DISTRIBUTION, MOVEMENTS, AND HABITAT USE OF BULL SHARKS (*Carcharhinus leucas*, Müller and Henle 1839) IN THE INDIAN RIVER LAGOON SYSTEM, FLORIDA

By

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To my grandparents, Stanley and Marjorie Faulkner, and Roland and Beth Curtis

Let your light from the lighthouse shine on me

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Distribution and habitat use of the bull shark (*Carcharhinus leucas*) were examined using fishery-independent sampling data, tagging, and ultrasonic telemetry to assess the potential role of the Indian River Lagoon (IRL) as a nursery area for this species. Fishery-independent sampling data were compiled and synthesized to examine patterns of seasonal occurrence, spatial distribution, and habitat associations. These data provided a comprehensive overview of bull shark ecology in the study site over a span of 30 years, based on data collected from 390 individual sharks. Tagging and acoustic telemetry methods were also employed to acquire more fine-scale information on shark movements, daily activities, and habitat utilization. A total of 50 sharks were marked with conventional tags, with four fish recaptured over the course of the study. Eleven of these sharks were tagged additionally with ultrasonic pingers, ten of which were tracked manually and one of which was monitored by moored listening stations (Vemco VR2). The manual tracking data provided fine-scale information on the patterns of movements of a small number of individuals. Integration of multiple methodologies provided a more complete picture of habitat use by this important apex predator in the IRL. Bull sharks occurred over a broad range of habitats, including depths of 0.2 – 4.0 m, temperatures of 18 – 37 °C, salinities of 1 – 42 ppt, dissolved oxygen concentrations of 3 – 8 mg/L, and water clarity levels of 70 – 170 cm. In addition, they were located over seagrass, sand, and mud substrates. Overall catch-per-unit-effort was low, relative to other systems. However, higher than average catch rates were observed at power plant outfalls and near freshwater creeks. These results may prove useful to the continued management and conservation of bull shark stocks in the northwest Atlantic.

CHAPTER 1
BACKGROUND AND OBJECTIVES

Introduction

Shark Fisheries

The expansion of commercial shark fisheries off the Atlantic coast of the United States over the past 30 years has led to population declines in many of the species taken (Figure 1-1) (Musick et al. 1993; NMFS 1993; 2006; Burgess et al. 2005). The rise of these fisheries has primarily been driven by the increased demand for shark fin products in Asia, as well as increased demand for shark meat in domestic and foreign markets (NMFS 1993; Brown 1999). The species captured in these fisheries, many from the family Carcharhinidae, are considered to have a *K*-selected life history (McArthur and Wilson 1967; Hoenig and Gruber 1990), meaning that they are long-lived, have slow growth rates, mature at a late age, and produce few, highly developed offspring (Pitcher and Hart 1982). Animals that are *K*-selected do not cope well with heightened levels of mortality, and take many years to repopulate an area once depleted (Jennings et al. 1998; Gedamke et al. 2007). According to the 1993 Fishery Management Plan for Sharks of the Atlantic Ocean (FMP), the abundance of the “large coastal species” management unit could have declined as much as 75% from the 1970s to the 1980s (NMFS 1993).

The FMP also identified an alarming lack of information on shark fisheries, and biological data needed for adequate fisheries management. It stated that delineation of essential fish habitat (EFH), specifically mating and nursery grounds, is of key importance. Estuarine nurseries were determined to be the habitats of greatest concern for coastal sharks, in that these areas continue to suffer from dramatic human-induced alteration and destruction. The re-authorized Magnuson-Stevens Fishery Conservation and Management Act (Sustainable Fisheries Act of 1996) also legally mandated that government fisheries agencies identify and protect EFH for commercially exploited species of fish. This continues to be an important component of the Magnuson-Stevens Reauthorization Act of 2007. Along with habitat degradation, impacts from water quality degradation in coastal areas were also identified as a potential threat, but the effects of these alterations on sharks remains mostly unknown (NMFS 1993). Before these impacts can be properly assessed, the spatial and temporal boundaries of shark nursery areas must first be isolated.

Shark Nursery Areas

In the most simplistic definition, shark nursery areas are part of a species' range where gravid females give birth to their pups, and where the young spend the first weeks, months, or years of their lives (Castro 1993). There are two main types of shark nursery areas. *Primary* nursery habitats are zones where parturition and young-of-the-year (YOY) sharks occur. *Secondary* nursery habitats are zones that are used only by juveniles and sub-adults (immature sharks at least 1 year old) of a species (Bass 1978). Many shark species use productive shallow coastal zones and estuaries as nursery areas because they are hypothesized to offer two key selective benefits, 1) low levels of predation from other larger sharks, and 2) an abundance of prey like small fishes and crustaceans (Springer 1967; Castro 1983; Branstetter 1990). In the northwest Atlantic and Gulf of Mexico, shark nurseries have been found along the U.S. coast from Massachusetts to Texas (McCandless et al. 2002; 2007).

This traditional definition of estuarine nursery areas functioning as critical habitats has recently met with some criticism. Beck et al. (2001) argued that just because the young of a species occur in a specific environment in high densities does not necessarily mean that that specific habitat is providing refuge from predation and abundant food resources. They suggested that an area is a nursery if its contribution per unit area of recruits to the adult population is greater than other areas where young individuals also occur. This contribution results from increases in numbers, rates of growth, juvenile survival, or facilitation of movement to adult habitats. Heithaus (2007) has further argued that an "essential" habitat could be defined as habitat where density-dependent selection occurs. With reference to shark nursery areas, he hypothesized that risk of predation and intraspecific competition should influence the habitat use of sharks within their nurseries. Both studies highlight the fact that information on the movements of species within their nurseries are lacking, yet are essential to understanding the factors influencing habitat selection. In a recent review of the shark nursery area concept, Heupel et al. (2007) attempted to reconcile the various proposed definitions for what constitutes a shark nursery area, and provided three testable criteria for an area to be characterized as a shark nursery: 1) density of juvenile sharks is greater in the putative nursery area relative to other areas, 2) juvenile sharks exhibit higher than average site fidelity to these areas, and 3) the area is used repeatedly by juvenile sharks across years. According to the authors, this definition does not discount the importance of prey availability, predation risk, and intraspecific competition in a potential nursery area, but provides the means to collect hard data in the field (through surveys, mark-recapture experiments, acoustic tracking, stable isotope analysis, genetic techniques, etc.) that will support or refute the characterization of a particular area as a nursery. If these three criteria are met, then the area is likely to support increased production in the shark population in question, as required by the Beck et al. (2001) definition of nursery habitat.

Study Species: The Bull Shark

The bull shark, *Carcharhinus leucas*, Müller and Henle 1839, is a cosmopolitan species in tropical to subtropical coastal waters, typically occurring in waters less than 30 m deep (Compagno 1984). Few studies have examined the movements and patterns of habitat use of the bull shark (Thorson 1971; Steiner 2002). However, the general biology and life history of the bull shark has been studied in a number of populations around the world including the Gulf of Mexico (Springer 1940; Clark and von Schmidt 1965; Caillouet et al. 1969; Branstetter 1981; Branstetter and Stiles 1987; Cruz-Martinez et al. 2002; Neer et al. 2005), the Atlantic coast of Florida (Dodrill 1977; Snelson et al. 1984), Central America (Thorson et al. 1966; Thorson 1976; Tuma 1976; Thorson and Lacy 1982; Montoya and Thorson 1982), Brazil (Sadowsky 1971; Thorson 1972), South Africa (Bass et al. 1973; Cliff and Dudley 1991), in addition to studies in captivity (Weihs et al. 1981; Schmid et al. 1990; Schmid and Murru 1994).

The bull shark frequents brackish estuarine waters and has been documented to penetrate rivers and into numerous freshwater lakes around the world (Tuma 1976; Garrick 1982; Compagno 1984; Martin 2005). There are verified records of bull sharks captured from the Peruvian Amazon River up to 3,480 km from the Atlantic (Thorson 1972), and a record from Alton, Illinois, 2,800 km up the Mississippi River (Thomerson et al. 1977). A population in Lake Nicaragua in Central America, previously believed to be a completely landlocked and separate species, *C. nicaraguensis*, has since been shown to be comprised of *C. leucas* that navigate the rapids of the San Juan River from the Caribbean Sea into the lake (Thorson et al. 1966; Thorson 1971). The bull shark’s unique physiology and osmoregulatory capabilities enable its euryhaline habits (Thorson 1962; Oguri 1964; Thorson et al. 1973; Pillans et al. 2005).

The bull shark can grow to lengths of 350 cm TL and weigh over 230 kg, making it one of the largest of its genus and order (Castro 1983). Consequently, the size at birth is also large at 60-80 cm TL (Clark and von Schmidt 1965, Dodrill 1977). In the northern Gulf of Mexico maturity is reached at 210-220 cm TL (14-15 years) for males, and >225 cm TL (18+ years) for females, which also tend to reach greater total lengths (Branstetter and Stiles 1987, Neer et al. 2005). Bull sharks are opportunistic roving predators, their diet primarily consisting of teleosts and smaller elasmobranchs (Compagno 1984, Snelson et al. 1984). Its large size, its tendency to inhabit shallow coastal zones, and its opportunistic feeding habits make the bull shark one of the most dangerous sharks, being implicated in at least 75 unprovoked attacks on humans around the world, 23 of those resulting in fatality (G. Burgess, unpubl. data, International Shark Attack File, University of Florida).

Most of the existing literature on the life history, ecology, and distributions of *C. leucas* in Florida waters has come from multi-species surveys (Clark and von Schmidt 1965; Snelson and Williams 1981; Hueter and Manire 1994; Hueter and Tyminski 2002). For example, the seasonal occurrence, size, reproductive habits, and diet of bull sharks were examined along with 16 other species of sharks that occur along Florida's central Gulf Coast by Clark and von Schmidt (1965). The bull shark was the most abundant species in their catch (N = 135), ranging in size from 88-264 cm TL. They were captured year-round, though catch was highest from March to October, particularly during the summer months. Adult individuals of both sexes were equally represented in their seasonal distribution, indicating no seasonal sexual segregation. They found that parturition occurred in April, following a gestation period of 10-11 months. The mating season was determined to be in June and July. Analysis of stomach contents revealed a diet dominated by bony fishes – *Archosargus probatocephalus*, *Caranx* spp., *Centropomus undecimalis*, *Euthynnus alletteratus*, *Arius felis*, *Acanthostracion quadricornis*, *Megalops atlanticus*, *Mugil* spp., and *Prionotus* spp., as well as parts of sharks, crustaceans, and mollusks. Other surveys have yielded complementary information on the diets of Florida bull sharks (Snelson et al. 1984; Hueter and Manire 1994; Michel 2002). Bull sharks also opportunistically scavenge on marine mammal carcasses (Compagno 1984; M. Stolen, Hubbs-SeaWorld Research Institute, pers. comm.).

Purpose and Need for Research

Many large coastal shark populations have been overfished along the Atlantic coast of the United States, in recent decades (NMFS 1993). Effective management measures to rebuild these depleted stocks have been unsuccessful, undoubtedly due in part, to a lack of data on shark life history, population dynamics, distribution, and habitat requirements (NMFS 2006). The impacts of ever-increasing coastal development and habitat alteration of nearshore regions has made the delineation of shark estuarine nursery areas a priority. Although progress has been made in recent years to help identify essential habitats for sharks (e.g. Simpendorfer and Milward 1993; McCandless et al. 2002; 2007), seasonal distribution and habitat use information is incomplete for most shark species. More information is needed to help characterize critical nursery areas for commercially exploited species. This is particularly true for species that may rely on disturbed and heavily impacted inshore systems. The recovery of these species may be dependent upon the ability to protect their essential habitats before they are lost or permanently altered by anthropogenic activities.

To maintain sustainable exploitation of shark resources, it is prudent to protect immature portions of the stocks and the habitats on which they rely (NMFS 1993; Cortes 2002). As a result, there has been a recent increase in the number of studies investigating the distribution and habitat use of sharks within their nursery areas (Simpfendorfer and Milward 1993; Hueter and Manire 1994; Merson and Pratt 2001; Michel 2002; McCandless et al. 2002; 2007). Bull sharks have been commercially harvested off the southeastern U.S. for over 30 years, and as a member of the large coastal shark management complex, may currently be overfished (Cortes et al. 2002; NMFS 2006). More effective management requires a better understanding of how exploited sharks, such as the bull shark, utilize their essential nursery habitats. A few recent studies have focused on the abundance, distribution, and habitat use of juvenile bull sharks in some of their

Gulf of Mexico nursery areas (Michel 2002; Simpfendorfer et al. 2005; Blackburn et al. 2007), but potential Atlantic coast nurseries such as the Indian River Lagoon (IRL) have not been studied since the recent rise of the U.S. shark fishery (Snelson et al. 1984). In addition, there is very little information available on the day-to-day movements, activities, and habitat preferences of immature bull sharks in their nursery areas. The purpose of this study is to describe the historic and current distribution of bull sharks within the IRL, and provide much-needed insights into daily movements and habitat use of the young sharks that utilize this coastal lagoonal system.

Objectives

This study takes two primary approaches to address the needs described above. The first is to use fishery-independent sampling methods to collect, tag, and release immature bull sharks in the IRL. Augmentation of this data with existing fishery-independent data sets for bull sharks in the IRL is used to provide a robust and comprehensive synthesis of information for this site. Catch rates are used as predictors of habitat use, and tag recaptures provide insights into movements.

The second approach is to actively track the movements of individual YOY and juvenile bull sharks via acoustic telemetry. This is the most effective method to examine the short-term, high-resolution movements of fishes in their natural environment (Nelson 1990; Sundström et al. 2001; Sibert and Nielsen 2001). This technique provides information on the daily activities, swimming behaviors, and patterns of habitat use of these young sharks relative to the environmental parameters of temperature, depth, dissolved oxygen, and salinity.

With these data I addressed the following research questions:

Question 1. Do immature bull sharks show any distinct patterns of habitat use in the IRL with regards to depth, temperature, salinity, water clarity, dissolved oxygen, or substrate?

Question 2. Do bull sharks of different size/age classes (YOY vs. juvenile) have similar activity spaces, and habitat utilization patterns?

Question 3. Do immature bull sharks exhibit any diel changes in activity levels or space use?

Question 4. Does the Indian River Lagoon system meet the definition of a shark nursery area, as proposed by Heupel et al. (2007)?

With a better understanding of how this commercially-important shark utilizes this important coastal environment, we will be better equipped to develop more effective management and conservation strategies for the species and its EFH. By delineating and protecting this EFH, it may help increase the survivorship of juveniles, and therefore promote successful recruitment to the adult stocks and fisheries (Cortes 2002). Thus, a primary contribution of this study is to increase our understanding of the ecology and behavior of bull sharks, and provide information needed to help conserve bull sharks and their EFH.

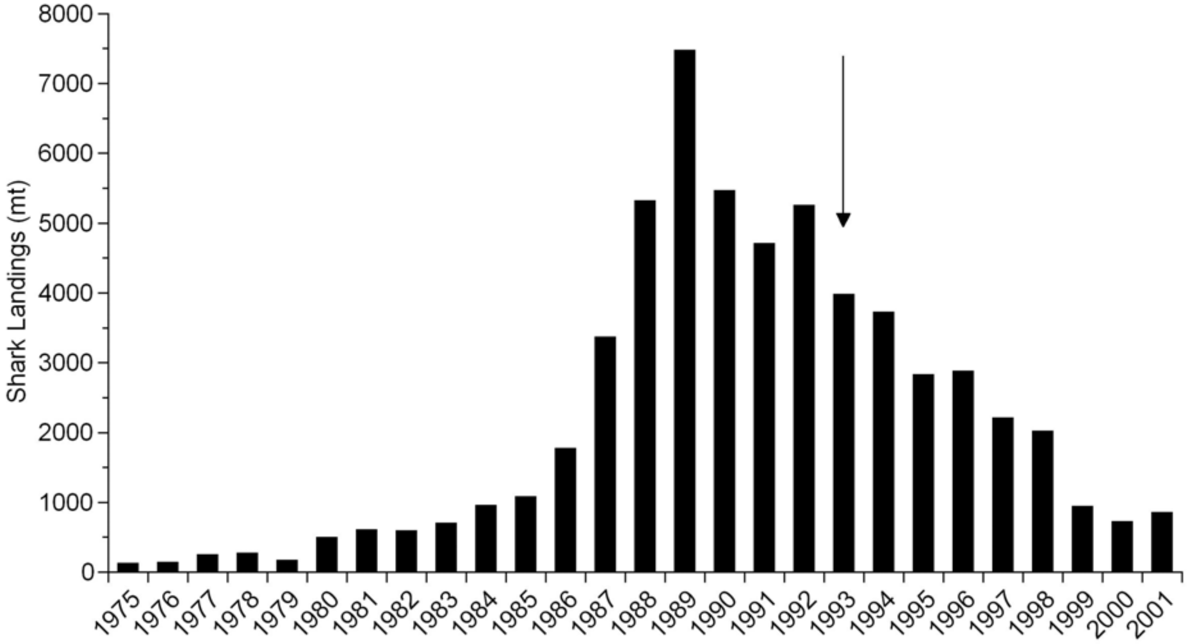

Figure 1-1. Annual U.S. Atlantic landings of large coastal sharks, 1975 to 2001. The arrow indicates the year that shark management was implemented in the U.S..

CHAPTER 2
REVIEW OF THE DISTRIBUTION AND HABITAT OF BULL SHARKS IN THE INDIAN RIVER LAGOON SYSTEM

Introduction

Fishery-independent surveys are one of the primary methods for assessing the distribution and habitat use of sharks (Simpfendorfer and Heupel 2004). Gillnet and hook gear surveys have proven particularly useful for sharks in shallow coastal and estuarine areas, often used as nursery grounds for coastal species (Clarke 1971; Snelson and Williams 1981; Simpfendorfer and Milward 1993; Hueter and Manire 1994; Carlson and Brusher 1999; Merson and Pratt 2001; Heithaus et al. 2002; Michel 2002; McCandless et al. 2002; 2007; Simpfendorfer et al. 2005; Wiley and Simpfendorfer 2007). Studies such as these have dramatically improved our knowledge of the distribution and habitat associations of a variety of shark species in a variety of environments around the world, and have proven useful for fishery managers in the conservation of depleted shark stocks. Distribution and habitat information for many species, however, is still lacking. Furthermore, even where species-specific data is available, site-specific information is needed to shed light on spatio-temporal patterns of utilization, since most sharks utilize a great variety of habitats within their ranges.

As a component of the NMFS multi-species “large coastal shark” management complex, the bull shark is a commercially exploited shark species for which more information on life history, movements, and habitat associations are needed. The current stock status of the large coastal shark group is unknown due to data deficiencies for robust species-level stock assessments (NMFS 2006), but has been classed as overfished and experiencing overfishing in previous stock assessments (Cortes et al. 2002). Additionally, other large coastal species including sandbar (*Carcharhinus plumbeus*) and dusky sharks (*C. obscurus*), have been assessed and found to be overfished. The World Conservation Union (IUCN) Red List of Threatened

Species classifies *C. leucas* as “near threatened” due to evidence of population declines in certain locations around the world (e.g. Thorson 1982; Cliff and Dudley 1991). The bull shark may be particularly at risk because its life history traits make it vulnerable to overfishing (Thorson and Lacy 1982; Branstetter and Stiles 1987; Cruz-Martinez et al. 2002; Wintner et al. 2002; Neer et al. 2005) and its coastal/inshore distribution may disproportionately expose this species to adverse anthropogenic environmental impacts and habitat loss (Garrick 1982; Compagno 1984). However, the most recent stock assessment of large coastal sharks stated that because of their nearshore distribution off the southern United States, bull shark populations may not be as impacted by fishing mortality as other species (NMFS 2006). It states, “Commercial shark fishing effort [in nearshore waters] has been limited or eliminated for more than a decade, which has helped to maintain a large biomass” (NMFS 2006). A species-specific bull shark population stock assessment is likely warranted to confirm this assertion.

The Indian River Lagoon (IRL) is an anthropogenically impacted waterway (Gilmore 1995) that is utilized by immature bull sharks (Snelson et al. 1984; Castro 1993). The seasonal occurrence and diet of bull sharks in the IRL was previously described by Snelson et al. (1984), but information on distribution and habitat use patterns in the nursery area were not discussed in detail. The study also only surveyed a portion of the northern IRL, so data has not been reported for much of the remainder of the expansive lagoon system. Due to the bull shark’s current conservation status and the apparent importance of this Atlantic coast estuary to their young (Snelson et al. 1984), more detailed information could prove beneficial to fisheries management and conservation efforts. This information will also help to further describe the ecology of this apex lagoon predator.

The objectives of this chapter are to compile and synthesize all available bull shark records from the IRL, including records from the scientific literature, unpublished fishery-independent data, and personal communications, to provide a comprehensive description of their seasonal distribution and habitat utilization patterns in this intra-coastal environment. These data will help to determine whether the IRL functions as a bull shark nursery area (Heupel et al. 2007).

Methods

Study Site

The IRL is a shallow, estuarine, barrier island system that stretches over one third of Florida’s central Atlantic coast, between the latitudes of 29º 04’ N (Ponce de Leon Inlet) and 26º 56’ N (Jupiter Inlet) (Figure 2-1). This system is comprised of three main water bodies: Mosquito Lagoon, Indian River Lagoon proper, and Banana River Lagoon, which are interconnected by canals. There are five inlets along the length of the system which connect these bodies to the ocean. The study area covered the northern half of the lagoon between Ponce de Leon Inlet (Volusia County) and Sebastian Inlet (Brevard County) (Figure 2-1). Portions of the study area fall under the jurisdiction of Canaveral National Seashore, Merritt Island National Wildlife Refuge, and the National Aeronautics and Space Administration’s (NASA) Kennedy Space Center (KSC). The IRL spans a climatic transition zone between tropical and warm-temperate environments (Phlips et al. 2002), and therefore contains a diverse ichthyofauna (Gilmore 1995). In addition, IRL contains a variety of habitat types including seagrass beds, fringing mangroves, saltmarshes, oyster bars, open sand bottom, lagoon reefs, tidally influenced freshwater tributaries, and ocean inlets (Gilmore 1977; Kupschus and Tremain 2001). It is home to at least 397 species of temperate to tropical fishes, many of these juvenile phases of offshore species (Gilmore 1977; 1995). The mean annual salinity for the entire IRL is 25.6 ppt, and water temperatures can annually range from 11 – 32.5 ºC (Figure 2-2) (Gilmore 1977).

Data Sources

To synthesize bull shark distribution information from the IRL, verified bull shark capture and sighting records were compiled from three main sources: (1) the scientific literature (Dodrill 1977; Snelson and Williams 1981; Snelson et al. 1984, Schmid and Murru 1994; Tremain et al. 2004); (2) fishery-independent sampling data: the Florida Fish and Wildlife Conservation Commission (FWC) Fishery-Independent Monitoring Program; sea turtle netting studies at the University of Central Florida (UCF) and the KSC/Dynamac Corporation; sampling efforts conducted as part of the current tagging study; and (3) personal communications from cooperating scientists and local fishermen. Table 2-1 summarizes the data sources, the gears used, the years represented, and the number of sharks captured in each of these studies.

Capture Methods

Sampling effort, spatial distribution, and techniques varied considerably between each of the studies from which data were compiled. The distribution of sampling effort spanned approximately half the length of the IRL, from Ponce de Leon Inlet at the north end of Mosquito Lagoon, to Sebastian Inlet, 145 km to the south (Figure 2-1). The primary capture gears were gillnet and bottom longline, but also included rod and reel and haul seine (Table 2-1). Direct visual observations were also included in this synthesis.

Hook gear, including bottom longlines and rod and reel, was utilized by Dodrill (1977) to collect sharks in the IRL and off Melbourne Beach between 1974 and 1977. The longline was 200 m in length, and was comprised of 1590-kg test nylon mainline. Ten baited hooks were evenly spaced along the length of the mainline, on 3.7 m long steel chain gangions. The hooks alternated in size, and included Mustad 51 mm and 63 mm shark hooks, and 14/0 tuna hooks.

As part of a sea turtle monitoring study, Snelson and Williams (1981) used large-mesh gillnets to capture elasmobranchs in the northern IRL between 1975 and 1979. Details of the bull shark catch data were described by Snelson et al. (1984). The gillnets were comprised of braided nylon twine with stretch mesh of 305 – 406 mm, net lengths from 90 – 230 m, and a net depth of 3.7 m. The nets were deployed monthly in Mosquito Lagoon and the northern IRL for periods of 24 – 147 h, as described by Snelson et al. (1984). Catch-per-unit-effort (CPUE) was calculated as the number of sharks captured per 24-h net day (NetDay24 = [m net deployed/100] x [h net deployed/24]).

Schmid and Murru (1994) used small bottom longlines to capture neonate bull sharks from the IRL for captive study and display at Sea World of Florida, Orlando. Collecting occurred during the summer of 1985 near the power plant outfalls at Port St. John (Mr. F. Murru, Sea World, pers. comm.). No detailed information on fishing effort or habitat associations were available.

The bull shark data contributed by FWC was from gillnet captures in the IRL between 1990 and 1997 (Figure 2-3), and from haul seine captures in 2000 and 2001. The gillnets used were multi-panel monofilament gillnets, 208 m in length and 1.8 m deep, with 127-mm diameter polypropylene float line and 127-mm diameter lead core lead-line. The net consisted of five panels; a 25-m long panel of 50-mm stretch mesh, and four 45.7-m panels, with 76-, 102-, 127-, and 152-mm stretch mesh (Adams and Paperno 2007). All sets were conducted during crepuscular or nighttime periods. Soak times ranged from 1.53 – 4.25 h (mean = 2.65 h). The haul seine was 183 m long and 3 m deep, with 38-mm meshes (D. Adams, FWC, pers. comm.). Water temperature, salinity, and dissolved oxygen measurements were collected at all sampling sites. All sharks were sexed and measured to the nearest mm, and then tagged below the first dorsal fin with a spaghetti-style dart tag.

Sampling gear in the present study, included a 50-hook bottom longline, comprised of 305 m of 6.4-mm braided nylon mainline. Gangions were made of braided nylon, 1.5-m in length, with 1.6-mm stainless steel cable leader attached to a baited 12/0 circle hook (with barbs depressed for easier release). On some occasions only half of the mainline was set with 25 hooks. Gangions were spaced evenly along the length of the longline. Bait included fresh or frozen fish (*Mugil* spp., *Alosa* spp., *Dorosoma petenense*, *Elops saurus*, *Arius felis*, *Dasyatis* spp., *Caranx* spp.). The line ends were anchored, and marked by visible surface floats. Soak time (defined as the time between the setting of the last hook and the retrieval of the first hook) varied depending on environmental conditions, and ranged from 20 – 65 min, but the majority of sets soaked for 45 min. Short soak times were intended to minimize incidental mortality of the captured sharks. This longline design is the same as that used by Pratt et al. (1998). Rod and reel was also used at many locations where setting the longline was not feasible, using the same terminal tackle and bait, attached to 13.6-kg (30-lb) test monofilament fishing line. While rod and reel fishing, the boat was anchored, and lines were soaked until the bait degraded or a fish was caught. CPUE was measured as the number of sharks captured per 100 hook hours (hh) of effort (1 hh = 1 baited hook soaking for 1 h).

At each sampling location (Figure 2-4) the date, time of day, latitude and longitude, water depth, bottom type, wind velocity and direction, air temperature, surface water temperature, salinity, dissolved oxygen (DO) concentration, and water clarity (Secchi depth) were recorded (Table 2-2). All captured sharks immediately had the hook removed and were restrained on the deck. Straight-line fork (FL) and total length (TL) were measured with a meter stick to the nearest cm. Sex of sharks was determined by external examination for the presence of claspers. A small fin clip was also removed from the second dorsal fin for subsequent genetic analysis by other researchers. Each shark was ID-tagged with a numbered plastic rototag (Dalton Co., UK) punched through the first dorsal fin, which included tag-return instructions to the NMFS Apex Predators Program, Narragansett, RI. The sharks were then promptly released. Handling time was normally less than 3 min, to minimize the stress experienced by the shark during capture and tagging. The condition of the shark at release was classified as “excellent”, “good”, “fair”, or “poor”, depending on how vigorously the shark swam upon release. The direct visual observation of free-swimming bull sharks was also recorded, and location and habitat data were noted at the time of observation.

Additional observations were provided by Jane Provancha (KSC), Sharon Tyson (Florida Dept. of Environmental Protection), Megan Stolen (Hubbs – Sea World Research Institute), and several resident lagoon sport fishermen.

Data Analysis

For the purposes of this synthesis, the study site was divided into three sub-regions: (1) Mosquito Lagoon (ML), (2) northern Indian River and Banana River (NIR), and (3) the Melbourne – Sebastian (MS) area (Figure 2-1). All known bull shark capture and sighting locations were plotted using Geographic Information Systems (GIS) software (ArcView 3.2, Environmental Systems Research Institute Inc., Redlands, California). Descriptive statistics were used to characterize the catch and habitat parameters observed from each of these sub-regions, and for the study site overall. CPUE was summarized by region and season for each study from which sampling effort information was available: i.e., Snelson et al. (1984) and the current study. The designation of seasons follows Snelson et al. (1984): Winter = December – February; Spring = March – May; Summer = June – August; and Fall = September – November.

Habitat data were available from Snelson et al. (1984), FWC, KSC, and this study. Linear correlation analysis was used to examine potential relationships between CPUE from the current study and habitat parameters, including depth, temperature, salinity, and DO.

Results

Population Structure

All the data sources combined represented a total of 390 individual bull shark records from the IRL from 1975 – 2005 (Table 2-1). Shark capture locations are shown in Figures 2-5 and 2-6. The population of bull sharks in the IRL was dominated by immature sharks (mean ± 1 sd = 121 ± 38 cm TL), including neonates (less than *c*. 75 cm TL), YOY (less than *c*. 90 cm TL), juveniles (less than *c*. 190 cm TL), and maturing subadults (less than *c*. 210 cm TL) (Figure 2-7). Of the sharks in which sex was noted, 86 were male and 113 were female, yielding a male to female ratio of 1:1.3. Juvenile bull sharks (*c*. 90 – 190 cm TL) were the dominant size/age class in the lagoon, and were captured year round in the IRL (Figure 2-8). The few adult-sized sharks were only captured during the late spring/early summer. Neonate-sized sharks, with fresh umbilical scars, were only captured between May and August (Figure 2-8). The smallest free-swimming bull shark captured in the IRL was 61 cm TL, and was captured in August 1985 (Schmid and Murru 1994). The smallest bull shark captured during the current study was a 66 cm TL male, weighing 1.8 kg, that was captured in June near the power plant outfall at Delespine, FL (Figure 2-5).

To date, the only mature bull sharks captured within the IRL (N = 6) have been gravid females approaching parturition (Dodrill 1977; Snelson et al. 1984). Dodrill (1977) discussed a large (> 250 cm TL) female bull shark harpooned by a fisherman north of Sebastian Inlet in late

Spring/early Summer 1976. Snelson et al. (1984) captured two large mature females (*c*. 225 – 249 cm TL) in ML; one in May 1975 and one in May 1979. One shark was not fully examined but appeared gravid. The other carried 12 near-term embryos, 60.8 – 70.6 cm TL. An anecdotal report from a local sport fisherman also indicated the observation of a large (> 250 cm TL) shark, presumably *C. leucas*, of unknown sex off the “Whale Tail” at the southern end of ML in May 2005. A large bull shark (sex unknown) was also reported from the southern IRL near Ft. Pierce Inlet in August 2002 (Capt. S. Bachman, Ft. Pierce, FL, pers. comm.). Additionally, an adult female bull shark that was tagged at Walker’s Cay, Bahamas with a pop-up satellite archival tag in April 2003 traveled 210 km and into the southern IRL through St. Lucie Inlet, where its tag popped off after 12 days at liberty (Brunnschweiler and Buskirk 2006).

Mature male bull sharks have not been documented within the IRL. Although all size classes less than 210 cm TL are represented in the catch, the length frequency of IRL bull sharks appears to be bimodal (Figure 2-7), with a peak at the 70 – 109 cm TL size classes and a peak at the 150 – 169 cm TL size class.

Spatio-Temporal Patterns of Distribution

In general, bull shark occurrence was lower in ML, the northernmost portion of the study site, than in the NIR or MS regions, with 70 sharks caught in ML, 127 sharks in the NIR, and 122 sharks in the MS area (Figure 2-9). Although somewhat influenced by the spatial distribution of fishing effort, the spatial distribution of catches was not homogeneous in any of the sub-regions. Catches of sharks tended to be clustered at specific sites within each sub-region (Figures 2-5 and 2-6). In ML, most sharks were captured south of Haulover Canal along the western shoreline of the lagoon (Figure 2-5). In the NIR, shark catches were clustered near the power plant outfalls at Frontenac and Delespine (Figure 2-5). In the MS area, most bull shark catches occurred within or adjacent to the freshwater creeks that flow into the lagoon from its western shoreline, and also at Sebastian Inlet (Figure 2-6). Few sharks were captured in deeper mid-lagoon waters, or from the intracoastal waterway which runs through the entire study site.

Bull sharks were captured year round in the IRL, although based upon all available catch data, there appears to be some variation in their seasonal distribution and occurrence (Figure 2-9). In ML, sharks were only captured between March and November. During winter months, no sharks were captured in ML despite various levels of sampling effort (Tables 2-3 and 2-4). In the NIR and MS areas, sharks were documented year round, though with less frequency during the winter. Only five bull sharks were documented in the NIR during winter, three of which were dead or moribund following severe hypothermal events in the lagoon (Dodrill 1977; Snelson and Bradley 1978; Snelson et al. 1984). The other two sharks were tagged individuals which were recaptured in the NIR (see Tag-Recapture Data). The MS area, however, yielded the capture of 13 juvenile bull sharks during the winter, primarily near Sebastian Inlet. This is the only area sampled where non-moribund bull sharks were regularly captured during winter. During spring months, juvenile bull sharks were present in all three lagoon regions, though most common in the NIR and least common in ML (Figure 2-9). During the summer, with the influx of neonate sharks (Figure 2-8), numbers peaked in ML and MS areas, and dropped somewhat in the NIR. Sharks remained abundant in all regions into the fall, particularly in the NIR and MS areas, until dropping off as winter approached (Figure 2-9).

The available CPUE data reflect these patterns of occurrence in both Snelson et al. (1984) and the present study (Table 2-5). In the current study, CPUE was greatest in the MS region and lowest in ML (Table 2-5). Snelson et al. (1984) also found that CPUE was notably lower in ML than in the NIR (Table 2-5). Across seasons, catch rates in ML ranged from 0.0 – 0.18 sharks per NetDay24, and in the NIR, catch rates ranged from 0.0 – 0.69 sharks per NetDay24 (Table 2-

5). Seasonal catch rates in the current study were highest (6.52 sharks per 100 hh) during summer in the MS region. CPUE was substantially lower (0 – 1.42 sharks per 100 hh) in all other regions and seasons (Table 2-5). Snelson et al. (1984) reported the highest seasonal CPUE of their study (1.15 sharks per NetDay24) during fall 1976 in ML and NIR. Other temporal trends in shark distribution may have been more apparent had more effort data been available for analysis.

Tag-Recapture Data

Tagging efforts conducted by FWC (Tremain et al. 2004) and during the current study led to the tag and release of 50 bull sharks in the IRL between 1991 and 2005. A total of 25 sharks were tagged by FWC between 1991 and 1997, and 25 sharks were tagged in the current study between 2003 and 2005. Two bull sharks were recaptured by each program in the IRL, yielding a total of 4 recaptures (8%). Time at liberty ranged from 3 – 214 days, and the minimum distance traveled between tag and recapture locations ranged from 0.1 – 34.5 km. No bull sharks were recaptured outside of the IRL. One juvenile bull shark that was tagged south of the Frontenac power plant on 25 October 1995 was recaptured 33 km to the north near Haulover Canal on 14 December 1995. A YOY bull shark that was tagged on 24 June 1996 in the northern Banana River KSC no-entry zone was subsequently recaptured in the NIR near the Rt. 405 causeway in Titusville on 23 January 1997 (Tremain et al. 2004). The two bull sharks recaptured from the current study moved very little over comparatively short times at liberty. One neonate was tagged off the Delespine power plant, and recaptured by a sportfisherman three days later less than 100 m from the tagging location. The other recaptured shark, a YOY male that was tagged south of Crane Creek in Melbourne, was recaptured by the author less than 1 km from its tagging location after two weeks at liberty.

Habitat Utilization

There are broad ranges of physical and biological habitats in the IRL system (Table 2-2; Figure 2-2; Gilmore 1995); most of which are utilized by bull sharks at least occasionally. The available habitats also varied to some degree between each of the sub-regions (Table 2-2; Figure 2-2). The water temperatures encountered during sampling ranged from 12.1 – 37.0 ºC, with bull sharks being captured in 20.0 – 37.0 ºC waters (Table 2-6). The mean temperature of occurrence was 29.7 ± 3.5 ºC. The single shark captured at 37 ºC, a juvenile swimming in the heated effluent of the Delespine power plant in August 2004, appeared emaciated and weak. YOY bull sharks were captured in a warmer and narrower temperature range than juveniles (Table 2-6). The mean temperature of capture was 30.4 ± 1.8 ºC for YOY and 29.7 ± 3.3 ºC for juveniles. Although there was no significant correlation between CPUE and water temperature detected in the current study, CPUE was highest in 27 – 33 ºC water temperatures (Figure 2-10).

The range of salinities encountered during sampling was 0.7 – 42.0 ppt (Table 2-2), with bull sharks captured at salinities of 1.2 – 42.0 ppt (23.2 ± 10.0 ppt, mean ± 1SD) (Table 2-6). YOY bull sharks tended to be captured in lower salinity waters (17.0 ± 7.7 ppt) than juveniles (21.6 ± 7.9 ppt) (Table 2-6). There was no significant correlation between CPUE and salinity, but CPUE was high in 9 – 15 ppt and 28 – 30 ppt salinity levels (Figure 2-10).

The range of DO concentrations encountered during sampling was 2.4 – 10.2 mg/L (Table 2-2), with bull sharks captured at concentrations of 3.2 – 9.2 mg/L (Table 2-6). The mean DO of occurrence was 5.5 ± 1.5 mg/L. YOY bull sharks were captured in areas with a slightly lower mean DO level (4.8 ± 1.5 mg/L) than juveniles (6.0 ± 1.2 mg/L) (Table 2-6). There was no correlation between CPUE and DO, but CPUE was highest between 4.5 and 7.5 mg/L (Figure 2-10).

Most depths available in the IRL (0.2 – 6.0 m) were sampled for bull sharks. Despite this, sharks were captured in depths of 0.2 – 3.4 m (Table 2-6). The mean depth of occurrence was 1.0 ± 0.6 m, which was equivalent for both YOY and juvenile sharks (Table 2-6). However, there was no significant correlation between CPUE and depth, but CPUE was highest in depths less than 2 m (Figure 2-10).

The water clarity levels encountered during sampling, as measured by Secchi depth, ranged from 0.2 – 3.0 m (Table 2-2). Bull sharks were captured in Secchi depths of 0.3 – 1.5 m (Table 2-6). The mean Secchi depth where sharks occurred was 0.9 ± 0.3 m, and was similar for both YOY and juveniles (Table 2-6).

Discussion

Based on thirty years of bull shark capture data, it appears that the northern IRL is commonly utilized by immature *C. leucas*, and appears to function as a nursery area. In addition, bull sharks of several size/age classes are seasonally distributed throughout the lagoon system and occupy a broad range of habitats. These findings are mostly consistent with the findings of previous studies on bull sharks in the IRL (Dodrill 1977; Snelson et al. 1984), as well as for bull sharks in some other documented nursery areas (Simpfendorfer et al. 2005; Blackburn et al. 2007). This chapter is intended to provide a comprehensive review of bull shark captures in the IRL and provides a reference source for management and conservation efforts for bull sharks and their habitats in the IRL.

The reduced frequency of bull sharks in the 110 – 129 cm TL size class may be an artifact of gear bias, and variation in the sampling techniques and effort of the different studies included in this synthesis. There did appear to be some differences in gear selectivity, with the mean TL of sharks captured by hook gear (98 ± 31 cm, N = 97) being notably less than the length of sharks captured by gillnet (135 ± 34 cm, N = 160). The reduced frequency of bull sharks in that size classes could indicate that the gears utilized were inefficient at capturing sharks of that size, rather than their reduced occurrence in the study site. Snelson et al. (1984), a study that utilized large-mesh nets, failed to capture any sharks in the 86 – 116 cm TL length range, and postulated that this was also a result of gear bias, rather than absence from the lagoon. Bull shark data from the other sources compiled herein corroborate that conjecture. In fact, sharks 90 – 109 cm TL appear to be the dominant size class in the lagoon (Figure 2-7). These findings underscore the importance of using gears of various size selectivities for characterizing shark populations in nursery areas.

The low catches of sharks greater than 190 cm TL, however, was not considered to be influenced by gear bias, as large bull sharks were readily taken by certain gears (Dodrill 1977; Snelson et al. 1984), and would likely have been visually observed if they were more abundant. Sharks greater than *c*. 190 cm TL appear to be at the size which they may leave the nursery and fully transition to offshore adult habitats (Figure 2-7). According to age at length estimates for bull sharks (Neer et al. 2005), individuals of that size are approximately 9 years of age. In the Caloosahatchee River estuary on Florida’s Gulf of Mexico coast, Simpfendorfer et al. (2005) captured bull sharks 68 – 189 cm stretched TL, and estimated their ages at 0 – 10 years. Blackburn et al. (2007) also reported that bull sharks in coastal Louisiana waters ranged from 44 – 136 cm FL (*c*. 55 – 166 cm TL), and Steiner et al. (2007) reported that bull sharks in Florida’s Ten Thousand Islands estuary were 43 – 120 cm precaudal length (*c*. 60 – 162 cm TL). Based on these length ranges (see Neer et al. 2005 for length conversions), bull sharks from both of Florida’s coasts and the Gulf of Mexico appear to transition from nursery to adult habitats at lengths of *c*. 160 – 180 cm TL. Bull shark length frequency data from U.S. Atlantic large coastal shark fisheries may help confirm this by examining the length at recruitment to the fishery.

Bull sharks primarily utilize the northern half of the IRL (Sebastian Inlet to Ponce de Leon Inlet) during spring, summer, and autumn (Figure 2-9). In the late spring, gravid adult female bull sharks enter the lagoon via one of the inlets, and parturition occurs between May and August, after which time the adult sharks exit the lagoon (Figure 2-8; Dodrill 1977; Snelson et al. 1984; Brunnschweiler and Buskirk 2006). The occurrence of gravid female bull sharks in nursery areas prior to parturition was also observed by Bass (1978) in South Africa. Beginning in October or November, YOY and juvenile sharks appear to migrate out of the northern portions of ML and the NIR. It is not currently known if the bull sharks exit ML via Ponce de Leon Inlet to the north, or through Haulover Canal and into the NIR. While a few sharks remain in the NIR during winter, particularly near the heated power plant outfalls (Figure 2-5), it is speculated that most sharks leave the area either presumably moving either offshore or south in the IRL. The higher catches of bull sharks near Sebastian Inlet, at the southern extent of the study site, in December seem to support this hypothesis. Additionally, Dodrill (1977) captured YOY bull sharks off the ocean beaches outside of the IRL in November and January. Based on the available data, it is not known if bull sharks also occur during winter in the IRL south of Sebastian Inlet, but based on the increases in winter catches with decreasing latitude (Figure 2-9), it is likely that they utilize or transit the southern portions of the lagoon during this time. Bull sharks begin to migrate back into the northern IRL around March of each year.

Snelson et al. (1984) noted that emigration from the lagoon during winter could be difficult to differentiate from reduced activity of sharks that could actually remain within the IRL. Since bull sharks are ectothermic, dropping water temperatures during winter could depress metabolism and activity to a degree that could allow the sharks to avoid capture in passive gears like gillnets and longlines. Though further research will be necessary to investigate this possibility, it may be unlikely for a few reasons. First, a significant amount of fishing effort was expended in the ML and NIR sub-regions during winter (Tables 2-3 and 2-4) and few sharks were captured or visually observed. Of those that were observed in the NIR, they were primarily located in warm power plant effluents (Figure 2-2), or were moribund from hypothermal (4 ºC) conditions (Dodrill 1977; Snelson and Bradley 1978; Snelson et al. 1984). Second, based on data from other nursery areas, young bull sharks tend to avoid water temperatures below 18 – 21 ºC (Hueter and Tyminski 2002; Wiley and Simpfendorfer 2007). Lower temperatures are commonly experienced in the shallow water of ML and the NIR during winter periods (Gilmore 1977; Gilmore et al. 1978; Snelson and Bradley 1978; Figure 2-2). Third, bull sharks in south Florida nursery areas, such as the Everglades National Park region, show no clear trends in seasonal abundance and are present year round (Wiley and Simpfendorfer 2007). This is consistent with the latitudinal gradient of winter bull shark occurrence discussed above. Many other carcharhinid shark species migrate south along the Atlantic coast of the U.S. during winter (Kohler et al. 1998), and immature bull sharks do not appear to be an exception (Hueter and Manire 1994). This suggests that migration, rather than inactivity, is a more plausible explanation for the lack of bull shark catches in the northern IRL in winter months. Given the low catch rates of bull sharks in ML, even during warmer summer and fall months, and the low reported catches of immature bull sharks in estuaries north of ML (McCandless et al. 2002), ML may represent the northern extent of bull shark nursery habitat along the Atlantic coast.

A primary determinant in the occurrence of bull sharks in the study site, as well as in their geographic range, is water temperature, as dictated by the sharks’ physiological tolerance of this environmental parameter. In broad terms, the range of the bull shark is limited to tropical and subtropical climes (Garrick 1982; Compagno 1984). Since the northern IRL is located in a climatic transition zone (Gilmore 1995), and temperatures seasonally fluctuate (Gilmore 1977; Figure 2-2), sometimes dramatically (e.g., Snelson and Bradley 1978), bull shark occurrence in the system should fluctuate in response. The avoidance of low water temperatures by bull sharks has been documented in a few studies (Hueter and Tyminski 2002; Simpfendorfer et al. 2005; Wiley and Simpfendorfer 2007), and unusually low water temperatures (< 10 ºC) can clearly be lethal to small sharks (Dodrill 1977; Snelson and Bradley 1978). Healthy (non-moribund) immature bull sharks have been recorded from water temperatures as low as 15 ºC (Blackburn et al. 2007). Bull sharks in putative nursery areas appear to be limited to temperatures greater than 20 ºC (McCandless et al. 2007). This temperature range may be a migratory cue for immature bull sharks at higher latitudes, inducing them to seek warmer waters. This is supported by the seasonal distribution of bull sharks in the IRL (Figure 2-9). The locations of bull shark captures during winter months were almost exclusively limited to areas with mean water temperatures greater than 20 ºC during those months. These include Sebastian Inlet and the power plant outfall areas (Figure 2-2), the latter of which is thought to function as a thermal refuge (Snelson et al. 1984). Other lagoon species, including manatees (*Trichechus manatus latirostris*) utilize these same heated power plant outfalls as thermal refugia during winter (Deutsch et al. 2003; Laist and Reynolds 2005). This hypothesis is further supported by the year round presence of immature bull sharks in nursery areas with warmer mean temperatures than the IRL (Wiley and Simpfendorfer 2007).

The distribution of bull sharks in the IRL also appeared to be influenced by salinity to some extent. Even though the sharks occurred in freshwater, brackish water, and even hypersaline conditions (Table 2-6), a finding consistent with numerous bull shark studies (e.g., Snelson et al. 1984; McCandless et al. 2002; 2007; Simpfendorfer et al. 2005), there was evidence of preferences for salinities ranging from 10 – 29 ppt (Figure 2-10). YOY bull sharks tended to occur in lower salinity conditions than juveniles (Table 2-6). This pattern of size segregation was also observed by Simpfendorfer et al. (2005), and was thought to be associated with either the need for YOY sharks to avoid larger predators, or a physiologically driven preference to reduce the metabolic costs of osmoregulation. The bull shark's ability to osmoregulate in low salinity environments (e.g., Thorson et al. 1973; Pillans et al. 2005), and the use of such areas by immature sharks as nurseries, may give this species a distinct survival advantage as compared to other coastal species that are less euryhaline. The risk of predation by larger sharks is certainly reduced in such shallow, low salinity regions (Branstetter 1990; Simpfendorfer et al. 2005), the only natural predators being larger bull sharks (Snelson et al. 1984). More research is needed to address the salinity preferences of YOY and juvenile bull sharks in the IRL, and to understand the factors that influence salinity selection.

The influence of DO on elasmobranch distribution has been examined in a few studies, but has not been found to be a significant predictor of habitat use (Grubbs and Musick 2002; McCandless et al. 2002; 2007). Since DO is often not limited in shallow, well-mixed estuarine areas like the IRL, temperature and salinity tend to be more important factors for elasmobranchs in coastal environments (Matern et al. 2000; Grubbs and Musick 2002; Hopkins and Cech 2003; Simpfendorfer et al. 2005). It is therefore not surprising that there was no discernible pattern or correlation between bull shark distribution and DO in this study (Table 2-6; Figure 2-10). Certainly the DO levels commonly occurring in the IRL (Table 2-2) meet the minimum oxygen demands for bull shark respiration, although oxygen consumption experiments would more completely define these demands (e.g., Miklos et al. 2003).

While temperature, salinity, and DO are habitat conditions that are selected at least in part based on physiological requirements, other environmental factors including water clarity, bottom substrate, depth, and habitat complexity are less influenced by physiological tolerance than by biological factors such as predator avoidance or the distribution of prey. The prevalence of YOY and juvenile bull sharks in waters less than 2 m deep may be linked to the distribution of prey species that utilize productive seagrass beds, the dominant substrate at those depths (Gilmore 1995). Primary prey species such as stingrays, catfishes, and mullet are abundant in these shallow areas of the IRL (Snelson and Williams 1981; Snelson et al. 1989; Curtis unpubl. data). Prey density may also influence the bull shark’s frequent utilization of power plant effluents and the freshwater creeks near Melbourne in the IRL. The plumes of warm water flowing from the power plant outfalls may attract forage species, particularly during colder periods. The availability of structure such as piers, used as a shelter for a variety of lagoon species, may also draw bull sharks into low salinity areas like Crane Creek (Figure 2-6). Few studies have investigated the relationships between shark distribution and prey distribution, and those that have found mixed results (Heupel and Hueter 2002; Torres et al. 2006; Heupel et al. 2007; Heithaus 2004; 2007). Similar investigations in the IRL, a nursery area with few shark predators, may provide greater insights into the habitat selection patterns of bull sharks.

Recent fishery management needs in the U.S., including the need to define EFH for federally managed species (NMFS 1999), have driven renewed interest in the habitat associations and critical nursery habitats in all fishes, including sharks. Bull shark habitat utilization patterns in nursery areas have been described in several studies (Bass 1978; Snelson et al. 1984; Hueter and Manire 1994; Michel 2002; McCandless et al. 2002; 2007; Simpfendorfer et al. 2005; Wiley and Simpfendorfer 2007), and the findings of this study are largely consistent the results of these other studies. The bull sharks captured in the IRL were found in a variety of habitat types including ocean inlets, brackish and freshwater creeks, around piers, over seagrass flats, open sand and muddy bottoms, and in dredged channels. The physical characteristics of these habitats were also broad (Table 2-6), and represent a large portion of habitats available in the IRL (Table 2-2). The increased frequency of bull sharks in specific habitats, however, is suggestive of selection for such areas (Table 2-6; Figure 2-10).

Tag-recapture data provided limited insights into the movements of bull sharks in the IRL. Unfortunately, only four tagged sharks were recaptured over the span these studies; two of which were recaptured less than two weeks from their initial release. No sharks were recaptured outside of the study site to provide insights into large scale movements, and no sharks were recaptured in years subsequent to their release that might support evidence of philopatry (Hueter et al. 2005) or other information such as mortality rates. Other bull shark tagging studies have shown that large scale movements tend to be comparatively limited (Thorson 1971; Bass 1978; Hueter and Manire 1994; Kohler et al. 1998; Bullen and Mann 2000; Kohler and Turner 2001; Tremain et al. 2004; Brunnschweiler and Buskirk 2006). The maximum known tag-recapture distance for bull sharks is 643 km (Kohler and Turner 2001), and movements are largely limited to coastal and continental shelf waters (Kohler et al. 1998).

One of the earliest bull shark tagging efforts was conducted by Thorson (1971), who tagged 2,200 bull sharks in the Lake Nicaragua/San Juan River system in Central America. The 220 recaptured sharks offered definitive proof that the sharks in Lake Nicaragua were not landlocked as previously believed, but readily traversed the 175 km of the San Juan River to the

Caribbean Sea in as little as one day. Of 60 YOY and juvenile bull sharks tagged in Tampa Bay by Hueter and Manire (1994), seven were recaptured, including one YOY female that was tagged in July 1993 and recaptured in December 1993, 194 km south in San Carlos Bay. The other six sharks were recaptured no more than 5 km from their tagging locations after times at liberty of up to 113 days (Hueter and Manire 1994). Bullen and Mann (2000) reported similar findings for immature *C. leucas* tagged in South Africa between 1984 and 1999 (N = 254). Of 16 bull (= Zambezi) sharks recaptured, five were recaptured at the site of their initial release after times at liberty of 10 – 573 days. The maximum distance traveled was 539 km over 572 days (0.94 km/day). For comparison, the maximum distances traveled by the closely-related *C. limbatus* and *C. obscurus* are 2,146 km and 3,800 km, respectively (Kohler and Turner 2001). It appears that, in general, bull sharks show relatively high levels of site fidelity, punctuated by limited migratory movements up and down coastlines. IRL bull sharks may exhibit similar patterns, but acoustic, satellite, and archival tagging studies will help to better describe these seasonal, large scale movement patterns.

The consistent presence of immature bull sharks in the IRL, clearly demonstrates this estuary's importance to the northwestern Atlantic population of this species. However, how does the IRL compare with other known bull shark nursery areas in the region? Along the Atlantic and Gulf of Mexico coasts of the U.S., potential bull shark nursery areas appear to extend from North Carolina to Texas (McCandless et al. 2002; 2007), although the frequency of immature bull shark captures appears to taper off north of ML on the Atlantic coast (McCandless et al. 2002; 2007). Even though habitat use patterns are quite similar across these nursery areas, bull shark occurrence appears to be greater in the Gulf of Mexico than in Atlantic coast nurseries. Specifically, immature bull shark catches appear higher than the IRL's in the following nursery areas: the Florida Keys (Hueter and Tyminski 2007), Everglades National Park and Florida Bay (Wiley and Simpfendorfer 2007), the Ten Thousand Islands estuary (Michel 2002; Steiner et al. 2007); the Caloosahatchee River estuary (Simpfendorfer et al. 2005), Charlotte Harbor and Tampa Bay (Hueter and Tyminski 2007), the Mississippi River estuary and coastal Louisiana (Blackburn et al. 2007), and several bay systems in Texas (Jones and Grace 2002; Hueter and Tyminski 2007). Texas, in particular, appears to contain some very productive bull shark nursery areas, with over 3,500 bull sharks captured between 1975 and 1995, including 2,118 YOY individuals (Jones and Grace 2002). In this region, YOY and juvenile bull sharks were present between March and December in temperatures of 18.6 – 33.5 ºC, and in salinities of 0 – 51 ppt. Consistent with evidence of overfishing, CPUE of bull sharks declined significantly over the course of this study (Jones and Grace 2002). Bull shark nursery areas may also extend along the coast of Mexico, but no data is currently available from this region. If absolute numbers of bull sharks from these areas can be used as an index of nursery area productivity, then Gulf of Mexico nursery areas likely contribute more recruits than the IRL to bull shark stocks in the northwest Atlantic. In fact, given the results of these other studies, the IRL may represent the northern/eastern extent of bull shark nursery areas for the region.

Although bull sharks may not be as abundant in the IRL as other nursery areas (McCandless et al. 2007), the lagoon may still serve as an important contributor to adult bull shark populations. The relative absence of large sharks (i.e., predation pressures) in the IRL in conjunction with its abundant prey resources may supply the ideal circumstances for a nursery area, in terms of maximizing survival. Although empirical mortality estimates are lacking for juvenile bull sharks, the mortality of juvenile sharks of other species that must remain in more saline waters appears to be relatively high (Heupel and Simpfendorfer 2002; Bush and Holland

2003). Bull sharks in the IRL and other enclosed, low salinity areas, may be relatively free from predation, and have more freedom to forage, thereby increasing energy intake to maximize their growth rates and overall fitness (Heithaus 2007). Conversely, the bull shark's proximity to coastal development, habitat alteration and degradation in inshore regions like the IRL, may expose young sharks to adverse water quality conditions, or reduced suitable habitat for foraging. The impacts of habitat loss and water pollution on shark nursery areas have received very little attention, even though such anthropogenic impacts could negate the beneficial functions of nearshore nursery areas. Bull sharks in intracoastal regions are documented to bio-accumulate high levels of contaminants (Adams and McMichael 1999; Johnson-Restrepo et al. 2005), but the possible effects of such contamination remains unknown. Further research is needed to address the relative productivity of different shark nurseries, and to determine if certain nursery areas have become compromised by detrimental habitat impacts. Given the current status of large coastal shark stocks, protection of vulnerable nursery areas should be a high priority.

Table 2-1. Summary of IRL bull shark data sources used for analysis, 1975 to 2005.

Source	Sharks	Locations	TL Range (cm)	Years	Gear
Dodrill (1977)	19	19	70-250	1975-1977	Hook
Snelson et al. (1984)	150	31	73-249	1975-1979	Gillnet
Schmid and Murru (1994)	5	1	61-68	1985	Hook
FWC - FIM	40	27	72-144	1991-2001	Gillnet
UCF/KSC Turtle Bycatch	52	4	130-200	1996-2005	Gillnet
Personal Communications	34	8	70-250	2003-2005	Hook, Observation
Current Study	90	90	66-130	2003-2005	Hook, Observation
Total	390	180	61-250	1975-2005	

Table 2-2. Range of environmental parameters sampled in the IRL by sub-region, during the current study, 2003 to 2005.

Parameter	ML	NIR	MS
Depth (m)	0.4 - 6.0	0.4 - 4.0	0.4 - 3.4
Temperature (ºC)	20.3 - 31.9	12.1 - 37.0	17.4 - 33.4
Salinity (ppt)	20.6 - 36.6	16.4 - 29.4	0.7 - 31.1
Dissolved Oxygen (mg/L)	2.4 - 9.9	3.7 - 10.2	3.2 - 8.3
Secchi Depth (m)	0.8 - 1.5	0.2 - 3.0	0.2 - 1.5

Table 2-3. Catch of bull sharks and gillnet effort (NetDay24) in the IRL by sub-region and season from Snelson et al. (1984), 1976 to 1979.

Region	ML		NIR	
	NetDay24	Sharks	NetDay24	Sharks
Winter	25.5	0	34.5	0
Spring	102.4	7	39.8	23
Summer	160.4	21	61.3	16
Fall	131.0	24	46.2	32
Total	419.3	52	181.8	71

Table 2-4. Catch of bull sharks and hook gear effort (hh = hook hours) in the IRL by sub-region and season during the current study, 2003 to 2005.

Region	ML		NIR		MS	
	hh	Sharks	hh	Sharks	hh	Sharks
Winter	7.0	0	565.3	0	0.0	0
Spring	2.0	0	572.7	7	210.7	3
Summer	383.8	4	685.5	3	184.0	12
Fall	472.2	0	116.3	0	0.0	0
Total	865.0	4	1939.7	10	394.7	15

Table 2-5. CPUE of bull sharks in the IRL by sub-region and season from Snelson et al. 1984 (NetDay24), and the current study (hh).

	Snelson et al. (1984)		Present Study		
	ML	NIR	ML	NIR	MS
Winter	0.00	0.00	0.00	0.00	0.00
Spring	0.07	0.58	0.00	1.22	1.42
Summer	0.13	0.26	1.04	0.44	6.52
Fall	0.18	0.69	0.00	0.00	0.00
Total	0.12	0.39	0.46	0.52	3.80

Table 2-6. Summary of habitat use by bull sharks in the IRL by life stage, 1975 to 2005.

Life Stage	N		Temperature (°C)	Salinity (ppt)	Oxygen (mg/L)	Depth (m)	Secchi Depth (m)
YOY	41	Mean	30.4	17.0	4.8	1.0	0.9
		Range	27.9 - 33.5	1.6 - 34.2	3.2 - 9.0	0.2 - 3.4	0.3 - 1.1
Juvenile	71	Mean	29.7	21.6	6.0	1.0	1.0
		Range	20.0 - 37.0	1.2 - 31.1	3.8 - 7.9	0.3 - 3.0	0.3 - 1.5
Total	136	Mean	29.7	23.2	5.5	1.0	0.9
		Range	20.0 - 37.0	1.2 - 42.0	3.2 - 9.2	0.2 - 3.4	0.3 - 1.5

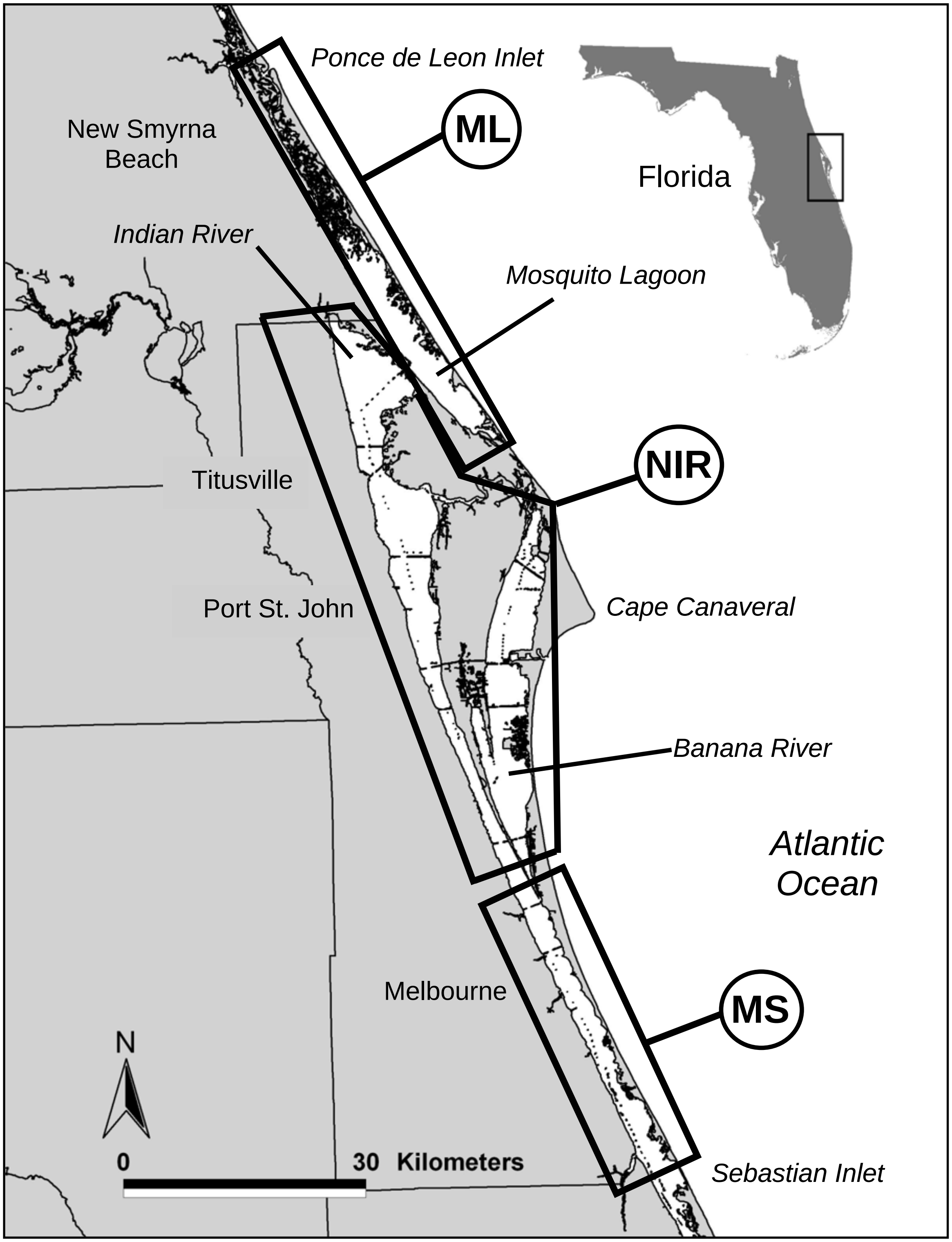

Figure 2-1. Chart of the Indian River Lagoon, FL study site. The boxes delineate the three lagoonal sub-regions described in the Methods: ML = Mosquito Lagoon; NIR = northern Indian River/Banana River; MS = Melbourne – Sebastian area.

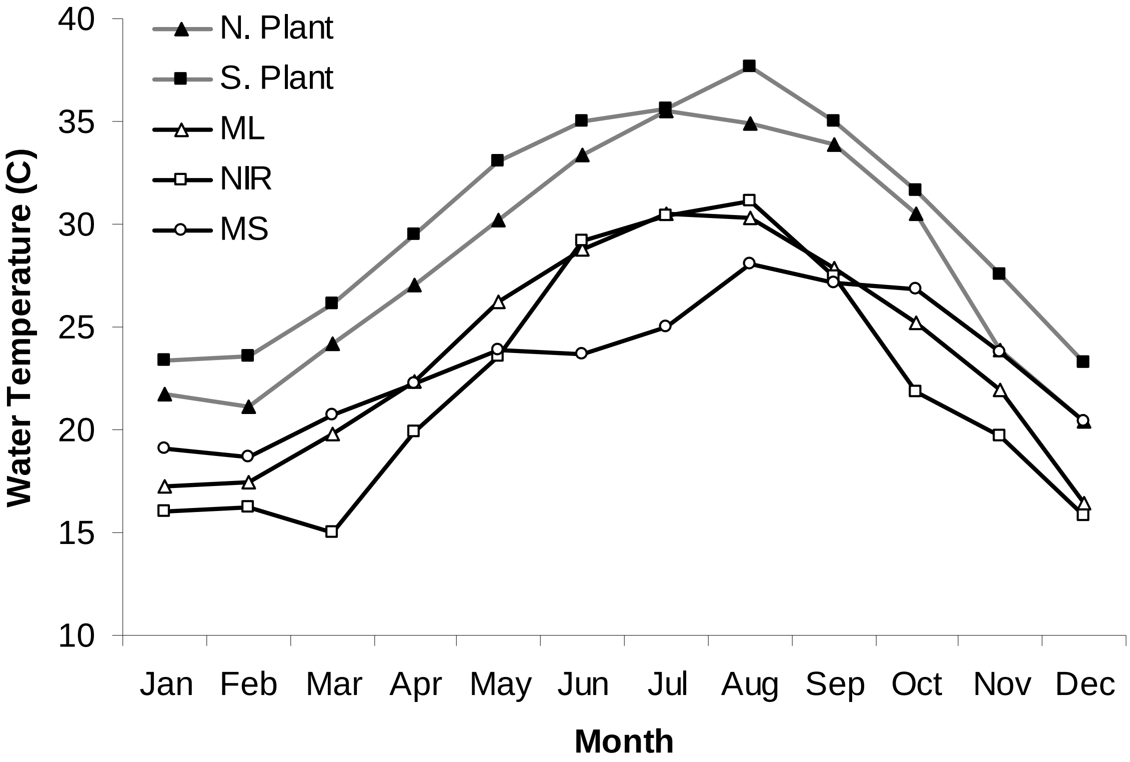

Figure 2-2. Mean monthly water temperatures (ºC) from the three sub-regions of the IRL study site and two power plant outfalls near Port St. John, 2004-2005. Sources: ML, Haulover Canal (USGS 2007); NIR and N. Plant, Mr. W. Baker (Reliant Energy, unpubl. data); MS, Sebastian Inlet (Florida Institute of Technology); and S. Plant, Mr. R. Hix (Florida Power and Light, unpubl. data).

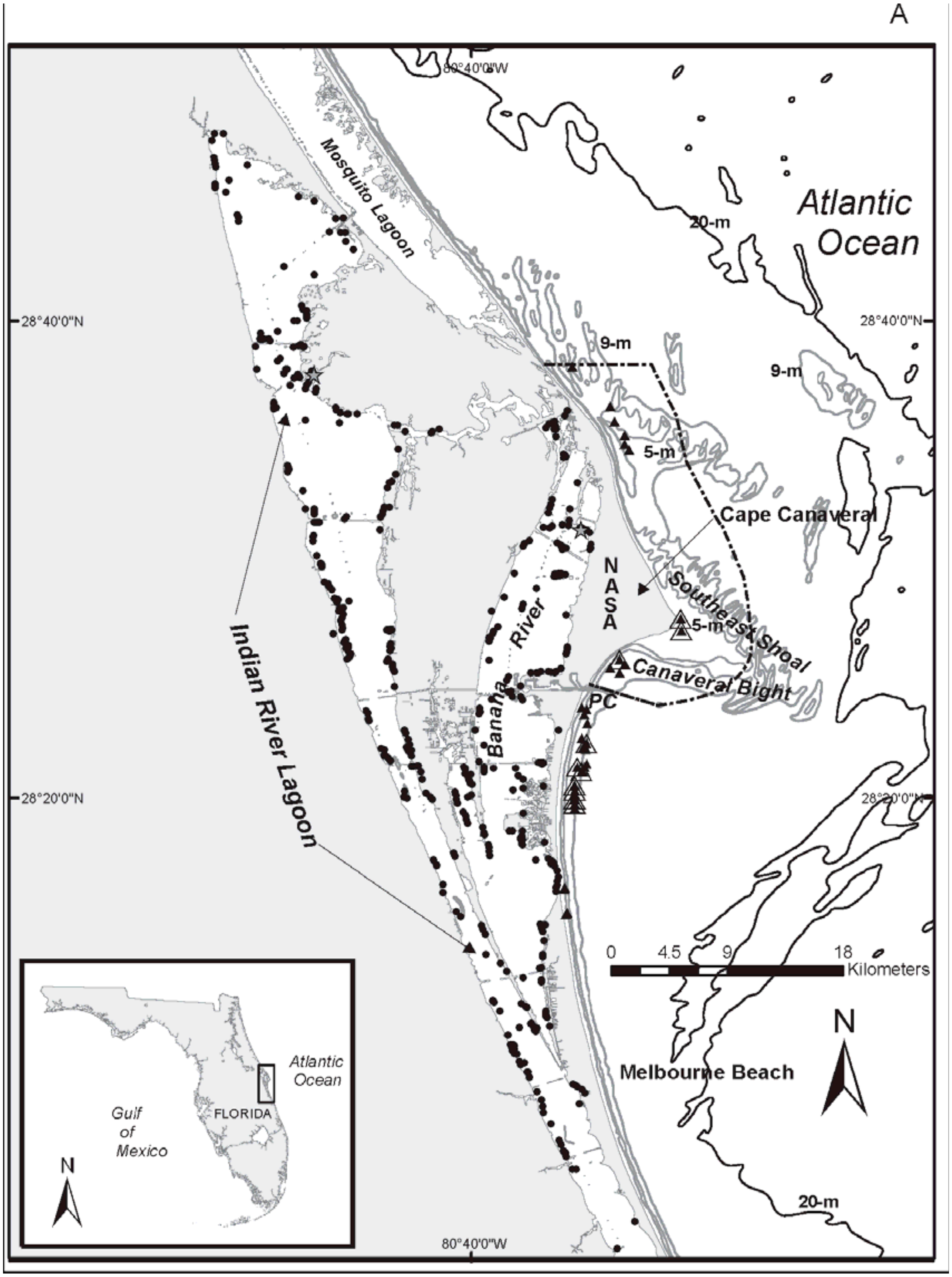

Figure 2-3. Distribution of gillnet sampling locations (N = 1,133) in the IRL carried out by FWC, 1990 to 1997. The dashed line delineates the boundary of the NASA Security Zone. Circles represent IRL gillnet sets. Triangles represent nearshore gillnet sets. Stars represent locations of fixed-station gillnet sets. Large open triangles represent capture locations of *Sphyrna lewini*. Taken from Adams and Paperno (2007), with permission.

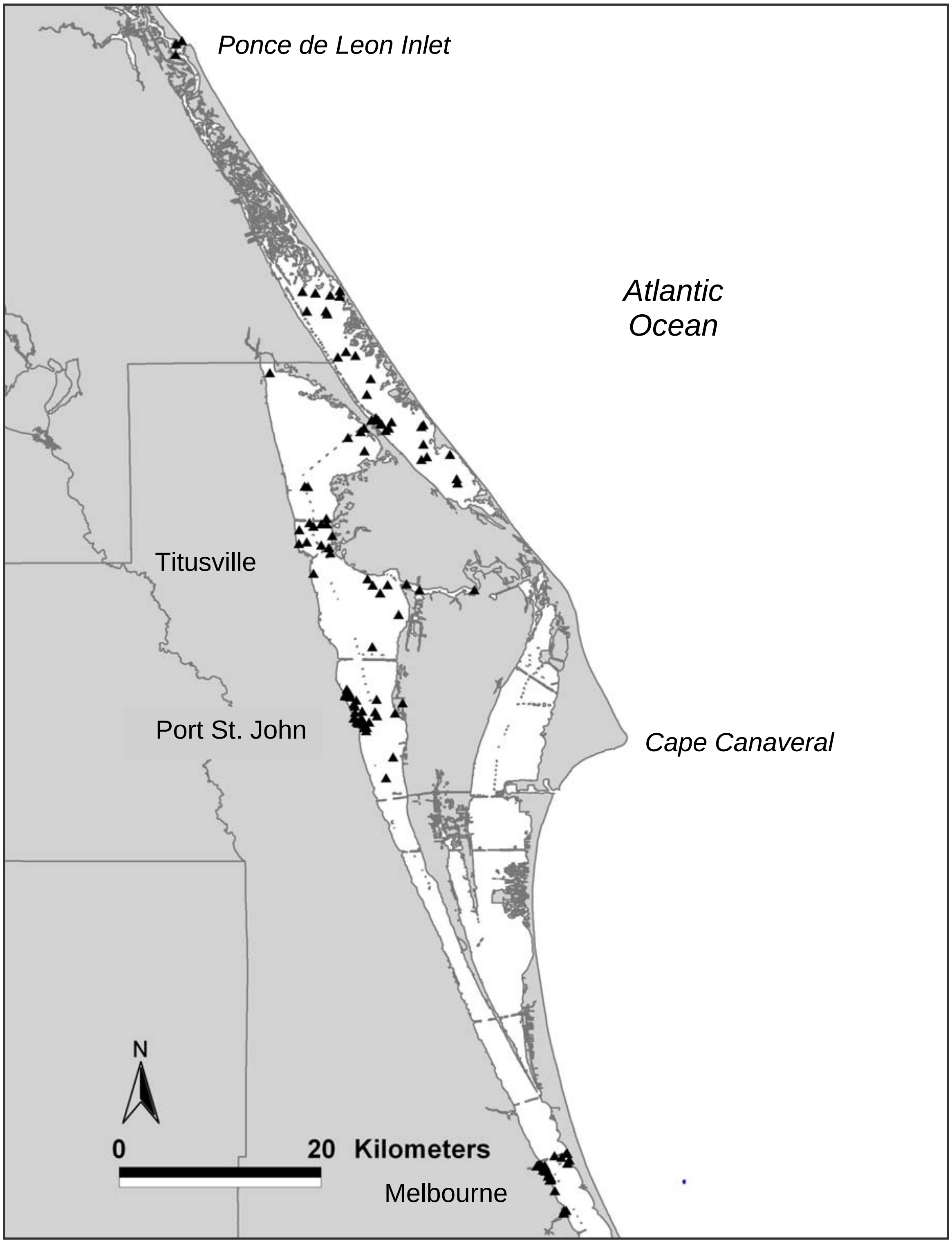

Figure 2-4. Distribution of hook and line sampling locations (N = 155) in the IRL during the current study, 2003 to 2005.

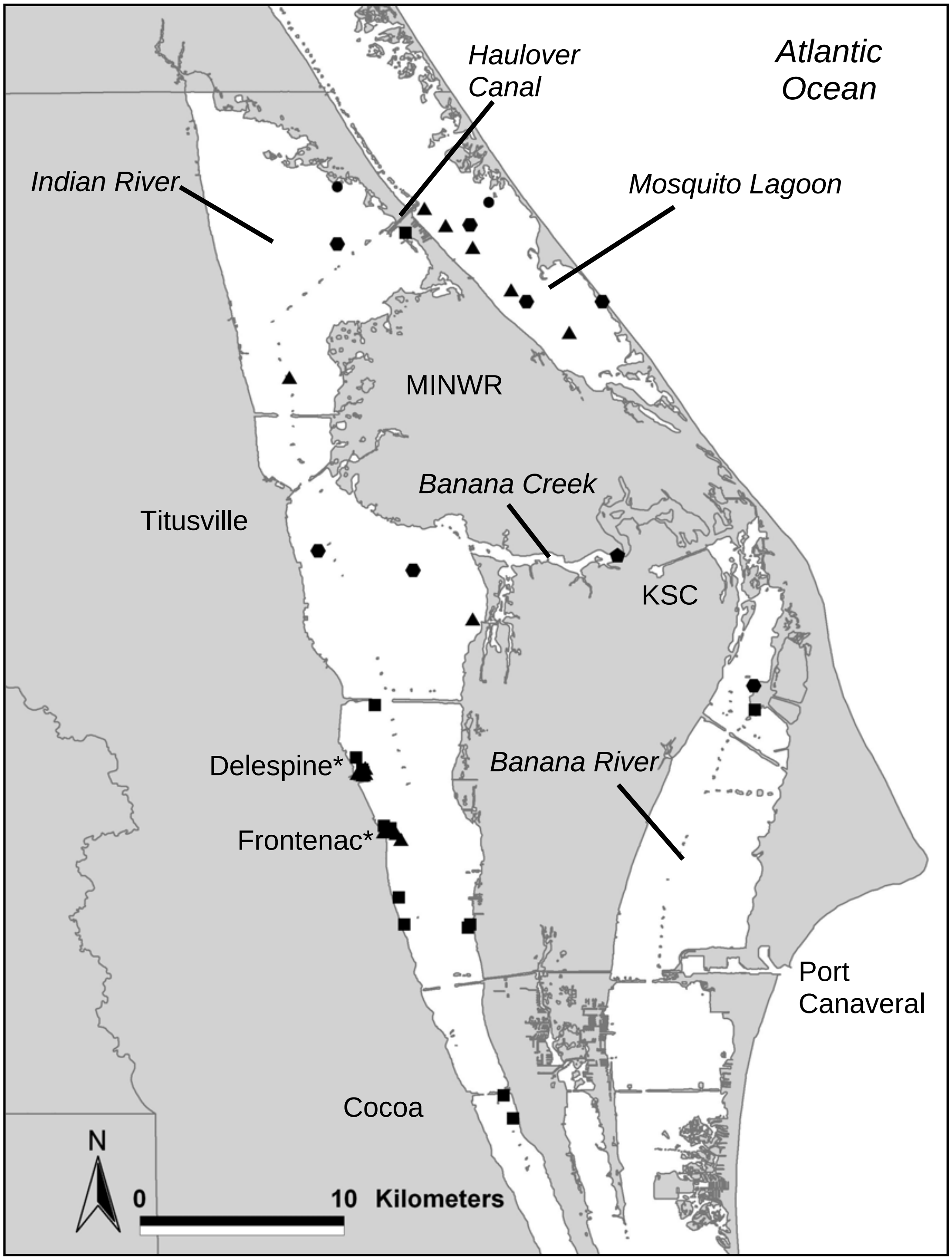

Figure 2-5. Locations of bull shark captures and observations in ML and the NIR, 1975 to 2005. Pentagons = Dodrill (1977); hexagons = Snelson et al. (1984); squares = FWC; circles = KSC; and triangles = present study. Note: many of the points represent multiple shark captures. *Indicates the locations of power plants.

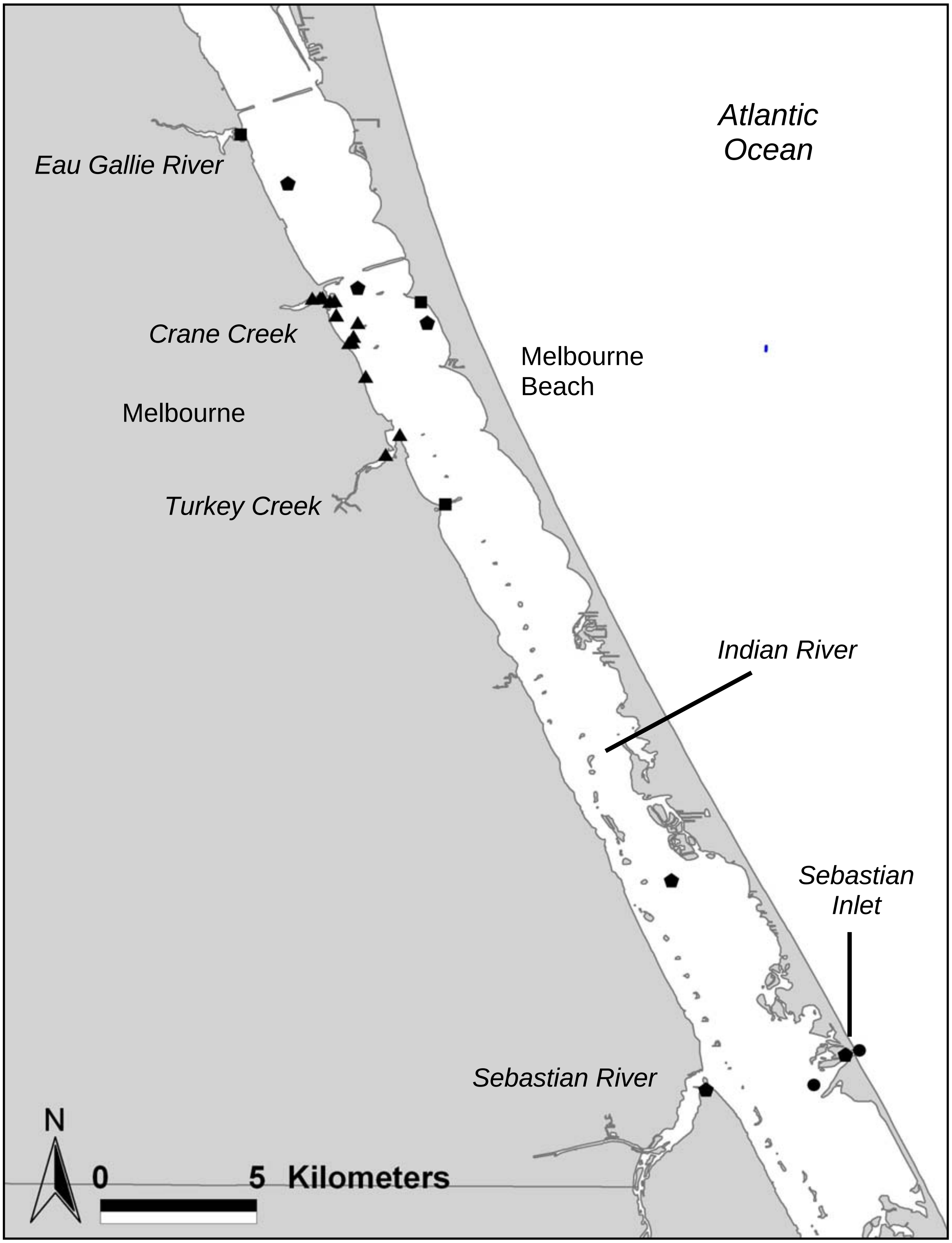

Figure 2-6. Locations of bull shark captures and observations in the MS sub-region, 1975 to 2005. Pentagons = Dodrill (1977); squares = FWC; circles = UCF; and triangles = present study. Note: many of the points represent multiple shark captures.

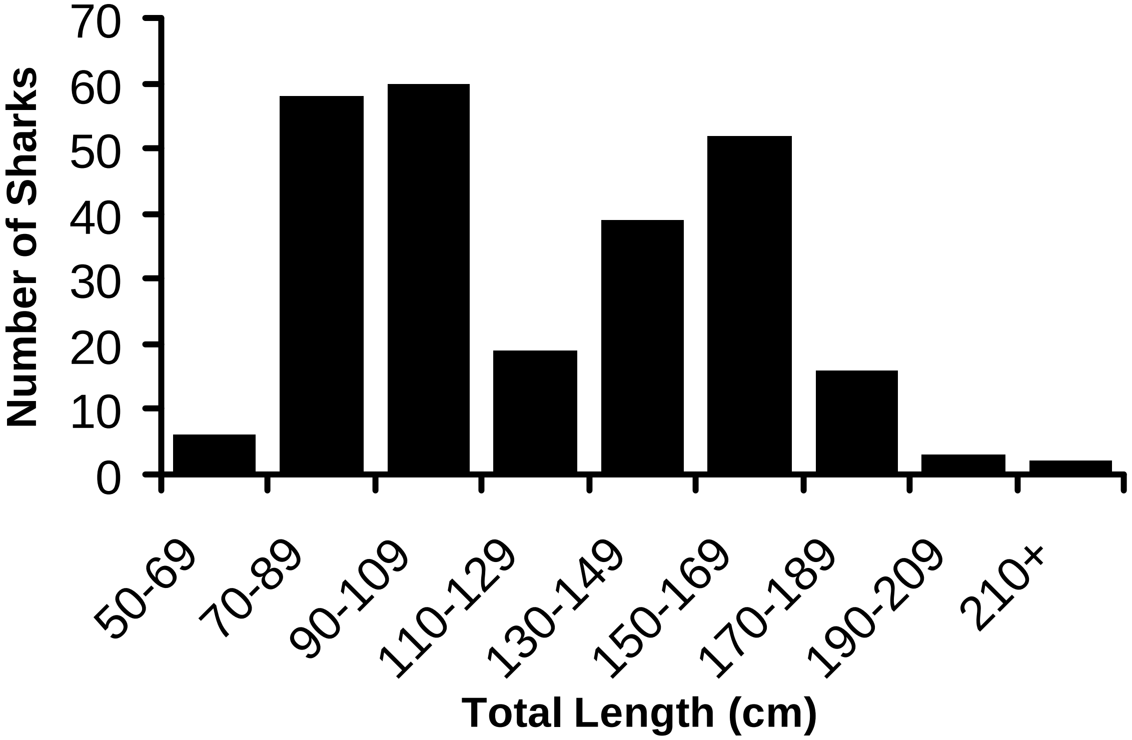

Figure 2-7. Length frequency of bull sharks captured in the IRL, 1975 to 2005 (N = 256).

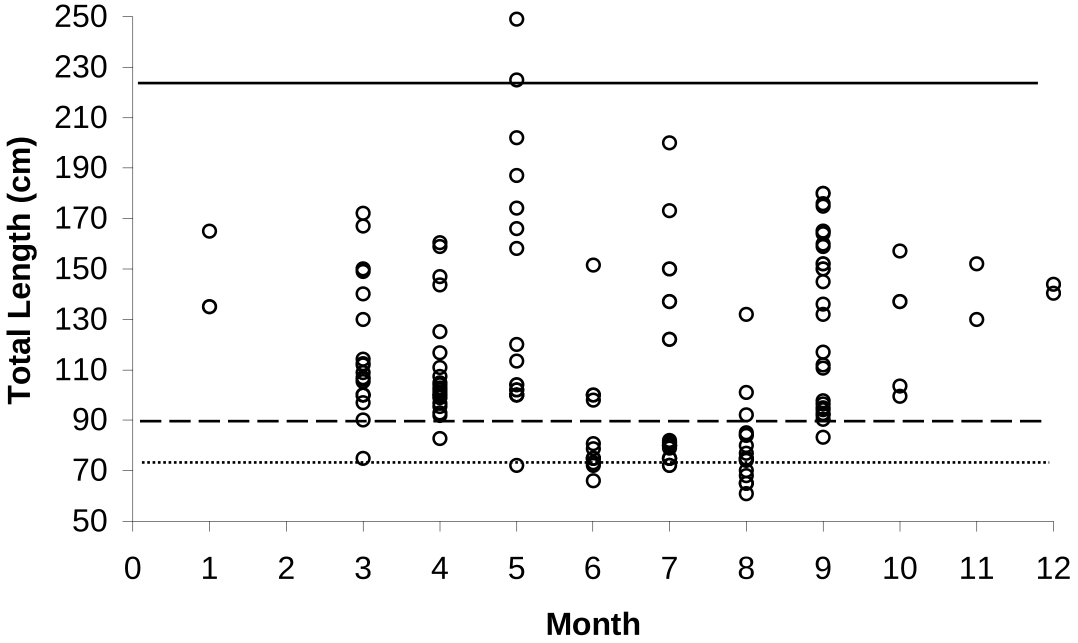

Figure 2-8. Lengths of captured bull sharks from the IRL by month, 1975 to 2005. The dotted line indicates the approximate length dividing neonate from YOY sharks, the dashed line indicates the approximate length dividing YOY and juvenile sharks, and the solid line indicates the approximate length at maturity for female bull sharks.

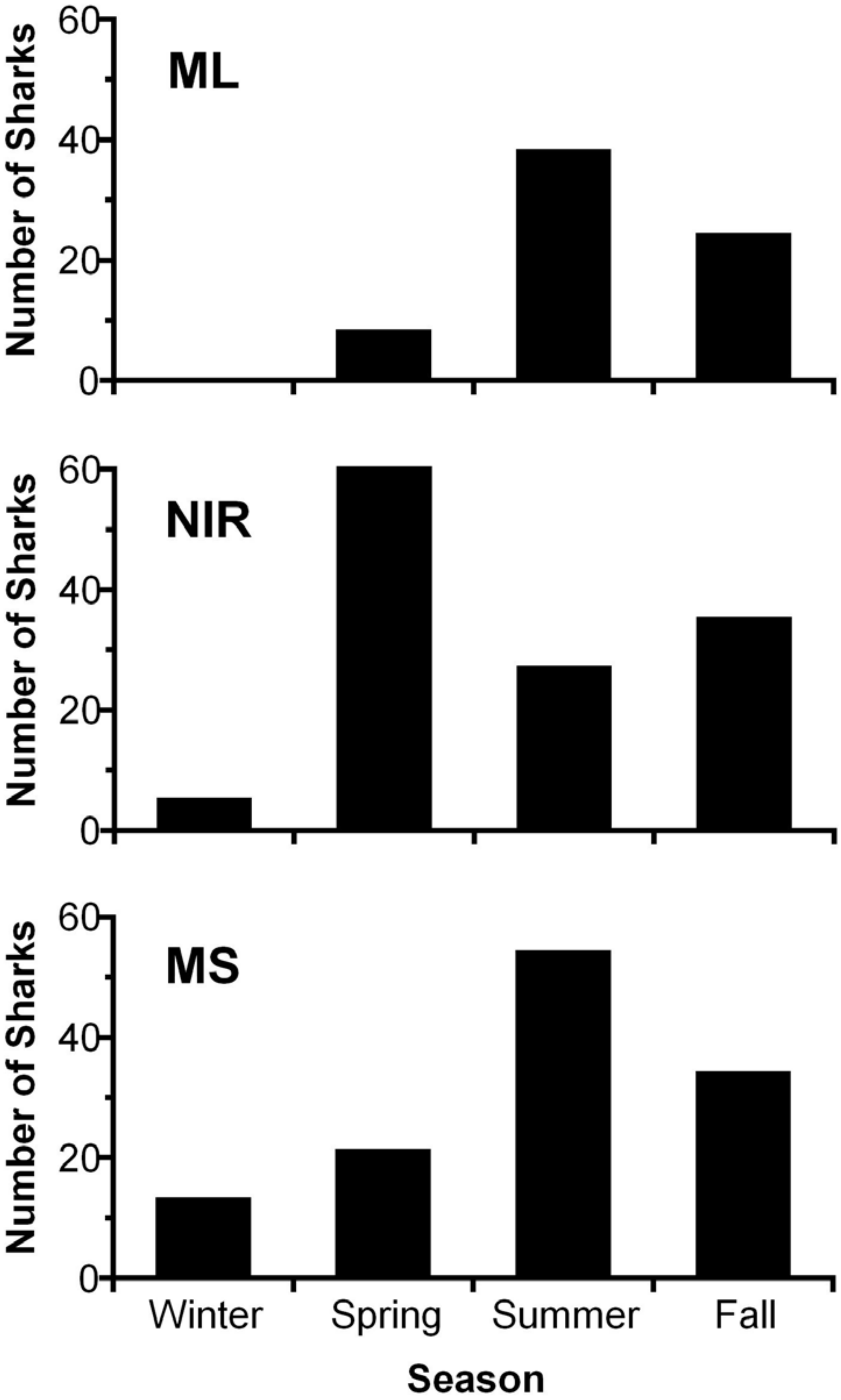

Figure 2-9. Frequency of bull shark captures (N = 319) in the IRL by sub-region and season, 1975 to 2005.

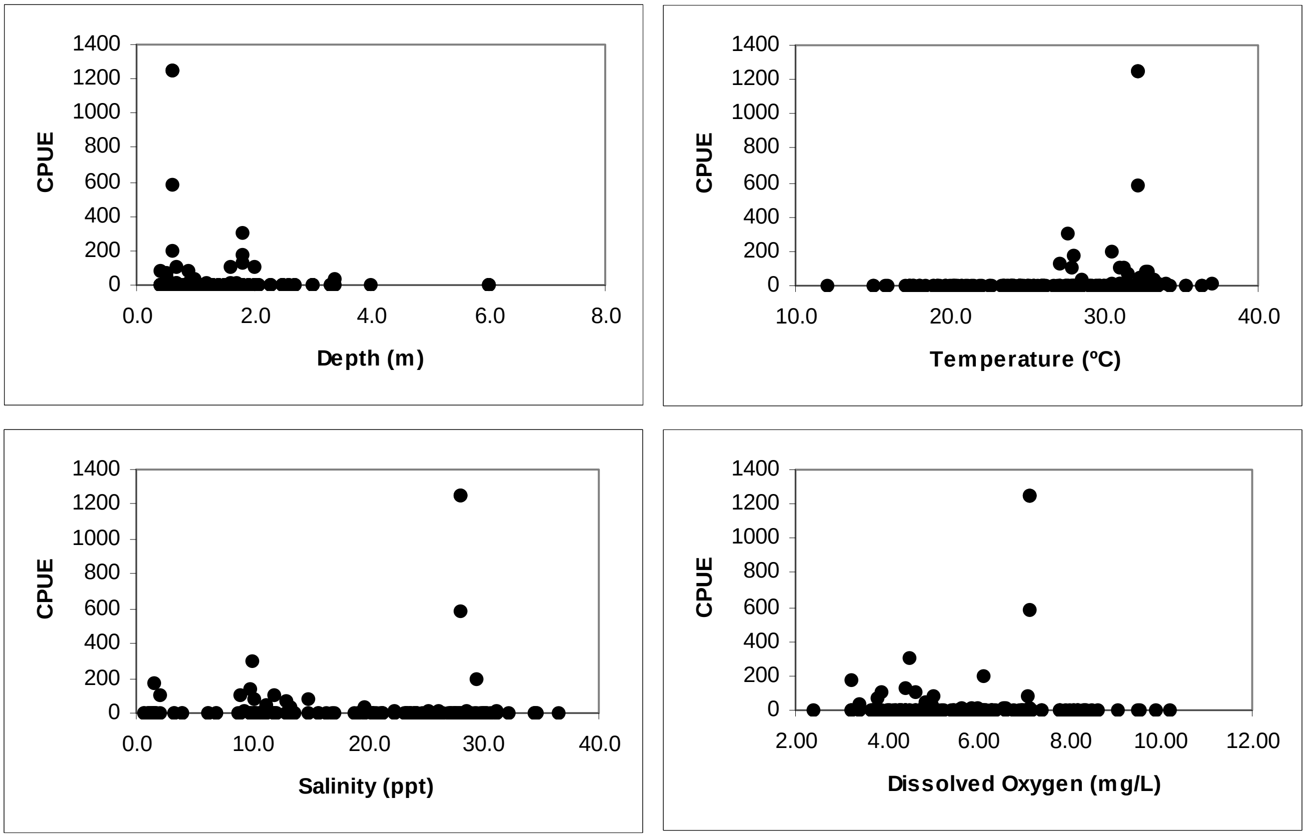

Figure 2-10. CPUE of bull sharks versus habitat parameter gradients in the IRL from the current study, 2003 to 2005.

CHAPTER 3
SHORT-TERM MOVEMENTS AND HABITAT USE OF YOUNG-OF-THE-YEAR AND JUVENILE BULL SHARKS

Introduction

Ultrasonic telemetry and active tracking of sharks have been useful tools for determining short-term movements (Nelson 1978; Nelson 1990), diel cycles of migration (e.g., Sciarotta and Nelson 1977; Tricas et al. 1981), home range (e.g., Holland and Wetherbee 1999; Morrissey and Gruber 1993a), habitat use and preference (e.g., Morrissey and Gruber 1993b; Heithaus et al. 2002), horizontal and vertical swimming behavior (e.g., Carey and Scharold 1990; Klimley et al. 2002), physiology (e.g., Carey et al. 1982; Lowe and Goldman 2001), and social interactions (Klimley and Nelson 1984). Traditionally, shark nursery areas and habitat use have been delineated through the use of catch rates from fishery-independent sampling (e.g. Snelson and Williams 1981; Castro 1993; Simpfendorfer and Milward 1993; Merson and Pratt 2001; McCandless et al. 2002, Simpfendorfer and Heupel 2004; Chapter 2). Acoustic telemetry has also been used to help identify and delineate shark nursery areas, and shark habitat use within these regions (Holland et al. 1993; Wetherbee et al. 2001; Heupel and Hueter 2001; Simpfendorfer et al. 2002; Steiner 2002; Rechisky and Wetherbee 2003, Simpfendorfer and Heupel 2004). This method has been used on a variety of shark species in widespread geographic locations, environments, and circumstances (for reviews see Nelson 1990; Sundström et al. 2001). The results garnered from these studies are not only proving to be useful for fisheries management, but are also providing novel behavioral insights that are difficult to obtain with other methods.

Most of the information known about the movements of juvenile and adult bull sharks has been derived from studies using externally attached conventional tags (Thorson 1971; Hueter and Manire 1994; Kohler et al. 1998; Kohler and Turner 2001; Tremain et al. 2004; Chapter 2).

These studies were important in providing some initial insights into movements and migrations, but are generally coarse in scale. These studies demonstrate that, in general, bull sharks do not migrate as widely as many other carcharhinid sharks, with the maximum reported tag-recapture distance being 643 km (Kohler and Turner 2001). In addition, while their distribution and migrations appear primarily limited to neritic waters (Kohler et al. 1998), lengthy excursions into riverine systems have been observed (e.g., Thomerson et al. 1977). A tag-recapture study by Thorson (1971) definitively described how bull sharks reached Lake Nicaragua from the Caribbean Sea via the San Juan River, previously considered a physical barrier to the sharks. Because of the limited data on individual movements, such methods of tagging are unable to provide insights into fine-scale movements on a short-term temporal scale. Telemetry is one of the only methods to effectively acquire such information.

Despite their relative abundance in a variety of coastal locations worldwide, their importance in many fisheries, and their notoriety for attacks on humans, movements of bull sharks have only been examined along coastal areas in southwest Florida (Steiner 2002). With their inshore distribution, the bull shark population present in the IRL is a particularly good candidate for an acoustic tracking study. Their seasonal occurrence and dietary habits in this region were described by Snelson et al. (1984) (also see Chapter 2). However, little is known about their daily movements and activities, home ranges, or patterns of habitat use in the IRL region. The goal of this chapter is to investigate such activities and add to the growing knowledge of the behavior of bull sharks in their young life stages. Specifically, this study set out to estimate the size of bull sharks’ daily activity space, their rates of movement, describe fine scale habitat use, and investigate any potential rhythmic diel patterns of movement.

Methods

Tagging and Tracking

Immature bull sharks were captured either with rod and reel or on a 50-hook bottom longline set for periods of 65 min or less, with a 12/0 Mustad circle hook baited with cut pieces of baitfish (*Mugil* spp., *Alosa* spp., *Dorosoma petenense*, *Elops saurus*, *Arius felis*, *Dasyatis* spp., *Caranx* spp.) (see Chapter 2, Methods). Once captured, sharks were brought aboard the boat, measured to the nearest centimeter (FL and TL), and then tagged through the ceratotrichia of the first dorsal fin with a NMFS Cooperative Shark Tagging Program blue or yellow rototag (Dalton Co., UK) (Kohler et al. 1998). Ultrasonic transmitters (Vemco V16-4H and V16-6H, 51-81 kHz) with pulse periods of 1.5 seconds and a minimum battery life of over 150 days were externally attached to sharks by a tether of monel wire which was wrapped to the stem of the rototag. The transmitter trailed between the first and second dorsal fins of the shark as it swam. The wire would eventually unwrap or corrode and drop from the shark. Transmitters weighed less than 1% of the sharks' body weight in air, and based on visual observations, did not appear to hinder the sharks' normal swimming behavior. Only sharks in good condition at the time of release were tracked. The capture, tagging, and release process normally took less than 5 min.

Once released, the transmitter signal was tracked using an acoustic receiver (Vemco VR60) and directional hydrophone (Vemco VH10). Range tests revealed a maximum detection range of approximately 500 m, but this varied depending on transmitter frequency, ambient noise, depth, temperature, water clarity and salinity profile. During each track, geographic positions were manually recorded at 15-minute intervals using a hand-held GPS (Garmin eTrex Legend, Olath, KS, accurate to 3 m). Water temperature, salinity, and dissolved oxygen concentration (DO) were recorded every 1-2 hours during each track using a water quality meter (YSI 85, Yellow Springs, Ohio, USA), and water clarity was measured using a secchi disk (during daylight only). The presence of known bull shark prey species (Snelson et al. 1984) was also noted when visually observed. The tracking vessel was preferably kept at a distance of 50 – 100 m from the shark, but at times when a shark entered very shallow water (< 0.5 m), it had to be followed much more closely because of transmitter signal attenuation. Efforts were taken to minimize interference with the sharks' movements, and the boat's engine was turned off whenever feasible in shallow water. The boat followed the course of the sharks' movements during tracking, with the assumption that the boat location, as determined by the handheld GPS, represented the location of the shark. Those GPS coordinates were then used in subsequent spatial analyses. An additional bull shark had a long-life (641-day) coded transmitter (Vemco V16-4H, 69 kHz, pulse period 30 – 79 seconds) surgically implanted into its body cavity. The presence/absence of this individual was monitored by moored acoustic listening stations (Vemco VR2, detection range approximately 800 m) placed near the outfalls of the two power plants in the northern IRL.

Juvenile and YOY bull sharks were actively tracked in the IRL between August 2003 and August 2005**,** primarily during the summer months when the sharks were more abundant (Snelson et al. 1984; see Chapter 2). Tracking was conducted in three distinct regions of the lagoon: in the southern portion of Mosquito Lagoon (N=1), in the Indian River near Port St. John (N=2), and in the Indian River near Melbourne (N=7) (Figure 2-1). All of these areas had similar depth and substrate characteristics, with shallow areas (<1 m) of seagrass (*Thalassia testudinum* and *Syringodium filiforme*) and sand close to shore. Deeper channels (3 – 4 m in depth) and segments of the intracoastal waterway (ICW) were present in the mid-lagoon, further away from shore. The tracks that occurred in the Port St. John area were in the vicinity of two large power-generating plants that discharge warm water as effluent into the lagoon year-round

(Figure 2-5). The temperature regimes found at these locations were therefore not homogeneous with the rest of the lagoon system. The Melbourne area is also different from the other regions in that a series of small freshwater creeks empty into the lagoon from its western shoreline (Figure 2-6), often reducing the salinity of the lagoon during rainfall events, and providing uncommon freshwater (<10 ppt) habitats for the sharks.

Data Analysis

The manually recorded 15-min GPS position fixes were plotted using ArcView 3.2 GIS software. The total distance traveled by each shark was calculated as the sum of the distances between each 15-min track segment. The rate of movement (ROM) over ground, defined as the distance between two successive positions divided by the time taken to travel that distance, was calculated to provide an indication of swimming speed (e.g. Klimley et al. 2002; Kelly et al. 2006). In active-tracking studies on fishes, ROM is used as a measure of swimming speed, though is considered an underestimate of true swimming speed (Sundström et al. 2001). It can also be used as an indicator of activity level, with heightened ROM being suggestive of migrating or foraging behavior (Klimley et al. 2002; 2005), and is useful for detecting diel patterns of activity (Nelson 1990). The mean ROM of YOY and juvenile sharks were compared, as were the mean ROM between day and night by using descriptive statistics.

The activity space, or size and shape of the area used by telemetered sharks, was analyzed using two methods: the minimum convex polygon (MCP) method (Odum and Kuenzler 1955), and a fixed-kernel utilization distribution (UD) method (Worton 1989), using the Animal Movement Analysis extension for ArcView 3.2 (Hooge et al. 1999). Core area was defined as the area of the 50% UD, and total activity space was defined as the area of the 95% UD (e.g. Cartamil et al. 2003, Heupel et al. 2006). The term activity space rather than home range is most often used to define the area utilized by sharks during manual tracking, because the duration of tracking is rarely long enough to encompass the entire home range of the individuals tracked (Sundström et al. 2001).

To describe the shape of the activity space of each shark, an index of eccentricity (ECC), was calculated using the formula (3-1):

$$ECC = L/W \tag{3-1}$$

where L is the maximum length of MCP, and W is the maximum width of the MCP area. When ECC = 1, the activity space would be considered symmetrical. When ECC > 1, the activity space would be considered more elongate and asymmetrical (Rechisky and Wetherbee 2003).

A measure of site attachment, the linearity index (LI), was also calculated for each shark track (Bell and Kramer 1979; Rechisky and Wetherbee 2003) (3-2):

$$LI = (F_n - F_1)/D \tag{3-2}$$

where F_n is the final position of the shark, F_1 is the first position of the shark, and D is the total distance traveled by the shark. If LI = 1, the movements of the shark would be considered linear, with little reuse of area within the activity space. A LI near zero suggests site fidelity.

To summarize the directionality of observed movements, circular histograms were plotted using circular statistics software (Oriana 2.00, Kovach Computing Services). Additionally, the vector of angular concentration (r) and the circular standard deviation (*csd*) were calculated for each track (Zar 1984). Values of r range from 0 to 1, where 0 indicates that bearings are uniformly distributed, and 1 indicates that all heading are concentrated in the same direction. A doubling of angles procedure was used for diametrically bimodal data to facilitate the calculation of *r* and *csd* which could otherwise not be calculated (Zar 1984). Rayleigh's *z* test was used to test if *r* was statistically different from a uniform distribution, therefore implying directional movement (e.g., Klimley et al. 2005). Due to low sample size in some tracks, circular statistics were only estimated for tracks longer than 10 h. Due to the largely restricted water flow within the IRL, tidal flow was not considered to be a factor in this study, and therefore was not assumed to influence directionality.

Descriptive statistics were used to examine patterns of habitat use for the following parameters: depth, water temperature, salinity, DO, and secchi depth. Simple linear correlation analysis was also used to describe the relationship between bull shark activity space and salinity. Bottom substrate type was described qualitatively by visual observations.

Results

Ten immature bull sharks were manually tracked in the IRL between August 2003 and August 2005 (Table 3-1). All of the sharks were tracked between the months of March and September. Five of the sharks were YOY (60-71 cm FL), and five were juveniles (79-94 cm FL). The duration of tracking ranged from 1.5 to 23 h total for each shark (mean ± 1 sd = 13.4 ± 8.7 h, N=10), yielding a total of 134 tracking hours for all sharks combined. A total of 242 positions were recorded for YOY sharks, and 243 positions were recorded for juvenile sharks. Many of the tracks, however, were performed intermittently in separate tracking periods spanning days to weeks. Characteristics of the patterns of movement of the sharks are summarized in Table 3-2. Due to the low sample size, and the lack of independence in observations from each individual shark, tests of statistical significance could not be performed to compare data from sets of tracks.

Bull Shark Tracks

Shark B1

The first bull shark tracked (B1), a YOY female (71 cm FL), was captured and tagged on 22 August 2003 at 15:15 hrs in Mosquito Lagoon (Figure 3-1). She was continuously tracked until 02:30 hrs, 23 August, when lightning storms forced us to abandon the track. The shark was relocated at 08:15 hrs, 23 August, and tracked for another 5.5 h until 13:45 hrs. Ten days later, on 2 September, the shark was once again relocated at 10:30 hrs in the vicinity of the previous track, and tracked for an additional 5 hours, yielding a total of 22.5 h of total tracking time over an 11-day period.

Shark B2

Bull shark B2 was captured and tagged on 11 March 2004, in the Indian River just south of the Florida Power and Light (south) power plant in Frontenac (Figure 3-2). This shark was a juvenile male, measuring 94 cm FL. The shark's tag signal was lost upon release at 15:15 hrs, but relocated at 10:30 hrs, 12 March, directly in front of the power plant outfall. A seasonal manatee closure zone surrounding the outfall area prevented us from following the shark in the normal tracking method, but the shark's positions were calculated by recording the compass bearing from the boat to the shark, and the signal strength identified by the acoustic receiver which could be used as a proxy of distance (based on transmitter range tests). The shark was continuously tracked in this manner for 15.5 h, until 02:00 hrs, 13 March. The shark was again relocated at 05:45 hrs, 13 March, and tracked until 13:00 hrs when the signal was lost. Six days later on 19 March, B2 was once again relocated in the same location, and tracked for an additional 2 h from 10:00-12:00 hrs. Subsequently, on 3 April, the transmitter signal was detected back near the tagging location, but was immobile, and presumably detached from the shark. This shark was tracked for a total of 23 h over an 8-day period.

Shark B3

This juvenile female bull shark, 82 cm FL, was captured and tagged at 16:00 hrs on 7 May 2004 near the outfall of the Reliant (north) power plant, in the Indian River near Port St. John. She was tracked continuously for 2 h, until 18:00 hrs when the signal was lost due to deteriorating sea surface conditions (Figure 3-3). The shark was never relocated.

Shark B4

Bull shark B4, a 79 cm FL juvenile female, was captured and tagged at 14:19 hrs on 10 June 2004, off the mouth of Crane Creek in Melbourne (Figure 3-4). The transmitter signal was lost almost immediately, but the shark was relocated at 07:45 hrs the following morning inside Crane Creek (Figure 3-4). The shark was then tracked continuously until midnight, and then again relocated at 08:45 hrs, 12 June. Tracking ended at 14:00 hrs, 12 June, yielding a total of 18.75 h of tracking over a 48-h period.

Shark B5

Bull shark B5 was an 82 cm FL juvenile female that was captured at 11:45 hrs, 17 May 2005, inside Crane Creek (Figure 3-5). Upon release, the shark swam out of the creek and into the lagoon where the transmitter signal was lost, and could not be immediately relocated. The shark was relocated near its tagging location in the creek one week later on 24 May, at 09:30 hrs, and tracked continuously for 12.5 h. By 17:45 hrs the shark had moved over 1 km south of the creek, but at approximately 18:00 hrs the shark began to make a directed movement northward back toward Crane Creek, which it re-entered at 19:06 hrs. By 19:15 hrs, less than an hour before sunset, the shark was back at its tagging location within the creek boat basin, where it remained until the track was broken off at 22:00 hrs. Shark B5 was relocated again the following day at 12:30 hrs, but the track was ended at 13:30 hrs. This shark was tracked for a total of 15 h over an 8-day period.

Shark B6

Bull shark B6, an 83 cm FL juvenile female, was captured and tagged at 10:45 hrs, 18 May 2005, in Crane Creek (Figure 3-6). She was tracked continuously until 18:00 hrs, when it became too windy to track. The shark was then relocated the following day at 08:00 hrs, back near its tagging location in Crane Creek. It was tracked for an additional 8 h, and it remained within the creek boat basin until the track ended at 16:00 hrs, 19 May. The shark was therefore tracked for 15.25 h over a 29-h period. During the 8-h tracking period on 19 May, however, there was very little movement detected, and it is possible that the transmitter had detached from the shark, and was lying on the bottom.

Shark B7

Bull shark B7 was a 60 cm FL YOY female, tagged on 7 June 2005 at 19:05 hrs in Crane Creek (Figure 3-7). The shark was tracked continuously for 12.25 h, until 07:00 hrs, 8 June, but it is suspected that the shark either shed the tag or died at approximately 22:00 hrs because movement of the shark ceased at this time. Due to the exceptionally small core areas utilized by these sharks, tracking was continued throughout the night to discern whether or not small movements were occurring. Only the first 3 h of this track are considered to be valid for the purposes of these analyses.

Shark B8

Bull shark B8 was a 66 cm FL YOY male, initially captured and tagged at 14:15 hrs, 20 July 2005, south of Crane Creek along the edge of the seagrass bed that runs along the western shore (Figure 3-8). The shark's signal was soon lost due to deteriorating sea surface conditions at 16:00 hrs. He was relocated the following day, however, at 07:30 hrs, less than 1 km from his tagging location, but further from shore. The shark was tracked continuously for 15 h, until 22:30 hrs. Two weeks later, on 4 August 2005, this shark was recaptured on hook and line several hundred meters from its original capture location. The transmitter had been shed, but the rototag remained intact, and the shark appeared to be in a healthy condition. A second transmitter was attached, and the shark was tracked for an additional 6 h. The shark was tracked for a total of 22.5 h over a 15-day period.

Shark B9

Bull shark B9, a 65 cm FL YOY male, was tagged at 11:45 hrs, 23 July 2005, on a seagrass bed south of Crane Creek (Figure 3-9). The shark was tracked for 4.5 h, until the weather deteriorated and the signal was lost. It was relocated the following day at 09:15 hrs, approximately 1.5 km southeast of its last position the previous day, and was tracked for another 6 h until 15:15 hrs, yielding a total of 10.5 h of tracking over a 27.5-h period.

Shark B10

Bull shark B10 was a 61 cm FL YOY female that was tagged at 11:45 hrs, 2 August 2005, just south of the mouth of Crane Creek (Figure 3-10). The shark was tracked for 1 h in extremely shallow water (<0.2 m), before the signal was lost. It was relocated the next day at 10:30 hrs on the eastern side of the lagoon, about 2 km from its last detected position. Position fixes were taken over the next 1.5 h, and it was determined that the transmitter signal was immobile, so the shark had either shed the tag or died.

Shark B11

This YOY male bull shark (60 cm FL) was tagged and monitored by acoustic listening stations (Vemco VR2) placed near the outfalls of each power plant in the northern IRL. The shark was tagged on 5 June 2004, off the Delespine (north) power plant, and was detected at one of the two outfalls on 123 of the subsequent 156 days leading up to 3 November 2004, after which it was no longer detected (Figure 3-11). The shark spent most of its time off the north power plant, but also spent a significant amount of time off the south power plant. On several days, the shark was detected at both listening stations which were approximately 3.4 km apart from each other. During this period the shark also made a single foray to a third listening station approximately 6 km north of Delespine.

Activity Space

The activity spaces (95% UD) of these bull sharks during their tracks were relatively small, ranging from 0.02 – 3.49 km^2 (mean = 1.40 ± 1.40 km^2) (Table 3-2). For several of these tracks, particularly when the sharks spent much of their time close to shore, the 95% UD (as calculated by the ArcView 3.2 Animal Movements Extension) overestimates activity space to some degree by including areas of land within the UD area (e.g. Figures 3-5, 3-9). The core area (50% UD) calculations were less affected by this bias. Core area sizes ranged from 0.0001 – 0.911 km^2 (mean = 0.275 ± 0.320 km^2), and usually included small areas utilized by multiple bull sharks (tagged and un-tagged individuals). There were notable differences between the sizes of YOY and juvenile bull shark activity spaces. Juvenile sharks had a mean activity space of 0.29 ± 0.41 km^2, and YOY sharks had a mean activity space of 2.27 ± 1.36 km^2 (Table 3-2). There was also an order of magnitude difference in the size of the core areas between juvenile and YOY sharks. Juveniles had a mean core area size of 0.04 ± 0.07 km^2, and YOY sharks had a mean core area size of 0.46 ± 0.35 km^2, despite the low number of sharks tracked, which precluded statistical analysis (Table 3-2).

The shape of the MCP activity spaces, as defined by the index of eccentricity (ECC), were >1 for all of the tracked sharks, and ranged from 1.36 – 3.34 (mean = 1.99 ± 0.69) (Table 3-2). This index shows that the bull shark activity spaces tended to be asymmetrical, and the space utilized tended to have an oblong shape that predominantly ran parallel to the shoreline (e.g., Figure 3-1). This pattern was consistent in both YOY and juvenile sharks, and though YOY sharks had higher average ECC values, there was no notable difference in ECC between the two age classes (Table 3-2).

Horizontal Swimming Behavior

Due to the difficulties in estimating the positions of shark B2, and the inherent error associated those positional estimates, data from this track were excluded from this analysis. The mean ROM for each of the remaining 9 bull sharks tracked in this study ranged from 0.033 – 0.387 m sec^{-1} (mean = 0.154 ± 0.107 m sec^{-1}) (Table 3-2). Although it appeared that most YOY bull sharks had a slightly higher mean ROM than juveniles (0.193 ± 0.128 m sec^{-1}, and 0.106 ± 0.059 m sec^{-1}, respectively). There was also no distinct diel change in ROM detected that would be suggestive of increased nocturnal activity (Figures 3-12 and 3-13).

To investigate the possibility of a post-release stress response in the tagged sharks, mean ROM from early in a track (0 – 2 h post-release) were compared to the mean ROM from late in a track (>12 h post-release). The tracks of four individuals (B1, B6, B8, B9) had sufficient data to make this comparison (Figure 3-14). In three out of four sharks, the initial post-release ROMs were slower than the ROMs after 12 h of tracking. In a single individual, the initial ROM was faster (Figure 3-14). Low sample size prohibited the evaluation of whether or not these differences were statistically significant.

The LI for each of these tracks was used as an indicator of site fidelity and home ranging behavior. Overall, the LIs for these sharks were quite low, ranging from 0.01 – 0.65, indicating a high level of area reuse during their tracks. The two tracks with the highest LI values (B3 and B10) were also the two shortest tracks (Table 3-1), suggesting that the high LI in these tracks was an artifact of low sample size. Had these sharks been tracked for longer periods, it is likely that the LI would have decreased. The mean LI for all tracks was 0.18 ± 0.21 (median = 0.09). The mean LI for YOY sharks was 0.25 ± 0.25, and 0.11 ± 0.15 for juvenile sharks (Table 3-2). As with the size of core areas noted above, the juvenile sharks had lower LI values than YOY sharks, demonstrating that juveniles tend to exhibit a higher level of site attachment than do YOY sharks.

The directionality of each shark was examined to determine if the angular orientation of their movements were uniformly distributed, or whether there were nonrandom and directional patterns of movement as they reused their activity space (e.g., Klimley et al. 2005). Circular histograms showed that in several cases bull shark movements did appear to be nonrandom, though not linear in concentration. For example, sharks B1, B5, and B8 each had equivalent proportions of track segment bearings that ran at both northwest and southeast headings (Figures 3-1, 3-5, and 3-8). Shark B4 showed a pattern of primarily east and west movements (Figure 3-4), and shark B9 had a pattern of more north and south movements (Figure 3-9). Values of *r* ranged from 0.078 ($p=0.577$) for shark B8, to 0.503 ($p < 0.0001$) for shark B5 (Table 3-2). Rayleigh's Test indicated that sharks B1, B4, B5, and B9 had angular distributions significantly different from uniform (Table 3-2), suggesting varying degrees of directional movement in these individuals.

Habitat Use

The bull sharks were found in a broad range of environmental conditions with respect to depth, temperature, salinity, DO, secchi depth, and bottom type (Table 3-3). However, some patterns of habitat utilization were observed that may be suggestive of some preferences. With regards to depth, the tracked sharks swam in waters as shallow as 0.2 m and their dorsal fins often exposed above the surface. Although we could not definitively determine the position of the sharks in the water column except by visual observation, they were tracked in areas with water depths of up to 3.9 m, in the deepest portions of the ICW channels (Table 3-3). When visual observation of free-swimming sharks was possible (occasionally at depths of up to about 1.5 m), the sharks typically swam just above the bottom. However, they were also occasionally observed to swim at or just beneath the surface when over deeper waters, particularly within Crane Creek. The majority (65%) of positions however, were recorded at depths of less than 2.0 m, with a peak of utilization between 1.0-1.5 m (mean = 1.6 ± 0.5 m) (Figure 3-15a). These depths, however, represent the majority of the lagoon's overall depth distribution. There did not appear to be any strong differences in the mean depth utilized by the sharks between day and night, nor between YOY (mean = 1.8 ± 0.5 m) and juvenile (mean = 1.3 ± 0.4 m) sharks.

The sharks were tracked in water temperatures ranging from 18.5 – 34.2 °C (mean = 28.3 ± 3.2 °C) (Table 3-3). However, the sharks spent over 68% of their tracks in waters warmer than 28 °C (Figure 3-15b). These temperatures coincided with the water temperatures that occur during the season of the sharks' peak abundance in the IRL during the summer and fall (see Chapter 2). The coldest temperatures were recorded from shark B2, which was tracked in mid-March near a power plant outfall (Figure 3-2). Temperatures closest to the outfall were as high as 32 °C, but the shark was initially captured, and made occasional forays, over a kilometer from the outfall where water temperatures were significantly colder. It is believed that this juvenile shark was using the power plant outfall area as a thermal refuge throughout the winter months (Snelson et al. 1984). There was no observable difference in temperatures of habitat utilized between day and night, nor between YOY (mean = 30.9 ± 1.9 °C) and juvenile (mean = 27.8 ± 3.6 °C) sharks.

The immature sharks were tracked in freshwater creek habitats with salinities as low as 1.2 ppt, and in open lagoon habitats with salinities as high as 31.9 ppt (mean = 19.0 ± 7.7 ppt) (Table 3-3). The salinities utilized by the sharks showed a bimodal distribution, with separate peaks at salinities of 10-15 ppt (32%) and 25-30 ppt (26%) (Figure 3-15c). Peaks in salinity utilization essentially correlate to the time spent inside or outside of Crane Creek. There was some evidence of diel changes in salinity preference, with some sharks spending daylight hours in more saline lagoon waters, and their nights in the less saline creek habitats (B5, Figure 3-5). This may be a function of either salinity preference, or of other aspects of the creek versus lagoon environments (e.g. depth, forage, refuge). However, this could not be determined conclusively. There was also some evidence of size/age segregation by salinity, with juvenile sharks spending more time in higher salinity waters (mean = 20.7 ± 7.9 ppt) than YOY sharks (mean = 13.7 ± 6.4).

The space utilized by the bull sharks tracked near Crane Creek varied between dry periods and wet periods, as measured by the salinity regimes near Crane Creek (Figures 3-16, 3-17, 3-18, 3-19). Utilization of the creek habitats was higher during dryer periods, when the creek salinity was greater than 10 ppt, and the open lagoon salinity was above 30 ppt. Following rain events, which lowered creek salinities below 10 ppt, and open lagoon salinity to below 20 ppt, the sharks utilized habitats in the open lagoon adjacent to the creek more often (Figure 3-16). There was definitely some overlap, and use of the full range of salinities by some sharks, but 75% of tracking positions during both wet and dry periods were in salinities greater than 11 ppt (Figure 3-18), even though the spatial distributions were substantially different (Figures 3-16 and 3-17). Although sample size was small (N=7), linear correlation analysis revealed an inverse relationship between the size of bull shark activity spaces and the salinity measured in Crane Creek ($r^2 = 0.820$) (Figure 3-19).

The movements of the sharks did not appear to be greatly influenced by DO. Though the sharks experienced a DO range of 1.8 – 8.2 mg/L (mean = 5.6 ± 1.3), 64% of positions were in the 5-8 mg/L range (Figure 3-15d). The lowest DO measurements were recorded from deep channel waters during the night. Water column DO, driven by primary production, naturally oscillates between day and night (Brown et al. 1999). Regardless, DO utilization was similar between YOY (mean = 5.1 ± 1.1 mg/L) and juvenile (mean = 6.1 ± 1.5 mg/L) sharks.

Water clarity, as measured by secchi depth, does not tend to vary greatly in highly-productive estuaries such as the IRL (Brown et al. 1999). During their tracks, these sharks experienced waters with secchi depths from 0.7 – 1.7 m, with a mean of 1.2 ± 0.3 m (Table 3-3, Figure 3-15e). However, water clarity was similar for YOY (mean = 1.8 ± 0.5 m) and juvenile (mean = 1.3 ± 0.4 m) sharks with regards to their secchi depth. Since secchi depth can not be recorded during the night, no comparisons of diel changes relative to water clarity were made.

The bull sharks swam over a variety of bottom substrate types during their tracks, including sand, seagrass, mud, and in deep channels. Most individual sharks utilized more than one primary substrate type. The sharks tracked near the power plants (B2, B3) primarily swam over sandy bottoms, which predominate near these particular areas. The remainder of observations were made over shallow seagrass beds or the muddy bottoms in dredged channels.

Discussion

Few studies have examined the movements of elasmobranchs along Florida’s east coast. While the seasonal occurrence and diet of bull sharks has been described for bull sharks in the

IRL region of Florida (Snelson et al. 1984) (see Chapter 2), the present study is the first to use acoustic telemetry on elasmobranchs in the IRL. In addition, it is only the second study to report both short-term movements and activity space of this apex predator (Steiner 2002). The 10 bull sharks that were manually tracked in this study displayed variability in their individual movements and behaviors, but there were notable patterns among them as well. Since contact with five of the sharks was lost soon after release, and later relocated (see *Bull Shark Tracks*), these sharks had presumably recovered from the stress of their capture and were behaving normally. In three of four sharks with sufficient comparable data, the ROM of sharks immediately post-was slightly slower than was observed after 12 h of tracking (Figure 3-14), also indicating that the tagging process did not adversely affect the sharks in a measurable way. In general, daily activity spaces of the sharks were relatively small, with high levels of area reuse in most tracks. Both juvenile and YOY sharks occupied a broad range of available environmental parameters in the lagoon (Table 3-3), but their increased frequency in some habitats (Figure 3-15) suggested evidence of selection for specific habitats.

The estimated activity spaces, movements, and habitat use of bull sharks in the IRL were similar to those calculated for 11 juvenile bull sharks tracked by Steiner (2002) in the Ten Thousand Islands (TTI) estuary off southwest Florida, using the similar methods and similar durations (2.5 – 23.2 h). The TTI estuary is physically different from the IRL, with numerous mangrove-fringed islets divided by channels, small bays, tide-influenced creeks, and rivers running through the system. However, based on observation-area curves of tracking data, Steiner (2002) found that bull shark activity space size did not significantly increase after tracking durations of 9 – 16 h (mean = 11.6 h). This suggests that this tracking duration was adequate for quantifying juvenile bull shark activity space. Activity spaces quantified using

MCP for TTI bull sharks ranged from 0.17 – 3.59 km^2 (mean = 1.26 ± 1.24 km^2), compared to 0.11 – 3.06 km^2 (mean = 1.13 ± 1.19 km^2) for IRL bull sharks in this study (if sharks tracked for less than 10 h are excluded from the analysis for the sake of comparison, Table 3-1). TTI bull sharks also predominantly showed similar movement patterns, including patrolling parallel to shore, milling about in deep channels, and reusing the same space repeatedly during tracking. In addition, some sharks were actually observed to remain stationary and "rest" in tidal currents for periods of up to 1.5 h. The orientation of their movements was not influenced by tidal flow, however, as has been observed in two other carcharhinid species, the blacktip (*Carcharhinus limbatus*) and sandbar (*C. plumbeus)* sharks (Steiner 2002; Medved and Marshall 1983; Rechisky and Wetherbee 2003). Most of the TTI bull sharks utilized similar ranges of depth, temperature, salinity, DO, and water clarity as IRL bull sharks. The movements and activities of the TTI bull sharks were mostly limited to backwater areas and river mouths, and hypothesized to be primarily influenced by the distribution of prey (Steiner 2002).

Larger individuals, across many animal taxa, typically have larger home ranges than smaller conspecifics (McNab 1963; Kelt and Van Vuren 2001). Although this observation has not been expressly tested in most sharks, it appears to hold true for some species (Morrissey and Gruber 1993a; Steiner 2002; Heupel et al. 2004) and not in other species (Goldman and Anderson 1999; Rechisky and Wetherbee 2003). The observation in the present study that small YOY sharks seem to have higher average activity spaces and core area sizes than larger juveniles is therefore more similar to these latter studies, although more data may be needed to fully support this pattern.

Contrary to my results, juvenile and YOY bull sharks tracked in the TTI estuary, showed a pattern of MCP area increasing with shark length (Steiner 2002). Juvenile lemon sharks

(*Negaprion brevirostris*) tracked in the Bahamas also showed a positive correlation between body size and home range size, utilizing larger portions of their lagoon nursery as they grew (Morrissey and Gruber 1993). Heupel et al. (2004) used passive acoustic monitoring to show that YOY blacktip sharks expanded their home ranges during their first months of life in their natal nursery areas. Following parturition in early summer, blacktip shark home ranges were restricted to a very small portion of the study site in Tampa Bay. As the summer progressed, all of the tagged sharks rapidly expanded their activities throughout the study site. There was no significant difference in activity space detected between neonate and juvenile sandbar sharks tracked in their Delaware Bay summer nursery (Rechisky and Wetherbee 2003).

One of the only other shark species reported to show the pattern of larger sharks having smaller activity spaces is the white shark (*Carcharodon carcharias*), tracked off the Farallon Islands, California by Goldman and Anderson (1999). Large adult and subadult white sharks seasonally aggregate at this site to hunt pinnipeds. They suggested that smaller, inexperienced white sharks had not yet learned the most successful feeding locations or hunting strategies, and therefore roamed over broad areas in search of prey. The larger sharks were more familiar with the terrain, and limited their space utilization to areas where they had experienced higher predation success during previous seasons. This could also be the case with bull sharks in the IRL. Older, larger, juvenile bull sharks may limit their activities to discrete areas where they have learned to feed successfully, while neonate bull sharks are more naïve, and have not yet learned the most suitable feeding sites or strategies. Also, since larger juvenile bull sharks are known predators of YOY bull sharks (Snelson et al. 1984), the smaller YOY sharks may actively avoid locations with high densities of juveniles (as observed by Simpfendorfer et al. 2005), and be forced to conduct their activities over broader areas. Competitive exclusion by juvenile bull sharks may occur in the IRL, however, it was not detected by the methods applied in this study. Habitat selection may also play a role in this pattern for bull sharks in the IRL, since salinity had an influence activity space (Figures 3-17 and 3-19). It should be noted that these observations likely only hold true for white sharks and bull sharks when they are seasonally found at the sites where they were tracked. Juvenile and adult white sharks are known to make long-distance, oceanic migrations during specific times of the year (Weng et al. 2007). I speculate that bull sharks migrate south and out of lagoon waters during winter months (see Chapter 2), where their behaviors may differ appreciably.

The overall activity space size range of 0.05 – 3.49 km^2 (mean = 1.40 ± 1.40 km^2) for IRL bull sharks is comparable to that reported for daily activity spaces and home ranges of other carcharhiniform shark species tracked in nursery areas. Juvenile lemon sharks tracked in the Bahamas had home ranges of 0.23 – 1.26 km^2 (Morrissey and Gruber 1993a), juvenile scalloped hammerhead sharks (*Sphyrna lewini*) tracked in Hawaii had home ranges of 0.46 – 3.52 km^2 (Holland et al. 1993), and juvenile blacktip sharks tracked off the west coast of Florida had daily activity spaces of 0.28 – 6.61 km^2 (Steiner 2002) and 0.019 – 13.0 km^2 (Heupel et al. 2004). In contrast, YOY and juvenile sandbar and bonnethead sharks (*S. tiburo*) tended to have larger activity spaces (Rechisky and Wetherbee 2003; Heupel et al. 2006). Immature sandbar sharks tracked in Delaware Bay were reported to have daily activity spaces as high as 315.4 km^2 (mean = 62.4 km^2), while bonnethead sharks tracked in Charlotte Harbor, Florida had daily activity spaces as high as 74.41 km^2 (mean = 8.31 km^2) (Rechisky and Wetherbee 2003; Heupel et al. 2006). These interspecific variations (and similarities) in activity space could be influenced by a number of biological and physical factors that require further investigation. Such studies may help to shed further light on how sharks select habitats within their nursery areas.

The distribution of prey species may have also influenced the movements of these sharks during their tracks. Although prey distribution was not quantified, presence of known primary prey species (mullet, catfishes, stingrays) was noted when observed. When directionality histograms are overlaid on each plotted shark track, it can be clearly observed that the diametrically bimodal distribution of bearings in some of the shark tracks can be attributed to their behavior of predominantly swimming back-and-forth parallel to the adjacent shoreline (e.g., Figures 3-1, 3-4, 3-5). This swimming pattern is indicative of a patrolling-style hunting strategy (Morrissey and Gruber 1993a; Klimley et al. 2001). In addition, during some tracks, the sharks appeared to exhibit foraging behavior consistent with observed foraging behaviors of untagged sharks. Both in Crane Creek and on nearby seagrass beds, young bull sharks were seen chasing schooling mullet, which were very dense in the area at times. Bull sharks were observed on a number of instances to actually breach clear of the water in pursuit. Although no sharks were visually observed feeding on catfishes or stingrays, both known prey items (Snelson et al. 1984), they were abundant in the study area (based on catch data and direct observations), and may have influenced the use of deeper habitats frequented by these species (Snelson et al. 1989).

The tradeoff between predator avoidance and prey distribution (i.e., energy intake) is thought to be a major biotic influence on shark habitat selection in nursery areas (Branstetter 1990; Heithaus 2007), although this concept has been difficult to test in the field (Heupel et al. 2007). The use of shallow habitats by sandbar sharks in Delaware Bay was postulated to be correlated to predator avoidance, distribution of preferred prey, avoidance of strong tidal currents, or a combination of those factors (Rechisky and Wetherbee 2003). Holland et al. (1993) showed that juvenile scalloped hammerhead sharks had rhythmic diel patterns of activity in which they utilized small core areas during the day, and much broader areas during the night, a pattern that was considered to be influenced by predator avoidance. Heupel and Hueter (2002) demonstrated that juvenile blacktip shark habitat use was not correlated to prey distribution, and was therefore hypothesized to be influenced more by predator avoidance. In Florida's Caloosahatchee River estuary, YOY bull sharks were spatially segregated from juveniles, and were more abundant in low salinity, riverine habitats than their larger conspecifics, which occupied the adjacent Pine Island Sound (Simpfendorfer et al. 2005). This size segregation was believed to be related to predator avoidance behavior of the YOY sharks.

At these sites, young sharks and their potential predators (i.e. larger sharks) occupy adjacent or overlapping habitats. Immature bull sharks in the IRL, however, are effectively free from predation risk since adult bull and lemon sharks, the only documented juvenile shark predators known to occur within the lagoon, are exceptionally rare (Snelson and Williams 1981). Although YOY bull sharks have been cannibalized by larger juvenile bull sharks, this does not appear to be a frequent occurrence (Snelson et al. 1984). The only other potential predators of YOY and juvenile bull sharks in the IRL are American alligators (*Alligator mississippiensis*), which I observed to be abundant along certain shorelines adjacent to low salinity creeks, and occasionally seen in the open lagoon in salinities as high as 25 ppt, particularly around Merritt Island. Alligators, however, have not been documented to prey on sharks in Florida intracoastal waters, and generally seem to prefer to feed on smaller teleosts (Rice 2004; Rice et al. 2007). However, other crocodilians have been documented to prey on small sharks (Whitfield and Blaber 1979), so the possibility does exist in the IRL. It should be noted that in this study, few sharks were captured or tracked where there were particularly high densities of alligators (e.g. Banana Creek, Gator Creek, see Figure 2-2), although lone alligators were occasionally sighted during some of the shark tracks in Crane Creek. Nevertheless, predation pressures do not appear to significantly impact young bull sharks in the IRL, so their movements and habitat use are more likely related to the distribution of their preferred prey items. Indeed, some bull sharks had activity spaces in which known prey were visibly dense, and sharks were observed feeding within these areas. Their observed patrolling behavior is certainly consistent with the hunting strategies employed by other sharks, including lemon sharks (Morrissey and Gruber 1993) and white sharks (Klimley et al. 2001). Additionally, bull sharks commonly utilized prey-rich seagrass habitats, which have been documented to support 54% of the IRL's ichthyofaunal diversity (Gilmore 1995). Further research and standardized experimentation are needed to more accurately define the importance of these factors in the habitat selection of bull sharks in the IRL, which appears to be a low predation-risk environment. This unique feature may provide benefits to the sharks through increased growth and survival, as compared to areas where predation risks would be greater.

The abiotic habitat features monitored during the tracking of these sharks included water temperature, salinity, DO, depth, and secchi depth (Table 3-3, Figure 3-15). The importance of temperature in the distribution and movements of elasmobranchs has been described in several studies (e.g. Matern et al. 2000; Grubbs and Musick 2002; Simpfendorfer et al. 2005), and is generally thought to influence distribution at a broad scale; i.e., within the physiological tolerances of the species in question. Since water temperatures below 10 °C can be lethal to small bull sharks (Dodrill 1977; Snelson and Bradley 1978), bull sharks likely migrate out of cooler northern IRL waters to warmer offshore and southern waters during the winter (see Chapter 2). Even though bull sharks were tracked in temperatures as low as 18.5 °C in this study, most activities were observed in temperatures greater than 28 °C, and as high as 34.2 °C (Figure 3-15b). This is consistent with findings from other bull shark habitat studies (Michel

2002; Simpfendorfer et al. 2005; Blackburn et al. 2007), and is also reflected in the predominantly tropical distribution of this species around the world (Compagno 1984).

The euryhaline tolerance of bull sharks has been previously documented and investigated (e.g. Thorson 1972; Thorson et al. 1973; Pillans et al. 2005), and is further supported by this study. The broad range of salinities utilized by the bull sharks in the IRL (1.2 – 31.9 ppt) is also consistent with results from other nursery area studies (e.g. Simpfendorfer et al. 2005; Blackburn et al. 2007; Chapter 2). Since bull sharks have well known euryhaline habits and broad salinity tolerances, one may not expect there to be distinct preferences in relation to salinity. However, the overall trend implies that the bull sharks near Crane Creek were mostly selecting habitats with salinities > 11 ppt (Figure 3-18), even when lower salinity habitats were available to them (Figure 3-16).

If these young sharks can physiologically tolerate freshwater, why do they appear to preferentially avoid it (Figure 3-19)? Simpfendorfer et al. (2005) found that YOY and juvenile bull sharks in the Caloosahatchee River estuary segregate themselves by salinity, similar to the pattern observed in this study (Table 3-3). They observed that YOY sharks preferred more brackish habitats with salinities between 7 and 17.5 ppt. In contrast, juvenile sharks preferred higher salinities, and the habitats of adjacent San Carlos Bay and Pine Island Sound. This segregation was speculated to reduce intraspecific cannibalism and predation by larger sharks on the YOY bull sharks. As a result, lower salinity river habitats provided a refuge for the youngest sharks in the population. However, the YOY sharks still appeared to avoid salinities below 7 ppt.

For the IRL, if predator avoidance can be ruled out as discussed above, then few other explanations for this pattern remain. One possibility is that reduced salinities only indirectly affect bull shark movements, and their distribution shift may be mediated by the movements of their prey, which directly respond to environmental changes. There are numerous euryhaline fishes that occur in the IRL (Gilmore 1977; 1995), many of which are documented prey of bull sharks (Snelson et al. 1984). Salinity has been shown to be a significant factor in the distribution and species associations of these fishes (Kupschus and Tremain 2001; Paperno et al. 2006), and as these fish redistribute themselves following a rain event, the bull sharks may follow. Some qualitative observations support this explanation. Multiple untagged and tagged sharks (tracks B4, B5, B6, and Figs. 3.4, 3.5, 3.6, respectively) were observed feeding on mullet, which shoaled in large numbers in Crane Creek during periods of low precipitation. When sharks were tracked during wet periods (Figs. 3.7, 3.8, 3.9, 3.10), mullet were visibly much less dense in Crane Creek, and more abundant in the open lagoon over seagrass beds. If mullet were indeed the major dietary component of bull sharks during this time, and/or other key prey species followed the same distribution shift (e.g. catfish), then it would make sense for the bull sharks to redistribute themselves in the lagoon accordingly. More detailed dietary analysis and prey distribution monitoring will be needed to adequately determine if these interactions truly exist.

An alternative explanation is that bull sharks directly respond to salinity changes because the sudden drop in salinity following a precipitation event disrupts homeostasis, possibly resulting in short-term, extraneous energetic costs. These costs (or homeostatic imbalances) may prompt individual sharks to seek out the salinity in which they were previously acclimated to, rather than linger and acclimate over time to the new medium. This possibility was proposed by Simpfendorfer et al. (2005) as another alternative to explain bull sharks' avoidance of extremely low salinities (< 7 ppt) in the Caloosahatchee River. They cited salinity selection experiments on other fish species, such as the killifish (*Fundulus heteroclitus*), that showed that even though killifish can tolerate a broad range of salinity, they repeatedly selected waters with salinity closest to their own cellular osmolarity (10 ppt) (Kidder 1997; Kidder et al. 2006). Kidder et al. (2006) hypothesized that euryhaline fishes may minimize their osmotic energy demand by selecting waters that are isotonic with their own body fluids. Even though elasmobranchs osmoregulate differently than bony fishes (Evans et al. 2004; Hammerschlag 2006), this "behavioral osmoregulation" could explain the pattern observed in IRL bull sharks. If YOY bull sharks select habitats that minimize the energetic costs for osmoregulating and maintaining homeostasis, more energy could be devoted to growth, thereby increasing their survival. Even though Crane Creek may be a preferred habitat because of its refuge and forage benefits, the acute salinity drops observed during this study could cause enough of an ionic imbalance in the sharks to influence them to move to the open lagoon. In the open lagoon, prey items would not be as spatially concentrated as they were in the creek, hence activity space (i.e., the foraging arena) is much larger. The physiological (i.e., histological, molecular) responses of euryhaline elasmobranchs to reduced salinity have been examined in several studies (e.g. Oguri 1964; Thorson et al. 1973; Piermarini and Evans 1998; Pillans et al. 2005). As stated by Simpfendorfer et al. (2005), future research should focus on investigating the potential energetic costs of osmoregulation and acclimation to varying salinities. Acute responses as well as chronic acclimation should be addressed, even though such responses may be difficult to quantify given the complexities of elasmobranch osmoregulation (Evans et al. 2004).

Power plant outfall areas in the IRL appear to be heavily utilized by young bull sharks. This is based on observations and catch rates in this, and previous studies (Snelson et al. 1984; Chapter 2), and is also supported by the movements of the bull sharks that were actively tracked in these vicinities. Bull sharks B2 and B3 both utilized core areas directly in front of outfalls for periods of 2 to 23 h (Figures 3-2 and 3-3). This site attachment behavior was not only limited to short-term periods, however. Shark B11 heavily utilized these areas during summer and fall 2004 (Figure 3-11). Based on anecdotal information, power plant outfall areas located further south in the IRL are also regularly utilized by bull sharks. The increased density of bull sharks at these outfall areas makes them particularly susceptible to capture, especially during winter months when they appear to use the outfalls as a thermal refuge. These areas are also utilized by a variety of other lagoon species during the winter, including manatees (Laist and Reynolds 2005), stingrays (*Dasyatis sabina* and *D. say*), spotted eagle rays (*Aetobatis narinari*), catfish (*Bagre marinus* and *Arius felis*), tarpon (*Megalops atlanticus*), ladyfish (*Elops saurus*), and other teleosts and invertebrates (Curtis, unpubl. data). Daily activity patterns, predator-prey dynamics, and other interspecific interactions in these confined outfall areas may be dramatically different during cold months, and warrant further investigation.

These outfall areas should be priorities for protection to aid in the conservation of the threatened and endangered species that rely on them during winter months. Indeed, some of the power plant outfall areas in the IRL are seasonally closed to boat access and fishing to protect vulnerable manatee aggregations creating *de facto* marine reserves for the sharks and other species that occur within those areas. The anthropogenic impacts of such sites on the health of lagoon sharks and other species should also be assessed. Bull sharks in the IRL and elsewhere have been shown to bioaccumulate high levels of contaminants such as mercury, polybrominated diphenyl ethers (PBDEs), and polychlorinated biphenyls (PCBs) (Adams and McMichael 1999; Johnson-Restrepo et al. 2005), as well as numerous human pharmaceuticals (Gelsleichter and Szabo 2007). The effects of these compounds on the physiology of the sharks are largely unknown. Johnson-Restrepo et al. (2005) calculated that the concentrations of PBDEs and PCBs in bull shark tissues increased exponentially between 1993 and 2004, indicating an alarming rate of increase in contamination levels of the IRL food web. Juvenile bull sharks are particularly at risk of accumulating these toxic chemicals due to their intracoastal distribution and their role as apex predators in the lagoon. Subsequently, this may also put humans at risk, since humans occasionally consume IRL bull sharks (Curtis, unpubl. observation). Further investigations are needed to more clearly describe the impacts of these contaminants on the IRL food web. The site fidelity of juvenile bull sharks to altered habitats such as power plant outfalls and heavily-trafficked creeks exposes them to a variety of potentially harmful wastewater pollutants, which could have far-reaching effects on their survival and population recovery.

Table 3-1. Details of ten bull sharks tracked in the IRL between 2003 and 2005.

Shark No.	FL (cm)	Sex	YOY/Juv	Start Date	Hours Tracked	Positions	Intermittent?
B1	71	F	Y	8/22/2003	22.50	89	Y
B2	94	M	J	3/11/2004	23.00	102	Y
B3	82	F	J	5/7/2004	2.00	8	N
B4	79	F	J	6/10/2004	18.75	63	Y
B5	82	F	J	5/17/2005	15.00	45	Y
B6	83	F	J	5/18/2005	15.25	25	Y
B7	60	F	Y	6/7/2005	3.00	12	N
B8	66	M	Y	7/20/2005	22.50	90	Y
B9	65	M	Y	7/23/2005	10.50	40	N
B10	61	F	Y	8/2/2005	1.50	11	Y

Table 3-2. Summary of movement and activity space parameters estimated for ten bull sharks tracked in the IRL.

Shark No.	Total Dist. (km)	ROM (m/s)	MCP (sq. km)	95% UD (sq. km)	50% UD (sq. km)	LI	ECC	*r*	*csd* (º)	Rayleigh p-value
B1	30.95	0.387	3.06	3.492	0.566	0.02	1.73	0.295	89.5	0.0004
B2	11.79	n/a	0.40	0.280	0.020	0.05	1.57	n/a	n/a	n/a
B3	1.11	0.154	0.03	0.104	0.018	0.37	1.53	n/a	n/a	n/a
B4	6.25	0.084	0.18	0.078	0.011	0.01	1.71	0.240	96.8	0.021
B5	8.10	0.154	0.42	1.011	0.161	0.09	2.13	0.503	67.2	<0.0001
B6	2.11	0.033	0.11	0.051	0.008	0.01	1.69	0.215	100.4	0.25
B7	0.38	0.050	0.01	0.020	0.0001	0.18	1.36	n/a	n/a	n/a
B8	18.58	0.229	2.44	2.341	0.254	0.08	1.72	0.078	129.4	0.577
B9	7.70	0.178	1.33	3.161	0.911	0.30	3.14	0.275	92.1	0.048
B10	2.79	0.119	0.39	2.360	0.550	0.65	3.34	n/a	n/a	n/a
Mean	8.66	0.154	0.837	1.402	0.275	0.177	1.992			
sd	10.03	0.107	1.086	1.403	0.320	0.208	0.688			

Table 3-3. Environmental parameters observed during the tracks of ten bull sharks in the IRL.

	Temperature (ºC)			Salinity (ppt)			DO (mg/L)			Depth (m)			Secchi Depth (m)			Bottom Substrate
Shark No.	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	
B1	29.8	29.5	30.0	24.9	22.0	27.5	6.2	5.6	6.9	1.4	0.6	2.1	1.0	1.0	1.0	seagrass, mud
B2	21.4	18.5	32.2	28.2	27.5	29.1	7.2	5.5	8.1	1.3	0.7	3.0	2.0	2.0	2.0	sand
B3	28.3	28.1	28.5	28.3	28.2	28.3	8.0	7.8	8.2	0.9	0.6	1.2	1.0	1.0	1.0	sand
B4	30.1	27.5	33.5	21.7	7.4	31.9	4.8	1.8	7.6	2.0	0.4	3.9	0.9	0.8	1.0	creek/seagrass
B5	30.1	28.3	31.6	14.8	8.9	17.5	5.4	3.0	6.0	1.3	0.3	3.2	1.5	1.5	1.5	creek/seagrass
B6	28.9	26.3	30.6	10.7	5.5	13.8	4.9	3.4	5.8	1.1	0.3	3.1	1.1	0.7	1.3	creek/seagrass
B7	28.3	27.3	30.0	9.0	1.2	17.2	3.3	2.0	4.3	2.3	0.9	3.5	1.0	1.0	1.0	creek
B8	32.7	30.4	33.6	11.3	9.4	12.4	5.9	5.1	7.1	2.2	0.4	3.6	1.4	1.1	1.7	seagrass/ICW
B9	32.5	31.7	34.2	11.0	10.6	11.2	5.2	3.9	7.2	1.8	0.2	3.0	1.2	1.0	1.4	seagrass/ICW
B10	31.2	31.0	31.3	12.1	12.0	12.2	4.8	4.6	4.9	1.3	0.2	3.0	1.0	1.0	1.0	seagrass, mud
TOTAL	28.3	18.5	34.2	19.0	1.2	31.9	5.6	1.8	8.2	1.6	0.2	3.9	1.2	0.7	1.7	

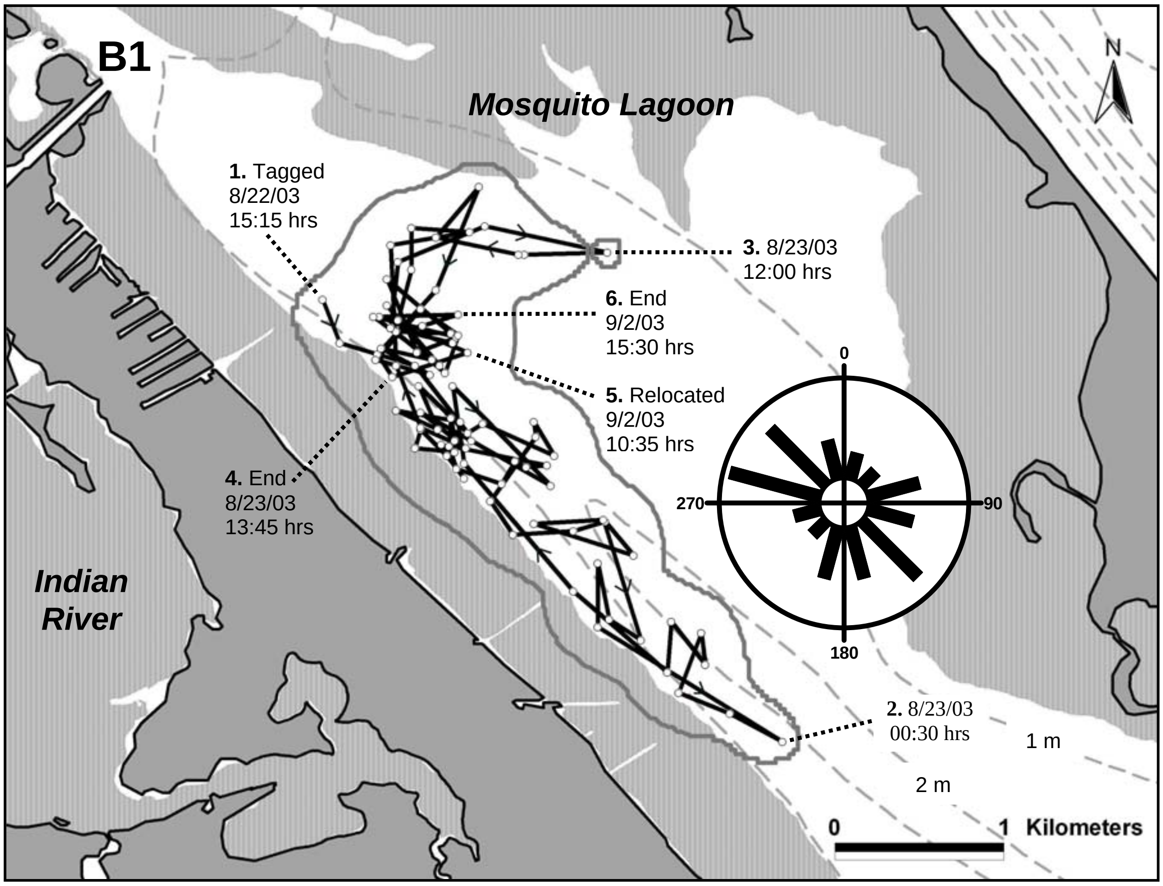

Figure 3-1. Manual acoustic track of bull shark B1, a 71 cm FL female, in Mosquito Lagoon between 22 August and 2 September, 2003. Points represent 15-min tracking positions. The dashed lines represent 1 m depth contours, and the lightly stippled area represents seagrass beds. The gray line surrounding the track positions represents the 95% KUD. In the inset directionality histogram, the outer edge of the circle represents 15 observations.

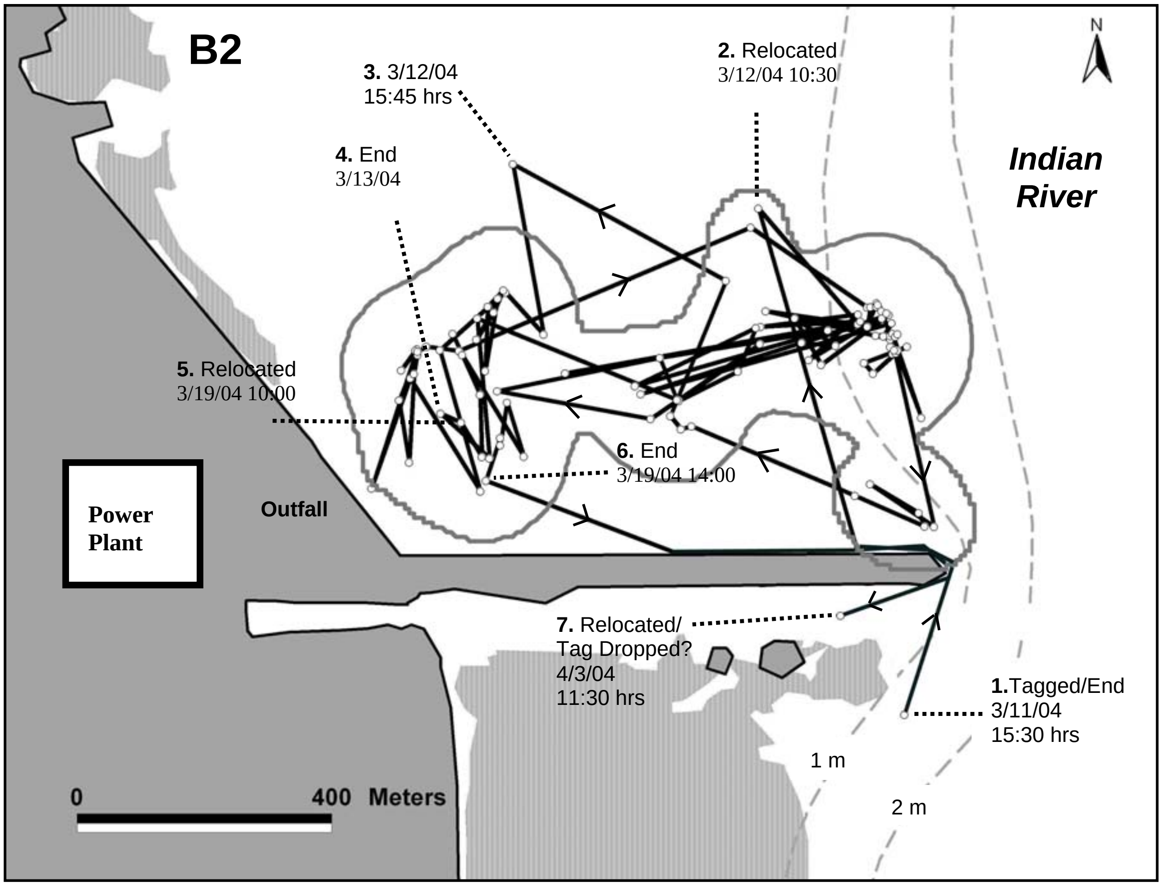

Figure 3-2. Manual acoustic track of bull shark B2, a 94 cm FL male, in the IRL between 11 March and 3 April, 2004. Points represent 15-min tracking positions. The dashed lines represent 1 m depth contours, and the lightly stippled area represents seagrass beds. The gray line surrounding the track positions represents the 95% KUD.

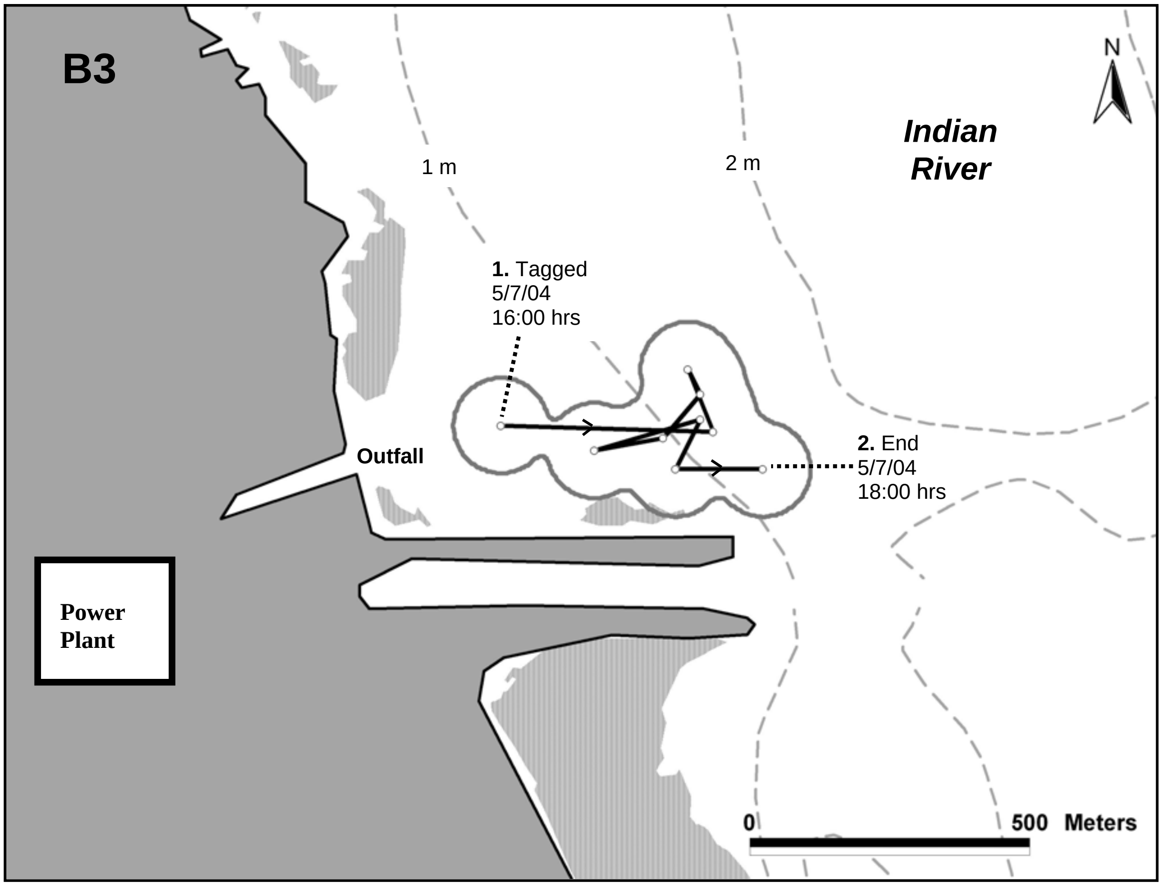

Figure 3-3. Manual acoustic track of bull shark B3, a 82 cm FL female, in the IRL on 7 May, 2004. Points represent 15-min tracking positions. The dashed lines represent 1 m depth contours, and the lightly stippled area represents seagrass beds. The gray line surrounding the track positions represents the 95% KUD.

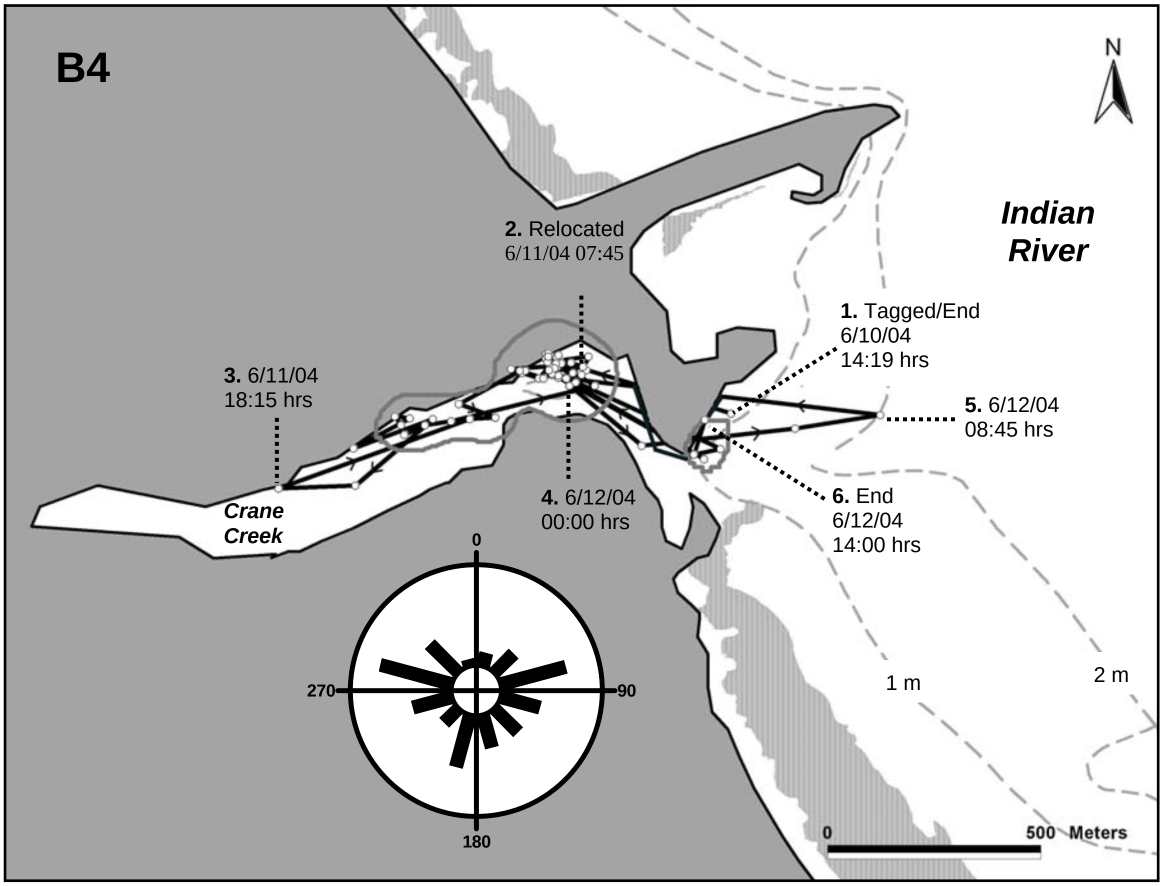

Figure 3-4. Manual acoustic track of bull shark B4, a 79 cm FL female, in the IRL between 10 and 12 June, 2004. Points represent 15-min tracking positions. The dashed lines represent 1 m depth contours, and the lightly stippled area represents seagrass beds. The gray line surrounding the track positions represents the 95% KUD. In the inset directionality histogram, the outer edge of the circle represents 15 observations.

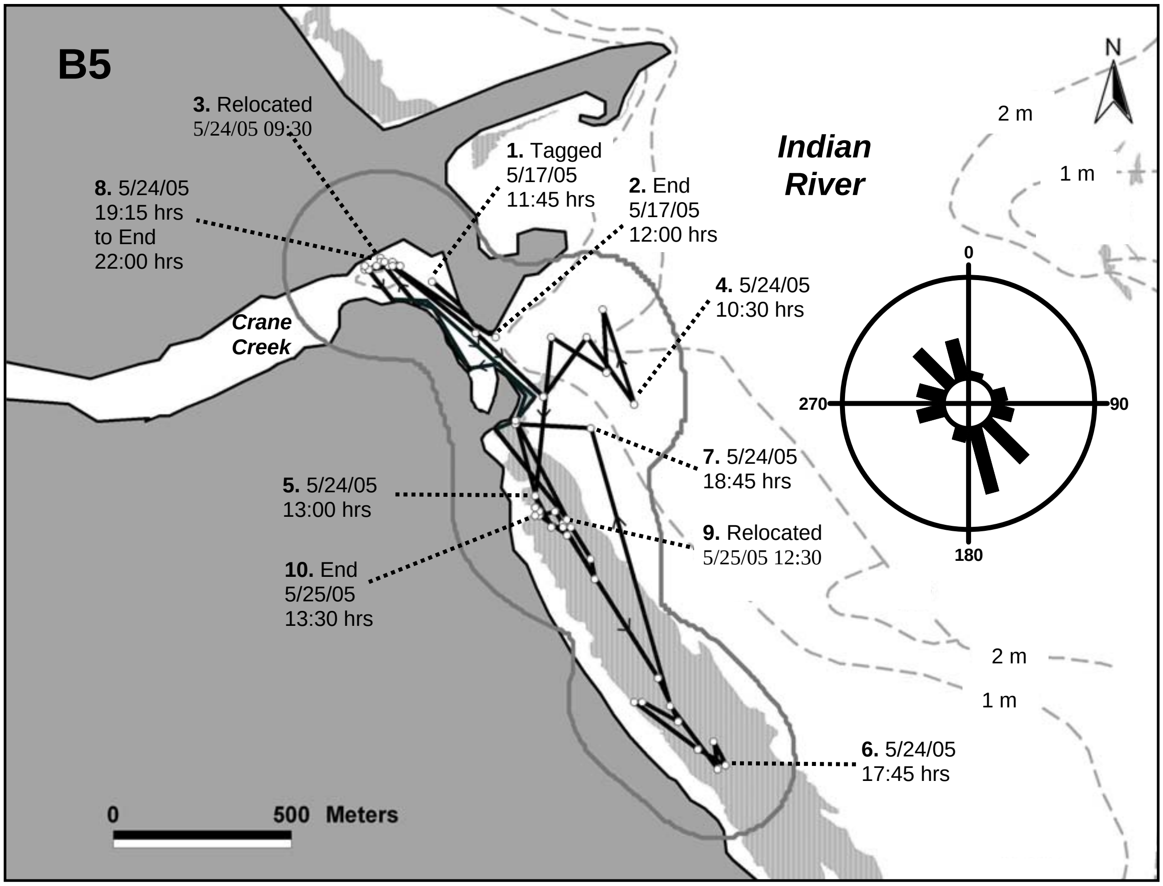

Figure 3-5. Manual acoustic track of bull shark B5, a 82 cm FL female, in the IRL between 17 and 25 May, 2005. Points represent 15-min tracking positions. The dashed lines represent 1 m depth contours, and the lightly stippled area represents seagrass beds. The gray line surrounding the track positions represents the 95% KUD. In the inset directionality histogram, the outer edge of the circle represents 15 observations.

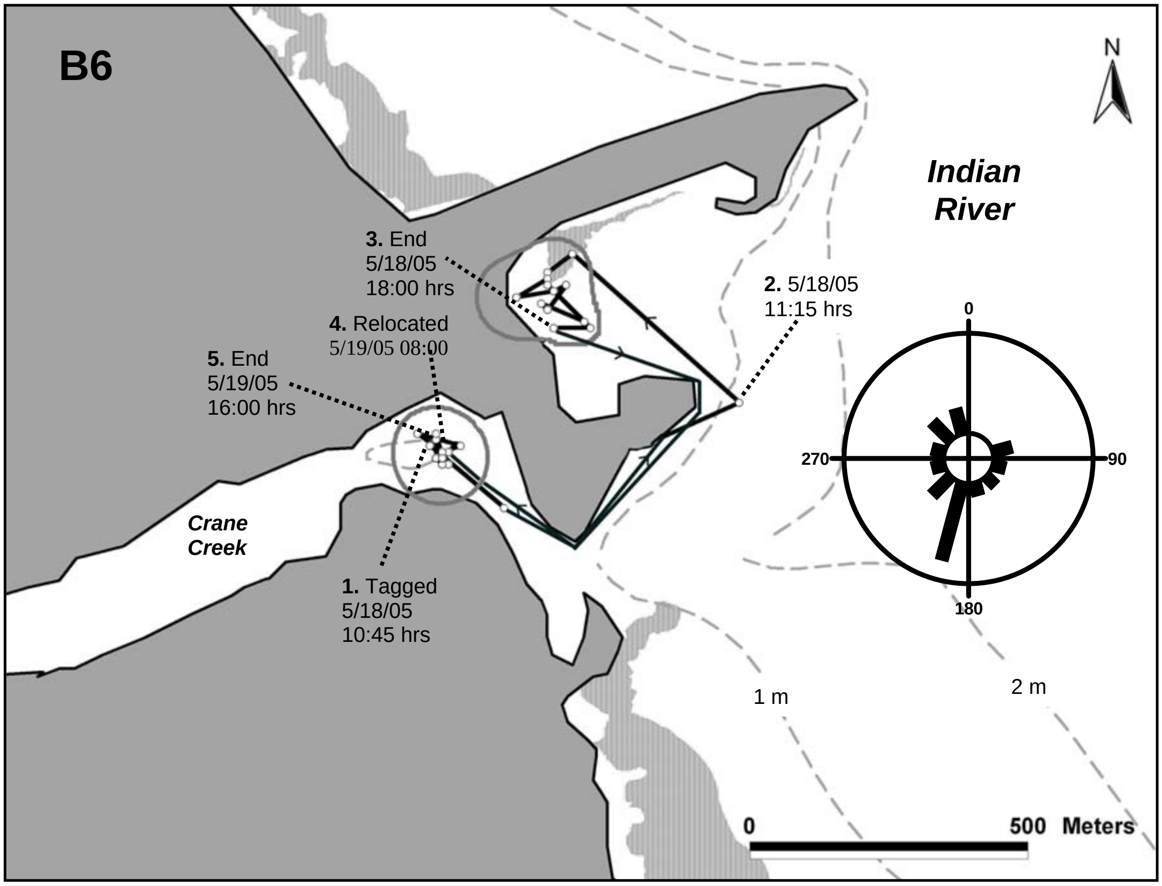

Figure 3-6. Manual acoustic track of bull shark B6, a 83 cm FL female, in the IRL between 18 and 19 May, 2005. Points represent 15-min tracking positions. The dashed lines represent 1 m depth contours, and the lightly stippled area represents seagrass beds. The gray line surrounding the track positions represents the 95% KUD. In the inset directionality histogram, the outer edge of the circle represents 15 observations.

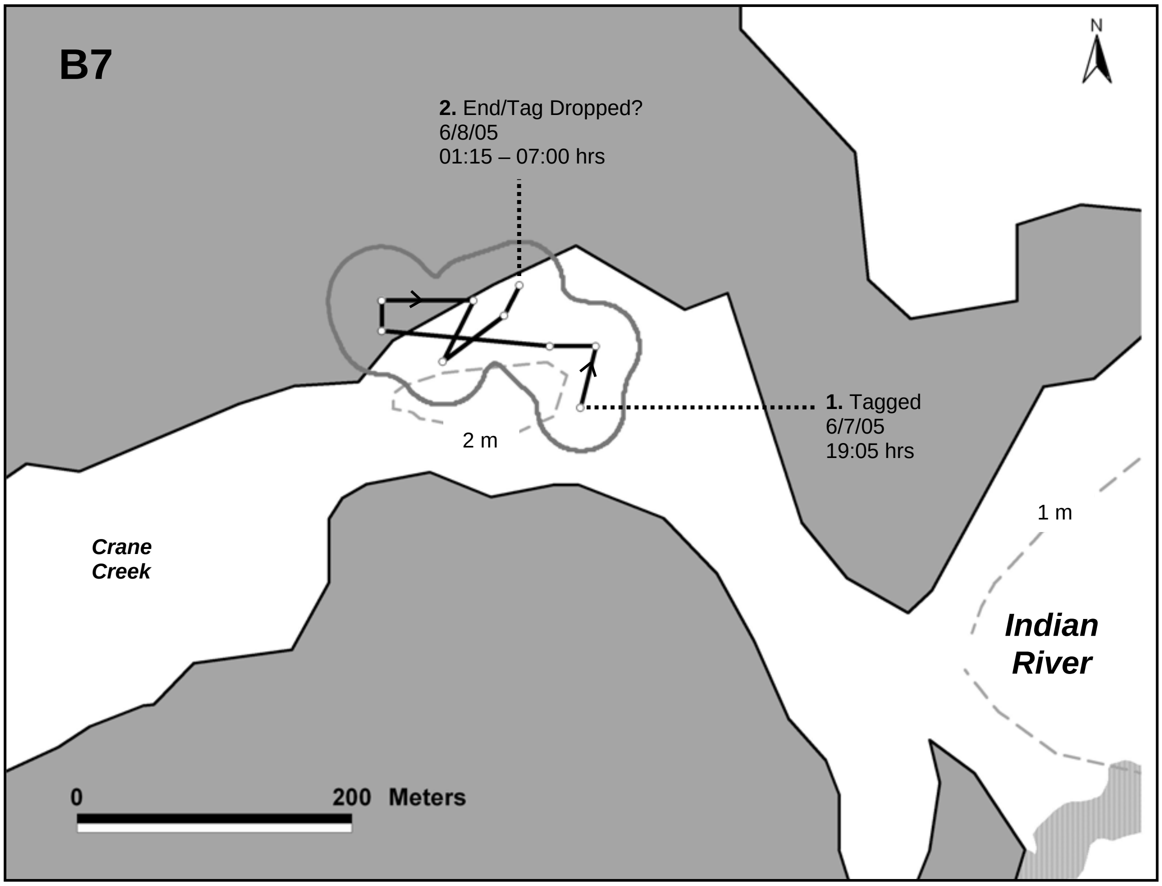

Figure 3-7. Manual acoustic track of bull shark B7, a 60 cm FL female, in the IRL between 7 and 8 June, 2005. Points represent 15-min tracking positions. A couple positions appear to overlap land because of the coarse resolution of the GIS coastline data at this scale. The dashed lines represent 1 m depth contours, and the lightly stippled area represents seagrass beds. The gray line surrounding the track positions represents the 95% KUD.

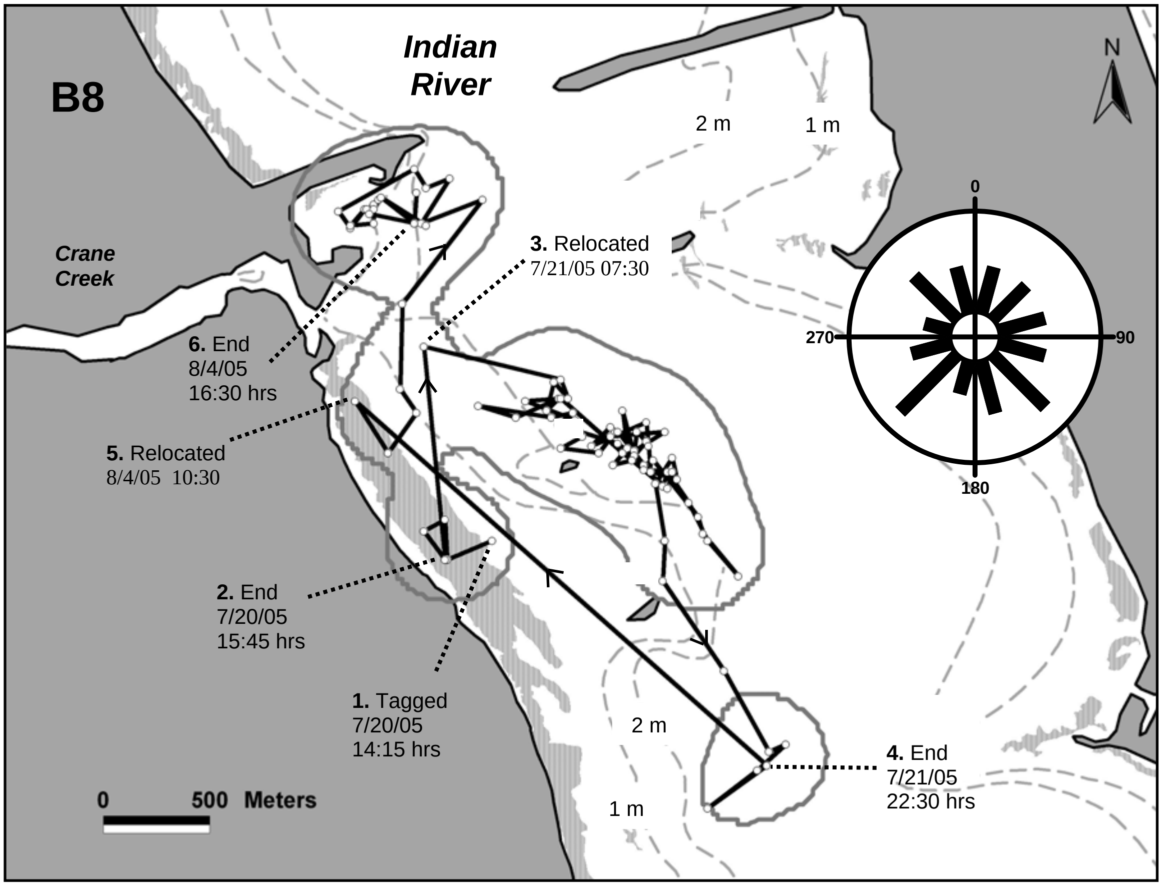

Figure 3-8. Manual acoustic track of bull shark B8, a 66 cm FL male, in the IRL between 20 July and 4 August, 2005. Points represent 15-min tracking positions. The dashed lines represent 1 m depth contours, and the lightly stippled area represents seagrass beds. The gray line surrounding the track positions represents the 95% KUD. In the inset directionality histogram, the outer edge of the circle represents 15 observations.

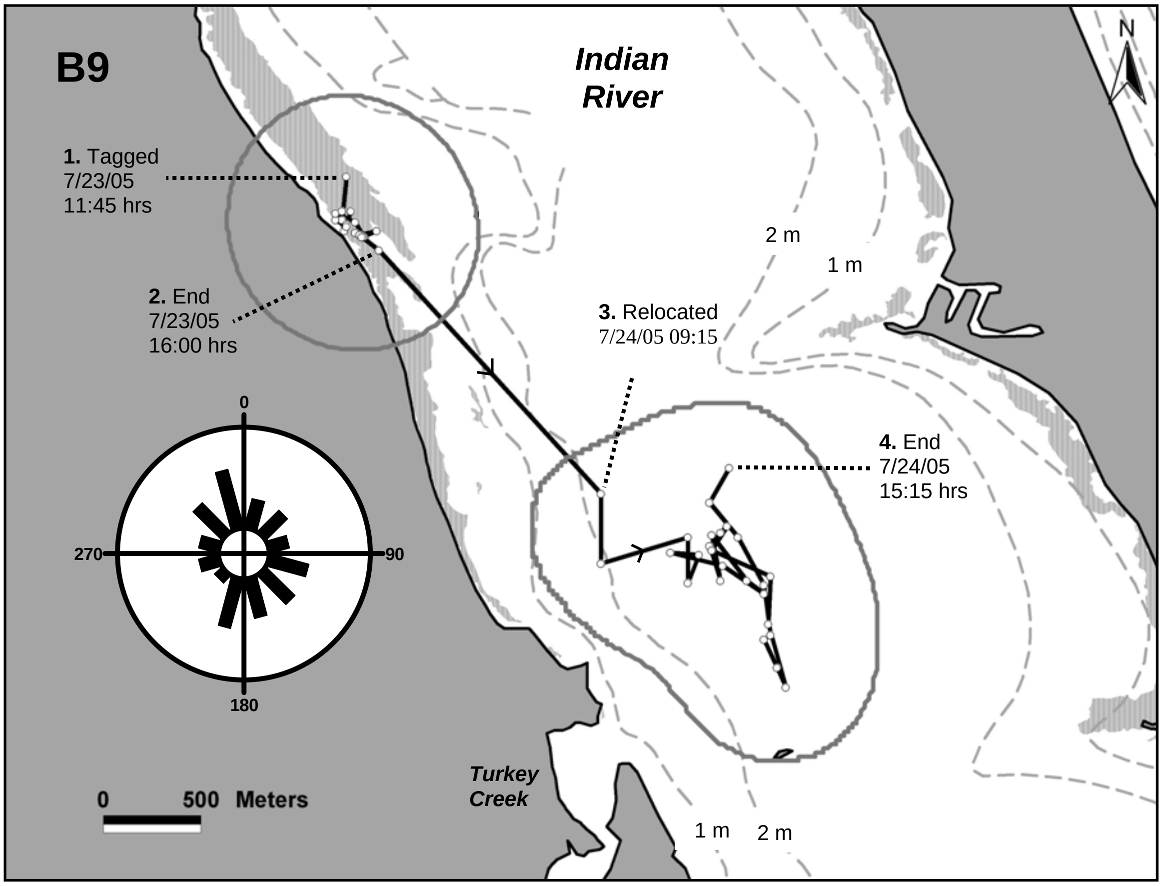

Figure 3-9. Manual acoustic track of bull shark B9, a 65 cm FL male, in the IRL between 23 and 24 July, 2005. Points represent 15-min tracking positions. The dashed lines represent 1 m depth contours, and the lightly stippled area represents seagrass beds. The gray line surrounding the track positions represents the 95% KUD. In the inset directionality histogram, the outer edge of the circle represents 10 observations.

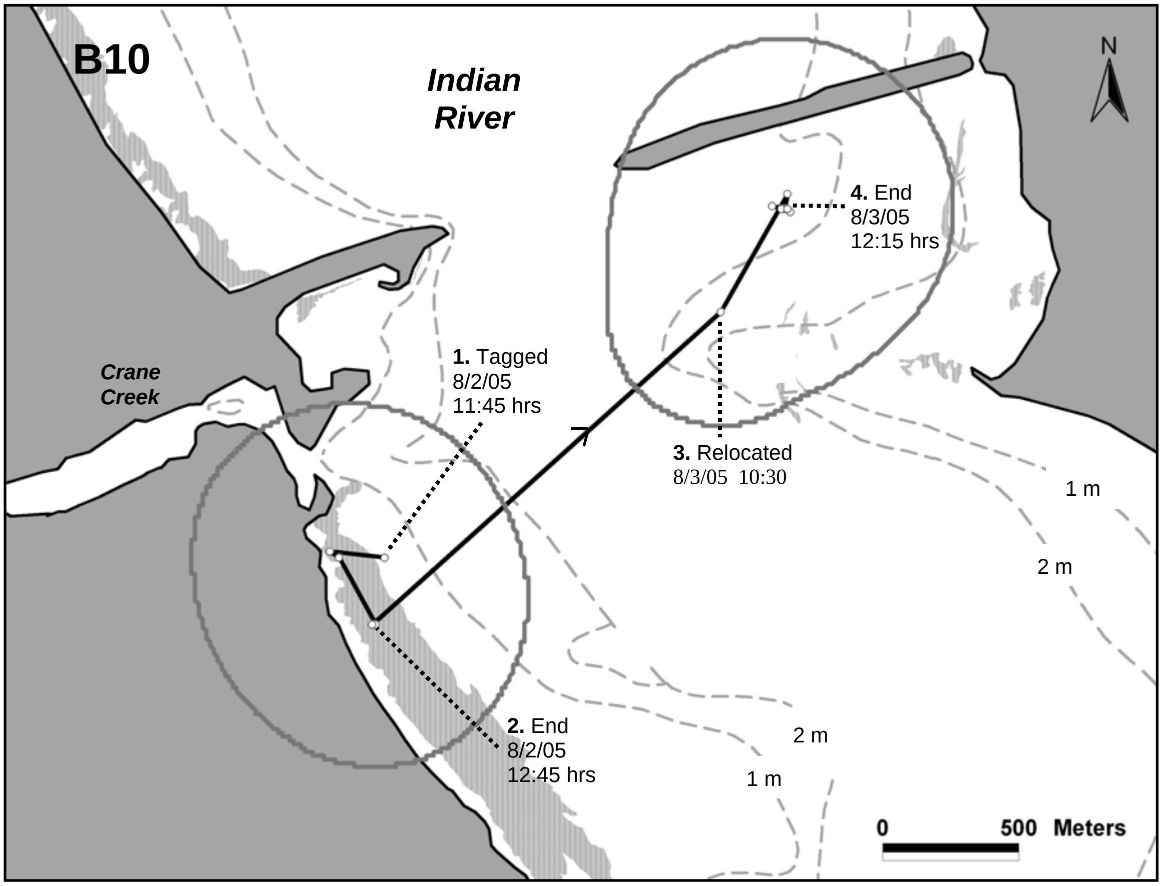

Figure 3-10. Manual acoustic track of bull shark B10, a 61 cm FL female, in the IRL between 2 and 3 August, 2005. Points represent 15-min tracking positions. The dashed lines represent 1 m depth contours, and the lightly stippled area represents seagrass beds. The gray line surrounding the track positions represents the 95% KUD.

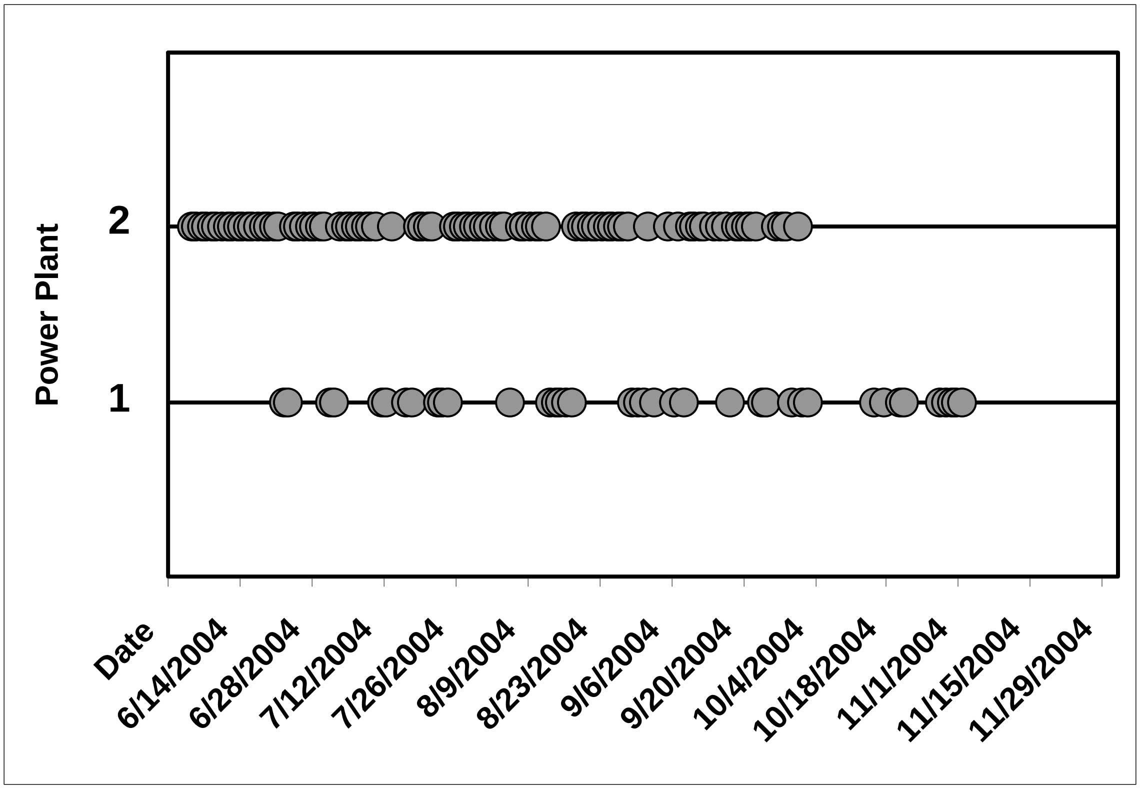

Figure 3-11. Site fidelity (days detected) of an acoustically tagged YOY bull shark (B11) at two power plants in the northern IRL during the summer and fall of 2004. Power plant 1 is the Florida Power and Light plant in Frontenac, FL, and power plant 2 is the Reliant Energy plant in Delespine, FL. The distance between the power plant outfalls is 3.4 km.

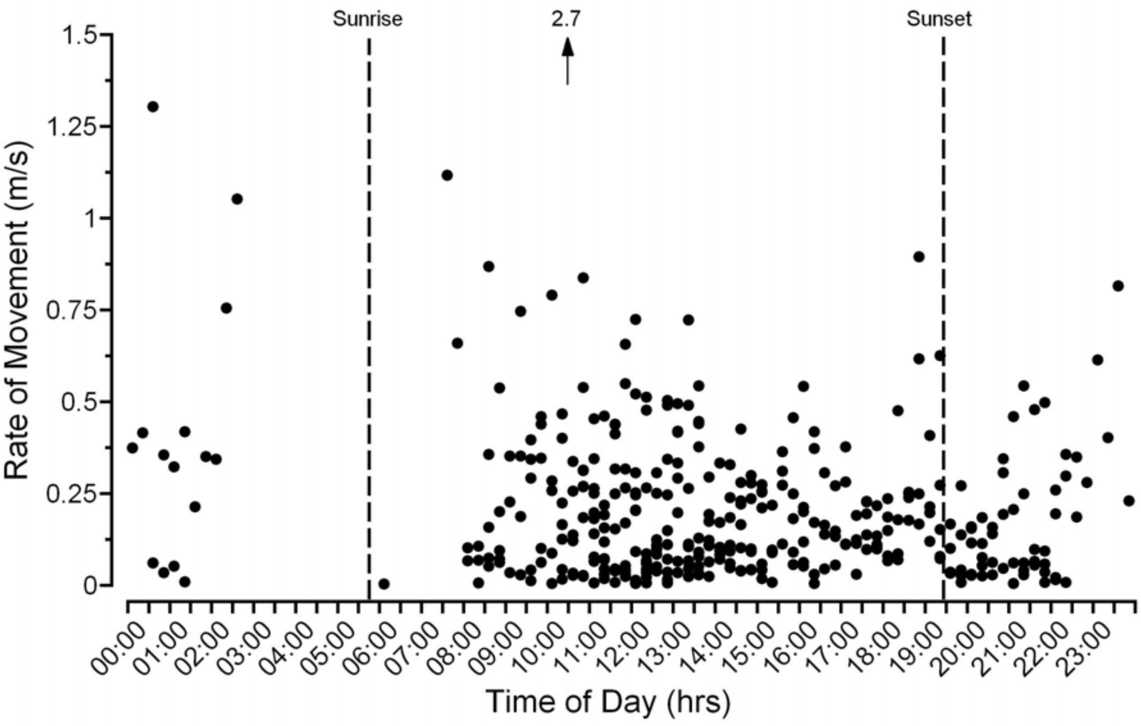

Figure 3-12. Scatter plot of ROM calculations versus the time of day for nine tracked bull sharks (B2 excluded due to positional error) in the IRL. The vertical dashed lines indicate the median times of sunrise and sunset across all tracks.

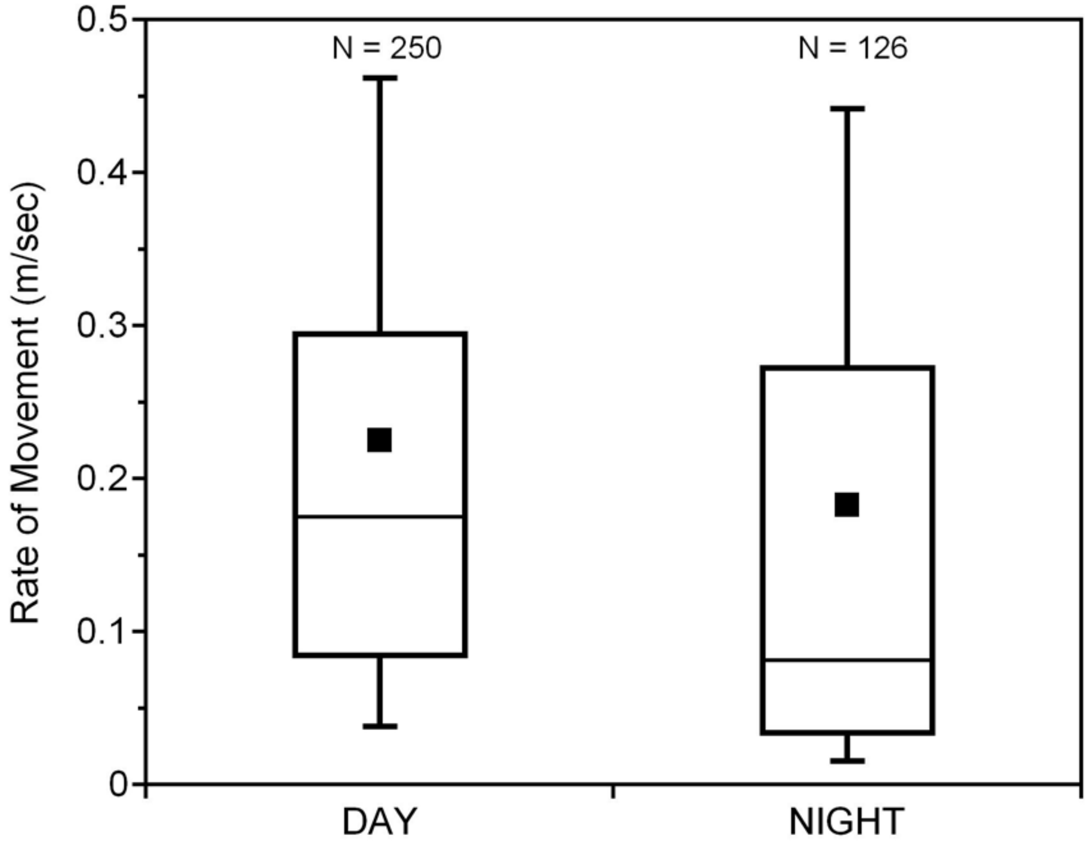

Figure 3-13. Box plots of ROM calculations comparing day and night observations to examine potential diel activity patterns. The box and whiskers represent (from bottom to top) the 10th, 25th, 50th, 75th, and 90th percentiles of observations. The square symbol represents the mean.

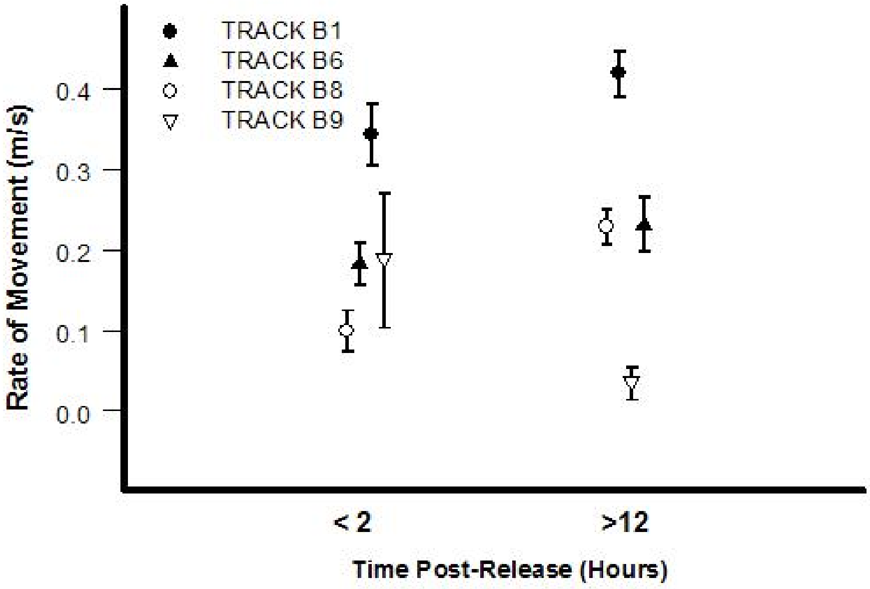

Figure 3-14. Comparison of rates-of-movement (mean ± 1 SE) obtained from ultrasonic tracking of four juvenile bull sharks captured in Indian River Lagoon, FL in the first 2 hours following release and after twelve hours post-release.

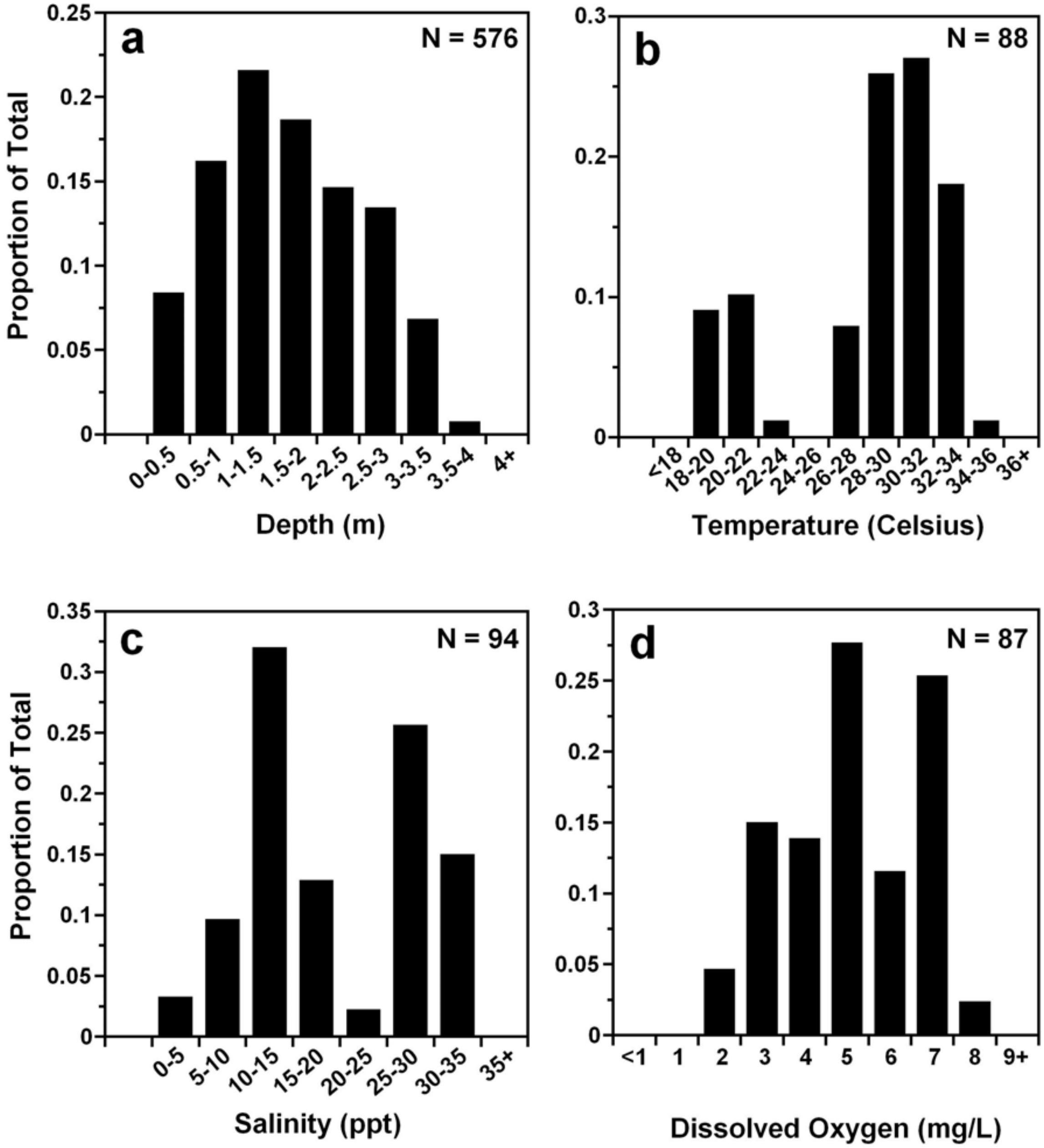

Figure 3-15. Environmental parameters observed during tracks of ten bull sharks in the IRL, including (a) depth, (b) temperature, (c) salinity, (d) dissolved oxygen concentration, and (e) secchi depth.

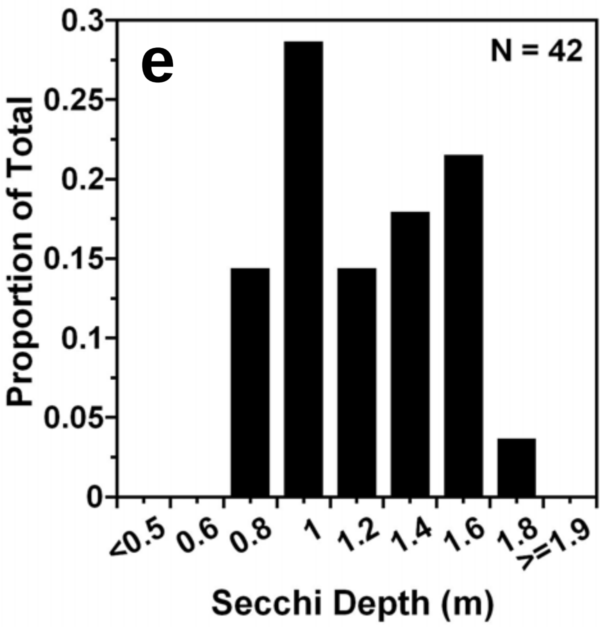

Figure 3-15. Continued

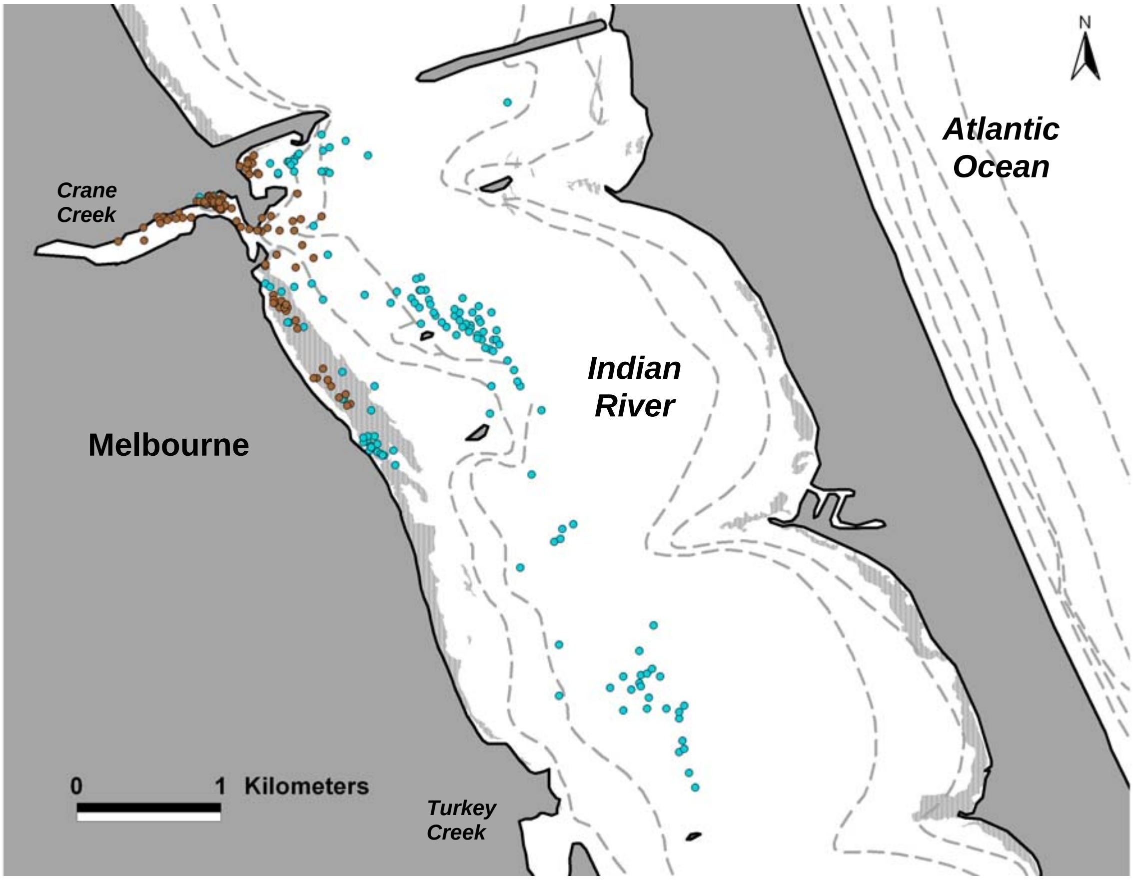

Figure 3-16. Tracking positions for seven bull sharks tracked near Crane Creek in the IRL during dry (brown positions, N=3) and wet (blue positions, N=4) periods, as defined by the surface salinity at the mouth of Crane Creek.

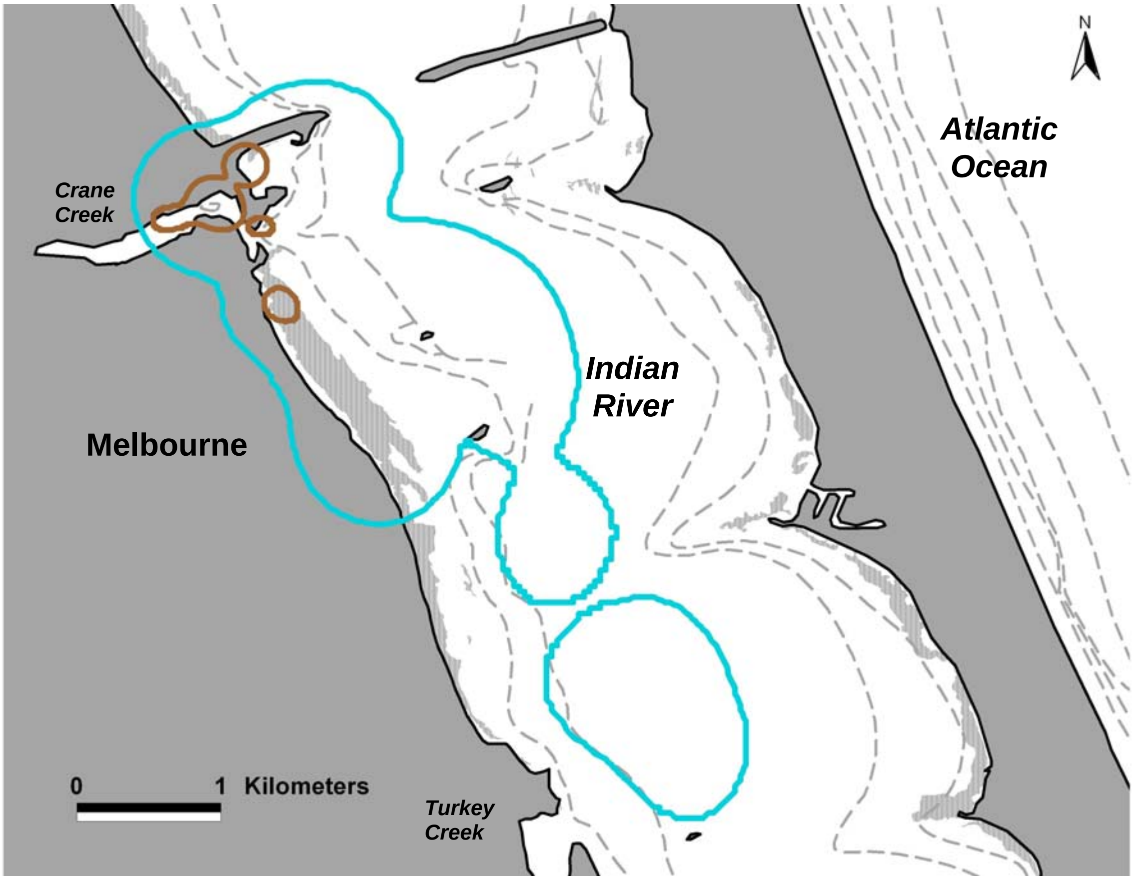

Figure 3-17. Cumulative 95% UDs for seven bull sharks tracked near Crane Creek in the IRL during dry (brown lines, N=3) and wet (blue lines, N=4) periods, as defined by the surface salinity at the mouth of Crane Creek (><10 ppt). Note the sharks' high site fidelity to the creek during dry periods.

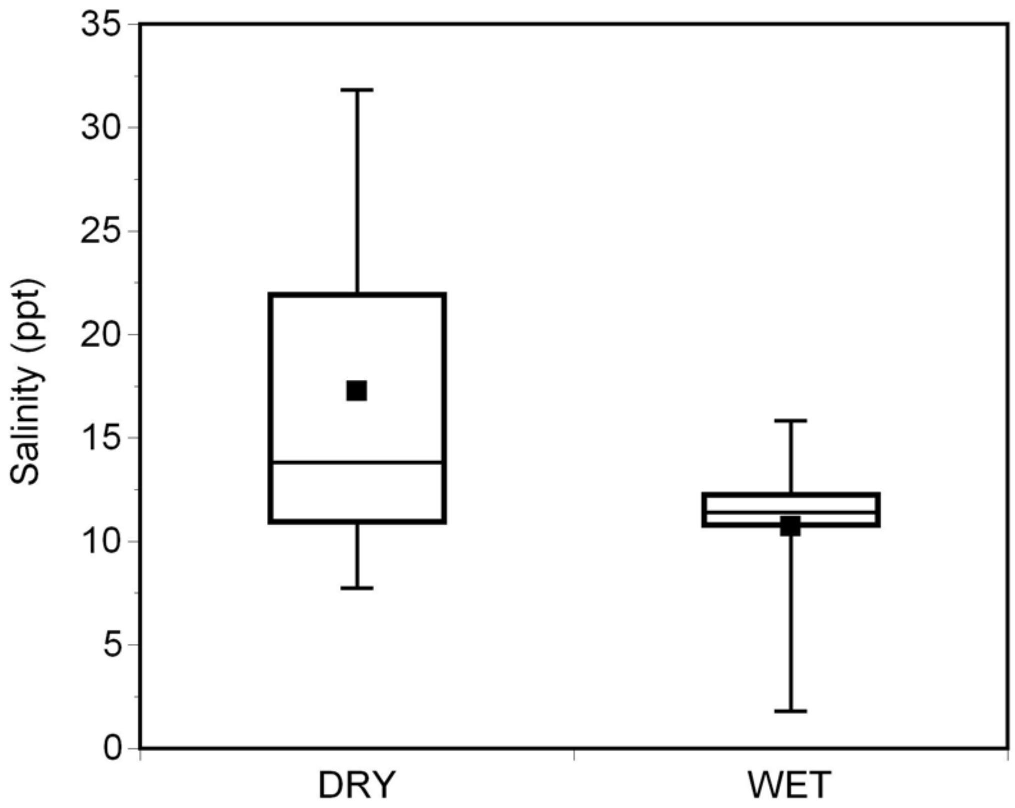

Figure 3-18. Box plots comparing the salinity utilization of seven bull sharks tracked near Crane Creek in the IRL during dry (N=3) and wet (N=4) periods, as defined by the surface salinity at the mouth of Crane Creek. Note that the 25th percentiles of observations are nearly equivalent at approximately 11 ppt.

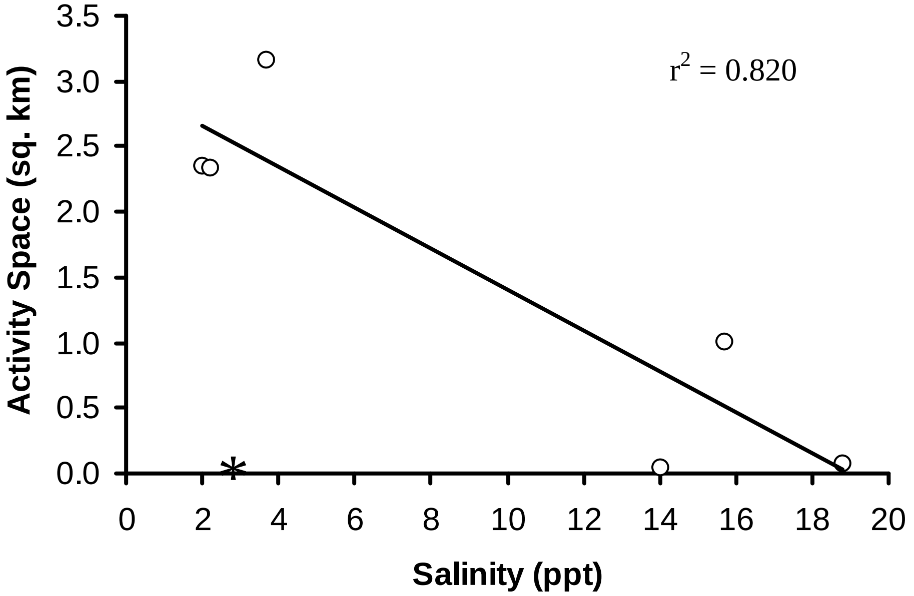

Figure 3-19. Linear correlation between bull shark activity space and salinity at the mouth of Crane Creek (N=6). * Indicates an outlier (B7) which was not included in the regression.

CHAPTER 4
CONCLUSIONS AND APPLICATIONS

This study utilized two primary methods to investigate bull shark distribution and habitat use in the IRL, and provided evidence for its role as a nursery area for this species. Fishery-independent sampling data were compiled and synthesized to provide insights into patterns of seasonal occurrence, spatial distribution, and habitat associations. These data provided a comprehensive, but coarse, overview of bull shark ecology in the study site over a span of 30 years, based on data collected from 390 individual sharks. Tagging and acoustic telemetry methods were also employed to acquire more fine scale information on shark movements, daily activities, and habitat utilization. A total of 50 sharks were marked with conventional tags, with four fish recaptured over the course of the study. Eleven of these sharks were additionally tagged with acoustic pingers, ten of which were manually tracked and one of which was monitored by moored listening stations (Vemco VR2). The manual tracking data provided fine-scale information on the patterns of movements of a small number of individuals. Integration of multiple methodologies provided a more complete picture of habitat use by this important apex predator the IRL. These results may prove useful to the continued management and conservation of bull shark stocks in the northwest Atlantic.

Bull Shark Ecology in the Indian River Lagoon

The IRL, a shallow, productive estuarine system, serves as a nursery area for bull sharks. All size classes of immature sharks are present in the system, including neonates, YOY, young and older juveniles, and maturing sub-adults. In addition, the only adults reported from the system have been gravid females that arrive in the lagoon in the late spring for parturition. The immature sharks appear to utilize the lagoon until approximately 9 years of age when they transition to offshore adult habitats. Bull sharks occur year round in the southern reaches of the study site, but appear to migrate out of the northernmost portions during winter months when temperatures drop below approximately 20 °C. As noted by Snelson et al. (1984), some bull sharks remained near heated power plant outfalls during winter months and appear to use these areas as thermal refugia. The sharks were generally more abundant in the system during spring, summer, and autumn. During this time they forage throughout the lagoon in shallow seagrass and sandy habitats, as well as in low salinity creeks, on various species of fish (Snelson et al. 1984). Given their size and broad dietary habits, juvenile bull sharks are among the lagoon's apex predators, and likely have an important function in maintaining the health of the ecosystem.

The short term movements and daily activities of YOY and juvenile bull sharks appear to be limited to comparatively small activity spaces. The sharks tend to show relatively high levels of area reuse and site attachment to areas such as power plant outfalls and freshwater creeks. These areas are presumably used either for foraging activities or as refugia from predators (i.e. larger bull sharks). Overall habitat use by bull sharks was broad, but there was more frequent use of depths between 1 and 2 m, temperatures of 28 – 34 °C, salinities of 10 – 25 ppt, DO concentrations of 4 – 7 mg/L, and water clarity levels of 0.8 – 1.4 m. Salinity appears to play an important role in the distribution and activity spaces of YOY and juvenile bull sharks. Young-of-the-year sharks tended to utilize lower mean salinity areas than juveniles, creating a level of size/age segregation in the population. The activity spaces of sharks were also notably larger during wet periods than dry periods in the vicinity of Crane Creek, supporting evidence of selection for low salinity environments in the lagoon. The mechanisms that drive these selection patterns require further investigation. These findings are largely consistent with the results of other recent investigations into bull shark nursery areas (Simpfendorfer et al. 2005; Wiley and Simpfendorfer 2007; McCandless et al. 2007).

Applications to Shark Management and Conservation

The concept of essential fish habitat (EFH) has driven much of the recent research into shark nurseries in U.S. waters (McCandless et al. 2002; 2007). The delineation, description, and conservation of such areas are necessary components of federal fishery management plans, and this study can be applied to the body of EFH information for bull sharks. The findings of the present study suggests that for most of the year, the IRL as a whole functions as a nursery area for this species, in the sense of Heupel et al. (2007). However, there are specific areas within the system that are candidates to be prioritized for protection: 1) The southern portion of Mosquito Lagoon, 2) the outfall areas of the Delespine (Reliant Energy) and Frontenac (Florida Power and Light) power plants, 3) Eau Gallie, Crane, and Turkey Creeks, and their adjacent shorelines in Melbourne, and 4) Sebastian Inlet. These areas had the highest catch rates of immature bull sharks and include important sites for parturition, foraging, refuge, and interchange with oceanic habitats for the sharks. Such locations may be critical to the continued survival of IRL bull sharks. Should the stock status of bull sharks require greater protection of EFH, these areas could be designated as Habitat Areas of Particular Concern. Given the dramatic rate of human development along Florida’s Atlantic coast (e.g. Gilmore 1995), the associated habitat alterations may presently be impacting sharks and other lagoon species in a detrimental manner. Given the close relationship between spawning stock and recruitment in many elasmobranchs (Hoenig and Gruber 1990; Cortes 2002), protection of juvenile portions of the population will tend to have direct, positive impacts on the rebuilding of depleted stocks.

Recommendations for Future Research

This research has expanded our understanding of the behavioral ecology of bull sharks in the IRL, but many important questions remain to be answered. Continued research efforts on bull sharks in this region will further benefit the species and its habitat. Before a more complete understanding of the bull shark's ecology in the IRL, and elsewhere, can be attained, this study identified several significant research questions that must be addressed. These include further investigations into abundance, movements, diet, habitat selection, and physiology of bull sharks in the IRL. Given the relatively low CPUE of bull sharks in much of the northern IRL (see Chapter 2), future focused studies may be more successful if centered in the Melbourne – Sebastian region and further south. These should include sampling in the southern IRL between Sebastian and Jupiter Inlets to investigate the seasonal distribution and habitat use of bull sharks in this region, from which little data is currently available.

Further ultrasonic tagging and tracking efforts, using both active and passive methods, will provide a great deal of valuable information on IRL bull sharks. Concurrent passive acoustic tracking studies of multiple species will also reveal new insights into predatory-prey dynamics and the complexity of how large consumers partition their habitats and activities in the lagoon. Acoustic tracking of bull sharks will also help answer questions on their seasonal occurrence, site fidelity, home ranges, and habitat selection patterns. This may be a particularly useful method to further investigate the apparent salinity preference differences between YOY and juvenile bull sharks. With the miniaturization and increase in the reliability of satellite tagging technology, these sophisticated devices may be attached to small sharks and will archive information on long term, large scale movements, as well as depth and temperature preferences. Telemetry techniques such as these should applied to a larger size range of bull sharks, so that ontogenetic changes in movements and migrations might be detected.

Based on the results of the current study, it can be postulated that the IRL is a low predation-risk environment, given the apparent relative absence of large predators of small sharks. A telemetry-based study of the mortality rates of juvenile sharks using survival analysis would refute or support this conjecture. In addition, the tradeoffs between foraging and predation-risk warrant further investigation. Well-designed studies on shark activity space in relation to prey density may support or refute an optimal foraging hypothesis. Updated diet studies, including stable isotope analyses, would also support such efforts. To date, similar studies have had mixed results in other shark nurseries, and investigators should be aware of the caveats and the importance of sampling design, including aspects of community structure, indirect interactions, anti-predator behavior of prey, and competition (Heithaus 2001; 2004; 2007).

The unique physiology of bull sharks, especially their osmoregulatory capabilities, also requires further investigation. Though several studies have described the physiological mechanisms of elasmobranch osmoregulation (e.g. Evans et al. 2004; Pillans et al. 2005), none have made the direct connection between physiology and ecology. What are the metabolic costs for immature bull sharks to acclimate to freshwater? Is there an energetic benefit for YOY sharks to remain in lower salinity waters than juveniles? Laboratory-based experiments may be required to investigate these questions, possibly by measuring oxygen consumption rates of small bull sharks acclimating to various salinities. Investigations into the physiological responses of bull sharks to water contaminants would also be valuable. Because of their position as apex predators and long lifespan, bull sharks bioaccumulate many harmful chemicals in their systems, including mercury, PCBs, PBDEs, and various pharmaceuticals (Adams and McMichael 1999; Johnson-Restrepo et al. 2005; Gelsleichter and Szabo 2007). It is not currently known if these chemicals are actually detrimental to the survival of young bull sharks. If water pollution in nearshore shark nursery areas does have an adverse impact on shark health, then the success of fishery-related management and conservation efforts could be limited or reduced. Above all, these recommendations underscore the importance of a multidisciplinary approach to address problems and questions of shark biology. With advancing technologies and analytical methods, future studies on the value of shark nursery areas should prove enlightening.

LIST OF REFERENCES

Adams DH, Paperno R (2007) Preliminary assessment of a nearshore nursery ground for the scalloped hammerhead off the Atlantic coast of Florida. Pages 165-174 in McCandless CT, Kohler NE, and Pratt HL Jr (eds). Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society, Symposium 50, Bethesda, Maryland.

Adams DH, McMichael RE (1999) Mercury levels in four species of sharks from the Atlantic coast of Florida. Fish Bull 97:372-379.

Bass AJ, D'Aubrey JD, Kistnasamy N (1973) Sharks of the east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). Invest Rep Oceanogr Res Inst 33:1-168.

Bass AJ (1977) Long-term recoveries of tagged sharks. Copeia 1977(3):574-575.

Bass AJ (1978) Problems in studies of sharks in the southwest Indian Ocean. Pages 545-594 in Hodgson ES, Matthewson RF (eds). Sensory Biology of Sharks, Skates, and Rays. Office of Naval Research, Dep Navy, Arlington, VA.

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51(8):633-641.

Bell WJ, Kramer E (1979) Search for anemotactic orientation of cockroaches. J Insect Physiol 25:631–640.

Blackburn JK, Neer JA, Thompson BA (2007) Delineation of bull shark nursery areas in the inland and coastal waters of Louisiana. Pages 331-343 in McCandless CT, Kohler NE, and Pratt HL Jr (eds). Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society, Symposium 50, Bethesda, Maryland.

Branstetter S (1981) Biological notes on the sharks of the north central Gulf of Mexico. Contr Mar Sci Univ Texas 24:13-34.

Branstetter S (1990) Early life-history implications of selected carcharhinoid and lamnoid sharks of the Northwest Atlantic. NOAA Tech Rep NMFS 90:17-28.

Branstetter S, Stiles R (1987) Age and growth of the bull shark, *Carcharhinus leucas*, from the northern Gulf of Mexico. Environ Biol Fish 20(3):169-181.

Brown S (1999) Trends in the commercial and recreational shark fisheries in Florida, 1980-1992, with implications for management. N Am J Fisheries Management 19:28-41.

Brown J, Colling A, Park D, Phillips J, Rothery D, Wright J (1999) Waves, tides, and shallow water processes. Bearman G (ed). Open University Press, England. 187 pp.

Brunnschweiler J, Buskirk JV (2006) Satellite tagging of bull sharks at Walker's Cay in the Bahamas. Bahamas Naturalist and J Sci 1(1):30-34.

Bullen E, Mann BQ (2000) Sedgewick's/ORI/WWF Tagging Programme: Zambezi shark (*Carcharhinus leucas*). Data Report, Oceanographic Research Institute 2000(11). 6 pp.

Burgess GH, Beerkircher LR, Cailliet GM, Carlson JK, Cortes E, Goldman KJ, Grubbs RD, Musick JA, Musyl MK, Simpfendorfer CA (2005) Is the collapse of shark populations in the northwest Atlantic Ocean and Gulf of Mexico real? Fisheries 30(10):19-26.

Bush A, Holland K (2003) Food limitation in a nursery area: estimates of daily ration in juvenile scalloped hammerheads, *Sphyrna lewini* (Griffith and Smith, 1834) in Kâne'ohe Bay, Ô'ahu, Hawai'i. J Exp Mar Biol Ecol 278:151–178.

Caillouet CW, Perret WS, Fontenot BJ (1969) Weight, length and sex ratio of immature bull sharks, *Carcharhinus leucas*, from Vermilion Bay, Louisiana. Copeia 1969:196-197.

Carey FG, Kanwisher JW, Brazier O, Gabrielson G, Casey JG, Pratt HL (1982) Temperature and activities of a white shark, *Carcharodon carcharias*. Copeia 1982:254-260.

Carey FG, Scharold JV (1990) Movements of blue shark (*Prionace glauca*) in depth and course. Mar Biol 106:329-342.

Carlson JK, Brusher JH (1999) An index of abundance for juvenile coastal species of sharks from the northeast Gulf of Mexico. Mar Fish Rev 61:37–45.

Cartamil DP, Vaudo JJ, Lowe CG, Wetherbee BM, Holland KN (2003) Diel movement patterns of the Hawaiian stingray, *Dasyatis lata*: implications for ecological interactions between sympatric elasmobranch species. Mar Biol 142(5):841-847.

Castro JI (1983) The Sharks of North American Waters. College Station, TX, Texas A&M University Press.

Castro JI (1993) The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environ Biol Fish 38:37-48.

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

Clarke TA (1971) The ecology of the scalloped hammerhead shark, *Sphyrna lewini*, in Hawaii. Pac Sci 25(2):133-144.

Cliff G, Dudley SFJ (1991) Sharks caught in the protective gill nets off Natal, South Africa. 4. The bull shark *Carcharhinus leucas* Valenciennes. S Afr J Mar Sci 10, 253-270.

Compagno LJV (1984) FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2 - Carcharhiniformes. Food Agric Org United Nations FAO Fisheries Synopsis 125(4, pt. 2):251-655.

Cortes E (2002) Incorporating uncertainty into demographic modeling: Application to shark populations and their conservation. Con Biol 16(4):1048-1062.

Cortes E, Brooks L, Scott G (2002) Stock assessment of large coastal sharks in the U.S. Atlantic and Gulf of Mexico. Sustainable Fisheries Division Contribution SFD-02/03-177. NMFS Southeast Fisheries Science Center, Panama City, Florida. 63 pp.

Cruz-Martinez A, Chiappa-Carrara X, Arenas-Fuentes V (2002) Age and growth of the bull shark *Carcharhinus leucas* from the southern Gulf of Mexico. Northwest Atlantic Fisheries Organization Scientific Council Meeting, September 2002, NAFO SCR Doc. 02/88. 11 pp.

Deutsch CJ, Reid JP, Bonde RK, Easton DE, Kochman HI, O'Shea TJ (2003) Seasonal movements, migratory behavior, and site fidelity of West Indian manatees along the Atlantic coast of the United States. Wildl Mono 151. 77 pp.

Dodrill JW (1977) A hook and line survey of the sharks found within five hundred meters of shore along Melbourne Beach, Brevard County, Florida. MSc Thesis. Florida Institute of Technology, Melbourne, Florida.

Evans DH, Piermarini PM, Choe KP (2004) Homeostasis: Osmoregulation, pH regulation, and nitrogen excretion. Pages 247-268 in Carrier JC, Musick JA, Heithaus MR (eds.) Biology of Sharks and Their Relatives. CRC Press, Boca Raton, Florida.

Garrick JAF (1982) Sharks of the genus *Carcharhinus*. NOAA Tech Rep NMFS circ 445.

Gedamke T, Hoenig JM, Musick JA, DuPaul WD, Gruber SH (2007) Using demographic models to determine intrinsic rate of increase and sustainable fishing for elasmobranchs: pitfalls, advances, and applications. N Am J Fisheries Management 27:605-618.

Gelsleichter J, Szabo N (2007) Are bull sharks on drugs? Preliminary observations on human pharmaceutical exposure and uptake in juvenile bull sharks (*Carcharhinus leucas*) residing in wastewater-impacted freshwater habitats. Proceedings of the 23rd Annual Meeting of the American Elasmobranch Society, St. Louis, Missouri.

Gilmore RG (1977). Fishes of the Indian River Lagoon and adjacent waters, Florida. Bull Florida State Mus, Biol Sci 22(3):101-148.

Gilmore RG, Bullock LH, Berry FH (1978). Hypothermal mortality in marine fishes of south-central Florida. Northeast Gulf Sci 2(2):77-97.

Gilmore RG (1995). Environmental and biogeographic factors influencing ichthyofaunal diversity: Indian River Lagoon. Bull Mar Sci 57(1):153-170.

Goldman KJ, Anderson SD (1999) Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, central California. Environ Biol Fish 56:351-364.

Grubbs RD, Musick JA (2002) Shark nurseries of Virginia: Spatial and temporal delineation, migratory patterns, and habitat selection; a case study. Pages 25-60 in McCandless CT, Pratt HL Jr, Kohler NE (eds). Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States: an overview. NMFS Internal Report to NOAA's Highly Migratory Species Office.

Hammerschlag N (2006) Osmoregulation in elasmobranchs: a review for fish biologists, behaviorists and ecologists. Mar Freshwater Behaviour and Physiol 39(3):209-228.

Heithaus MR (2001) Habitat selection by predators and prey in communities with asymmetrical intraguild predation. Oikos 92:542–554.

Heithaus MR, Dill LM, Marshall GJ, Buhleier B (2002) Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. Mar Biol 140:237-248.

Heithaus MR (2004) Predator-prey interactions. Pages 487-522 in Carrier JC, Musick JA, Heithaus MR (eds.) Biology of Sharks and Their Relatives. CRC Press, Boca Raton, Florida.

Heithaus MR (2007) Nursery areas as essential shark habitats: a theoretical perspective. Pages 3-13 in McCandless CT, Kohler NE, and Pratt HL Jr (eds). Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society, Symposium 50, Bethesda, Maryland.

Heupel MR, Hueter RE (2001) Use of an automated acoustic telemetry system to passively track juvenile blacktip shark movements. Pages 217-236 in Sibert JR, Nielsen JL (eds). Electronic Tagging and Tracking in Marine Fisheries. Kluwer Academic Publishers: Netherlands.

Heupel MR, Hueter RE (2002) The importance of prey density in relation to the movement patterns of juvenile sharks within a coastal nursery area. Mar Freshwater Res 53:543–550.

Heupel MR, Simpfendorfer CA (2002) Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. Can J Fisheries and Aquat Sci 59:624–632.

Heupel MR, Simpfendorfer CA, Hueter RE (2004) Estimation of shark home ranges using passive monitoring techniques. Environ Biol Fish 71:135–142.

Heupel MR, Simpfendorfer CA, Collins AB, Tyminski JP (2006) Residency and movement patterns of bonnethead sharks (*Sphyrna tiburo*) in a large Florida estuary. Environ Biol Fish 76(1):47-67.

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Mar Ecol Prog Ser 337:287-297.

Hoenig JM, Gruber SH (1990) Life-history patterns in the elasmobranchs: implications for fisheries management. NOAA Tech Rep NMFS 90:1-16.

Holland KN, Wetherbee BM (1999) Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. Mar Biol 134:665-673.

Holland KN, Wetherbee BM, Peterson JD, Lowe CG (1993) Movements and distribution of hammerhead shark pups on their natal grounds. Copeia 1993:495-502.

Hooge PN, Eichenlaub W, Solomon E (1999) The animal movement program. USGS, Alaska Biological Science Center.

Hopkins TE, Cech JJ (2003) The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California. Environ Biol Fish 66:279-291.

Hueter RE, Manire CA (1994) Bycatch and catch-release mortality of small sharks in the Gulf coast nursery grounds of Tampa Bay and Charlotte Harbor. Mote Marine Laboratory Tech Rep No 368. 183 pp.

Hueter RE, Tyminski JP (2002) Center for Shark Research (CSR) U.S. shark nursery research overview 1991-2001. Pages 116-135 in McCandless CT, Pratt HL Jr., Kohler NE (eds). Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States: an overview. NMFS Internal Report to NOAA's Highly Migratory Species Office.

Hueter RE, Tyminski JP (2007) Species-specific distribution and habitat characteristics of shark nurseries in Gulf of Mexico waters off peninsular Florida and Texas. Pages 193-223 in McCandless CT, Kohler NE, and Pratt HL Jr (eds). Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society, Symposium 50, Bethesda, Maryland.

Hueter RE, Heupel MR, Heist EJ, Keeney DB (2005) Evidence of philopatry in sharks and implications for the management of shark fisheries. J Northwest Atl Fishery Sci 35:239–247.

Jennings SD, Reynolds JD, Mills SC (1998) Life history correlates of responses to fisheries exploitation. Proc Royal Soc London B. 265:333-337.

Johnson-Restrepo B, Kannan K, Addink R, Adams DH (2005) Polybrominated diphenyl ethers and polychlorinated biphenyls in a marine foodweb of coastal Florida. Environ Sci Technol 39:8243-8250.

Jones LM, Grace MA (2002) Shark nursery areas in the bay systems of Texas. Pages 209-219 in McCandless CT, Pratt HL Jr., Kohler NE (eds). Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States: an overview. NMFS Internal Report to NOAA's Highly Migratory Species Office.

Kelly JT, Klimley AP, Crocker CE (2006) Movements of green sturgeon, *Acipenser medirostris,* in the San Francisco Bay estuary, California. Environ Biol Fish 79:281-295.

Kelt DA, Van Vuren DH (2001) The ecology and macroecology of mammalian home range area. Am Naturalist 157:637-645.

Kidder GW (1997) Behavioral osmoregulation in *Fundulus heteroclitus*. Bull Mount Desert Island Biological Laboratory 36:69.

Kidder GW, Petersen CW, Preston RL (2006) Energetics of osmoregulation: II. Water flux and osmoregulatory work in the euryhaline fish, *Fundulus heteroclitus*. J Exp Zoolog A Comp Exp Biol 305(4):318-327.

Klimley AP, Beavers SC, Curtis TH, Jorgensen SJ (2002) Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. Environ. Biol. Fish. 63:117-135.

Klimley AP, Nelson DR (1984) Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. Behav Ecol Sociobiol 15:45-54.

Klimley AP, Le Boeuf BJ, Cantara KM, Richert JE, Davis SF, Van Sommeran S, Kelly JT (2001) The hunting strategy of white sharks (*Carcharodon c*archarias) near a seal colony. Mar Biol 138:617–636.

Klimley AP, Kihslinger RL, Kelly JT (2005) Directional and non-directional movements of bat rays, *Myliobatis californica,* in Tomales Bay, California. Environ Biol Fish 74:79-88.

Kohler NE, Casey JG, Turner PA (1998) NMFS Cooperative Shark Tagging Program, 1962-93: an atlas of shark tag and recapture data. Mar Fish Rev 60(2).

Kohler NE, Turner PA (2001) Shark tagging: a review of conventional methods and studies. Environ Biol Fish 60:191-224.

Kupschus S, Tremain D (2001) Associations between fish assemblages and environmental factors in nearshore habitats of a subtropical estuary. J Fish Biol 58:1383-1403.

Laist DW, Reynolds JE (2005) Influence of power plants and other warm-water refuges on Florida manatees. Mar Mamm Sci 21(4):739-764.

Lowe CG, Goldman KJ (2001) Thermal and bioenergetics of elasmobranchs: bridging the gap. Environ Biol Fish 60:251-266.

Martin RA (2005) Conservation of freshwater and euryhaline elasmobranchs: a review. J Mar Biol Ass UK 85:1049-1073.

Matern SA, Cech JJ, Hopkins TE (2000) Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: evidence for behavioral thermoregulation? Environ Biol Fish 58:173-182.

McArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, New Jersey. 224 pp.

McCandless CT, Pratt HL Jr, Kohler NE (2002) Shark nursery grounds of the Gulf of Mexico and East Coast waters of the United States: an overview. NMFS Internal Rep to NOAA's Highly Migratory Species Office. 291 p.

McCandless CT, Kohler NE, and Pratt HL Jr (2007) Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society, Symposium 50, Bethesda, Maryland.

McNab BK (1963) Bioenergetics and the determination of home range size. Am Naturalist 894:133-140.

Medved RJ, Marshall JA (1983) Short-term movements of young sandbar sharks, *Carcharhinus plumbeus* (Pisces, Carcharhinidae). Bull Mar Sci 33:87-93.

Merson RR, Pratt HL Jr (2001) Distribution, movements and growth of young sandbar sharks, *Carcharhinus plumbeus*, in the nursery grounds of Delaware Bay. Environ Biol Fish 61:13-24.

Michel M (2002) Environmental factors affecting the distribution and abundance of sharks in the mangrove estuary of the Ten Thousand Islands, Florida, USA. PhD Dissertation. University of Basel, Switzerland. 134 pp.

Miklos P, Katzman SM, Cech JJ (2003) Effect of temperature on oxygen consumption of the leopard shark, *Triakis semifasciata*. Environ Biol Fish 66:15-18.

Montoya RV, Thorson TB (1982) The bull shark (*Carcharhinus leucas*) and largetooth sawfish (*Pristis perotteti*) in Lake Bayano, a tropical man-made impoundment in Panama. Environ Biol Fish 7(4):341-347.

Morrissey JF, Gruber SH (1993a) Home range of juvenile lemon sharks, *Negaprion brevirostris*. Copeia 1993:425-434.

Morrissey JF, Gruber SH (1993b) Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. Environ Biol Fish 38:311-319.

Musick JA, Branstetter S, Colvocorosses JA (1993) Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. Mid-Atlantic Coast. Pages 1–18 in S. Branstetter (ed) Conservation biology of elasmobranchs. NOAA Tech Rep NMFS 115.

Neer JA, Thompson BA, Carlson JK (2005) Age and growth of *Carcharhinus leucas* in the northern Gulf of Mexico: incorporating variability in size at birth. J Fish Biol 67:370-383.

Nelson DR (1978) Telemetering techniques for the study of free-ranging sharks. Pages 419-482 in Hodgson ES, Matthewson RF (eds). Sensory Biology of Sharks, Skates, and Rays. Office of Naval Research, Dep Navy, Arlington, VA.

Nelson DR (1990) Telemetry studies of sharks: a review, with applications in resource management. NOAA Tech Rep NMFS 90:239-256.

NMFS (1993) Fishery Management Plan for sharks of the Atlantic Ocean. U.S. Dep. Commer., NOAA, NMFS. 167 p.

NMFS (1999) Final Fishery Management Plan for Atlantic Tunas, Swordfish and Sharks. Highly Migratory Species Management Division, Office of Sustainable Fisheries, NMFS, Silver Spring, Maryland.

NMFS (2006) Final Consolidated Atlantic Highly Migratory Species Management Plan. National Oceanic and Atmospheric Administration, NMFS Highly Migratory Species Management Division, Silver Spring, Maryland. Public Document. 1600 pp.

Odum E, Kuenzler EJ (1955) Measurements of territory and home range size in birds. Auk. 72:128–137.

Oguri M (1964) Rectal glands of marine and fresh-water sharks: comparative histology. Science 144:1151-1152.

Paperno R, Tremain DM, Adams DH, Sebastian AP, Sauer JT, Dutka-Gianelli J (2006) The disruption and recovery of fish communities in the Indian River Lagoon, Florida, following two hurricanes in 2004. Estuaries and Coasts 29(6A):1004-1010.

Phlips E, Badylak S, Grosskopf T (2002) Factors affecting the abundance of phytoplankton in a restricted subtropical lagoon, the Indian River Lagoon, Florida, USA. Estuarine, Coastal and Shelf Sci 55:385-402.

Piermarini PM, Evans DH (1998) Osmoregulation of the Atlantic stingray (*Dasyatis sabina*) from the freshwater Lake Jesup of the St. Johns River. Florida. Physiol Zool 71:553-560.

Pillans RD, Good JP, Anderson WG, Hazon N, Franklin CE (2005) Freshwater to seawater acclimation of juvenile bull sharks (*Carcharhinus leucas*): plasma osmolytes and Na+/K+-ATPase activity in gill, rectal gland, kidney and intestine. J Comp Physiol B 175:37–44.

Pitcher TJ, Hart PJB (1982) Fisheries Ecology. The AVI Publishing Co., Inc. 414 pp.

Pratt HL Jr, McCandless CT, Kohler NE, Jensen C, Ulrich G, Gilligan M (1998) COASTSPAN: Report of the 1998 Apex Predators Program Cooperative Atlantic States Shark Pupping and Nursery Grounds Project. US Dep Commer, NOAA, NMFS, NEFSC, Narragansett, RI. 62 p.

Rechisky EL, Wetherbee BM (2003) Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus,* on their nursery grounds in Delaware Bay. Environ Biol Fish 68:113-128.

Rice AN (2004) Diet and condition of American alligators (*Alligator mississippiensis*) in three central Florida lakes. MSc Thesis. University of Florida. 89 pp.

Rice AN, Ross JP, Woodward AR, Carbonneau DA, Percival HF (2007) Alligator diet in relation to alligator mortality on Lake Griffin, Florida. Southeastern Naturalist 6(1):97-110.

Sadowsky V (1971) Notes on the bull shark, *Carcharhinus leucas*, in the lagoon region of Carmaneia, Brazil. Bolm Inst Oceanogr Sao Paulo 20(2):71-78.

Sciarrotta TC, Nelson DR (1977) Diel behavior of the blue shark, *Prionace glauca*, near Santa Catalina Island, California. Fish Bull 75(3):519-528.

Schmid TH, Murru FL, McDonald F (1990) Feeding habits and growth rates of bull (*Carcharhinus leucas*, Valenciennes), sandbar (*Carcharhinus plumbeus,* Nardo), sandtiger (*Eugomphodus taurus*, Rafinesque), and nurse (*Ginglymostoma cirratum,* Bonnaterre) sharks maintained in captivity. J. Aquariculture and Aquatic Sci. 5(4):100-105.

Schmid TH, Murru FL (1994) Bioenergetics of the bull shark, *Carcharhinus leucas,* maintained in captivity. Zoo Biol 13:177-185.

Sibert JR, Nielsen JL (2001) Electronic Tagging and Tracking in Marine Fisheries. Kluwer Academic Publishers: Netherlands.

Simpfendorfer CA, Milward NE (1993) Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environ Biol Fish 37:337-345.

Simpfendorfer CA, Heupel MR, Hueter RE (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Can J Fish Aquat Sci 59:23-32.

Simpfendorfer CA, Heupel MR (2004) Assessing habitat use and movement. Pages 553–572 in Carrier JC, Musick JA, Heithaus MR (eds), Biology of Sharks and Their Relatives. CRC Press, Boca Raton, Florida.

Simpfendorfer CA, Freitas GG, Wiley TR, Heupel MR (2005) Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a southwest Florida estuary. Estuaries 28(1):78-85.

Snelson FF, Bradley WK (1978) Mortality of fishes due to cold on the east coast of Florida, January, 1977. Florida. Sci. 41(1):1-12.

Snelson FF, Mulligan TJ, Williams SE (1984) Food habits, occurrence, and population structure of the bull shark, *Carcharhinus leucas*, in Florida coastal lagoons. Bull Mar Sci 34:71-80.

Snelson FF, Williams SE (1981) Notes on the occurrence, distribution, and biology of elasmobranch fishes in the Indian River lagoon system, Florida. Estuaries 4:110-120.

Snelson FF, Williams-Hooper SE, Schmid TH (1989) Biology of the bluntnose stingray, *Dasyatis sayi*, in Florida coastal lagoons. Bull Mar Sci 45(1):15-25.

Springer S (1940) The sex ratio and seasonal distribution of some Florida sharks. Copeia 1940:188-194.

Springer S (1967) Social organization of shark populations. Pages 149-174 in Gilbert PW, Matthewson RF, Rall DP (eds). Sharks, Skates, and Rays. Hopkins Press, Baltimore, Maryland.

Steiner PA (2002) A comparative study on the activity patterns of the bull shark, *Carcharhinus leucas*, and the blacktip shark, *Carcharhinus limbatus*, in the Ten Thousand Islands estuary, Florida. PhD Dissertation. University of Basel, Switzerland. 115 pp.

Steiner PA, Michel M, O'Donnell PM (2007) Notes on the occurrence and distribution of elasmobranchs in the Ten Thousand Islands estuary, Florida. Pages 237-250 in McCandless CT, Kohler NE, and Pratt HL Jr (eds). Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society, Symposium 50, Bethesda, Maryland.

Sundström LF, Gruber SH, Clermont SM, Correia JPS, de Marignac JRC, Morrissey JF, Lowrance CR, Thomassen L, Oliveira MT (2001) Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. Environ. Biol. Fish. 60:225-250.

Thomerson JE, Thorson TB, Hempel RL (1977) The bull shark, *Carcharhinus leucas*, from the upper Mississippi River near Alton, Illinois. Copeia 1977:166-168.

Thorson TB (1962) Partitioning of body fluids in the Lake Nicaragua shark and three marine sharks. Science 138:688-690.

Thorson TB, Watson DE, Cowan CM (1966) The status of the freshwater shark of Lake Nicaragua. Copeia 1966:385-402.

Thorson TB (1971) Movements of bull sharks, *Carcharhinus leucas*, between Caribbean Sea and Lake Nicaragua demonstrated by tagging. Copeia 1971:336-338.

Thorson TB (1972) The status of the bull shark, *Carcharhinus leucas*, in the Amazon River. Copeia 1972:601-605.

Thorson TB, Cowan CM, Watson DE (1973) Body fluid solutes of juveniles and adults of the euryhaline bull shark, *Carcharhinus leucas,* from freshwater and saline environments. Physiol Zool 46:29-42.

Thorson TB (1976) The status of the Lake Nicaragua shark: An updated appraisal. Pages 561-574 in Thorson TB (ed). Investigations of the Ichthyofauna of the Nicaraguan Lakes. University of Nebraska.

Thorson TB, Lacy EJ (1982) Age, growth rate and longevity of *Carcharhinus leucas* estimated from tagging and vertebral rings. Copeia 1982:110-116.

Thorson TB (1982) The impact of commercial exploitation on sawfish and shark populations in Lake Nicaragua. Fisheries 7(2):2-10.

Torres LG, Heithaus MR, Delius B (2006) Influence of teleost abundance on the distribution and abundance of sharks in Florida Bay, USA. Hydrobiologia 569:449-455.

Tremain DM, Harnden CW, Adams DH (2004) Multidirectional movements of sportfish species between an estuarine no-take zone and surrounding waters of the Indian River Lagoon, Florida. Fish Bull 102:533-544.

Tricas TC, Taylor LR, Naftel G (1981) Diel behavior of the tiger shark, *Galeocerdo cuvier*, at French Frigate Shoals, Hawaiian Islands. Copeia 1981:904-908.

Tuma RE (1976) An investigation of the feeding habits of the bull shark, *Carcharhinus leucas*, in the Lake Nicaragua - Rio San Juan system. Pages 533-538 in Thorson TB (ed). Investigations of the Ichthyofauna of the Nicaraguan Lakes. University of Nebraska.

Vorenberg MM (1962) Cannibalistic tendencies of lemon and bull sharks. Copeia 1962:455-456.

Weihs D, Keyes R, Stalls D (1981) Voluntary swimming speeds of two species of carcharhinid sharks. Copeia 1981:219-222.

Weng KC, Boustany AM, Pyle P, Anderson SD, Brown A, Block BA (2007) Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. Mar Biol 152(4):877-894.

Wetherbee BM, Rechisky EL, Pratt HL Jr, McCandless CT (2001) Use of telemetry in fisheries management: juvenile sandbar sharks in Delaware Bay. Pages 249-262 in Sibert JR, Nielsen JL (eds). Electronic Tagging and Tracking in Marine Fisheries. Kluwer Academic Publishers: Netherlands.

Whitfield AK, Blaber SJM (1979) Predation on striped mullet (*Mugil cephalus*) by *Crocodylus niloticus* at St. Lucia, South Africa. Copeia 1979(2):266-269.

Wiley TR, Simpfendorfer CA (2007) The ecology of elasmobranchs occurring in the Everglades National Park, Florida: implications for conservation and management. Bull Mar Sci 80(1):171-189.

Wintner SP, Dudley SFJ, Kistnasamy N, Everett B (2002) Age and growth estimates for the Zambezi shark, *Carcharhinus leucas,* from the east coast of South Africa. Mar Freshwater Res 53(2):557-566.

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

Zar JH (1984). Biostatistical Analysis, 2nd edition. Prentice-Hall, Inc, Englewood Cliffs, New Jersey.

BIOGRAPHICAL SKETCH

Tobey Hayward Curtis was born in Fitchburg, Massachusetts on February 19, 1978. He graduated from Lunenburg High School in 1996, and graduated with a Bachelor of Science in Marine Science in 2000 from Long Island University, Southampton, New York. Before starting his Master of Science in Fisheries and Aquatic Sciences at the University of Florida in 2003, Tobey worked as an intern at the Apex Predators Program of the NMFS Northeast Fisheries Science Center in Narragansett, Rhode Island, studying sandbar sharks and smooth dogfish in Delaware Bay. He also worked in California as a postgraduate researcher at the University of California – Davis, Bodega Marine Laboratory conducting telemetry studies on white sharks and bat rays, as well as laboratory studies on larval estuarine fishes. While in California, Tobey also worked as a scientific aide for the California Department of Fish and Game, and as a port sampler for the Pacific States Marine Fisheries Commission. In 2001 he moved to Florida and worked as a fishery observer and technician for the Florida Program for Shark Research at the Florida Museum of Natural History, Gainesville. Tobey currently works as a fishery policy analyst for the NMFS Northeast Regional Office in Gloucester, Massachusetts.