Age and growth of the scaled herring, *Harengula jaguana*, from Florida waters, as indicated by microstructure of the sagittae

Daryl J. Pierce

Behzad Mahmoudi

Florida Fish and Wildlife Conservation Commission
Florida Marine Research Institute
100 Eighth Avenue S. E.
St. Petersburg, Florida 33701-5095
Present address (for D. J. Pierce): RR1 71 Hack Road
                                     Dalton, Pennsylvania 18414
E-mail address (for D. J. Pierce): daryljp@aol.com

Raymond R. Wilson Jr.

College of Marine Science
University of South Florida
140 7th Avenue South
St. Petersburg, Florida 33071-5095

Scaled herrings, *Harengula jaguana* (Clupeidae), inhabit nearshore (40-m isobath, rarely 500-m) warm temperate and tropical waters of the western Atlantic Ocean from coastal New Jersey to off southern Brazil, including the waters of Bermuda, the Gulf of Mexico, and the Caribbean Sea (Whitehead, 1985). They are an important link in the nearshore neritic food web as predators of zooplankton and as common prey for many species of piscivorous fishes, sea birds, and marine mammals (Odum and Heald, 1972; Carr and Adams, 1973; Reintjes[1]). Although *H. jaguana* is popular live bait for anglers throughout Florida, it has relatively minor commercial importance as bycatch in regional purse-seine fisheries. However, Houde (1977) estimated a potential yield of 41–92 million kg per year for this species from a survey of *H. jaguana* eggs and larvae in the eastern Gulf of Mexico.

Limited age and growth information exists for *H. jaguana*. Martinez and Houde (1975) reported ages of up to three years determined from scale circuli of fish collected from Biscayne Bay, Florida. Hubold and Mazzetti (1982) identified three age groups of *H. jaguana* from Guanabara Bay, Brazil, with length-frequency analysis. How-

ever, daily growth increments of otoliths provide a better means of aging short-lived species (Pannella, 1974; Brothers et al., 1976) and are typically better for age determination than are scales (Jones, 1992). The objective of our study was therefore to determine ages from validated periodicities of otolith (sagitta) daily rings and to use the ages and lengths to compare growth rates of *H. jaguana* from the Atlantic coast with those from the Gulf coast of Florida.

Materials and methods

Adult *H. jaguana* were sampled monthly from commercial purse-seine catches from nearshore waters adjacent to West Palm Beach and Tampa Bay, Florida, between February 1992 and December 1993. By using cast nets, juvenile and adult fish were collected monthly in Tampa Bay and in alternate months near West Palm Beach. From each sample (purse-seine and cast net) the sex of approximately 100 fish was determined, and these fish were measured to the nearest 1.0 mm (standard, fork, and total lengths) and weighed to 0.1 g. Length-length and sex-specific weight-length relation-

ships were computed for each coast. Weight-length regressions from $\log_{10}$-transformed data were described by least-squares linear regression and tested for differences between sexes within each coast and between coasts by analysis of covariance (ANCOVA). A total of 4210 (30 to 174 mm FL) *H. jaguana* were collected from off West Palm Beach and 29,994 (30 to 179 mm FL) fish were collected from Tampa Bay.

Each month, sagittae were removed from four fish randomly selected from within each 10-mm-FL (fork length) size class, sex, and coast. Otoliths were cleaned and stored dry in labeled containers. Sagittae were then processed, sectioned (transverse), and aged as in Secor et al. (1991) using an Olympus BH-2 compound microscope with transmitted light at 500×. Sagittae were read three separate times by the same reader in random sequence with a two-week interval between counts. Increment counting began at the first identifiable increment around the core (presumed to be day one) and continued along the medial plane of the sulcal ventral lip. Age was taken as the arithmetic mean of the three counts of the daily rings and accepted for analysis if the range of the three did not vary more than 10% from the mean. All rejected sagittae were counted a fourth time to replace the most extreme count, but were removed from further analysis if rejected a second time. The sex-specific relationship of otolith radius (core to medial edge of the sagitta) to fish length (FL) was linearly regressed for aged fish from each coast to examine the relationship between otolith growth and somatic fish growth.

During fall 1995, *H. jaguana* (50–80 mm FL) were marked with tetracycline and held in indoor tanks (568-L Nalgene tanks with a subgravel filtration system) to validate daily increment formation. Aquariums were kept at water

Table 1

Length-length, weight-length, and otolith radius-fish length least-squares linear regressions of *H. jaguana* from off West Palm Beach and Tampa Bay, Florida. Two standard errors of the parameters are in parentheses. The length-length and pooled weight-length data include immature-size fish. TL = total length (mm); FL = fork length (mm); SL = standard length (mm); $Log_{10}(WT)$ = transformed total fish weight (g); $Log_{10}(FL)$ = transformed fork length (mm); OR = median otolith radius (mm) from the core to the ventral edge of the sulcus; Range = range of fork lengths (TL was used for TL vs. SL) included in regression relationships.

Y	X	n	Range	$Y=a+bX$ a	b	r^2
West Palm Beach						
SL	FL	682	34–166	–1.412 (0.1294)	0.964 (0.0013)	0.9987
FL	SL	682	34–166	1.581 (0.1321)	1.035 (0.0014)	0.9987
TL	FL	822	34–172	–2.116 (0.2521)	1.191 (0.0024)	0.9964
FL	TL	822	34–172	2.108 (0.2073)	0.836 (0.0017)	0.9964
TL	SL	676	30–172	–0.002 (0.3288)	1.231 (0.0035)	0.9944
SL	TL	676	30–172	0.489 (0.2656)	0.807 (0.0023)	0.9944
$Log_{10}(WT)$ (females)	$Log_{10}(FL)$	195	91–166	–5.104 (0.202)	3.172 (0.095)	0.9578
$Log_{10}(WT)$ (males)	$Log_{10}(FL)$	169	84–161	–4.956 (0.194)	3.105 (0.091)	0.9647
$Log_{10}(WT)$ (pooled)	$Log_{10}(FL)$	987	45–166	–5.138 (0.024)	3.187 (0.012)	0.9961
OR (females)	FL	22	91–166	–0.116 (0.098)	0.004 (0.0007)	0.8666
OR (males)	FL	22	98–161	–0.218 (0.113)	0.005 (0.0008)	0.8792
Tampa Bay						
SL	FL	1482	30–151	–1.140 (0.1136)	0.960 (0.0011)	0.9979
FL	SL	1482	30–151	1.382 (0.1166)	1.038 (0.0012)	0.9979
TL	FL	1475	30–151	–2.357 (0.1399)	1.281 (0.0014)	0.9980
FL	TL	1475	30–151	2.152 (0.1141)	0.831 (0.0009)	0.9980
TL	SL	1473	34–178	0.881 (0.1382)	0.799 (0.0011)	0.9968
SL	TL	1473	34–178	–0.742 (0.1739)	1.247 (0.0018)	0.9968
$Log_{10}(WT)$ (females)	$Log_{10}(FL)$	1742	74–151	–5.048 (0.056)	3.144 (0.027)	0.9678
$Log_{10}(WT)$ (males)	$Log_{10}(FL)$	1300	77–145	–4.983 (0.062)	3.114 (0.015)	0.9693
$Log_{10}(WT)$ (pooled)	$Log_{10}(FL)$	10,219	28–151	–5.088 (0.011)	3.163 (0.006)	0.9905
OR (females)	FL	84	76–146	–0.106 (0.055)	0.004 (0.0005)	0.8418
OR (males)	FL	73	77–145	–0.101 (0.064)	0.004 (0.0005)	0.8133

temperatures of 26–28°C and a salinity of 30–31‰ with an average photoperiod of 10 h/day. Fish were fed twice daily a combination of Tetramin® flake food and frozen brine shrimp. Fish were injected in the dorsal musculature with 0.05 mL of 0.06-mg oxytetracycline (OTC) solution/g body weight on 30 October, 14 November, and 6 December. Fish were sacrificed 7 days following the second (*n*=50) and third (*n*=30) injections. Otoliths were prepared and polished as previously described, examined with a combination of transmitted and incident ultraviolet light to fluoresce the OTC marks, and number of increments between all OTC marks were counted.

Forty transverse sections aged with the light microscope were also examined with a scanning electron microscope (SEM). Sagittae of unknown ages were selected by fish-size category and the quality of the section (i.e. core was on the surface of the section and there were no apparent large cracks) from those prepared for age analysis. The sections were etched with 0.12 N HCl for 1–5 seconds. Micrographs were read by using the same procedures and ac-ceptance criteria described above. A paired sample *t*-test (Zar, 1996) was used to determine if the difference ($d_j = X_{1j} - X_{2j}$) between the light and SEM counts was significantly different from zero.

Harengula jaguana growth rates were estimated from the aged sagittae and compared with modal analysis of length frequencies. For each coast, sex-specific growth rates were estimated by using the least-squares linear regression of age on FL. Analysis of covariance was used to compare growth rates between sexes. The data were pooled if there were no significant differences, and pooled growth rates were compared for Florida's coasts by analysis of covariance. Cohort modal groups were assigned an approximate spawning month based upon estimated ages from the sagittae samples representative of the mode. The difference of the mean lengths between the largest and smallest modes from the same spawning month divided by the number of days between the two modes was defined as the modal growth. All statistical analyses were made with SAS software (SAS Institute Inc., 1989).
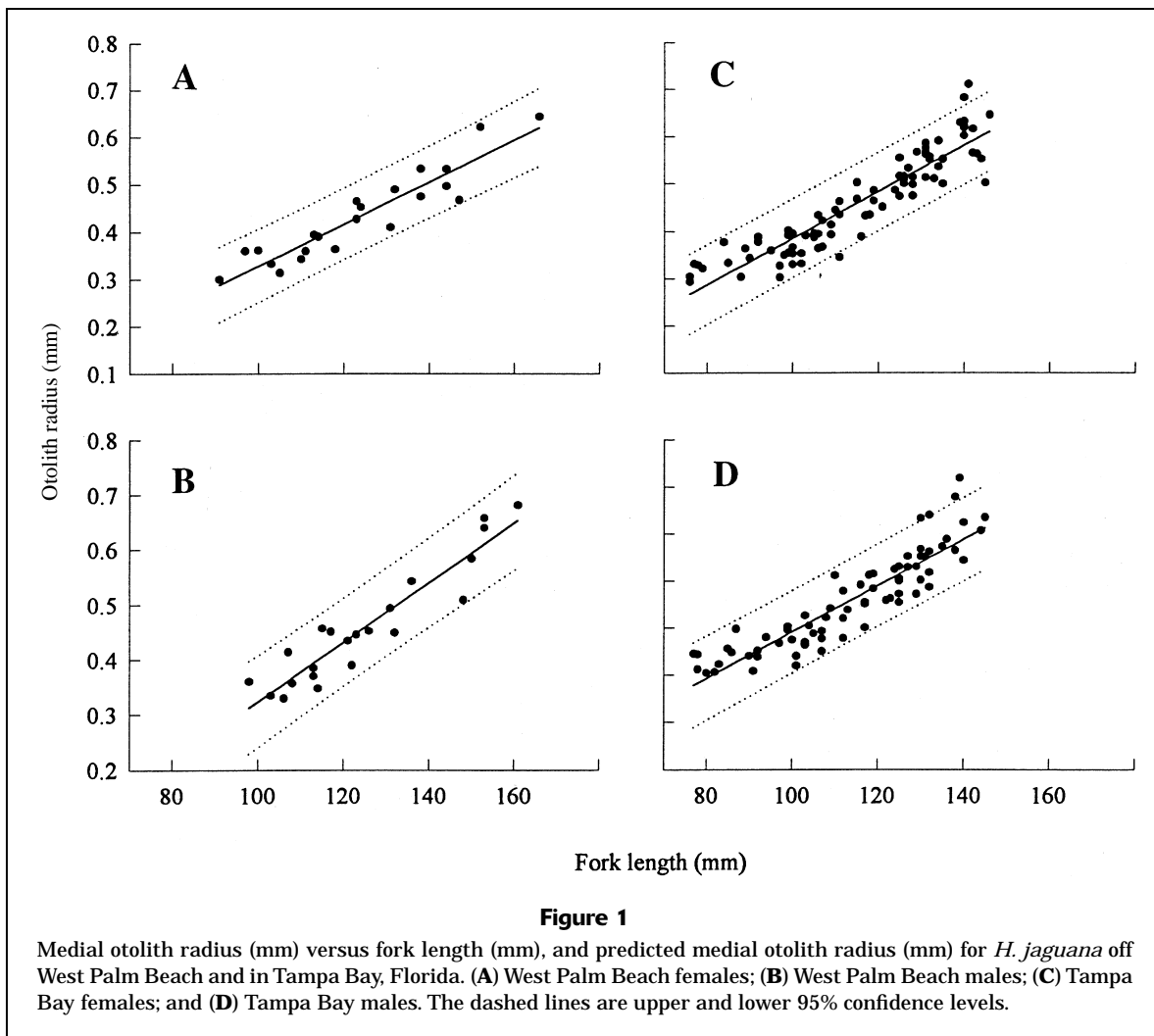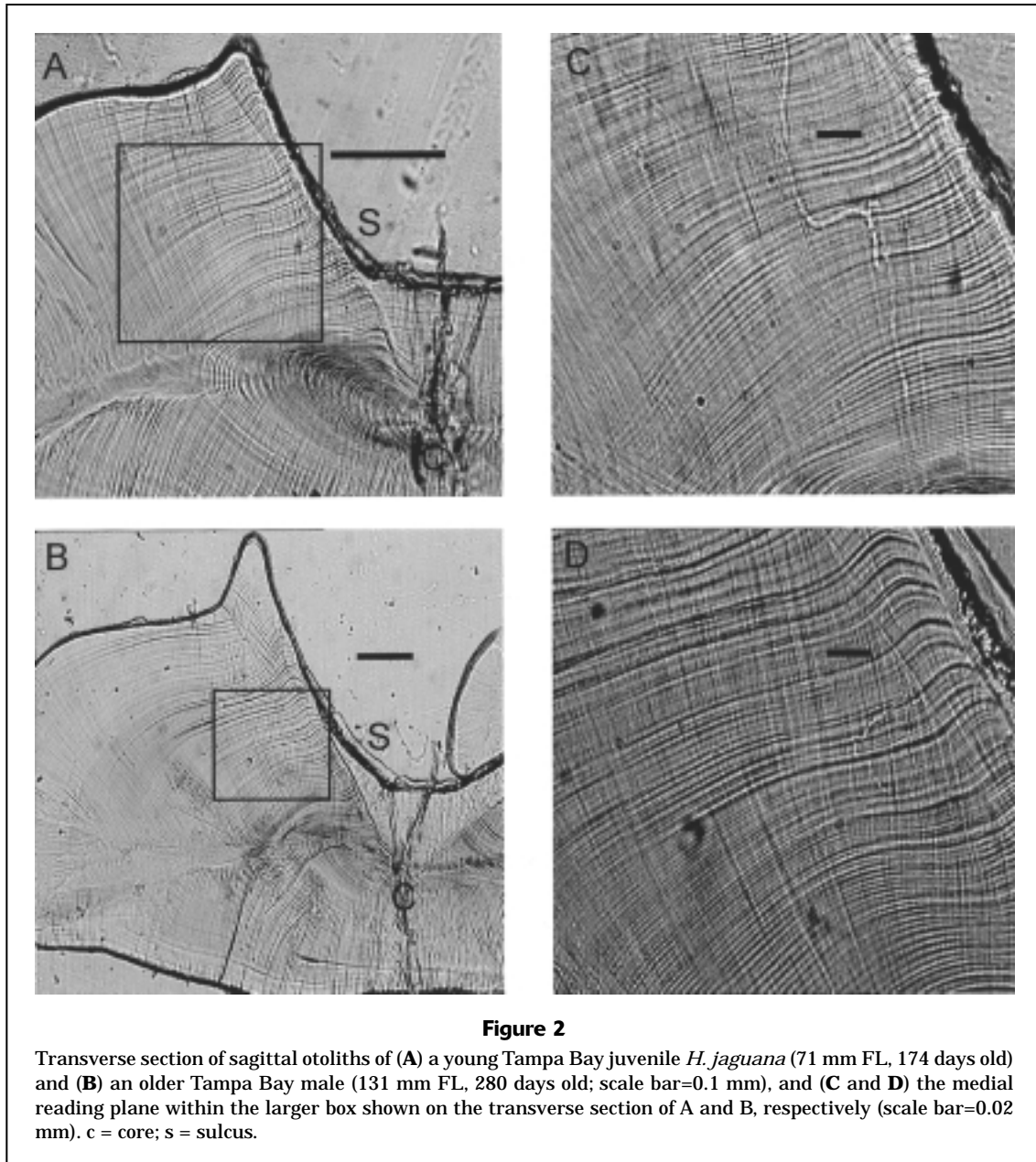
Figure 1

Medial otolith radius (mm) versus fork length (mm), and predicted medial otolith radius (mm) for *H. jaguana* off West Palm Beach and in Tampa Bay, Florida. (**A**) West Palm Beach females; (**B**) West Palm Beach males; (**C**) Tampa Bay females; and (**D**) Tampa Bay males. The dashed lines are upper and lower 95% confidence levels.

Table 2

Modeled least-squares regression growth rates of *H. jaguana* from off West Palm Beach and Tampa Bay, Florida. Numbers in parentheses are two standard errors of the estimated parameter. *AGE* = mean incremental counts (days); FL = fork length (mm); Range = range of age (days) included in the regression.

Capture site and sex of fish	n	Range	$FL = a + (b \times AGE)$		
			a	b	r^2
West Palm Beach					
females	18	175–269	32.337 (44.979)	0.4142 (0.2020)	0.5124
males	16	154–325	38.646 (24.444)	0.3569 (0.0963)	0.7968
pooled[1]	75	100–325	2.143 (10.263)	0.5050 (0.0519)	0.8381
Tampa Bay					
females	65	149–335	33.605 (13.642)	0.3542 (0.0592)	0.6944
males	57	141–370	50.034 (16.285)	0.2728 (0.0690)	0.5317
pooled[1]	178	78–370	13.902 (7.568)	0.4247 (0.0355)	0.7648

[1] Data include both immature and adult fishes.

Figure 2
Transverse section of sagittal otoliths of (**A**) a young Tampa Bay juvenile *H. jaguana* (71 mm FL, 174 days old) and (**B**) an older Tampa Bay male (131 mm FL, 280 days old; scale bar=0.1 mm), and (**C** and **D**) the medial reading plane within the larger box shown on the transverse section of A and B, respectively (scale bar=0.02 mm). c = core; s = sulcus.
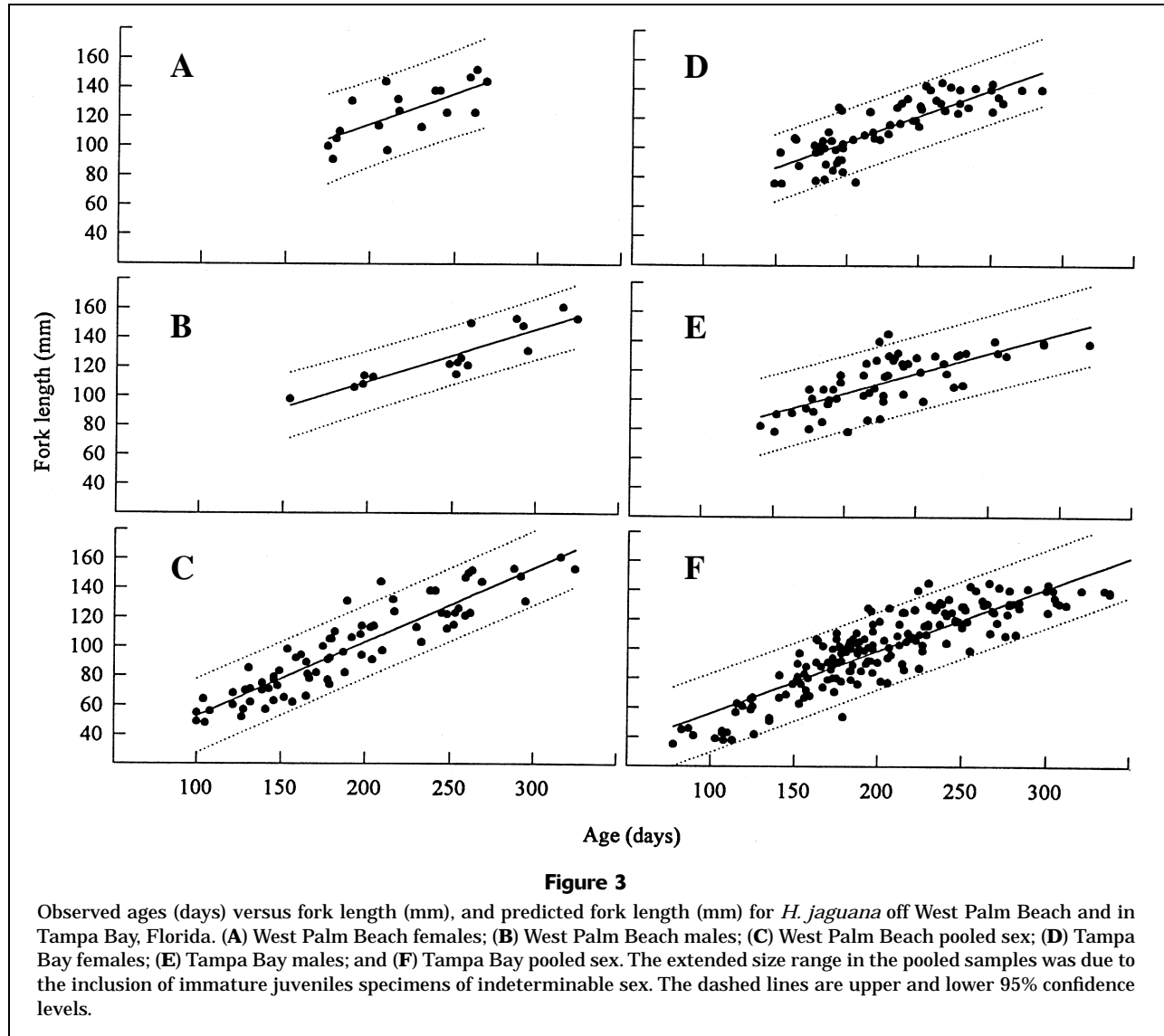
Results

Relationships between standard, fork, and total lengths, as well as weight-length regressions were calculated for fish off West Palm Beach and Tampa Bay (Table 1). The weight-length regressions between sexes for each coast showed no significant differences between slopes (ANCOVA, F=1.04, df=1, 360, P=0.309 for West Palm Beach; F=2.22, df=1, 3038, P=0.136 for Tampa Bay) or intercepts (ANCOVA, F=1.46, df=1, 361, P=0.227 for West Palm Beach; F=3.82, df=1, 3039, P=0.0508 for Tampa Bay). The pooled weight-length regressions for east and west coasts of Florida showed a significant difference between slopes (ANCOVA, F=5.50, df=1, 11,205, P=0.019) but not between intercepts

(ANCOVA, F=3.37, df=1, 11,205, P=0.066). Thus, fish from off West Palm Beach were heavier at length than fish from Tampa Bay. The relationship of sagittal medial axis (OR) to fish length (FL) was linear (Table 1; Fig. 1, A–D).

Harengula jaguana otoliths from field collections were difficult to interpret (Fig. 2, A–D). Fifty-five percent of the counted sagittae had to be examined a fourth time and overall 84 (25%) of the sagittae were rejected. Yet, increment formation appeared to be daily for the laboratory-reared fish. Forty-five otoliths produced an average of 14.5 increments (SE=0.20) between the first and second OTC marks in an elapsed time of 15 days. Eleven otoliths averaged 21.0 increments (SE=0.25) between the second and third OTC marks in 22 days. The mean age of the OTC-
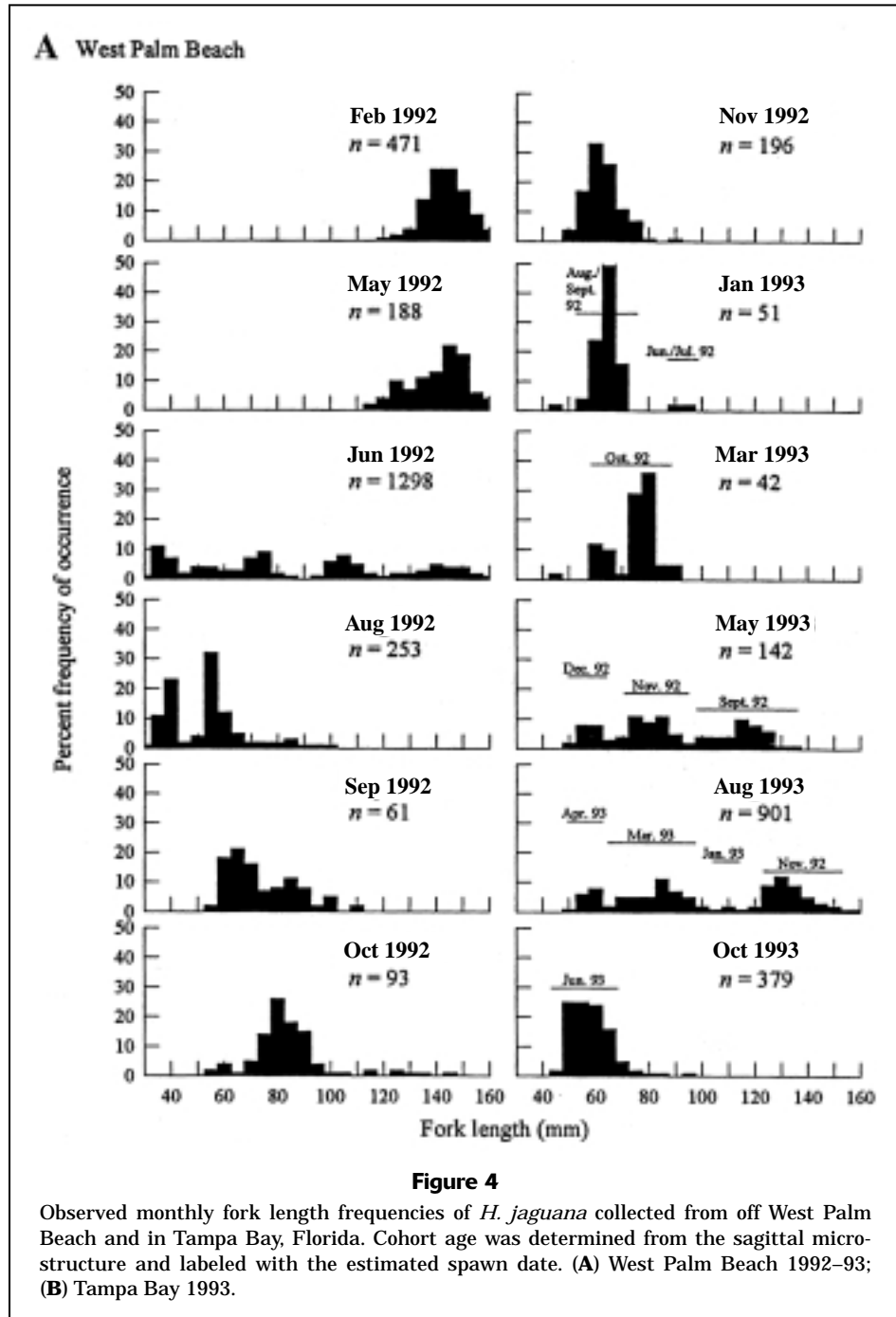
Figure 3

Observed ages (days) versus fork length (mm), and predicted fork length (mm) for *H. jaguana* off West Palm Beach and in Tampa Bay, Florida. (**A**) West Palm Beach females; (**B**) West Palm Beach males; (**C**) West Palm Beach pooled sex; (**D**) Tampa Bay females; (**E**) Tampa Bay males; and (**F**) Tampa Bay pooled sex. The extended size range in the pooled samples was due to the inclusion of immature juveniles specimens of indeterminable sex. The dashed lines are upper and lower 95% confidence levels.

injected fish was 141 days and ages varied from 125 to 165 days and lengths varied from 56 to 78 mm FL. Age estimated from 17 sagittae (41 to 131 mm FL) by using a SEM compared with transmitted light was not significantly different from zero (paired t=0.397, P>0.05).

Harengula jaguana grow rapidly and live little more than a year (Table 2; Fig. 3, A–F). Observed ages varied from 141 to 370 days for males and from 149 to 335 days for females. Growth rates (slope) were not significantly different for males and females in either West Palm Beach (ANCOVA, F=0.29, df=1, 30, P=0.595) or in Tampa Bay (ANCOVA, F=3.24, df=1, 118, P=0.074). Intercepts were also not significantly different in either West Palm Beach (ANCOVA, F=2.71, df=1, 31, P=0.109) or in Tampa Bay (ANCOVA, F=0.98, df=1, 119, P=0.325); therefore the data were pooled for each coast. Pooled growth rates (immature and adult) for Tampa Bay were significantly different from West Palm Beach (ANCOVA, F=6.09, df=1, 249, P=0.014).

Combined commercial purse-seine and cast-net length-frequency databases showed multiple juvenile recruitment peaks between June and November 1993 in Tampa Bay and between June and August 1992 from West Palm Beach (Fig. 4, A–B). Growth rates estimated from cohort length frequencies in Tampa Bay from February 1993 to May 1993 (spawned in September 1992) showed growth from 85 mm to 135 mm FL over 90 days, an average growth rate of 0.55 mm/day. A similar rate was obtained for fish at 45-mm mode in July 1993 (spawned in April 1993) that grew 125 mm FL by December 1993, a period of 150 days producing an average growth rate of 0.53 mm/day.

Discussion

Polished transverse sections of *H. jaguana* otoliths allowed enumeration of age in days. Houde et al. (1974) reported

Figure 4

Observed monthly fork length frequencies of *H. jaguana* collected from off West Palm Beach and in Tampa Bay, Florida. Cohort age was determined from the sagittal microstructure and labeled with the estimated spawn date. (**A**) West Palm Beach 1992–93; (**B**) Tampa Bay 1993.

that *H. jaguana* larvae <8.9-mm TL did not show any ossification and that maxillaries and dentaries in the head region were first to ossify at 14.0 mm TL; but these authors did not describe the formation of the otoliths (sagittae, lapilli, or asterisci) for laboratory hatched and reared larvae collected from south Florida. Therefore, the first identifiable increment about the core could form as early as 4–5 days (yolksac absorption) to 14 days (first ossification in the head region) after hatching but no later than transformation into juvenile (25 days after hatch-

ing). Thus, growth from the daily counts could be underestimated by 4–25 days.

Hubold and Mazzetti (1982) calculated a von Bertalanffy growth curve for *H. jaguana* in Guanabara Bay, Brazil, based upon three values of length-at-age assigned from length-frequency analyses of fish caught in July 1979. They identified only two modal length-at-age groups—105 mm (age 2) and 140 mm FL (age 3)—estimating the mean length at age 1 to be 40 mm FL. Applying either Houde and Palko's (1970) (0.7 mm TL/day growth rate for labora-

B Tampa Bay

Figure 4 (continued)
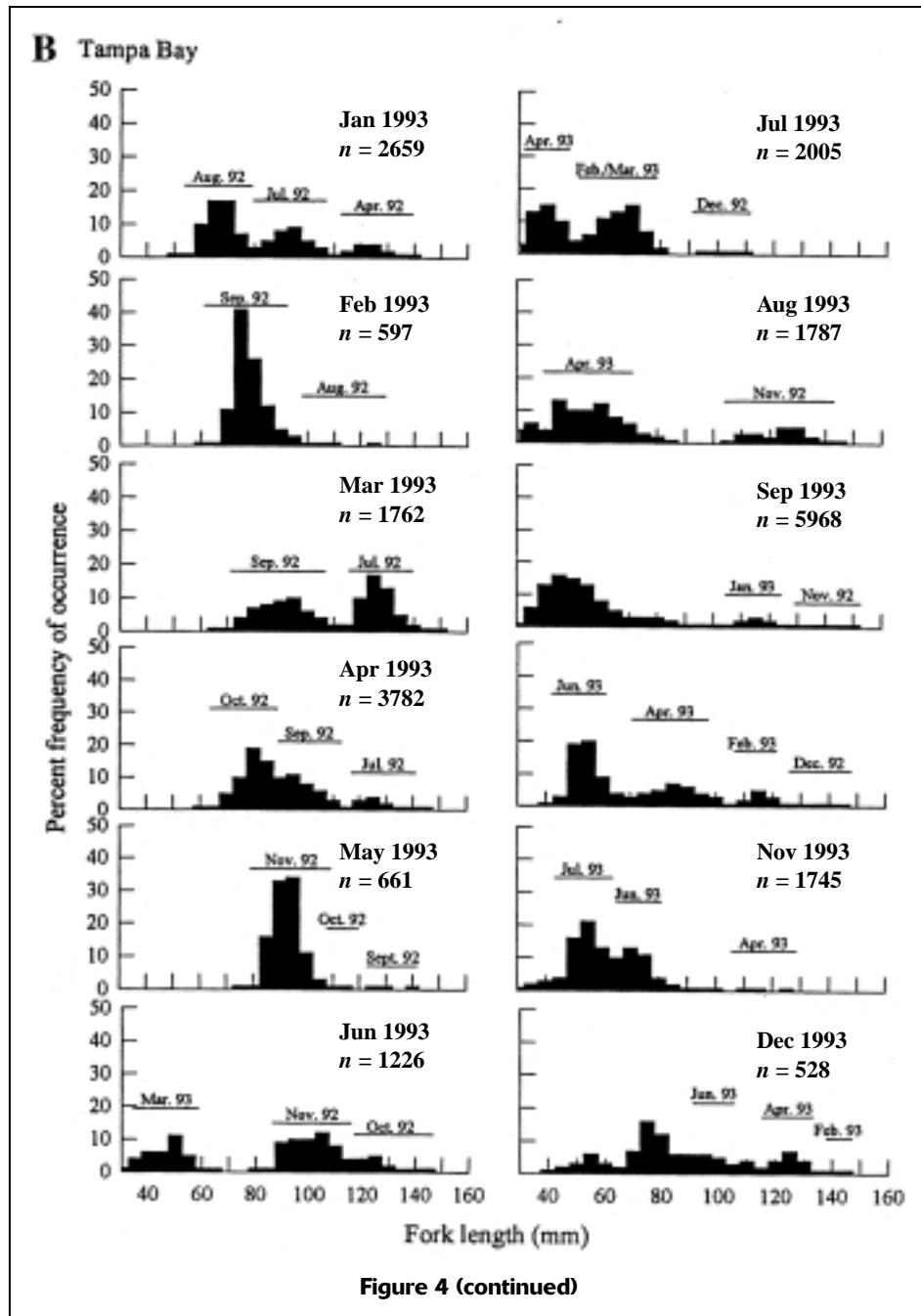
tory-reared juveniles) or our measured growth rates (0.5 mm FL/day) to Hubold and Mazzetti's (1982) length for age-1 fish (40 mm) suggests that the fish were not one year old, but probably only 30 to 40 days old. Using scales from *H. jaguana* collected in Biscayne Bay, Florida, Martinez and Houde (1975) cited fish lengths of age class one (106 mm SL), age class two (136.6 mm SL), and age class three (142 mm SL). The majority of the fish growth occurred in the first year; there was little increase in size between the second and third years.

Length-frequency modes (Fig. 4) corroborate the growth rates for *H. jaguana* derived from sagittal microstructure

and are consistent with estimates of 11–13 mm TL per month reported by Christmas and Waller (1973) for Mississippi waters, and 12.5 mm TL per month by Gunter (1945) for Texas. Low (1973) reported growth rates from 9 to10 mm TL per month for young-of-the-year fish in Biscayne Bay, Florida, which are close to those reported in our study. Identifying individual age cohorts is subjective, especially for older fish where modal groups tend to overlap.

Multiple recruitment periods are consistent with the serial spawning behavior of *H. jaguana* reported by Martinez and Houde (1975), who found fish maturing at 78–85 mm SL and continuous ripening of oocytes during a protracted

spawning season from February to August. Other authors (Gunter, 1945; Springer and Woodburn, 1960; Low, 1973; Modde and Ross, 1981) have noted one to two peak spawning events in April or September, or in both months. Observed length frequencies from our collections, specifically in Tampa Bay, suggest nearly continuous spawning year round. Fish spawned early could conceivably reach maturity and become a spawner in the fall of the same year.

In summary, *H. jaguana* are evidently fast-growing, short-lived fish. In coastal waters off West Palm Beach they appear to attain heavier weights and larger sizes at age than do fish inhabiting Tampa Bay. Although these differences might be genetically influenced, local environmental conditions seem the more likely cause of the observed significant variation in *H. jaguana* growth rates between coasts of Florida.

Acknowledgments

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