Cetaceans of the oceanic northern Gulf of Mexico: Distributions, group sizes and interspecific associations

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ABSTRACT

The Gulf of Mexico is a subtropical ocean basin with a diverse oceanic cetacean community. Cetacean research in the Gulf of Mexico has been driven by mandates of the US Marine Mammal Protection Act as well as concerns over the rapidly expanding oil and natural gas industry and related potential threats (e.g. seismic surveys, increased ship traffic, oil spills). Previously, cetacean distribution and abundances for specific Gulf of Mexico areas or species have been described based on work over periods of several years, and recently abundance estimates were made for the entire oceanic northern Gulf of Mexico (1996-2001). For each cetacean species, the paper describes distribution, group size, associated sea surface temperature and water depth and interspecific associations based on surveys conducted over 11 years that span the entire northern Gulf of Mexico. This dataset is the most comprehensive to date for the oceanic northern Gulf. Nine ship surveys totalling 45,462km of effort were conducted during spring seasons (1991-2001) in continental shelf-edge and oceanic waters ($\geqslant$100m) of the northern Gulf of Mexico. Eighteen species were identified from 1,868 sightings. Cetaceans were found throughout the area although some species had localised distributions or occurred in restricted ranges of water depths. Spinner dolphins (*Stenella longirostris*) had the largest mean group size (n = 40, $\bar{x}$ = 151.5, SE = 30.90), followed by melon-headed whales (*Peponocephala electra*), clymene dolphins (*S. clymene*), pantropical spotted dolphins (*S. attenuata*), Fraser's dolphins (*Lagenodelphis hosei*) and striped dolphins (*S. coeruleoalba*) (range of means 46.1-99.6). Beaked whales (Ziphiidae), Bryde's whales (*Balaenoptera edeni/brydei*), sperm whales (*Physeter macrocephalus*) and pygmy/dwarf sperm whales (*Kogia* spp.) were found in the smallest groups ($\bar{x}$ < 3). Twenty-seven sightings (1.4% of all sightings) were composed of two cetacean species. Common bottlenose dolphins (*Tursiops truncatus*) were recorded in mixed-species groups with more species than any other cetacean. Forty-five cetacean sightings (2.4% of all sightings) were associated with at least one bird species, and 21 (1.1% of all sightings) were associated with schools of fish. Contrary to previous reports, pantropical spotted dolphins were observed in association with both fish (including surface tunas) and seabirds, although to a lesser extent than for other tropical oceans. No mixed pantropical spotted and spinner dolphin groups were sighted despite their regular co-occurrence in other tropical oceans.

KEYWORDS: CETACEAN; GULF OF MEXICO; SURVEY-VESSEL; DISTRIBUTION; GROUP SIZE

INTRODUCTION

About 21 species of cetaceans regularly inhabit the northern Gulf of Mexico (i.e. waters within the boundary of the US Exclusive Economic Zone in the Gulf). The species are divided into two communities, the continental shelf community, comprised of the common bottlenose dolphin (*Tursiops truncatus*) and Atlantic spotted dolphin (*Stenella frontalis*), and the oceanic community, comprised of 19 additional species: the Bryde's whale (*Balaenoptera edeni/brydei*); sperm whale (*Physeter macrocephalus*); dwarf sperm whale (*Kogia sima*); pygmy sperm whale (*K. breviceps*); Cuvier's beaked whale (*Ziphius cavirostris*); Blainville's beaked whale *(Mesoplodon densirostris*); Gervais' beaked whale (*M. europaeus*); melon-headed whale (*Peponocephala electra*); pygmy killer whale (*Feresa attenuata*); false killer whale (*Pseudorca crassidens*); killer whale (*Orcinus orca*); short-finned pilot whale (*Globicephala macrorhynchus*); rough-toothed dolphin (*Steno bredanensis*); Risso's dolphin (*Grampus griseus*); Fraser's dolphin (*Lagenodelphis hosei*); pantropical spotted dolphin (*Stenella attenuata*); striped dolphin (*S. coeruleoalba*); spinner dolphin (*S. longirostris*) and clymene dolphin (*S. clymene*) (Mullin *et al.*, 1994a; b; 2004; Hansen *et al.*, 1996; Mullin and Hansen, 1999; Mullin and Hoggard, 2000; Fulling *et al.*, 2003). The cetacean community in the northern Gulf is essentially a tropical one. With the exceptions of Atlantic spotted dolphins and clymene dolphins, which are endemic to warm Atlantic Ocean waters, and common bottlenose dolphins, sperm whales and killer whales, which have nearly cosmopolitan distributions, all species occurring in the Gulf of Mexico inhabit deep, warm temperate to tropical waters throughout the world (Jefferson *et al.*, 1993).

Previous cetacean research in the Gulf of Mexico focused on abundance and distribution (Jefferson, 1996; Fulling *et al.*, 2003; Mullin *et al.*, 2004; Mullin and Fulling, 2004), habitat preferences (Baumgartner, 1997; Baumgartner *et al.*, 2001; Davis *et al.*, 1998; 2002), or detailed descriptions of sightings of specific species (Leatherwood *et al.*, 1993; Mullin *et al.*, 1994a; c; O'Sullivan and Mullin, 1997). Ballance and Pitman (1998) compared the cetacean communities (species composition, relative abundance, group sizes and associated species) in the eastern tropical Pacific Ocean, western tropical Indian Ocean and the Gulf of Mexico. They based their Gulf conclusions on results from spring cruises from 1991-1994 (Hansen *et al.*, 1995) and on personal observations by R.L. Pitman while participating in those cruises. Many of the conclusions on the Gulf cetaceans by Jefferson and Schiro (1997) and Mullin and Hansen (1999) were also based on the 1991-1994 data.

This paper summarises data from shipboard cetacean surveys of the shelf-edge and oceanic northern Gulf of Mexico conducted during nine spring seasons from 1991 to 2001 (the largest, most consistent dataset) to more adequately describe distribution, group sizes and interspecific associations for each cetacean species. The specific objectives are to describe: (1) the diversity of cetaceans; (2) the distribution of each species; (3) the group size, sea surface temperature and water depth for each species; and (4) the interspecific associations for each

species. It also provides quantitative support for and amends comments on these topics for the Gulf of Mexico by Jefferson and Schiro (1997), Ballance and Pitman (1998) and Mullin and Hansen (1999).

METHODS

Study area

The study area was continental shelf-edge (100-200m deep) and oceanic waters (>200m deep) of the US Gulf of Mexico (398,960km^2) (Fig. 1). The Gulf is a subtropical ocean basin in which the biological and physical oceanography are dynamic both spatially and temporally (Baumgartner *et al.*, 2001; Biggs and Ressler, 2001; Davis *et al.*, 2002). In the eastern Gulf the near-surface circulation is dominated by the Loop Current (LC), an extension of the Gulf Stream that enters the Gulf of Mexico via the Yucatan Channel, turns anticyclonically and exits through the Straits of Florida (Wiseman and Sturges, 1999). Pairs of anticyclonic (warm-core) – cyclonic (cold-core) eddies are regularly found in the central and western Gulf.

The mean state of productivity of the oceanic Gulf of Mexico is low (<0.1mg chl · m^{-3}), but there are a number of physical features that make the habitat heterogeneous both spatially and temporally (Biggs and Ressler, 2001). Upwelling often occurs at the LC periphery, where cyclonic eddies frequently develop. The LC periodically sheds anticyclonic eddies, which after separation, move slowly westward until their advance is hindered by shoaling topography over the northwestern continental slope (Davis *et al.*, 2002). Another major influence on the Gulf of Mexico oceanography is the large freshwater inflow from the Mississippi River.

Major bathymetric features of the northern Gulf include: the wide continental shelf off the Florida peninsula and off northern Texas and western Louisiana; the narrow shelf off the Florida Panhandle near DeSoto Canyon, off the Mississippi River Delta region, and off southern Texas; the two major canyon systems, the Mississippi and DeSoto canyons; and the salt domes and basins on the northwestern continental slope (Baumgartner, 1997).

Data collection

Nine spring surveys were conducted during 1991-1994, 1996-1997 and 1999-2001. Surveys were conducted aboard NOAA ships *Oregon II* (52m) and *Gordon Gunter* (68m), and were approximately 44 days in duration (two ~22 day legs), beginning in mid-April and ending in early June. These surveys were conducted in conjunction with ichthyoplankton sampling along a trackline uniformly spaced throughout oceanic waters of the northern Gulf (Fig. 1). The trackline was transited 24h/day to accommodate plankton sampling at stations spaced 55.6km (30 n.miles) apart.

There was less survey effort in the extreme western and southeastern areas since plankton stations in the extreme west were considered of lower priority. Stations in this region were also sometimes dropped due to time constraints arising from inclement weather or mechanical problems. During some years, researchers from the State of Florida, in collaboration with our agency, sampled the stations in the southeastern Gulf, making those of lower priority as well. An additional 10-day leg that was a dedicated cetacean line-transect survey (no plankton sampling) was conducted during most years in northwestern (1992-1994) or northeastern (1996-1997) shelf-edge and continental slope waters (100-2,000m deep).

Data were collected by two teams of three observers on the ship's flying bridge, located 9.2m (*Oregon II*) and 14.5m (*Gunter*) above the water's surface. Data were collected during daylight hours in favourable weather conditions (i.e. Beaufort sea state <6, no rain) at a ship's speed of 10 knots (18km h^{-1}). Two observers searched for cetaceans using 25× 'bigeye' binoculars, and the third observer recorded data and searched near the ship using hand-held binoculars and unaided eye. Teams alternated 2 hour watches throughout the day, and observers rotated positions every 30-40min to avoid fatigue. Sightings made by the on-watch observer team while following standard line-transect protocol were 'on-effort'. Sightings made under other circumstances (e.g. while the ship was stopped for ichthyoplankton sampling) were 'off-effort'.

Data were recorded on a computer using a BASIC data acquisition program interfaced with the ship's GPS. For each cetacean sighting the following data were recorded: bearing from the bow; linear distance from the ship; species; group size; behaviour; presence of calves; presence of remoras (Echeneidae) and wounds from cookie-cutter sharks (*Isistius* spp.); sea surface temperature (SST); water depth; and the presence of associated seabird and fish species. A suite of environmental sensors (e.g. SST) were integrated into the ship's scientific computer system which was constantly displayed, allowing observers to record SST. Water depth for each sighting was obtained from nautical charts using the latitude and longitude of the sighting. Visibility conditions were recorded and updated at least every 30-40min, including Beaufort sea state, wind direction, weather and glare.

The ship was typically diverted if a sighting was within a 5,550m corridor perpendicular to the transect-line to confirm species identifications and to make group size estimates. For mixed-species cetacean groups, a separate group size estimate was made for each species. Group size was estimated by a consensus of the on-watch observers. Cetacean species were considered 'associated' or in a 'mixed-species group' if they were swimming in a mixed school, bowriding the research vessel together, behaving aggressively toward one another or behaving in a similar manner within 300-400m of one another.

Cetaceans were identified to the lowest taxonomic level possible based on descriptions in field guides and scientific literature (e.g. Jefferson *et al.*, 1993; Leatherwood *et al.*, 1983). Pygmy and dwarf sperm whales were not consistently distinguished, and mesoplodont whales were difficult to distinguish at sea; therefore findings are reported for *Kogia* spp. and *Mesoplodon* spp. Sightings of *Mesoplodon* sp. were probably Gervais' or Blainville's beaked whale, based on stranding records from the Gulf (Jefferson and Schiro, 1997; Mead, 1989; Schmidly, 1981). Male Blainville's beaked whales were identified in two sightings by their unique high arching mouthline (Jefferson *et al.*, 1993). Short-finned and long-finned pilot whales cannot easily be distinguished at sea, but based on stranding records and known distributions (Bernard and Reilly, 1999; Schmidly, 1981), it seems most likely all pilot whale sightings were short-finned and they are reported thus here. We also believe the only balaenopterid whale sighted during these surveys was the Bryde's whale; therefore sightings of Bryde's whales, Bryde's/sei whales and *Balaenoptera* sp. were combined and treated as Bryde's whales. Each whale in these sightings had a large, falcate dorsal fin similar to that of Bryde's or sei whales, but when observers clearly saw the dorsal surface of the rostrum of at least one whale in a sighting (11 of 17 sightings), three ridges were present, a

diagnostic characteristic of Bryde's whales (Cummings, 1985). The five records of sei whales from the Gulf of Mexico are from strandings and are considered to be strays or accidental (Jefferson and Schiro, 1997). Finally, in some cases, animals could only be identified as unidentified Ziphiidae (Cuvier's beaked whale or *Mesoplodon* sp.), large whale (>7m long), small whale (non-dolphin, <7m), unidentified dolphin, *Stenella* sp., or odontocete.

Data analysis

All sightings used in analyses occurred in waters ≥100m. For group size summaries, off-effort and naked-eye sightings were deleted from the dataset (only on-effort sightings made with 25× binoculars were used), the latter because in most cases these sightings were believed to be a subset of a larger group that approached the ship to ride the bow. For distribution plots, all on-effort sightings were used. For analysis of mixed-species cetacean sightings, all sightings were used, including off-effort and naked-eye sightings. For SST data, temperatures not recorded to the nearest tenth of a degree due to observer error were deleted from the SST dataset. Descriptive statistics are reported as means and standard errors.

RESULTS

Effort

Line-transect effort for the nine spring surveys totalled 45,462km (Table 1, Fig. 1). Annual survey effort ranged from 4,048 to 5,844km. A total of 1,868 sightings were made, of which 1,736 were on-effort and 132 were off-effort. Annual total sightings ranged from 81 to 275.

Table 1
Survey effort and number of sightings by year.

Year	Effort (km)	Number of on-effort sightings	Number of off-effort sightings	Total number of sightings
1991	4,267	81	0	81
1992	5,756	236	16	252
1993	5,519	228	12	240
1994	5,601	259	16	275
1996	5,844	201	26	227
1997	5,724	205	15	220
1999	4,522	190	17	207
2000	4,048	181	10	191
2001	4,181	155	20	175
Grand total	45,462	1,736	132	1,868

Diversity

Eighteen species were identified (Table 2). These included male Blainville's beaked whales on two occasions and two distinct forms of *Kogia*, one with a large falcate dorsal fin and the other with a much more diminutive dorsal fin, that represent the two species, dwarf and pygmy sperm whales, respectively (Caldwell and Caldwell, 1989). Groups of pantropical spotted dolphins were the most commonly encountered species and made up about one third of all groups sighted. Sperm whales, which were frequently sighted, and Bryde's whales were the only great whales encountered.

Distribution, water depth and sea surface temperature

Cetaceans were found throughout the northern Gulf of Mexico; however, some species had more localised distributions (e.g. eastern, western) or occurred in more restricted ranges of water depths (Fig. 2a-l, Table 2). All five species in the genus *Stenella* regularly occurred in the northern Gulf. Atlantic spotted dolphins were found along the continental shelf break throughout the study area with the deepest sighting occurring at 362m. Pantropical spotted and striped dolphins had widespread distributions throughout oceanic waters in a wide range of depths. Spinner and clymene dolphins had nearly parapatric distributions, with most sightings of each species occurring east or west, respectively, of the Mississippi River. The mean depths of clymene, pantropical and striped dolphin sightings were twice that of spinner dolphins (Table 2).

Sperm whales were widely distributed but relatively concentrated near the mouth of the Mississippi and the area due west of the Florida Keys. *Kogia* spp. and Risso's dolphins were also widespread and occurred in a wide range of depths.

Common bottlenose dolphins occurred most commonly along the shelf-edge and upper continental slope. Most killer whales occurred in the central Gulf in waters >700m. There were few false killer whale sightings, but nearly all (9 of 11) occurred in the far eastern Gulf in a wide range of depths. Short-finned pilot whales were widespread throughout the continental slope of the western Gulf, west of 89°W, with the exception of one sighting near the Dry Tortugas in the eastern Gulf.

Melon-headed and pygmy killer whales occurred in waters >800m in a nearly identical range of depths, though the mean depth of pygmy killer whale sightings was about 1,000m deeper. Rough-toothed dolphins were widespread in

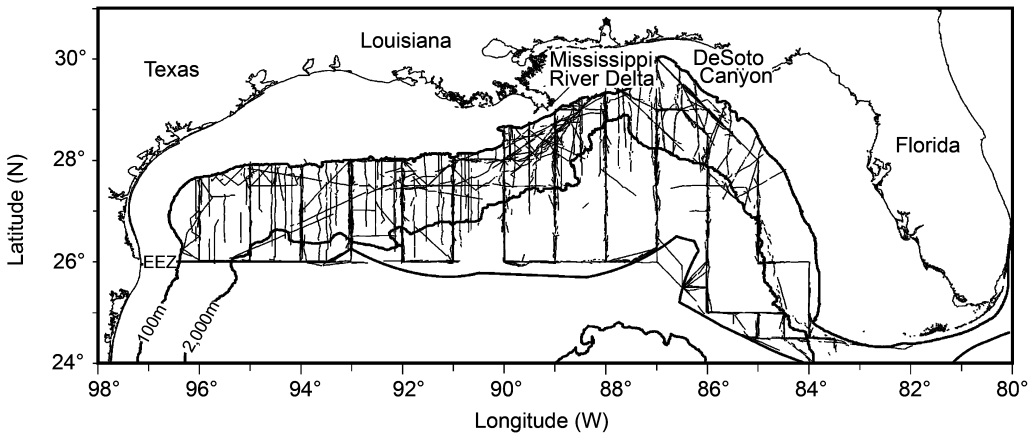

Fig. 1. Study area within the northern Gulf of Mexico. The 100m and 2,000m lines of bathymetry and the boundary of the US Exclusive Economic Zone (EEZ) are indicated by bold lines. Survey effort is indicated by the thinner lines.

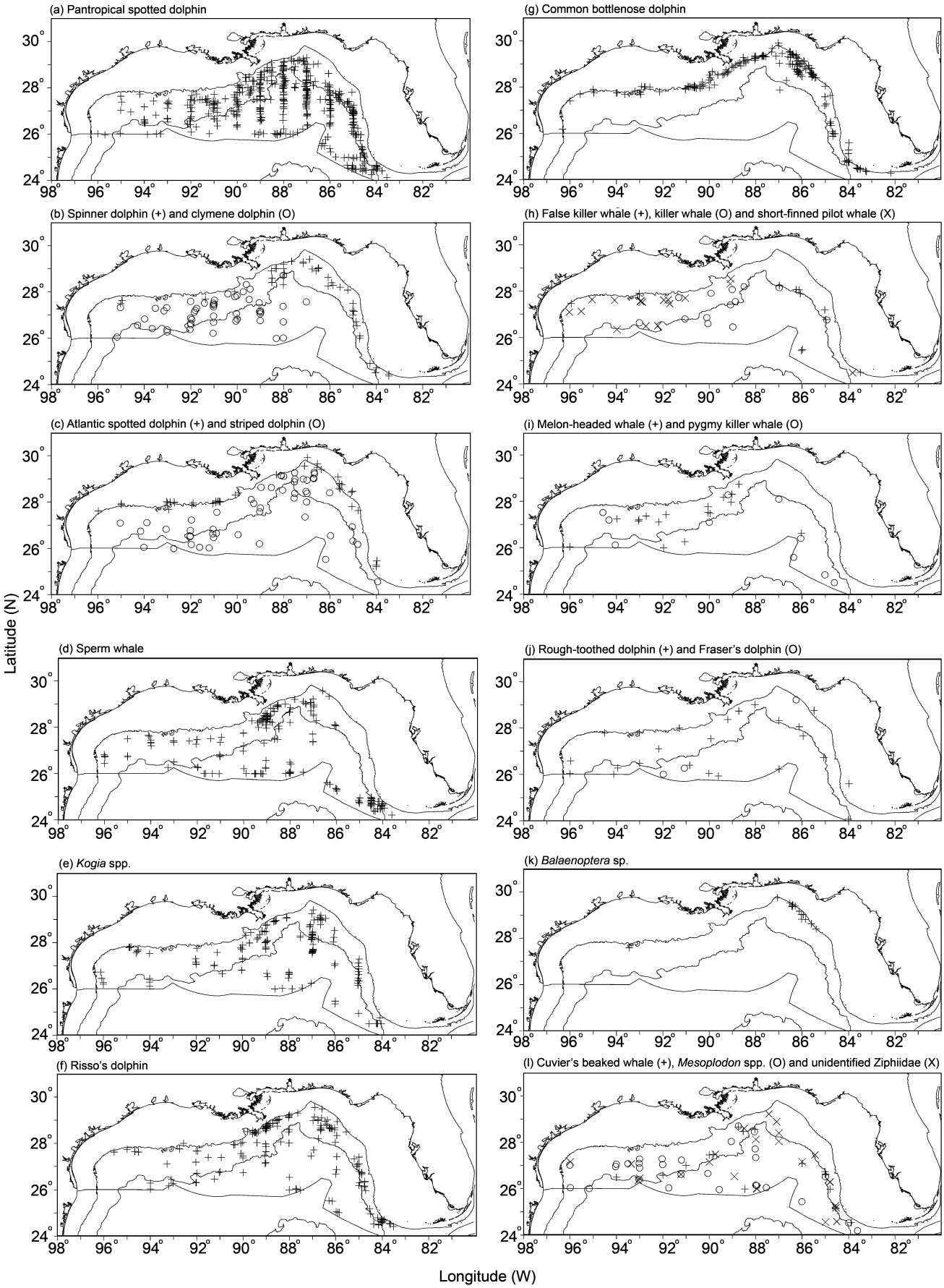

Fig. 2. Sighting locations for each species/taxonomic group observed. Each symbol represents one sighting. The 200m and 2,000m lines of bathymetry and the boundary of the US Exclusive Economic Zone (EEZ) are shown. (a) Pantropical spotted dolphin (*n*=432); (b) Spinner dolphin (*n*=42) and clymene dolphin (*n*=50); (c) Atlantic spotted dolphin (*n*=39) and striped dolphin (*n*=52); (d) Sperm whale (*n*=172); (e) *Kogia* spp. (*n*=135); (f) Risso's dolphin (*n*=160); (g) Common bottlenose dolphin (*n*=179); (h) False killer whale (*n*=11), killer whale (*n*=13) and short-finned pilot whale (*n*=18); (i) Melon-headed whale (*n*=17) and pygmy killer whale (*n*=10); (j) Rough-toothed dolphin (*n*=24) and Fraser's dolphin (*n*=3); (k) *Balaenoptera* sp. (*n*=15); (l) Cuvier's beaked whale (*n*=16), *Mesoplodon* spp. (*n*=29) and unidentified Ziphiidae (*n*=24).

Table 2

Descriptive statistics for group size, sea surface temperature (SST), and depth of on-effort sightings for each species/taxonomic group. Sample sizes (*n*) may be different for the three categories within species due to deletion of naked-eye sightings from group size data and deletion of SSTs without decimals for SST data (see Methods for details).

	Group size					SST (°C)					Depth (m)				
Species	*n*	Mean	SE	Max	Min	*n*	Mean	SE	Max	Min	*n*	Mean	SE	Max	Min
Bryde's whale	14	2.0	0.33	5	1	9	23.31	0.497	25.9	21.5	15	226.3	7.94	302	199
Sperm whale	164	2.6	0.16	11	1	148	26.02	0.154	29.7	21.1	172	1,732.4	73.54	3,462	198
Kogia spp.	133	2.0	0.12	8	1	116	26.60	0.155	29.5	22.7	135	1,670.6	88.25	3,422	339
Cuvier's beaked whale	15	1.8	0.30	4	1	15	26.01	0.334	28.3	24.3	16	1,884.6	172.03	3,221	1,179
Mesoplodon spp.	29	2.3	0.25	7	1	26	26.95	0.296	28.9	23.1	29	1,791.6	143.24	3,257	796
Unidentified Ziphiid	19	1.7	0.20	4	1	21	26.48	0.471	29.2	22.5	24	1,876.9	185.14	3,386	531
Killer whale	13	6.5	1.37	12	1	11	26.66	0.476	28.6	22.7	13	1,865.8	195.46	2,818	732
False killer whale	11	27.6	7.38	70	3	7	26.79	0.494	28.7	25.1	11	1,301.5	329.96	3,294	167
Short-finned pilot whale	18	24.9	4.41	85	3	16	26.47	0.293	28.4	24.4	18	984.3	111.34	2,105	553
Melon-headed whale	17	99.6	16.44	275	22	15	26.47	0.354	28.7	24.1	17	1,401.5	160.29	3,203	824
Pygmy killer whale	10	18.5	7.39	84	4	8	26.84	0.394	28.2	24.5	10	2,405.7	330.73	3,422	893
Risso's dolphin	147	10.2	0.56	40	1	142	26.20	0.163	29.2	20.4	160	1,155.5	71.98	3,440	110
Rough-toothed dolphin	21	14.1	1.60	28	2	21	25.87	0.379	28.8	22.3	24	1,572.0	226.84	3,294	128
Fraser's dolphin	3	65.3	26.03	117	34	3	25.77	0.371	26.5	25.3	3	1,483.5	616.86	2,141	251
Common bottlenose dol.	151	20.6	2.49	220	1	154	25.25	0.175	29.5	19.4	179	312.4	18.90	2,950	102
Pantropical spotted dol.	381	71.3	3.45	650	3	377	25.94	0.084	29.1	21.1	432	1,912.2	45.49	3,488	280
Striped dolphin	51	46.1	4.74	150	8	45	25.30	0.260	28.6	22.2	52	1,638.3	109.43	3,206	404
Spinner dolphin	40	151.5	30.90	800	6	37	25.42	0.355	29.6	22.2	42	825.7	88.36	2,525	275
Clymene dolphin	44	89.5	11.48	325	2	43	25.93	0.227	29.2	22.1	50	1,692.2	93.72	3,065	688
Atlantic spotted dolphin	35	25.7	2.58	68	1	34	24.99	0.335	28.3	21.3	39	179.6	10.54	362	101

both distribution and range of water depths. Only three sightings of Fraser's dolphins were made. All sightings of Bryde's whales except one were concentrated along the northeastern shelf-edge in the DeSoto Canyon area, and were in a very narrow water depth range (199-302m), more narrow than for any other taxonomic group. Beaked whales (*Mesoplodon* spp., Cuvier's beaked whale, and unidentified Ziphiidae) were widely distributed in waters >500m deep. Mean SST ranged from 23.31°C for Bryde's whales to 26.95°C for *Mesoplodon* spp. (Table 2).

Group size

The beaked whales, Bryde's whale, sperm whale and *Kogia* spp. occurred in the smallest groups, all with mean group sizes <3 (Table 2). Killer whales were also found in small groups of ≤12 whales. Spinner dolphins had the largest mean group size (n=40, $\bar{x}$ = 151.5, SE = 30.90) of any species and the largest cetacean group observed during all surveys (800 dolphins). After spinner dolphins, the largest mean group sizes were those of melon-headed whales, clymene dolphins, pantropical spotted dolphins, Fraser's dolphins and striped dolphins (range of means 46.1-99.6).

Interspecific associations

The vast majority of sightings consisted of single species groups, however 27 of the 1,868 sightings (1.4%) comprised two cetacean species (Tables 3 and 4). The most frequent mixed-species group, common bottlenose and Atlantic spotted dolphins, comprised 33.3% of all mixed-species sightings but only 0.48% of all sightings (9 of 1,868). The other species most commonly sighted in mixed-species groups were rough-toothed dolphins, melon-headed whales, Risso's dolphins, false killer whales and Fraser's dolphins.

In five of the mixed-species cetacean groups, aggressive interactions were observed between the two species. Two common bottlenose and Atlantic spotted dolphin sightings involved both species bowriding. In one instance, the Atlantic spotted dolphins were riding first and snapped their jaws and made fast approaches at the common bottlenose dolphins when they came to the bow. In the second instance, both species approached the bow together, with common bottlenose dolphins swimming in front and tail slapping, and Atlantic spotted dolphins butting the common bottlenose dolphins with their rostrum/head. In two different sightings of mixed-species groups bowriding, rough-toothed dolphins chased Atlantic spotted dolphins in one case, and in another, they chased melon-headed whales away from the bow while jaw snapping. On one occasion, a pod of seven killer whales separated up to three dolphins from a group of about 120 pantropical spotted dolphins. They chased and herded a single dolphin for approximately 1.5 hours, ramming and tossing it into the air, finally killing it (see Pitman *et al.*, 2003).

Of the 1,868 cetacean sightings, 45 (2.4%) were associated with at least one seabird species/taxonomic group (Table 3). Cetacean and seabird sightings included the following species of cetacean: pantropical spotted dolphin (21 sightings); spinner dolphin (5); clymene dolphin (3); Risso's dolphin (2); false killer whale (2); and pygmy killer whale, melon-headed whale, sperm whale, rough-toothed dolphin and striped dolphin (1). The majority of pantropical or spinner dolphin and seabird sightings, 61.9% and 80.0%, respectively, were associated with terns (sooty terns, *Sterna fuscata;* black terns, *Chlidonias niger*; sooty/bridled terns, *S. fuscata/S. anaethetus*; and *Sterna* sp.). The largest seabird flocks contained ~50 birds each and were all associated with pantropical spotted dolphins. Species most commonly involved in cetacean sightings were sooty tern (10 sightings); *Sterna* spp. (8); storm petrels (band-rumped, *Oceanodroma castro;* Leach's, *Oceanodroma leucorhoa*; or Wilson's, *Oceanites oceanicus*) (6); Audubon shearwater (*Puffinus lherminieri*) (4); pomarine jaegar (*Stercorarius pomarinus*) (3); and sooty/bridled tern (3).

Twenty-one (1.1%) cetacean sightings associated with fish schools were observed. Pantropical spotted dolphins were most commonly sighted with fish (8 sightings); other cetacean species were sighted with fish only on one or two

Table 3

Species sighted in mixed-species cetacean groups, associated with birds, and/or associated with fish. Total number of sightings includes on- and off-effort sightings. Percent values represent percentage of total sightings for each species.

		Mixed cetacean		With birds		With fish	
Species	Total no. sightings	No. sightings	%	No. sightings	%	No. sightings	%
Bryde's whale	17	0	0.0	0	0.0	1	5.9
Sperm whale	186	1	0.5	1	0.5	0	0.0
Cuvier's beaked whale	18	0	0.0	0	0.0	1	5.6
Mesoplodon spp.	29	0	0.0	0	0.0	1	3.4
Killer whale	13	1	7.7	0	0.0	0	0.0
False killer whale	11	3	27.3	2	18.2	0	0.0
Short-finned pilot whale	18	1	5.6	0	0.0	0	0.0
Melon-headed whale	17	5	29.4	1	5.9	0	0.0
Pygmy killer whale	11	0	0.0	1	9.1	0	0.0
Risso's dolphin	163	4	2.5	2	1.2	0	0.0
Rough-toothed dolphin	25	6	24.0	1	4.0	1	4.0
Fraser's dolphin	3	2	66.7	0	0.0	0	0.0
Common bottlenose dolphin	195	16	8.2	0	0.0	2	1.0
Pantropical spotted dolphin	468	1	0.2	21	4.5	8	1.7
Striped dolphin	54	0	0.0	1	1.9	1	1.9
Spinner dolphin	43	0	0.0	5	11.6	2	4.7
Clymene dolphin	53	1	1.9	3	5.7	1	1.9
Atlantic spotted dolphin	45	10	22.2	0	0.0	0	0.0

occasions. Pantropical spotted dolphins were associated with tuna (*Thunnus* spp.), flyingfish (Exocetidae), a whale shark (*Rhincodon typus*) and unidentified small fish. Of the eight pantropical spotted dolphin sightings associated with fish, five were also associated with seabirds.

DISCUSSION

Diversity

All of the cetacean species sighted during spring surveys appear to be regular, if not abundant, inhabitants of the Gulf of Mexico (Würsig *et al.*, 2000), although some species were not sighted during every year. Other species previously reported from the Gulf but not observed during the spring surveys are considered to be accidental, stray or extralimital. Jefferson and Schiro (1997) discussed seven reliable reports of fin whales (*Balaenoptera physalus*), all from summer, fall and winter. There are records of North Atlantic right whales (*Eubalaena glacialis*; 3 sightings, 1 stranding), blue whales (*B. musculus*; 2 strandings), sei whales (5 strandings) and a Sowerby's beaked whale (*M. bidens*; 1 stranding) (Würsig *et al.*, 2000; Southeast Fisheries Science Center [SEFSC] unpublished data). Common minke whales (*B. acutorostrata*; 10 strandings) and humpback whales (*Megaptera novaeangliae*; 6 sightings) are rare visitors to the Gulf of Mexico, but with most confirmed records occurring during winter and spring, they likely strayed during migration (Jefferson and Schiro, 1997; Weller *et al.*, 1996; Würsig *et al.*, 2000).

Distribution

With a few exceptions, the species distributions reported here are similar to those previously published, most of which were based on subsets of our dataset (Baumgartner, 1997; Baumgartner *et al.*, 2001; Hansen *et al.*, 1996; Mullin *et al.*, 1994a; b; c; Mullin and Hansen, 1999; Mullin and Hoggard, 2000; O'Sullivan and Mullin, 1997). One exception is for the rough-toothed dolphin reported almost exclusively in oceanic waters west of the Mississippi for surveys conducted during 1990-1994 (Mullin and Hansen, 1999). During subsequent aerial (Mullin and Hoggard, 2000) and ship surveys, groups were sighted both east of the Mississippi (Fig. 2j) and in continental shelf waters <100m deep (Fulling *et al.*, 2003). It is also important to note that Atlantic spotted, common bottlenose and rough-toothed dolphins are known to inhabit waters <100m deep in the Gulf (Fulling *et al.*, 2003), so our surveys of waters ≥100m deep did not cover the entire range of the distributions for these species.

The species distributions from spring surveys cannot necessarily be applied to other seasons. Seasonal aerial surveys of continental slope waters in the northwestern Gulf from 1992 to 1994 (summer, fall, winter, spring; Mullin *et al.*, 2004) and in the northeastern Gulf from 1996 to 1998 (summer, winter; Mullin and Hoggard, 2000) provided some evidence of seasonal changes in species abundance in slope waters. For example, during the 1996-1998 aerial surveys, five groups of clymene dolphins (3 summer, 2 winter) were sighted in the northeastern Gulf, an area where none were seen during spring ship surveys. These sightings were spatially sympatric with those of spinner dolphins during summer and winter (Mullin and Hoggard, 2000).

While the seasonal results of the aerial studies were not definitive, they demonstrated that cetaceans remained diverse (10-15 species) and abundant throughout the year and that no common species vacated slope waters seasonally. We suggest that the spring distributions reported here are similar to distributions for other seasons for the majority of species, but further surveys that span the entire oceanic northern Gulf during additional seasons are needed.

Studies of cetacean habitats in the Gulf, based wholly or in part on subsets of cetacean sightings from our dataset, have shown physiography (bottom depth, bottom depth gradient), mesoscale oceanographic features and zooplankton biomass to be significant variables in identifying species-specific cetacean habitat (Baumgartner, 1997; Davis *et al.*, 1998; 2002; Baumgartner *et al.*, 2001). However, prior to this study, direct comparisons of the habitats of specific species or groups of species have not been made.

Table 4

Species sighted in mixed-species cetacean groups, including associated species and number of sightings.

Species	*n*	Associated species in mixed-species groups (number of sightings)				
Common bottlenose dolphin	16	Atlantic spotted dolphin (9)	Risso's dolphin (3)	False killer whale (2)	Rough-toothed dolphin (1)	Unidentified dolphin (1)
Atlantic spotted dolphin	10	Common bottlenose dolphin (9)	Rough-toothed dolphin (1)			
Rough-toothed dolphin	6	Melon-headed whale (3)	Common bottlenose dolphin (1)	Atlantic spotted dolphin (1)	False killer whale (1)	
Melon-headed whale	5	Rough-toothed dolphin (3)	Fraser's dolphin (2)			
Risso's dolphin	4	Common bottlenose dolphin (3)	Unidentified dolphin (1)			
False killer whale	3	Common bottlenose dolphin (2)	Rough-toothed dolphin (1)			
Fraser's dolphin	2	Melon-headed whale				
Sperm whale	1	Clymene dolphin				
Clymene dolphin	1	Sperm whale				
Killer whale	1	Pantropical spotted dolphin				
Pantropical spotted dolphin	1	Killer whale				
Short-finned pilot whale	1	Unidentified dolphin				
Unidentified dolphin	3	Risso's dolphin (1)	Short-finned pilot whale (1)	Common bottlenose dolphin (1)		

All five species of the genus *Stenella* are known to occur in the Atlantic Ocean, and, to date, the northern Gulf is the only area with a large number of sightings of each. While this genus may in fact be polyphyletic (Rice, 1998; LeDuc *et al.*, 1999), similar external morphology suggests at least some level of ecological overlap, such as in prey size and energetic requirements. The distributions within the Gulf hint that some of the *Stenella* may avoid interspecific competition by spatial partitioning. Atlantic spotted dolphins are essentially parapatric with the other four oceanic species. Clymene and spinner dolphins appear nearly parapatric, at least in spring. Spatially, spinner and pantropical spotted dolphins are sympatric in eastern slope waters (200-2,000m), but they do not generally co-occur in abyssal waters (>2,000m) where pantropical spotted dolphins are abundant (Mullin and Fulling, 2004). Pantropical spotted dolphins are sympatric with striped dolphins throughout the northern oceanic Gulf and both are sympatric with clymene dolphins in the western Gulf.

Other species with a limited distribution in the Gulf include the Bryde's whale (found in the northeastern Gulf) and the melon-headed and short-finned pilot whales (primarily in the western Gulf). Most of these distributions have an east-west component; in general, the eastern and western northern oceanic regions have different physiographic and oceanographic characteristics (Baumgartner, 1997; Biggs and Ressler, 2001). Habitat heterogeneity in these waters may provide the opportunity for niche partitioning but more quantitative studies are needed.

Atlantic spotted dolphins do not occur in the oceanic waters of the Gulf far from the shelf-edge, although they do occur in oceanic waters in other parts of the Atlantic Ocean, including north of Cape Hatteras, North Carolina (Bero, 2001; Mullin and Fulling, 2003) and around the Azores archipelago (Silva *et al.*, 2003). While more study is needed, initial results indicate that Atlantic spotted and pantropical spotted dolphins do not generally co-occur in these areas[1]. Similarly, common bottlenose dolphins in the Gulf were rare seaward of the upper continental slope (i.e. >1,000m) but more common in deep waters north of Cape Hatteras (Kenney, 1990) and in the eastern tropical Pacific Ocean (ETP) (Scott and Chivers, 1990). Why the distributions of Atlantic spotted and common bottlenose dolphins do not extend further seaward in the Gulf of Mexico is not known, but it may be due to the oligotrophic mean state of the oceanic Gulf compared to the Atlantic Ocean north of the Gulf Stream Front and areas of the ETP where productive waters may afford these traditionally coastal species the opportunity to exploit oceanic habitats. In addition, where it occurs, the pantropical spotted dolphin may competitively exclude the Atlantic spotted dolphin from oceanic habitats.

Group size, sea surface temperature and depth

It is difficult to compare our results with previous studies of cetacean group size, SST and water depth in the Gulf because study areas have varied. For example, some previous studies only covered waters to a depth of 1,000 or 2,000m (e.g. Davis *et al.*, 1998; Mullin *et al.*, 1994b). Our

[1] A recent genetic study based on biopsy samples collected during research surveys has revealed four hybrids of the two species from the Gulf of Mexico and Atlantic. Personal communication from S.E. Kingston, NMFS/SEFSC, Marine Mammal Molecular Genetics Laboratory, 646 Cajundome Blvd. Rm. 219, Lafayette, LA 70506, USA, March 2004.

sample sizes are larger in most instances, and the ranges of group size, SST and depth tend to be broader than previously reported. Baumgartner *et al.* (2001) summarised data from three spring surveys (1992-1994, a subset of these data) for five cetacean species. The addition of sighting data from six additional surveys presented here did not affect group size descriptive statistics in most instances for these five species. In general, as with the distribution data, the present findings were similar to previous reports if differences in study area depth are taken into account.

The group size statistics reported here may be biased for some species. Groups were sighted during line-transect surveys and it is possible that larger groups were sighted disproportionally, particularly for those species with a large range of group sizes. For example, Mullin and Fulling (2004) estimated size-biased mean group sizes for pantropical spotted dolphin abundance estimates based on the regression of group size with perpendicular sighting distance (Buckland *et al.*, 2001), and found that the arithmetic mean overestimated mean group size by 27-52%. Sperm whale group sizes were estimated based on '10-minute' counts during line-transect surveys (once a sperm whale was sighted, all observers scanned 360° for 10 minutes to determine group size). Group sizes are certainly larger because sperm whale groups forage asynchronously (Whitehead, 1989; Whitehead and Weilgart, 1991; 2000; Whitehead, 1996). During a 2003 survey to obtain less biased estimates of sperm whale group size, 90-minute counts were conducted (observers scanned 360° for 90 minutes) that suggest mean group-sizes are at least 6-8 whales (SEFSC, unpublished data), considerably higher than the mean group-size of 2.6 reported here.

Interspecific associations

Similar to findings from vessel surveys, the percentage of mixed-species groups sighted during previous aerial surveys in the Gulf was low. Of 736 groups sighted during 12 seasonal aerial surveys conducted over the period from 1992-1998, only 9 sightings (1.4%) were of mixed-species groups (Mullin and Hoggard, 2000; Mullin *et al.*, 2004). However, there were mixed-species groups observed during aerial surveys that were not observed during ship surveys. Mullin *et al.* (1994b) sighted a mixed group of Risso's dolphins and *Globicephala* sp. during Gulf of Mexico aerial surveys. During another aerial survey study, Mullin *et al.* (2004) reported a mixed-species sighting of melon-headed whales, rough-toothed dolphins and Fraser's dolphins. No mixed groups of these three species were sighted during ship surveys, but rough-toothed and Fraser's dolphins were the only two species sighted with melon-headed whales, and the melon-headed whale was the only species sighted with Fraser's dolphins.

No dedicated seabird survey team was present during spring surveys, however, dedicated seabird surveys have been conducted in select areas of the oceanic Gulf (Davis and Fargion, 1996; Davis *et al.*, 2000). Although some species inhabit the Gulf year-round, the seasonal seabird composition varies (Hess and Ribic, 2000; Peake, 1999). Spring surveys produced the greatest species diversity of seabirds (28 species) and the second highest sighting rate after summer (Peake, 1999). Our findings on seabird species associated with cetaceans cannot necessarily be applied to other seasons; however, considering our observations were made during a time of high species diversity and high sighting rates, we suggest the general trend of few cetacean-seabird associated sightings applies year-round. Cetacean-seabird sightings during seasonal aerial surveys were also uncommon (Mullin and Hoggard, 2000; Mullin *et al.*, 2004).

The combinations of mixed-species groups reported here and the cetacean species that were observed associated with seabirds and fish are obviously not exhaustive. Additional effort may yield new combinations of associations, however, our results strongly suggest that interspecific interactions among cetaceans, seabirds and fish occur at low levels in the Gulf of Mexico.

Comparisons to areas outside the Atlantic Ocean

Most cetacean species that inhabit the oceanic Gulf are also distributed in warm waters throughout the world (Jefferson *et al.*, 1993). Comparisons of the relative abundances of cetacean species, group sizes, behaviours and associations (e.g. other cetacean species, birds, fish) from tropical regions throughout the world could provide an understanding of how they are affected by the biological and physical environment (Mullin *et al.*, 1994b). Ballance and Pitman (1998) compared cetacean communities in the ETP, western tropical Indian Ocean (WTIO) and the Gulf of Mexico. They noted that the major differences between the Gulf and ETP are that in the Gulf, pantropical spotted dolphins do not school with spinner dolphins, do not associate with surface tunas, are not accompanied by seabirds, and that the two species of *Stenella* exhibit largely parapatric distributions. The present data indicate these conclusions are essentially correct but can be quantified and refined.

Of 468 groups of pantropical spotted dolphins and 43 groups of spinner dolphins from our database, none were found in mixed-species groups with the other. Pantropical spotted dolphins in the Gulf were observed in association with fish in 4.5% of the sightings, including surface tunas, and were accompanied by seabirds in 0.2% of the sightings. The situation in the ETP and WTIO is very different where 58.9% and 58.3% of the pantropical spotted dolphin groups were found with seabirds and 33.5% and 58.3% were mixed with spinner dolphins, respectively (Au and Perryman, 1985; Au and Pitman, 1986; Ballance and Pitman, 1998).

Spinner dolphin sightings were widespread throughout continental slope waters of the eastern Gulf as were those of the pantropical spotted dolphin, so the two species are not parapatric. In addition, spinner dolphins were not associated with inshore waters, islands, banks or any other cetacean species. This supports the conclusion by Ballance and Pitman (1998) that association of spinner dolphins with these features in the open ocean is apparently not obligatory, as had been suggested previously (Norris *et al.*, 1994).

In the ETP, large flocks of seabirds accompanying dolphins, particularly pantropical spotted and spinner dolphins which are commonly associated with yellowfin tuna (*Thunnus albacares*), are a common and conspicuous sight. Purse-seine fishermen use the presence of seabird flocks as a reliable indication that tuna are accompanying the dolphins. Au and Perryman (1985) reported that 96.4%, 58.9% and 52.9% of groups of mixed pantropical spotted and spinner dolphins, pantropical spotted dolphins only and spinner dolphins only, respectively, occurred in association with seabird flocks in northern tropical waters of the ETP, and they assumed that their minimum flock size also indicated presence of tuna.

We found no indication that any interspecific interactions among any cetacean species, seabirds and tuna occurred in the Gulf at those levels. Our findings are more similar to those from the central and western Pacific, which also have

the species involved in such associations present, but lack the dolphin-seabird-tuna interactions (Au and Pitman, 1986). A variety of tuna species occur in the Gulf including yellowfin tuna, which are commercially harvested mainly by longline (during the years our surveys occurred, 1991-2001, commercial landings of yellowfin ranged from 1,327.5 to 4,155.2 metric tons[2]). However, large-bodied diving seabirds such as boobies (*Sula* spp.) that associate with dolphins and tunas in the ETP and feed on prey driven to the surface by them, are uncommon in the northern oceanic Gulf (Hess and Ribic, 2000).

The Gulf mixed-species cetacean interactions more closely resemble those obtained by Ballance and Pitman (1998) for the WTIO. Overall, mixed-species cetacean groups comprised only 4% of the total sightings in the WTIO and 1.4% in the Gulf. Some of the frequent associations between mixed-species cetacean groups in the WTIO were different than those reported here, such as the pantropical spotted and spinner dolphin association. However, in both the Gulf and WTIO, common bottlenose dolphins were recorded in mixed-species groups frequently and with more species than any other cetacean. Seabirds were recorded with cetaceans at a low level for both the WTIO (7%) and the Gulf of Mexico (2%), and in both places terns, especially sooty terns (*S. fuscata*), were among the most frequently recorded flocks associated with cetaceans.

Scott and Chivers (1990) reported that common bottlenose dolphin groups in the ETP were sighted in mixed-species cetacean groups most prevalently with short-finned pilot whales, Risso's dolphins, rough-toothed dolphins, pantropical spotted dolphins and spinner dolphins, and with at least eight other species. In the Gulf, they were recorded in mixed-species groups with four other cetacean species: Atlantic spotted dolphins; Risso's dolphins; false killer whales; and rough-toothed dolphins. In the Gulf therefore, they were obviously sighted with far fewer species, and those they most commonly associated with in the Gulf and ETP were different. However, in contrast to the ETP, common bottlenose dolphins in the Gulf are not commonly found seaward of the upper continental slope. Therefore, in the northern oceanic Gulf, one of the species that is most likely to form mixed-species groups does not generally co-occur with many of the species it associates with in the ETP.

An important factor to consider in regional comparisons is the size of each area, and the spatial and temporal scale of the oceanographic processes found in each. Of the ETP, WTIO and Gulf, the ecology of the ETP has been most thoroughly studied. The ETP study area is about 19 million km^2 (Wade and Gerrodette, 1993), almost 50 times larger than the northern oceanic Gulf. The vast area of the ETP has at least several persistent oceanographic regions, including 'tropical surface waters' and 'upwelling modified', where cetacean communities with different characteristics reside (Au and Perryman, 1985; Reilly, 1990) that do not occur in the Gulf. *Delphinus* spp. are absent in the Gulf but in the ETP they are common and are most abundant in the upwelling modified regions. Regions of the ETP where spinner dolphin-pantropical spotted dolphin-tuna-seabird associations are the most prevalent are those tropical surface waters (warm, low salinity) where the thermocline is sharp and shallow, and dolphins and tuna feed more frequently close to the surface where seabirds have access to the prey (Au and Perryman, 1985; Au and Pitman, 1986; Reilly, 1990). Neither of these oceanographic conditions exist in the Gulf on a similar scale, and when they do, they are largely ephemeral (Biggs and Ressler, 2001).

While Ballance and Pitman (1998) suggested that cetacean group sizes are generally similar in the ETP and the Gulf, there is a difference in the frequency of large groups (i.e. >300 animals) that occur and in their maximum sizes. Only 15 groups were that large in the Gulf and all were <1,000 animals. Large groups are much more common in the ETP and routinely exceed 1,000 animals (Au and Perryman, 1985; Leatherwood *et al.*, 1983).

We suggest that it is important to identify the region of the ETP used in comparisons, and that the Gulf and ETP may be less different when the large area at the western edge of the tropical surface and upwelling modified waters in the ETP is used in the comparison. Ballance *et al.* (1997) described this area as 'sooty tern-dominated'. In the ETP, <3% of all 'sooty tern flocks' (flocks with a large number of sooty terns) were associated with cetaceans, and waters where sooty tern flocks occurred were characterised by the deepest thermocline depth and the lowest surface productivity (Au and Perryman, 1985; Ballance *et al.*, 1997). A comparison of the oceanic northern Gulf and the sooty tern-dominated areas of the ETP may reveal fewer differences between the two. The seabirds that do occur routinely in the oceanic northern Gulf are terns, small shearwaters and storm petrels (Hess and Ribic, 2000). That is, small seabirds that can fly efficiently between patchy ephemeral food sources (Ballance *et al.*, 1997).

Comparisons to other areas of the Atlantic Ocean

During Cetacean and Turtle Assessment Program (CeTAP) surveys conducted between Cape Hatteras, North Carolina, and the northern Gulf of Maine during 1978-1982, 26 cetacean species were observed (CeTAP, 1982). Sixteen species were sighted in mixed-species groups, including sperm whales, common bottlenose dolphins, *Globicephala* spp., Risso's dolphins and striped dolphins. One of the most frequent mixed-species sightings was of common bottlenose dolphins and *Globicephala* spp. (n=84), a combination which we have not seen in the Gulf of Mexico. Also, striped dolphins were sighted with many different species, including sperm whales, common bottlenose dolphins and Risso's dolphins, but in the Gulf striped dolphins have not been sighted with any other cetacean species. Comparisons to CeTAP results should be made with caution however, as the term 'association' was used differently; in many instances during CeTAP, association simply meant animals sighted in the same general vicinity (Kenney, 1990).

During two ship surveys in the southeastern US Atlantic Ocean (US waters south of Maryland) conducted during summer 1998 and winter 2002, only 1.5% and 4.5% of all groups for the summer and winter surveys, respectively, were composed of mixed-species groups (SEFSC, unpublished data). The majority of mixed-species groups from the winter survey included species not found in the Gulf (*Delphinus* spp. and fin whale), whereas sightings from the summer survey included common bottlenose dolphins and *Globicephala* spp., again, a combination not seen in the Gulf. We hope that additional surveys in the southeastern US Atlantic will allow for better comparisons to this area, but preliminary findings suggest mixed-species groups occur at a low level, as they do in the Gulf.

In summary, the oceanic northern Gulf is physiographically complex and oceanographically dynamic, and has a diverse tropical cetacean community. The group

[2] Personal communication from the National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD, March 2004.

sizes, interspecific associations and species distributions we characterise here are different from those in other tropical regions where most of the same species occur. The underlying ecological reasons for these differences between tropical regions and for the intra-Gulf species distributions we observed are fertile areas for future research.

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REFERENCES

Au, D.W.K. and Perryman, W.L. 1985. Dolphin habitats in the eastern tropical Pacific. *Fish. Bull.* 83(4):623-43.

Au, D.W.K. and Pitman, R.L. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. *Condor* 88:304-17.

Ballance, L.T. and Pitman, R.L. 1998. Cetaceans of the western tropical Indian Ocean: distribution, relative abundance, and comparisons with cetacean communities of two other tropical ecosystems. *Mar. Mammal Sci.* 14(3):429-59.

Ballance, L.T., Pitman, R.L. and Reilly, S.B. 1997. Seabird community structure along a productivity gradient: importance of competition and energy constraint. *Ecology* 78(5):1502-18.

Baumgartner, M.F. 1997. The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. *Mar. Mammal Sci.* 13(4):614-38.

Baumgartner, M.F., Mullin, K.D., May, L.N. and Leming, T.D. 2001. Cetacean habitats in the northern Gulf of Mexico. *Fish. Bull.* 99(2):219-39.

Bernard, H.J. and Reilly, S.B. 1999. Pilot whales *Globicephala* Lesson, 1828. pp. 245-79. *In:* S. Ridgway and R. Harrison (eds.) *Handbook of Marine Mammals* Vol. 6 *The Second Book of Dolphins and the Porpoises*. Academic Press, San Diego. 486pp.

Bero, L. 2001. Population structure of the Atlantic spotted dolphin, *Stenella frontalis*, in the Gulf of Mexico and western North Atlantic. MSc Thesis, University of Charleston, Charleston, SC. 101pp.

Biggs, D.C. and Ressler, P.H. 2001. Distribution and abundance of phytoplankton, zooplankton, ichthyoplankton, and micronekton in the deepwater Gulf of Mexico. *Gulf of Mexico Science* 19(1):7-29.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK. xv+432pp.

Caldwell, D.K. and Caldwell, M.C. 1989. Pygmy sperm whale, *Kogia breviceps* (de Blainville, 1838); dwarf sperm whale, *Kogia simus* (Owen, 1866). pp. 235-60. *In:* S.H. Ridgway and R. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 4. *River Dolphins and the Larger Toothed Whales*. Academic Press, London and San Diego. 442pp.

CeTAP. 1982. A characterization of marine mammals and turtles in the mid- and north Atlantic areas of the US outer continental shelf. Report BLM/YR/TR-82/03, Bureau of Land Management, US Department of the Interior, Washington, DC, USA. 538pp.

Cummings, W.C. 1985. Bryde's whale – *Balaenoptera edeni* Anderson, 1878. pp. 137-54. *In:* S.H. Ridgway and R. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 3. *The Sirenians and Baleen Whales*. Academic Press, London and Orlando. xviii+362pp.

Davis, R.W. and Fargion, G.S. (eds.). 1996. Distribution and abundance of cetaceans in the north-central and western Gulf of Mexico: Final report. Volume II: Technical Report. OCS Study MMS 96-0027. US 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. and Mullin, K. 1998. Physical habitat of cetaceans along the continental slope in the north-central and western Gulf of Mexico. *Mar. Mammal Sci.* 14(3):490-507.

Davis, R.W., Evans, W.E. and Würsig, B. (eds.). 2000. Cetaceans, sea turtles and seabirds in the northern Gulf of Mexico: Distribution, abundance and habitat associations. Volume II: Technical report. OCS Study MMS 2000-003. US Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. 346pp.

Davis, R.W., Ortega-Ortiz, J.G., Ribic, C.A., Evans, W.E., Biggs, D.C., Ressler, P.H., Cady, R.B., Leben, R.R., Mullin, K.D. and Würsig, B. 2002. Cetacean habitat in the northern oceanic Gulf of Mexico. *Deep-Sea Research I* 49:121-42.

Fulling, G.L., Mullin, K.D. and Hubard, C.W. 2003. Abundance and distribution of cetaceans in outer continental shelf waters of the US Gulf of Mexico. *Fish. Bull.* 101(4):923-32.

Hansen, L.J., Mullin, K.D. and Roden, C.L. 1995. Estimates of cetacean abundance in the northern Gulf of Mexico from vessel surveys. NOAA, NMFS, Southeast Fisheries Science Center, Miami Laboratory Contribution No. MIA-94/95-25 (unpublished). 20pp. [Available from SEFSC, 3209 Frederic St., Pascagoula, MS 39567].

Hansen, L.J., Mullin, K.D., Jefferson, T.A. and Scott, G.P. 1996. Visual surveys aboard ships and aircraft. pp. 55-132. *In:* R.W. Davis and G.S. Fargion (eds.) Distribution and abundance of marine mammals in the north-central and western Gulf of Mexico: Final report. Volume II: Technical Report. OCS Study MMS 96-0027. Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. 357pp.

Hess, N.A. and Ribic, C.A. 2000. Seabird ecology. pp. 275-315. *In:* R.W. Davis, W.E. Evans and B. Würsig (eds.) Cetaceans, sea turtles and seabirds in the northern Gulf of Mexico: Distribution, abundance and habitat associations. Volume II: Technical Report. OCS Study MMS 2000-003. Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. 346pp.

Jefferson, T.A. 1996. Estimates of abundance of cetaceans in offshore waters of the northwestern Gulf of Mexico, 1992-93. *Southwest. Nat.* 41(3):279-87.

Jefferson, T.A. and Schiro, A.J. 1997. Distribution of cetaceans in the offshore Gulf of Mexico. *Mammal Rev.* 27(1):27-50.

Jefferson, T.A., Leatherwood, S. and Webber, M.A. 1993. *Marine Mammals of the World —FAO Species Identification Guide*. FAO, Rome. 320pp.

Kenney, R.D. 1990. Bottlenose dolphins off the northeastern United States. pp. 369-86. *In:* S. Leatherwood and R.R. Reeves (eds.) *The Bottlenose Dolphin*. Academic Press, San Diego. 653pp.

Leatherwood, S., Reeves, R.R. and Foster, L. 1983. *The Sierra Club Handbook of Whales and Dolphins*. Sierra Club Books, San Francisco. xvii+302pp.

Leatherwood, S., Jefferson, T.A., Norris, J.C., Stevens, W.E., Hansen, L.J. and Mullin, K.D. 1993. Occurrence and sounds of Fraser's dolphins, *Lagenodelphis hosei*, in the Gulf of Mexico. *Texas J. Sci.* 45(4):349-54.

LeDuc, R.G., Perrin, W.F. and Dizon, A.E. 1999. Phylogenetic relationships among the delphinid cetaceans based on full cytochrome b sequences. *Mar. Mammal Sci.* 15(3):619-48.

Mead, J.G. 1989. Beaked whales of the genus *Mesoplodon*. pp. 349-430. *In:* S.H. Ridgeway and R. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 4. *River Dolphins and the Larger Toothed Whales*. Academic Press Inc., London and San Diego. i-xix+442pp.

Mullin, K.D. and Fulling, G.L. 2003. Abundance of cetaceans in the southern US North Atlantic Ocean during summer 1998. *Fish. Bull.* 101(3):603-13.

Mullin, K.D. and Fulling, G.L. 2004. Abundance of cetaceans in the oceanic northern Gulf of Mexico, 1996-2001. *Mar. Mammal Sci.* 20(4):787-807.

Mullin, K.D. and Hansen, L.J. 1999. Marine mammals of the Gulf of Mexico. pp. 269-77. *In:* H. Kumpf, K. Steidinger and K. Sherman

(eds.) *The Gulf of Mexico Large Marine Ecosystem*. Blackwell Science, London. 704pp.
Mullin, K.D. and Hoggard, W. 2000. Visual surveys of cetaceans and sea turtles from aircraft and ships. pp. 111-72. *In:* R.W. Davis, W.E. Evans and B. Würsig (eds.) *Cetaceans, Sea Turtles, and Seabirds in the Northern Gulf of Mexico: Distribution, Abundance and Habitat Associations. Volume II: Technical Report*. OCS Study MMS 96-0027. Minerals Management Service, Gulf of Mexico OCS Region, New Orleans. 346pp.
Mullin, K.D., Higgins, L.V., Jefferson, T.A. and Hansen, L.J. 1994a. Sightings of the Clymene dolphin (*Stenella clymene*) in the Gulf of Mexico. *Mar. Mammal Sci.* 10(4):464-70.
Mullin, K.D., Hoggard, W., Roden, C.L., Lohoefener, R.R. and Rogers, C.M. 1994b. Cetaceans on the upper continental slope in the north-central Gulf of Mexico. *Fish. Bull.* 92(4):773-86.
Mullin, K.D., Jefferson, T.A., Hansen, L.J. and Hoggard, W. 1994c. First sightings of melon-headed whales (*Peponocephala electra*) in the Gulf of Mexico. *Mar. Mammal Sci.* 10(3):342-8.
Mullin, K.D., Hoggard, W. and Hansen, L.J. 2004. Abundance and seasonal occurrence of cetaceans in outer continental shelf and slope waters of the north-central and northwestern Gulf of Mexico. *Gulf of Mexico Science* 22(1):62-73.
Norris, K.S., Würsig, B., Wells, R.S. and Würsig, M. 1994. *The Hawaiian Spinner Dolphin*. University of California Press, Berkeley. 408pp.
O'Sullivan, S. and Mullin, K.D. 1997. Killer whales (*Orcinus orca*) in the northern Gulf of Mexico. *Mar. Mammal Sci.* 13(1):141-7.
Peake, D.E. 1999. Distribution and relative abundance of pelagic seabirds of the northern Gulf of Mexico. pp. 236-47. *In:* H. Kumpf, K. Steidinger and K. Sherman (eds.) *The Gulf of Mexico Large Marine Ecosystem*. Blackwell Science, London. 704pp.
Pitman, R.L., O'Sullivan, S. and Mase, B. 2003. Killer whales (*Orcinus orca*) attack a school of pantropical spotted dolphins (*Stenella attenuata*) in the Gulf of Mexico. *Aquat. Mamm.* 29(3):321-4.
Reilly, S.B. 1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. *Mar. Ecol. Prog. Ser.* 66:1-11.
Rice, D.W. 1998. *Marine Mammals of the World. Systematics and Distribution.* Special Publication No. 4. The Society for Marine Mammalogy, Allen Press Inc., Lawrence, Kansas. v-ix+231pp.
Schmidly, D.J. 1981. *Marine Mammals of the Southeastern United States and the Gulf of Mexico*. US Department of the Interior, US Fish and Wildlife Service Biological Services Program FWS/OBS-80/41. 165pp. [Available from NTIS, 5285 Port Royal Road, Springfield, VA 22161].
Scott, M.D. and Chivers, S.J. 1990. Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific Ocean. pp. 387-402. *In:* S. Leatherwood and R.R. Reeves (eds.) *The Bottlenose Dolphin*. Academic Press, San Diego. 653pp.
Silva, M.A., Prieto, R., Magalhães, S., Cabecinhas, R., Cruz, A., Goncalves, J.M. and Santos, R.S. 2003. Occurrence and distribution of cetaceans in the waters around the Azores (Portugal), summer and autumn, 1999-2000. *Aquat. Mamm.* 29(1):77-83.
Wade, P.R. and Gerrodette, T. 1993. Estimates of cetacean abundance and distribution in the eastern tropical Pacific. *Rep. int. Whal. Commn* 43:477-93.
Weller, D.W., Schiro, A.J., Cockcroft, V.G. and Ding, W. 1996. First account of a humpback whale (*Megaptera novaeangliae*) in Texas waters, with a re-evaluation of historical records from the Gulf of Mexico. *Mar. Mammal Sci.* 12(1):133-7.
Whitehead, H. 1989. Formations of foraging sperm whales, *Physeter macrocephalus*, off the Galapagos Islands. *Can. J. Zool.* 67(9):2131-9.
Whitehead, H. 1996. Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behav. Ecol. Sociobiol.* 38(4):237-44.
Whitehead, H. and Weilgart, L. 1991. Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour* 118(3-4):275-96.
Whitehead, H. and Weilgart, L. 2000. The sperm whale: social females and roving males. pp. 154-72. *In:* J. Mann, R.C. Connor, P. Tyack and H. Whitehead (eds.) *Cetacean Societies*. University of Chicago Press, Chicago. 433pp.
Wiseman, W.J., Jr. and Sturges, W. 1999. Physical oceanography of the Gulf of Mexico: processes that regulate its biology. pp. 77-92. *In:* H. Kumpf, K. Steidinger and K. Sherman (eds.) *The Gulf of Mexico Large Marine Ecosystem*. Blackwell Science, London. 704pp.
Würsig, B., Jefferson, T.A. and Schmidly, D.J. 2000. *The Marine Mammals of the Gulf of Mexico*. Texas A&M University Press, College Station. 232pp.

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