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Abundance and Seasonal Occurrence of Cetaceans in Outer Continental Shelf and Slope Waters of the North-Central and Northwestern Gulf of Mexico

KEITH D. MULLIN, WAYNE HOGGARD, AND LARRY J. HANSEN

Eight aerial line-transect surveys of outer continental shelf and continental slope waters (range 100–2,000 m deep) were conducted seasonally from summer 1992 through spring 1994 in the north-central and northwestern Gulf of Mexico to study the seasonal occurrence and spatial distribution of cetaceans and to estimate their abundances. The surveys sampled an 85,815 km^2 study area, resulting in 49,960 km of effort and sightings of at least 18 cetacean species and 365 cetacean groups. Eight species identified in four seasons included bottlenose dolphin (*Tursiops truncatus*), pantropical spotted dolphin (*Stenella attenuata*), Risso's dolphin (*Grampus griseus*), dwarf sperm whale (*Kogia sima*) and pygmy sperm whale (*Kogia breviceps*), sperm whale (*Physeter macrocephalus*), short-finned pilot whale (*Globicephala macrorhynchus*), rough-toothed dolphin (*Steno bredanensis*), and Atlantic spotted dolphin (*Stenella frontalis*). Clymene dolphin (*Stenella clymene*), striped dolphin (*Stenella coeruleoalba*), and beaked whales (*Mesoplodon* spp.) were sighted in three seasons. The number of species sighted seasonally ranged from 10 in fall to 15 in winter. The overall estimated abundance (number of animals) of five species, which accounted for 71% of the identified group sightings, were as follows: bottlenose dolphin, 2,890 (coefficient of variation [CV] = 0.20); pantropical spotted dolphin, 5,097 (CV = 0.24); Risso's dolphin, 1,237 (CV = 0.28); dwarf–pygmy sperm whale, 176 (CV = 0.31); and sperm whale, 87 (CV = 0.27). Melon-headed whales (*Peponocephala electra*) were sighted less frequently but were abundant (2,561; CV = 0.74) because of large group sizes. Common species were widely distributed spatially but occurred in different water depth ranges. In general, species abundance estimates varied seasonally, but the precision of estimates was usually poor (CV > 0.30) and provided little power to detect significant seasonal differences.

Before the early 1990s, cetacean studies in outer continental shelf and oceanic waters of the Gulf of Mexico (Gulf) consisted of two seasonal aerial survey studies confined to relatively small areas of the continental slope (Fritts et al., 1983; Mullin et al., 1994) and a series of ship surveys that covered the entire oceanic northern Gulf during spring (L. J. Hansen, K. D. Mullin, and C. L. Roden, unpubl.). These studies indicated that cetaceans in the oceanic northern Gulf are diverse (at least 20 species) and occur throughout the year and that a few species, such as the pantropical spotted dolphin (*Stenella attenuata*), are abundant and widely distributed during spring. Gulf species include the sperm whale (*Physeter macrocephalus*), which is listed as endangered under the U.S. Endangered Species Act (ESA) (Mullin and Hansen, 1999).

The U.S. Marine Mammal Protection Act and the ESA require that federal agencies ensure that activities under their purview do not lead to the depletion of cetacean populations or adversely affect endangered species. In U.S. waters, the National Marine Fisheries Service (NMFS) is responsible for protecting cetaceans and the Minerals Management Service (MMS) oversees oil and natural gas resources. The Gulf accounts for about 95% of the oil and gas production in North American waters (Neff, 1990). Gulf continental shelf waters (depths <200 m) have been heavily exploited. Development of continental slope waters (depths 200–2,000 m) began in the early 1990s, and by 2003 there were about 500 oil- and gas-related structures (MMS, unpubl. data).

Before large-scale exploration and development of oil and gas resources was to take place in deep Gulf waters, an assessment of cetacean abundances and distributions was needed so that changes possibly associated with future development could be detected. In 1992, the NMFS Southeast Fisheries Science Center, in cooperation with the MMS and Texas A&M

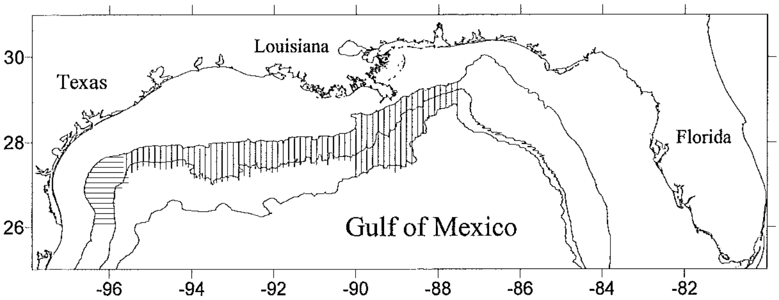

Fig. 1. Example of 74 transects surveyed by aircraft in north-central and northwestern Gulf of Mexico during eight seasonal surveys conducted from summer 1992 to spring 1994. The 100-, 1,000-, and 2,000-m isobaths are shown.

University at Galveston, initiated research (GulfCet I Program) to study cetaceans in the north-central and northwestern Gulf (Davis and Fargion, 1996; Jefferson, 1996). Our purpose here is to report on one aspect of the GulfCet I Program, aerial surveys of outer continental shelf and continental slope waters and to assess the seasonal diversity, distribution, and abundance of cetacean species.

Materials and Methods

Study area.—The study area (85,815 km^2) included outer continental shelf and upper continental slope waters (100–1,000 m deep) in the Gulf from the Florida–Alabama border west to the Texas–Mexico border (Fig. 1). Slope waters from 1,000–2,000 m deep east of 90.0°W (Mississippi River Delta region) were also surveyed because it was logistically feasible and because of the oil and gas industry's interest in this region.

Survey design.—The study was designed to survey the area uniformly once each season for 2 yr from summer 1992 through spring 1994 (eight seasonal surveys). The seasons were as follows: summer, Aug.–Sep.; fall, Nov.–Dec.; winter, Feb.–Mar.; and spring, May–June. On the basis of funding and projected availability of acceptable survey conditions, ≈6,400 transect km were planned each season along 74 transects placed equidistantly apart from a random start. The transects were oriented approximately perpendicular to major depth contours and consisted of 60 north–south and 14 east–west transects that ranged in length from 51–185 km (Fig. 1). A window of 45 d and 100 flight hr were allocated for each survey.

Survey methods.—The survey aircraft were a Partenavia (survey 1) and a DeHavilland Twin Otter (surveys 2–8). Both were twin-engine, turbo-prop aircraft modified with a large bubble window on each side of the aircraft that provided observers transect line visibility. Survey flights were conducted from an altitude of 229 m (750 feet) at a speed of 204 km · h^{-1} (110 nmi · h^{-1}) during Beaufort sea states 0–3. Survey flights typically began at 0800 hr and were of 4.5–6.5 hr duration. A pilot, copilot, and three observers participated in each flight. The observers were stationed at each of the two bubble windows and at a data entry station and rotated positions every ≈30 min. Observers searched waters primarily on and near the transect line and scanned periodically out to the horizon. Neither observer focused exclusively on the transect line.

Sighting and related environmental data were entered into a computer interfaced with a GPS/LORAN-C navigation receiver by means of a custom BASIC program. A suite of data characterizing survey conditions (e.g., sea state and weather), effort status, and observer locations were updated throughout the day. The date, time, latitude, longitude, and aircraft heading and speed were automatically recorded with each data record.

For cetacean sightings, the angle (θ) between the cetacean group and the transect line was measured with an inclinometer for $\theta < 60°$. The perpendicular sighting distance (y) from the transect line to the cetacean group was calculated as $y = \tan(\theta) \cdot 229$ m. Each bubble window was divided into seven 10° intervals and one interval >70° corresponding to interval endpoints with y equal to 40, 83, 132, 192, 273, 397, 629, or >629 m. If the inclinometer malfunctioned or for $\theta > 60°$, the interval was recorded.

When a cetacean group was sighted, the aircraft was diverted to circle the group. Before continuing the transect, the group was identi-

TABLE 1. Categories of cetaceans with similar sighting characteristics pooled to estimate $f(0)$ (n = number of sightings, P = number of parameters in the model, CV = coefficient of variation).

Category Species	n	Model	P	$f(0)$ (km^{-1})	CV[$f(0)$]
Category 1, inactive at the surface (<7 m)	69	Hazard rate	2	4.365	0.24
Dwarf sperm whale (*Kogia sima*) and pygmy sperm whale (*Kogia breviceps*)					
Cuvier's beaked whale (*Ziphius cavirostris*)					
Mesoplodon spp.					
Unidentified ziphiid					
Unidentified odontocete					
Unidentified small whale					
Unidentified dolphin					
Category 2, active at the surface (<7 m)	143	Hazard rate	3	3.538	0.09
Bottlenose dolphin (*Tursiops truncatus*)					
Atlantic spotted dolphin (*Stenella frontalis*)					
Bottlenose/Atlantic spotted dolphin					
Rough-toothed dolphin (*Steno bredanensis*)					
Risso's dolphin (*Grampus griseus*)					
False killer whale (*Pseudorca crassidens*)					
Short-finned pilot whale (*Globicephala macrorhynchus*)					
Category 3, very active at the surface (<7 m)	73	Half-normal	2	3.190	0.11
Pantropical spotted dolphin (*Stenella attenuata*)					
Striped dolphin (*Stenella coeruleoalba*)					
Spinner dolphin (*Stenella longirostris*)					
Clymene dolphin (*Stenella clymene*)					
Stenella spp.					
Melon-headed whale (*Peponocephala electra*)					
Fraser's dolphin (*Lagenodelphis hosei*)					
Pygmy killer/melon-headed whale (*Feresa attenuata/P. electra*)					
Category 4, large whales (>7 m)	30	Half-normal	1	1.986	0.15
Sperm whale (*Physeter macrocephalus*)					
Bryde's whale (*Balaenoptera edeni*)					
Unidentified large whale					

fied and the group size estimated by a consensus of the three observers. The identifying characteristics of each species and anecdotal information were recorded on a standardized form.

At least one observer on each flight had at least 1,000 hr experience conducting aerial surveys of marine life in the Gulf and western North Atlantic Ocean and was responsible for confirming all identifications. Cetaceans were identified to the lowest taxonomic level possible on the basis of descriptions in field guides and scientific literature (e.g., Leatherwood et al., 1976; Leatherwood and Reeves, 1983; Perrin et al., 1987). Identifications to species were not possible for some genera (Table 1). In some cases, identification was dependent on water clarity, sea state, or animal behavior (Würsig et al., 1998), and cetaceans could be identified only to genus, a group of species, as large whales (>7 m long), small whales (nondolphin, <7 m), dolphins, or odontocetes.

Analytical methods.—Line-transect analysis methods (Buckland et al., 1993) as implemented by the analysis program DISTANCE (Laake et al., 1993) were used to estimate cetacean abundance in the study area for the following: 1) each species for the entire study (i.e., all eight surveys combined); and for each species with ≥20 on-effort sightings, 2) annually for each of the 2 yr, and 3) for each season (summer, fall, winter, and spring) by combining the two annual surveys for the season. Estimates were not made for each seasonal survey because of the small number of sightings of each species.

Abundances (N) and associated variances and coefficients of variation (CV) were estimated as:

$$N = \frac{A \cdot n \cdot S \cdot f(0)}{2 \cdot L \cdot g(0)}$$

and CV $(N) = \sqrt{\mathrm{var}(N)}/N$ where N is the number of animals, A is the size of the study area, n is the number of sightings of the species within the temporal stratum, $f(0)$ is the probability density function evaluated at $y = 0$ (see below), S is the mean or size-bias adjusted group size of the species within the temporal stratum (see below), L is the total length of transect lines within the temporal stratum, and $g(0)$ is the probability of sighting a group on the transect line. The parameter $g(0)$ was not estimated, and $g(0) = 1$ was used for each abundance estimate. Abundance estimates were negatively biased because of the probability that observers missed groups on the transect line at the surface and some groups were under the surface while in the observation area; therefore $g(0) < 1$ (see Discussion). Each transect was considered a sampling unit and treated as a replicate in analyses. The variance was estimated as:

$$var(N) = N^2 \left(\frac{var(n)}{n^2} + \frac{var(S)}{S^2} + \frac{var[f(0)]}{f(0)^2} \right)$$

The formula used to estimate each component of the variance followed Buckland et al. (1993). Var(n) was transect length weighted and based on the variation in the number of on-effort group sightings between sampling units. As implemented on DISTANCE, log-normal 95% confidence intervals were estimated for N because they were a product of estimates and tend to have a skewed distribution.

Bubble window observers made 349 on-effort sightings. Sixteen on-effort sightings made by the pilots or the computer operator but missed by the observers were excluded from abundance analyses. For $\theta = 0–60°$, 286 groups were sighted; $\theta = 60–70°$, 32 groups; and $\theta > 70°$, 31 groups. For 26 groups sighted from 0–60° and all sightings from 60–70°, only the midpoint of the interval was recorded and it was used for y and treated as an exact distance. Sightings at angles >70° were bounded by the horizon. However, we assumed that they occurred at <1,300 m (about 80°) and the midpoint of the interval 70–80° was used. In trial runs, the value of the midpoint $\theta > 70°$ made little difference in estimates of $f(0)$.

When the frequency of all sightings was plotted against y, the frequency of sightings peaked near $y = 50$ m and decreased as y approached 0 m. From side-viewing aircraft there are probably a number reasons for this, which include better sighting conditions at $y > 50$ m due to glare on the transect line, longer observation periods for waters as y increases, and dorsal fins of animals breaking the surface being more easily seen in profile. Because the frequency distribution violated one of the assumptions of the line-transect theory (i.e., $f(x)$ is a monotonically decreasing function), it would have caused the abundance estimates to be negatively biased (Alldredge and Gates, 1985). Therefore, all analyses were made with the data left-truncated at 50 m using the left-truncation option on DISTANCE, and 38 sightings with a $y < 50$ m were excluded from analyses.

The number of sightings of most species was too small to obtain an accurate and precise estimate of $f(0)$. Therefore, sightings of species with similar characteristics that were intuitively believed to affect their sightability from aircraft (i.e., body size and surface behavior tendencies) were pooled into four categories, and an estimate of $f(0)$ was made for each category (Table 1). For each species, the value of $f(0)$ and its variance for that species' category were used in each abundance estimate. If the individual detection functions of each species within a category in Table 1 were indeed very similar, by pooling, the variance of $f(0)$ was probably underestimated because it was based on an artificially high sample size. Conversely, if the true detection functions of the species within a category were highly variable, the variance of $f(0)$ for an individual species was probably overestimated.

Exploratory analyses using various y distance interval combinations were performed to achieve a good fit of the model to the data (i.e., low χ^2 value and decreased CV[$f(0)$]). For categories 1–3, a model was fit to the y data grouped into intervals: 50–150, 151–250, 251–400, 401–630, and 631–1,300 m. The intervals for category 4 were: 50–200, 201–400, 401–630, and 631–1,300 m. The hazard rate, half-normal, and uniform models were considered in each case, and DISTANCE selected one of these based on Akaike's Information Criterion.

In cases where larger groups were easier to see than smaller groups as y increased, the arithmetic mean of group size would overestimate the true mean group size and lead to a positively biased abundance estimate (Buckland et al., 1993). DISTANCE tests for this potential bias using a linear regression of group size by y and estimates a mean "size-biased adjusted group size." The adjusted mean group size was used for abundance estimates if it was significantly smaller than the arithmetic mean group size ($P < 0.15$).

RESULTS

All proposed transect lines were completed each season except for fall 1992, when only 80% of the effort was completed because of poor weather. The effort ranged from 5,330–6,592 km per survey and 11,756–12,942 km for each season. For the entire study, 97% of the proposed effort (49,960 km) was surveyed.

In total, 365 cetacean groups and at least 17 species were sighted on-effort (Table 2). The only sighting of killer whales (*Orcinus orca*) occurred off-effort. Five species accounted for 71% of the identified sightings and included: bottlenose dolphin (*Tursiops truncatus*), pantropical spotted dolphin (*S. attenuata*), Risso's dolphin (*Grampus griseus*), dwarf sperm whale (*Kogia sima*) and pygmy sperm whale (*Kogia breviceps*), and sperm whale (*P. macrocephalus*). Eight species were identified in four seasons and, in addition to the five species listed above, included: short-finned pilot whale (*Globicephala macrorhynchus*), rough-toothed dolphin (*Steno bredanensis*), and Atlantic spotted dolphin (*Stenella frontalis*). Clymene dolphins (*Stenella clymene*), striped dolphins (*Stenella coeruleoalba*), and *Mesoplodon* spp. were sighted in three seasons. Seven species were sighted in one or two seasons. By season, the number of species sighted ranged from 10 in fall to 15 in winter (Table 2).

Overall, mean group sizes ranged from 315 animals for melon-headed whales (*Peponocephala electra*) to less than four animals for Brydes's whale (*Balaenoptera edeni*), dwarf and pygmy sperm whales, sperm whales, and all ziphiids. Except for the Atlantic spotted dolphin, group sizes of stenellid dolphins averaged more than 40 individuals (Table 2).

Of species sighted 10 or more times, Atlantic spotted and bottlenose dolphins were sighted at depths averaging <300 m. Mean depths for Risso's dolphins, short-finned pilot whales, and dwarf and pygmy sperm whales ranged from 500–1,000 m. The mean depths for sperm whales and the pantropical spotted dolphins were more than 1,000 m. Other species were seen almost exclusively at depths >500 m (Table 2).

With sightings from all surveys combined, cetacean groups were sighted throughout the study area and at all water depths surveyed. Seasonal distributions of all cetaceans combined appeared similar, except that only one cetacean group was sighted in the vicinity of the DeSoto Canyon during summer and fall, whereas groups were common in this area during winter and spring (Fig. 2). Plots of sighting locations of each species by season can be found in Hansen et al. (1996). In summary, most species sighted >10 times were widely distributed in the study area. Short-finned pilot whales were predominantly encountered in the central and western portions of the study area. There was a concentration of sperm whale sightings south of the Mississippi River delta. The two sightings of Fraser's dolphins (*Lagenodelphis hosei*) were within 50 km of each other, with one occurring in spring and the other in winter. All four of the spinner dolphin (*Stenella longirostris*) sightings were in the eastern half of the study area.

Sightings where two or more species were in a mixed group occurred four times. Both sightings of Fraser's dolphin were associated with melon-headed whales, with one that also included rough-toothed dolphins. Bottlenose dolphins were sighted with Atlantic spotted dolphins on one occasion and with rough-toothed dolphins on another.

Abundance.—Overall, pantropical spotted dolphins were the most abundant species (5,097; CV = 0.24) followed by melon-headed whales (2,561; CV = 0.74), bottlenose dolphins (2,890; CV = 0.20), and Risso's dolphins (1,237; CV = 0.28) (Table 3). The overall abundance of sperm whales was estimated to be 87 whales (CV = 0.27) and of dwarf and pygmy sperm whales, 176 (CV = 0.31). Other delphinid species were represented by <1,000 individuals each, and ziphiids, <100 individuals each. Based on one sighting, two Bryde's whales were estimated to inhabit the study area.

For species sighted ≥20 times, abundance estimates varied annually and seasonally in some cases, although CVs were generally high (>0.30) and provided little statistical power to test for significance (Gerrodette, 1987) (Table 4). The abundance of sperm whales, dwarf and pygmy sperm whales, and bottlenose dolphins was similar each year. About twice as many pantropical spotted dolphins and Risso's dolphins were estimated for the second year of the study compared with the first. Seasonally, sperm whale abundance ranged from 47 whales in winter to 121 in spring. Dwarf and pygmy sperm whale abundance was <100 for fall and winter and >200 for summer and spring. Bottlenose dolphin abundance estimates were about two to three times greater in summer than in the other seasons. Pantropical spotted

TABLE 2. Cetaceans sighted, number of group sightings (*n*), number of sightings each season (SU = summer, FA = fall, WI = winter, SP = spring), and mean group size and water depth of sightings from aerial surveys conducted in the Gulf of Mexico from summer 1992 to spring 1994.

		Group size			Water depth (m)			Groups–season			
Species	*n*	Mean	SE	Range	Mean	SE	Range	SU	FA	WI	SP
Bryde's whale	1	1.0			213			0	0	1	0
Sperm whale	28	2.3	0.4	1–12	1,046	68	499–2,108	6	7	6	9
Dwarf/pygmy sperm whale	37	1.4	0.1	1–3	808	61	151–1,856	14	2	6	15
Cuvier's beaked whale	1	3.0			1,521			0	0	0	1
Mesoplodon spp.	4	3.5	0.3	3–4	878	103	630–1,066	1	2	1	0
Unidentified ziphiid	8	2.5	0.4	1–4	984	132	197–1,470	1	2	2	3
Melon-headed whale	4	315.0	31.2	175–400	1,081	257	641–1,815	0	0	1	3
Melon-headed/pygmy killer whale	5	13.8	4.8	3–25	895	213	431–1,572	1	2	2	0
False killer whale	2	27.5	7.5	20–35	1,033	59	974–1,091	2	0	0	0
Killer whale[a]	1	10.0			826			1	0	0	0
Short-finned pilot whale	11	20.4	3.6	5–50	761	116	241–1,876	3	3	3	2
Rough-toothed dolphin	9	14.6	3.8	3–48	907	135	85–1,393	2	1	1	5
Fraser's dolphin	2	31.0	14.0	17–45	934	99	835–1,033	0	0	1	1
Bottlenose dolphin	83	14.5	1.5	1–68	298	25	65–1,316	27	8	24	24
Risso's dolphin	39	12.7	2.0	2–78	585	57	102–2,088	4	3	16	16
Pantropical spotted dolphin	47	49.0	4.5	5–210	1,185	60	435–2,121	15	4	12	16
Atlantic spotted dolphin	12	22.4	3.9	5–48	221	35	76–546	3	1	5	3
Striped dolphin	8	46.3	16.0	7–150	1,212	206	561–2,101	0	2	4	2
Spinner dolphin	4	91.3	36.4	48–200	954	177	519–1,366	1	0	3	0
Clymene dolphin	7	59.0	19.5	9–168	1,363	197	601–2,018	1	0	2	4
Bottlenose/Atlantic spotted dolphin	7	9.9	2.5	2–25	229	61	54–623	1	0	3	3
Stenella spp.	10	22.2	7.2	2–65	693	93	98–1,091	3	1	3	3
Unidentified dolphin	13	5.1	1.3	1–20	667	129	95–1,808	4	4	3	2
Unidentified small whale	10	1.9	0.3	1–4	1,124	109	693–1,748	5	2	0	3
Unidentified large whale	4	1.3	0.3	1–2	1,211	164	914–1,556	2	1	1	0
Unidentified odontocete	9	2.7	1.4	1–15	952	178	93–1,728	2	5	1	1

[a] Off-effort sighting.

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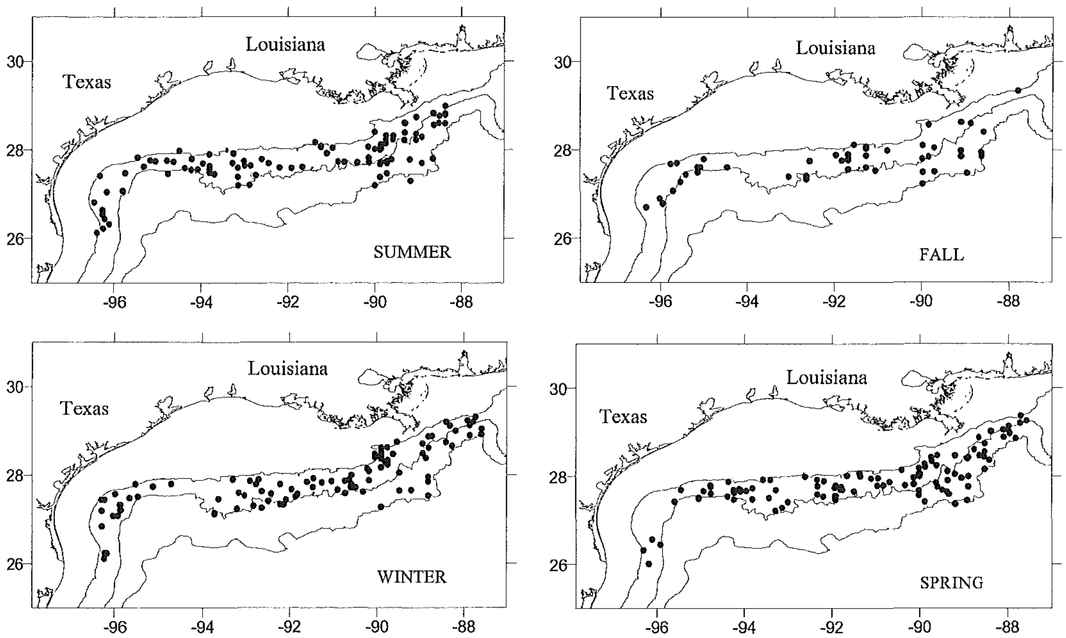

Fig. 2. Locations of sightings of cetacean groups during summer (n = 98), fall (n = 50), winter (n = 101), and spring (n = 116) during eight seasonal aerial surveys conducted from summer 1992 to spring 1994 in the north-central and northwestern Gulf of Mexico. The 100-, 1,000-, and 2,000-m isobaths are shown.

dolphin and Risso's dolphin abundance estimates were three to five and four to seven times, respectively, less in fall than in the other seasons.

Of species sighted fewer than 20 times, both false killer whale (*Pseudorca crassidens*) sightings were in summer; most of the sightings of melon-headed whales (4/4 sightings), Clymene dolphins (6/7), spinner dolphins (3/4), and striped dolphins (6/8) were in winter and spring. Rough-tooth dolphins sightings (5/11) were concentrated in spring. Short-finned pilot whale sightings were distributed throughout the year (Table 2).

DISCUSSION

The primary findings on cetacean species, relative abundance, and distribution on the upper continental slope from this study are similar to those from previous or contemporaneous Gulf studies (Fritts et al., 1983; Mullin et al., 1994; Hansen et al., 1996; Jefferson, 1996; L. J. Hansen, K. D. Mullin, and C. L. Roden, unpubl.). Except for Atlantic spotted and Clymene dolphins, which are endemic to warm Atlantic Ocean basin waters, cetacean species that occur in the Gulf are pantropical or broader in distribution (Jefferson et al., 1993). The upper continental slope is also the meeting place of two cetacean communities that are nearly parapatric in the northern Gulf. Bottlenose and Atlantic spotted dolphins inhabit the continental shelf and shelf-edge region (Mills and Rademacher, 1996; Fulling et al., 2003), with another 18-plus species essentially oceanic in distribution (Mullin and Hansen, 1999).

In other locations, such as the eastern tropical Pacific, the northwestern Atlantic, and the Pacific adjacent to California (e.g., CeTAP, 1982; Leatherwood and Reeves, 1983; Barlow, 1994; Forney et al., 1994), many of the same species that occur in the Gulf are in groups that regularly exceed 350 animals and routinely occur in multicetacean species groups. However, maximum group sizes in the northwestern Gulf were generally small, and groups were almost exclusively made up of a single species. The largest group in our study was estimated to contain 400 melon-headed whales. Only 1% (4/365) of the groups contained two or more cetacean species. As is common in other areas, Fraser's dolphins in the Gulf were associated with melon-headed whales (e.g., Wade and Gerrodette, 1993). Other species such as bottlenose dolphins and Risso's dolphins that are regularly found in multispecies groups in other areas (CeTAP, 1982; Scott and Chivers, 1990) were common in this study but seldom occurred with other species.

TABLE 3. Estimates of parameters used to estimate the overall abundance (N) of cetaceans in the study area (n = groups sighted; S = average or size-bias adjusted group size; D = animals·1,000 km^{-2}; CV = coefficient of variation).

Species	n	S	CV(S)	D	N	CV	95% CI
Bryde's/sei whale	1	1.0	1.00	0.02	2	1.08	0–10
Sperm whale	25	2.0	0.12	1.01	87	0.27	52–146
Dwarf/pygmy sperm whale	33	1.4	0.09	2.04	176	0.31	97–317
Cuvier's beaked whale	1	3.0	0.58	0.13	11	0.71	3–40
Mesoplodon spp.	4	3.5	0.08	0.61	52	0.30	18–152
Unidentified ziphiid	7	2.7	0.16	0.83	71	0.53	27–189
Melon-headed whale	3	311.7	0.22	29.84	2,561	0.74	698–9,396
Pygmy killer/melon-headed whale	2	14.5	0.72	1.02	88	1.03	8–925
False killer whale	2	27.5	0.27	1.94	167	0.72	45–614
Killer whale[a]							
Short-finned pilot whale	10	22.5	0.17	7.96	684	0.48	284–1,656
Rough-toothed dolphin	7	11.2	0.44	2.76	237	0.59	74–758
Fraser's dolphin	2	31.0	0.45	1.69	146	1.00	26–810
Bottlenose dolphin	70	13.6	0.12	33.67	2,890	0.20	1,955–4,270
Risso's dolphin	34	12.0	0.19	14.41	1,237	0.28	727–2,102
Pantropical spotted dolphin	43	43.3	0.15	59.40	5,097	0.24	3,207–8,100
Atlantic spotted dolphin	11	17.8	0.21	6.94	596	0.39	288–1,233
Striped dolphin	6	52.5	0.39	10.05	863	0.60	276–2,699
Spinner dolphin	4	91.3	0.40	11.65	1,000	0.66	291–3,433
Clymene dolphin	5	35.0	0.21	5.59	479	0.44	209–1,101
Bottlenose/Atlantic spotted dolphin	5	8.2	0.52	1.45	125	0.67	2–478
Stenella spp.	8	28.5	0.31	7.28	624	0.51	235–1,660
Unidentified dolphin	10	5.0	0.36	2.18	187	0.55	67–526
Unidentified small whale	6	2.2	0.18	0.56	49	0.51	19–124
Unidentified large whale	4	1.3	0.19	0.10	9	0.53	3–23
Unidentified odontocete	8	3.0	0.57	1.05	90	0.71	23–350

[a] One off-effort sighting.

Abundance and distribution.—There are no other abundance estimates that are directly comparable with these estimates for the study area. Other estimates are from spring ship surveys that covered the entire oceanic northern Gulf (L. J. Hansen, K. D. Mullin, and C. L. Roden, unpubl.) or covered a much larger continental slope study area (Hansen et al., 1996; Jefferson, 1996). In general, density estimates for each species from the ship surveys were of the same magnitude as those from this study.

Except for the short-finned pilot whale, commonly sighted species were widely distributed in the study area. Species sightings were too few to speculate about seasonal differences in their spatial distributions. Although there was no evidence of seasonal shifts in distribution within the study area, differences in seasonal abundance, if significant, indicate that cetaceans had moved out of the study area. In a much larger study area in the temperate northwestern Atlantic, many odontocete species appeared either to shift distribution seasonally within the area or move out of it completely (CeTAP, 1982). Similarly, Forney and Barlow (1998) report significant winter–summer differences in the abundance of some small odontocete species (e.g., Risso's dolphins) in United States waters off of California.

In this study, generally fewer cetaceans were sighted in fall than in other seasons, but this may not be the case every year. On the north-central Gulf slope, the peak sighting rate of cetaceans found by Mullin et al. (1994) occurred during fall, whereas the minimum occurred during summer. The weather may have negatively biased our fall results. Average Beaufort sea states during fall surveys, weighted by effort, were 2.1 and 2.4 whereas, during other seasons, the averages ranged from 1.2 to 1.8. Rougher water could have increased the magnitude of perception bias on the transect line (see below) and resulted in lower estimated abundances for fall.

In general, primary productivity in tropical marine ecosystems is much less seasonally variable compared with that of higher latitudes. Because the distribution of apex predators such as cetaceans is tied to primary productivity, seasonal distributions of cetaceans are

TABLE 4. Estimates of parameters used to estimate the annual and seasonal abundance (N) of cetaceans in the study area sighted 20 or more times (n = groups sighted; S = average or size-bias adjusted group size; D = animals·1,000 km^{-2}; CV = coefficient of variation).

Species	n	S	CV(S)	D	N	CV	95% CI
Sperm whale							
Year 1	10	2.1	0.19	0.85	73	0.33	35–153
Year 2	15	2.0	0.16	1.16	100	0.33	54–186
Summer	5	2.2	0.26	0.84	72	0.52	27–192
Fall	7	2.1	0.26	1.26	109	0.43	47–250
Winter	5	1.4	0.17	0.55	47	0.54	18–127
Spring	8	2.3	0.21	1.41	121	0.43	54–274
Dwarf/pygmy sperm whale							
Year 1	17	1.4	0.12	1.96	168	0.36	85–334
Year 2	16	1.5	0.11	2.04	176	0.37	88–352
Summer	13	1.8	0.13	3.87	333	0.38	161–688
Fall	2	1.5	0.33	0.55	48	0.90	10–227
Winter	5	1.2	0.17	1.03	89	0.58	31–255
Spring	13	1.3	0.10	2.71	233	0.38	114–478
Bottlenose dolphin							
Year 1	30	11.6	0.22	25.15	2,158	0.33	1,141–4,081
Year 2	40	13.3	0.16	36.70	3,150	0.25	1,959–5,064
Summer	24	18.2	0.19	59.73	5,126	0.30	2,867–9,163
Fall	6	18.2	0.32	16.40	1,407	0.71	395–5,011
Winter	20	9.0	0.16	25.09	2,154	0.29	1,241–3,737
Spring	20	11.3	0.22	31.61	2,713	0.37	1,356–5,428
Risso's dolphin							
Year 1	12	10.4	0.20	9.07	779	0.41	359–1,689
Year 2	22	12.8	0.30	19.49	1,673	0.34	861–3,249
Summer	3	30.7	0.77	12.57	1,079	0.97	133–8,777
Fall	2	9.0	0.22	2.70	232	0.74	62–872
Winter	14	11.1	0.17	21.87	1,877	0.32	1,019–3,459
Spring	15	9.4	0.17	19.72	1,693	0.35	874–3,279
Pantropical spotted dolphin							
Year 1	19	30.3	0.26	37.67	3,233	0.37	1,586–6,590
Year 2	24	58.1	0.14	86.86	7,453	0.27	4,413–12,587
Summer	14	35.1	0.17	58.89	5,053	0.33	2,674–9,549
Fall	4	41.1	0.25	22.32	1,915	0.50	726–5,050
Winter	10	41.5	0.32	52.49	4,504	0.49	1,766–11,486
Spring	15	55.1	0.24	104.16	8,938	0.37	4,383–18,224

probably less variable in tropical waters such as the Gulf. Nevertheless, although the mean state of Gulf oceanic waters is oligotrophic, productivity is significantly enhanced in local areas by a variety of dynamic processes that are spatially and temporally variable (Biggs and Ressler, 2001). These include the Loop Current (LC), which pushes variably north into the eastern Gulf, sometimes as far as the Mississippi–Alabama Shelf. The LC periodically sheds anticyclonic (warm core) eddies 200–300 km in diameter, which drift slowly (≈5 km·d^{-1}) to the west and spin down as they interact with the continental slope in the western Gulf. Upwelling occurs along the LC front and in cyclonic (cold core) eddies that routinely form in association with the LC front or eddies. Nutrient-rich shelf waters are periodically entrained into the confluence of these cyclone–anticyclone pairs and transported to oceanic water. Nutrient-rich Mississippi River water is also variably entrained, and the river plume periodically extends across the narrow shelf into the oceanic north-central Gulf. These processes almost certainly affect the spatial and temporal distribution of cetaceans in the Gulf (see

Baumgartner, 1997; Davis et al., 1998, 2002; Baumgartner et al., 2001).

Bias and precision.—This study was designed to meet the assumptions of the line-transect theory (Buckland et al., 1993). Meeting the central assumption, that objects (e.g., cetacean groups) on the transect line are detected with certainty, was problematic. Because this assumption was violated in two ways, the resulting abundance estimates are negatively biased. Cetaceans dive and can remain out of view much longer than the time the aircraft is overhead. Therefore, some groups on the line are missed because they are not available to be seen (availability bias; Marsh and Sinclair, 1989). Species-specific behavioral studies of dive behavior will have to be completed to assess the magnitude of this bias, but it is probably largest for species that feed at greatest depths or during the day. Cetacean groups that are on the transect line and visible are also missed by observers (perception bias; Marsh and Sinclair, 1989). The magnitude of this is dependent on species, group size, behavior, and weather. The 16 groups missed by the primary observers, but sighted by pilots or the data recorder during our study, indicate that one or both biases occurred. Only groups missed on the transect line ($g(y) = 0$) contributed to bias, but y was not measured for the missed groups.

The left-truncated sighting distribution was an artifact of perception bias. The left-truncation option on DISTANCE should have minimized this bias. Forney et al. (1994) used a third observer who concentrated on the transect line from the aircraft's belly port to help ensure that groups on and near the transect line were not missed and to estimate $g(0)$. Their estimates of $g(0)$ ranged from 0.67 to 0.85 for small cetaceans (e.g., Risso's dolphins) and was 0.95 for large cetaceans (e.g., sperm whales).

Another problematic assumption of line-transect theory is that the probability of detecting a cluster (e.g., cetacean group) has to be independent of its size. Violations of this assumption have been found by others (see Buckland et al., 1993) and would result in positive bias if not corrected. Corrections were made here using a regression estimator implemented on DISTANCE. The regression was significant in several cases (generally those with large sample sizes or large mean group sizes [or both]) (see Hansen et al., 1996). For example, the arithmetic mean group sizes of pantropical spotted dolphins were estimated to be from 16% (overall) to 53% (winter) larger than the adjusted means in Tables 3 and 4.

A wide variety of human activities in the Gulf of Mexico could potentially affect cetacean populations and include fishing, oil- and gas-related activities, shipping, and military training. If these activities adversely affect cetaceans in the Gulf, they will most likely be chronic in the form of habitat degradation from noise and physical disturbance. For chronic effects, monitoring strategies for acute effects, such as the risk aversion plan implemented by the NMFS for fisheries where cetacean mortalities are directly observed and extrapolated to the entire fishery (Barlow et al., 1995), will be not useful. Because of the diversity and density of cetaceans in the Gulf, the sample sizes for each species obtained by our study, despite a great deal of effort, were generally small. Statistical power, the ability of a statistical test to reject a null hypothesis (e.g., no intersample change in abundance; Gerrodette, 1987), is therefore poor. Clearly, monitoring the effects of human activities on cetaceans in the Gulf of Mexico is not trivial.

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