Vertebrate Ecology and Systematics—A Tribute to Henry S. Fitch
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Parameters of Two Populations of Diamondback Terrapins (*Malaclemys terrapin*) on the Atlantic Coast of Florida

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INTRODUCTION

The diamondback terrapin, *Malaclemys terrapin* has several attributes which would seem to make it an interesting subject for ecological study. These include a unique habitat for chelonians (brackish water), an extremely wide linear range (Massachusetts–Texas), and the distinction of being the "most celebrated of American turtles," a reflection of the popularity of this turtle as a gourmet food item in the early 20th century (Conant 1975). Despite these features, our knowledge of the life history of this species remains surprisingly limited. Studies of terrapins in the wild have dealt mainly with reproduction (Finneran 1948; Reid 1955; Burger and Montevecchi 1975; Montevecchi and Burger 1975; Burger 1976a, 1976b, 1977; Auger and Giovannone 1979; Seigel 1980b, 1980c), epizoic fouling (Jackson and Ross 1971; Ross and Jackson 1972; Jackson *et al.* 1973), mortality (Seigel 1978, 1980a) and hibernation (Lawler and Musick 1972; Yearicks *et al.* 1981). Data on the population biology of *Malaclemys* are few, especially under natural conditions. Cagle (1952) reported growth rates and age at maturity for Louisiana intergrades (*M. t. pileata* × *littoralis*), and Hurd *et al.* (1979) described the size structure and population size of *M. t. terrapin* from Delaware. Most data on population biology are based on captives (Hildebrand 1929, 1932; Allen and Littleford 1955), and must be viewed with caution due to the unnatural conditions under which the turtles were maintained (Carr 1952; Burnley 1969).

From 1977 to 1979 I studied the life history and ecology of the Florida east coast terrapin, *M. t. tequesta,* at the Merritt Island National Wildlife Refuge, Brevard County, Florida. This paper presents data on the growth rates, population structure, and age at maturity for two populations of *Malaclemys* under natural conditions.

MATERIALS AND METHODS

The Merritt Island refuge consists of three large, brackish water lagoons, each surrounded by a series of canals and ditches which are permanently filled with water. A more detailed description of the area is presented elsewhere (Seigel 1979). For the purposes of this study, terrapins were collected primarily from the northern ends of two lagoons, known locally as the Indian and Banana rivers (Fig. 1). Indian River turtles were collected by deploying small mesh (maximum diameter = 6 cm) gill nets along a narrow canal bordering a dike road. Two nets were set perpendicular to the shoreline to block off a 100 m section of the canal. Turtles moving up and down the canal became entangled in the nets and were removed within two hours of capture. Turtles from the Banana River were collected by walking surveys around a small man-made spoil island. Turtles were captured by hand while they basked along the shoreline, or while they swam and fed in the clear waters surrounding the island.

The following straight-line measurements were recorded to the nearest 0.1 cm using vernier calipers; carapace (CL) and plastron (PL) length, length of the right abdominal scute, and medial length of visible abdominal annuli. Wet body weight was recorded to the nearest 10 g with a spring balance. All turtles were given an individual mark (Ernst *et al.* 1974) and released at point of capture.

Plastral annuli have been used to estimate the growth rate and age of several species of turtles, using a variety of techniques (see Graham 1979 for review). In my study, age was estimated using the method of Sexton (1959). Growth was estimated using Sergeev's (1937) formula of $L_1/L_2 = C_1/C_2$, where C_1 represents the annuli length, C_2 the abdominal scute length, L_1 the plastron length when the annuli was formed, and L_2 the current plastron length. Since large, female *Malaclemys* >16 cm PL often lacked one or more annuli, they were excluded from this analysis.

Statistical tests follow Ott (1977). Means are followed by ± one standard deviation.

RESULTS AND DISCUSSION

Growth and Sexual Maturity.—One hundred thirteen *Malaclemys* were examined from the

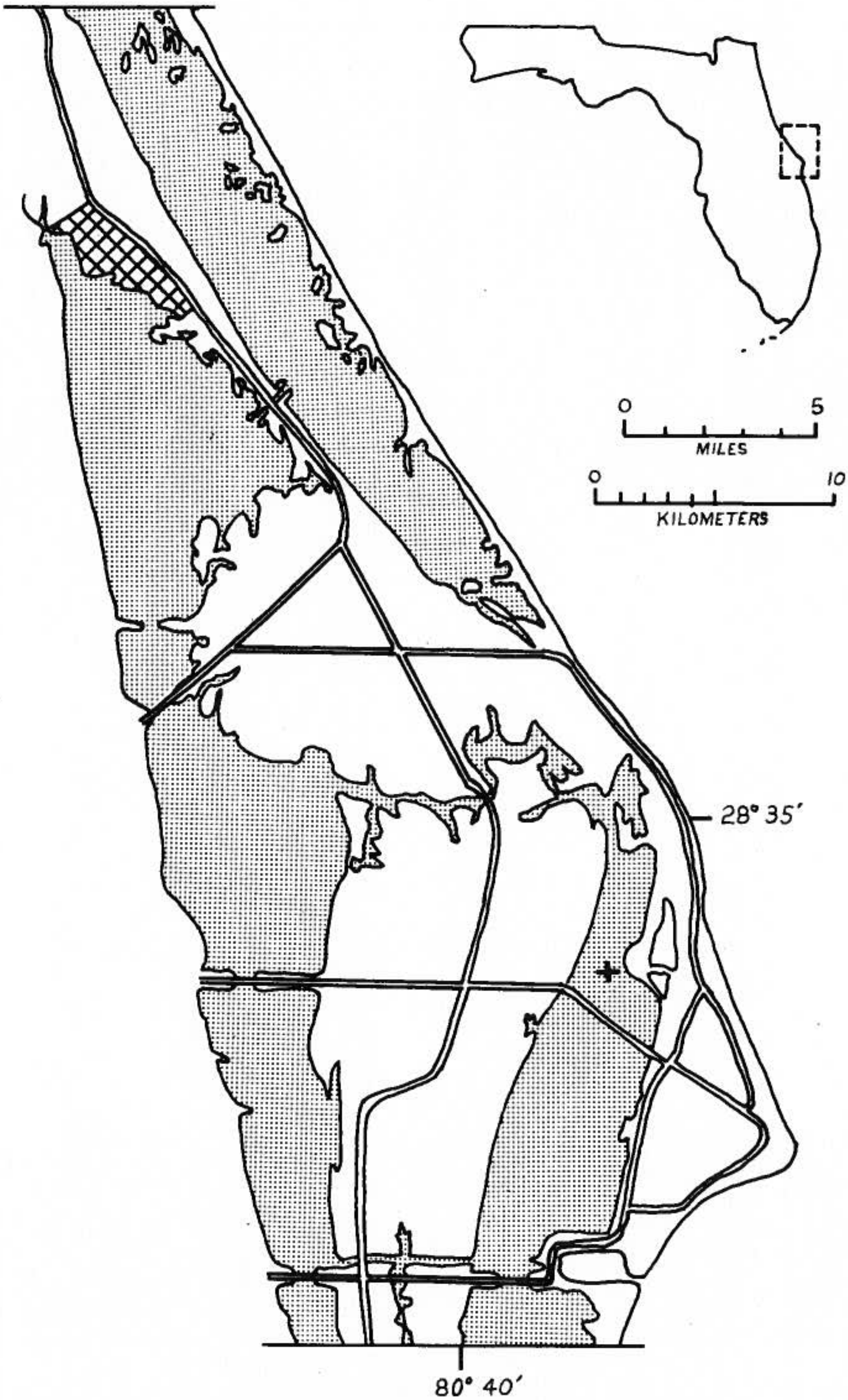

FIG. 1. Merritt Island National Wildlife Refuge. Shaded areas represent lagoonal waters. Indian River study site is shown by cross-hatching, Banana River study site by cross.

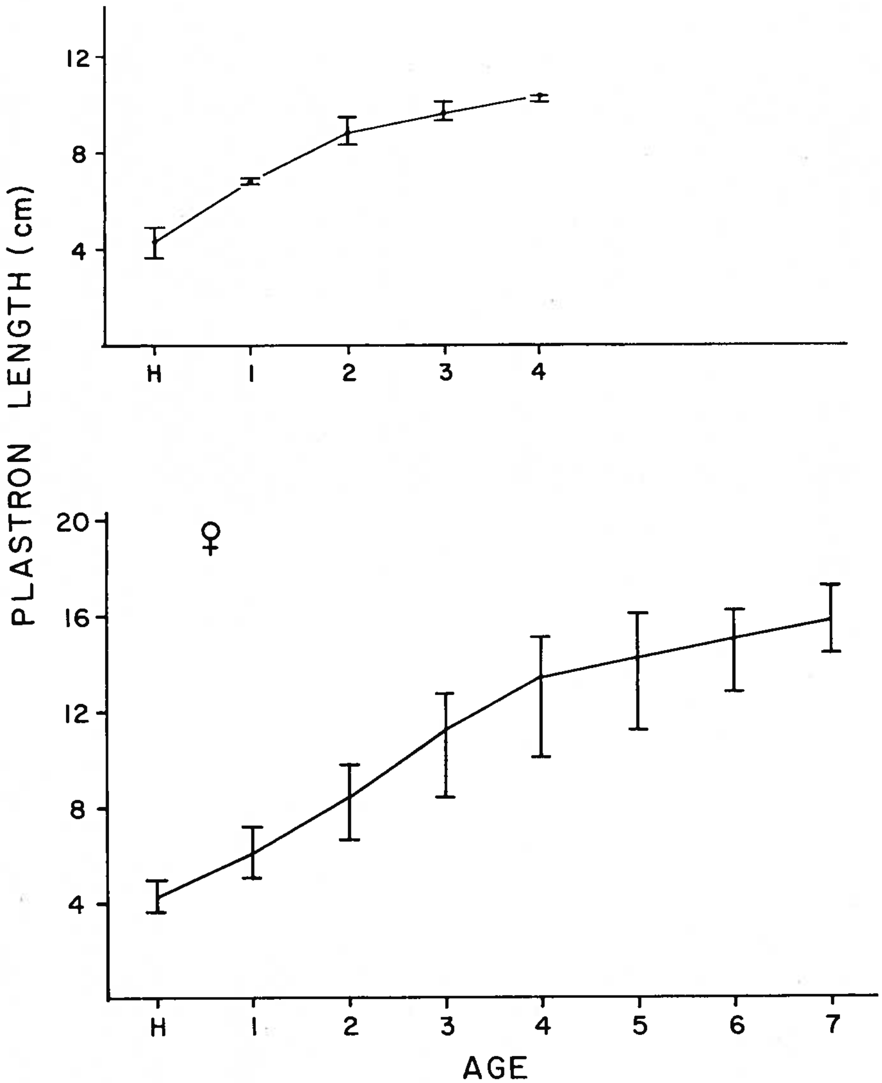

FIG. 2. Relationship between age and plastron length in 53 female and 13 male *Malaclemys* from the Indian River. Vertical bars represent sample range.

Indian River and 44 from the Banana River. Fifty-three of the Indian River turtles bore distinct growth annuli, but heavy shell damage from barnacles (Seigel 1983) obliterated most annuli on terrapins from the Banana River. Ontogenetic change in the relative size of the abdominal scute, such as that noted by Moll and Legler (1971) for tropical *Pseudemys scripta,* was minor in this study (<2%), so no correction factor was needed.

Fig. 2 shows the relationship between age and plastron size. The wide variability in size within a particular age class observed in *Malaclemys* frequently occurs in other turtles (Gibbons 1968; Ernst 1971, 1975, 1977; Plummer 1977b). Growth of the sexes is relatively constant and similar for the first two years of life, but begins to diverge after age three, when male growth rates decline, but females continue to grow at a steady rate. The curve for both sexes shows a marked decline in growth as sexual maturity is reached (see below). Fig. 3 shows the relationship between percent growth/year and plastron size. Most

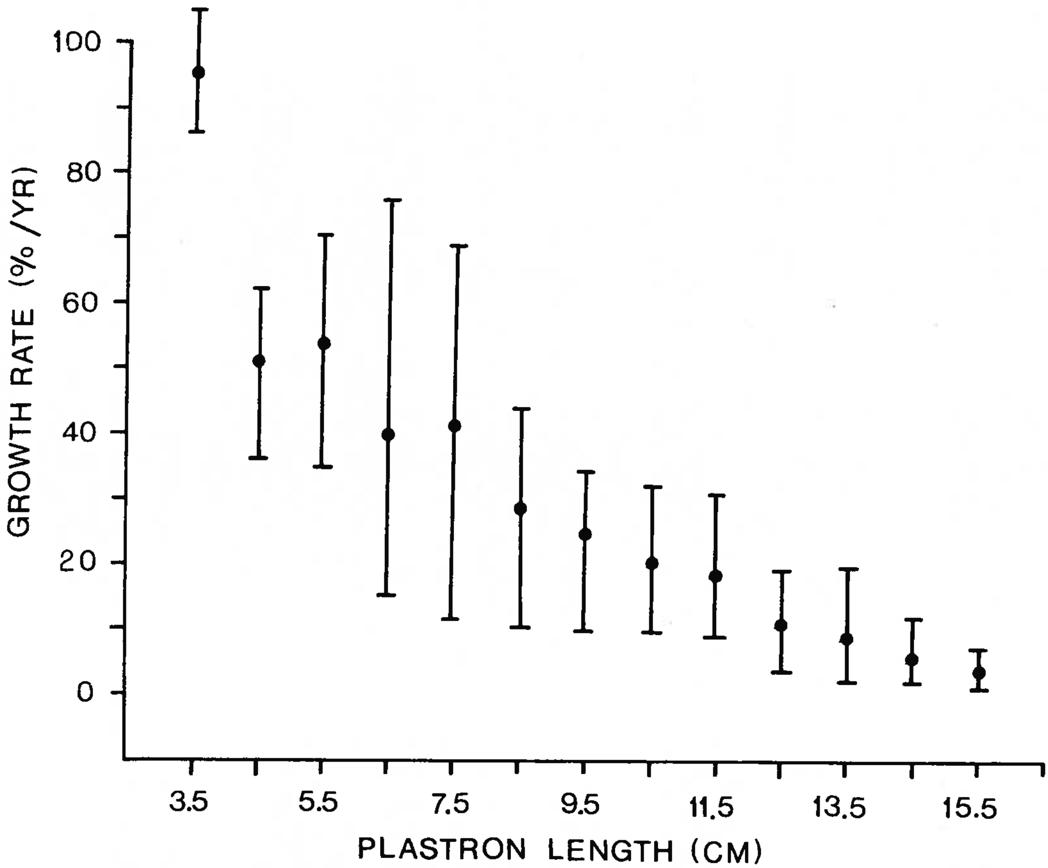

FIG. 3. Relationship between growth rate (%/year) and plastron length for Indian River *Malaclemys*. Vertical bars represent sample range.

rapid growth occurs at PL 3–3.9 cm, followed by a sharp decrease, and then a more gradual decline in growth to <5%/year in mature individuals. This pattern is similar to that of most other freshwater turtles, especially the genera *Chrysemys* and *Pseudemys* (see Bury 1979 for review). Limited data from turtles recaptured after six months or more support the above growth estimates. Two mature females of 13.8 and 14.6 cm PL grew at annual rates of 5.4% and 2.9% respectively. Six mature females of >15.0 cm PL grew at a mean annual rate of 2.2% (range = 0–7.1%). Based on these values, the largest female in the Indian River population (PL = 17.7 cm) would be approximately 15 years old. Longevity in this population is estimated to be about 20 years.

Fig. 4 compares the PL/age relationships of *Malaclemys* from different parts of the range. Florida *Malaclemys* grow at a slightly faster rate than terrapins from North Carolina or Louisiana (Cagle 1952). Although Florida *Malaclemys* are larger at hatching than turtles from the other populations (Seigel 1980c), this difference in initial size is insufficient to account for the differences in Fig. 4. Gibbons (1967) showed that even local populations of *Chrysemys picta* varied widely in growth rates because of differences in local feeding habits and food quality. Most data suggest that the feeding habits of *Malaclemys* are relatively similar throughout its range (Cagle 1952; Wood 1976; Hurd *et al.* 1979; R. Seigel, pers. obs.; but see Cochran 1976), with no comparable dramatic differences such as Gibbons (1967) noted. It therefore seems unlikely that the differences in growth rates seen in Fig. 4 are due to differences in local feeding habits. However, the North Carolina turtles were captives, and were fed fish as supplements to their normal food

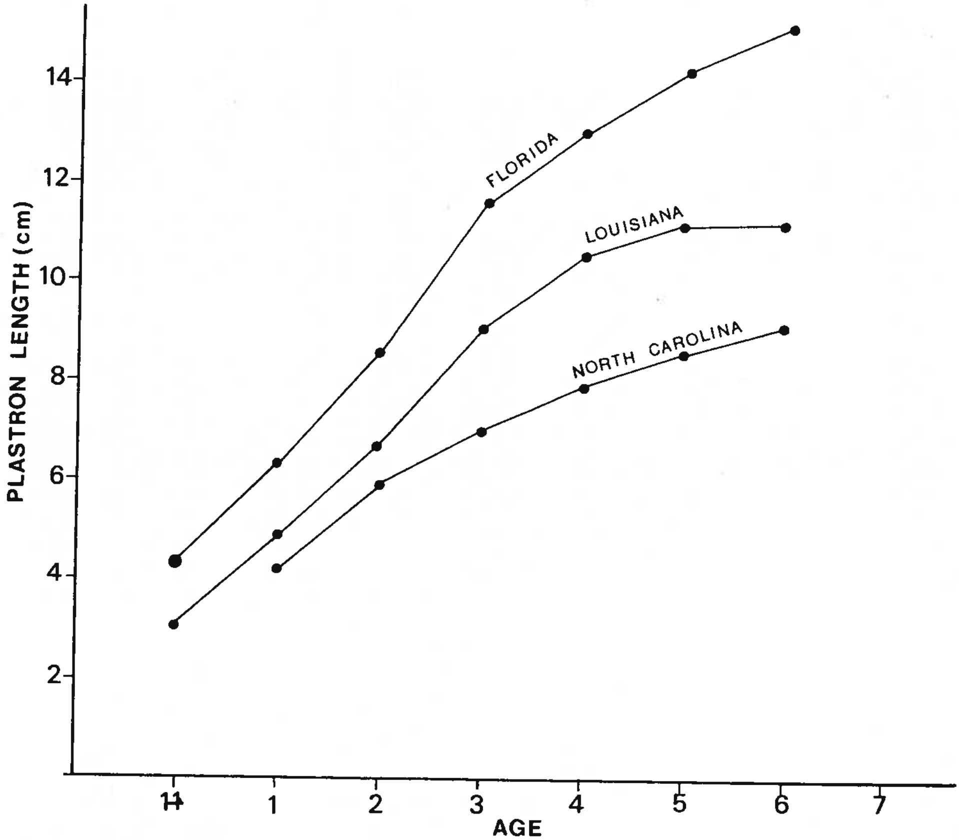

FIG. 4. Comparison of growth rate of *Malaclemys* from different parts of the range (sexes combined). See text for data sources.

(mollusks), so their growth may have been somewhat affected. The differences in Fig. 4 may reflect the longer activity and growing season of *M. t. tequesta,* which at Merritt Island is active from mid-February to late November (Seigel, unpub. data), whereas North Carolina captives were only active from May to October (Hildebrand 1932). No data on the activity season of Louisiana terrapins are available, but from a climatic viewpoint, it is probably more similar to Florida than North Carolina.

The smallest female showing evidence of sexual maturity (oviducal eggs or corpora lutea) was 13.5 cm PL, and all females >14.0 cm PL were mature. Fig. 2 shows that most females reach 13.5–14.0 cm by age four, but that some may not attain maturity until age five. The smallest male considered mature (based on secondary sexual characteristics and enlarged testes) was 9.1 cm PL, and all males >9.5 cm PL were considered mature. According to Fig. 2, males may reach this size as early as the second year of life, but most probably do not mature until age three. Hildebrand (1932) suggested that sexual maturity in *Malaclemys* was related to size rather than age, and my results support this idea. Table 1 shows the size and age at maturity for *Malaclemys* from different parts of the range. Size at maturity is rather uniform for both sexes, while age at maturity is more variable.

Bury (1979) summarized the data on growth and sexual maturity for freshwater, mainly north-temperate turtles, and made the following conclusions: 1) males often mature earlier and at a smaller size than females; 2) growth is most rapid before maturity is reached; 3) in temperate regions, individuals in southern populations mature earlier than northern conspecifics; 4) sexual

TABLE 1. Size and age at sexual maturity for male and female *Malaclemys terrapin* from different parts of the range.

Subspecies (locality)	♀ size (plastron length) and age (yrs) at maturity	♂ size (plastron length) and age (yrs) at maturity	Authority
terrapin (New Jersey)	13.2 cm/? yrs	—	Montevecchi and Burger (1975)
terrapin[1] (North Carolina)	13.7 cm/7 yrs	9.0 cm/5 yrs	Hildebrand (1932)
pileata × *littoralis* (Louisiana)	16.0 cm/6 yrs	9.9 cm/3 yrs	Cagle (1952)
tequesta (Florida)	13.5 cm/4–5 yrs	9.5 cm/2–3 yrs	This study

[1] Captive population.

maturity is usually related to attaining a certain size rather than a certain age. The data from subtropical *Malaclemys* appear to conform closely to these patterns.

Sexual Dimorphism.—The sexes of *M. t. tequesta* are highly dimorphic, both for external characters and body size. Male terrapins have smaller, narrower heads, darker carapacial markings, and larger carapacial keels than females. In addition, adult males have long, thick tails, with the vent posterior to the margin of the carapace, while adult females have short, narrow tails with the vent beneath the overhanging carapace. The mean PL and weight of 113 Indian River females was 15.4 ± 1.00 cm, and 886 ± 193 g. The same measurements for 13 Indian River males were 10.4 ± 0.69 cm, and 283 ± 50.9 g. Using the terminology of Fitch (1981), *M. t. tequesta* has a FMR (female to male ratio) for length and weight of 148 and 313, respectively. Thus, while females are ca. 1.5 times male length, they are >3 times male weight. Fitch (1981) reported that other turtle species showed similar variation in FMR between length and weight.

Berry and Shine (1980) and Fitch (1981) reviewed sexual size dimorphism in turtles and other reptiles, and related such dimorphism to intrasexual competition and divergent reproductive strategies. The greater body size of female *M. t. tequesta* probably evolved as a means to increase reproductive potential, since clutch size is positively correlated with body size in *Malaclemys* (Montevecchi and Burger 1975; Seigel 1980c). Large males on the other hand, would gain no reproductive advantage over smaller males, because male combat for mates is apparently absent in *Malaclemys* (Seigel 1980b). However, small body size permits males to mature at a younger age than females, possibly increasing lifetime reproductive potential.

Population Structure.—The size class structure of Indian and Banana river females, and that of Indian River males are shown in Figs. 5 and 6. Too few Banana River males were captured for analysis. The age structure of Indian River terrapins is shown in Fig. 7. There is a noticeable lack of small or immature individuals in both populations. The under-representation of small terrapins is probably the result of sampling error which favored adults. Small *Malaclemys* (<9 cm PL) were rarely seen at either study site, and it seems likely that behavioral differences exist between adults and juveniles that reduce the probability of capturing small terrapins. Hurd *et al.* (1979) advanced a similar hypothesis to explain the lack of small individuals in a Delaware population of *M. t. terrapin,* but also noted that local habitat destruction may have caused "catastrophic mortality" among young terrapins. No evidence for such habitat destruction exists at Merritt Island (at least recently), and I suggest that sampling error, rather then heavy mortality, is sufficient explanation for the lack of immature individuals.

The population size structures of Indian and Banana river females are significantly different (Mann-Whitney U test, $P < 0.01$), with the most striking differences reflected in the 17.0 cm and larger size classes (Fig. 5). Thirty-one percent of the female turtles from the Banana River were >17.0 cm PL, compared to only 3% of the Indian River terrapins in the same size range. Conceivably, these differences could be artifacts of the different sampling techniques used, but this seems

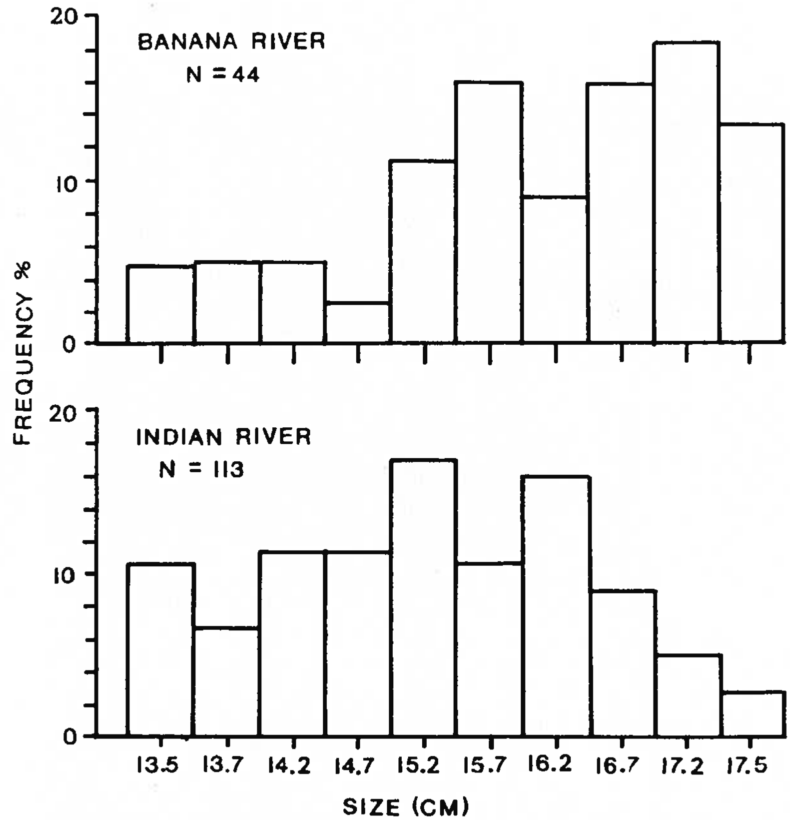

FIG. 5. Size structure of female *Malaclemys* from the Indian and Banana rivers 1977–1979. Size distributions did not differ between sampling periods (Mann-Whitney U test, $P > .10$), so data are combined for presentation.

unlikely, since both techniques were effective in capturing large individuals and it was in the larger size classes that most of the differences between the populations were found. Gibbons (1967) found that local populations of *C. picta* may vary widely in size structure, reflecting differences in feeding habits, food quality and growth rates. I was unable to determine if Indian and Banana river *Malaclemys* grew at different rates, but qualitative analysis of stomach contents from females from the two sites showed no striking differences (Seigel, unpub.), and it seems improbable that feeding habits varied sufficiently to account for the differences in size structure seen in Fig. 5. An alternative hypothesis is differential mortality. Elsewhere (Seigel 1980a) I have shown that Indian River females are subject to raccoon predation during the nesting season. No comparable predation was observed along the Banana River. Each time an Indian River female nests, there is a small but definite risk of encountering a predator and being eliminated from the local population. Because *M. t. tequesta* may nest up to three times/year (Seigel 1980c), the probability of Indian River females surviving many nesting seasons may be low. This may result in a lower proportion of females surviving to reach the larger (i.e. older) size classes that might otherwise occur in the absence of predation. The under-representation of larger females in the Indian River when compared to the Banana River might be a reflection of the higher mortality rate among mature Indian River females.

Sex Ratio.—The ratio of females/males for Merritt Island *Malaclemys* is shown in Table 2. Ratios varied seasonally, but were always significantly different from unity (binomial distribution, $P < 0.05$). The samples showing the least skewed ratios (March–April) were taken during

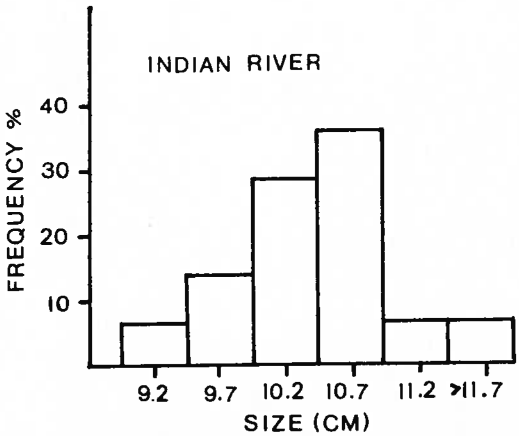

FIG. 6. Size structure of male *Malaclemys* from the Indian River, 1977–1979. Differences in size structure between sampling periods were insignificant (Mann-Whitney *U* test, $P > .10$), so combined data are shown.

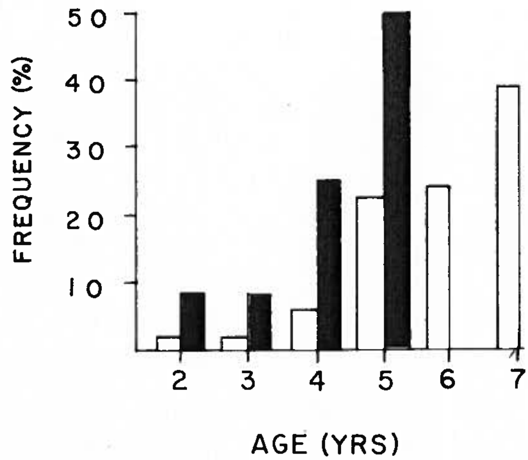

FIG. 7. Age structure of 12 male and 107 female *Malaclemys* from the Indian River, based on age-size relationships calculated from growth annuli. Males >5 years old, and females >7 years old, could not be accurately aged, so they are included with the oldest classes. Males are represented by shaded bars, females by open bars.

the spring mating season (Seigel 1980b), at a time when males reach their greatest representation in local populations. The 5:1 ratio taken at this time probably represents the best estimate of the "true" sex ratio in this population. Hildebrand (1932), Hurd *et al.* (1979), and Yearicks *et al.* (1981) have also reported female-biased sex ratios in *Malaclemys,* although Cagle (1952) noted the opposite trend in offshore populations from Louisiana.

The skewed sex ratios in Merritt Island *Malaclemys* are not the result of sampling bias or investigator error as suggested by Gibbons (1970) for other studies where the sex ratio was not 1:1. The different sampling techniques used, as well as the number of populations examined, probably precluded most bias due to sampling error, and the distinct sexual dimorphism in *Malaclemys* (see above) greatly reduced the chances of mistaking juvenile males for females, as Gibbons (1970) suggested. Bury (1979) found that of 39 studies of sex ratio in freshwater turtles, skewed ratios were reported in only 13 (33%). Assuming no bias due to sampling error, cases of skewed sex ratio such as that of *M. t. tequesta* are in the minority. Such skewed ratios may be the result of differential juvenile mortality (which has been neither confirmed or rejected), or temperature-modified sex determination during incubation, for which extensive evidence exists (see Bull and Vogt 1979; Yntema 1979 and references therein). If skewed sex ratios among adult turtles are a reflection of incubation temperatures, it remains to be determined if such ratios occur fortuitously (depending on the nest site choosen by the female) or if these ratios have been selected for by such factors as resource abundance, as was suggested by Nichols and Chabreck (1980) for *Alligator mississipiensis.*

Population Size.—Schnabel population size estimates and 95% confidence limits (Overton, 1969) for the Indian and Banana rivers were 404.7 (95% C.L. = 182.8–790.5) and 212.5 (95% C.L. = 58.7–627.3), respectively. The wide variability in the confidence limits are probably a result of two factors: 1) a low recapture rate which did not exceed 50% until the last sampling period, and 2) the apparent ability of *Malaclemys* to freely move into and out of the study area for short time periods (due to the lack of natural

TABLE 2. Sex ratio (females/males) of Merritt Island *Malaclemys* during different sampling periods.

Study site	Sampling period	Sex ratio	N
Banana River	February–November	9:1	47
Indian River	February–November	10:1	99
Indian River	March–April	5:1	26

barriers restraining movement). Plummer (1977a) found that temporary movements of *Trionyx muticus* out of his Kansas study site greatly increased the variability of his population size estimates. Although *Malaclemys* at Merritt Island showed relatively long-term (ca. 18 months) fidelity to a particular area (Seigel 1979), it is probable that short-term movements took place at both study sites, so the above estimates may be somewhat biased.

These population estimates and the size limits of the two sampling areas were used to construct density estimates. The Indian River sampling area covered 2.27 acres, yielding a density of 178.3 individuals/acre; the Banana River sampling area was 1.62 acres, yielding a density of 131.1 individuals/acre. These figures are somewhat higher than most reports of density in freshwater turtle populations (Bury 1979), but are not as high as the 239 individuals/acre reported by Ernst (1971) for *C. picta*. Biomass estimates, based on the above figures and wet body weight were 390.0 kg/ha for the Indian River, and 355 kg/ha for the Banana River. Both the density and biomass estimates may be somewhat inflated as a result of a) an arbitrary and possibly unrealistically low estimate of the population boundaries, and/or b) the tendency of *Malaclemys* to form large aggregations during the breeding season (Seigel 1980b). However, it seems clear that Merritt Island *Malaclemys* may attain a considerable density and biomass in local areas, at least during certain times of the year.

Summary

The growth rates, age at maturity, population size and population structure of the Florida east coast terrapin, *Malaclemys terrapin tequesta* were studied from 1977 to 1979 at the Merritt Island National Wildlife Refuge, Brevard County, Florida. Data from two areas (Indian and Banana rivers) are presented. Growth was most rapid immediately after hatching, declining to <5%/year in mature turtles. Females matured at a plastron length of 13.5–14.0 cm, at an age of 4–5 years. Male terrapins reached maturity at a plastron length of 9.0–9.5 cm, at an age of 2–3 years. Female terrapins attain a much larger body size than do males, with a mean FMR (female to male size ratio) of 148 for length and 313 for weight. Such dimorphism probably reflects divergent reproductive strategies between the sexes; females benefit from large body size via increased reproductive potential, whereas males attain only a small body size, but reach maturity earlier than females. The two study populations differed significantly in size structure, with the Banana River population having relatively more individuals in the larger size classes. This may reflect higher mortality among Indian River females. The sex ratios of both populations were significantly different from 1:1, with females outnumbering males by at least 5:1. Schnabel population size estimates for the Indian and Banana rivers were 404.7 and 212.5, respectively, and it appears that *Malaclemys* may attain a considerable density and biomass in local areas.

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