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The Status of the Lake Nicaragua Shark: An Updated Appraisal

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INTRODUCTION

In 1966, my co-workers and I (Thorson, Watson and Cowan) presented data refuting the traditional claim that the sharks of Lake Nicaragua originated as a population of Pacific sharks, trapped, by volcanic damming, in the Nicaraguan Depression, which gradually became a freshwater lake and overflowed to form the present channel of the Río San Juan. According to this explanation the sharks became landlocked, and Atlantic sharks were prevented from entering the lake by way of the effluent Río San Juan by the presence of several rapids. By careful morphometric comparison of sharks from both ends of the lake, the river, and the rivermouth, we confirmed the conclusion of Bigelow and Schroeder (1961) that *Carcharhinus nicaraguensis* belongs in the synonymy of *C. leucas*, the bull shark of the Atlantic Ocean. Since *C. leucas* is a euryhaline shark, known to ascend many rivers and to enter a number of lakes in the tropics and subtropics, and since we found that the rapids did not stop boats, including small freight barges, from ascending and descending the river, we proposed that the sharks probably move freely up and down the river between the sea and the lake.

Since 1966, an extensive tagging program has demonstrated beyond any further doubt (Thorson, 1971) that the sharks move from the Caribbean Sea to Lake Nicaragua and vice versa. At the time of this writing, of 1450 post-juvenile sharks tagged at the various river mouths on the Caribbean Coast, ten have been recovered in Lake Nicaragua; and of 146 tagged at San Carlos, where the river leaves the lake, 28 have been recovered along the Caribbean Coast, most of them at the various outlets of the Río San Juan. Except for these basic facts, the results of the tagging program have not yet been published.

The myth of the landlocked shark, of Pacific origin, must now certainly have been laid to rest, although it will no doubt persist for many years in the public mind. This, however, makes it no less a unique and interesting species. The Lake Nicaragua - Río San Juan population of *C. leucas* remains the classic example of "freshwater" sharks, and there probably is no other concentration of this widely-distributed species as great as at the various mouths of the Río San Juan, especially that branch known as the Río Colorado.

Although a number of questions about this species still remain unanswered or poorly understood, several aspects of its biology have been investigated, and some questions now have at least partial answers.

THE QUESTION OF REPRODUCTION IN THE LAKE

Among the most basic of these questions is whether or not the bull shark reproduces in Lake Nicaragua. This question was studied by Jensen (1976), whose results are presented elsewhere in this volume.

The discredited idea that the lake sharks are landlocked implies that the fresh water of the lake provides the ecological requirements for completion of the shark's life cycle, including copulation, gestation and parturition. Disproving that the sharks are landlocked does not in itself necessarily eliminate this possibility.

Marden (1944) and Carr (1953) supported the occurrence of freshwater reproduction, stating that pregnant females were taken by fishermen in Lake Nicaragua and that young were sometimes aborted when the females were landed. Herre (1955, 1956) stated flatly that neither sharks nor sawfish reproduce in lakes and rivers, but that they return to the sea to breed. He pointed out that no proof has ever been provided that the sharks breed in Lake Nicaragua. Astorqui (1967) agreed that the sharks probably breed in the sea. Reports of births in the lake have been based solely on accounts by fishermen and local residents. I know of no verification based on preserved specimens, photographs or specific reports in the zoological literature. Therefore, I looked into a report (Anon., 1965) in a popular magazine that fetal shark meat had been served to a party of fishermen at a fishing camp on the Río San Juan just above Rápidos Toro, about 130 km up the river from the sea (Thorson, 1965). The pups were three in number, 45 to 59 cm in length (slightly under birth size), and they were documented by photographs. Another pregnant female with 10 young, 51 to 58 cm long (within the range of full-term pups), was taken in Jensen's study at El Castillo, a few km below the location where the first litter was taken. Jensen took no pregnant females at San Carlos, nor were any to my knowledge ever taken there in my tagging program. Jensen studied 66 pregnant or slightly post-pregnant females, all except the El Castillo one taken in the vicinity of the two mouths of the Río Colorado. He concluded that reproduction normally takes place around the river mouths, as stated by Springer (1963), but he pointed out the possibility that occasionally a female may drop her young in the lake.

I have had persistent reports to that effect from fishermen, some of whom I have good reason to believe. Tagging results indicate that an undetermined fraction of the sharks at the river mouth, apparently in no special pattern, eventually make their way up the river and into the lake. The passage up the river appears to have little or no screening effect on sex or size except on the largest females. Although females up to 251 cm in length were taken at the river mouths, the largest taken any place up the river was 206 cm (at San Carlos). Otherwise, we have taken both males and females of all post-juvenile sizes at San Carlos. The two pregnant females taken near El Castillo attest to at least the occasional movement of pregnant females up the river. If they should find themselves in the lake at full term, parturition would undoubtedly proceed. Such random occurrences are very likely the basis for the reports of Marden (1944), and Carr (1953) and fishermen that females drop their young in the lake.

Survival of young in Fresh Water

There is no reason to doubt that the pups would survive if born in the lake. Of the 1335 juvenile sharks taken at Barra del Colorado, most were taken from fresh water, although a few were taken outside the river mouth, possibly in salt or brackish water. Their greatest concentrations were definitely in fresh water, especially in Laguna Agua Dulce, a body of standing water that extends from near the mouth of the Río Colorado about 12 km northward, parallel to the sea. They also occur abundantly below the rapids at El Castillo, indicating that some move up the river. Although only one juvenile shark was taken in my tagging program at San Carlos, fishermen and local residents reported taking them farther downstream and in tributaries of the Río San Juan. They are occasionally taken in Lake Nicaragua by hook and line, and have also been taken there in seining operations (Hagberg, 1968). Whether these were born in the lake or moved up the river is of course unknown. Their concentration at El Castillo would indicate the latter to be more likely.

Fetal pups already have the full range of urea tolerance for a euryhaline life. Their body fluids, reflecting those of their mothers, range from the hyperuremic condition of sharks residing in sea water to the reduced urea levels found when they are in fresh water (Thorson and Gerst, 1972). We placed near-term young taken from pregnant females and neo-natal young taken with hook and line in tanks of water ranging from fresh water to full-strength sea water. Although for various reasons we had difficulty keeping sharks alive in our holding facilities, the young sharks appeared to do equally well in fresh water and sea water.

We also tagged 86 *ex utero* pups and released them in the river near its mouth. Nine were recovered in fresh water from five to 17 days later, so we know that they survived and were taking bait. One of these was caught in fresh water after five days, was released a second time and caught in fresh water a third time 16 days later for a total of 21 days at liberty. Six were released a second time and so far have not been recovered.

Obstacles to Freshwater Reproduction

The hypothetical completion of all aspects of reproduction in fresh water appears to encounter no difficulty concerning parturition or the ability of the young to survive in fresh water. However, some uncertainties remain. The first is the initiation of mating behavior and actual copulation. These have to my knowledge never been observed in any of their phases in *C. leucas* in fresh water; nor have they been seen in marine or brackish water, in the wild. Pursuit and nipping of the females by the males have been observed in captive bull sharks (held in sea water) by W. Weiler and G. Klay (pers. comm.); and cuts and abrasions on females, presumably the result of the courting behavior of males, have been reported in large, free-ranging carcharhinids in general, although not specifically in *C. leucas*, by Springer (1967). Since *C. leucas* occurs regularly is sea water along the whole Atlantic Coast, from Brazil to well up the East Coast of the United States, and since the young are apparently normally dropped in brackish water along the coast, it appears likely that the preliminaries to reproduction and the actual copulation also occur along the coast. No evidence is at present available, but investigation may show whether or not a saline medium is essential for pheromones or other stimuli to trigger the steps in the mating behavior.

A second uncertainty concerns the activation of sperm and transfer of sperm from male to female. Gilbert and Heath (1972) have recently presented their own and previous observations concerning the clasper-siphon sac structure and function of elasmobranchs, especially as exemplified by *Squalus acanthias* and *Mustelus canis*. As summarized by them, during breeding activity, the male shark pumps sea water into its siphon sacs by repeated flexing of its claspers. The claspers are inserted, one at a time, into the oviducts of the female. A compressor muscle forces out the content of the siphon sac, including the sea water and a clear, sticky secretion of the goblet-like cells in the siphon sac lining. Semen, expelled from the urogenital papilla, is washed by the sea water through the clasper groove into the oviduct. The siphon sac secretion lubricates the claspers before insertion and may have an activating action on the sperm and may stimulate contraction of the oviduct, thus facilitating passage of the sperm as well as fertilization.

Although not claimed by Gilbert and Heath, and no direct evidence is available, the possibility must be considered that brackish or sea water is required for the activation of sperm and effective fertilization of the ova. Sperm cells of most animals require rather narrow limits of physical conditions such as pH and salinity. It appears unlikely that such a fragile entity as a spermatozoon would be capable of functioning effectively in fresh water if its physiological design were adapted to functioning in sea water. Most elasmobranchs certainly copulate in sea water and *Carcharhinus leucas* is known to occur commonly in sea water and apparently drops its young in coastal waters, so it is reasonable to expect copulation to take place in the sea. If this is the normal procedure, it seems improbable that copulation would occur in fresh water, and if it did, it would likely be unsuccessful in affecting fertilization. It must be noted, however, that the South American freshwater stingrays of the family Potamotrygonidae, which have abandoned the retention of high concentrations of urea, so universally found in marine elasmobranchs (Thorson, Cowan and Watson, 1967; Thorson, 1970), also reproduce in fresh water, so their sperm have obviously become adapted to freshwater activation. The euryhaline sawfish, *Pristis perotteti*, although it has, like *C. leucas*, retained its urea-concentrating ability (Thorson 1967), appears to reproduce in fresh water (Thorson, 1976). Whether or not it may also reproduce in the sea remains unknown, and its requirements for sperm activation, as well as those of *C. leucas*, require further study.

Life History Considerations

Further questions regarding the completion of the life cycle entirely in fresh water arise when the size distribution of *C. leucas* is examined. Total length measurements have been tabulated and graphed (Fig. 1) for 3121 sharks taken near the three outlets of the Río San Juan during a five-year tagging program (1966–1970). Fig. 1 shows that the bull shark population around the river mouth and estuary consists of large numbers of juveniles from about 50 to 79 cm

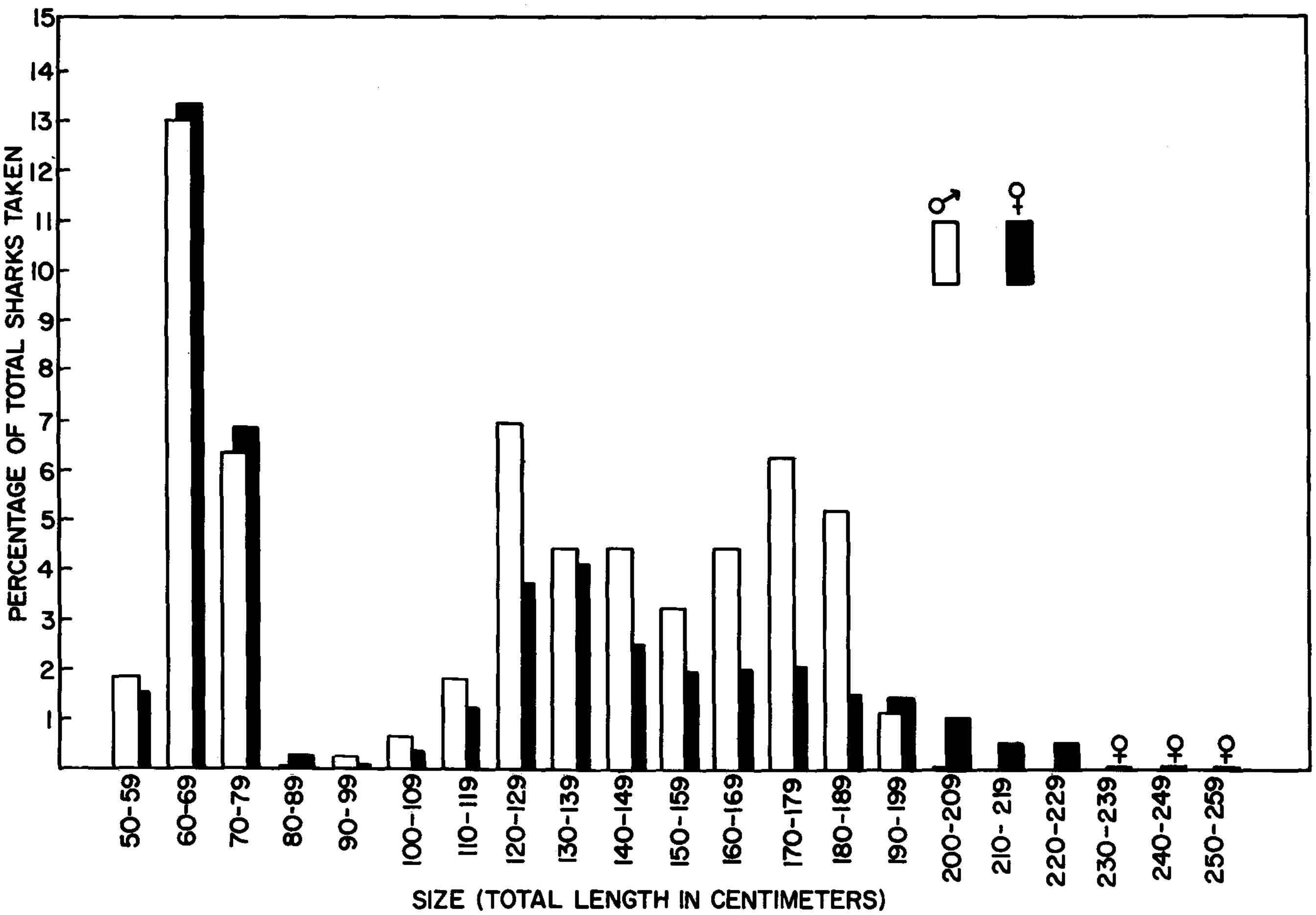

FIGURE 1. Size distribution of 3121 *Carcharhinus leucas* taken at the three mouths of the Río San Juan, 1966 through 1970. Through 89 cm total length, they are considered juveniles; 90 cm or more, post-juveniles; at approximately 160-170 cm, they become sexually mature.

in total length and post-juveniles 100 cm or more in length, but that there is an almost total absence of intermediate sizes (80 to 99 cm). What happens to sharks of this size range has not been determined, but they apparently go to sea for an unknown period. Whether or not this represents an obligatory sojourn in salt water is not know, but if so, it would prevent the life cycle from occurring strictly in fresh water. Although neo-natal sharks occur abundantly in fresh water, it is also not known if this is obligatory, since they definitely can tolerate both fresh water and full strength sea water from birth. However, it appears likely that the life cycle normally begins in fresh water and that this phase continues until they have reached the size of the missing part of the range, when they may for a time experience a marine phase. Following this, at lengths of about 100 cm, the sharks begin to reappear in the estuarine population as post-juveniles, which are now apparently thoroughly euryhaline. As shown by tag recoveries, they move freely about the freshwater channels, in and out the river mouths, and sometimes various distances up the river and into Lake Nicaragua. Furthermore, a large percentage of those tagged in Lake Nicaragua are recovered in the coastal areas.

There is no evidence that post-juvenile *C. leucas* has an obligatory freshwater period; nor is there evidence of any general seasonal migration up or down the river, or that the sharks that move upstream are of any special size group or are fulfilling any special requirement of their life cycle. There are occasional claims made locally that sharks are most plentiful, for instance below the El Castillo rapids, at certain times of the year. This may well be so, but fluctuations in numbers are almost certainly related to periods of high and low water and possibly to the movements of prey species. There is as yet no evidence of any kind of mass movement in the river related to reproduction or other aspects of the life cycle.

There is, however, a depression in the size distribution curve, reaching its lowest level between 150 and 159 cm, with peaks on each side (Fig. 1). The first peak is reached at a smaller size by males (120–129 cm) than by females (130–139 cm). Preliminary observations indicate a growth rate too slow for this peak to indicate a distinct year class. However, the decrease in numbers that follows it corresponds with the period preceding and during sexual maturation, as determined by Jensen (1976), who found that sexual maturity is attained at approximately 160 to 170 cm in females and 160 to 165 cm in males. I would suggest that the relative scarcity of sharks of this size range represents a period in the life cycle during which both sexes are maturing reproductively, when they again tend to disappear from the estuarine population, perhaps moving to deeper waters along the coast. If the size at sexual maturity were uniform, both within and between sexes, the depression would presumably be deeper and more distinct, but because of these variables and because of unequal growth rates, both within and between sexes, the depression is partially obscured. The second peak, although evident in both sexes, is more pronounced in males than in females. The maximum size of all males captured was 201 cm, while for females it was 251 cm.

It must be pointed out that, to date, my study has been confined largely to the months of June, July and August. A year-round program of observations is planned, which, together with a detailed analysis of the results of my tagging program (to be published elsewhere), may further elucidate the life cycle.

WHAT ATTRACTS THE SHARKS TO FRESH WATER?

The Lake Nicaragua- Río San Juan bull sharks are clearly most numerous in the lower reaches of the river, become decreasingly common up the river and are least numerous at the far (northwest) end of the lake. The vast majority of tagged sharks recovered have remained in the channels and lagoons near the coast and only a small percentage apparently ever reaches the lake. Those that do so appear to be a random assortment of sizes and sexes and, as stated, the upstream movement does not appear to be related to, or required by, the life cycle. Why, then, do the sharks invade fresh water here and elsewhere?

The question of calcium

The suggestion has been made, both in the zoological literature and to me in verbal discussions, that the sharks are attracted to streams originating in, or flowing through, limestone deposits, and therefore having water of high calcium content. This idea has its roots in the work of Ringer (1883), who reported that calcium salts added to distilled water sustained the life of fishes longer than salts of sodium and potassium, and Breder (1934), who considered a relatively high calcium content in fresh water as the prime factor in the adaptation of marine teleost fishes to a hypoosmotic environment. Homer Smith (1936, p. 65) first suggested that a high calcium content favored the transition of elasmobranchs to fresh water, although he made it clear that he did not exclude elasmobranchs from fresh water on physiological grounds and he believed that under appropriate ecological conditions, most of the smaller forms could survive as well in fresh water as in the ocean. The role of calcium in freshwater adaptation has also been supported or suggested by Gunter (1938), Heuts (1944), Black (1957) and Hulet *et al.* (1967). Severin (1953) in a popular article proposed calcium specifically as the attractant for sharks in the Lake Nicaragua-Río San Juan System.

In order to test this theory, I have, as the opportunity has arisen, measured the calcium content and total hardness of twenty tropical rivers and lakes, while also investigating the occurrence of sharks and sawfish in the same places.

Tests were conducted with a small Hach field kit, which measures calcium (as calcium carbonate) and total hardness, both in terms of grains per gallon. Results, to date, appear in Table 1.

All of the rivers tested in Mexico and Guatemala had both calcium and total hardness higher than in the rivers of any of the other regions. Sharks or sawfish, or both, are known to occur occasionally in these Mexican rivers, but are not common in any of them. Both sharks and sawfish are fairly common in the Lake Izabal-Río Dulce System of Guatemala (Thorson, Cowan and Watson, 1966), and it must be pointed out that the water sample tested was taken from the upper Río Dulce, just below the point where it leaves Lake Izabal and above the stretches that pass between limestone cliffs. A sample taken at the mouth of the Río Dulce might show a considerably higher calcium content.

TABLE 1. Calcium content and total hardness of some rivers and lakes entered by elasmobranchs. All values expressed in grains per gallon.

Body of Water	Point sampled	Calcium	Total hardness
Atlantic drainage, Lake Nicaragua–Lake Managua–Río San Juan			
Lake Managua	Managua	2	8
Lake Nicaragua	San Carlos	3	5
Río Frío	San Carlos	1	2
Río Sábalo	Near mouth	3	5
Río Poco Sol	Near mouth	<1	<1
Río San Carlos	Near mouth	2	4
Río Sarapiquí	Near mouth	2	4
Río San Juan	Delta	2	3
Atlantic drainage, México and Guatemala			
Río Soto la Marina	Soto la Marina	13	17
Río Tecolutla	Tecolutla	5	7
Río Papaloapan	Tlacotalpan	5	7
Río Coatzacoalcos	Coatzacoalcos	9	14
Río Grijalva	Villahermosa	7	13
Río Usumacinta	Tenosique	13	19
Río Dulce	San Felipe, Guatemala	5	8
Pacific drainage, Central America			
Río Lempa, El Salvador	Cantón San Nicolás Lempa	2	
Río Bayano, Panamá	Interamerican Highway bridge, 40 km beyond Chepó	3	4
South America			
Rio Solimões (Amazon)	Above confluence with Rio Negro	<2	2
Rio Negro	Below Manaus	<1	1
Africa			
Benue River	Makurdi, Nigeria	<1	2
Reference samples			
Sea water	Monterey, Calif.	65	
Hard tap water	Lincoln, Nebraska	11	
Very hard tap water	Ciudad del Carmen, Campeche, México	25	

These data by themselves might suggest support for a role for calcium in attracting elasmobranchs. However, the classical example of both sharks (*Carcharhinus leucas*) and sawfish (*Pristis perotteti*) in fresh water is the Lake Nicaragua-Río San Juan System, where both species are very common. Throughout this system, both calcium and total hardness are uniformly in the low part of their ranges (except for Lake Managua, which will be discussed later). Lake Nicaragua, the Río San Juan and all of the major tributaries listed commonly harbor sharks (and presumably sawfish), probably in greater numbers than in any other freshwater body.

The two rivers draining into the Pacific both have sharks and sawfish, at least occasionally, and both have low calcium.

The Amazon River has calcium and total hardness slightly lower than those of the Río San Juan, but it is also known to have sharks, at least 2300 miles up the river (Myers, 1952; Thorson 1972), and sawfish, nearly 1000 miles up (Thorson, 1974).

The Rio Negro, with the lowest calcium and hardness figures of any river tested, probably harbors neither sharks nor sawfish (Thorson 1972, 1974). However, their absence appears to be related to the acidity and relativly low productivity of the "black water" of that river (Sioli, 1967). It should be noted that freshwater stingrays, largely *Potamotrygon* spp., are found in the Rio Negro and its tributaries, so the elasmobranchs are represented there.

Stingrays, *Dasyatis* (formerly *Potamotrygon*) *garouaensis*, also occur in the fresh waters of the Benue River of Nigeria and Cameroon (Stauch and Blanc, 1961; Castello, 1973; Thorson and Watson, 1975), where calcium and total hardness are also very low. Sharks and sawfish have not been reported in the Benue.

There is no discernible pattern to the freshwater occurrence of elasmobranchs in relation to calcium concentration. The figures offer no support for the presence of high levels of calcium as an attractant or a requirement for life of elasmobranchs in fresh water and the explanation for their invasion of fresh water must be sought elsewhere.

The role of food; competition with sawfish.

The most reasonable explanation appears to be that the sharks are simply taking advantage of an ecological opportunity for a large, aggressive predator. Being common inshore, and in the brackish and fresh waters of coastal lagoons and estuaries, the sharks apparently make their way, in pursuit of food, into any channel available to them. Eventually they may find themselves well inland, and if the river originates there, in a lake.

Carcharhinus leucas is an indiscriminate opportunist in its food habits, taking virtually any kind of animal food or bait available (Tuma, 1976). Its biggest food item is fish, perhaps more because of its availability than preference, according to Tuma. The Río San Juan and its tributaries and Lake Nicaragua with its affluents support a substantial population of fish of many kinds, as well as a few other aquatic or semi-aquatic vertebrates and invertebrates large enough to be of value as food. There are a few other consumers of this food, including some of the larger fish species, but there are none that can offer substantial competition to the shark, with the possible exception of the sawfish.

Crocodilians, once numerous, have been decimated and would in any case compete mainly around the margins, in the shallows. Sawfish, on the other hand, although of somewhat different habits, take the same baits as sharks, on the same fishing gear, often in exactly the same places. They are undoubtedly in competition with the sharks and encounters between the two have been attested to by more than 20 records of sharks taken in my study bearing the unmistakable evidence of a row of evenly spaced punctures inflicted by the rostral teeth of a sawfish. Of the 101 shark stomachs examined by Tuma (1976), only one, at San Carlos, contained sawfish flesh, a piece of a caudal fin. A fisherman also reported finding a sawfish rostrum in a net, the sole remains of a small sawfish obviously eaten by sharks. In neither case was it known whether or not the sawfish was dead before it was devoured. A few sawfish taken at San Carlos had pieces missing from their fins which may have been taken by sharks. I have no other evidence of sharks attacking live sawfish. However, Dahl and Medem (1964) reported seeing a large *Pristis*, caught in a net and attacked by a shark (*Carcharhinus leucas*), but the sawfish almost cut the shark in two with a slash of its rostrum.

Sharks and sawfish maintained in the same tanks for public display at Marineland, Florida, do not ordinarily interact antagonistically, according to the curator, Cliff Townsend (pers. comm.). Whether or not they interfere extensively with each other in nature is unknown.

Physiological Tolerance to Fresh Water.

The question now arises, why is *Carcharhinus leucas* virtually the only species of shark whose post-juveniles are found extensively in fresh water? Several species have been reported to occur at times in fresh or brackish coastal waters (Bigelow and Schroeder, 1948; Springer, pers. Comm.). North, South and Central America, the Philippines, New Guinea, and Fiji (Englehardt, 1913; Smith, 1936; Boeseman, 1964). However, when allowance is made for synonymy and some probable misidentification, and when we eliminate species of accidental or rare occurrence in the mouths of rivers or in brackish coastal lagoons, and the juveniles of several species, the sharks that occur regularly in fresh water, far from the sea, in appreciable numbers, are reduced to *Carcharhinus leucas* and very closely allied species or subspecies included in the *C. leucas-C. gangeticus* group of Garrick and Schultz (1963).

Numerous species of elasmobranchs occur along the Caribbean coast of Central America, several of which are reported to occur at times in fresh or brackish coastal waters (Bigelow and Schroeder, 1948; Springer, pers. Comm.). Stewart Springer has kindly provided me with raw data recorded by B. W. Winkler on the Borden Company boat "Dusky", from September 1 to December 12, 1948. The boat was based at Bluefields, Nicaragua, and was engaged in taking sharks for liver oil at largely unspecified locations off the Nicaraguan and Costa Rican coasts, but including the mouth of the Río San Juan off San Juan del Norte, Nicaragua, and the mouth of the Río Colorado off Barra del Colorado, Costa Rica. The gear was probably selective for large sharks, although a few of certain species were taken as small as 76 cm in length. Winkler's records include a few collections made in relatively shallow water (under 12 fathoms) near shore. At the mouth of the Río San Juan, at 9-12 fathoms, in addition to *Carcharhinus leucas*, they took the small black-tipped shark, *C. limbatus*; the sandbar shark, *C. milberti*; the tiger shark, *Galeocerdo cuvieri*; the hammerhead shark, *Sphyrna mokarran*; and the sharp-nosed shark, *Rhizoprionodon* sp. (probably *R. porosus*). At the mouth of the Río Colorado, at 12 fathoms, they took *C. leucas* and *S. mokarran*. At unspecified locations, probably not far from the two river mouths, they took *C. leucas* and *C. limbatus* in "shallow, brackish water"; *C. leucas* and *C. limbatus* at eight fathoms; and *C. leucas*, *C. limbatus*, *S. mokarran* and *Rhizoprionodon* sp. at five fathoms.

The Borden catches reported by Winkler farther offshore and at greater depths (20-125 fathoms) included six-gilled sharks, *Hexanchus* spp., nurse sharks, *Ginglymostoma cirratum*, lemon sharks, *Negaprion brevirostris*, silky sharks, *Carcharhinus falciformis*, large black-tipped sharks, *C. maculipinnis*, and dusky sharks, *C. obscurus*.

In extensive collecting and contact with fishermen at the mouth of the Río San Juan in Nicaragua and its larger fork, the Río Colorado, in Costa Rica, I have never known of a shark of any species other than *C. leucas* taken more than a few hundred meters inside the river mouth.

During calm weather, when the river was low, the fishermen went outside the river mouth to fish and they occasionally took the small black-tip (*C. limbatus*), the hammerhead (*Sphyrna* sp.), the nurse shark (*Ginglymostoma cirratum*), the tiger shark (*Galeocerdo cuvieri*) and possibly others. As in other rivers that empty into the sea, the water leaving the rivermouth spreads out, producing a large freshwater fan extending two or three kilometers into the sea. The lighter fresh water forms a shelf, one or two meters or more in depth, over the denser sea water. The more turbid fresh water fan, clearly visible from the air, is washed down the coast by the prevailing current and gradually dissipates. A number of species of sharks probably venture close to the rivermouth in the brackish intrusion under the freshwater layer and may therefore be taken occasionally by fishermen quite close to the mouth of the river. However, they rarely, if ever, venture into the river itself and *Carcharhinus leucas* remains the only species of shark ever reported up the river or in Lake Nicaragua.

This environmental screening effect is clearly related to the degree of euryhalinity of the various species present in the area. As among bony fishes, the elasmobranchs range from species that can tolerate only sea water, as in offshore, deepwater forms, to those that can live only in fresh water (the stingrays of the family Potamotrygonidae in South American rivers). Marine sharks deal with the marine medium in which they live by maintaining their body fluids at a concentration slightly hyperosmotic to the sea water, largely through retention of an extremely large quantity of urea. Being slightly hyperosmotic to the sea, they take up sufficient water to form urine that is relatively concentrated and small in quantity. They throw off excess salts by way of a rectal gland capable of secreting sodium chloride more concentrated than that in sea water and of twice the concentration found in the body fluids. The freshwater stingrays of South America have abandoned the retention of urea, their rectal gland is reduced and presumably nonfunctional, and they osmoregulate much as the freshwater teleosts do.

There are no fully freshwater sharks known, but the bull shark is capable, as are certain salmonids, eels and lampreys, of functioning in either fresh or marine water. The sharks differ from the latter, however, in that they can move between the two media freely and repeatedly, in a pattern not necessarily related to their life cycle (Thorson, unpublish data). When they spend extended periods in fresh water, their urea content drops to about 30 to 50 percent of the marine level, their rectal gland stops functioning, and their urine becomes many-fold more copious and dilute (Thorson, 1967). Seven adult *C. leucas* taken from marine waters off the coast of Florida had a mean serum urea level of 356 mM/1, with a range of 289-450; sixteen taken in Lake Nicaragua had serum with 169 mM/1 urea (range 121-194); and twenty-eight individuals taken at the river mouth had a mean of 220, but ranged from 147 to 357, indicating a mixed recent environmental history (Thorson, Cowan and Watson, 1973).

Many attempts have been made to transfer a number of species of sharks from sea water to fresh water. In no case have I heard of any species, except *C. leucas*, being transferred successfully for more than a few days to dilutions of sea water beyond 50% without some degree of over-hydration, loss of inorganic salts and fall in hematocrit, leading to death if the fish were not returned to the original medium (Thorson, Cowan and Watson, 1973). On the other hand, *C. leucas* survives for long periods of time in fresh water (Thorson, unpublished data) without untoward effects. Hematocrit values for *C. leucas* are slightly higher in fresh water than in marine specimens, rather than lower, as would be the case if dilution of body fluids occurred when they enter fresh water (Thorson, Cowan and Watson, 1973). Furthermore, total body water of *C. leucas* from Lake Nicaragua is nearly identical (72.1% of body weight) with the average of three marine species of sharks (71.5%), as is the pattern of water apportionment among the major body fluid compartments (Thorson, 1962a; 1962b).

The osmoregulatory equipment of *C. leucas* is fully capable of effective functioning throughout the full range of environmental salinities usually encountered by the species. Its presence in fresh water is apparently a matter of the exploitation of an ecological opportunity by a species that is equipped to tolerate fresh water and deal physiologically with the osmotic problems found there. Species that cannot do so are excluded from fresh water.

Attacks on Humans

This subject will be treated in more detail elsewhere, so I shall only say here that (1) there are documented instances of loss of human life to *Carcharhinus leucas* both in marine situations and in the Lake Nicaragua-Río San Juan System; (2) in the latter, verified cases within the past 30 years exist, but are rare, and (3) although statements have been published that bull sharks are more ferocious and dangerous when in fresh water, no evidence exists that they are either more or less so.

Is This an Accessory Population?

Springer (1963) proposed that the concept of accessory populations might apply to the bull shark of the Lake Nicaragua-Río San Juan System. By his definition, an accessory population is one more or less isolated from the main population, characterized by smaller size and, perhaps because of a genetic deficiency, unable to compete with the more robust members of the primary population.

The subject population is indeed smaller in body size than the members of the species reported from both the northern and southern portions of the species range. Figure 1 indicates the size distribution for the Lake Nicaragua-Río San Juan population, the maximum sizes being 201 cm for males and 251 cm for females. Young are born at approximately 50 to 75 cm (Jensen, 1976). Bigelow and Schroeder (1948) included in their study material a *C. leucas* male 231 cm long and they stated that the species certainly reaches 10 feet and perhaps somewhat longer. They based this figure on a report by Bell and Nichols (1921) of taking a male 10 feet long off the coast of North Carolina. Schwartz (1959) reported two males in Chesapeake Bay, Maryland, each approximately 252 cm in length, and (1960) a female 259 cm long. Clark and von Schmidt (1965), reporting on 129 bull sharks taken over a period of nine years in the Gulf of Mexico in the general vicinity of Sarasota, Florida, gave 249 cm as the maximum length of males taken and 264 cm for females. They gave 74–75 cm as the length at birth, while Bigelow and Schroeder (l.c.) gave 65–70 cm. Springer (pers. comm.) stated that the population at the mouth of the Río San Juan consists of individuals appreciably smaller than those off the mouth of the Mississippi, but appreciably larger than those at the mouth of the Orinoco. However, in Brazil, at the southern end of the West Atlantic range, Sadowski (1971) reported females up to 275.5 cm in length. In South Africa, Bass *et al.* (1973) gave 299 cm (males) and 300 cm (females) as the maximum length of more than 400 specimens of *C. leucas* taken in the Natal area.

Whether or not the Lake Nicaragua–Río San Juan population is genetically inferior to the main population is at this point entirely problematical.

It is also impossible to determine to what extent the subject population remains isolated from and retains its own identity from the main population. Results of my tagging program, although inconclusive on this subject, suggest some degree of isolation. The tagging included only sharks from the fresh water of the lake and the river and from the fan of fresh to brackish water that spreads out from the river mouth. Of more than 2800 sharks tagged, approximately 450 have been recovered, some as many as four times. The recoveries represented movements between many pairs of points, but they were almost all made someplace within the system where the tagging took place. A number of these recoveries demonstrated movements between the three outlets of the Río San Juan (Río San Juan, Río Colorado and Laguna Samay). Only four sharks moved up or down the coast beyond these outlets: three were recovered at Boca Tortuguero, 20 km down the coast from Laguna Samay, and one was recovered at Río Maiz, 50 km north of the San Juan outlet. We see then that, to date, 8 years after the first tagging, not a single recovery has been logged more than 50 km from the fresh water where the subject population occurs. It is quite possible that tags are lying in the houses of fishermen with rewards unclaimed and that eventually more extended movements will come to light. However, it appears unlikely that, if extended movement up and down the coast is the rule, some such movements would not by this time have come to my attention.

There is nevertheless evidence that suggests the possibility of some liaison between coastal concentrations of bull sharks. *Carcharhinus leucas* is a common and widespread species in Western Atlantic waters from approximately New York to Brazil (Bigelow and Schroeder, 1948). It is found in fully marine situations, usually in relatively shallow water, although it may occur to at least 90–100 fathoms (B.W. Winkler *via* S. Springer, unpublished data). It is best known as a shark that is attracted to brackish and fresh water around river mouths and in coastal lagoons, and that penetrates rivers and lakes available to it. It has been reported in rivers from the Amazon (Myers, 1952; Thorson, 1972) to the Mississippi (Gunter, 1938). On the Atlantic side of Mesoamerica bull sharks have been reported in the Ríos Papaloapan and Usumacinta of *Mexico* (Miller, 1966), Lake Izabal-Río Dulce of *Guatemala* (Miller, 1966; Thorson *et al.*, 1966) and Río Patuca of *Honduras* (Bigelow and Schroeder, 1948), besides Lake Nicaragua-Río San Juan of *Nicaragua* and *Costa Rica*. Information from popular sources, correspondence and conversations with ichthyologists and interviews with local residents and fishermen indicate the occurrence of sharks (not identified, but probably *Carcharhinus leucas*), farther inland than the mouths, in several other rivers. In addition to those mentioned, these include: in *México*, the Ríos Grande, Soto la Marina, Tuxpan, Tecolutla, Coatzacoalcos, Grijalva, San Pedro (tributary of the Usumacinta); *Belize*, Belize; *Guatemala*, Motagua; *Honduras-Nicaragua* border, Coco; *Nicaragua*, Grande de Matagalpa, Huahuasan, Escondido, Maiz, Indio; and *Costa Rica*, Tortuguero, Pacuare, Matina. Based on the same type of evidence, sharks are found on the Pacific side in the following rivers: *El Salvador*, Lempa; *El Salvador-Honduras*, Goascoran; *Honduras*, Choluteca; *Costa Rica*, Grande de Térraba; and *Panamá*, Bayano. In addition, they have been recorded in the Río Chucunaque (Breder, 1927) and in the Miraflores Locks in the Panama Canal (Bigelow and Schroeder, 1948).

The widespread occurrence of bull sharks in fresh water leads me to believe that they may be expected to penetrate any coastal body of fresh water within their range if it has a connection with the sea, is deep enough for navigation, has suitable temperature and elevation gradient, and has sufficient animal food to attract them.

It does not seem likely that the concentrations of bull sharks around each of these river mouths would be discrete populations with no gene flow between them. That there is some movement between the various river mouths from Río Maiz to Río Tortuguero is demonstrated by the tagging results cited above. Furthermore, numerous post-juvenile *C. leucas* occur in deeper water, farther offshore than the freshwater aggregations from which most of our information comes. Four hundred and twenty-four bull sharks were recorded along the coast of Nicaragua and Costa Rica by Winkler (see above) at depths ranging up to nearly 100 fathoms, but largely under 40 fathoms. In length, they ranged from 132 to 216 cm (males) and 142 to 262 cm (females). The maximum size of both sexes was a few cm longer than that of our specimens in fresh water (by 15 cm in males; 6 cm in females). Whether the Winkler specimens were actually larger is uncertain, since differences in measuring techniques can lead to discrepancies of this magnitude. We measured total length between perpendiculars from the long axis taken at the end of the snout and the end of the caudal fin held up in a "natural" position. How the tail is held, or whether it is held up or not, or is stretched out in the long axis, makes an appreciable difference in the figures obtained. In any case, the occurrence of bull sharks offshore in deeper water suggests that they probably also cruise up and down the coast for some distance, and provide for some gene flow between estuarine populations. The fact remains that there is no direct proof except the limited movement so far demonstrated by tag recoveries.

Decline in Shark Population in Lake Nicaragua

It has become very obvious that the population of sharks in Lake Nicaragua has decreased markedly from the levels of many years ago. This decline has continued noticeably during the past decade, when I have had the opportunity to make observations.

No reliable information is available on the actual population density of the sharks in the Río San Juan or in Lake Nicaragua in years past. Long-time residents of the area uniformly recall larger numbers of sharks "in the old days," but only Severin (1953) offers figures that are indicative of what these larger numbers might represent. He mentioned a woman at San Carlos who took 2008 sharks in six months from her house over the Río San Juan. He also cited a fisherman who took 7000 sharks from the Río San Juan in an eight-month commercial operation. Today there is virtually no commercial fishing for sharks in the upper San Juan or in Lake Nicaragua, except that which is incidental to the sawfish fishery (INFONAC, 1974; Davies, 1976; Thorson, 1976).

At the far (northwest) end of Lake Nicaragua the situation is the same. At one time many years ago, the City of Granada offered a bounty for sharks, which were considered a menace to bathers. Squier (1852) cited the presence of numerous sharks swimming about near the old fortress at Granada[1]. In 1960, I had no trouble being supplied with sharks near Granada, while in recent years my same supplier (Sr. Armando Vega B.) reports that there are virtually no sharks at the northwest end of the lake. Until the late 1960s, a few hours of fishing would usually yield several sharks, but now one may fish several days without getting one.

A possible explanation for this decline in the shark population might be sought in pollution of the water of the lake by industrial and agricultural chemicals, so common in many parts of the world. In this instance, however, Granada is the only sizable population center on the lake and it is not heavily industrialized. There are some cultivated areas in the lake's drainage system, where heavy crop dusting and spraying have been practiced, but it seems unlikely that concentration of these chemicals would build up in the lake to levels sufficient to kill sharks without similarly affecting the rest of the ichthyofauna. Rainfall is heavy, the Río San Juan carries a heavy discharge of water and the turnover in the lake is relatively rapid. In Lake Managua, which for practical purposes has no outlet except under flooding conditions, solutes become more concentrated than in Lake Nicaragua (Table 1) and pollutants would be more likely to become concentrated and create a problem for the organisms inhabiting it. I know of no study that has been made nor figures that are available on pollutants in Lake Nicaragua or Lake Managua. It would be very desirable that such a study be made.

My study was not designed to provide figures on population density, but a tabulation of the sharks and sawfish taken at San Carlos in 1963 through 1974 discloses a very interesting shift in the ratio of sharks to sawfish (Table 2). There is no way to determine accurately the take in relation to fishing effort, since the fishermen fished when and where they wanted to. The number of days in the first column of Table 2 simply indicates the total number of days that members of my crew were present in San Carlos to receive, tag and pay for sharks and sawfish.

From 1963 through 1971, a regular shift took place, from a preponderance of sharks (3.5:1) to one of sawfish (1:13). During these years, especially 1966 through 1970, my tagging program was in progress, primarily at the mouth of the river at Barra del Colorado, Costa Rica, and we took more than 4000 sharks of all sizes for all purposes. Most of these were tagged and released, so they were not removed from the population, and the effect on the lake population was probably minimal.

The explanation for the decline of the lake population appears to be the small-scale, but sustained commercial fishing at the mouth of the Río Colorado branch of the Río San Juan. There has probably always been a small but sporadic fishery for shark at the river mouths. There has been an occasional market for the skins, although those coming from fresh water have been regarded as inferior because of

TABLE 2. Ratio of sharks to sawfish taken at San Carlos, Nicaragua, in 1963 to 1974.

Year	No. of fishing days	Sharks taken	Sawfish taken	Shark: sawfish ratio
1963-67	25	39	11	3.5:1
1968	37	42	22	2:1
1969	47	64	53	7:6
1970	43	51	252	1:5
1971	3	2	26	1:13
1972	2	13	9	1.4:1
1974	5	8	1	8:1

soft spots attributed to external parasites. The Borden Company refused to purchase freshwater skins (Springer, pers. comm.). Most recently (1964) a small shark skin processing operation was set up at Barra del Colorado, but it had terminated by 1966. Since then, only the fins, jaws and dried and salted meat have had a market. The latter is sold under various false names, particularly *bacalao* (cod), sometimes specifically *bacalao frances* or *bacalao noruego*.

Starting in 1968, the shark fishery intensified when three or four enterprising people began to buy shark and process the fins, jaws and meat for the market in San José. The fishing pressure, sustained the year-round, has not been documented, but undoubtedly resulted in several thousand sharks being taken from the Río Colorado mouth annually, into the early 1970s. The taking of even a few thousand sharks each year undoubtedly has an effect on the population around the river mouths, as well as the numbers that go upstream. Over a period of several years, this would certainly result in the reduction of the population in the lake, since the sharks do not normally reproduce in the lake (Jensen, 1976).

In 1972, the shark:sawfish ratio changed sharply (from 1:13 in favor of the sawfish in 1971 to a preponderance of sharks, 1.4:1 in 1972). Since only two days of fishing were involved, I did not take this very seriously, but in October, 1974, five days of fishing showed it even more dramatically when eight sharks were taken to only one sawfish.

The explanation for this reversal may lie partially in the reported decline in shark fishing at Barra del Colorado in the past two or three years. However, there can be no doubt that the primary reason is the development of a rather intensive sawfish fishery in Lake Nicaragua. This is discussed in another paper (Thorson, 1976) and I shall only state here that it has been concentrated at the south end of Lake Nicaragua, where the sawfish have been most plentiful and has already, since only 1970, reduced the sawfish population to a point where commercial fishing will soon be forced to stop.

Since the shark population in Lake Nicaragua does not rely on reproduction for its perpetuation, but on new arrivals from the sea, it does not appear that the species will become extinct in the lake simply because of fishing pressure. Barring other influences, if fishing is reduced at the river mouth, the lake population can be expected to return slowly to the levels of recent years. If all fishing were to cease throughout the whole system, the population around the mouths of the Río San Juan system would almost certainly recover over a period of a decade or two, and the numbers in the lake might return, possibly even to near the levels of the Nineteenth Century.

However, shark fishing will never be totally eliminated, nor will "other influences" completely disappear. The

[1]Squier's reference to the fins above the surface of the water suggests the possibility that he may have been seeing tarpon. The fins of bull sharks are seldom seen cutting the surface.

prognosis does not appear to include a return of the shark in greater numbers than have been present during the early 1960s and, given certain developments (see below), *Carcharhinus leucas* (as well as *Pristis perotteti*) might be eliminated from the lake for all time.

Absence of Sharks From Lake Managua

One of the most frequently asked questions concerning the "Lake Nicaragua Shark" is "Why are there no sharks in Lake Managua?" That there are none is well known, even though uninformed writers of popular accounts now and then ascribe sharks to both lakes. Occasionally even better-informed writers (*e. g.*, Marden, 1944; McCormick *et al.*, 1963) have treated the absence of sharks (and tarpon and sawfish) in Lake Managua as a mystery. However, the reason for their absence, in light of recent findings, is simple and obvious: There is a well-known, insurmountable physical barrier in the Río Tipitapa that prevents movement of sharks or other fishes from Lake Nicaragua to Lake Managua.

The history and present physical nature of the Río Tipitapa is carefully described by Villa (1976b) elsewhere in this volume and he discusses it as a distributional barrier to the ichthyofauna of Lakes Nicaragua and Managua.

The numerous accounts of this area by early travellers, engineers and naturalists have almost invariably noted the interrupted flow of the Río Tipitapa and mentioned the dry "falls", variously estimated by most to have a drop of 12 to 16 feet (von Humboldt, 1826; Stephens, 1841; Bailey, 1849; Childs, 1852; Squier, 1852; Stout, 1859; Froebel, 1859; Pim, 1863; Günther, 1869; Walker, 1899; Simmons, 1900; Carr, 1953). Some of these writers examined the river themselves, casually or carefully; others quoted canal surveys or earlier reports; but they were all aware of the falls, which have been clearly visible to travellers from the old stone bridge, and a later iron bridge that still crosses the Río Tipitapa within sight of the present Pan American Highway.

Lake Managua lies at an elevation of about 8.5 m (28.5 ft) above that of Lake Nicaragua. According to Hayes (1899), and confirmed by others (*e. g.*, Swain, 1966), the two lakes were at one time parts of one large lake, lying in a *graben*, the Nicaraguan Depression, and called by Villa (1968) the Great Nicaraguan Lake (*El Gran Lago de Nicaragua*). This body of fresh water gradually rose to a level 15 or more meters above the present level of Lake Nicaragua. Possibly after a period of draining into the Pacific, it overflowed, near the present location of El Castillo, draining toward the Caribbean Sea. It gradually eroded the channel of the Río San Juan, and the lake dropped to the present level of Lake Nicaragua. When the level had dropped to near the present level of Lake Managua, a vein of rock prevented the portion of "*El Gran Lago*" which now forms Lake Managua from dropping further. As the stabilized Lake Managua continued to drain into the incipient Lake Nicaragua, a sizeable river developed (the Río Tipitapa) and a waterfall formed over the rock sill in its upper reaches.

Stout (1859) said that an eruption of the Volcano Masaya in 1670 separated Lake Nicaragua and Lake Managua, and Froebel (1859) stated that the Río Tipitapa dried up as a result of an earthquake in 1844, but I know of no firm evidence for either of these claims.

In any case, the flow of water has gradually been reduced until today for long periods there may be no flow except that produced by seepage, springs or local rain runoff (Villa, 1976b). The lower 25 km of the Río Tipitapa is a permanent estuary (*estero*), the *Paso de Panaloya*, actually an arm of Lake Nicaragua. In dry seasons, sections of the river above the *estero* stand separated from one another by sections of dry river bed. The Pan American Highway, which crosses the Río Tipitapa within a few hundred meters of Lake Managua, has not been provided with a bridge over the river, but the road bed drops a few feet as it crosses the river bed, providing a spillway for Lake Managua water in the rare instances when it overflows. A small culvert under the road permits a trickle of water which in effect, at that point, is the visible Río Tipitapa for long periods of time. I have crossed the "river" at that point many times in the past ten years and have never seen water running across the road, nor in appreciable quantities under the road. This is the usual observation of others who have had much more experience with the situation than I have.

Nevertheless, it is common knowledge that overflows do occasionally occur. Apparently no records have been kept of these overflows, but Marden (1944) and McCormick *et al.* (1963) suggest that they occur about once in ten years. The report of the Nicaraguan Canal Commisson survey of 1897–1899 (Walker, 1899) includes two photographs just below the falls which show more water than I have seen, including a stream of water gushing from one of the fissures in the rock ledge and possibly several other small trickles. Walker reported a gage placed in the river about 100 yards above the Tipitapa falls and said that "During low water the river was too sluggish above the falls for accurate measurements with current meters, and gagings were made from the bridge below the falls. As the river rose it became very turbulent and swift at the bridge, but at the same time the velocity in the upper river increased and good measurements were made above the falls."

Claims have been made that there is noticeably less flow through the Río Tipitapa now than in the 19th Century. The account of the 1897–1899 survey might be taken as evidence for this view. However, Squier's (1852) account of his study of the Tipitapa gives a picture much like that of today, and he discounted even then that there was any noticeable change occurring.

The cutting of both the Río San Juan channel and the Río Tipitapa bed have taken place through relatively soft materials (Hayes, 1899; Villa, 1976b), and it appears very likely that the lakes have assumed their present forms and levels rapidly in terms of geological time. The rock vein that has preserved the higher level of Lake Managua is of relatively soft material also, exhibiting potholes and strangely eroded patterns. Deep fissures through this ledge suggest that if the earlier flow from Lake Managua had been maintained, eventually the ledge might have eroded back to the lake, permitting the draining of most of the present Lake Managua.

In light of the present knowledge that the sharks of Lake Nicaragua enter the lake from the Caribbean Sea, the physical barrier of the Tipitapa falls is the obvious explanation for the absence of sharks in Lake Managua. However, the "mystery" of their absence might be justified if the old theory were correct that the lakes formed from an embayment of the Pacific Ocean cut off from the sea by volcanic action. If the Lake Nicaragua sharks were landlocked animals that had been trapped and gradually adapted to the fresh water in all aspects of their life cycle, they would have been present in the Great Nicaraguan Lake. When it separated into the two modern lakes, the shark would have been present in both and might be expected to occur in Lake Managua today. However, the information reported above, demonstrating that they do not normally reproduce in Lake Nicaragua, probably do not depend on the lake for any part of their life cycle, and may possibly have one or two marine periods in their lives, would preclude their survival in Lake Managua, so no mystery remains.

Boyle (1868) reported that he had been told that freshwater sharks and large alligators abound in a crater lake near Managua, the lake that Squire (1852) said had hieroglyphics on some of its rock walls. This was the lake Squier called Nihapa, but according to Villa (1976a) it is not the modern Nejapa, but rather Asososca of Managua. Since the lake had no outlet, Boyle wondered how the sharks came to be there. He speculated seriously that a waterspout may have brought them since such phenomena are common in Nicaragua. There are of course no sharks in any of the crater lakes, but Boyle's suggestion is no more fanciful than the explanation often heard in Nicaragua that the sharks in Lake Nicaragua come in through an underground passage from the Pacific Ocean.

Canalization of the Río San Juan and Lake Nicaragua

Ever since the early explorers discovered how close the Atlantic and Pacific oceans lie to each other, potentates and financiers have dreamed of a water connection between the two. Since it was found that Lake Nicaragua and the Río San Juan brought the oceans within only 12 or 13 miles of each other, and they were separated only by a low ridge, at its lowest point less than 50 feet above the level of the lake, the area has been the focus of almost continual international maneuvering for control. Several countries have conducted more than a dozen surveys of the prospective canal route over almost two centuries, but eventually, by a narrow margin, the Panamanian route was selected rather than the Nicaraguan. As recently as 1970, however, the Nicaragua route was under consideration for a second trans-isthmian canal, but the Atlantic-Pacific Inter-oceanic Canal Study Commission finally discarded the route (Nicaragua-Costa Rica, No. 8) because of its expense compared to others (Anderson, 1970). The commission estimated that, if dug by conventional means, the canal through Nicaragua would cost 11 billion dollars; if done by nuclear blasting, it would cost only five billion; but 675,000 inhabitants would have to be re-located at unacceptable social and economic cost. The United States and Nicaragua have since that time terminated their 1914 agreement (Bryan-Chamorro Treaty) which granted the U.S. the right in perpetuity to build a canal across Nicaragua. The prospect of a trans-isthmian canal thus appeared finally to have come to an end.

However, soon after the abrogation of the Bryan-Chamorro Treaty, Nicaragua and Costa Rica started negotiations and plans for a large dam (or two smaller ones) on the Río San Juan, for purposes of improving navigation and the production of hydroelectric energy. Locks would provide passage of vessels of up to 12-foot draught. The final plan also calls for a canal and locks between the lake and the Pacific and between Lakes Nicaragua and Managua, some years after the construction on the Caribbean side.

A large dam below the confluence of the San Juan and the Río San Carlos would create a huge new lake in the watershed of the upper San Juan and its major tributaries, with obvious results to the local fauna and flora and to the species of fish that presently use the Río San Juan for passage from the sea to food sources in fresh water, including Lake Nicaragua. A dam would effectively bar passage not only to the shark and sawfish, but also to marine telosts such as the *sábalo* (tarpon), *Megalops atlanticus*; *róbalo* (snook), *Centropomus parallelus*; *roncador* (grunt), *Pomadasys boucardi*; and possibly others.

We have noted that movement of bull sharks into Lake Nicaragua does not appear to be a requirement of their life cycle; that they do not normally reproduce in Lake Nicaragua; that the population of sharks in the lake is apparently sustained by new arrivals from the sea; and it does not appear, as formerly thought, that the requirements for the complete life cycle are met in fresh water. It can therefore be predicted that, if a dam were to cut off the recruitment of sharks to the lake population, *Carcharhinus leucas* would disappear from the lake.

How long the disappearance of the last sharks from the lake would take would depend on several factors not yet well-understood. In particular, it would involve the life span of *C. leucas* and its long-term independence of sea water. It is now well-established that both the juveniles and adults of this species have the full range of tolerance to environmental salinities from fresh water to full strength sea water and they are capable of moving freely back and forth between the two media. It has also been shown by tag recoveries that individual sharks may be taken three or even four times in fresh water over an extended period of time; and the original tagging of a post-juvenile shark and the recovery of the tag, both in fresh water, have been separated by as much as approximately five years, to date. These observations indicate long periods spent in fresh water, although there is no way of knowing if the sharks remained in fresh water for the whole time. As far as their osmoregulation is concerned, they are probably capable of surviving in fresh water for their entire normal life span. It must be remembered, however, that there may be a period in their first year or two of life, when they normally go to sea, and possibly another period, just before reaching sexual maturity, which they also may spend at sea. We do not know yet if either of these are obligatory marine phases.

There are insufficient data at present to determine accurately the life span of *Carcharhinus leucas*. Until more actual measurements are available for both time of tagging and time of recovery, and until the final tag recoveries have been made, I can only give six years as a minimum figure, one year as juveniles (up to 100 cm total length) and five years post-juvenile (determined from maximum time at large up to this time). The juvenile period may prove to be longer than one year and the post-juvenile period is almost certainly longer than five years, judging from very limited information on growth rates. Records of bull sharks in captivity are of little help in determining the life span, as one and one-half years is the maximum time reported by Clark (1963) at Marine Studios, Marineland, Florida, and four years by Wallace (1972) at the Oceanographic Research Institute in Durban, South Africa.

From the time a dam bars the passage of sharks upstream from the Caribbean, the population in the lake can be expected to start declining. They will probably become rare within four or five years, or possibly less, and their extinction will almost certainly be complete within five or ten years. If their life span proves to be longer than this, a rare individual might conceivably survive more than ten years, but it is highly unlikely.

It has been suggested to me that, since the sharks have been heading upstream presumably at least for millennia, they will congregate in the waters below the dam and find their way up through the locks. It is conceivable that this might happen occasionally, but a strong suggestion that it would not occur commonly is contained in the absence of sharks from Lake Gatún in the Panama Canal, a situation somewhat analogous to the Lake Nicaragua one. Lake Gatún is a large freshwater lake created by the damming of the Chagres River when the canal was constructed, and accessible by locks from both the Atlantic and Pacific sides. *Carcharhinus leucas* occurs in the sea at both ends of the canal. At the Pacific end there is an actual record of a bull shark taken at the Miraflores Locks (Bigelow and Schroeder, 1948). However, C. E. Dawson (pers. comm.), who has made a number of collections of fishes during the "dewatering" and cleaning of both the Gatún and Miraflores Locks, reports that he has never seen any elasmobranchs among the fishes trapped when the water was drained from the locks. I have made numerous inquiries locally and have received no reliable reports of sharks occurring in Lake Gatún.

Only speculation can be offered regarding the effect that the removal of sharks and sawfish from the lake would have on the rest of the ichthyofauna. Removal of the top predators would decrease the competition now experienced by the next level of carnivores, which might then increase in numbers. However, the consequences of environmental manipulations of any kind are notoriously unpredictable. There is insufficient knowledge available about the whole food web of Lake Nicaragua to foretell confidently what readjustments in interspecies relationships and population densities would occur. Nicaragua and Costa Rica would be well-advised to study carefully, by all means available, the potential consequences of the construction of a hydroelectric dam and shipping canal *before* they are constructed. Whether the effects would be regarded as good or bad for the countries, their peoples, their economies and their natural resources, including the fauna and flora, the two nations should inform themselves in advance of what can be expected.[1]

The construction of a dam and canal may well benefit Nicaragua economically and make a port of Granada and perhaps later of Managua; but if so, these benefits will be exchanged for the unique distinction, presently enjoyed by Nicaragua, of having within its boundaries the classical population of sharks (as well as of sawfish) existing in an inland body of fresh water. The many tales, some true and some false, of savage attacks on bathers, sharks following boats, waiting for them to capsize, bounties paid for sharks, dorsal fins cutting the water, volcanic dams and underground passages from the Pacific, will undoubtedly persist as stories from the olden days; but they will probably be supplemented by new legends, perhaps also passed for truth. One can imagine a ready explanation for all extraordinary occurrences such as the disappearance of a wading cow or a human bather, the tearing of fishermen's nets or breaking up of their dugouts. It was surely The Shark, a real *grandote*, twenty feet long, that lurks in a cave, always escapes the hook and the net, and of course is never seen.

An era, extending from the *conquistadores* to the present, will have come to an end.

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SUMMARY

The sharks in Lake Nicaragua are identical with the bull sharks (*Carcharhinus leucas*) in the Caribbean Sea and they move freely between the sea and the lake in both directions.

They reproduce along the coast, near the river mouths, rather than in the lake. *Ex utero* and neo-natal pups survive in both fresh and salt water, so if a female should occasionally drop her young in the lake, they would likely survive. However, this probably occurs only rarely, and it is very unlikely that copulation and actual fertilization of the eggs occur in fresh water.

The neo-natal young (50 to 80 cm total length) tend to congregate in freshwater nursery grounds. The young sharks are almost completely absent from the freshwater environment at lengths of 80 to 100 cm, when they are presumably in the sea, but they reappear in large numbers after reaching 100 or 110 cm. There may be a tendency to remain in the sea again for a period just preceding sexual maturity, which is reached at lengths of about 160 to 170 cm. It is not known if either freshwater or marine sojurns are obligatory. The sharks appear to be thoroughly euryhaline, both as neo-natal pups and as post-juveniles. The movement up the river and into the lake does not appear to be related to any life cycle requirement.

Movement into fresh water represents the exploitation of an ecological opportunity for a large, aggressive, predatory species which can also cope physiologically with the osmotic demands of the freshwater environment. *C. leucas* probably occurs in all rivers of Mexico and Central America that have suitable characteristics for its entrance and feeding. It is the only species of shark known to penetrate the Lake Nicaragua-Río San Juan system beyond the immediate vicinity of the river mouths. There is no evidence that a high calcium content in the water is required to attract it to fresh water or to maintain it there.

C. leucas is an indiscriminate opportunist in its eating habits. Its only enemy or serious competitor in Lake Nicaragua, besides Man, is the sawfish, *Pristis perotteti*. It is known to attack humans occasionally, but the special ferocity that has been attributed to it in fresh water is completely undocumented.

Members of the Lake Nicaragua-Río San Juan population are somewhat smaller than those of oceanic populations in the northern and southern parts of the species' Atlantic range. Results of a tagging program suggest that this population may be partially isolated from other coastal populations.

The shark population in the lake has declined markedly

[1]As this goes to press, a beginning is being made by a feasibility study, which is to include an environmental component, conducted by *Ministerio Obras Publicas*.

in recent years, most likely because of small-scale, but sustained, commercial fishing activity at the mouth of the Río Colorado, where the largest concentration of bull sharks occurs.

Since the sharks normally breed in the sea, it would appear that they cannot complete their life cycle in fresh water alone. Therefore, the construction of a proposed dam across the Río San Juan would almost certainly eliminate *Carcharhinus leucas* from Lake Nicaragua.

Resumen

Los tiburones del Lago de Nicaragua son taxonomicamente idénticos con los "Bull Sharks" del Mar Caribe (*Carcharhinus leucas*), y se mueven libremente entre el lago y el mar, en ambas direcciones.

Se reproducen a lo largo de la costa, cerca de la desembocadura de los ríos, pero no en el lago. Los tiburones *ex utero* y recién nacidos pueden sobrevivir en agua dulce o salada, por lo que si una hembra ocasionalmente pariese en el lago, sus jóvenes probablemente sobrevivirían. Sin embargo, esto probablemente ocurre raramente, y es poco probable que la cópula y la fertilización de los huevos ocurran en el lago.

Los tiburones recién nacidos (de 50 a 80 cm de longitud total) tienden a congregarse formando criaderos en aguas dulces. Los tiburones jóvenes (de 80-100 cm) se encuentran casi totalmente ausentes en aguas dulces, cuando se presume que se encuentran en el mar. Sin embargo, después de alcanzar 100-110 cm, reaparecen en abundancia. Puede existir una tendencia a permanecer, de nuevo, en el mar, por un período inmediatamente antes de madurar sexualmente, lo que ocurre cuando miden unos 160-170 cm. No se sabe si éstas temporadas, en agua dulce o salada, son obligatorias. Los tiburones parecen ser completamente eurihalinos cuando son recién nacidos o post-juveniles.

El movimiento río arriba, y hacia el lago, no parece estar ligado a ningún requisito de su ciclo vital. Representa la explotación de una oportunidad ecológica para un depredador grande y agresivo, que puede además adaptarse fisiologicamente a las demandas osmóticas del ambiente dulceacuícola. *C. leucas* probablemente se encuentra en todos los ríos de México y Centro América que posean características adecuadas para su entrada y alimentación. Es la única especie de tiburón que se sabe que penetra en el sistema Lago de Nicaragua-Río San Juan mas allá de la inmediata vecindad de la desembocadura de los ríos. No existe evidencia de que sea necesario un alto contenido de calcio en el agua para atraerlos o mantenerlos alli.

C. leucas es oportunista e indiscriminante en sus hábitos alimenticios. Su único enemigo ó competidor serio en el Lago de Nicaragua, además del hombre, es el pez sierra (*Pristis perotteti*). Se sabe que ocasionalmente ataca al hombre, pero la ferocidad especial que se le atribuye en agua dulce no está documentada.

Los tiburones del sistema Lago de Nicaragua-Río San Juan son algo mas pequeños que los de poblaciones oceánicas en el norte o el sur de la distribución de esta especie. Los resultados del programa de marca y recaptura sugieren que esta población puede estar parcialmente aislada de las otras poblaciones costeras.

La cantidad de tiburones en el Lago ha declinado marcadamente en años recientes, probablemente debido a una actividad pesquera comercial pequeña, pero sostenida, en la boca del Río Colorado, donde está la mayor concentración de estos tiburones.

Debido a que los tiburones normalmente se reproducen en el mar, parece que no pueden completar su ciclo vital solamente en agua dulce. Por lo tanto, la construcción de las proyectadas exclusas en el Río San Juan interrumpirá el movimiento de los tiburones, y casi ciertamente los eliminará del Lago de Nicaragua.

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