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Distribution and Habitat Partitioning of Immature Bull Sharks (*Carcharhinus leucas*) in a Southwest Florida Estuary

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ABSTRACT: The distribution and salinity preference of immature bull sharks (*Carcharhinus leucas*) were examined based on the results of longline surveys in three adjacent estuarine habitats in southwest Florida: the Caloosahatchee River, San Carlos Bay, and Pine Island Sound. Mean sizes were significantly different between each of these areas indicating the occurrence of size-based habitat partitioning. Neonate and young-of-the-year animals occurred in the Caloosahatchee River and juveniles older than 1 year occurred in the adjacent embayments. Habitat partitioning may reduce intraspecific predation risk and increase survival of young animals. Classification tree analysis showed that both temperature and salinity were important factors in determining the occurrence and catch per unit effort (CPUE) of immature *C. leucas*. The CPUE of <1 year old *C. leucas* was highest at temperatures over 29°C and in areas with salinities between 7‰ and 17.5‰. Although they are able to osmoregulate in salinities from fresh to fully marine, young *C. leucas* may have a salinity preference. Reasons for this preference are unknown, but need to be further investigated.

Introduction

Bull sharks (*Carcharhinus leucas*) are common worldwide in tropical and subtropical coastal, estuarine, and some riverine environments. This species grows to a large size, with a reported maximum size of 340 cm (Compagno 1984). The young are born at 56–81 cm, and maturity occurs at approximately 160–225 cm in males and 180–230 cm in females (Last and Stevens 1994). *C. leucas* is the only species of shark that is known to be physiologically capable of spending extended periods in freshwater (Thorson et al. 1973). This ability has resulted in this species being recorded in many rivers and lakes, including those in the U.S. (Gunter 1938; Thomerson et al. 1977), Central America (Thorson 1971; Montoya and Thorson 1982), South America (Myers 1952; Thorson 1972), Africa (Bass et al. 1973), Australia (Taniuchi et al. 1991a; Last and Stevens 1994), Papua New Guinea (Taniuchi et al. 1991b), and Asia (Compagno 1984).

Like many species of sharks, *C. leucas* use nursery areas. These areas are believed to provide newborn animals with protection from predation and abundant food to ensure high survival and rapid growth (Branstetter 1990; Simpfendorfer and Milward 1993). *C. leucas* nurseries have been reported most commonly in estuarine areas (Caillouet et al. 1969; Snelson and Williams 1981; Montoya and Thorson 1982) and rarely in freshwater areas (Bass et al. 1973; Montoya and Thorson 1982).

In Florida, *C. leucas* is a commonly encountered species in coastal and estuarine areas. Snelson and Williams (1981) and Snelson et al. (1984) reported that juveniles were common inhabitants of the Indian River Lagoon system on the east coast. Michel (2002) reported that in the Ten Thousand Islands region of southwest Florida juvenile *C. leucas* were common, especially in backwater areas where salinities were lowest. As part of a study on the elasmobranch fauna of the Charlotte Harbor ecosystem in southwest Florida, *C. leucas* were regularly captured on longlines set in the Caloosahatchee River, San Carlos Bay, and lower Pine Island Sound. The aim of this study was to examine the distribution of immature *C. leucas* within the Caloosahatchee River–Pine Island Sound estuarine system to investigate if there was habitat partitioning within the system and to examine environmental parameters that may influence their distribution.

Materials and Methods

STUDY AREA

This study was conducted in southern Charlotte Harbor in southwest Florida. For the purposes of examining habitat partitioning the study site was divided into three sampling areas, the Caloosahatchee River, San Carlos Bay, and lower Pine Island Sound (Fig. 1) based on differences in habitat type and water quality parameters.

The Caloosahatchee River connects Lake Okeechobee with the southwest coast of Florida. The river has been substantially modified over the past 100 years. Presently there are two locks to allow boat passage through Lake Okeechobee and dams to regulate the flow of water down the river. The regulation of flow is used to maintain water storage

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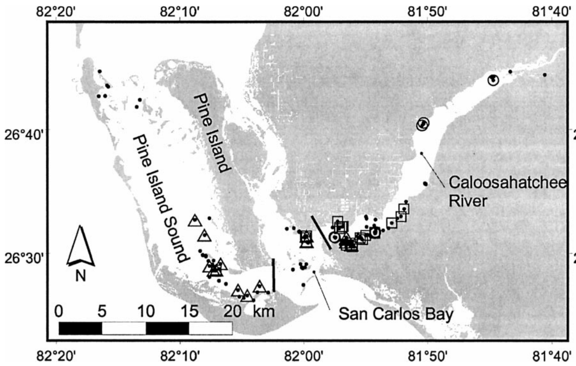

Fig. 1. Location of the study site in Florida, sampling stations, and location of captures by life stage. Points indicate longline survey locations, open circles indicate neonate capture locations, open squares indicate young-of-the-year captures, open triangles indicate juvenile captures, and solid lines indicate the boundaries between the three study areas.

within the lake for use in agriculture, to supply freshwater flow through the Everglades ecosystem, and to provide flow through the Caloosahatchee River and estuary (South Florida Water Management District 2000). The lowest lock on the river (Franklin Locks, S79) is 42 km from the mouth and below this point the river is euryhaline. During periods when freshwater releases from the lake and rainfall are low, salinities at S79 reach as high as 20‰, but are more normally <8‰ (South Florida Water Management District 2000). During high releases or high rainfall periods the river below S79 becomes oligohaline with salinities near the mouth reaching as low as 0.2‰ (Simpfendorfer et al. unpublished data). The lower reaches of the river are highly urbanized, and extensive canal systems have been cut from the main river channel. The lower reaches of the river up to S79 were historically lined by mangroves (mostly *Rhizophora mangle*), but much of this native shoreline vegetation has been removed by urbanization.

The Caloosahatchee River flows into San Carlos Bay (Fig. 1). The northern portion of the bay is dominated by shallow seagrass beds, extensive oyster reefs, and spoil islands. These shallow habitats are cut by several deep channels that run north-south and drain lower Pine Island Sound and Matlacha Pass to the Gulf of Mexico. The Intracoastal Waterway runs east-west through this area. Salinity variation in the bay is considerably less than in the Caloosahatchee River because of the proximity of the Gulf of Mexico. During periods of low freshwater flow from the Caloosahatchee River salinities in San Carlos Bay reflect those of the Gulf (approximately 35‰), and during high flow salinity drops to 15–20‰ (South Florida Water Management District 2000).

Lower Pine Island Sound is protected from the Gulf of Mexico by a series of barrier islands. The Sound is a relatively shallow environment with extensive seagrass beds (especially *Thalassia testudinum, Syringodium filiforme,* and *Halodule wrightii*) in areas less than 2 m deep. The deepest sections of the Sound occur along its center line and reach approximately 5 m. The Intracoastal Waterway runs through the Sound and, in places, is dredged to maintain the navigable channel. The shore of the Sound is mostly lined by mangroves (mainly *R. mangle*). The lack of significant freshwater flow from the islands bordering lower Pine Island Sound, and strong tidal mixing with San Carlos Bay make salinity values similar between these two study areas.

Field Sampling

Sampling was carried out using 400–800 m long bottom-set longlines. Longlines consisted of a mainline of 8-mm braided nylon rope anchored at both ends. Gangions were constructed of 1 m of 5-mm braided nylon cord and 1 m of stainless steel wire leader. Mustad tuna circle hooks ranging in size from 12/0 to 16/0 were baited with frozen mullet (*Mugil cephalus*) and fresh catfish (*Arius felis*), jacks (Carangidae) or ladyfish (*Elops saurus*). Fresh bait was only used when available, and at least half of the hooks on all lines were baited with frozen mullet. Longlines were set for periods from 30 min to 2 h, with most set for approximately 1.5 h.

A total of 128 longline sets were made between April 2001 and October 2003; 75 in the Caloosahatchee River, 19 in San Carlos Bay, and 34 in Pine Island Sound (Fig. 1). The main aim of sampling was the capture of smalltooth sawfish (*Pristis pectinata*) and so was ad hoc in relation to *C. leucas.* Sets were made in all seasons, but the majority occurred between May and September in each year. The time, date, and location of all sets were recorded. Physical parameters (depth, water temperature, and salinity) were recorded at each sampling location midway between the surface and bottom.

C. leucas caught were identified and sexed. Four measurements of length (to the nearest 0.5 cm) were taken: precaudal, fork, total (TL), and stretched total (STL). All sharks were examined for the presence of an open umbilical scar, indicating that they had been recently born. Individuals with open or partly closed umbilical scars were classified as neonates. Individuals that had been born less than 12 mo previously (based on size-at-age data, see below, and the months of occurrence of neonates), but that were not neonates, were classified as young-of-the-year (YOY). Individuals older than 12 mo, but not mature, were classified as juveniles. Ages of sharks were estimated from length data based on the growth curve of *C. leucas* in the northern Gulf of Mexico (Branstetter and Stiles 1987). We found that this length-at-age relationship overestimated the age of young sharks in our sampling area. For example, neonate *C. leucas* from our sampling area were of similar size to 1 year olds collected in the northern Gulf of Mexico. We adjusted our age estimates by subtracting 1 year from the age of individuals as determined from the growth curve of Branstetter and Stiles (1987). On the basis of these data we assumed the size at 1 year of age was 90 cm TL or 92 cm STL. All live sharks were tagged with plastic headed dart tags positioned at the base of the first dorsal fin, and a subsample was double tagged with a plastic ear tag (rototag or jumbo rototag) placed through the first dorsal fin. Sharks were revived if necessary and released.

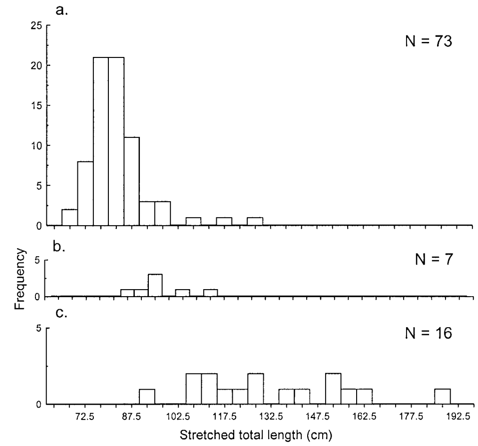

Fig. 2. Size frequency distributions of immature *Carcharhinus leucas* in (a) the Caloosahatchee River, (b) San Carlos Bay, and (c) Pine Island Sound.

Data Analysis

Comparisons of shark lengths between the three study areas were tested using a single factor analysis of variance (ANOVA). A post-hoc Duncan's test was used to identify which study areas had different mean lengths. The catch per unit effort (CPUE) of *C. leucas* for each longline set was expressed as the number of sharks caught per 1,000 hook hours. CPUEs were calculated by dividing the number of *C. leucas* caught by the number of hooks and the soak time of the set (measured in hours) and then multiplying by 1,000. Soak time was taken as the time from the first hook going in the water to the last hook coming out of the water. CPUE was calculated for all immature *C. leucas* and for individuals less than 1 year old (i.e., neonates and YOY).

To identify physical parameters that were important in determining the presence of *C. leucas* classification tree (CT) analysis was used (Breiman et al. 1984). This type of analysis was selected as the sampling design was ad-hoc and would not support more rigorous statistically techniques (e.g., ANCOVA). This technique uses binary-recursive partitioning based on values of predictor variables, which can be categorical or ordinal. Since the dependent variable must be categorical CPUE was divided into three groups: no catch (CPUE = 0), low (CPUE = 0.01–20 sharks per 1,000 hook hours), and high (CPUE > 20 sharks per 1,000 hook hours). Division of CPUE at 20 sharks per 1,000 hook hours was chosen to divide the number of positive sets approximately in half. Misclassification costs were set as equal between all groups. Goodness of fit was determined using the Gini measure. Tree size was determine by FACT-style direct stopping, with trees pruned until the minimum cross validation cost was achieved. Since the data set was relatively small, cross validation costs were determined using v-fold cross validation with three subsamples (Statsoft 2004). If two or more trees had equal cross validation costs, then the simplest was selected. Three physical factors were included in CT analysis: depth, water temperature, and salinity. Month or season was not used as a predictor variable because it was correlated with temperature. CT analysis was performed on two groups of individuals: all immature (neonates, YOY, and juveniles) and <1 year old (neonate and YOY) sharks.

Physical parameters that CT analysis identified as having high predictive power for *C. leucas* CPUE (as identified by their Importance Ranking) were further investigated by pooling into sets of 6 and 8 groups for salinity and temperature, respectively. CPUE data were then compared between groups using nonparametric Kruskal-Wallis ANOVA. The value of α was set to 0.05 for all statistical tests.

Results

A total of 96 immature *C. leucas* were captured: 73 in the Caloosahatchee River, 7 in San Carlos Bay, and 16 in Pine Island Sound (Fig. 1). Twenty-one neonates were captured ranging in size from 70 to 82 cm STL, all in the Caloosahatchee River in June and July. Forty-five YOY were captured ranging in size from 68 to 89 cm STL, 43 from the Caloosahatchee River and 2 from San Carlos Bay. Thirty juveniles were captured ranging in size from 91 to 189 cm STL and were captured in all three study areas (San Carlos Bay, 5; Caloosahatchee River, 9; Pine Island Sound, 16).

The mean lengths of *C. leucas* were significantly different between the three sampling areas (Fig. 2; ANOVA, F = 90.15, df = 2, $p < 0.0001$). Individ-

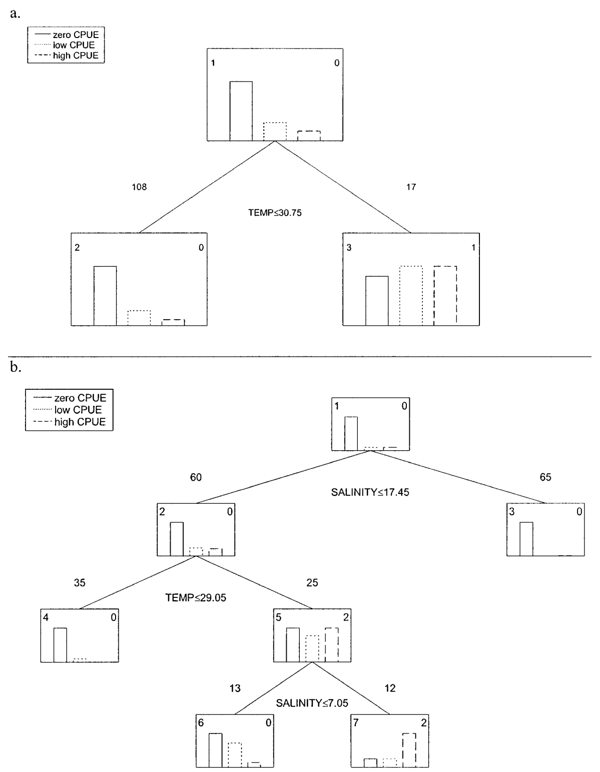

Fig. 3. Classification trees for (a) all immature and (b) neonate and young-of-the-year *Carcharhinus leucas*. Boxes indicate nodes of trees. Histograms in nodes indicate the numbers of each CPUE group assigned to each node (zero, low, or high). Number in top left of nodes is the node number, and the number in the top right indicates the predicted node value (0 is zero CPUE, 1 is low CPUE, and 2 is high CPUE). Condition below nodes indicates splitting variable and its value. Numbers adjacent to lines joining nodes indicate sample sizes assigned to each of the lower nodes.

uals caught in the Caloosahatchee River ranged in size from 68 to 127 cm STL, with the mean length being 82.9 cm STL. Sharks caught in San Carlos Bay ranged in size from 89 to 112 cm STL (1–3 years of age) and had a mean length of 94.7 cm STL. Individuals caught in Pine Island Sound ranged in size from 91 to 189 cm STL (1–10 years of age), with most larger than 105 cm STL (>2 years of age) and a mean length of 149.2 cm STL. The mean length of individuals caught in the river were significantly smaller than those caught in San Carlos Bay (post-hoc Duncan's test, $p = 0.026$) and Pine Island Sound (post-hoc Duncan's test $p < 0.001$). Individuals caught in San Carlos Bay had a significantly smaller mean length than those caught in Pine Island Sound (post-hoc Duncan's test, $p = 0.0001$).

Longline sets were carried out in temperatures ranging from 14.6°C to 32.1°C, salinities from 0.2‰ to 35.6‰, and depths from 0.3 to 6.2 m.

TABLE 1. Results of Kruskal-Wallis nonparametric ANOVA results for environmental factors influencing the catch per unit effort of immature bull sharks. All tests were based on 126 longline sets, and sets were grouped into categories based on each of the factors for analysis. Bold probability (p) values indicate significant differences between groups for a factor for either < 1 year olds or all immature sharks.

		< 1 Year		All Immature	
Parameter	df	H	p	H	p
Temperature	5	16.64	**0.005**	12.22	**0.032**
Salinity	7	18.24	**0.011**	19.82	**0.006**
Depth	5	4.84	0.435	4.96	0.421

The CT analysis for all immature *C. leucas* produced a classification tree that had two terminal nodes with a single split based on temperature at 30.75°C (Fig. 3). At temperatures below 30.75°C the tree predicted zero catches, while above 30.75°C low CPUE was predicted. No terminal node predicted high CPUE, but the histogram of the >30.75°C node indicated that low and high CPUE sets occurred in equal numbers. A more complex tree (six terminal nodes) shared the same cross validation cost, but was rejected because of the existence of the simpler tree. The Importance Ranking values indicated that temperature (100) had the greatest influence on the split, while salinity (84) also had relatively high influence. Depth had a low Importance Ranking (24).

The <1 year old regression tree had four terminal nodes and three splits; two based on salinity and one on temperature (Fig. 3). The tree indicates that no <1 year old animals were caught above 17.45‰, very few were caught below 29.05°C, and high CPUE occurred above 7.05‰. Histograms in the terminal nodes indicate that few individuals were caught at temperatures below 29.05°C and salinities below 7.05‰. No terminal node predicted low CPUE. The Importance Rankings indicated that salinity (100) was the most influential in tree construction, closely followed by temperature (98); depth (42) was of moderate influence.

Nonparametric ANOVAs indicated that there were significant differences in CPUE between temperature and salinity groups for both <1 year old sharks and all immature sharks (Table 1). There were no differences in CPUE between depth groups. CPUE was highest at lower salinities (Fig. 4): 5–20‰ for immatures and 5–15‰ for <1 year olds. CPUE was more variable among temperatures. For both immature and <1 year old sharks the highest CPUE occurred at >29°C, but catches were made in water as cool as 18°C. Few captures of <1 year olds were made in water less than 29°C.

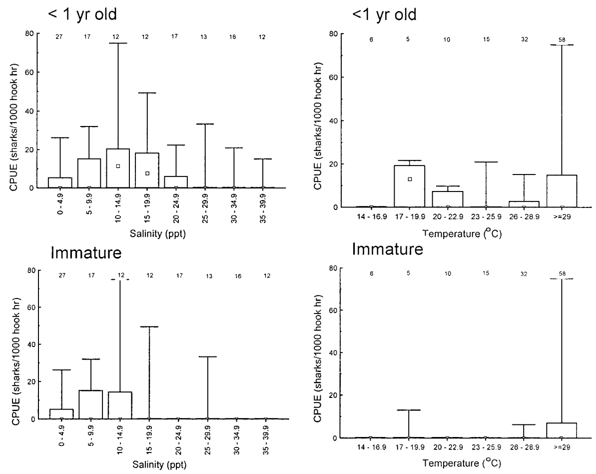

Fig. 4. Catch rates as a function of salinity and temperature for all immature *Carcharhinus leucas* and neonate and young-of-the-year *C. leucas*. Squares represent medians, boxes represent 25–75% quantiles, and error bars represent ranges. Numbers above bars indicate the sample size for each group.

Discussion

While the role of estuarine areas as nurseries for *C. leucas* is well known, there is almost no information available on the structure of the population within these areas. The results of this study show that immature *C. leucas* partition the estuarine habitats within the Caloosahatchee River–Pine Island Sound system based on size (and age). The smallest and youngest animals occur in the Caloosahatchee River, with neonate individuals recorded in June and July. It is unclear if parturition occurs within the river, or if the neonates migrate into this area after birth. Once individuals grow to greater than 95 cm STL they are most likely to move out of the river and into the more open areas of northern San Carlos Bay and finally into Pine Island Sound. This ontogenetic partitioning is the reverse of that observed by Bass et al. (1973) in the St. Lucia system on the KwaZulu-Natal coast of South Africa. In this system, the smallest animals were recorded in the lower part of the system and the juveniles were more common in the lakes further inland. Larger animals were recorded in the ocean outside of the estuarine system. Several factors may account for this reversed pattern. During the period that Bass et al. (1973) studied the St. Lucia system the upstream lake area was in fact hypersaline due to a lack of freshwater input and so the juveniles were moving into more saline areas (as did the sharks in the Caloosahatchee River–Pine Island Sound system). The second factor is that the Franklin Locks on the Caloosahatchee River also prevent juveniles moving up into the higher reaches of the river. The tendency of juvenile *C. leucas* to move upstream in rivers was also observed in the San Juan River–Lake Nicaragua system in Central America (Thorson 1971). To retain partitioning in the Caloosahatchee River–Pine Island Sound system *C. leucas* may reverse the previously observed pattern. Distributional data from other populations may yield interesting comparisons to the partitioning observed in the current study and may help understand why these patterns exist.

Based on the growth parameters given by Branstetter and Stiles (1987) the animals that moved out of the Caloosahatchee River and into San Carlos Bay (95 cm STL) were approximately 1 year old, while those that moved from San Carlos Bay into lower Pine Island Sound (110 cm STL) were approximately 2 years old. It appears that newborn *C. leucas* spend their first year within the Caloosahatchee River, their second year close to the river mouth in San Carlos Bay, and thereafter normally occur in lower Pine Island Sound. It is likely that the neonate and YOY *C. leucas* that occur in the Caloosahatchee River remain throughout the summer after they are born. It is currently unknown whether any or all of the juveniles that occur in lower Pine Island Sound or San Carlos Bay were born in the Caloosahatchee River, or if juveniles from other primary nursery areas also use this area. Two rivers that enter the northern section of Charlotte Harbor (Peace and Myakka) are also known to be primary nursery areas for *C. leucas* (Simpfendorfer unpublished data) and could easily contribute animals to this area. The larger size of the animals that occur in the embayments may mean that this segment of the population moves more widely and that these areas represent only one of several habitats in which they occur. Tagging, tracking, and genetic studies currently underway aim to address these questions.

Two main factors are acknowledged as being important in the selection of nursery areas for sharks: predation risk and food resources (Branstetter 1990; Simpfendorfer and Milward 1993). The first of these factors can be applied to habitat partitioning by *C. leucas*. Physically separating animals less than a year of age from juveniles (>1 year old) significantly reduces the potential for intraspecific predation. Snelson et al. (1984) reported that *C. leucas* were cannibalistic in the Indian River Lagoon on Florida's east coast, with a 162 cm juvenile consuming a small (presumably YOY) animal. The larger juveniles that inhabit lower Pine Island Sound may represent a significant predatory threat to the smaller animals (neonate and YOY), and by maintaining separation, survival of the youngest animals is increased. Less is understood about the role of food availability for *C. leucas* within this system, and further study will need to be undertaken to determine if this factor is important to the observed distribution pattern.

Physical parameters also appear to be important in determining the distribution and occurrence of *C. leucas* in the Caloosahatchee River–Pine Island Sound system. Depth was the only physical factor examined that did not have a significant effect on CPUE. Temperature was important for both <1 year olds and all immatures, with both groups having high catch rates at the highest temperatures. Given that temperature varies mostly on a seasonal basis it is most likely to have a role in terms of occurrence within the general area, rather than in more fine-scale distribution patterns. The role of temperature in wide-scale distribution patterns of sharks is well known (Simpfendorfer and Heupel 2004). The CT analysis indicated that the temperatures at which the two different groups had higher catch rates were different, with the <1 year old sharks present at lower temperatures when compared to the all immatures group. The persistence of the youngest sharks in their summer nursery area beyond that of larger immature animals may be a strategy to reduce predation risk. By remaining later the <1 year old sharks can exit their nursery area with a reduced risk of predation by larger *C. leucas*.

The results indicate that salinity was an important factor in determining the distribution and occurrence of *C. leucas*. Comparison of CPUE between salinity groups indicated that there were differences for both <1 year olds and all immatures, with CPUE higher at lower salinities. The CT analysis results had only the <1 year old group with nodes based on salinity, although salinity had a high Importance Ranking for the all immature group. The CT results indicate that the <1 year old group was most common in salinities between 7‰ and 17.5‰. Since salinity within estuaries, including the Caloosahatchee River–Pine Island Sound system, fluctuate on a relatively short time scale (hours to days) this factor is likely to be responsible, at least in part, for influencing the short-term movements of *C. leucas*. Since the Caloosahatchee River is the only place within the system where salinities less than 17.5‰ regularly occur, this factor may also be important in structuring the size-based partitioning observed.

The role of salinity as a factor influencing the distribution of immature *C. leucas* has rarely been considered. It is generally believed that since they are able to osmoregulate in fresh, estuarine, and marine waters (Thorson et al. 1973), that salinity would not be important in influencing their distribution. Data from the current study indicate that this may not be the case. The data support the conclusion that juvenile *C. leucas* have a preference for salinities between 7‰ and 17.5‰. A similar pattern of salinity selection was observed during behavioral experiments by Kidder (1997) with killifish (*Fundulus heteroclitus*). Like *C. leucas, F. heteroclitus* can osmoregulate over a wide range of salinities, including freshwater. *F. heteroclitus* introduced into a salinity gradient repeatedly selected areas with salinity closest to their own cellular osmolarity (10‰). This type of salinity selection has been shown in some species of euryhaline teleost fishes related to minimizing the energetic costs of osmoregulation (e.g., Marais 1978; Barton and Barton 1987). It would not be unexpected that euryhaline elasmobranches would also aim to minimize energetic costs associated with osmoregulation. This is likely to be especially important for smaller elasmobranches (such as neonate or YOY animals) as they have the highest surface-area-to-volume ratio and so are subjected to the highest energetic cost per unit weight for osmoregulating. By selecting areas where the energetic costs of osmoregulating are minimized, young sharks can expend more energy on growth and reach a size where the risk of predation by other sharks is reduced. Further research to determine the energetic costs of osmoregulation at different salinities will be required to test this hypothesis.

This selection for areas with salinities between 7‰ and 17.5‰ may account for the one individual *C. leucas* smaller than 100 cm STL that was captured in Pine Island Sound. This animal was caught during a period when the salinities in the Caloosahatchee River and lower Pine Island Sound were very low (0.2‰ at the mouth of the river and 17.5‰ in the Sound). This suggests that during periods of high flow in the river neonate and YOY *C. leucas* may move out of the Caloosahatchee River and San Carlos Bay into the more open waters of Pine Island Sound. While this may compromise their survival by exposing them to increased predation risk from larger *C. leucas* and other large shark species present in the area (e.g., *Negaprion brevirostris*), it may be a physiologically related trade off. Since larger *C. leucas* were still present within lower Pine Island Sound at the time of this observation (Heupel unpublished data), this observation also supports the hypothesis that salinity rather than predation risk forced the movement of the small individual.

The results of this research are important for understanding how changes in the flow pattern of the Caloosahatchee River can change its use as a primary nursery for *C. leucas*. Current water management practices result in large and rapid changes in salinity within the river during summer. During periods of high flow and rainfall the salinity may get so low that neonate and YOY *C. leucas* move out of the river to the adjacent embayments. This may result in higher than normal mortality as young animals move out into areas occupied by potential predators. Such an occurrence may have an adverse impact on the population if it occurs over a substantial period of time. Historic flows of the Caloosahatchee River were much lower than present, and as such the population of *C. leucas* was rarely subjected to these types of changes in the environment.

The results of this research have provided new insights into the utilization of estuarine habitats by *C. leucas*. Not only do they partition the habitat between size classes, they also appear to show a preference for areas based on salinity. A great deal more research is required to fully validate these observations and understand the mechanisms that drive them. Such research will provide an understanding of the factors that are important in influencing the distribution of large mobile estuarine fauna and how habitat alterations can affect fish populations.

Acknowledgments

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Literature Cited

Barton, M. and A. C. Barton. 1987. Effects of salinity on oxygen consumption of *Cyprinodon variegates*. *Copeia* 1987:230–232.

Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy. 1973. Sharks of the east coast of southern Africa. 1. The genus *Carcharhinus* (Carcharhinidae). *Oceanographic Research Institute (Durban) Investigational Report* 33:1–168.

Branstetter, S. 1990. Early life history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. National Oceanic and Atmospheric Administration Technical Reports, U.S. National Marine Fisheries Service 90:17–28.

Branstetter, S. and R. Stiles. 1987. Age and growth estimates of the bull shark, *Carcharhinus leucas,* from the northern Gulf of Mexico. *Environmental Biology of Fishes* 20:169–181.

Breiman, L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. Classification and Regression Trees. Chapman and Hall, New York.

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

Compagno, L. J. V. 1984. FAO species catalogue, Volume 4. Sharks of the world; an annotated and illustrated catalogue of shark species known to date, Part 2. Carcharhiniformes. *FAO Fisheries Synopsis* 125:251–655.

Gunter, G. 1938. Notes on invasion of freshwater by fishes of the Gulf of Mexico, with special reference to the Mississippi-Atchafalaya river system. *Copeia* 1938:69–72.

Kidder, III, G. W. 1997. Behavioral osmoregulation in *Fundulus heteroclitus*. *Bulletin of the Mount Desert Island Biological Laboratory* 36:69.

Last, P. R. and J. D. Stevens. 1994. Sharks and Rays of Australia. Commonwealth Scientific and Industrial Research Organisation, Melbourne, Australia.

Marais, J. F. K. 1978. Routine oxygen consumption of *Mugil cephalus, Liza dumerili,* and *L. richardsoni* at different temperatures and salinities. *Marine Biology* 50:9–16.

Michel, M. 2002. Environmental factors affecting the distribution and abundance of sharks in the mangrove estuary of the Ten Thousand Islands, Florida, U.S. Ph.D. Dissertation, University of Basel, Basel, Switzerland.

Montoya, R. V. and T. B. Thorson. 1982. The bull shark (*Carcharhinus leucas*) and largetooth sawfish (*Pristis perotteti*) in Lake Bayano, a tropical man-mad impoundment in Panama. *Environmental Biology of Fishes* 7:341–347.

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

Simpfendorfer, C. A. and M. R. Heupel. 2004. Assessing habitat use and movement, p. 553–572. *In* J. C. Carrier, J. A. Musick, and M. R. Heithaus (eds.), Biology of Sharks and Their Relatives. CRC Press, Boca Raton, Florida.

Simpfendorfer, C. A. and N. E. Milward. 1993. Utilisation of a tropical nursery area by sharks of the families Carcharhinidae and Sphyrnidae. *Environmental Biology of Fishes* 37:337–345.

Snelson, Jr., F. F., T. J. Mulligan, and S. E. Williams. 1984. Food habits, occurrence, and population structure of the bull shark, *Carcharhinus leucas,* in Florida coastal lagoons. *Bulletin of Marine Science* 34:71–80.

Snelson, Jr., F. F. 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.

South Florida Water Management District. 2000. Caloosahatchee Water Management Plan. South Florida Water Management District. West Palm Beach, Florida.

Statsoft. 2004. Electronic Statistics Textbook. Statsoft, Tulsa. WEB: http://www.statsoft.com/textbook/stathome.html.

Taniuchi, T., M. Shimuzu, M. Sano, O. Baba, and P. R. Last. 1991a. Description of freshwater elasmobranchs collected from three rivers in northern Australia, p. 11–26. *In* M. Shimizu and T. Taniuchi (eds.), Studies on Elasmobranchs Collected from Seven River Systems in Northern Australia and Papua New Guinea, Volume 3. The University Museum, the University of Tokyo, Nature and Culture, Tokyo, Japan.

Taniuchi, T., T. T. Kan, S. Tanaka, and T. Otake. 1991b. Collection and measurement data and diagnostic characters of elasmobranchs collected from three river systems in Papua New Guinea, p. 27–41. *In* M. Shimizu and T. Taniuchi (eds.), Studies on Elasmobranchs Collected from Seven River Systems in Northern Australia and Papua New Guinea, Volume 3. The University Museum, the University of Tokyo, Nature and Culture, Tokyo, Japan.

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. 1971. Movements of bull sharks, *Carcharhinus leucas,* between the Caribbean Sea and Lake Nicaragua demonstrated by tagging. *Copeia* 1971:336–338.

THORSON, T. B. 1972. The status of the bull shark, *Carcharhinus leucas,* in the Amazon River. *Copeia* 1972:601–605.

THORSON, T. B., C. M. COWAN, AND D. E. WATSON. 1973. Body fluid solutes of juveniles and adults of the euryhaline bull shark *Carcharhinus leucas* from freshwater and saline environments. *Physiological Zoology* 46:29–42.

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