# Dolphin Distribution on the West Florida Shelf Using Visual Surveys and Passive Acoustic Monitoring

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### Abstract

A combination of autonomous acoustic recorders and visual surveys was used to determine the seasonal and spatial distribution of dolphins on the West Florida Shelf (WFS), Gulf of Mexico, USA. Acoustic detection rates were calculated using a model that adjusted the theoretical detection range for variations in ambient noise, which was found to be highly variable. Both acoustic and visual techniques indicated dolphins were present on the WFS year-round. Acoustic detections were not identified to species, but bottlenose dolphins (Tursiops truncatus), Atlantic spotted dolphins (Stenella frontalis), and a single group of rough-toothed dolphins (Steno bredanensis) were visually sighted, with the highest sighting rates for bottlenose dolphins. Both dolphin acoustic detection rates and bottlenose dolphin visual sighting rates decreased from inshore to offshore waters, and were especially high in waters adjacent to Tampa Bay, a major estuary. Dolphin acoustic detection rates and bottlenose dolphin visual sighting rates also suggested a habitat shift from deeper to shallower water in summer and/or autumn. Atlantic spotted dolphins were rarely observed in water shallower than 20 m, and appeared to move into shallower and more northerly waters during the summer. Both spatial and temporal variations in dolphin acoustic detection and visual sighting rates can potentially be explained by the habitat preferences and seasonal movements of their prey. This study is the first investigation of dolphin distribution on the WFS using both visual and acoustic methodologies over a synoptic scale, and the combined techniques

allowed for a more complete assessment of the temporal and spatial patterns of WFS dolphins.

Key Words: acoustics, distribution, bottlenose dolphin, *Tursiops truncatus*, Gulf of Mexico, Atlantic spotted dolphin, *Stenella frontalis* 

## Introduction

A fundamental question in biology is how animal distribution fluctuates over space and time. Various methods have been developed to measure animal distribution (e.g., abundance estimates; Buckland et al., 2001), each with associated benefits and disadvantages in terms of accuracy, precision, and logistical considerations. Measuring cetacean distribution is complicated by several factors, including their tendency to (1) spend large amounts of time underwater, (2) in some cases travel long distances, and (3) live in regions that are sometimes inaccessible for researchers.

One commonly used method for determining cetacean distribution involves visual counts from boat-based surveys. This method allows for reliable species identification, group size estimation, and concurrent data collection (e.g., photographic identification, distance sampling, behavioral observations, acoustic surveys, and environmental measurements; Wells, 1991; Barlow & Taylor, 2005). While visual surveys have advantages, they are weather and daylight dependent, and results are often based on datasets using single vessels and relatively short time periods (Mellinger & Barlow, 2003; Mellinger et al., 2007).

As cetaceans produce a variety of sounds, and sound propagates well in the aquatic environment (see Au & Hastings, 2008, for review), cetacean distribution can also be investigated using stationary autonomous acoustic recorders. These recorders can be relatively inexpensive and logistically simple, and they can operate in poor weather, darkness, and inaccessible locations over large spatial and temporal scales (Mellinger et al., 2007; Marques et al., 2012). Acoustic recordings are permanent records that can be reanalyzed at a later time if spurious results appear or new processing techniques develop. Cetaceans also produce sounds when they are not visible at the surface, thereby increasing their probability of detection through acoustic monitoring. Disadvantages to this method include the necessity of animals to be making sound in order to be detected; variability in the sound production of cetaceans (e.g., by location [Jones & Sayigh, 2002] and behavior [Nowacek, 2005]); masking by ambient noise; greater uncertainty about species identification, group size, and behavior (Mellinger et al., 2007; Marques et al., 2012); and the logistic considerations of deploying and recovering equipment in the marine environment (Dudzinski et al., 2011).

Given that each method has advantages and disadvantages, the concurrent use of visual surveys and stationary passive acoustic recorders can provide a more complete assessment of cetacean distribution. For example, distribution patterns of harbor porpoises (Phocoena phocoena) and common bottlenose dolphins (Tursiops truncatus, henceforth referred to as bottlenose dolphins) in the Moray Firth, Scotland, determined with acoustic data from three pairs of T-PODs (timing-porpoise detectors), were corroborated by land-based visual surveys and previously published distribution patterns (Bailey et al., 2010). Bottlenose dolphin presence in the Shannon Estuary, Ireland, was also investigated with a shore-based observation post and a single T-POD, and acoustic detections corresponded with visual detections (Philpott et al., 2007). In a large spatial and temporal scale study, the distribution patterns of ten cetacean species were documented in the coastal waters of New Jersey, using a combination of autonomous recorders ("pop-ups") and ship-board and aerial visual surveys (Geo-Marine, Inc., 2010).

The purpose of this study was to investigate spatial and temporal variation in dolphin distribution over large spatial and temporal scales on the central West Florida Shelf (WFS), eastern Gulf of Mexico, using both boat-based visual surveys and autonomous bottom-mounted acoustic recorders. Bottlenose and Atlantic spotted dolphins (*Stenella frontalis*) are known to inhabit the WFS (Griffin & Griffin, 2003, 2004). While several detailed studies exist on the seasonal and spatial patterns of bottlenose dolphins found in estuarine and lagoon communities (e.g., Irvine et al., 1981; Wells, 1991), far less is known about large-scale distribution and seasonality of dolphin species on the WFS. As each method has advantages and disadvantages, the use of both methods concurrently was expected to provide a more complete understanding of dolphin distribution patterns. This is the first study to investigate cetacean distribution on the WFS over a synoptic scale using both methodologies.

# Methods

The study took place on the central WFS, in an area bounded approximately by the shoreline of the Gulf of Mexico (outside of bays and lagoons) to the 100-m isobath, and 27.10° to 28.15° N (Figure 1) from April to September 2008 and from April 2009 to June 2010. The study area was divided into ten analysis regions (see Figure 1; black lines) using *ArcGIS* (ESRI, Redlands, CA, USA) with bathymetry and landform data from the Florida Fish and Wildlife Conservation Commission (2012) and Price (2012). Since dolphin distribution and species composition vary greatly with depth in many areas (including the WFS, e.g., Fritts et al., 1983; Griffin & Griffin, 2004), geographic regions were defined partially by depth.

Coastal regions extended from the shoreline (seaward edges of barrier islands, with straight lines connecting adjacent land) to 2 km from shore (approximately 5 m water depth). The seaward extent of this region was based on the results of Fazioli and colleagues (2006) who found that bottlenose dolphin groups containing only dolphins resident to bay and estuary areas occurred on average up to 0.8 km from shore (SD = 1.03 km), and mixed groups of dolphins resident to bay and estuary waters and to the open continental shelf waters of the Gulf of Mexico occurred on average 1.9 km from shore (SD = 1.03). Therefore, the Coastal regions were assumed to be heavily influenced by the movements and distributions of the resident dolphins from the local bays and estuaries. The Inner Shelf regions (> 2 km from shore to the 20-m  $\pm$ isobath) extended seaward from the Coastal regions. Previous studies found that in this depth range, most bottlenose dolphins were resident to the open Gulf of Mexico, and very few Atlantic spotted dolphins were present (Griffin & Griffin, 2004; Fazioli et al., 2006). The 20-m isobath is also the boundary for the National Marine Fisheries Service (NMFS) stock boundary dividing "coastal" and "shelf" bottlenose dolphins (Waring et al., 2013). Further from shore, the Mid Shelf regions (> 20 to 45 m) delineate where Atlantic spotted dolphins become abundant (Griffin & Griffin, 2004). The seaward edge of the Mid Shelf regions is also near a transition of shelf circulation, inshore of which Ekman layer divergence results in a cross-shelf pressure gradient that impacts coastal circulation (Weisberg et al., 2001, 2005). This division of physical processes could potentially have biological responses that could influence the distribution of large predators such as dolphins. The most seaward region (Outer Shelf) was defined as an area extending from the Mid Shelf regions to the 100-m isobath. This region is a physical buffer between the inner shelf processes and those that occur near the shelf break (Weisberg et al., 2005). The 100-m isobath was chosen as it was near the seaward boundary of acoustic recorder deployments and most visual surveys.

In order to investigate changes in dolphin distribution in the alongshore (north-south) direction, the Coastal, Inner Shelf, and Mid Shelf regions were subdivided into three latitude-based regions. Fazioli and colleagues (2006) suggested that the Gulf of Mexico waters off Tampa Bay were a confluence of several continental shelf bottlenose dolphin communities. In addition, Tampa Bay is a large estuary that significantly impacts the oceanography of the adjacent WFS (Weisberg & Zheng, 2006; Wall et al., 2008), which could in turn result in different spatial and temporal patterns in dolphin distribution. Therefore, latitude regions were defined as their position in relation to Tampa Bay: North (approximately 27° 45' to 28° 15' N), Central (approximately 27° 30' to 27° 45' N), and South (approximately 27° 10' to 27° 30' N). The Outer Shelf region was not subdivided into latitude-based regions due to the low amounts of data in comparison to other regions.

Oceanographic and biological patterns on the WFS fluctuate seasonally (Hixon et al., 1980; Weisberg et al., 2005; Fazioli et al., 2006). Therefore, the study period was divided into spring (1 April–30 June 2008, 2009, and 2010), summer (1 July–30 September 2008 and 2009), autumn (1 October–31 December 2009), and winter (1 January–31 March 2010). These seasonal periods were based on climate and oceanographic patterns of the area (Weisberg et al., 2005)

### Field Methods: Autonomous Acoustic Recorders

Autonomous acoustic recorders (Digital SpectroGram [DSG] recorders, Loggerhead Instruments, Sarasota, FL, USA) were deployed at 19 stations on the WFS from June through September 2008 in a grid with 25 km spacing between recorders (approximately 28.1° to 27.0° N, and out to the 30-m isobath; Figure 1). These recorders operated with a duty cycle of either 6 or 11 s/h, and recordings were made at a 50-kHz sample rate with a 3-pole (-18 dB/octave) low-pass filter with a 35-kHz corner frequency, resulting in a bandwidth for analysis of up to 25 kHz. Recorders were also deployed at 63 stations from June 2009 through June 2010 in a grid with 20 km spacing between recorders (approximately 28.1° to 27.2° N, and out to the 100-m isobath; Figure 1).



Figure 1. Map of analysis regions (shaded areas), recovered DSG recorders with station numbers (circles indicate June-September 2008 deployment, and triangles indicate June 2009–June 2010 deployment), and DSG recorders not recovered ("X")

These recorders operated with a 6 s/h duty cycle and a 37-kHz sample rate with a 3-pole (-18 dB/octave) low-pass filter with a 35 kHz corner frequency, resulting in a bandwidth for analysis of up to 18.5 kHz. As the corner frequency of the low-pass filter (35-kHz) was above the Nyquist frequencies of the recordings (25 kHz in 2008, 18.5 kHz in 2009-2010), the change in analysis bandwidth was not expected to change detection probabilities as echolocation and whistle energy up to 35 kHz was aliased into the spectrograms. All hydrophones were HTI-96-MINs (-170 or -186 dBV/  $\mu$ Pa, flat response 2 Hz to 37 kHz [+/- 3 dB], High Tech, Inc., Long Beach, MS, USA), and recordings were stored on 16 GB HDSD cards. All electronics and a D-cell power supply were housed in watertight PVC housings and moored to the bottom (for details, see Dudzinski et al., 2011; Simard, 2012). The recorders in both the 2008 and 2009 deployments operated for variable periods of time as some recorders were replaced mid-deployment, while others operated for the entire deployment.

The primary goal of the recorder deployments was to record dolphin sounds that can extend into higher frequencies. For example, whistle fundamental frequencies for bottlenose and Atlantic spotted dolphins normally range up to 18 kHz (Herzing, 1996; Frankel et al., 2014). Echolocation for these species has energy that typically ranges to above 130 kHz (Au & Herzing, 2003; Au et al., 2012), although echolocation energy below 20 kHz is not uncommon (Houser et al., 2005), especially when recorded off-axis (Au et al., 2012). The sample rates and duty cycles chosen for this study were a balance between sufficient recordings of high-frequency sounds (favoring many recordings at high sample rates) and the digital memory constraints during long deployments (favoring fewer recordings at low sample rates).

### Field Methods: Visual Surveys

Visual surveys were conducted on the WFS from 7 April through 29 September 2008 and 8 April 2009 through 18 June 2010, departing from St. Petersburg or Sarasota, Florida. Cruises were conducted by the University of South Florida (USF) aboard research vessels of 9 to 35 m lengths. USF visual surveys were mostly conducted during acoustic recorder deployment and recovery cruises; therefore, cruise tracklines were based on the locations of acoustic recorders. Additional cruises were conducted specifically to investigate dolphins (see Frankel et al., 2014); tracklines were based on weather conditions and maintaining an even cruise distribution in the study area. Cruises were also conducted in nearshore WFS waters by the Sarasota Dolphin Research Program (SDRP) and the Eckerd College Dolphin Project (ECDP) with vessels of 4.2 to 6.7 m lengths. SDRP visual surveys were conducted along a standard survey route determined by depth, tide, and weather conditions. ECDP cruises did not follow a standard route but were based on depth and weather conditions and maintaining an even cruise distribution in the ECDP study area. All cruises had a minimum of two experienced cetacean observers who continuously visually scanned for cetaceans (naked eye) during daylight hours in a 180° arc in front of the survey vessel. On visual surveys, data collected included times of observation of dolphin groups, species, group size, distance from boat when a group was first sighted (USF, ECDP), and automatically recorded GPS positions of vessel survey tracklines. Survey tracklines were considered all vessel tracks when observers were actively searching for cetaceans. Survey tracklines were discontinued during times when researchers were working with cetacean groups on concurrent projects. Environmental data were also collected and included wave and swell height, wind speed, and for SDRP, a sightability index from 0 (excellent conditions, very unlikely to miss dolphins) to 4 (likely to miss dolphins) and 5 (off survey). Cetaceans were identified to the lowest possible taxonomic level.

#### Acoustic Data Analysis

Dolphin sounds were identified by the lead author by manual inspection of individual 6- or 11-s spectrograms (512 point resolution, Blackman-Harris windowing function) in *Adobe Audition* (Adobe Systems Inc., San Jose, CA, USA). For this study, a presence-absence score for any dolphin sound (e.g., whistles and echolocation; see Au & Hastings, 2008) in each 6 or 11 s file was used as a measure of dolphin presence at that particular time and location. No attempts were made to identify species from acoustic recordings in this study.

Post-identification analysis was conducted using custom written MATLAB routines (Mathworks Inc., Natick, MA, USA). Acoustic detection rates (dolphin detections/km<sup>2</sup>/h) were calculated for each region and season. Dolphin detections were defined as the number of individual files in each region and season with any dolphin sound (e.g., whistle and echolocation), and the time component was calculated as the sum of the recording time of all 6 and 11 s recordings within the region and season. The detection area of the recorders was based on static estimates of detection range geometry, transmission loss, signal source level, signal directionality, and detection threshold (see Au & Hastings, 2008). As this model was developed for omnidirectional recorders, the area of a circle was used to convert detection range to detection area (area =  $\pi \times r^2$ , where r = radius or detection range). The detection area was estimated with the formula

Detection Area = 
$$\pi \left( 10 \left( \frac{SL - DT - AN}{TL} \right) \right)^2$$

where SL is the signal source level, DT is the detection threshold, AN is the ambient noise of the recording (25 or 18.5 kHz Nyquist frequency, 2-kHz high-pass filter) adjusted for the frequency resolution of the analysis spectrogram, and TL is the transmission loss spreading coefficient. The components of this model are discussed here.

Source Level (SL)—This model used a dolphin whistle source level estimate for the active space calculation. Whistles are only weakly directional (Lammers & Au, 2003; Branstetter et al., 2012); however, echolocation and burst-pulses are highly directional, and the degree of directionality is frequency dependent (Au et al., 2012; Branstetter et al., 2012). This makes the development of a detection function for pulsed dolphin sounds very complex as the orientation of the dolphin to the hydrophone would change the received level. Therefore, for this model, the detection function developed for whistles was assumed to be proportionately appropriate for echolocation and burstpulses, assuming the orientation of dolphins to the hydrophone is random. Frankel and colleagues (2014) determined the median whistle source level for both bottlenose and Atlantic spotted dolphins on the WFS to be 138 dB re 1  $\mu$ Pa; therefore, this value was used as the source level estimate in this acoustic model.

Detection Threshold (DT)-The detection threshold was calculated by measuring the root mean square (RMS) of the highest amplitude section of 40 whistles considered "barely detectable" by the lead author in a 512 point spectrogram (20 from 50 kHz sample rate recordings; 20 from 37 kHz sample rate recordings). The RMS noise levels immediately adjacent to the whistle and at the same frequency bandwidth were used to determine the detection threshold using a 512 point fast Fourier transform (FFT). As the frequency by time resolution was different for the different sample rates used, the detection threshold between years was statistically tested and found to be not significant (t = 0.39, p = 0.0774). Therefore, the overall mean detection threshold value was used in the model (9.8 dB re 1  $\mu$ Pa; range 4.7 to 14.8 dB re 1  $\mu$ Pa).

Ambient Noise (AN)—Ambient noise levels were calculated using the RMS amplitude for each individual file. As most dolphin sounds are produced at higher frequencies (Au & Hastings, 2008), the files were high-pass filtered (2-kHz corner frequency) in order to limit the ambient noise values to the bandwidth that would impact signal detection. In order to adjust the broadband ambient noise measurement to the same frequency resolution as the analysis spectrogram, the measured ambient noise level (*RMS*) was adjusted with the formula:

$$AN = RMS - 10 \log_{10}[(NR - CF) / (SR / R)]$$

where AN is the adjusted ambient noise level, NR is the Nyquist rate (25.0 or 18.5 kHz), CF is the corner frequency of the high-pass filter (2 kHz), SR is the sample rate (50 or 37 kHz), and R is the spectrogram resolution (512 points). Therefore, AN is the spectrum level of ambient noise measured above 2 kHz, and we are assuming the AN values are applicable to the results of the DT calculation as the latter is the ratio of signal to noise. Mean ambient noise values were calculated for the monthly time-integrated detection rates used in this study.

Transmission Loss (TL)-Frankel and colleagues (2014) used a Bellhop propagation model to determine the transmission loss of a dolphin whistle in depths from 15 to 38 m on the WFS. Their results indicated that transmission loss curves were similar for the depths investigated, and transmission loss was described by a logarithmic function  $[TL = C \ x \ log_{10}(range)]$ . The value of the spreading coefficient C was between 18.01 and 18.92 for all depths; therefore, a logarithmic function using C = 18.5 was used in this study. We are assuming that this value is a good estimate for all frequencies across the range of dolphin whistle frequencies. In the same study, the observed propagation data for both bottlenose and Atlantic spotted dolphin whistles provided in situ confirmation for the transmission loss model.

### Visual Survey Data Analysis

Data were not collected in a manner to allow for distance sampling (e.g., the angular distances from the vessel track lines were not recorded; see Buckland et al., 2001); however, the number of dolphins per linear kilometer of survey effort was calculated (dolphins/km, cf. Fazioli et al., 2006). GPS survey and sightings data from the different projects were lumped for analysis. GPS track lines (while vessels were "on survey": vessel moving, observers on deck and actively searching for dolphins but no dolphins present) and dolphin sighting locations were analyzed in ArcGIS to calculate seasonal/regional sighting rates (dolphins/km) for bottlenose and Atlantic spotted dolphins. For comparisons with acoustic detection rates, visual sighting rates for all dolphins combined were also calculated.

Several potential biases could be introduced due to differences in survey protocols. For example, while ECDP cruises were conducted on small boats and in good weather, USF cruises often took place on larger vessels with higher observer height, increasing the probability of visually detecting cetaceans at long distances. USF cruises were also conducted in poorer weather conditions as their objectives were also to switch out acoustic recorders, therefore, potentially decreasing the probability of detecting cetaceans. Thus, all effort data (GPS tracks while on survey) and visual detections collected during poor weather (wave or swell height > 1 m) or when dolphins were estimated to be more than 500 m away from the vessel were omitted from analysis to reduce the bias of multiple vessels and survey protocols used.

## Statistical Analysis

A factorial ANOVA was conducted to determine if depth and/or season had significant effects on the calculated area of detection. Depth was classified into the four depth-related regional divisions (Coastal, Inner Shelf, Mid Shelf, and Outer Shelf). For both acoustic detection rates and visual sighting rates, G-tests with Šidák corrections for multiple tests were used to test for significant variation in rates from even distribution both spatially (within seasons, between regions) and temporally (within regions, between seasons). Spearman correlations were used to determine the degree of correlation between acoustic detection rates and visual sighting rates. As acoustic detection rates and visual sighting rates using low amounts of data may not accurately represent the area or time period in question, regions or seasons with less than one full month of acoustic recording from at least one recorder were not used in analysis. Similarly, regions and seasons with less than 25 km visual survey effort were not included in analysis.

## Results

### Acoustic Data

Recorders were recovered from and successfully recorded at 37 stations (Figure 1). These recorders operated from 10 June to 29 September 2008 and 1 June 2009 to 10 June 2010, resulting in 134,922 files totaling 269 h 43 min of noncontinuous recording time (Table 1). All regions and seasons exceeded the minimum threshold of data quantity for analysis (at least one full month of recording from at least one recorder). Dolphin whistles, echolocation, burst-pulses, low-frequency burst-pulse like sounds were recorded (see Herzing, 1996; Au

**Table 1.** Summary of recovered DSG recorders in each region and season, with sum time of recording (Sum Time, s), mean detection area  $\pm 1$  SD (Det Area, km<sup>2</sup>), and pooled detection rates from all stations within the region (Det Rate, detections/km<sup>2</sup>/h); note that the Coastal South region did not have any DSG recorders and is not included here. -- denotes no data.

Region		Spring	Summer	Autumn	Winter
Coastal North	Sum Time	5,145	19,707		
	Det Area	0.14 (0.00)	0.25 (0.06)		
	Det Rate	24.27	17.10		
Inner Shelf North	Sum Time	12,746	37,099	15,478	15,167
	Det Area	1.69 (0.73)	0.60 (0.15)	1.37 (0.64)	4.50 (0.19)
	Det Rate	18.54	30.06	25.16	19.62
Mid Shelf North	Sum Time	42,933	68,676	77,403	70,186
	Det Area	1.90 (1.49)	2.82 (3.14)	3.62 (2.99)	5.78 (3.48)
	Det Rate	8.40	12.10	7.70	12.09
Coastal Central	Sum Time	3,391			
	Det Area	0.27 (0.00)			
	Det Rate	42.63			
Inner Shelf Central	Sum Time	9,736	11,534		
	Det Area	1.63 (1.34)	0.22 (0.22)		
	Det Rate	28.08	69.38		
Mid Shelf Central	Sum Time	8,931	39,938	30,784	18,778
	Det Area	4.81 (1.71)	4.68 (0.92)	6.07 (1.75)	5.84 (4.08)
	Det Rate	10.24	7.74	8.06	9.03
Inner Shelf South	Sum Time	12,887	36,034	9,216	
	Det Area	1.34 (1.33)	1.08 (1.08)	0.26 (0.10)	
	Det Rate	16.74	33.87	54.63	
Mid Shelf South	Sum Time	39,835	63,458	43,799	30,239
	Det Area	2.88 (2.40)	2.37 (2.55)	2.23 (1.76)	5.64 (3.11)
	Det Rate	12.88	12.80	14.08	9.40
Outer Shelf	Sum Time	53,439	75,087	59,545	51,400
	Det Area	11.31 (11.68)	6.48 (4.44)	5.09 (2.76)	4.29 (3.08)
	Det Rate	2.81	4.11	4.71	5.49

& Hastings, 2008; Simard et al., 2011). No sounds from other cetaceans were found; however, as acoustic files were browsed for relatively highfrequency dolphin sounds, some low-frequency cetacean sounds may have been overlooked (e.g., 100 Hz calls of Bryde's whales [*Balaenoptera edeni*]; Würsig et al., 2000; Heimlich et al., 2005).

Using the ambient noise from each file, mean detection areas ranged from 0.14 km<sup>2</sup> (Coastal North, spring) to 11.31 km<sup>2</sup> (Outer Shelf, spring) (Table 1). The factorial ANOVA indicated that the detection area varied significantly with depth (Table 2), increasing from inshore to offshore

(Table 1). In addition, detection area varied significantly with season (Table 2), increasing in cooler seasons. With these detection range estimates, the detection rate for dolphin sounds ranged between 2.81 detections/km<sup>2</sup>/h (Outer Shelf, spring) to 69.38 detections/km<sup>2</sup>/h (Inner Shelf Central, summer) (Table 1).

#### Visual Survey Data

Between 7 April and 23 September 2008 and between 8 April 2009 and 18 June 2010, visual surveys were conducted over 12,135 km, and 506 dolphin groups were observed while on survey (Figure 2). Only

**Table 2.** Results of factorial ANOVA (detection area, season, and depth); depth was categorized as Coastal, Inner Shelf, Mid Shelf, and Outer Shelf. Sum of squares (SS), degrees of freedom (*df*), mean square (MS), F ratio (F), and probability (*p*) are provided. \* = statistically significant,  $\alpha = 0.05$ .

	SS	df	MS	F	р
Season	6.543	1	6.543	5.715	0.0314*
Depth	63.916	2	31.958	27.913	< 0.0001*
Season * Depth	42.508	7	6.073	5.304	0.0039*
Error	16.029	14	1.145		



Figure 2. Map of analysis regions (shaded areas), visual survey tracklines (thin grey lines), and locations of dolphin groups, bottlenose dolphins (Tt), Atlantic spotted dolphins (Sf), and rough-toothed dolphins (Sb), in April through September 2008 and April 2009 through June 2010; breaks in survey tracklines are due to vessel going off survey (e.g., poor weather, darkness).

oceanic dolphins (Family Delphinidae) were identified in this study. Bottlenose dolphins were observed 477 times throughout the study area, while Atlantic spotted dolphins were observed 26 times, with only two sightings at depths shallower than 20 m (at approximately 10 and 14 m). A single group of rough-toothed dolphins (*Steno bredanensis*) was observed in a mixed group with bottlenose dolphins (at approximately 12 m depth). Eleven groups of dolphins were observed that could not be identified to species.

The survey effort and sighting rates (individual dolphins/km) for bottlenose and Atlantic spotted dolphins are found in Table 3. Regions/seasons not meeting the minimum threshold of data quantity for analysis (at least 25 km of survey effort)

**Table 3.** Summary of visual survey data in each region and season, with survey effort in km and sighting rate (dolphins/km of survey effort) for bottlenose and Atlantic spotted dolphins; note that sighting rates for regions and seasons with less than 25 km of survey effort are presented here (in italics) but are not used in statistical analysis. -- denotes no data.

Region		Spring	Summer	Autumn	Winter
Coastal North	Effort (km)	8.0	3.52		
	Bottlenose (dol/km)	0.50	1.99		
	Atlantic spotted (dol/km)	0.00	0.00		
	All (dol/km)	0.50	1.99		
Inner Shelf North	Effort (km)	144.9	366.2	19.8	
	Bottlenose (dol/km)	0.00	0.07	0.00	
	Atlantic spotted (dol/km)	0.00	0.02	0.00	
	All (dol/km)	0.00	0.08	0.00	
Mid Shelf North	Effort (km)	148.1	460.5	200.8	
	Bottlenose (dol/km)	0.00	0.00	0.00	
	Atlantic spotted (dol/km)	0.02	0.01	0.00	
	All (dol/km)	0.02	0.01	0.00	
Coastal Central	Effort (km)	491.1	329.9	89.2	79.3
	Bottlenose (dol/km)	0.52	0.66	0.85	0.64
	Atlantic spotted (dol/km)	0.00	0.00	0.00	0.00
	All (dol/km)	0.52	0.66	0.85	0.64
Inner Shelf Central	Effort (km)	482.7	315.7	66.9	
	Bottlenose (dol/km)	0.24	0.11	0.06	
	Atlantic spotted (dol/km)	0.00	0.01	0.00	
	All (dol/km)	0.24	0.12	0.06	
Mid Shelf Central	Effort (km)	372.4	158.5	102.0	
	Bottlenose (dol/km)	0.03	0.00	0.02	
	Atlantic spotted (dol/km)	0.16	0.00	0.02	
	All (dol/km)	0.19	0.00	0.04	
Coastal South	Effort (km)	1,616.0	768.3	463.4	367.2
	Bottlenose (dol/km)	0.25	0.33	0.27	0.11
	Atlantic spotted (dol/km)	0.00	0.00	0.00	0.00
	All (dol/km)	0.25	0.33	0.27	0.11
Inner Shelf South	Effort (km)	1,923.4	44.9	61.3	0.5
	Bottlenose (dol/km)	0.07	0.13	0.03	0.00
	Atlantic spotted (dol/km)	0.00	0.00	0.00	0.00
	All (dol/km)	0.07	0.13	0.03	0.00
Mid Shelf South	Effort (km)	2,062.4	14.4		
	Bottlenose (dol/km)	0.12	0.28		
	Atlantic spotted (dol/km)	0.13	0.00		
	All (dol/km)	0.25	0.28		
Outer Shelf	Effort (km)	730.9	0.0	350.2	
	Bottlenose (dol/km)	0.01		0.04	
	Atlantic spotted (dol/km)	0.18		0.09	
	All (dol/km)	0.20		0.12	

are included in Table 3 but were not used in further analysis. For the entire study, the sighting rate for bottlenose dolphins was 0.17 dolphins/ km, while the sighting rate for Atlantic spotted dolphins was 0.04 dolphins/km. Sighting rates for both species were 0.00 dolphins/km in several cases but ranged up to 0.85 dolphins/km for bottlenose dolphins (Coastal Central, autumn) and up to 0.18 dolphins/km for Atlantic spotted dolphins (Outer Shelf, spring).

# Temporal Variation of Acoustic Detection and Visual Sighting Rates Within Regions

G-tests were calculated for eight regions (Table 4; null hypothesis of no seasonal variation in acoustic detection rates within regions). No acoustic data were available for Coastal South, and only one season of data was available for Coastal Central. Acoustic detection rates varied significantly between seasons in the Inner Shelf Central and Inner Shelf South regions. In these regions, acoustic detection rates increased from spring to summer (Figures 3 & 4; no data available in winter months). Rates continued to increase into the autumn for Inner Shelf South (Figures 3-5; no autumn data were available for Inner Shelf Central). All other temporal results were not significant (Table 4).

G-tests were also conducted to test if seasonal visual survey sighting rates within each region were significantly different from even distribution (null hypothesis of no seasonal variation in visual sighting rates within regions). For bottlenose dolphins, G-tests were conducted for nine regions (insufficient data were available for Coastal North and Mid Shelf South due to low survey effort; Table 4). Visual survey sighting rates for bottlenose dolphins varied significantly between seasons in two Coastal regions (Central, South), three Inner Shelf regions (North, Central, South), Mid Shelf Central, and Outer Shelf. Data over four seasons were available for the regions Coastal Central, where bottlenose dolphin sighting rates peaked in autumn, and Coastal South, where bottlenose dolphin sighting rates peaked in summer (Figures 3-6). Inner Shelf North and South also peaked in summer (Figures 3 & 4), although no autumn data were available for Inner Shelf North. Inner Shelf Central showed a different pattern, with sighting rates much higher in the spring and decreasing through the summer and autumn (Figures 3-5). In Mid Shelf Central, sighting rates were highest in spring, decreased to 0.00 dolphins/ km in the summer, and increased in the autumn (Figures 3-5). Sighting rates for the Outer Shelf region were only available for spring and autumn, and sighting rates for bottlenose dolphins were much higher in the autumn (Figures 3-5).

For Atlantic spotted dolphins, G-tests were conducted for five regions (Table 4). In order to not inflate statistical significance by including regions where Atlantic spotted dolphins are not known to be found (see Griffin & Griffin, 2004), all Coastal regions were omitted from this analysis. Insufficient data were available for statistical testing in Mid Shelf South due to lack of survey effort. Visual survey sighting rates for Atlantic spotted dolphins varied significantly between seasons in the Inner Shelf North, Mid Shelf North, Mid Shelf Central, and Outer Shelf regions. In the Mid Shelf North, Mid Shelf Central, and Outer Shelf regions, sighting rates for Atlantic spotted dolphins were highest in the spring and lower in the summer and autumn (Figures 3-5). This pattern was not observed in the shallower Inner Shelf North region, where no sightings occurred in the spring but did occur in the summer (Figures 3 & 4; no data available for autumn).

# Spatial Variation of Acoustic Detection Rates and Visual Sighting Rates Within Seasons

G-tests were conducted to test if the regional acoustic detection rates and the bottlenose and Atlantic spotted dolphin visual sighting rates were significantly different from even distribution (Table 5; null hypothesis of no regional variation in sighting rates within seasons). All sighting rates varied significantly between regions in all seasons, except for acoustic detection rates during the winter. No Atlantic spotted dolphins were observed in winter when only Coastal regions were surveyed.

In general, acoustic detection rates and bottlenose dolphin visual sighting rates decreased from inshore to offshore in spring through autumn (in winter, this decrease was not significant for acoustic detection rates, and only coastal visual survey data were available; Figures 3-6). However, acoustic detection rates in the summer were lower for Coastal North than immediately offshore in Inner Shelf North (Figure 4). Acoustic detection rates and bottlenose dolphin visual sighting rates were also highest in the regions adjacent to Tampa Bay (Coastal Central and Inner Shelf Central; Figures 3-6). In spring and autumn, Atlantic spotted dolphins were only observed in the Mid Shelf and Outer Shelf regions, with sighting rates highest in the Outer Shelf (Figures 3 & 5). During the summer, Atlantic spotted dolphins were observed in waters shallower than 20 m (Inner Shelf North and Central), and the sighting rates increased toward the northeast of the study area (maximum sighting rate in Inner Shelf North; Figure 4). Only Coastal regions were visually surveyed in winter, where Atlantic spotted dolphins are not known to be present (e.g., Griffin & Griffin, 2004).

or $\alpha = 0.0102$	? (Atlant	ic spotted visi	ual, 5 tests).	, )		)		×			
		Coastal North	Coastal Central	Coastal South	Inner Shelf North	Inner Shelf Central	Inner Shelf South	Mid Shelf North	Mid Shelf Central	Mid Shelf South	Outer Shelf
Acoustic	df P	1.250 2 0.5353	1 1 1	1 1 1	3.598 3 0.3083	18.063 2 0.0001*	21.250 2 < 0.0001*	1.668 3 0.6441	0.426 3 0.9348	1.037 3 0.7923	0.938 3 0.8162
Bottlenose (visual)	df $df$		1,496.403 3 < 0.0001*	698.807 3 < 0.0001*	57.619 1 < 0.0001*	68.524 2 < 0.0001*	206.352 2 < 0.0001*	0.000 2 1.0000	43.563 2 <0.0001*	1 1 1	86.222 1 < 0.0001*
Atlantic spotted (visual)	df P		1 1 1		7.301 1 0.0069*	0.382 2 0.8261	0.000 2 1.0000	10.058 2 0.0065*	82.384 2 < 0.0001*	1 1 1	269.510 1 < 0.0001*

Table 4. Temporal statistical results of acoustic detection rates and visual detection rates for bottlenose and Atlantic spotted dolphins within regions and between seasons; G-test results for null hypothesis of no variation in detection rates between seasons. G-test statistic (G), degrees of freedom (df), and probability (p) are provided. -- = insufficient data for testing



Figure 3. Maps showing bottlenose and Atlantic spotted dolphin visual sighting rates (dolphins/km) and dolphin acoustic detection rate (detections/km<sup>2</sup>/h) in spring (2008, 2009, 2010); numbers overlaying analysis regions are visual sighting rates and acoustic detection rates (ND = no data). Bottlenose and Atlantic spotted dolphin sighting rates and acoustic detection rates were significantly different from even distribution (see Table 5).



Figure 4. Maps showing bottlenose and Atlantic spotted dolphin visual sighting rates (dolphins/km) and dolphin acoustic detection rate (detections/km<sup>2</sup>/h) in summer (2008, 2009); numbers overlaying analysis regions are visual sighting rates and acoustic detection rates (ND = no data). Bottlenose and Atlantic spotted dolphin sighting rates and acoustic detection rates were significantly different from even distribution (see Table 5).



**Figure 5.** Maps showing bottlenose and Atlantic spotted dolphin visual sighting rates (dolphins/km) and dolphin acoustic detection rate (detections/km<sup>2</sup>/h) in autumn (2009); numbers overlaying analysis regions are visual sighting rates and acoustic detection rates (ND = no data). Bottlenose dolphin sighting rates, Atlantic spotted dolphin sighting rates, and acoustic detection were rates significantly different from even distribution (see Table 5).



Figure 6. Maps showing bottlenose and Atlantic spotted dolphin visual sighting rates (dolphins/km) and dolphin acoustic detection rate (detections/km<sup>2</sup>/h) in winter (2010); numbers overlaying analysis regions are visual sighting rates and acoustic detection rates (ND = no data). Bottlenose dolphin sighting rates and acoustic detection rates were significantly different from even distribution; however, there were insufficient data for statistical testing of Atlantic spotted dolphin sighting rates (see Table 5).

**Table 5.** Spatial statistical results of acoustic detection rates and visual survey sighting rates for bottlenose and Atlantic spotted dolphins within seasons and between regions; G-test results for null hypothesis of no variation in detection rates between regions. G-test statistic (G), degrees of freedom (*df*), and probability (*p*) are provided. -- = no or insufficient data for a G-test; \* = statistically significant; Šidák corrected  $\alpha = 0.0127$  (acoustic and bottlenose visual, 4 tests each) or  $\alpha = 0.0169$  (Atlantic spotted visual, 3 tests).

Density estimates		Spring	Summer	Autumn	Winter
Acoustic	G	63.027	118.279	79.416	9.839
	df	8	7	5	4
	р	< 0.0001*	< 0.0001*	< 0.0001*	0.0432
Bottlenose (visual)	G	795.659	593.719	306.601	68.384
	df	8	6	6	1
	р	< 0.0001*	< 0.0001*	< 0.0001*	< 0.0001*
Atlantic spotted (visual)	G	850.221	20.118	75.565	
	df	8	6	6	
	р	< 0.0001*	0.0026*	< 0.0001*	

**Table 6.** Spearman correlation results for seasonal acoustic and visual detection rates, Spearman's rho (r), degrees of freedom (df), and probability (p) are provided. Note that insufficient data were available for correlations in winter. \* = statistically significant positive correlation,  $\alpha = 0.05$ .

		Spring	Summer	Autumn
Acoustic – bottlenose (visual)	r	0.9187	0.7857	0.2432
	df	6	3	2
	p	0.001*	0.079	0.741
Acoustic – Atlantic spotted (visual)	r	-0.6477	0.2337	-0.483
	df	6	3	2
	р	0.071	0.694	> 0.999
Acoustic – All dolphins (visual)	r	0.6675	0.4846	-0.2830
	df	6	3	2
	p	0.059	0.381	0.698

**Table 7.** Spearman correlation results for regional acoustic and visual detection rates, Spearman's rho (*r*), degrees of freedom (*df*), and probability (*p*) are provided. Note that insufficient data were available for correlations for all regions not included in table. Data fields labeled "n/av" indicate where sighting rates = 0.00, correlations not possible; and \* = statistically significant positive correlation,  $\alpha = 0.05$ .

		Mid Shelf North	Mid Shelf Central	Inner Shelf South
Acoustic – bottlenose (visual)	r	n/av	0.8277	-0.4441
	df	1	1	1
	р	n/av	0.237	0.654
Acoustic – Atlantic spotted (visual)	r	0.1480	0.9999	n/av
	df	1	1	1
	р	0.891	< 0.001*	n/av
Acoustic – All dolphins (visual)	r	0.1480	0.9965	-0.4441
	df	1	1	1
	р	0.891	0.001*	0.654

# Correlations Between Dolphin Acoustic Detection Rates and Visual Sighting Rates

As several regions had no data in some seasons, correlations between acoustic detection rates and visual sighting rates were limited to spring, summer, and autumn seasons (Table 6). Correlations between acoustic detection rates and bottlenose dolphin visual sighting rates were all positive; however, a strong and significant correlation was only found in the spring. Correlations between acoustic detection rates and Atlantic spotted dolphin visual survey sighting rates and between acoustic detection rates and visual sighting rates for all dolphins combined were generally weak, frequently negative, and not significant. Regional correlations between acoustic detection rates and visual detection rates were limited to regions with data available for at least three seasons. This restricted analysis to the regions Mid Shelf North, Mid Shelf Central, and Inner Shelf South (Table 7). Significant correlations were found in Mid Shelf Central between acoustic detection rates and Atlantic spotted dolphin visual sighting rates, and between acoustic detection rates and visual sighting rates for all dolphins combined. Other regional correlations were generally weak, frequently negative, and not significant.

### Discussion

The spatial and temporal distribution patterns of bottlenose and Atlantic spotted dolphins were investigated on the WFS using visual surveys and recordings from autonomous acoustic recorders. The use of both methodologies allowed for a more complete assessment of dolphin distribution, especially considering the large spatial and temporal scales. For example, the winter of 2010 was particularly severe, and the use of autonomous acoustic recorders allowed for data collection in offshore areas even though visual surveys were often not possible. In addition, dolphin sound production varies with species (e.g., Oswald et al., 2008), group size (Jones & Sayigh, 2002; Quick & Janik, 2008), activity (Jones & Sayigh, 2002; Nowacek, 2005), community (Jones & Sayigh, 2002), foraging preferences (Deecke et al., 2005), and ambient noise or disturbance level (Van Parijs & Corkeron, 2001: Buckstaff, 2004). Therefore, the absence of dolphin sounds on a recording does not necessarily indicate the absence of dolphins in the area, and acoustic detections can only serve as a proxy for distribution, making concurrent visual surveys a valuable tool. This is especially true when species cannot be identified from acoustic recordings.

There were several limitations to this analysis. Both the acoustic and the visual survey data were spatially and temporally sparse. Acoustic recorders had a low duty cycle (one 6 or 11 s recording/h) and were up to 25 km apart, limiting the probability of detection of phonating cetaceans. Visual surveys were infrequent in noncoastal areas, and a wide variety of vessels with different speeds and observer heights were used. Missing data (seasons and regions) made comparisons difficult and restricted the statistical analysis. In addition, the detection range model did not have sound propagation data from multiple seasons available. Although these limitations necessitate interpreting our results cautiously, this study adds to the sparse knowledge of dolphin distribution on the WFS, and the use of both methods concurrently allowed for a more comprehensive study (e.g., synoptic coverage and reliable species identification).

### Detection Area Model

The estimated area of acoustic detection varied greatly between seasons and depths, indicating considerable ambient noise differences on the WFS. Although temperature and depth-related variations in sound propagation is important, ambient noise has been suggested as the most important limitation of sound detection by human and animal observers (Hastie et al., 2005; Au & Hastings, 2008), and the large variations in estimated detection areas from ambient noise suggest that this is the case in this study.

The detection area varied significantly with depth, with Coastal regions having smaller estimated detection areas (and, therefore, higher ambient noise levels) than more offshore regions. The detection area also varied significantly with season, with warmer seasons having smaller estimated detection areas (and, therefore, higher ambient noise levels). In the analysis bandwidth used in the algorithm (2 to 18.5 or 2 to 25 kHz), most ambient noise was caused by snapping shrimp (Alpheidae) and boats.

Snapping shrimp produce broadband, highintensity sounds (< 5 to > 200 kHz, 183 to 189 dB<sub>PP</sub> re 1  $\mu$ Pa), which dominate the soundscape in many tropical and subtropical areas (Everest et al., 1948; Au & Banks, 1998; Ferguson & Cleary, 2000). Throughout their range, these shrimp, and their associated noise, are more common in shallow water (< 55 m depth; Everest et al., 1948). In many tropical and subtropical areas, seasonal variations in snapping shrimp sound production are negligible (Everest et al., 1948). However, snapping shrimp sound production may decrease significantly during cooler weather in areas with more variable water temperature (Radford et al., 2008). In the recordings from this study, snapping shrimp noise was negligible or absent in deep water recordings and ubiquitous in Coastal recordings, while seasonal changes in snapping shrimp sound production were present but not as dramatic. These patterns of snapping shrimp sound production help to explain the observed patterns in this study of smaller estimated detection ranges in shallower waters and in warmer seasons.

Boat noise is typically dominant in low frequencies (Ogden et al., 2011); however, harmonics can extend into ultrasonic frequencies (> 20 kHz; P. Simard, unpub. data, 2008-2014). Boat traffic in western Florida is some of the highest in the U.S., and boat traffic is far higher in inshore waters than in offshore waters (Sidman et al., 2004). Boat traffic also peaks in warmer months in western Florida (April-July; Sidman et al., 2004). In this study, boat noise was noticeably more common in Coastal recordings than in offshore recordings; however, less dramatic variation was observed seasonally. Therefore, the patterns of boat noise also help to explain the observed patterns in this study of smaller estimated detection ranges in shallower waters and in warmer seasons.

### General Patterns of Dolphin Distribution

The results of this study indicate that dolphins are present on the WFS in all seasons. Dolphin sounds were detected on recordings from all recorders, and, therefore, dolphin sounds were detected in all regions and seasons where data were available. Visual surveys also indicated that bottlenose and Atlantic spotted dolphins make extensive use of the central WFS year-round, although winter survey effort was limited to Coastal regions where Atlantic spotted dolphins have not been observed (this study; Griffin & Griffin, 2004). Previous studies have also found that bottlenose and Atlantic spotted dolphins are found on the WFS in all seasons (Fritts et al., 1983; Mullin & Hoggard, 2000; Griffin & Griffin, 2003, 2004; Fazioli et al., 2006). In this study, the overall sighting rate for bottlenose dolphins (0.17 dolphins/km) was higher than the overall sighting rate for Atlantic spotted dolphins (0.04 dolphins/km); however, previous studies have indicated that Atlantic spotted dolphins are more abundant than bottlenose dolphins in Gulf of Mexico continental shelf waters (Mullin & Hoggard, 2000; Fulling et al., 2003; Griffin & Griffin, 2004; Waring et al., 2013). The species composition of the WFS may fluctuate on various time scales in relation to environmental conditions (Griffin & Griffin, 2004), and, therefore, relative abundances of bottlenose and Atlantic spotted dolphins may not be comparable between studies conducted at different times. In addition, the visual survey effort of this study was not random or systematic, and it may be biased by the lower amounts of offshore survey effort where Atlantic spotted dolphins are more abundant.

Apart from one sighting of rough-toothed dolphins found in a mixed group with bottlenose dolphins, no other cetaceans were observed, suggesting that species other than bottlenose and Atlantic spotted dolphins are only rarely present on the central WFS. This is supported by previous studies of cetacean distribution on the WFS that only report sporadic sightings of other species (see Waring et al., 2013). Rough-toothed dolphins are more commonly seen in off-shelf waters (Davis et al., 2002); however, several sightings on continental shelf waters of the Gulf of Mexico suggest that this species is normally found there in low numbers (Fulling et al., 2003; Griffin & Griffin, 2003). Mixed groups of rough-toothed and bottlenose dolphins have been previously documented in the Gulf of Mexico (Maze-Foley & Mullin, 2006) and the eastern tropical Pacific (Scott & Chivers, 1990).

### Spatial Variation in Dolphin Distribution

A general decrease was observed in both acoustic detection rates and bottlenose dolphin visual sighting rates from inshore to offshore waters. However, in winter, this decrease was not significant in acoustic detection rates, suggesting a more spatially homogeneous distribution of dolphins in this season; and for visual surveys in winter, only Coastal data were available. Previous visual survey studies also found that bottlenose dolphin sightings decreased from inshore to offshore on the WFS (Irvine et al., 1982; Fritts et al., 1983), and this pattern has been observed in other areas and species (e.g., Mediterranean Sea short-beaked common dolphins [Delphinus delphis]; Cañadas & Hammond, 2008). Higher numbers of bottlenose dolphins close to shore are likely influenced by foraging habitat. Inshore WFS waters have increased bathymetric variation (e.g., coastlines, shipping channels), nutrient input (Heil et al., 2007), and lower trophic level biomass (e.g., zooplankton; Sutton et al., 2001). Fish abundance on the WFS is also generally higher closer to shore, including important prey items for Gulf bottlenose dolphins (Barros & Odell, 1990) such as pinfish (Lagodon rhomboides), pigfish (Orthopristis chrysoptera), and silver perch (Bairdiella chrysoura) (Darcy & Gutherz, 1984; Pierce & Mahmoudi, 2001).

Atlantic spotted dolphins were largely restricted to waters deeper than 20 m. This distribution pattern has been previously noted for the WFS (e.g., Griffin & Griffin, 2003). The highest visual sighting rates for this species were found in southern and offshore waters (Mid Shelf South and Central, Outer Shelf). This distribution pattern may reflect foraging preferences. For example, stomach contents from Gulf of Mexico Atlantic spotted dolphins indicate that squid are an important prey item (Perrin et al., 1987), and most squid species are more common beyond the 40-m isobath in the Gulf of Mexico (Hixon et al., 1980).

In all seasons, both acoustic detection rates and bottlenose dolphin visual detection rates were especially high near Tampa Bay (Coastal Central and Inner Shelf Central regions). Aerial surveys for bottlenose dolphins on the shallow WFS also found relatively high densities off Tampa Bay (Irvine et al., 1982; Weigle et al., 1991), and increased bottlenose dolphin numbers adjacent to estuaries were identified in the Gulf of California (Ballance, 1992). In addition, the waters off Tampa Bay have been identified as a potential confluence of several bottlenose dolphin communities, and relatively large mixed groups of bottlenose dolphins resident to inshore waters and those resident to open Gulf of Mexico waters have frequently been found there (Wells et al., 1987; Fazioli et al., 2006). Tampa Bay is the largest estuary on Florida's west coast and is characterized by various shipping channels, shallow areas, and manmade structures that modify the circulation in and out of the bay (Weisberg & Zheng, 2006). Estuarine outflow can influence the adjacent WFS (e.g., estuarine plumes and associated chlorophyll increases; Wall et al., 2008). The WFS adjacent to Tampa Bay has high levels of bathymetric variability and hard bottom structures (e.g., artificial reefs; Dupont, 2008). Bathymetric variability and bottom structure, and their influence on circulation, can lead to increased biological productivity (e.g., Mann & Lazier, 2006). Areas of high-relief bathymetry were preferential foraging areas for bottlenose dolphins in Anclote Key and John's Pass, Florida (Allen, 2000; Allen et al., 2001); Moray Firth, Scotland (Hastie et al., 2004; Bailey & Thompson, 2010); and southern California (Hanson & Defran, 1993). The Tampa Bay estuary and adjacent Gulf waters are important for many fish species, including known prey species of local bottlenose dolphins (e.g., pinfish; Nelson, 2002). Therefore, high numbers of bottlenose dolphins on the WFS adjacent to Tampa Bay are likely due to increased foraging opportunities for this species.

# Temporal Variation in Dolphin Distribution

For much of the WFS, temporal variation in acoustic detection rates was generally low, suggesting that dolphin density in a given area did not vary greatly over seasons. However, significant seasonal variation was found in shallower waters where acoustic detection rates increased from spring to summer (Inner Shelf Central) and from spring to autumn (Inner Shelf South). Bottlenose dolphin sighting rates also peaked in shallower waters during the summer (Coastal South) and autumn (Coastal Central). This suggests an influx of bottlenose dolphins into the Coastal WFS in the summer and autumn months. This seasonal influx is further supported by the decrease in bottlenose dolphin sightings in the Inner Shelf Central and Inner Shelf South regions from spring to summer (little data were available for Mid Shelf North and South regions). However, acoustic detections increase from spring to summer in the Inner Shelf Central region. These contradictory results may reflect the small increase in Atlantic spotted dolphins in this area during the summer, acoustic behavioral changes, or could simply be due to the limitations of our study design. Inshore distribution shifts of Gulf of Mexico bottlenose dolphins during the warmer months have been reported previously for the WFS (Fritts et al., 1983; Fazioli et al., 2006). However, a more recent study using mark recapture estimates found that coastal dolphin abundance decreased as the summer progressed (Wells et al., 2011). In addition, the resident bottlenose dolphins from Sarasota Bay were found to increase their use of the shallow WFS in from late autumn to early spring (Irvine et al., 1981; Scott et al., 1989), which could be expected to increase bottlenose density in the shallow WFS.

For Atlantic spotted dolphins, the highest sighting rates (>0.1 dolphins/km) were found in deeper and more southern waters in spring (Mid Shelf South, Mid Shelf Central, and Outer Shelf). The only time this species was observed in shallower northern waters (Inner Shelf North and Central) was during the summer. Although our data are sparse, this suggests a seasonal movement of this species into shallow and more northern waters during the summer. Inshore and northerly distribution shifts of Gulf of Mexico Atlantic spotted dolphins during the warmer months were reported previously for the WFS (Fritts et al., 1983, and references therein; Mills & Rademacher, 1996). Griffin & Griffin (2004) investigated seasonal density trends on the WFS and found that Atlantic spotted dolphin densities were highest from November to May, and they concluded that little evidence for an inshore spring movement was found. As both the seasonal period and spatial scale used by Griffin & Griffin were different than this study (smaller study area and seasons divided into June-October and November-May), it is possible that the seasonal movements suggested in this study are too fine-scale temporally and spatially to be found in the Griffin & Griffin study. In addition, very few autumn and winter visual survey data were collected in noncoastal waters in this study, so a comparison of all seasons was not possible.

An inshore migration of continental shelf bottlenose dolphins and an inshore/northward

migration of Atlantic spotted dolphins in warmer months may be due to a variety of factors; however, prey movements are likely important. For example, Atlantic spotted dolphins and continental shelf bottlenose dolphins in the Gulf of Mexico are known to feed on squid (Perrin et al., 1987, and references therein; Barros & Odell, 1990), and several species of squid migrate to shallower continental shelf waters on the WFS in the spring and summer (Hixon et al., 1980; Marelli & Arnold, 1998). Inshore movements of Atlantic spotted dolphins in warmer months have also been related to the movements of carangid fish (e.g., jacks; Würsig et al., 2000). In addition, several estuarine fish species important to bottlenose dolphins resident to the Gulf of Mexico (Leatherwood, 1975; Barros & Odell, 1990) return to the Gulf waters for spawning in the summer through autumn such as gulf menhaden (Brevoortia patronus; Lassuy, 1983), sand seatrout (Cynoscion arenarius; Sutter & McIlwain, 1987), and striped mullet (Mugil cephalus; Hoese & Moore, 1998). The seasonal movements of striped mullet are believed to influence the seasonal distribution patterns of bay and estuary bottlenose dolphins in the Tampa Bay area as well (Scott et al., 1990; Weigle, 1990).

# Correlations Between Acoustic Detection Rate and Visual Sighting Rate

In several smaller spatial and temporal scale studies, acoustic detections and visual sightings have been well-correlated. For example, in the Shannon Estuary in Ireland, 82% of bottlenose dolphin groups sighted within 500 m of an acoustic recorder operating on a 1 min on/1 min off duty cycle were acoustically detected (Philpott et al., 2007). Despite general similarities between the acoustic and visual datasets in this study (e.g., decreased acoustic detection rates and bottlenose dolphin visual sighting rates from inshore to offshore waters), specific correlations were rarely significant. This was possibly due to changes in acoustic behavior (e.g., dolphins present but changing their sound production behavior), inaccuracies in analysis (e.g., the detection area model), or inaccuracies due to the sparse nature of the dataset.

A significant positive correlation was found between acoustic detection rates and bottlenose dolphin visual sighting rates in spring. In most regions, more visual survey effort was available for spring than in other seasons, suggesting that insufficient survey effort resulted in the low levels of correlation between the datasets. However, significant positive correlations were also found between acoustic detection rates and the visual sighting rates for Atlantic spotted dolphins (and all dolphins combined) for the Mid Shelf Central region, which did not have unusually high visual survey effort. This indicates that insufficient survey effort is not wholly responsible for the lack of significant correlations. For example, the larger detection areas of recorders in the Mid Shelf Central region result in greater overlap between acoustic detection areas and visual surveys. Although the number of significant correlations was low in this study, this type of analysis is important for the continuing development of methods to analyze cetacean abundance from acoustic recordings and is likely more reliable in less sparse datasets.

### Conclusion

The estimated area of acoustic detection on the WFS was highly variable, reflecting ambient noise levels from snapping shrimp and boats. Although both bottlenose and Atlantic spotted dolphins appear to be present on the WFS yearround, dolphin distribution appears to be spatially and seasonally nonrandom. Dolphin acoustic detection rates and bottlenose dolphin visual sighting rates were higher in shallow water and adjacent to Tampa Bay. Atlantic spotted dolphins were generally found beyond the 10-m isobath. Both species appear to have seasonal movements into more shallow waters in the summer and/or fall. These spatial and temporal distribution patterns appear to reflect the spatial and temporal patterns of potential prey species; however, the diet of Gulf of Mexico bottlenose and Atlantic spotted dolphins and the details of prey movements are not fully understood, and other factors could potentially be influencing dolphin movement (e.g., predation risk, although little is known about predation risk on the WFS). The use of both visual surveys and acoustic monitoring in this study allowed for a more thorough analysis of the distribution patterns of dolphins, and future studies with less sparse datasets will allow for more detailed comparisons of these methodologies.

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