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Distribution, Habitat Partitioning, and Abundance of Atlantic Spotted Dolphins, Bottlenose Dolphins, and Loggerhead Sea Turtles on the Eastern Gulf of Mexico Continental Shelf

ROBERT B. GRIFFIN AND NANCY J. GRIFFIN

We surveyed cetaceans and marine turtles from Nov. 1998 to Nov. 2000 along a series of prescribed transects between Tampa Bay and Charlotte Harbor, Florida, and between the coast and the 180-m isobath. Vertical profiles of temperature, salinity, and chlorophyll concentration were collected at 65 stations, and continuous surface data on these variables and transmittance were collected while underway. Habitat partitioning among Atlantic spotted dolphins (*Stenella frontalis*), bottlenose dolphins (*Tursiops truncatus*), and loggerhead sea turtles (*Caretta caretta*) was examined by canonical correspondence analyses of environmental characteristics at sighting locations. Environmental characteristics and primary productivity of *S. frontalis* and *T. truncatus* habitat on the eastern Gulf of Mexico continental shelf significantly differed. In shelf waters shallower than 20 m, *T. truncatus* were the dominant cetacean species, whereas *S. frontalis* were the most common shelf species at depths of 20–180 m. Environmental preferences of *C. caretta* were intermediate between the two dolphin species and showed no apparent relationship with depth. The continental shelf in the eastern Gulf of Mexico is broad, with distances from coast to slope as great as 200 km. Although *S. frontalis* habitat has elsewhere been described as ubiquitous over the shelf, our data suggest that *S. frontalis* in the eastern Gulf of Mexico prefer midshelf habitat.

Two delphinid species that predominate on the Gulf of Mexico continental shelf are the bottlenose dolphin (*Tursiops truncatus*) and Atlantic spotted dolphin (*Stenella frontalis*) (Mills and Rademacher, 1996; Jefferson and Schiro, 1997). Among species of marine turtles, the loggerhead sea turtle (*Caretta caretta*) is the most abundant in the Gulf of Mexico (Henwood, 1987). Research in the Gulf of Mexico has focused primarily on abundance of these species, and little work has compared habitat-use patterns.

Current population estimates (using aerial surveys) for *T. truncatus* in the U.S. Gulf of Mexico suggest that approximately 50,000 dolphins live on the outer continental shelf (from approximately 9 km seaward of the 18-m isobath to the continental slope and from the United States–Mexico border to the Florida Keys) and 17,600 dolphins live in coastal and inner shelf waters (from shore to the outer shelf boundary) (Waring et al., 1997). Abundance of *T. truncatus* within 37 km of the Gulf of Mexico coast (estimated using aircraft strip transects) was 16,000 (Mullin et al., 1990).

Population estimates for *S. frontalis* in the Gulf of Mexico are incomplete, with an estimate of 3,200 dolphins in the northern Gulf of Mexico (from approximately the 200-m isobath along the U.S. coast to the seaward extent of the U.S. Exclusive Economic Zone) (Waring

et al., 1997). This is considered a partial stock estimate because continental shelf areas were generally not covered. Yet, data from 7 yr of opportunistic effort on the continental shelf in the northern and eastern Gulf of Mexico showed that the primary depth range for *S. frontalis* was between 15 and 100 m (Mills and Rademacher, 1996), with highest sighting rates east of the Mississippi River. Beyond the continental shelf, this species is sighted exclusively along the upper continental slope (Mullin and Hansen, 1999).

A shipboard survey along the continental slope in the north-central and western Gulf of Mexico from the Florida–Alabama border (87.5°W) to the Texas–Mexico border (26.0°N) and between the 100- and 2,000-m isobaths found that habitat partitioning of these two species was best explained by bottom depth (Davis et al., 1998, 2002; Baumgartner et al., 2001). *Stenella frontalis* were consistently found on the continental shelf and shelf break, whereas *T. truncatus* were found primarily in deeper waters along the upper slope. Although *T. truncatus* are also found on the Gulf of Mexico shelf, these surveys were limited to shelf-break regions and did not examine habitat partitioning between these species on the continental shelf.

Little is known of sea turtle distributions and abundance in the Gulf of Mexico. Aerial sur-

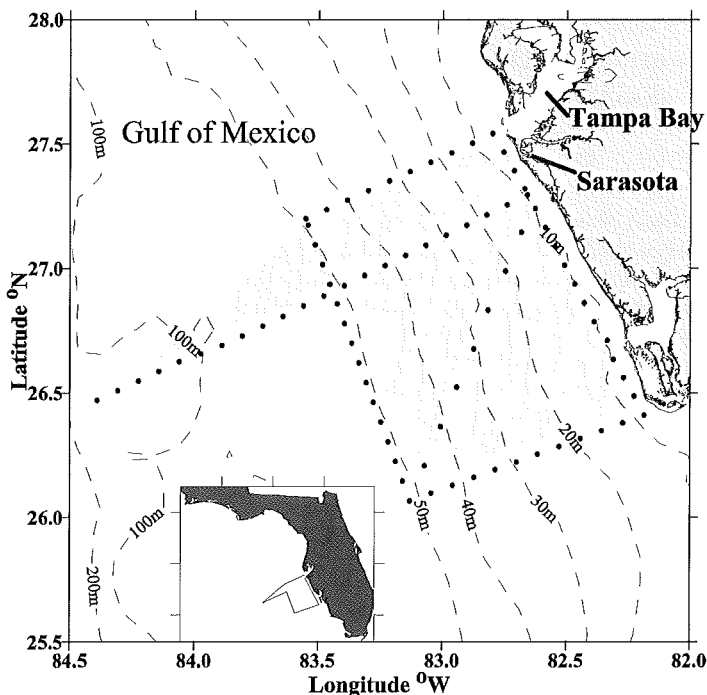


Fig. 1. Location of study area. Solid lines represent ECOHAB synoptic survey track line. Abundance estimates refer to region contained within ECOHAB block ($\approx 14,400 \text{ km}^2$). Conductivity-temperature-depth station locations (filled circles) are shown.

veys of a 9,000- km^2 area, 50 km south of Mobile, AL (Levenson et al., 1992), yielded a combined density estimate of 0.01 turtles km^{-2} for three turtle species (*C. caretta*; leatherback turtle, *Dermodochelys coriacea*; and green turtle, *Chelonia mydas*) during Nov. 1991–April 1992. *Caretta caretta* densities of 0.04 turtles km^{-2} were reported for the northeastern Gulf of Mexico (Mullin and Hoggard, 2000). Satellite sea-surface temperature data and aerial survey data were used to identify an upper (28 C) and lower (13.3 C) limit of preferred sea-surface temperatures for *C. caretta* (Coles and Musick, 2000). The study suggests that sea turtles are not randomly distributed geographically but stay within preferred temperature ranges that are seasonally variable.

Partitioning of habitat between the primary aquatic tetrapods on the west Florida continental shelf, *T. truncatus*, *S. frontalis*, and *C. caretta*, has not been studied, and *S. frontalis* and *C. caretta* population densities have not been examined in this region. We examined habitat partitioning of *T. truncatus* and *S. frontalis* with reference to physical and biotic oceanographic parameters, testing the hypothesis of minimal habitat overlap between these species on the continental shelf, as found by others on the

continental slope (Davis et al., 1998). Habitat use by these two closely related taxa was also compared with that of *C. caretta*.

METHODS

We gathered cetacean- and turtle-sighting data from Nov. 1998 through Nov. 2000. Monthly shipboard oceanographic surveys aboard the R/V *Suncoaster* (Florida Institute of Oceanography) transected an area of the west Florida continental shelf bounded by 82°–84.5°W and 26°–28°N (Fig. 1). General survey design was generated by the Ecology of Harmful Algal Blooms (ECO HAB) research group at the University of South Florida, St. Petersburg, FL, for purposes of understanding physical and biological mechanisms underlying blooms of the toxic dinoflagellate, *Karenia brevis*. Surveys included a series of repeatable transects, with 79 oceanographic stations, at 9-km intervals (Fig. 2). Two cross-shelf transects between 10- and 50-m depths, as well as one cross-shelf transect between 10- and 180-m depth, were surveyed on a monthly basis throughout the study period. Surveys consisted of 3–4 d of effort per month, covering approximately 100 km^2 /d. Surveys were completed each month

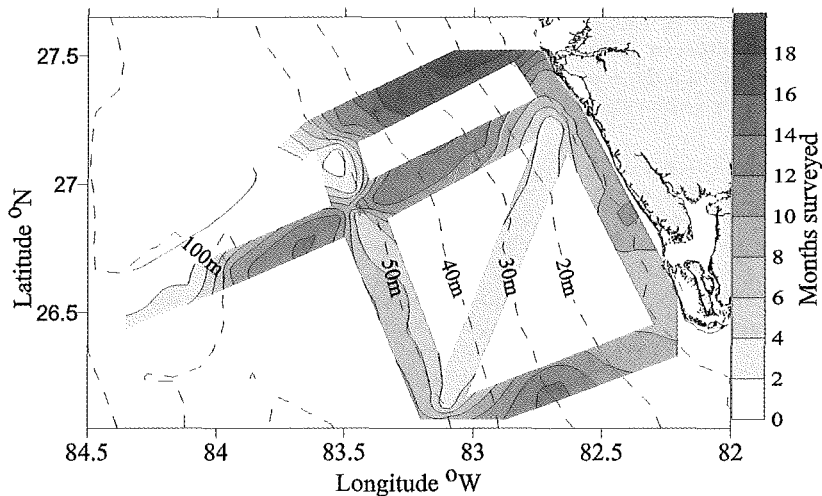


Fig. 2. Contour of cetacean sighting effort (months surveyed) along track, between Nov. 1998 and Nov. 2000.

during the study, with the exception of July and Sep. 1999 and Oct. 2000. Other transects surveyed during a part of the study period included 1) 10-m isobath coastal transect (Dec. 1998–June 2001; Nov. 2001); 2) 10- to 50-m-deep diagonal transect (Dec. 1998–Aug. 1999; May, Sep., and Dec. 2001); 3) 50-m isobath (Nov. 1998–Nov. 1999; June 2001). During surveys, vertical profiles of temperature, salinity, chlorophyll concentration, and transmittance were collected at oceanographic stations by conductivity–temperature–depth (CTD) bathythermograph (Seabird SPE25 Sealogger). Fluorescence was measured as a proxy for chlorophyll using a Chelsea Instruments AQUA-tracka Mk III fluorometer. Continuous underway surface data on temperature, salinity, chlorophyll concentration, and transmittance were collected using a Falmouth Scientific Instrument Micro-CTD3 integrated with a Seapoint Chlorophyll fluorometer manufactured by Seapoint Sensors, Inc. (Kingston, NH), a Wet Labs C-Star transmissometer, and a Seapoint turbidity meter, mounted on the port deck in a plastic vessel through which near-surface seawater (~2 m deep) passed continuously.

During surveys, observers were on watch during transit between stations (approximately 30 min) and then broke from effort for 15–20 min while data were gathered at oceanographic stations. Surveys were conducted by three observers, with two observers on effort during duty rotations. Additional observers permitted duty rotation, enabling additional break time. Two observers maintained a watch from the bow while underway during daylight hours,

scanning with naked eye for the presence of cetaceans and turtles. Biological and physical data within “transect segments” (9-km effort unit between oceanographic stations) were collected by observers to document conditions between oceanographic stations. These data included observations of surface biological manifestations (e.g., birds, flying fish, schooling fish, cnidarians), descriptors of sea-state and sighting conditions, and number of cargo, fishing, and recreational vessels present. Handheld binoculars (7 × 50) were used to sight and identify species when cues or animals were found. When cetaceans or sea turtles were encountered, data collected included time and location of sighting, bearing and distance to animals when initially sighted, species, total group size, and number of calves. Bearing was estimated using a 360° course plotter. Distances to animals when sighted were estimated by observers with prior training and experience in distance approximation. Estimation skills were periodically tested by comparing estimated distances to buoys with distances obtained by ship’s radar. Calves were defined as dolphins having ≤75% the body length of associated maternal escort. Species identifications were assigned by experienced observers. For some sightings, the vessel was diverted from track to allow for species identifications.

Abundances of *S. frontalis*, *T. truncatus*, and *C. cavelta* were estimated using the program DISTANCE (Thomas et al., 1998). Sightings from all months were pooled for these analyses. Data were right truncated to exclude the greatest 5% of perpendicular distances. Detec-

TABLE 1. Variables used in canonical correspondence analysis of *Tursiops truncatus*, *Stenella frontalis*, and habitat use. Surface values of temperature, salinity, density, chlorophyll, and transmittance at cetacean locations were extracted from the continuous underway surface data set. Water column properties at cetacean locations were calculated as means of CTD values at casts bracketing transect segments where sightings were made.^a

1	Surface temperature (C) at sighting location or at midsegment where no sighting was made
2	Surface minus bottom temperature (C) in 9-km transect segment associated with sighting location
3	Stratified (1) or nonstratified (0) water column defined as the presence or absence of a well-developed thermocline in given transect segments
4	Surface salinity (PSU) at sighting location or at midsegment where no sighting was made
5	Mean surface minus bottom salinity (PSU) in 9-km transect segment
6	Density (Sigma-T, kg m ⁻³) at sighting location or at midsegment where no sighting was made
7	Mean surface minus bottom density (Sigma-T) in 9-km transect segment
8	Surface transmittance (%) at sighting location or at midsegment where no sighting was made
9	Maximum chlorophyll (µg liter ⁻¹) in the water column in 9-km transect segment
10	Surface chlorophyll (µg liter ⁻¹) at sighting location or at midsegment where no sighting was made
11	Latitude of sighting
12	Longitude of sighting
13	Closest distance of sighting from land (km)
14	Depth (m) at sighting location or at midsegment where no sighting was made
15	Month
16	Year
17	Sequential date (day of year, from 1 to 366)
18	Cos of sequential date (cos and sine of sequential date analyzed to test for cyclical temporal variation)
19	Sine of sequential date

^a CTD, conductivity-temperature-depth.

tion function and group size were estimated globally by species, and analyses were poststratified by sighting-depth ranges: 0–10 m, 10–20 m, 20–30 m, 30–40 m, 40–50 m, and >50 m. The >50-m stratum included waters between 50 m and 180 m, the maximum depth in the survey area. Data were combined in this stratum because of relatively low sighting effort in individual 10-m increments in depth. For *S. frontalis* densities, effort within the 0- to 10-m stratum was not used for the density estimate because the minimum depth of sighting locations for this species was 16 m. Three models were tested (i.e., uniform+cosine, half-normal+cosine, and half-normal+hermite polynomial), and Akaike's information criterion (Akaike, 1973) was used to select the most parsimonious model for each analysis. Regressions of observed group size against distance were not significant at an alpha level of 0.15; hence, mean group sizes were calculated as the mean of observed values.

Relationships of cetacean species and habitat use to the physical and biological environment were analyzed by canonical correspondence analyses (CCA) (ter Braak, 1986, 1995; ter Braak and Verdonschot, 1995) using the program CANOCO 3.10 (ter Braak, 1992). These analyses have been successful in understanding cetacean distributions in the eastern

tropical Pacific (Fiedler and Reilly, 1994; Reilly and Fiedler, 1994). Differences in habitat characteristics and temporal use patterns were tested by CCA of 19 environmental, spatial, and temporal variables (Table 1). We included cos and sine transformations of sighting sequential dates to test for the influence of cyclical annual variation. Analyses were done by a forward selection process to minimize the number of variables used in ordination, and variables significantly contributing to explaining species variance (tested by Monte Carlo simulation with 999 permutations) were retained. Addition of variables to the ordination ended when the contribution of the variable under consideration was insignificant ($P > 0.05$).

Canonical correspondence analysis is an eigenvector ordination technique, which relates community composition to variation in the environment, using an iterative procedure to directly relate species ordinations to environmental variables. In CCA, species are ordinated along synthetic axes that are constrained to be linear combinations of environmental variables. Axes are generated subject to the restriction that they be uncorrelated with previous axes. Biplots of species' ordinations and environmental vectors permit direct interpretation of relationships between species' distributions and the environment. In CCA ordination dia-

grams, species points are plotted at their "optima" locations (center of species curve) along the axes, representing a two-dimensional niche center. Environmental variables are plotted as eigenvector axes, leading away from the origin in the direction of increasing value. Relative lengths of environmental vectors are proportional to the importance of the environmental variable in explaining species distributions. Similarities in direction of environmental vectors are related to degree of correlation between environmental parameters.

For these analyses, effort and sighting data gathered where sighting conditions included Beaufort sea states of ≤ 3 were used, and "sites" were defined as the 9-km transect segments between oceanographic stations. Sighting data were weighted in these analyses by natural logarithms of the group size estimates within each sighting to minimize the effect of errors in the estimates of the size of larger groups and to reduce the relative influence of larger groups on these analyses. Although group size in delphinids may reflect availability of food sources, additional factors that are not related to suitability of habitat may influence group size (e.g., aggregation for mating, perceived risk of predation, or age and sex of group members) (Evans, 1987).

Community ordination diagrams were constructed using CCA results to relate cetacean and turtle distributions to physical and biological variables making significant contributions. Species scores, or ordination coordinates, were calculated as weighted mean sample scores in all tests. Interspecies ordination distances approximate their chi-square distances when this scaling is used. Kruskal-Wallis test and the Mann-Whitney U-test (Sokal and Rohlf, 1981) were used to test for differences in axes scores between cetacean species and to examine differences in species means of physical and biological variables associated with species distributions.

RESULTS

Monthly sighting effort (Fig. 2) within the study area varied as a function of daylight length and scientific operations aboard the vessel. The three cross-shelf transects were consistently surveyed for cetaceans, whereas the diagonal transect received the least attention. Over 7,000 km of survey effort was completed in the study area during the 2-yr period, with 267 on-effort dolphin sightings [119 *S. frontalis* sightings, 663 dolphins; 113 *T. truncatus* sightings, 316 dolphins; one rough-toothed dolphin

(*Steno bredanensis*) sighting, seven dolphins; 34 unidentified dolphin sightings, 94 dolphins] for an overall sighting rate of 0.154 dolphins km^{-1} . Mean (SD, median) group size was 2.8 (2.27, 2) for *T. truncatus* and 5.6 (5.29, 4) for *S. frontalis*. Group sizes of *S. frontalis* ranged from 1 to 48 dolphins, whereas *T. truncatus* group sizes ranged from 1 to 15 dolphins. Approximately 81% of *S. frontalis* groups sighted approached the vessel to bow-ride, compared with 42% of *T. truncatus* groups. This difference was highly significant (chi-square test; $\chi^2 = 46.49$, $P < 0.001$). Three species of marine turtles were sighted, including 36 *C. caretta*, three *D. coriacea*, and one Kemp's Ridley (*Lepidochelys kempi*), along with 21 turtles not identified to species.

Stenella frontalis sightings tended to be in deeper waters farther from the coast (Fig. 3) compared with *T. truncatus* sightings, whereas *C. caretta* were more often seen at median depths and distances. The minimum depth for *S. frontalis* sightings was 16 m, with only eight sightings at depths < 20 m, whereas *T. truncatus* and *C. caretta* were found throughout the study area. Mean (SD, median) sighting depths for the two dolphin species were 40 m (19.1, 37 m) and 23 m (16.1, 13 m), respectively, whereas mean (SD, median) distances from coast were 71 km (36.0, 68 km) and 37 km (39.3, 17 km), respectively. Mean (SD, median) *C. caretta* sighting depth was 30 m (17.5, 30), and mean distance from land was 55 km (42.6, 54 km).

Using Akaike's information criterion, the half-normal+cosine model was selected for abundance estimates of *S. frontalis* and *T. truncatus*, whereas the uniform+cosine method was selected for *C. caretta* estimates. The effective strip width (ESW) of *S. frontalis* was 202 m, compared with an ESW of 168 m for *T. truncatus*. Pooled data showed an abundance of 3,703 *S. frontalis* (2,635–5,202, 95% Confidence Interval (CI)) and 1,346 *T. truncatus* (959–1,889, 95% CI) in the study area. Overall density of *S. frontalis* was 0.260 dolphins km^{-2} , whereas overall *T. truncatus* density throughout all depth strata was 0.093 dolphins km^{-2} . Density estimates stratified by sighting depth (Fig. 4) indicate a primary depth range of 20–50 m for *S. frontalis* in this region, whereas *T. truncatus* are more likely to be sighted from the coast to 20-m depth.

Effective strip width for *C. caretta* was 182 m. Estimated abundance of *C. caretta* within the study area was 181 (114–286, 95% CI), with an overall density of 0.013 turtles km^{-2} . No relationship was apparent between *C. caretta* sighting densities and depth strata (Fig. 4).

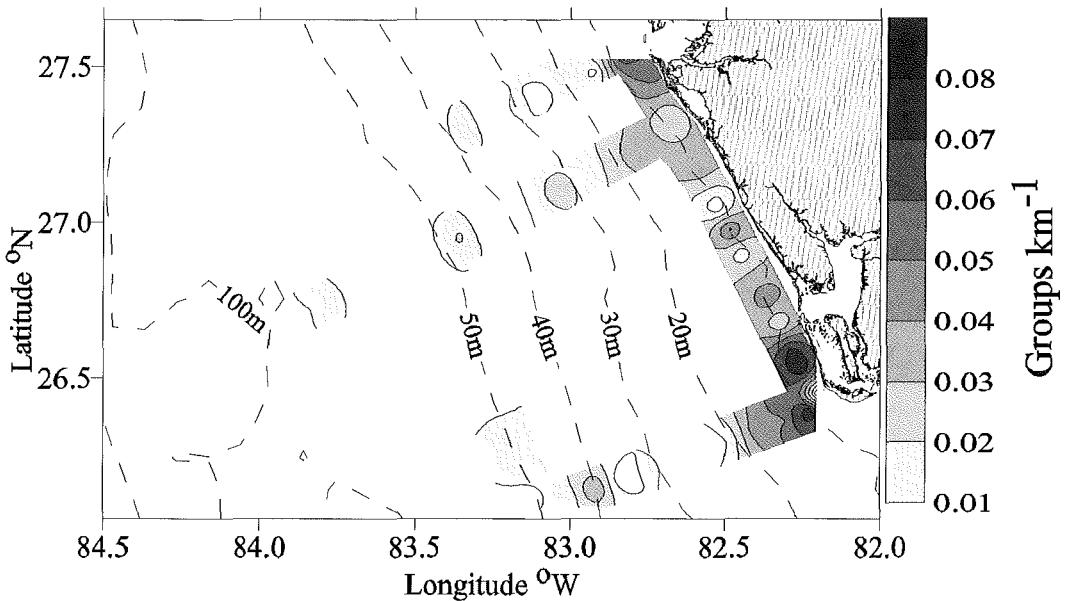
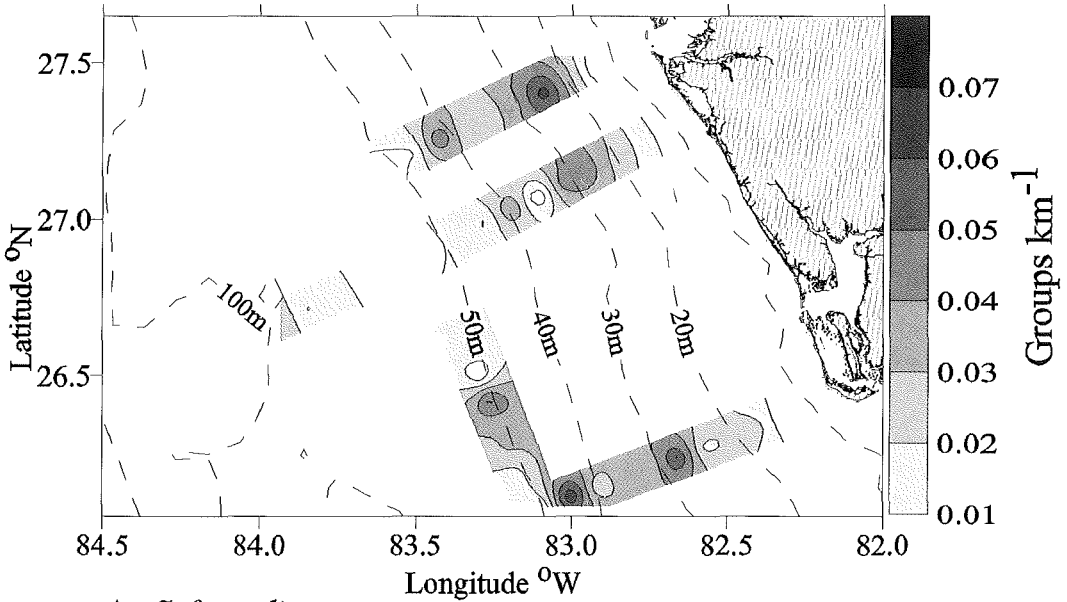


Fig. 3. Group sightings per kilometer in transect segments during study period.

Canonical correspondence analyses.—Of 19 physical and biological variables used in CCA, four made significant contributions to explaining variance in cetacean habitat characteristics: transmittance, surface temperature, surface salinity, and difference between surface and bottom salinity. Correlation values (Table 2) suggest that canonical axis 1 represented variation in transmittance and surface minus bottom sa-

linity, whereas canonical axis 2 represented variation in surface temperature. Variation in surface salinity contributed to both axes. For *S. frontalis* and *T. truncatus*, CCA explained ~29% and ~25% of the species variation (Table 3), respectively, whereas ~27% of *C. cava* variation was explained. Axis 1 was more important in explaining *S. frontalis* variation. Axis 2 was more important in explaining characteristics

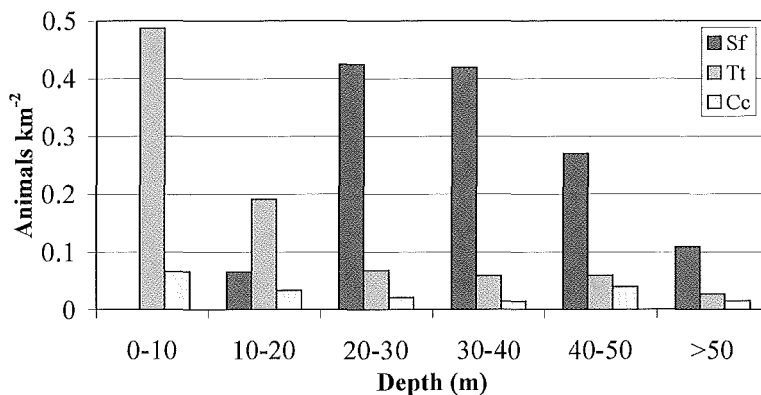


Fig. 4. Estimated densities (animals per square kilometer) of *Stenella frontalis* (Sf), *Tursiops truncatus* (Tt), and *Caretta caretta* (Cc) by depth stratum (m) for 2-yr pooled data.

of *C. caretta* habitat, whereas both axes were important in explaining *T. truncatus* habitat.

Species-environment ordination biplots indicated environmental similarities and differences in optimal habitat (represented by axes location) of the three species. Axis 1 (Fig. 5) separated the *S. frontalis* habitat characteristics from those of *T. truncatus* and *C. caretta*, whereas axis 2 separated the *C. caretta* environmental conditions from the two dolphin species habitats. Canonical ordination suggests that *S. frontalis* are likely to be found in waters with greater surface salinity, lower or negative surface minus bottom salinity values, and greater transmittance (corresponding with lower chlorophyll values) compared with *C. caretta* or *T. truncatus*. *Caretta caretta* are more likely found in warmer waters than *S. frontalis* or *T. truncatus*.

Plotting of weighted species CCA standard deviations along each axis (Fig. 6) provided a measure of niche breadth (Carnes and Slade, 1982) and permitted an examination of niche separation between species, as described by environmental characteristics. Standard deviation ellipses about estimated optimum environments overlap for all species combinations but do not coincide. Although variation in environmental conditions at sighting locations was

large, Mann-Whitney U-test shows that these species significantly differed in location in canonical space (Table 4). *Stenella frontalis* and *T. truncatus* ordinations significantly differed along axis 1, which was most important in explaining variation between species. Axis 1 (salinity and transmittance) separated *S. frontalis* from *T. truncatus* and *C. caretta*, whereas axis 2 (temperature and salinity) separated *C. caretta* from the two dolphin species.

Mean values of many of the environmental variables tested by CCA significantly differed by species (Tables 5, 6), providing further evidence of differences in habitat conditions indicated by canonical ordination. Transmittance of light through water was greater and chlorophyll content was lower in waters where *S. frontalis* were found than in waters where *T. truncatus* were sighted. *Tursiops truncatus* were sighted in water with significantly less salinity and smaller water column temperature gradient compared with *C. caretta* and *S. frontalis*. *Caretta caretta* were sighted in waters with a minor water column salinity gradient. All species differed in mean sighting depth and mean distance from shore, with *C. caretta* intermediate between the two dolphin species.

TABLE 2. Correlations of canonical axes with significantly ($P < 0.05$) contributing variable ($n = 605$).

Variable	Axis 1	Axis 2
S-B salinity ^a	-0.375	0.027
Temperature	-0.014	0.385
Salinity	0.121	0.164
Transmittance	0.154	0.050

^a S-B indicates surface minus bottom.

TABLE 3. Percentage of variation explained by canonical axes, by species.

Species	Axes		Total
	1	2	
<i>Stenella frontalis</i>	27.60	1.10	28.70
<i>Tursiops truncatus</i>	13.85	11.63	25.48
<i>Caretta caretta</i>	9.50	17.18	26.68

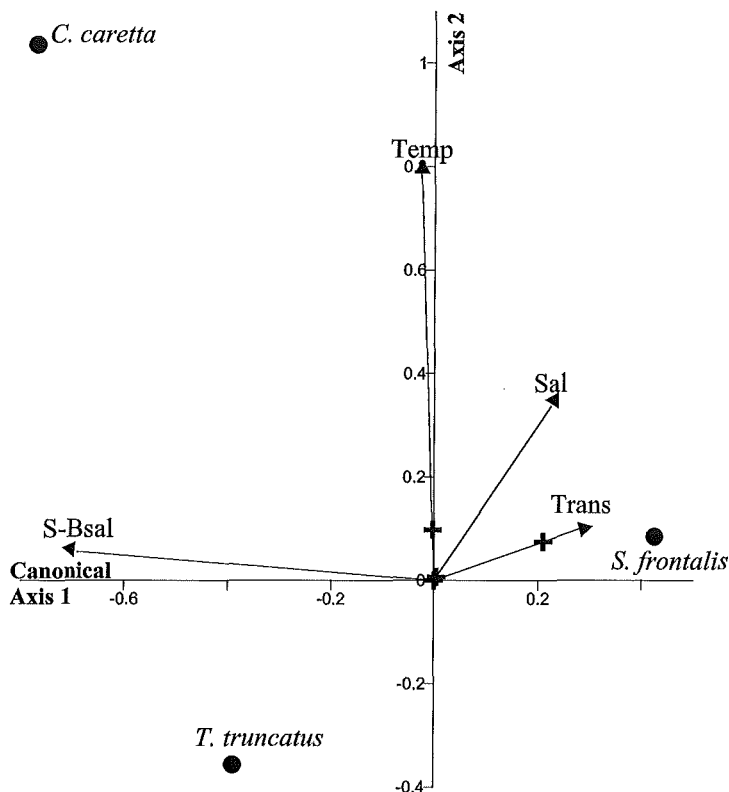


Fig. 5. Ordination for model with abundance logarithmically transformed. All variables significantly contributed ($P < 0.05$). Arrows point in direction of variable increase, and crosses represent variable grand means. Species ordinations: Sf, *Stenella frontalis*; Tt, *Tursiops truncatus*; Cc, *Caretta caretta*. S - B Sal, mean value for surface salinity - bottom salinity; Trans, surface transmittance; Salinity, surface salinity; Temp, surface temperature.

DISCUSSION

We found that densities of *S. frontalis* (0.260 dolphins km^{-2}) in the eastern Gulf of Mexico were greater than densities of *T. truncatus* (0.093 dolphins km^{-2}). Aerial surveys in the northeastern Gulf of Mexico (Mullin and Hoggard, 2000) reported a greater density of *T. truncatus* (0.148 dolphins km^{-2}) on that area of the shelf (waters <100 m in depth) and a lower density of *S. frontalis* (0.089 dolphins km^{-2}). Differences in survey methodology make comparisons of our results with earlier work difficult. It is not known whether the apparent dissimilarity among studies on relative density of these two species between the eastern and northeastern Gulf of Mexico is an artifact of methodology or represent true regional differences. Observed differences between the two regions suggest ecological variation between broad-shelf habitat in the eastern Gulf of Mexico and narrow-shelf habitat in the north.

The importance of *S. frontalis* habitat of greater than 20-m depth agrees with earlier findings indicating that *S. frontalis* principally occupy waters 15–100 m in depth (Mills and Rademacher, 1996). In that study, *S. frontalis* distribution on the entire Gulf of Mexico continental shelf was examined using opportunistic data gathered from various National Marine Fisheries Service resource surveys.

Because *C. caretta* spend 90% of their time submerged during any given season (Renaud and Carpenter, 1994), with average submergence times as great as 171 min., abundances for this species are probably underestimated. In addition, unidentified turtles that could potentially increase *C. caretta* density estimates were not included in these analyses. Mean sea-surface temperature (26.3 C) associated with our *C. caretta* sightings was in agreement with mean sea-surface temperature reported elsewhere for *C. caretta* distributions (13.3–28 C; Coles and Musick, 2000).

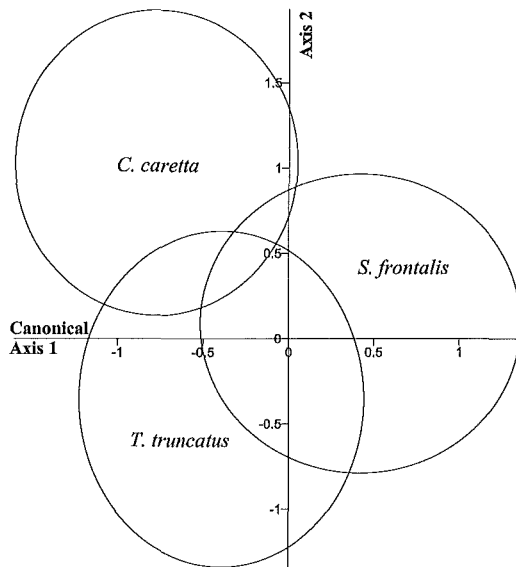


Fig. 6. Ellipses of uncertainty (95% CI) about species ordinations on the first and second canonical axes, taken from canonical correspondence analysis of environmental data. Ellipses are ± 1 SD about the estimated optimal location for each species on the first and second canonical axes. Sf, *Stenella frontalis*; Tt, *Tursiops truncatus*; Cc, *Caretta caretta*.

Some assumptions of line transect theory were violated in this study. It is not likely that all animals on track line were seen. Further, it is likely that dolphins were often aware of the vessel's approach before they were detected. Some initial sightings were made while dolphins approached the vessel, which may reduce calculated ESW, and lead to an inflated abundance estimate (Turnock and Quinn, 1991). Although some bow-riding groups may have initially been on the track line, a higher proportion of *S. frontalis* bow-riders suggests that *S. frontalis* may be more likely to approach the vessel than *T. truncatus*, potentially leading to an artificial increase in relative abundance of this species.

The greater number of *S. frontalis* (663) than *T. truncatus* (316) seen by observers during this study may reflect relative densities of dolphin species. This could also have resulted from greater visibility and the differential attraction of *S. frontalis* to the research vessel. Work has shown that these two species show 0% avoidance reaction toward ships (Würsig et al., 1998); yet, no work has been done to examine relative detectability of these two species as a function of response to vessel. *Stenella frontalis* approaching the vessel to bow-ride tended to display "exhibitory behaviors" (pers. obs.)

TABLE 4. *P* values for Mann-Whitney U-test, comparing canonical axes scores by species.

Species	<i>Stenella frontalis</i>		<i>Tursiops truncatus</i>	
	Axis 1	Axis 2	Axis 1	Axis 2
<i>T. truncatus</i>				
Axis 1	0.003			
Axis 2		0.14		
Axis 1	<0.001		0.15	
Axis 2		0.005		<0.001

(e.g., porpoising, leaping, splashing, and breaches), whereas *T. truncatus* seldom displayed these behaviors. Such behaviors may enable observer detection of groups at a greater relative distance. The greater ESW reported in this study for *S. frontalis* supports this hypothesis of early detection for this species. Although abundance estimates reported in this study may be positively biased, they can be useful for detection of seasonal and interannual trends within species.

The four variables significantly contributing to CCA represent parameters that reflect nearshore vs offshore regions (e.g., greater salinity and "blue" water at greater distances from the coast). The eastern Gulf of Mexico exhibits environmental variability between nearshore and offshore waters, with consistent differences in primary productivity, temperature, and salinity. Nearshore chlorophyll concentrations are relatively high, and chlorophyll concentrations rapidly decline beyond 10 km from the coast. Nearshore waters are often well mixed, whereas offshore waters may be thermally stratified. Greater transmittance with distance from the coast, as in *S. frontalis* optimum habitat, results from lower primary productivity in offshore waters. High gradients in surface to bottom salinity can result from 1) less mixing in the water column, 2) input of higher-salinity water from offshore regions, or 3) high freshwater outflow from estuaries such as Tampa Bay and Charlotte Harbor.

Salinity and transmittance of water (a proxy for primary production) were important in describing variation in species' habitat use and may reflect differences in water masses and associated productivity. Salinity is a conservative characteristic, useful for identification of water masses. Salinity levels in the region are elevated by intrusion of Loop Current filaments, whereas freshwater flow from coastal bays and estuaries results in a relatively strong salinity gradient of fresher water. Thermal fronts were often located at boundaries between well-

TABLE 5. Results from Kruskal–Wallis analysis of variance (ANOVA) by ranks, testing for differences in variable mean values at species' sighting locations, and Mann–Whitney U-test comparing variable means between species pairs. Sf = *Stenella frontalis*, Tt = *Tursiops truncatus*, Cc = *Caretta caretta*.

Variable	Kruskal–Wallis ANOVA	Mann–Whitney U-test		
		Sf-Tt	Sf-Cc	Tt-Cc
Depth	<0.0001	<0.001	0.002	<0.001
Distance from shore (km)	<0.0001	<0.001	0.004	<0.001
Temperature	0.003	0.29	0.003	0.001
Salinity	0.0001	<0.001	0.60	0.03
Sigma-T ^a	<0.0001	<0.001	<0.001	0.49
Chlorophyll	<0.0001	<0.001	0.35	0.003
Transmittance	0.05	0.02	0.26	0.70
S–B ^b temperature	0.02	0.007	0.87	0.06
S–B ^b salinity	0.02	0.63	0.007	0.02
S–B ^b density	0.10	0.04	0.27	0.89

^a Sigma-T = density (kg m⁻³) minus 1000.

^b S–B indicates surface minus bottom.

mixed and stratified waters in this study, and we frequently sighted dolphins near boundary fronts. Other variables (e.g., secondary productivity, proximity to thermal fronts) that were not measured or included in these analyses would be useful in understanding differences in habitat characteristics between these species.

Warm-water filaments and cool cyclonic eddies originating in the Loop Current system affect oceanographic variability on spatial and temporal scales. Loop Current cyclonic and anticyclonic eddies were important oceanographic features explaining distributions of oceanic *Stenella* species (Evans et al., 2000). Advanced Very High Resolution Radiometer satellite images reveal intrusion of Loop Current filaments onto shelf areas, where *S. frontalis* are found. Loop Current flow and filaments may directly affect salinity and primary productivity levels and influence trophic dynamics in the eastern Gulf of Mexico. In another study, cetacean distributions were partially explained by entrainment of water masses by Gulf Stream features in the northeast Atlantic (Griffin, 1999), a system similar to the Loop Current.

Data provide support for our hypothesis of minimal habitat overlap between these species. Our study indicates that *S. frontalis* were more common than *T. truncatus* in waters 20–180 m deep. The importance of canonical axis 1 in separating *S. frontalis* and *T. truncatus* habitat descriptions, together with the significant differences in oceanographic variables between these species, provides evidence for spatial separation of habitat on temporal scales. A partitioning of habitat between species on the inner shelf is apparent, where *T. truncatus* are more

likely found nearshore, *S. frontalis* densities are highest in midshelf waters, and *C. caretta* are more likely found in intermediate habitat.

The continental shelf in the eastern Gulf of Mexico is up to 200 km wide (Roberts et al., 1999) and is much broader than elsewhere on the eastern coast of the United States. The nearest similarly broad-shelf habitat along eastern North America is Georges Bank in the northwest Atlantic, an area where climatic conditions are very different from those in our study area. Research has shown that *S. frontalis* in the Gulf of Mexico are genetically distinct from conspecifics in adjacent Atlantic Ocean waters (Bero, 2001). Studies of genetic variation are needed to learn whether ecological adaptations to broad-shelf habitat have given rise to multiple populations of this species in the Gulf of Mexico. Future work will examine seasonality and interannual variability in dolphin populations on the west Florida continental shelf.

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TABLE 6. Means (\pm SD) of biotic and abiotic variables associated with dolphin and turtle sightings.

	<i>Stenella frontalis</i>	<i>Tursiops truncatus</i>	<i>Caretta caretta</i>	<i>n</i>
Depth (m)	40.7 (\pm 18.14)	17.7 (\pm 16.07)	29.5 (\pm 17.38)	40
Distance (km)	76.7 (\pm 35.63)	26.4 (\pm 38.86)	54.9 (\pm 42.50)	40
Temperature (C)	24.6 (\pm 3.15)	24.0 (\pm 3.72)	26.3 (\pm 3.17)	33
Salinity (psu)	35.850 (\pm 0.5369)	34.885 (\pm 1.7629)	35.696 (\pm 0.8433)	33
Sigma-T ^a	24.097 (\pm 0.09540)	23.512 (\pm 1.1543)	23.507 (\pm 0.3441)	33
Chlorophyll (μ g liter ⁻¹)	0.241 (\pm 0.1912)	0.639 (\pm 0.8718)	0.342 (\pm 0.3654)	33
Transmittance (%)	39.1 (\pm 26.33)	31.5 (\pm 24.51)	34.6 (\pm 25.98)	31
S-B ^b temperature (C)	1.55 (\pm 2.100)	1.06 (\pm 2.099)	1.68 (\pm 2.582)	32
S-B ^b salinity (psu)	-0.189 (\pm 0.3751)	-0.128 (\pm 0.3035)	-0.003 (\pm 0.2069)	32
S-B ^b density (kg m ⁻³)	-0.596 (\pm 0.7111)	-0.389 (\pm 0.5259)	-0.518 (\pm 0.7437)	32

^a Sigma-T = density (kg m⁻³) minus 1000.^b S-B indicates surface minus bottom.

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