# Maturation and reproductive seasonality in bonefish, *Albula vulpes*, from the waters of the Florida Keys

**Roy E. Crabtree***
**Derke Snodgrass**
**Christopher W. Harnden**

*Florida Marine Research Institute, Department of Environmental Protection*
*100 Eighth Avenue SE, St. Petersburg, Florida 33701-5095*
*E-mail address: crabtree_r@sellers.dep.state.fl.us

**Abstract.**—We examined 528 bonefish to estimate length and age at sexual maturity and to describe seasonal patterns in gonadal development. These fish ranged from 21 to 702 mm fork length (FL) and were collected in South Florida waters from 1989 to 1995. Gonads of 437 bonefish were examined histologically, and gonadosomatic indices (GSI) were calculated for 449 bonefish. Male bonefish reached 50% sexual maturity (the predicted size and age at which half the individuals are expected to be sexually mature) at 418 mm FL (95% confidence interval 393–443 mm) and an age of 3.6 years (95% confidence interval 3.3–3.9 years). Females reached 50% sexual maturity at 488 mm FL (95% confidence interval 472–504 mm) and 4.2 years (95% confidence interval 3.9–4.6 years). Lengths and ages at 50% maturity for males and females were significantly different. The smallest sexually mature male was 425 mm FL, and the smallest sexually mature female was 358 mm FL. The youngest sexually mature male was 3 years old, and the youngest sexually mature female was 2 years old. Gonadal activity was seasonal and peaked during November–May. Vitellogenic oocytes were present in ovaries in every month except August and September and were most abundant during November–May. Median GSI's were greatest during November–May and least during July–September for both males and females. No fully hydrated ovaries or postovulatory follicles were found, therefore we could not estimate spawning periodicity or batch fecundities. Total fecundity ranged from 0.4 to 1.7 million oocytes and had a significant positive relation to fish weight. The absence of fully hydrated ovaries and postovulatory follicles in the bonefish we sampled suggests that bonefish spawn outside the traditional shallow-water (<2 m) fishing grounds in the Florida Keys.

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Bonefish, *Albula* spp., frequent coastal and inshore waters of tropical seas worldwide and are the basis of economically important recreational fisheries in many areas of their range. Although 23 nominal *Albula* species have been described (Whitehead, 1986), only two Atlantic species, *A. vulpes* and *A. nemoptera*, are recognized (Rivas and Warlen, 1967). In the western Atlantic, *A. vulpes* is common in the Florida Keys, the Bahama Islands, and throughout the Caribbean Sea (Hildebrand, 1963). *Albula nemoptera* appears to have a more restricted distribution than *A. vulpes* and has been reported from the Guianas, Venezuela, Columbia, Panama, Jamaica, and Hispaniola (Rivas and Warlen, 1967; Uyeno et al., 1983). The single record of *A. nemoptera* from Florida waters is considered questionable (Robins and Ray, 1986), and the species has not been reported from the Bahama Islands (Böhlke and Chaplin, 1993).

Bonefish are esteemed for their wariness and fighting abilities, and fishing for them provides an important source of income to Florida Keys and Bahamian fishing guides. Commercial sale of bonefish in Florida is prohibited, and regulations on the recreational fishery restrict catches to one fish per angler per day and the length of captured fish to a minimum total length of 457 mm (390 mm fork length). Most bonefish caught in Florida waters are released.

The life history of bonefish has not been adequately described. Crabtree et al. (1996) described the age and growth of bonefish from South Florida and found that bonefish can attain ages of 19 years. Female and male growth models were significantly different; females were slightly longer than males of the same age. Although the age and growth of Florida Keys bonefish have been studied, important questions remain regarding bonefish reproduction. Bruger (1974) reported sexually mature females as small as 210 mm standard length (221 mm fork length) and as young as 1 year from waters off the Florida Keys, but his sample size was inadequate to determine the age or length at 50% maturity (the predicted size and age at which half the individuals are expected to be sexually mature). Bruger found ripe female bonefish throughout the year in waters off the Florida Keys and concluded that reproduction was not seasonal, but his sample size was small ($n$=148) and his conclusions equivocal. In other areas, bonefish reproduction appears to be seasonal according to patterns of larval and juvenile abundance (Alexander, 1961; Pfeiler, 1984; Pfeiler et al., 1988; Mojica et al., 1995). There

is also no published information on bonefish fecundity. In this article, we estimate the age and length at which sexual maturity is attained and describe the seasonal cycle of gonadal development in bonefish from waters off the Florida Keys. We also estimate the total fecundity of 33 bonefish collected from these waters.

## Methods

### Sampling

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 the Keys. Supplemental collections of small bonefish (<425 mm) were made with various-size seines and gill nets in waters off the Keys. Ages, based on validated sectioned otoliths and growth rates of these bonefish, were described by Crabtree et al. (1996).

Fork length (FL) was measured to the nearest millimeter (mm), and fish were weighed to the nearest gram. Sex, gonad condition, and gonad weight (g) were recorded. Gonad samples for histology and for estimation of fecundity were removed from the fish and preserved in 10% buffered formalin; they were later soaked in water for one hour and then stored in 70% ethanol. Histological sections of gonads from 437 bonefish ranging from 228 to 702 mm were prepared and assessed for reproductive state. Gonad samples were processed histologically with a modification of the periodic acid Schiff's (PAS) stain for glycol-methacrylate sections, with Weigert's iron-hematoxylin as a nuclear stain and metanil yellow as a counterstain (Quintero-Hunter et al., 1991).

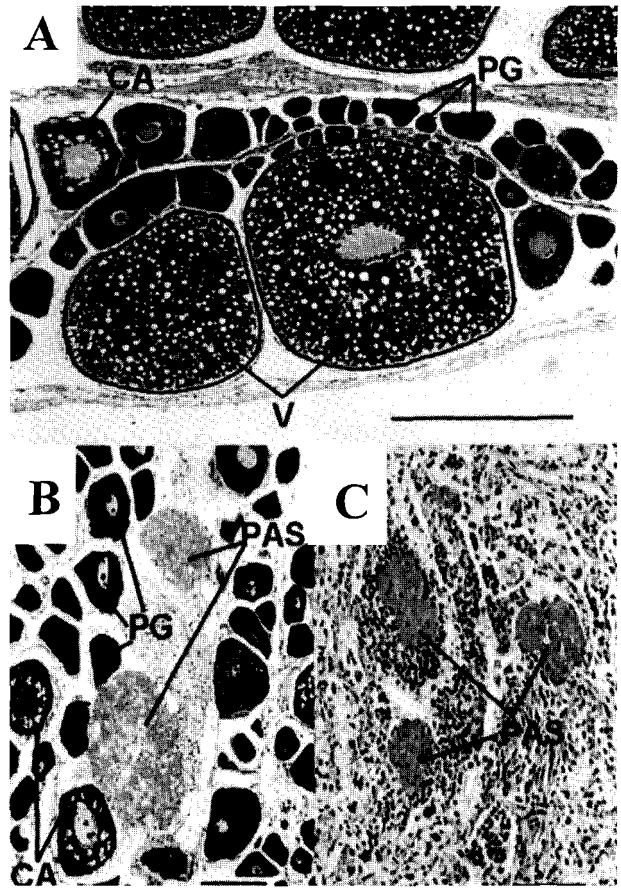


**Figure 1**

(**A**) A histological section from an ovary of a 677-mm-FL bonefish, *Albula vulpes*, showing oocyte stages. PG = primary growth oocytes, CA = cortical alveolar oocytes, and V = vitellogenic oocytes. Scale bar = 400 microns. (**B**) A histological section showing PAS-positive melanomacrophage centers (PAS), cortical alveolar oocytes, and primary growth stage oocytes in a regressed ovary from a 692-mm-FL bonefish. When stained with periodic acid Schiff's stain, melanomacrophage centers are brilliant purple. Scale bar = 100 microns. (**C**) A histological section showing PAS-positive melanomacrophage centers in a regressed testis from a 586-mm-FL bonefish. Scale bar = 50 microns.

### Oocyte staging

Oocytes were staged and counted from histological preparations at 100× with a compound microscope attached to a digital image-processing system. Three oocyte stages were recognized in bonefish ovaries: primary growth, cortical alveolar, and vitellogenic (Wallace and Selman, 1981; Fig. 1A). In addition, we counted PAS-positive melanomacrophage centers (Ravaglia and Maggese, 1995), which were present in many ovaries (Fig. 1B). When stained with the PAS stain, these structures are brilliant purple. Melanomacrophage centers are thought to be active in degrading atretic oocytes, postovulatory follicles, and residual cells of the spermatogenic cycle (Chan et al., 1967; Ravaglia and Maggese, 1995). At least 300 combined oocytes and melanomacrophage centers per slide were staged and counted in arbitrarily chosen fields, and frequencies were expressed as a percentage of the total count. We counted all structures that had at least 50% of their area visible in a field before moving to the next field. The presence of atretic hydrated oocytes was also noted.

## Length and age at sexual maturity

Females were considered sexually mature if vitellogenic oocytes were present or if the histological sections appeared disorganized, highly vascularized, and contained widespread evidence of atresia. Documentation of atresia followed the classification of Hunter and Macewicz (1985). Immature females had small (gonadosomatic index <0.35), well-organized gonads that contained little evidence of atresia. We interpreted the widespread occurrence of PAS-positive melanomacrophage centers in inactive ovaries as evidence of past gonadal development, and we considered bonefish that had regressed (no vitellogenic oocytes present) ovaries containing many of these structures to be sexually mature (Fig. 1B). Males were considered sexually mature if the testes contained evidence of ongoing spermatogenesis, residual sperm, or widespread PAS-positive melanomacrophage centers associated with gonadal recrudescence (Fig. 1C).

Sometimes distinguishing between the gonads of sexually immature bonefish and the regressed gonads of mature fish was difficult. We reduced the probability of misclassifying regressed and immature fish by eliminating all bonefish collected during June–October from our analyses of age and length at sexual maturity. June–October was the season of minimal gonad development in bonefish, and most of the regressed bonefish in our sample were captured during this period. By excluding the postreproductive months from our analysis, we eliminated 84% of the regressed females and 63% of the regressed males in our sample. Hunter et al. (1992) recommended that only fish collected early in the spawning season be used to estimate the length at 50% maturity, but our sample size was not large enough to allow us to restrict our analysis to this extent.

To describe age and length at sexual maturity, we used nonlinear regression procedures to determine the inflection point of a logistic function fitted to the percentage of males and females that were sexually mature and to their respective lengths and ages. Parameter $b$ in Table 1 is the inflection point and is the estimate of length or age at 50% maturity. Likelihood-ratio tests were used to compare the overall regression models and parameter estimates for males and females (Kimura, 1980).

## Seasonality of gonad development

Monthly median gonadosomatic indices (GSI) of sexually mature males and females were plotted to show seasonal reproductive patterns. GSI's were calculated for 449 bonefish ranging from 228 to 702 mm as

$$GSI = (GW/(TW - GW)) \times 100,$$

where $GW$ = total gonad weight (g); and
$TW$ = total fish weight (g).

We also plotted the monthly frequency of occurrence of the various oocytes stages that we counted for fish

**Table 1**

Percentage mature-age, percentage mature fork length, and weight-fecundity regressions for bonefish, *Albula vulpes*, from the waters of the Florida Keys. Wt = weight (g), FL = fork length (mm), AGE = age in years, FEC = fecundity. Values in parentheses are standard errors.

| $Y$ | $X$ | $n$ | $a$ (1 SE) | $b$ (1 SE) | $r^2$ | Range of $X$ for regressions |
|---|---|---|---|---|---|---|
| | | | $Y = \left(1/\left(1+e^{(-a(X-b))}\right)\right)\times 100$ | | | |
| % Mature (Females) | FL | 150 | 0.028 (0.0064) | 487.6 (8.14) | 0.632 | 228–702 |
| % Mature (Females) | AGE | 143 | 1.122 (0.2345) | 4.24 (0.192) | 0.445 | 1–19 |
| % Mature (Males) | FL | 116 | 0.545 (2.8227) | 417.5 (12.59) | 0.735 | 322–687 |
| % Mature (Males) | AGE | 109 | 1.618 (0.3674) | 3.60 (0.156) | 0.464 | 2–19 |
| | | | $Y = a + bX$ | | | |
| $\log_{10}$FEC | $\log_{10}$Wt | 33 | 1.936 (0.4708) | 1.131 (0.1312) | 0.706 | 1,790–5,790 |

collected in the years during which we had regular monthly collections.

### Fecundity

The total fecundity (the standing stock of advanced yolked oocytes) of 33 bonefish was estimated gravimetrically. Ovaries were subsampled from anterior, middle, and posterior portions of each ovary to evaluate spatial variations in oocyte size within the ovary and between ovaries. Subsamples of ovary containing 1,000–1,500 vitellogenic oocytes were weighed to the nearest 0.01 mg, and total fecundity was calculated on the basis of the mean number of oocytes per gram of ovary. Ovaries that contained widespread atresia, which suggested that partial spawning might have occurred, were not used for fecundity estimation.

## Results

Two of the bonefish that we examined were statistically significant outliers (Crabtree et al., 1996); both were exceptionally small for their estimated ages and the weights of their otoliths were exceptionally light. Crabtree et al. excluded both fish from growth models, age-frequency distributions, and otolith weight-age regressions, and we also excluded them from our analyses. One was a 351-mm female that was 7 years old and the other was a 458-mm female that was 18 years old. 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 whose ovaries contained vitellogenic oocytes. The 458-mm female had oocytes that were in the nuclear migratory stage, and these were the most advanced oocytes we found in any bonefish.

### Length and age at sexual maturity

Male bonefish reached 50% sexual maturity at a length of 418 mm (95% confidence interval 393–443 mm) and an age of 3.6 years (95% confidence interval 3.3–3.9 years); females reached 50% sexual maturity at a length of 488 mm (95% confidence interval 472–504 mm) and an age of 4.2 years (95% confidence interval 3.9–4.6 years; Fig. 2; Table 1). The lengths at 50% maturity ($\chi^2$=124.43, df=1, $P$<0.001) and the ages at 50% maturity ($\chi^2$=5.59, df=1, $P$=0.018) for males and females were significantly different. In addition, the overall logistic equations for length at 50% maturity ($\chi^2$=51.18, df=2, $P$<0.001) and for age at 50% maturity ($\chi^2$=11.55, df=2, $P$=0.003) for males and females were significantly different. The smallest sexually mature male was 425 mm long, and the smallest sexually mature female was 358 mm long. The youngest sexually mature male was 3 years old, and the youngest sexually mature female was 2 years old. All males longer than 477 mm and all females longer than 594 mm were sexually mature. All males older than 5 years and all females older than 7 years were sexually mature.

Primary growth stage oocytes were present in all ovaries in which we counted oocytes (Fig. 3A). Cortical alveolar oocytes were present only in ovaries from fish longer than about 400 mm and older than 2 years and were common only in fish longer than about 475 mm and older than 4 years (Fig. 3B). Vitellogenic oocytes were found only in fish longer than 450 mm and were common only in fish longer than 550 mm and older than 5 years (Fig. 3C). PAS-positive melanomacrophage centers were common only in females longer than about 550 mm and older than 5 years (Fig. 3D): the same length and age as those for females that contained vitellogenic oocytes.

### Seasonality of gonad development

Bonefish gonadal activity was seasonal. Vitellogenic oocytes were present in greatest numbers during November–May, and their numbers declined during May–June (Fig. 4). There were no vitellogenic oocytes in any ovaries from females collected during August–September of any of the three summers during which we sampled. Cortical alveolar oocytes were present during all months but were least abundant during July–October. Primary growth stage oocytes were present in all females examined and made up at least 20% of the total number of oocytes present. PAS-positive melanomacrophage centers were most abundant in the gonads of spent and regressed males and females and were most abundant in ovaries at the end of the spawning season in June–August (Fig. 5). They were least abundant in ovaries immediately before the initiation of spawning in November, when recrudescence was complete and most ovaries were ripening to spawn during winter–spring. We saw no evidence of recent or imminent spawning, such as postovulatory follicles or fully hydrated females. Only six ovaries contained atretic hydrated oocytes, and no single histological preparation contained more than a few hydrated oocytes.

Seasonal GSI patterns suggest that bonefish spawned during a prolonged period from November to June (Fig. 6). Median GSI's were greatest during November–May and were least during July–September. The decrease in female GSI's during July–September corresponded with the decrease in the number of vitellogenic oocytes present in ovaries and with the increased abundance of spent and regressed fish during late summer.

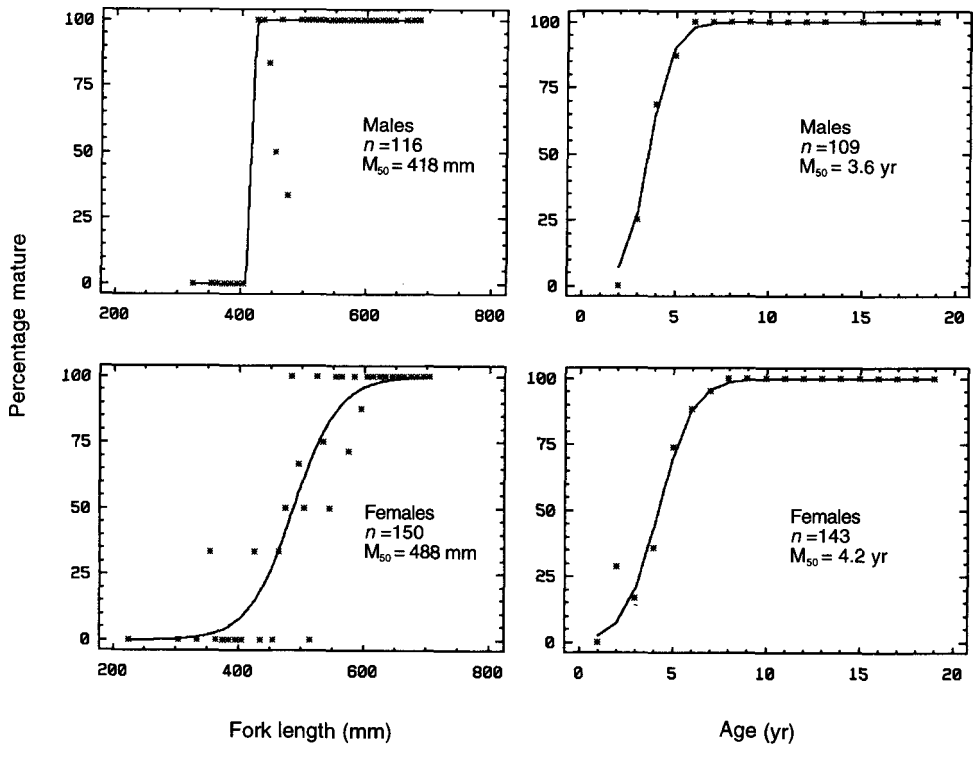


**Figure 2**

Length-maturity and age-maturity relations for male and female bonefish, *Albula vulpes*. Lengths plotted are the midpoints of 10-mm size classes. The solid line represents the predicted relation from the logistic regressions presented in Table 1. $M_{50}$ is the length or age predicted by the logistic regression at which 50% of the bonefish were sexually mature.

## Fecundity

Bonefish total fecundity estimates ranged from 0.4 to 1.7 million oocytes and had a significant positive relation to fish weight (Table 1; Fig. 7). Relative fecundity (the number of oocytes per gram fish weight) ranged from 159 to 385 oocytes/g (mean=259 oocytes/g, SD=47.1, $n$=33) for fish ranging in length from 485 to 702 mm. There was no significant relation between relative fecundity and fish length ($n$=33, $r^2$=0.014, $P$=0.514 ) or weight ($n$=33, $r^2$=0.043, $P$=0.247), but there was a significant positive relation between relative fecundity and age ($n$=32, $r^2$=0.248, $P$=0.003).

Oocyte development among areas within the ovary was homogeneous. We used a two-factor analysis of variance to compare oocyte densities with side (right or left) and position (anterior, middle, or posterior section of the ovary) as the effects. The number of late vitellogenic oocytes per gram of wet ovary weight was not significantly different between left and right ovaries (ANOVA, df=1, $P$=0.648) or among subsamples from anterior, middle, or posterior sections of the ovary (ANOVA, df=2, $P$=0.709). Furthermore, we found no significant interaction between side and position from which subsamples were taken (ANOVA, df=2, $P$=0.702). Weights of left and right ovaries from sexually mature females were not significantly different (paired $t$-test, $n$=112, $t$=0.480, $P$=0.632), but right testes from sexually mature males were significantly larger than left testes (mean difference=9.1 g, SD=18.62; paired $t$-test, $n$=98, $t$=4.826, $P$<0.001).

# Discussion

## Length and age at sexual maturity

The bonefish we examined reached sexual maturity at an older age and larger size than reported by Bruger (1974). He reported sexually mature females that were 1 year old and ranged from 221 to 352 mm FL (reported as 210 to 338 mm standard length). Bruger considered these small bonefish to be sexually mature on the basis of the presence of vitellogenic oocytes, one of the criteria that we used. He did not report how many of these small sexually mature fe-

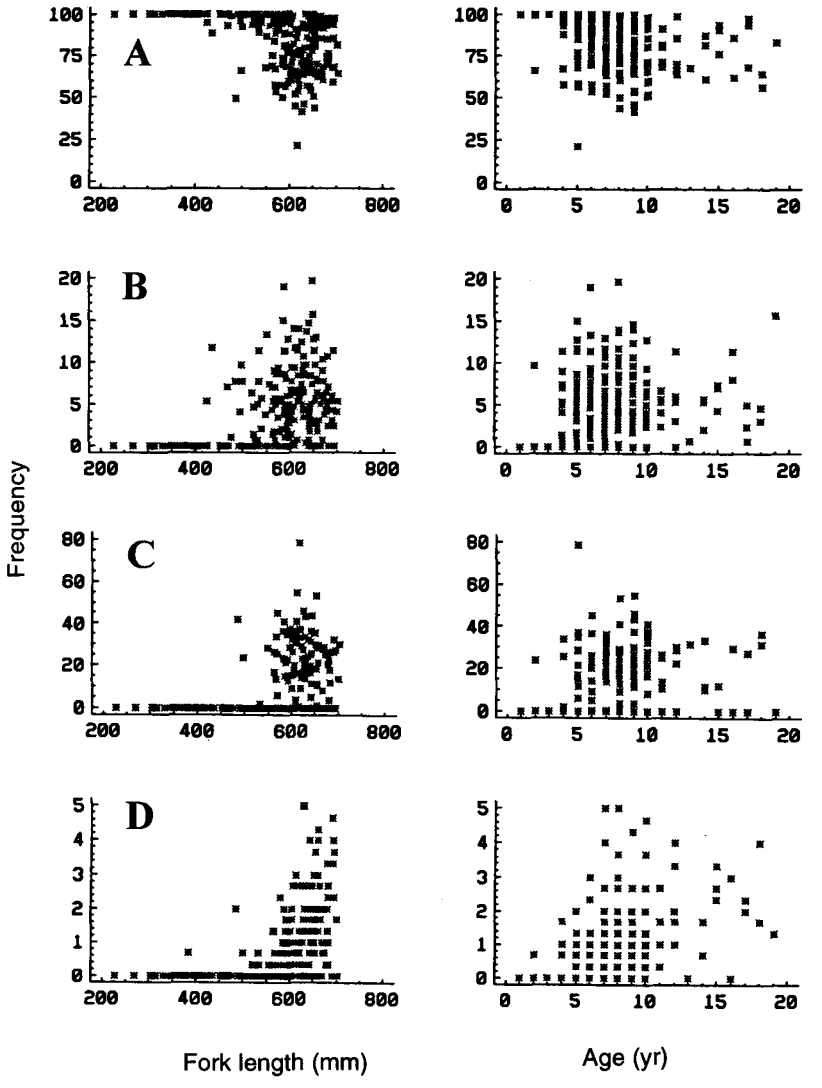


**Figure 3**

The percent frequency of occurrence of (**A**) primary growth oocytes, (**B**) cortical alveolar oocytes, (**C**) vitellogenic oocytes, and (**D**) PAS-positive melanomacrophage centers in bonefish, *Albula vulpes*, ovaries as a function of fork length (mm; $n$=248) and age (years; $n$=241).

males were captured or the typical length and age at sexual maturity. Some of the sexually mature females he collected were smaller than the 351-mm sexually mature female that we considered an outlier and excluded from our analysis. Furthermore, the lengths of Bruger's fish were substantially shorter than our estimated length at 50% maturity for females (488 mm). We also did not find any 1-year-old bonefish that were sexually mature; the youngest sexually mature fish we examined was 2 years old. All of the small mature females reported by Bruger were caught in deeper water (9.1–12.2 m) than that surveyed for bonefish in our sample; most of our fish were caught in water less than 2 m deep. Both Bruger (1974) and Crabtree et al. (1996) considered the possible existence of a cryptic bonefish species in waters off the Florida Keys as a potential explanation for the presence of exceptionally small and sexually mature bonefish, but additional study is needed to resolve this question.

Little is known regarding bonefish maturation in other areas. Pfeiler et al. (1988) reported 12 *Albula* sp., ranging in length from 205 to 264 mm (SL) from the Gulf of California, that had ripe or ripening gonads; this finding suggests a smaller length at sexual maturity there than we found in the Keys. The *Albula*

line gear until after they had completed the resorption of recognizable postovulatory follicles. This possibility seems unlikely because most collections of premetamorphic bonefish larvae are from offshore waters (Alexander, 1961); thus spawning bonefish probably move out of the shallow waters (<2 m) where fishing usually occurs. Alexander (1961) suggested that bonefish either spawn offshore or in areas where currents are likely to carry the eggs offshore.

### Fecundity

We did not examine any bonefish ovaries containing oocytes in the final stages of oocyte maturation or showing definitive evidence of recent spawning, such as postovulatory follicles. Consequently, we do not know if bonefish are isochronal or multiple-batch spawners, and we could not estimate batch fecundity. If annual fecundity in bonefish is indeterminate (Hunter et al., 1992), our estimate of total fecundity may not accurately represent total annual egg production. The bonefish spawning season is prolonged, and the potential exists for additional vitellogenic oocytes to mature from the standing stock of unyolked oocytes during the spawning season. Some ovaries contained vitellogenic oocytes, widespread atresia, and were loosely organized and highly vascularized. These females may have spawned earlier in the season and were developing an additional batch of oocytes that would have been spawned later in the season. It is unclear whether these oocytes were recruited from the standing stock of unyolked oocytes after previous spawning or if they were vitellogenic oocytes already present in the ovary that did not ovulate during previous spawning. Another bias of our fecundity estimates is that we could not correct them for atretic losses of vitellogenic oocytes during the spawning season; these losses could have caused us to overestimate egg production.

## Acknowledgments

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