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Cetacean habitat in the northern oceanic Gulf of Mexico

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Abstract

Cetaceans (whales and dolphins) are diverse and abundant upper trophic level predators in the Gulf of Mexico, a semi-enclosed, intercontinental sea with a total area of about 1.5 million km². The objectives of this study were to better define the habitat of cetaceans in the northern oceanic Gulf of Mexico. An integrated methodology was used that included visual surveys and hydrographic collections from ships. Near real-time sea surface altimetry from the TOPEX/POSEIDON and ERS satellites was used during ship surveys to determine the location of hydrographic features (e.g., cyclones, anticyclones and confluence zones). Archival satellite sea surface altimetry data were also used to retrospectively determine the location of hydrographic features for analysis with earlier cetacean sightings. We estimated zooplankton and micronekton biomass using both net and acoustic sampling to indicate the amount of potential food available for higher trophic level foraging by cetaceans. Nineteen cetacean species were identified during ship surveys. Cetaceans were concentrated along the continental slope in or near cyclones and the confluence of cyclone–anticyclone eddy pairs, mesoscale features with locally concentrated zooplankton and micronekton stocks that appear to develop in response to increased nutrient-rich water and primary production in the mixed layer. A significant relationship existed between integrated zooplankton biomass and integrated cephalopod paralarvae numbers, indicating that higher zooplankton and micronekton biomass may correlate with higher concentrations of cetacean prey. In the north-central Gulf, an additional factor affecting cetacean distribution may be the narrow continental shelf south of the Mississippi River delta. Low salinity, nutrient-rich water may occur over the continental slope near the mouth of the Mississippi (MOM) River or be entrained within the confluence of a cyclone–anticyclone eddy pair and transported beyond the continental slope. This creates a deep-water environment with locally enhanced primary and secondary productivity and may explain the presence of a resident, breeding population of sperm whales within 100 km of the Mississippi River delta. Overall, the results suggest that the amount of potential prey for cetaceans may be consistently greater in the cyclone, confluence areas, and south of the MOM, making them preferential areas for foraging. However, this may not be true for bottlenose dolphins, Atlantic spotted dolphins and possibly Bryde's whales,

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which typically occur on the continental shelf or along the shelf break outside of major influences of eddies. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The Gulf of Mexico is a dynamic body of water dominated by two major circulation features (Fig. 1). The Loop Current, formed by the interconnection of the Yucatan and Florida Currents, governs the circulation of the eastern (east of the ca. 87.5°W longitude) Gulf. In the central (ca. 87.5–94.0°W longitude) and western (ca. west of 94.0°W longitude) Gulf, anticyclonic (warm-core) eddies and their associated cyclonic

(cold-core) eddies are the primary circulatory features. The Loop Current periodically penetrates deep into the eastern Gulf and sheds large anticyclonic eddies. Satellite altimeter data from the TOPEX/POSEIDON and ERS satellites have been used to map the sea surface topography in the Gulf and monitor the eddy shedding process (Sturges and Leben, 2000). After separation from the Loop Current, the anticyclonic eddies drift westward until their progress is eventually constrained by shoaling topography over the

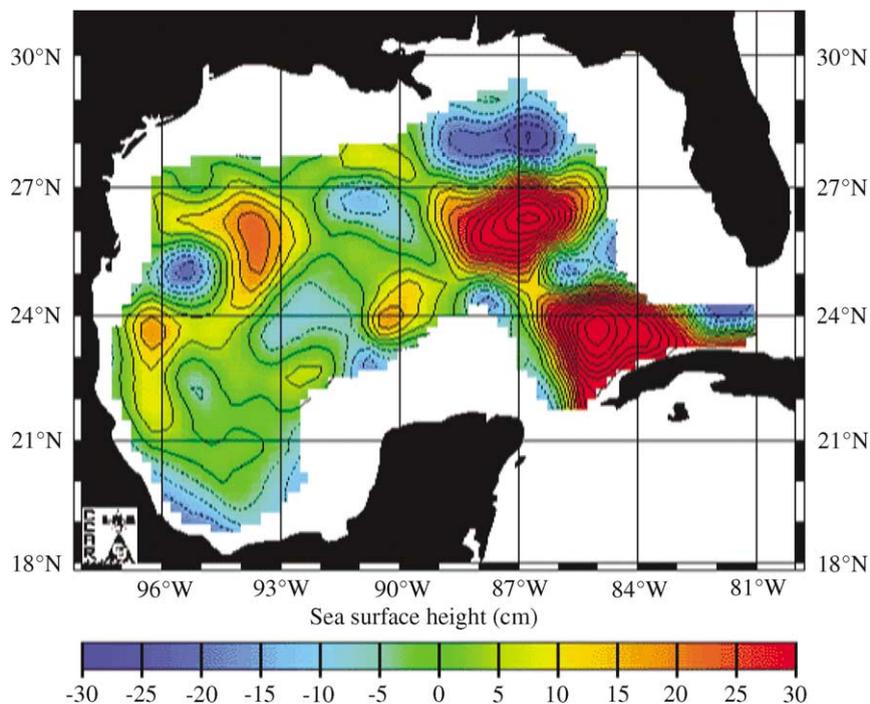


Fig. 1. Contour map of the SSH for the Gulf of Mexico showing major hydrographic features of the region. Data were collected by altimeters aboard the TOPEX/POSEIDON and ERS-2 satellites and used to objectively map the height field for August 1, 1997. The northward penetration of the Loop Current (red) into the eastern Gulf has resulted in the separation of an anticyclone (warm-core eddy), identified by the large region of closed contours in red around a high in the SSH. Cyclonic, cold-core eddies (blue) are lows in the SSH and visible on the periphery of the anticyclone. The eddy field in the western gulf is made up of anticyclones and companion cyclones that are remnants of an older Loop Current eddy interacting with the continental slope along the Texas and Mexican coasts. Data for ocean depths less than 200 m have been masked.

northwestern continental slope of the Gulf. They remain in this region, coalescing with existing or approaching eddies until ultimately dissipating. The general circulation in the Gulf is dominated by the currents associated with the Loop Current and these large anticyclonic eddies.

The dynamics of the Gulf are made more complex by the large fresh water inflow. Nearly two-thirds of the U.S. mainland and half the area of Mexico drain into the Gulf. The Mississippi River discharges into the northern Gulf through the Balize and Atchafalaya delta regions. Approximately 30% of the Mississippi River enters the northern Gulf through the Atchafalaya, and the remaining 70% goes through the Balize bird-foot delta. The Mississippi and other rivers with their associated pollutants, nutrients, and sediment loads have a great impact on all aspects of continental shelf oceanography in the northern Gulf. The input of nutrients ensures high phytoplankton production and thus higher zooplankton productivity (Lohrenz et al., 1990; Biggs, 1992). Twenty-eight percent of the total U.S. commercial fish catch is from the Louisiana/Texas shelf (Walker and Rouse, 1993). Spawning of key fish species, such as Gulf menhaden (*Brevoortia patronus*), is also concentrated around the Mississippi delta. River discharge into the Gulf is distinctly seasonal, with the highest flow occurring from March through May, and the lowest flow occurring from August through October. Wind forcing and shelf currents are major factors controlling the distribution of Mississippi River outflow onto the continental shelf. Loop Current eddies and filaments provide the major control of plume circulation over the continental slope and into the northern oceanic Gulf. The fresh water of the Mississippi River affects the spatial and temporal distribution of areas of higher primary and secondary production.

Until recently, relatively little was known about cetaceans inhabiting deeper waters of the Gulf of Mexico. The most extensive survey of cetaceans in the offshore waters (100–2000 m deep) of the northern Gulf of Mexico was conducted jointly by National Marine Fisheries Service, Southeast Fisheries Science Center and Texas A&M University from 1992–98 and called the GulfCet I and

GulfCet II Programs (Jefferson, 1995; Davis and Fargion, 1996; Baumgartner, 1997; Jefferson and Schiro, 1997; Davis et al., 1998, 2000; Würsig et al., 2000). This six-year, two-part study provided synoptic information on the distribution and abundance of cetaceans using both visual and acoustic survey techniques. Twenty-eight cetacean species are known to occur in the northern Gulf of Mexico (Table 1). Pantropical spotted dolphins

Table 1
Cetaceans of the Gulf of Mexico

Balaenidae	
Northern right whale	<i>Balaena glacialis</i>
Balaenopteridae	
Blue whale	<i>Balaenoptera musculus</i>
Fin whale	<i>Balaenoptera physalus</i>
Sei whale	<i>Balaenoptera borealis</i>
Bryde's whale (S) ^a	<i>Balaenoptera edeni</i>
Minke whale	<i>Balaenoptera acutorostrata</i>
Humpback whale	<i>Megaptera novaeangliae</i>
Physeteridae	
Sperm whale (S)	<i>Physeter macrocephalus</i>
Kogiidae	
Pygmy sperm whale (S)	<i>Kogia breviceps</i>
Dwarf sperm whale (S)	<i>Kogia sima</i>
Ziphiidae	
Cuvier's beaked whale (S)	<i>Ziphius cavirostris</i>
Blainville's beaked whale	<i>Mesoplodon densirostris</i>
Sowerby's beaked whale	<i>Mesoplodon bidens</i>
Gervais' beaked whale	<i>Mesoplodon europaeus</i>
Delphinidae	
Melon-headed whale (S)	<i>Peponocephala electra</i>
Pygmy killer whale (S)	<i>Feresa attenuata</i>
False killer whale (S)	<i>Pseudorca crassidens</i>
Killer whale (S)	<i>Orcinus orca</i>
Short-finned pilot whale (S)	<i>Globicephala macrorhynchus</i>
Rough-toothed dolphin (S)	<i>Steno bredanensis</i>
Fraser's dolphin (S)	<i>Lagenodelphis hosei</i>
Bottlenose dolphin (S)	<i>Tursiops truncatus</i>
Risso's dolphin (S)	<i>Grampus griseus</i>
Atlantic spotted dolphin (S)	<i>Stenella frontalis</i>
Pantropical spotted dolphin (S)	<i>Stenella attenuata</i>
Striped dolphin (S)	<i>Stenella coeruleoalba</i>
Spinner dolphin (S)	<i>Stenella longirostris</i>
Clymene dolphin (S)	<i>Stenella clymene</i>

^a The (S) next to the common name indicates species that were sighted during this study.

are the most abundant species with a minimum estimate of 46,625 animals followed by 11,251 spinner dolphins and 10,093 Clymene dolphins (Davis et al., 2000). Minimum estimates for bottlenose dolphins, striped dolphins, melon-headed whales, Atlantic spotted dolphins, Risso's dolphins, and short-finned pilot whales ranged from 5618 to 1471. Minimum abundances of all other species were less than 900.

There are many factors that may influence the spatial and temporal distribution of cetaceans. These factors include physiographic and hydrographic characteristics, prey distribution, breeding and calving areas, and predation. Anthropogenic factors such as ship activity, oil and gas production, and seismic exploration (Richardson et al., 1995) may also influence whale and dolphin distribution. Previous studies have demonstrated correlations of cetacean distribution with physiographic features such as ocean depth and seafloor slope (Evans, 1975; Hui, 1979, 1985; Selzer and Payne, 1988; Sutcliffe and Brodie, 1977; Payne et al., 1986; Whitehead et al., 1992; Jaquet and Whitehead, 1996; Baumgartner, 1997; Davis et al., 1998). Some studies have also demonstrated correlations between cetacean distribution and hydrographic characteristics that may secondarily affect prey availability (Reilly, 1990; Reilly and Thayer, 1990; Waring et al., 1993; Reilly and Fielder, 1994; Jaquet et al., 1996; Jaquet and Whitehead, 1996; Croll et al., 1998; Fiedler et al., 1998; Tynan, 1997; Goold, 1998; Griffin, 1999). During an earlier study, we were unable to correlate cetacean distribution with hydrographic variables in the northern Gulf of Mexico (Davis and Fargion, 1996; Davis et al., 1998). This may have resulted from: (1) the small number of cetacean sightings with simultaneous hydrographic data, (2) the dynamic hydrography of the Gulf with periodic intrusion of the Loop Current and the formation of anticyclones and cyclones that move across the northern Gulf and (3) factors other than hydrographic features that influence the wide-ranging movements of cetaceans. Physiographic and hydrographic features alone may not fully explain cetacean distribution. Instead, the distribution of cetaceans may be better explained by prey availability,

which is secondarily influenced by hydrographic features.

The objective of this study was to characterize cetacean habitat in the northern oceanic Gulf of Mexico. Correlation of environmental features and zooplankton biomass with sighting data may improve our understanding of cetacean ecology and indicate which, if any, physical and biological oceanographic variables influence cetacean distribution. During two cruises, we conducted visual cetacean surveys and simultaneously collected data on the marine environment and zooplankton biomass in the northeastern oceanic Gulf. Cetacean-habitat associations were statistically analyzed for six physical and biological oceanographic variables. In addition, we retrospectively analyzed satellite remote sensing data for sea surface height (SSH) anomaly and shipboard cetacean sightings from an earlier study (GulfCet I) to examine the relationship between cetacean distribution and hydrographic features for the entire oceanic northern Gulf. We hypothesized that hydrographic features in the study area had different levels of potential prey that influence cetacean distribution. We further hypothesized that these food stocks would be locally concentrated in nutrient-rich areas offshore from the Mississippi River, within cyclonic eddies, and along the high-shear edges of cyclonic eddies.

2. Methods

2.1. Cruise data

This study was part of a larger project (GulfCet II) designed to determine the distribution, minimum abundances and habitat associations of cetaceans in the northern Gulf of Mexico (Davis et al., 2000). To determine the relationship between cetacean distribution and habitat characteristics, two dedicated cruises aboard the R/V *Gyre* were conducted in the eastern Gulf of Mexico in late summer of 1996 and mid-summer of 1997 (Table 2, Fig. 2). Simultaneous data were collected on cetacean distribution and zooplankton biomass. In addition, the *Gyre* received near real-time plots from the Colorado Center for Astrody-

Table 2

Cruises used in the cetacean habitat analysis^a

	Vessel	Survey no.	Season	Project	Start date	End date
NMFS	<i>Oregon II</i>	199	Spring 92	GulfCet I	4/22/92	6/7/92
NMFS	<i>Oregon II</i>	203	Winter 93	GulfCet I	1/6/93	2/12/93
NMFS	<i>Oregon II</i>	204	Spring 93	GulfCet I	5/4/93	5/28/93
TAMU	<i>Longhorn</i>	1	Spring 92	GulfCet I	4/14/92	4/30/92
TAMU	<i>Pelican</i>	2	Summer 92	GulfCet I	8/10/92	8/24/92
TAMU	<i>Pelican</i>	3	Fall 92	GulfCet I	11/8/92	11/21/92
TAMU	<i>Pelican</i>	4	Winter 93	GulfCet I	2/12/93	2/25/93
TAMU	<i>Pelican</i>	5	Spring 93	GulfCet I	5/24/93	6/4/93
TAMU	<i>Pelican</i>	6	Summer 93	GulfCet I	8/27/93	9/7/93
TAMU	<i>Pelican</i>	7	Winter 93	GulfCet I	12/4/93	12/14/93
NMFS	<i>Oregon II</i>	220	Spring 96 and Early Summer	GulfCet II	4/16/96	6/9/96
NMFS	<i>Oregon II</i>	225	Spring 97 and Early Summer	GulfCet II	4/16/97	6/10/97
TAMU	<i>Gyre</i>	Gyre96G06	Late Summer 96	GulfCet II	10/11/96	10/29/96
TAMU	<i>Gyre</i>	Gyre97G08	Summer 97	GulfCet II	8/6/97	8/20/97

^a NMFS = National Marine Fisheries Service, Southeast Fisheries Science Center, TAMU = Texas A&M University.

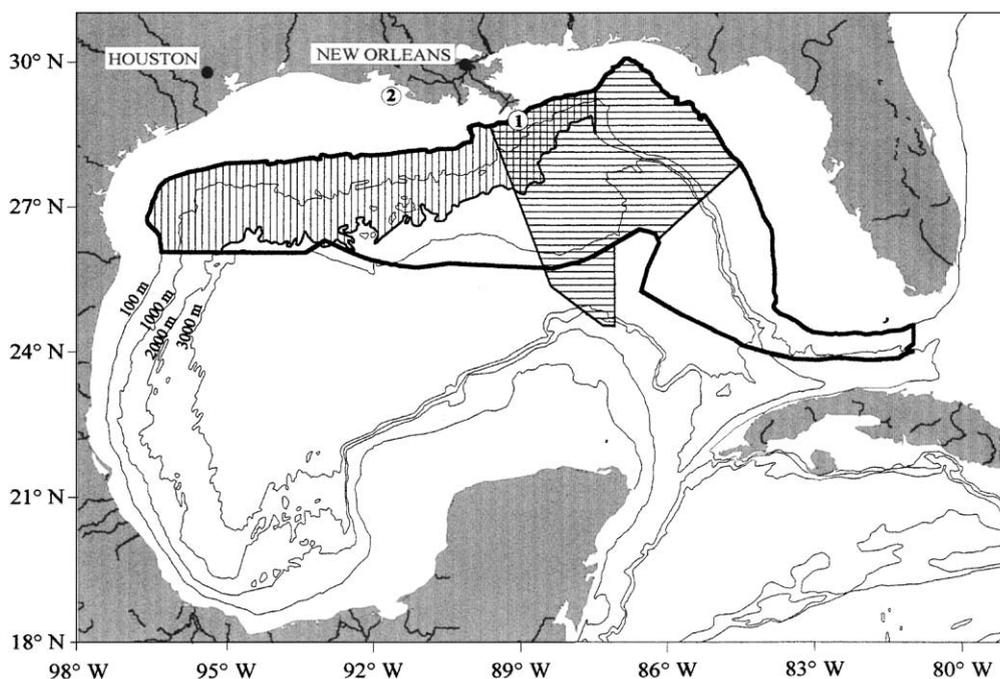


Fig. 2. The U.S. oceanic northern Gulf of Mexico (bold line; 396,960 km²), GulfCet I study area (vertical line pattern; 154,621 km²), GulfCet II Gyre cruises Gyre96G06 and Gyre97G08 study area (horizontal line pattern), Mississippi River Balize delta region (1) and Atchafalaya Bay (2).

namics Research of SSH anomaly, which identified hydrographic features such as anticyclones and cyclones. This enabled us to direct the ship's course into features that may have directly

influenced the distribution of cetaceans or their prey. In this way we attempted to sample within both cyclonic and anticyclonic eddies, and along the high-shear edges of the eddies.

In addition to the two dedicated cruises described above, we used cetacean sighting data from 10 previous cruises in the north-central and western Gulf of Mexico collected from 1992–94 during the GulfCet I Program (Davis and Fargion, 1996; Davis et al., 1998) (Table 2, Fig. 2). These sighting data were combined with similar data collected during two additional GulfCet II cruises (1996–97) conducted by the R/V *Oregon II* in the northern oceanic Gulf (Table 2, Fig. 2). Data from the GulfCet I study have been analyzed previously for cetacean-habitat associations using bathymetric and shipboard hydrographic data (Davis and Fargion, 1996; Davis et al., 1998). For the current analysis, we retrospectively determined SSH anomaly from satellite remote sensing data for GulfCet I cetacean sightings and combined these data with comparable GulfCet II data (all four cruises) for the eastern and northern oceanic Gulf. This large data set from 14 cruises (Table 2) was analyzed for correlations between cetacean distribution, hydrographic features (based on satellite remote sensing of SSH anomaly), ocean depth and seafloor slope.

2.2. Cetacean sightings

During all 14 cruises, line transect data were collected by two teams of three observers during daylight hours, weather permitting (i.e., no rain, Beaufort sea state <4) using standard vessel survey data collection methods for cetaceans (Buckland et al., 1993; Davis et al., 2000). Each team had at least two members experienced in shipboard cetacean observation and identification techniques. Two observers searched for cetaceans using 25 × 150 binoculars mounted on the ship's flying bridge. The third observer maintained a search of the area near the ship using unaided eye or 7 × 50 hand-held binoculars, and recorded data. The observers rotated through each of these three stations every 30–40 min, and each team alternated 2-h watches while there was daylight. The vessel speed was usually 15–18 km/h but varied with sea conditions. Sighting effort was interrupted to approach a group of animals to confirm identification, or by weather conditions. On-effort transect

segments located within a range of 5 km from each other were considered as the same segment. Cetaceans were identified to the lowest taxonomic level possible based on descriptions in field guides and scientific literature (e.g., Leatherwood and Reeves, 1983; Perrin et al., 1987; Jefferson et al., 1993). The ability to identify animals was dependent on water clarity, sea state and the animals' behavior.

2.3. Hydrography and satellite remote sensing of sea surface height anomaly

Hydrographic data collection during the late and mid-summer *Gyre* cruises (Table 2) is described in Biggs et al. (2000) and Davis et al. (2000). Briefly, dynamic SSH anomaly (DHA), mixed layer depth (MLD) and 15°C depth were determined from closely spaced (ca. 18 km) conductivity-temperature-depth (CTD) and expendable bathythermograph (XBT) stations. The *Gyre* was equipped with a through-the-hull pumped seawater system. Sea surface temperature (SST) and conductivity (salinity) were measured with Sea-Bird Electronics Corporation in-line sensors, and fluorescence (a measure of chlorophyll concentration) was measured with an in-line Turner Designs model 10 fluorometer. Sensor data were logged every 2 min (distance between data points varied depending on speed; the average distance was 0.4 km) with the ship's Serial ASCII Interface Loop (SAIL) system.

Hydrographic features for all 14 shipboard surveys were characterized using coincident altimetry from the TOPEX/POSEIDON and ERS-1&2 satellites. Daily fields of SSH topography on a $\frac{1}{2}$ degree grid were estimated by adding the height anomaly fields, interpolated from the available along-track altimeter data, to a model mean surface. To quantify the relationship between sightings and the remotely sensed physical environment, the SSH anomaly was computed for each sighting location from the gridded height fields.

Ocean depths for cetacean sightings were determined from the Global Relief Data (National Geophysical Data Center, NOAA), a matrix with a resolution of 9.26 km. Ocean depth gradient was

calculated for each point in the bathymetric database to produce a seafloor slope in units of meters per km.

2.4. Acoustically estimated mean biomass (EMB) of zooplankton in the MLD

A 153 kHz narrow-band Rowe Deines Instruments (RDI) Acoustic Doppler Current Profiler (ADCP) mounted on the *Gyre* was used to collect acoustic backscatter (S_v) data throughout (i.e., day and night) the late summer and mid-summer *Gyre* cruises only in the eastern Gulf of Mexico (see Davis et al., 2000; Wormuth et al., 2000 for details). Acoustic data were used to estimate zooplankton and micronekton biomass in the water column. Biomass estimations were based on empirical calibration of the acoustic signal from the ADCP with samples of zooplankton and micronekton collected with a Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS; 1 m² mouth area and 333 μm mesh) (Flagg and Smith, 1989; Zhou et al., 1994; Ashjian et al., 1994; Ressler et al., 1998; Zimmerman and Biggs, 1999). For each MOCNESS tow, the mean S_v measured at a given depth during the tow was matched with the measured displacement volume biomass from the corresponding depth-discrete net sample. Linear regression of the log₁₀ of MOCNESS displacement volume biomass (cm³ m⁻³) as a function of mean S_v (in dB re m⁻¹ 4π⁻¹) was used as a first-order empirical model of estimated mean biomass (EMB; cm³ m⁻³). The EMB values (based on S_v data averaged every 300 s) had a horizontal resolution of 0.3–1.5 km, depending on ship speed, and a vertical resolution of 4 m. Depth discrete EMB estimates were vertically integrated from 10 to 50 m to give a summary EMB value (cm³ m⁻²) within the MLD. The MOCNESS samples were sorted for paralarval cephalopods and myctophids, and the numbers per square meter of sea surface were calculated. Cephalopod paralarvae were used as an indirect assessment of adult cephalopods (which are an important cetacean prey item) because the latter evade capture by nets.

2.5. Statistical methods

2.5.1. Cetacean categories

Cetaceans observed during this study were divided into four subgroups based on the following criteria: large body size and deep diving ability (sperm whales), intermediate body size and dietary preference for squid (squid-eaters), phylogenetic relationship and occurrence in deep water (>200 m) habitats (oceanic stenellids), or preference for shallow water (<200 m) habitats (bottlenose and Atlantic spotted dolphin). Some species could belong to more than one category. For example, sperm whales and the oceanic stenellids (pantropical spotted dolphin, spinner dolphin, Clymene dolphin and striped dolphin) are also squid-eaters (Perrin et al., 1973; Clarke, 1996; Ridgway and Harrison, 1994). Nevertheless, grouping was necessary to reduce the number of species and increase the sample size for statistical analysis. Cetacean sightings were grouped as follows:

1. Cetaceans (all species identified).
2. Sperm whales.
3. Squid-eaters (except for sperm whales). Dwarf and pygmy sperm whales, false killer whales, melon-headed whales, pilot whales, pygmy killer whales, Risso's dolphins, rough-toothed dolphins and all the members of the Family Ziphiidae.
4. Oceanic stenellids. Oceanic dolphins from the genus *Stenella*: Clymene dolphins, pantropical spotted dolphins, spinner dolphins and striped dolphins.
5. Bottlenose dolphins and Atlantic spotted dolphins.

2.5.2. GulfCet II data for the eastern Gulf of Mexico

For the late and mid-summer *Gyre* cruises (Fig. 2), where multiple environmental variables were collected, the presence of cetacean categories was modeled with logistic regression for each cruise (Hosmer and Lemeshow, 1989). The environmental variables used for all but cetacean category 5 analyses were bottom depth (m), bottom depth gradient (m km⁻¹), sea surface salinity (SSS, practical salinity scale), dynamic

SSH anomaly (DHA, dyn cm), surface chlorophyll concentration ($\mu\text{g l}^{-1}$), and EMB ($\text{cm}^3 \text{m}^{-2}$). Bottom depth and bottom depth gradient only were used in the cetacean category 5 analysis. The SST was not used in the analysis because of the almost uniformly warm surface water in the Gulf during the summer. Cetacean survey transects were divided into 18.5 km-long (10 nautical miles) segments. If a segment of on-effort transect were less than 9.25 km, it was added to the previous segment. If it were greater than 9.25 km, it was treated as a separate segment. A total of 335 transect segments were obtained. The occurrence of cetacean sightings and the value of environmental variables at the closest hydrographic station were determined for each segment. For all but cetacean category 5, segments located in water deeper than 800 m, which had values for all environmental variables, were used in the analysis. Cetacean category 5 used all transects regardless of depth. Step-wise logistic regression was run using S-plus 4.5 software (Mathsoft, 1997). A summary of our observations on sperm whale-habitat has been previously reported (Biggs et al., 2000).

2.5.3. *GulfCet I and II data for the oceanic northern Gulf of Mexico*

For all 14 cruises in the oceanic northern Gulf of Mexico (Table 2), the occurrence (presence/absence) of cetacean species or species groups was compared to ocean depth and hydrographic features. The oceanic northern Gulf was divided into four ocean depth categories: continental shelf (<200 m), upper continental slope (200–1000 m), lower continental slope (1000–2000 m), and abyssal region (>2000 m). The study area was also divided into four hydrographic features based on DHA for GulfCet II data and SSH anomaly for GulfCet I data. The four features were: (1) anticyclone; (2) cyclone; (3) confluence; and (4) other. Criteria to delineate hydrographic features varied for each cruise. For GulfCet I *Pelican* and *Longhorn* cruises in the north-central and western Gulf (Table 2), SSH anomaly ≥ 10 cm was considered an anticyclone; SSH anomaly < -10 cm was considered a cyclone. The SSH anomaly < 10 and > -10 cm was classified as “confluence” or “other” depending on its location

relative to a cyclone–anticyclone pair. For the GulfCet I *Oregon II* cruises, hydrographic features were determined using SSH anomaly as well as depth of the 15°C isotherm obtained from CTD and XBT casts. This was necessary because some of these surveys were conducted in the northeastern Gulf, where SSH anomaly was not as accurate as it is in the north-central and western Gulf. This reflects the fact that the Loop Current is temporally persistent but spatially variable in the location of its northern perimeter, which makes it difficult to establish a spatially accurate, model mean surface for the evaluation of SSH anomaly data from the northeastern Gulf.

Hydrographic features for GulfCet II *Gyre* cruises were determined using DHA. For the 1996 late summer cruise, a cyclone was classified as any area with DHA 0 to -12 cm. An area with DHA 25–50 cm was classified as an anticyclone. An area of confluence (0–22 cm) occurred between cyclone and anticyclone pairs (from 26.2°N to 26.6°N and 86.5°W to 87.5°W). For the 1997 mid-summer *Gyre* cruise, a cyclone was defined as 0 to -13 cm and an anticyclone as 25–71 cm. A confluence area (0–24 cm) was observed from 26.9°N to 27.9°N and 86.3°W to 87.8°W. For the GulfCet II *Oregon II* cruises, we used SSH anomaly as described in the paragraph above to delineate the four hydrographic features, because very few deep water (>800 m) CTD and XBT data were available.

Occurrence of sightings from each cetacean category, ocean depth region and hydrographic feature were determined for all transect segments. The resulting contingency tables were analyzed with a Chi-square test for independence. Freeman–Tukey deviates were calculated to determine which cells were not fit well by the independence model (Bishop et al., 1975); significance was assessed at an alpha of 0.10.

3. Results

3.1. *Hydrographic features for summers 1996 and 1997*

Satellite remote sensing showed a broad area of temporally persistent but spatially variable cyclonic circulation in the northeastern Gulf

throughout 1996 and 1997 (for details, see Davis et al., 2000; Biggs et al., 2000). The MLD and 15°C depth were shallower in the cyclone than in the confluence or anticyclone during late summer 1996 and mid-summer 1997. The deep chlorophyll maximum (DCM) was located at or just above the depth at which nitrate was first detectable; this averaged 50 m below the surface in the cyclone and 100 m in the anticyclone. The cyclones were also distinguishable by SST, salinity and chlorophyll. In late summer of 1996, surface waters of the cyclone averaged 1°C cooler and 1 unit (practical salinity scale) less saline than surface waters of the anticyclone. Surface chlorophyll was lower than 0.05 µg l⁻¹ in the warm, nutrient-depleted surface waters of the anticyclone, while within the cyclone and over the rest of the continental margin, surface chlorophyll concentrations ranged 0.05–0.3 µg l⁻¹. The highest surface chlorophyll concentrations were encountered near the continental shelf in areas of greatest freshwater input from the Mississippi River. In mid-summer of 1997, surface temperatures over most of the continental margin were 30–31°C, while surface temperatures in the cyclone ranged from 29°C to 30°C. Freshwater from the Mississippi River was entrained into the flow confluence between cyclone–anticyclone pair and reached much farther offshore than in 1996. Surface chlorophyll levels in the interior of the cyclone ranged 0.05–0.15 µg l⁻¹, while in the interior of the anticyclone, surface chlorophyll concentrations were extremely low (<0.05 µg l⁻¹).

3.2. *Estimated mean biomass (EMB) of zooplankton*

The EMB during daytime was low throughout the study area, with values ranging from 0.2 to 1.2 cm³ m⁻² during late summer 1996 and 0.7–2.2 cm³ m⁻² during mid-summer 1997 (for details, see Davis et al., 2000; Wormuth et al., 2000). It was lowest in the anticyclone (0.2–0.7 cm³ m⁻² for late summer 1996 and 0.7–1.2 cm³ m⁻² mid-summer 1997) and in patches at the western and eastern edges of the cyclone during both cruises. EMB was highest (as high as 1.2 cm³ m⁻² for late summer 1996 and 2.2 cm³ m⁻² for mid-summer 1997) near the mouth of the Mississippi (MOM)

along the continental slope, in the center of the cyclones, and throughout the confluence between the cyclone–anticyclone. At night, EMB was higher than during daytime (maximum = 3.2 cm³ m⁻² during both cruises) due to diel vertical migration of zooplankton and micronekton. Nevertheless, EMB was still highest in the center of the cyclones, in areas along the continental slope and in the confluence zone; EMB was lowest in the anticyclones. Generally, EMB was higher during mid-summer 1997 than during late summer 1996.

A comparison between the mantle lengths of cephalopod paralarvae collected by both the 1-m² MOCNESS and a 15' Issacs Kidd Midwater Trawl (IKMT; mouth opening 14.7 m² and mesh size of 4 mm) was completed using a matrix of 95% confidence intervals. The analysis used only genera contained within the five most abundant families. In 9 of 16 cases, mantle lengths of the specimens collected with the IKMT were significantly larger than those collected with the MOCNESS. Additionally, the average mantle length of all genera collected by the IKMT was larger than those collected by the MOCNESS. The IKMT was more efficient at catching larger (older) individuals. Both net systems contained similar taxonomic composition with changes in rank order of abundance of the five most abundant families.

Higher zooplankton and micronekton biomass may indicate richer concentrations of cetacean prey, since the number of cephalopod paralarvae per m² found in the 1-m² MOCNESS tows was significantly correlated with zooplankton biomass (cm³/m²) (Spearman Rank Correlation Coefficient = 0.73, $p < 0.001$, $n = 36$ tows from 333 samples; see Wormuth et al., 2000 for details). The five most abundant families of cephalopod paralarvae collected were Enoploteuthidae, Ommastrephidae, Pyroteuthidae, Cranchiidae, and Onychoteuthidae. Previous studies have shown that each of these families is preyed on by cetaceans (Clarke, 1996).

3.3. *GulfCet II data: eastern Gulf of Mexico (logistic regression analysis)*

3.3.1. *Late summer 1996 cruise*

Visual survey effort, hydrographic features and bathymetry for the late summer *Gyre* cruise are

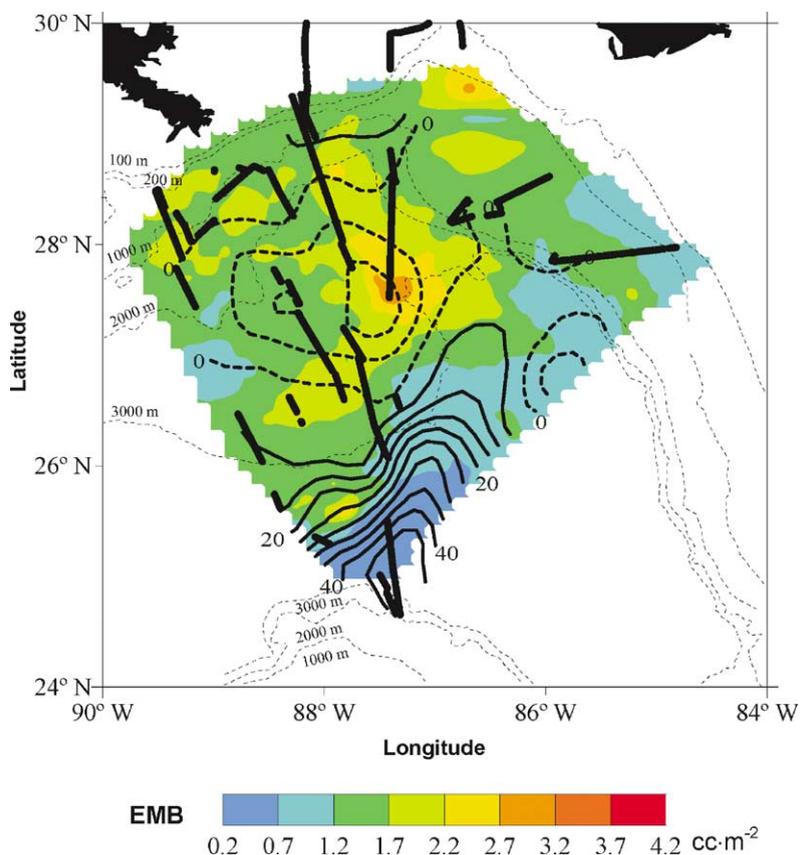


Fig. 3. Visual survey effort (very bold lines) for the late summer 1996 cruise. Thin dashed lines represent isobaths. Bold solid (positive) and bold dashed (negative) lines are sea surface dynamic height anomaly (DHA, cm) relative to the 100 cm mean. Contour intervals are 5 cm. The cyclone is between 0 and -12 cm, the confluence between 0 and 22 cm, and the anticyclone between 25 and 50 cm. The color contours indicate nighttime estimated mean biomass (EMB, $\text{cm}^3 \text{m}^{-2}$) in the interval 10–50 m.

illustrated in Fig. 3. “On-effort” time covered all four hydrographic features. The presence of all cetaceans (Category 1) was related to depth, depth gradient, and chlorophyll. Cetaceans were more likely to be seen in areas where depth was shallower, depth gradient was less steep and chlorophyll concentrations were higher (Fig. 4). Areas where cetaceans were seen had a mean depth of 1754 m (SE = 195, $n = 23$), a mean depth gradient of 13.2 m/km (SE = 2.2) and a mean chlorophyll concentration of $0.144 \mu\text{g l}^{-1}$ (SE = 0.010). Areas where cetaceans were not seen had a mean depth of 2170 m (SE = 84, $n = 97$), mean depth gradient of 16.6 m/km (SE = 1.8) and a mean chlorophyll concentration of $0.125 \mu\text{g l}^{-1}$ (SE = 0.004). Note that only deepwater (depth

> 800 m) sightings were used in the analysis, although a number of shallow water sightings are also shown in Fig. 4.

The presence of sperm whales (Category 2) was related to ocean depth, depth gradient, DHA and EMB. Sperm whales were more likely to be seen in areas where depth was shallower, depth gradient was less steep, DHA was negative and EMB was higher (Fig. 5). Areas where sperm whales were seen had a mean depth of 1581 m (SE = 227, $n = 10$), mean depth gradient of 12.8 m/km (SE = 0.5), DHA of -2.86 cm (SE = 1.79) and mean EMB of $0.86 \text{ cm}^3 \text{ m}^{-2}$ (SE = 0.08). The largest number of sightings occurred south of the MOM and extended southeast into the cyclone. Areas where sperm whales were not seen had a

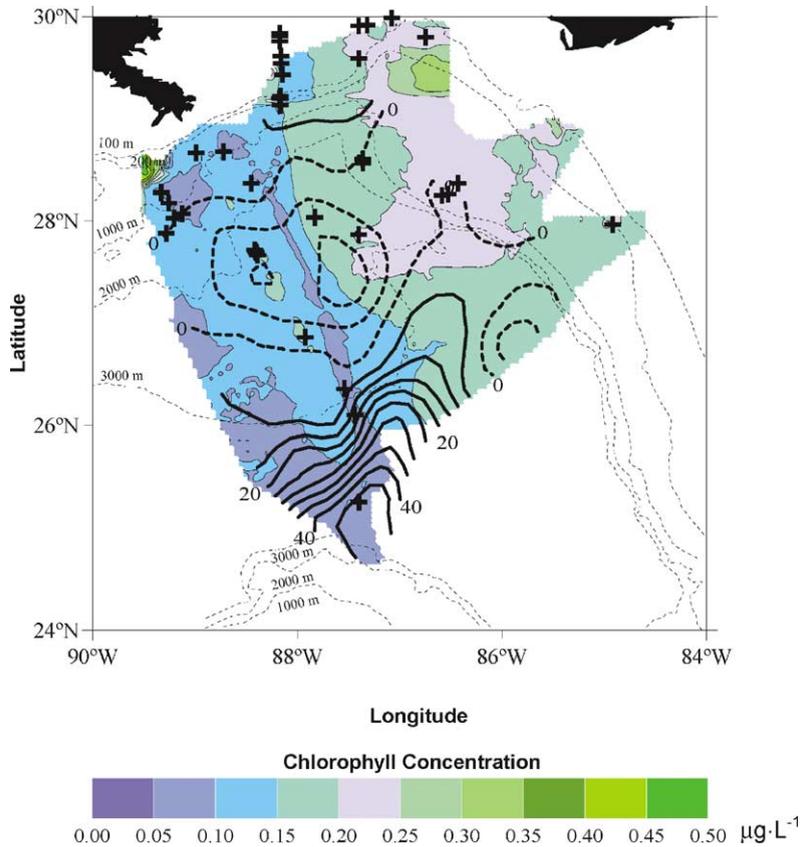


Fig. 4. Cetacean (Category 1, all identified species) sightings (+) during the late summer 1996 cruise. Thin dashed lines represent isobaths. Bold solid (positive) and bold dashed (negative) lines are sea surface dynamic height anomaly (DHA, cm) relative to the 100 cm mean. Contour intervals are 5 cm. The cyclone is between 0 and -12 cm, the confluence between 0 and 22 cm, and the anticyclone between 25 and 50 cm. The color contours indicate surface chlorophyll concentration ($\mu\text{g}\cdot\text{L}^{-1}$).

mean depth of 2170 m ($\text{SE} = 84$, $n = 97$), mean depth gradient of 16.6 m/km ($\text{SE} = 1.7$), mean DHA of 4.16 cm ($\text{SE} = 1.37$) and mean EMB of $0.73 \text{ cm}^3 \text{ m}^{-2}$ ($\text{SE} = 0.02$).

There were not enough sightings of squid eaters (Category 3) to analyze. Of the two sightings beyond the shelf break, one occurred along the lower slope and the other over abyssal depths, in a cyclone. There were seven sightings of *Stenella* (Category 4), but these sightings were not statistically explained by any of the environmental variables considered in the models. All were along the lower slope or over abyssal depths (Fig. 6). Four sightings were within a cyclone, two in an area of confluence, and one in an anticyclone.

The presence of bottlenose dolphins and Atlantic spotted dolphins (Category 5) was related to ocean depth. Bottlenose dolphins and Atlantic spotted dolphins were more likely to be seen in areas where depth was shallower. Areas where bottlenose dolphins and Atlantic spotted dolphins were seen had a mean depth of 104 m ($\text{SE} = 29$, $n = 13$), and areas where they were not seen had a mean depth of 1555 m ($\text{SE} = 107$, $n = 106$). All of the sightings were on the continental shelf or along the shelf break.

3.3.2. Mid-summer 1997 cruise

Visual survey effort, hydrographic features and bathymetry for the mid-summer *Gyre* cruise are

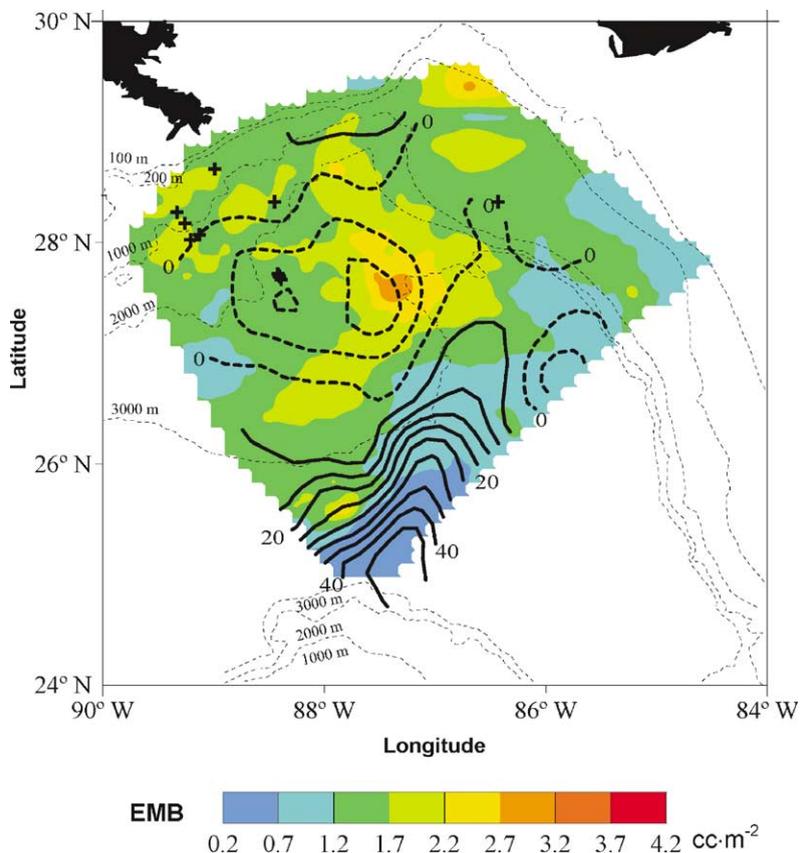


Fig. 5. Sperm whale (Category 2) sightings (+) during the late summer 1996 cruise. Thin dashed lines represent isobaths. Bold solid (positive) and bold dashed (negative) lines are sea surface dynamic height anomaly (DHA, cm) relative to the 100 cm mean. Contour intervals are 5 cm. The cyclone is between 0 and -12 cm, the confluence between 0 and 22 cm, and the anticyclone between 25 and 50 cm. The color contours indicate nighttime estimated mean biomass (EMB, $\text{cm}^3 \text{m}^{-2}$) in the interval 10–50 m.

illustrated in Fig. 7. “On-effort” time covered all four hydrographic features. The presence of all cetaceans (Category 1) was related to ocean depth. The presence of cetaceans was associated with shallower depths (mean = 1863 m, SE = 124, $n = 59$) compared to areas where cetaceans were not seen (mean depth = 2335 m, SE = 75, $n = 83$) (Fig. 8). Sightings occurred in all four hydrographic features, although most sightings occurred in the cyclone, around the periphery of the cyclone and in the confluence zone. Again, only deepwater (depth > 800 m) sightings were used in the analysis although a number of shallow water sightings are also shown in Fig. 8.

The presence of sperm whales (Category 2) was related to depth gradient. The presence of sperm

whales was associated with steeper depth gradients (mean = 44.5 m/km, SE = 12.1, $n = 12$) compared to areas where sperm whales were not seen (mean = 16.3 m/km, SE = 2.6, $n = 83$) (Fig. 9). This was probably due to a cluster of sightings during this cruise along the Florida escarpment, an area of steep depth gradient. Most of the sightings occurred along the lower slope and over abyssal depths less than 3000 m in the cyclone or confluence zone; one sighting occurred in the anticyclone.

The presence of squid eaters (Category 3) was associated with higher salinity (mean = 35.653, SE = 0.437, $n = 6$) compared to areas where squid eaters were not seen (mean salinity = 33.992, SE = 0.249, $n = 83$). Most sightings occurred along the

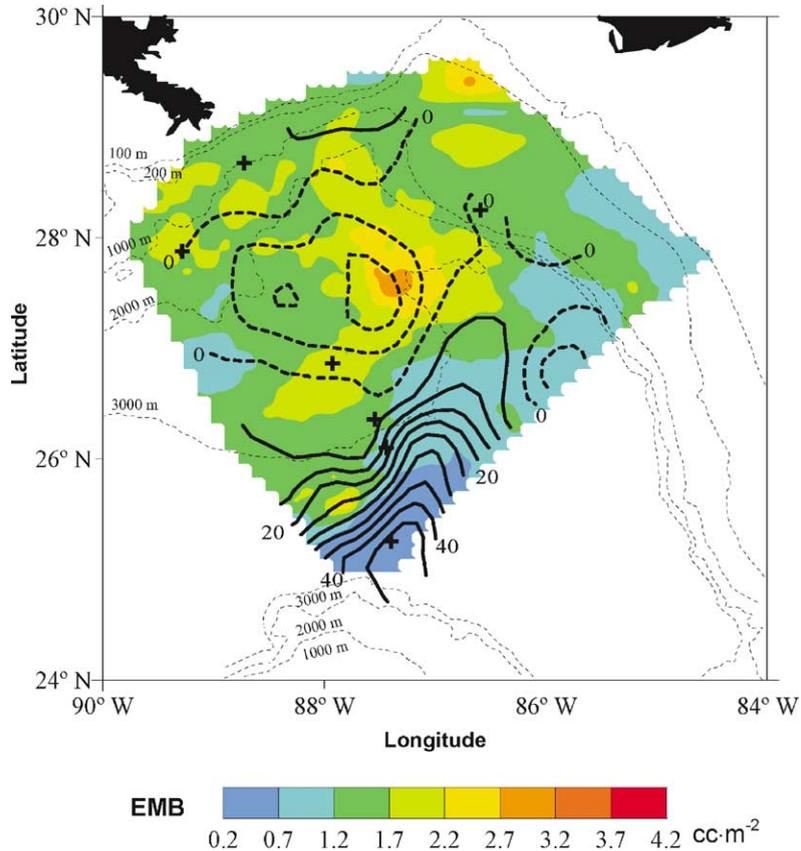


Fig. 6. Stenellid (Category 4, see text for list of species) sightings (+) during the late summer 1996 cruise. Thin dashed lines represent isobaths. Bold solid (positive) and bold dashed (negative) lines are sea surface dynamic height anomaly (DHA, cm) relative to the 100 cm mean. Contour intervals are 5 cm. The cyclone is between 0 and -12 cm, the confluence between 0 and 22 cm, and the anticyclone between 25 and 50 cm. The color contours indicate nighttime estimated mean biomass (EMB, $\text{cm}^3 \text{m}^{-2}$) in the interval 10–50 m.

lower slope and over abyssal depths on the periphery of the cyclone or in the confluence zone; one sighting occurred in the anticyclone.

The presence of oceanic stenellids (Category 4) was associated with areas of lower DHA (mean = 0.82 cm, SE = 2.62 , $n = 27$) compared to areas where stenellids were not seen (mean DHA = 16.34 cm (SE = 2.6 , $n = 83$). Oceanic stenellids were seen from the upper slope to abyssal depths; most occurred in the cyclone, on the periphery of the cyclone or in the confluence zone (Fig. 10).

Bottlenose dolphins and Atlantic spotted dolphins (Category 5) were more likely to be seen in areas where depth was shallower. Areas where

bottlenose dolphins and Atlantic spotted dolphins were seen had a mean depth of 208 m (SE = 91 , $n = 13$), and areas where they were not seen had a mean depth of 2029 m (SE = 105 , $n = 89$). All sightings occurred on the continental shelf or along the shelf break.

3.4. GulfCet I and II data: oceanic northern Gulf of Mexico

All groupings of cetaceans in the oceanic northern Gulf were sighted differentially with respect to ocean depth ($p < 0.001$, all tests). Cetaceans in general (Category 1) were concentrated along the upper continental slope (200–

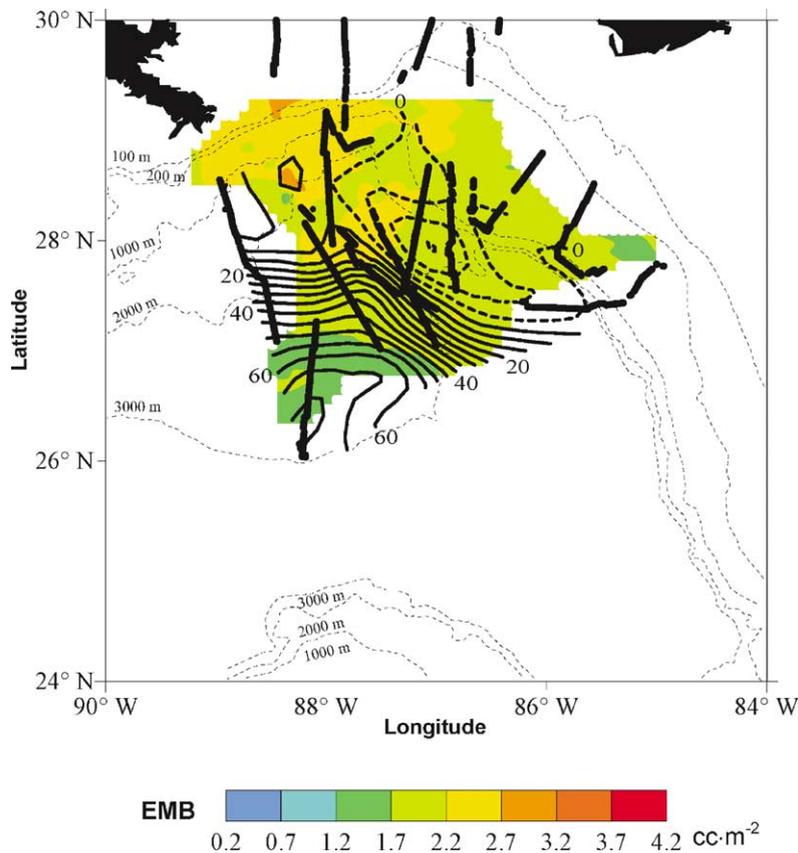


Fig. 7. Visual survey effort (very bold lines) for the mid-summer 1997 cruise. Thin dashed lines represent isobaths. Bold solid (positive) and bold dashed (negative) lines are sea surface dynamic height anomaly (DHA, cm) relative to the 105 cm mean. Contour intervals are 5 cm. The cyclone is between 0 and -13 cm, the confluence between 0 and 24 cm, and the anticyclone between 25 and 71 cm. The color contours indicate nighttime estimated mean biomass (EMB, $\text{cm}^3 \text{m}^{-2}$) in the interval 10–50 m.

1000 m) and were sighted less frequently than expected (based on a Chi-square analysis) over abyssal regions (>2000 m). Sperm whales (Category 2) occurred more frequently along the lower slope (1000–2000 m), and the squid-eaters (Category 3) were concentrated along the upper slope. However, commonly sighted species such as Risso's dolphin heavily influenced the preferred ocean depth range for squid-eaters and disguised the fact that some less frequently sighted species (e.g., *Mesoplodon* spp., Clarke, 1996) occurred over the lower slope and abyssal areas. Oceanic stenellids (Category 4) occurred more frequently over the lower slope and in abyssal areas. Bottlenose dolphins and Atlantic spotted dolphins (Category 5) occurred most frequently on the

continental shelf (<200 m) and along the upper slope; they had a lower than expected occurrence along the lower slope and in abyssal areas.

Groupings of cetaceans were sighted differentially with respect to hydrographic features. Cetaceans in general (Category 1) ($X^2 = 22.0$, $df = 3$, $p < 0.001$) and oceanic stenellids (Category 4) ($X^2 = 25.8$, $df = 3$, $p < 0.001$) were concentrated in cyclones and were less frequently observed in anticyclones. Sperm whales (Category 2) were infrequently seen near anticyclones when these nutrient-poor features were surveyed during GulfCet II. However, when sperm whale sightings from GulfCet I and II were combined, sperm whales in the oceanic northern Gulf were sighted in proportion to the survey effort expended in all four

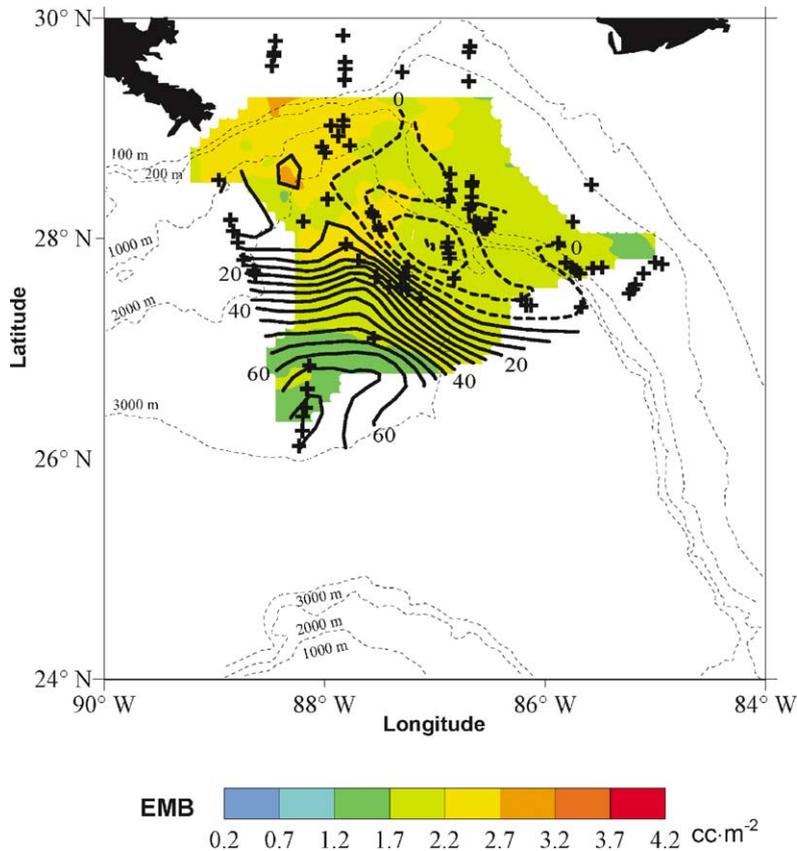


Fig. 8. Cetacean (Category 1, all identified species) sightings (+) during the mid-summer 1997 cruise. Thin dashed lines represent isobaths. Bold solid (positive) and bold dashed (negative) lines are sea surface dynamic height anomaly (DHA, cm) relative to the 105 cm mean. Contour intervals are 5 cm. The cyclone is between 0 and -13 cm, the confluence between 0 and 24 cm, and the anticyclone between 25 and 71 cm. The color contours indicate nighttime estimated mean biomass (EMB, $\text{cm}^3 \text{m}^{-2}$) in the interval 10–50 m.

hydrographic categories ($X^2 = 1.1$, $df = 3$, $p = 0.077$). Similarly, squid-eaters (Category 3) were sighted in proportion to survey effort ($X^2 = 3.1$, $df = 3$, $p = 0.38$). Bottlenose dolphins and Atlantic spotted dolphins (Category 5) occurred mostly in features other than cyclones, anticyclones and confluence areas, probably because they were concentrated along the continental shelf and upper slope where these features do not normally occur.

4. Discussion

The results support our hypotheses that hydrographic features in the study area had different

levels of potential prey that influence cetacean distribution and that these food stocks would be locally concentrated in nutrient-rich areas offshore from the Mississippi River, within cyclonic eddies, and along the high-shear edges of cyclonic eddies. However, there was much unexplained variability in the data that may indicate seasonal, inter-annual and geographic variability in cetacean-habitat association.

Combining the results from the logistic regression and Chi-square analyses, cetaceans in general were concentrated along the continental slope in areas of cyclonic circulation where chlorophyll was elevated. They were less likely to occur over water deeper than 2000 m and in anticyclones. Sperm whales tended to occur along the lower slope and,

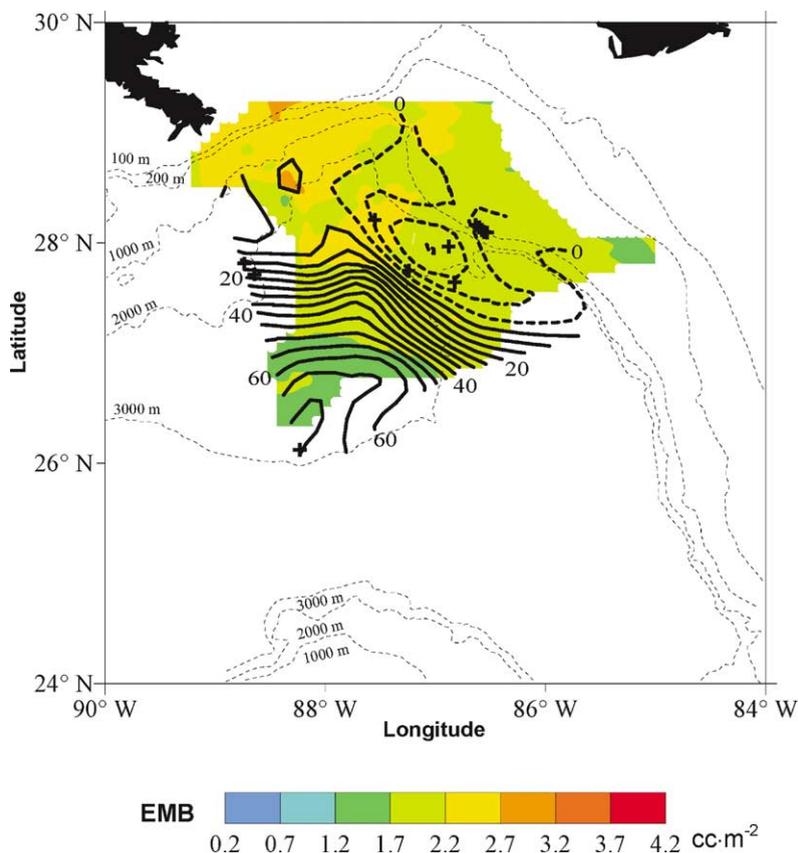


Fig. 9. Sperm whale (Category 2) sightings (+) during the mid-summer 1997 cruise. Thin dashed lines represent isobaths. Bold solid (positive) and bold dashed (negative) lines are sea surface dynamic height anomaly (DHA, cm) relative to the 105 cm mean. Contour intervals are 5 cm. The cyclone is between 0 and -13 cm, the confluence between 0 and 24 cm, and the anticyclone between 25 and 71 cm. The color contours indicate nighttime estimated mean biomass (EMB, $\text{cm}^3 \text{m}^{-2}$) in the interval 10–50 m.

in some areas, in cyclonic eddies (i.e., low DHA) with elevated EMB. Squid-eaters occurred more frequently along the upper slope in areas outside of anticyclones. Oceanic stenellids occurred more often over the lower slope and abyssal regions in areas of cyclonic or confluence circulation.

Recent studies have used acoustic techniques to assess zooplankton and micronekton biomass as a direct or indirect index of food resources for cetaceans (Croll et al., 1998; Macaulay et al., 1995; Beardsley et al., 1996; Fiedler et al., 1998). Although there was a pronounced diel fluctuation in the vertical migration of sound-scattering organisms during this study, integrated EMB was always greater in cyclones than in anticyclones (Davis et al., 2000; Wormuth et al., 2000). These

former areas have a shallower MLD and lower dynamic SSH due to doming of cold, deep water. Our results show that cyclones and confluence zones are areas of locally concentrated zooplankton and micronekton, including cephalopod paralarvae, which we suggest result from nutrient-rich water and locally high primary production in the mixed layer (Biggs et al., 1988, 2000; Davis et al., 2000; Wormuth et al., 2000). Cetaceans were concentrated in these mesoscale features (Figs. 4 and 8). In the plots for sperm whales, most of the sightings occurred in the cyclones, confluence zones or the MOM area where EMB was highest. A comparison of Figs. 5 and 9 shows that, although sperm whales were seen in the MOM area in late summer 1996, more of them were seen

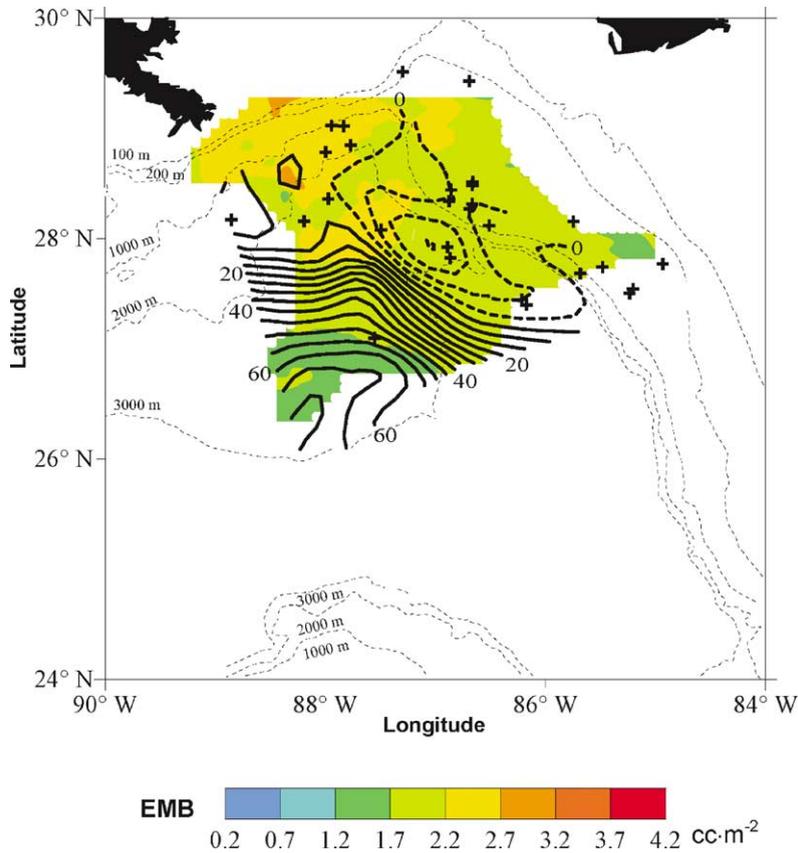


Fig. 10. Stenellid (Category 4, see text for list of species) sightings (+) during the mid-summer 1997 cruise. Thin dashed lines represent isobaths. Bold solid (positive) and bold dashed (negative) lines are sea surface dynamic height anomaly (DHA, cm) relative to the 105 cm mean. Contour intervals are 5 cm. The cyclone is between 0 and -13 cm, the confluence between 0 and 24 cm, and the anticyclone between 25 and 71 cm. The color contours indicate nighttime estimated mean biomass (EMB, $\text{cm}^3 \cdot \text{m}^{-2}$) in the interval 10–50 m.

100–200 km due east over the DeSoto Canyon in mid-summer 1997. In 1996, the MOM area was strongly cyclonic, but the next year the cyclone was centered farther east, and sperm whale occurrence shifted similarly. Since cyclones in the northern Gulf are dynamic and usually associated with westward moving cyclone–anticyclone pairs, cetacean distribution will be dynamic. However, with near real-time satellite remote sensing of SSH anomaly, these features can be tracked and used to predict where cetaceans may be concentrated.

Twenty-eight cephalopod families are eaten by cetaceans, and cephalopods are the main food constituent of 28 odontocetes (toothed whales) (Clarke, 1996). Of these cephalopod families, the

ommatrephids, onychoteuthids, cranchiids and enoploteuthids are numerically important in the diets of sperm whales, members of the Family Ziphiidae, dwarf and pygmy sperm whales, false killer whales, melon-headed whales, pilot whales, Risso’s dolphin, pantropical spotted dolphins, spinner dolphins and striped dolphins (Clarke, 1996; Perrin et al., 1973; Wolff, 1982). The paralarvae of all of these cephalopod families were found in our trawl samples, although the family Enoploteuthidae was by far the most abundant. Although the number of trawls in this study was too small to detect a difference in squid paralarvae abundance in the different hydrographic features, a statistically significant

relationship existed between integrated zooplankton biomass and integrated cephalopod paralarvae numbers (Davis et al., 2000; Wormuth et al., 2000). This implies that higher zooplankton and micronekton biomass indicate richer concentrations of squid in the cyclones and confluence regions than in the anticyclones. These results suggest that the amount of prey for cetaceans may be consistently greater in the cyclone and confluence areas (as opposed to anticyclones) making them preferential areas for foraging. The capture of larger cephalopods by the IKMT provides evidence that cephalopods of different life stages may not be horizontally segregated within the mesoscale features in the Gulf of Mexico. Most species of adult cephalopods perform diel vertical migration, and many also perform ontogenetic vertical migration (Goldman, 1994; Hopkins 1982; Roper and Young 1975; Sweeney et al., 1992). Evidence exists that some species migrate from open ocean to near shore environments to spawn (Bower et al., 1999), possibly to provide their young with advantageous feeding conditions. Conversely, paralarvae of most species are planktonic and live in the epipelagic zone, resulting in a possible vertical segregation between adults and their paralarvae. The mesoscale oceanographic features may provide the cephalopods with a better foraging habitat during all life stages than normally found in the oligotrophic waters of the Gulf of Mexico. Our samples show that cephalopods of multiple life stages were found in the study area. Patterns of abundance and taxonomic composition of paralarval and juvenile-adult cephalopods were similar, implying that the distribution of paralarvae does reflect the presence of older cephalopods, although adults were not directly sampled. While we have no direct evidence to support the contention that adult cephalopods were found in abundance within the nutrient enriched cyclone and confluence, it seems reasonable that mesoscale oceanographic features would provide suitable habitat for adult cephalopods as well as the paralarvae caught in our nets.

In addition to the presence of hydrographic features, ocean depth influences cetacean distribution in the northern Gulf. In earlier studies (Davis and Fargion, 1996; Baumgartner, 1997; Davis

et al., 1998; Mullin et al., 1994), the distribution of cetaceans in the north-central and western Gulf of Mexico in waters deeper than 100 m was differentiated most clearly with ocean depth. Atlantic spotted dolphins were consistently found in the shallowest water on the continental shelf and along the shelf break. Bottlenose dolphins were found most commonly along the upper slope in water significantly deeper than that for Atlantic spotted dolphins. All the other species and species categories were found over deeper ocean depths; these were Risso's dolphins, short-finned pilot whales, pygmy/dwarf sperm whales, rough-toothed dolphins, spinner dolphins, sperm whales, striped dolphins, *Mesoplodon* spp., pantropical spotted dolphins, Clymene dolphins and unidentified beaked whales (Ziphiidae). Risso's dolphins and short-finned pilot whales occurred along the upper slope and, as a subgroup, were significantly different from striped dolphins, *Mesoplodon* spp., pantropical spotted dolphins, Clymene dolphins, and unidentified beaked whales, which occurred in the deepest water. Pygmy/dwarf sperm whales, rough-toothed dolphins, spinner dolphins, and sperm whales occurred at intermediate depths between these two subgroups and overlapped them. In terms of cetacean distribution based on ocean depth, our results for the combined GulfCet I and II data for the northern oceanic Gulf are consistent with these earlier results.

The enhanced presence of cetaceans along the slope instead of abyssal areas of the northern Gulf probably results from the collision of mesoscale eddies with the continental margin, which enhances primary and secondary productivity, especially along the upper continental slope. Skipjack (*Katsuwonus pelamis*), blackfin tuna (*Thunnus atlanticus*), swordfish (*Xiphias gladius*), and blue marlin (*Makaira nigricans*) have been reported by fisherman to be locally abundant in these areas (Roffer's Ocean Fishing Forecasting Service, pers. com.). The presence of large, apex-predators such as tuna, billfish and cetaceans indicates reliable food resources along the continental slope.

In the north-central Gulf, an additional factor affecting cetacean distribution may be the narrow continental shelf (only 20 km wide at its narrowest point) south of the Mississippi River delta. Low

salinity, nutrient-rich water may occur over the continental slope near the MOM or be entrained within the confluence of a cyclone–anticyclone eddy pair and transported beyond the continental slope. This creates a deep-water environment with locally enhanced primary and secondary productivity and may explain the presence of a resident, breeding population of endangered sperm whales within 100 km of the Mississippi River delta (Townsend, 1935; Berzin, 1972; Davis and Fargion, 1996; Davis et al., 2000; Weller et al., 2000). Previous studies have shown that sperm whales in the north-central Gulf occur along the mid-to-lower slope (Collum and Fritts, 1985; Davis et al., 1998). The results from the late and mid-summer cruises are in agreement with these earlier studies and show sperm whales inhabiting areas along the lower slope where DHA is low (i.e., within cyclones or confluence zones) and EMB is higher (Figs. 5 and 9). Similar associations with cyclones and higher EMB were obtained for the squid-eaters and oceanic stenellids, although squid-eaters occurred along the upper slope and oceanic stenellids along the lower slope and in water greater than 2000 m deep (Jennings, 1982). Along the continental slope of Nova Scotia and the northeastern United States, male sperm whales have been observed over similar ocean depths (200–1500 m; Whitehead et al., 1992.) and in areas of increased productivity along frontal systems (Waring et al., 1993; Griffin, 1999). In the South Pacific, sperm whales occur in areas with high secondary productivity and steep underwater topography (Jaquet and Whitehead, 1996; Jaquet et al., 1996). However, it should be noted that the association of sperm whales with low DHA and elevated EMB was statistically significant only for the late summer cruise; most of the sperm whale sightings during the mid-summer cruise occurred in the MOM region and cyclone–anticyclone confluence zone, two other areas that have enhanced primary and secondary productivity. Sperm whale sightings for the entire oceanic northern Gulf (GulfCet I and II sightings combined) showed no significant relationship with hydrographic features. The inconsistent results for sperm whales indicate important problems with this type of analysis that may result from: (1) the

difficulty in obtaining large numbers of sightings with simultaneous environmental data for some species, (2) combining sightings collected over large geographic and temporal scales in which important but subtle factors may be obscured, (3) the low resolution (> 60 nm) of many environmental variables and (4) the lack of data on cetacean behavior (e.g., diving, social and sexual) and at-sea movements. The relationships between physical and biological processes are subtle and complex, and factors other than hydrographic features and potential prey abundance may also influence the distribution of sperm whales and other cetaceans (Jaquet and Whitehead, 1996; Jaquet et al., 1996). For example, the seasonal movements of sperm whales and other cetaceans may be affected by reproductive behavior, for which we currently have little information.

Unlike the other cetaceans, the distribution of bottlenose dolphins and Atlantic spotted dolphins was not correlated with the cyclones that occur in deeper waters beyond the shelf break. The preference of these two species for the shallow waters of the continental shelf and upper slope generally precludes them from feeding around cyclones and areas of confluence. The same appears to be true of Bryde's whales, which have been sighted in the northeastern Gulf in water 100 m deep (Davis et al., 1998, 2000) and along the shelf break (Mullin et al., 1994). We have little information on the environmental variables that influence the distribution of these species or their prey because hydrographic surveys have concentrated on deeper waters beyond the continental shelf.

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References

- Ashjian, C.J., Smith, S.L., Flagg, C.N., Mariano, A.J., Behrens, W.J., Lane, P.V.Z., 1994. The influence of a Gulf Stream meander on the distribution of zooplankton biomass in the slope water, the Gulf Stream, and the Sargasso Sea, described using a shipboard Acoustic Doppler Current Profiler. *Deep-Sea Research I* 41, 23–50.
- Baumgartner, M.F., 1997. Distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. *Marine Mammal Science* 13, 614–638.
- Beardsley, R.C., Epstein, A.W., Chen, C., Wishner, K.F., Macaulay, M.C., Kenney, R.D., 1996. Spatial variability in zooplankton abundance near feeding right whales in the Great South Channel. *Deep-Sea Research II* 43, 1601–1625.
- Berzin, A.A., 1972. *Kashalot. Izdatelstvo Pishchevaya Promyshlennost, Moskva (The Sperm Whale)*. Israel Program for Scientific Translations, Jerusalem (English Translation, 394pp).
- Biggs, D.C., 1992. Nutrients, plankton and productivity in a warm-core ring in the western Gulf of Mexico. *Journal of Geophysical Research* 97, 2143–2154.
- Biggs, D.C., Vastano, A.C., Ossinger, R.A., Gil-Zurita, A., Perez-Franco, A., 1988. Multidisciplinary study of warm and cold-core rings in the Gulf of Mexico. In: Margalef, R. (Ed.), *Memorias del Congreso Iberoamericano y del Caribe*. Fundacion La Salle de Ciencias Naturales. Caracas, Venezuela, pp. 11–31.
- Biggs, D.C., Leben, R.R., Ortega-Ortiz, J.G., 2000. Ship and satellite studies of mesoscale circulation and sperm whale habitats in the northeast Gulf of Mexico during GulfCet II. *Gulf of Mexico Science* 18, 15–22.
- Bishop, Y.M.M., Fienberg, S.E., Holland, P.W., 1975. *Discrete Multivariate Analysis: Theory and Practice*. The MIT Press, Cambridge, 557pp.
- Bower, J.R., Seki, M.P., Young, R.E., Bigelow, K.A., Hirota, J., Flament, P., 1999. Cephalopod paralarvae assemblages in Hawaiian Islands waters. *Marine Ecology Progress Series* 185, 203–212.
- Buckland, S.T., Anderson, D. R., Burnham, K. P., Laake, J. L., 1993. *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman & Hall, London, 446pp.
- Clarke, M.R., 1996. Cephalopods as prey. III. Cetaceans. *Philosophical Transactions of the Royal Society of London B: Biological Science* 351, 1053–1065.
- Collum, L.A., Fritts, T.H., 1985. Sperm whales (*Physeter catodon*) in the Gulf of Mexico. *Southwestern Naturalist* 30, 101–104.
- Croll, D.A., Tershy, B.R., Hewitt, R.P., Demer, D.A., Fiedler, P.C., Smith, S.E., Armstrong, W., Popp, J.M., Kiekhefer, T., Lopez, V.R., Urban, J., Gendron, D., 1998. An integrated approach to the foraging ecology of marine birds and mammals. *Deep-Sea Research II* 45, 1353–1371.
- Davis, R.W., Fargion G.S. (Eds.), 1996. *Distribution and Abundance of Cetaceans in the North-Central and Western Gulf of Mexico: Final Report. vol. II: Technical Report. OCS Study MMS 96-0027*. Prepared by Texas Institute of Oceanography and National Marine Fisheries Service. U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA, 357pp.
- Davis, R.W., Fargion, G.S., May, N., Leming, T.D., Baumgartner, M., Evans, W.E., Hansen, L.J., Mullin, K.D., 1998. Physical habitat of cetaceans along the continental slope in the north-central and western Gulf of Mexico. *Marine Mammal Science* 14, 490–507.
- Davis, R.W., Evans, W.E., Würsig, B. (Eds.), 2000. *Cetaceans, Sea Turtles and Seabirds in the Northern Gulf of Mexico: Distribution, Abundance and Habitat Associations. vol. II:*

- Technical Report. Prepared by Texas A&M University at Galveston and the National Marine Fisheries Service. U.S. Department of the Interior, Geological Survey, Biological Resources Division, USGS/BRD/CR-1999-0006 and Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA, OCS Study MMS 2000-003, 346pp.
- Evans, W.E., 1975. Distribution, Differentiation of Populations and Other Aspects of the Natural History of *Delphinus delphis* Linnaeus in the Northeastern Pacific. Unpublished Ph.D. Dissertation, Department of Biology, University of California, Los Angeles, CA, 145pp.
- Fiedler, P.C., Barlow, J., Gerrodette, T., 1998. Dolphin prey abundance determined from acoustic backscatter data in eastern pacific surveys. Fishery Bulletin 96, 237–247.
- Flagg, C.N., Smith, S.L., 1989. On the use of the Acoustic Doppler Current Profiler to measure zooplankton abundance. Deep-Sea Research 36, 455–474.
- Goldman, D.A., 1994. Seasonal occurrence and horizontal and vertical distribution of paralarval cephalopods off the Florida Keys from May 1989 to May 1990. Masters' Thesis, University of Miami, Coral Gables, FL, 179pp.
- Goold, J.C., 1998. Acoustic assessment of populations of common dolphin off the west Wales coast, with perspectives from satellite infrared imagery. Journal of the Marine Biological Association of the UK 78, 1353–1364.
- Griffin, R.B., 1999. Sperm whale distributions and community ecology associated with a warm-core ring off Georges Bank. Marine Mammal Science 15, 33–51.
- Hopkins, T.L., 1982. The vertical distribution of zooplankton in the eastern Gulf of Mexico. Deep-Sea Research 29, 1069–1083.
- Hosmer, D.W., Lemeshow, S., 1989. Applied Logistic Regression. Wiley, New York, 307pp.
- Hui, C.A., 1979. Undersea topography and distribution of dolphins of the genus *Delphinus* in the southern California Bight. Journal of Mammalogy 60, 521–527.
- Hui, C.A., 1985. Undersea topography and the comparative distributions of two pelagic cetaceans. Fishery Bulletin 83, 472–475.
- Jaquet, N., Whitehead, H., 1996. Scale-dependant correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Marine Ecology Progress Series 135, 1–9.
- Jaquet, N., Whitehead, H., Lewis, M., 1996. Coherence between 19th century sperm whale distributions and satellite-derived pigments in the tropical Pacific. Marine Ecology Progress Series 145, 1–10.
- Jefferson, T.A., 1995. Distribution, abundance and some aspects of the biology of cetaceans in the offshore Gulf of Mexico. Ph.D. Dissertation, Texas A&M University, College Station, TX, 232pp.
- Jefferson, T.A., Schiro, A.J., 1997. Distribution of cetaceans in the offshore Gulf of Mexico. Mammalogy Review 27, 27–50.
- Jefferson, T.A., Leatherwood, S., Webber, M.A., 1993. Marine Mammals of the World. United Nations Environment Program, FAO of the United Nations, Rome, 320pp.
- Jennings, R., 1982. Pelagic sightings of Risso's dolphin, *Grampus griseus*, in the Gulf of Mexico and Atlantic Ocean adjacent to Florida. Journal of Mammalogy 63, 522–523.
- Leatherwood, S., Reeves, R.R., 1983. The Sierra Club Handbook of Whales and Dolphins. Sierra Club Books, San Francisco, 302pp.
- Lohrenz, S.E., Dagg, M.J., Whitlege, T.E., 1990. Enhanced primary production at the plume/oceanic interface of the Mississippi River. Continental Shelf Research 10, 639–664.
- Macaulay, M.C., Wishner, K.F., Daly, K.L., 1995. Acoustic scattering from zooplankton and micronekton in relation to a whale feeding site near Georges Bank and Cape Cod. Continental Shelf Research 14, 509–537.
- Mathsoft. 1997. S-PLUS 4 Guide to Statistics. Mathsoft Inc., Seattle, WA.
- Mullin, K.D., Hoggard, W., Roden, C.L., Lohofener, R.R., Rogers, C.M., Taggart, B., 1994. Cetaceans on the upper continental slope in the north-central Gulf of Mexico. Fishery Bulletin 92, 773–786.
- Payne, P.M., Nicholas, J.R., O'Brien, L., Powers, K., 1986. The distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, *Ammodytes americanus*. Fishery Bulletin 84, 271–277.
- Perrin, W.F., Warner, R.R., Fiscus, C.H., Holts, D.B., 1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fishery Bulletin 71, 1077–1092.
- Perrin, W.F., Mitchell, E.D., Mead, J.G., Caldwell, D.K., Caldwell, M.C., van Bree, P.J.H., Dawbin, W.H., 1987. Revision of the spotted dolphins, *Stenella* spp. Marine Mammal Science 3, 99–170.
- Reilly, S.B., 1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. Marine Ecology Progress Series 66, 1–11.
- Reilly, S.B., Thayer, V.G., 1990. Blue whale (*Balaenoptera musculus*) distribution in the eastern tropical Pacific. Marine Mammal Science 6, 265–277.
- Reilly, S.B., Fiedler, P.C., 1994. Interannual variability of dolphin habitats in the eastern tropical Pacific I. Research vessel surveys, 1986–1990. Fishery Bulletin 92, 434–450.
- Ressler, P.H., Biggs, D.C., Wormuth, J.H., 1998. Acoustic estimates of zooplankton and micronekton biomass using an ADCP. Proceedings of the 16th International Congress on Acoustics and the 135th Meeting of the Acoustical Society of America, Seattle, WA, 20–26 June 1998. The Acoustical Society of America (ASA), Woodbury, NY, pp. 2167–2168.
- Richardson, W.J., Greene Jr., C.R., Malme, C.I., Thomson, D.H., 1995. Marine Mammals and Noise. Academic Press, San Diego, 576pp.
- Ridgway, S.H., Harrison, R., 1994. Handbook of Marine Mammals, vol. 5: The First Book of Dolphins. Academic Press, London, 416pp.

- Roper, C.F., Young, R.E., 1975. Vertical Distribution of Pelagic Cephalopods. Smithsonian Contributions to Zoology. No. 209, 51pp.
- Selzer, L.A., Payne, P.M., 1988. The distribution of white-sided (*Lagenorhynchus acutus*) and common dolphins (*Delphinus delphis*) vs. environmental features of the continental shelf of the northeastern United States. Marine Mammal Science 4, 141–153.
- Sturges, W., Leben, R.R., 2000. Frequency of ring separations for the Loop Current in the Gulf of Mexico. Journal of Physical Oceanography 30, 1814–1819.
- Sutcliffe, W.H., Brodie, P.F., 1977. Whale Distribution in Nova Scotia Waters. Fisheries and Marine Service Technical Report 722. Fisheries and Marine Service, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, 83pp.
- Sweeney, M.J., Roper, C.F., Mangold, K.M., Clarke, M.R., Boletzky, S.v. (Eds.), 1992. “Larval” and juvenile cephalopods: a manual for their identification. Smithsonian Contributions to Zoology. No. 513, 282pp.
- Townsend, C.H., 1935. The distribution of certain whales as shown by logbook records of American whale ships. Zoologica 19, 3–50.
- Tynan, C.T., 1997. Cetacean distributions and oceanographic features near the Kerguelen Plateau. Geophysical Research Letters 24, 2793–2796.
- Walker, N.D., Rouse, L.J., 1993. Satellite assessment of Mississippi River discharge plume variability. OCS Study MMS 93-0044. U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Regional Office, New Orleans, LA, 50pp.
- Waring, G.T., Fairfield, C.P., Ruhsam, C.M., Sano, M., 1993. Sperm whales associated with Gulf Stream features off the northeastern USA shelf. Fisheries Oceanography 2, 101–105.
- Weller, D.H., Würsig, B., Lynn, S.K., Schiro, A.J., 2000. Preliminary findings on the occurrence and site fidelity of photo-identified sperm whales (*Physeter macrocephalus*) in the northeastern Gulf of Mexico. Gulf of Mexico Science 18, 35–39.
- Whitehead, H., Brennan, S., Grover, D., 1992. Distribution and behaviour of male sperm whales on the Scotian Shelf, Canada. Canadian Journal of Zoology 70, 912–918.
- Wolff, G., 1982. A Study of Feeding Relationships in Tuna and Porpoise Through the Application of Cephalopod Beak Analysis. Unpublished Ph.D. Dissertation, Department of Oceanography, Texas A&M University, College Station, TX, 233pp.
- Wormuth, J.H., Ressler, P.H., Cady, R.B., Harris, E.J., 2000. Zooplankton and micronekton in cyclones and anticyclones in the northeast Gulf of Mexico. Gulf of Mexico Science 18, 23–34.
- Würsig, B., Jefferson, T.A., Schmidly, D.J. 2000. The Marine Mammals of the Gulf of Mexico. Texas A&M University Press, College Station, TX, 232pp.
- Zhou, M., Nordhausen, W., Huntley, M., 1994. ADCP measurements of the distribution and abundance of euphausiids near the Antarctic Peninsula in winter. Deep-Sea Research 41, 1425–1445.
- Zimmerman, R.A., Biggs, D.C., 1999. Patterns of distribution of sound-scattering zooplankton in warm- and cold-core eddies in the Gulf of Mexico, from a narrowband Acoustic Doppler Current Profiler survey. Journal of Geophysical Research 104, 5231–5262.