regime affected the periodicity of annulus formation. However, we saw no change in the appearance or widths of the alternating translucent

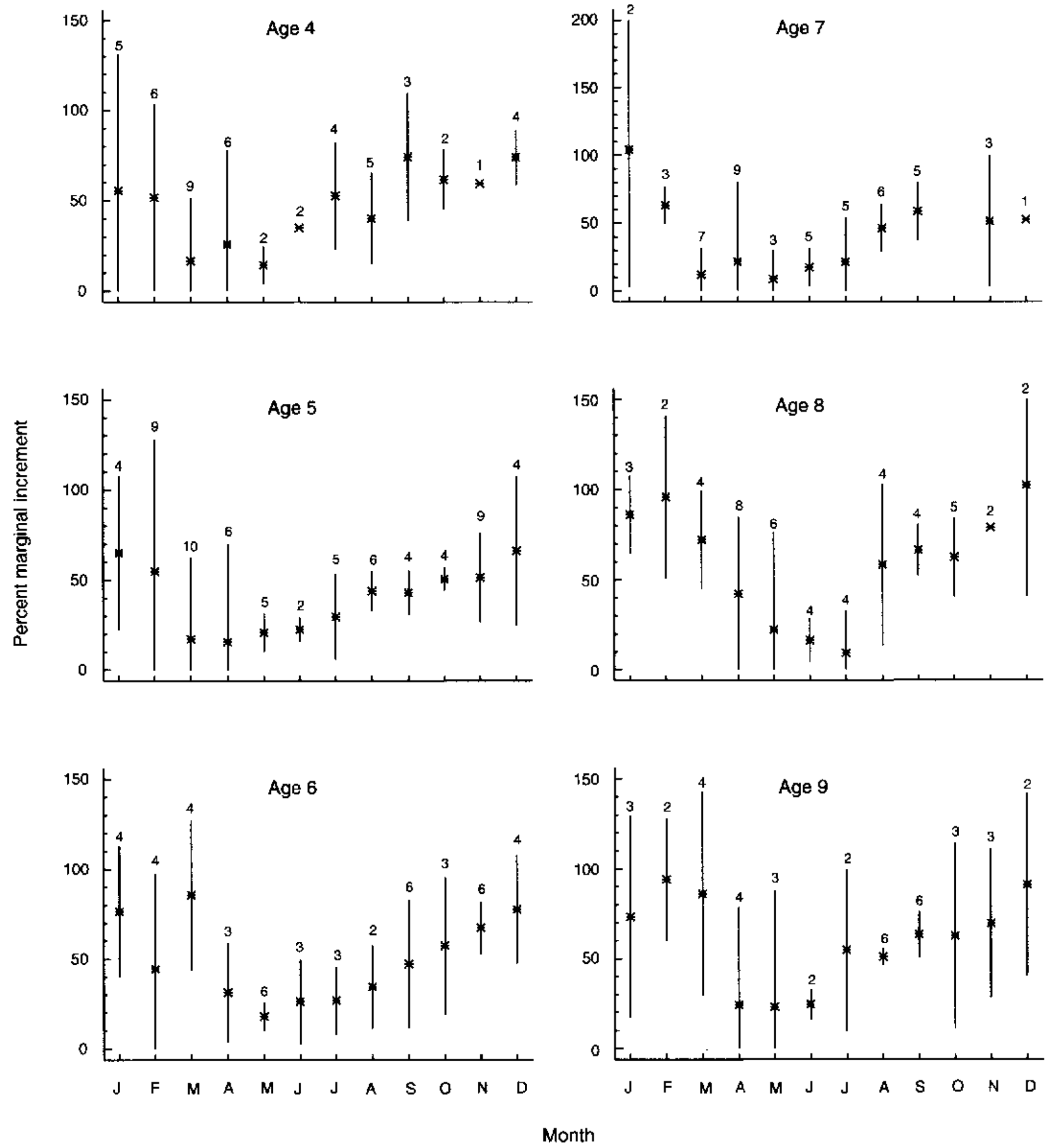

Figure 4

Monthly median percent marginal increment and interquartile range for bonefish otoliths for individual bonefish, *Albula vulpes*, age classes 4–9.

and opaque zones on otolith sections distal to the OTC mark to suggest that otolith growth had been fundamentally altered.

Our findings suggest that scales may not be suitable for ageing bonefish older than 6–9 years, the point at which our length-at-age data reached an asymptote. Scale-derived estimates of bonefish longevity by Bruger (1974) are lower than our otolith-derived estimate of 19 years. The oldest fish Bruger reported was estimated to be 12 years old, but he presented age-at-length data for only 140 bonefish ages 1–9. The number of fish in Bruger's sample declined quickly after age 6, and he apparently found only one fish older than age 9. In contrast, we found bonefish ages 3–9 to be abundant, and small numbers of fish were present in each age class from ages 10 to 19 yr (Fig. 6). The truncated age structure of Bruger's sample is probably an artifact of his ageing technique, but because we did not directly compare scale-derived and otolith-derived ages, we cannot rule out the possibility that Bruger's sample contained only one fish older than age 9.

Table 3

Average observed and predicted fork lengths (mm) for male and female bonefish, *Albula vulpes*, and average observed fork lengths for unsexed bonefish. Values in parentheses are standard error and sample size.

Age (yr)	Male		Female		Unsexed
	Average observed	Predicted	Average observed	Predicted	Average observed
1	320 (8.8; 7)	288	311 (13.4; 9)	284	
2	362 (4.7; 5)	370	374 (19.5; 8)	381	
3	401 (9.2; 19)	435	403 (10.9; 11)	454	399 (7.0; 2)
4	493 (11.6; 22)	486	499 (12.7; 27)	509	437 (37.0; 2)
5	531 (10.1; 33)	525	567 (8.1; 38)	551	538 (1)
6	559 (13.6; 20)	557	585 (7.2; 31)	583	608 (1)
7	588 (8.4; 17)	581	605 (6.3; 33)	606	597 (1)
8	619 (7.0; 19)	600	633 (4.2; 31)	625	635 (1)
9	608 (7.0; 17)	615	641 (7.4; 25)	638	
10	614 (7.6; 6)	627	651 (8.1; 16)	649	
11	618 (10.8; 7)	637	638 (25.0; 7)	657	
12	637 (17.0; 3)	644	672 (6.9; 5)	662	668 (1)
13	660 (1)	650	670 (29.0; 2)	667	
14		654	635 (18.0; 2)	670	
15	672 (1)	658	674 (13.6; 3)	673	
16		661	654 (3.0; 3)	675	
17	644 (1)	663	679 (5.7; 5)	676	
18	659 (22.0; 2)	664	642 (1.2; 3)	677	
19	641 (1)	666	650 (1)	678	

Table 4

Parameter estimates for the von Bertalanffy growth model for bonefish, *Albula vulpes*, collected from the waters of the Florida Keys. Values in parentheses are standard errors.

Sex	n	L_∞ (mm)	K	t_0	r^2
Males	181	670.7 (14.74)	0.242 (0.0256)	–1.318 (0.3205)	0.770
Females	260	680.9 (8.55)	0.279 (0.0195)	–0.934 (0.2031)	0.792

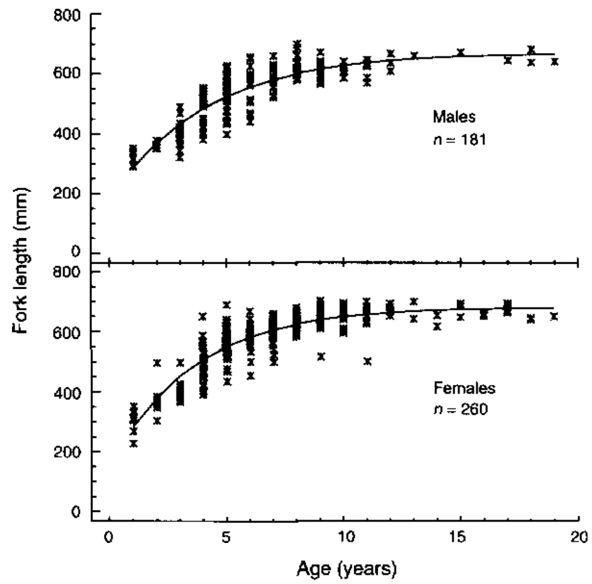

Figure 5

Observed and predicted lengths from the von Bertalanffy growth model for male and female bonefish, *Albula vulpes*.

Although our growth models for male and female bonefish were significantly different, the differences were small. This is reflected in our findings that individual growth parameters were not significantly different, that the two growth curves appeared similar (Fig. 5), and that the maximum sizes attained by both sexes were similar. Observed lengths at age for females were larger than those for males in all but two age classes, which is consistent with the higher growth rates for females. The median length of the

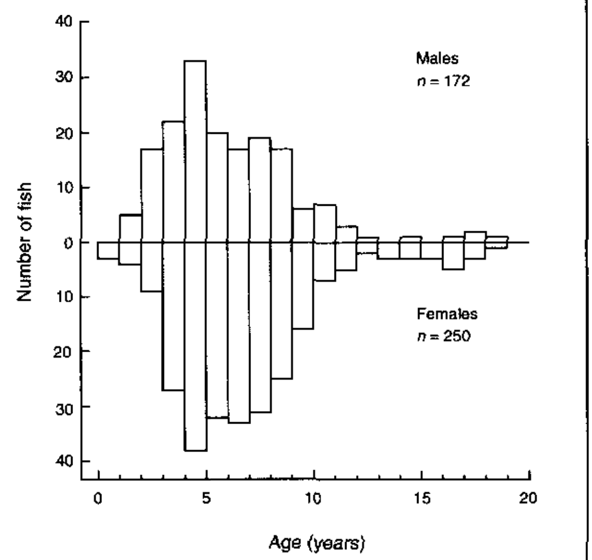

Figure 6

Age-frequency distributions for male and female Florida Keys bonefish, *Albula vulpes*, caught with hook-and-line gear.

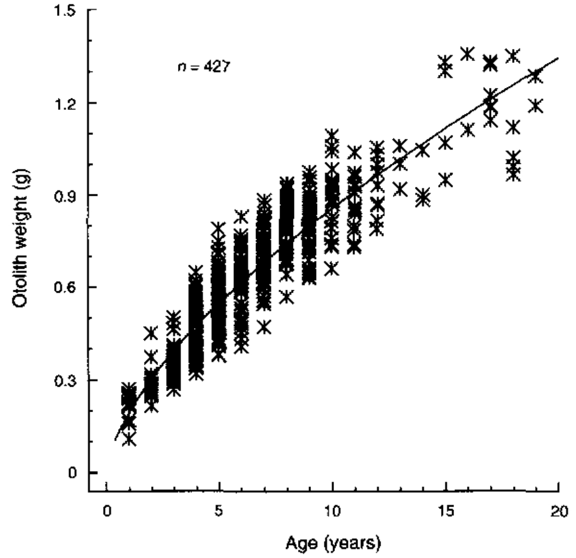

Figure 7

Growth of otoliths (g) of male and female bonefish, *Albula vulpes*. The equation for the regression of $\log_{10}$-transformed data is presented in Table 2.

females in our sample was slightly but significantly larger than that of males. This is also consistent with a small but significant difference in sex-specific growth rates; however, this finding is confounded by the significantly older median age of females, which would also contribute to the observed difference in the sex-specific size-frequency distributions. There is no readily apparent biological explanation for the slightly older age-frequency distribution of females in relation to males.

The only other estimates of von Bertalanffy growth parameters for bonefish are by Morales-Nin (1994) for 31 fish caught off Mexico's Pacific coast. She used a length-frequency analysis to estimate K=0.275 and L_∞ = 473 mm; her estimate of K is close to our Florida estimates, but her estimate of L_∞ is much less. Her small sample size could have seriously biased her parameter estimates. Furthermore, Pfeiler (1996) presented allozyme data that suggested that an undescribed species of *Albula* occurs off Mexico in the Gulf of California. It is unclear whether *A. vulpes* actually occurs off Mexico's Pacific coast or whether Morales-Nin's growth parameter estimates apply to *A. vulpes* or to Pfeiler's undescribed species.

The estimated instantaneous total mortality rate for bonefish was low. Our estimated range for natural mortality (0.2–0.3) included our total mortality estimates, suggesting that there is little fishing mortality. This was expected because the commercial harvest of bonefish from Florida waters is prohibited and most bonefish caught by recreational anglers are released. The low estimate for total mortality suggests that the mortality rate of bonefish caught with hook-and-line gear and then released was low, and that there was little mortality of bonefish as bycatch in commercial net fisheries operating in Florida Keys waters.

Otolith weight is not a precise estimator of bonefish age, but it could be used to approximate age distributions in situations where annulus counts are not available. Otolith weight accounted for more of the variability in age (84.9%) than fish length (77.0% for males and 79.2% for females). The Florida Keys are on the northern edge of the range of bonefish in the western North Atlantic. In specimens from the more tropical and less seasonal portions of the species' range, annuli may be more difficult to count and thus be less useful in age determination. This has been observed in other elopomorph species. Crabtree et al. (in press) reported that estimating age by sectioned otoliths was more difficult with tarpon from Costa Rican waters than it was with those from Florida waters; they rejected as unreadable more than twice as many otoliths from Costa Rican tarpon as those from Florida tarpon.

We cannot explain the presence of the two exceptionally small, old, and sexually mature female bonefish in our sample. Variable growth rates and stunting of some early maturing females is a possible explanation. We cannot eliminate the possible existence of a cryptic species in the Keys, but the one specimen retained in our collection has no obvious morphometric or meristic characters to support this idea. Bruger (1974) also reported the occurrence of small bonefish from 221 to 352 mm FL with mature ovaries in the Florida Keys, but he found no morphometric or meristic evidence to suggest the presence of a second species. Additional specimens are needed to resolve this issue.

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