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Movement and Distribution of Juvenile Bull Sharks, Carcharhinus leucas, in Response to Water Quality and Quantity Modifications in a Florida Nursery

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ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Movement and Distribution of Juvenile Bull Sharks, *Carcharhinus leucas,* in Response to

Water Quality and Quantity Modifications in a Florida Nursery

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ABSTRACT

Movement, distribution, and habitat use of juvenile bull sharks were examined in

two studies using manual and passive acoustic telemetry. Research was conducted in the

Caloosahatchee River, which serves as nursery habitat for this species, and is highly

impacted due to anthropogenic alterations in water quality and quantity via dams and

locks. Manual tracking yielded fine-scale results for eight individuals on home range

size, rate of movement, swimming depth, linearity, direction of travel, tidal influence,

diel pattern, as well as correlation with environmental variables. Changes in salinity,

temperature, dissolved oxygen, turbidity, and pH played a role on the distribution of bull

sharks. Passive monitoring of twelve individuals allowed for examination of trends in

residency, home range, depth, and distribution in response to water quality alterations.

Both studies documented a shift in the distribution of animals in response to significant

modifications in salinity and flow levels. Sharks were distributed throughout the river at

low flow rates, but were located only near the river mouth, or exited the river at

discharges rates above 75 m^3s^{-1}. Current water management policies are examined and

recommendations are made which include the physiological preferences of this top-level

predator.

CHAPTER ONE: INTRODUCTION

An expansion of commercial shark fisheries has resulted in the drastic population decline of many coastal shark species of the Atlantic over the past 30 years (NMFS 1993; Burgess et al. 2005). The Fisheries Management Plan for Sharks of the Atlantic Ocean (FMP) stated that abundance has potentially declined as much as 75 % from the 1970s to the 1980s (NMFS 1993). Most shark species are not capable of rebounding quickly to population reduction since they generally have slow growth, late maturity, and low fecundity compared to bony fishes (Camhi et al. 1998). Significant elasmobranch population reduction affects their prey species and also may have second and third degree affects through trophic linkages (Stevens et al. 2000; Schindler et al. 2002). Bull sharks are managed as part of the large coastal shark fishery complex in the Gulf of Mexico and the Atlantic Ocean. They are taken both commercially and recreationally and the complex is regarded as overfished (Cortés et al. 2002). The FMP recognized a disturbing lack of information regarding shark fisheries and biological data required for appropriate fisheries management.

The FMP identified estuarine nurseries as areas of great concern for coastal sharks due to the direct exposure of these locations to anthropogenic alteration (NFMS 1993). Although the effect is unknown, the degradation of water quality in estuaries has been identified as a potential threat to coastal shark populations (NMFS 1993). Only a few estuarine systems exist globally that remain unaffected by the upstream alteration of their

1

freshwater inflow (Alber 2002), and approximately 60% of the worldwide storage of freshwater is held behind registered dams (Vörösmarty and Sahagian 2000). These areas are at risk from alteration in natural flow rates, which may have disastrous consequences downstream (Alber 2002). High levels of variation in river flow discharge and salinity have been found to affect the distribution of aquatic species (Bain and Finn 1988; Moser and Gerry 1989; Paperno and Brodie 2004; Harrison and Whitfield 2006), and specifically on bull sharks (Heupel and Simpfendorfer 2008, Curtis 2008).

Bull sharks are cosmopolitan in tropical and subtropical coastal, estuarine, and riverine waters (Garrick 1982, Compagno 1984). This elasmobranch species is able to reside in both freshwater and saltwater for extended periods of time due to unique physiology and osmoregulatory capabilities (Thorson 1971; Thorson et al. 1973; Montoya and Thorson 1982). This enables them to travel long distances in freshwater systems, which has been documented throughout the world (Sadowsky 1968, Branstetter 1981, Jensen 1976, Pillans et al. 2006). Females are thought to give birth in estuaries or in proximity to river mouths and juveniles tend to move upstream after parturition (Thorson 1972; Last and Stevens 1994). Juveniles are rarely found in marine environments following birth (Branstetter and Stiles 1987; Thorson et al. 1973; Thorson 1976), possibly due to an inability to up-regulate urea (Pillans and Franklin 2004), and have exhibited a distinct preference for estuarine water. The bull shark is one of the most common large shark species in Florida's coastal and estuarine areas, many of which are believed to provide important nursery habitat (Snelson et al. 1984; Michel 2002; Simpfendorfer et al. 2005). Habitat utilization by this species has received limited

scientific attention despite its broad distribution and known use of freshwater and coastal systems.

The Caloosahatchee River in southwest Florida served as the site of this study and is a nursery for bull sharks in their first year of life (Simpfendorfer et al. 2005). This system is highly impacted with major changes in its historic hydrology due to significant modifications in land and canal development (Barnes 2005). The South Florida Water Management District (SFWMD) manages water flow into the river and water quality parameters can change rapidly, on a scale from hours to days (Simpfendorfer et al. 2005), depending on precipitation levels and discharge regimes. Regulatory releases of freshwater from Lake Okeechobee have created large changes in the natural quantity, timing, and quality of flow to the estuary (Barnes 2005). Alteration in flow rate has an influence on salinity, which is a critical determinant of estuarine habitat characteristics and can affect distribution of rooted vegetation, and sessile and motile biota (Alber 2002). Increased river discharge has been linked to behavioral changes in several bony fish species by altering their habitat selection (Brenden et al. 2006; Albanese et al. 2004) and abundance (Flannery et al. 2002). Modifications in the Caloosahatchee River are often made without considering the biological integrity of the system (Haunert et al. 2000). It is believed that the river has declined in the abundance, distribution, and species richness of juvenile fish due to changes in the natural salinity regime and freshwater discharge, although current data does not yet exist to substantiate (Barnes 2005). In heavily regulated systems, such as the Caloosahatchee River, it is essential to understand the effect that modifications to environmental parameters have on resident species. A population decline of many coastal shark species necessitates research to

understand both habitat use and response to habitat modification in order to formulate appropriate management policy.

This study utilized both manual and passive acoustic telemetry to aid in the understanding of juvenile bull shark habitat use within nursery grounds. Manual tracking provided data on short-term, fine-scale movement patterns while passive tracking allowed for a broader view of how animals were distributed throughout the estuary. The purpose of study one was to gain an understanding of detailed daily movement patterns and habitat use as well as examine the relationship between river habitat modification and movement. The purpose of study two was to examine in closer detail the relationship between distribution and abundance of juvenile bull sharks and physical factors, specifically flow rate and salinity, over a longer period of time. With these goals, I addressed the following research questions for the short term, manual tracking study:

1. How are juvenile bull sharks utilizing the estuarine nursery habitat?

2. Do juvenile bull sharks exhibit diel habitat use patterns in regards to home range size, rate of movement, depth, linearity, direction, or tidal influence?

3. Do changes in salinity, temperature, turbidity, dissolved oxygen, or pH influence juvenile bull shark movement and habitat use?

The following research questions were addressed for the long term, passive monitoring study:

1. How are juvenile bull sharks utilizing the nursery over a longer time period?

2. What is the impact of high discharge rates on the residency and distribution of juvenile bulls sharks?

3. What would be an appropriate management regime for this top-level predator?

A comprehensive examination of movement on both short and long term scales provides a more complete understanding of how juvenile bull sharks utilize habitat as well as how water management practices influence shark behavior. An understanding of how juvenile bull sharks utilize nursery habitat in response to significant artificial water quality modification is necessary for both biological and management purposes. Bull sharks are a commercially-important species and are currently believed to be overfished. In order to maintain a sustainable population and healthy ecosystem, it will be necessary to protect immature stocks and essential habitats (Cortes et al. 2002). This study aims to contribute to the knowledge of how juvenile bull sharks utilize nursery habitat as well as how they are affected by water management decisions.

CHAPTER TWO:

HOME RANGE, MOVEMENT PATTERNS, AND WATER QUALITY

PREFERENCES OF JUVENILE BULL SHARKS, *Carcharhinus leucas,* IN A

FLORIDA NURSERY

Abstract

Acoustic telemetry was used to examine home range size, small-scale movement

patterns, and water quality preferences of juvenile bull sharks in the Caloosahatchee

River, Florida. Movement pattern analysis included home range size, rate of movement,

swimming depth, linearity, direction, tidal influence, diel pattern, and correlation with

environmental variables. Manual tacking occurred before and after a large freshwater

influx which divided the sharks into two groups based on movement patterns. The first

group displayed increased rate of movement, distance traveled, and space utilization at

night, and movements correlated with salinity, temperature, and dissolved oxygen. The

second group had an increased rate of movement, distance traveled, and space utilization

during the day, and movements correlated with temperature, dissolved oxygen, turbidity

and pH. These juvenile bull sharks displayed distinct diel movement patterns that were

influenced by physical factors, which may account for the distribution of this top-level

predator in the Caloosahatchee River.

Introduction

The life history and ecology of euryhaline elasmobranchs is poorly understood, as is the extent of their ecological role in freshwater and brackish systems (Martin 2005; Curtis 2008). Understanding behavior, especially movement patterns, will help define the ecological role of species within these systems. Movement is an essential process that enables fishes to fulfill their resource requirements in spatially and temporally changing environments (Schlosser and Angermeier 1995). Through movement, fish are able to choose the most suitable habitats in order to optimize survival and growth (Gowan and Fausch 2002). Although physical barriers such as dams or other habitat features have an obvious impact on movement patterns, the role of environmental factors as drivers of movement patterns has received less attention. Since many aquatic systems are being increasingly modified, it is especially important to study the relationship between movement and ecological characteristics of mobile residents in order to predict how animals will respond to environmental change. Due to the close proximity of freshwater systems to human development, elasmobranchs that utilize reduced salinity environments may be especially vulnerable to anthropogenic habitat modification, making it essential to gain a better understanding of their habitat utilization and environmental preferences.

Bull sharks, *Carcharhinus leucas*, are one of the few elasmobranch species known to be physiologically capable of tolerating freshwater for extended periods of time (Thorson et al. 1973), and are found throughout the world in warm subtropical and tropical coastal, estuarine and riverine waters (Bass et al. 1973; Compagno 1984; Curtis 2008). The bull shark is one of the most common large shark species in Florida's near-shore coastal waters (Snelson et al. 1984; Wiley and Simpfendorfer 2007), and is well

7

known for its ability to travel long distances in freshwater systems. In South Africa, *C. leucas* has been reported to travel up to 1,120 km from the sea in the Zambezi River system (Bass et al. 1973). Bull sharks have also been reported 2,800 km up the Mississippi River (Thomerson et al. 1977). Movement of bull sharks into freshwater systems has also been reported in Brazil (Sadowsky 1968; 1971), the Gulf of Mexico (Springer 1940; Clark and Von Schmidt 1965; Branstetter 1981), Lake Nicaragua (Thorson et al. 1966; Jensen 1976; Tuma 1976), Australia (Thorson et al. 1973; Pillans et al. 2006) and the Indian River Lagoon system in Florida (Curtis 2008). Despite its broad distribution and known use of freshwater systems, habitat utilization by this species has received limited scientific attention.

The movement and behavior patterns of elasmobranchs have been the subject of study for several decades. With the use of acoustic telemetry, these studies have examined many aspects of movement including short-term movement patterns, home range size, rate of movement, and depth distribution (e.g. McKibben and Nelson 1986; Gruber et al. 1988; Carey and Scharold 1990; Morrissey and Gruber 1993b). However, most of these studies focused on pelagic or coastal species with little telemetry data available for species utilizing freshwater or estuarine systems (Heupel et al. 2006; Simpfendorfer 2006; Collins et al. 2007; Curtis 2008). Telemetry research has highlighted the variety of temporal and spatial patterns displayed by elasmobranchs in movement characteristics such as rate of movement and horizontal migrations (Sundström et al. 2001). Several physical factors may interact to define elasmobranch movement patterns, including water temperature (Morrissey and Gruber 1993a; Matern et al. 2000), oxygen levels (Parsons and Carlson 1998), diel periodicity (Tricas et al. 1981;

8

McKibben and Nelson 1986; Klimley et al. 1988; Holland et al. 1992), tides (Ackerman et al. 2000; Medved and Marshall 1983) and salinity (Curtis 2008; Heupel and Simpfendorfer 2008). Furthermore, few species have been tracked for a full diel period, making it difficult to understand the relationship between environmental characteristics and elasmobranch movement patterns.

The Caloosahatchee River and San Carlos Bay in southwest Florida is a nursery area for bull sharks during their first year of life until reaching approximately 95 cm standard total length (STL) (Simpfendorfer et al. 2005). Although it is known that young bull sharks utilize this system, there is a lack of information regarding the relationship between environmental factors and habitat utilization. The goal of this research was to investigate short-term detailed space utilization, movement patterns, and to determine whether environmental variables influence short-term movement patterns of juvenile *C. leucas*. With a better understanding of habitat requirements for this euryhaline species, we make recommendations for water management in this environmentally sensitive river system.

Materials and Methods

Study Site

The Caloosahatchee River extends 105 km and links Lake Okeechobee to San Carlos Bay on Florida's southwest coast (Barnes 2005). The river is the primary provider of freshwater to southern Charlotte Harbor (Figure 1). Sharks were tracked in the Caloosahatchee Estuary which consists of approximately 32 km of river habitat. Due to the long and narrow configuration of the river, the estuary experiences large water quality fluctuations generated by wind, tide, runoff, and precipitation. These changes are

9

compounded by the artificial release of freshwater from Lake Okeechobee, with variable

discharge rates that have reached as high as 1278 m^3s^{-1} (South Florida Water

Management District 2008). The unnatural, rapid flow of freshwater may cause severe

damage to estuarine organisms and communities, especially during the wet season when

freshwater release is at its highest levels (Barnes 2005). Conditions within the system

can alter abruptly, on a scale from hours to days (Simpfendorfer et al. 2005), providing an

ideal location to examine *C. leucas* movement patterns in relation to environmental

fluctuations.

Figure 1: The Caloosahatchee estuary. Inset: Location of the study site in Florida and

showing connections to Lake Okeechobee and the Gulf of Mexico.
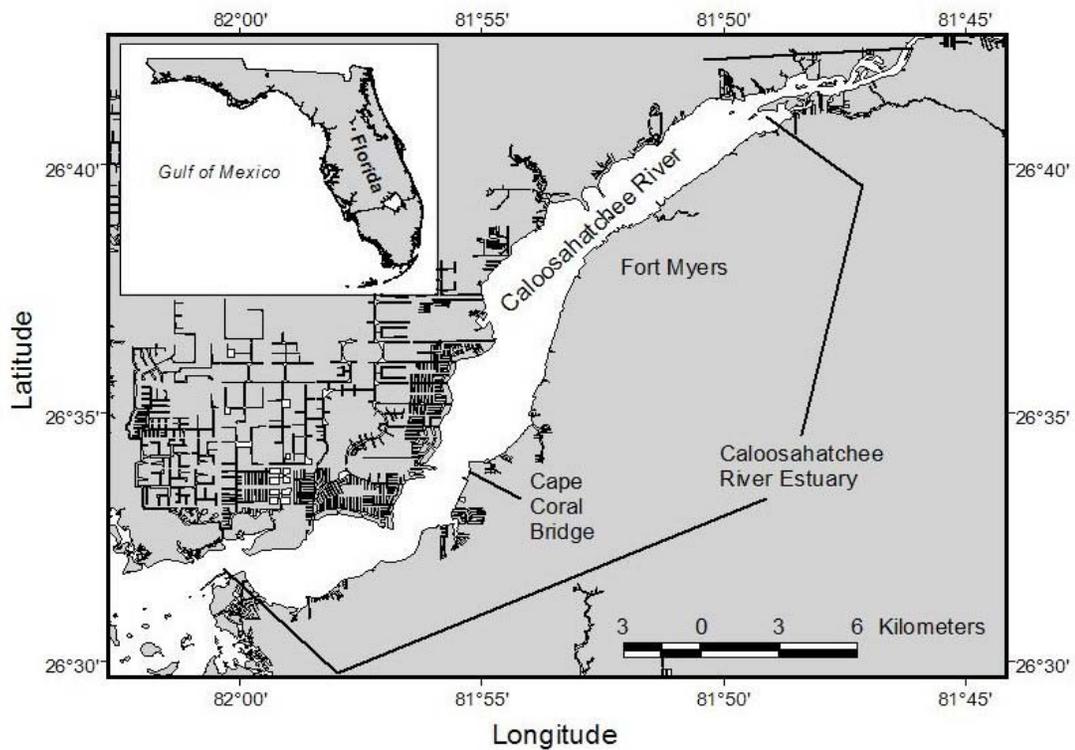
Eight juvenile sharks were collected from June to August of 2006 via rod and reel fishing using circle hooks and frozen mullet, *Mugil cephalis* or fresh catfish, *Arius felis* and *Bagre marinus*. Captured individuals were weighed, measured (stretch total length – STL), sexed, and tagged with a single-barb plastic dart tag inserted into the dorsal musculature adjacent to the first dorsal fin. In addition, a V13P (Vemco Ltd) acoustic depth sensing transmitter was attached to the dorsal fin via a rototag. Transmitters (13 x 84 mm) pulsed continuously on one of four acoustic frequencies (75, 78, 81, or 84 kHz). Two transmitters of each frequency were used. One shark was tracked at a time and transmitters on the same frequency were spaced out during the course of the research to avoid signal overlap.

A Vemco VR100 acoustic receiver and directional hydrophone mounted on the boat were used to manually track shark movements. In order to eliminate potential influence on shark movement, an estimated minimum distance of 100 m between the shark and the boat was maintained. Shark location was recorded every 15 minutes for up to 24-hours using a global positioning system. Water quality samples were collected at the surface and bottom every 15 minutes using a Niskin bottle and tested for several parameters including salinity, temperature, dissolved oxygen, turbidity, and pH using a water quality meter, pH meter and turbidimeter.

Data Analysis

Home Range

Positional fixes derived from active tracking were plotted over a digital orthoquad of the Caloosahatchee River and analyzed using ESRI ArcView 3.3 geographic

information systems software. The maximum size of activity space used by each animal was determined for day, night, and 24 hour (total) periods using minimum convex polygon analysis in the Animal Movement Extension for ArcView (Hooge and Eichenlaub 2000). Movements between positions recorded from 0700 to 1900 were categorized as daytime and movements between 1900 and 0700 were categorized as nighttime in order to coincide with local sunrise and sunset times. A Brainerd-Robinson Similarity Coefficient Analysis, which measures the similarity of assemblages by comparing the proportional representation of each category within the assemblage, was used to determine whether there was a difference in day and night home range size between tracks. Hierarchical cluster analysis using the average linkage method and squared euclidean distance measure was conducted to support those results. A Wilcoxon signed rank test based on groupings from the cluster analysis was used because the data were paired and non-normal. The test was performed to determine if there was a significant diel difference in home range size, however, only one cluster (n = 4) was used because the second cluster was too small (n = 2) to perform any tests.

Movement

In order to describe movement patterns, six variables were used: swimming depth, rate of movement (ROM), linearity of movement, direction of travel (upriver, downriver, shoreline), tidal stage, and diel period. The rate of movement was calculated using the distance traveled between successive positional fixes divided by the sampling interval. In order to achieve normality, ROM data were normalized using a log transformation. A linearity index was calculated to determine if there was a linear or random trend to shark

movement. The linearity index values were determined using the formula from Bell and

Kramer (1979):

$$LI = (F_n - F_1)/D$$

where F_n was the last fixed location of the animal, F_1 was the first fixed location, and D

was the total distance traveled by the shark. Values of linearity ranged from 0 to 1, with

values near zero representing random movements and values approaching 1 indicating

linear travel. Direction of travel in degrees (a_i), or the angle of movement between fixes,

was calculated between successive fixes using the formula described in Kernohan et al.

(2001), with (x_i, y_i) representing the first fix and (x_{i+1}, y_{i+1}) representing the following fix.

The degree of travel was calculated by the following criteria:

$$a_i = \quad \arctan (Y_i/X_i)(180°/\pi) \qquad\qquad \text{if } X_i > 0$$

$$180° + \arctan (Y_i/X_i)(180°/\pi) \qquad \text{if } X_i < 0$$

$$90° \qquad\qquad\qquad\qquad\qquad \text{if } X_i = 0 \text{ and } Y_i > 0$$

$$270° \qquad\qquad\qquad\qquad\qquad \text{if } X_i = 0 \text{ and } Y_i < 0$$

The distance of the X vector was calculated as:

$$X_i = x_{i+1} - x_i$$

The distance of the Y vector was calculated as:

$$Y_i = y_{i+1} - y_i$$

The formula computed angles calculated in radians that were converted to degrees. This

angle was then converted to a bearing from true north (b_i) with the equation:

$$B_i = 90 - a_i$$

If b_i was negative, a value of 360° was added to the result to make the value positive.

These results were used to determine if an individual was moving upriver (1), downriver

(-1), or towards the shoreline (0). If movement was between 330º and 120º, movement was categorized as upriver, between 120º and 150º or 300º and 330º was considered towards the shoreline, and between 150º and 300º was considered downriver. These angles were chosen because they most closely reflected the northeast to southwest trajectory of the river where the tracks occurred.

A multivariate analysis of variance (MANOVA) was conducted to assess whether there was a difference in shark depth, ROM, or linearity in relation to directional travel. A Tukey's post-hoc test was used to identify if ROM changed upriver, downriver, or perpendicular to the shoreline. A univariate general linear model (GLM) determined if there were significant changes in ROM, shark depth, and linearity among the tracks. A univariate GLM was also conducted to elucidate if swimming depth, ROM, linearity, or directional travel displayed diel differences within tracks. Spearman correlation analysis was used to determine relationships between depth and ROM, linearity, or direction of travel. Spearman analysis was also used to determine if there was a tidal influence on ROM, depth, linear movement, or direction of travel.

Water Quality

To understand how water quality changed over time, a univariate GLM was used to determine if top and bottom values for salinity, temperature, dissolved oxygen (DO), turbidity, and pH were different among tracks (i.e. over time) and if there were significant diel differences within each track for each variable. A correlation analysis was conducted to ensure that water quality variables were independent. Variables were considered correlated if values fell between 0.3 and 0.8, however the largest correlation was minimal at 0.32, supporting the independent analysis of each variable. Preference

14

for each of the water quality variables was analyzed using multiple linear regression comparing average habitat condition with the latitudinal shark position. Latitude was chosen as the position variable due to the north-south orientation of the river and the higher degree of latitudinal heterogeneity in habitat characteristics. Based on an analysis of the residual error, multiple regressions were again performed with the tracks separated into two groups, as determined via cluster analysis. Both groups of data were analyzed using Cook's and Mahalanobis distance and two outliers were removed per group because they fell outside two standard deviations from the mean. Statistical tests were performed with Statistica (1999) and SPSS (15.0), and a rejection level of 0.05 was employed.

<div align="center">Results</div>

From June to August of 2006, 509 positional fixes were obtained for eight juvenile *C. leucas* that were actively tracked for periods of up to 24 hours. Six of these tracks were considered to be full tracks (i.e. >21 hours) and were used in all statistical analyses (individuals 3 and 8 were omitted), data are shown in Table 1 and Figure 2. Animals 1 through 3 were caught in the same section in the northern portion of the estuary in salinities of 7.6 – 11.1 ‰. Following a large freshwater influx, the salinity in that location dropped to approximately 2.6 ‰, after which no additional sharks were captured despite extensive fishing efforts. After moving closer to the mouth of the river, an individual was caught in 6.5 ‰ within 45 minutes. All subsequent individuals were captured in this lower portion of the estuary in salinities ranging between 6.5 and 12.5 ‰ at time of capture. Results were reported as pooled data for all tests where a uniform trend was determined. However, in each case where uniformity between the six

individuals was not the result, animal behavior patterns clustered by tracks 1-2 and 4-7, and results were reported by cluster.

Table 1: Summary data for eight juvenile *C. leucas* tracked using acoustic telemetry within the Caloosahatchee River, FL in 2006. Size is indicated as stretch total length (STL) in centimeters.

Track	Sex	Size- STL	Date	Latitude of capture	Longitude of capture	Duration (h)	Total positional fixes
1	M	80	14-Jun-07	26.64392	-81.89285	24	75
2	F	77	28-Jun-07	26.64474	-81.88980	24	62
3	F	78	06-Jul-07	26.64983	-81.88493	7	13
4	M	80	18-Jul-07	26.64942	-81.86473	21	74
5	M	84	01-Aug-07	26.55795	-81.92523	24	79
6	M	77	03-Aug-07	26.55847	-81.92476	24	82
7	F	82	08-Aug-07	26.55818	-81.92437	24	74
8	M	104	23-Aug-07	26.52864	-81.96098	6	20

Figure 2: Movement of eight actively tracked bull sharks within the Caloosahatchee
River. Inset maps provide closer detail of the movements within the two clusters.
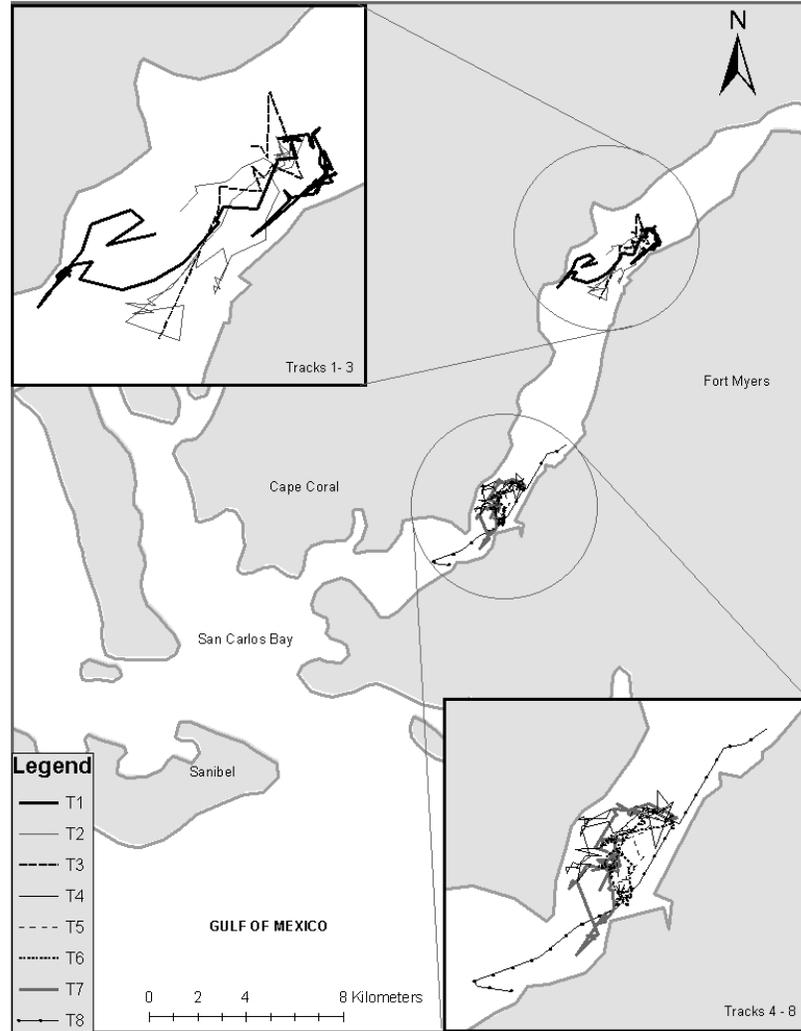
Home Range

Activity space for the six complete tracks varied from 1.2 to 4.3 km^2 (mean = 2.5
km^2, median = 2.4 km^2). When calculated as a distance measurement, sharks utilized a
1.9 to 4.8 km linear stretch of river. With all six tracks pooled, a larger space was used
during the night (mean = 1.3 km^2, median = 0.7 km^2) than during the day (mean = 0.9
km^2, median = 0.9 km^2). However, results from the Brainerd-Robinson Similarity

17

Coefficient Analysis showed tracks 1 and 2 were highly related in regards to home range size with a correlation value of 0.92, and tracks 4 though 7 were highly related, with all correlation values above 0.90. Hierarchical cluster analysis supported a cluster of two groups, with the upriver tracks completed in June (n = 2) grouping and the downriver tracks conducted in July and August (n = 4) forming the second cluster. With data separated according to cluster membership, it was shown that tracks 1 and 2 had larger nighttime home range sizes and tracks 4 through 7 had significantly (Wilcoxon, $p <$ .0001) larger daytime home ranges (Figure 3).

Figure 3: Estimates of diel spatial usage of six actively tracked individuals as measured by minimum convex polygon.
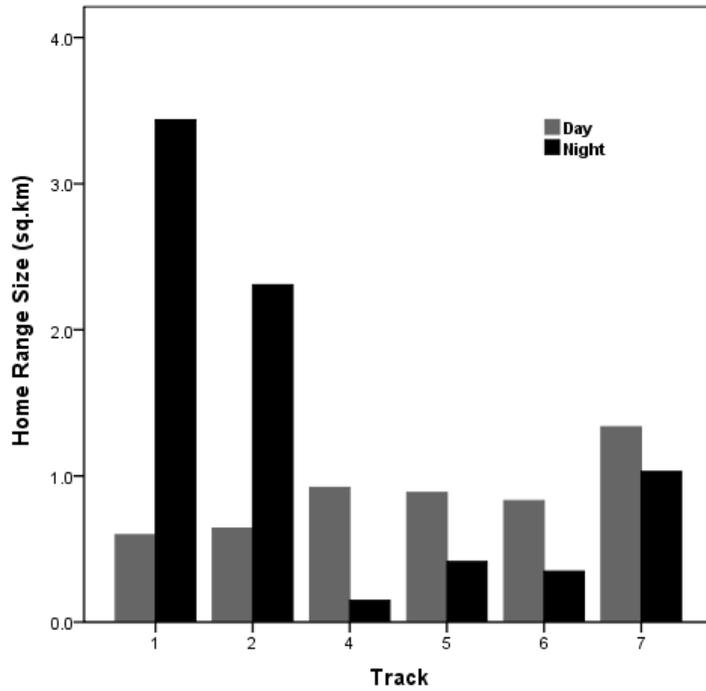
Total distance traveled by all individuals per 24 hour period ranged from 9.7 to 20.6 km, with a mean of 14.9 km. Sharks 1 and 2 traveled 4.32 and 7.22 km farther at night than during the day. Shark 4 had a slightly higher total distance traveled during the night, but the difference was small (1.65 km). Sharks 5 through 7 had small diel variation (range 1.28 – 1.69 km) but generally displayed increased daytime travel distances, corresponding with diel spatial usage patterns, as shown in Table 2.

Table 2: Summary of movement variables separated by diel period for same sharks tracked within the Caloosahatchee River.

Track	Diel	Total dist (km)	ROM (m/min)	Shark Depth (m)	Linearity
1	Day	8.13	11.5	2.2	0.2
	Night	12.45	18.5	0.8	0.3
	Total / Mean	20.60	15.1	1.4	0.2
2	Day	5.49	10.2	1.0	0.4
	Night	12.71	19.1	0.4	0.2
	Total / Mean	18.20	15.1	0.7	0.3
3	Day	7.20	21.4	1.2	0.4
	Night	N/A	N/A	N/A	N/A
	Total / Mean	7.20	21.4	1.2	0.4
4	Day	6.33	11.5	0.9	0.2
	Night	7.98	11.0	0.5	0.3
	Total / Mean	14.30	11.2	0.7	0.2
5	Day	6.21	9.2	1.7	0.4
	Night	4.74	7.1	0.5	0.2
	Total / Mean	10.90	8.1	1.1	0.3
6	Day	5.48	7.1	1.6	0.4
	Night	4.20	5.6	0.5	0.3
	Total / Mean	9.70	6.3	1.0	0.3
7	Day	8.56	14.9	1.7	0.4
	Night	6.87	9.2	0.6	0.3
	Total / Mean	15.40	12.1	1.1	0.3
8	Day	12.00	31.0	0.9	0.6
	Night	N/A	N/A	N/A	N/A
	Total / Mean	12.00	31.0	0.9	0.6

There was a significant difference in the rate of movement (ROM) between all six tracks (GLM, df = 5, F = 12.991, p < .0001). The first two tracks showed an overall higher ROM (mean = 15.1 m/min) than the second cluster of individuals (mean = 9.3 m/min). These two individuals also moved faster during nighttime hours (mean = 18.8 m/min) than during the day (mean = 10.9 m/min). In contrast, individuals in tracks 4 through 7 moved faster during the day (mean = 10.8 m/min) than at night (mean = 8.2 m/min) (Figure 4).

Figure 4: Diel rate of movement for the six actively tracked bull sharks.
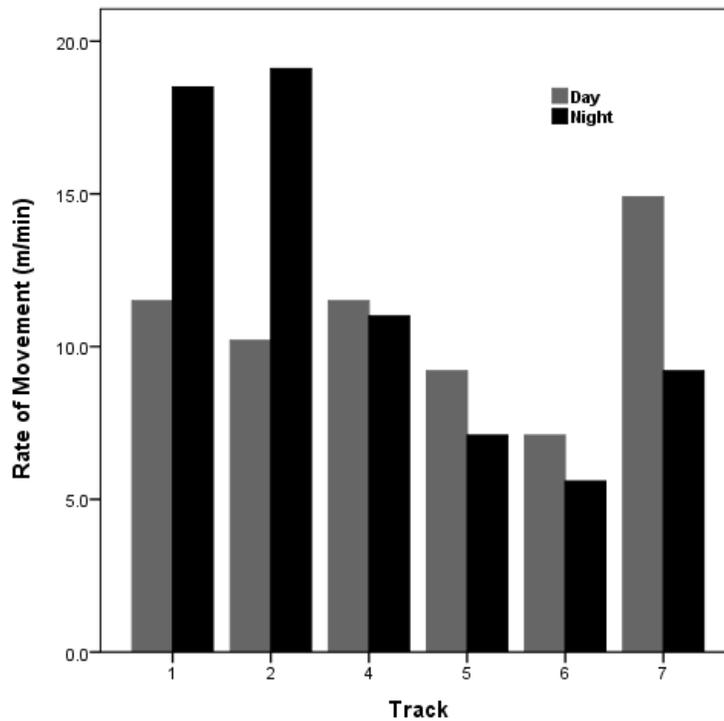
Significantly different swimming depth was observed among the six tracks (GLM, df = 5, F = 8.8128, p < .0001). Mean bottom depth in tracking locations was 2.4 m and mean shark depth was 1 m from the surface. All six individuals displayed the same trend regarding depth and were therefore analyzed together. Each shark swam significantly closer to the surface during the night (mean = 0.6 m) and were deeper in the water column during the day (mean = 1.5 m) (GLM, df = 6, F = 29.2176, p < .0001).

There was no significant difference in linearity either among tracks or between night and day within tracks for any individual (Table 2). No significant relationship existed between either linearity or shark depth with direction of travel (MANOVA, p > .05). However, all sharks moved at a different rate relative to direction of travel (MANOVA, df = 5, F = 5.034, p = .007). All sharks moved at an elevated speed as they traveled upriver (mean = 17.5 m/min) but there was no difference in ROM between travel downriver (mean = 13.5 m/min) or toward the shoreline (12.5 m/min). Spearman correlation analysis showed significant relationships between tidal stage and shark depth (p = .004), linearity (p < .001), and direction of travel (p = .027), but no relationship was present with ROM (p = 0.637). Sharks swam slightly deeper in the water column during a falling tide (mean = 1.1 m) versus a rising tide (mean = 0.9 m). Individuals displayed more random movements during a rising tide (mean = 0.262) than during a falling tide (mean = 0.321). All individuals followed the tide, traveling upriver during a rising tide and downriver during a falling tide. Relationships between shark depth and linearity (Spearman, p = .005) and ROM and linearity (Spearman, p = .011) were also significant. Each individual showed a higher degree of random movements at shallower depths and more linear travel in deeper depths. Animals also displayed a faster ROM when

22

swimming a linear trajectory than when traveling a random pattern. No other movement

variables showed significant correlations.

Water Quality

There were significant differences for all surface and bottom values of salinity,

temperature, dissolved oxygen (DO), turbidity, and pH when compared across tracks.

Water conditions therefore changed significantly over time (Table 3). All top and bottom

water quality variables, except bottom pH, showed significant diel differences within

each track (Table 3). However, when water quality from all tracks was analyzed

together, it became evident that few variables exhibited clear diel trends. Surface

temperature was always higher and surface and bottom pH was always lower during the

day.

Table 3: Results from univariate general linear models testing whether there was a significant difference in surface and bottom water quality variables between each track and for diel differences in surface and bottom water quality variables within each track. "T" denotes surface of the water column and "B" denotes the bottom of the water column.

	Water quality statistics			Difference in WQ between tracks			Diel difference in WQ within tracks		
Variable	Min	Max	Mean	df	F	p	df	F	p
T Salinity	2.4	12.8	7.5	5	45.30	0.001	6	7.13	0.001
B Saliinity	5.4	17.0	10.7	5	42.30	0.001	6	11.86	0.001
T Temp	27.0	37.3	30.4	5	68.90	0.001	6	18.70	0.001
B Temp	28.0	32.0	30.4	5	629.00	0.001	6	17.00	0.001
T DO	3.6	9.4	5.9	5	32.81	0.001	6	6.90	0.001
B DO	2.2	8.7	4.6	5	72.71	0.001	6	2.75	0.012
T Turbidity	1.4	5.9	3.0	5	117.92	0.001	6	15.83	0.001
B Turbidity	1.7	15.2	4.4	5	11.19	0.001	6	2.55	0.020
T pH	7.3	8.6	8.1	5	368.00	0.001	6	15.00	0.001
B pH	7.4	8.9	8.0	5	13.82	0.001	6	0.75	0.606

Linear regression showed a significant relationship between shark location and salinity ($p < .0001$), temperature ($p < .0001$), and dissolved oxygen ($p = .012$) for tracks 1-2, and the model accounted for 0.609 of the sample variation. Tracks 4 through 7 were related to temperature ($p = .017$), dissolved oxygen ($p < .0001$), turbidity ($p < .0001$) and pH ($p < .0001$), and the model accounted for 0.560 of the sample variation (Tables 4, 5). No significant relationship was yielded between shark swimming depth and water quality variables ($p > .05$).

Table 4: Linear regression model summarizing water quality influence on actively tracked bull sharks 1 – 2.

Variables	Coefficient	t Value	p	Model Summary	
Salinity	-0.003	-8.207	0.001		
Temperature	-0.003	-4.198	0.001		
Diss. Oxygen	0.001	2.562	0.012		
Turbidity	0.001	1.548	0.124	N	125
pH	-0.004	-1.078	0.283	R^2	0.609
Diel	-0.008	-7.298	0.001	Standard error of est.	0.005
Constant	26.783	915.213	0.001	Significance (p-value)	0.001

Table 5: Linear regression model summarizing water quality influence on actively tracked bull sharks 4 – 7.

Variables	Coefficient	t Value	p	Model Summary	
Salinity	0.0000548	0.349	0.727		
Temperature	0.001	2.400	0.017		
Diss. Oxygen	0.001	4.085	0.001		
Turbidity	-0.001	-4.590	0.001	N	284
pH	-0.016	-5.797	0.001	R^2	0.560
Diel	-0.006	-11.956	0.001	Standard error of est.	0.004
Constant	26.644	951.004	0.001	Significance (p-value)	0.001

Discussion

Utilization of estuarine regions by euryhaline sharks has largely gone unstudied. Bull sharks, *C. leucas*, are widely reported to utilize fresh and brackish waters throughout their range (Bass et al. 1973; Compagno 1984). Recently, Pillans and Franklin (2004) reported the presence of bull sharks along an entire salinity gradient in Australia with smallest individuals found in the freshwater reaches of the system. They suggested that physiological limitations (the inability to upregulate urea) may explain the lack of juvenile bull sharks in fully marine water. However, they also suggested that the movement of bull sharks should be investigated to further define use of habitats and potential physiological implications of use of estuarine regions. We have found that young bull sharks in a dynamic Florida estuarine system display distinct movement patterns within that habitat and may respond to environmental changes which affect their movements and distribution.

The home range size of young bull sharks in the Caloosahatchee River (1.2 – 4.3 km^2) were similar to that described for other juvenile sharks including scalloped hammerheads, *Sphyrna lewini* (0.5 – 3.5 km^2; Holland et al. 1993a) and sandbar sharks, *C. plumbeus* (1.9 – 14.7 km^2; Medved and Marshal 1983). Results were also similar to the home range size found for juvenile bull sharks in Florida's Indian River Lagoon (0.02 – 3.49 km^2; Curtis 2008). Similarity among juvenile sharks suggests that this space utilization may be typical for young sharks. In addition, home range size was consistent among individuals within the study despite the fact that individuals were collected in different portions of the estuary.

26

When examined using cluster analysis, the six tracks were divided into two distinct groups. This grouping indicated movement patterns of individuals tracked in the northern part of the study site were different from those tracked approximately 10 km downriver in the southern region, suggesting that either individual differences or differences in location may be influencing movement patterns. Heupel and Simpfendorfer (2008) suggested that changes in environmental conditions within the Caloosahatchee River caused synchronous downriver movement of an entire monitored population (c. 18 sharks per year) of bull sharks. Movement in relation to changes in salinity was also documented on Florida's east coast, where individuals moved between a creek and an open lagoon, depending on precipitation levels, to remain within a preferred salinity range (Curtis 2008). If this movement pattern is consistent, individuals captured in the southern portion of the site during this study may have been displaced from further upriver due to the large freshwater influx that occurred between tracks 3 and 4. Thus, differences in movement patterns between the two clusters may be related to location within the river (at a given point in time) and differences in habitat in those regions. The upriver portion of the estuary is slightly wider, shallower and more natural than downriver areas.

Examination of diel patterns revealed distinct differences in day and night movement patterns and locations for most individuals. The first two tracked animals displayed a larger nighttime space use accompanied by an increased ROM and distance traveled during the night. This result was not unexpected since many shark species have been reported to increase home range size and swimming speed at night (Gruber et al. 1988; Klimley and Nelson 1984; Holland et al. 1992; Ackerman et al. 2000; Vaudo and

27

Lowe 2006). Tracks 5 through 7, however, showed larger daytime home ranges with a faster ROM and larger distances traveled during the day. Those individuals were also shown to utilize more random movement patterns in shallow water at night. A substantial shift in environmental parameters could be the impetus for behavioral change between the two groups of juvenile bull sharks in this study. The magnitude of the freshwater influx that occurred prior to the tracking of sharks 4-7 moved the salt-wedge downriver and likely displaced many bony fish species upon which they prey (Snelson et al. 1984). Increased river discharge has been linked to behavioral changes in several bony fish species by altering their habitat selection (Brenden et al. 2006; Albanese et al. 2004). A positive relationship was also found between freshwater inflow and fish abundance in a southwest Florida estuary (Flannery et al. 2002). This relationship may drive predators downstream during freshwater influx events to maintain favorable foraging conditions.

The ROM, or speed of movement over ground (as opposed to swimming speed), is affected by the linearity of shark movement and is an approximation since the position of the shark cannot be fixed exactly. Although ROM is not an accurate measure of swimming speed, it is helpful in elucidating temporal behavioral changes. The ROM of the six sharks examined here ranged from 0 - 73.5 m/min (0 - 4.41 kmh^{-1}), with a mean of 11.07 m/min (0.67 kmh^{-1}). This is lower than the mean reported for adult bat rays, *Myliobatis californica* (8.84 kmh^{-1}; Matern et al. 2000), adult leopard sharks, *Triakis semifasciata* (4.9 kmh^{-1}; Ackerman et al. 2000), and the range of 0 – 38.2 kmh^{-1} for juvenile lemon sharks, *Negaprion brevirostris* (Sundström et al. 2001). This result, however, approximates the mean ROM of 1.53 kmh^{-1} reported for neonate and juvenile

sandbar sharks, *C. plumbeus* (Rechisky and Wetherbee 2003) and the mean ROM of 0.55 kmh^{-1} (0.154 m/s) reported for juvenile and young-of-the-year bull sharks on Florida's east coast (Curtis 2008).

Analysis of depth data showed that approximately 60% of all shark fixes were recorded when the shark was swimming where water depth was less than 1 m. This depth preference is similar to that of 1.0 – 1.5 m reported for young bull sharks in a Florida lagoon, where 65% of the positions were recorded in less than 2.0 m (Curtis 2008). This suggests shallow portions of the estuary are key habitat for this species. Bull sharks in this study exhibited a uniform trend of spending a large amount of time during the day in the middle of the river and closer to the banks at night. Correspondingly, this meant that sharks were slightly deeper in the water column during the day than at night. Similarly, gray reef sharks (*C. amblyrhynchos*) were reported to display predictable diel patterns of utilizing deeper water during the day and moved to shallower areas at dusk, likely for foraging (Nelson and Johnson 1980).

A linearity index helps to determine if sharks are traveling in long-ranging linear paths, or making small, random movements. Examination of this movement parameter provides information on how individuals are using habitat and may provide clues to behavior during those periods. Morrissey and Gruber (1993b) calculated a linearity index value of 0.044 for juvenile lemon sharks and concluded they were highly site attached due to regular re-visitation of preferred areas. Rechisky and Wetherbee (2003) reported a linearity index of 0.2 (range = 0.02 – 0.62) for neonate and juvenile sandbar sharks indicating a more linear pattern of movement. In the Caloosahatchee River, juvenile bull sharks had a linearity index of 0.29 (range = 0.04 – 1.0) indicating more linear paths than

29

both juvenile lemon sharks and sandbar sharks. This result is not unexpected as lemon sharks were tracked in an open lagoon, sandbar sharks in a large bay, and bull sharks in a narrow river which provided physical constraints to movement. Bull sharks in this study also exhibited more linear travel than that of bull sharks tracked in the Indian River Lagoon, Florida (mean = 0.18; Curtis 2008). Although there were periods when *C. leucas* traveled a linear path, random movements were more common. Individuals displayed a higher degree of circular or random movements at shallower depths and more linear travel in greater depths. Movement within a shallow nursery habitat by young sandbar sharks was attributed to predator avoidance, avoidance of currents, and distribution of prey (Rechisky and Wetherbee 2003). Since there are no natural predators of bull sharks in the Caloosahatchee River (Heupel unpublished data), and generally minimal current speed, it is likely that a large portion of juvenile bull shark movement patterns may be attributed to the distribution of and search for prey. Little is known about the movement patterns of their primary prey species, ariid catfishes and dasyatid stingrays, however, *D. sabina* was found to have small, restricted movements in a shallow tidal lagoon (Schmid 1988). Nursery areas provide abundant food sources and it is probable that the movement patterns of bull sharks are reflecting the distribution and movement patterns of their prey species.

The results demonstrated that tidal flow within the estuary had a significant effect on movements. Shark depth, linearity of movement, and direction of travel were all significantly correlated with tidal stage. Sharks have been reported to move in relation to environmental variables in previous studies and may have been using tidal transport as a means of conserving energy. For example, sandbar sharks and Atlantic stingrays have

been reported to move with tidal flow (Teaf 1978; Medved and Marshall 1983; Rechisky and Wetherbee 2003). Leopard sharks also used currents for movement to and from muddy littoral zones that contained an abundance of food (Ackerman et al. 2000). Based on this pattern, Ackerman et al. (2000) determined that leopard sharks potentially conserved 6% of their total energy expenditure by swimming with currents. This would suggest that bull sharks may be utilizing passive transport in order to conserve or reallocate energy. A second explanation for this behavior could lie in environmental variables within the region. If bull sharks have preferences for specific environmental conditions as suggested by Simpfendorfer et al. (2005), Heupel and Simpfendorfer (2008), and Curtis (2008), then this movement may be a means of remaining in a desired environmental regime. Movement downriver and swimming closer to the bottom on a falling tide would allow individuals to remain in potentially more saline or well-mixed water and avoid freshwater in the upper portion of the water column. Movement with tides may further be an indirect result from foraging for prey which are likely to be tidally influenced. Many bony fish have exhibited movement patterns that correlate to tidal activity (Kanou et al 2005; Krumme 2004; Dresser and Kneib 2007). Therefore, movement is likely a means of optimizing energy allocation either via passive transport and/or maintenance of favorable environmental and foraging conditions.

Movements of juvenile *C. leucas* may also be directly related to changes in water quality, specifically salinity, in order to decrease energy expended for osmoregulation. The process of osmoregulation in seawater was determined to require 6 to 10% of the total energy budget of the euryhaline killifish, *Fundulus heteroclitus* (Kidder et al. 2006). This expenditure was suggested to be enough for behavioral osmoregulation, a process of

seeking a medium isotonic with body fluids, to be a significant driving force in killifish

movement (Kidder et al. 2006). While bull sharks are capable of osmoregulating in a

wide salinity range (Pillans and Franklin 2004; Pillans et al. 2005; Pillans et al. 2006),

Heupel and Simpfendorfer (2008) reported that young bull sharks remained within a

salinity range of 7 to 20 ‰, and avoided areas of less than 7 ‰. Curtis (2008) reported

that despite a range of available habitats, bull sharks selected locations with salinities

above 11 ‰. In previous studies, salinity and temperature were found to be the most

important factors determining the distribution and abundance of four elasmobranch

species including the bull shark in Florida (Heupel and Simpfendorfer 2008), and the bat

ray, *M. californic*a, leopard shark, *T. semifasciata* and brown smoothhound shark,

Mustelis henlei, in California (Hopkins and Cech 2003). These two environmental

factors were also determined to influence the location of cownose rays, *Rhinoptera*

bonasus, in the Chesapeake Bay (Smith and Merriner 1987). Thus, changes in these

variables may be key to juvenile bull shark movement and distribution. Water quality

parameters may also play an indirect role in bull shark movement due to the influence of

fluctuating conditions on the distribution of prey species. Temperature and salinity were

found to be primary factors influencing movement (Harrison and Whitfield 2006) and

community assemblages (Vega-Cendejas and Hernández de Santillana 2004) of fishes in

estuaries. These water quality variables were specifically determined to be important in

structuring estuarine assemblages on Florida's east coast (Kupschus and Tremain 2001;

Paperno and Brodie 2004). *Arius felis* and *B. marinus*, two primary food items for bull

sharks, are known to prefer salinity above 10 ‰ (Muncy and Wingo 1983). Therefore,

during high freshwater influx events, these species may be displaced downriver to remain

within a certain salinity range. The downriver movement of the sharks may have been in efforts to follow the prey population, the distribution of which changed in order to fulfill physiochemical requirements.

Although significant differences in water quality variables over time and diel differences within tracks were reported, aside from the large freshwater influx event, changes were generally subtle. Locations of the first two sharks were related to salinity, temperature, and dissolved oxygen, while locations for sharks 4 through 7 were related to temperature, dissolved oxygen, turbidity and pH. These differences are likely due to the different locations in the river. Although dissolved oxygen, pH and turbidity influenced shark distribution it is unclear what role these factors play in influencing movement patterns. It is difficult to define the role that small variations in water quality have on movement over a short period of time, especially for a species that is known to have considerable environmental tolerances. This makes it necessary to examine short-term movement patterns with long-term trends. For example, temperature is more likely to have a role in shark presence over a longer period, showing seasonal variation (e.g. Simpfendorfer et al. 2005; Grubbs et al. 2007; Heupel 2007). Although there is evidence that salinity plays a role in long-term distribution of bull sharks in this estuary (Heupel and Simpfendorfer 2008), small variability in water quality made it impossible to determine movement drivers in the short-term. Therefore, mechanisms driving short-term movement patterns of bull sharks within the Caloosahatchee River may be dependent on a number of confounding variables and conditions. It did appear, however that a large influx of freshwater changed the location of individuals within this habitat

supporting the conclusion of Heupel and Simpfendorfer (2008) and suggesting water

management practices causing large changes should be carefully examined.

Habitat alterations in the Caloosahatchee River due to canals, locks, and dams

have been substantial in the last century. Increasing urbanization of the lower sections

has resulted in a loss of mangroves and other native vegetation (Barnes 2005;

Simpfendorfer et al. 2005). Water flow in the Caloosahatchee River is managed by the

South Florida Water Management District to maintain water supply for agricultural

purposes, to sustain appropriate levels in Lake Okeechobee and to supply water to the

Everglades (South Florida Water Management District 2000). Anthropogenic hydrologic

modifications have altered not only the water quality throughout the river, but also the

magnitude, timing, and distribution of flows to the estuary (Haunert et al. 2000).

Historically, rainfall runoff was contained within the undeveloped watershed during the

wet season which prevented heavy, fast freshwater flows into the river. Thus,

populations of *C. leucas* were probably not frequently exposed to large environmental

fluctuations. Water management practices currently create large, rapid changes in

salinity which appear to have a direct effect on the distribution of juvenile *C. leucas.* The

flow rate documented between tracks 3 and 4 was 86 m^3s^{-1}, more than double the average

flow of 36 m^3s^{-1} during 2006. There appears to be a critical threshold between these flow

rates which influences the population distribution. In periods of high rainfall and

augmented river flow, salinity in the river may drop low enough to require young sharks

to move out of the protected nursery areas into the bay where they will face a higher risk

of predation (Simpfendorfer et al. 2005). This may have severe consequences for this

population if continued for an extended period. The Caloosahatchee River is likely to

undergo restoration as part of the Greater Everglades Region and it will be necessary to have an understanding of how resident species are affected by water management practices. In order to develop less invasive use of water resources, the behavior and biology of mobile estuarine species should be considered. An understanding of how these species respond to environmental stressors will provide a basis for well-informed management decisions.

CHAPTER THREE:

HABITAT USE OF JUVENILE BULL SHARKS, *Carcharhinus leucas*, IN A

FLORIDA NURSERY AND THE INFLUENCE OF WATER QUALITY AND

QUANTITY MODIFICATION

Abstract

There is a population decline in many coastal shark species accompanied by a

lack of information on which to base appropriate management policies. Estuarine areas

serve as nursery habitat for many plant and animal species and are at high risk from

anthropogenic modification. This study examined the relationship between changes in

water quality and quantity and the distribution and residency patterns of juvenile bull

sharks in a Florida estuarine nursery. Individuals displayed distinct movement patterns in

relation to alterations in flow rates and salinity. Sharks were distributed throughout the

river at low flow rates, but were located only near the river mouth, or exited the river, at

discharges rates above 75 m^3s^{-1}. This paper examines current water management policy

and makes recommendations based on the physiological preferences of this top-level

predator.

Introduction

There has been a drastic population decline in many coastal shark species of the

Atlantic over the past 30 years (NMFS 1993; Burgess et al. 2005). The 1993 Fisheries

Management Plan for Sharks of the Atlantic Ocean (FMP) recognized a disturbing lack

of information regarding shark fisheries and biological data required for appropriate fisheries management. Estuarine nurseries were specifically identified by the FMP as areas of great concern for coastal sharks because these locations are directly exposed to anthropogenic alteration (NFMS 1993). The increasing level of coastal development makes it necessary to determine what constitutes estuarine shark nursery areas and how these habitats are used by juvenile sharks. The definition of a shark nursery has been vague and these areas have generally been considered as locations in which protection from predation and adequate food supplies are provided (Springer 1967; Bass 1978; Branstetter 1990). However, in a recent effort to define nurseries in a way that allows for quantitative determination, these sites were attributed with three testable criteria; they contain a higher density of juveniles in relation to other areas, individuals tend to remain or return for extended periods, and the habitat is used repeatedly over a period of years (Heupel et al. 2007). The Caloosahatchee Estuary in southwest Florida qualifies as a nursery for bull sharks and is highly impacted by anthropogenic alterations in flow rates and salinity levels. The purpose of this research was to examine in closer detail the relationship between distribution and abundance of juvenile bull sharks in a coastal estuarine environment and physical factors, specifically flow rate and salinity.

The degradation of water quality in estuaries has been identified as a potential threat to coastal shark populations, however the effects of this alteration is unknown (National Marine Fisheries Service (NMFS 1993). High levels of variation in river flow discharge and salinity have been found to affect the distribution of aquatic species (Bain and Finn 1988; Moser and Gerry 1989; Paperno and Brodie 2004; Harrison and Whitfield 2006), and specifically on bull sharks (Heupel and Simpfendorfer 2008, Curtis 2008).

This study was conducted to complement previous research (Chapter 1) which examined short term movement patterns of juvenile bull sharks in relation to environmental fluctuations. That study also found a direct relationship between significant modifications in water quality and quantity and the distribution of bull sharks over a short period of time due to a direct physiological or indirect prey-driven influence. However, due to the short-term nature of the study, it was difficult to investigate in detail the role that water quality played on shark distribution. Those results necessitated further research to determine how fluctuations in environmental parameters affect the distribution of *C. leucas* over a longer period of time.

Bull sharks are cosmopolitan in tropical and subtropical coastal marine waters (Garrick 1982). This elasmobranch species has unique physiology and osmoregulatory capabilities which enable it to reside in both freshwater and saltwater for extended periods (Thorson 1971; Thorson et al. 1973; Montoya and Thorson 1982). Females are thought to give birth in estuaries or in proximity to river mouths and juveniles tend to move upstream after parturition (Thorson 1972; Last and Stevens 1994). Juveniles have exhibited a preference for fresh or estuarine water following birth and are rarely found in marine environments (Branstetter and Stiles 1987; Thorson et al. 1973; Thorson 1976), possibly due to an inability to up-regulate urea in marine environments (Pillans and Franklin 2004). Bull sharks are a common shark species in Florida's coastal and estuarine areas, many of which are believed to provide important nursery habitat (Snelson et al. 1984; Michel 2002; Simpfendorfer et al. 2005).

The Caloosahatchee River in southwest Florida served as the site of this study and is a nursery for bull sharks in their first year of life (Simpfendorfer et al. 2005). Water

38

flow into the river is managed by the South Florida Water Management District (SFWMD) and water quality parameters can change rapidly, on a scale from hours to days (Simpfendorfer et al. 2005), depending on precipitation levels and discharge regimes. In heavily regulated systems, such as the Caloosahatchee River, it is essential to understand the effect that modifications to environmental parameters have on resident species. An understanding of how these animals are affected by anthropogenic modification within the estuary will aid in developing informed management decisions.

Materials and Methods

Study Site

This study was conducted in the Caloosahatchee River, in southwest Florida. The Caloosahatchee River serves as an artificial hydrologic connection between Lake Okeechobee and the Gulf of Mexico and has been highly impacted over the previous 100 years due to heavy urbanization and channelization. Water flow throughout the system is currently regulated by the SFWMD via dams for hydrologic and agricultural purposes. Episodic freshwater discharge from the dams, up to 1278 m^3s^{-1} (SFWMD et al. 2008), can create rapid, dramatic fluctuations in water quality variables downstream, particularly salinity. During periods of high freshwater discharge, salinity may drop to less than 5 ‰ at the river mouth, and conversely, salinity may exceed 10 ‰ at the head of the river during periods of low discharge. Time needed to transition between these extremes may be less than a week (SFWMD 2002). This study was completed in the estuarine section of the river and encompassed approximately 26 km of river habitat.

Field Methods

Twelve *C. leucas* were collected between June and July 2006 via long line fishing. An 800 m longline was employed, which consisted of an 8-mm braided nylon rope anchored at both ends. Frozen mullet (*Mugil cephalus*), ladyfish (*Elops saurus*), and fresh catfish (*Arius felis, Bagre marinus*) were used as bait on Mustad tuna circle hooks ranging from 12/0 to 14/0 in size. Soak time was approximately one to two hours. The location, date, time, duration of set, and environmental conditions were recorded at each fishing location.

Once on board, sharks were weighed, measured, sexed, and tagged externally with both a dart and rototag for identification. Dart tags were inserted at the base of the first dorsal fin and rototags were attached to the dorsal fin. All individuals were surgically fitted with Vemco V13P transmitters. Surgical procedures were identical to those described by Heupel and Hueter (2001) where a 2-3 cm incision was made in the abdomen and the transmitter inserted. These transmitters were identical in size and shape to those used for active tracking (see Chapter 1). The long-term transmitters pulsed once per minute at 69.0 kHz and at randomly spaced intervals between 45 and 75 seconds. Transmitters also reported the depth at which the individual was swimming based on a pressure sensor. Each transmitter was programmed to produce a unique pulse series per individual and had a battery life of at least 12 months. Random signal transmission times helped to avoid signal overlap and the blocking of detections. After insertion of the transmitter, the incision was closed via running nylon sutures in both the muscle and skin layers. Individuals were revived on board and released in good condition.

The long-term presence and movement patterns of sharks fitted with transmitters were

monitored via a series of 25 acoustic receivers (Vemco VR2) moored within the

Caloosahatchee Estuary (Figure 5). Methods for deploying receiver stations are

described in Heupel & Heuter (2001). Receivers were located in the estuarine section of

the river between the mouth and approximately 26 km upstream. Each receiver recorded

the time, date, and transmitter code, which identified the individual, when an animal

swam within range of a receiver. Receivers were omnidirectional, single frequency, and

had a detection range of approximately 600 m (Heupel unpublished data), depending on

variables such as ambient noise, depth, and water clarity. This detection range often

allowed sharks to be detected at more than one station simultaneously. The array allowed

for continuous monitoring of sharks for most of the time they were present in the study

location. Data was downloaded from the receivers once every month at which time any

necessary maintenance was conducted. At each receiver station, surface and bottom

temperature, salinity, and dissolved oxygen were measured using a YSI 85 water quality

meter.

Figure 5: The location of the Caloosahatchee River study site, with inset showing location of study site in Florida. Filled circles indicate locations of acoustic receiver stations.
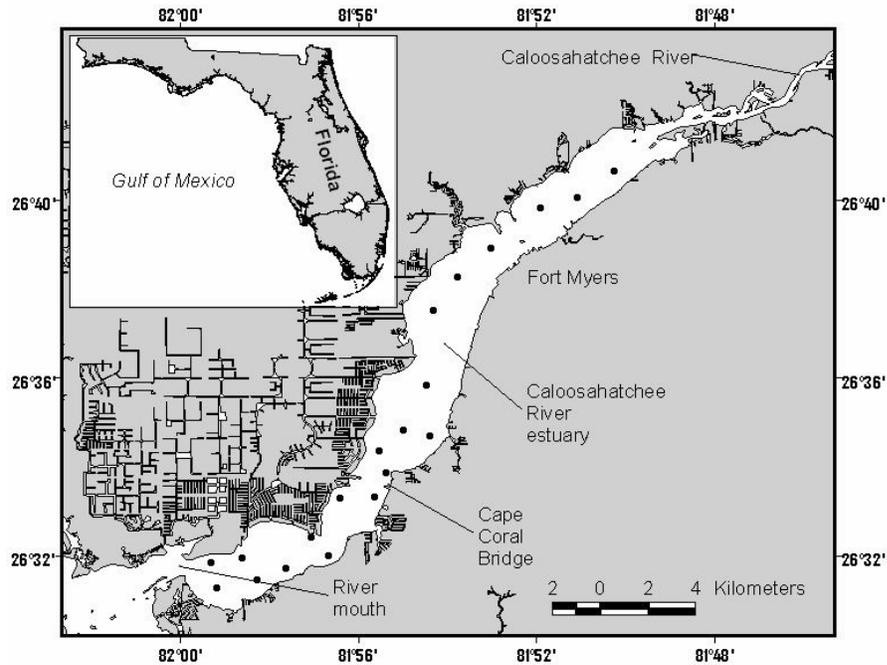
Data Analysis

Residency

Data from the acoustic monitoring array were used to determine the residence period and movement patterns of *C. leucas* within the estuary. A shark was considered to be present on a particular day if more than one signal was detected from that individual. The total number of days that an individual was present in the study site, as well as the number of consecutive days, was calculated to determine if any pattern was evident between individuals. Three individuals were not included in analyses due to early mortality; two animals died within days of release and the third within six weeks.

42

Home Range and Depth

Data from acoustic receivers was condensed and analyzed using a custom written FORTRAN program (see Simpfendorfer et al. 2008 for details). The program yielded shark position in the estuary every 30 minutes on a linear scale, with the river position of 2 km located at the mouth and 26 km located at the northern section of the study site. Position estimates were used to determine daily minimum, maximum, and mean river location for each animal. The extent of river space used per day was calculated as the difference between the maximum and minimum mean river locations (in river kilometer) and served as a proxy for home range. This was the most accurate method of calculating spatial usage due to the linear configuration of receivers in the river, which would have influenced the size of an area measurement. Kruskal-Wallis determined if there was a difference in daily home range size by individual. Position within the river was separated into day and night bins and Wilcoxon paired samples tests were performed to determine if there were diel differences in either river location or home range size. Fixes that were recorded between the hours of 0700 and 1900 were considered daytime and between 1900 and 0700 were considered nighttime. A Kruskal-Wallis test determined if home range size changed significantly over weekly or monthly periods. Data for these analyses were examined from the onset of monitoring, in June or July, 2006 and concluded in November 2006 since only two animals remained in the estuary past that month.

To determine if there was a difference among individuals in average depth within the water column, a Kruskal-Wallis test was used. A Wilcoxon paired samples test was conducted to determine if individuals displayed a diel depth pattern. A Pearson Correlation determined if there was a relationship between location in the river and depth

in the water column. A Kruskal-Wallis test was performed to determine if depth changed

significantly over time. Four individuals were not used in depth analyses because three

did not survive and depth was not accurately recorded by the receiver for another

individual. Statistical tests were performed with SPSS, version 16.0.

Water Quality and Quantity

The number of sharks present each day was calculated and compared to daily

river flow and salinity levels using linear regression. Flow rate data was recorded at the

Franklin Locks, an area upriver from the study area and 35 km from the mouth of the

river. Salinity was a daily mean of the continuously measured value recorded at the Cape

Coral Bridge, 10.5 km from the river mouth. Salinity and flow data were obtained from

the SFWMD and the values at Cape Coral were used as indicators of the regimes present

in the river on each day. These daily values have been determined to be accurate

measures of conditions throughout the river (P. Doering, Pers comm.). To examine

relationships between shark location with salinity and flow, the daily mean river distance

for each animal was also compared to these variables using linear regression. Regression

analysis was also conducted to determine if there was a significant relationship between

salinity and flow rate.

To further investigate the relationship between water quality and shark location

within the estuary, the mean river distance of each shark on days when receivers were

downloaded, thus when water quality parameters were recorded, was compared to water

quality variables. Values between all stations were highly correlated, as determined by a

Pearson correlation, therefore, water quality data were compared to a single station.

Linear regression was used to elucidate potential relationships between shark location with salinity, temperature, dissolved oxygen, and turbidity.

Results

Residency

The movements of twelve neonate bull sharks were recorded beginning in June (n = 5) and July (n = 7), 2006 and ending in March, 2007. Seven individuals were females, five were males, and the animals ranged in size from 74 to 83 cm stretch total length (STL); sampling data is shown in Table 6. Two individuals remained within the study site until March 2007, however the remainder of the sharks were absent after November 2006. Duration of residency throughout the study ranged from 13 to 285 days, with sharks utilizing the nursery for an average of 138 days (Figure 6). Individuals regularly moved in and out of the detection range of the acoustic system, with sharks leaving the estuary for varying amounts of time. Sharks were present in the study site for consecutive periods of 1- 81 days, with a mean of ten days continuously present.

Table 6: Biological data for bull sharks monitored within the Caloosahatchee estuary. ID indicates transmitter number, size is indicated as Standard Total Length (STL), Fate is defined as S = apparent survival and D = individuals that died within the study site.

| Shark ID	Sex	Size - STL	Fate	Monitoring Dates	Total days monitored
241	F	83	S	6/17/06 - 3/28/07	285
242	F	70	S	6/14/06 - 11/06/06	146
243	F	74	D	6/16/06 - 6/16/06	1
244	M	76	S	6/19/06 - 3/18/07	273
245	F	78	S	7/03/06 - 11/01/06	122
246	F	81	S	6/15/06 - 7/31/06	47
247	M	82	S	7/03/06 - 10/23/06	113
248	M	77	S	7/03/06 - 7/15/06	13
249	F	82	S	7/03/06 - 11/13/06	134
250	F	82	D	7/03/06 - 7/13/06	11
251	M	82	D	7/03/06 - 8/17/06	46
252	M	76	S	7/03/03 - 11/07/06	128

Figure 6: Presence and absence of neonate bull sharks monitored within the

Caloosahatchee River during 2006 and 2007.
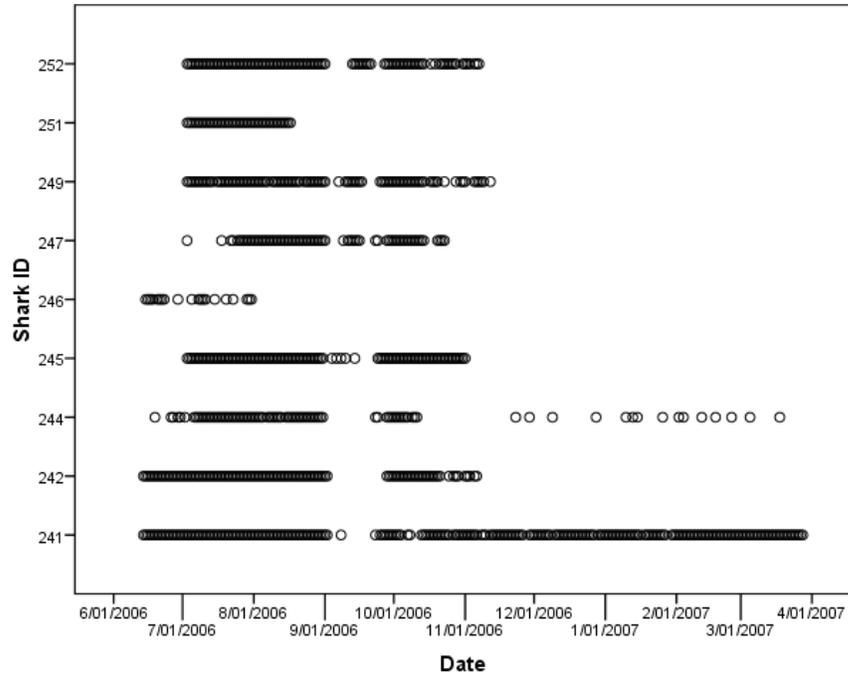
In order to elucidate patterns in residency, the proportion of the monitored

population that was present in the estuary throughout the study period was examined.

The proportion of individuals present ranged from 0 to 89 % per day (mean = 35 %,

median = 22 %), with the highest number of individuals being detected in July, August,

and October of 2006, and few from November 2006 – March 2007, (Figure 7a,c).

Figure 7: Proportion of neonate bull sharks present, shown in grey, within the
Caloosahatchee River relative to a) freshwater inflow as indicated by rates measured at
Franklin Locks and c) salinity as indicated by values measured at the Cape Coral Bridge.
Flow and salinity are each represented by black lines. Scatterplots show the proportion
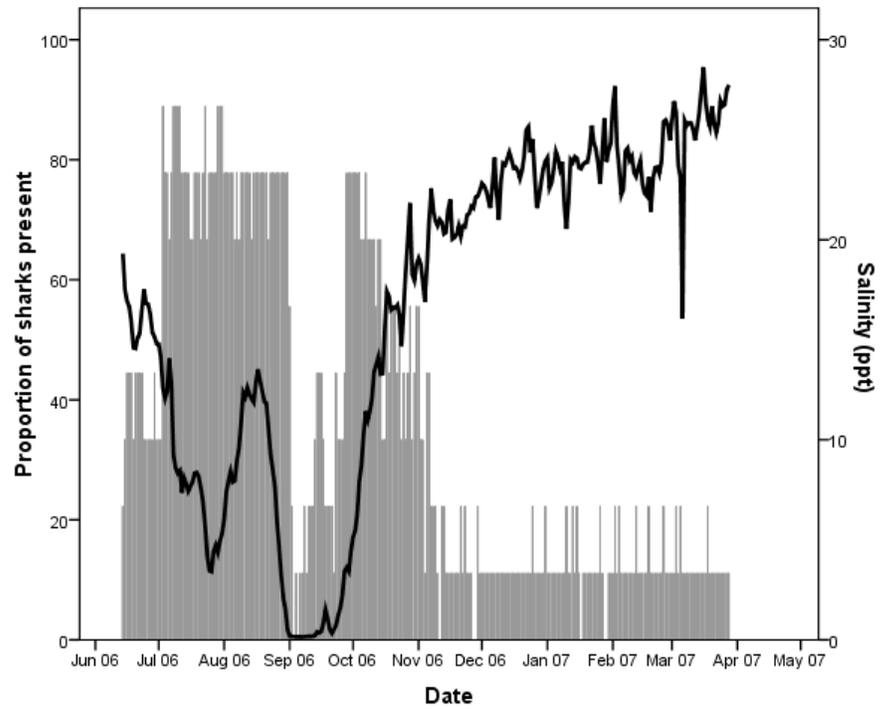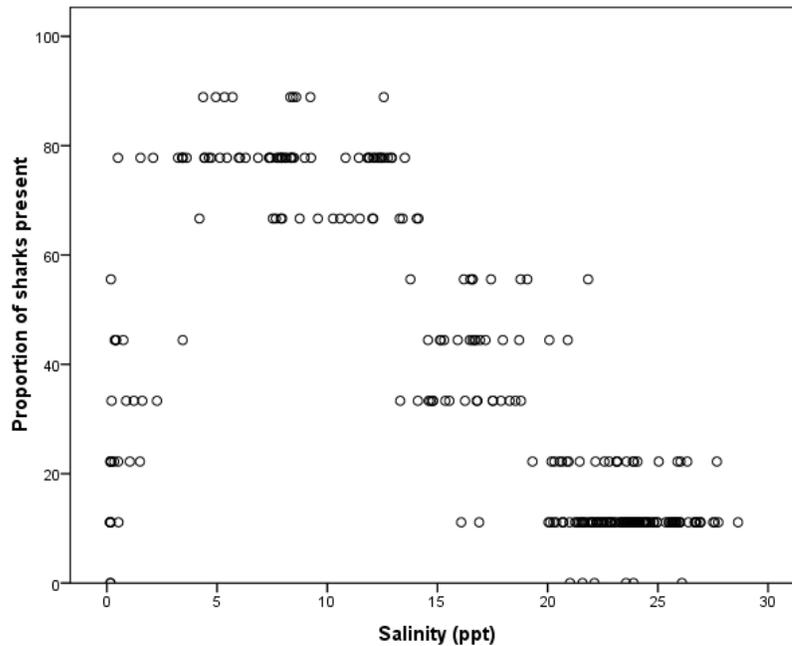of sharks present versus b) flow rate and d) salinity.

a.

b.

c.

49
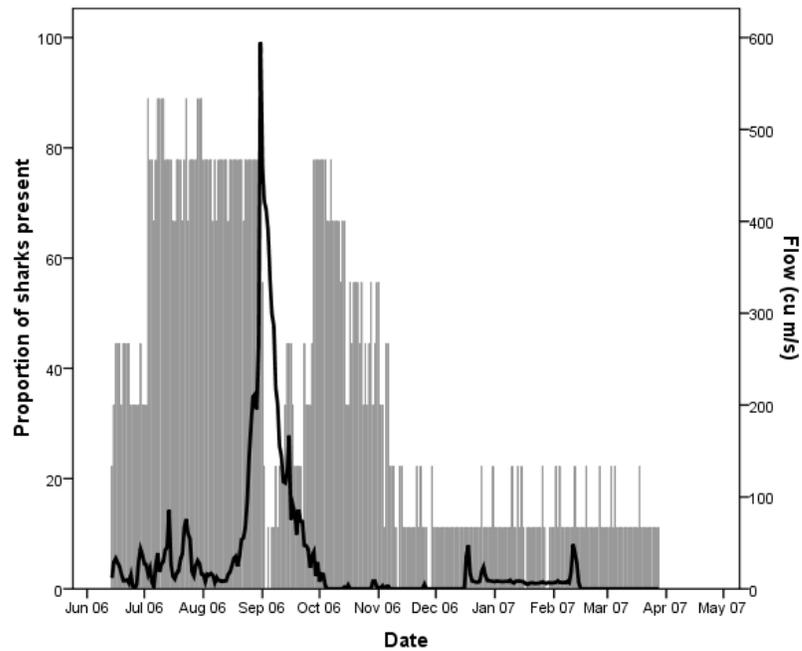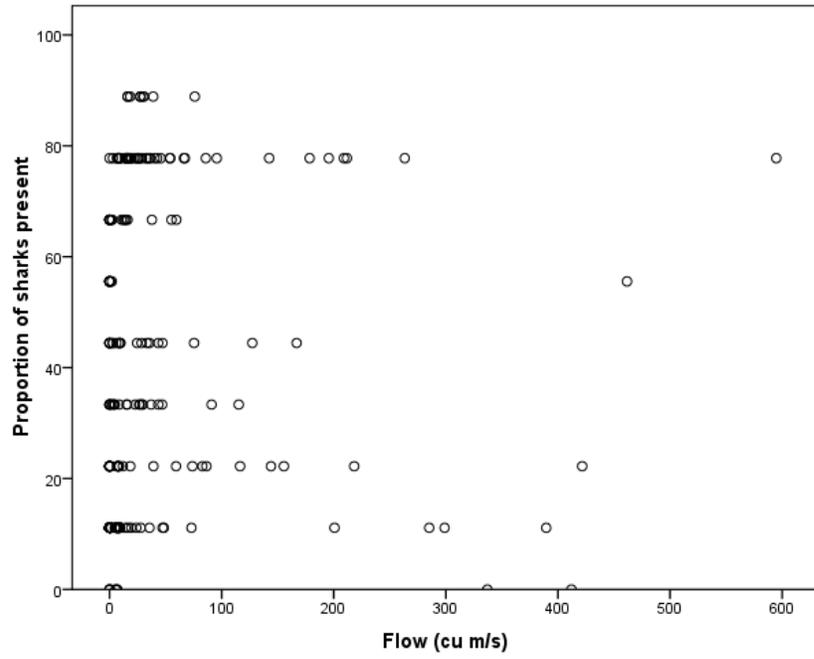
d.

Home Range and Depth

Linear distance traveled served as a proxy for home range of the nine individuals, and ranged from 0.1 to 8.83 km per day (mean = 1.8 km, median = 1.4 km), as shown in Figure 8. Results showed a significant difference in home range size by individual (Kruskal-Wallis, df = 8, p < 0.0001). Daily home range size differed significantly based on diel period (Wilcoxon, Z = -10.203, p < 0.0001); sharks displayed an increased home range size at night (mean = 1.94 km) than during the day (mean = 1.27 km). Home range size changed significantly on a weekly basis (Kruskal-Wallis, df = 40, p < 0.0001), but did not exhibit any uniform change over time. Home range size did not change significantly based on the month (Kruskal-Wallis, df = 5, p = 0.146). However, there was a population wide expansion of home range size in October, 2006 (mean = 3.23 km) with the smallest average home range size observed the following month, in November, 2006 (mean = 0.62 km). Throughout the study, individuals spent 46 % of their time

50

within 14 km of the river mouth; mean river location is shown in Figure 9. The

difference in daily mean river location for all sharks based on diel period was negligible

(day = 13.74 km, night = 13.58 km).

Figure 8: Daily home range of animals, shown in grey, present from June 2006 to

November 2006 relative to a) freshwater flow and b) salinity. Flow and salinity each

represented by black lines.
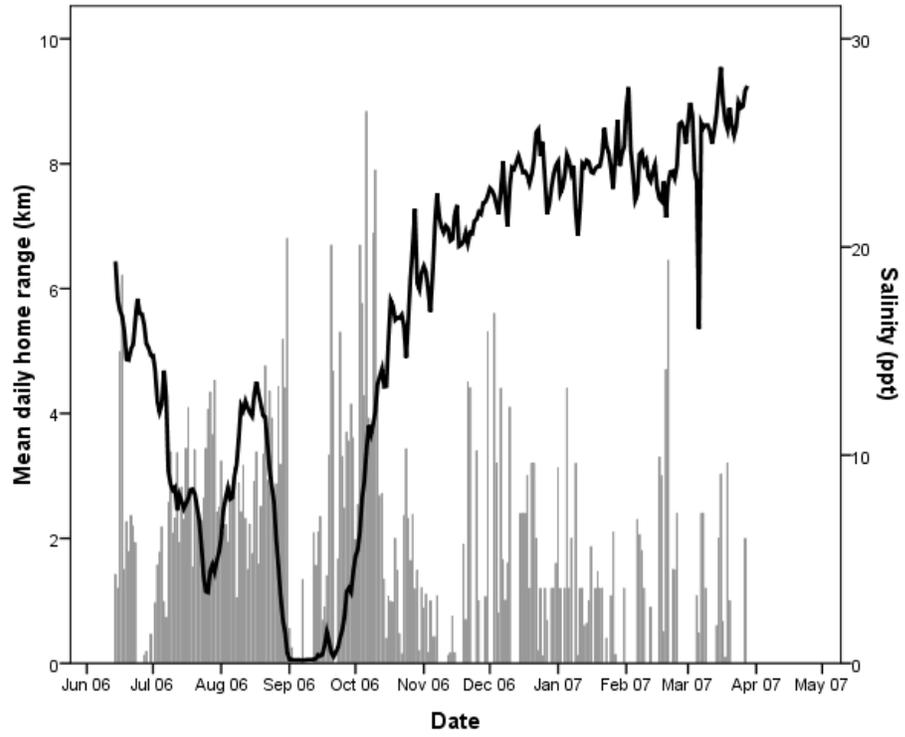
a.
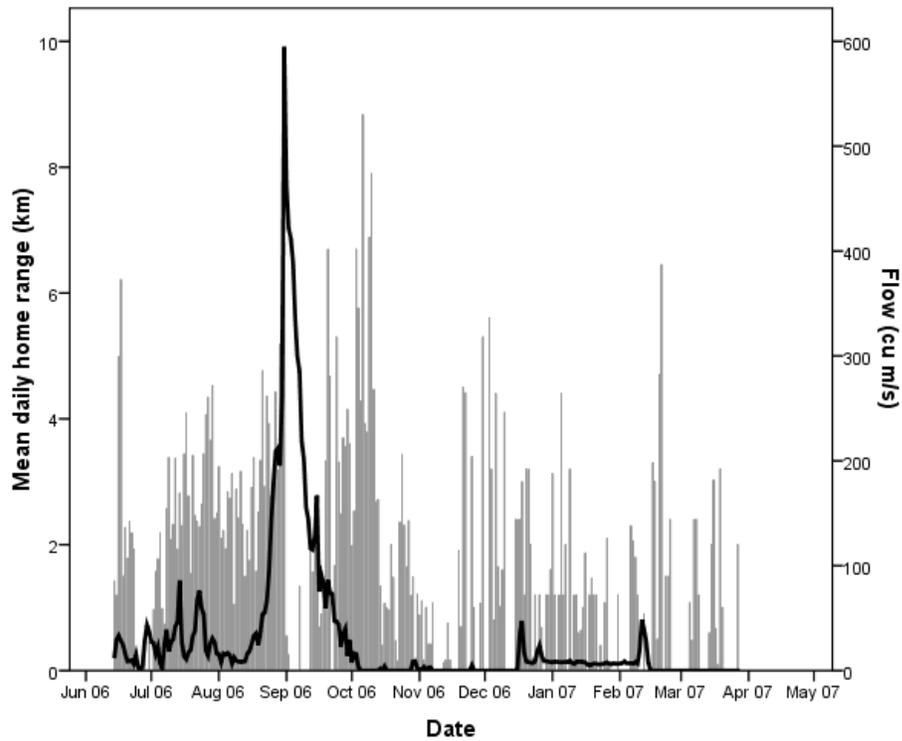
b.

Figure 9: Relationship between distribution of acoustically tagged bull sharks within the Caloosahatchee River relative to a) freshwater influx and c) daily average salinity. Scatterplots show daily mean river location relative to b) freshwater and d) salinity. Mean river location is shown in the grey shaded area and the black lines represent the water quality variable.

a.
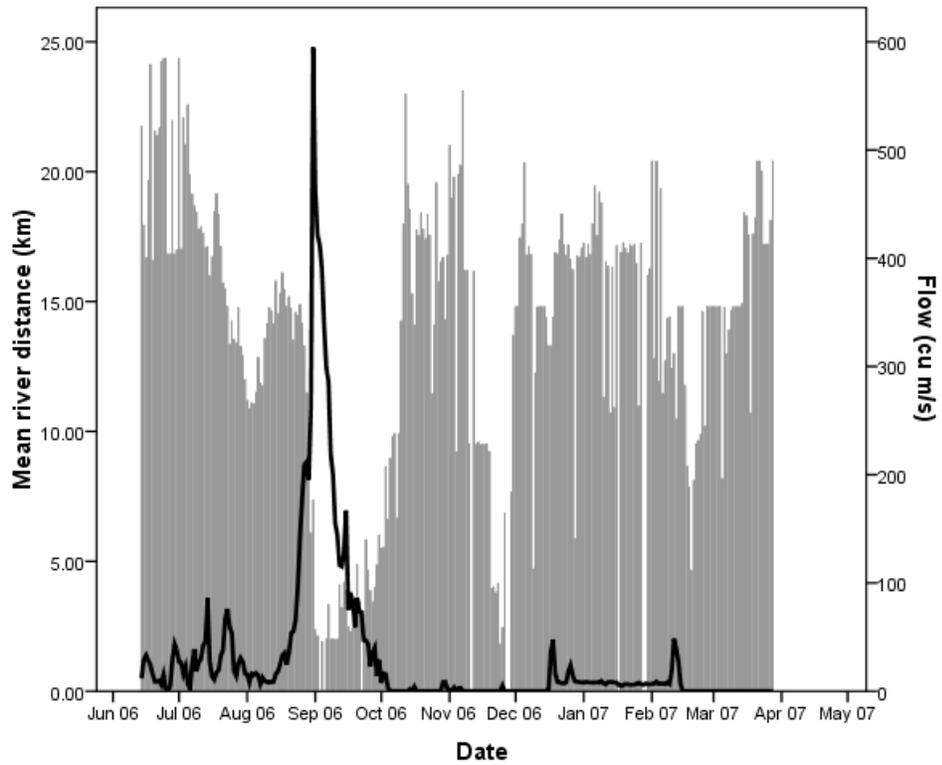
b.
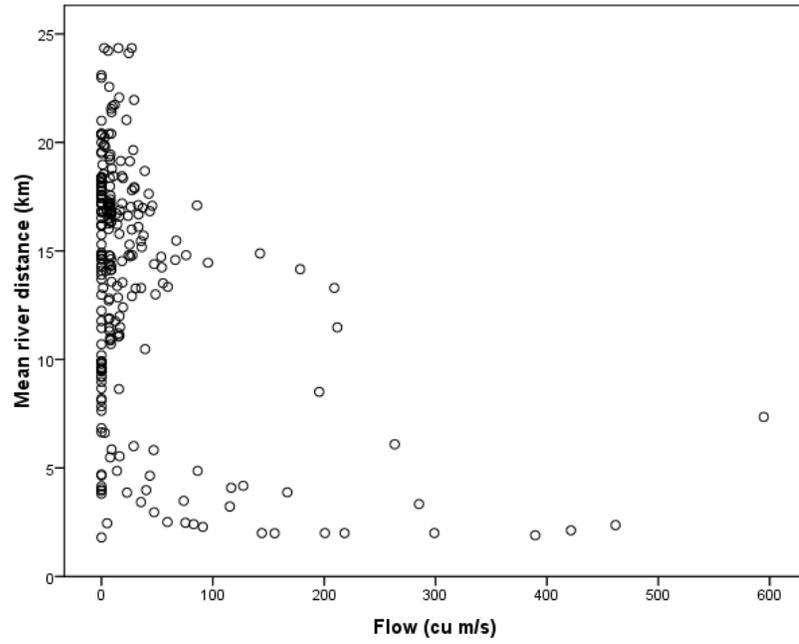
c.
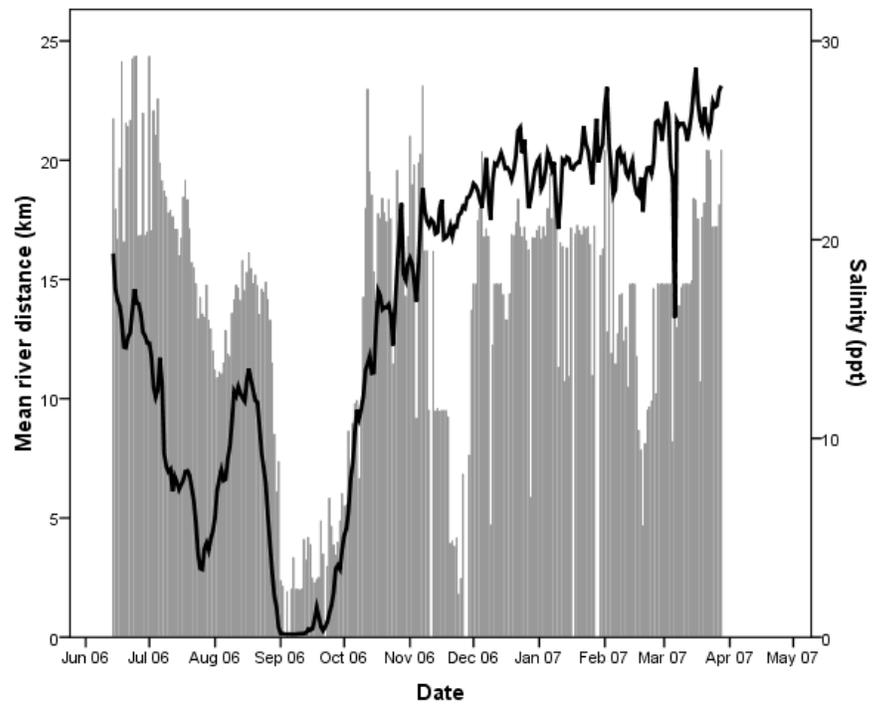
d.
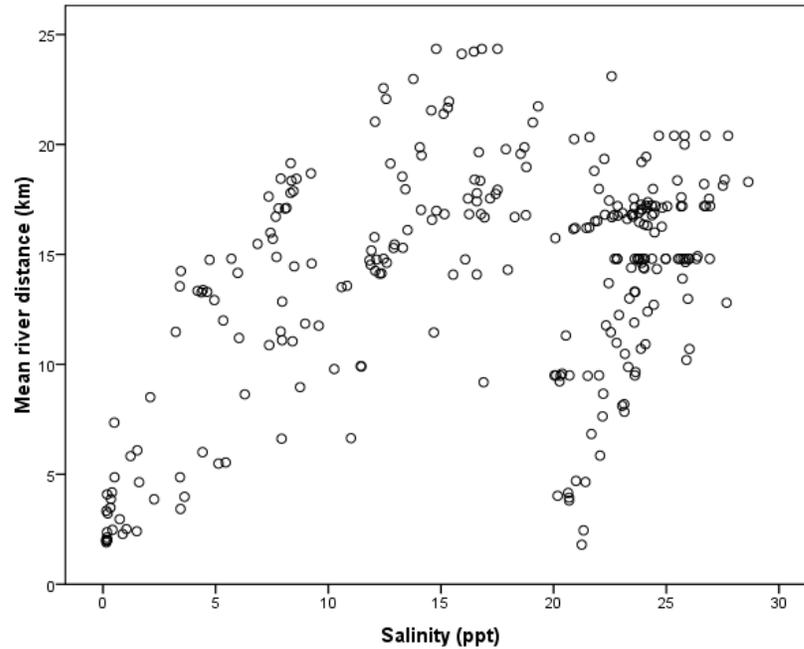
Daily average swimming depth ranged from 0.0 to 3.3 m. There was a significant difference between individuals in daily average depth (t-test, df = 732, p < 0.0001). Individuals exhibited a diel trend in average depth (Wilcoxon, Z = -13.518, p < 0.0001), with animals swimming deeper in the water column during the day. The mean daily day depth was 1.07 m and the average daily night depth was 0.81 m. There was a significant correlation between location in the river and average daily depth (Pearson, p < 0.0001), with sharks swimming deeper in the water column as they approached the river mouth. There was no difference in shark depth over time (Kruskal-Wallis, df = 5, p = 0.493).

Water Quality and Quantity

From June 14, 2006 to March 28, 2007, individuals were exposed to a salinity range of 0.15 – 28.64 ‰ (mean = 16.48 ‰, median = 19.67 ‰) and flow rates from 0 – 596 m^3s^{-1} (mean = 31 m^3s^{-1}, median = 7 m^3s^{-1}). There was a significant positive relationship between the daily proportion of animals resident and average daily salinity (R^2 = 0.434, slope = 0.707, p < 0.0001) and a significant negative relationship with daily mean flow (R^2 = 0.115, slope = -3.926^{-5}, p < 0.0001). A higher proportion of individuals were present in the river during conditions of low flow (< 50 m^3s^{-1}) and salinities approximately 5- 12 ‰. There was also a significant negative relationship between the log of salinity and the log of river flow (Figure 10) which confirmed that increased flow rates throughout the river were accompanied by decreases in salinity levels (R^2 = 0.618, slope = -2.058, p < 0.0001).

Figure 10: Scatterplot of daily salinity versus river flow.
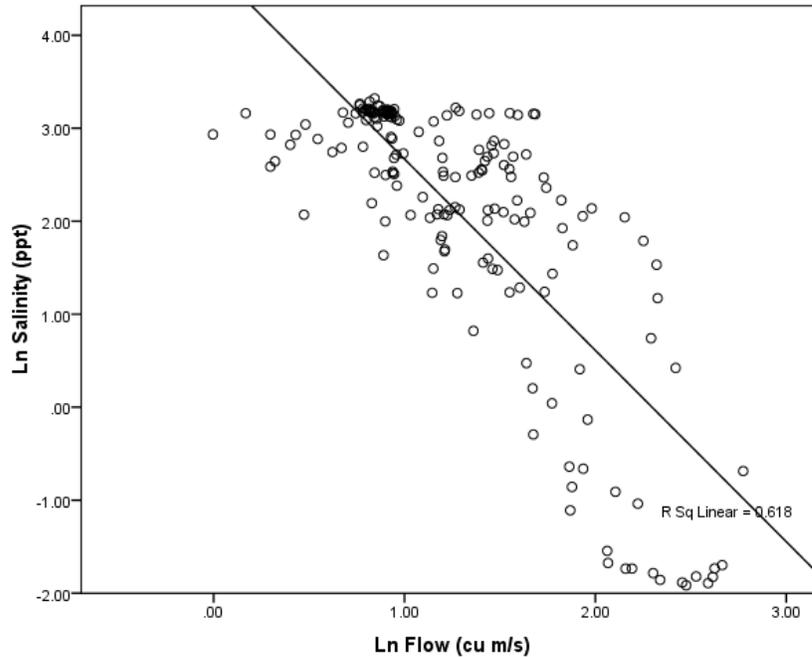
Examination of shark distribution within the estuary in relation to daily salinity and flow data showed a strong relationship. Analysis of shark location in the river yielded a significant positive linear relationship for salinity ($R^2 = 0.516$, slope = 1.469, p < 0.0001) indicating that as salinity in the river increased, sharks traveled away from the river mouth. Conversely, as salinity decreased, sharks moved towards the mouth of the river. Shark position in the river had a negative linear relationship with flow ($R^2 = 0.341$, slope = -1.106, p < 0.0001) showing that at flow rates below 50 m^3s^{-1}, sharks were distributed throughout the river. However, as flows increased above approximately 75 m^3s^{-1} animals were located in close proximity to the mouth of the river. Although the strength of the relationship differed, both salinity and flow rate exhibited a significant influence on shark location.

Environmental parameters were recorded at each receiver station during download events, and these values showed a significant relationship with the mean river location of the sharks. Comparison of mean river location showed a significant positive relationship with salinity (R^2 = 0.869, slope = 0.351, p = 0.002), but no relationship with temperature (R^2 = 0.504, slope = -0.470, p = 0.074), turbidity (R^2 = 0.847, slope = -1.770, p = .080), or dissolved oxygen (R^2 = 0.121, slope = 1.148, p = .445). The positive relationship between river location and salinity on days in which the receivers were downloaded supports the significant result between shark position and daily SFWMD salinity values. This further strengthens the hypothesis that salinity was a primary factor in bull shark distribution.

Discussion

Bull sharks are managed as part of the large coastal shark fishery complex in the Gulf of Mexico and the Atlantic Ocean. They are taken both commercially and recreationally and the complex is regarded as overfished (Cortés et al. 2002). During the past 30 years, there has been a serious decline in the population of many shark species on the Atlantic coast due to the expansion of commercial shark fisheries (NMFS 1993; Burgess et al. 2005). The Fisheries Management Plan for Sharks of the Atlantic Ocean (FMP) stated that the abundance of large coastal species in the Atlantic Ocean has potentially declined as much as 75 % from the 1970s to the 1980s (NMFS 1993). These data are especially concerning since most sharks have slow growth, are late maturing, and have very low fecundity compared to bony fishes (Camhi et al. 1998). Most shark species are consequently not capable of rebounding quickly to population reduction and cannot tolerate high levels of fishing without stock collapse (Camhi et al. 1998; Musick

1999). A high level of population reduction in elasmobranchs not only affects this top-level predator, but also their prey species and may have second and third degree affects through trophic linkages (Stevens et al. 2000; Schindler et al. 2002). Despite these significant top-down effects, there is a serious lack of information on shark fisheries (NMFS 1993). It is necessary to protect immature stocks and their habitats in order to provide a sustainable fisheries population (Cortes et al. 2002). An effective management plan will benefit by a clear understanding of what constitutes a shark nursery and how juveniles utilize these habitats. Specifically, how shark distribution is affected by significant artificial modification of water conditions within a nursery is important for both biological and management purposes.

The Caloosahatchee River flows into San Carlos Bay, a shallow bay which is cut by many deep channels which run longitudinally, and drains lower Pine Island Sound and Matlacha Pass to the Gulf of Mexico. The bay has less variation in salinity than the river due to its close proximity to the Gulf and during periods of high flow, juveniles may be forced to move into this open region and face an increased threat of predation. Typically, the smallest and youngest individuals stay within the river and neonates are found in June and July (Simpfendorfer et al. 2005). Simpfendorfer et al. (2005) suggested that neonate and young-of-the-year *C. leucas* which are found in the Caloosahatchee River remain through the summer after parturition. After animals reach approximately 95 cm STL, they tend to move out of the river and into northern San Carlos Bay and later into Pine Island Sound (Simpfendorfer et al. 2005). Of the nine individuals which survived throughout the duration of this study, seven utilized the estuary through October of 2006 and two remained for ten months post capture.   Duration of residency for young bull

sharks within the Caloosahatchee (13 - 285 days) exceeded that of bonnethead sharks *Sphyrna tiburo* (1 - 173 days; Heupel et al. 2006) and cownose rays *Rhinoptera bonasus* (1 – 102 days; Collins et al. 2007) in adjacent regions.

Variation in proportional residency appeared to relate to both fluctuations in salinity and freshwater discharge. In many shark nurseries, it has been documented that presence is influenced by seasonal changes in temperature or photoperiod (Grubbs et al. 2007; Heupel 2007; Merson and Pratt 2001). However, it appeared that presence of juvenile bull sharks within this system was largely influenced by acute fluctuations in water quantity and related changes in quality rather than by moderate changes over time. There were a reduced proportion of sharks present during periods of high flow and low salinity. Conversely, periods of low flow and moderate salinity resulted in a greater proportion of individuals present (Fig 3). The mean daily flow rate during this study was 31 m^3s^{-1}, however, in August, 2006 there was an extreme discharge event of 596 m^3s^{-1}, which reduced salinity throughout the river to less than 0.5 ‰ for approximately two weeks. During this period, the proportion of sharks present in the river dropped from 80 % to approximately 20 %. These results concur with the findings by Heupel and Simpfendorfer (2008), which determined that habitat use within estuary and river systems was influenced by salinity and flow, especially for bull sharks less than one year of age. Although young bull sharks are physiologically capable of gradual (Pillans et al. 2005) and acute (Pillans et al. 2006) transition between freshwater and saltwater, previous research has shown they exhibit consistent salinity preferences. Based on CPUE results, Simpfendorfer et al. (2005) determined that salinity was an important variable in determining the distribution and presence of *C. leucas,* and individuals less than one year

of age were present most frequently in salinities between 7‰ and 17.5‰.   This was supported by Heupel and Simpfendofer (2008) who reported a salinity preference of 7 ‰ to at least 20 ‰ and suggested that young bull sharks may select moderate salinity levels to reduce osmoregulatory costs and allow more energy to be allocated to growth functions.

There has been considerable research regarding how euryhaline fishes physiologically cope with salinity fluctuations (Pillans and Franklin 2004; Pillans et al. 2005; Pillans et al. 2006; Kidder et al. 2006), however there has been little focus on how movement is used to stay within a preferable range of conditions (Heupel and Simpfendorfer 2008). Small bull sharks tend to remain within fresher areas whereas large individuals are more commonly found in marine waters (Pillans and Franklin 2004; Simpfendorfer et al. 2005). Small individuals may not be able to up-regulate urea (Pillans and Frankin 2004), suggesting that they are physiologically limited to fresher locations until they are further developed. Previous research has shown that fishes use behavioral osmoregulation to remain within iso-osmotic conditions (Kidder et al. 2006) and higher growth rates were exhibited in the teleost, *Oreochromis niloticus*, when reared in iso-osmotic conditions rather than fresh or saltwater (Woo et al. 1997). Distribution of young bull sharks in this study appeared to be directly related to environmental change. A potential explanation for this behavior is that young sharks may conserve energy by seeking salinity equal to that in which they were acclimated prior to a high discharge event rather than remaining to acclimate to new conditions. In either case, behavioral osmoregulation is likely due to either physiological limitations or efforts to conserve energetic costs.

61

This study was performed to complement the previous study on the short-term movements of juvenile bull sharks in the Caloosahatchee River (Chapter 1). That study examined general movement patterns as well as a relationship between movement and water quality variables. The mean daily linear activity space (0.1 – 8.83 km) approximated the results from the short-term study (1.9 – 4.8 km). Animals in both studies displayed an increased use of space at night. Diel depth trends (day = 1.07 m, night = 0.81 m) also approximated that for individuals in the short-term study (day = 1.5 m, night = 0.6 m), with sharks consistently swimming deeper in the water column during the day.

The short-term study examined relationships between shark location and salinity, temperature, dissolved oxygen, turbidity, and pH.   Although all variables were found to be significant, the strength of the relationship varied. In this study, movement was compared to salinity and flow gathered from both daily values recorded by the SFWMD as well as water parameters recorded on days when receivers were downloaded. Flow and salinity were found to be significant in affecting the distribution of bull sharks for each test while temperature, dissolved oxygen, and turbidity had no influence. The results for the three water parameters were inconclusive between studies, suggesting that further research needs to be done to determine what relationship, if any, these variables have on shark movement.

The Caloosahatchee River and estuary is a highly impacted system with major changes in its historic hydrology due to significant modifications in land and canal development (Barnes 2005).   Regulatory releases of freshwater from Lake Okeechobee have created large changes in the natural quantity, timing, and quality of flow to the

estuary (Barnes 2005). These hydrologic changes are associated with alterations in salinity which is a critical determinant of estuarine habitat characteristics and can affect distribution of rooted vegetation, and sessile and motile biota (Alber 2002). Modifications in the Caloosahatchee River are often made without considering the biological integrity of the system (Haunert et al. 2000). This system is sensitive to high salinity levels and provides an indicator of the health of the entire watershed. The Caloosahatchee River serves as a nursery ground for many estuarine and coastal plant and animal species (Barnes 2005; South Florida Water Management District 2000b). Although current data does not yet exist to substantiate, it is expected that the river has declined in juvenile fish abundance, distribution, and species richness due to changes in the natural salinity regime and freshwater discharge (Barnes 2005).

The state of Florida requires the five Water Management Districts to develop Minimum Flows and Levels (MFLs) for all priority water bodies, and the South Florida Water Management District is responsible for the Caloosahatchee River. An MFL is the limit at which further withdrawals would be significantly harmful to the water resources or ecology of the area (Barnes 2005). Although the rule specifically addresses MFL's in order to assess the damage to water resources from low flows, research also explores damage from high discharge events. Scientific deficiencies were identified in the initial effort to set MFLs for the Caloosahatchee River, including a lack of documentation on the effects of MFL flows on downstream estuarine biota (SFWMD 2002). In response, the SFWMD took a Valued Ecosystem Component based approach for setting inflow requirements and therefore chose an important set of resources and tailored environmental policy based on the requirements of specific resources (Alber 2002). For

the Caloosahatchee River, proposed MFL's were created by examining the salinity tolerance of three species of seagrass, *Vallisneria americana*, *Halodule wrightii*, and *Thalassia testudinum*, with the assumption that salinity and flow conditions in which these species thrive will also be preferable for other organisms in the estuary (Alber 2002; Chamberlain and Doering 1998). This research determined that flow above the 71 - 85 m^3s^{-1} range (SFWMD 2002) was detrimental to tapegrass, *Vallisneria americana,* whereas a flow rate of approximately 8 m^3s^{-1} was optimal. A flow rate of 8 m^3s^{-1} yields an average daily salinity of 10 ‰ at the Ft. Myers salinity monitoring site, however this is highly variable depending on seasonal precipitation levels and contribution from downstream tidal basin inflows (SFWMD 2002). This proposed flow regime would be appropriate for juvenile bull sharks, however, MFL's are currently not being met and flow rates continue to be highly variable which provides an inadequate level of resource protection (SFWMD 2002).

The Caloosahatchee estuary is a connected segment of the Greater Everglades Ecosystem due to its connection with Lake Okeechobee and is therefore included in the Comprehensive Everglades Restoration Plan (CERP) (SFWMD 2002). The CERP addresses water supply needs throughout South Florida and has projects in place that will provide total flows to the estuary, distribute total flow between upstream and downstream areas, and affect the spatial and temporal variability of salinity within the estuary. Specifically, the plan includes an above ground storage reservoir within the Caloosahatchee watershed to supplement Lake Okeechobee water storage which will help to reduce the effects of too much or too little freshwater entering the estuary. Currently, the CERP goal is to have these structural components in place by 2011 (SFWMD and

USACOE 2002). Since high discharge rates have been shown to have an effect on the distribution of juvenile bull sharks, oftentimes forcing them out of the nursery area to remain within preferred conditions, attainment of the CERP goal would beneficial for this species.

The Lake Okeechobee Watershed Construction Project Phase II Technical Plan was created by state agencies to consolidate the numerous initiatives which addressed restoration of the Everglades, including CERP (SFWMD et al 2008). This Plan re-defined the optimal flow rate range as $13 - 798$ m^3s^{-1} and reported that levels have largely remained in that range since the inception of MFLs in 2000, however extreme high flow events of greater than 1278 m^3s^{-1} have continued to occur (SFWMD et al. 2008). Although this range was determined optimal, data from this research suggests that this adjusted flow regime may not be appropriate for juvenile bull sharks. Young bull sharks in this study all exhibited behavior of moving towards the river mouth during an extreme discharge event, with most sharks exiting the study area. Juveniles were shown to exhibit behavioral osmoregulation at flow rates above 75 m^3s^{-1}. These data substantiate the findings of Heupel and Simpfendofer (2008) who reported that juvenile bull sharks were found throughout the river at low flow rates, (< 57 m^3s^{-1}), but were only near the mouth at flows over 113 m^3s^{-1}.

The Caloosahatchee system provides nursery habitat to many species of animals and plants. In order to ensure protection for these estuarine communities, further research will be necessary to develop water management practices which establish appropriate freshwater inflow criteria. Current water management practices have been found to be inadequate for juvenile *C. leucas* as there continues to be highly variable flow

rates and releases that are high enough to affect the distribution of the population. We recommend that the physiological requirements of this top-level predator are considered in the formulation and enforcement of comprehensive water management policies.

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