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Spatiotemporal Variation in Abundance and Social Structure of Bottlenose Dolphins in the Florida Coastal Everglades

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SPATIOTEMPORAL VARIATION IN ABUNDANCE AND SOCIAL STRUCTURE

OF BOTTLENOSE DOLPHINS IN THE FLORIDA COASTAL EVERGLADES

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by

Robin Elizabeth Sarabia

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To: Dean Kenneth G. Furton
    College of Arts and Sciences

This thesis, written by Robin Elizabeth Sarabia, and entitled Spatiotemporal Variation in Abundance and Social Structure of Bottlenose Dolphins in the Florida Coastal Everglades, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this thesis and recommend that it be approved.

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Date of Defense: November 9, 2012

The thesis of Robin Elizabeth Sarabia is approved.

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Dean Kenneth G. Furton
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Florida International University, 2012

DEDICATION

This manuscript is dedicated to Carol Sarabia.

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ABSTRACT OF THE THESIS

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Professor Michael Heithaus, Major Professor

Bottlenose dolphins (*Tursiops truncatus*) are large-bodied predators that are locally

abundant in the coastal Everglades. Because of their potential to exert strong top-down

effects on their communities, it is important to understand how spatiotemporal variation

in biotic and abiotic factors affects the abundance and behavior of dolphins. This study

combined two years of transect surveys with photographic identification methods to

assess spatiotemporal variation in the abundance and group sizes of bottlenose dolphins

across four large regions of the coastal Everglades including the Shark and Harney

Rivers, Whitewater Bay, and coastal oceans of the Gulf of Mexico and Florida Bay.

Dolphin abundance was similar across wet and dry seasons, except in river habitats where

abundances were higher during the dry season. Group sizes were largest in Florida Bay

and open water. Dolphins may be relatively resilient to abiotic changes in the coastal

Everglades, with the possible exception of river habitats.

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INTRODUCTION

The Florida Everglades is a system of subtropical wetlands comprising a number of distinct habitats that terminates in oligotrophic mangrove estuaries adjacent to Florida Bay and the Gulf of Mexico (Childers 2006). Within the coastal Everglades, there is an assemblage of multiple, distinct aquatic habitats including sloughs, creeks, rivers, shallow bays with mangrove islands, and coastal oceans. Urbanization of the surrounding land and global climate change have reduced freshwater flow in volume and duration, thus changing patterns of dissolved oxygen, salinity, primary production, and consequently the distribution of many species of consumers (e.g., Turner et al. 1999, Chick et al. 2004, Rehage and Trexler 2006). Diminished freshwater flow that has resulted from anthropogenic activities has reduced fish populations, and in turn, limited populations of some upper trophic level predators (e.g., wading birds) though decreased food availability (Lorenz and Serafy 2006, Trexler and Goss 2009).

The Comprehensive Everglades Restoration Plan (CERP) was created to restore and preserve the natural water function and resources by capturing fresh water that now flows to the Atlantic Ocean and the Gulf of Mexico and redirecting it back to the Everglades (see CERP: evergladesplan.org). The project, budgeted at $7.8 billion, will result in considerable changes throughout the Everglades, including in the coastal estuaries (Perry 2004, Davis et al. 2005, Gaiser 2009). In order to predict and understand the impact this will have on native species, as well as to assess the quality of "restoration," it is critical to have a functional understanding of how spatiotemporal variation in biotic and abiotic factors, and their interaction, affects the abundance and behavior of key species.

Most published studies of Everglades ecosystems, especially in coastal estuaries, has focused on organisms at relatively low trophic levels (e.g., Trexler et al. 2005, Williams and Trexler 2006; but see Wiley and Simpfendorfer 2007, Heithaus et al. 2009, Mazzotti et al. 2009 for studes of large predators). The oligohaline ecotone region, however, is predicted to be dramatically affected by habitat restoration and sea level rise because of drastic changes in abiotic conditions. Thus, an understanding of how these changes will impact upper trophic level species, and their roles in estuarine communities and ecosystems, is important. Previous work on large predators in the coastal Everglades has suggested that they may play an important role in upstream transport of marine-derived nutrients into the oligohaline ecotone (e.g.,, Matich et al. 2011, Rosenblatt and Heithaus 2011). However, the predators that have been studied - bull sharks (*Carcharhinus leucas*) and alligators (*Alligator mississipiensis*) - are poikilothermic and have low metabolic rates (Coulson et al. 1989, Schmid and Murru 1994), particularly when compared to mammalian metabolism. Consequently, the overall ecological impacts of these species through consumptive effects may not be as sizeable as those of abundant mammalian predators.

Bottlenose dolphins (*Tursiops truncatus*) are large-bodied predators that can be locally abundant in coastal and estuarine habitats (Ballance 1992), including those of South Florida. They have high metabolic rates, and may consume a large percentage of total productivity, potentially impose strong top-down effects on community structure through direct predation (Bowen 1997, Young and Phillips 2002, Williams et al. 2004), and may serve as an indicator of ecosystem health (Torres and Urban 2005.) Therefore,

understanding spatiotemporal variation in the abundance of dolphins and their feeding

ecology in the coastal Everglades is important for elucidating the dynamics of the

ecosystem and for successful management of this system. However, no previous work on

dolphins in the inshore waters of the coastal Everglades has been published, and their

trophic relationships and ecological roles are poorly known in the area. Currently

available data on dolphins within the boundaries of the Everglades National Park come

from studies conducted in the marine waters of Florida Bay (Torres 2007, Torres et al.

2008) and are focused on marine habitat affinities of dolphins. Furthermore, the current

NOAA Marine Mammal Stock Assessment examines only the bottlenose dolphins

residing in Florida Bay and does not consider the potential role dolphins may play in the

trophic dynamics and nutrient flow of the more inshore waters of the coastal Everglades

(NOAA 2010). The last known descriptions of dolphins within the estuarine Everglades

are sporadic notes on dolphin distribution from the early 1950's (Moore 1953).

Bottlenose dolphins are capable of rapid long-distance movements. For example, Wells

et al. (1999) recorded one animal that moved 4,200 km in 47 days. Therefore, they could

serve as mobile links between ecosystems, although not all populations or individuals

display such pronounced distributions. Indeed, many populations in the waters of the

southeastern United States tend to display high site fidelity and what may initially appear

to be a continuous coastal distribution is often a mosaic of localized resident groups with

limited population exchange among these groups (Irvine et al. 1981, Gubbins 2002, Irwin

and Würsig 2004). In extreme cases, two or more genetically separate populations that

differ in foraging ecology may be sympatric (Fernandez et al. 2011). Home range sizes,

however, can vary greatly. In some populations, individuals may occupy areas as small as 0.4 km^2 while others exhibit movements across more than 2000 km (e.g., Caldwell 1955, Bassos 1993). In Sarasota Bay, Florida, USA the approximately 100 resident animals have a year-round community home range of about 125 km^2, comprised of the overlapping core areas of different groups and individuals (Wells 1993). Their distribution is often correlated with environmental factors, but the nature and strength of the relationship is confounded with fish distribution and is difficult to critically assess (Allen et al. 2001, Torres et al. 2008). For example, dolphin distributions in Florida Bay are more tightly correlated with environmental characteristics than measures of prey distribution based on otter trawls (Torres and Read 2008).

Habitat preferences of dolphins have been studied in multiple locations around the world. Food availability, predation risk, social and maternal factors, as well as abiotic conditions have been identified as potential drivers, with their relative importance varying within and among study locations (Wells 1993, Heithaus and Dill 2002, Torres et al. 2008, Yeates and Houser 2008, McHugh et al. 2011a). Changes in habitat use and abundance of dolphins within locations can be driven by numerous factors tidal variation (Gregory and Rowden 2001), the interaction of submarine characteristics with foraging tactics and seasonally abundant prey (Hastie et al. 2004), overall prey availability (Shane et al. 1986, Heithaus et al. 2002), predation risk (Heithaus and Dill 2002, 2006) or environmental factors including dissolved oxygen, salinity, turbidity and temperature (Barco et al. 1999, Wilson et al. 1997, Stocktin et al. 2006, Miller and Baltz 2010). The extent to which some of these relationships are causal, particularly for physical and abiotic drivers,

remains poorly understood. For example, physical characteristics may indirectly affect

dolphins through their impacts on the abundance and distribution of dolphin predators

and prey (e.g., Toth et al. 2011).

Even in adjacent areas, the drivers of temporal and spatial variation in abundance can

differ; such as in New South Wales, Australia, where tidal phase and an interaction of

season and tidal phase influence dolphins habitat use in the Clarence River, but neither

tidal phase nor season influences spatial distributions in the nearby Richmond River

(Fury and Harrison 2011). The degree to which various factors shape dolphin

abundances, therefore, likely is context-dependent. Some of this context dependence may

be driven by the extent to which spatial and temporal variation in dolphin abundance is

the result of spatial shifts within home ranges versus immigration and emigration of

individuals. Such dynamics, however, are poorly understood in many dolphin

populations (e.g., Stocktin et al. 2006, Wilson et al. 1997).

Group size is one of the main defining characteristics of social organization of a

population (Wilson 1975). In cetaceans, group sizes vary considerably within and among

species and populations. Like other taxa, grouping patterns are influenced by the

abundance and predictability of resources as well as predation risk (See Gowans et al.

2008 for a summary). Larger group sizes are favored when predation risk is higher,

grouping can enhance resource acquisition of individuals, and clumping of resources

promotes social coexistence (e.g., Alexander 1974, Bertram 1978). Group sizes, however,

are mediated by costs such as increased probabilities of predator and parasite encounter

and resource competition (Bertram 1978). For coastal populations of bottlenose dolphins, group sizes are typically smaller where the habitat is complex and resources are predictable (e.g., Campbell et al. 2002) and larger in open water with unpredictable and spatially fluctuating resources (e.g., Defran and Weller 1999). Importantly, because of the high mobility and relatively low energetic cost of travel to dolphins, group sizes and composition can be highly dynamic on scales of hours or even less (e.g., Connor et al. 2001). Thus, individuals can select appropriate group sizes and compositions on the basis of current requirements (i.e., behavioral state) or in response to changing trade-offs through ontogeny or across sex and reproductive states.

Social structure is one of the best-studied aspects of bottlenose dolphin behavior, and varies considerably between regions in response to environmental and social factors (e.g., Connor et al. 2000). In Sarasota Bay, a residential inshore population is typified by fluid groups largely defined by age and sex (Wells et al. 1987, Wells 1991, Curry and Smith 1997, Barros et al. 2010). The most common types of groups include juvenile bands, male pairs/trios, and nursery bands comprised of females of multiple generations and calves as well as older calves of both sexes. Nursery groups tend to include females with long-term associations that share home ranges, although the composition of these groups is highly variable (Wells et al. 1987). Subadult groups are formed by juveniles of both sexes and individuals remain in these groups for many years, often over a decade (Wells et al. 1987). Roving male pairs/trios are long-term, stable associations capable of lasting for decades, although some males are largely solitary (Wells et al. 1987, Wells 1991). These groups select different parts of the population's home range; females in nursery

bands select protected shallow-waters much more often than subadults or males (Wells 1993).

In contrast to Sarasota Bay, in Shark Bay, Western Australia, male Indo-Pacific bottlenose dolphins may form pairs and trios that are part of a large, multi-level male alliance system or be a part of larger "superalliances" that are one of the most complex non-human societies (Connor et al. 1992, 1999). Also, female groups appear to be more fluid in Shark Bay than those in Sarasota Bay (Smolker et al. 1992). In comparison to Sarasota Bay females' selection of safer habitats for nursery groups, females in Shark Bay may switch habitats adaptively to take advantage of both safer resting habitats and more energetically profitable but riskier foraging habitats (Heithaus and Dill 2002). Unlike these sex- and maturity-defined group structures, common bottlenose dolphins in Moray Firth, Scotland, exhibit groups composed of both adults of both sexes with no preferential associations among males (Wilson et al. 1997).

It is critical to note that the social structure of dolphins may be dynamic as environmental conditions change. For example, in Moreton Bay, Australia, changes in food sources led to shifts in social structure with dolphins shifting from two separate sympatric communities to a more integrated single society with smaller groups sizes, different patterns of association, and different foraging patterns as one of the food sources became less available (Ansmann et al. 2012).

Bottlenose dolphins also display considerable variation in foraging behavior within and among populations. Indeed, even within populations innovative foraging tactics arise, apparently in response to ecological conditions, and often are maintained through social learning (Connor 2001, Krutzen et al. 2005, Sargeant et al. 2007). Some foraging behaviors are specific to the local environment; for example, dolphins in Shark Bay have been observed using marine sponges as foraging tools; sponging is the predominant mode of foraging for some individuals, but is only used by a small number of individuals with the behavior being passed down through matrilines (Mann et al. 2008). Similar tactical variation has been observed in Florida Bay. Three distinct foraging methods have been observed – deep diving, which is a common tactic in multiple populations, a herd-and-chase tactic in which a barrier such as a mud-bank or mangrove island is used to herd the fish, and mud-ring feeding, a foraging behavior never observed elsewhere and requiring the cooperation of multiple individuals (Torres and Read 2009). Each tactic is correlated with a particular habitat type and location in the bay, varying with depth and bathymetric features; dolphins appear to limit their overall movements to coincide with the habitats predicted by their preferred tactic (Torres and Read 2009). Of particular interest are the site-specific "mud-plume" strategy (Lewis and Schroeder 2003) and the similar "mud-ring" feeding behavior (Torres and Read 2009), which are thought to be unique to south Florida. Other behaviors are seen across many populations, such as the use of shallow mud-flats for intentional stranding to capture prey herded onto the bank (Silber and Fertl 1995). Both environmental heterogeneity (Sargeant et al. 2007) and unexploited niches (Patterson and Mann 2011) have been postulated to lead to the development of new and unique foraging behaviors.

Prey selection by dolphins appears to be a function of both prey availability and behavioral tactics being employed by dolphins. Dolphins using inland waters bordering the Gulf of Mexico often feed heavily on common seagrass-associated fish, particularly larger, solitary, soniferous fish (Barros and Wells 1998, Gannon et al. 2005, McCabe et al. 2010.) It is believed that this preference reflects a passive listening foraging tactic (Gannon et al. 2005). Variation in foraging tactics may reflect differences in preferred prey. For example, mud-ring feeding in the Florida Keys appears to exclusively target mullet (Lewis and Schroeder 2003).

The objective of my study was to conduct preliminary investigations of spatiotemporal variation in the abundance and behavior of bottlenose dolphins in the Florida Coastal Everglades in order to gain insights into their potential ecological roles. Specifically, I estimated the number of individual dolphins using different regions of the FCE, investigated spatial and temporal variation in dolphin densities and group sizes, and conducted preliminary investigations into spatial variation in group composition and age/sex classes.

MATERIALS AND METHODS

Study site

The Florida Coastal Everglades is a spatially and temporally heterogeneous system which extends from small creeks where freshwater marshes transition to mangrove forests through mangrove-lined channels and inland bays to the coastal oceans of the Gulf of Mexico and Florida Bay (Childers 2006). The system is relatively oligotraophic and

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phosphorous-limited. Phosphorous inpts in this estuary have a marine source, rather than a terrestrial one, creating an "upside down" estuary with no productivity peak in the oligohaline zone (Childers et al. 2006). Instead, productivity decreases from the mouths of rivers to upstream marshes. Salinity varies both spatially and temporally as the region alternates between a high precipitation wet season (July - December) and a low precipitation dry season (January – June) (Schomer and Drew 1982). During the dry season, salinities measuring >20 ppt may occur up to 17 km from the mouth of the estuary (Rosenblatt and Heithaus 2011) while salinities where the channels meet the coastal oceans can fall to <15 ppt in the wet season (Childers et al. 2006). Seasonal changes in precipitation lead to marked spatiotemporal variation in aquatic communities. Fish from freshwater marshes enter creeks and channels during marsh dry down creating a pulse of increased prey availability to estuarine predators (Rehage and Loftus 2007).

My study was conducted from July 2010 – June 2012 in five major areas of the Everglades National Park: 1) Whitewater Bay, 2) Joe River, 3) Shark River Slough from Tarpon Bay to the mouths of the Harney and Shark Rivers, 4) coastal waters of Ponce de Leon Bay and a strip up to 4 km offshore and extending south to Cape Sable ("Gulf of Mexico"), and 5) the northernmost portion of Florida Bay extending from Flamingo to Cape Sable (See Figure 1).
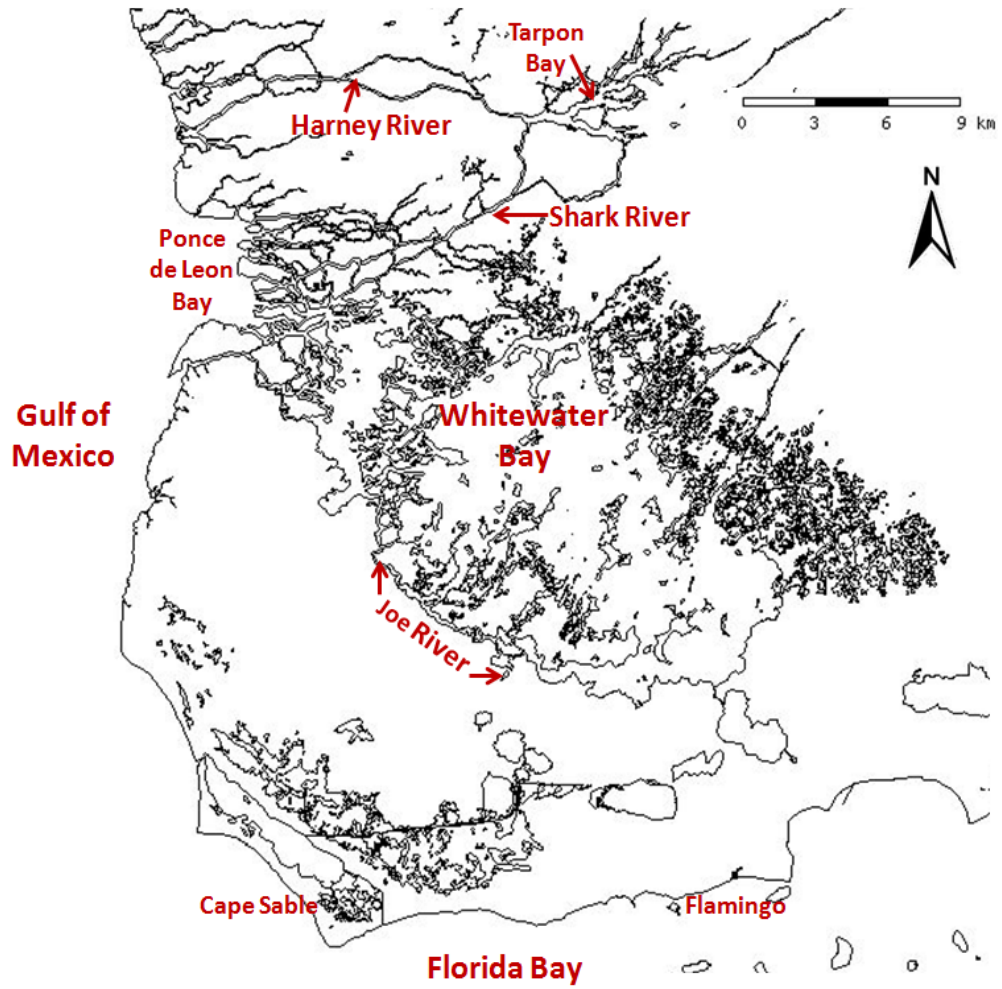
Figure 1: The study was conducted in the coastal and inland waters of southwest Florida's coastal Everglades. Transects were conducted in the Shark and Harney Rivers, Joe River, Whitewater Bay, the Gulf of Mexico, and Florida Bay.

Whitewater Bay is a large (approximately 200 km^2) and shallow enclosed bay with relatively uniform depth (0.75 -1.75m,) and characterized by small tidal variation. Salinities were observed to range from 33 ppt in the wet season to as low as 5 ppt in the dry season (R. Sarabia, unpublished data). A number of small red mangrove (*Rhizophora mangle*) islands of varying sizes are scattered throughout the bay and water clarity varies with location in the bay. The Shark and Harney Rivers are comprised of deeper water channels (2.5-4.5 meters deep, with an average width of 100 meters) lined with mangroves and a salinity gradient ranging from marine levels of up to 35 ppt at the river mouth to values as low as <4 ppt in Tarpon Bay. Tarpon Bay is a narrow (100-500 meters), shallow (1-2 meters), mangrove-lined bay bordering the sawgrass ecotone (Figure 2), and was the upriver terminus for this study.
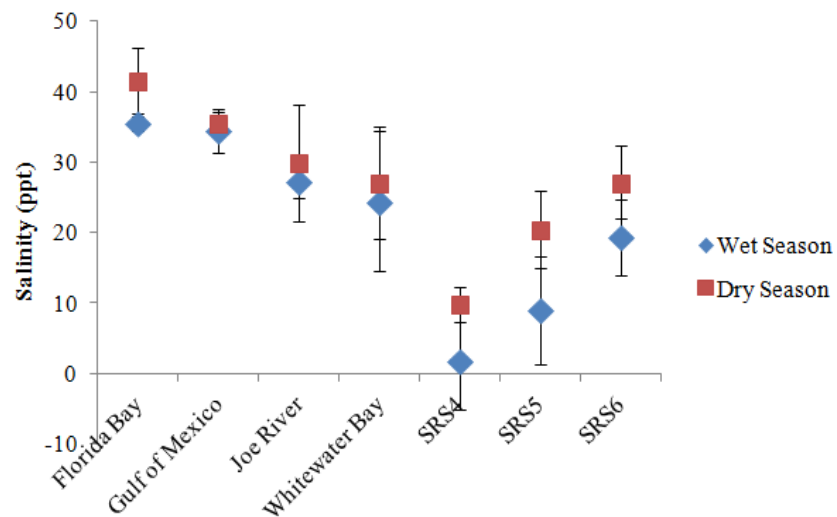
Figure 2: Spatial and seasonal variation in salinity in the study system. SRS 4, 5 and 6 are monitoring stations in the Shark River, with SRS4 being the furthest upstream and SRS6 being the furthest downstream. Other data were taken by the author during the course of this study. Error bars show standard error.

Florida Bay is a shallow basin, connected to the Gulf of Mexico at its western margin and to the Straits of Florida to the south through multiple channels between the islands of the Florida Keys. Mean salinity during the dry season can exceed 40 ppt in the areas surveyed (Boyer et al. 1997). Water clarity, depth and benthic habitats vary regionally; the area covered by this study is characterized by a muddy bottom, very turbid water and depths ranging from 0.5 to 3 meters (Torres and Read 2009).

Study Methods

I established transects in five regions (three estuarine, two in the coastal ocean), including Whitewater Bay (55 km in length), the Shark and Harney Rivers and Ponce de Leon Bay (50 km), Joe River (20 km), coastal waters of the Gulf of Mexico (33 km) and Florida Bay (15 km) (Figure 3). Transects were run onboard a 6.4 m vessel with three trained observers. Transects were run at 15 kph and only in Beaufort sea conditions 3 or less.

Figure 3 – Location of sampling transects in the Florida Coastal Everglades. Image
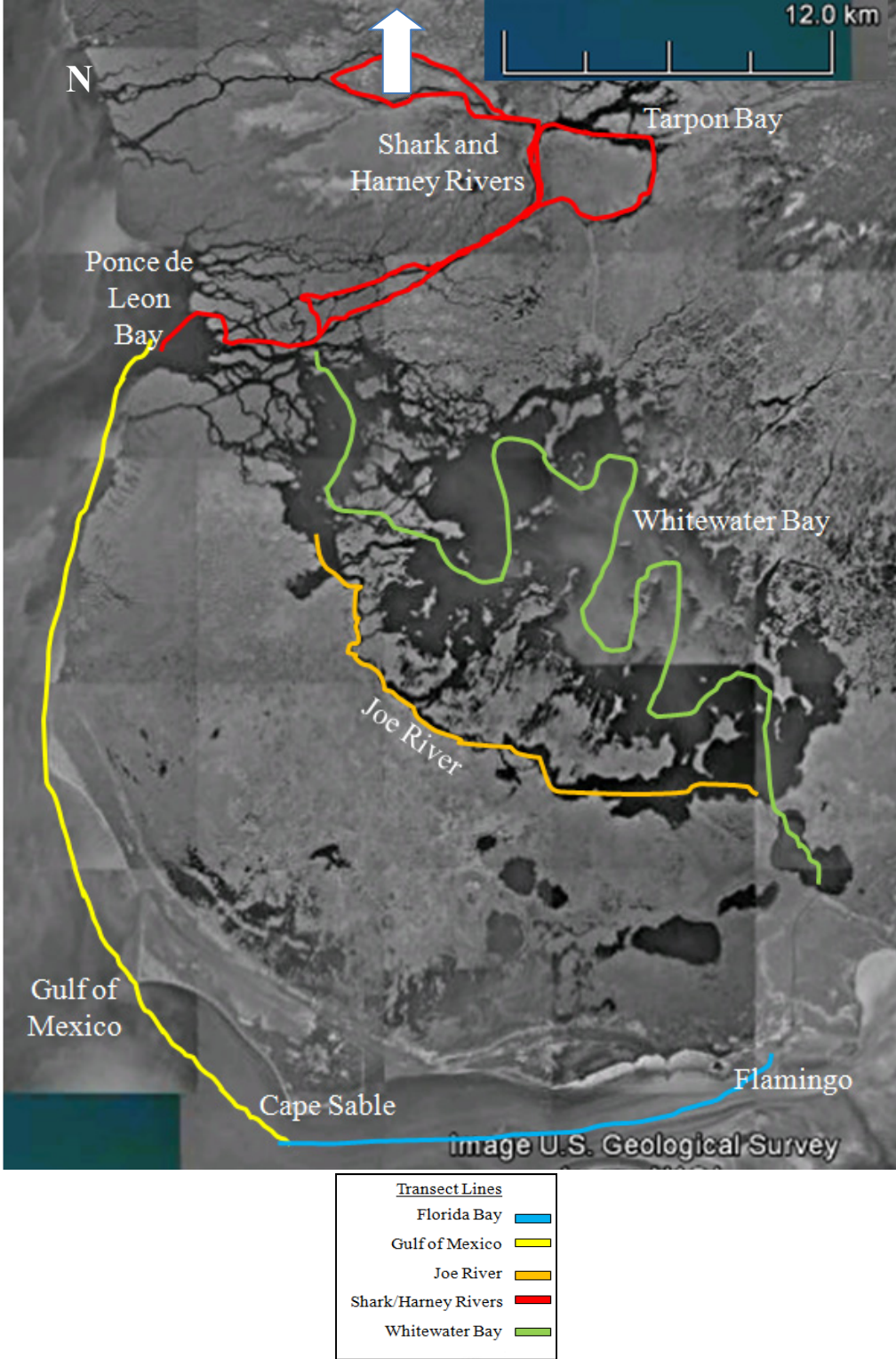from Google Earth 6.1

When a dolphin group was encountered during a transect, I marked the location on the transect and left the transect to survey the group. For the purposes of this study, a group was defined as all animals in close proximity to one another (<100m) engaged in similar behaviors (Shane 1990). During the survey, I recorded the group GPS position, environmental conditions (salinity, water temperature, dissolved oxygen, Beaufort sea state, tidal conditions, water depth and habitat type), behavior, and group size. Due to equipment malfunctions I was unable to record salinity, water temperature, and dissolved oxygen for some surveys. Predominate group behavior was determined at first sighting and categorized according to a modification of the Sarasota Bay Research Program guidelines (e.g., McHugh et al. 2011b). *Traveling* dolphins were those seen surfacing with persistent directional movement and surfacing at regular intervals. *Resting* dolphins were observed at or near the surface but not engaged in any obvious surface behavior, exhibited slow movements, and often occurred in tight groups. *Socializing* dolphins were those observed chasing or making bodily contact with one another, including a suite of possible behaviors linked with play and/or mating. *Foraging* dolphins were those observed making any effort to capture prey. Behaviors included, but were not limited to, tail-out grubbing in the mud, herding prey, chasing prey, and rapid surfacing at varying intervals with no consistent heading. If the dolphins were first observed reacting to the presence of the researchers (e.g., approaching the boat to bow ride), their behavior was classified as unknown.

I took photographs of the dorsal fins of every individual in a group using a Canon EOS 10D SLR. These photos were used to create a catalog of dorsal fins to identify

individuals on the basis of variation in dorsal fin size and shape, along with the nicks and scars acquired though the animal's lifetime (e.g.,, Wursig and Wursig 1977) (Figure 4). The catalog was continuously updated with new individuals and current photographs of the animals, and all new photographs were compared to the catalog for identification.

Figure 4: Examples of distinctive dorsal fin morphology and markings allowing for consistent identification of individuals through time.

Photographs from each sighting were sorted by individual and all the photographs of an individual from a given sighting were then sorted to obtain the highest quality picture for comparison to the catalog. The sex of individuals was determined opportunistically, either by observing the presence of a dependent calf in the echelon position with a particular animal during multiple surveys (e.g., Elliser and Herzing 2011) or by directly observing the external genitalia. Calves were identified by size and behavior and sorted into three categories: juveniles, calves, and neonates. Juveniles were defined as animals smaller than adult size but greater than half an adult body length. A calf was defined as

an animal smaller than half an adult body length, and was typically found closely associated with its mother, particularly while surfacing. Neonates were identified by the presence of visible fetal folds and stereotypical awkward surfacing during breathing (e.g. Shane 2004).

Photographs were also used to examine individuals for evidence of scars from shark bites. Scars were considered to have been inflicted by sharks in they were characteristically crescent-shaped or had deep and widely spaced tooth marks (Heithaus 2001.) I determined the proportion of individuals with wounds by comparing the number of known individuals with wounds to the total number of individuals identified. This method underestimates actual wounding rates since only a small portion of the body is surveyed for evidence of shark bites (e.g., Heithaus 2001).

Statistical Methods

Statistical tests were carried out using JMP Pro 9^{TM} software. To test for adequate sampling, a rarefaction analysis was performed. Cumulative individual curves were generated by resampling group compositions for 1000 randomly selected groups to calculate a mean and variability estimate of the cumulative number of individuals for each group. This mean cumulative number of individuals was then plotted against the randomly pooled number of groups; a linear regression was then performed on the last four points to determine if the slope of the line was significantly different from zero (e.g., Bizzarro et al. 2007).

To determine spatial and temporal variation in dolphin abundance, I calculated both the densities of groups (number of group sightings per km^2) and individuals (number of individual animals per km^2). Area sampled was calculated by multiplying transect length by 0.8km, which represents sightings within 400 meters of the boat (the distance at which groups were sighted during a sea state of Beaufort 3). Because all of the channels sampled were narrower than 0.8 km, instead of 0.8 km, a mean width was calculated by averaging channel width derived from measurements every 100m along transects. Data were non-normal and transformations were unsuccessful, necessitating the use of non-parametric statistical methods (Kruskal-Wallis and Mann Whitney tests). To determine if dolphins preferentially used areas near mangrove islands in Florida Bay, I used logistic regression to compare the probability of encountering a group within 100 meters of a mangrove island relative to that more than 100m from islands.

Because of the turbidity of water in most sampling regions, I calculated group size using the total number of unique individuals photographed during a sample and estimates of minimum group size (i.e., number of individuals surfacing simultaneously). These data were also non-normal, and no transformations successful. Therefore, I used a series of Kruskal-Wallis tests to investigate the effects of season (Wet or Dry), group composition (the presence or absence of calves), behavior (at first sighting), and region. For tests showing significant effects, Mann-Whitney tests were used to determine statistically significant paired contrasts where necessary.

The distance a group was found upstream in the Shark and Harney Rivers was calculated as river distance from a central point in Ponce de Leon Bay. We used Kruskal-Wallis tests to investigate whether dolphins moved further upstream during particular seasons or if particular age/sex classes were more likely to be encountered further upstream. A series of Kruskal-Wallis tests were used to examine the proportion of calves encountered per total individuals sampled by season, region, behavior, and distance upstream. A simple logistic regression was performed to test if group encounter rate was higher within 100 m of mangrove islands.

RESULTS

From August 2010 – June 2012, I completed a total of 67 transects (34 in the dry season, 33 in the wet season). These transects involved over 268 hours of observation and covered *ca.* 2650 kilometers (Table 1). Overall, I encountered 148 groups, 34 of which were foraging, 14 were socializing, and 63 were traveling. I was not able to determine the behavior of 27 groups. Resting groups of dolphins were not observed. Multiple foraging behaviors were observed; the most common behavior was a tail-out mud grubbing behavior that was observed on 15 occasions, while using mangrove roots to herd fish was observed on seven occasions. Although not observed during quantitative sampling, intentional stranding on mud banks was observed near the mouth of the Harney River.

I recorded over 12,000 photographs that resulted in identifying 174 unique individuals. A total of 31 animals were identified in Florida Bay, 30 in the Gulf of Mexico, 9 in the

Shark and Harney Rivers, and 92 in Whitewater Bay. All 14 individuals identified in Joe River were also observed in Whitewater Bay. Three animals were observed using both Whitewater Bay and the Shark River, four were observed using both the coastal ocean and either Whitewater Bay or Shark River, and two animals were observed in both Florida Bay and the Gulf of Mexico. No animals from the estuary were observed in Florida Bay or vice versa. Juveniles were observed on 51 occasions, calves on 17 occasions, and neonates were sighted only twice. Most calves were not cataloged as individuals, because of a lack of identifying features early in life. Definitive shark bite scars were observed on two individuals, with possible bites occurring on seven others resulting in a minimum estimate of 1-5% of the population having been bitten by sharks along their dorsal surfaces.

Rarefaction analysis showed that the identification rate of new individuals in Whitewater Bay has reached an asymptote with a slope nonsignificantly different from zero, showing that the region was sampled sufficiently to capture most of the individuals using this habitats (Figure 5). However, all of the other subregions (Joe River, the Shark and Harney Rivers, Florida Bay and the Gulf of Mexico) had rates of identification of new animals significantly different from zero, indication that these regions were not surveyed sufficiently to identify a large proportion of the individuals in the area (Figure 5). Given the small sampling area relative to the likely size of individual dolphin home ranges in these areas, this result is not surprising. However, when the rarefaction analysis was performed, only the analysis of all individuals from all regions showed a slope nonsignificantly different from zero, indicating adequate sampling (p=0.188). The slopes

of the identification rates of new individuals in Florida Bay (p=0.0005), the Gulf of Mexico (p=0.020), Joe River (p=0.005) and the Shark and Harney Rivers (p=0.0004) were all significantly different from zero, indicating that new individuals were still being discovered. The identification rate of new individuals in Whitewater Bay was borderline significant (p=0.046).

Table 1.Seasonal and regional survey effort and dolphin sightings.

| Transect		# transects	# dolphins	# of Groups	Group Size		% Calf
					Mean ± SD	Range	
Florida Bay		**7**	**89**	**7**	**12.71 ± 9.59**	**2-31**	**8.73**
	Dry	4	32	4	8.0 ± 6.48	2-17	11.25
	Wet	3	57	3	19 ± 10.44	12-31	5.38
Gulf of Mexico		**10**	**69**	**13**	**5.31 ± 4.70**	**1-15**	**5.17**
	Dry	6	63	10	6.3 ± 4.90	1-15	6.72
	Wet	4	6	3	2.0 ± 1.73	1-4	0
Joe River		**12**	**97**	**26**	**3.73 ± 2.75**	**1-12**	**9.57**
	Dry	6	54	13	4.15 ± 3.28	1-12	8.54
	Wet	6	43	13	3.31 ± 2.13	1-9	10.51
Shark/Harney Rivers		**16**	**42**	**20**	**2.1 ± 1.65**	**1-6**	**4.25**
	Dry	9	27	11	2.45 ± 1.63	1-5	7.08
	Wet	7	15	9	1.67 ± 1.65	1-6	0
Whitewater Bay		**22**	**454**	**82**	**5.54 ± 4.05**	**1-18**	**8.81**
	Dry	9	188	33	5.69 ± 4.72	1-18	9.56
	Wet	13	266	49	5.42 ± 3.57	1-8	8.37
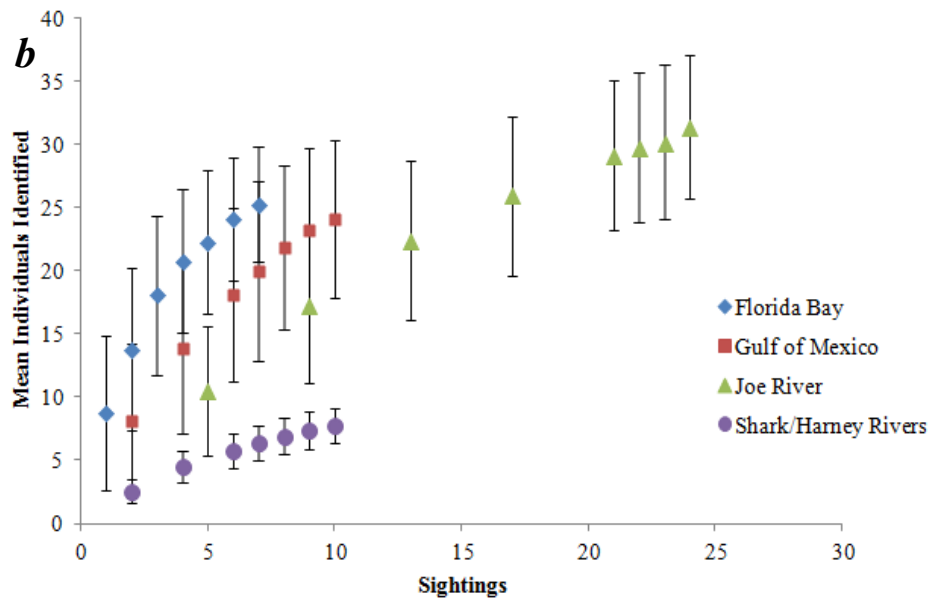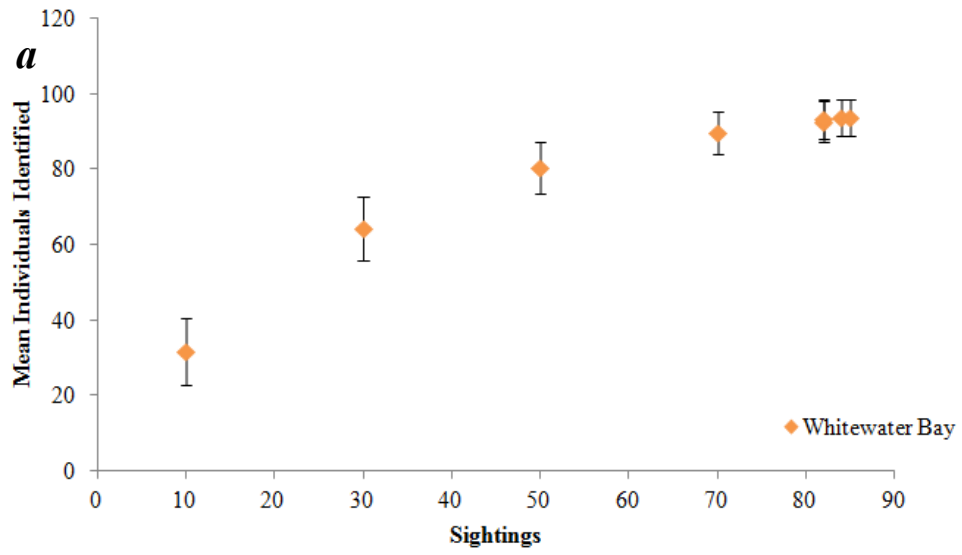
Figure 5 Cumulative individual curves generated by resampling group compositions for 1000 randomly selected groups within Whitewater Bay (a) and the four other regions of the study area (b). Points show means, error bars show standard error.

Both densities of individuals (Kruskal-Wallis Statistic = 20.18, P=0.0168) (Figure 6) and densities of groups (Kruskal-Wallis Statistic = 23.55, P=0.0044) (Figure 7) varied significantly in space and in time. Within the rivers, densities of individuals were greater in the dry season (mean=0.73 dolphins per km^2 ± 0.19 SD) than the wet season (mean=0.14 dolphins per km^2 ±0.08 SD) (Kruskal-Wallis Statistic = -2.34, P=0.02). Densities of individuals were similar across regions, with the exception of higher abundances in the Joe River in both wet and dry seasons (Kruskal-Wallis Statistic =18.34, P=0.001) and Florida Bay in the wet season. During the wet season, Florida Bay and Joe River had the highest density of individuals (mean=1.94 dolphins/km^2 ± 1.29 SD and mean=1.27 ± 0.60 SD respectively), and the density in the Gulf of Mexico was significantly less than in Joe River (mean=0.37 ± 0.54 SD). Densities in Whitewater Bay (mean=0.56 ± 0.25 SD) and the Shark and Harney Rivers (mean=0.14 ± 0.22 SD) were not significantly different from those of the Gulf of Mexico but were significantly different from densities in all other regions including each another. Interestingly, the density of foraging animals did not vary across regions (Kruskal-Wallis Statistic= 2.66, P=0.62) and did not change seasonally (Kruskal-Wallis Statistic= 0.21, P=0.98). Within Whitewater Bay, the probability of encountering groups was higher within 100m of mangrove islands than more than 100 m from islands (Z = 4.58, P=0.03).

The presence versus absence of calves did not vary among regions (Chi-Square Statistic =4.70, P=0.32) within the estuary (Chi-Square Statistic =4.43, P=0.11), or among channels, open water, and mangrove edges within Whitewater Bay (Chi-Square Statistic=5.35, P=0.13).   Interestingly, during the dry season in the rivers, groups with

calves were encountered further upstream than those without calves (Kruskal-Wallis Statistic =2.28, P=0.02). I was unable to assess whether this pattern occurred in the wet season because only one group with calves was encountered.

I did not detect seasonal variation in group sizes overall or within regions (overall Kruskal-Wallis Statistic =0.84, P=0.89, Florida Bay Kruskal-Wallis Statistic =1.24, P=0.22, Gulf Kruskal-Wallis Statistic =-1.46, P=0.14, Joe River Kruskal-Wallis Statistic =-0.36, P=0.72, Shark/Harney River Kruskal-Wallis Statistic =-1.29, P=0.20, Whitewater Bay Kruskal-Wallis Statistic =-0.29, P=0.77).
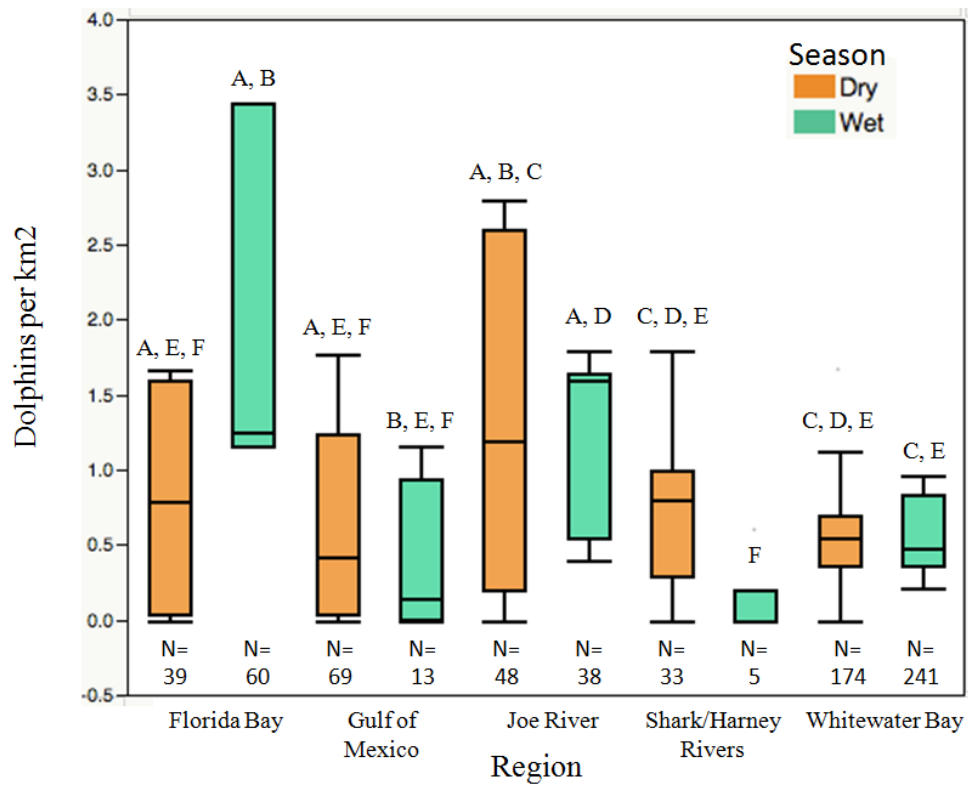

Figure 6 – Spatiotemporal variation in the density of dolphins in the Florida Coastal Everglades. Boxplots show median, quartile, minimum and maximum values; bars with the same letter are not significantly different from one another. .
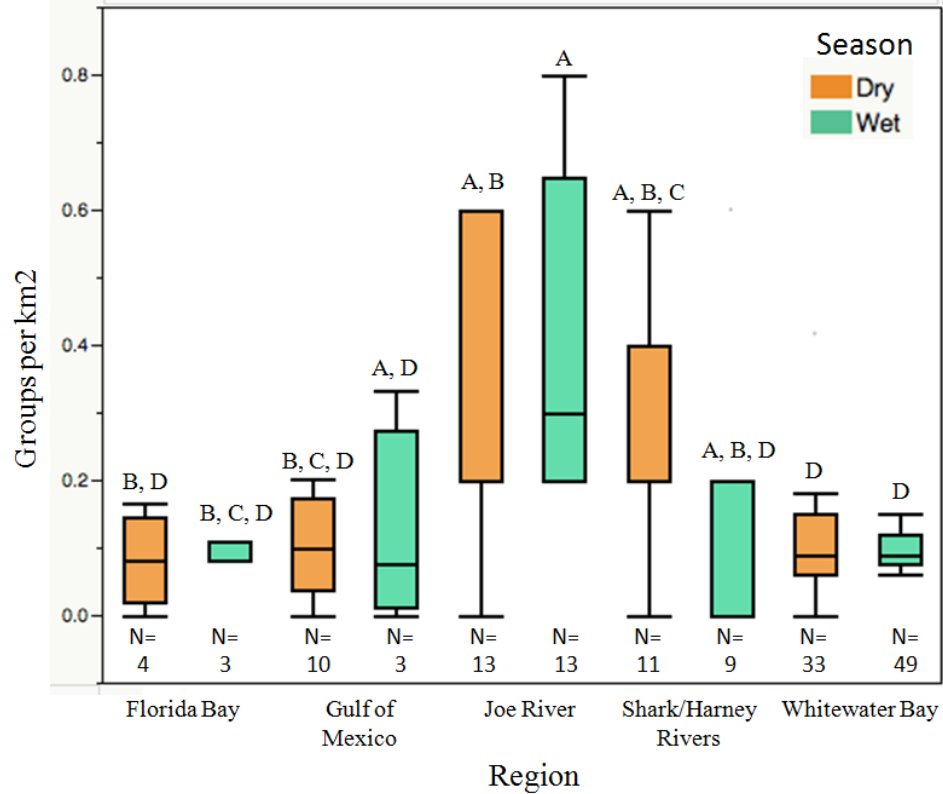
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Figure 7 – Spatiotemporal variation in the density of dolphin groups in the Florida

Coastal Everglades. Boxplots show median, quartile, minimum and maximum values;

bars with the same letter are not significantly different from one another.

Group sizes varied across regions (Kruskal-Wallis Statistic = 25.88, P<0.0001) and

among habitats within Whitewater Bay (Kruskal-Wallis Statistic = 17.24, P=0.0002).

The smallest groups were found in the rivers (mean=2.10 ± 1.65 SD) and the largest were

found in Florida Bay (mean=12.71 ± 9.59 SD). Mean group sizes were intermediate in

the Gulf of Mexico (mean=5.31 ± 4.70 SD), Joe River (mean=3.73± 2.75 SD), and

Whitewater Bay (mean=5.37±4.04 SD) (Figure 8, 9). Interestingly, Whitewater Bay had

significantly larger groups than Joe River, despite the high degree of connectivity

between the regions. Across habitats within Whitewater Bay, groups were largest in

open water and smallest around mangrove islands (Figure 10). Finally, when examining

groups while excluding calves, groups with juveniles, calves, or neonates were much

larger than those without younger age classes within estuarine regions (Figure 13;

Kruskal-Wallis Statistic =15.60, P=0.004) (Figure 11).
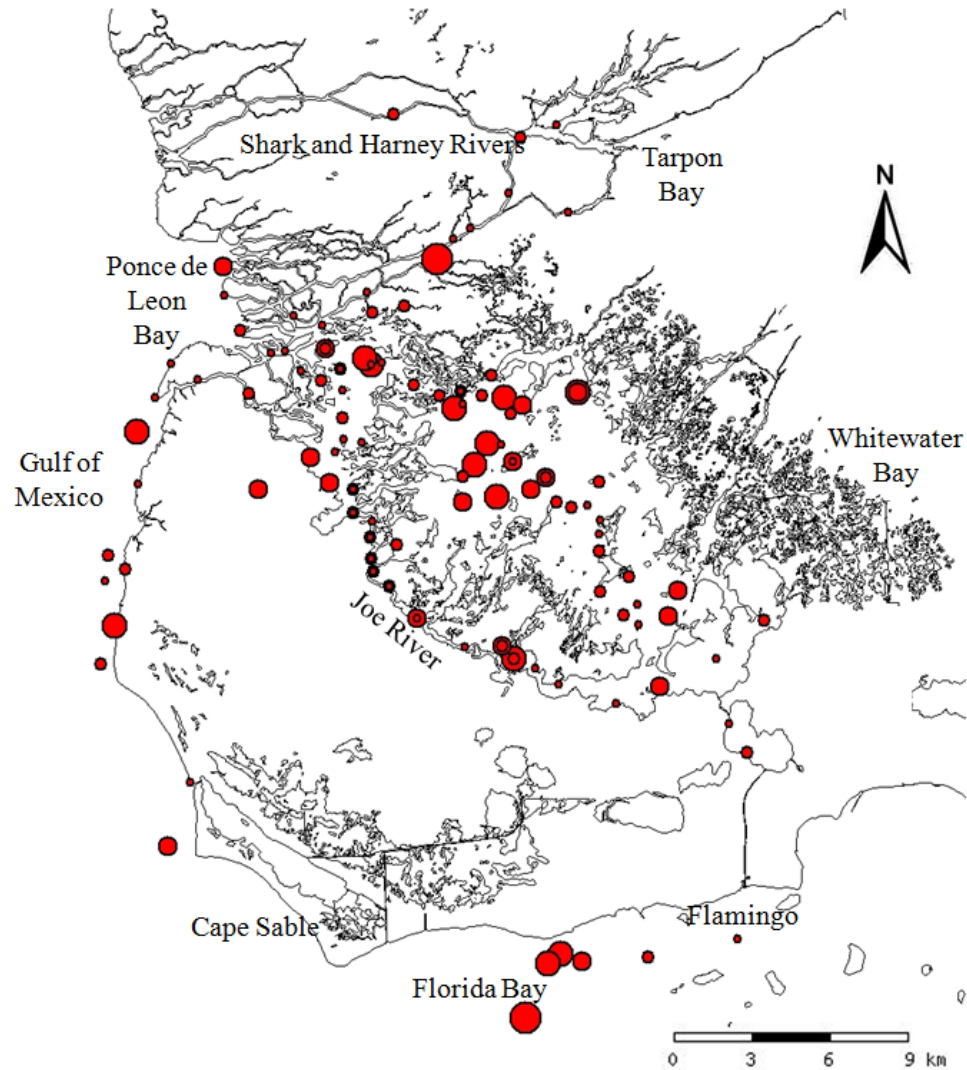
Figure 8- Map showing locations of all groups encountered. Dot size is proportional
to group size.
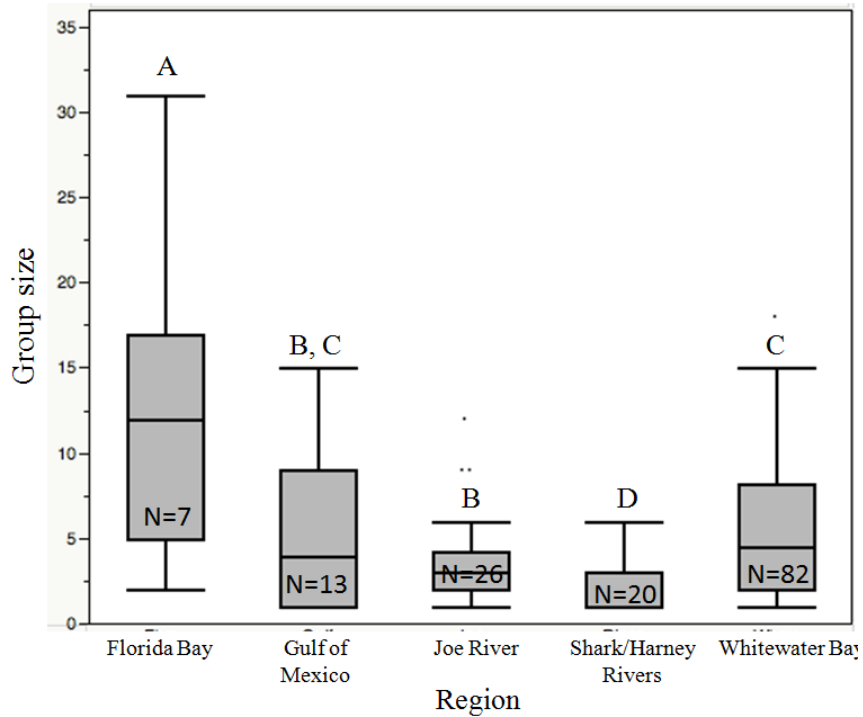
Figure 9 – Regional variation in mean group sizes. There was no seasonal variation in group sizes. Boxplots show median, quartile, minimum and maximum values; bars with the same letter are not significantly different from one another.

Group size varied among behavioral states; traveling groups were significantly smaller (mean=4.58 ± 3.34 SD) than the larger socializing groups (mean=7.92, SD=6.01); foraging groups were nonsignificantly different from either socializing or traveling groups (Kruskal-Wallis Statistic=12.72, P=0.0053).
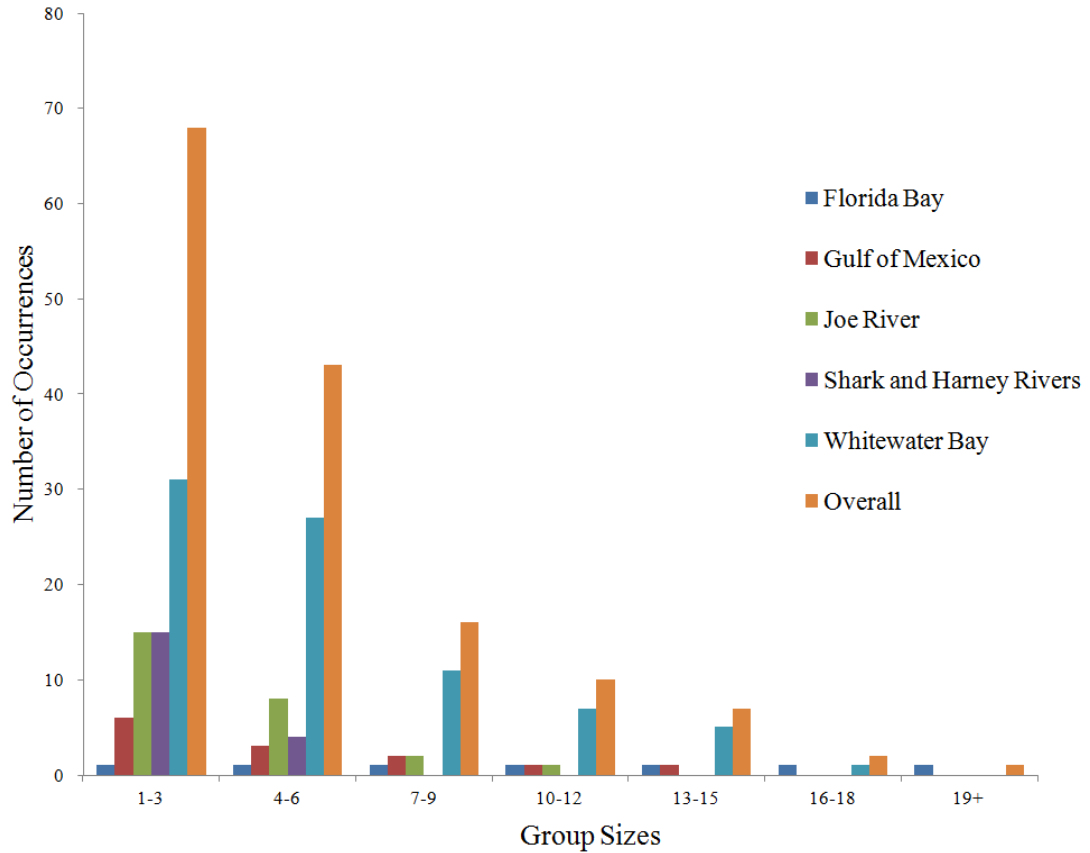
Figure 10 - Distribution of group sizes across the five study zones. Overall, the smallest groups were the most common. Groups in Whitewater Bay most closely resembled overall patterns; group sizes in river habitats were smallest, and group sizes in Florida Bay had the widest variation in size, including the largest groups encountered.
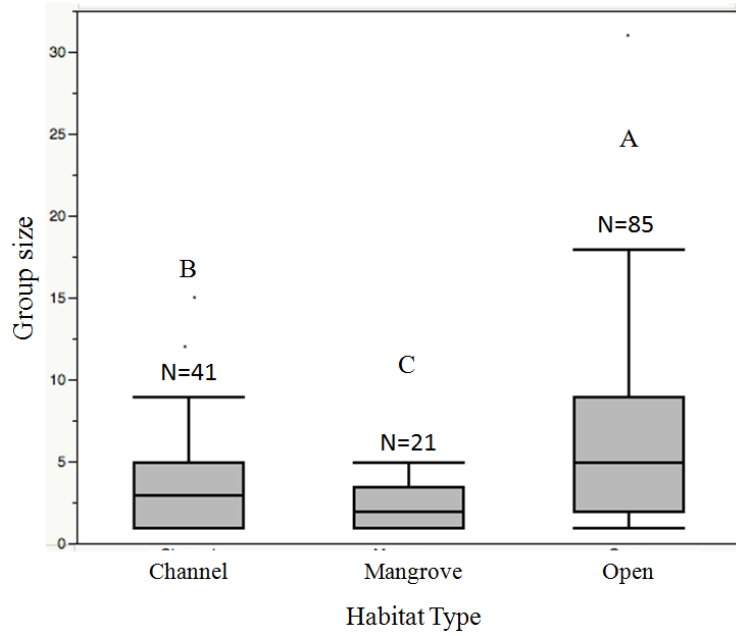
Figure 11 – Variation in group sizes among estuarine habitats. Boxplots show median, quartile, minimum and maximum values; bars with the same letter are not significantly different from one another.
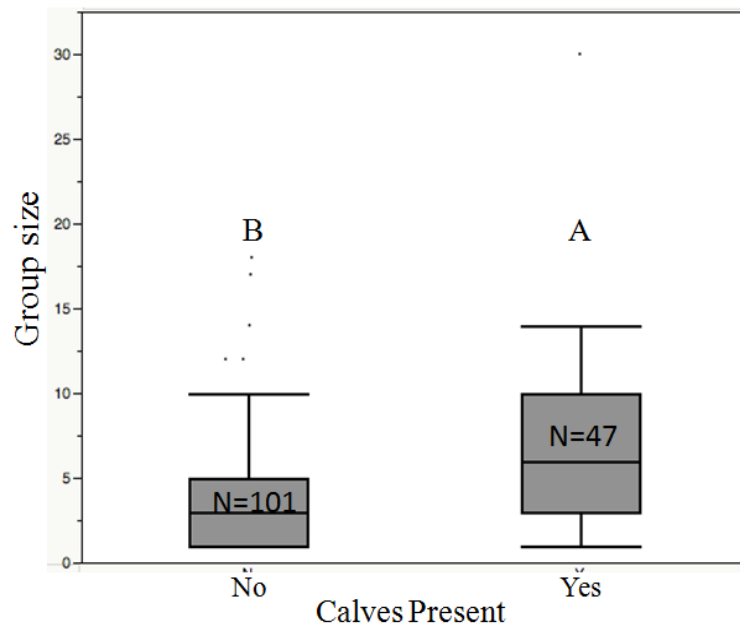
Figure 12 – Influence of group type (presence or absence of calves) on group sizes. Boxplots show median, quartile, minimum and maximum values; bars with the same letter are not significantly different from one another.

DISCUSSION

Bottlenose dolphins are known to use coastal and estuarine habitats around the world (Wells and Scott 1999). However, few areas exhibit the considerable diversity of habitat types encompassed by the Florida coastal Everglades (FCE). In addition, most studies of estuarine dolphins have occurred in areas with relatively high human densities (e.g., Barros and Wells 1998, Gregory and Rowden 2001, Hastie et al. 2004). Although water flow into the FCE is highly modified and managed by humans, the current study site is typified by low densities of boats and direct human impacts (Ault et al. 2008). I discovered that in spite of considerable seasonal variation in abiotic conditions, bottlenose dolphins in this temporally dynamic environment exhibit relatively stable densities and group sizes within regions, but show considerable variation in their use of regions in the estuary and coastal ocean.

There are three main population types that might be observed in an estuarine system: year-round residents (Wells 1991, Williams et al. 1993, Zolman 2002), temporarily resident seasonal migrants (Scott et al. 1990), or transient animals (Hansen 1990, Bearzi et al. 1997, Defran and Weller 1999). Often, animals from multiple populations are temporarily sympatric (Wells 2003), but there appears to be little genetic interchange despite these periods of intermingling (Hoelzel et al. 1998). Social structure differs

among these population types. Resident animals tend to be found in small groups that are differentiated by sex and reproductive state and feature a variety of association types (see Wells 1991, Connor et al. 2000) while migratory groups are often large and include all ages and sexes, and associations are more fluid (Defran and Weller 1999).

In the FCE it is clear that there is a year-round residential population, at least in Whitewater Bay and Joe River. Out of the 50 animals sighted four or more times, 45 were sighted in both seasons. The presence of either a seasonal resident or a transient population is possible since 125 animals were observed three times or fewer, with 62 animals sighted only once. Of the individuals sited only once, 36 were from the Gulf of Mexico or Florida Bay. At this time, however, it is not possible to reject the possibility that these rarely sighted individuals are part of a resident population, and simply were not frequently encountered because the survey transects may have only included a small portion of their home ranges. For example, although the transect through Whitewater Bay sampled 33 km^2, this is only *ca.*16.5% of the total area available to dolphins. Additionally, if dolphins in Whitewater Bay exhibited small-scale shifts in habitat use or home ranges similar to those observed in other locations (e.g., Nowacek et al. 2001), they may become unavailable for observation within the transect area.

Residency patterns of dolphins encountered in the Shark and Harney Rivers are similarly difficult to assess; of the 19 animals identified in these rivers, only three were ever sighted elsewhere in the estuary. It is likely that these animals are part of a nearshore population occasionally exploiting the rivers since it is unlikely dolphins were present but

not sited during river transects due to the narrow width of the transect and calm water conditions. The presence of a nearshore population occasionally entering the estuary could explain the low resighting rates of these animals (only two of the 19 individuals were sighted four times or more). Three animals were observed to switch habitats from estuarine to nearshore Gulf of Mexico; a pattern also observed in Sarasota Bay (Owen et al. 2002). Of the 31 animals identified in Florida Bay, two were later identified in the Gulf of Mexico. No animals seen in any other regions were sighted in Florida Bay. The lack of resightings may be indicative of a separate population or simple isolation by distance. Ponce de Leon Bay is the nearest entrance point to the estuarine Everglades from Florida Bay, which is 32 km away. Future genetic or isotopic studies may help elucidate population structure in the coastal Everglades region (e.g., Olin et al. 2012).

Dolphin densities varied considerably among regions. Densities of individuals in Florida Bay were consistently high despite having similar group densities to other areas, which is reflective of larger group sizes in Florida Bay. In the Shark and Harney Rivers, the densities of individuals during the dry season were not significantly greater than those found in the rest of the estuarine system, but the densities of groups were greater than those in Whitewater Bay. It was somewhat surprising that densities of both individuals and groups were considerably higher in Joe River than the adjacent Whitewater Bay since they should experience very similar water temperatures and salinities throughout the year. In addition, all of the individuals observed in Joe River were also observed in Whitewater Bay at some time. Because the abundance of large sharks is low in both Whitewater Bay and Joe River (Wiley and Simpfendorfer 2007) and rates of shark-inflicted injuries are

low, it is unlikely that Joe River provides a refuge from predation. The possibility that dolphins are using Joe River for foraging reasons is not testable at this time because of a lack of data of prey abundance and generally low sample sizes of foraging individuals. However, it is possible that dolphins select Joe River because the greater proportion of mangrove-lined shores facilities foraging. For example, in the Moray Firth, dolphins preferentially foraged over steep seabed gradients that may either provide higher concentrations of prey or increased foraging efficiency (Hastie et al. 2004).

The lack of measurable seasonal variation in dolphin densities (except within rivers) within regions was somewhat surprising given the dynamic nature of the ecosystem. However, the subtropical climate of south Florida, likely facilitates year-round residence and may lead to similar densities within the region across seasons. For example, even at higher latitudes (i.e., south of North Carolina along the Atlantic coast) dolphins tend to be year-round residents (Wells and Scott 1999, Gubbins 2002). The seasonal increase in dolphin abundances in rivers during the dry season is consistent with dolphins taking advantage of foraging opportunities. Indeed, during the dry season there is a pulse of freshwater fish entering the rivers as marsh taxa seek refuge from drying marshes (Rehage and Loftus 2007). In addition, increases in salinity dung the dry season may reduce the physiological costs of accessing these, and resident estuarine, potential prey. Stable isotope (e.g. Matich et al. 2011, Rosenblatt and Heithaus 2011) and fatty acid (Belicka et al. 2012) analysis could provide insights into the contribution of freshwater and estuarine taxa to the diets of dolphins using river habitats.

The proportion of individuals with scars or wounds from shark bites was quite low (1-5%) compared to other locations. For example, boat-based observations of free-swimming animals documented scars of 74.2% of individuals in Shark (Heithaus 2001) and 36.6% of individuals in Moreton Bay, Australia (Corkeron et al. 1987). In Sarasota Bay, attack rates are lower. Even though animals were captured and the entire body was assessed, only 31% of individuals had evidence of having been bitten by sharks (Urian et al. 1998). It is likely that some of the differences in scarring rates between the FCE and these locations is driven by poorer observation conditions in the FCE (e.g. tubid waters, free-swimming animals). When viewed in light of low catch rates of large sharks within the FCE (e.g. Wiley and Simpfendorfer 2007, P. Matich unpublished data), however, scarring data suggest that risk to dolphins is low. Yet, predation rates need not be high in order to elicit strong anti-predator behavior and low scarring rates could be the result of effective anti-predator behavior (e.g. Lima and Dill 1990).   Indeed, even though predation pressure is relatively low in Sarasota Bay, dolphins were still found to preferentially use shallower, more complex habitats during the times when bull sharks were most prevalent (Wells et al. 1980).

There appeared to be a general trend of increasing group size with increasing habitat openness, even within estuarine waters. Whitewater Bay had significantly larger groups than Joe River or the Shark and Harney Rivers and groups in channel habitats were smaller than those in open water habitats. Florida Bay had by far the largest group sizes compared to all other regions. In open water regions, prey tend to aggregate in larger patches (Ritz et al. 2011), which may result in larger groups through foraging

aggregations or facilitate larger groups through the benefits of cooperative foraging (e.g.
Creel and Creel 1995, Blundell et al. 2002). The open waters of Florida Bay likely have
somewhat higher risk of predation than estuarine habitats (e.g. Torres et al. 2006, Wiley
and Simpfendorfer 2007), so it is not possible to distinguish between foraging
considerations and anti-predator behavior as drivers of spatial variation in group sizes. In
other bottlenose dolphin populations, spatial variation in group sizes has been attributed
to age/sex variation in grouping patterns and habitat use (Wells 1993), activity-specific
habitat use and group size variation (Miller and Baltz 2010) and multiple dolphin
communities that may or may not share overlapping core areas of their home ranges but
vary in group sizes (Chilvers et al. 2001, Toth et al. 2012).

Groups with juveniles, calves and neonates were larger in the estuarine regions than in
the coastal oceans. In general, it is thought female bottlenose dolphins form nursery
bands with loose associations among individuals to reduce the risk of predation to their
calves (Wells et al. 1987). In Sarasota Bay, females with calves are most sociable and
occupy the largest groups – usually within estuaries - when their calves are younger
(Scott et al. 1990, Barco et al. 1999). Interestingly, in my study, the probability of
sighting a group with calves did not vary across regions. Based on patterns observed in
Florida Bay, higher probabilities of sighting calves would have been expected in
estuarine waters. Thus, it is possible that there are two separate populations or
communities within the study area, specifically an estuarine community and a coastal
ocean community. It is possible, however, that use of the river is influenced by predators
of dolphins. Groups containing calves were found further upstream than those without

calves. Juvenile bull sharks (*Carcharinhus leucas*) use upstream areas of the rivers to reduce the risk of predation from large sharks (Heithaus et al. 2009). Sharks large enough to be predators of juvenile sharks and young dolphins are encountered only at the mouth of the Shark River and coastal oceans (Wiley and Simpfendorfer 2007; Matich unpublished data), so moving upstream could reduce predation risk.

The results of my study suggest that the impacts of the planned Everglades restoration project will vary across the population. The animals using the Shark and Harney Rivers appear to be the most likely to be impacted. The upcoming CERP restoration will increase the amount of fresh water flowing through the system, potentially reducing the magnitude of dry-down and resulting prey pulses. In addition, salinities will be reduced throughout the system, potentially increasing metabolic costs to dolphins using some areas. Long-term studies will allow more detailed investigations of the biotic and abiotic factors impacting dolphin densities and habitat use and provide important insights into likely responses to restoration. In addition, incorporating stable isotopic or fatty acid analysis would provide insights into the foraging ecology of dolphins and be an important first step in elucidating their ecological roles in the coastal Everglades.

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