BULLETIN OF MARINE SCIENCE, 34(1): 71-80, 1984

FOOD HABITS, OCCURRENCE, AND POPULATION STRUCTURE OF THE BULL SHARK, *CARCHARHINUS LEUCAS*, IN FLORIDA COASTAL LAGOONS

Franklin F. Snelson, Jr., Timothy J. Mulligan and Sherry E. Williams

ABSTRACT

The bull shark, *Carcharhinus leucas*, is the most common shark in the brackish Indian River lagoon system on the central east coast of Florida. The biology of the lagoon population was studied between May 1975 and May 1979. There was substantial spatial and seasonal variation in catch rates with gill nets. Bull sharks were usually most abundant in the low-salinity lagoon basins. Catch rates were generally highest in the spring and fall and were always higher at night than day. No specimens were netted during the winter although bull sharks are known to be present during that season.

The permanent lagoon population was composed entirely of newborn young and juveniles up to 202 cm TL. As they approach maturity, the subadults leave the estuary. Pregnant adult females return to lagoon waters in late spring and summer to give birth. One pregnant female 249 cm TL was captured during this study. Juvenile bull sharks in the lagoon system fed primarily on stingrays and marine catfishes.

The bull shark, *Carcharhinus leucas* (Valenciennes), is one of the most common large sharks in the near-shore coastal waters of Florida. It is also the most abundant shark species in the extensive Indian River lagoon system along Florida's east coast (Snelson and Williams, 1981). Several papers have contributed to the basic biology and natural history of the bull shark in Florida waters (Nichols, 1917; Springer, 1938; 1940; 1960; 1963; Vorenberg, 1962; Clark and von Schmidt, 1965; Dodrill, 1977), but none have dealt specifically with the population inhabiting the brackish east-coast lagoons. This paper describes the food habits, occurrence, and population structure of *C. leucas* in the Indian River lagoon system and outlines a proposed life history scheme for the population in east-central Florida.

METHODS

The study was carried out in the northern part of the Indian River lagoon system on the central east coast of Florida, between latitudes 28°25′N and 28°52′N (Fig. 1). The lagoon system in this region consists of three partially isolated bodies of water, Mosquito Lagoon, Indian River, and Banana River. These basins are interconnected by canals, and the system communicates with the ocean through inlets located 28 km north (Ponce de Leon Inlet) and 80 km south (Sebastian Inlet) of the study area. Lagoon waters are mesohaline, with an average salinity of about 29–30‰ in the study area. The ichthyofauna in this region was discussed by Snelson (1983), and the area was more thoroughly described by Gilmore (1974; 1977), Snelson (1976; 1980), Snelson and Williams (1981), and Mulligan and Snelson (1983).

Sampling was conducted from May 1975 to May 1979, with the most intense effort during the period March 1977 to November 1978. During the study, 150 bull sharks were recorded; but not all individuals were examined in detail. Except for two specimens collected during a hypothermal fish kill (Snelson and Bradley, 1978), all sharks were collected by netting. Fourteen small specimens were provided by a commercial fisherman who gill-netted for mullet (*Mugil* sp.). His nets were 274 m long, 7.9–8.9 cm stretch mesh, and made of monofilament nylon. The fisherman worked exclusively at night and fished on the average about three nights per week year-round during the period 1975–1976, primarily in the Indian River. The majority of our specimens were captured in large-mesh gill nets set for the primary purpose of collecting sea turtles (Snelson and Williams, 1981; Mendonca and

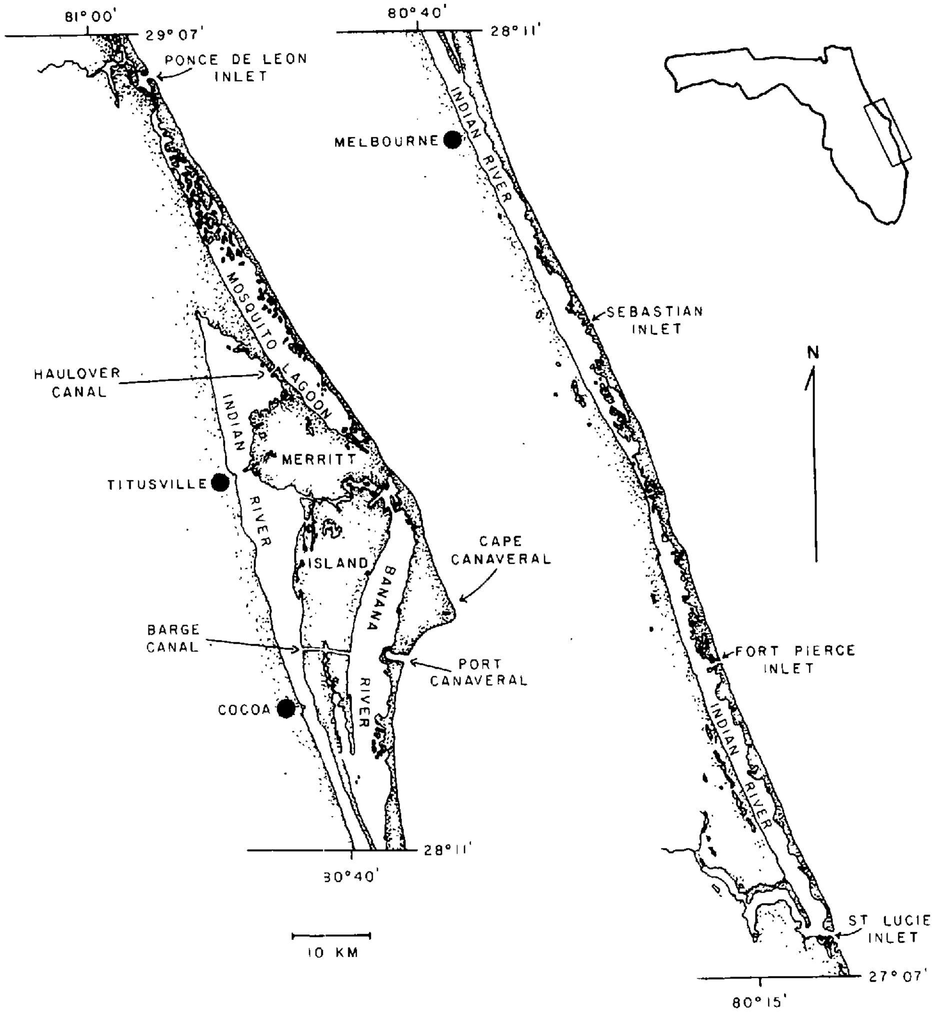

Figure 1. Map of the Indian River lagoon system, Florida.

Ehrhart, 1982). The nets were constructed of braided nylon twine. Length varied from 90–230 m, stretch mesh ranged from 30.5–40.6 cm, and depth was 3.7 m. The nets were deployed, either singly or in series, at least once each month in Mosquito Lagoon and Indian River and bimonthly in Banana River. Deployment averaged 5 days per month, but effort was more intense during the warm months, May through September. When deployed, the nets were left in place for as little as 24 h to as long as 147 h. Nets were checked and the contents removed at least three times daily, at dawn, mid-day, and dusk. Occasionally they were checked at night.

Because detailed records were kept on all collecting with large-mesh gill nets, it was possible to quantify the sampling effort. A 24-h net day (NetDay24) is defined as 100 m of net fished for 24 h, calculated as follows:

$$\text{NetDay24} = \text{m net deployed}/100 \times \text{h net deployed}/24.$$

Fishing effort was also calculated separately for daylight and night-time sampling as follows:

$$\text{NetDay12 or NetNite12} = \text{m net deployed}/100 \times \text{daylight (night-time) h net deployed}/12.$$

The hours of 0600 and 1800 were used as the change-over times between night and day. Catch-per-unit-effort data are summarized by season as follows: December–February = Winter, March–May = Spring, June–August = Summer, September–November = Fall.

Eight-one of the sharks captured were returned to the laboratory for examination. Specimens were weighed while fresh to the nearest 0.1 kg on a platform balance or spring scale. They were then either measured and autopsied fresh or frozen for examination at a later date. A series of measurements was taken, but only straight-line total length (TL) is used herein. Sex and maturity status were evaluated on the basis of clasper and gonad morphology (males) or gonad and uterine development (females) (Springer, 1960; Clark and von Schmidt, 1965). Stomach contents were identified to the lowest possible taxon.

RESULTS

Diet

Sixty-four *C. leucas* stomachs were examined; 14 were empty and 50 (78%) contained some food material. The following food items were found (numbers following items are, first, the number of stomachs containing the item and, last, the total number of that item found): Crustacea—*Callinectes* sp. 5, 5; *Panaeus* sp. 1, 1; unidentified crustacean remains 1, ?; Pisces—*Archosargus probatocephalus* 2, 3; Ariidae 17, 20; *Brevoortia* sp. 4, 10; Carangidae 2, 2; *Carcharhinus leucas* 1, 1; *Cynoscion* sp. 2, 2; *Dasyatis* sp. 13, 13; *Elops saurus* 1, 1; *Lagodon rhomboides* 1, 1; *Mugil* sp. 5, 9; *Ophichthus* sp. 1, 1; *Opsanus tau* 1, 1; *Synodus foetens* 1, 1; *Trinectes maculatus* 1, 1; unidentified teleost remains 21, ?.

The diet consisted almost exclusively of fishes. Items most frequently encountered were ariid catfishes, *Arius felis* and *Bagre marinus*, and stingrays, primarily *Dasyatis sabina* and *D. sayi*. Stingrays are common in the lagoon system (Snelson and Williams, 1981) and the fact that their tail spines were often found imbedded in the jaws, jaw musculature, and in various organs in the body cavity of bull sharks suggests that they may be more important food items than reflected in the above data. The head of a small shark, found in the stomach of a 162 cm TL *C. leucas* collected 8 September 1976, was identified as that of a bull shark on the basis of the jaws and teeth (Springer, 1938). Based on tooth size, the shark eaten was 80–90 cm TL. One *C. leucas* 181 cm TL had eaten six menhaden (*Brevoortia* sp.). Since all were in a similar state of digestion, it appeared that they had all been ingested during one feeding bout.

Abundance and Seasonality

Seasonal fishing effort and bull shark captures in the three lagoon basins are summarized in Table 1. The overall capture rate was 0.20 sharks/NetDay24. However, capture rate varied substantially among the three basins. Based only on the data for seasons during which there was some netting in all three bodies of water (Spring 1977 through Fall 1978), capture rates were 0.08/NetDay24 for Mosquito Lagoon, 0.41/NetDay24 for Indian River, and 0.36/NetDay24 for Banana River.

Capture rates also exhibited substantial temporal variation (Fig. 2). No *C. leucas* were netted during the winter season. Otherwise, there were no clear seasonal trends. The peak catch rate in the fall of 1976 was caused by high and virtually identical values in both Mosquito Lagoon and Indian River (Table 2), especially during the month of September. Catch rates were also high in the fall, especially October, of 1978 in Indian River and in the spring, especially April, of 1977 in Banana River. Seasonal discrepancies between the three bodies of water were dramatic. For example, during the fall of 1978, the catch-per-unit-effort was 1.26 in Indian River but was zero in both Mosquito Lagoon and Banana River.

Because of spatial and seasonal variability in catch rates and missing 1976 data in Banana River, it is difficult to identify any meaningful annual differences in abundance. The overall spring through fall catch rates for 1977 and 1978 were

Table 1. Summary of sampling effort and *Carcharhinus leucas* caught during netting operations in the Indian River lagoon system, Florida

Year and Season	Mosquito Lagoon		Indian River		Banana River	
	Sampling Effort NetDay24	Sharks Caught	Sampling Effort NetDay24	Sharks Caught	Sampling Effort NetDay24	Sharks Caught
1976						
Summer	2.15	0	10.69	3	—	—
Fall	19.89	23	11.35	13	—	—
1977						
Winter	11.06	0	21.37	0	—	—
Spring	51.05	7	19.29	11	2.34	3
Summer	106.60	8	29.62	7	10.19	6
Fall	83.11	1	20.89	9	3.80	0
1978						
Winter	12.18	0	8.52	0	4.63	0
Spring	51.39	0	15.79	8	2.34	1
Summer	51.64	13	8.40	0	2.43	0
Fall	27.98	0	7.92	10	2.22	0
1979						
Winter	2.24	0	—	—	—	—
Totals	419.29	52	153.84	61	27.95	10

very similar, 0.16 and 0.19/NetDay24, respectively. Despite the unusually high catch rate in the fall of 1976, the catch rate for the summer of 1976 (0.23/NetDay24) was not substantially different than the summer catch rate for 1977 (0.14) and 1978 (0.21).

Bull sharks were caught at a higher rate during darkness than during daylight (Fig. 2). This difference was consistent throughout the study in all three lagoon basins. Tank studies have shown that this species can visually discriminate between nets of several colors (Wallace, 1972). Therefore, it was unclear whether low catch rates during daylight hours reflected reduced activity, altered movements, or net avoidance.

Population Characteristics

The size distribution of the 80 specimens measured is shown in Table 2. Most of the specimens captured but not measured were estimated in the field to be 125–180 cm TL. The 14 small specimens ranged from 73.5–85.8 cm TL ($\bar{x}$ = 77.6) and were collected in the months of June (4 specimens), July (9), and August (1). Several of these specimens retained fresh umbilical scars.

Of the 122 *C. leucas* sexed, 57 were males and 65 were females. Except for one female, every specimen that was critically examined was sexually immature. The largest immature male was 182.5 cm; the largest immature female was 201.6 cm. The single mature female was collected 8 May 1975 in Mosquito Lagoon. This specimen was 249 cm TL, weighed 168 kg, and carried 12 near-term embryos. The embryos, seven males and five females, measured 60.8–70.6 cm TL ($\bar{x}$ = 66.4) and weighed 1.84–2.82 kg ($\bar{x}$ = 2.39). One other unusually large female was netted 6 May 1979 in Mosquito Lagoon, but it could not be returned to the laboratory for examination. Field records indicated that it was in excess of 7 ft TL and had an unusually large girth with a distinctively bulging abdomen. We believe that this individual was another pregnant female.

Weight data for 78 immature *C. leucas* were log transformed and plotted against

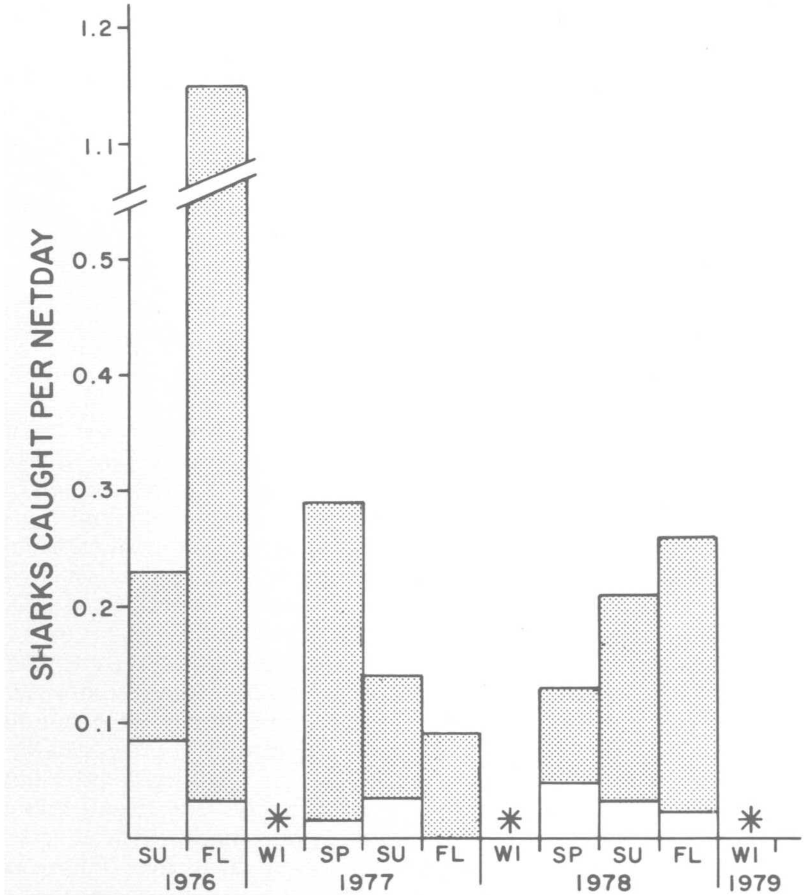

Figure 2. Seasonal catch of *Carcharhinus leucas* per NetDay in the Indian River lagoon system, Florida. The height of each seasonal bar indicates sharks caught per NetDay24. The open portion of each bar is day-time catch (sharks per NetDay12) and the shaded portion of each bar is the night-time catch (sharks per NetNite12). Data from the three lagoon basins are pooled. SU = summer, FL = fall, WI = winter, SP = spring; * indicates value of zero.

total length. The scatter of points assumed nearly a straight-line relationship, and the statistics for the least-squares linear regression were: $\log_{10}\text{wt} = -0.270 + (0.011)(\text{TL})$; $r = 0.98$; $P(F) < 0.0001$.

Discussion

Our data reveal that the lagoon population of *C. leucas* feeds almost exclusively on fishes, as has been reported for bull sharks elsewhere in Florida (Clark and von Schmidt, 1965; Dodrill, 1977). The species is generally acknowledged to be predisposed to feeding on other elasmobranchs and that observation is supported by the importance of stingrays (*Dasyatis* sp.) in the diet of the Indian River population. Other than the "shark-eat-shark" episodes provoked by Vorenberg (1962), this study documents the first case of cannibalism in this species (Gudger, 1932; Tuma, 1976), although other sharks are regularly eaten (Springer, 1960;

Table 2. Length-class frequency distribution for *Carcharhinus leucas* from the Indian River lagoon system, Florida

Sex	Total Length Size Group (cm)									$\bar{x}$ TL (cm)	N
	70–89	90–109	110–129	130–149	150–169	170–189	190–209	210–229	230–249		
Males	9	—	3	10	19	1	—	—	—	135.8	42
Females	5	—	3	11	10	7	1	—	1*	145.3†	38
Total	14	—	6	21	29	8	1	—	1	140.2†	80

* Mature, pregnant.
† Mean excludes one pregnant female 248.9 cm TL.

1963; Sadowsky, 1971; Bass et al., 1973; Tuma, 1976). Ariid catfishes, the most abundant food item found in Indian River bull sharks, are also major dietary items in Brazilian lagoons (Sadowsky, 1971).

Sadowsky (1971) noted that *C. leucas* in Brazilian lagoons did not feed on puffers of the genus *Sphoeroides*, even though they were abundant and regularly consumed by other sharks. Likewise, puffers, especially *S. nephelus*, are common in Florida lagoons (Snelson, 1983) but were not consumed by bull sharks. The related *Chilomycterus schoepfi*, also common in the lagoon system, seems to be an important food item for Indian River lemon sharks, *Negaprion brevirostris*, (Snelson and Williams, 1981) but was never consumed by bull sharks. Despite a substantial population of sea turtles, especially small *Chelonia mydas*, in the Indian River lagoons (Ehrhart, 1983), no sea turtle remains were found in bull shark stomachs. The species occasionally feeds on sea turtles in other parts of its range (Bass et al., 1973; Tuma, 1976).

Sharks captured by passive gill-netting are a reflection of both abundance and activity. Without more refined data, it is impossible to speculate on how these two variables affected the catch rates reported herein. The large-mesh gill nets were not set for the explicit purpose of capturing bull sharks. Instead, sharks were an incidental catch in nets set primarily for capturing sea turtles. If more attention had been paid to the details of capturing sharks, it is likely some of the temporal variability in catch rates could have been reduced.

Although no bull sharks were netted in the winter season (December–February), they are known to be present during every month of the year except December. Snelson and Bradley (1978) reported two immature bull sharks killed in Banana River by cold weather on 21 January 1977, and Dodrill (1977) and Gilmore et al. (1978) noted three immature individuals killed in Banana Creek (an Indian River tributary) during the same cold period. Furthermore, on two occasions, we observed immature *C. leucas* concentrated around the heated outflow of power plants on the Indian River during the month of February. Thus, the absence of gill-net captures during the winter season may reflect depressed activity caused by low water temperatures (typically 10–15°C in January and February) rather than emigration from lagoonal waters.

Because of seasonal variability, differences in catch rates between the three lagoon basins are difficult to interpret. However, we feel that the overall low catch rate in Mosquito Lagoon compared to the other two basins is real. Substantial effort was expended in Mosquito Lagoon at diverse localities because sea turtles were more susceptible to netting there (Ehrhart, 1983). In contrast, sea turtles were never netted in Banana River and very little netting effort was expended there. In view of the very limited netting in Banana River, the catch rate suggests a rather substantial population of immature bull sharks there, as in Indian River.

Within the study area, Mosquito Lagoon, of the three basins studied, has the shortest and most direct connection to an ocean inlet (Ponce de Leon Inlet). Therefore, proximity to ocean access does not appear to enhance bull shark abundance. We know of no environmental factor except salinity that might influence differential abundance in the lagoon basins. Mosquito Lagoon was substantially more saline ($\bar{x}$ = 32.5‰) than Indian River ($\bar{x}$ = 29.6‰) or Banana River ($\bar{x}$ = 26.7‰). Mosquito Lagoon was often hypersaline during the dry season, and salinities as high as 42‰ have been recorded (Snelson and Williams, 1981). Coastal bull shark populations appear to prefer low salinity waters (Springer, 1960; Caillouet et al., 1969), and the species often enters strictly fresh water (Myers, 1952; Thorson et al., 1966a; 1966b; Bass et al., 1973; Thomerson et al., 1977; Burgess and Ross, 1980). Bull sharks in our study area may have actively avoided the higher salinity waters of Mosquito Lagoon.

Sharks 86–116 cm TL were not recorded during this study. This hiatus probably is an artifact produced by gear bias. All of the small individuals were collected in the small-mesh gill nets, whose strength and mesh size seemed to preclude the capture of larger specimens. The commercial fisherman often reported tears and holes in his nets that he felt were caused by larger sharks. On the other hand, the large-mesh gill nets we employed clearly were unsuitable for the capture of small bull sharks. Thus, the size hiatus probably resulted because neither net type was suitable for sampling individuals 86–116 cm TL. Dodrill (1977) recorded two individuals in the missing size range from further south in the Indian River system, a female 98.8 and a male 92.1 cm TL, both captured in April 1976. An alternative explanation, however, for the virtual absence of sharks 86–116 cm TL from the lagoons is that they leave the estuary temporarily during this phase of their life. Thorson (1976) noted greatly reduced abundance of *C. leucas* 80–109 cm TL in the Rio San Juan system and suggested that they went to sea for an unknown period before returning to the river system.

The absence of immature sharks larger than about 200 cm TL is significant since the large-mesh gill nets are known to effectively capture both bull and lemon sharks as large as 250–260 cm TL (Snelson and Williams, 1981). Bull sharks in Florida begin to mature at about 200–215 cm TL (Springer, 1960). The smallest breeding male and pregnant female recorded from Florida waters are 225 and 233 cm TL, respectively (Clark and von Schmidt, 1965). Bull sharks apparently emigrate from the lagoons as they approach sexual maturity. Thorson (1976) noted a similar pattern in the Nicaragua population of *C. leucas*.

Because of gear bias and selectivity, our data contribute virtually nothing toward understanding growth rates in lagoon bull sharks. Limited observations presented by Clark and von Schmidt (1965), Sadowsky (1971), and Dodrill (1977) suggest that young attain about 100 cm TL in their first year. Dodrill (1977) thought that 150–200 cm TL bull sharks were about 22–36 months old. Based on these suggestions, immature bull sharks may reside in lagoonal waters for about three years. However, these suggested growth rates are far greater than those reported for *C. leucas* in the Lake Nicaragua–Rio San Juan system by Thorson and Lacy (1982). They estimated that bull sharks 150–200 cm TL were 6–11 years old and that three-year-old individuals were no larger than about 120 cm TL.

Life History Outline

Data presented herein and by Dodrill (1977), along with data or observations on bull sharks elsewhere, make it possible to piece together an outline of the probable life history pattern of the *C. leucas* population on the central east coast of Florida. Although some points in this story are tenuous, other aspects appear to be adequately supported by the available evidence.

Maturing and adult *C. leucas* apparently reside primarily in deeper waters off the coast of central Florida, and perhaps further south (Springer, 1963). Adult bull sharks generally have been recognized as primarily summertime residents in Florida waters (Springer, 1940; Clark and von Schmidt, 1965), and no adults are present along east coast beaches between November and April (Dodrill, 1977). Females 240–265 cm TL, most carrying near-term embryos, begin to appear in shallow inshore waters in late April (Clark and von Schmidt, 1965; Dodrill, 1977). They apparently enter the Indian River lagoons between May and July to give birth. Dodrill (1977) never captured a female carrying full-term embryos from Brevard County beaches in June, July, or August; nor did he capture newborn young along the beaches in that time period. In contrast, this study has documented both a pregnant female with near-term embryos and newborn pups in the lagoons in late spring and summer months. Dodrill (1977) also recorded an abundance of small *C. leucas* in the Indian River during summer.

In Florida, *C. leucas* are born at a size of 60–80 cm TL, with an average of about 75 cm (Clark and von Schmidt, 1965; Dodrill, 1977). Parturition apparently takes place in lagoonal waters in June and July. The pregnant female we report was captured in May and carried embryos that averaged 66 cm TL. The small free-living specimens captured in the lagoons were in the right size range (73.5–85.8 cm) and collected in the right time frame (June–August) to be neonates. Furthermore, several of these specimens had fresh umbilical scars.

Some newborn *C. leucas* may move seaward through inlets to populate inshore coastal waters. Based on two specimens <1 m TL collected from the Atlantic beaches in November and January, Dodrill (1977) suggested that the young did not spend their first winter in lagoonal waters. In fact, there may be a period, corresponding to the missing size range noted herein, during which the young obligatorily return to the sea. As noted above, however, the absence of winter captures of young sharks in the lagoons may reflect inactivity rather than emigration. If pups do leave the estuary during their first winter, many of them return the following spring. Juveniles 120–180 cm TL are present in lagoon waters year-round and apparently reside there, for an unknown period of time, until they begin sexual maturation. Juveniles also are present along ocean beaches throughout the year (Dodrill, 1977). If there is annual winter emigration from the lagoons, its magnitude is unclear.

Adult females apparently leave the lagoons after parturition (Dodrill, 1977). Mating may occur in June or July (Clark and von Schmidt, 1965; Dodrill, 1977). However, mature males are rare in the inshore waters of east Florida, and mating may occur elsewhere (Dodrill, 1977). Females do not necessarily bear young every year, and the available data suggest a gestation period of 10–12 months (Clark and von Schmidt, 1965; Jensen, 1976; Dodrill, 1977).

Acknowledgments

The netting operations that produced most of the sharks reported herein were under the direction of Dr. L. M. Ehrhart. We are indebted to him and his students and technicians, the sea turtle study group at the University of Central Florida, for the long hours and special efforts required to provide us with specimens. The following individuals deserve special recognition: T. R. Clabaugh, R. J. Demmer, J. D. Galluzzo, M. A. McGehee, M. T. Mendonca, and B. Z. Thompson. We thank A. Heredia for providing small sharks collected in his commercial netting operations. For assistance in collecting and examining sharks, we acknowledge W. K. Bradley, Jr., R. A. Byles, H. L. Large, J. A. Phillips Provancha, M. J. Provancha, J. S. Turner, and J. D. Wetherington. We thank J. W. Dodrill for permission to cite unpublished data from his M.S. Thesis. An earlier version of this manuscript was critically reviewed by G. H. Burgess, Eugenie Clark, J. W. Dodrill, Stewart Springer, and T. B. Thorson. Financial support was provided through a contract with the John F. Kennedy Space Center, National Aeronautics and Space Administration (NAS 10-8986); and space and logistic support were provided by the Merritt Island National Wildlife Refuge. This paper is contribution number 32 in the Merritt Island Ecosystems Studies series.

LITERATURE CITED

Bass, A. J., J. D. D'Aubrey and N. Kistnasamy. 1973. Sharks of the east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). Oceanogr. Res. Inst. Invest. Rept. No. 33. 168 pp.

Burgess, G. H. and S. W. Ross. 1980. *Carcharhinus leucas* (Valenciennes), Bull Shark. Page 36 *in* D. S. Lee et al. Atlas of North American freshwater fishes. N.C. State Mus. Natur. Hist., Raleigh. 854 pp.

Caillouet, C. W., Jr., W. S. Perret and B. J. Fontenot, Jr. 1969. Weight, length and sex ratio of immature bull sharks, *Carcharhinus leucas,* from Vermilion Bay, Louisiana. Copeia 1969: 196–197.

Clark, E. and K. von Schmidt. 1965. Sharks of the central Gulf coast of Florida. Bull. Mar. Sci. 15: 13–83.

Dodrill, J. W. 1977. A hook and line survey of the sharks found within five hundred meters of shore along Melbourne Beach, Brevard County, Florida. M.S. Thesis, Florida Institute of Technology, Melbourne. 304 pp.

Ehrhart, L. M. 1983. Marine turtles of the Indian River lagoon system. Fla. Sci. 46: 337–346.

Gilmore, R. G. 1974. A regional description and checklist of fishes of the Indian River. Pages 119–183 *in* Indian River Study, 1973–1974 Annual Rept. Vol. I. Harbor Branch Consortium, Florida.

———. 1977. Fishes of the Indian River lagoon and adjacent waters, Florida. Bull. Fla. St. Mus., Biol. Sci. 22: 101–148.

———, L. H. Bullock and F. H. Berry. 1978. Hypothermal mortality in marine fishes of south-central Florida, January, 1977. Northeast Gulf Sci. 2: 77–97.

Gudger, E. W. 1932. Cannibalism among the sharks and rays. Sci. Monthly 34: 403–419.

Jensen, N. H. 1976. Reproduction of the bull shark, *Carcharhinus leucas,* in the Lake Nicaragua-Rio San Juan system. Pages 539–559 *in* T. B. Thorson, ed. Investigations of the ichthyofauna of Nicaraguan lakes. School of Life Sciences, University of Nebraska, Lincoln. 663 pp.

Mendonca, M. T. and L. M. Ehrhart. 1982. Activity, population size and structure of immature *Chelonia mydas* and *Caretta caretta* in Mosquito Lagoon, Florida. Copeia 1982: 162–168.

Mulligan, T. J. and F. F. Snelson, Jr. 1983. Summer-season populations of epibenthic marine fishes in the Indian River lagoon system, Florida. Fla. Sci. 46: 250–276.

Myers, G. S. 1952. Sharks and sawfishes in the Amazon. Copeia 1952: 268–269.

Nichols, J. T. 1917. Ichthyological notes from a cruise off southwest Florida, with a description of *Gobiesox yuma* sp. nov. Bull. Amer. Mus. Natur. Hist. 37: 873–877.

Sadowsky, V. 1971. Notes on the bull shark, *Carcharhinus leucas* in the lagoon region of Cananeia, Brazil. Bolm Inst. Oceanogr. Sao Paulo 20: 71–78.

Snelson, F. F., Jr. 1976. A study of a diverse coastal ecosystem on the Atlantic coast of Florida: ichthyological studies. Vols. I, 122 pp. and II, 287 pp. Final Rept., Grant NGR-10-019-004. NASA, J. F. Kennedy Space Center, Florida.

———. 1980. A continuation of base-line studies for environmentally monitoring space transportation systems at John F. Kennedy Space Center. Vol. III, Pt. 1, 119 pp. Ichthyological Studies; Ichthyological survey of lagoonal waters. KSC TR 51-2, NASA Contract Report 163122, J. F. Kennedy Space Center, Florida.

———. 1983. Ichthyofauna of the northern part of the Indian River lagoon system, Florida. Fla. Sci. 46: 187–206.

——— and W. K. Bradley, Jr. 1978. Mortality of fishes due to cold on the east coast of Florida, January, 1977. Fla. Sci. 41: 1–12.

——— and S. E. Williams. 1981. Notes on the occurrence, distribution, and biology of elasmobranch fishes in the Indian River lagoon system, Florida. Estuaries 4: 110–120.

Springer, S. 1938. Notes on the sharks of Florida. Proc. Fla. Acad. Sci. 1939: 9–41.

———. 1940. The sex ratio and seasonal distribution of some Florida sharks. Copeia 1940: 188–194.

———. 1960. Natural history of the sandbar shark, *Eulamia milberti.* Fish. Bull. 61: 1–38.

———. 1963. Field observations on large sharks of the Florida-Caribbean region. Pages 95–113 *in* P. W. Gilbert, ed. Sharks and survival. D. C. Heath Co., Boston. 578 pp.

Thomerson, J. E., T. B. Thorson and R. L. Hempel. 1977. The bull shark, *Carcharhinus leucas,* from the upper Mississippi River near Alton, Illinois. Copeia 1977: 166–168.

Thorson, T. B. 1976. The status of the Lake Nicaragua shark: an updated appraisal. Pages 561–574 *in* T. B. Thorson, ed. Investigation of the ichthyofauna of Nicaraguan lakes. School of Life Sciences, University of Nebraska, Lincoln. 663 p.

——— and E. J. Lacy, Jr. 1982. Age, growth rate and longevity of *Carcharhinus leucas* estimated from tagging and vertebral rings. Copeia 1982: 110–116.

———, C. M. Cowan and D. E. Watson. 1966a. Sharks and sawfish in the Lake Izabal–Rio Dulce system, Guatemala. Copeia 1966: 620–622.

———, D. E. Watson and C. M. Cowan. 1966b. The status of the freshwater shark of Lake Nicaragua. Copeia 1966: 385–402.

Tuma, R. E. 1976. An investigation of the feeding habits of the bull shark, *Carcharhinus leucas*, in the Lake Nicaragua–Rio San Juan system. Pages 533–538 *in* T. B. Thorson, ed. Investigation of the ichthyofauna of Nicaraguan lakes. School of Life Sciences, University of Nebraska, Lincoln. 663 pp.

Vorenberg, M. M. 1962. Cannibalistic tendencies of lemon and bull sharks. Copeia 1962: 455–456.

Wallace, L. 1972. Reactions of the sharks *Carcharhinus leucas* (Muller & Henle) and *Odontaspis taurus* (Rafinesque) to gill net barriers under experimental conditions. Oceanogr. Res. Inst. Invest. Rept. No. 30, 24 pp.

DATE ACCEPTED: August 16, 1982.

ADDRESS: *Department of Biological Sciences, University of Central Florida, Orlando, Florida 32816;* PRESENT ADDRESSES: *(T.J.M.) Department of Zoology, University of Maryland, College Park, Maryland 20742; (S.E.W.) Miller and Miller, Inc., 214 East Lucerne Circle, Orlando, Florida 32801.*