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PHYSICAL HABITAT OF CETACEANS ALONG THE CONTINENTAL SLOPE IN THE NORTH-CENTRAL AND WESTERN GULF OF MEXICO

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Abstract

The physical habitat of cetaceans found along the continental slope in the north-central and western Gulf of Mexico was characterized from shipboard sighting data, simultaneous hydrographic measurements, and satellite remote sensing. The study area was encompassed by the longitude of the Florida-Alabama border (87.5°W), the southernmost latitude of the Texas-Mexico

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border (26.0°N), and the 100-m and 2,000-m isobaths. Shipboard surveys were conducted seasonally for two years from April 1992 to May 1994. A total of 21,350 km of transect was visually sampled in an area of 154,621 km^2.

Sighting localities of species in the study area were differentiated most clearly with bottom depth. Atlantic spotted dolphins (*Stenella frontalis*) were consistently found in the shallowest water on the continental shelf and along the shelf break. In addition, the bottom depth gradient (sea floor slope) was less for Atlantic spotted dolphins than for any other species. Bottlenose dolphins (*Tursiops truncatus*) were found most commonly along the upper slope in water significantly deeper than that for Atlantic spotted dolphins. All the other species and species categories were found over deeper bottom depths; these were Risso's dolphins (*Grampus griseus*), short-finned pilot whales (*Globicephala macrorhynchus*), pygmy/dwarf sperm whales (*Kogia* spp.), rough-toothed dolphins (*Steno bredanensis*), spinner dolphins (*Stenella longirostris*), sperm whales (*Physeter macrocephalus*), striped dolphins (*Stenella coeruleoalba*), *Mesoplodon* spp., pantropical spotted dolphins (*Stenella attenuata*), Clymene dolphins (*Stenella clymene*) and unidentified beaked whales (Ziphiidae). Risso's dolphins and short-finned pilot whales occurred along the upper slope and, as a subgroup, were significantly different from striped dolphins, *Mesoplodon* spp., pantropical spotted dolphins, Clymene dolphins, and unidentified beaked whales, which occurred in the deepest water. Pygmy/dwarf sperm whales, rough-toothed dolphins, spinner dolphins, and sperm whales occurred at intermediate depths between these two subgroups and overlapped them.

Key words: cetacean, habitat, Gulf of Mexico.

Twenty-eight species of cetaceans are known to occur in the Gulf of Mexico (Jefferson 1995, Jefferson and Shiro 1997). Studies of continental slope waters (*i.e.*, bottom depths between 180 and 3,000 m) of the northern Gulf have revealed this to be an area of high cetacean diversity with at least 19 species (Fritts *et al.* 1983, Mullin *et al.* 1994, Hansen *et al.* 1996). Of these, the pantropical spotted dolphin, bottlenose dolphin, Clymene dolphin, Atlantic spotted dolphin, spinner dolphin, melon-headed whale (*Peponocephala electra*), Risso's dolphin, short-finned pilot whale, rough-toothed dolphin, and sperm whale occur commonly in this part of the Gulf. Cryptic species such as the pygmy sperm whale (*Kogia breviceps*) and dwarf sperm whale (*Kogia simus*) and certain species of beaked whales (Ziphiidae) may also be common but are difficult to observe. Despite recent studies of distribution and abundance (*e.g.*, Jefferson 1995), we know little about the natural history and ecology of pelagic cetaceans in the Gulf of Mexico.

There are many factors that influence the spatial and temporal distribution and abundance of cetaceans. The factors may be broadly divided into environmental, biotic, and anthropogenic (Borcard *et al.* 1992). Environmental variables include those that are physicochemical, climatological, and geomorphological. Environmental factors operate on time scales ranging from less than a day to many millennia. Diel, seasonal, interannual, and decadal patterns of variability or periodicity may occur for each factor. Biotic variables include prey distribution, competition among animals, reproduction, and predation. Anthropogenic factors include, among others, historical hunting, pollution,

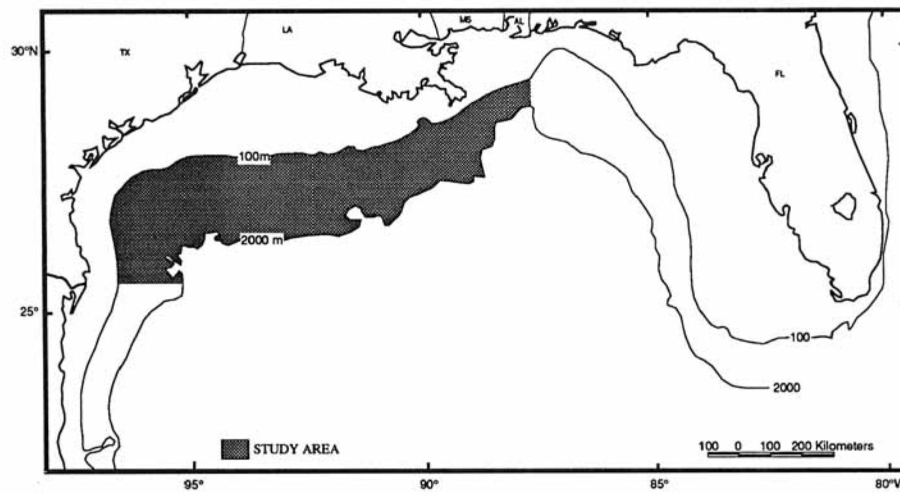

Figure 1. Study area between the 100- and 2,000-m isobaths, extending as far east as the Florida-Alabama border and as far southwest as the Texas-Mexico border.

ship activity, commercial and recreational fishing, oil and gas development and production, and seismic exploration. The spatial and temporal structuring of marine mammal communities may be influenced by many of these variables, the relative contributions of which are difficult to quantify (Jaquet 1996).

The correlation of environmental features with sighting data can improve our understanding of cetacean ecology and indicate which, if any, oceanographic variables may be affecting cetacean distribution (Volkov and Moroz 1977, Smith and Gaskin 1983, Hui 1985, Kenney and Winn 1986, Smith *et al.* 1986, Brown and Winn 1989, Reilly 1990, Waring *et al.* 1993). The purpose of this study was to characterize the physical habitat of cetaceans along the continental slope in the north-central and western Gulf of Mexico based on shipboard sighting data and simultaneous oceanographic measurements using hydrographic sampling techniques and satellite remote sensing.

Materials and Methods

Cetacean surveys—This study was part of a larger research program designed to determine the distribution and minimum abundances of cetaceans in a 156,621-km^2 area of the north-central and western Gulf of Mexico (Davis and Fargion 1996). The study area was encompassed by the longitude of the Florida-Alabama border (87.5°W), the southernmost latitude of the Texas-Mexico border (26.0°N), and the 100-m and 2,000-m isobaths (Fig. 1). This area includes much of the continental slope in the northern Gulf and is currently of interest to the Minerals Management Service, U.S. Department of the Interior, for oil and gas exploration and development. Shipboard visual surveys were conducted seasonally for two years from April 1992 to May 1994 along north-south transect lines spaced equidistantly over the study area (for details, see Hansen *et al.* 1996). Seasons were defined as: summer, July–September; fall, October–December; winter, January–March; and spring, April–June. A total of 21,350 km of transect were sampled on 10 cruises during the two-year period.

Cetacean sightings were recorded by two trained observers using high-power (25 × 150) binoculars mounted on each side of the ship's flying bridge (Holt and Sexton 1987). The binoculars were mounted on a graduated base to determine the bearing of a sighting relative to the survey track-line and fitted with a graduated eyepiece (reticle) to measure radial distance of the sighting. The third member of the survey team recorded data and searched the area near the track-line either without visual aids or with hand-held binoculars. The observers rotated through each of the three stations every 30–40 min, and teams alternated between 2-h watches. The survey data were collected only during daylight hours and favorable weather conditions (*i.e.*, no rain and Beaufort sea state <6). Sighting data were recorded on standard marine mammal visual sampling forms (Hill *et al.* 1991) or with a data logger interfaced with a global positioning system (GPS) or LORAN-C navigation receiver. Data collected included species, group size, bearing, reticle reading, and environmental observations (*e.g.*, Beaufort sea state, cloud cover, visibility, and solar elevation) which could impair the observers' ability to sight animals. Other data recorded included the time of day, latitude and longitude coordinates, behavior, and associated animals.

Cetaceans were identified to the lowest taxonomic level possible based on descriptions in field guides and scientific literature (*e.g.*, Leatherwood *et al.* 1976, Leatherwood and Reeves 1983, Perrin *et al.* 1987, Jefferson *et al.* 1992). The ability to make an identification was dependent on water clarity, sea state, and animal behavior. Identifications to species were not possible for some genera or groups of species.

Hydrographic and satellite remote sensing data—A detailed description of the hydrographic and remote sensing data collection and analysis may be found in Fargion *et al.* (1996). Briefly, hydrographic stations were located at the 100- and 2,000-m isobaths and at 74-km (40-nmi) intervals along the cruise track. Vertical salinity and temperature profiles were measured using a CTD (conductivity-salinity-depth) instrument and rosette that were lowered to the sea bottom or to a maximum depth of 800 m. Niskin bottles were closed on the upcast, and data from these samples were later used to verify CTD data. The actual depths sampled were variable, because the standard cruise plan called for water samples at the surface, mid-depth, and the bottom. Expendable bathythermographs (XBTs) were launched half-way between CTD stations. Location, surface water salinity, and temperature were recorded at 60-sec intervals using a continuous-flow thermo-salinograph on the ship. Sea-surface temperature measurements were also extracted from NOAA-AVHRR satellite images during periods when equipment failure precluded the use of the thermo-salinograph data. The satellite data were acquired within 24 h of cetacean sightings along the survey track-lines. The data were analyzed using standard techniques that are described in detail elsewhere (Fargion *et al.* 1996).

Data integration and analysis—A geographic information system (GIS) was used to integrate the cetacean sightings with the following environmental data: sea-surface temperature, sea-surface temperature gradient, depth of the 15°C isotherm, water temperature at 100 m, surface salinity, bottom depth, and bottom-depth gradient. The environmental data were aggregated into cells which were 1.1 × 1.1 km in size. The sightings data and environmental measurements were converted into raster or vector maps (Aronoff 1989) as appropriate, and displayed and analyzed with the Advanced Geographic Information System (Delta Data Systems, Inc., Picayune, Mississippi) installed on a UNIX workstation or personal computer. The environmental data were extracted at the location of each sighting and along all of the survey tracklines. Environmental profiles consisting of the arithmetic mean, median, minimum, and maximum observed values were tabulated for each of the 13 most abundant species or species groups.

To test whether species could be differentiated with regards to environmental variables, the species or species groups that had 10 or more sightings were analyzed for each variable using the Kruskall-Wallis one way analysis of variance with *a posteriori* comparisons (significance defined as $\alpha = 0.05$) (Conover 1980). Significant differences between species or species groups were illustrated with box plots (Tukey 1977). Low sample sizes and missing data precluded a full multivariate analysis (see Reilly and Fiedler 1994). Data reduction and statistical analyses were conducted with the UNIX version of the Statistical Analysis System (SAS Institute, Inc., Cary, North Carolina) and SYSTAT for Windows, version 5 (SYSTAT, Inc. 1992).

Results

Sea-surface temperature (SST)—Eight species or species categories were found along a gradient of cooler to warmer water ($KW = 20.7$, df = 7, $P = 0.004$) (Table 1, Fig. 2). Specifically, Atlantic spotted dolphins, striped dolphins, and sperm whales occurred in the coolest water and, as a group, were found at temperatures significantly different from the warmest waters, where pantropical spotted dolphins were found. Bottlenose dolphins, Risso's dolphins, pygmy/dwarf sperm whales, and unidentified beaked whales were seen in water temperatures that fell between and overlapped the coolest and warmest temperatures.

Sea-surface temperature gradient—As with sea-surface temperature, there was a significant difference in SST gradient values among the eight species or species categories ($KW = 15.7$, df = 7, $P = 0.03$) (Table 1, Fig. 2). Atlantic spotted dolphins and striped dolphins occurred in the shallowest SST gradients and, as a group, were found in significantly different SST gradients from unidentified beaked whales, which were found in the steepest SST gradients. Bottlenose dolphins, Risso's dolphins, pantropical spotted dolphins, sperm whales, and pygmy/dwarf sperm whales were found at intermediate SST gradient values and overlapped the ends of the SST gradient.

Depth of the 15°C isotherm—There was no significant difference among nine

Table 1. Environmental profiles for the study area along the survey track-line and for cetacean species or species categories that had 10 or more sightings for most of the variables.

Species or species category	Sample statistic	SST (°C)	SST gradient (°C/1.1 km)	Depth of 15°C isotherm (m)	Temperature at 100 m (°C)	Surface salinity (psu)	Bottom depth (m)	Bottom-depth gradient (m/1.1 km)
Study area	mean	24.5	0.04	198.8	19.8	35.61	984.2	16.4
	median	24.0	0.02	192.5	19.4	36.05	1,011.4	12.4
	n	9,895	9,785	12,367	12,050	7,638	13,318	13,318
	minimum	14.0	0.0	117.1	16.8	5.24	100.0	0.03
	maximum	31.0	1.15	358.1	26.0	36.61	1,999.8	141.6
Atlantic spotted dolphin	mean	22.6	0.09	184.20	19.30	34.94	197.1	11.2
	median	22.5	0.02	185.20	19.19	36.00	173.4	7.1
	n	19	19	18	18	8	30	30
	minimum	17.9	0.0	141.2	18.2	27.4	102	1
	maximum	28.7	0.6	216.6	22.6	36.2	589	37
Bottlenose dolphin	mean	24.2	0.08	188.70	19.06	33.60	293.5	16.4
	median	23.8	0.05	190.75	18.83	35.93	216.6	12.0
	n	84	81	68	68	19	149	149
	minimum	14.6	0.0	150.9	16.9	15.8	101	0
	maximum	30.7	0.5	271.6	22.6	36.5	1,226	120
Risso's dolphin	mean	24.4	0.09	194.54	19.32	34.88	713.7	23.3
	median	24.3	0.05	195.40	18.92	35.72	571.0	20.9
	n	38	38	31	31	11	67	67
	minimum	19.0	0.0	145.7	18.1	24.8	150	3
	maximum	29.5	0.3	256.4	23.0	36.6	1,997	58
Pygmy/dwarf sperm whale	mean	24.6	0.09	205.41	19.72	35.57	928.5	20.6
	median	24.5	0.07	199.7	19.75	35.75	860.8	17.1
	n	34	34	29	28	4	72	72
	minimum	18.9	0.0	145.3	17.7	34.7	176	2
	maximum	29.7	0.3	277.1	22.0	36.1	1,989	91

Table 1. Continued.

Species or species category	Sample statistic	SST (°C)	SST gradient (°C/1.1 km)	Depth of 15°C isotherm (m)	Temperature at 100 m (°C)	Surface salinity (psu)	Bottom depth (m)	Bottom-depth gradient (m/1.1 km)
Sperm whale	mean	23.7	0.07	194.80	19.91	35.82	1,104.9	24.2
	median	23.3	0.05	194.60	19.59	36.21	1,009.3	18.8
	n	37	36	41	38	15	65	65
	minimum	18.1	0.0	160.9	17.3	33.4	480	3
	maximum	29.5	0.4	254.8	24.4	36.3	1,957	90
Mesoplodon spp.	mean	25.2	0.09	195.35	20.25	36.01	1,196.9	14.8
	median	26.6	0.09	188.40	19.64	35.86	1,126.5	13.5
	n	6	6	10	10	3	13	13
	minimum	18.2	0.0	160.5	18.9	35.8	680	4
	maximum	28.6	0.2	256.4	22.4	36.4	1,933	26
Clymene dolphin	mean	24.3	0.04	190.35	19.22	36.15	1,261.0	17.5
	median	23.5	0.02	175.90	19.19	36.39	1,304.0	16.1
	n	9	9	17	17	5	22	22
	minimum	21.3	0.0	150.4	17.6	35.5	612	2
	maximum	27.4	0.1	284.1	22.5	36.4	1,979	40
Pantropical spotted dolphin	mean	25.3	0.07	197.82	19.24	35.64	1,241.9	19.0
	median	25.4	0.05	196.30	19.24	35.99	1,287.2	16.5
	n	60	58	69	57	31	103	103
	minimum	19.1	0.0	145.3	17.0	31.8	364	2
	maximum	29.7	0.5	266.9	22.4	36.6	1,999	120
Striped dolphin	mean	23.6	0.02	200.47	19.24	34.72	1,235.2	24.5
	median	22.2	0.01	199.05	18.93	34.82	1,214.9	23.0
	n	13	12	12	12	7	18	18
	minimum	19.6	0.0	160.6	17.9	32.6	570	6
	maximum	30.0	0.1	248.9	22.4	36.3	1,997	71

Table 1. Continued.

Species or species category	Sample statistic	SST (°C)	SST gradient (°C/1.1 km)	Depth of 15°C isotherm (m)	Temperature at 100 m (°C)	Surface salinity (psu)	Bottom depth (m)	Bottom-depth gradient (m/1.1 km)
Spinner dolphin	mean	24.1	0.53	187.01	18.96	36.09	1,111.0	23.3
	median	23.4	0.03	184.80	18.89	36.09	927.0	22.4
	n	7	7	8	8	2	13	13
	minimum	18.1	0.0	154.8	17.3	36.0	526	7
	maximum	29.7	0.1	230.0	21.5	36.2	1,776	38
Rough-toothed dolphin	mean	25.1	0.11	208.07	19.92	35.23	950.5	18.4
	median	25.4	0.02	197.10	19.24	34.83	1,066.6	13.3
	n	9	9	7	7	3	16	16
	minimum	21.9	0.0	180.5	18.5	34.7	194	7
	maximum	27.9	0.6	267.3	22.9	36.1	1,524	73
Short-finned pilot whale	mean	24.0	0.03	174.69	19.09	35.72	863.4	17.0
	median	22.8	0.01	165.20	18.87	35.98	716.8	11.5
	n	9	8	8	8	3	21	21
	minimum	21.7	0.0	157.1	17.9	35.0	246	3
	maximum	29.0	0.1	203.6	21.0	36.2	1,906	69
Unidentified beaked whale	mean	24.8	0.12	173.47	18.66	35.84	1,273.7	17.9
	median	24.7	0.10	165.35	18.79	35.80	1,292.7	19.3
	n	12	12	6	7	4	16	16
	minimum	21.5	0.0	159.3	17.9	35.5	253	3
	maximum	28.8	0.3	203.1	19.3	36.2	1,852	33

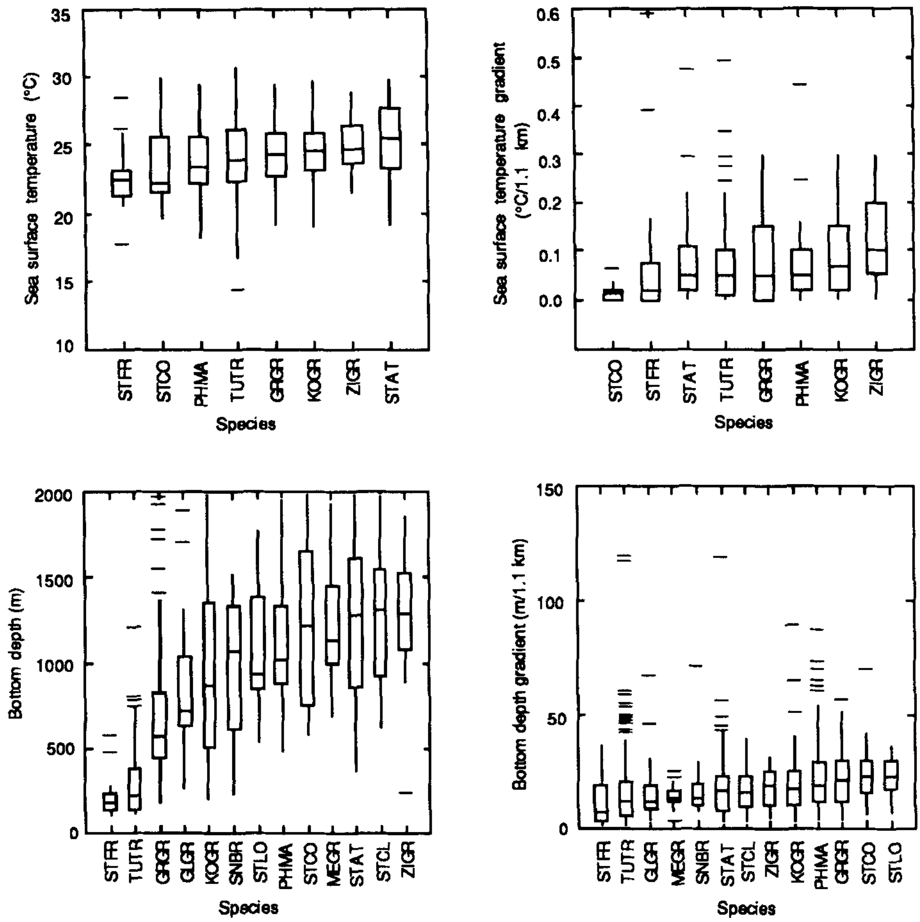

Figure 2. Box plots of the sea-surface temperature, sea-surface temperature gradient, bottom depth, and bottom-depth gradient associated with the sightings of the 8–13 cetacean species or species groups. The mid-line is the median, the box encompasses the interquartile range, and the vertical lines are 1.5 × the interquartile range. Outlying points are shown individually as horizontal bars. Codes: STFR = Atlantic spotted dolphin, TUTR = bottlenose dolphin, GRGR = Risso's dolphin, GLGR = short-finned pilot whale, KOGR = pygmy/dwarf sperm whale, SNBR = rough-toothed dolphin, STLO = spinner dolphin, PHMA = sperm whale, STCO = striped dolphin, MEGR = *Mesoplodon* spp., STAT = pantropical spotted dolphin, STCL = Clymene dolphin and ZIGR = beaked whale.

species or species categories (KW = 11.8, df = 8, P = 0.16) with regard to the depth of the 15°C isotherm (Table 1). The overall mean for the nine species or species categories was 205.3 m ± 30.2 (SD).

Water temperature at 100 m—There was no significant difference among nine species or species categories (KW = 14.6, df = 8, P = 0.07) with regard to water temperature at 100 m (Table 1). The overall mean for the nine species or species categories was 19.5°C ± 0.44 (SD).

Surface salinity—Only four of the 13 species or species categories had 10 or more sightings with measured surface salinity, and there was no significant difference among these four (KW = 2.4, df = 3, P = 0.49) (Table 1). The overall mean was 34.98 psu ± 0.99 (SD).

Bottom depth—There was a significant difference among the 13 species or species categories (KW = 362.6, df = 12, $P < 0.001$) with regard to bottom depth that allowed them to be differentiated into three groups (Table 1, Fig. 2).

The Atlantic spotted dolphin was found at the shallowest bottom depths, while bottlenose dolphins were found at intermediate bottom depths. The mean water depth for Atlantic spotted dolphins was significantly shallower than that for bottlenose dolphins. On average, Atlantic spotted dolphins occurred on the continental shelf while the bottlenose dolphins were seen along the shelf break.

All the other species and species categories were found over the deepest bottom depths; these were Risso's dolphins, short-finned pilot whales, pygmy/dwarf sperm whales, rough-toothed dolphins, spinner dolphins, sperm whales, striped dolphins, *Mesoplodon* spp., pantropical spotted dolphins, Clymene dolphins, and unidentified beaked whales. Even within this group, species were found over a gradient of water depths. Risso's dolphins and short-finned pilot whales occurred along the upper slope and, as a subgroup, were significantly different from striped dolphins, *Mesoplodon* spp., pantropical spotted dolphins, Clymene dolphins, and unidentified beaked whales, which occurred in the deepest water. Pygmy/dwarf sperm whales, rough-toothed dolphins, spinner dolphins, and sperm whales occurred at depths that were between the values for the two subgroups and overlapped them.

Bottom-depth gradient—There was a significant difference among the 13 species or species categories (KW = 53.1, df = 12, $P < 0.001$) with regard to bottom-depth gradient (Table 1, Fig. 2). Atlantic spotted dolphins occurred over the shallowest bottom depth gradient and were found at gradient values significantly different from the group found in the steepest gradients; this group consisted of sperm whales, Risso's dolphins, striped dolphins, and spinner dolphins. The other species occurred over bottom-depth gradients in the middle and overlapped the values found for the other two groups.

Discussion

The mean, annual marine environment in the upper layer of the study area is subtropical to tropical in temperature, with normal seasonal variation in the depth of the mixed layer (*i.e.*, deepest [35–110 m] in the winter and shallowest [<50 m] in the summer). Salinity ranges from 34.9–36.6 psu, excluding areas affected by the Mississippi River effluent (Fargion *et al.* 1996). The surface circulation is dominated by persistent warm-core (anticyclonic) eddies 100–300 km in diameter that separate from the Loop Current in the eastern Gulf and drift westward until they dissipate along the continental slope (Hofmann and Worley 1986, Biggs 1992, Biggs *et al.* 1996). Generally, one or more of these warm-core eddies is present in the Gulf at any one time. These dynamic circulation features transport large quantities of high-salinity, nutrient-poor water across the near-surface environment of the northern Gulf. Cold-core (cyclonic) eddies can be generated as the anticyclonic eddy interacts with the continental margin. As a result, the temperature and salinity in the upper 200–300 m can vary depending on whether measurements are taken inside or outside of these distinctive but ephemeral circulation features. Below a depth of several hundred meters, the Gulf has stable temperature-salinity characteristics that are unaffected by warm-core or cold-core eddies.

The cetaceans in this study occurred in water with a relatively narrow range of annual SSTs, similar to those reported previously for cetaceans in the northern Gulf (Fritts *et al.* 1983) and for pantropical spotted and spinner dolphins in the eastern tropical Pacific (Au and Perryman 1985, Perrin and Gilpatrick 1994, Perrin and Hohn 1994, Perrin *et al.* 1994*b*). The seasonal variation in SST in the Gulf typically ranges from 5°–7°C, with little interannual variation (Table 1; Müller-Karger *et al.* 1991). It is noteworthy that the deep-diving species (*e.g.*, Risso's dolphins, sperm whales, pygmy/dwarf sperm whales, and unidentified beaked whales) in this study occurred in water with the steepest SST gradient. These species are known to feed on squid and may be foraging along thermal fronts associated with eddy systems. These areas may be associated with cold-core eddies that are more productive than the warmer, oligotrophic surface water within warm-core eddies and the Loop Current (Biggs 1992, Biggs and Müller-Karger 1994). SST gradient also seems to be a reasonable correlate to the distribution and migration of yellowfin tuna which feed on many of the same organisms as the dolphin species encountered (Perrin *et al.* 1973, Sharp and Dizon 1978).

The mean values for the depth of the 15°C isotherm (<250 m), the temperature at 100 m (<22°C) and surface salinity (<36.6 psu) indicate that most of the cetacean sightings were outside of the oligotrophic Subtropical Underwater that flows into the Gulf through the Yucatan Straits and is found in the region of the Loop Current and warm-core rings derived from that current (Table 1; Hofmann and Worley 1986). As the warm-core rings move westward across the northern Gulf, they mix with Gulf Common Water. Discharge from the Mississippi and Atchafalaya rivers gives rise to a band of low-salinity water that usually flows westward over the continental shelf but can have a freshening influence as far south as 26°N (Nowlin 1972). The relatively constant, mean surface salinity beyond the shelf edge is probably responsible for the absence of any significant difference for this environmental variable among cetacean species in the study area. However, the large range of salinities recorded (some as low as 15.8 psu) for those species frequently observed along the shelf break in the north-central Gulf reflects the mixing of the Mississippi River discharge and near shore water.

Sightings of species in the study area were differentiated most clearly with bottom depth. Atlantic spotted dolphins were consistently found in the shallowest water on the continental shelf and along the shelf break. In addition, the bottom-depth gradient was less for Atlantic spotted dolphins than for any other species. This agrees with observations of this species along the west Florida shelf (Mullin, unpublished data). Mullin *et al.* (1994) sighted Atlantic spotted dolphins in offshore waters along the Louisiana coast south of the Mississippi River delta that were in deeper water (mean depth 367 m) than those seen in this study. However, the continental shelf is very narrow with a steep bottom gradient in this region, so that small movements offshore result in a rapid change in depth. Overall, it appears that Atlantic spotted dolphins prefer shallow water with a gently sloping bottom typical of the continental shelf, although they may also occur along the shelf break and upper continental slope. Their occurrence in shallow shelf waters may be related to prey preference and foraging strategies. Atlantic spotted dolphins are known to feed on small cephalopods, fish, and benthic invertebrates (Perrin *et al.* 1994*a*). A rehabilitated Atlantic spotted dolphin that was monitored with a satellite-linked time-depth recorder along the continental shelf of the Texas coast for 24 d spent most of its time at depths less than 10 m. However, the dolphin consistently made dives that were on or near the seafloor in 30 m of water (Davis *et al.* 1996*b*).

The bottlenose dolphins in this study were found most commonly along the upper slope in water significantly deeper than that for Atlantic spotted dolphins. Both species also occur in shallower waters along the continental shelf in the northern Gulf of Mexico, but the bottlenose dolphin is more abundant in this area (Perrin *et al.* 1994*a*). However, morphometric, hematological, and hemoglobin differences indicate that the larger, offshore bottlenose dolphins may not mix with the nearshore population (Hersh and Duffield 1990). Pelagic bottlenose dolphins feed on a variety of epipelagic and mesopelagic fish, squid, and crustaceans (Walker 1981, Barros and Odell 1990).

The deep-water cetaceans of this study were diverse in size, diving ability, and prey preference. Large species such as the sperm whale, *Mesoplodon* spp. and unidentified beaked whales are known or believed to be deep divers that feed on squid and mesopelagic or deep-water benthic fish (Raun *et al.* 1970, Berzin 1971, Clarke 1986, Heyning 1989, Rice 1989, Findlay *et al.* 1992). Sperm whales are capable of exploiting most of the water column in the study area and regularly occur in water over 1,000 m deep. Previous sightings of sperm whales in the Gulf were in waters of similar depth to that of this study (Fritts *et al.* 1983, Collum and Fritts 1985, Mullin *et al.* 1994). Their frequent occurrence near the Mississippi Canyon suggests that this may be an important part of their habitat in the north-central Gulf. However, sperm whales were not commonly sighted to the east near DeSoto Canyon in the Gulf, and submarine canyons were apparently not important habitat for sperm whales off the North Atlantic coast (Kenney and Winn 1987). The combination of deep water within 20 km of the Mississippi River delta and the enhanced primary productivity associated with the river discharge may increase the abundance of squid and be responsible for the year-round occurrence of sperm whales in this part of the north-central Gulf. Of the 42 species of cephalopods known to occur in the Gulf, most are also found in the North Atlantic (Voss 1956).

Less than 10% of these species are endemic to the Gulf, and apparently these are confined to benthic species.

Risso's dolphins and short-finned pilot whales occurred most commonly along the mid-to-upper slope, often in areas with a steep bottom gradient. A similar range of bottom depths was observed for these species for the northern Gulf (Fritts *et al.* 1983, Mullin *et al.* 1994, Baumgartner 1997), by Dohl *et al.* (1981) along the California coast and by Findlay *et al.* (1992) along the South African coast. The deeper water and steep bottom gradient characteristic of Risso's dolphin and pilot whale habitat may be linked to their diet of squid (Clarke and Pascoe 1985, Evans 1987, Würtz *et al.* 1992, Jefferson *et al.* 1993).

Pygmy/dwarf sperm whales feed on squid, benthic and mesopelagic fish, and crustaceans (Fitch and Brownell 1968). Their bottom-feeding habits and considerable body oxygen stores for their size suggest that they make deep dives along the continental slope (Raun *et al.* 1970, Caldwell and Caldwell 1989). The apparent preference of dwarf sperm whales for areas over or near the shelf break (Raun *et al.* 1970, Caldwell and Caldwell 1989) is consistent with their greater frequency of sightings in this study. Nevertheless, pygmy sperm whales have historically stranded more frequently in the Gulf than have dwarf sperm whales (Schmidly and Scarbrough 1990, Davis *et al.* 1996*a*). Without surveying the entire Gulf, inferences about preferred bottom depth of these two species remain speculative.

Rough-toothed, spinner, Clymene, pantropical spotted, and striped dolphins are all small cetaceans that occur over deep water beyond the continental shelf (Jefferson *et al.* 1993), although their small size probably limits them to the upper 250 m of the water column (Williams *et al.* 1993). Their occurrence in deep water may be linked to the offshore location of their prey (Ridgway and Harrison 1994). For example, striped dolphins off the coast of Japan feed on myctophid fish and squid, many with luminous organs, associated with the deep scattering layer (Miyazaki *et al.* 1973). In the eastern tropical Pacific, spinner dolphins also feed on vertically migrating fish, especially myctophids (Fitch and Brownell 1968).

Although the study area covered 154,621 km^2 (about 10% of the Gulf), it undoubtedly represents only part of the home range for individuals of the species observed. A strong differentiation of species distributions by ocean bottom depth was identified most likely because the study area was limited to the continental slope. Differentiation of species sightings by the other oceanographic variables was weak and may have resulted from the fact that: (1) the oceanography of the Gulf of Mexico is very dynamic with periodic intrusion of the Loop Current and the formation of warm-core eddies that move across northern Gulf and (2) cetaceans are large, warm-blooded mammals whose wide-ranging movements are not physiologically constrained by water temperatures and other hydrographic features of the northern Gulf. The distribution of cetaceans is probably better explained by the availability of prey, which may be influenced secondarily by oceanographic features. Future studies should include an assessment of regional food stocks of zooplankton and nekton. In addition, satellite-linked telemeters will enable us to use cetaceans as platforms for measuring oceanographic variables in order to better define and monitor their habitat.

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