entered the sea. Juvenile crocodiles were most evident when hatchling turtles were emerging from their nests on the beach and during periods of heavy rain.

The successful attacks on solitary turtles and the absence of predation on *arribada* turtles suggests that *arribada* behavior may deter predation by crocodiles. Observations from the present study make it difficult to accurately assess the predatory pressures American crocodiles impose on the olive ridley sea turtle population at Playa Nancite. However, the depredation of 1 or 2 sea turtles by American crocodiles between arribadas ranging from 1000 to 20,000 turtles is at a low level, having little or no effect on the nesting population of olive ridleys at Playa Nancite. Instead, predation of crocodiles upon turtles at Playa Nancite may actually enhance the survival of this population of crocodiles which persists as a small, fragmented remnant of the original population on the Pacific coast.

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Growth and Reproductive Estimates from Alligator Snapping Turtles, *Macroclemys temminckii*, taken by Commercial Harvest in Louisiana

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The alligator snapping turtle (*Macroclemys temminckii*) is a large freshwater chelydrid restricted to drainages of the Gulf Coastal Plain and the Mississippi River Valley of the USA (Lovich, 1993). In comparison to other North American turtles, many aspects of its biology remain poorly known (Ernst et al., 1994) even though the species has been exploited heavily by the soup industry for decades (Pritchard, 1989). Populations of *Macroclemys* are considered low or depleted because of overharvesting, yet the actual status is poorly known (George, 1987).

Many biological details about *Macroclemys* have been learned by analyzing specimens gathered by commercial turtle trappers (Dobie, 1971; Pritchard, 1989; Sloan and Lovich, 1995; Sloan et al., 1996). Ancillary information gleaned from commercial harvesting provides useful, albeit fragmentary data, in situations analagous to salvage archeology. There are compelling reasons to collect and report salvage biology whenever a harvested species is incompletely known or of conservation concern.

In this paper we summarize reproductive and growth data gathered from a large sample of *Macroclemys* that were processed at a commercial facility in Louisiana in 1986. The data were compared to a similar study conducted two decades earlier in the same region (Dobie, 1971). Because growth and reproductive parameters are vital elements in the recovery plans for *Macroclemys*, the information has implications for the proposed size limits in commercial harvesting of the species.

Methods. — A processing facility in Jonesville, Louisiana, saved *Macroclemys* viscera and carapaces which were bagged, labelled, and frozen for later analysis. Both sexes were collected initially in March and April, but from May to October, only females were saved by the processor because of limited freezer space, even though both sexes were still processed. Sample sizes varied because some individual samples were incomplete, e.g., the carapace was salvaged but not the viscera.

Midline carapace length (ML, straightline measurement to the nearest 0.1 cm) was used for analyses of body

size because that measurement has the greatest standardization among researchers. A sexual dimorphism index was calculated as a ratio of mean adult body size between the larger and smaller sex (Gibbons and Lovich 1990). Turtles were sexed by visual examination of the reproductive organs and the detailed descriptions given by Dobie (1971). Maturity was assessed by the visual appearance of the gonads. Adult males had purple testes with enlarged cream-colored, coiled vas deferens; immature males had small straight vas deferens. Adult females were identified by enlarged, highly convoluted oviducts and the presence of eggs, vitellogenic follicles, or corpora lutea, whereas immature females had small straight oviducts and no enlarged follicles within the ovaries. Sex ratios were compared among immatures and adults by χ^2 tests.

We quantified seasonal changes in the female reproductive cycle by measuring the mean number and size of previtellogenic and vitellogenic follicles, eggs, and corpora lutea during each month from April to August. Diameters of reproductive structures were measured to the nearest mm with calipers. Reproductive stages were categorized following Moll and Legler (1971) as previtellogenic follicles (Class I: 1–6 mm) or vitellogenic follicles (Class II: 7–12 mm, Class III: 13–18 mm, Class IV: 19–24 mm, and Class V: 25–30 mm). Because *Macroclemys* produces only one clutch per year (Dobie, 1971), annual reproductive output for each female could be estimated as the highest number of either vitellogenic follicles, oviductal eggs, or corpora lutea. Estimates based on follicle counts may be overestimates if follicular atresia occurred. We examined relationships for size-specific fecundity by least squares linear regression.

Age (in whole years) was estimated by detaching the second right costal scute, soaking it in water, backlighting it, and counting growth annuli (Zangerl, 1969; Dobie, 1971). Scutes were examined (by KNS) under a dissecting microscope and counts were made three times on each scute to achieve consistent counts. We assumed that scute growth rings were deposited annually as found in the earlier study of *Macroclemys* from the same region (Dobie, 1971). Age estimates were acknowledged minimums as rates of annulus erosion or deposition were impossible to know from single samples of individual turtles. We examined the relationship between age and fecundity by least squares linear regression.

We chose a von Bertalanffy equation to fit length at age relationships as there were insufficient data on small size classes to use a logistic or Gompertz function. The model used was

$$\mathbf{x} = a(1 - be^{-kt})$$

where $\mathbf{x}$ = midline carapace length (ML), $\mathbf{t}$ = age (yrs), b is related to the size at hatching (time 0), and a (asymptotic length) and k (intrinsic growth rate) were parameters to be estimated. We used the average hatchling carapace length of 4.2 cm (Dobie, 1971; Drummond and Gordon, 1979) as an initial estimate of b and allowed parameter values for the asymptote (a) and the intrinsic growth rate (k) to vary freely during iterations.

Growth curves were fitted by a quasi-Newton search algorithm (MacCurveFit 1.1, © K. Raner, 1995) to minimize the summed squares of deviation and derive 95% confidence intervals for each parameter. We also examined growth curves for the earlier study of Louisiana *Macroclemys* by digitizing (Digigraf 1.4, © S. Tortike, 1994) a graph of size at age (Fig. 9 in Dobie, 1971) to capture x and y coordinates for the datapoints. We compared growth curves from Dobie's data with our growth curves to look for evidence of long term changes in growth over the intervening two decades.

Means are reported with ± 1 sd and sample size. If the assumptions of normality and homogeneity of variance were not met for parametric statistical tests, an appropriate transformation was applied or an equivalent non-parametric test was used. Tests of statistical significance used an alpha = 0.05.

RESULTS

A total of 93 specimens were examined (73 females and 20 males) that were collected from 27 March to 26 October 1986. Although the trappers were reluctant to give precise locations for the collection, the processor indicated that most turtles had been collected in Louisiana with a few taken in Arkansas and Mississippi.

Female Reproductive Cycle. — Females were taken from March through August except for one taken in October. Data from the October female were atypical and are considered separately. Several general reproductive trends were evident. Vitellogenic follicles were already enlarged in

Table 1. Seasonal occurrence of ovarian follicles, corpora lutea, and oviductal eggs in *Macroclemys temminckii* in Louisiana. Measurements are mean diameters in mm. Follicle size classes are I: 1–6 mm, II: 7–12 mm, III: 13–18 mm, IV: 19–24 mm, and V: 25–30 mm.

		Follicle Size Classes					Corpora		Female Size	
Sample Period	*n*	I	II	III	IV	V	Lutea	Eggs	Mean	Range
27 March – 14 April	14	+	+	+	+	+	14.9	39.3	40.4	36.3–46.5
18–30 April	15	+		+	+	+	13.0	35.0	40.3	37.0–46.2
3–6 May	4	+			+	+	11.0	36.0	40.4	35.8–45.4
21–27 May	7	+			+	+	11.8	31.7	38.3	39.0–47.2
8–19 June	9	+		+	+	+	10.8	—	37.9	32.7–43.4
25–27 June	10	+		+	+		9.6	—	41.3	34.3–45.8
10–26 July	6	+		+	+		8.3	—	42.2	37.0–45.9
7–11 August	4	+			+	+	6.0	—	40.0	37.2–42.3

April and May and a decline in average follicle size in June reflected a loss of ovulated follicles (Table 1). Follicle numbers were depleted for a month after nesting but average follicle size increased again during July and August as follicles for the next year's clutch became vitellogenic (Table 1). Follicles attained an average size by August that was not significantly different than the follicle size in April, evidence that vitellogenesis for an upcoming year was largely completed by the end of summer and the follicles retained over winter. The pattern was evident by an increase in the minimum follicle size after oviposition since the maximum follicle size remained relatively constant. Following ovulation in April, corpora lutea became progressively smaller in diameter ($p = 0.0001$, Fig. 1A) even though the average number of detectable scars was relatively constant for the period of April – August (Table 1).

Oviductal eggs were present from late March through late May but were absent by early June. Average egg diameters declined slightly through this period ($p = 0.002$, Fig. 1B) as did the average reproductive output ($p = 0.02$, Fig. 1C). The reproductive declines were unrelated to smaller females nesting later because female body size did not decline concomitantly ($p = 0.43$).

Reproductive periodicity was predominantly annual except for an anomalous female collected in October. This female (40.7 cm ML) examined on 26 October contained 10 vitellogenic follicles (up to 26 mm in diameter), 26 soft-shelled eggs (up to 38 mm), and corpora lutea (up to 13 mm). The presence of large corpora lutea well after the normal breeding season (Fig. 1A), the soft-shelled eggs indicating very recent ovulation, and a lack of a second set of smaller corpora lutea ruled out the possibility of this being a second clutch for the season. Eggs ovulated very late in a season were apparently retained in the oviduct rather than oviposited and a low number of follicles were in vitellogenesis for the next season.

Size-Specific Fecundity. — Female body size (ML) was significantly related ($p = 0.02$) to the overall estimate of reproductive output (Fig. 2), but not to number of vitellogenic follicles ($p = 0.39$), number of corpora lutea ($p = 0.39$), or to egg size ($p = 0.17$). Despite an overall positive correlation for female body size and fecundity, low coefficients of determination signified high individual variance in reproductive output for females of given body size.

Age-Size-Maturity Relationships. — Immature females in the sample averaged 16.0 yrs (sd = 3.7 yrs, range 12–21 yrs, $n = 5$) and 33.8 cm ML (sd = 1.9 cm, range 31–37 cm, $n = 6$). Adult females in the sample averaged 21.4 yrs (sd = 6.0 yrs, range 13–38 yrs, $n = 36$) and 40.4 cm ML (sd = 3.6 cm, range 32.7–47.2 cm, $n = 67$). Immature males in the sample averaged 16.8 yrs (sd = 4.7 yrs, range 10–21 yrs, $n = 6$) and 34.5 cm ML (sd = 5.0 cm, range 26.0–41.0 cm, $n = 6$). Adult males in the sample averaged 29.3 yrs (sd = 12.5 yrs, range 11–45 yrs, $n = 8$) and 48.7 cm ML (sd = 5.2 cm, range 37.8–55.2 cm, $n = 13$). Females attained maturity between 13–21 yrs and at sizes between 32.7–37.0 cm ML; males attained maturity between 11–21 yrs and at sizes between 37.8–41.0 cm ML.

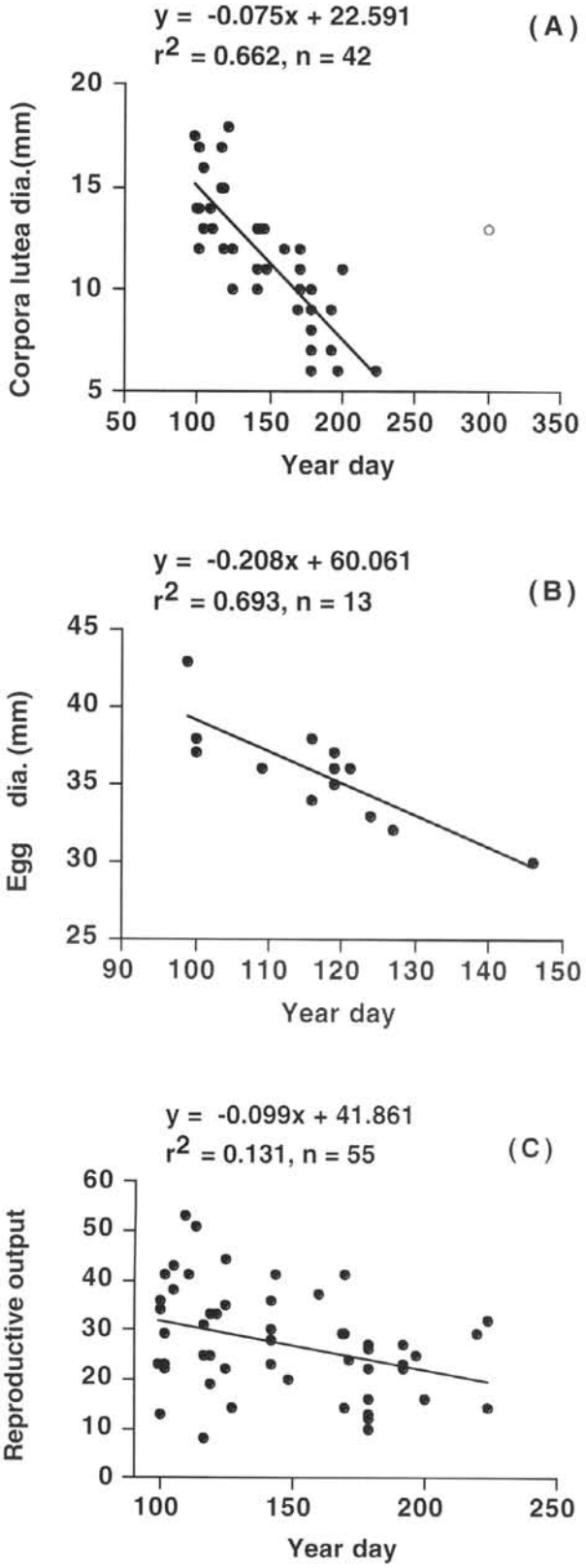

Figure 1. Least squared linear regressions for relationships between (**A**) corpora lutea diameter (mm) through the reproductive season, (**B**) egg diameter (mm) through the reproductive season, and (**C**) reproductive output (maximum number of vitellogenic follicles, eggs, or corpora lutea) through the reproductive season for *Macroclemys temminckii* in Louisiana. In A, the open circle indicates a female sampled in October.

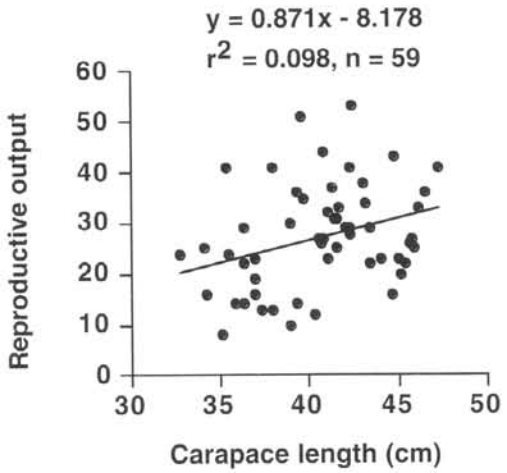

Figure 2. Relationship between female body size (midline carapace length, cm) and reproductive output (maximum number of vitellogenic follicles, eggs, or corpora lutea) for *Macroclemys temminckii* in Louisiana.

Mean size of adult males was significantly larger than for adult females (1 way *t*-test on ln(ML), 42 df, $t = 2.04$, $p = 0.02$). Adult males were on average 1.2 times larger than adult females as indicated by the sex dimorphism index (–1.2). The ten largest females ($\bar{x} = 45.7$ cm, sd = 0.7 cm) and males ($\bar{x} = 51.0$ cm, sd = 2.92) in the sample showed a similar male bias in the sex dimorphism index (–1.1). The mean age of harvested males was significantly older than for females (1 way *t*-test on ln(ML), df = 78, $t = 6.55$, $p = 0.0001$). The oldest ages assigned from scute counts were 39 yrs for females and 45 yrs for males. For the ten largest individuals of each sex, 60% of the females and 50% of the males had scute counts that were unreadable and consequently omitted from growth curve calculations. Variation in age and size at maturity obscured any clear relationship between female age and fecundity ($p = 0.27$).

Adult sizes were within the 95% confidence intervals for asymptotic size calculated for the two Louisiana datasets (present study and Dobie, 1971) combined (Table 2, Fig. 3). Asymptotic sizes for females were similar in our sample (39.9 cm) and the earlier study (40.1 cm), but our sample estimated a smaller asymptotic size for males (50.3 cm) than the earlier study (57.6 cm). Omission of an outlier data point for a single large male in Dobie's (1971) study gave convergence to a similar asymptotic value in growth functions of both data sets (Table 2, Fig. 3).

Table 2. Estimated parameters of the von Bertalanffy growth model for male and female *Macroclemys temminckii*. Data include present study, data for the same region two decades earlier (Dobie, 1971), and combined. r^2 = coefficient of determination; a = asymptotic value; k = characteristic growth rate estimated from the von Bertalanffy growth model.

Data set	sex	r^2	$a \pm 1$ s.e. (cm)	95% CI for a (cm)	$k \pm 1$ s.e.
Present study	m	0.93	50.3±3.3	43.8–56.8	0.082±0.017
	f	0.89	39.9±0.9	38.1–41.7	0.269±0.155
Dobie, 1971	m	0.98	57.6±3.9	50.0–65.2	0.071±0.010
	f	0.97	40.1±1.7	36.8–43.4	0.170±0.030
Combined	m	0.95	51.0±2.3	46.5–55.5	0.084±0.011
	f	0.92	40.3±0.9	38.5–42.1	0.186±.0270

DISCUSSION

Female Reproductive Cycle. — Many of the findings concerning the female reproductive cycle were similar to an earlier study of *Macroclemys* in Louisiana (Dobie, 1971). However, additional July and August samples demonstrated that *Macroclemys* begins its pre-reproductive period for an upcoming spring breeding season in July and August (Table 1). The presence of Class III–V follicles in August indicates that vitellogenesis was largely completed by the end of summer, well before the December sample reported by Dobie (1971). This evidence contradicts an earlier suggestion that large follicles found in December undergo atresia and that vitellogenesis occurs in spring (Dobie, 1971). A reinterpretation is supported by comparison with *Chelydra serpentina*, a chelydrid whose reproductive cycle is well characterized (White and Murphy, 1973).

The pre-reproductive phase in *C. serpentina* extends from mid-August to mid-May with vitellogenesis occurring largely during warm months; little additional yolk develops over winter (White and Murphy, 1973). A similar reproduc-

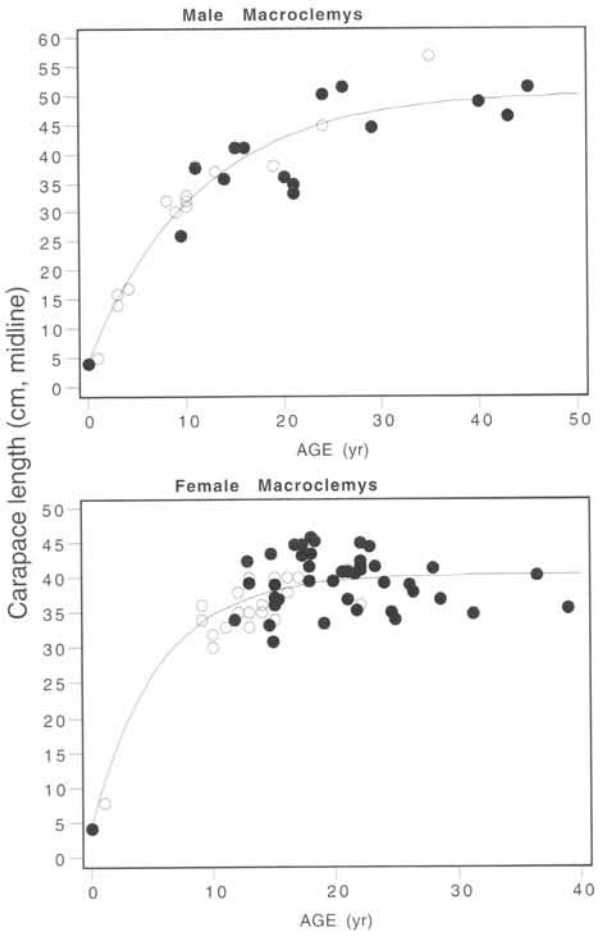

Figure 3. Von Bertalanffy growth curves for male and female *Macroclemys temminckii* from a commercial harvest in Louisiana. Dots are data from the present study; open circles are data from Dobie (1971). Curves are simultaneous fits for both data sets.

tive cycle is typical for turtles that lay a single clutch annually (Moll, 1979). Thus, any enlarged follicles found in August were in vitellogenesis for the next breeding season. In addition, ovarian follicles undergo atresia primarily during the latent period after reproduction (June – July for *Macroclemys*) so December samples simply record the arrested state of vitellogenic follicles developed during the warmer months. There is no energetic reason to remobilize lipids already committed to reproduction unless a female were under metabolic stress from an injury or disease or as a bet-hedging strategy for an environmentally unfavorable season. Furthermore, there is little physiological means for doing so in winter, a time of metabolic depression for ectotherms. We do not question that large follicles are present in over-wintering *Macroclemys*, but the comparative evidence in *Chelydra* does not support a view that follicles undergo atresia during hibernation or that vitellogenesis occurs in spring.

Interpretation becomes necessarily more complex for turtles laying more than one clutch annually or with variable reproductive periodicity. Latitudinal differences in vitellogenic cycles are known in some turtles, e.g., northern populations of *Chrysemys picta* complete vitellogenesis before hibernation, whereas southern populations have follicular enlargement occurring between spring emergence and nesting (Moll, 1979). However, this example concerns a species that lays multiple clutches, whereas chelydrids only produce one clutch annually.

The samples gave no evidence of adult females that did not breed, but we cannot state categorically that all females breed annually. Dobie (1971) suggested that some females may skip a year based on the absence of vitellogenic follicles in August. As the lipids allocated to reproduction are accumulated in the year(s) prior to ovulation, we would not be surprised if some females forego breeding after a season of poor foraging. Also, the female that contained eggs in October suggests that some females may not oviposit eggs under unusual circumstances. Apart from *Deirochelys reticularia*, egg retention by free-living turtles after a normal nesting season is only associated with unsuitable environmental conditions or pathological states (reviewed by Buhlmann et al., 1995).

Reproductive Characteristics. — Mean clutch sizes or variances were not significantly different in Louisiana *Macroclemys* measured two decades apart (present study and Dobie, 1971). Reproductive stasis was noted in Florida *Macroclemys* measured across the same time scale (Ewert and Jackson, 1994). Both Louisiana populations produced lower clutch sizes and had smaller average female size (mean 40.3 cm ± 3.4 cm, n = 39, range 34–47.2) than in Florida (mean 45 cm ± 2.8, n = 10, range 41.8–51). Ewert and Jackson (1994) speculated that a difference in clutch size may arise from selective removal of larger, older females in Louisiana harvests compared to their relatively undisturbed population in Florida. Both Louisiana studies found evidence for size-specific fecundity (Dobie, 1971; this study). For *Macroclemys*, it appears that female body size is more tightly linked to fecundity than egg size; indeed there was no statistical evidence for the latter relationship.

Age-Size Relationships. — For harvested samples, it was impossible to test accuracy of age estimates but growth rings are reliable and validated for juvenile *Chelydra serpentina* (Galbraith and Brooks, 1987). Dobie (1971) obtained reliable annuli counts on 41% (34/84) of his sample while 58.5% of the carapaces in our sample gave consistent annulus counts. *Macroclemys* that could not be aged due to eroded annuli were invariably larger and presumably older individuals, i.e., in this study 80% of the largest turtles of each sex were excluded from growth curve calculations because of eroded annuli.

The high coefficients of determination (r^2 from 0.89–0.98) indicated that age-size relationships for Louisiana *Macroclemys* are reasonably described by von Bertalanffy growth models (Table 2), even though the model underestimated size of the largest individuals. Despite considerable variation in body size at any given age, the average adult size for both sexes was near the asymptotic value. To reiterate Frazer et al. (1990), parameter estimates for the asymptotic size (a) are not an absolute size limit or the size of the largest individuals, but instead represent an average size for individuals once growth has slowed (once maturity is attained). Additional growth is obviously not precluded, as some impressively large *Macroclemys* are known (reviewed by Pritchard, 1989) that far exceed the asymptotic estimate from this commercial harvest.

The practical limitations of attempting to age turtles from eroded or missing annuli (Galbraith and Brooks, 1987) often exclude older and larger animals from size-age calculations. All researchers validly share the same concerns about whether more or less than one growth mark is deposited per year. If back-calculation methods can account for missing annuli (Sexton, 1959; Parham and Zug, in press), it may be reasonable to attempt an age estimate for the purpose of recalculating growth curves since a lack of data on large animals will bias estimates of asymptotic size (Frazer et al., 1990). However, estimates of ages and sizes at maturity may be biased anyway if fewer large turtles remain in a heavily harvested species. For these reasons, proposed minimum size limits on harvested *Macroclemys* in Louisiana (Sloan and Lovich, 1995) or elsewhere in their range should be viewed with appropriate care.

Size-Selective Harvests. — It has been suggested that a proposed minimum size limit of 15 inches (38 cm carapace length) will not affect size distributions of *Macroclemys* since commercial trappers who are paid by turtle weight take as many of whatever size turtles are available (Sloan and Lovich, 1995). However, size limits are ineffective conservation tools if inappropriately selected and the proposed limits afford virtually no protection to adult*Macroclemys*. For example, 71% of adult females and 100% of adult males from the harvested sample were vulnerable to a size-selective harvest of 38 cm.

If a hypothetical management scenario were to protect half the adult population of either sex, size limits near the

asymptotic value would be desirable since average adult size is assumed to be normally distributed about the asymptote (Frazer et al., 1990). As a representative example, using our data, size limits set progressively at 38, 39, 40, 41, or 42 cm (values within the 95% confidence limits for a 40 cm female asymptote, Table 2) would afford protection for only 29, 32, 44, 54, or 66%, respectively, of the adult female *Macroclemys* in the sample. In view of the threatened status for this species, a stronger degree of protection is warranted than offered by the proposed size limit.

Minimum size limits are intended to prevent growth overfishing and recruitment overfishing (Hilborn and Walters, 1992), and the simplicity of imposing size limits makes them a popular management option. However, a size-selective harvest will have immediate consequences on population structure and should not be adopted without due consideration of the long-term consequences. Minimum sizes are generally set at a smallest size for sexually mature animals, but a consequence of a size-selective harvest may be to remove individuals of highest reproductive value from the population before they replace themselves demographically (Hilborn and Walters, 1992). Only by iteroparity and high adult survivorship do turtles accomplish this (Congdon et al., 1993; Congdon et al., 1994; Cunnington and Brooks, 1996). If harvest pressure is heavy, size-selection may create shifts in population structure as larger females are removed (Ewert and Jackson, 1994). Furthermore, the size-fecundity relationship (Fig. 2) means that the smaller females that remain will be less capable of meeting the recruitment levels needed for a stable or healthy population. Effects on age at maturity and growth rate are less simple to predict. Managers should be alert to the potential effects of size-selective harvests since a bet-hedging reproductive strategy of long-lived turtles gives little capacity to buffer harvests of adults by reproductive compensation or increased survivorship.

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