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The Soundscape of the St. Johns River and its Potential Impacts on the Habitat Use Patterns of Bottlenose Dolphins

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THE SOUNDSCAPE OF THE ST. JOHNS RIVER AND ITS POTENTIAL IMPACTS ON THE HABITAT USE PATTERNS OF BOTTLENOSE DOLPHINS

by

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Abstract

The development of effective management plans for animal populations relies on an understanding of how the population is utilizing the habitat as well as the identification of any critical habitat areas. The St. Johns River (SJR), an urban estuary with a high level of anthropogenic disturbance, is home to a resident population of bottlenose dolphins (*Tursiops truncatus*). In chapter one, SJR dolphin habitat use patterns, the factors that influenced these patterns, and the critical habitat areas were identified. Significant associations were found in most pair-wise comparisons between season, behavioral state, group size, water depth, and location, indicating that the overall habitat use patterns of SJR dolphins were influenced by complex interactions among these variables. Additionally, two critical habitat areas were identified. Both critical habitats had high levels of anthropogenic activity and the SJR will undergo further development during the Jacksonville Port expansion project. In conjunction with increasing levels of activity, anthropogenic sound can have numerous effects on cetaceans including the masking of signals, alterations in behavior, abandonment of critical habitats, and physiological stress. In chapter two, the soundscape of the SJR was characterized to evaluate the potential impacts of anthropogenic sound on SJR dolphins. Sound levels in the SJR were consistently high and anthropogenic sound was pervasive throughout the river. Therefore, the dolphins in the SJR are at risk of experiencing long-term behavioral and physiological stress due to anthropogenic sound. Together, this work provides valuable knowledge about dolphin habitat use and the soundscape ecology of an urbanized estuary that will enable more informed management decisions and hopefully lead to more effective conservation practices.

Introduction

Bottlenose dolphins (*Tursiops truncatus*) have a global distribution and exhibit complex patterns of habitat use. Habitats are not uniform in their composition (Ballance, 1992; Fortin et al., 2009), and dolphins will exhibit preferential use of certain areas depending on the quality and quantity of resources within each habitat patch (Ballance, 1992; Ingram and Rogan, 2002; Hastie et al., 2004; Parra, 2006; Gibson et al., 2013). Numerous factors influence area utilization including environmental variables (e.g., water depth, surface water temperature, distance from coast, tidal state), prey availability, predation risk, physiological factors, behavior of both con- and heterospecifics, seasonal fluctuations of dolphin abundance, and anthropogenic activity (Wilson et al., 1997; Williams et al., 1992; Allen and Read, 2000; Allen et al., 2001; Heithaus and Dill, 2002; Ingram and Rogan, 2002; Torres et al., 2005; Parra, 2006; Rossi-Santos et al., 2006; Balmer et al., 2013; Pirotta et al., 2013). Levels of anthropogenic activity in coastal systems have been steadily growing in the last few decades due to coastal development and increasing levels of commercial and recreational vessel traffic. Disturbance from anthropogenic activity can influence dolphin behavior within their habitat (Lusseau, 2003; Pirotta et al., 2013; Pirotta et al., 2015) and/or may reduce dolphin abundance within certain areas due to an overall habitat shift (Bejder et al., 2006; Pirotta et al., 2013). Dolphins have been shown to adjust their behavior in response to high levels of vessel traffic, which is also a potential source of acoustic harassment for these animals (Buckstaff, 2004; La Manna et al., 2013; Luís et al., 2014, Bas et al., 2014; Pirotta et al., 2015). In addition to eliciting behavioral responses, anthropogenic sound can lead to elevated levels of physiological stress (Romano et al., 2004; Wright et al., 2007; Rolland et al., 2012) and exposure to intense sound can cause auditory damage (Finneran et al., 2005; Mooney et al., 2009). Anthropogenic noise produced in the biologically relevant mid-

frequency range (0.5-25kHz), which overlaps with dolphin hearing and vocalization ranges, will have the largest behavioral and physiological effects on bottlenose dolphins (Haviland-Howell et al., 2007; Hildebrand, 2009; Marley et al., 2016). To understand the potential impacts of anthropogenic sound on dolphins within a specific habitat it is useful to identify the habitat use patterns and critical habitat areas for dolphin populations in coastal regions that have high levels of anthropogenic disturbance and are being actively developed.

Assessing dolphin habitat use provides valuable baseline data for monitoring a population, and the identification of critical habitat areas (high-use areas of fundamental importance; Ingram and Rogan, 2002) can aid in the development of effective management plans (Wilson et al., 1997; Ingram and Rogan, 2002; Lusseau and Higham, 2004; Bas et al., 2014). The habitat use patterns of dolphins have been documented in many study locations around the world including the Shannon Estuary, Ireland (Ingram and Rogan, 2002), Moray Firth, Scotland (Wilson et al., 1997), Shark Bay, Australia (Heithaus and Dill, 2002), Mississippi Sound, USA (Miller et al., 2013), and Doubtful Sound, New Zealand (Lusseau, 2003; Lusseau, 2004). To add to this body of knowledge, chapter 1 documented the habitat use of dolphins within the St. Johns River (SJR), Jacksonville, FL. The SJR is a highly-urbanized estuary that is actively being developed. Additionally, this study was one of the few that examined dolphin habitat use during multiple behavioral states. The two objectives for chapter one were to: (1) identify overall habitat use patterns and the factors that influence these patterns, and (2) identify the critical habitat areas for foraging, socializing, and resting dolphin groups.

Chapter two builds upon the identification of habitat use patterns and critical habitat areas for SJR dolphins by determining the potential impacts of anthropogenic sound on the dolphins in the river. Identifying patterns of anthropogenic disturbance within a system and comparing these

patterns to dolphin distribution can inform management decisions by indicating areas where dolphins are at risk of disturbance (Marley et al., 2016). Given the importance of sound in dolphin behavior, rising levels of vessel traffic and coastal development make anthropogenic sound a growing source of disturbance for these animals. The soundscape of the SJR and the impact of anthropogenic sound on the behavior of the dolphins in the river are unknown. Therefore, the two objectives for chapter two were to: (1) characterize the soundscape of the SJR by measuring median sound levels, identifying common sound sources, and documenting the prevalence of anthropogenic sound, and (2) determine the impact of anthropogenic sound on SJR dolphin habitat use.

Together, this work provided a rare opportunity to compare dolphin habitat use with soundscape patterns within an urbanized estuary. Identification of habitat use patterns provides management agencies with valuable information for determining where the dolphins are likely most vulnerable to disturbance from anthropogenic activity. This knowledge can then be used to develop management plans that would help maintain a viable SJR dolphin community. Additionally, only three previous studies (Pamlico Sound, North Carolina: Lillis, 2014; Kaipara Harbour, New Zealand: Pine, 2015; Swan-Canning River, Western Australia: Marley, 2016) have explored the soundscape of an estuary. Therefore, this study is a significant contribution to the body of knowledge on estuarine soundscapes. Furthermore, the impact of sound on marine mammals is a growing field of interest. Human activity in marine ecosystems has increased exponentially within the last few generations and is likely to continue increasing into the future. It is essential to understand the impacts of sound produced by human activities on marine mammals in order to effectively manage and protect these species.

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Chapter 1

Identification of bottlenose dolphin (*Tursiops truncatus*) habitat use patterns and critical habitat areas in an urban estuary

Abstract

Coastal development poses a significant risk to cetacean populations, and development of site-specific regulations is necessary to adequately manage and protect these populations. The St. Johns River (SJR), Jacksonville, FL is an urban estuary with high levels of anthropogenic disturbance. Prior to the commencement of the large-scale Jacksonville port expansion project, it is essential to understand the habitat use of, and identify critical habitat areas for, the SJR bottlenose dolphin (*Tursiops truncatus*) community. The objectives for this project were to identify habitat use patterns and the factors that influence these patterns, while also identifying the critical habitat areas for foraging, resting, and socializing dolphin groups. Data were collected weekly on boat-based photo-identification surveys from June 2011 to May 2016. General habitat use patterns were identified by testing the associations among season, behavioral state, group size, water depth, and location in the SJR. The critical habitat areas for foraging, socializing, and resting dolphin groups were then identified using their 50% utilization distributions. The overall habitat use patterns of SJR dolphins were influenced by complex interactions among all variables tested. Two critical habitat areas were identified in this study: stratum two and stratum four. Stratum two (Mile Point) was a year-round and a warm-season

critical habitat area for foraging and socializing dolphin groups, respectively. Stratum four (first JaxPort shipping terminal and entrance to Mill Cove) was a year-round critical habitat for socializing and resting dolphin groups. High levels of anthropogenic activity are already present throughout the dolphins' range within the SJR and approximately 20km of the river, including both dolphin critical habitat areas, will undergo further development during the port expansion project. Future increases in anthropogenic activity could potentially exceed the tolerance thresholds of the dolphins to disturbance, resulting in large-scale impacts.

Introduction

Bottlenose dolphins (*Tursiops truncatus*) have a global distribution and can be found in a wide variety of habitats ranging from shallow, coastal waters to deep waters along continental shelves (Ballance, 1992; Bas et al., 2014; Ingram and Rogan, 2002; New et al., 2013; Rossi-Santos et al., 2006; Smolker et al., 1992; Wilson et al., 1997). The different ecological pressures present in these various habitats will dictate the home ranges (area occupied by an individual during its everyday activities; Burt, 1943) of the dolphins living within each region. The overall size of a dolphin's home range and their preferential use of certain areas is determined by the quality and quantity of resources within the habitat (Balance, 1992; Ingram and Rogan, 2002; Gibson et al., 2013; Hastie et al., 2004; Parra, 2006). Additionally, due to their low energetic costs of movement (Williams et al., 1992), dolphin home ranges can be quite large and vary greatly among populations and individuals. For example, within the northeast Florida estuarine system, estimated dolphin home ranges were between 116-217 linear kilometers in size (Nekolny, 2014). These home range estimates were determined from the combined data sets of six research teams that covered a total area of 253 linear kilometers. Thus, an individual dolphin's home range may span beyond the boundaries of a single research study area. However,

core areas of use (regions that are heavily utilized and typically contain essential habitat) can be reliably identified within study sites (Ingram and Rogan, 2002; Nekolny, 2014).

Variations in area utilization occur because habitats are not uniform in their composition; rather they vary physically, biologically, and temporally (Ballance, 1992; Fortin et al., 2009). Factors that influence dolphin habitat use patterns include environmental variables (e.g., water depth, surface water temperature, distance from coast, tidal state), prey availability, predation risk, anthropogenic activity, physiological factors, behavior of both con- and heterospecifics, and seasonal fluctuations of dolphin abundance (Wilson et al., 1997; Williams et al., 1992; Allen and Read, 2000; Allen et al., 2001; Heithaus and Dill, 2002; Ingram and Rogan, 2002; Torres et al., 2005; Parra, 2006; Rossi-Santos et al., 2006; Balmer et al., 2013; Pirotta et al., 2013). To balance these diverse ecological pressures, bottlenose dolphins live in fission-fusion societies (Connor et al., 2000), in which group size and composition change frequently. These fluid societies allow dolphins to optimally adjust behavioral state, group size, and habitat use in response to changing pressures (Heithaus and Dill, 2002; Fortin et al., 2009), while also allowing for association preferences (Irvine et al., 1981; Connor et al., 2000; Gero et al., 2005). For example, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) inhabiting the pristine waters of Shark Bay, Australia, preferentially used deep water habitats and associated in larger groups while resting which decreased their risk of encountering tiger sharks (*Galeocerdo cuvier*; Heithaus and Dill, 2002). Documentation of such variation in area utilization (i.e., the amount of time a certain area is utilized by individuals in a population), can indicate the ecological function of a certain habitat patch (Hastie et al., 2004) as well as the location of preferred core areas (Johnson, 1980; Allen et al., 2001).

Ecological parameters, especially food resources, significantly influence the habitat use patterns of a population (Ingram and Rogan, 2002; Hastie et al., 2004; Miller et al., 2013; La Manna et al., 2016). Food resources are spatially and temporally distributed, and behavior will fluctuate accordingly to reduce resource competition (van Schaik et al., 1983; Hoare et al., 2004). For example, many coastal populations use deeper channels of fast moving water (Ingram and Rogan, 2002; Hastie et al. 2004) and estuary mouths as foraging sites because these locations concentrate prey (Ballance, 1992; Wilson et al., 1997; Parra, 2006; Steiner, 2012). Estuarine systems are preferred because they serve as important nursery grounds for fish larvae as well as habitat for adult fish (DeMort, 1991). Habitat utilization is further dictated by seasonal changes in productivity (Ballance, 1992; Wilson et al., 1997; Allen et al., 2001; Gubbins et al., 2003; Heithaus and Dill, 2002; Hastie et al., 2004; Miller et al., 2013; Bas et al., 2014). Typically, estuarine productivity is lowest during the cold season, and seasonal shifts in dolphin distribution, home range size, and abundance have been observed within estuarine regions (United States southeast coast: Gubbins et al., 2003; Torres et al., 2005; Speakman et al., 2010; Balmer et al., 2013; Miller et al., 2013; Brusa et al., 2016; Shannon Estuary, Ireland: Ingram and Rogan, 2002; and Moray Firth, Scotland: Wilson et al., 1997). For example, within the Mississippi Sound, bottlenose dolphin abundance was lowest during the winter months and highest during the summer. This shift in abundance was most likely due to dolphins moving to deeper, coastal waters during the winter in search of prey (Miller et al., 2013). However, this directional pattern may not apply to all populations that exhibit seasonal shifts in dolphin abundance (see Durden et al., 2017). Seasonal shifts in productivity and the movement of prey species will influence the habitat use patterns of individuals within a population because areas of

higher prey abundance will often be favored over areas with low prey abundance (Ballance, 1992; Miller, 2017).

Many estuarine systems are also heavily utilized by humans for recreational and commercial purposes, resulting in repeated interactions between dolphins and humans. These repeated interactions create a need to monitor the status of estuarine dolphin populations, and assessing dolphin habitat use patterns provides valuable baseline data for monitoring purposes. Specifically, if a population changes their habitat use patterns (e.g., stop utilizing a certain foraging patch) this could also indicate changes in activity budgets, and long-term changes to activity budgets can result in significant, negative impacts to the population (Lusseau and Higham, 2004; Tyack, 2008; Bas et al., 2014). In addition to monitoring the status of a population, it is essential to identify critical habitat areas (high-use areas of fundamental importance; Ingram and Rogan, 2002) for the development of effective management plans (Wilson et al., 1997; Ingram and Rogan, 2002; Lusseau and Higham, 2004; Bas et al., 2014). Repeated or increasing levels of anthropogenic disturbance (e.g., boat traffic and dredging) create a need for updated management plans because these disturbances may influence dolphin behavior within their habitat (Lusseau 2003; Pirotta et al., 2013; Pirotta et al., 2015), or may reduce dolphin abundance within certain areas due to an overall habitat shift (Bejder et al., 2006; Pirotta et al., 2013). In Doubtful Sound, New Zealand, socializing and resting dolphins altered their habitat use (i.e., left the area) due to disturbances from boating traffic (Lusseau, 2003; Lusseau, 2004). Similar displacement from certain habitat areas due to coastal development that modified the habitat and led to increased boat traffic has even been documented in bottlenose dolphin populations that were previously habituated to relatively high levels of disturbance (Pirotta et al. 2013). The dolphins in Aberdeen Harbor, Scotland could tolerate short-term peaks

in disturbance (e.g., frequent vessel traffic and maintenance dredging), but once the disturbance reached a threshold level (i.e., long-term dredging during a port expansion) the habitat was abandoned until the disturbance stopped (Pirotta et al., 2013). Therefore, it is essential to identify the habitat use patterns and critical habitat areas for dolphin populations in coastal regions prior to the commencement of large-scale development projects.

Along the northeast coast of Florida, the St. Johns River (SJR) is an urban estuary that is currently undergoing the initial stages of a large-scale port expansion project to accommodate larger vessels and alleviate cross-currents on vessel navigation. The Jacksonville port expansion project will entail dredging the main channel from 12.5m to a maximum depth of 15.2m, underwater blasting to loosen bedrock during dredging as well as at specific locations in the river to create turn-around points for cargo ships, and the relocation of the training wall at Mile Point (convergence point for the Intracoastal waterway and the SJR; U.S. Army Corp, 2014; Harbor Deepening, 2017). Such a large-scale habitat change within the SJR may impact both the resident and transient bottlenose dolphins that utilize the river (Nekolny, 2014; Ermak et al., 2017).

The habitat use patterns of the SJR dolphin community are not yet known; therefore, the two objectives for this project were to: (1) identify overall habitat use patterns and the factors that influence these patterns, and (2) identify the critical habitat areas for foraging, resting, and socializing dolphin groups. Baseline data on the habitat use patterns of the SJR dolphin community will be essential for detecting changes in habitat use during and/or following port expansion and will enable any necessary mitigation efforts to be employed in a timely manner. Additionally, knowledge of the critical habitat areas is crucial to ensuring that these areas are adequately protected to maintain the health and viability of this community (Ingram and Rogan, 2002; Bas et al., 2014).

Methods

Study Area

The study site for this project was the St. Johns River (SJR) in Jacksonville, FL. The 500km SJR is the longest river in Florida and one of the few rivers in North America that flows northward (Pinto et al., 2016). The SJR is a dark blackwater system that drains into the Atlantic Ocean at the Mayport Inlet in Jacksonville, Florida. The tidal range at the Mayport Inlet is about 2m and water depth is tidally influenced up to 170km upriver (Pinto et al., 2016). The study area is located in the mesohaline riverine zone of the Lower St. Johns River Basin, and is typically well-mixed and deep with a fast flow rate (Pinto et al., 2016). The lower SJR has relatively poor water quality (Pinto et al., 2016) and has a high potential for anthropogenic disturbance. Sources of disturbance include an international shipping port with three major terminals, a U.S. Naval station, U.S. Coast Guard station, Carnival cruise ship port, commercial fishing fleet, and heavy use by recreational boats. Additionally, work on the Jacksonville port expansion project began in May 2016.

Photo-Identification surveys

Weekly boat-based photo-identification surveys of dolphins were conducted from June 2011 to May 2016 along a 40km fixed transect from the river mouth (Mayport Inlet: N30.39904, W-81.39396) to downtown Jacksonville (Hart Bridge: N30.31479, W-81.62987; Figure 1). The direction of travel was alternated each week to randomize data collection in relation to tidal and diel patterns. Surveys were conducted using a 7.9m Twin Vee catamaran or 6.4m Carolina skiff traveling at 10-12km/hour until dolphins were sighted.

During dolphin sightings, the dorsal fins of all individuals within the group were photographed using a professional grade digital camera with 400mm telephoto lens for later

identification and confirmation of group size (Würsig and Jefferson, 1990). Group membership was determined using the conservative 10m chain rule, which states that a dolphin is a member of the group if it is within 10m of at least one other dolphin in the group (Smolker et al., 1992). Behavioral data collected during sightings included predominant behavioral state, group size and composition, movement with respect to tidal state, and surfacing patterns. Environmental data were also collected during sightings and included the latitude and longitude of the start and end location of each sighting, Beaufort sea state, water depth, water temperature, and salinity.

Habitat use patterns

Identifying habitat use patterns of dolphins can be challenging due to the highly mobile nature of these animals and the limited amount of time they are visible at the surface (Hastie et al., 2004; La Manna et al., 2016). Therefore, habitat use patterns are frequently inferred from the distribution patterns of a population as a whole (Parra, 2006; Rossi-Santos et al., 2006; Bas et al., 2014; Brusa et al., 2016). In this study, the sighting locations of dolphin groups were used to determine the distribution of dolphins within the SJR. Also, the location of sightings was used as a proxy for measuring the amount of time different areas were utilized (more sightings in an area indicate that it was utilized more frequently). Analyses excluded sightings from incomplete surveys, sightings with unknown behavioral state, and same day re-sightings of groups with compositions that were less than 30% different. In addition, incomplete sightings (sightings in which not all of the individuals were photographed) of small groups (one-two individuals) were also excluded from analyses. Incomplete sightings of small groups typically occurred when the dolphin(s) were only seen once at the surface or were seen from a distance making it difficult to record the predominant behavioral state. However, to avoid biasing the data towards small group sizes, all sightings of medium and large groups (three-seven and ≥ eight individuals,

respectively) were included in analyses because the probability of fully documenting group membership decreased with increasing group size. Finally, sightings with traveling dolphins were excluded from the critical habitat analyses but included in all other analyses.

Habitat use has been shown to be influenced by complex interactions between season (Wilson et al., 1997; Speakman et al., 2010; Miller et al., 2013), behavioral state (Allen et al., 2001; Hastie et al., 2004), group size (Heithaus and Dill, 2002; Fortin et al., 2009), water depth (Ingram and Rogan, 2002) and location in relation to river/estuary mouths (Ballance, 1992; Parra, 2006). Therefore, to determine how these variables influenced the habitat use patterns of SJR dolphins, all sightings were classified based on season and behavioral state, then further stratified based on group size, water depth, and strata (location). Dolphin abundance in the SJR is highest during the summer and lowest during the winter (Nekolny, 2014), and anecdotal shifts in distribution have been observed in conjunction with this shift in abundance (Gibson, unpublished data). Therefore, sightings were separated into two seasons based on mean daily water temperatures: warm (> 16°C) and cold (≤ 16°C; Heithaus and Dill, 2002; Gubbins et al., 2003; Caldwell, 2016). Residency status was not included in this study; therefore, the habitat use patterns identified during the warm season were determined using sightings composed of residents, seasonal residents, and transients.

Dolphin behavioral states were separated into four categories: traveling, foraging, socializing, and resting (Table 1). If multiple behavioral states were observed during a sighting, the sighting was classified based on the behavioral state that was observed for the greatest amount of time (predominant behavioral state) for the entire group. Sightings were further classified based on group size (small groups: one-two individuals; medium groups: three-seven individuals; large groups: eight or more individuals). These group size classifications reflected

the 1st quartile, median, and 3rd quartile values. Water depth was measured at the beginning of each sighting using a Garmin depth finder, and sightings were separated into one of six depth categories (0-2.9m, 3-5.9m, 6-8.9m, 9-11.9m, ≥ 12m). These depth categories were selected because they provided fine-enough resolution for the habitat use analyses without oversimplifying the data.

Finally, to assess fine-scale changes in habitat use, the locations of all sightings were assigned to one of ten strata (Figure 1) using ArcMap 10.3 software (ESRI, Redlands, CA). Stratum one was located at the Mayport Inlet and stratum ten was located 40km upriver at downtown Jacksonville. The strata were created based on the predominant level and type of anthropogenic activity within each stratum, and as such, varied in size (Table 2). Anthropogenic activity was used to separate strata because different types of activity result in different modifications to the SJR such as docks, jetties, riprap, and bridge pillars. For example, stratum ten contained two major high-traffic bridges in downtown Jacksonville, stratum eight was primarily residential (private docks), stratum four contained the first JaxPort shipping terminal, and stratum one at the Mayport Inlet had two military bases and rock jetties along both shores. Most strata were between 4-6.4km in length, with the only exception being stratum five (> 10km in length). Stratum five (Mill Cove) was unique because it was not located on the survey transect line due to the shallow nature of the stratum. Thus, most sightings obtained in stratum five were opportunistic; if dolphins were visible from the main transect line, the survey vessel would attempt to approach for data collection. The typical water depth in stratum five was ≤ 2m and only the narrow entrance was reliably passable in the survey vessel. Thus, many sightings collected in stratum five were incomplete because the survey vessel was unable to follow groups into the cove or approach groups further inside the cove.

The sighting categorizations were then used to determine the association between behavioral state and season/group size/water depth/location as well as the association between group size and location using row x column G-tests of independence ($\alpha = 0.05$ for all tests). To account for the seasonal shifts in dolphin abundance, warm and cold season data were analyzed separately in the tests among behavioral state, group size, water depth, and location. For the location analyses, all ten strata were included during the warm season and only strata one-six were included during the cold season due to the lack of data (no samples in one or more strata or behavioral state rows/columns) from strata seven-ten. Multiple comparisons were made with each G-test; therefore, a significant result indicated the variables were associated but not which comparison was significant. Bonferroni corrections were not conducted because the multiple comparisons in each G-test would have made the criteria for finding significance too restrictive.

To identify large-scale patterns of habitat use, the 95% and 50% utilization distributions (UD) were calculated using ArcGIS 10.3 software. Sighting locations were first weighted based on the number of dolphins in each group using the population field in the sighting record. Kernel density estimates (KDEs) were then generated for each behavioral state and season combination using the kernel density tool in the ArcGIS Spatial Analyst toolbox. Raster grid sizes were generated by ArcGIS based on the minimum of the inputs (smallest distance between points on a cell-by-cell basis) from the sighting location shapefile. Land areas were then removed from the KDEs with the Spatial Analyst masking tool using a St. Johns River shapefile. The 95% and 50% UDs were then calculated by dividing each KDE into 20 regions of use using the natural breaks (Jenks) classification scheme in ArcGIS. For the 95% utilization distribution, region one was excluded and for the 50% utilization distribution regions one-ten were excluded (Warning and Benedict, 2015; Warning, *personal communication*). At the population level, the 95% UD

indicates the representative home range and the 50% UD indicates critical areas (Ingram and Rogan, 2002; Parra, 2006; Brusa et al., 2016).

Results

Sample Size

A total of 1,481 group sightings were analyzed in this study: 1,210 group sightings were collected during the warm season (107 survey days) and 271 group sightings were collected in the cold season (39 survey days). Overall, traveling groups were observed most frequently (57% of all sightings), followed by foraging groups (27% of all sightings), then socializing groups (12% of all sightings), and resting groups were seen the least (4% of all sightings). Warm season sightings were most frequently of medium sized groups (three-seven individuals; 39% of sightings). Cold season sightings were primarily of small groups (one-two individuals; 43% of sightings). Large groups (≥ eight individuals) were sighted the least in both seasons (28% of sightings in the warm season and 19% of sightings in the cold season). Mean group size was 6.4 individuals (SD = 4.0) during the warm season and 4.8 individuals (SD = 4.7) during the cold season.

Identification of SJR dolphin habitat use patterns

A significant association was found between season and behavioral state ($G = 8.32$, $X^2_{Crit} = 7.81$, $p = 0.04$). The proportion of sightings that contained foraging groups remained the same between the two seasons (Figure 2). For both socializing and resting groups the proportion of sightings slightly decreased from the warm to the cold season ($\Delta = 0.03$). Finally, the proportion of sightings of traveling groups slightly increased from the warm to the cold season ($\Delta = 0.05$).

Behavioral state was also significantly associated with location (strata) in both seasons (warm: $G = 88.45$, $X^2_{Crit} = 40.11$, $p < 0.0001$; cold: $G = 39.64$, $X^2_{Crit} = 18.31$, $p = 0.0001$). Sightings were not weighted based on group size in these analyses, thus these results represent the proportion of group sightings rather than the proportion of dolphins observed in each location. With the exception of stratum five, which was rarely used for foraging, there was relatively low variation in the proportion of foraging sightings among the strata (Figure 3). During the warm season, the highest proportion of foraging group sightings was in stratum seven (0.15), whereas stratum nine (0.08) had the lowest proportion of foraging group sightings ($\Delta = 0.07$) when stratum five was excluded. In contrast, during the cold season, foraging groups exhibited a clear spatial pattern in which the strata closest to the river mouth were utilized more frequently than those further upriver (Figure 4). The highest proportion of foraging group sightings was in stratum two (0.31) and the lowest in stratum six (0.01; $\Delta = 0.3$) when stratum five was excluded. Socializing groups clearly utilized specific locations more than others. In the warm season, stratum four had the highest proportion of socializing group sightings (0.21) and was utilized at least two times more often than six other strata (excluding stratum five). The next most frequently utilized area was stratum two (0.16). Stratum six (0.05) and stratum ten (0.04) were utilized relatively infrequently by socializing groups. This pattern of concentrated use was more pronounced during the cold season. Half of the socializing group sightings in this season were in stratum four (0.5); all other strata had proportions ≤ 0.16. Traveling dolphin groups were primarily observed in the regions closest to the river mouth in both seasons, with the proportion of sightings generally decreasing with increasing distance from the inlet. Specifically, the highest proportion of traveling group sightings was collected in stratum one (warm: 0.21; cold: 0.46), and the lowest proportion in stratum ten (warm season: 0.04; $\Delta = 0.17$) and stratum six (cold

season: 0.05; $\Delta = 0.41$). The only exception to this general pattern was stratum five (warm: 0.02; cold: 0.01); however, this was likely due to the opportunistic nature of sightings in this stratum. Finally, resting dolphin groups did not exhibit clear patterns of habitat utilization during the warm season. In general, stratum two had the highest proportion of resting group sightings (0.18) and stratum 10 had the lowest proportion (0.02; $\Delta = 0.16$). Strata three, seven, and nine were also utilized less often compared to the other strata. Area utilization of resting groups was not examined during the cold season due to insufficient sample size (N = 4). Three of these sightings were collected in stratum four and the other in stratum two.

A significant association between group size and location (strata) was also found within both seasons (warm: $G = 57.15$, $X^2_{Crit} = 28.87$, $p < 0.0001$; cold: $G = 21.84$, $X^2_{Crit} = 18.31$, $p = 0.005$). During the warm season, groups of all sizes were observed throughout the river (Figure 5). Small groups (one-two individuals) did not exhibit a clear pattern of habitat use based on location. The highest proportion of sightings of small groups (0.15) were observed in strata one and seven, whereas the lowest proportion was collected in stratum nine (0.07; $\Delta = 0.08$) when stratum five was excluded. In contrast to small groups, the proportion of medium (three-seven individuals) and large (≥ eight individuals) group sightings exhibited greater variation among strata in the warm season. Generally, the proportion of sightings decreased with increasing distance from the river mouth. The only exception to this pattern was stratum five, which is being treated as an outlier due to the opportunistic nature of any sightings collected in this stratum. For medium-size groups, stratum one (0.18) contained the highest proportion of sightings. The lowest proportion of medium group sightings was collected in stratum ten (0.05; $\Delta = 0.15$). For large groups in the warm season, stratum two (0.22) had the highest proportion of sightings. For stratum six through ten, the proportion of large group sightings were overall much

lower (≤0.08) than those collected in the first four strata. During the cold season, the proportion of sightings for all three group size categories generally decreased with increasing distance from the river mouth (Figure 6). Stratum one had the highest proportion of small and medium group sightings (0.42 and 0.39, respectively) and stratum two had the highest proportion of large group sightings (0.36). A low proportion of sightings for all group sizes were collected in stratum six (small: 0.01, $\Delta = 0.4$; medium: 0.08, $\Delta = 0.31$; large: 0.02, $\Delta = 0.34$). In the cold season, strata seven-ten were not included in this analysis due to insufficient sample size for the G-test; thus, stratum six was the furthest upriver and was utilized the least.

Behavioral state and group size were also significantly associated during both seasons (warm: $G = 167.133$, $X^2_{Crit} = 12.59$, $p < 0.0001$; cold: $G = 59.90$, $X^2_{Crit} = 12.59$, $p < 0.0001$). Foraging groups were predominantly small in both seasons, but the proportion of small foraging group sightings was much lower in the warm season (0.53; Figure 7) compared to the cold season (0.75; Figure 8). Foraging groups that were medium to large were also observed year-round, but more frequently in the warm season (medium: 0.36; large: 0.11) than the cold season (medium: 0.16; large: 0.09). Socializing groups were primarily medium-large in size year-round. In the warm season, the highest proportion of sightings were of large socializing groups (0.57), and small socializing groups were infrequently observed (0.07; $\Delta = 0.5$). Conversely in the cold season, the proportion of medium and large socializing group sightings were exactly equal (0.48) and small socializing groups were again observed the least (0.04; $\Delta = 0.44$). In general, traveling dolphin groups were most often medium-sized year-round (warm: 0.4; cold: 0.46). In the warm season, overall low levels of variation were observed between the three group size categories (small/large: 0.3; $\Delta = 0.1$). In contrast, during the cold season small traveling groups were observed more (0.35) than large groups (0.18). Finally, the proportion of medium-sized resting

group sightings was highest year-round. In the warm season, over half of the resting group sightings were of medium groups (0.55), while small and large resting groups were observed in similar proportions (small: 0.22; large: 0.24). Overall, resting dolphin groups were observed most frequently during the warm season, with only four sightings collected during the cold season. Of these sightings half (0.5) were of medium sized resting groups, and a quarter (0.25) were of small and large resting groups.

Finally, a significant association was found between water depth and behavioral state during the warm season, but not during the cold season (warm: $G = 37.32$, $X^2_{Crit} = 24.99$, $p = 0.001$; cold: $G = 14.28$, $X^2_{Crit} = 18.31$, $p = 0.164$). The main channel of the SJR was between 12-15m deep on average, with fluctuations in depth above 15m depending on the tidal state. Across all behavioral states, the highest proportion of warm season sightings was observed in water depths ≥ 12m (Figure 9). Generally, within each behavioral state the proportion of sightings increased with water depth. Accordingly, the lowest proportions of sightings were collected in water depths from 0-2.9m. During the cold season, water depths ≥ 12m also had the highest proportion of sightings, but the proportions were much higher compared to the warm season (FOR: $\Delta = 0.24$; SOC: $\Delta = 0.04$; TRV: $\Delta = 0.14$; Figure 10). Rest was excluded from the cold season water depth analysis due to insufficient sample size ($N = 4$), but these sightings were collected in either 3m or 6m of water. All other water depth categories were utilized in much lower proportions (all ≤ 0.18) during the cold season.

Identification of the 95% utilization distributions and critical habitat areas

The warm season 95% utilization distributions (UD) of foraging (Figure 11a) and traveling (Figure 12a) dolphin groups indicated the entire study area was utilized during these behavioral states. Socializing (Figure 13a) and resting (Figure 14a) dolphin groups also utilized

most regions of the SJR although a few areas were not utilized. Socializing groups did not utilize small sections of strata one, two, and six, while resting groups did not utilize small sections of strata six and seven. In contrast to the warm season pattern, habitat use was more fragmented during the cold season. Foraging dolphin groups consistently utilized the region between the river mouth and 18km upriver (strata one-four) as well as two regions of relatively low use approximately 23km and 26km upriver (in stratum seven; Figure 11c). Traveling dolphin groups utilized most regions of the SJR during the cold season (Figure 12b). The areas that were most heavily utilized were between the river mouth and 18km upriver (strata one-four). Socializing groups had seven distinct regions of use identified in the cold season 95% utilization distribution (Figure 13c). Five of these regions were also located in the area between the river mouth and 18km upriver (strata one-four), and the remaining two were located 20km (stratum six) and 34km (stratum nine) upriver. Resting dolphin groups only utilized a small region approximately 16km upriver (stratum four) during the cold season (Figure 14c). Overall, the entire SJR study area was largely utilized during all behavioral states in the warm season, while only certain regions were utilized during each behavioral state in the cold season. The majority of regions utilized during the cold season were also located towards the river mouth, indicating habitat use shifts downriver in this season.

Two critical areas (50% UDs) were identified for foraging behavior during the warm season: stratum ten (downtown Jacksonville) and stratum two (Mile Point; Figure 11b). Stratum two was more heavily utilized by the dolphins compared to stratum ten based on the color-coding scheme generated in ArcGIS. During the cold season, stratum two was the only critical area identified for foraging groups (Figure 11d). Socializing dolphins also had two critical areas during the warm season: stratum two and stratum four (Figure 12b). Stratum four was more

heavily utilized than stratum two. Stratum four was also identified as a critical area for socializing groups during the cold season (Figure 12d). Similarly, resting groups had two warm season critical areas identified: stratum three and four with stratum four more heavily utilized than stratum three (Figure 13b). The only critical area identified for resting groups during the cold season was stratum four (Figure 13d). Only four sightings of resting dolphin groups were collected during the cold season; however, three of these sightings were within stratum four. Overall, SJR dolphins utilized stratum two and stratum four as year-round critical habitat areas for multiple behavioral states.

Discussion

Seasonal changes in habitat use

Seasonal, large-scale shifts in habitat use were observed in the St. Johns River (SJR). During the warm season, dolphins utilized the entire 40km survey area (strata one-ten), but concentrated their habitat use closer to the river mouth (strata one-six) in the cold season. This seasonal shift in habitat use was also seen in the 95% utilization distributions (UD) of foraging, socializing, traveling, and resting dolphin groups. The strata and 95% UD analyses were two methods for examining the same data set, and ultimately the same general trend in habitat use was identified. Overall, there was more wide-spread habitat utilization during the warm season and more concentrated use during the cold season.

The fluctuations in habitat use that were shown by the strata and 95% UD analyses could be due to seasonal changes in dolphin abundance and/or movements of prey to deeper waters (Wilson et al., 1997; Miller et al., 2003). In Moray Firth, Scotland, Wilson et al. (1997) observed dolphins shifting their habitat use in response to the summer influx of non-resident

dolphins, with resident dolphins utilizing different areas of the Firth than non-residents. Like the Moray Firth residents, SJR resident dolphins may be moving farther up river in the warm season due to changes in population abundance. Dolphin abundance in the SJR was highest during the spring/summer (warm season) due to an influx in transients/seasonal residents (Nekolny, 2014). Preliminary analyses indicate that resident SJR dolphins preferentially associate with other residents and rarely associate with transients (Gibson, unpublished data). Therefore, social factors may be causing the dolphins to expand their range farther upriver during the warm season. Increased dolphin abundance also correlates with higher levels of resource competition (Belovsky and Slade, 1995; Parrish and Edelstein-Keshet, 1999; Fortin et al., 2009; Ermak et al., 2017). The population density of dolphins in the summer is exceptionally high in the SJR compared to other study sites (Ermak et al., 2017), indicating resource competition could be a significant driver of habitat use patterns (Parra, 2006). Therefore, it is likely that SJR dolphins adjusted their habitat use seasonally to reduce competition. With respect to prey movements, estuarine productivity is lowest during the winter, and this could cause SJR dolphins to move towards the river mouth in search of prey (Irvine et al., 1981; Steiner, 2012; Miller et al., 2013). Numerous finfish species live within the SJR (DeMort, 1991; Pinto et al., 2016), and fish species that are commonly consumed by dolphins include drums, croakers, seatrout, and mullet (Barros and Odell, 1990; Gannon et al., 2005; Miller et al., 2013). Seasonal changes in the abundance and distribution of these fish species could potentially influence the habitat use patterns of SJR dolphins. For example, mullet leave the SJR and head south to warmer waters during the autumn (Mullet Run, 2017), which is consistent with our finding that dolphins shifted their habitat use to the regions (strata) closer to the river mouth during the cold months. Overall, the observed seasonal changes in habitat use patterns of SJR dolphins were likely due to both changes in

dolphin abundance and prey availability; thus, further research is necessary to determine the degree of influence these factors have on habitat use. Additionally, the habitat use patterns of resident and non-resident dolphins should be examined separately to determine how residency status influences habitat use.

Behavioral state and location (strata)

The SJR dolphins did not utilize the SJR equally during all behavioral states; rather, they exhibited varying patterns of habitat use. For example, during the cold season, foraging dolphin groups exhibited a clear pattern of habitat use: the mouth of the river (strata one and two) was more heavily utilized than stratum six (limit of the cold season strata analyses). In general, the proportion of foraging group sightings decreased with increasing distance from the river mouth. Dolphins in estuarine systems often move towards deeper water during the cold season in search of prey (Steiner, 2012; Miller et al., 2013), and this likely explains why the strata near the river mouth were utilized more by foraging dolphin groups. In contrast, the warm season strata analysis did not reveal a clear pattern of habitat use by foraging groups or indicate preferred foraging areas. Although there was relatively little variation among strata, the strata that were utilized more than others likely contained some habitat feature(s) that made them more profitable foraging patches. For example, stratum two may have been a high-quality foraging habitat because the Intracoastal Waterway (ICW) crosses the SJR at this location creating fast cross-currents which help to concentrate prey items (Ingram and Rogan, 2002). Additionally, stratum seven was relatively narrow and a major tributary (Trout River) joins the SJR just upriver in stratum eight. Therefore, it is likely that fast currents were also present in stratum seven, causing it to be a profitable foraging patch. More research is necessary to determine if the strata that were

utilized slightly more than others were more advantageous foraging areas (e.g., higher prey density) or if the differences in utilization were due to chance.

Unlike foraging groups, socializing groups preferentially utilized specific strata year-round. For example, in the warm season, socializing groups utilized stratum four twice as often as they utilized other strata. Stratum two was also heavily utilized in this season. Since the dolphins exhibited preference for strata two and four, these areas likely contain some feature(s) that make them favorable to socializing dolphins. Stratum four contains the eastern entrance to Mill Cove (stratum five) and the area around the entrance was relatively shallow (typically < 3m in depth). Socializing in dolphins is often linked to reproduction (Lusseau, 2004), and the shallow water may allow males to maintain greater control over a cycling female. Also, fewer vessels pass through this shallow area compared to the northern part of the stratum where the first JaxPort shipping terminal is located. Therefore, it may be safer to socialize in the shallow regions where less vigilance for vessel traffic is required during periods of intense socialization. Additionally, stratum two may have been favored by socializing dolphin groups due to the diversity of available associates during the warm season (e.g., transients or seasonal residents). The ICW crosses the SJR in stratum two, therefore this location could act as a mixing area for residents in the northern and southern ICW communities as well as coastal and SJR dolphins. Thus, dolphins may be able to interact with new or infrequently encountered associates in this location. However, residency status was not examined in this study, so further research is necessary to clarify how residents and non-residents utilize the SJR. In the cold season, socializing dolphin groups continued to predominantly utilize stratum four, but did not utilize stratum two differently from the other strata. SJR males continued to herd females during the cold season (non-breeding season; Karle, 2016), and the shallow water region of stratum four

would also continue to offer increased protection from vessel traffic. Therefore, it was likely beneficial for all types of socializing groups to utilize stratum four year-round.

Traveling dolphin groups exhibited clear patterns of habitat use year-round with utilization generally decreasing with increasing distance from the river mouth. Stratum one, which had the highest proportion of traveling group sightings, may be heavily utilized in both seasons because dolphins that are moving between estuarine and coastal waters likely pass through this stratum.

Finally, resting dolphin groups did not exhibit clear patterns of habitat use during the warm season, although variations in utilization were observed. Some strata were utilized approximately twice as often as other strata (e.g., strata two and four) and there was a slight trend of decreasing utilization with increasing distance from the river mouth. The lack of clear habitat use patterns by resting groups was unexpected because certain strata should be less favorable for rest compared to others. For example, strata that typically have fast currents (e.g., stratum two) should be utilized less by resting dolphins because the currents would quickly push the dolphins into a new area where, due to decreased vigilance levels during rest, they would likely be more vulnerable to interactions with vessel traffic. Therefore, some currently unknown, component or feature of the habitat may have made some strata more favorable for resting groups compared to the other strata. Alternatively, the SJR may not contain ideal resting habitat for the dolphins resulting in them resting in the same areas that were utilized during the other behavioral states. Finally, the small sample size for resting groups could have contributed to the lack of distinct patterns in habitat use. More research is necessary to determine why certain strata were utilized more than others or if the observed variation in habitat use was instead due to chance. Resting behavior was rarely observed in the cold season with only four sightings collected during this

study, so resting dolphin groups were not included in the strata analyses during the cold season due to insufficient data (small sample size). However, three of these sightings were collected within a small area in stratum four near the entrance to Mill Cove, which was also an area that was utilized by socializing groups in the cold season.

In conjunction with the behavioral state analyses, the habitat use patterns of differently sized dolphin groups were also examined. The group size strata analyses did not take behavioral state into account, instead the purpose of these analyses was to determine if different strata (locations) were primarily utilized by groups of a specific size.

In the warm season, variations in habitat use were not identified for small groups, but were for medium and large groups. Small groups did not exhibit a clear pattern of habitat use; with the exception of stratum five, there was relatively little variation among strata. Medium sized groups exhibited a slight trend of increased utilization of stratum one and decreased utilization of stratum ten. However, little difference in habitat use by medium sized groups was observed in strata three to eight (excluding stratum five). Finally, large groups in the warm season exhibited a strong pattern of habitat use; habitat utilization decreased with increasing distance from the river mouth.

In the cold season, groups of all sizes exhibited the same general pattern of habitat utilization: the regions closest to the river mouth were utilized the most. Both small and medium sized groups utilized stratum one at least twice as often as they utilized the other strata. Large groups utilized stratum two slightly more than they used stratum one. Finally, all groups utilized stratum six the least in the cold season (excluding stratum five).

In general, the patterns of habitat utilization identified by the group size strata analyses coincided with the patterns identified in the behavioral state strata analyses because group size is

typically dependent on behavioral state (Hoare et al., 2004; Fortin et al., 2009; New et al., 2013). For example, no clear pattern of habitat use was determined for small groups in the warm season. Foraging dolphin groups were often small in this study; thus, it is likely that no pattern was found because foraging groups also did not exhibit a clear pattern of habitat use during the warm season. Traveling dolphin groups were usually medium sized, and traveling groups and medium-sized groups followed the same pattern of habitat utilization year-round (decreasing use with increasing distance from the river mouth). In addition, socializing groups were commonly large in the warm season and utilized the same strata (e.g., stratum two) that were also used most often by large groups overall. It should be noted that the group size strata analyses did not take behavioral state into account, and groups of all sizes were observed for each behavioral state. Therefore, the patterns observed in the group size strata analyses were likely influenced by a particular behavioral state depending on the group size (e.g., small groups and foraging groups), but were not completely determined by the habitat use patterns of dolphins engaged in that behavioral state. Finally, dolphins in groups of all sizes generally concentrated their habitat use in the strata closest to the river mouth during the cold season. This pattern of utilization likely reflects the overall habitat shift, regardless of behavioral state, towards the river mouth in the cold season. All together the behavioral state strata analyses and group size strata analyses indicate that all locations in the SJR were not utilized equally, rather specific regions were favored, or alternatively rarely utilized, depending on the season, behavioral state, and group size.

In all strata analyses, stratum five was problematic because it was not included in the main survey transect. Due to the issues with data collection in this stratum, it was expected that the lowest proportion of sightings for each behavioral state and group size would be collected in

stratum five. However, socializing groups (year-round), resting groups (warm season), small groups (cold season), and large groups (cold season) did not follow this expectation. In these cases, the proportion of sightings collected in stratum five were greater than or equal to the proportion of sightings obtained in one to four other strata. Although the differences in the proportion of sightings were likely not biologically meaningful, this result was still interesting because it indicated that stratum five was utilized more than was initially expected. If the survey vessel could reliably enter stratum five, it is predicted that utilization of this stratum would increase, especially for socializing and resting dolphin groups. Stratum five would likely be an important habitat for socializing and resting groups because of its shallow nature. The shallow water would likely allow males greater control over females (like the shallow region in stratum four) and would provide greater protection from vessels during resting and socializing, behavioral states with reduced vigilance (shallow water restricts vessel navigation). More research is necessary to determine the extent to which stratum five is utilized compared to the strata along the main channel.

Comparison between strata and utilization distribution analyses

The strata and UD analyses each had multiple strengths and weaknesses. One strength of the strata analyses was that the number of sightings were analyzed so even a single sighting in a stratum was included giving a more complete picture of how the dolphins utilized the SJR during each behavioral state. The strata analyses also determined if an association was present between the variables tested, and were a quantitative rather than qualitative measurement of habitat use. However, one weakness of the strata analyses was the requirement for every category (row and column) to contain data (≥ 1 sighting) for the G-test of independence to be properly conducted, and all behavioral states were analyzed together. Therefore, in the cold season analyses, strata

seven-ten were excluded because one or more of the categories (stratum and/or behavioral state) did not contain any data (zero sightings) even though not all of the categories lacked data. For example, traveling and foraging groups were sighted in stratum eight but socializing groups were not, thus stratum eight was excluded from the cold season analysis. The UD analyses did not have this same weakness because each behavioral state was examined separately. Thus, one strength of the UDs was that the lack of data or limited sample size from one behavioral state did not influence the results obtained for the other behavioral states. Additionally, it was possible to calculate a UD even from a small sample size. For example, only 4 sightings of resting dolphin groups were collected during the cold season, but it was still possible to generate 95% and 50% UDs for that behavioral state. Additionally, using the 95% UDs, it was determined that some areas further upriver than stratum six were utilized during the cold season, but that the eastern regions of the river (strata one-six) were more heavily utilized. One weakness of the UD analyses was that it analyzed the density of points (sightings) rather than the number, so areas with a low density of sightings (e.g., a single sighting) were not highlighted on the UD map. Altogether, it was beneficial to conduct both strata and UD analyses because the combination of the results obtained from each analysis type gave a complete picture of the SJR dolphins' habitat use patterns.

The strata and UD analyses allowed for both quantitative and qualitative examination of SJR dolphin habitat use patterns, and when compared enabled the identification of essential habitat areas. For example, the habitat use patterns identified by the strata and 50% UD analyses were similar for socializing groups. In the strata analyses, the highest proportions of socializing group sightings were observed in stratum two (warm season) and stratum four (year-round). The 50% UD analyses also determined that stratum two was a warm season critical habitat and

stratum four was a year-round critical habitat area for socializing groups. Additionally, stratum four was utilized more frequently than stratum two in both analyses. Thus, these two separate analyses identified the same locations as key habitat areas and the same temporal patterns of utilization for socializing groups. However, there were some key differences between the results of the strata and 50% UD analyses for foraging and resting groups. These differences can be explained by the strata analyses not accounting for group size. In the UD analyses sighting locations were weighted based on group size to more accurately reflect the number of dolphins utilizing a particular area. In contrast, the strata analyses examined the proportion of group sightings (unweighted), rather than the proportion of dolphins, that were utilizing the different strata. The strata analyses did not reveal a clear pattern of habitat use by foraging groups in the warm season, but in the cold season foraging groups utilized the strata closest to the river mouth (e.g., strata one and two) more frequently than strata farther upriver. For comparison, the 50% UD analyses identified stratum two (year-round) and stratum ten (warm season) as critical habitat areas for foraging dolphin groups. Although no clear pattern was found in the strata analyses, both stratum two (year-round) and stratum ten (warm season) were among the strata with the highest proportions of foraging group sightings. Therefore, these strata were still identified as important, and were most likely preferred, habitat areas by the strata analyses. Finally, the warm season strata analysis also showed that resting groups did not exhibit a clear pattern of habitat use in the warm season (rest was excluded from the cold season strata analysis). In contrast, stratum three and stratum four were classified as warm season critical habitat areas for resting groups. While no pattern was observed in the strata analysis, stratum four did have one of the highest proportions of resting group sightings, thus the strata analysis also found it to be a frequently utilized resting habitat. Together the results from these analyses

indicate that resting groups may be relatively evenly distributed among the strata, but that larger resting groups may utilize strata three and four. Larger groups would contain more dolphins and thus would have higher densities in the UD analyses, resulting in these strata being identified as critical habitat areas. Overall, the strata and UD analyses both provided valuable information about how dolphins utilize the SJR. When considered together, these analyses indicated key areas that served as essential habitat during specific behavioral states and are likely important for maintaining a viable SJR dolphin population.

Behavioral state and group size

Group size is frequently dependent on behavioral state (Hoare et al., 2004; Fortin et al., 2009; New et al., 2013), and the fission-fusion nature of dolphin societies allows them to maximize the benefits of group living while minimizing the costs (Heithaus and Dill, 2002; Pearson, 2011; Tsai and Mann, 2013). Overall, SJR dolphins associated in larger groups ($\bar{x}$ ± SD = 6.08 ± 6.46 individuals, SE = 0.17) compared to dolphins in other Florida study sites. For example, the mean group size of dolphins was 2.45 ± 2.70 individuals in the Indian River Lagoon (Durden et al., 2017), and 4.8 individuals (SE = 0.16) in Sarasota (Irvine et al., 1981). Competition for food resources is reduced and foraging efficiency is increased with small group sizes (van Schaik et al., 1983; Hoare et al., 2004; Pearson, 2011; Tsai and Mann, 2013). Accordingly, foraging groups in the SJR were predominantly small (one-two individuals) year-round. Similar group sizes (≤ 2 individuals) were reported for foraging bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia (Heithaus and Dill 2002). Although foraging groups of all sizes were observed in the SJR year-round, small foraging groups were observed the most and large foraging groups the least. However, the proportion of small foraging group sightings was much higher in the cold season than the warm season (0.75 vs 0.53). The proportion of large

foraging group sightings remained approximately equal between the two seasons, but medium sized foraging groups were more prevalent during the warm season than cold season. This seasonal change in the relative proportion of small and medium foraging group sightings was likely a result of the change in population density between the two seasons. The probability of encountering another individual increases with increased population density, thus a positive linear relationship exists between group size and population density (Olupot et al., 1994). Although dolphins may prefer small group sizes while foraging, it may not be possible for individuals to spread out into smaller groups during periods when dolphin density is high. Thus, foraging group sizes were generally larger in the warm season because numerous individuals would gather in the same area to utilize a desired resource (e.g., food). Consequently, SJR dolphins likely experience higher levels of foraging competition during the warm season compared to the cold season.

While small groups are beneficial for foraging due to the decreased competition, larger group sizes are advantageous for activities that reduce vigilance for predators (e.g., socializing and resting) because larger groups help to reduce predation risk (Gauthier-Clerc et al., 1998; Parrish and Edelstein-Keshet, 1999; Heithaus and Dill, 2002; Hoare et al., 2004; Fortin et al., 2009). In the SJR, the majority of socializing groups were large (≥ eight individuals) during the warm season, whereas medium (three-seven individuals) and large groups were equally common in the cold season. Small socializing groups were rarely observed in either season. This pattern may be explained in part due to the relatively high spring/summer population density in the SJR, caused by the influx of individuals during the breeding season (Ermak et al., 2017), which results in high encounter rates and interactions. Thus, the prevalence of large socializing groups during the warm season is likely a result of this high population density (Wrangham et al., 1993; Olupot

et al., 1994) combined with the high levels of breeding (mating and calving) activity during this time of year. In contrast, resting dolphins in the SJR were primarily observed in medium-sized groups (three-seven individuals) year-round. For comparison, the dolphins in Shark Bay experience high levels of predation risk and resting dolphins typically associated in larger groups than dolphins in other behavioral states (warm season mean group size: ~5.5 individuals; cold season mean group size: ~4.5 individuals; Heithaus and Dill, 2002). Thus, resting SJR dolphins associated in groups of similar sizes as those in Shark Bay. However, due to the low incidence of shark bite scars in the SJR population (Gibson, unpublished data), predation risk due to sharks in the SJR is likely much lower than in Shark Bay. It is probable that SJR resting group sizes were due to some other ecological pressure (e.g., population density or density of boats). However, it is important to note that only four resting dolphin groups were observed during the cold season, thus this year-round trend of medium-sized resting groups could be an artifact of low sample size. In addition, the relatively infrequent observations of resting groups compared to the other behavioral states could also indicate a lack of suitable resting habitat in the SJR.

Finally, medium-sized traveling groups were observed most often year-round. In the warm season, small and large traveling groups were observed in equal proportions, but the difference in proportions of medium and small/large groups was relatively minimal (range = 0.1). Therefore, the difference in the proportion of small, medium, and large traveling group sightings was likely not biologically significant during the warm season. In contrast, during the cold season the proportion of small and medium traveling group sightings increased, while the proportion of large traveling group sightings decreased. Both small and medium sized traveling groups were observed more than twice as often as large groups; thus, this difference was likely biologically significant. The observed decrease in the proportion of large traveling group

sightings during the cold season was likely due to the low abundance during this time. In summary, the patterns observed suggest that group sizes in the SJR fluctuated to reduce competition while foraging, increase protection while socializing or resting, and in response to seasonal changes in dolphin abundance.

Behavioral state and water depth

The SJR dolphins exhibited a strong pattern of habitat use in relation to water depth, with the proportion of sightings in an area generally increasing with water depth. Deep water areas (≥ 12m) were utilized the most during all behavioral states, and shallow water areas (< 3m) were utilized the least. The main channel of the SJR is routinely dredged to stay between 12-15m deep; therefore, based on the utilization pattern observed, it appears that the SJR dolphins exhibited preferred use of the main channel during all behavioral states and in both seasons (excluding rest during the cold season). Deep water habitats help to concentrate prey and are typically favored by foraging dolphins (Ingram and Rogan, 2002), thus the increased utilization of deep water habitats during foraging was expected. Furthermore, the main channel likely has faster water currents compared to the shallow regions close to shore and traveling dolphins may experience energetic benefits from utilizing the main channel. In contrast, the utilization of deep water habitats by socializing and resting groups was unexpected due to high current speed and increased risk of vessel collisions. Socializing and resting dolphin groups would have to expend more energy to maintain group cohesion and to maintain their position in the river in regions with fast moving currents, and as such, were expected to prefer shallow habitats. Additionally, socializing and resting groups would be more vulnerable (due to reduced vigilance) to interactions with fast moving vessels while in the main channel. The utilization of deep water habitats during all behavioral states could potentially be explained by bias in the survey methods.

The survey transect line followed the main channel of the river, so dolphins utilizing the main channel were more likely to be observed than those not in the channel. Also, the observed preference of socializing and resting groups for deep water may have been an artifact of how the water depth data were collected. Based on anecdotal field observations in which socializing dolphins were typically observed in shallow water (< 3m) areas, it was initially expected that socializing dolphin groups would utilize shallow water habitats more than deep water habitats. However, shallow water restricted the survey vessel's ability to closely approach these groups; thus, the water depth measurement reflected the boat's location instead of the dolphin group's. Additionally, the water depth was sometimes recorded when the dolphin group was greater than 20m from the research vessel and did not accurately reflect the water depth the group was utilizing. In the future, efforts should be made to ensure that water depth is only recorded once the survey vessel is less than 20m away from the dolphin group. Despite these potential sources of bias, a preference for deeper water has also been shown for bottlenose dolphins in Moray Firth, Scotland (water depths of 25-50m; Hastie et al., 2004) and the Shannon Estuary, Ireland (water depths of 31-50m; Ingram and Rogan, 2002). Although the SJR is not as deep as Moray Firth or the Shannon Estuary, all study sites had a range of water depths available to the dolphins and higher use of the respective deep water areas was observed.

Critical habitat areas and the implications for management

The SJR was determined to be an important, year-round habitat for bottlenose dolphins. A previous study by Caldwell (2001) did not find that the SJR was utilized as a year-round habitat. Therefore, utilization of the SJR has increased since 2001, and the present study provided valuable new information about the SJR dolphin community. Additionally, all behavioral states were observed throughout the study area, indicating the SJR contained suitable

and favorable habitats that could be utilized for foraging, socializing, resting, and/or traveling. It was expected that more critical habitat areas would be identified during the warm season due to the high population density. Competition for food resources increases with increasing population density; thus, the dolphins should utilize more areas while foraging to reduce competition. However, only two critical habitat areas were identified during the warm season for each behavioral state indicating the dolphins did not spread out or distribute their habitat use as much as expected. The preferential use of just two habitat areas per behavioral state indicates these areas must contain unique features (e.g., fast currents or access to shallow water) that make them attractive despite the high dolphin density. Residency status may have also influenced which dolphins utilized each critical area. A previous preliminary study only observed residents using the upper regions of the survey area and did not observe residents associating with transient dolphins (Gibson, unpublished data). The only warm season critical habitat area that was likely utilized primarily by residents was stratum ten (foraging groups) based on the results of the previous study. However, all other warm season critical habitat areas were in regions of the river that were also utilized by transients and/or seasonal residents (Gibson, unpublished data). Therefore, in the future, the habitat use patterns of residents and non-residents should be analyzed separately to better clarify which community of dolphins is utilizing a specific habitat/critical area.

The importance of the SJR as a year-round habitat for dolphins in all behavioral states is somewhat surprising considering that it is also heavily utilized by humans for recreational and commercial purposes. In habitats where humans and dolphins frequently interact, the health and sustainability of the affected dolphin population or community depends on the development of effective management practices. Previous management efforts in other areas have been aided

through the identification of critical habitat areas (Wilson et al., 1997; Ingram and Rogan, 2002; Lusseau and Higham, 2004; La Manna et al., 2016; Bas et al., 2014); therefore, the SJR dolphin critical habitat areas were assessed primarily to support management efforts. This study identified two year-round critical habitat areas for the SJR dolphins: stratum two (foraging groups) and stratum four (socializing and resting groups).

As a year-round critical area for foraging groups, stratum two was an essential habitat patch for the SJR dolphins. The physical features of this stratum contributed to its importance as a foraging area. The Intracoastal Waterway crosses the SJR in stratum two, and strong cross-currents have been recorded in this area. Dolphins in the Shannon Estuary, Ireland (Ingram and Rogan, 2002) and Sarasota, Florida (Irvine et al., 1981) were observed preferentially foraging and utilizing areas with fast tidal currents. Therefore, the strong currents in stratum two may help to concentrate prey (Ingram and Rogan, 2002) at this location making it a profitable foraging patch for the SJR dolphins. In addition to being a critical foraging habitat, high levels of anthropogenic activity occur in stratum two, including recreational boating and shipping traffic. Recreational traffic can pass through this area at any time, but the movements of large cargo ships are restricted to certain tidal states due to the strong cross-currents. The present levels of vessel traffic likely reduce the foraging efficiency of SJR dolphins (Pirotta et al., 2015), and future declines in habitat quality could have severe implications for the health of this community. Survival depends on the ability to efficiently obtain food resources, and failure to meet energy demands can have significant consequences (Wright et al., 2007; Pirotta et al., 2015). If an animal is unable to obtain enough food, lipid stores will begin to be metabolized and the animal will ultimately be forced to leave the area or risk starving to death (Wright et al., 2007; Bas et al., 2014). Animals that are displaced to different areas face additional challenges including

increased competition if the new area is already occupied (Wilson et al., 1997) and decreased knowledge about resources and potential predators (Breed and Moore, 2012; Tsai and Mann, 2013). Within the SJR, dolphins that are displaced from foraging sites in stratum two could potentially utilize stratum ten (warm season critical habitat) more frequently or move out to the coast to find new foraging habitats. Increased use of stratum ten may not be a realistic solution for several reasons. First, stratum ten has lower salinity levels ($\bar{x}$ = 8.5 ppt) compared to stratum two ($\bar{x}$ = 25.2 ppt), and dolphins are better adapted to high salinity environments. For example, extended exposure to freshwater can result in dolphins developing freshwater lesions on their skin. Second, the prey density in stratum ten may not support increased levels of predation from the dolphins. If too many dolphins utilize a single foraging patch, the prey availability in that area would sharply decline and the dolphins would again be forced to find a new foraging patch. Finally, the dolphin's prey species are also mobile and could potentially leave stratum ten in response to increased predation from dolphins. Displacement to a new foraging area along the coast would also present the dolphins with many new challenges including decreased foraging rates due to less knowledge about the habitat, decreased prey availability, increased exposure to predators, and increased levels of competition with conspecifics that were already present in the new habitat. It is also possible that no other high quality foraging patches are available to the dolphins, either within the SJR or along the coast. Further research is necessary to determine if SJR dolphins adjust their foraging behavior in relation to vessel traffic (e.g., concentrate foraging during times when vessel traffic is lowest; Pirotta et al., 2013) and to determine their sensitivity to habitat disturbance.

In addition to serving as a core foraging area, stratum two was identified as a warm season critical area for socializing dolphins in conjunction with stratum four, which was utilized

as a year-round critical habitat area for socializing and resting dolphins. The physical features of stratum four likely influence its quality for socializing and resting dolphins. The southern edge of stratum four was relatively shallow (water depths < 3m), while the northern edge contained the main channel (water depths between 12-15m). Miller et al. (2013) found that dolphin groups in the Mississippi sound preferentially utilized shallow waters along the coast (mean depth 3m) during the summer. The presence of a large shallow area in stratum four likely made this a good area for both socializing and resting groups. Specifically, shallow water likely gives males greater control over females while socializing and fewer vessels pass through the shallow area making it a safer resting habitat compared to the main channel. Socializing and resting are both key behavioral states for maintaining the health and viability of a population and the individuals within it. Social behavior is directly related to the reproductive output of dolphins and less time spent socializing may result in lower reproductive success and population growth (Lusseau, 2004). Additionally, animals must rest and failure to do so can result in significant physiological effects (Siegel, 2008). Like stratum two, high levels of anthropogenic activity occur within stratum four. The current major sources of anthropogenic activity in this stratum include activity at the first JaxPort shipping terminal and vessel traffic from recreational boats and crab fishermen. Socializing and resting dolphins are both sensitive to disturbance by boats (Lusseau and Higham, 2004; Lusseau, 2004; Steiner, 2012), and an increase in vessel traffic past their tolerance threshold could cause the dolphins to leave stratum four (Bejder et al., 2006). If anthropogenic activity in stratum four reaches the threshold where socializing and resting dolphins stopped utilizing this area, the dolphins may choose to move to stratum two or three (respectively) or to a new location entirely. However, moving to new habitats could decrease or change the associates available during socializing (potentially affecting the overall social

structure of the population) and/or decrease resting rates (which were already low in the SJR). Displacement to a new habitat could also result in increased levels of predation risk (e.g., increase their encounter rates with sharks), and socializing and resting dolphins are already more vulnerable to predators due to the decreased levels of vigilance associated with these behavioral states (Heithaus and Dill, 2002). Further research is necessary to determine how strongly the SJR dolphins react to disturbance from vessel traffic, to determine the distance at which they begin to experience this disturbance, and to determine how long it takes the dolphins to recover/resume their previous behavioral state after disturbance. Additional exploration into the reactions of SJR dolphins to vessel traffic could provide insight into their tolerance thresholds to disturbance.

Stratum two and stratum four were not the only locations in the SJR that experienced high levels of anthropogenic activity. The entire study area within the SJR was heavily utilized for recreational, commercial, and military purposes. Even on the coldest days of the year, it was normal to see recreational boaters on the water (Gibson, unpublished data). In the summer months, recreational activity was extensive throughout the study area. Additionally, with three international shipping terminals, a U.S. Navy base, and a U.S. Coast Guard station, commercial and military traffic were constant, year-round sources of anthropogenic activity. Anthropogenic activity is pervasive throughout the SJR and chronic exposure to this activity can have numerous impacts on the dolphins including communication masking (Miller et al., 2000; Clark et al., 2009; La Manna et al., 2013), alterations in surfacing behavior (Nowacek et al., 2001), and increased levels of physiological stress (Wright et al., 2007; Rolland et al., 2012). Although the dolphins may be able to move to different habitats within the SJR, this does not necessarily reduce these negative effects because all regions of the river are impacted by anthropogenic activity. Furthermore, the level of anthropogenic activity and disturbance to the SJR will be

increasing with the port expansion project. This project will cause significant changes/degradation to the habitat via dredging and underwater blasting (Pirotta et al., 2013) and will ultimately result in increased traffic by larger shipping vessels. The project entails three major operations: relocating the training wall at Mile Point (located in stratum two), confined underwater blasting, and dredging the main channel. The purpose of relocating the training wall was to reduce the strength of cross-currents from the ICW, and this portion of the project was completed during the summer of 2016 (data collection for this study ended prior to the commencement of the Mile Point project). The underwater blasting and dredging operations will begin soon. The confined underwater blasting (charge is placed in the bedrock and covered with inert material) will be used to pretreat the bedrock prior to dredging and to assist in creating two turn-around points (located in stratum four and stratum six) for large cargo ships (U.S. Army Corp, 2014). Dredging operations are expected to last for five years as the main channel will be dredged from a depth of 12.5m to a maximum depth of 15.2m starting at the river mouth to approximately 20km upriver (stratum six).

Overall, the SJR dolphins will likely experience both direct and indirect effects from the port expansion project. Some of the direct effects from the blasting and dredging operations include physiological (e.g., auditory changes) and behavioral responses (e.g., habitat displacement). These operations will also indirectly affect the dolphins by impacting their prey species. Fish experience several physiological impacts (e.g., rupture of the swim bladder and increased mortality) from exposure to underwater blasting and dredging, and these in turn will reduce the amount of prey available to the dolphins.

The effects of the underwater blasting and dredging operations on the dolphins will be similar, but occur over very different time-scales. The blasting will be an acute source of

disturbance where impacts will be intense but over a relatively short time-frame (minutes). The main documented physiological impacts of underwater explosions are temporary or permanent auditory threshold shifts (Finneran et al., 2000). Temporary threshold shifts represent short-term changes in hearing thresholds, while permanent threshold shifts represent irreversible damage to auditory structures. Dredging operations also produce intense sounds (Hildebrand, 2004) that could also result in auditory damage and can reduce the foraging efficiency of dolphins due to communication masking and increased turbidity levels (Pirotta et al., 2013). The dredging operations will be a chronic source of disturbance for SJR dolphins and will have numerous impacts that occur over an extended time-frame (years). The main channel in strata one-six will be dredged (approximately 20km), and both year-round critical habitat areas fall within the dredging zone. The presence of dredging in both critical habitat areas could potentially cause the SJR dolphins to abandon these habitats (Bryant et al., 1984; Pirotta et al., 2013).

Few studies have been conducted that directly assessed the impact of dredging operations on large marine predators, such as bottlenose dolphins. One study that assessed these impacts was conducted by Pirotta et al. (2013) in Aberdeen Harbor, Scotland, one of Europe's busiest ports. Aberdeen Harbor was identified as an important foraging habitat for bottlenose dolphins and had high baseline levels of anthropogenic activity (e.g., recreational and commercial traffic and routine maintenance dredging). Unlike the SJR, Aberdeen harbor was only utilized by foraging groups and the dolphins utilized different habitats outside of the harbor during the other behavioral states. Additionally, these dolphins began using the harbor when vessel traffic was already high and as such exhibited high levels of tolerance to vessel traffic. Maintenance dredging took place in the harbor during the summers of 2008 and 2009, and large-scale dredging took place in 2012 to widen the main channel as part of a harbor expansion project.

Although the Aberdeen harbor dolphins were previously habituated to high levels of anthropogenic disturbance, the dredging operations exceeded their tolerance threshold causing them to leave the area. The dolphins were observed less often during the maintenance dredging operations, and they completely left the harbor for five weeks in 2012 when dredging operations were the most intense. Once the dredging operations began to decrease, the dolphins started returning to the harbor, but they spent proportionally less time in the harbor than they did before the dredging began. Additionally, Pirotta et al. (2013) noted that group size was not affected by the presence of dredgers indicating that all individuals in a group chose to leave the harbor rather than just a few individuals. Finally, the Aberdeen harbor dolphins also exhibited dynamic responses to vessel traffic levels by leaving the harbor when traffic was highest and returning once it decreased. Pirotta et al. (2013) stated that the increased levels of vessel traffic that result from dredging and expansion projects could cause dolphins to modify their long-term habitat use patterns.

The results from the Aberdeen harbor study have important implications for the SJR port expansion project. First, the SJR is utilized during all behavioral states, and abandonment of the SJR would result in the loss of foraging, socializing, and resting habitats. Long-term displacement from a habitat utilized for multiple behavioral states will have greater consequences for the future viability of the SJR dolphin community (e.g., decreased reproductive output and increased mortality rates) compared to the loss of key habitat for a single behavioral state. Second, the Aberdeen harbor dolphins had been previously exposed to routine maintenance dredging, but still abandoned the harbor in response to the intense dredging that was part of the harbor expansion project. Thus, it is highly likely that SJR dolphins will exhibit similar responses to the large-scale dredging operations and may ultimately leave the river for the entire

length of the dredging project (which is predicted to take up to five years to complete). The loss of habitat for five years will have much greater population-level consequences than the loss of habitat for five weeks. Lastly, the purpose of the port expansion project is to increase the size and number of large cargo ships that can dock at the JaxPort terminals. This increase in vessel traffic may cause the dolphins to modify their habitat use patterns and potentially decrease the amount of time they utilize the SJR even after the project is completed.

Dredging and shipping operations also displaced gray whales (*Eschrichtius robustus*) from one of their primary breeding lagoons in Baja California, Mexico. The gray whales abandoned this lagoon for ten years until the dredging and shipping operations completely ceased (Bryant et al., 1984; Tyack, 2008). Additionally, the gray whales did not return to the breeding lagoon immediately after these disturbances ended, rather it took several years before the number of whales in the lagoon gradually began to increase. The dredging operations in the SJR will also take many years, and it is possible that the dolphins will behave similarly to the gray whales and not immediately return to the river once the expansion project is completed. If the dredging operations in the SJR cause the dolphins to abandon either critical habitat area and/or additional areas in the SJR, the health of the population will ultimately be at risk (Lusseau and Higham, 2004; Wright et al., 2007; Pirotta et al., 2013; Bas et al., 2014; Pirotta et al., 2015).

Blasting and dredging in the SJR may also indirectly affect the dolphins by impacting their prey species. Underwater blasting can have numerous impacts on fish including rupturing of their swim bladders and disorientation (Gordon et al., 2005). A fish with a ruptured swim bladder will be unable to modify its position in the water column, potentially making it more vulnerable to predators, if the rupture itself is not immediately fatal. Fish can also become disoriented after exposure to an underwater explosion often causing them to remain in the blast

area and potentially be exposed to additional blasts (Gordon et al., 2005). Furthermore, dredging operations increase the amount of sediment that is suspended in the water column and the turbidity levels within the system (Wilber and Clarke, 2001). Increased levels of sediment suspension can negatively impact numerous fish species by causing delayed hatching and/or increased egg/larvae mortality (Wilber and Clarke, 2001). Adult estuarine fish can also experience negative effects from increased levels of suspended sediments. For example, the foraging success of adult Atlantic croaker (*Micropogonias undulatus*) was reduced when turbidity was high, and extended periods of lowered feeding success could result in increased adult mortality (Wilber and Clarke, 2001). Altogether, these impacts will result in a decline in the amount of prey available to the dolphins. If prey abundance in the SJR declines to a critical level, the dolphins will be unable to meet their energetic demands and will need to find new foraging habitats.

The underwater blasting and dredging operations will have numerous direct and indirect effects on the dolphins in the SJR. Ultimately, the dolphins may reach a threshold where the level of disturbance from anthropogenic activity outweighs the benefits of an area, causing the dolphins to move to a different habitat (Bejder et al., 2006; Lusseau, 2003; Lusseau, 2004). The exact threshold between when dolphins will continue utilizing a habitat and when they leave the habitat is not known and likely varies depending on the population and/or community (Bejder et al., 2006; Pirotta et al., 2013). Thus, even a slight increase in anthropogenic disturbance could result in large-scale consequences, and the SJR Port expansion project will be a significant source of disturbance.

The current, high levels of anthropogenic activity and the projected increase in activity due to port expansion project indicate a need for updated regulations to better protect the SJR

dolphin community (Hawkins et al., 2017). These dolphins are part of the Jacksonville Estuarine Stock (JES), and are protected under the Marine Mammal Protection Act (MMPA) of 1972. The MMPA limits the number of animals (or "take") that can be impacted by human activities, and it defines different levels of harassment. Level A harassment is defined as the potential to cause injury to a marine mammal and Level B harassment is defined as the potential to cause disruption of behavioral patterns. Although bottlenose dolphins are not listed as endangered, the JES is listed as a strategic stock because it is likely that relatively few injuries or mortalities would exceed the potential biological removal (PBR) level that is necessary to maintain a viable population (NOAA Fisheries, 2016). Since the JES stock is listed as strategic and the port expansion project will involve at least Level B harassment and likely Level A harassment as well, new management regulations need to be implemented.

To provide the maximum level of protection for the SJR dolphins, regulations need to be established to prevent further habitat degradation in strata two and four. Without the implementation of policies to preserve these critical habitats, the SJR dolphins may be displaced to different habitats (Bryant et al., 1984; Bejder et al., 2006; Pirotta et al., 2013) and the overall health of the stock may begin to decline (Lusseau, 2003; Lusseau, 2004; New et al., 2013; Hawkins et al., 2017). While it is not possible to exclude or prevent vessels from traveling through these habitats, it is possible to establish slow speed zones in these areas (Bas et al., 2014; Lusseau and Higham, 2004). Dolphins exhibit the strongest reactions to fast-moving vessels (Bas et al., 2014), so reducing the speed of all vessels should also reduce their impact on the dolphins. Slow speed zones have already been established close to shore in most areas of the SJR to protect the Florida manatee (*Trichechus manatus*), which were recently downgraded from endangered to threatened under the Endangered Species Act. Thus, these zones could be

expanded to cover both critical habitat areas. To reduce the impact of cargo ship traffic on the dolphin critical habitat areas, regulations should be established so that only one cargo ship can pass through a critical area at a time. Limiting the number of actively moving cargo ships to one would provide the dolphins more room to maneuver around the ship and reduce the compounding impacts of multiple ships moving in the same area at the same time (Lusseau, 2004; Bejder et al., 2006).

The plans for the port expansion project also need to be re-evaluated to establish additional mitigation procedures to minimize the impact the project will have on the SJR dolphins. Currently, the port expansion project contains minimal mitigation procedures for the protection of animals within the river (News4Jax, 2017). The mitigation procedures that have been outlined primarily focused on the underwater blasting operations but not the dredging operations. During blasting operations, four blast zones will be implemented for the protection of marine mammals: the exclusion zone (point where injury is likely and blasts will not occur; 152m from detonation point), the danger zone (point at which injury or mortality is unlikely to occur; 530m from the detonation point), the safety zone (point at which injury is unlikely to occur; 756m from detonation point), and the watch zone (1,135m from detonation point; U.S. Army Corp, 2014). Marine mammal observers (MMOs) will be stationed in the air, on moving vessels, and on a stationary barge to monitor for dolphins and manatees and to alert operation managers when an animal is sighted within one of the blast zones. However, these blast zones will likely not adequately protect either dolphins or manatees. Dolphins can travel large distances in a short period of time (Williams et al., 1992), and the turbid and curving nature of the SJR will make it difficult for the observers to detect them before they are too close to the detonation point. The high turbidity in the SJR makes it impossible to see the dolphins (or manatees) unless they

are at the surface of the water, and both species can hold their breath for several minutes at a time (bottlenose dolphins: up to 12 minutes, Schreer and Kovacs, 1997; manatees: up to 16 minutes, Irving, 1939). Manatees are also difficult to spot as they typically only raise their snout above the water surface. Therefore, it is likely that dolphins and manatees would enter the blast zones without being detected. If a dolphin or manatee were in the exclusion zone during detonation, they will experience significant injury and potentially death. To increase the probability of detecting a dolphin/manatee, the blast zones should be expanded and the number of MMOs in the area should be increased. The exclusion zone should be expanded to a minimum of 500m (same distance utilized during seismic exploration; Wright and Cosentino, 2015), and the other zones should be expanded accordingly. For example, the danger zone could be expanded to 600m, the safety zone could be expanded to 800m, and the watch zone to 1,200m. These distances would facilitate earlier detection of marine mammals while still being logistically feasible to monitor. Additionally, increasing the number of MMOs would assist in the early detection of dolphins and/or manatees. A minimum of two MMOs should be stationed on each observation platform, and they should rotate regularly to prevent observer fatigue.

The port expansion plans also included possible regulations to protect the fish in the river from the blasting operations. To reduce the impacts of underwater blasting on fish, a small, unconfined explosive (termed a “scare” blast) will be set of 30-sec before the main blast to drive fish away. However, the effectiveness of this “scare” blast is not known, and it is likely that a 30-second interval would not give fish enough time to leave the area before the main blast. Additionally, this “scare” blast could potentially cause dolphins to move into the exclusion zone (closer to the blast) to catch prey that were stunned or hurt by the “scare” blast. If a “scare” blast

is utilized, the time interval should be increased (i.e., to 1-2 minutes) to give the fish enough time to leave the area and help ensure no dolphins entered the area in search of easy prey.

Finally, mitigation procedures need to be included in the port expansion project plans to better protect dolphins from the impacts of dredging. Dolphins are predicted to detect the sounds produced during dredging up to 6km away (Pirotta et al., 2013), and will likely interpret these sounds as a source of risk thereby eliciting avoidance responses like those exhibited by the Aberdeen harbor dolphins and Baja California gray whales (Bryant et al., 1984; Tyack, 2008; Pirotta et al., 2013). To reduce the impact dredging operations have on SJR dolphins, dredging should be restricted to the cold season when dolphin abundance is lowest. This restriction would limit the number of dolphins exposed to dredging and reduce the impact dredging has on newborn calves (born during the warm season). Newborn calves will be the most sensitive to the dredging operations because of their small body size (U.S. Army Corps, 2014). Additionally, if dolphins avoid/leave the SJR in response to a single dredger operating, then multiple dredgers could be operated at the same time to speed up the dredging process and make up for time lost during the warm season. Reducing the amount of time dredging operations are taking place will also help to reduce how long dolphins leave/avoid the SJR. However, if the dolphins continue to utilize parts of the SJR during the dredging operations, then only a single dredger should be utilized to prevent further disturbance to the dolphins. The dredging operations will have numerous impacts on SJR dolphins and mitigation procedures need to be included in the port expansion plans to reduce/limit these impacts.

In summary, the development of new regulations in the SJR is necessary to maintain the viability of the strategic JES of bottlenose dolphins. First, slow speed zones should be established in both critical habitat areas to reduce the impact of current and future vessel traffic

on dolphins utilizing these areas. Second, additional regulations need to be implemented during the expansion project including the expansion of the blast zones and the restriction of dredging operations to the cold season. The establishment of slow speed zones and development of additional mitigation procedures for the port expansion project would help to better protect and maintain a viable SJR dolphin population. If these regulations are successfully implemented, they could potentially be used as a framework for developing revised management plans in urban estuaries around the world.

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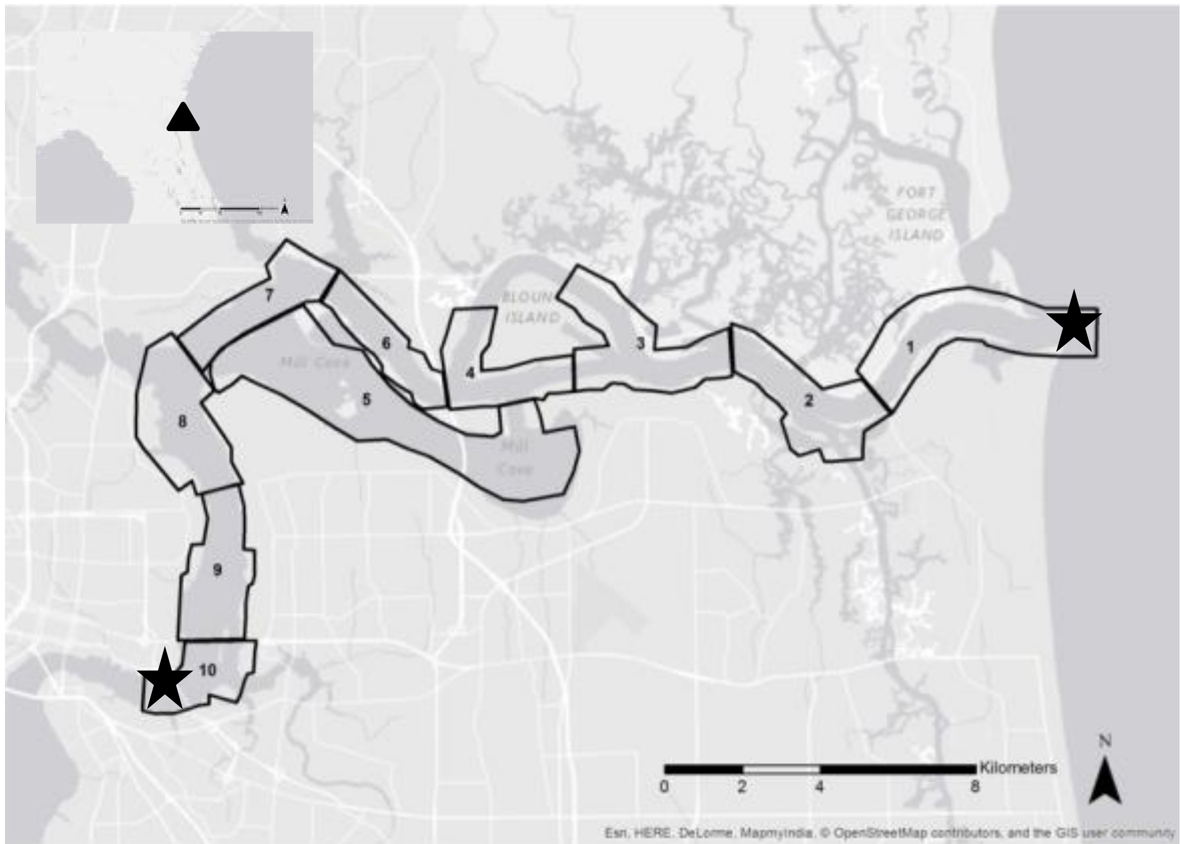


Figure 1: Study area within the St. Johns River, Jacksonville, FL (triangle). Stratum one was at the Mayport Inlet and stratum ten was in the downtown Jacksonville area approximately 40km upriver. Strata were identified based on the type and level of anthropogenic activity present in the area. The start and end locations of the photo-identification surveys are denoted by the stars.

Table 1. Ethogram of behavioral states (adapted from Mann and Watson-Capps, 2005). Activity categories are mutually exclusive.

Activity	**Definition**
Travel	Steady, moderate, or fast (>3 km/h) directional movement.
Forage	Fast swimming, rapid direction changes, fish catches, and fish fleeing.
Social	Rubbing, petting (flipper or flukes actively moving on a body part of another), displays, chasing, mounting, poking, contact swimming, and other forms of active contact
Rest	Slow (< 3 km/h) nondirectional movement, frequent hanging at the surface.

Table 2. Predominant types of anthropogenic activity present within each stratum, and its approximate size and distance from the river mouth

Stratum	**Predominant type of anthropogenic activity**	**Approx. Size**	**Distance from Inlet**
One	Multiple public and private marinas/docks and the U.S. Navy and Coast Guard bases. Rock jetties along both shores at the Mayport Inlet	6.4km	At Inlet
Two	Location where Intracoastal Waterways cross the SJR (Mile Point), heavy vessel traffic	5.6km	~8km
Three	U.S.M.C. shipping depot and a residential area with private docks	6.4km	~12km
Four	First JaxPort shipping terminal and major bridge (Dames Point) at western end	4.8km	~16km
Five	Large, shallow cove (Mill Cove) primarily utilized by recreational and crab fishermen, and crossed by a major bridge (Dames Point). Not included in dolphin survey transect	>10km	~16-24km
Six	Carnival cruise ship terminal, second JaxPort shipping terminal, and major bridge (Dames Point) at eastern end	4km	~20km
Seven	Three oil docks, heavy recreational and commercial shipping traffic	4.8km	~24km
Eight	Residential area- mostly private docks and recreational fishing	6.4km	~27km
Nine	Third JaxPort shipping terminal	6.4km	~32km
Ten	Two major bridges (Hart and Mathews) and a dry dock facility	4km	~40km

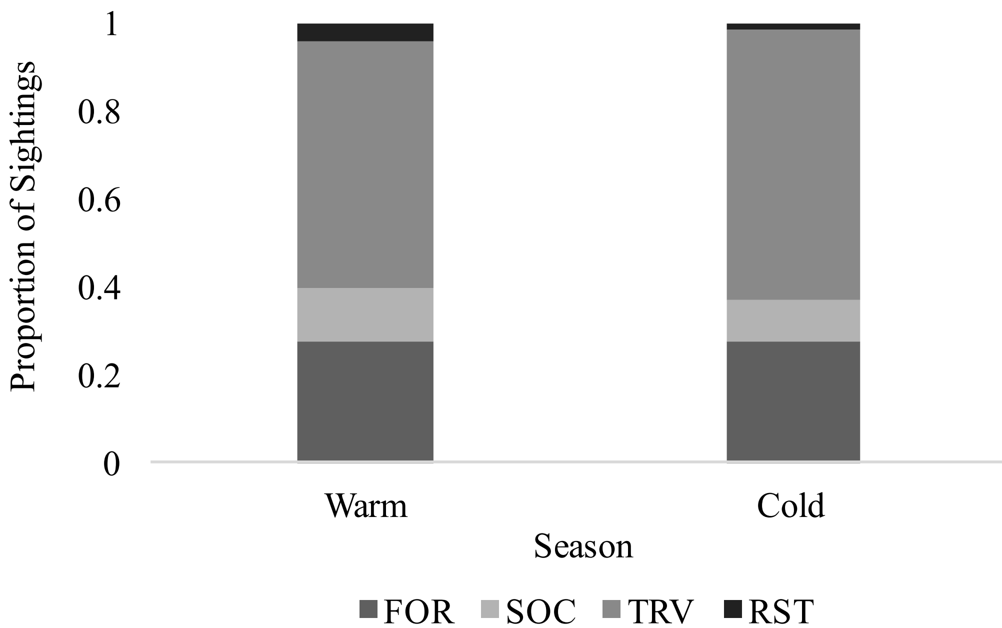


Figure 2: Seasonal changes in the proportion of sightings for each behavioral state.

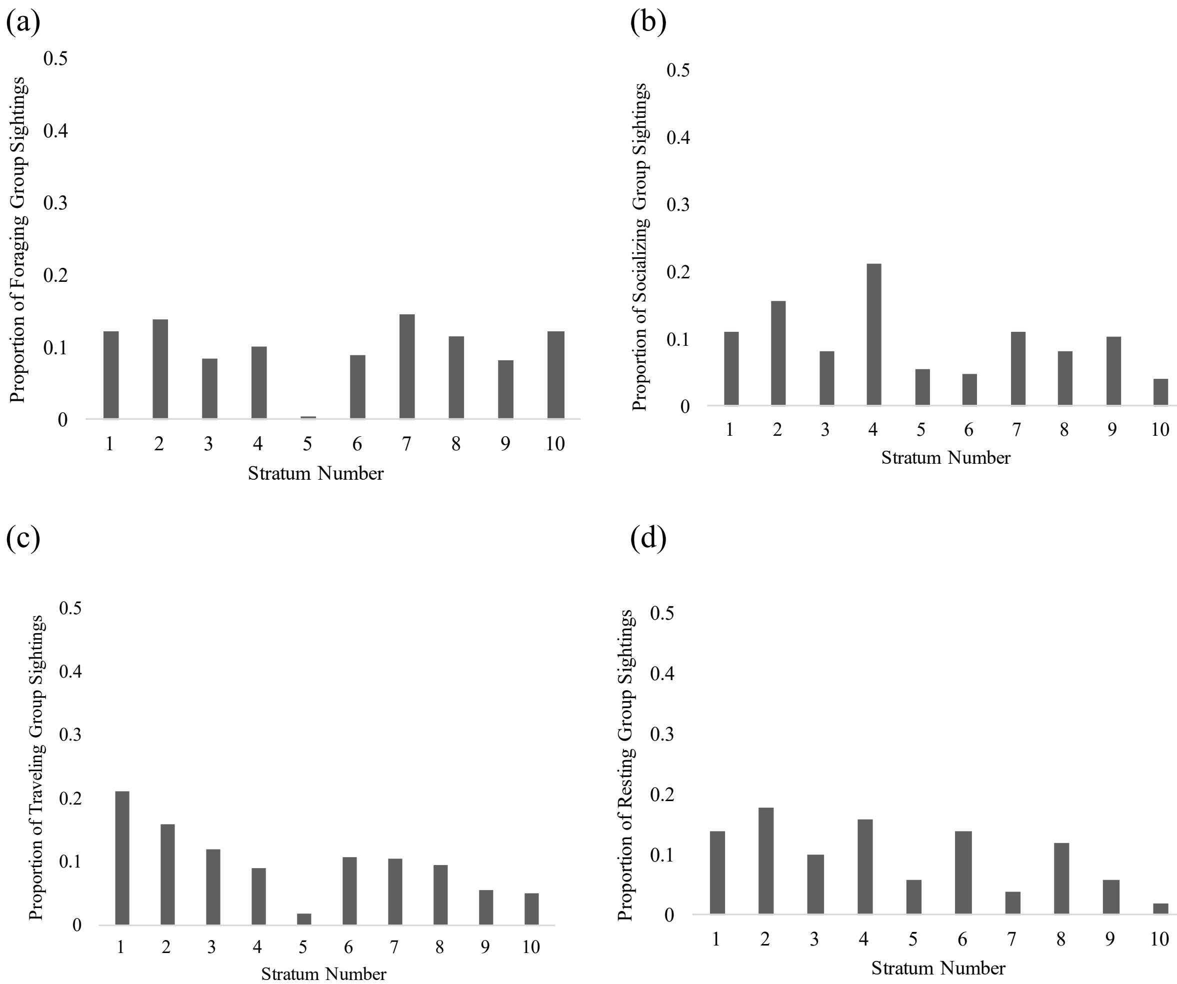


Figure 3a-d: Warm season associations between predominant behavioral state and location (strata) in the SJR. Stratum one was located at the Mayport Inlet and stratum ten was located 40km upriver. Stratum five was not included on the survey transect so any sightings in that stratum were collected opportunistically. Additionally, sightings were not weighted based on group size.

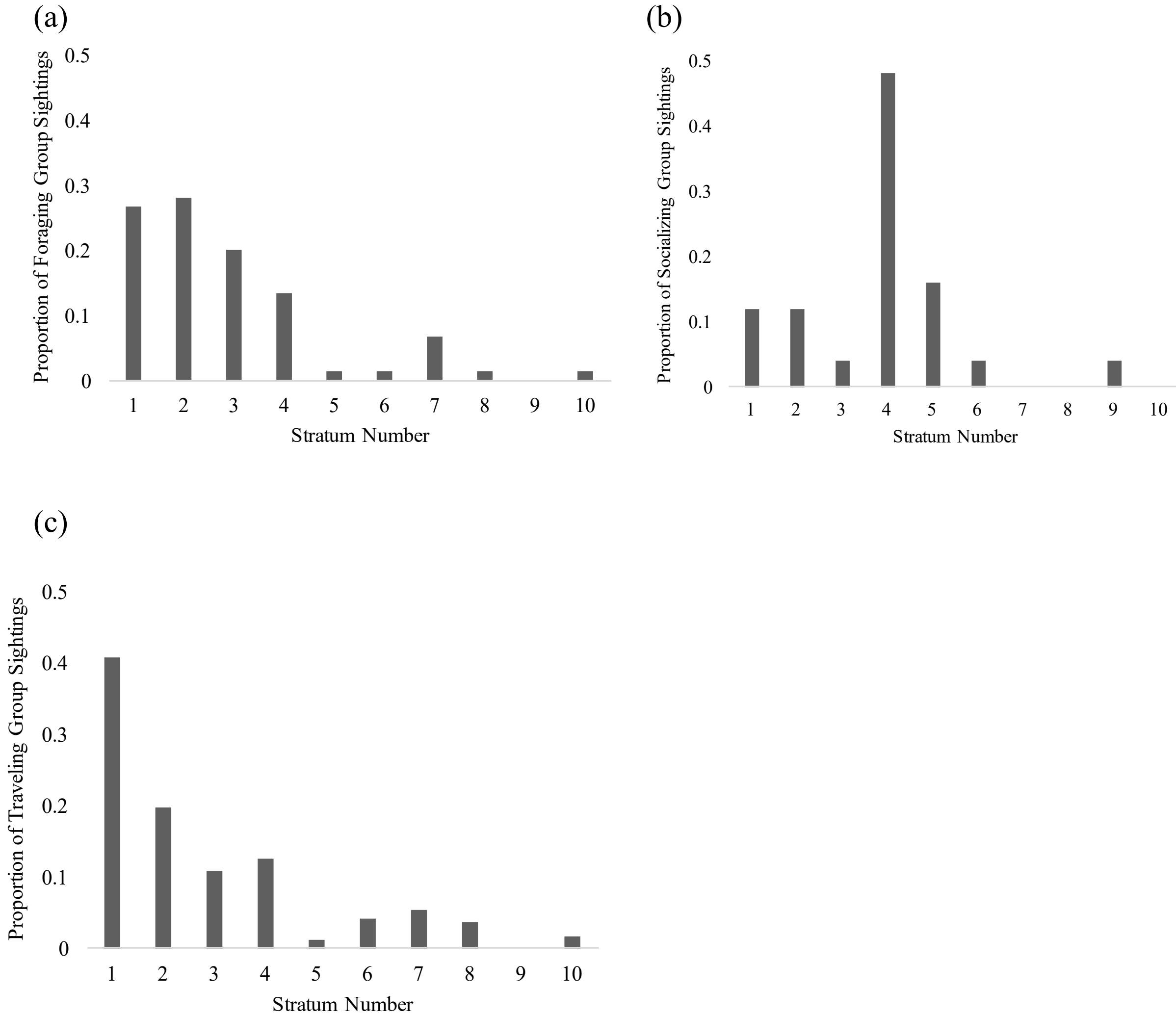


Figure 4a-c: Cold season associations between predominant behavioral state and location (strata) in the SJR. Strata seven-ten and resting groups were excluded from the G-test calculations due to the lack of data. Stratum one was located at the Mayport Inlet and stratum six was located approximately 20km upriver. Stratum five was not included on the survey transect so any sightings in that stratum were collected opportunistically. Additionally, sightings were not weighted based on group size.

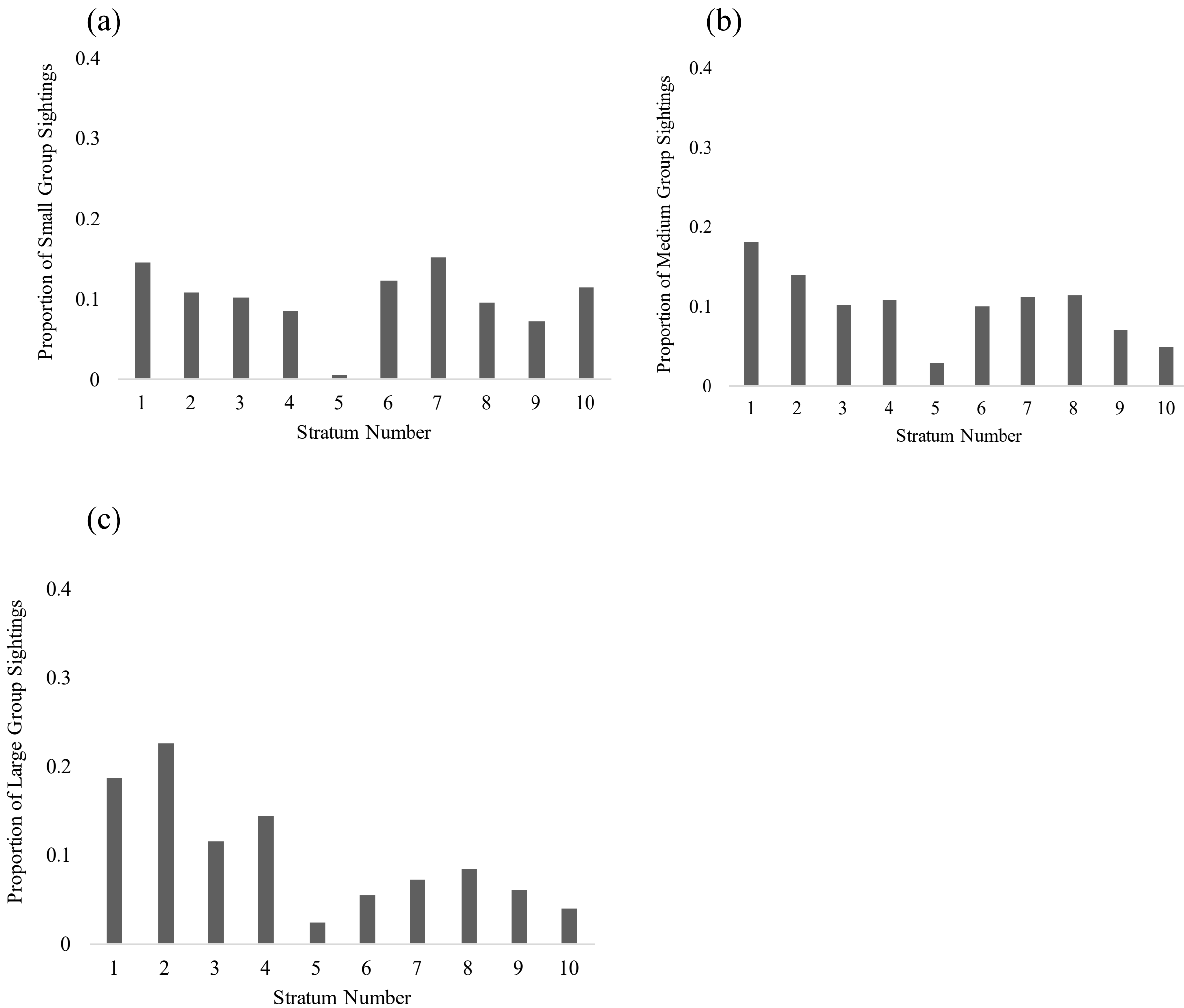


Figure 5a-c: Warm season associations between group size and location (strata)in the SJR. Stratum one was located at the Mayport Inlet and stratum ten was located 40km upriver. Stratum five was not included on the survey transect so any sightings in that stratum were collected opportunistically.

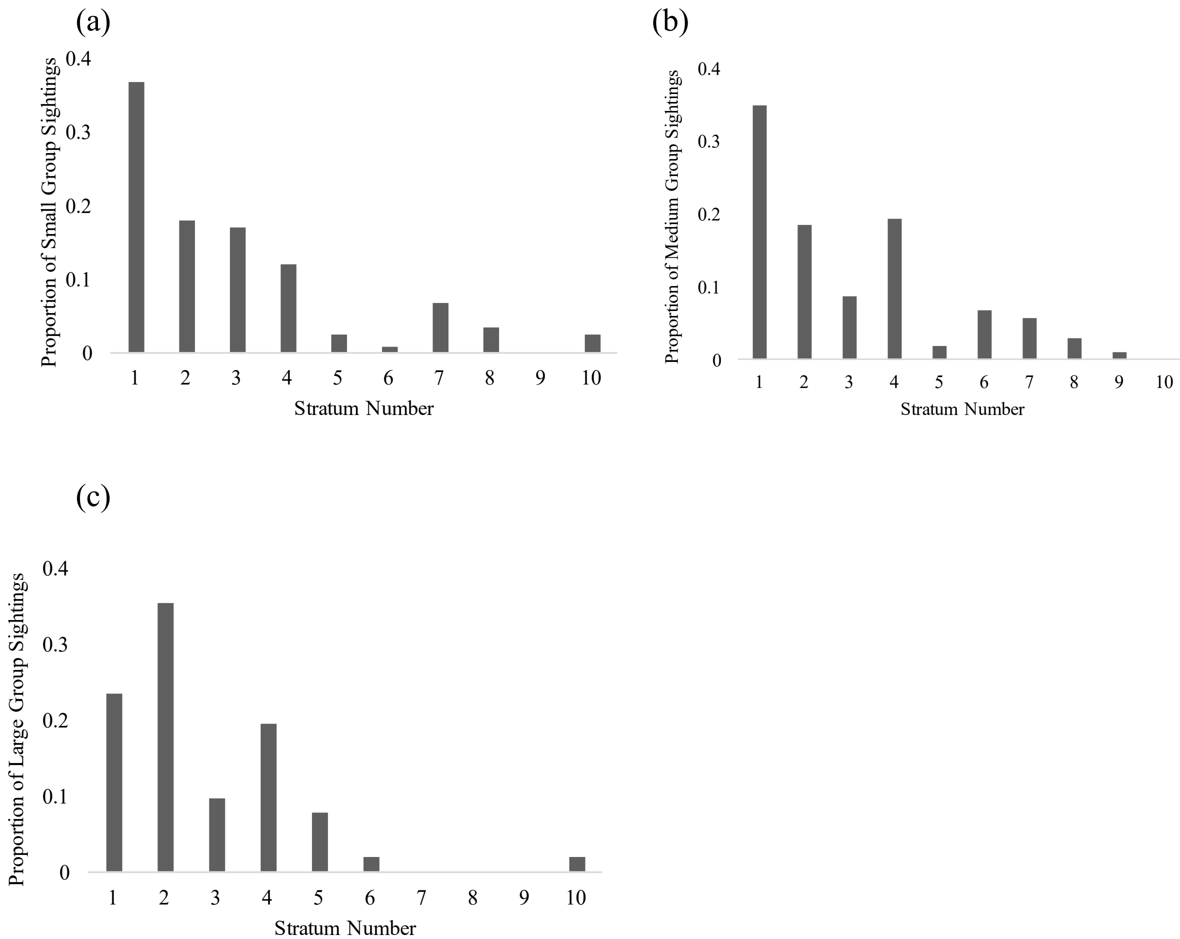


Figure 6a-c: Cold season associations between group size and location (strata) in the SJR. Stratum one was located at the Mayport Inlet and stratum six was approximately 20km upriver. Strata seven-ten were excluded from G-test calculations due to the lack of data. Stratum five was not included on the survey transect so any sightings in that stratum were collected opportunistically.

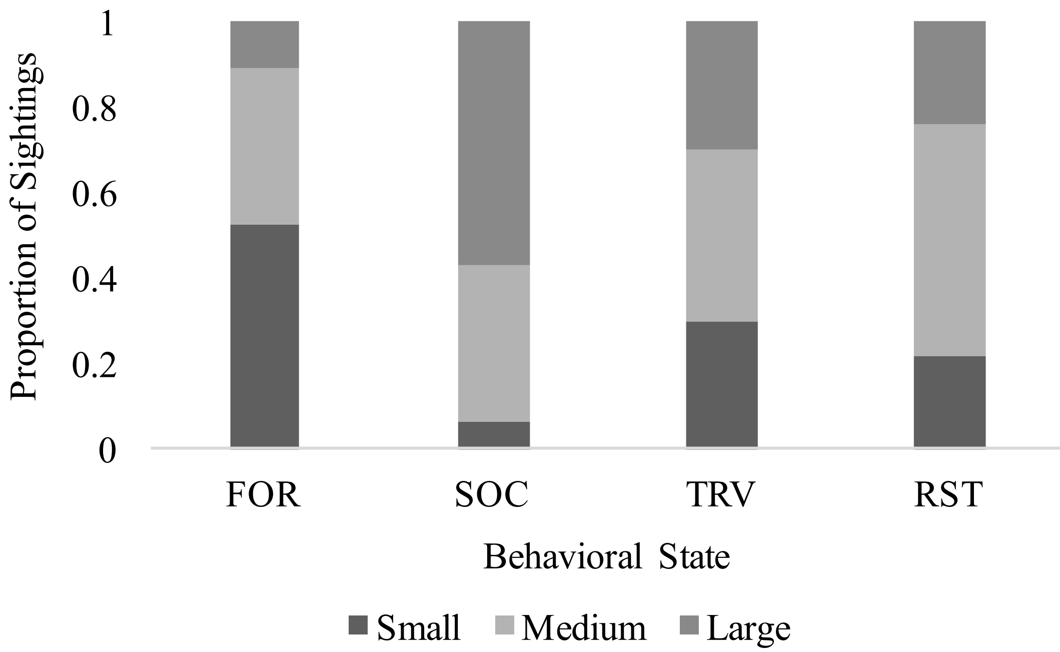


Figure 7: Warm season associations between behavioral state and group size. Small groups included one-two individuals, medium groups included three-seven individuals, and large groups included ≥ eight individuals. Proportion of sightings was calculated for each behavioral state separately.

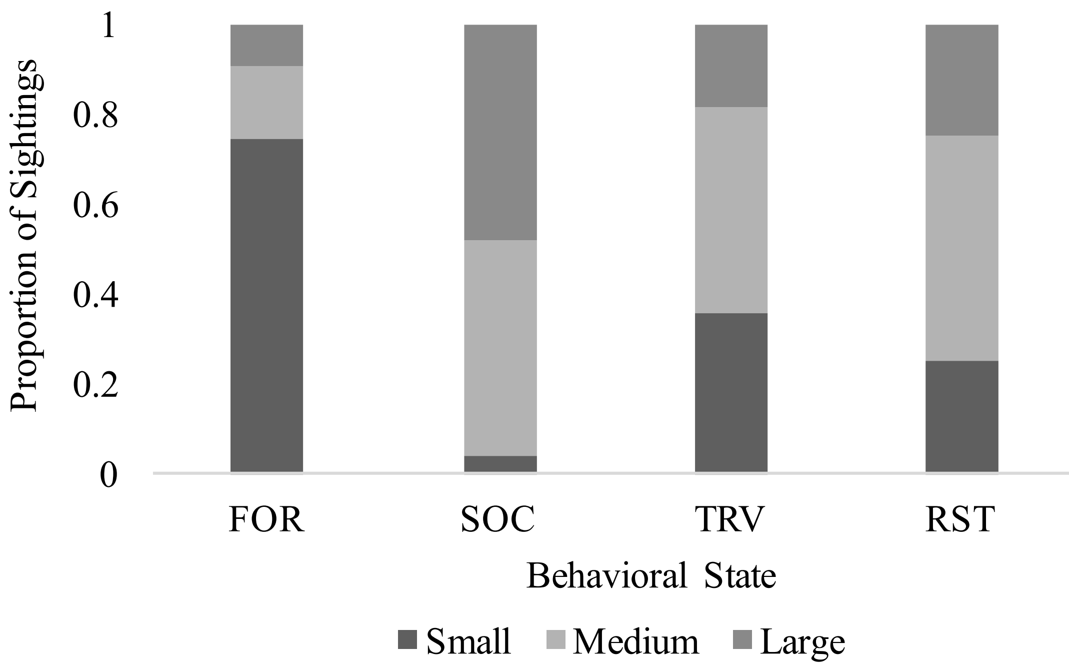


Figure 8: Cold season associations between behavioral state and group size. Small groups included one-two individuals, medium groups included three-seven individuals, and large groups included ≥ eight individuals. Proportion of sightings was calculated for each behavioral state separately.

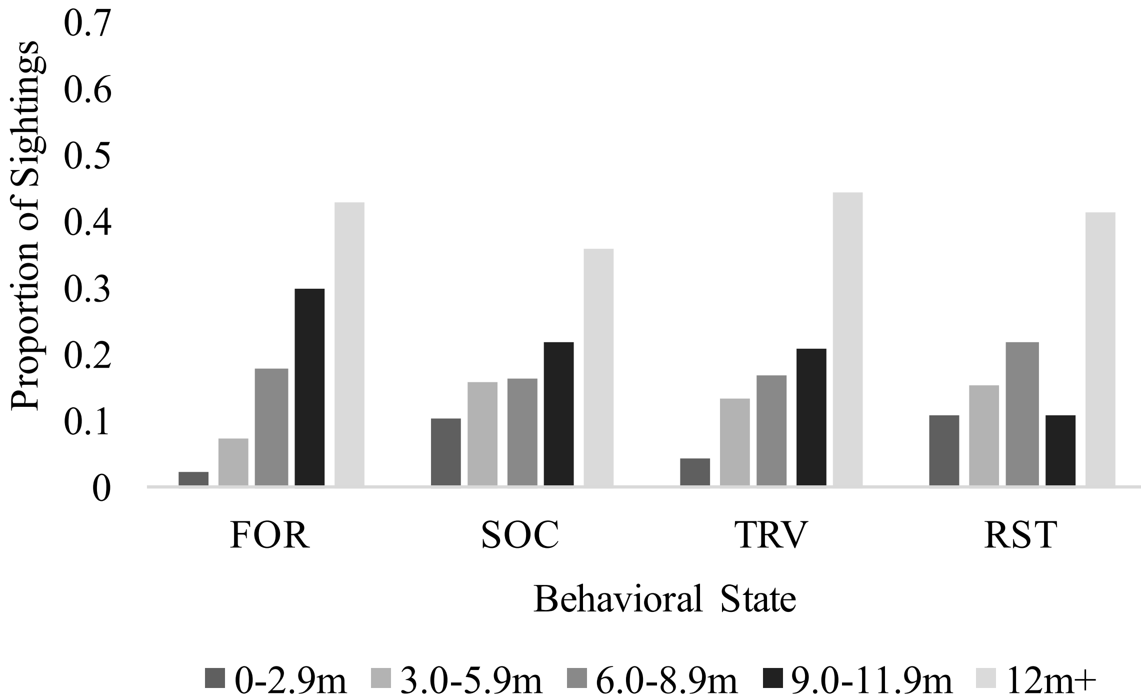


Figure 9: Warm season associations between behavioral state and water depth.

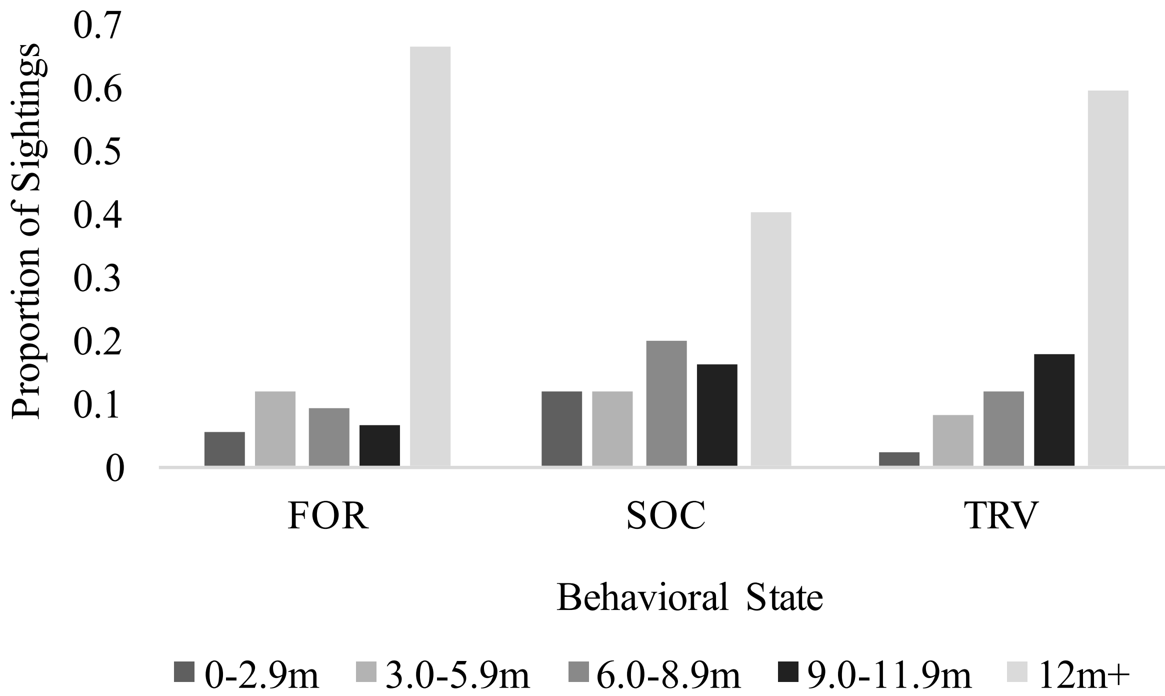
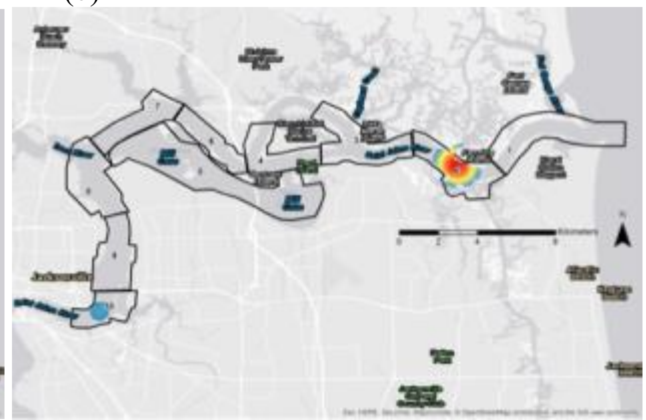


Figure 10: Cold season associations between behavioral state and water depth. Resting groups were excluded due to insufficient sample size.

(a)

(b)



(c)

(d)

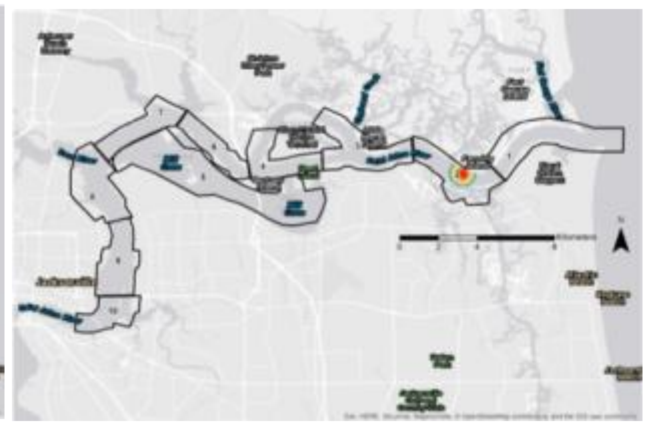


Figure 11a-d: Foraging dolphin groups 95% (a and c) and 50% (b and d) utilization distributions in the warm (> 16°C; a and b) and cold (≤ 16°C; c and d) seasons. Areas of high use are indicated by the red, medium use by the yellow, and areas of low use are indicted by the blue.

(a) (b)

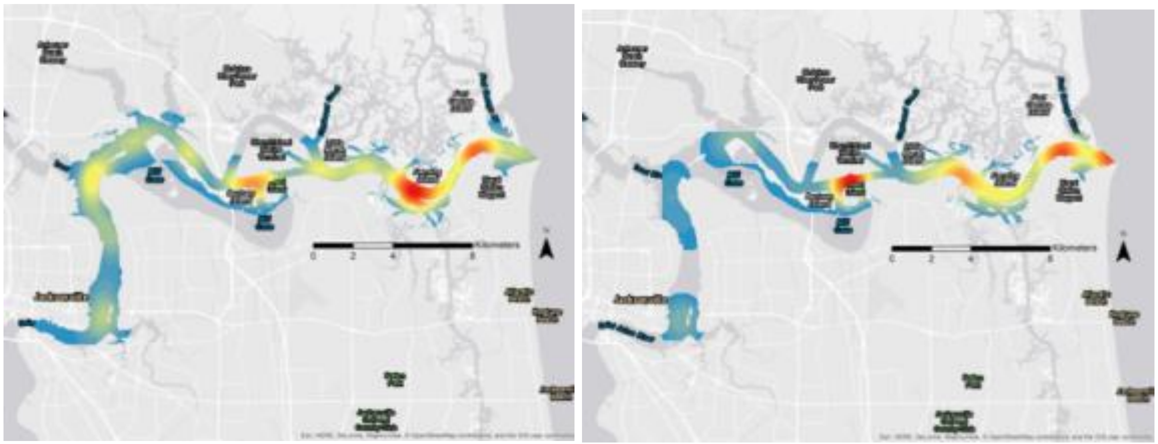
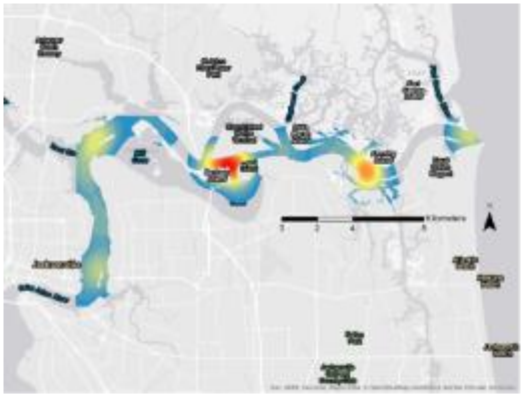
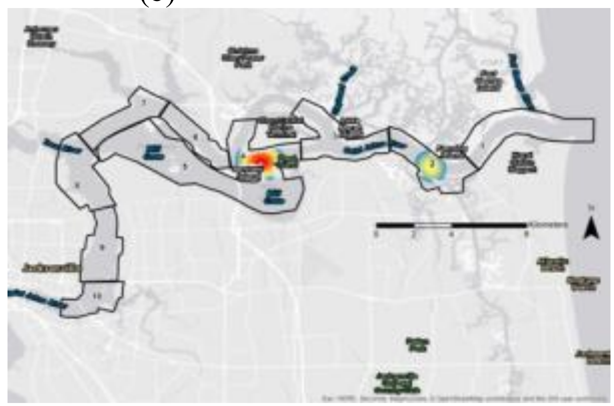


Figure 12a-b: Traveling dolphin groups 95% utilization distributions in the warm (> 16°C; a) and cold (≤ 16°C; b) seasons. Areas of high use are indicated by the red and areas of low use are indicted by the blue.

(a)



(b)



(c)

(d)

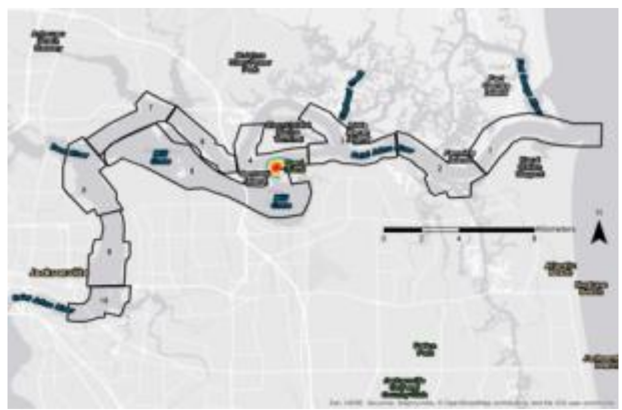


Figure 13a-d: Socializing dolphin groups 95% (a and c) and 50% (b and d) utilization distributions in the warm (> 16°C; a and b) and cold (≤ 16°C; c and d) seasons. Areas of high use are indicated by the red and areas of low use are indicted by the blue.

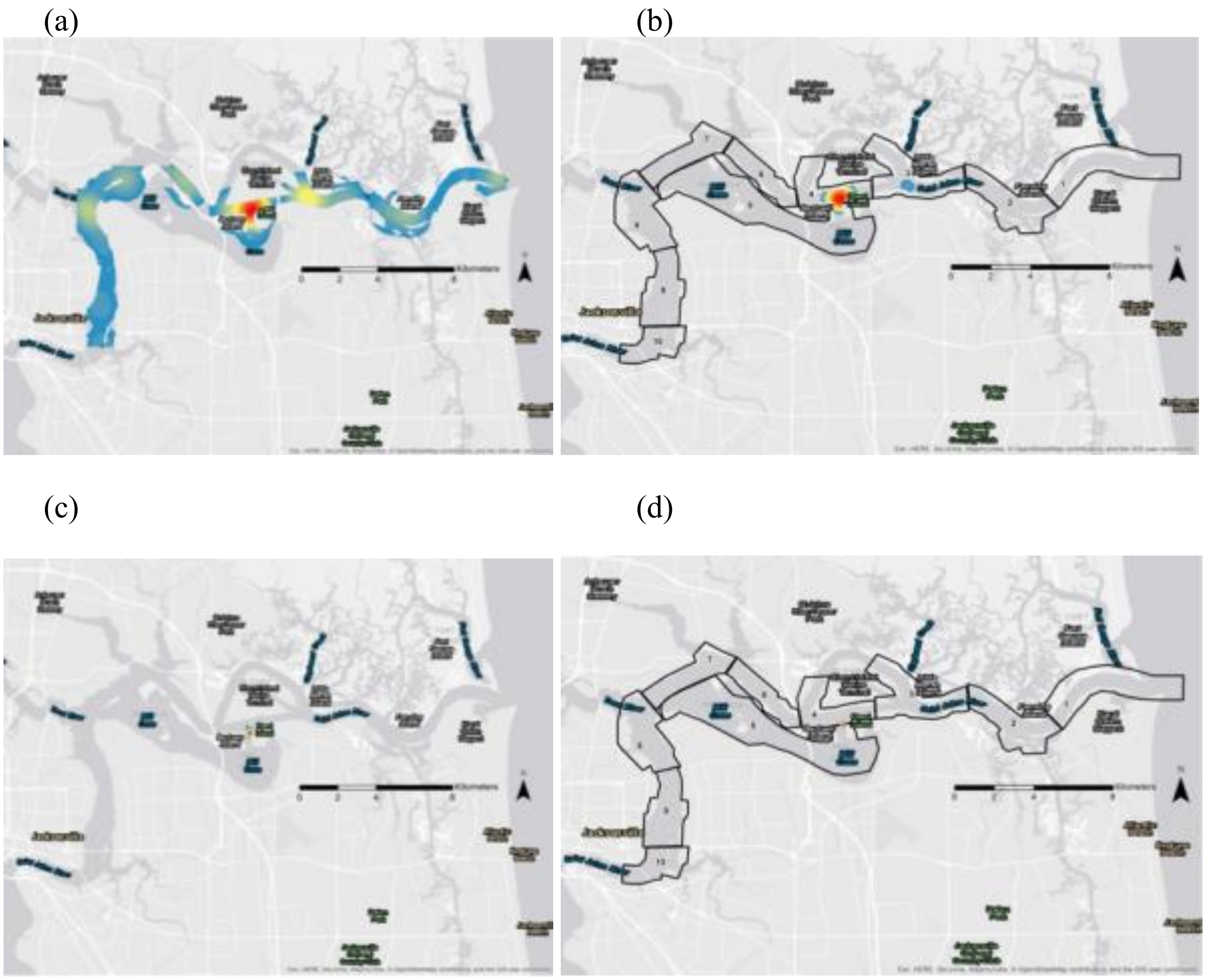


Figure 14a-d: Resting dolphin groups 95% (a and c) and 50% (b and d) utilization distributions in the warm (> 16°C; a and b) and cold (≤ 16°C; c and d) seasons. Areas of high use are indicated by the red and areas of low use are indicted by the blue. Only four sightings of resting dolphin groups were collected during the cold season in this study.

Chapter 2

The soundscape of the St. Johns River and the impact of chronic anthropogenic sound on the behavior of bottlenose dolphins (*Tursiops truncatus*)

Abstract

Anthropogenic activity within coastal systems has been steadily increasing, and as such anthropogenic noise is now becoming a more pervasive and intense source of disturbance in aquatic systems. The St. Johns River (SJR), an urban estuary with a high level of anthropogenic disturbance, is home to a resident population of bottlenose dolphins (*Tursiops truncatus*). The aims of this study were to (1) characterize the soundscape of the SJR and (2) determine the impact of anthropogenic sound on the habitat use patterns of dolphins in the river. To identify soundscape patterns, the SJR was divided into 71 quadrants (800m x 800m). Boat-based acoustic recordings were collected from June 2016 – May 2017 (N=688) using a HTI-96-MIN hydrophone and a Marantz handheld solid state recorder. Autonomous recordings were collected over multiple deployments in Fall 2016 and Spring 2017 (N=6) using a Cetacean Research Technologies µRUDAR-XL or nRUDAR-mk2 system. Sound sources were identified in RavenPro 1.5 and sound levels (dB re 1µPa) at the 3.15kHz 1/3rd octave band for each quadrant were measured using the Cornell Bioacoustics MATLAB script. To identify the impacts of anthropogenic sound on dolphin behavior median sound levels were compared with the habitat use patterns and critical areas identified in chapter 1. Sound levels in the SJR were consistently

high throughout the river (median ± SD = 136.38dB ± 2.72). These levels were notably higher than those measured in two other coastal systems, and anthropogenic sound was pervasive throughout the river. Additionally, SJR dolphins were unable to modify their habitat utilization to avoid high sound levels because there were no sound refuges available to them. Therefore, these dolphins are likely at risk of experiencing long-term behavioral and physiological stress due to anthropogenic sound. The development of new management practices to better protect the SJR dolphins from chronic anthropogenic activity is recommended to ensure the health and viability of this population.

Introduction

An organism's habitat is an intricate and complex system composed of a myriad of interacting biotic and abiotic factors. Studying how an organism interacts with its environment provides insight into the life history and behavior of a species and this knowledge can ultimately be used for the conservation and management of populations (Wilson et al., 1997; Ingram & Rogan, 2002; Rossi-Santos et al., 2006; Miller et al., 2013; Bursa et al., 2016; La Manna et al., 2016). Sound is a significant habitat component that can have numerous impacts on organisms, and yet is relatively understudied. To fill this knowledge gap, soundscape ecology was developed to represent the relationship between a landscape and the sounds present within it (Pijanowski et al., 2011; Marley et al., 2016). Soundscapes change dynamically depending on ecological factors (e.g., time of day, weather, and season), and are influenced by environmental variables (e.g., bathymetry, salinity, temperature, and sediment type) that affect the propagation speed of sound (Nowacek et al., 2001; Quintana-Rizzo et al., 2006). Thus, the distance at which sound sources can be detected depends on the conditions of the immediate environment

(Hildebrand, 2009; Erbe et al., 2015a; Erbe et al., 2015b). In general, sound sources within the soundscape can be divided into three major categories: biophony, geophony, and anthrophony (Hildebrand, 2009; Pijanowski et al., 2011; Erbe et al., 2015a; Erbe, et al., 2015b). Biophony is defined as sounds that are biological in nature such as animal vocalizations. Geophony includes non-biological sounds such as wind and rain, while human made sounds are classified as anthrophony.

In aquatic ecosystems, most animals use acoustic cues to collect information about their environment (Popper, 2003; Pijanowski et al., 2011; Dekeling, 2014). Sound travels quickly and efficiently through water, causing aquatic environments to be highly connected acoustically (Houghton et al., 2015; McWilliam and Hawkins, 2013). Invertebrates, fish, and marine mammals utilize acoustic cues for behaviors such as larval settlement, navigation, territory defense, detection of con- and heterospecifics, communication, and reproduction (Miller et al., 2000; Rolland et al., 2012; Lillis et al., 2014; Pine et al., 2015; Marley et al., 2016). Within coastal environments, invertebrate cues (or sounds) are predominately made by various species of snapping shrimp (genera *Crangon, Alpheus,* and *Synalpheus*) whose snaps can raise ambient sound levels by approximately 20dB (Tyack, 1998; Gannon et al., 2005; Hildebrand, 2009; McWilliam and Hawkins, 2013; Lillis et al., 2014). The vocalizations of soniferous fish can also be important components of coastal/estuarine soundscapes (Lillis et al., 2014). For example, the nighttime soundscape of Perth Canyon, Western Australia, was dominated by a fish chorus (Erbe et al., 2015b). Finally, marine mammals depend on sound as a key source of environmental and social information, and different species will produce a variety of vocalizations in a range of frequencies (Miller et al., 2000; Nowacek et al., 2007; Weilgart, 2007; Clark et al., 2009). For example, right whales (*Eubalaena glacialis*) produce low frequency (~50-400Hz) stereotyped

upcalls to maintain social contact (Parks et al., 2011), while bottlenose dolphins (*Tursiops truncatus*) produce mid-frequency (4-18kHz) whistles during social interactions (Herzing, 1996).

In undisturbed systems, biophony is often the dominant contributor to the ambient soundscape; however, anthropogenic noise is now becoming more pervasive and intense in aquatic systems (Wright et al., 2007; Hildebrand, 2009; Jensen et al., 2009; Rolland et al., 2012). Sounds produced by anthropogenic activity can be classified along a spectrum with pure-tone signals (sounds produced at a specific frequency and for a varying length of time) and impulsive signals (brief sounds produced over numerous frequencies that have high peak levels; Finneran et al., 2000) located at either end of the spectrum. An example of a pure-tone signal would be military sonar and an impulsive signal would be an underwater explosion (Finneran et al., 2000). The pervasive nature of anthropogenic sound is due in part to the increased use of coastal systems by recreational boaters and commercial fishing, as well as the increased size and number of cargo/shipping vessels. Large shipping vessels are one of the strongest sources of broad spectrum sound within marine environments (Wright et al., 2007; Hildebrand, 2009; Erbe et al., 2015b), and can raise total noise levels by approximately 20dB (Merchant et al., 2014). Shipping vessels produce noise at a variety of frequencies depending on the rotation rate of propeller blades and individual engine tones/overtones (Erbe et al., 2015b). As a result, anthropogenic sound levels have increased across a broad range of frequencies (Wright et al., 2007; Merchant et al., 2014)

The widespread occurrence of vessel traffic in coastal systems and the highly-connected nature of marine acoustic environments creates a need for studies that evaluate the impact of anthropogenic activities on the soundscape (McWilliam and Hawkins, 2013). High levels of anthropogenic sound can have numerous effects on marine animals, especially cetaceans, in

these systems because anthropogenic sounds are typically produced in the same frequency ranges as those utilized by these animals (Nowacek et al., 2007; Wright et al., 2007; Pine et al., 2016). Negative impacts of anthropogenic sound include the masking of signals, alterations in behavior, abandonment of critical habitats, and physiological stress/damage (Buckstaff, 2004; Finneran et al., 2005; Wright et al., 2007; Weilgart, 2007; Clark et al., 2009; Mooney et al., 2009; Parks et al., 2011; Rolland et al., 2012; McWilliam and Hawkins, 2013; Pirotta et al., 2013; Dekeling, 2014; Merchant et al., 2014).

The potential for communication masking is one of the main long-term effects of anthropogenic sound that has been assessed, especially for baleen whales (Miller et al., 2000; Wright et al., 2007; Clark et al., 2009; Parks et al., 2011). Specific types of communication that can be affected by anthropogenic sound include contact calls and mating calls used to maintain proximity between mother and calf or group members (Parks et al., 2011; Rossi-Santos, 2015; Redfern et al., 2017). For example, Miller et al. (2000) observed that male humpback whales (*Megaptera novaeangliae*) increased the length of their songs when low-frequency active sonar was present. They hypothesized that the whales were adjusting their vocal behavior to compensate for sonar interference. North Atlantic right whales have also been documented to compensate for communication masking. Parks et al. (2011) observed that right whales increased the amplitude (volume) of their upcalls (contact calls) as background noise levels increased. High levels of anthropogenic sound have also been associated with high stress levels in right whales. Ambient noise levels in the Bay of Fundy, Canada decreased by 6dB during a temporary reduction in large vessel traffic after the events of September 11, 2001 (Rolland et al., 2012). Concurrently, the fecal adrenal glucocorticoids (stress hormones) secreted by right whales in the bay decreased indicating lower stress levels in the whales. However, by 2002, vessel traffic in

the Bay of Fundy had resumed normal levels and right whale glucocorticoids had returned to baseline levels (Rolland et al., 2012).

The impacts of anthropogenic sound on baleen whales have been the focus of numerous research studies because of the overlap of sounds within the low-frequency range (Tyack, 2008; Clark et al., 2009). However, anthropogenic sounds also affect the mid-frequency range of the sound spectrum that is utilized by many odontocetes (Hildebrand, 2004; Houghton et al., 2015; Pine et al., 2016), including bottlenose dolphins (*Tursiops truncatus*). Sound plays an important role in both the social and foraging behavior of bottlenose dolphins (Herzing, 1996, 2014). These animals are highly social and live in fission-fusion societies in which group composition changes frequently (Connor et al., 2000). To mediate their complex social interactions and maintain group cohesion, dolphins produce a variety of vocalizations (Smolker et al., 1993; Herzing, 1996; Quick and Janik, 2008; King et al., 2016). Whistles are the most common type of social vocalization and generally occur in the frequency range of 0.2-24kHz (Herzing, 1996; Berta and Surmich, 1999; Buckstaff, 2004; Boisseau, 2005; Haviland-Howell et al., 2007). While foraging, dolphins utilize echolocation and passive listening (Smolker et al., 1993; Gannon et al., 2005). The echolocation system in dolphins is highly advanced and is used for detecting and locating prey or objects within their environment. Echolocation clicks are generally produced in the frequency range of 30-150kHz and echolocation razor buzzes have a frequency range of 2-6kHz (Herzing, 1996; Berta and Surmich, 1999). In some populations dolphin prey includes soniferous fish, thereby allowing dolphins to first utilize passive listening for initial prey detection (Barros and Wells, 1998; Gannon et al., 2005), then further investigate sound sources via echolocation (Gannon et al., 2005).

Sound plays a vital role in behavior, and dolphins are known to detect sound frequencies from about 75Hz to 160kHz (Johnson, 1967; Au et al., 2002; Finneran et al., 2008). Sound is an especially important sensory modality for dolphins living in areas with poor water quality because the effective range of visual cues is greatly diminished. The exact hearing threshold of an individual dolphin depends on a variety of factors including the frequency of the sound, the sound pressure level, and the age and sex of the dolphin (Houser and Finneran, 2006; Weilgart, 2007). The hearing threshold of an individual can also be altered by exposure to intense sound. A temporary threshold shift (TTS) occurs when the hearing sensitivity of an individual is briefly lowered, but eventually returns to normal. Conversely, a permanent threshold shift (PTS) is when the individual's auditory structures are damaged (sensory hair cells in the inner ear are lost) and hearing sensitivity is permanently reduced. The extent of a threshold shift and the recovery time varies depending on the frequency and duration of the sound exposure (Mooney et al., 2009). In addition to causing auditory disturbance/damage, anthropogenic sound can also cause behavioral changes in dolphins (Finneran et al., 2000). Anthropogenic sound, such as that from recreational boating traffic, which is produced in the same frequency bands used by dolphins will have the largest effect on them (Jensen et al., 2009). Small boats with either inboard or outboard engines produce sounds that generally peak in the biologically relevant mid-frequency (0.5-25kHz) range (Haviland-Howell et al., 2007; Hildebrand, 2009; Marley et al., 2016). Increased noise levels from vessel traffic can interfere with dolphin acoustic communication due to an overlap between the frequency and amplitude of dolphin vocalizations and vessel noise (Wright et al., 2007; Jensen et al., 2009; La Manna et al., 2013; Merchant et al., 2014; Pirotta et al., 2015). Thus, high levels of vessel traffic are a potential source of acoustic harassment for these animals (Nowacek et al., 2001), and dolphins have been shown to adjust their acoustic behavior to avoid signal

masking by boat traffic (Buckstaff, 2004; La Manna et al., 2013; Luís et al., 2014; Pirotta et al., 2015). Increased levels of ship noise can induce avoidance responses in dolphins (Lusseau, 2003; Tyack, 2008; Merchant et al., 2014; Houghton et al., 2015). Given the importance of sound in dolphin behavior, rising levels of vessel traffic make anthropogenic sound a growing source of disturbance for these animals (Nowacek et al., 2001).

In addition to acoustic harassment, marine vessel presence is a significant driver of behavioral transitions or changes in bottlenose dolphins (Bas et al., 2014; Pirotta et al., 2015). Dolphins have been observed leaving an area or shortening the length of their dives, in response to boats passing within 200m of them (Nowacek et al., 2001; Papale et al, 2012; La Manna et al, 2013). These short-term changes in behavior can lead to larger impacts on the overall energy budgets of the dolphins (Lusseau, 2004). For example, dolphins in the Istanbul straight reduced socializing and resting behavior in response to increased commercial fishing vessel traffic (Bas et al., 2014). Similarly, in Doubtful Sound, New Zealand, dolphins were less likely to continue resting or socializing and more likely to begin traveling after interacting with tour boats (Lusseau, 2003). Eventually, these short-term energy costs will accumulate and may lead to dolphins abandoning an area (Allen and Read, 2000; Pirotta et al., 2013; Bas et al., 2014). If displaced to areas that are already occupied, dolphins may then experience higher levels of competition for resources (Wilson et al., 1997). Additionally, high levels of anthropogenic disturbance could reduce the foraging efficiency of dolphins that remain in the area and ultimately reduce the carrying capacity of the environment (Allen and Read, 2000; Heithaus and Dill, 2002; Pirotta et al., 2015).

In coastal systems, dolphins are at increased risk of chronic exposure to various anthropogenic disturbances. Some anthropogenic sources of disturbance exhibit temporal

variation that parallel normal human routines, such as increased vessel traffic at mid-day and on the weekends, and increased construction/dredging during the week (Haviland-Howell et al., 2007; Marley et al., 2016), while other disturbances are more continuous (commercial shipping traffic; Merchant et al., 2012). Identifying patterns of anthropogenic noise within a system and comparing these patterns to dolphin distributions can inform management decisions by indicating areas where dolphins are at risk of disturbance due to anthropogenic activity (Jensen et al., 2009; Marley et al., 2016; Redfern et al., 2017).

The St. Johns River (SJR), Jacksonville, FL is an urban estuary that is home to a resident population of bottlenose dolphins. These dolphins are part of the Jacksonville estuarine stock (JES), which is one of two estuarine stocks recognized by NOAA fisheries on the east coast of Florida (NOAA Fisheries, 2016). The JES is also listed as a strategic stock by NOAA fisheries. Thus, significant disturbance to SJR dolphins could have implications for the management of this stock. The lower SJR has relatively poor water quality (Pinto et al., 2016), thereby increasing the importance of sound for the dolphins (Quintana-Rizzo et al., 2006). The SJR is extremely turbid and visual cues would only be effective over very short distances. Therefore, the dolphins would rely more on auditory cues than visual cues to collect information about their environment, maintain group cohesion/social contact, and while foraging. The SJR also has a high potential for anthropogenic disturbance. Sources of potential disturbance include an international shipping port with three terminals, a Carnival cruise ship port, a U.S. Naval station, a U.S. Coast Guard station, commercial fishing fleet, and heavy use by recreational boats. Additionally, work on the Jacksonville Port expansion project began in early 2016. This project entails dredging the main channel from a depth of 12.5m to a maximum depth of 15.2m, underwater blasting, and the

relocation of a training wall to alleviate cross-currents for shipping traffic (U.S. Army Corp, 2014; Harbor Deepening, 2017).

Relatively few studies have characterized the soundscape of an estuary (Lillis et al., 2014; Pine et al., 2015; Marley et al., 2016), and establishing baseline data is integral to evaluating anthropogenic impacts on these ecosystems (Merchant et al., 2014; Marley et al., 2016). Therefore, the first aim of this study was to characterize the soundscape of the SJR by measuring median sound levels (dB re 1 µPa), identifying common sound sources, and documenting the prevalence of anthropogenic sound. The second aim was to determine the impact of anthropogenic sound on the habitat use patterns of dolphins in the river. It was hypothesized that dolphins would preferentially utilize areas of the river with lower sound levels for critical behaviors such as socializing and resting. Characterizing the soundscape and identifying patterns of anthropogenic disturbance in the SJR will provide valuable insight into how human activities influence estuarine environments. Furthermore, determining the potential impacts of anthropogenic disturbance on the habitat use patterns of a cetacean species that commonly inhabits estuarine systems will enable more informed management decisions in other coastal systems that also have high levels of human activity (Marley et al., 2016; Pine et al., 2016).

Methods

Study site

The St. Johns River (SJR) in Jacksonville, FL is a northward flowing blackwater river that drains into the Atlantic Ocean at the Mayport Inlet (30.399073°N 81.386612°W; Pinto et al., 2016). The tidal range at Mayport Inlet is about 2m and water depth is influenced up to 170km

upriver (Pinto et al., 2016). The study area for this project ranged from the Mayport Inlet to approximately 40km upriver. This section of the river is in the mesohaline riverine zone of the Lower St Johns River Basin, and is typically well-mixed and deep (main channel 12-15m) with a fast flow rate (Pinto et al., 2016).

Data Collection

Acoustic data were collected through a combination of boat-based and autonomous recordings. The boat-based recordings provided short snap-shots of the SJR soundscape over an extended time period and a large geographic range. However, these recordings did not allow for the analysis of diel patterns in the soundscape. Therefore, the autonomous recordings were collected to examine diel sound patterns in the SJR, but due to logistical constraints these were taken during a much more restricted sampling period and geographic range. Combined, these recording methods allowed for a comprehensive characterization of the SJR soundscape.

Boat-based Recordings:

From June 2016 through May 2017, boat-based recordings were obtained using a High-Tech Inc. HTI-96-MIN marine mammal hydrophone (sensitivity: -171.3dB re 1V/µPa and 30dB pre-amplifier gain) and a Marantz Professional PMD661 MKII handheld solid state recorder (24-bit, 96kHz sampling rate). The SJR study area was divided into 71- 800m x 800m quadrants (Figure 1a). Quadrant size was set at $800m^2$ because bottlenose dolphins begin to react and exhibit behavioral modifications when vessels are approximately 400m away (Buckstaff, 2004; Bas et al., 2014). Therefore, a dolphin in the center of each quadrant would experience disturbance from a vessel moving anywhere within the quadrant. Quadrant location and central GPS coordinates were identified using ArcGIS 10.3 software (ESRI, Redlands, CA). Quadrant 1 was located 40km upriver in downtown Jacksonville and quadrant 73 was located at the Mayport

Inlet. It should be noted that originally 73 quadrants were identified, but two (48 and 49) were eliminated part-way through the study because they were in areas that were too shallow (<1m) for the research vessel to safely reach. Enough recordings had been collected that it was decided the quadrants would not be re-numbered. During recording sessions, the hydrophone was deployed at or near the center of each quadrant (based on GPS location) and a minimum of 2 minutes were recorded per deployment (McWilliam and Hawkins, 2013). The hydrophone was held at a depth of 0.5m below the water surface while the research vessel engines were turned off. Detailed notes were taken during each recording session describing the type and frequency of anthropogenic activity observed, the timing of events at the surface (e.g., when a boat passed), environmental variables (i.e., water depth, salinity, Beaufort sea state, and water temperature), and dolphin behavior if present within the quadrant.

Due to the high number of quadrants, not every quadrant was recorded during a single day. Instead, all of the odd or all of the even numbered quadrants were recorded during an acoustic survey. The starting location and which quadrants were recorded (odd vs. even) were alternated each survey to randomize the data and account for variation in sound levels due to tidal state, shipping schedule, recreational activity, day of the week, and time of day (i.e., morning vs evening). A minimum of one acoustic survey was conducted per month, and all boat-based recordings were collected during the day (0700-1800 hrs.). A total of 688 boat-based recordings were collected ($\bar{x} \pm$ SE = 9.69 ± 0.33 recordings per quadrant; $\bar{x} \pm$ SE = 23.5 ± 0.85 minutes recorded per quadrant).

<u>Autonomous Recordings:</u>

Autonomous recordings were collected using the Cetacean Research Technologies (CRT) μRUDAR-XL (August-September 2016) and nRUDAR-mk2 (February-April 2017) autonomous

recording systems. Each recording apparatus contained a SQ26-05 CRT hydrophone, batteries, and Tascam DR-22WL recorder. The μRUDAR-XL system had a hydrophone sensitivity of -167.86dB re.1V/μPa with a 20dB gain and a 24-bit, 96kHz sampling rate. The μRUDAR-XL was only used for the August-September deployments because it disappeared mid-deployment in September. The nRUDAR-mk2 system had the same gain and recorder settings as the μRUDAR-XL and had a hydrophone sensitivity of -169.11dB re.1V/μPa. This recording system was used for all 2017 deployments. Both recorders were deployed using the same anchoring system. The hydrophone was suspended 1m above the river bottom (Haviland-Howell et al., 2007; Tellechea et al., 2014; Pine et al., 2015), and was attached to the rope that connected the surface buoy to the main anchor. A secondary anchor was attached to the main anchor with approximately 2m of rope. Rope was used instead of chain to reduce flow noise and recording artifacts. The recorders were deployed at two locations in the SJR. Each deployment lasted for two days during which acoustic data were collected continuously. The first deployment location was in Quadrant 53 (a primarily residential area), approximately 13km from the Mayport Inlet. The second deployment location was in Quadrant 17 (near the third JaxPort terminal), approximately 28km from the Mayport Inlet. The autonomous recorder was deployed at these two locations because they were roughly equal distances from each other and either end of the study area (Figure 1a). Additionally, it was logistically more reasonable to deploy the autonomous recorder at two consistent sites rather than attempt to deploy it in all quadrants.

The autonomous recorders were deployed during different months of the year (approximately six months apart) to account for any potential seasonal effects on the diel sound patterns. Overall, the autonomous recorders were deployed six times during this study with three deployments per location. The Quadrant 17 deployments took place in August 2016 (Aug. 16-18;

44 hours recorded) and February 2017 (Feb. 14 and Feb. 21-22; 3 and 31 hours recorded, respectively) for a total of 78 hours recorded. Only 3 hours were recorded on February 14th because of memory card failure, and the recorder batteries died after 31 hours during the February 21-22nd deployment. The Quadrant 53 deployments took place in September 2016 (Sep. 6-8; 48 hours recorded), February 2017 (Feb. 28-Mar. 2; 47 hours recorded), and April 2017 (Apr. 13-15; 47 hours recorded) for a total of 142 hours recorded. No equipment issues occurred during the Quadrant 53 deployments.

Data Analyses

Soundscape

The overall soundscape of the SJR was characterized using a combination of boat-based and autonomous recordings. Boat-based recordings provided short snap-shots of the SJR soundscape over an extended time period and greater geographic range, allowing for identification of SJR sound sources and fine-scale sound level variations throughout the study area. Spectrograms for each recording were generated in RavenPro 1.5 beta with a 2639-point Hann window (3dB bandwidth = 52.3Hz), 80% overlap, and 4096-point DFT. Sound sources and common sound patterns were visually and acoustically identified and measured using these spectrograms. The median sound levels at the 3.15kHz 1/3rd octave band (Heenehan, 2016) were averaged over 10-second intervals and measurements were done using the Cornell Bioacoustics MATLAB script (MathWorks software, Natick, MA). Median sound levels were measured because these provided an indication of the typical sound levels present in each quadrant (Clark et al., 2009; Merchant et al., 2015; Pine et al., 2015). All sound levels were calculated in dB re 1 µPa. Analyses focused on the 3.15kHz 1/3rd octave band because this band was well within the hearing range of bottlenose dolphins, and was influenced by both anthropogenic and biotic

sounds (Heenehan, 2016). As such, it indicated the typical sound levels in a frequency band that was biologically relevant for SJR dolphins.

Boat-based recordings did not allow for analyses of diel changes in sound level, thus, autonomous recordings were utilized to identify these patterns. Diel changes in sound intensity were qualitatively identified via time-frequency (kHz) and third-octave band (TOB) central frequency (Hz) spectrograms. Changes in sound intensity were identified visually using a color-coded scale that represented dB level. Within this color-scheme, red indicated high sound intensity (> 140dB) and dark blue indicated low sound intensity (< 110dB). Spectrograms were generated using a custom MATLAB script from the Cornell Bioacoustics research program (2048-point Hann window, sound averaged over 10-second intervals). Seasonal soundscape patterns were not assessed using either recording method because of insufficient sample size in the cold season (≤ 16°C). However, the combination of both recording methods allowed for a comprehensive characterization of the overall SJR soundscape.

Prevalence of anthropogenic sound

Anthropogenic disturbance in the river was determined by identifying individual sound sources and calculating the prevalence of anthropogenic sound using the boat-based recordings. Initial sound source identification was performed in the field during recording sessions through observations of human activity in the quadrant and written notations regarding sounds heard. Visual and auditory confirmation of anthropogenic sound sources were conducted using the spectrograms generated in RavenPro 1.5 beta. Anthropogenic sounds have distinct sound signatures (visually and acoustically) compared to biotic sounds, thereby enabling accurate identification. The prevalence of anthropogenic sound in the SJR was determined by examining all recordings in RavenPro for the presence of anthropogenic sound and then calculating the

proportion of recordings per quadrant that contained anthropogenic sound (Marley et al., 2016). Additionally, the proportion of time anthropogenic sound was recorded in each quadrant was calculated (in minutes) to provide fine-scale resolution of anthropogenic disturbance. Pearson correlation analyses were then run in SPSS v24 (IBM Predictive Software, Armonk, NY) to determine if the median sound levels present in each quadrant were correlated with the presence of anthropogenic sound and/or the amount of time anthropogenic sound was recorded.

Impact of anthropogenic sound on dolphin habitat use

The impact of anthropogenic sound on bottlenose dolphin habitat utilization was determined through a comparison of dolphin habitat use patterns (see Chapter 1) and median sound levels. To simplify analyses, each quadrant was nested into one of ten strata (Figure 1b), and each stratum was identified based on the predominant type of anthropogenic activity present within it (defined in table 1 and see chapter 1). Anthropogenic activity was used to identify the strata because different types of activity produce different sounds. For example, stratum one (at the Mayport Inlet) contained a U.S. Naval base, U.S. Coast Guard base, and multiple marinas, and stratum six (approximately 20km upriver) contained the second JaxPort shipping terminal and the Carnival cruise ship terminal. The median sound levels of each stratum at the 3.15kHz 1/3rd octave band were then compared to the habitat use patterns of the SJR dolphins. Habitat use patterns were identified by determining the proportion of sightings with foraging, socializing, resting, and traveling (defined in table 2) as the predominant behavioral state in each stratum. Pearson correlation analyses were then run in SPSS v24 to determine if sound levels affect how dolphins utilize the SJR. The proportion of sightings of foraging, socializing, and resting groups per stratum was individually assessed for correlation with median sound levels because sound could have varying effects on the dolphins depending on their behavioral state. Traveling groups

were not included in the correlation analyses because dolphins are most sensitive to disturbance while foraging, socializing, and resting (Lusseau, 2004; Pirotta et al., 2015). Finally, dolphin critical habitat areas (see Chapter 1) were visually compared to median sound levels to determine the degree of sound exposure for dolphins utilizing those areas.

Results

Soundscape

Sound sources

Sound sources were identified using the boat-based recordings. Geophony was not a major contributor to the SJR soundscape. Rainfall was recorded on a few occasions, but was difficult to detect visually on spectrograms and acoustically during playbacks. Waves hitting the side of the research vessel and flow noise around the hydrophone were frequently recorded during the boat-based sessions. However, these sounds were artifacts of the recording method and were not considered components of the soundscape (Merchant et al., 2014; Erbe et al., 2015b).

Biophony and anthrophony both significantly contributed to the SJR soundscape. The most common biological sound sources recorded were bigclaw snapping shrimp (*Alpheus heterochaelis*), oyster toadfish (*Opsanus tau*), red drum (*Sciaenops ocellatus*), and bottlenose dolphins. The snapping shrimp were the most substantial source of biological sound in the SJR. The snaps typically occurred in the frequency range of 1-15kHz, with overtones visible into the upper frequency (> 20kHz) bands on the spectrograms. Snapping shrimp were recorded in all locations and recording sessions, and were typically louder in shallow areas (water depths ≤ 3m) compared to deeper regions (water depths ≥ 9m). Additionally, it was often difficult to hear (in the field) or identify (in the lab via spectrograms) other biological sound sources due to the

pervasive nature of the snapping shrimp sounds. The presence of oyster toadfish and red drum were both definitively identified from spectrographic analyses. Their vocalizations occurred in the frequency range of approximately 0.2-2kHz. It was highly likely that other soniferous fish species were also recorded but their vocalizations were not identified. Bottlenose dolphin vocalizations, including whistles, squeaks, buzzes, clicks, and burst pulses, were also frequently recorded during boat-based sessions. These vocalizations occurred over a wide-frequency range from approximately 0.4kHz to 48kHz. Whistles generally occurred in the mid-frequency range (5-20kHz) and echolocation vocalizations occurred in the high-frequency range (25-48kHz).

Numerous sources of anthrophony were identified during this study with the most common sound source being vessel engine noise. The types of vessels recorded include recreational boats, shrimp trawlers, cargo ships, ferries, tug boats, and military (U.S. Navy and U.S. Coast Guard) ships. The recreational boats were comprised of jet skis, personal fishing boats, sailboats, crab fishing boats, and yachts. The exact frequency range of the sound produced by each individual vessel depended on the size of the vessel, the type of engine, and the speed at which the vessel was travelling. Overall, vessel noise typically occurred within the frequency range of 0.8-35kHz, with some vessels producing sounds in frequencies up to 43kHz. Additional anthropogenic sound sources included dredging, construction at ports and ferry docks, loading/unloading of cargo ships, helicopters, and traffic on bridges. These sound sources occurred over different time scales (seconds to minutes) and in approximately the same frequency bands as vessel noise.

3.15kHz 1/3rd octave band sound levels

Consistently high sound levels at the 3.15kHz 1/3rd octave band (TOB) were measured for each quadrant from the boat-based recordings (Figure 2). The maximum median sound level

measured was 138.79dB re 1 μPa in Quadrant 13. The minimum median sound level was recorded in quadrant 73 and was 128.34dB re 1 μPa. Overall, the median sound level across all quadrants was 136.38dB re 1 μPa with a standard deviation of 2.42dB. The median sound levels at the 3.15kHz 1/3rd octave band for each stratum were also high (Table 3). The lowest stratum sound level was 135.82dB re 1 μPa and the highest was 137.03dB re 1 μPa.

Diel soundscape patterns

The spectrograms generated from the autonomous recordings at Quadrant 17 indicated that diel sound patterns were present during the August 2016 deployment but not during the February deployments. The sound levels on the time-frequency spectrogram were lower (approximately 10-20dB) in the 10-40kHz frequency range during the night compared to day-time levels (Figure 3a). However, a peak in sound intensity was also observed during the middle of the night in the 315-630Hz TOBs. To determine the source of this peak in sound intensity, a random sample was analyzed in RavenPro from 0100-0200 hours on August 17, 2016. During this time frame, numerous dolphin vocalizations (whistles and echolocation clicks) and a red drum chorus were audible and visible on the spectrogram. Throughout the entire hour there was also a constant engine or mechanical noise that ranged from approximately 0-20kHz. Unlike the August deployment, the February deployments in Quadrant 17 did not have any diel changes in sound intensity (sound levels remained the same regardless of time of day) in both the time-frequency and the time-TOB central frequency spectrograms (Figure 3b-c). Similarities between the August and February deployments included similar sound intensity levels in the 0-10kHz frequency range (~120-130dB; time-frequency spectrograms) and high sound intensities measured in the 10-80Hz TOB (~140-150 dB; time-TOB central frequency spectrograms). Also, similar to the August deployment, the February 14th deployment had high sound intensities in the

315-630Hz TOBs, but these levels were continuous throughout the three hours recorded and this recording was collected during the day (Figure 3b). Overall, it was determined that no seasonal influences were observed in the Quadrant 17 deployments due to the degree of similarity among the spectrograms.

Diel sound patterns were not observed in any of the spectrograms generated from the Quadrant 53 deployments (Figure 4a-c). The time-frequency (kHz) spectrograms all had a high degree of variability in this quadrant. In general, the higher frequencies (20-45kHz) had lower intensity levels (approximately 10-20dB) than the low frequencies (0-20 kHz). The time-TOB central frequency (Hz) spectrograms also had a high degree of variability above 80Hz. Each spectrogram had peaks in sound intensity but the peaks did not occur in consistent diel patterns (day vs night). Conversely, below 80Hz all of the TOBs had constant, high sound intensities (approximately 145dB). Due to the high level of similarity among all of the spectrograms, it was determined that no seasonal influences were observed in the Quadrant 53 deployments.

Finally, given the lack of diel sound patterns in the Quadrant 17 February deployments and all deployments in Quadrant 53, the diel patterns observed in the Quadrant 17 August deployment were likely an anomaly rather than a consistent pattern within the SJR soundscape. Overall, no major differences in the sound level patterns were observed within or between the deployment locations.

Prevalence of anthropogenic sound

Anthropogenic sound was prevalent in all areas of the river (Figure 5a-b). Only one quadrant (46) did not have an anthropogenic sound source present in any recordings; however, this was most likely due to the small sample size (1 recording) for that quadrant. All other quadrants had anthropogenic sound present in them. A total of 688 recordings were collected

($\bar{x}$ ± SE = 9.69 ± 0.33 recordings per quadrant); of these, 81% contained anthropogenic sound. Additionally, anthropogenic sound was present for 71% of the recorded time ($\bar{x}$ ± SE = 16.74 ± 0.85 minutes of anthropogenic sound per quadrant), and the source of the sound was usually vessel engines. Locations in the SJR where anthropogenic sound was present in every recording included two of the three JaxPort shipping terminals (Quadrants 11, 13, 17, 37, 40-42) and the Mayport Inlet (Quadrant 69) near the Navy base (Figure 5a). In Quadrants 13 and 17, all recording sessions also had anthropogenic sound present the entire time (Figure 5b). No significant correlation was found between median sound levels at the 3.15kHz TOB and the prevalence of anthropogenic sound per quadrant (number of recordings: r = 0.179, N = 71, p = 0.136; amount of recorded time: r = 0.161, N = 71, p = 0.179).

Impact of anthropogenic sound on dolphin habitat use

Median sound levels at the 3.15kHz TOB were consistently high with little variation among the different strata (Table 3). However, variation was observed in the habitat use patterns of the dolphins. The dolphins utilized certain strata more than others and these habitat use preferences differed depending on their behavioral state (Table 3 and see chapter 1). No correlation was found between median sound levels and the proportion of foraging, socializing, and resting group sightings collected in the strata (foraging: r = 0.563, N = 10, p = 0.09; socializing: r = 0.084, N = 10, p = 0.817; resting: r = -0.021, N = 10, p = 0.954).

Two critical habitat areas were identified for dolphins in the SJR; stratum two (foraging year-round and socializing during the warm season) and stratum four (socializing and resting year-round; Figure 6 and see Chapter 1). These critical areas both had quadrant median sound levels in the 3.15kHz TOB that were at or within one standard deviation (SD = 2.4dB) of the overall median sound level (136.38dB re 1 µPa) for the SJR. Therefore, sound levels were

consistent across the critical areas and the dolphins did not appear to modify their habitat use in relation to sound levels.

Discussion

SJR Soundscape Ecology

This study was the first to examine the soundscape of the St. Johns River, and one of the few to examine the soundscape of an estuarine system (Lillis et al., 2014; Pine et al., 2015; Marley et al., 2016). Lillis et al. (2014) and Pine et al. (2015) compared the natural soundscapes between two different estuarine habitat types (oyster reef vs soft-sediment in Pamlico Sound, North Carolina and subtidal mudflat vs seagrass beds in Kaipara Harbor, New Zealand, respectively). Marley et al. (2016) examined the soundscape at a single site in Western Australia (the Narrows in the Swan-Canning river system). Estuarine soundscapes are relatively understudied compared to other marine or terrestrial soundscapes, thus this study is a valuable addition to the growing field of soundscape ecology.

Similar biotic sound sources were identified in the three previous estuarine soundscape studies and the present study: snapping shrimp, soniferous fish, and bottlenose dolphins. Snapping shrimp were major contributors to the soundscape in all studies and the dominant source of biotic sound in the SJR. In the SJR, snapping shrimp were recorded in every quadrant throughout the study period (June 2016-May 2017). The pervasive and intense nature of snapping shrimp sounds often made it difficult to identify other biotic sound sources, both in the field and in the lab (via auditory and visual examination). Additionally, snapping shrimp were typically louder in the shallow ($\leq$ 3m) areas compared to the deep ($\geq$ 12m) areas. Heithaus and Dill (2002) observed a similar pattern in snapping shrimp sound intensity in Shark Bay, Australia. The exact difference in sound intensity was not measured in this study because it

would have been difficult to isolate the snapping shrimp sounds to perform these measurements with the software available. Soniferous fish vocalizations were also important components of the estuarine soundscape in all studies. Multiple species of soniferous fish live in the SJR, and the two species that were identified based on their vocalizations were oyster toadfish and red drum. Individuals of both species were frequently recorded vocalizing alone or as part of a chorus, and they were recorded throughout the river. Interestingly, oyster toadfish were not recorded throughout the study period, instead they were recorded from June-September 2016 and again from January-May 2017. In contrast to oyster toadfish, red drum were recorded throughout the year (June 2016-May 2017). Further research is necessary to determine why the oyster toadfish only vocalized for part of the year while red drum vocalized throughout the year. Finally, bottlenose dolphin (Narrows: *Tursiops aduncus*; SJR: *Tursiops truncatus*) vocalizations were important components of the estuarine soundscapes in the Marley et al. (2016) study and the present study. Dolphin vocalizations were not a focus in the Lillis et al. (2014) and Pine et al. (2015) studies. Multiple different types of dolphin vocalizations were recorded in the SJR including whistles, buzzes, squeaks, pops, burst-pulses, and clicks. Foraging dolphin groups were infrequently observed at the surface during recording sessions, but it was possible infer that they were present based on the observation of echolocation clicks on the spectrograms. In contrast, socializing groups were easily spotted at the surface if they were present in the quadrant and all vocalization types were recorded from groups engaged in social behavior. No resting groups were observed during a recording session, and traveling groups often did not vocalize while they were passing the research vessel. Interestingly, this trend was not followed during a single recording session in May 2017 when a mother-calf group with three newborns traveled

past the research vessel. When this mother-calf group passed, they were being very vocal and numerous different vocalizations were recorded.

While similar biotic sound sources were identified in all of the estuarine soundscape studies, differences in spatial and temporal patterns were observed in all but the present study. Lillis et al. (2014) examined spatial variation in natural soundscape patterns and found significant differences between the oyster reef and soft-bottom habitats. Specifically, the reef habitats had higher sound intensities in the high frequency range, but the habitat types did not vary in sound intensity in the low frequency range. Lillis et al. (2014) did not examine or test for temporal soundscape patterns. Pine et al. (2015) also compared natural soundscape patterns between two habitat types as well as temporal variations in the soundscapes. They found both seasonal and diurnal variability within and between the two study sites in broadband sound levels, octave band sound levels, and diurnal sound levels. Marley et al. (2016) examined the soundscape characteristics at a single site and found clear temporal variation in sound levels that paralleled human activity patterns. Sound levels were highest when human activity levels were also high, and sound levels varied between weekends vs. weekdays. In contrast to these three studies, it was determined that the soundscape of the SJR had low variation in sound levels with no distinct, repeated patterns based on location or time of day. Median sound levels were consistent across all quadrants and no diel soundscape patterns were identified in the majority of the autonomous recordings. Additionally, this study was the first to examine soundscape patterns across numerous sites (71 quadrants). The lack of clear spatial and temporal acoustic patterns in the SJR compared to the other study sites was most likely due to the prevalence of anthropogenic sound identified in this study.

The previous soundscape studies and the current study differ in the occurrence of anthropogenic sound (anthrophony). Lillis et al. (2014) and Pine et al. (2015) both designed their studies to specifically exclude anthropogenic sound to examine natural soundscape patterns and differences between the habitat types. However, Marley et al. (2016) examined the soundscape of an urban estuary and as such recorded numerous sources of anthrophony including a ferry, recreational boating traffic, and vehicle traffic on bridges. In the SJR, the same sources of anthropogenic sound were recorded as well as helicopters, commercial shipping traffic, activity at the shipping terminals (e.g., construction and loading/unloading of cargo ships), military vessels (U.S. Navy and U.S. Coast Guard), and dredging. Thus, the SJR had more sources of anthropogenic sound than were recorded in the Swan-Canning Narrows. Anthrophony was also present in a greater number of recordings in the present study compared to what was observed by Marley et al. (2016). Overall, the three previous estuarine soundscape studies had similar sources of biotic sound, identified temporal variations in sound levels, and had lower levels of anthropogenic activity relative to the SJR. The major differences found between the previous studies and the present study were likely due to the high levels and diversity of anthropogenic sound in the SJR.

The constant presence of anthropogenic activity in the SJR was also most likely a key contributor to the low levels of variation found in the median sound levels at the 3.15kHz 1/3rd octave band (TOB; Heenehan, 2016). Median sound levels at the 3.15kHz TOB were measured because this band was influenced by both biotic and anthropogenic sound, and was well within the hearing range of bottlenose dolphins. Therefore, sound levels in this band were biologically relevant to SJR dolphins. The difference between the highest and lowest quadrant median sound level at the 3.15kHz TOB in the SJR was 10.45dB re 1 µPa, with an overall median sound level

of 136.38 ± 2.42dB re 1 μPa. If median sound levels at a lower TOB band (e.g., 800Hz) were analyzed, the sound levels measured would likely have been higher because anthropogenic sound generally dominates the lower frequency bands (Clark et al., 2009). However, lower frequency bands are also influenced by flow noise as well as the sound of waves hitting the side of the boat. Since these are both recording artifacts that often have high intensity levels, the median sound levels measured at a lower frequency band would have been artificially elevated by flow and wave noise. Thus, it would have been difficult to determine if the sound levels measured at a low frequency band were due to anthropogenic sound or recording artifacts. Median sound levels at a high frequency TOB (e.g., 16kHz) could also have been measured, and they would likely have been lower than the levels at the 3.15kHz band because high frequency bands are mainly influenced by biotic sound sources. The absence of anthropogenic sound, a significant source of high intensity sound, would result in overall lower sound levels. Therefore, it was valuable to measure median sound levels at the 3.15kHz TOB because it was influenced by both biotic and anthropogenic sounds but was minimally influenced by any recording artifacts.

The median sound levels at the 3.15kHz TOB did not vary as greatly as was initially expected, which indicates that the SJR had low levels of acoustic heterogeneity. Like environmental heterogeneity, increased acoustic heterogeneity can be an indicator of the quality or health of the landscape (Pijanowski et al., 2011; Lillis et al., 2014; Marley et al., 2016). Homogenous landscapes occur when there are low levels of species or resource diversity, and homogenous soundscapes follow the same pattern in relation to sound sources. Thus, the low levels of acoustic heterogeneity in the soundscape suggest the SJR ecosystem is threatened and potentially declining. Although the documented 10.45dB difference among quadrants was not statistically significant, every 3dB increase represents a doubling in sound intensity due to the

logarithmic nature of the dB scale (Hildebrand, 2009); therefore, it is highly likely this difference was biologically significant. In the Bay of Fundy, Canada, a 6dB decrease in sound intensity was enough to cause the stress hormone levels in there North Atlantic right whales to decrease (Rolland et al., 2012). Thus, SJR dolphins may experience different levels of physiological stress depending on the sound levels present in their immediate area.

With respect to other coastal locations, the SJR overall median sound level at the 3.15kHz TOB (136.38 ± 2.42dB re 1 μPa) was much higher. The Intracoastal waterway in Wilmington, North Carolina, had a mean received sound level of 116 dB_{rms} re 1 μPa (measured across all frequency bands), and the maximum received level was 127 dB_{rms} re 1 μPa (Haviland-Howell et al., 2007). The dolphins in Wilmington, NC, were deemed at risk of chronic noise exposure due to the daily high mean received sound levels. However, the median sound level in Wilmington at the 3-4kHz band was approximately 83dB_{rms} re 1 μPa, which was considerably lower than those at the 3.15kHz TOB recorded in the SJR. In comparison to four Hawaiian bays (Makako, Kealakekua, Honaunau, and Kauhako) also impacted by anthropogenic activity (recreational and U.S. Navy), the SJR median sound levels at the 3.15kHz TOB were approximately 39-40dB higher than the levels recorded in Hawaii (96-97dB re 1 μPa; Heenehan, 2016). Thus, SJR bottlenose dolphins are likely at a greater risk of chronic noise exposure due to the higher median sound levels in conjunction with increased anthropogenic activity.

The absence of diel soundscape patterns was also likely due to the high levels of anthropogenic activity present in the SJR. Sound levels remained consistent throughout the day and night in all the autonomous recordings, except for the August 2016 deployment in quadrant 17. Also, all of the autonomous recordings contained a peak in sound intensity in the TOBs below 80Hz. Anthropogenic sound is typically the most intense in the lower frequency bands

(Tyack, 2008; Clark et al., 2009); thus, this peak was most likely due to anthropogenic sound. Additionally, no major differences were observed among the deployments based on location (quadrant), time of day, or time of year. Therefore, it was determined that the SJR soundscape did not exhibit any diel patterns. Two potential sources of bias may have contributed to this absence of diel soundscape patterns. First, autonomous recordings were only collected in two locations. Ideally, more autonomous deployments would have been conducted in quadrants spread throughout the river to provide a more accurate representation of the SJR soundscape. However, this was not possible in the current study due to the loss of the μRUDAR-XL system, equipment malfunction, and time restrictions. The second source of bias could be the large difference in recording time between Quadrant 17 and Quadrant 53. Quadrant 17 had fewer hours recorded due to memory card failure and bad batteries. Future studies should attempt to obtain autonomous recordings in more locations throughout the SJR and for the same amount of time to correct these possible sources of bias. Nevertheless, the low levels of variation in the median sound levels measured from the boat-based recordings and the lack of distinct diel sound patterns in the autonomous recordings indicated that the soundscape of the SJR was heavily influenced by high levels of anthropogenic activity (Merchant et al., 2012; Pine et al., 2016).

Overall, anthropogenic activity was a constant source of acoustic disturbance in the SJR. Most of the boat-based recordings (81% of recordings and 71% of recorded time) collected over a 12-month period contained anthropogenic sound. Anthrophony was present in all the recordings collected in 15 quadrants, and in two of these quadrants anthropogenic sound was heard 100% of the time. These quadrants were mostly located at major transit points in the river such as the JaxPort shipping terminals (strata four, six, and nine) and the Mayport Inlet (stratum one), thus it was expected that high levels of anthropogenic sound would be observed in these

locations. The prevalence of anthropogenic sound was first analyzed by determining the number of recordings that contained anthropogenic sound using a presence/absence approach. This approach was used because it was often difficult to distinguish among different types of anthropogenic sound. For example, jet skis and recreational fishing boats have similar sound signatures, and boats produce differing noise levels depending on their size and speed (Hildebrand, 2009; Jensen et al., 2009; Houghton et al., 2015; Pine et al., 2016). Additionally, it was not always possible to determine how many vessels were producing sound during a recording session. Recreational fishing boats frequently clumped together, and some would have their engines on while others would not. Cargo ships also often blocked recreational boats or tug boats from view while they were passing the research vessel. Thus, it was sometimes difficult to determine the number and type of vessels present. Lastly, the presence/absence of anthropogenic sound was a better metric for determining the prevalence of anthropogenic sound than counting the number/type of vessels because it was a more conservative assessment of the incidence of anthropogenic sound (Marley et al., 2016). The proportion of time anthropogenic sound was present in each quadrant was also analyzed to provide a finer-scale assessment of the prevalence of anthropogenic sound in the SJR. Numerous different types of anthrophony were recorded in this study, some with very short durations and others with long durations, thus determining the amount of time anthropogenic sound was present provided an indication of the extent to which the soundscape was influenced by human sound. The general patterns observed from both prevalence analyses were extremely similar, most likely because vessel engine noise was the dominant and most common anthropogenic sound source identified. If a vessel was heard during a recording, it was frequently heard for most, if not all, of the recording. Additionally, the sounds produced by vessel engines traveled large distances in the SJR and it was normal to begin

hearing engine noise before the vessel entered the quadrant (sometimes >1600m away) and frequently before it was even visible. Finally, no correlation was found between median sound levels and the prevalence of anthropogenic sound per quadrant; however, this was most likely due to the low levels of variation in both the median sound levels and the prevalence of anthropogenic sound. Overall, anthropogenic activity, especially vessel traffic, was a pervasive source of acoustic disturbance in the SJR.

Activity at the international shipping terminals was another source of acoustic disturbance in the SJR. In addition to recording the sounds produced by cargo ship engines while they were entering and leaving the SJR, sounds produced by construction at the ports and the loading/unloading of cargo ships were recorded on numerous occasions throughout this study. Automatic identification system (AIS) ship tracking also showed that cargo ships were coming into and leaving the Jacksonville ports throughout the day and night (Marine Traffic, 2017). An example of the high levels of human activity at the terminals even during the night was observed in the August 2016 autonomous recorder deployment in Quadrant 17 near the third JaxPort shipping terminal (Figure 3a). A peak in sound intensity was observed in this recording during the middle of the night (approximately 2100-0400) in the 315-630Hz TOBs. Although both red drum and dolphin vocalizations were identified in the recording, this peak was most likely due to anthropogenic activity because it occurred below the frequency range of typical fish choruses (1-2kHz; Erbe et al., 2015b) and dolphin vocalizations (Herzing, 1996). It should be noted that a distinct peak in the 315-630Hz TOBs was not found in the other autonomous recorder deployments, so this result may be an exception rather than a general pattern. However, high sound intensities were observed in the same TOBs (just not in a distinct peak) in all the other autonomous recordings. Therefore, anthropogenic activity may not have been as continuous

during the August 2016 deployment compared to the other deployments. Further research is necessary to determine if activity at the international shipping terminals is truly continuous or if temporal patterns in activity are present.

Impacts of the SJR Soundscape on Dolphin Habitat Use

The final aim of this study was to determine the potential impacts of anthropogenic sound on SJR dolphin habitat use patterns. The median sound levels among the different strata did not vary (only a 2dB range), and no correlation was found between sound levels and the proportion of sightings for each behavioral state (foraging, socializing, and resting) observed in each stratum. However, the dolphins did utilize some strata more than others depending on their behavioral state (see chapter 1). For example, stratum four was preferentially utilized by socializing dolphins year-round. Furthermore, the two year-round critical habitat areas for foraging, socializing, and resting dolphin groups (see Chapter 1) were in areas with both high sound levels and high levels of anthropogenic disturbance. The median sound levels measured in each quadrant were higher and had less variation than initially predicted. Therefore, it is likely SJR dolphins were unable to modify their habitat use in response to sound levels because there were no relatively quiet areas. The continued utilization of the SJR despite high baseline sound levels could indicate that dolphins were accustomed to the chronically high sound levels (Merchant et al., 2014), had learned to behaviorally regulate the negative effects of sound disturbance (Wright et al., 2007), or were unable to move to a different habitat (possibly due to high levels of competition or lack of resources). Even if the dolphins were acclimated to the sound levels, sound disturbance can still be a chronic source of stress (Wright et al., 2007; Tyack, 2008). Extended exposure to high levels of noise and the resulting chronic stress response may lead to numerous physiological issues including sickness-like symptoms, suppression of

reproduction, and accelerated aging (Wright et al., 2007). Thus, the consistently high median sound levels in the SJR could cause long term health issues for the SJR dolphins.

Chronic exposure to anthropogenic sound has been associated with increased levels of stress hormones (Weilgart, 2007; Wright et al., 2007; Rolland et al., 2012), can cause changes in hearing sensitivity (Finneran et al., 2000; Finneran et al., 2005; Mooney et al., 2009), and can result in reduced communication space (Lusseau, 2004; Jensen et al., 2009; Parks et al., 2011; Erbe et al., 2015a; Pine et al., 2016). Elevated glucocorticoid levels were linked to chronic exposure to shipping traffic noise in right whales (Rolland et al., 2012), and stress hormone levels (norepinephrine, epinephrine, and dopamine) were significantly higher in a captive beluga whale (*Delphinapterus leucas*) one hour after exposure to high intensity sound (seismic water gun) compared to pre-sound exposure (Romano et al., 2004). SJR dolphins may experience high stress levels when they are in the quadrants with the highest median sound levels, but have lower stress levels when they are in the (relatively) quieter quadrants. However, even the relatively quiet quadrants in the SJR had elevated sound levels compared to other study sites. Alternatively, the dolphins may experience chronically elevated stress levels due to their frequent movements throughout the SJR and high baseline sound levels. Dolphins can efficiently travel large distances (Williams et al., 1992), so their frequent movements into areas with high sound intensity may also cause their stress levels to remain high. It is most likely that the dolphins' stress levels remain chronically high because it likely takes more time for stress levels to decrease than it does for the dolphins to travel between different regions in the river (e.g., stress levels in a beluga whale were still significantly elevated one hour post-sound exposure; Romano et al., 2004). Chronic exposure to intense anthropogenic sound can also cause changes in hearing sensitivity. Finneran et al. (2005) found that exposure to 3kHz pure-tones for 2-8 seconds with

sound exposure levels (SEL) ≥ 195dB re 1μPa^{2}s was sufficient to cause significant temporary threshold shifts (TTS) in two captive male bottlenose dolphins. Mooney et al. (2009) also tested for TTS in a single, male bottlenose dolphin after varying exposure to tones produced at five different frequencies. Like Finneran et al. (2005), Mooney et al. (2009) observed TTS after exposure to a 5.6kHz tone for 7.5, 15, and 30 minutes. The SEL for these durations was 192.5dB re 1μPa^{2}s, which correlated with sound pressure levels of 166dB re 1 μPa (7.5 min), 163dB re 1 μPa (15 min), and 160dB re 1 μPa (30 min). Therefore, exposure (ranging from 2 seconds to 30 minutes) to intense anthropogenic sounds produced at similar frequencies to that tested in the current study were sufficient to cause TTS in captive dolphins. Repeated and prolonged exposure to these intense sounds could ultimately result in permanent threshold shifts (PTS; Mooney et al., 2009). Additionally, even short-term TTS could result in injury or death in wild animals due to the missed detection of a hazard (e.g., fast moving boat) or a predator (e.g., shark; Weilgart, 2007). Reduced communication space can also have numerous negative impacts on animals including reduced group cohesion or identification, masking of mating calls, and restricted contact between mothers and their infants (Erbe et al., 2015a). For example, vocalizations are essential to maintain contact between dolphin mother-calf pairs, especially during temporary separations (Smolker et al., 1993; Connor et al., 2000; Quintana-Rizzo et al., 2006). Thus, communication masking due to high sound levels could potentially impact the ability of a female dolphin to reunite with her calf (Smolker et al., 1993; King et al., 2016). The negative impacts of communication masking are likely exacerbated for SJR dolphins due to their reliance on sound to collect information about their environment. The SJR is an extremely turbid system and at the surface visibility is often limited to about 0.5-1m. Thus, the effective range of visual cues is very small and dolphins would have to rely more heavily on auditory cues to navigate their physical

and social environment. Although communication masking can negatively influence healthy individuals, it will have a greater impact on animals that are already compromised in some way (Wright et al., 2007; Tyack, 2008). An animal that is already experiencing stress (e.g., from illness, injury, or lack of rest) is more likely to interpret an ambiguous signal negatively, and so may miss foraging opportunities or waste energy avoiding potential predators (Nowacek et al., 2001; Wright et al., 2007). The high sound levels and chronic exposure to anthropogenic sound likely cause negative physiological consequences and reduced communication space for SJR dolphins (Wright et al., 2007; Mooney et al., 2009; Pine et al., 2016).

Anthropogenic sound can also impact the foraging behavior and efficiency of dolphins (Allen and Read, 2000; Pirotta et al., 2015; Pine et al., 2016). Many of the prey species bottlenose dolphins eat are soniferous fish, and some dolphins will use passive listening techniques to initially locate their prey (Gannon et al., 2005). Elevated sound levels could potentially mask the soniferous fish vocalizations and reduce the effective range of the dolphin's echolocation (mask echolocation signals), thereby reducing the dolphin's overall foraging efficiency (Popper, 2003; Jensen et al., 2009; Pirotta et al., 2015). More time spent foraging will result in less time spent engaged in other behaviors (such as socializing and resting), resulting in a change in the overall activity budget of the individual (Lusseau, 2004). Long-term changes to activity budgets can result in significant, negative impacts to the population (Lusseau and Higham, 2004; Tyack, 2008; Bas et al., 2014). Eventually, the dolphins may reach a threshold where the costs of remaining in a certain habitat patch outweigh the benefits, causing them to move to a different habitat (Lusseau, 2003; Bejder et al., 2006; Pirotta et al., 2013). Anthropogenic sound may also indirectly affect the dolphins by influencing the behavior of their prey (Gordon et al., 2003; Popper, 2003). Exposure to anthropogenic sound could cause fish to

leave an area or freeze/remain in the habitat (Popper, 2003). If the fish leave the habitat, the quality of the habitat for the dolphins will decrease and they will likely also leave to follow the fish. Alternatively, if the fish were startled into remaining in the habitat, then this could also cause the dolphins to stay and continue being exposed to the sound (Gordon et al., 2003). Therefore, anthropogenic sound could both directly and indirectly affect the foraging behavior and efficiency of dolphins.

Furthermore, the consistently high median sound levels and the lack of diel patterns indicate that dolphins within the SJR did not have a refuge, physically or temporally, from anthropogenic activity. It was initially hypothesized that Mill Cove (stratum five) would act as a sound refuge for the dolphins because it would have little to no anthropogenic activity due to its shallow, restrictive nature (Nowacek et al., 2001). However, anthropogenic activity was recorded in all but one quadrant within Mill Cove. Recreational boats frequently traveled through Mill Cove, and even boats moving within the main channel of the river were still clearly audible, often at a distance > 1600m. Consequently, Mill Cove was not a refuge from anthropogenic sound for the SJR dolphins, despite being more restrictive to vessel traffic than the main channel. Moreover, very few dolphin resting groups were observed in the SJR (see Chapter 1), and this lack of resting behavior could be due to the absence of a sound refuge. Lack of rest can have serious physiological effects (Siegel, 2008), thus the absence of quality resting habitat could be another source of stress for the dolphins. Ultimately, lack of rest can decrease the health of an individual (making them more susceptible to illness) and/or decrease vigilance (making them more vulnerable to predators; Siegel, 2008).

Future anthropogenic impacts to SJR soundscape

Anthropogenic activity has already begun to increase within the past year due to the Jacksonville Port expansion project. This project entails modifying a training wall to alleviate strong cross-currents, underwater blasting, and dredging the main channel from a depth of 12.5m to a maximum depth of 15.2m (Harbor Deepening, 2017). The training wall portion of the project has already been completed; however, the underwater blasting and dredging operations will begin in the near future. The underwater blasting will be used to loosen bedrock during dredging operations and to create turn-around points for the large cargo ships. However, the explosions involved will likely negatively impact the SJR dolphins (Gordon et al., 2003; Nowacek et al., 2007; Buckstaff et al., 2013). Buckstaff et al. (2013) found that dolphins in Sarasota, Florida, avoided the area around a bridge while it was under construction (which included blasting). Additionally, dolphins in a captive setting exhibited behavioral responses (avoided testing station) after exposure to simulated underwater explosions (Finneran et al., 2000). The intense sounds produced by the underwater blasting could also exceed SEL of 192dB re 1$\mu Pa^2 s$ and cause TTS or even PTS (Finneran et al., 2005; Mooney et al., 2009). Thus, the underwater blasting in the SJR could cause the dolphins to exhibit short-term avoidance responses and result in auditory damage. The dredging required to deepen the main channel will be another significant source of anthropogenic activity and sound (Pirotta et al., 2013). Dredging was recorded on numerous occasions during this study and it produced a variety of high-intensity sounds. However, the maintenance dredging activity that was recorded occurred over a much shorter time period (days) compared to the dredging that will be necessary for the Port expansion project (years). The dredging of the main channel could potentially cause the dolphins to abandon certain regions of the SJR, as has occurred elsewhere during similar port expansion

projects (Tyack, 2008; Pirotta et al., 2013). For example, dredging operations over the span of five-weeks caused the bottlenose dolphins in Aberdeen harbor, Scotland, to temporarily abandon an important foraging habitat (Pirotta et al., 2013). These dolphins were already habituated to high levels of vessel traffic and routine maintenance dredging (similar to the SJR dolphins); however, the port expansion dredging operations appear to have exceeded their tolerance levels causing them to leave the harbor. Additionally, Aberdeen harbor was utilized primarily as a foraging habitat. In comparison, the SJR is utilized by the dolphins during all behavioral states and the dredging for the SJR Port expansion project is projected to take five years with yearly maintenance afterwards (U.S. Army Corp, 2014; Harbor Deepening, 2017). Consequently, it is possible that the dolphins may abandon parts of the river for the entire length of the dredging project. For example, gray whales (*Eschrichtius robustus*) in Baja California, Mexico, abandoned one of their primary breeding lagoons for the ten years that dredging was taking place in the lagoon (Bryant et al., 1984). Finally, deepening the main channel will allow the New Panamax class vessels to dock at the JaxPort terminals, making Jacksonville the first U.S. east coast port of call capable of accommodating these ships (Harbor Deepening, 2017). Larger ships produce more sound and carry more cargo (Redfern et al., 2017), which increases the amount of time it takes to process, unload, and reload the shipping containers. Altogether, the underwater blasting (short-term), dredging operations (long-term), and the addition of the New Panamax vessels to the current SJR vessel traffic levels (long-term) will cause anthropogenic activity to have an increasing impact on the soundscape (Jensen et al., 2009; Redfern et al., 2017).

Conclusions

It was determined that the soundscape of the SJR was heavily impacted by anthropogenic activity. Extremely high sound levels were measured throughout the study area, and these levels

were most likely driven by pervasive anthropogenic activity. Anthropogenic sound contributed to the limited variability found in the soundscape of the river and the lack of clear diel patterns within it. Anthropogenic sound was observed in most recordings collected and in most quadrants of the river. The SJR median sound levels were significantly higher than the levels obtained at other estuarine and coastal sites and are a cause for concern. Exposure to chronically high sound levels and constant anthropogenic disturbance can ultimately affect the behavior and health of these dolphins (Nowacek et al., 2001; Wright et al., 2007; Weilgart, 2007). Chronically high sound levels can degrade the quality of the habitat by increasing the risk of signal masking, decreasing foraging efficiency (Tyack, 2008; Merchant et al., 2014; Pirotta et al., 2015), and may lead to elevated levels of physiological stress and possibly cause auditory damage (Finneran et al., 2005; Wright et al., 2007; Mooney et al., 2009; Rolland et al., 2012) for local bottlenose dolphins. Understanding the impact of anthropogenic sound on the soundscape of the SJR is important for the management and protection of the dolphins in the river (Bejder et al., 2006; Merchant et al., 2014; Redfern et al., 2017). The development of new management regulations is recommended to better protect the SJR dolphins from chronic anthropogenic activity and ensure the health and survival of this population.

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(a) (b)

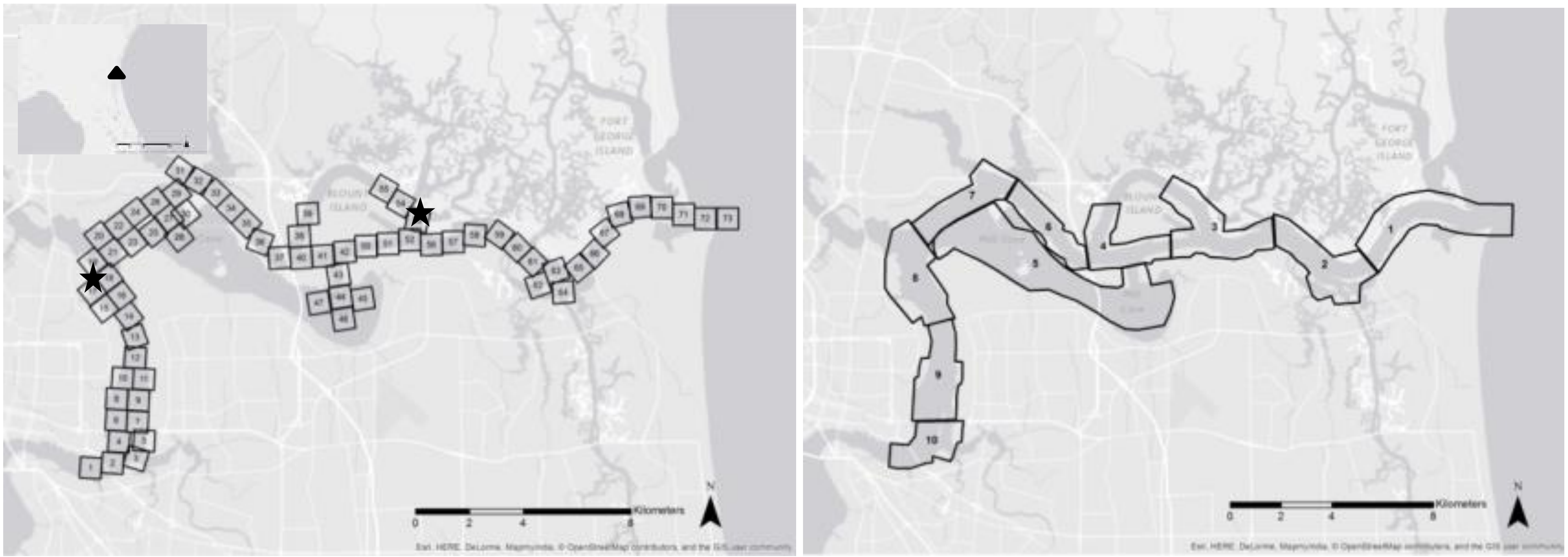


Figure 1: Study area within the St. Johns, River, Jacksonville, FL (triangle). The (a) quadrants (800m x 800m) and (b) strata were used to distinguish different areas of the SJR. The strata were identified based on the predominant level and type of anthropogenic activity present. Quadrant 1 (within stratum 10) was in the downtown Jacksonville area approximately 40km upriver from the Mayport Inlet and Quadrant 73 (within stratum 1) was at the mouth of the river. The deployment locations of the autonomous recorder are represented by the stars on the map (a).

Table 1. Predominant types of anthropogenic activity present within each stratum, and its approximate size and distance from the river mouth.

Stratum	**Predominant type of anthropogenic activity**	**Approx. Size**	**Distance from Inlet**
One	Multiple public and private marinas/docks and U.S. Navy and Coast Guard bases	6.4km	At Inlet
Two	Location where Intracoastal Waterways cross the SJR (Mile Point), heavy vessel traffic	5.6km	~8km
Three	U.S.M.C. shipping depot and a residential area with private docks	6.4km	~12km
Four	First JaxPort shipping terminal and major bridge (Dames Point) at western end	4.8km	~16km
Five	Large, shallow cove (Mill Cove) primarily utilized by recreational and crab fishermen, and crossed by a major bridge (Dames Point). Not included in dolphin survey transect	>10km	~16-24km
Six	Carnival cruise ship terminal, second JaxPort shipping terminal, and major bridge (Dames Point) at eastern end	4km	~20km
Seven	Three oil/fueling docks, heavy recreational and commercial shipping traffic	4.8km	~24km
Eight	Residential area- mostly private docks and recreational fishing	6.4km	~27km
Nine	Third JaxPort shipping terminal	6.4km	~32km
Ten	Two major bridges (Hart and Mathews) and a dry dock facility	4km	~40km

Table 2. Ethogram of behavioral states (adapted from Mann and Watson-Capps, 2005). Activity categories are mutually exclusive.

Activity	**Definition**
Travel	Steady, moderate, or fast (>3 km/h) directional movement.
Forage	Fast swimming, rapid direction changes, fish catches, and fish fleeing.
Social	Rubbing, petting (flipper or flukes actively moving on a body part of another), displays, chasing, mounting, poking, contact swimming, and other forms of active contact
Rest	Slow (< 3 km/h) nondirectional movement, frequent hanging at the surface.

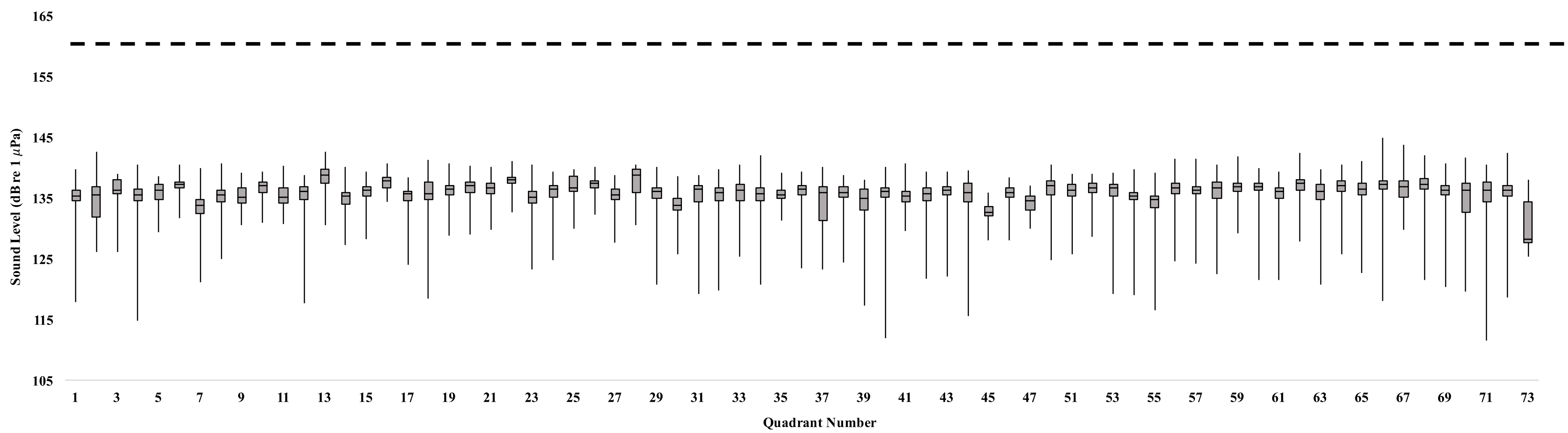
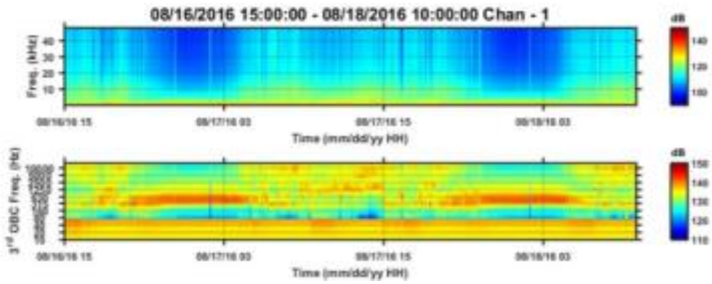


Figure 2: Sound levels (dB re 1µPa) at the 3.15kHz 1/3rd octave band. Box plots were generated from the 1st quartile, median, and 3rd quartile sound levels in each quadrant. Quadrant 73 was located at the mouth of the river and Quadrant 1 was located approximately 40km upriver. Highest median sound levels were recorded at quadrant 13 and the lowest levels at quadrants 73. The dashed line at 160dB re 1µPa indicates the threshold at which a bottlenose dolphin exhibited temporary threshold shifts after exposure to a 5.6kHz tone for 30 minutes (Mooney et al., 2009).

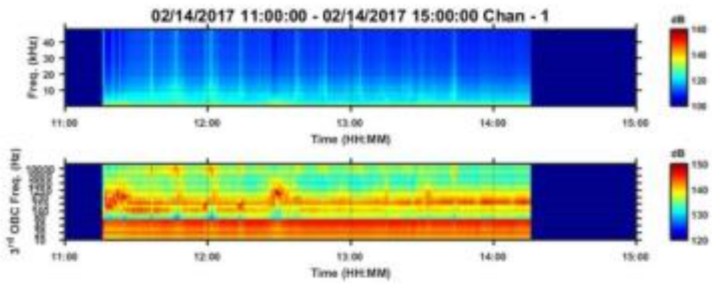
Table 3: Comparison between the median sound levels at the 3.15kHz 1/3rd octave band, the total number of sightings, and the proportion of sightings for each behavioral state by stratum. Stratum one was located at the Mayport Inlet and stratum ten was located approximately 40km upriver in downtown Jacksonville. Stratum five was not included on the survey transect so any sightings in that stratum were collected opportunistically.

Stratum	**Median sound level (re 1μPa)**	**Total number of sightings**	**Proportion of foraging sightings**	**Proportion of socializing sightings**	**Proportion of traveling sightings**	**Proportion of resting sightings**
One	136.53 dB	297	0.15	0.11	0.25	0.13
Two	136.80 dB	244	0.17	0.15	0.17	0.18
Three	136.30 dB	160	0.11	0.08	0.12	0.09
Four	135.92 dB	177	0.11	0.25	0.10	0.16
Five	135.88 dB	33	0.005	0.07	0.02	0.09
Six	136 dB	124	0.07	0.05	0.09	0.13
Seven	137.03 dB	151	0.13	0.09	0.09	0.04
Eight	136.44 dB	127	0.10	0.07	0.08	0.11
Nine	136.69 dB	83	0.07	0.09	0.04	0.05
Ten	135.82 dB	85	0.10	0.04	0.04	0.02

(a)



(b)



(c)

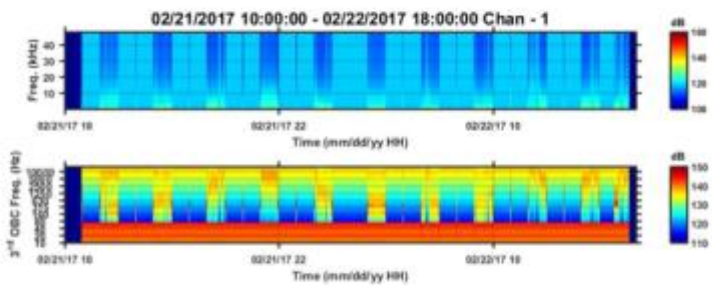
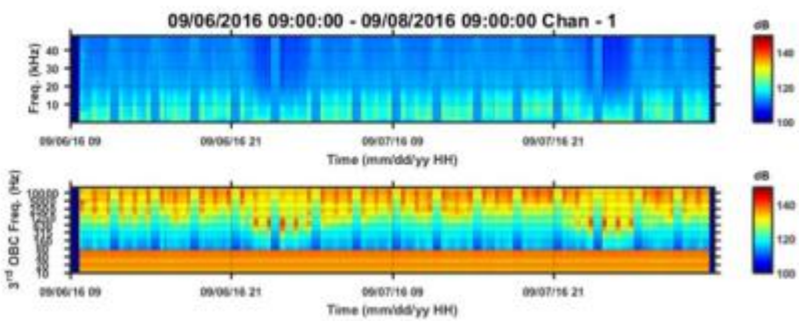


Figure 3a-c: Spectrogram images generated in MATLAB for the autonomous recorder deployments in Quadrant 17. The y-axis denotes frequency (kHz for top images and Hz for bottom images) and the x-axis denotes time for all spectrograms. The dB color scale to the right of each image represent the sound intensities present in the spectrograms. High intensity (loud) sounds are represented by the hot colors. The solid dark blue regions in (b) and (c) were due to the absence of sound. The top spectrograms in (a)-(c) represent the intensity of sound across all frequencies recorded while the bottom spectrograms represent the mean sound intensity for the central frequency of each 1/3rd octave band recorded.

(a)



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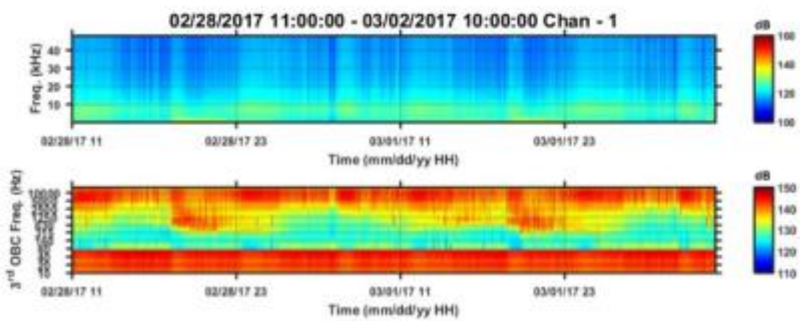

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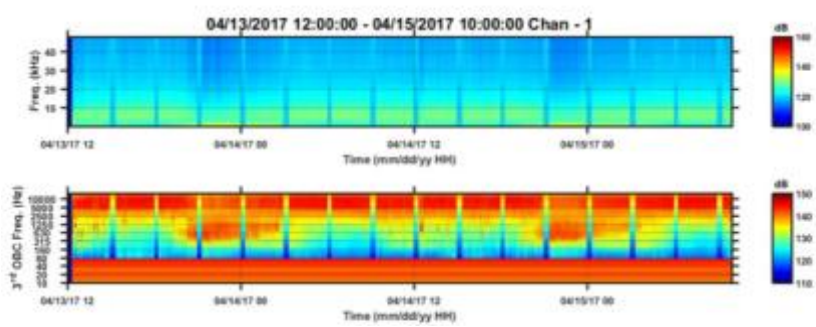

Figure 4a-c: Spectrogram images generated in MATLAB for the autonomous recorder deployments in Quadrant 53. The y-axis denotes frequency (kHz for top images and Hz for bottom images) and the x-axis denotes time for all spectrograms. The dB color scale to the right of each image represent the sound intensities present in the spectrograms. High intensity (loud) sounds are represented by the hot colors. The solid dark blue regions in (a) were due to the absence of sound. The top spectrograms in (a-b) represent the intensity of sound across all frequencies recorded while the bottom spectrograms represent the mean sound intensity for the central frequency of each 1/3rd octave band recorded.

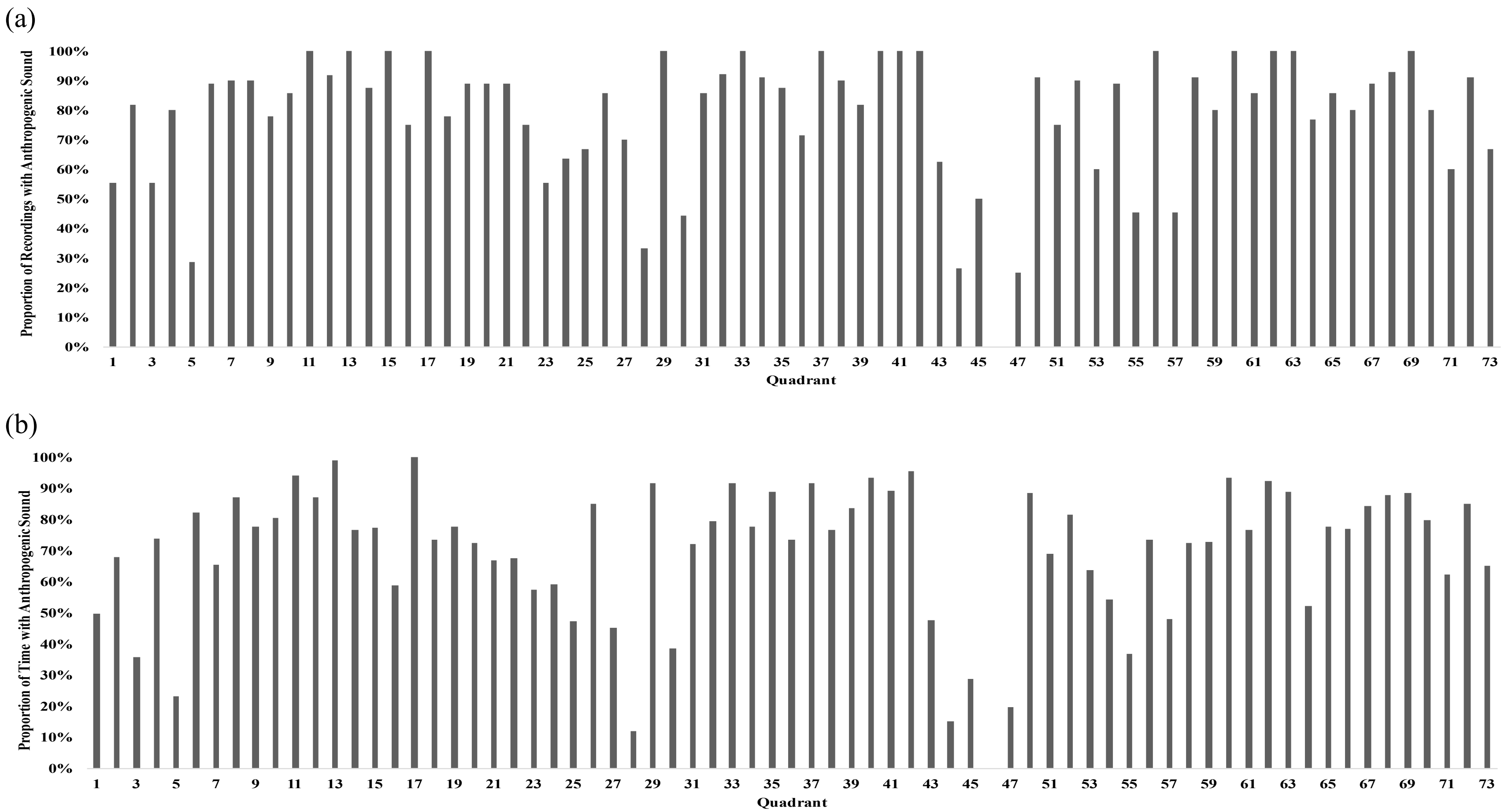

Figure 5a-b: Prevalence of anthropogenic sound in the St. Johns River. The proportion of recordings containing anthropogenic sound (a) and the proportion of time anthropogenic sound was present (b) for each quadrant. Quadrant 1 was located 40km upriver in downtown Jacksonville and quadrant 73 was located at the Mayport Inlet. Across all quadrants combined, anthropogenic sound was found in 81% of the recordings obtained. Of those recordings, anthropogenic sound was present for 71% of the time.

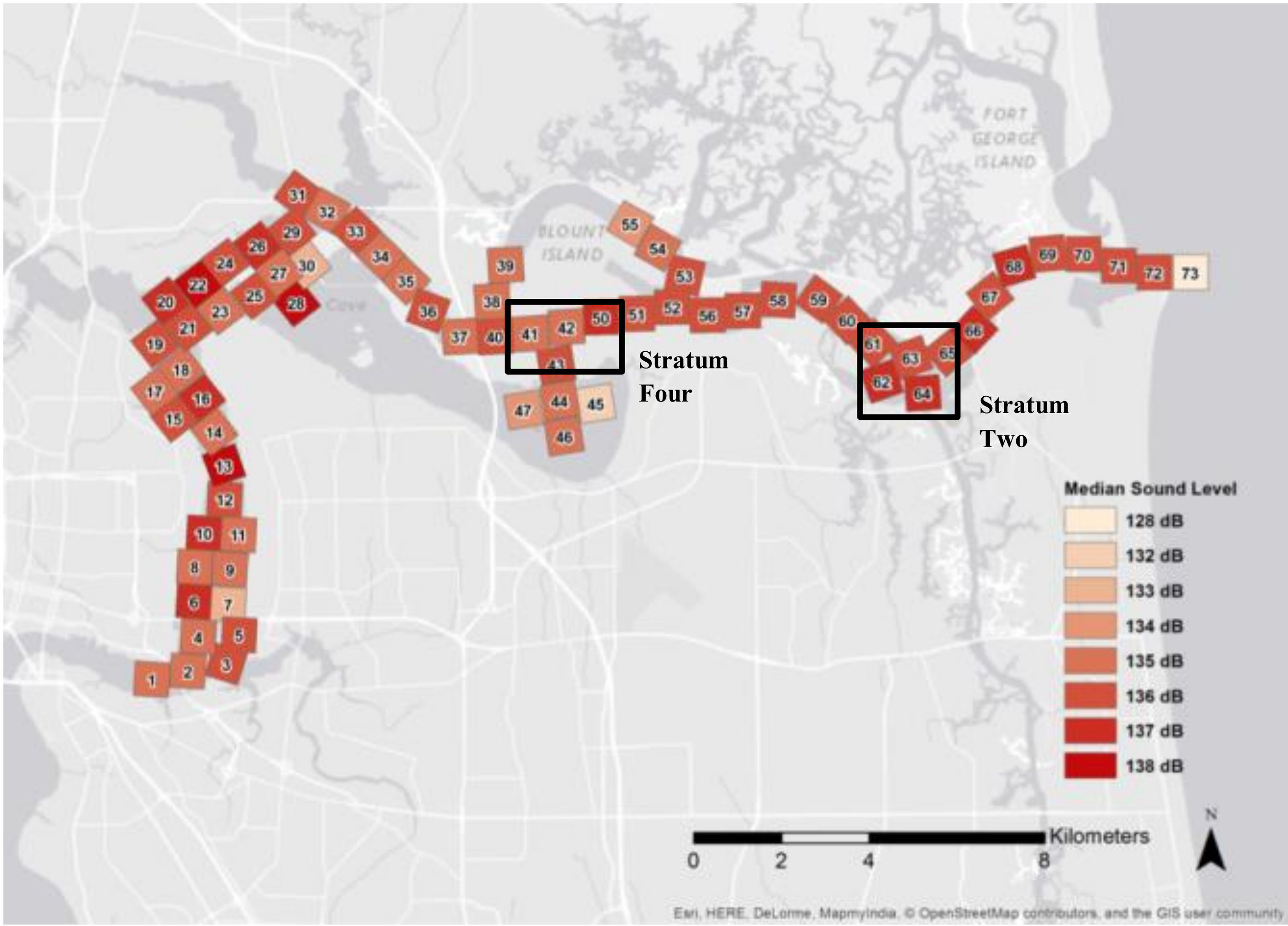

Figure 6: Median sound level (dB re 1 μPa) at the 3.15kHz 1/3rd Octave Band obtained in each quadrant. Intensity of sound indicated by the color of the quadrant; darker colors represent more intense sound. The dolphin critical habitat areas are outlined by the boxes; stratum four is on the left and stratum two on the right

VITA

Carissa graduated with her B.S. in biology from the University of Northern Colorado (UNC) with a minor in chemistry. During her time at UNC, Carissa gained experience in the fields of behavioral ecology and bioacoustics. Since arriving in Jacksonville at the University of North Florida (UNF), Carissa focused her time on dolphin behavioral ecology research and expanding her knowledge about the field of bioacoustics. She has presented portions of her research at numerous domestic and international conferences. Carissa plans to publish her research collected at the University of North Florida and continue her career as a behavioral ecologist and bioacoustician.