

Abstract—Surveys were conducted in the northern Gulf of Mexico during the spring seasons of 1992, 1993, and 1994 to determine the distribution, abundance, and habitat preferences of oceanic cetaceans. The distributions of bottlenose dolphins (*Tursiops truncatus*), Risso's dolphins (*Grampus griseus*), *Kogia* spp. (pygmy [*Kogia breviceps*] and dwarf sperm whales [*Kogia sima*]), pantropical spotted dolphins (*Stenella attenuata*), and sperm whales (*Physeter macrocephalus*) were examined with respect to depth, depth gradient, surface temperature, surface temperature variability, the depth of the 15°C isotherm, surface chlorophyll concentration, and epipelagic zooplankton biomass. Bottlenose dolphins were encountered in two distinct regions: the shallow continental shelf (0–150 m) and just seaward of the shelf break (200–750 m). Within both of these depth strata, bottlenose dolphins were sighted more frequently than expected in regions of high surface temperature variability which suggests an association with ocean fronts. Risso's dolphins were encountered over the steeper sections of the upper continental slope (200–1000 m), whereas the *Kogia* spp. were sighted more frequently in waters of the upper continental slope that had high zooplankton biomass. The pantropical spotted dolphin and sperm whale were similarly distributed over the lower continental slope and deep Gulf (>1000 m), but sperm whales were generally absent from anticyclonic oceanographic features (e.g. the Loop Current, warm-core eddies) characterized by deep occurrences of the 15°C isotherm. Habitat partitioning, high-use areas, species accounts, environmental sampling limitations, and directions for future habitat work in the Gulf of Mexico are discussed.

Cetacean habitats in the northern Gulf of Mexico

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Studies of cetacean distribution in the northern Gulf of Mexico have largely relied on stranding, opportunistic sighting, and limited survey data (Jefferson and Schiro, 1997) until recently (Mullin et al., 1994; Davis and Fargion¹; Davis et al.²). During the past decade, both aerial and shipboard assessment surveys in the oceanic (>200 m depth) northern Gulf have identified and characterized the abundance and distribution of 20 species of cetaceans, all but one of which were odontocetes (Mullin et al., 1994; Mullin and Hansen, 1999; Hansen et al.³; Mullin and Hoggard⁴). Only two of these species, the bottle-

² (*continued*) abundance and habitat associations, vol. I: executive summary. U.S. Department of the Interior, Geological Survey, Biological Resources Division, USGS/BRD/CR-1999-0006 and Minerals Management Service, OCS (outer continental shelf) Study MMS 2000-003, 27 p. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

³ Hansen, L. J., K. D. Mullin, T. A. Jefferson, and G. P. Scott. 1996. Visual surveys aboard ships and aircraft. In Distribution and abundance of cetaceans in the north-central and western Gulf of Mexico: final report, vol. II: technical report (R. W. Davis and G. S. Fargion, eds.), p. 55–128. U.S. Department of the Interior, Minerals Management Service, OCS Study MMS 96-007. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

⁴ Mullin, K. D., and W. Hoggard. 2000. Visual surveys of cetaceans and sea turtles from aircraft and ships. In Cetaceans, sea turtles and seabirds in the northern Gulf of Mexico: distribution, abundance and habitat associations, vol. II: technical report (R. W. Davis, W. E. Evans, and B. Würsig, eds.), p. 111–171. U.S. Department of the Interior,

¹ Davis, R. W., and G. S. Fargion. 1996. Distribution and abundance of cetaceans in the north-central and western Gulf of Mexico: final report, vol. I: executive summary. U.S. Department of the Interior, Minerals Management Service, OCS Study MMS 96-007, 29 p. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

² Davis, R. W., W. E. Evans, and B. Würsig. 2000. Cetaceans, sea turtles and seabirds in the northern Gulf of Mexico: distribution,

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nose dolphin (*Tursiops truncatus*) and Atlantic spotted dolphin (*Stenella frontalis*), occur regularly over the continental shelf (Fritts et al., 1983; Mullin et al., 1994; Davis et al., 1998). In contrast, the oceanic Gulf supports a wide diversity of cetacean species by potentially supplying a large number of ecological niches. Although predator avoidance, interspecific competition, and reproductive strategies all affect cetacean distribution to some extent, energetic budget studies indicate that most cetaceans must feed every day (Smith and Gaskin, 1974; Lockyer, 1981; Kenney et al., 1985; CETAP⁵) and thus habitat is assumed to be primarily determined by the availability of food (Kenney and Winn, 1986). The distribution of the oceanic species, then, is presumably linked to the rather dynamic oceanography of the Gulf of Mexico through physical-biological interactions and trophic relationships between phytoplankton, zooplankton, micronekton, and cetacean prey species. For most cetaceans in the Gulf of Mexico, specific prey species are not known but likely include epi- and mesopelagic fish and cephalopods (Fitch and Brownell, 1968; Perrin et al., 1973; Würtz et al., 1992; Clarke, 1996).

The physical and biological oceanography of the northern Gulf of Mexico is highly variable in both space and time. The eastern Gulf contains the Loop Current, an extension of the Gulf Stream system that enters the Yucatan Channel, turns anticyclonically, and exits through the Straits of Florida. The northward penetration of the Loop Current into the Gulf of Mexico normally varies between 24° and 28°N on a quasi-annual basis (Sturges and Evans, 1983). Cold, potentially biologically rich, upwelling features are frequently found at the edge of the Loop Current and often develop into cyclonic, cold-core eddies (Vukovich et al., 1979; Maul et al., 1984; Vukovich and Maul, 1985; Richards et al., 1989). Large, anticyclonic, warm-core eddies can shed from the Loop Current during its maximum northerly penetration into the Gulf (Cochrane 1972; Hurlburt and Thompson, 1982) after which they move slowly westward at an average speed of 5 km/day. More than one of these warm-core eddies can be found in the western Gulf of Mexico because their translation (net) speed and decay are slow (Elliot, 1982). During their transit from the eastern to western Gulf of Mexico, these warm-core features can also have associated cyclonic features at their peripheries which are biologically productive (Biggs, 1992). Another major source of nutrients that can drive primary productivity in the oceanic Gulf is the Mississippi River. The Mississippi River Delta protrudes into the Gulf

in a region where the continental shelf is narrow and the continental slope is steep. The river's nutrient-rich fresh water plume extends over the deep Gulf and supports high rates of primary productivity and large standing stocks of chlorophyll and zooplankton biomass (El-Sayed, 1972; Dagg et al., 1988; Ortner et al., 1989).

Our study examines the distribution of five commonly encountered cetacean species or species groups in the northern Gulf of Mexico with respect to several physical, biological, and physiographic variables. These species are the bottlenose dolphin, Risso's dolphin (*Grampus griseus*), Kogia spp. (pygmy [*Kogia breviceps*] and dwarf sperm whale [*Kogia sima*]), pantropical spotted dolphin (*Stenella attenuata*) and sperm whale (*Physeter macrocephalus*). The environmental and cetacean survey data for our study were collected by the U.S. National Marine Fisheries Service. Subsets of these data have been analyzed by Baumgartner (1997) to characterize the distribution of Risso's dolphins with respect to the physiography of the northern Gulf of Mexico and by Davis et al. (1998) to describe cetacean habitats over the continental slope in the northwestern Gulf. One of the major objectives of these surveys was to help assess the impact of large-scale oil and gas exploration and development in the northern Gulf of Mexico on cetaceans. An understanding of the habitat preferences of each of these species will greatly improve management and conservation efforts by providing a context for interpreting future anthropogenic influences on cetacean distribution.

Materials and methods

Data collection and treatment

We examined the distribution of each cetacean species with respect to seven environmental variables (Table 1) to characterize habitat. These variables were selected because they represent specific oceanographic or physiographic features or conditions. Depth and depth gradient (sea floor slope) were included to represent the physiography of the Gulf of Mexico because the distribution of some cetaceans has been associated with specific topographic features in the Gulf (Baumgartner, 1997; Davis et al., 1998) and elsewhere (Evans, 1975; Hui, 1979, 1985; Selzer and Payne, 1988; CETAP⁵; Dohl et al.⁶; Dohl et al.⁷; Green et al.⁸). A com-

⁴ (continued from previous page) Geological Survey, Biological Resources Division, USGS/BRD/CR-1999-0006 and Minerals Management Service, OCS Study MMS 2000-003. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

⁵ CETAP (Cetacean and Turtle Assessment Program). 1982. A characterization of marine mammals and turtles in the mid- and north Atlantic areas of the U.S. outer continental shelf. U.S. Department of the Interior, Bureau of Land Management, contract AA551-CT8-48. 584 p. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161.]

⁶ Dohl, T. P., K. S. Norris, R. C. Guess, J. D. Bryant, and M. W. Honig. 1978. Summary of marine mammal and seabird surveys of the Southern California Bight area 1975-78, vol. III: Investigators' Reports, part II: Cetacea of the Southern California Bight. U.S. Department of the Interior, Bureau of Land Management, Contract AA550-CT7-36, 414 p. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161.]

⁷ Dohl, T. P., R. C. Guess, M. L. Duman, and R. C. Helm. 1983. Cetaceans of central and northern California, 1980-1983. Status, abundance and distribution. U.S. Department of the Interior, Minerals Management Service, contract 14-12-0001-29090, 284 p. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161.]

mon measure of bottom relief, contour index (Evans, 1975), was omitted because it does not distinguish between significantly different topographies in the northern Gulf of Mexico (Baumgartner, 1997). Many oceanographic features, such as eddies or river discharge, have strong sea surface temperature signatures, whereas areas where different water masses abut (frontal zones) are often characterized as regions of high surface temperature variability. Meso-scale warm-core eddies in the Gulf of Mexico are easily detected in hydrographic transects by the deep occurrence of the 15°C isotherm. Finally, surface chlorophyll concentration and zooplankton biomass represent rough measures of the standing stocks on which higher trophic consumers might feed.

Cetacean surveys were conducted during the spring seasons of 1992, 1993, and 1994 from NOAA Ship *Oregon II* in the Gulf of Mexico approximately north of a line connecting Brownsville, Texas, and Key West, Florida, and primarily in waters deeper than 200 m (Fig. 1). Sighting data were collected with 25× binoculars and standard line-transect survey methods for cetaceans (e.g. Barlow, 1995; Hansen et al.³). Time and the ship's position were recorded automatically every two minutes, and at regular intervals the survey team recorded ancillary data, such as sea state, sighting conditions, and effort status. These ancillary data were appended to the time and position records. Environmental data were extracted from the appropriate data sets (discussed below) and also appended to the time and position records. These records comprise the effort data set which provides a complete history of the sighting conditions, survey effort, and environmental observations. The cetacean sighting records were also appended with the environmental and ancillary data and collectively represent the cetacean sighting data set.

Surface temperature was recorded at one-minute intervals with a flow-through thermosalinograph (SeaBird Electronics, Inc, Bellevue, WA). The temperature measurements were low-pass filtered to reduce high frequency and high wave number variability. The filter was a simple 5-min running mean which, at an average vessel speed of 5 m/s (10 knots), is equivalent to averaging over 1.5 km.

Conductivity, temperature, and depth (CTD) or expendable bathythermograph (XBT) casts were conducted every 55 km (30 nmi) along the survey transect. CTD casts were

Table 1
Environmental variables used in the habitat analyses.

Variable	Source	Units
Depth	digital bathymetry	m
Depth gradient	digital bathymetry	m/1.1 km
Surface temperature	thermosalinograph	°C
Surface temperature standard deviation	infrared satellite imagery	°C
Depth of 15°C isotherm	CTD and XBT casts	m
Surface chlorophyll concentration	surface samples	mg/m ³
Zooplankton biomass	oblique bongo tows	cc/100 m ³

generally made to 500 m or just off the sea floor, whichever was shallower. XBT probes capable of operating to depths of 200 to 1000 m were used in appropriate depths. Surface water samples were collected every 55 km and chlorophyll *a* was measured in these samples by using fluorometric and spectrophotometric techniques described in Strickland and Parsons (1972) and Jeffery and Humphrey (1975). Plankton tows were also conducted at 55-km intervals by using a 61-cm diameter bongo equipped with 0.333-mm mesh nets and flowmeters. The nets were towed obliquely from 200 m or just off the sea floor, whichever was shallower. Samples from one of the bongos were analyzed by the Polish Sorting and Identification Center in Szczecin, Poland. Zooplankton biomass was computed as the ratio of the displacement volume of the sample after organisms larger than 2.5 cm were removed (after Smith and Richardson, 1977) to the volume of water filtered during the tow.

Remotely sensed sea surface temperature (SST) data from the advanced very high resolution radiometer (AVHRR) carried aboard the National Oceanic and Atmospheric Administration (NOAA) polar orbiting environmental satellites were acquired from the U.S. National Environmental, Satellite and Data Information Service. The raw, level 1B data from the NOAA 9, 10, and 11 satellites were warped to a 0.01° · 0.01° linear latitude-longitude projection by using the supplied satellite navigation information, coregistered to a digital coastline and converted to sea surface temperatures by using separate day and night multichannel SST equations. Because of the lower accuracy and relative paucity of the satellite-derived SST data, the *in-situ* surface temperature from the shipboard thermosalinograph was used in the analyses of cetacean habitat. However, these remotely sensed data are well suited to detecting horizontal gradients in SST due to their synoptic coverage. These gradients are often resolved by using digital image gradient operators (e.g. Sobel, Prewitt, or Roberts operators), but we chose another approach after Smith et al. (1986). Because horizontal gradients in SST can be measured as horizontal variability, we computed the standard deviation of the remotely sensed SST within a 10-km radius of each transect and sighting position.

Water depth was extracted from a digital bathymetric data set compiled from NAVOCEANO's DBDB5 5-minute · 5 minute gridded bathymetry, National Ocean Service's high

⁸ Green, G. A., J. J. Brueggeman, R. A. Grotefendt, C. E. Bowlby, M. L. Bonnell, and K. C. Balcomb III. 1992. Cetacean distribution and abundance off Oregon and Washington, 1989–1990. *In Oregon and Washington marine mammal and seabird surveys* (J. J. Brueggeman, ed.), p. 1–100. U.S. Department of the Interior, Minerals Management Service, contract 14-12-0001-30426. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161.]

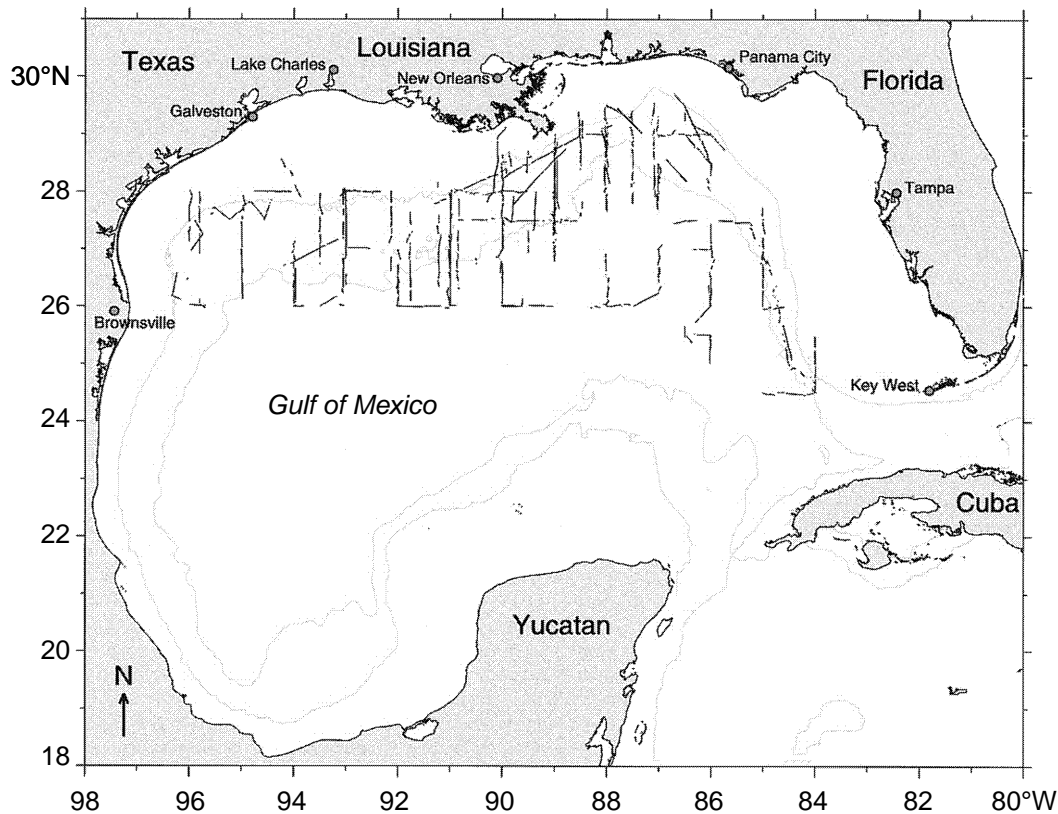


Figure 1

Map of shipboard surveys transects conducted by NOAA Ship *Oregon II* in the spring seasons of 1992, 1993, and 1994. Only transects conducted during active searches for cetaceans during adequate sighting conditions are shown. The 200-m and 2000-m isobaths are indicated in gray.

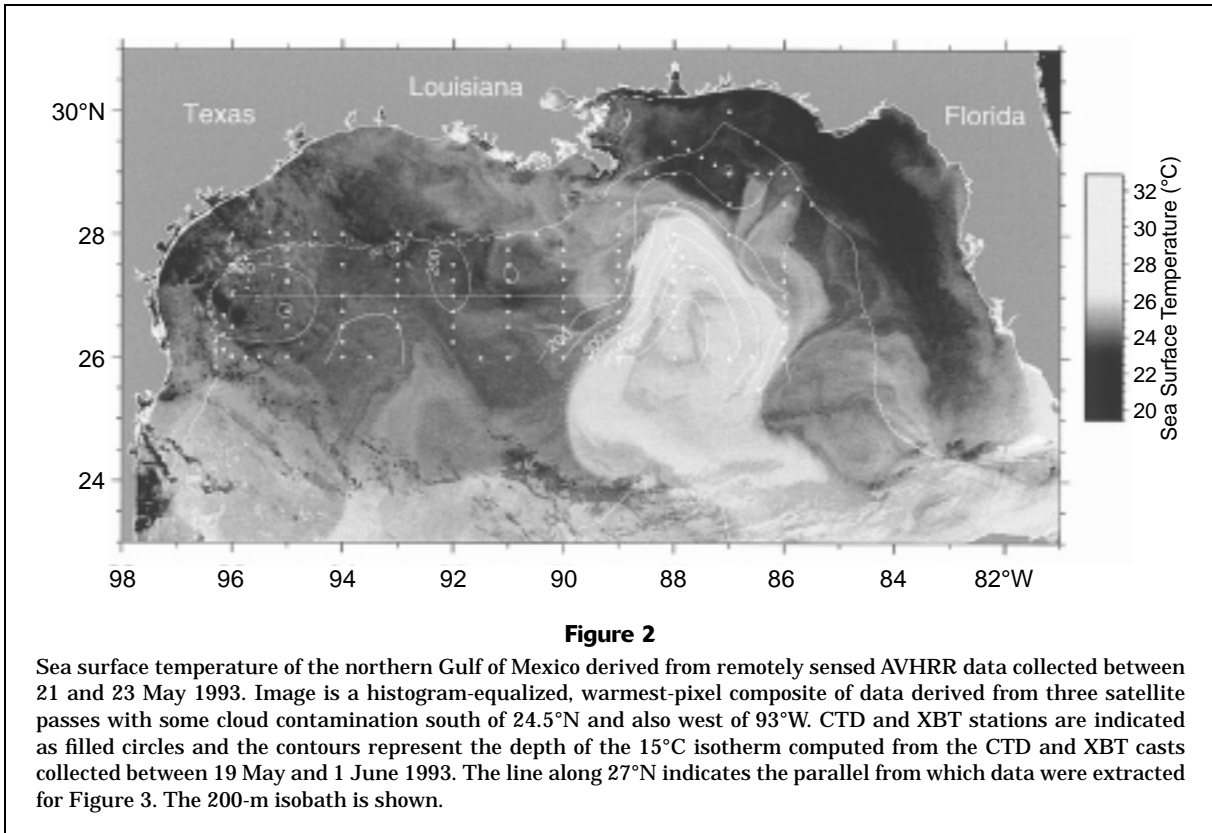
resolution coastal bathymetric data set and Texas A&M University's digitized bathymetric charts (Herring⁹). This depth data set was provided on a $0.01^\circ \times 0.01^\circ$ linear latitude-longitude grid with a nominal resolution of 1.1 km for the entire Gulf of Mexico. Depth gradient or sea floor slope was derived from the depth grid by using a 3×3 pixel Sobel gradient operator. The resulting product had the same base resolution and spatial coverage as the bathymetry data set. For descriptive purposes, the following physiographic terms will be used to denote specific depth ranges or features: continental shelf (0–200 m), shelf break (~200 m), continental slope (200–2000 m), upper continental slope (200–1000 m), lower continental slope (1000–2000 m), and deep Gulf (>2000 m).

A single descriptor of the vertical temperature structure in the upper ocean was selected to quantify the influence of mesoscale features such as eddies on cetacean distribution. Reilly (1990) chose the depth of the 20°C isotherm

as an approximate indicator of thermocline depth in his study of cetacean habitat in the eastern tropical Pacific. We used a similar approach by extracting the depth of the 15°C isotherm from each CTD and XBT profile. This variable is not intended to represent the depth of the thermocline, however. The low-frequency, large-scale temperature variability along this isotherm is associated with the mesoscale features of interest and it occurs deep enough that it never reaches the sea surface during the spring in the northern Gulf of Mexico.

The discrete samples of the depth of the 15°C isotherm, surface chlorophyll concentration and zooplankton biomass from each cruise leg (9–17 days in duration) were interpolated on a regular $0.1^\circ \times 0.1^\circ$ linear latitude-longitude grid by using the kriging method (Golden Software, 1994). Surface chlorophyll was log-transformed before interpolation because the observed chlorophyll concentrations had a log-normal distribution and spanned several orders of magnitude (0.02–13.02 mg/m³). The interpolation method provided consistent results when compared with other data sets (e.g. Fig. 2). Because no interpolation method will capture the true spatial structure of these variables, the accuracy of the interpolated values in the effort and sighting datasets is undoubtedly low. Despite these errors, however, the horizontal variability associated

⁹ Herring, H. J. 1993. A bathymetric and hydrographic climatological atlas for the Gulf of Mexico (draft report). U.S. Department of the Interior, Minerals Management Service, contract 14-12-0001-30631, 191 p. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161.]



with mesoscale oceanographic features is much larger than these errors and therefore the interpolated fields represent these features reasonably well (e.g. Fig. 2).

The base unit of effort for this study was defined as 1 km of actively surveyed transect during adequate sighting conditions. To conform to this definition, each contiguous transect in the effort data set was broken into 1-km linear sections and all the environmental variables measured along each 1-km section were averaged. This provided a single set of observed environmental variables for each unit of effort. Only those 1-km sections that were actively surveyed (i.e. those where the observers were on-effort) during adequate sighting conditions (defined as Beaufort sea states of 3 or less) were used for analysis. Similarly, only those cetacean sightings that occurred while observers were on-effort and in Beaufort sea states of 3 or less were used for analysis. All of the following analyses were conducted on cetacean group sightings and therefore do not account for group size.

Some portions of the described data have been previously published by Davis et al. (1998) and Baumgartner (1997). Davis et al. (1998) examined cetacean habitat in the northwestern Gulf of Mexico with respect to a variety of physical oceanographic and physiographic variables. We have included the sighting data and some of the environmental data from that study here (less than 40% of our total data set) to examine cetacean habitat throughout the entire northern Gulf of Mexico with an expanded set of environmental variables and new statistical analyses.

With regard to Risso's dolphin habitat, we have used the same sighting, depth, and depth gradient data presented in Baumgartner (1997). To these, we have added physical and biological oceanographic variables to test and extend the conclusions of Baumgartner (1997) and to strengthen the univariate and multivariate interspecies comparisons described below.

Analytical methods

The analysis of the sighting and effort data sets was conducted in two parts: 1) univariate and multivariate interspecies comparisons of the environmental variables measured at each cetacean sighting and 2) comparisons of each species' distribution with respect to the environmental variables to that of the effort. The former analysis examined the null hypothesis that each species had similar distributions with respect to each of the environmental variables. This was tested with Mood's median test (Conover, 1980) and the Kruskal-Wallis test (Sokal and Rohlf, 1981) as nonparametric substitutes for a one-way analysis of variance. Multivariate analysis of variance (MANOVA) and canonical linear discriminant function (LDF) analysis (Huberty, 1994; Johnson, 1998) with rank-transformed environmental variables were used to further examine interspecies differences. These analyses were conducted with the CANDISC procedure of the Statistical Analysis System (SAS, 1989), version 6.12. The MANOVA detects species group differences in multivariate space and

the canonical LDF analysis describes which environmental factors contribute most to these group differences. The canonical LDF analysis is accomplished by finding a linear combination of the environmental variables that best discriminates between the species groups. These linear combinations (canonical variables) are then examined by using the LDF structure correlations (Huberty, 1994) to assess their ecological meaning and significance. The structure correlations are essentially the correlations between the canonical variables and the original environmental variables and their interpretation is analogous to the interpretation of factor loadings in factor analysis.

The second analysis uses univariate and bivariate chi-squared (χ^2) tests, Mann-Whitney tests, Monte Carlo tests, and equal-effort sighting rate distribution plots to determine the specific relationships between the distribution of each species and each of the environmental variables. For the χ^2 analysis, the effort data were used to compute expected uniform distributions for each species with respect to the individual environmental variables. Classes were chosen such that each contained an equal amount of effort (Kendall and Stuart, 1967). This approach "normalized" the sighting rates by creating class sizes of equal sighting probability based on the effort and guaranteed that the analysis would not be distorted by classes with exceptionally low or high amounts of effort. For a complete description of the methods used to compute the uniform distribution, see Baumgartner (1997). The actual distributions were then compared with the predicted uniform distributions by using the χ^2 statistic. Equal-effort sighting rate distribution plots were constructed directly from the contingency tables used in the χ^2 analyses. In some cases, the sample size was lower than the minimum required for a conservative χ^2 test ($n=25$), therefore the species' and effort distributions were compared by using a Mann-Whitney test.

Of the five species examined here, each had a distribution with respect to depth that was significantly different from a uniform distribution. Further analyses with Monte Carlo (randomization) tests were conducted to determine if the distribution of a particular species with respect to the other environmental variables was an artifact of that species' distribution with depth. For example, consider a hypothetical species that is only found on the continental shelf. The continental shelf in the northern Gulf of Mexico is characterized by low depth gradients, whereas the continental slope has high depth gradients and the abyssal plains of the deep Gulf have low depth gradients. Because this species occurs on the continental shelf, it would have distributions with respect to both depth and depth gradient that were significantly different from a uniform distribution. However, this species' distribution with respect to depth gradient is merely an artifact of its distribution with respect to depth because of a correspondence between shallow depths and low depth gradients over the continental shelf.

The Monte Carlo tests consisted of randomly choosing n transect sections from the effort data set that had the same depth distribution as the n sightings of the species of interest. These transect sections represent n "virtual" cetacean sightings that have the same depth distribution as the species of interest but have a random distribution

with respect to all of the other environmental variables. A χ^2 analysis was then conducted to determine if the distribution of the "virtual" sightings with respect to the particular environmental variable of interest (e.g. depth gradient in the example above) was different from a uniform distribution predicted by the effort. The process of choosing n "virtual" sightings and of conducting the χ^2 analysis was performed 10,000 times. The proportion of the resulting 10,000 χ^2 statistics that exceeded the χ^2 statistic associated with the species' actual distribution with respect to the environmental variable of interest was considered a P -value. This P -value represented the probability that the actual χ^2 statistic could have been observed by chance and was used to test the null hypothesis that the species' distribution with respect to the environmental variable of interest was the same as a uniform distribution given its distribution with respect to depth.

Results

NOAA Ship *Oregon II* completed 113 days of effort during the spring surveys from 1992 to 1994 and sampled the entire oceanic northern Gulf of Mexico once each year. A total of 9101 1-km transect sections (units of effort) were completed during adequate sighting conditions. The amount of environmental data available for each transect section was dependent on survey design, on instrument availability and performance, and, in the case of the remotely sensed sea surface temperature variability, on satellite orbital parameters and cloud conditions (Table 2).

The Loop Current penetrated into the eastern Gulf to at least 27.5°N during each of the surveys and warm-core eddies could usually be found in the central and western Gulf (Fargion et al.¹⁰). Both the Loop Current and the warm-core eddies were often accompanied by cold-core features at their peripheries. Examples of the major oceanographic features of the northern Gulf are shown in the composite AVHRR sea surface temperature image and the contoured depth of the 15°C isotherm (Fig. 2). The Loop Current is easily identifiable as the broad region in the eastern Gulf where the 15°C isotherm was at depths below 250 to 300 m and sea surface temperatures reached a local maximum. The remnants of a warm-core eddy (Eddy V) are evident in the northwestern Gulf centered at about 27.0°N, 95.5°W (Jockens et al., 1994; Fargion et al.¹⁰). Warm-core features like the Loop Current were characterized by depressed isotherms and were often accompanied by warm surface temperatures and low zooplankton biomass (Fig. 3). Surface temperature gradients were high at the edge of these mesoscale features when

¹⁰ Fargion, G. S., L. N. May, T. D. Leming, and C. Schroeder. 1996. Oceanographic surveys. *In* Distribution and abundance of cetaceans in the north-central and western Gulf of Mexico: final report, vol.II: technical report (R.W. Davis and G.S. Fargion, eds.), p. 207–269. U.S. Department of the Interior, Minerals Management Service, OCS Study MMS 96-007. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

Table 2
Number of 1-km transect sections (units of effort) with valid data for each environmental variable.

Variable	1992	1993	1994	Total
Depth	3454	2373	3274	9101 (100%)
Depth gradient	3454	2373	3274	9101 (100%)
Surface temperature	1414	2245	2915	6574 (72%)
Surface temperature standard deviation	688	1084	498	2270 (25%)
Depth of 15°C isotherm	2357	1939	2669	6965 (77%)
Surface chlorophyll concentration	2844	2277	2859	7980 (88%)
Zooplankton biomass	2127	1103	1419	4649 (51%)

Table 3

Correlation matrix of environmental variables. Correlation coefficients for surface chlorophyll and zooplankton biomass were computed from the station samples (not from the interpolated fields). SD = standard deviation.

Variable	Depth	Depth gradient	Surface temperature	Surface temperature SD	Depth of 15°C isotherm	Surface chlorophyll
Depth gradient	-0.003					
Surface temperature	0.104**	0.098**				
Surface temperature SD	-0.067**	0.032	0.019			
Depth of 15°C isotherm	0.297**	-0.139**	0.199**	0.365**		
Surface chlorophyll	-0.341**	0.013	-0.250*	-0.165	-0.166	
Zooplankton biomass	-0.224**	-0.064	-0.192	0.141	-0.380**	0.710**

* indicates $P < 0.05$.

** indicates $P < 0.01$.

their surface temperature signatures were strong.

Many of the environmental variables in the effort data set were significantly correlated with one another ($P < 0.05$), but correlation coefficients were less than 0.3 in most cases (Table 3). The high correlation between surface chlorophyll and zooplankton biomass was strongly influenced by stations on the continental shelf where both surface chlorophyll and zooplankton biomass were typically quite high. The surface chlorophyll measurements collected on the shelf were significantly higher than those from oceanic waters (Mann-Whitney, $U=4.44$, $P < 0.0001$), whereas the median zooplankton biomass measured on the shelf ($10.1 \text{ cc}/100 \text{ m}^3$) was almost twice as large as the median of the oceanic observations ($5.4 \text{ cc}/100 \text{ m}^3$). The correlation coefficient between the surface chlorophyll and zooplankton biomass measured in oceanic waters was not significantly different from zero ($P > 0.05$). This contrast between the continental shelf and

Table 4

Number of group sightings (n), sighting rate (group sightings per 100 km) and mean, standard deviation (SD), minimum (Min) and maximum (Max) group size of the five most frequently encountered species or species groups.

Species	n	Sighting rate	Group size			
			Mean	SD	Min	Max
Bottlenose dolphin	89	0.98	14.7	22.7	1	150
Risso's dolphin	67	0.74	10.8	7.3	2	40
<i>Kogia</i> spp.	56	0.62	2.1	1.6	1	8
Pantropical spotted dolphin	107	1.18	51.8	42.4	3	180
Sperm whale	43	0.47	2.5	1.9	1	11

more oceanic waters was also manifested in the inverse relationships detected between depth and surface chlorophyll and between depth and zooplankton biomass.

Of the 614 cetacean groups sighted between 1992 and 1994, the most frequently encountered species were the bottlenose dolphin, Risso's dolphin, *Kogia* spp., pantropical spotted dolphin, and sperm whale (Table 4). The *Ko-*

gia spp. group was made up of sightings of dwarf sperm whales ($n=32$), pygmy sperm whales ($n=7$), and those small whales that could only be identified to the genus *Kogia* ($n=17$). The spatial distributions of sightings suggest high use areas for each species (Fig. 4), but these are heavily influenced by the distribution of the sighting effort. To better capture the true spatial distributions, the location of each sighting and 1-km transect section was projected onto the 200-m isobath (by using the minimum distance to this isobath) and equal-effort sighting distributions were gener-

ated with respect to the distance along the 200-m isobath (Fig. 4). Chi-squared analyses indicated that all of the species' distributions, except the *Kogia* spp. group, were significantly different from a uniform distribution ($P<0.01$). The northwestern Gulf of Mexico (west of the Mississippi River Delta) had much lower group sighting rates of each cetacean species when compared with the northeastern Gulf (east of the Mississippi River Delta). To the south of New Orleans, the Mississippi Canyon and just seaward of the Mississippi River Delta were regions of high group encounter rates for bottlenose dolphins, Risso's dolphins, and sperm whales. Just to the east of this region and south of Mobile Bay, pantropical spotted dolphin sighting rates reached a local maximum. Along the steep upper continental slope of the Florida Escarpment between Tampa and Key West, very high relative abundances of Risso's dolphins, pantropical spotted dolphins, and sperm whales were observed.

Examination of the mean, median, first and third quartiles, and standard deviation of the environmental variables for each species suggested significant interspecies differences (Fig. 5). The null hypothesis of equal medians for each species was rejected for depth, depth gradient, surface temperature, and zooplankton biomass (Mood's median test, $P<0.01$). Similarly, the null hypothesis of equal "locations" was rejected with a Kruskal-Wallis test for depth, depth gradient, zooplankton biomass ($P<0.01$), and surface temperature ($P<0.05$). The bottlenose dolphin had the lowest median depth, depth gradient, and surface temperature of all the species. The Risso's dolphin had the highest median depth gradient and surface temperature and the *Kogia* spp. had the highest median zooplankton biomass. The bottlenose dolphin's median habitat was so different from the others that if this species was removed from each of the Mood's median tests, the null hypothesis of equal medians between species would be rejected for only depth ($P<0.01$) and zooplankton biomass ($P<0.05$).

Despite clear heterogeneity of variances (Fig. 5A), a one-way analysis of variance indicated that the cetacean distributions with respect to depth were significantly different. Furthermore, a Duncan's multiple range test suggested species groupings by depth ($P<0.05$) that were qualitatively accurate and in agreement with earlier results (Mullin et al., 1994). These species groupings were 1) bottlenose dolphins, 2) Risso's dolphins and *Kogia* spp., and 3) pantropical spotted dolphins and sperm whales. Bottlenose dolphins were encountered predominantly over the continental shelf and were never sighted seaward of the 750-m isobath. Risso's dolphins and *Kogia* spp. were distributed mostly over the upper continental slope, whereas pantropical spotted dolphins

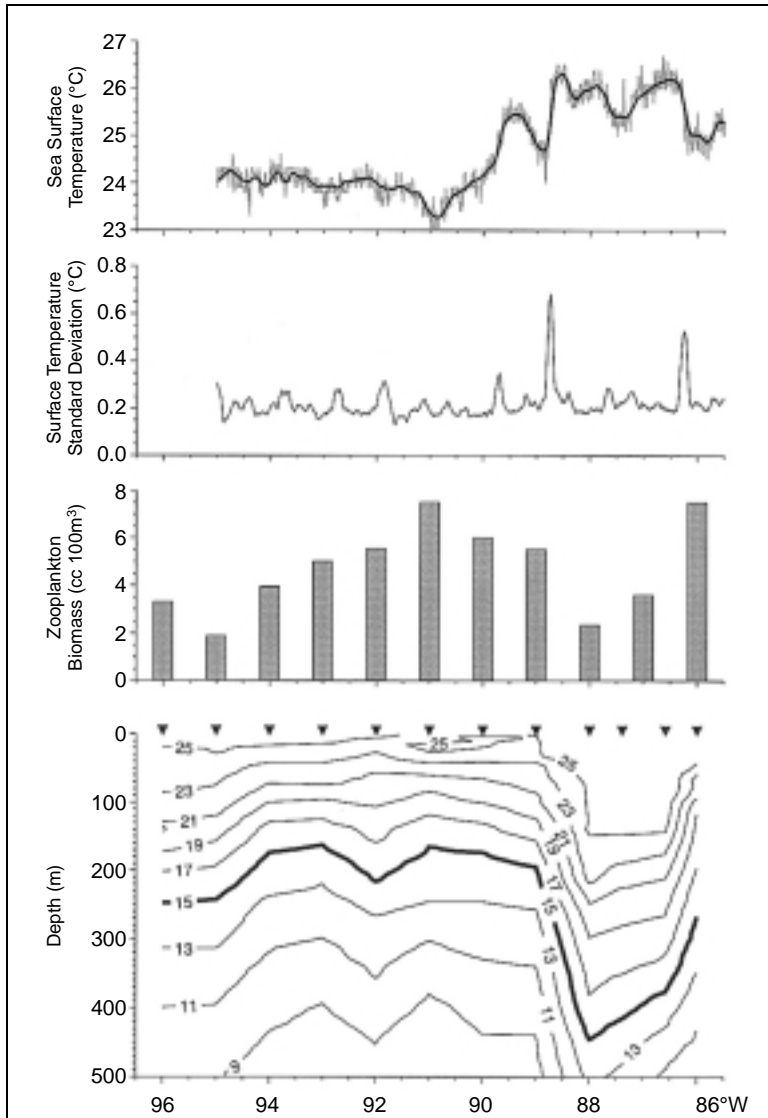


Figure 3

Surface temperature (raw temperatures in gray, 10 km radius average in black), surface temperature variability (standard deviation in 10 km radius), epipelagic zooplankton biomass and vertical temperature structure along 27°N observed between 19 May and 1 June 1993. Surface temperature and surface temperature variability were obtained from the composite satellite image shown in Figure 2. The inverted triangles indicate CTD/XBT station locations from which the temperature section was derived.

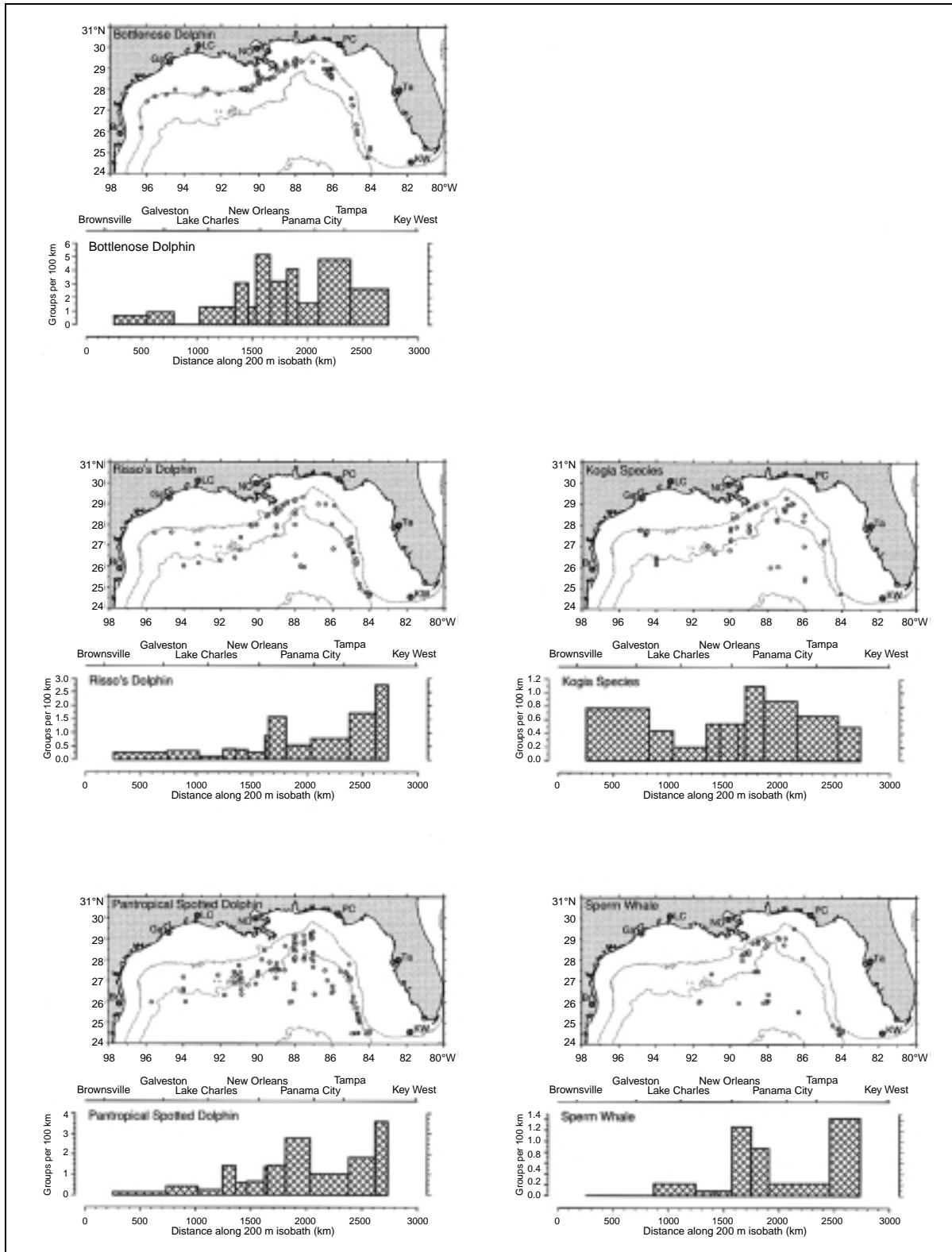


Figure 4

Spatial distribution of group sightings and sighting rates for each species. Sightings and 1-km transect sections (effort) were projected onto the 200-m isobath and the group sighting rate distributions were computed by using equal-effort class sizes. The sighting rate distribution of the bottlenose dolphin only includes effort from 1000 m depth and shallower because no bottlenose dolphins were encountered seaward of the 750-m isobath. The sighting maps and sighting rate distribution plots are aligned geographically to facilitate comparison. The 200- and 2000-m isobaths are shown in the sighting maps.

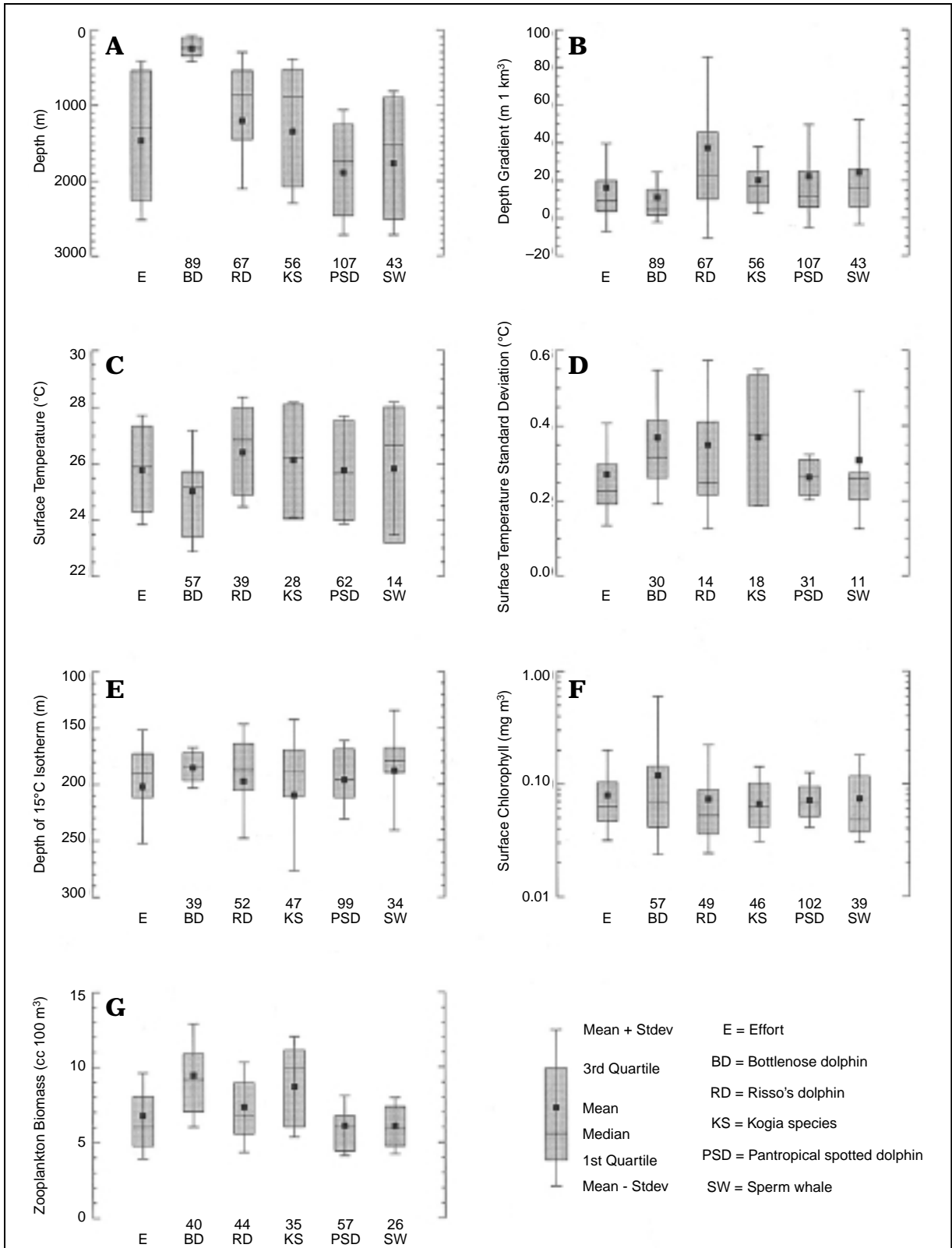


Figure 5

Mean, median, interquartile range, and standard deviation of (A) depth, (B) depth gradient, (C) surface temperature, (D) surface temperature variability, (E) depth of the 15°C isotherm, (F) surface chlorophyll, and (G) epipelagic zooplankton biomass for each species and the 1-km transect sections (effort). The sample size (*n*) is shown above each species abbreviation.

and sperm whales had distributions that extended from the upper continental slope to the deep Gulf. Mann-Whitney tests between Risso's dolphins and *Kogia* spp. for each of the environmental variables indicated that only their distributions with respect to depth gradient ($U=2.12$, $P<0.05$) and zooplankton biomass ($U=1.69$, $P<0.05$) were significantly different. Similar tests between pantropical spotted dolphins and sperm whales indicated that their distributions with respect to the depth of the 15°C isotherm ($U=2.26$, $P<0.05$) alone were significantly different.

Differences between species were also detected with MANOVA and canonical linear discriminant function analysis. Unfortunately, low sample size for both sea surface temperature and sea surface temperature variability precluded their use in the multivariate analyses. Of the remaining variables, the sample sizes for each species were as follows: bottlenose dolphins ($n=18$), Risso's dolphins ($n=35$), *Kogia* spp. ($n=25$), pantropical spotted dolphins ($n=51$), and sperm whales ($n=19$). The null hypothesis of equal mean vectors was rejected in the MANOVA (Wilks' $\lambda=0.446$, $P<0.0001$). The first two canonical variables in the canonical LDF analysis accounted for 94.5% of the

total variability, and likelihood ratio tests indicated that only the first two canonical variables were significant ($P<0.01$ for each). The structure correlations indicated that low depths and high zooplankton biomass were associated with positive values of the first canonical variable, whereas shallow occurrences of the depth of the 15°C isotherm and low surface chlorophyll concentration were associated with positive values of the second canonical variable (Fig. 6A). The separation between groups along canonical axis 1 supports the importance of depth in habitat partitioning in the northern Gulf of Mexico. The significance of zooplankton biomass in this first canonical variable was due to the inclusion of the bottlenose dolphin in the analysis and the presence of high zooplankton biomass on the continental shelf. Note that the bottlenose dolphin was clearly separated from the other species along canonical axis 1 and the sperm whale was separated from the other species on both canonical axes.

Because inclusion of the bottlenose dolphin strongly influenced the results of the multivariate analysis, a second analysis was conducted for just the oceanic species. The null hypothesis of equal mean vectors was rejected

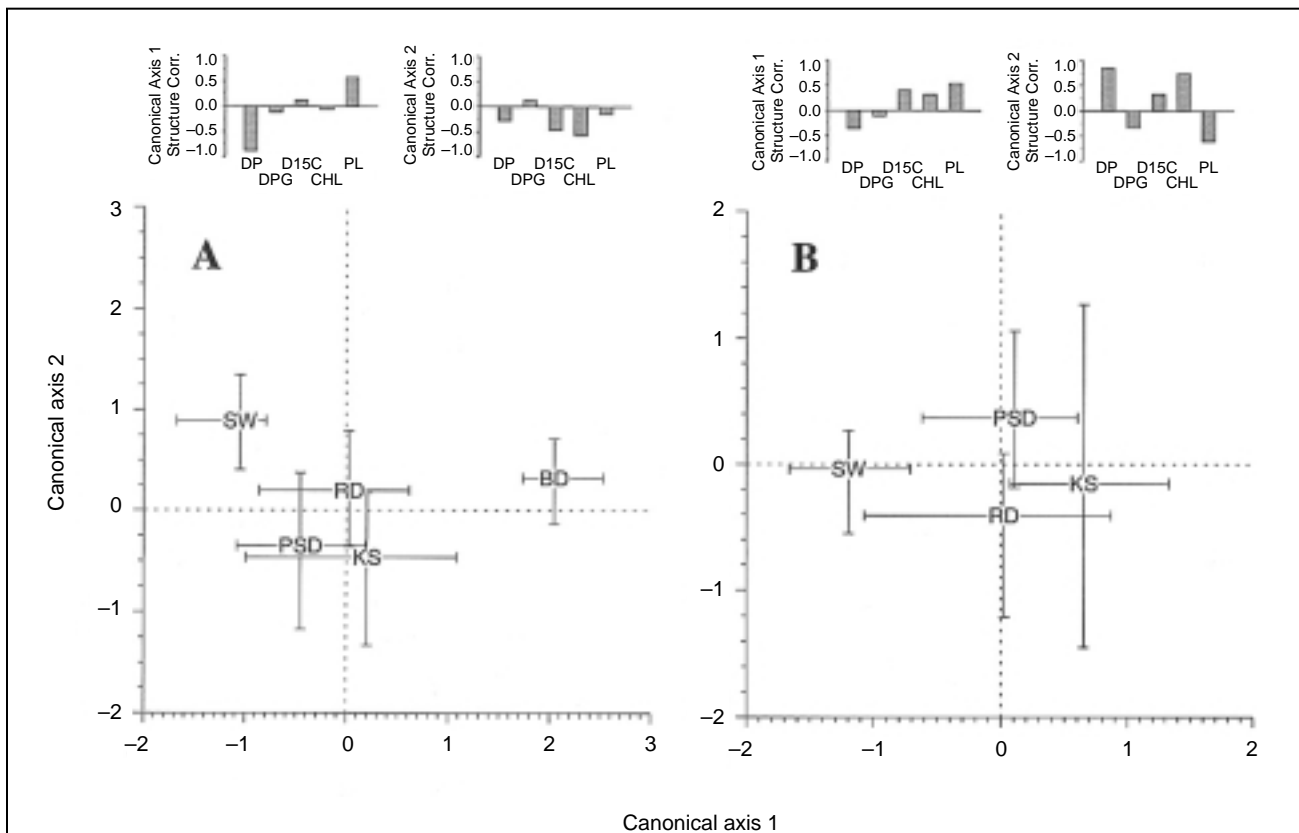
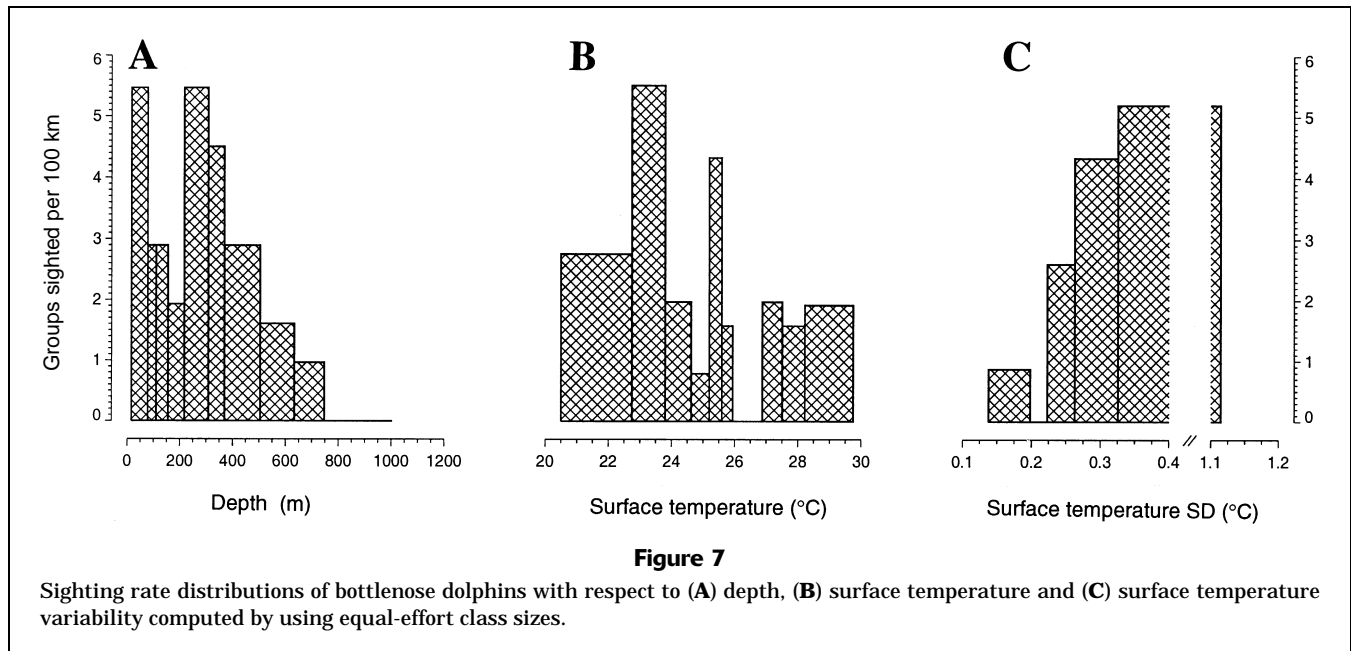


Figure 6

Means and interquartile ranges (error bars) of the canonical linear discriminant function variables for (A) all species and (B) all species except the bottlenose dolphin. The structure correlations associated with each canonical axis represent the approximate correlations between the canonical variables and depth (DP), depth gradient (DPG), depth of the 15°C isotherm (D15C), surface chlorophyll concentration (CHL), and epipelagic zooplankton biomass (PL). Species abbreviations are the same as those shown in Figure 5.



again in the MANOVA (Wilks' $\lambda=0.675$, $P<0.0001$). The first two canonical variables in the canonical LDF analysis accounted for 94.2% of the total variability, and likelihood ratio tests indicated that only these first two canonical variables were significant ($P<0.0001$ for the first, $P<0.05$ for the second). The correlation structure suggested that high values of zooplankton biomass and deep occurrences of the depth of the 15°C isotherm were associated with positive values of the first canonical variable, whereas high values for depth and surface chlorophyll were associated with positive values of the second canonical variable (Fig. 6B). Although there seems to be considerable overlap between the Risso's dolphin, pantropical spotted dolphin, and *Kogia* spp. in the canonical space, the sperm whale is separated from the other species primarily along canonical axis 1 (Fig. 6B).

Bottlenose dolphin

Because the bottlenose dolphin was never encountered seaward of the 750-m isobath, only the surveyed transect sections shallower than 1000 m were used in the comparisons between the sightings and the effort. The distributions of this species with respect to depth, depth gradient, surface temperature, and surface temperature variability were significantly different from a uniform distribution (Table 5). Monte Carlo tests suggested that the distribution with respect to depth gradient may have been an artifact of the distribution with respect to depth ($P>0.05$; Table 5). The sighting rate distribution of the bottlenose dolphin with respect to depth (Fig. 7A) was bimodal as indicated by the peak in the sighting rate at the shallowest depth class (<75 m) and another peak just seaward of the shelf break. Although no coherent pattern was apparent in the sighting rate distribution with respect to surface temperature (Fig. 7B), group sighting rates

increased with increasing surface temperature variability (Fig. 7C).

Interpretation of the sighting rate distributions for surface temperature and surface temperature variability was confounded by this species' bimodal distribution with respect to depth. To address this, the sightings were separated into a shelf group (<150 m) and a shelf break group (>150 m) by using the local minimum in the sighting rates with respect to depth as the separation criterion (Fig. 7A). The shelf dolphins ($n=24$) were found in cooler surface waters in relation to that observed during the sighting effort (Mann-Whitney test, $U=2.23$, $P<0.05$), whereas the distribution of the shelf break dolphins ($n=33$) with respect to surface temperature was not significantly different from the effort (Mann-Whitney test, $U=1.03$, $P>0.05$; χ^2 test, $\chi^2=9.7$, $df=5$, $P>0.05$). Both the shelf ($n=16$, $U=3.23$, $P<0.01$) and shelf break bottlenose dolphins ($n=14$, $U=2.93$, $P<0.01$) were encountered in regions of significantly higher surface temperature variability in relation to the effort.

It should be noted that the bottlenose dolphin appears to have a distribution with respect to zooplankton biomass that is significantly different from the effort for all depths (Fig. 5G). In fact, a Mann-Whitney test supports this assertion ($U=5.42$, $P<0.0001$). Once the analysis is restricted to the continental shelf and upper continental slope (0–1000 m), however, the distribution of the bottlenose dolphin with respect to zooplankton biomass is not significantly different from the effort ($U=0.19$, $P>0.05$). This apparent discrepancy is due to higher zooplankton biomass over the continental shelf than anywhere else in the northern Gulf of Mexico.

Risso's dolphin

The distribution of the Risso's dolphin was significantly different from a uniform distribution for both depth and depth gradient (Table 5) and there was strong evidence

Table 5
Results for univariate χ^2 , Mann-Whitney, and Monte Carlo tests. Values of 0.0000 for P indicate $P < 0.0001$.

	n	χ^2 test			Mann-Whitney		Monte Carlo
		χ^2	df	P	U	P	P
Bottlenose dolphin							
Depth	89	57.6	11	0.0000**			—
Depth gradient	89	23.1	11	0.0174*			0.7474
Surface temperature	57	26.8	9	0.0015**			0.0224*
Surface temperature standard deviation	30	17.3	4	0.0017**			0.0018**
Depth of 15°C isotherm	39	6.0	6	0.4184			0.4909
Surface chlorophyll	57	12.2	9	0.1999			0.4095
Zooplankton biomass	40	1.9	6	0.9268			0.9720
Risso's dolphin							
Depth	67	53.9	12	0.0000**			—
Depth gradient	67	57.4	12	0.0000**			0.0000**
Surface temperature	39	9.9	6	0.1296			0.1527
Surface temperature standard deviation	14				1.69	0.0456*	
Depth of 15°C isotherm	52	16.3	9	0.0603			0.0971
Surface chlorophyll	49	9.2	8	0.3232			0.3227
Zooplankton biomass	44	7.3	7	0.3970			0.7056
<i>Kogia</i> spp.							
Depth	56	42.6	9	0.0000**			—
Depth gradient	56	20.4	9	0.0155*			0.0690
Surface temperature	28	4.8	4	0.3038			0.3540
Surface temperature standard deviation	18				1.98	0.0238*	
Depth of 15°C isotherm	47	7.2	8	0.5125			0.5371
Surface chlorophyll	46	3.4	7	0.8441			0.8560
Zooplankton biomass	35	31.6	5	0.0000**			0.0014**
Pantropical spotted dolphin							
Depth	107	50.6	11	0.0000**			—
Depth gradient	107	25.1	11	0.0088**			0.0687
Surface temperature	62	13.5	11	0.2614			0.3616
Surface temperature standard deviation	31	7.5	4	0.1096			0.1148
Depth of 15°C isotherm	99	19.1	11	0.0593			0.0748
Surface chlorophyll	102	20.6	11	0.0380*			0.0985
Zooplankton biomass	57	16.4	9	0.0588			0.3522
Sperm whale							
Depth	43	14.5	7	0.0431*			—
Depth gradient	43	13.7	7	0.0566			0.0965
Surface temperature	14				0.27	0.3921	
Surface temperature standard deviation	11				1.14	0.1268	
Depth of 15°C isotherm	34	11.0	5	0.0508			0.0388*
Surface chlorophyll	39	11.5	6	0.0741			0.0749
Zooplankton biomass	26	3.5	4	0.4729			0.7053

* indicates $P < 0.05$.

** indicates $P < 0.01$.

that the distribution with respect to depth gradient was not an artifact of the depth distribution ($P < 0.0001$). The distribution with respect to surface temperature variability was significantly different from the effort ($P < 0.05$; Table 5) and surface temperature variability at Risso's

dolphin sightings was generally higher than the effort (Fig. 5D). The sighting rate distribution with respect to depth was modal about the upper continental slope (Fig. 8A), whereas group sighting rates increased with increasing depth gradient (Fig. 8B).

Kogia spp.

The distributions of the *Kogia* spp. with respect to depth, depth gradient, and epipelagic zooplankton biomass were significantly different from a uniform distribution (Table 5); however, the distribution with respect to depth gradient may have been an artifact of the depth distribution ($P>0.05$; Table 5). The distribution with respect to surface temperature variability was significantly different from the effort ($P<0.05$; Table 5), and the median value of surface temperature variability for *Kogia* spp. was the highest of all the species examined (Fig. 5D). *Kogia* spp. had a modal distribution about the upper continental slope (Fig. 9A) and group sighting rates increased with increasing zooplankton biomass (Fig. 9B). A bivariate χ^2 analysis (after Baumgartner, 1997) indicated that the distribution of *Kogia* spp. was significantly different from a uniform distribution with respect to both depth and zooplankton biomass ($\chi^2=29.2$, $df=4$, $P<0.0001$) and that in waters of high zooplankton biomass over the upper continental slope, group sighting rates were 2.5 times the average.

Pantropical spotted dolphin

The distribution of the pantropical spotted dolphin was significantly different from a uniform distribution of depth, depth gradient, and surface chlorophyll (Table 5); however, the distributions with respect to depth gradient and surface chlorophyll may have been an artifact of the depth distribution ($P>0.05$; Table 5). This species was encountered only once near the shelf break (Fig. 10) and if the χ^2 analysis was limited to sightings and effort deeper than 500 m, then the depth distribution would not be significantly different from a uniform distribution ($\chi^2=14.5$, $df=11$, $P>0.05$).

Sperm whale

The distribution of the sperm whale with respect to depth was significantly different from a uniform distribution

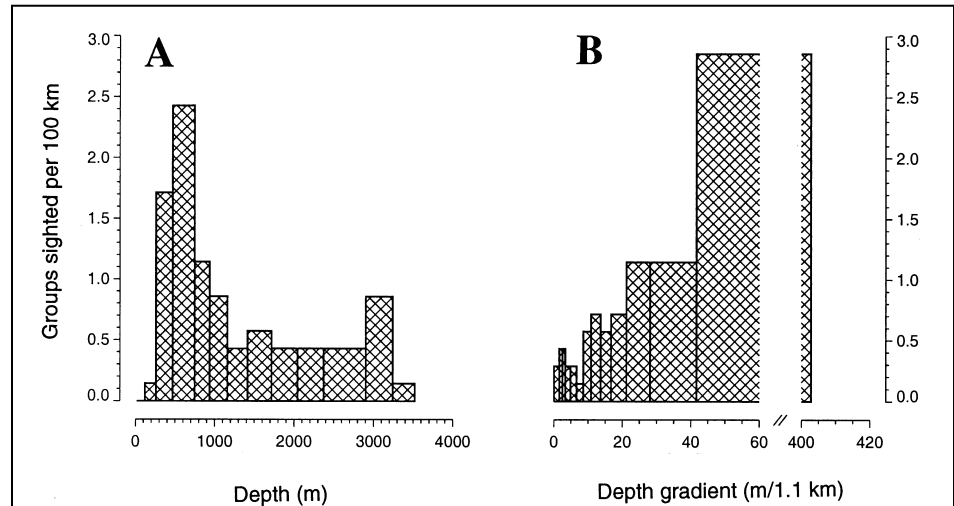


Figure 8

Sighting rate distributions of Risso's dolphins with respect to (A) depth and (B) depth gradient.

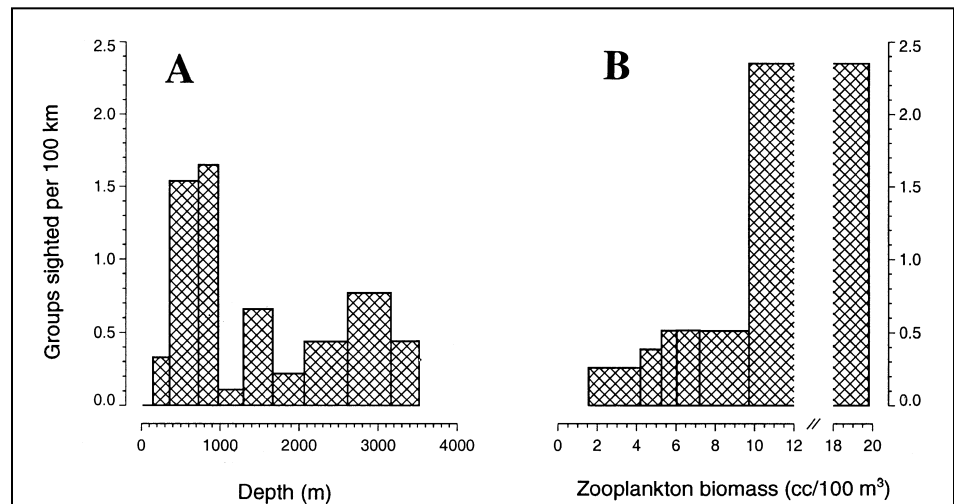


Figure 9

Sighting rate distributions of *Kogia* spp. with respect to (A) depth and (B) epipelagic zooplankton biomass.

(Table 5; Fig. 11A). Only one group of sperm whales was encountered near the shelf break and if the χ^2 analysis was limited to sightings and effort deeper than 500 m, then the depth distribution would not be significantly different from a uniform distribution ($\chi^2=2.2$, $df=7$, $P>0.05$). There is evidence to suggest that the distribution with respect to the depth of the 15°C isotherm was significantly different from a uniform distribution when the depth distribution is taken into consideration (Monte Carlo test, $P<0.05$; Table 5). In waters where the 15°C isotherm was deeper than 200 m, the group sighting rate of sperm

whales was less than a quarter of the average and was one-sixth the sighting rate in waters where the depth of the 15°C isotherm was shallower than 200 m (Fig. 11B)

Discussion

Previous studies have indicated that cetacean habitat within several hundred kilometers of the coast is most effectively partitioned by depth (Davis et al., 1998; CETAP⁵; Dohl et al.⁶; Dohl et al.⁷; Green et al.⁸; Davis et al.¹¹). In the northern Gulf of Mexico, each of the five species examined in our study could be distinguished from at least three of the others by its distribution with depth alone. Although the distributions of Risso's dolphin and the *Kogia* spp. with respect to depth overlapped on the upper continental slope, their distributions over the upper slope could be distinguished by using depth gradient and zooplankton biomass. The distributions of pantropical spotted dolphins and sperm whales with respect to depth were very similar over the continental slope and deep Gulf, but their distributions differed with respect to the depth of the 15°C isotherm. These results suggest that cetaceans partition the northern Gulf of Mexico according to each species' habitat preferences which are presumably based on different prey distributions. It is important to note that this partitioning does not necessarily imply spatial separation. Given the right conditions (e.g. waters 500–750 m deep over a steep section of the continental slope with high zooplankton biomass in the upper 200 m), many of these cetaceans could be encountered in the same area. Some of the environmental variables that are important descriptors of cetacean habitat (e.g. zooplankton biomass, depth of the 15°C isotherm, and surface temperature variability) vary over time, and therefore the locations and spatial extent of each species' habitat may vary over time as well.

Two regions of the northern Gulf of Mexico seem to be particularly important habitats for some of the more fre-

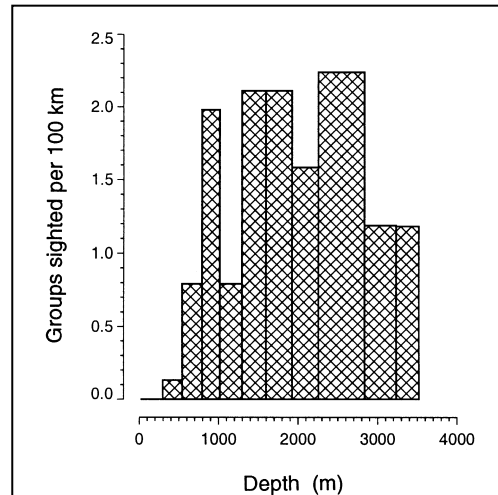


Figure 10
Sighting rate distribution of pantropical spotted dolphins with respect to depth.

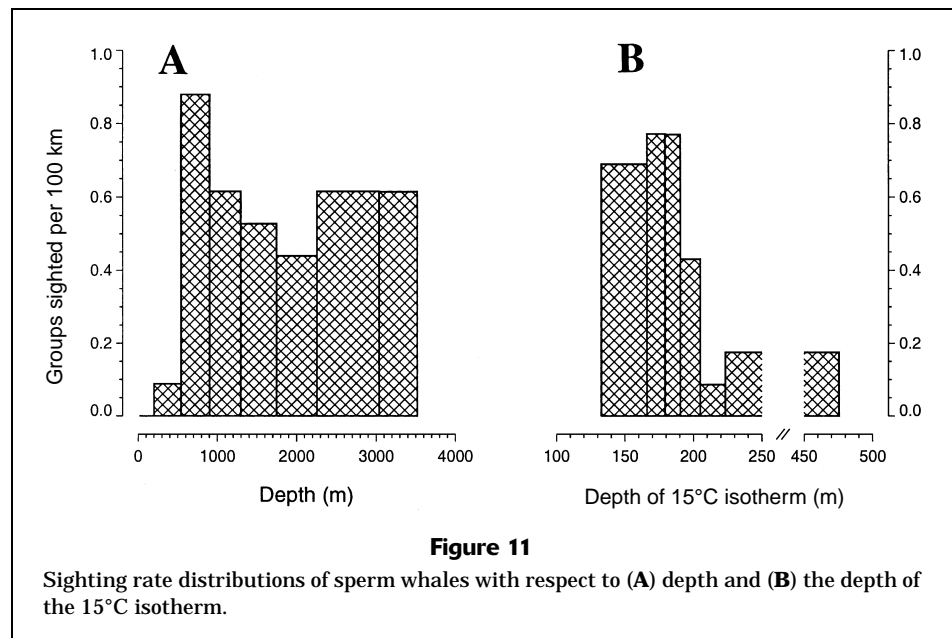


Figure 11
Sighting rate distributions of sperm whales with respect to (A) depth and (B) the depth of the 15°C isotherm.

quently encountered species during the spring (Fig. 4): the vicinity of the Mississippi River plume and just seaward of the southwestern Florida continental shelf. The Mississippi River injects nutrients into an otherwise oligotrophic oceanic Gulf in a region where the continental shelf is very narrow and the upper continental slope is quite steep. The rate of primary productivity and the standing stocks of chlorophyll and plankton associated with the nutrient-rich, fresh-water plume are high in relation to other regions in the oceanic Gulf (El-Sayed, 1972; Dagg et al., 1988; Ortner et al., 1989; Müller-Karger et al., 1991). Consequently, the plume region may provide feeding oppor-

¹¹ Davis, R. W., G. S. Fargion, W. E. Evans, L. N. May and T. D. Leming. 1996. Cetacean habitat. In Distribution and abundance of cetaceans in the north-central and western Gulf of Mexico: final report, vol. II: technical report (R. W. Davis and G. S. Fargion, eds.), p. 329–349. U.S. Department of the Interior, Minerals Management Service, OCS Study MMS 96-007. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

tunities for cetaceans through local trophic interactions. Likewise, the area west of the southwestern Florida shelf break may be another region of high productivity. The physical oceanography of this region is characterized by the formation of a cyclonic meander or eddy in the spring between the Loop Current to the west and the steep Florida Escarpment to the east (Cochrane, 1972; Vukovich et al., 1979; Vukovich and Maul, 1985). Maul et al. (1984) observed that bluefin tuna catch per unit of effort inside a cold-core meander in this region was three times higher than in the central Gulf the previous year. Between 83–86°W and 24–27°N in oceanic waters, the sighting rates of Risso's dolphins, pantropical spotted dolphins, and sperm whales were 3.8, 2.6, and 2.8 times higher than the average sighting rate and 4.9, 3.0, and 3.3 times higher than the sighting rate outside of this region, respectively.

Bottlenose dolphin

The bottlenose dolphin's distribution in the northern Gulf of Mexico is markedly different from the other species examined in our study. This species and the Atlantic spotted dolphin are the only cetaceans that are routinely encountered on the continental shelf (Fritts et al., 1983; Mullin et al., 1994; Jefferson and Schiro, 1997; Hansen et al.³). Caution is warranted when interpreting the bimodal distribution of bottlenose dolphin sighting rates with respect to depth (Fig. 7A). Effort on the continental shelf was neither extensive nor distributed uniformly throughout the northern Gulf. During the CETAP study (Kenney, 1990; CETAP⁵), a distinct bimodal distribution of bottlenose dolphins was observed north of Cape Hatteras. Bottlenose dolphins were concentrated during warm months in waters less than 25 m and year round near the 1000-m isobath and some groups were sighted in waters as deep as 4712 m (CETAP⁵). This bimodal distribution is suggestive of the inshore (coastal) and offshore forms of bottlenose dolphins described by others (Norris and Prescott, 1961; Walker, 1975; Leatherwood and Reeves, 1982; Shane et al., 1986; Kenney, 1990; Walker¹²) and supported by mitochondrial DNA (Dowling and Brown, 1993; Curry and Smith, 1997), hematological (Duffield et al., 1983; Hersh and Duffield, 1990), and morphological (Hersh and Duffield, 1990) evidence. The spatial distribution of bottlenose dolphin group sightings from aerial surveys on the continental shelf of the Gulf of Mexico (Blaylock et al., 1995) and off the southeast U.S. coast south of Cape Hatteras (Blaylock and Hoggard, 1994), however, was not characterized by any large-scale discontinuities in bottlenose dolphin distribution similar to those observed north of Cape Hatteras.

The shelf bottlenose dolphins were found in regions with cooler than expected surface waters and high surface tem-

perature variability. These oceanographic characteristics are consistent with the cool and fresh water side of fronts associated with river plumes and, indeed, sighting rates of the shelf bottlenose dolphins were particularly high near the Mississippi River Delta. Sighting rates of the shelf break bottlenose dolphins were more evenly distributed in the central and eastern Gulf and the high surface temperature variability observed near these dolphins suggests a potential association with shelf break fronts.

Risso's dolphin

Baumgartner (1997) examined the same 1992–94 spring cruise data used in our study with the intent of defining Risso's dolphin habitat in terms of the physiography of the northern Gulf of Mexico. Using both univariate and bivariate analyses, he determined that the sighting rate of Risso's dolphin groups between the 350- and 975-m isobaths and in depth gradients exceeding 24 m per 1.1 km was nearly 5 times the average. Of the groups encountered outside this region, 40% were sighted within 5 km of it. Aerial survey data collected during all seasons between 1992 and 1994 were used to independently assess this habitat model. Sighting rates from these surveys were nearly 6 times the average inside this core habitat, and of the groups encountered outside of this region, 73% were sighted within 5 km of it.

The distribution of Risso's dolphin along the continental slope has been noted in several studies (Würtz et al., 1992; CETAP⁵; Dohl et al.⁶; Dohl et al.⁷; Green et al.⁸; Davis et al.¹¹) and some evidence exists to support this species' association with the steeper sections of the upper continental slope elsewhere. Off the Oregon and Washington coasts, Green et al.⁸ observed that Risso's dolphin encounter rates over the continental slope (200–2000 m) were seven times greater than on the shelf and that the groups sighted on the shelf were very close to the shelf break. Compared with the northern Gulf of Mexico, almost the entire Oregon–Washington continental slope can be considered steep with depth gradients in excess of 22 m per 1.1 km (Fig. 11 in Green et al.⁸). Dohl et al.⁷ found a similar distribution off central and northern California, where the majority of Risso's dolphin sightings were between the 183- and 1830-m (100–1000 fathom) isobaths. As is the case off Oregon and Washington, virtually all of the continental slope off central and northern California can be considered very steep (Fig. 1 in Dohl et al.⁷). The physiography of the northwestern Atlantic Ocean is much more like that found in the northern Gulf of Mexico and the CETAP study (Hain et al., 1985; Kenney and Winn, 1986; CETAP⁵) found Risso's dolphins concentrated at the shelf break (mode of 478 sightings was 183 m depth) and distributed over the entire continental slope (average of 478 sightings was 1092 m).

Baumgartner (1997) hypothesized that Risso's dolphins aggregate along the upper continental slope because of the presence of a persistent ocean front separating the relatively cool and fresh waters of the continental shelf and the more warm and salty waters of the oceanic Gulf. This shelf break front may provide greater feeding opportuni-

¹² Walker, W. A. 1981. Geographical variation in morphology and biology of bottlenose dolphins (*Tursiops*) in the eastern North Pacific. Southwest Fisheries Center Administrative Report LJ-81-03C, 52 p. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.]

ties because of enhanced local productivity or because it forms a border between two separate, exploitable ecosystems. The observations of higher than expected surface temperature variability at Risso's dolphin sightings seem to support this hypothesis, but the evidence is rather tenuous given the small sample size ($n=14$).

Kogia spp.

Kogia spp. were predominantly encountered along the upper continental slope in regions with high epipelagic zooplankton biomass. Their distribution with respect to depth in the northern Gulf of Mexico is in agreement with inferences drawn from a stomach content study of stranded *Kogia* spp. in South Africa where cephalopods typical of the continental slope were identified as the largest constituent of the stranded whales' stomach contents.¹³ Further stomach content and stable isotope analyses suggest that pygmy and dwarf sperm whales consume different prey species and therefore may occupy different habitats.^{14,15} No such separation was detectable in our study because of the low sample size for the individual species and the difficulty of positively identifying each at sea. Some diet overlap was observed between the two species off South Africa¹⁴ and therefore the association between *Kogia* spp. and high epipelagic zooplankton biomass in the northern Gulf of Mexico may be due to the utilization of zooplankton in the diet of one or more of their common prey species.

Of all the cetaceans, *Kogia* spp. had the highest median value for surface temperature variability which suggests a similar association with ocean fronts as that observed for Risso's dolphins. Sample size for this variable was unfortunately low ($n=18$) however; therefore it is difficult to accurately describe this potential association. Because the upper continental slope can be a region of persistent frontal activity, it is conceivable that the distribution of both Risso's dolphins and *Kogia* spp. with respect to surface temperature variability may have been a consequence of their distribution with depth. The low sample sizes for each of these species precludes any analysis that may have been able to further support or refute these hypotheses.

Pantropical spotted dolphin

The distribution of the pantropical spotted dolphin was not significantly different from a uniform distribution with respect to any of the environmental variables, except depth. Pantropical spotted dolphins are rarely encountered on the continental shelf in the northern Gulf of Mexico (Jefferson and Schiro, 1997) and from the results

obtained in our study, are probably evenly distributed with depth over the continental slope and deep Gulf. These results were surprising in light of this species' spatial distribution in the northern Gulf of Mexico (Fig. 4). Local maxima in group encounter rates occurred southwest of Panama City and along the Florida Escarpment northwest of Key West. The coherent pattern in Figure 4 strongly suggests the existence of high-use areas for this species, but the characteristics that make these regions attractive to pantropical spotted dolphins were not observed in the chosen set of environmental variables used in our study. Davis et al.¹⁶ reported that oceanic stenellids (pantropical spotted dolphins, striped dolphins [*Stenella coeruleoalba*], spinner dolphins [*Stenella longirostris*], and Clymene dolphins [*Stenella clymene*]) were more frequently encountered in cyclonic, cold-core eddies and less frequently encountered in anticyclonic, warm-core eddies than expected based on the distribution of the GulfCet program sighting effort in the northern Gulf of Mexico. Although no such relationship was detected in our study, species grouping, confounding by other environmental or behavioral factors or temporal variability in habitat associations (or both) or prey availability could easily account for the apparent discrepancy between these two studies.

Sperm whale

Like the pantropical spotted dolphin, the sperm whale was never encountered on the continental shelf and appears to have a roughly even distribution with respect to depth over the continental slope and deep Gulf. The distributions of these two species with respect to the depth of the 15°C isotherm were significantly different, however, and the canonical LDF analysis suggested that this variable contributed to the separation between sperm whales and the other oceanic cetaceans (Fig. 6B). Sperm whales were encountered much less frequently in regions where the depth of the 15°C isotherm was quite deep (Fig. 11B), which suggests that this species avoids the interior of anticyclonic, warm-core features such as the Loop Current or warm-core mesoscale eddies. Waring et al. (1993) and Griffin (1999) described similar results from studies of sperm whale distributions in and around the periphery of warm-core eddies associated with the Gulf Stream in the north-west Atlantic Ocean. Davis et al.¹⁶ and Biggs et al. (2000) reported that sperm whales were not only encountered outside of anticyclonic features in the northeastern Gulf of Mexico, but most of the visual and acoustic contacts with

¹³ Klages, N. 2000. Personal commun. Port Elizabeth Museum at Bayworld, P.O. Box 13147, Humewood 6013, South Africa.

¹⁴ Plön, S. 2000. Personal commun. School of Biological Sciences, Thomas Building, Level 2, Univ. Auckland, Private Bag 92019, Auckland, New Zealand.

¹⁵ Barros, N. 2000. Personal commun. Center for Marine Mammal and Sea Turtle Research, Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL 34236-1096.

¹⁶ Davis, R. W., J. G. Ortega-Ortiz, C. A. Ribic, W. E. Evans, D. C. Biggs, P. H. Ressler, J. H. Wormuth, R. R. Leben, K. D. Mullin, and B. Würsig. 2000. Cetacean habitat in the northern Gulf of Mexico. In *Cetaceans, sea turtles and seabirds in the northern Gulf of Mexico: distribution, abundance and habitat associations*, vol. II: technical report (R. W. Davis, W. E. Evans, and B. Würsig, eds.), p. 217–253. U.S. Department of the Interior, Geological Survey, Biological Resources Division, USGS/BRD/CR-1999-0006 and Minerals Management Service, OCS Study MMS 2000-003. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

sperm whales during the GulfCet II focal cruises were in regions characterized by cyclonic mesoscale features.

Jaquet (1996) reviewed a variety of sperm whale habitat studies that seemed to have contradictory conclusions regarding the primary oceanographic processes influencing sperm whale distribution (namely upwelling and downwelling). Jaquet attributed these discrepancies to a problem of defining the appropriate spatial and temporal scales, and she and others illustrated this point by demonstrating a varying but positive correlation between historical sperm whale catches and surface chlorophyll over increasing temporal and spatial scales in the equatorial Pacific (Jaquet et al., 1996). These results seem to indicate that upwelling, which contributes to increased surface phytoplankton biomass, is a predominant factor in influencing sperm whale distribution in the equatorial Pacific. Historical catches in temperate waters, however, are not at all correlated with surface chlorophyll (see Fig. 1 of Jaquet, 1996 and Fig. 1 of Jaquet et al., 1996) which suggests that other oceanographic processes or physiographic influences may be important (e.g. downwelling or biological-physical processes associated with continental slopes). At comparatively short time scales and small spatial scales, we found no evidence to suggest a relationship between the distribution of sperm whales and surface chlorophyll in the northern Gulf of Mexico. Even at longer temporal and larger spatial scales, we would expect this same result because the oceanic Gulf is persistently oligotrophic both in time and space (Müller-Karger et al., 1991; Longhurst, 1998).

Berzin (1971) examined harvest records from the worldwide sperm whale fishery and suggested that sperm whale distribution was closely linked to processes that supported the meso- and bathypelagic food webs. Because sperm whales feed almost exclusively on mesopelagic or demersal cephalopods (Clarke, 1986, 1996), they probably aggregate in areas where these prey are abundant. These deep-water prey species are entirely dependent on the rain of organic matter from the surface for their sustenance and so these species will be found in regions where the export of detritus from the surface is enhanced. This process occurs in convergence zones where downwelling forces surface biomass and oxygen into the deep ocean, such as in the middle of anticyclonic eddies, at the peripheries of cyclonic eddies, to the right (left) of surface ocean currents in the northern (southern) hemisphere, in the middle of the large-scale anticyclonic ocean gyres (e.g. the Sargasso Sea), or along fronts where surface water masses abut. The global sperm whale distribution maps provided by Townsend (1935) and Berzin (1971) do indeed suggest that this species was frequently harvested in or near large-scale oceanic convergence zones, especially along the subtropical convergence zones and the Antarctic polar front.

The distribution of sperm whales in the northern Gulf of Mexico and northwestern Atlantic Ocean (Waring et al., 1993; Griffin, 1999) seems contradictory to Berzin's hypothesis, however. Features such as the Loop Current or warm-core eddies rotate anticyclonically and have convergent centers in which downwelling occurs. According to Berzin's hypothesis, the interior of these features would be favorable to sperm whales because of the enhanced export

of surface biomass to the deep ocean and the resultant increase in prey species. The interior of anticyclonic eddies in the northern Gulf of Mexico are, however, low in surface zooplankton biomass (Biggs, 1992). Although the rate of detrital export to the deep is enhanced by increased vertical velocities within these features, the amount of biomass actually exported may be too small to support large populations of deep-water prey.

Another possible explanation for the distribution of sperm whales with respect to the depth of the 15°C isotherm is related to the availability of prey. Berzin (1971) characterized cephalopods as thermophilic and thus indicated that they are distributed within a narrow range of ocean temperatures according to their species-specific thermal requirements or to the thermal requirements of their prey. These requirements not only govern the horizontal distribution of cephalopods, but their vertical distribution as well. Because warm-core features are characterized by depressed isotherms (e.g. Fig. 3), cephalopods within these features may be hundreds of meters deeper in the water column than in the waters outside these features. Despite their well-known ability to dive to great depths, foraging continuously at greater depths under warm-core features would be much more energetically expensive than foraging outside these features. Thus, when prey abundance inside and outside of warm-core eddies are equivalent, sperm whales may feed on prey distributed at shallower depths outside of these features to reduce their energy expenditure.

Caveats

It is important to remember that this study was limited to surveys conducted during the spring season. The spatial distribution of cetaceans may be different in other seasons because the oceanographic conditions of the northern Gulf of Mexico change over the course of the year. The northward penetration of the Loop Current into the Gulf varies on a quasi-annual basis (Vukovich et al., 1979; Sturges and Evans, 1983; Vukovich, 1995) and the variability in the position of the Loop Current affects the generation and positions of both anticyclonic and cyclonic eddies. This variability may, in turn, greatly influence the productivity and availability of prey species in the eastern Gulf of Mexico. In the northwestern Gulf, the slow march of warm-core eddies from east to west toward the "eddy graveyard" over the continental slope also varies with time and may affect the seasonal distribution of cetaceans. Hansen et al.³ observed seasonal differences in cetacean abundance in the western and central regions of the northern Gulf of Mexico that may have been influenced by temporal changes in the local oceanography.

Another potential limitation of our study was the rather coarse environmental sampling. Although the CTD/XBT sampling strategy was sufficient to identify the large-scale oceanographic features, some of the most biologically significant processes in the oceanic Gulf of Mexico occur on smaller spatial scales. In particular, the outer edge of the Loop Current is frequently a site of upwelling and these divergent features often develop into cyclonic meanders

and eddies at the northern and eastern sides of the Loop Current (Vukovich and Maul, 1985). These cyclonic features are usually much smaller than the Loop Current itself or the warm-core features of the central and western Gulf (Cochrane, 1972). Along the latitude of 27°N and within 40 km of the Loop Current (near 88.8°W) in late spring, 1993, for instance, the satellite-borne AVHRR detected surface temperatures 1.5°C cooler than the Loop Current itself, but the vertical temperature structure, surface chlorophyll and zooplankton biomass associated with this narrow feature were not captured because of the coarse sampling strategy (Figs. 2 and 3). The recent GulfCet II program (Davis et al.¹⁰) examined cetacean habitat associations in the vicinity of cyclonic-anticyclonic eddy pairs in the northeastern Gulf of Mexico and demonstrated that these mesoscale hydrographic features can indeed influence cetacean distribution. In addition to the cyclonic features associated with the Loop Current, the CTD and XBT sampling strategy of our study did not resolve other potentially productive features that occur on smaller spatial scales, such as nutrient-rich Mississippi River plume waters entrained at the edge of the Loop Current (Maul, 1977; Müller-Karger et al., 1991) and shelf break fronts.

Future studies of cetacean habitats in the Gulf of Mexico should continue to consider these smaller scale features as potential sites of large cetacean aggregations because of their high levels of biological activity. These features could potentially 1) have high rates of primary productivity that is converted into prey biomass over short temporal and spatial scales, 2) concentrate prey through solely physical mechanisms or through physical-biological interactions or 3) make local prey more accessible to surface-bound cetaceans. Although investigating these processes is undoubtedly a challenge, it is important to elucidate what processes affect cetacean distribution and at what spatial and temporal scales these processes operate if we are to understand how oceanographic conditions affect cetacean ecology.

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