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Common bottlenose dolphins (*Tursiops truncatus*) are behaviorally flexible cetaceans that have adapted to a wide variety of habitats. In the San Luis Pass area near Galveston, Texas, there are two populations of bottlenose dolphins, distinguished through long-term photo-identification studies, which use adjacent habitat in different ways. A small resident population makes use of the shallow bay system, while the larger, more transient population remains outside the bay along the Gulf of Mexico coastline. A 13-mo study was conducted to examine the behavior of these populations and to explore the hypothesis that although they overlap geographically, each population utilizes the area differently. The behavior of focal groups was assessed by instantaneous sampling, and a time budget of each behavior per unit effort was calculated. When these populations mix in Gulf of Mexico waters, social activity and travel were the primary behaviors observed. Resident dolphins foraged predominantly in the bays and pass, and displayed group foraging behavior. In contrast, Gulf dolphins were only observed foraging in coastal waters, and did so individually. These behavioral differences may reflect strategies based on habitat variation, but may also be indicative of distinct social structures between resident and Gulf populations. There was a seasonal component to behavior and group size, with larger mixed groups and more social behavior occurring in summer. Finally, resident dolphin behavior varied by time of day, with a peak in foraging in the morning and socializing in the afternoon. The results of this study suggest that these adjacent groups are distinct populations that have partitioned their habitat into separate niches, and thus should be treated separately in management decisions.

The common bottlenose dolphin (*Tursiops truncatus*) is one of the most cosmopolitan cetaceans, ranging in diverse habitats from cold temperate to tropical waters in much of the Northern and Southern hemispheres (Wilson et al., 1997, 1999; Rossbach and Herzing, 1999; Lusseau et al., 2003). Bottlenose dolphins inhabit small seas and open oceans (Bearzi et al., 1999), coastal waters (Hanson and Defran, 1993; Defran et al., 1999), and shallow protected bays (Wells et al., 1987). Their use of such wide-ranging and variable habitats is due not only to their almost-global distribution, but to the variety of prey available in each area. Therefore, investigations of this species in a range of habitats provide information on not only their own adaptations, but also of the characteristics of the ecosystem as a whole.

The study of animal behavior offers insight into possible causes of those behaviors, such as movement of prey, escape from predation, or habitat association. For example, foraging behavior of bottlenose dolphins off California's coast includes high fluke dives of long duration, consistent with the need to access their preferred benthic prey (Hanson and Defran, 1993). Similarly, mating and social strategies, or socio-sexual behavior of dolphins vary by species, sex, and age class, and social interactions are often an outgrowth of a species' mating strategy. Most bottlenose dolphin societies exist in a tactile fission–fusion society where groups constantly fluctuate in size and composition, and sexual behavior may act as a means of recognition and communication, occurring between all age classes and sexes (Connor et al., 2000). Behavioral studies can also provide information about daily and seasonal habitat use and movement patterns. Bottlenose dolphins in California have higher rates of feeding in the morning and afternoon, and decreased feeding but increased traveling at midday (Hanson and Defran, 1993).

Environmental factors such as sea temperature, tidal activity, depth, seafloor slope, and sediment type can also affect cetacean behavior (Würsig and Würsig, 1979; Ingram and Rogan, 2002; Hastie et al., 2004). Several studies have demonstrated an increase in the foraging activity of bottlenose dolphins in deep channel areas with steep slopes (Wilson et al., 1997; Ingram and Rogan, 2002). This increase in foraging may indicate a higher concentration of prey as they bottleneck in narrow channels, or perhaps the steep slopes aid dolphins in herding and catching fish. In addition, there are often seasonal shifts in behavior, including increased migration, seasonal use of bays or inlets, and variation in duration and modes of behavior

(Wilson et al., 1997; Weller, 1998; Barco et al., 1999).

This paper explores the behavior of bottlenose dolphins that habitually use a portion of the northwestern Gulf of Mexico (GoM) coastline and the shallow bay system of San Luis Pass/Chocolate Bay (SLP/CB) off Galveston Island, Texas. Two groups of dolphins inhabit this area; one group is designated "resident," whereas the others are considered "Gulf" animals (Maze and Würsig, 1999). Residents are defined as being sighted in three of four seasons, with continued sightings in two of four seasons (Irwin and Würsig, 2004). These dolphins appear to remain in the area all year, although there is a seasonal trend of favoring the shallow bays in summer and the channel and GoM in winter (Maze and Würsig, 1999; Irwin and Würsig, 2004). In contrast, Gulf dolphins are rarely resighted (e.g., Henningsen, 1991; Bräger et al., 1994), and may be moving up and down the coastline. The Gulf animals may display seasonal residency in some parts of their range, similar to the bottlenose dolphins of the North American Atlantic coast (Barco, et al.; 1999; Connor, 2001), but we have no information on this point for those animals.

Bottlenose dolphins in SLP have been studied for almost 10 yr, but their behavior has not been systematically categorized. This is an important step in answering the question of disparate habitat use by resident and Gulf dolphins. Despite the fact that residents exhibit a seasonal movement pattern, it is unknown whether their day-to-day activity has a corresponding seasonal pattern. Similarly, although the Gulf dolphins are seen in the coastal area year-round, their specific use of the habitat has not been examined. The objectives of this study were to 1) determine if and how behavioral states differed between resident and Gulf dolphins, 2) determine what, if any, changes occur when these dolphins interacted, and 3) identify factors that influenced behavior, and to determine if those influences created a daily or seasonal component to behavior.

MATERIALS AND METHODS

Study area.—San Luis Pass and Chocolate Bay are at the southwestern end of Galveston Island and the Galveston Bay estuary. This region is approximately 65 km^2, and in previous dolphin studies carried out in this area it was divided into four sections based on habitat characteristics: CB, SLP, West Bay (WB), and the GoM (Maze and Würsig, 1999; Irwin and Würsig, 2004). The current study also includes an adjacent bay,

Bastrop Bay (BB), and divides the GoM into two sections: North GoM (NG) and South GoM (SG), separated by SLP. It also incorporates additional coastline to the south as well as the Surfside Shipping Channel (SC), which connects the GoM to the Intracoastal Waterway (ICW) (Fig. 1). The sections surveyed in this study were BB, NG, SG, SC, SLP, WB, and CB/ICW. These areas vary in size and habitat characteristics, and will therefore each be considered separately; however, CB and ICW were combined into one study section because they were adjacent and always surveyed together.

Both CB and BB vary in bottom depth, but are relatively shallow (mean = 1.80 ± 1.26 m) and have a generally muddy bottom scattered with numerous oyster reefs. CB is bisected by a shipping channel, and is bordered on the southwest by the ICW, both of which are much deeper. WB is more consistent in depth, but is still shallow (mean = 2.33 ± 0.577 m), with sediment composed of mud and silt. SLP, the channel between the GoM and WB, is marked with dense sand bars that shift constantly in the rapid movement of the tides, and can be extremely shallow except during high tides (mean = 1.14 ± 0.77 m). These areas are all used by small recreational vessels; in addition, the ICW and CB shipping channels are regularly traversed by large barges. The two GoM sections run northeast to southwest along the coasts of Galveston and Follet's Islands, and have sandy bottoms and greater depths (mean = 5.07 ± 2.22 m). Surveys in the GoM were run on two tracks, one approximately 0.25 km offshore and the other approximately 0.75 km offshore. At the southwestern edge of this study, the SC is a deep channel (mean = 13.10 ± 4.74 m) with considerable boat traffic, both large and small. Shrimp trawling occurs in the GoM, SC, and the channel area of CB, but cannot be accommodated by the shallow bays or SLP.

Data collection.—After a pilot study from September through November 2002, data were gathered for 13 consecutive months, from December 2002 through December 2003. Behavioral data from the pilot study were not used for analysis. A 5.1-m Boston Whaler with a four-stroke, 200-hp motor was used to survey the study area. Every survey covered a minimum of two sections of the study area, though most surveys covered three or more. Surveys were only conducted in sea states of Beaufort 3 or less. There were a minimum of three observers on each survey so that surveillance could be maintained for 360 degrees. Previous work had determined that track lines were not suitable for
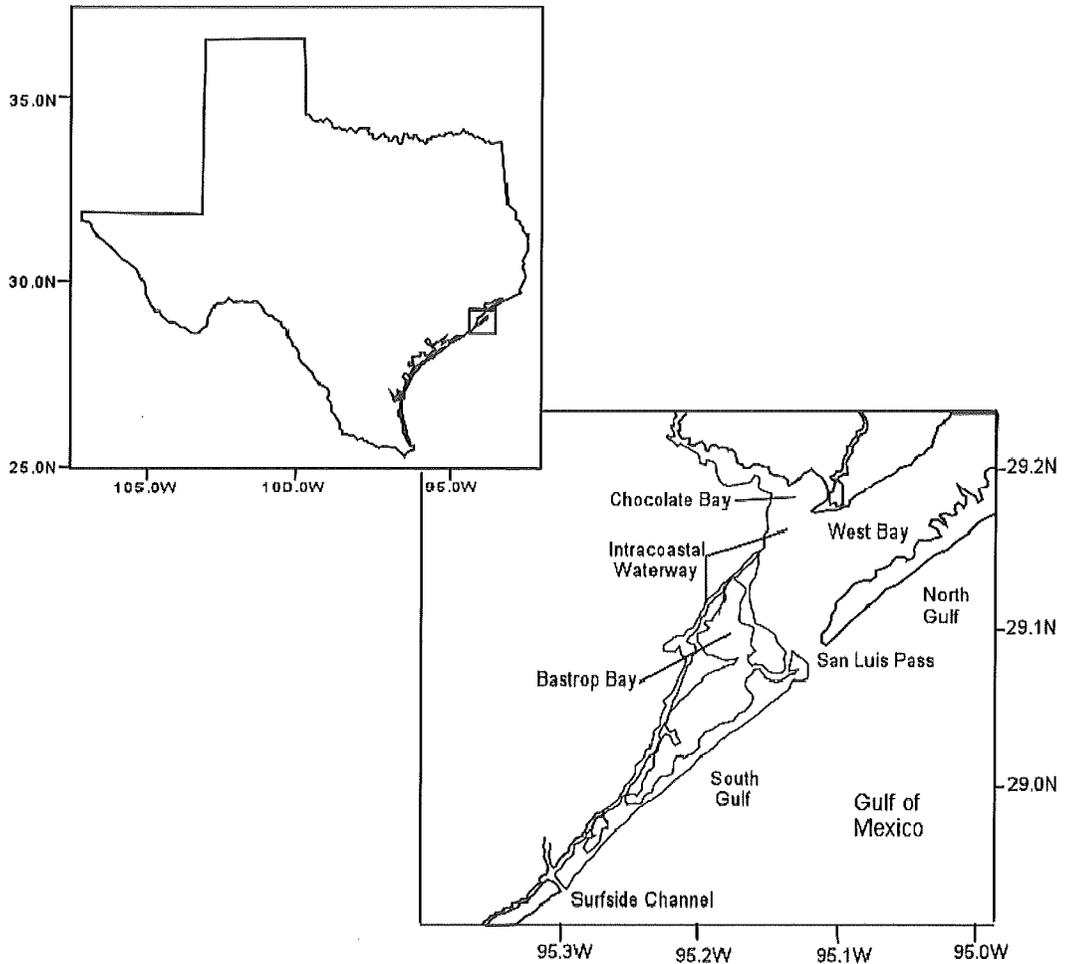
Fig. 1. San Luis Pass/Chocolate Bay study area.

most of this area (Irwin and Würsig, 2004), so survey routes were set and followed using a Garmin 45 GPS Personal Navigator. Survey speed was maintained between 10 and 12 knots (18.52–22.22 km/hr) until a group of dolphins was located, then speed was reduced to match the pace of the group. Groups were defined as all dolphins in apparent association, generally engaged in the same behavior (Shane, 1990; Bräger et al., 1994; Karczmarski, 1999), and group composition was recorded, including numbers of neonates, calves, and juveniles based on body length and position (as in Irwin and Würsig, 2004). Photographs were taken of all members of each group using a Nikon D-1 digital camera, with an 80–400-mm zoom lens. We stayed with each group until all members were photographed, environmental conditions worsened, or the group was not sighted for more than 9 min.

Environmental data were taken at the end of each group encounter, as well as every hour in order to compare conditions with and without dolphins present. These data included salinity, depth, Beaufort sea state, swell, cloud cover, and wind speed and direction. Salinity was measured using a VISTA A366ATC refractometer, and depth measurements were taken with a Depth-mate Model 605-024 portable depth sounder. Each location was also correlated with bottom type and depth: deep sandy bottom (NG and SG), shallow muddy bottom with oyster reefs (CB and BB), deep channels (ICW and SC), and shallow sandy bottom with sand bars (SLP). Seasons were combined into two periods: warm (May–Oct.) and cold (Nov.–April) (e.g. Irwin and Würsig, 2004).

Dolphins were photo-identified using natural markings on their backs and dorsal fins, particularly scars and nicks on the trailing edge of the

fin (Würsig and Würsig, 1977; Defran et al., 1990; Würsig and Jefferson, 1990). Photographs of each individual were examined for quality; the top three quality categories were excellent, good, or fair for the following criteria: contrast, relative size of fin in photograph, focus, parallax, and proportion of fin visible. Those in the top quality categories were entered into a fin-recognition assistance program called Finscan (Hillman et al., 2003). Photographs were then matched within the catalog from this study, as well as against catalogs compiled by Irwin and Würsig (2004) and Maze and Würsig (1999) to determine status and duration of residency. Groups in this study were categorized based on the composition of their members: resident groups consisted of all resident animals, mixed groups consisted of both resident and Gulf animals, and Gulf groups consisted of only Gulf animals.

Behavioral sampling.—A start time was taken upon joining a group, and behavior samples were recorded on the focal group using the instantaneous sampling method (Altmann, 1974; Mann, 1999; Rose, 2000). Behavioral categories were defined as follows: foraging, traveling, socializing, milling, or other, with the majority of the group performing the same behavior. Foraging was indicated by a variable direction of movement, with high arching dives, possible fish chasing, and generally remaining in the same area. Traveling consisted of all individuals moving in the same direction steadily or rapidly, often with synchronous and frequent surfacings. Socializing was marked by a variable direction of movement, with individuals in close proximity or touching and frequent surface active behaviors. Finally, milling was indicated by the animals remaining in one area with no physical contact; surface active behavior; or long, deep dives and by slow swimming speeds (definitions followed Shane, 1990; Ballance, 1992; Hanson and Defran, 1993). The behavior category "other" included all behaviors that were not readily identifiable and is likely a combination of all behavior categories. Therefore, it is not considered in any analyses so as not to bias the identifiable behavioral categories. Behavior categories could also be combined if more than half of the group was engaged in more than one activity, such as foraging/traveling, traveling/socializing, or socializing/foraging. These behavioral samples were taken every 3 min, or upon the first surfacing of the majority of the group after the 3-min interval mark. If no dolphins were observed during the entire 3-min interval, then that sample was counted as not applicable (NA).

Behavioral sampling continued until photographs were taken of all dolphins in a group, or after three consecutive recordings of NA when the dolphins were presumed lost. A behavior index (sightings per unit effort) was then calculated of the number of times a given behavior was observed divided by the total number of samples taken per group sighting (Sorensen et al., 1984; Akashi and Terazawa, 2005). This behavior index was calculated for all possible behavior categories, so a value of zero (no instances of that behavior during that sighting) was possible. Additionally, the mixed categories of behavior were split and calculated as one-half toward each of the three possible behaviors of traveling, foraging, or socializing, in order to make the behavioral trends more apparent and robust (Hanson and Defran, 1993; Würsig et al., 2003). This behavior index also controls for pseudoreplication due to uneven sampling durations with each group encounter. Finally, time budgets of all behaviors were calculated for each group category (resident, Gulf, and mixed) in each section of the study area where dolphins were sighted (CB/ICW, SLP, NG, SG, and SC), and environmental and seasonal factors were compared with behaviors to determine if they differed seasonally, by time of day, or by bottom type, bottom depth, or salinity.

Analysis.—Due to nonnormal distributions, behavioral indices were examined using Kruskal–Wallis nonparametric analysis of variance (ANOVA) and Dunnett's T3 post hoc tests to determine if frequency of behaviors varied between resident or Gulf dolphins, and if behaviors varied by habitat type. Behaviors were also examined for daily and seasonal trends using multivariate generalized linear models, and were compared to environmental data using MANOVA and Kruskal–Wallis ANOVA tests. Additionally, all group encounters in which behavioral sampling occurred for 5 min or less were discarded, leaving 44 groups for analysis. All statistical analyses were carried out with SPSS for Windows Version 11.0.

RESULTS

There were 38 survey days, 20 in the cold season and 18 in the warm season, with 156 hr on the water; 28.5 hr were spent with dolphins. Forty-four groups were encountered; 17 of those were Gulf groups, 19 were resident groups, and eight were mixed groups. Overall, resident dolphin behavior was fairly well distributed across the four main behavior categories, where-
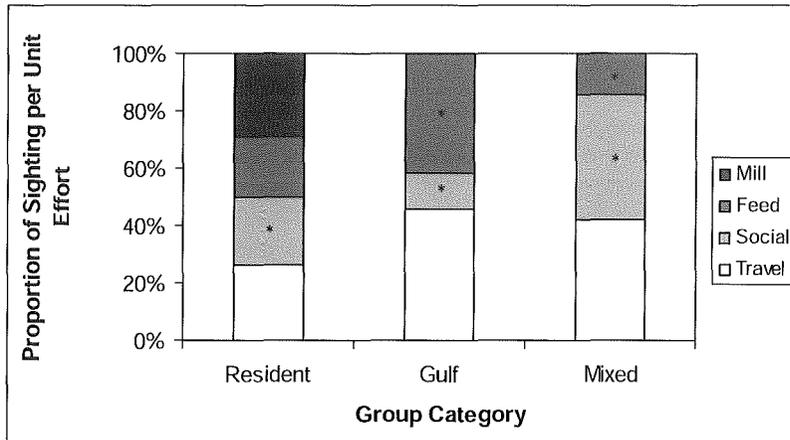
Fig. 2. Overall sighting per unit effort of each behavior for all group categories. An asterisk indicates significant results ($p < 0.05$) for rates of behavior compared across group categories.

as Gulf dolphins spent the majority of their time traveling and foraging, and mixed groups spent most of their time socializing and traveling (Fig. 2). Foraging ($\chi^2 = 6.21$, $p = 0.045$) and socializing ($\chi^2 = 9.42$, $p = 0.009$) varied significantly between group categories. In post hoc analysis, foraging was seen more in Gulf groups than in mixed groups ($p = 0.007$), whereas socializing was seen more in resident and mixed groups than in Gulf groups ($p = 0.018$ and 0.029, respectively). Residents were the only group observed milling.

Table 1 outlines the time budgets of behavior for each group (resident, Gulf, mixed) in each study area. Resident groups were only observed in CB/ICW and SLP, except for one occurrence in SG, whereas Gulf groups were only observed in the GoM (NG and SG) and SC. Mixed groups were observed largely in the GoM (NG and SG), and only once each in CB/ICW and SLP. No groups were observed in WB or BB.

The only environmental factors that appeared to have an influence on behavior were bottom depth and bottom type. Most foraging occurred in the shallowest (< 2 m) and deepest (> 10 m) areas. Socializing was never seen in water deeper than 8 m, whereas traveling occurred in all depths, but slightly more in shallower depths. Traveling varied significantly by bottom type for all groups ($\chi^2 = 12.03$, $p = 0.007$), with post hoc analysis indicating more traveling in the deep sandy areas than in shallow sandy areas ($p = 0.022$), whereas the opposite categories, shallow sandy bottom and deep channels, had more foraging.

The group type encountered varied significantly by season ($\chi^2 = 3.98$, $p = 0.046$), as well as by the study area in which the dolphins were found ($\chi^2 = 23.13$, $p < 0.001$). For resident groups, both foraging ($\chi^2 = 8.87$, $p = 0.012$) and socializing ($\chi^2 = 7.06$, $p = 0.029$) varied by time of day (Fig. 3), with foraging seen predominantly in the morning, and socializing seen predominantly in the afternoon. The frequency of both foraging (F = 2.65, $p = 0.048$) and social behavior (F = 3.75, $p = 0.011$) varied significantly with group size ($\Lambda = 0.030$), with larger groups socializing more than smaller ones. No other seasonal or time-of-day trends were statistically detectable, perhaps because of small sample size.

DISCUSSION

Dolphins in the area of SLP were not uniformly distributed, nor did they utilize this habitat equally. Resident dolphins rarely ventured farther than SLP without mixing with Gulf dolphins, presumably to socialize because the rate of socializing increased in mixed groups. Socializing also only occurred in water shallower than 8 m, possibly indicating that Gulf dolphins ventured closer to the coastline in order to facilitate socializing with resident dolphins. The resident population size has remained constant for at least 10 yr, with new calves born every year. It is possible but remains unproved that the resident group represents one or more matrilines, as has been observed in other populations with long-lasting female bands (Wells, 1991). Females and young calves may utilize the bay system while older males disperse, perhaps joining a coastal migration by Gulf dolphins, if that does in fact occur. An increase in calf births coincides with the summer peak in social behavior and group size in mixed groups, which

TABLE 1.   Mean sighting per unit effort of behaviors for group categories by study area. Behavioral sightings per unit effort calculated as number of samples of that behavior divided by total number of behavior samples. A dash indicates no observations of that group category in that area. Behaviors with more than 50% sightings per unit effort are in bold. The study areas West Bay and Bastrop Bay are not included because no sightings were made in those areas. The mixed categories of behavior were split and calculated as one-half towards each of the three possible behaviors of travel, forage, or social; therefore, the total sighting per unit effort may equal more than 100%.

Group category	Behavior	Study area[a]				
		CB/ ICW	SLP	NG	SG	SC
Resident	Travel	**0.60**	0.21	—	**0.67**	—
	Social	0.45	**0.61**	—	0.00	—
	Forage	0.34	**0.80**	—	0.22	—
	Mill	**0.63**	0.00	—	0.00	—
Gulf	Travel	—	—	**0.74**	**0.50**	**1.00**
	Social	—	—	0.24	0.25	0.04
	Forage	—	—	0.22	**0.62**	**0.98**
	Mill	—	—	0.22	0.22	0.00
Mixed	Travel	0.35	0.00	**0.59**	**0.52**	—
	Social	**0.65**	**0.50**	**0.69**	0.45	—
	Forage	0	0.00	0.14	0.2	—
	Mill	0	0.00	0.00	0.00	—

[a] CB, Chocolate Bay; ICW, Intracoastal Waterway; SLP, San Luis Pass channel; NG, north Gulf of Mexico; SG, south Gulf of Mexico; SC, Surfside Shipping Channel.

may indicate that resident females are mating with Gulf males in the summer, although a genetic examination of both resident and Gulf dolphins is necessary for confirmation. Alternatively, the females could be dispersing from the area in order to mate and then returning to the bay with their young, as was observed by Fertl (1994) in Galveston Bay for at least one female. Finally, it is possible that there is no gender correlation in the animals that remain in the bay vs those that disperse, and thus it would be equally likely that both males and females might employ either strategy.

Although as not well established in bottlenose dolphins, some patterns of dispersal have been documented in other marine mammal species. Resident, fish-eating killer whales (*Orcinus orca*) in the U.S. Pacific Northwest have low dispersal rates from their natal groups by either males or females. Sperm whales (*Physeter macrocephalus*) also form clans, often based on matrilineal lines, with females and immature animals remaining together while mature males disperse and "rove" individually (Whitehead, 1997; Christal and Whitehead, 2001; Whitehead and Rendell, 2004); this may be the case for the SLP/CB residents as well.

Foraging behavior also differed markedly by habitat type. The Gulf dolphins rarely entered SLP or CB, and the few times they did, were
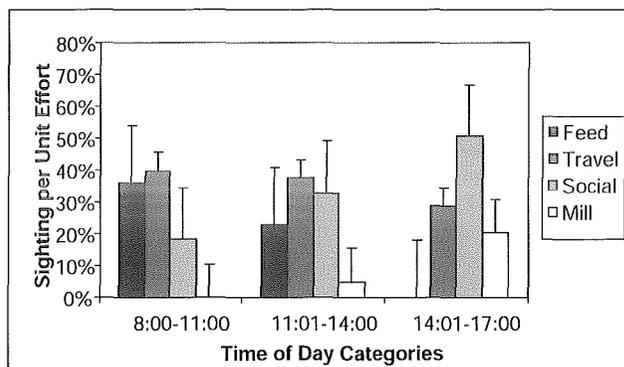

Fig. 3.   Mean sighting per unit effort of each behavior by time of day for resident groups. Error bars represent standard deviation.

never observed feeding in these shallow areas. However, they were frequently observed foraging in the deeper GoM waters and the SC. Their foraging behavior was marked by long dives and largely occurred individually or in small groups, with no apparent interactions between individuals. In contrast, resident dolphins were predominantly observed foraging in the shallow, sandy- or muddy-bottomed areas of SLP and CB in larger groups, with some interaction or cooperation between dolphins, such as chasing fish toward the broadside of another individual, or multiple animals chasing fish together.

There are several possible explanations for the different foraging strategies between resident and Gulf groups. Perhaps the use of SLP/CB solely by resident dolphins indicates resource partitioning, a behavior also noted in other dolphins that seasonally inhabit bays (Ingram and Rogan, 2002). Therefore, the foraging behavior observed in each area could be merely an artifact of the bottom characteristics of the area, and these in turn may differ between resident and Gulf dolphins because of their exclusive use of each area. However, it may also be that the possible cooperative foraging behavior observed in resident dolphins is additionally due to their long-term associations. Cooperative feeding has been observed in other bottlenose dolphin populations, in the form of group herding and synchronous capture behavior (Tayler and Saayman, 1972; Würsig, 1986). All cetacean species that demonstrate cooperative feeding behavior, such as sperm whales, killer whales, bottlenose dolphins, and pilot whales (*Globicephela* sp.), also seem to demonstrate long-term associations and lower intergroup competition (Christal and Whitehead, 2001). Both resident and transient killer whale pods form long-term associations and both forage cooperatively (Hoelzel, 1993; Baird and Whitehead, 2000). Sperm whales also seem to demonstrate unique foraging strategies between clans, even in sympatric areas, which may indicate cultural transmission of foraging strategies (Whitehead and Rendell, 2004).

Resident dolphins also display a seasonal use of the bay system, with an increase in bay use in summer months. In Moray Firth, Scotland, dolphins occupy the outer bay year-round, but enter the deeper parts of the bay only in summer. It is at this time of year that foraging increases in the narrow, deep entrances into inlets, and it is also the time of year when salmon, a known prey species, are most likely to be migrating through the area (Hastie et al., 2004). The seasonal movements of resident dolphins in SLP may also be mirroring the

spawning migrations of prey species in the area. Catch data gathered by the National Marine Fisheries Service from 1976 to 2002 in the SLP and CB areas (M. Fisher, pers. comm.) show a significantly higher abundance of six species of fish in the bay in the warm season. These six species, Atlantic croaker (*Micropogonias undulates*), silver perch (*Bidyanus bidyanus*), sand seatrout (*Cynoscion arenarius*), spot (*Leiostomus xanthurus*), striped mullet (*Mugil cephalus*), and white mullet (*Mugil curema*), were shown to be the most commonly consumed fish by bottlenose dolphins in the Texas GoM (Gunter, 1942; Barros and Odell, 1990). Therefore, it is likely that resident dolphins are following these fish into the bays in the summer.

Further observations of behavior, particularly foraging and socializing, need to be carried out with both resident and Gulf dolphins to better identify the strategies behind observed differences. Actual feeding was difficult to see from the surface, and therefore documented occurrences of foraging behavior could be skewed downward. Further work with additional recording techniques, such as in-air video cameras for detailed behavior descriptions, and underwater acoustic monitoring, are recommended. Additionally, comparisons with other photo-identification catalogs from the GoM should be carried out to determine the extent of the migratory range of Gulf dolphins, as well as possible sightings of dispersed animals from this population. Finally, genetic work is necessary to determine the true nature of the relationship among residents, and between the resident and Gulf dolphins. The resident group is a distinct population living in a human-degraded and heavily populated area. If the resident dolphin population is even partially genetically discrete, the implementation of conservation efforts becomes increasingly important.

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