

Identifying Foraging Hotspots of Bottlenose Dolphins in a Highly Dynamic System: A Method to Enhance Conservation in Estuaries

Paula Moreno¹ and Michael Mathews²

¹*University of Southern Mississippi, Gulf Coast Research Laboratory, Division of Coastal Sciences, 703 Beach Boulevard, Ocean Springs, MS 39654, USA*

E-mail: Paula.Moreno@usm.edu

²*2302 Sandy Lane, Bryan, TX 77801, USA*

Abstract

Estuaries are biologically productive systems that support many cetacean populations and serve as important nursery grounds for their prey but face continued habitat degradation from increasing coastal development. Because estuaries are highly dynamic systems with fine-scale environmental gradients and microhabitats, it is challenging to identify foraging hotspots. To investigate whether bottlenose dolphin (*Tursiops truncatus*) foraging hotspots occur at fine spatial (500 m) and temporal (time of day and season) scales in a large estuary in the northern Gulf of Mexico, we conducted boat surveys from January to December 2001 in five subareas of Galveston Bay, totaling 3,815 km. Using geospatial techniques, we analyzed the number of dolphins, group behavior, and environmental variables (e.g., water temperature, salinity, turbidity, number of boats and seabirds, and distance to the Gulf) on a 500-m resolution grid. We observed 1,802 dolphins in 262 groups, 57% of which were foraging. Two subareas, Bolivar Roads and the Galveston Ship Channel, comprising only one-fifth of the total surveyed area, accounted for 91% of foraging groups. We identified six foraging hotspots in these two areas that were used throughout the day and in every season. Hotspots were located in deeper channels where dolphins often foraged with bottom trawl shrimp vessels, near ferry landings, and along the jetties where prey are likely exposed or aggregated by currents and tidal fronts. In addition, a greater number of seabirds and vessels were recorded in hotspots relative to where dolphins were not observed. We suggest that this fine spatio-temporal scale approach is a valuable tool for the conservation of vulnerable estuarine cetacean populations, particularly if paired with population and site-fidelity studies. Specifically, determining prime foraging habitat and identifying baseline hotspot density (number of foraging dolphins per unit area) provides useful metrics for detecting changes in

habitat usage resulting from habitat degradation or restoration efforts.

Key Words: foraging, hotspots, cetacean, estuaries, bottlenose dolphin, *Tursiops truncatus*, conservation, Galveston Bay, Gulf of Mexico

Introduction

Habitat degradation is one of the most widespread threats to cetaceans, particularly estuarine populations that are exposed to both direct and indirect disturbance from a multitude of anthropogenic sources such as urban and industrial areas, agricultural discharges, and vessel traffic. As human populations grow exponentially along coastal zones, the level of disturbance experienced by estuarine cetacean populations is likely to increase. This situation is concerning since estuarine populations are often small and thus more vulnerable to adverse impacts, especially extreme events such as oil and chemical spills that can result in high dolphin mortality (Hayes et al., 2017). A recent example of the long-lasting impacts of industrial accidents is the extended time to recover to pre-oil spill abundance from the Deepwater Horizon accident (estimated to range from 31 to 52 years), the largest marine oil spill in United States history for three impacted estuarine populations of bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico (GOM) (Schwacke et al., 2017).

Minimizing impacts to critical areas such as foraging habitat is crucial for the conservation of slow-growing, vulnerable species. Designation of “hotspots,” including foraging hotspots, is becoming a valuable tool to guide marine conservation, particularly in efforts to preserve seabirds (Urmy & Warren, 2018) and long-lived, slow growth marine mega-fauna such as sea turtles (Wingfield et al., 2011) and cetaceans (Croll et al., 2005; Moulins et al., 2008; Jones et al., 2014). In open ocean and coastal zones, conservation has targeted high

productivity regions caused by static and dynamic features such as slopes and upwelling (Yen et al., 2004; Scales et al., 2014). In the Pacific Ocean off the Baja California Peninsula (Ulloa Bay), the California Current System brings high concentrations of nutrients, which are accompanied by high zooplankton and red crab densities, attracting predators such as sea turtles, tuna, sharks, and whales and forming an ecological hotspot (Wingfield et al., 2011). Submarine canyons are also likely to concentrate prey for many cetacean species and represent important foraging habitat (Moors-Murphy, 2014; Santora et al., 2018). For example, the canyon off the east coast of Canada known as the Gully has been designated as a Marine Protected Area (Hooker et al., 1999). Hotspots for several cetacean species were also identified in association with canyons and steep slopes in the Mediterranean Sea (Moulins et al., 2008). However, ascertaining whether foraging hotspots occur in estuaries can be challenging because the distribution of predators and prey is highly dynamic, driven by the interplay of abiotic and biotic processes operating from very short (e.g., over several hours as a result of tides or storms) to long (e.g., over months) time scales combined with spatial gradients created by topography, river discharge, distance to the ocean, etc. (Day et al., 2013). Therefore, to fully capture the range of environmental variability in estuaries and reliably identify cetacean foraging hotspots in estuaries requires fine spatio-temporal scale surveys across seasons, especially when the species is highly mobile and only visible when surfacing.

The bottlenose dolphin is the most common cetacean species in estuaries from tropical to temperate latitudes and also inhabits coastal and offshore waters. Despite being one of the most studied species, efforts to ascertain the occurrence and spatio-temporal stability of bottlenose dolphin foraging hotspots in estuaries are lacking, in part due to the need for intensive, year-round survey effort to be able to detect and adequately characterize foraging hotspots. In addition to being highly mobile predators, bottlenose dolphins are generalists and opportunistic consumers with a diverse diet and high plasticity in foraging strategies, which further complicates determining foraging hotspots. For instance, bottlenose dolphins are known to forage in association with tidal fronts, channels (Shane, 1990; Mendes et al., 2002; Hastie et al., 2003, 2004), and shrimping vessels (Fertl, 1994a; Delgado-Estrella, 1997; Kovacs & Cox, 2014), which presumably enhance foraging efficiency. The assumption is that since most of their foraging energy is spent searching for prey, foraging in areas with higher densities of prey should be energetically advantageous (Pianka, 1994). Foraging microhabitats are likely to occur in estuaries as long as prey occurrence is predictable.

The GOM estuaries, from Texas to Florida, support 31 populations of bottlenose dolphins managed as distinct stocks (Hayes et al., 2017). Galveston Bay (GB) is a highly productive estuary of national significance and is the second largest in the GOM. Bordered to the north by Houston, the fourth largest city in the U.S., the area surrounding GB is highly industrialized, including the second largest petrochemical industrial complex and the second highest shipping activity in the world. Notably, the GB shrimp fishery was valued at \$45 million in 2016 (National Oceanic and Atmospheric Administration Fisheries [NOAA Fisheries], 2017). Bottlenose dolphins occur in GB year-round but are more abundant in the spring and summer, which has been attributed to an influx of dolphins from coastal waters (Henningsen, 1991; Bräger, 1993; Fertl, 1994a, 1994b). More than 1,000 individuals have been identified and at least one-fifth are considered residents (Henningsen, 1991; Bräger, 1993); however, current abundance estimates for this population are not available (Hayes et al., 2017).

Recently, the GB bottlenose dolphin stock was designated as a high priority for research and monitoring due to the numerous threats posed by human activities (Phillips & Rosel, 2014), notably the high incidence of oil spills, which have averaged 175/year since 1998. The largest oil spill in GB (635,949 liters) occurred in 2014. More recently, in the aftermath of Hurricane Harvey, an estimated 2.65 million liters of toxic chemicals were discharged into the GB (Houston Advanced Research Center/Galveston Bay Foundation [HARC/GBF], 2017). An effective response to contain spills and avoid further degradation of important ecological habitat for this bottlenose dolphin population is needed. Damage to the environment can be reduced by timely and proper use of response resources. Identifying foraging hotspots is an important step to help in planning cleanup efforts to ensure the adequate and timely deployment of containment and recovery equipment in case of a spill. More broadly, a rapid assessment to characterize foraging hotspots (i.e., the number, size, density, and location) for bottlenose dolphin populations would provide a baseline from which changes of foraging habitat due to pollution or other threats could be measured helping to prioritize conservation and restoration efforts for the 30+ estuarine bottlenose dolphin populations in the GOM. In addition, a better understanding of the environmental attributes of foraging hotspots can provide insights into the ecological processes underlying prime foraging habitat for bottlenose dolphins in estuaries.

We hypothesized that the GB bottlenose dolphins forage consistently in certain areas of the estuary where detection and capture of prey may be enhanced. Our goals were to (1) determine whether

areas with high incidence of foraging occur in the GB estuary and, if so, to characterize these hotspots and determine whether they are stable for short and long temporal scales (i.e., throughout the day and across seasons); (2) evaluate the proportion of foraging relative to non-foraging activities (i.e., the foraging budget); and (3) estimate the mean group size during foraging and determine whether it varies with location.

Methods

Study Area and Data Collection

The Galveston Bay estuary (29° 30' N, 94° 40' W), located on the east Texas coast, is the second largest estuary on the northern Gulf of Mexico (Figure 1). It is 50 km long and 27 km wide, with an area of 1,600 km². GB is a shallow estuary (average depth of 3 m) with mud and sand flats and dredged channels of up to 12 m in depth that are maintained for commercial navigation. In addition

to shipping, commercial and recreational fisheries are also important human uses of the GB. The main inlet to the GOM, Bolivar Roads (BRD), is jettied and accounts for 80% of the tidal exchange (Galveston Bay Estuary Program [GBEP], 2002). As is typical of most GOM estuaries (Nelson & Monaco, 2000), GB contains three salinity zones: (1) tidal fresh (< 0.5 ppt), (2) mixing zone (0.5 to 25 ppt), and (3) a seawater zone (> 25 ppt). The boundaries of these salinity zones vary seasonally. The lower GB surveyed area, comprised of 221 km², was divided into five adjacent locations with different natural and anthropogenic environmental conditions: (1) Bolivar Roads (BRD), (2) Galveston Ship Channel (GSC), (3) Houston Ship Channel (HSC), (4) Back Bay (BB), and (5) West Bay (WB) (Figure 1). We conducted 367 surveys in 5 and 6 m vessels over 124 d from 22 January to 29 December 2001 for a total of 3,814.77 km on-effort. Surveys were stratified by location/month/time of day. If weather conditions

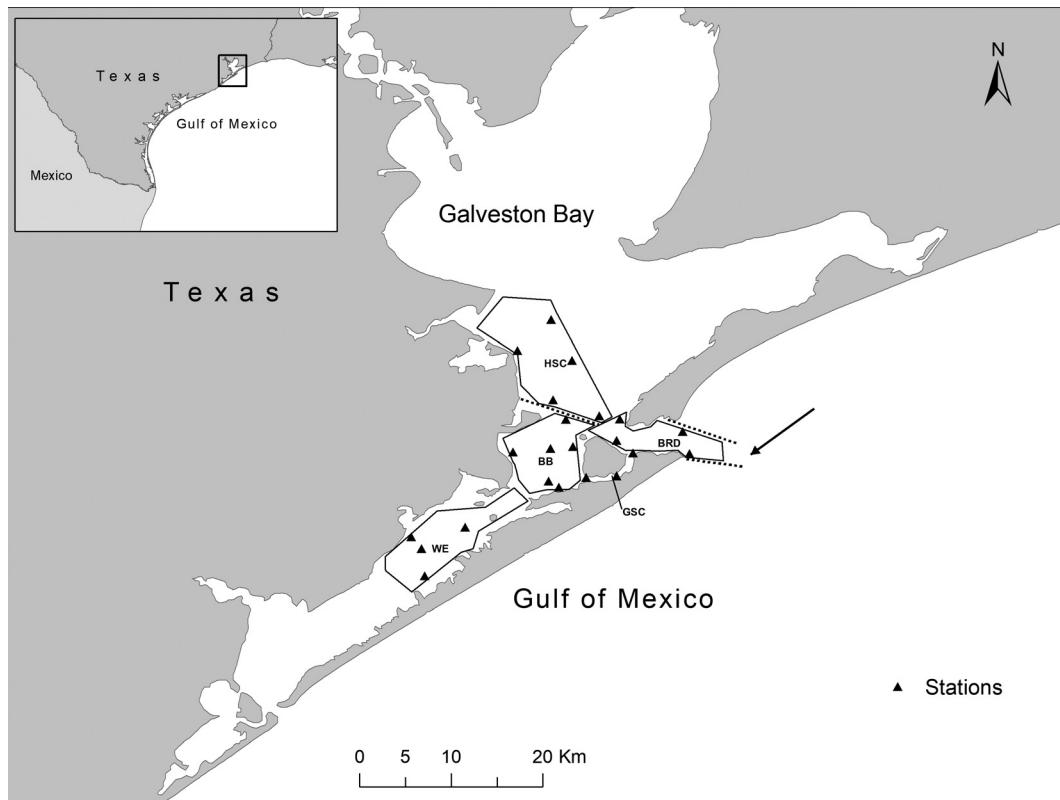


Figure 1. Map of Galveston Bay (square within inset), Texas, and the five surveyed locations: West Bay (WE; Area: 55.08 km²), Back Bay (BB; Area: 47.34 km²), Houston Ship Channel (HSC; Area: 83.36 km²), Bolivar Roads (BRD; Area: 31.58 km²), and Galveston Ship Channel (GSC; Area: 3.95 km²). Environmental data were collected at fixed stations (triangles) or after sightings. Jetties shown as dotted lines. The end of the jetties represents the zero-distance (arrow) from the Gulf of Mexico.

allowed, each location was surveyed at least once a month in the morning, midday, and afternoon. Time of day categories were formed by dividing the hours between sunrise and sunset into three equal intervals. Survey tracks consisted of pre-defined routes traveled at an average speed of 14 km h⁻¹. Geographic positions were recorded by GPS at 1-min intervals for subsequent estimation of effort and mapping of dolphins and environmental data.

When a group of dolphins was first sighted, search effort ceased. The number of adult dolphins and calves was estimated, and group behavior was classified using scan sampling and instantaneous recording (Martin & Bateson, 1993) for 5 min. A group was defined as all dolphins within 100 m of their nearest neighbor either moving together, performing similar activities, or interacting (adapted from Wells et al., 1987). Behaviors were classified as foraging, which includes following a shrimp vessel, traveling, socializing, resting, and unknown (adapted from Shane, 1990; Hanson & Defran, 1993). Foraging is searching for and capturing prey, identified by behaviors such as frequent dives, often with changes in direction, with body and peduncle arched; tossing fish; and fish in the mouth and includes the behaviors described above when foraging with shrimp vessels. Because foraging is the focus of this study, we pooled traveling, socializing, and resting into a single category ("Other"). Since more than one behavior may occur in the same group, when the animals in a group were engaged in foraging and another behavior, we assigned the group to "Foraging," except when analyzing activity budget in which case they were assigned to "Mixed Foraging."

To maintain consistent detection of dolphins, we implemented the following protocol: (1) surveys were only conducted at or below Beaufort sea state 3; (2) one observer covered 90° from the bow to the right, and a second observer covered 90° to the left; (3) groups detected when off search effort (e.g., while following another group or while collecting environmental data) were excluded; and (4) groups detected beyond 200 m from the survey position were excluded *a posteriori* using *ArcGIS* (Environmental Systems Research Institute [ESRI], 2004).

We recorded environmental data at 22 fixed stations (Figure 1) and after a group scan when the group was detected more than 500 m from a station or if more than 1 h had elapsed since the previous measurement. We recorded surface salinity (ppt measured with a refractometer), surface water temperature (°C with a digital thermometer), turbidity (meters determined with a Secchi disk), and Beaufort sea state scale as descriptors. In addition, we recorded the number of shrimp vessels,

the number of non-shrimp boats, and the number of seabirds within a 200-m radius using 1-min scan sampling. Shrimp vessels within 200 m of the transect line were counted on-effort.

For the seasonal analysis, we used temperature and salinity seasons. Salinity seasons were defined as dry (February, May, July, August, and November) and wet (remaining months) by classifying months according to whether the estimated monthly freshwater balance in GB—as computed by the Texas Water Development Board (TWDB) (n.d.)—fell above or below the annual mean calculated over a 9-y period (1992 to 2000). Likewise, temperature seasons were assigned to warm (April to November) and cold (remaining months) depending on whether monthly water temperature rose above or fell below the annual mean calculated over a 5-y period (1996 to 2000) (National Oceanic and Atmospheric Administration [NOAA], 2004; Texas Coastal Ocean Observation Network [TCOON], n.d.).

Geospatial Data Preparation

Using *ArcGIS* geospatial tools (ESRI, 2004), we created a 500-m cell grid of the water surface of GB. To optimally represent observed environmental conditions, surface maps of environmental variables measured during the same survey strata (location/date/time of day) were created by Inverse Distance Weighted interpolation on the gathered data. When more than one measurement was available per cell, the mean value was used. Dolphin counts and shrimp vessels were continuously recorded on-effort and, thus, were not interpolated.

In addition to the environmental data recorded during the surveys, we calculated mean depth and distance to the main pass to the GOM (BRD; Figure 1) for each cell. Depth was obtained from GEODAS 7.5 min × 7.5 min bathymetric maps with a 30-m cell resolution (NOAA/National Centers for Environmental Information [NCEI], n.d.). To obtain the depth of each cell, we overlaid 184,703 soundings with the grid of the study area and calculated the mean value for each cell. To calculate the distance of each cell to the GOM, we used the *ArcGIS* CostDistance function to calculate the shortest path by water from each cell grid to the GOM.

To calculate *on-effort* distances, we parsed the GPS survey tracks into on-effort sets of points as determined by recorded stop/resume times. These sets were used to construct line segments, which were intersected with the grid cells and were integrated with the other georeferenced datasets (i.e., dolphin, shrimp vessel, and environmental data). We defined *mean foraging rate* as the mean number of dolphins foraging standardized by

survey effort (i.e., the number of times that the cell was surveyed).

To calculate the proportion of observed behaviors (i.e., behavioral budget) and group size, a matrix stratified by date, time of day, and cell were used. This matrix was then aggregated to the level of month, time of day, and cell for the remaining analysis. Medians were used due to the skewed distribution of most of the variables. We refer to *occurrence* as a data point that represents one to two groups of dolphins encountered in the same month, time of day, and cell. Of the total occurrences, only six resulted from combining multiple groups. Because individual dolphins can be resighted during surveys, number of dolphins does not imply number of distinct individuals.

Statistical Analysis

Foraging densities (mean foraging rates/km²) were calculated using a kernel density analysis with a 10-m raster resolution and 1-km search radius. We performed separate kernel density analyses for subsets of seasons (warm and cold) and time of day (morning, midday, and afternoon). We defined a *foraging hotspot* (hereafter hotspot) as a region with foraging density at or above 2 standard deviations (SDs) above the mean.

To determine whether foraging occurrences exhibited a spatial pattern or were randomly distributed, we used the Global Moran's I function on the mean foraging rate using the Euclidean distance. A Moran's I value near +1.0 indicates clustering, a value near -1.0 indicates dispersion, and the z-score value indicates if it is statistically significant (Cressie, 1993; ESRI, 2004).

To evaluate the level of clustering of sightings with high and low mean foraging rates, we used the Getis-Ord General G Index (Cressie, 1993; ESRI, 2004). A high/low index value indicates that high/low values are clustered within the study area and z scores indicate whether the index value is statistically significant.

To compare the location of the overall mean center of the hotspots in different seasons and times of day, we obtained the mean center based on Euclidean distance and weighted by foraging density. All geospatial analyses were performed in *ArcGIS*.

To test the null hypotheses that foraging group size is the same in GSC and BRD, we used the median test, a distribution-free procedure, which is suitable for small samples and assumes that all samples have the same shape but is stable when the sample shapes are not quite the same (Zar, 1996). Median tests were also used to compare environmental conditions in the hotspots to those in the overall study area and in the main foraging locations (GSC and BRD) where dolphins were not observed. In the above median

tests, we used the Yates adjustment to correct for the upward bias of the Chi-squared test for 2x2 comparisons (Yates, 1934). The latter tests were bootstrapped 1,000 times (on overall area subset) and 2,000 times (on the GSC/BRD subset) on random subsamples ($n = 100$) of environmental conditions where dolphins were not sighted. To test the null hypothesis that foraging density was the same among hotspots, the non-parametric Kruskal-Wallis test was used. Statistical analyses were performed with the *SPSS 12.0* and *R 2.0.1* packages.

Results

From January to December 2001, 1,802 dolphins were observed in 262 groups. Foraging was the most commonly observed behavior, representing 56.87% of the total groups (Figure 2) and 66.52% of identified behaviors. Of the foraging groups, which could include resightings of individuals throughout the year, about one-third (33.56%) consisted of mixed behavior groups; most groups were exclusively foraging and numbered 632 dolphins (Figure 3).

The foraging group size ranged from 1 to 30, and the median was six, even when foraging groups with mixed behaviors were excluded. Likewise, the median group size for non-foraging groups was six (Table 1). Foraging group size was significantly smaller ($p < 0.001$) in GSC (median = 4) than in BRD (median = 7) ($\chi^2[1] = 16.119, p < 0.001$). In GSC, the mode was two dolphins per group; and in BRD, it was three-fold higher. It is noteworthy that BRD is five-fold wider (2.5 vs 0.5 km) and twice the length of GSC (11 vs 6.5 km), or about 10 times the area of GSC (Table 1).

Behavioral Budget

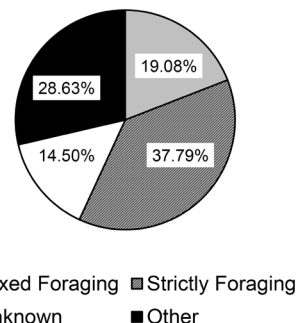


Figure 2. Behavioral budget shown as a percentage of behaviors for dolphin groups ($n = 262$). Mixed Foraging = foraging and other behavior(s) in the same group, Strictly Foraging = only foraging in the same group, Unknown = undetermined, and Other = not foraging. Foraging is comprised of Mixed and Strictly Foraging.

Table 1. Summary statistics for group sizes of the overall foraging in Bolivar Roads (BRD), Galveston Ship Channel (GSC), and in all locations combined (when including mixed groups, F+Fmix, and excluding mixed groups, F). Non-foraging groups (Other) found in all locations.

	Area	<i>n</i>	Mean	SE	Median	Mode	Min.	Max.
BRD	31.58 km ²	59	9.03	± 0.74	7.00	6	1	30
GSC	3.95 km ²	76	5.63	± 0.47	4.00	2	1	19
F+Fmix		149	6.90	± 0.41	6.00	6	1	30
F		99	6.38	± 0.50	6.00	2†	1	30
Other		59	7.63	± 0.74	6.00	8	1	25

†Multiple modes exist. The smallest value is shown.

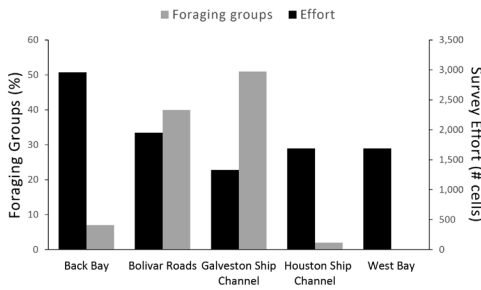


Figure 3. Percentage of total foraging groups and survey effort (total number of cells sampled) by location: Back Bay (BB), Bolivar Roads (BRD), Galveston Ship Channel (GSC), Houston Ship Channel (HSC), and West Bay (WE).

Of 149 foraging groups, 135 were found in GSC (*n* = 76) and BRD (*n* = 59). These two locations comprise about one-fifth (21.49%) of the surveyed area, yet accounted for the majority (91%) of the foraging groups (Figure 3). The higher percentage of foraging groups in GSC and BRD relative to the other areas is not a result of disproportionate sampling: WE has a level of effort similar to BRD but the lowest proportion of foraging groups, while GSC has the lowest sampling effort but accounts for the largest proportion of foraging groups (Figure 3).

The foraging rate (i.e., number of foraging dolphins standardized by survey effort) in BRD (mean = 7.30; SE = 0.83) was more than two-fold higher than in GSC (mean = 3.02; SE = 0.35; Table 2).

The higher mean foraging rate observed in BRD was not an artifact caused by differences in range of detection in the wider expanse of BRD compared to GSC since a constant search distance (200-m radius) was used, and all groups that were beyond this distance were excluded to ensure equal detectability.

The distribution of foraging events exhibited a highly clustered pattern with a less than 1% likelihood of occurring by chance (Moran’s I Index = 0.14; *z* = 5.5). In terms of the overall foraging distribution, the clusters of low foraging rate sightings exhibited a higher degree of aggregation than did the clusters of high foraging rate sightings (General G Index = 0.084; *z* = -2), indicating large continuous areas where no foraging was observed. The overall foraging density (mean foraging rate km²) was clustered into six foraging hotspots: GSC1 and GSC2 inside the GSC; BRD4, BRD8, and BRD10 in BRD; and GSC3 at the confluence of GSC and BRD (Figure 4).

Foraging density differed among hotspots (Kruskal-Wallis *H* = 35.08; *p* < 0.001). The main foraging hotspots were BRD8 and GSC3, where foraging density surpassed 3 SD (above 42.86 mean foraging rate/km²), followed by BRD4 and GSC2 (Figure 5). The lowest density hotspots were BRD10 and GSC1. The most persistent foraging hotspot across seasons and time of day was GSC3, followed by BRD8 and BRD10. The weighted mean center of foraging hotspots shifted slightly with temperature season and time of day. In the cold season (Figure 6a), the mean center was located inside the GSC; and in the warm

Table 2. Summary statistics for the foraging rate (number of foraging dolphins/number times cell sampled) in Bolivar Roads (BRD) and Galveston Ship Channel (GSC)

	<i>n</i>	Mean	SE	Median	Min.	Max.
BRD	57	7.30	± 0.83	5.00	0.50	30.00
GSC	72	3.02	± 0.35	2.00	0.20	15.00

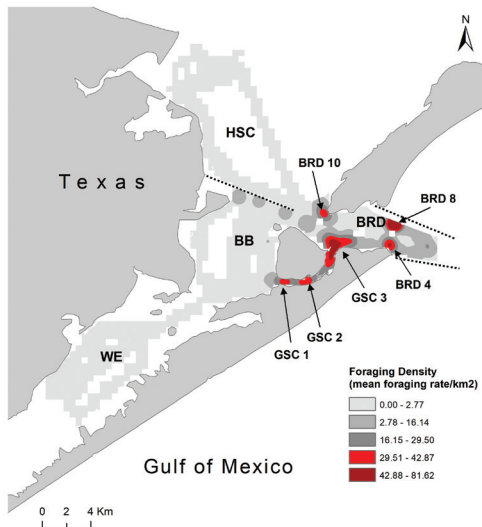


Figure 4. Location and densities (mean foraging rate/ km^2) of foraging hotspots for all seasons and time of day. Hotspots (red shades) include foraging densities that are 2 SD = [29.51, 42.87] and 3 SD = [42.88, 81.62] above the mean.

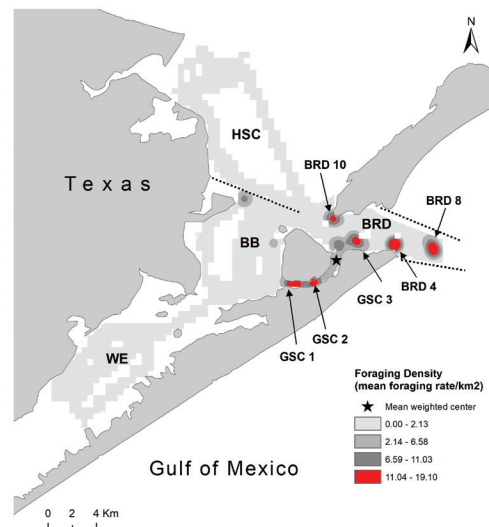


Figure 6a. Location and densities (mean foraging rate/ km^2) of foraging hotspots during the cold season. Hotspots (red) include foraging densities that are 2 SD = [11.04, 19.10] above the mean. The mean weighted center of the hotspots is indicated (star).

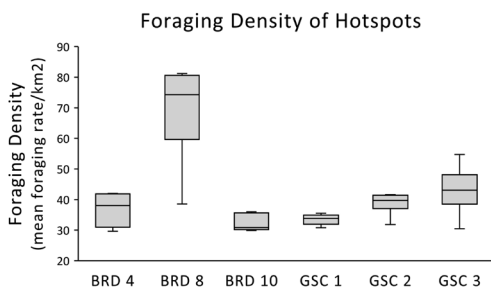


Figure 5. Foraging density of hotspots for all seasons and time of day (morning, midday, and afternoon) in Bolivar Roads (BRD 4, BRD 8, and BRD 10) and in Galveston Ship Channel (GSC 1, GSC 2, and GSC 3).

season (Figure 6b), the mean center was situated in BRD. Similarly, the mean center was positioned in the GSC in the morning (Figure 7a) and in BRD from midday (Figure 7b) to afternoon (Figure 7c).

Overall, the environmental conditions in the five locations were highly variable and covered a wide range of habitat types as illustrated—for example, by distance to the GOM (0.75 to 38 km) and depth (0.2 to 14 m) (Table 3). Except for turbidity and water temperature, environmental conditions in the hotspots compared to those in the entire study area where dolphins were not observed differed

significantly (Table 4). In general, foraging hotspots were deeper and closer to the GOM and exhibited higher salinity and higher number of boats, seabirds, and shrimp vessels (Table 5).

In GSC and BRD, comparing the environmental conditions in the hotspots to environmental conditions outside of the hotspots where dolphins were not observed revealed that the hotspots were deeper and tended to have higher numbers of seabirds (Table 6). Other environmental parameters (e.g., distance, water temperature, turbidity, salinity, and number of shrimp vessels and other boats) were not significantly different (Table 7).

Discussion

There is a growing need for effective tools for the conservation of cetacean populations in estuaries as the impacts from human activities in estuaries intensify and expand. While conservation efforts in coastal and offshore waters often target foraging hotspots (as well as biodiversity hotspots) to protect cetaceans and other marine megafauna, this approach has not been pursued in estuaries. Our study showed the importance of GB as a foraging area for bottlenose dolphins and, more significantly, demonstrated that foraging hotspots occur and are stable over the course of a year in a dynamic estuarine environment. These foraging hotspots offer candidate areas for enhanced

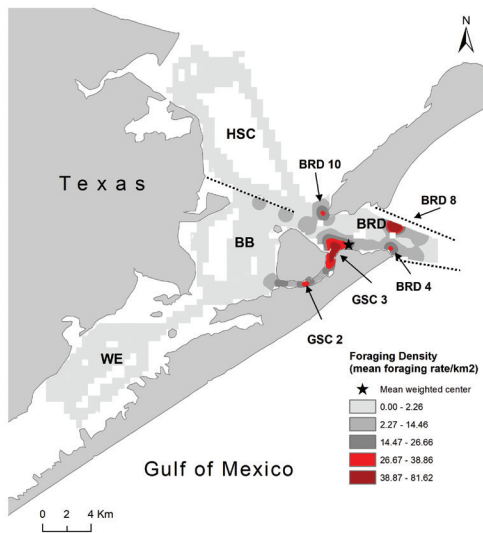


Figure 6b. Location and densities (mean foraging rate/km²) of foraging hotspots during the warm season. Hotspots (red shades) include foraging densities that are 2 SD = [26.67, 38.86] and 3 SD = [38.87, 81.62] above the mean. The mean weighted center of the hotspots is indicated (star).

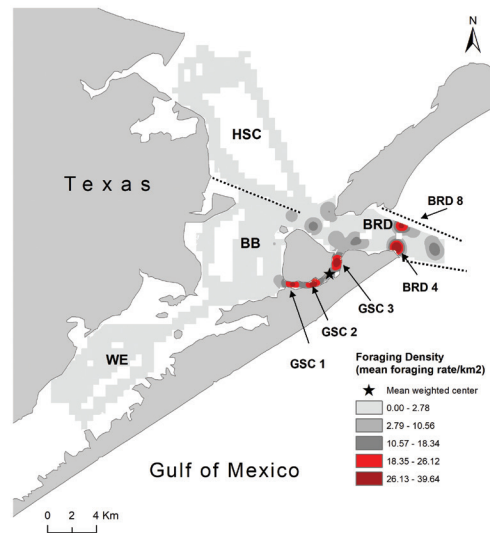


Figure 7a. Location and densities (mean foraging rate/km²) of foraging hotspots in the morning. Hotspots (red shades) include foraging densities that are 2 SD = [18.35, 26.12] and 3 SD = [26.13, 39.64] above the mean. The mean weighted center of the hotspots is indicated (star).

conservation that may be beneficial for bottlenose dolphins as well as other species.

Foraging Budget

Foraging was the predominant activity (57% of groups when groups with mixed behaviors are included) for bottlenose dolphins in the GB estuary during daylight hours and is within the range reported previously in the GB and adjacent coastal waters. For instance, Henningsen (1991) found that foraging comprised 42% of all behaviors, and Bräger (1993) reported substantial variation between the summer (0 to 95%) and fall (40 to 70%). In the westernmost portion of GB, Maze & Würsig (1999) reported that foraging was the prevalent behavior, while Henderson & Würsig (2007) found a difference between resident dolphins (only about 20% foraging) in the same area and GOM dolphins (up to about 43% foraging). Although some of these differences among GB studies can be attributed to methodological differences (e.g., in behavioral categories and the assignment of concurrent behaviors in the same group), it is also likely that other factors such as annual variation in prey availability and the influx of transient dolphins influence the proportion of foraging observed. In other estuaries, foraging is also highly variable for *Tursiops* sp. For example, a lower proportion of foraging (28%) was observed for bottlenose dolphins in the Shannon estuary in Ireland (Baker et al., 2017) than in the

highly urbanized Port River Estuary in Adelaide, South Australia, where foraging varied between ~35 to 47% for the Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Steiner, 2012).

A high incidence of dolphin foraging activity is not surprising considering the role of estuaries as nurseries for many fish species (Alongi, 1998; McLusky & Elliot, 2004) that comprise a large portion of the bottlenose dolphin's diet. The most important prey species for bottlenose dolphins in GOM estuaries (Atlantic croaker [*Micropogonias undulatus*], pinfish [*Lagodon rhomboids*], and spot [*Leiostomus xanthurus*]) (Barros & Odell, 1990; Barros & Wells, 1998; Gannon & Waples, 2004) are very abundant year-round in GB (Nelson, 1992; Nelson & Monaco, 2000). Shrimp fishing vessels that operate year-round in parts of GB are also a reliable source of prey. Bottlenose dolphins were observed foraging with shrimp vessels, either behind the nets or at the side of the vessel feeding on discards. This association with bottom-trawling has been described previously for GB (Fertl, 1994a, 1994b) and throughout the GOM as well as in other regions around the world (Delgado-Estrella, 1997; Fertl & Leatherwood, 1997; Kovacs & Cox, 2014).

Foraging Areas and Group Size

The main foraging areas for bottlenose dolphins in the lower GB were the GSC and BRD (two out of the five surveyed locations), which accounted for

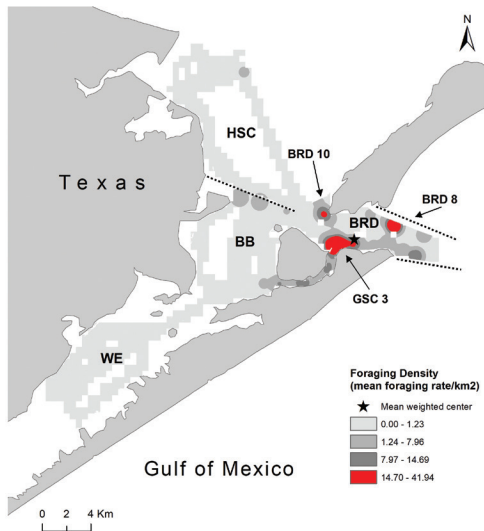


Figure 7b. Location and densities (mean foraging rate/ km^2) of foraging hotspots in the midday. Hotspots (red) include foraging densities that are 2 SD = [14.70, 41.94] above the mean. The mean weighted center of the hotspots is indicated (star).

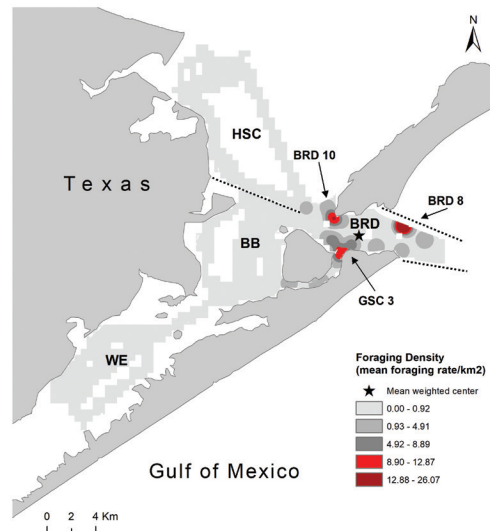


Figure 7c. Location and densities (mean foraging rate/ km^2) of foraging hotspots in the afternoon. Hotspots (red shades) include foraging densities that are 2 SD = [8.90, 12.87] shown in red and 3 SD = [12.88, 26.07] above the mean. The mean weighted center of the hotspots is indicated (star).

91% of the foraging groups. This is likely related to the higher occurrence of dolphins in these two areas (Henningson, 1991; Henningson & Würsig, 1991). BRD is at the mouth of the estuary, which is considered a mixing area for GB resident and transient dolphins from the GOM.

The preference of dolphins for the southern part of the GB (GSC and BRD) cannot be accounted for strictly by the presence of shrimp vessels since shrimpers are almost absent from BRD while being common in the northern part of the bay (HSC). The increasing trend of fish size, from smaller in the north to larger in the south (Patillo et al., 1995), and greater diversity of prey species in GSC and BRD (Nelson & Monaco, 2000) are also possible explanations. Perhaps more importantly, some of the preferred prey of bottlenose dolphins in estuaries (e.g., Atlantic croaker, pinfish, and spot) are most abundant in conditions of moderate (0.5 to < 25 ppt) and high (> 25 ppt) salinity, which are prevalent in GSC and BRD (Nelson, 1992; Nelson & Monaco, 2000). Allen et al. (2001) found that in two distinct inshore sites on the GOM (off eastern Florida), bottlenose dolphins foraged preferentially in non-seagrass habitat where the size of their preferred prey (pinfish) was larger. Therefore, it is possible that the fishes that are preferred prey occur in greater numbers or larger size at the mouth of the GB, which is

supported by the higher salinity measured in the foraging hotspots compared to the lower salinity recorded in locations of the GB where dolphins were not detected.

Although a high proportion of the foraging groups were sighted in GSC, the mean foraging rate was higher in BRD, indicating that more dolphins forage in this area at any given time. This difference is explained by the lower mean group size observed in GSC (~6) than in BRD (~9), suggesting that the physical environment is an important determinant of group size. Although both channels are approximately 10 m deep on average, GSC is substantially smaller than BRD, which is longer and four to five times wider. Spacing and orientation among group members are important elements of the sociality of cetaceans (Norris & Dohl, 1980; Shane et al., 1986). It is possible that in a narrow channel with heavy vessel traffic, such as GSC, a larger group size would impede dolphins from maintaining optimal social spacing. Food availability has also been noted to be a determinant of group size in delphinids (Würsig, 1978); thus, the larger foraging groups and higher mean foraging rate in BRD could result from higher food availability in BRD. Larger groups in BRD may also be related to distinct foraging strategies (i.e., a wider area being conducive to more cooperative strategies).

Table 3. Summary statistics of the environmental variables measured in Galveston Bay from January to December 2001 ($n = 4,298$ cells)

Environmental variables	Mean	SD	Min.	Max.	Range
Depth (m)	3.56	±3.22	0.20	13.99	13.79
Distance to the Gulf (GOM) (km)	18.79	±8.87	0.75	38.08	37.33
Turbidity (m)	0.51	±0.19	0.10	1.30	1.20
Salinity (ppt)	19.13	±5.68	0.03	35.00	34.97
Water temperature (°C)	22.99	±6.49	8.59	32.65	24.06
No. seabirds	9.37	±15.02	0.00	150.00	150.00
No. boats	0.49	±0.80	0.00	9.00	9.00
No. shrimp vessels	0.04	±0.19	0.00	4.00	4.00

Table 4. Test statistics from the median test comparing environmental variables in the entire Galveston Bay where dolphins were not observed to those in foraging hotspots. An example from the bootstrapping procedure (1,000 repetitions) is shown.

	Median	χ^2	df	p	Yates' Continuity Correction		
					χ^2	df	p
Depth (m)	5.57	50.05	1.00	0.00*	47.97	1.00	0.00*
Distance to the GOM (m)	12,769.61	51.96	1.00	0.00*	49.85	1.00	0.00*
Turbidity (m)	0.51	2.89	1.00	0.09	2.41	1.00	0.12
Salinity (ppt)	20.50	10.15	1.00	0.001*	9.22	1.00	0.002*
Water temperature (°C)	24.50	0.26	1.00	0.61	0.13	1.00	0.72
No. seabirds	8.01	58.37	1.00	0.00*	56.13	1.00	0.00*
No. boats	0.50	27.71	1.00	0.00*	26.17	1.00	0.00*
No. shrimp vessels	0.00	13.80	1.00	0.00*	11.81	1.00	0.00*

*Denotes test was significant ($p < 0.05$).

Spatial and Temporal Changes in Distribution and Density of Foraging Hotspots

For highly mobile predators and prey, such as dolphins and fish, foraging efficiency depends on optimizing search and capture times. Search time may be decreased by a higher density of prey, while hunting time may be reduced as a result of conditions that facilitate capture of prey. Since food resources in estuaries are typically patchy, and dolphins are opportunistic foragers that have the ability to locate and exploit favorable foraging conditions (e.g., exploiting shrimp trawl discards), we hypothesized that bottlenose dolphins would consistently forage in high-prey patches, or hotspots, thereby benefiting from the reduction of search and hunting (or capture) time.

We observed that hotspots may shift, expand, or contract and that they can also appear and disappear on a seasonal basis or at shorter temporal

intervals (i.e., time of day); however, the two main hotspots, approximately 3 km², were stable across temperature seasons. From the warm to the cold season, the foraging density decreased, and the spatial center of the combined hotspots shifted from BRD to GSC. The warm season (April to November) largely overlaps with the peak of dolphins in the GB (spring to fall; Henningsen, 1991; Bräger, 1992; Fertl, 1994a) and corresponds to the highest number of fish species in the GB (March to October; Nelson & Monaco, 2000).

The seasonal shift of the center of foraging activity from BRD (warm months) to GSC (cold months) suggests that during the cold months, dolphins in the GB may rely more heavily on shrimpers fishing in GSC, possibly because of the overall reduction of fish in the bay. The higher foraging density in warm months could be due to an increase in the number of dolphins in the bay—attracted to a

Table 5. Frequency of observations less or equal (\leq) and above ($>$) the median (\bar{x}) of environmental variables in the entire Galveston Bay (GB) where dolphins were not observed compared to foraging hotspots. An example from the bootstrapping procedure (1,000 repetitions) using subsets of 100 randomly selected cells is shown.

Environmental predictors	GB – No dolphins		Foraging hotspots	
	$\leq \bar{x}$	$> \bar{x}$	$\leq \bar{x}$	$> \bar{x}$
Depth*	73	27	17	66
Distance to the GOM*	26	74	66	17
Turbidity	56	44	36	47
Salinity*	61	39	31	52
Water temperature	52	48	40	43
No. seabirds*	76	24	16	67
No. boats*	68	32	24	59
No. shrimp vessels*	99	1	70	13

*Denotes median test was significant ($p < 0.05$). Details in Table 4.

Table 6. Frequency of observations less or equal (\leq) and above ($>$) the median (\bar{x}) of environmental variables in the Bolivar Roads (BRD) and Galveston Ship Channel (GSC) where dolphins were not observed compared to foraging hotspots. An example from the bootstrapping procedure (2,000 repetitions) using subsets of 100 randomly selected cells is shown.

Environmental predictors	BRD & GSC – No dolphins		Foraging hotspots	
	$\leq \bar{x}$	$> \bar{x}$	$\leq \bar{x}$	$> \bar{x}$
Depth*	59	41	29	54
Distance to the GOM	52	48	42	41
Turbidity	58	42	35	48
Salinity	47	53	45	38
Water temperature	49	51	43	40
No. seabirds*	58	42	34	49
No. boats	56	44	36	47
No. shrimp vessels	92	8	70	13

*Denotes median test was significant ($p < 0.05$). Details in Table 7.

higher prey availability—and/or a higher degree of aggregation of foraging dolphins. Although previous studies have reported higher numbers of dolphins in the GB during the summer and fall, and speculated that this could be attributed to an influx of transient dolphins, a conclusive resolution would require a mark-recapture study to identify GB residents and determine migration rates into and out of the bay.

Hotspots were confined to two connected and equally deep (~10 m), dredged channels with heavy vessel traffic. BRD is a wide (2.5 km) jet-tied area at the mouth of the estuary and the main inlet, accounting for 80% of tidal exchange with the GOM. GSC is a much shorter and narrower

channel (~0.5 km), where shrimp trawling is frequent year-round. Conditions that are common in deep channels around jetties and regions with strong currents promote the aggregation of fish. Fish often select the bottom of deep channels where salinity and temperature conditions are more stable (Patillo et al., 1995). Jetties constructed of large boulders line half of BRD's length, offering fish a food supply and shelter from predators and currents (Bohnsack & Sutherland, 1985; Bohnsack, 1989; Pickering & Whitmarsh, 1997; Walker et al., 2002). Tidal fronts concentrate nutrients and phytoplankton which create favorable feeding conditions for a variety of predators, including fish, seabirds, and dolphins

Table 7. Test statistics from the median test comparing environmental variables in the Bolivar Roads and Galveston Ship Channel where dolphins were not observed to those in foraging hotspots. An example from the bootstrapping procedure (1,000 repetitions) is shown.

	Median	χ^2	df	p	Yates' Continuity Correction		
					χ^2	df	p
Depth (m)	9.09	10.52	1	0.001*	9.58	1	0.002*
Distance to the GOM (m)	9,774.30	0.04	1	0.85	0.002	1	0.97
Turbidity (m)	0.50	4.55	1	0.03*	3.94	1	0.06
Salinity (ppt)	22.00	0.95	1	0.33	0.68	1	0.41
Water temperature (°C)	25.40	0.14	1	0.71	0.05	1	0.82
No. seabirds	12.99	5.27	1	0.02*	4.61	1	0.03*
No. boats	2.89	2.89	1	0.09	2.41	1	0.12
No. shrimp vessels	2.62	2.62	1	0.11	1.92	1	0.17

*Denotes test was significant ($p < 0.05$).

(Dustan & Pinckney, 1989). While these zones of high turbidity may offer protection to fish from visual predators, fish still remain susceptible to echolocating dolphins that can take advantage of this congregation of prey. Furthermore, bottlenose dolphins are known to feed against the current, a counterforce thought to act as a boundary that limits fish movements and, hence, facilitates their capture (Shane, 1990).

The affinity of foraging bottlenose dolphins with high turbulence zones is well-documented elsewhere, including estuaries, bays, and other coastal systems. In Moray Firth, Scotland, the higher abundance of bottlenose dolphins feeding at the mouth of the estuary is thought to result from a bottleneck restricting the dispersion of fish (Wilson et al., 1997; Mendes et al., 2002; Hastie et al., 2003, 2004, 2006). Similarly to our study, bottlenose dolphins in the Moray Firth preferentially foraged in deeper, narrow channels with steep seabed slope. While in the Moray Firth, there was no significant difference in sightings with tidal or diurnal cycles; sightings peaked in the summer (June-July), which was attributed to the salmon migration. Topography and physical properties of the Moray Firth, such as strong currents and haloclines, were suggested as factors that lead to re-orientation and aggregation of salmon, thereby facilitating capture by dolphins. A recent fine-scale investigation of the hydrodynamics of a hotspot of harbor porpoises (*Phocoena phocoena*) in Moray Firth also confirmed this species' preference for high turbulence regions (Jones et al., 2014).

The funneling effect of channels on prey at the mouth of an estuary likely occurs in the jettied channel of BRD. However, finer-scale circulation

patterns (e.g., around pilings, ferry landings, and breaks in the jetties) may also contribute to the formation of hotspots. Off the Sein Island in Brittany, strong currents around submersed rocks also characterize one of the main feeding sites for bottlenose dolphins (Liret, 2001).

We propose that the main hotspots constitute areas where fish aggregate or where prey capture is facilitated by a combination of static and dynamic environmental features, including jetties, estuarine plumes, shrimp trawling vessels, and ferries churning up the bottom. A hotspot in BRD was located adjacent to a break in the jetty, a structure that also creates high turbulence. One of the hotspots was located where two channels, GSC and BRD, meet—a zone of confluence where estuarine plumes are often visible at the surface. Shrimp vessels that trawl in the GSC often haul nets in this confluence area and discard fish, attracting dolphins and seabirds. In addition, we observed hotspots at the end points of the ferry crossings. Ferries stir up bottom sediments that may have a similar confining effect as currents, or their undersea wake may simply dislodge or startle fish from the bottom. Future studies that take into account the hydrodynamic conditions in the hotspots and adjacent waters would provide further insights into the mechanisms that create them. Since the GB has a small tidal amplitude (0.5 m; Salas-Monreal et al., 2017), rather than investigating the role of tides, a better understanding of hotspot dynamics would be gained from characterizing the currents at fine scale within the southern part of the GB while concurrently quantifying prey densities using an echo-sounder or bottom trawl nets.

It should be noted that other factors, namely predation by sharks (Heithaus & Dill, 2002), bottlenose dolphin social structure (Urian et al., 2009), or environmental factors that were not measured (e.g., dissolved oxygen, which is known to affect prey distribution and dolphin foraging habitat), may also influence foraging distribution.

Environmental Attributes of Foraging Hotspots

To characterize prime foraging habitat for bottlenose dolphins in the GB, we examined the environmental conditions within the hotspots. When compared to the entire study area where we did not observe dolphins, hotspots tended to be closer to the GOM, in deeper waters with higher salinity, and, as mentioned above, in zones of confluence where estuarine plumes and strong currents may play an important role in aggregating prey.

Hotspots were associated with higher numbers of seabirds, shrimp vessels, and other boats. This suggests that these hotspots are also relevant for seabirds. Although associations of dolphins foraging with seabirds and shrimp boats have frequently been noted, and the effects of vessel traffic on bottlenose dolphins have also been examined, seabirds have only rarely been used in spatially explicit studies of bottlenose dolphin foraging habitat in estuaries (Torres, 2009); and to our knowledge, vessels have not been previously used and appear to be useful at least when fishing and vessel traffic are intensive.

Boats may have both direct (e.g., prey discarded from shrimp boats and fish attracted by bait deployed from recreational fishing boats) and indirect effects on prey distribution. Stationary vessels (e.g., tankers anchored in BRD) may lead to the aggregation of fish seeking shelter from predators. On the other hand, shrimp bottom trawlers and ferries stir up the bottom as evidenced by the mud plumes trailing these vessels. Dislodged from the bottom or shelter, prey may become disorientated and are more vulnerable to predation. Unfortunately, we cannot ascertain whether the association with boats is coincidental (i.e., resulting from the higher occurrence of recreational fishing in favorable feeding areas) or whether the boats themselves may be attracting prey. Although bottlenose dolphins avoid boat traffic in certain estuaries, the positive correlation of dolphin occurrence with the deeper channels in GB suggests that under certain ecological conditions, such as co-occurrence of boats with abundant food resources, the benefits of foraging may outweigh the presumed negative impact of boat traffic. Notably, bottlenose dolphins in Tampa Bay, Florida, disproportionately use dredged channels with heavy boat traffic relative to the dominant shallow habitat (McHugh et al., 2011).

Liret (2001) also found that a harbor with intense boat traffic was a primary habitat for bottlenose dolphins, in this case for resting. In Liret's study, the reaction of bottlenose dolphins to boats was monitored, revealing the majority of the interactions to be null reactions. This contrasts with other studies (Janik & Thompson, 1996; Nowacek et al., 2001; Hastie et al., 2003) that reported behavioral changes associated with boat traffic.

Unsurprisingly, when we focused only in GSC and BRD, fewer environmental descriptors were required to distinguish the hotspots from surrounding habitat where dolphins were not detected since the combined GCS and BRD area is more environmentally homogenous than the study area as a whole. In GSC and BRD, only the number of seabirds and depth were significantly higher in hotspots. The persistence of the high number of seabirds associated with hotspots corroborates the foraging potential offered by these sites. The change in environmental descriptors when considering the entire study area vs the smaller area with hotspots reinforces a key ecological concept: the usefulness of environmental descriptors is both site- and scale-dependent (Levin, 1992).

While there have been many studies of bottlenose dolphin habitat in estuaries (e.g., Ingram & Rogan, 2002), to our knowledge, this is the first to characterize foraging hotspots. Other studies have examined environmental conditions associated with foraging habitat at fine spatial (50 to 500 m) and temporal (daytime to month) scales in an effort to capture the dynamic environment of estuaries (e.g., Allen et al., 2001; Torres et al., 2008; Miller & Baltz, 2009; Torres, 2009). The suite of environmental variables and the metrics employed for the occurrence of dolphins (e.g., we used number of dolphins, while Torres et al. [2008] used presence/absence and Miller & Baltz [2009] used minimum group size) differed among these studies, hindering a direct comparison of findings. Importantly, there are marked differences even among the four GOM estuaries both topographically and in the type and intensity of dominant human activities (Allen et al., 2001; Torres et al., 2008; Miller & Baltz, 2009; Torres, 2009; and this study). For instance, the maximum depth in Florida Bay is 3 m (Torres et al., 2008; Torres, 2009), while in our study area, depth reaches nearly 14 m. Therefore, it is not surprising that the environmental parameters that were useful for classifying areas as bottlenose dolphin foraging habitat varied greatly across these estuaries suggesting that a single, small set of environmental properties that characterize prime foraging habitat for bottlenose dolphin in estuaries may not be practical. This emphasizes

the environmental complexity of estuaries and the need to carefully consider the set of environmental variables that influence dolphin foraging in each estuary. However, in spite of locational variations, deeper waters and dredged channels emerged as common features of prime foraging habitat, except in estuaries that are very shallow (Torres et al., 2008; Torres, 2009).

Foraging Hotspots: Implications for Conservation

Estuaries are essential nurseries for many species, exhibiting high biodiversity and providing many ecosystem services. However, conservation and/or restoration of estuaries, especially large estuaries that have been utilized by humans for decades, is expensive and resources are limited. Fine-scale mapping of cetacean foraging habitat based on environmental proxies of prey distribution has been proposed as a method to improve the conservation of cetaceans in estuaries (Torres et al., 2008). Herein, we demonstrate that, at the spatial and temporal scales examined, foraging hotspots of bottlenose dolphins are well-defined and persistent, offering the opportunity to more directly identify critical foraging habitat compared to model-based approaches that rely on environmental predictors.

The main applications of this study to conservation are four-fold. First, this study can guide the prioritization of cetacean habitat for conservation (i.e., maximize the benefits by selecting prime foraging habitat)—for instance, to aid in planning of response and mitigation measures to minimize impacts from oil/chemical spills on critical habitat. Second, this study provides a framework to promote an ecosystem-based approach to conservation and management by simultaneously protecting habitat that supports high densities of prey, which, in turn, support multiple species of predators, including protected seabirds (e.g., Brown pelicans [*Pelecanus occidentalis*]). Third, this study contributes to our understanding of the environmental factors (natural and anthropogenic) that determine prime foraging habitat by identifying the locations and attributes of the hotspots, which can focus research efforts by generating new hypotheses (e.g., higher densities of prey occur within the hotspots as a result of fronts, strong currents, or available refuge). Finally, in the GB, this study provides a baseline of prime dolphin foraging habitat that can be monitored over time to evaluate the effects of anthropogenic impacts (e.g., oil/chemical spills) or restoration measures that can be achieved with a much lower resource requirement than what is necessary to monitor the entire estuary (i.e., strategically selecting focal monitoring sites that require lower resources but have high performance impact in

conservation). Identifying and monitoring foraging hotspots could serve as a useful methodology to evaluate the effectiveness of restoration efforts on the recovery of estuarine bottlenose dolphin populations throughout the GOM, in particular the three populations in Barataria Bay, the Mississippi Sound, and adjacent waters that were most impacted by the Deepwater Horizon oil spill.

We recommend the continued systematic mapping of foraging hotspots in the GB to identify trends in their distribution by comparison to the baseline established in this study. Of particular interest would be to monitor the foraging hotspots for the years following an extreme event such as the 2014 oil spill or Hurricane Harvey. Future studies should also investigate which hotspots are the most important sites for GB resident bottlenose dolphins since this population is at higher risk from habitat degradation. Complementing foraging studies with monitoring of population abundance would allow using the bottlenose dolphin as an indicator of the health of the GB. Presently, the health of the GB is assessed based on 19 indicators ranging from water quality, pollution events, and seagrasses to wildlife (HARC/GBF, 2017). While oysters, shrimp, fish, and seabird populations are assessed, bottlenose dolphin populations are not despite the importance of GB as foraging habitat for this protected species. Used as a sentinel species to monitor the health trends of this estuary, the bottlenose dolphin would enhance the existing set of wildlife indicators by including a marine mammal.

Acknowledgments

This project was made possible through the collaboration and with the support of many individuals and institutions, and we are grateful to all of them—in particular, to B. Würsig for ideas, discussion, and support. Special thanks to each of the 30+ dedicated Marine Mammal Research Program interns, especially to Kristie Plyer, Nicole Remington, Wendy Schrader, Leo Flach, and Patricia Amaral. We also thank Kait Frasier for helpful comments on a draft of the manuscript. The primary funding support was provided by the Fulbright Fellowship program and the Science and Technology Foundation (Fundação para a Ciência e Tecnologia), Portugal (Grant PRAXIS XXI/BD/16224/98, Sub-Programa Ciência e Tecnologia do 2º Quadro Comunitário de Apoio). Supplemental funding was provided by the Texas Institute of Oceanography, Texas A&M University at Galveston, and the Waterford Yacht Club. Data were collected under NOAA-NMFS permit #550-1441.

Literature Cited

- Allen, M. C., Read, A. J., Gaudet, J., & Sayigh, L. S. (2001). Fine-scale habitat selection of foraging bottlenose dolphins *Tursiops truncatus* near Clearwater, Florida. *Marine Ecology Progress Series*, 222, 253-264. <https://doi.org/10.3354/meps222253>
- Alongi, D. M. (1998). *Coastal ecosystem processes*. New York: LLC, CRC Press.
- Baker, L., O'Brien, J., McHugh, K., & Berrow, S. (2017). An ethogram for bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. *Aquatic Mammals*, 43(6), 594-613. <https://doi.org/10.1578/AM.43.6.2017.594>
- Barros, N., & Odell, D. (1990). Food habits of bottlenose dolphins in the southeastern United States. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 309-328). New York: Academic Press. <https://doi.org/10.1016/B978-0-12-440280-5.50020-2>
- Barros, N., & Wells, R. S. (1998). Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Journal of Mammalogy*, 79(3), 1045-1059. <https://doi.org/10.2307/1383114>
- Bohnsack, J. A. (1989). Are high densities of fishes at artificial reefs the result of habitat limitation or behavioural preference? *Bulletin of Marine Science*, 44(2), 631-645.
- Bohnsack, J. A., & Sutherland, D. L. (1985). Artificial reef research: A review with recommendations for future priorities. *Bulletin of Marine Science*, 37(1), 11-39.
- Bräger, S. (1992). *Untersuchungen zur Ortstreue und zum Vergesellschaftungsmuster des Grossen Tümmlers, Tursiops truncatus* (Montagu, 1821) [Investigation on the site fidelity and socialization pattern of bottlenose dolphins, *Tursiops truncatus* (Montagu, 1821)] (Master's thesis). Christian-Albrechts-Universität, Kiel, Germany.
- Bräger, S. (1993). Diurnal and seasonal behavior patterns of bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, 9(4), 434-438. <https://doi.org/10.1111/j.1748-7692.1993.tb00477.x>
- Cressie, N. A. C. (1993). *Statistics for spatial data* (Revised ed.). New York: John Wiley & Sons.
- Croll, D. A., Marinovic, B., Benson, S., Chavez, F., Black, N., Ternullo, R., & Tereshy, B. R. (2005). From wind to whales: Trophic links in a coastal upwelling system. *Marine Ecology Progress Series*, 289, 117-130. <https://doi.org/10.3354/meps289117>
- Day, J. W., Jr., Crump, B. C., Kemp, W. M., & Yáñez-Arancibia, A. (Eds.). (2013). *Estuarine ecology* (2nd ed.). Hoboken, NJ: Wiley-Blackwell.
- Delgado-Estrella, A. (1997). Relación de las toninas, *Tursiops truncatus*, y las toninas moteadas, *Stenella frontalis*, con la actividad camaronera en la Sonda de Campeche, México [Relationship of dolphins, *Tursiops truncatus*, and speckled dolphins, *Stenella frontalis*, with the shrimp activity in the Bay of Campeche, Mexico]. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México. Serie Zoología*, 68(2), 317-338.
- Dustan, P., & Pinckney, J. L., Jr. (1989). Tidally induced estuarine phytoplankton patchiness. *Limnology and Oceanography*, 34(2), 410-419. <https://doi.org/10.4319/lo.1989.34.2.0410>
- Environmental Systems Research Institute (ESRI). (2004). *ArcGIS desktop: Release 9*. Redlands, CA: ESRI.
- Fertl, D. (1994a). *Occurrence, movements, and behavior of bottlenose dolphins (Tursiops truncatus) in association with the shrimp fishery in Galveston Bay, Texas* (Master's thesis). Texas A&M University, College Station.
- Fertl, D. (1994b). Occurrence patterns and behavior of bottlenose dolphins (*Tursiops truncatus*) in the Galveston ship channel, Texas. *Texas Journal of Science*, 46(4), 299-317.
- Fertl, D., & Leatherwood, S. (1997). Cetacean interactions with trawls: A preliminary review. *Journal of Northwest Atlantic Fishery Science*, 22, 219-248. <https://doi.org/10.2960/J.v22.a17>
- Galveston Bay Estuary Program (GBEP). (2002). *The state of the bay: A characterization of the Galveston Bay ecosystem* (2nd ed.). Webster, TX: GBEP.
- Gannon, D., & Waples, D. M. (2004). Diets of coastal bottlenose dolphins from the U.S. Mid-Atlantic coast differ by habitat. *Marine Mammal Science*, 20(3), 527-545. <https://doi.org/10.1111/j.1748-7692.2004.tb01177.x>
- Hanson, M. T., & Defran, R. H. (1993). The behaviour and feeding ecology of the Pacific coast bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals*, 19(3), 127-142.
- Hastie, G. D., Wilson, B., & Thompson, P. M. (2006). Diving deep in a foraging hotspot: Acoustic insights into bottlenose dolphin dive depths and feeding behaviour. *Marine Biology*, 148(5), 1181-1188. <https://doi.org/10.1007/s00227-005-0143-x>
- Hastie, G. D., Wilson, B., Tufft, L. H., & Thompson, P. M. (2003). Bottlenose dolphins increase breathing synchrony in response to boat traffic. *Marine Mammal Science*, 19(1), 74-84. <https://doi.org/10.1111/j.1748-7692.2003.tb01093.x>
- Hastie, G. D., Wilson, B., Wilson, L. J., Parsons K. M., & Thompson, P. M. (2004). Functional mechanisms underlying cetacean distribution patterns: Hotspots for bottlenose dolphins are linked to foraging. *Marine Biology*, 144(2), 397-403. <https://doi.org/10.1007/s00227-003-1195-4>
- Hayes, S. A., Josephson, E., Maze-Foley, K., & Rosel, P. E., (Eds.). (2017). *U.S. Atlantic and Gulf of Mexico marine mammal stock assessments – 2016* (NOAA Technical Memorandum NMFS-NE-241). Woods Hole, MA: National Oceanic and Atmospheric Administration.
- Heithaus, M. R., & Dill, L. M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, 83, 480-491. [https://doi.org/10.1890/0012-9658\(2002\)083\[0480:FAATSP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0480:FAATSP]2.0.CO;2)
- Henderson, E. E., & Würsig, B. (2007). Behavior patterns of bottlenose dolphins in San Luis Pass, Texas. *Gulf of Mexico Science*, 25(2), 153-161. <https://doi.org/10.18785/goms.2502.06>
- Henningsen, T. (1991). *Zur Verbreitung und Ökologie des Grossen Tümmlers (Tursiops truncatus) in Galveston, Texas* [On the distribution and ecology of bottlenose dolphins (*Tursiops truncatus*) in Galveston, Texas] (Master's thesis). Christian-Albrechts-Universität, Kiel, Germany.

- Henningsen, T., & Würsig, B. (1991). Bottle-nosed dolphins in Galveston Bay, Texas: Numbers and activities. *European Research on Cetaceans*, 5, 36-38.
- Hooker, S. K., Whitehead, H., & Gowans, S. (1999). Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. *Conservation Biology*, 13(3), 592-602. <https://doi.org/10.1046/j.1523-1739.1999.98099.x>
- Houston Advanced Research Center/Galveston Bay Foundation (HARC/GBF). (2017). Retrieved from www.galvbaygrade.org/wp-content/uploads/2017/08/2017_Galveston_Bay_Full_Report.pdf
- Ingram, S. N., & Rogan, E. (2002). Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. *Marine Ecology Progress Series*, 244, 247-255. <https://doi.org/10.3354/meps244247>
- Janik, V. M., & Thompson, P. M. (1996). Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. *Marine Mammal Science*, 12(4), 597-602. <https://doi.org/10.1111/j.1748-7692.1996.tb00073.x>
- Jones, A. R., Hosegood, P., Wynn, R. B., De Boer, M. N., Butler-Cowdry, S., & Embling, C. B. (2014). Fine-scale hydrodynamics influence the spatio-temporal distribution of harbour porpoises at a coastal hotspot. *Progress in Oceanography*, 128, 30-48. <https://doi.org/10.1016/j.pocean.2014.08.002>
- Kovacs, C., & Cox, T. (2014). Quantification of interactions between common bottlenose dolphins (*Tursiops truncatus*) and a commercial shrimp trawler near Savannah, Georgia. *Aquatic Mammals*, 40(1), 81-94. <https://doi.org/10.1578/AM.40.1.2014.81>
- Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73(6), 1943-1967. <https://doi.org/10.2307/1941447>
- Liret, C. (2001). *Domaine vital, utilisation de l'espace et des ressources: Les grands dauphins, Tursiops truncatus, de l'île de Sein* [Home range, use of space and resources: The bottlenose dolphins, *Tursiops truncatus*, in the island of Sein] (Doctoral dissertation). Université de Bretagne Occidentale, France.
- Martin, P., & Bateson, P. (Eds.). (1993). *Measuring behaviour: An introductory guide* (2nd ed.). New York: Cambridge University Press. <https://doi.org/10.1017/CB09781139168342>
- Maze, K. S., & Würsig, B. (1999). Bottlenose dolphins of San Luis Pass, Texas: Occurrence patterns, site-fidelity, and habitat use. *Aquatic Mammals*, 25(2), 91-103.
- McHugh, K. A., Allen, J. B., Barleycorn, A. A., & Wells, R. S. (2011). Natal philopatry, ranging behavior, and habitat selection of juvenile bottlenose dolphins in Sarasota Bay, Florida. *Journal of Mammalogy*, 92(6), 1298-1313. <https://doi.org/10.1644/11-MAMM-A-026.1>
- McLusky, D. S., & Elliot, M. (Eds.). (2004). *The estuarine ecosystem: Ecology, threats and management* (3rd ed.). Oxford, UK: Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780198525080.001.0001>
- Mendes, S., Turrell, W., Lütkebohle, T., & Thompson, P. (2002). Influence of the tidal cycle and a tidal intrusion front on the spatio-temporal distribution of coastal bottlenose dolphins. *Marine Ecology Progress Series*, 239, 221-229. <https://doi.org/10.3354/meps239221>
- Miller, C. E., & Baltz, D. M. (2009). Environmental characterization of seasonal trends and foraging habitat of bottlenose dolphins (*Tursiops truncatus*) in northern Gulf of Mexico bays. *Fishery Bulletin*, 108(1), 79-86.
- Moors-Murphy, H. B. (2014). Submarine canyons as important habitat for cetaceans, with special reference to the Gully: A review. *Deep-Sea Research II*, 104, 6-19. <https://doi.org/10.1016/j.dsr2.2013.12.016>
- Moulins, A., Rosso, M., Ballardini, M., & Würtz, M. (2008). Partitioning of the Pelagos Sanctuary (north-western Mediterranean Sea) into hotspots and coldspots of cetacean distributions. *Journal of the Marine Biological Association of the United Kingdom*, 88(6), 1273-1281. <https://doi.org/10.1017/S0025315408000763>
- National Oceanic and Atmospheric Administration (NOAA). (2004). *Extratropical water level guidance*. Retrieved from co-ops.nos.noaa.gov/data_res.html
- NOAA Fisheries. (2017). *Fisheries of the United States, 2016 report* (Annual report of the National Marine Fisheries Service). Retrieved from <https://www.fisheries.noaa.gov/resource/document/fisheries-united-states-2016-report>
- NOAA/National Centers for Environmental Information (NCEI). (n.d.). Retrieved from www.hgdc.noaa.gov/mgg/geodas/geodas.html
- Nelson, D. M. (Ed.). (1992). *Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries* (Vol. I: Data summaries; ELMR Report No. 10). Silver Spring, MD: National Oceanic and Atmospheric Administration/National Ocean Service, Strategic Environmental Assessments Division.
- Nelson, D. M., & Monaco, M. E. (2000). *National overview and evolution of NOAA's Estuarine Living Marine Resources (ELMR) program*. (NOAA Technical Memo NOS NCCOS CCMA 144). Silver Spring, MD: National Oceanic and Atmospheric Administration/National Ocean Service, Center for Coastal Monitoring and Assessment. <https://doi.org/10.5962/bhl.title.4815>
- Norris, K. S., & Dohl, T. P. (1980). The structure and functions of cetacean schools. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and processes* (pp. 211-261). New York: John Wiley & Sons.
- Nowacek, S., Wells, R. S., & Solow, A. R. (2001). Short-term effects of boat traffic on bottlenose dolphin, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science*, 17(4), 673-688. <https://doi.org/10.1111/j.1748-7692.2001.tb01292.x>
- Patillo, M., Rozas, L. P., & Zimmerman, R. J. (1995). *A review of salinity requirements for selected invertebrates and fishes of U.S. Gulf of Mexico estuaries*. Galveston, TX: Southeast Fisheries Science Center.
- Phillips, N. M., & Rosel, P. E. (2014). *A method for prioritizing research on common bottlenose dolphin stocks through evaluating threats and data availability: Development and application to bay, sound and estuary stocks in*

- Texas (NOAA Technical Memo NMFS-SEFSC-665). Silver Spring, MD: National Oceanic and Atmospheric Administration. <https://doi.org/10.7289/V5F769H8>
- Pianka, E. R. (Ed.). (1994). *Evolutionary ecology* (5th ed.). New York: HarperCollins College Publishers.
- Pickering, H., & Whitmarsh, D. (1997). Artificial reefs and fisheries exploitation: A review of the "attraction versus production" debate: The influence of design and its significance for policy. *Fisheries Research*, 31(1-2), 39-59. [https://doi.org/10.1016/S0165-7836\(97\)00019-2](https://doi.org/10.1016/S0165-7836(97)00019-2)
- Salas-Monreal, D., Anis, A., & Salas-de-Leon, D. A. (2017). Galveston Bay dynamics under different wind conditions. *Oceanologia*, 60(2), 232-243. <https://doi.org/10.1016/j.oceano.2017.10.005>
- Santora, J. A., Zeno, R., Dorman, J. G., & Sydeman, W. J. (2018). Submarine canyons represent an essential habitat network for krill hotspots in a large marine ecosystem. *Scientific Reports*, 8, Article number 7579. <https://doi.org/10.1038/s41598-018-25742-9>
- Scales, K. L., Miller, P. I., Hawkes, L. A., Ingram, S. N., Sims, D. W., & Votier, S. C. (2014). On the front line: Frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, 51(6), 1575-1583. <https://doi.org/10.1111/1365-2664.12330>
- Schwacke, L. H., Thomas, L., Wells, R. S., McFee, W. E., Hohn, A. A., Mullin, K. D., . . . Schwacke, J. H. (2017). Quantifying injury to common bottlenose dolphins from the Deepwater Horizon oil spill using an age-, sex- and class-structured population model. *Endangered Species Research*, 33, 265-279. <https://doi.org/10.3354/esr00777>
- Shane, S. H. (1990). Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 245-264). New York: Academic Press. <https://doi.org/10.1016/B978-0-12-440280-5.50016-0>
- Shane, S. H., Wells, R. S., & Würsig, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: A review. *Marine Mammal Science*, 2(1), 34-63. <https://doi.org/10.1111/j.1748-7692.1986.tb00026.x>
- Steiner, A. (2012). Temporal determinants of Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) activity in the Port River Estuary (Adelaide, South Australia). *Aquatic Mammals*, 38(3), 267-278. <https://doi.org/10.1578/AM.38.3.2012.267>
- Texas Coastal Ocean Observation Network (TCOON). (n.d.). *Project summary*. Retrieved from <http://cbi.tamucc.edu/TCOON>
- Texas Water Development Board (TWDB). (n.d.). Retrieved from www.twdb.gov
- Torres, L. G. (2009). A kaleidoscope of mammal, bird and fish: Habitat use patterns of top predators and their prey in Florida Bay. *Marine Ecology Progress Series*, 375, 289-304. <https://doi.org/10.3354/meps07743>
- Torres, L. G., Read, A. J., & Halpin, P. (2008). Fine-scale habitat modeling of a top marine predator: Do prey data improve predictive capacity? *Ecological Applications*, 18(7), 1702-1717. <https://doi.org/10.1890/07-1455.1>
- Urian, K. W., Hofmann, S., Wells, R. S., & Read, A. J. (2009). Fine-scale population structure of bottlenose dolphin (*Tursiops truncatus*) in Tampa Bay, Florida. *Marine Mammal Science*, 25(3), 619-638. <https://doi.org/10.1111/j.1748-7692.2009.00284.x>
- Urmy, S. S., & Warren, J. D. (2018). Foraging hotspots of common and roseate terns: The influence of tidal currents, bathymetry, and prey density. *Marine Ecology Progress Series*, 590, 227-245. <https://doi.org/10.3354/meps12451>
- Walker, B. K., Henderson, B., & Spieler, R. E. (2002). Fish assemblages associated with artificial reefs of concrete aggregates or quarry stone offshore Miami Beach, Florida. *Aquatic Living Resources*, 15, 95-105. [https://doi.org/10.1016/S0990-7440\(02\)01154-3](https://doi.org/10.1016/S0990-7440(02)01154-3)
- Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In H. H. Genoways (Ed.), *Current mammalogy* (pp. 247-305). New York: Plenum. https://doi.org/10.1007/978-1-4757-9909-5_7
- Wilson, B., Thompson, P. M., & Hammond, P. S. (1997). Habitat use by bottlenose dolphins: Seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology*, 34(6), 1365-1374. <https://doi.org/10.2307/2405254>
- Wingfield, D. K., Peckham, S. H., Foley, D. G., Palacios, D. M., Lavaniegos, B. E., Durazo, R., . . . Bograd, S. J. (2011). The making of a productivity hotspot in the coastal ocean. *PLOS ONE*, 6(11). <https://doi.org/10.1371/journal.pone.0027874>
- Würsig, B. (1978). Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine bay. *The Biological Bulletin*, 154(2), 348-359. <https://doi.org/10.2307/1541132>
- Yates, F. (1934). Contingency table involving small numbers and the χ^2 test. *Supplement to the Journal of the Royal Statistical Society*, 1, 217-235.
- Yen, P. P. W., Sydeman, W. J., & Hyrenbach, K. D. (2004). Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: Implications for trophic transfer and conservation. *Journal of Marine Systems*, 50, 79-99. <https://doi.org/10.1016/j.jmarsys.2003.09.015>
- Zar, J. H. (1996). *Biostatistical analysis* (3rd ed.). Upper Saddle River, NJ: Prentice-Hall.