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THE DISTRIBUTION OF RISSO'S DOLPHIN (*GRAMPUS GRISEUS*) WITH RESPECT TO THE PHYSIOGRAPHY OF THE NORTHERN GULF OF MEXICO

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ABSTRACT

The distribution of Risso's dolphin (*Grampus griseus*) was examined with respect to two physiographic variables, water depth and depth gradient (sea floor slope), in the northern Gulf of Mexico, using shipboard and aerial survey data collected from 1992 to 1994. Univariate χ^2 analyses demonstrated that Risso's dolphins are distributed non-uniformly with respect to both depth and depth gradient. A bivariate analysis of the shipboard data indicated that Risso's dolphins utilize the steep sections of the upper continental slope in the northern Gulf of Mexico. This narrow core habitat is in waters bounded by the 350-m and 975-m isobaths with depth gradients greater than 24 m per 1.1 km and consists of only 2% of the surface area of the entire Gulf of Mexico. Sighting rates inside this region were nearly 5 and 6 times the average for the shipboard and aerial surveys, respectively. Of the groups sighted outside this region, 40% (shipboard) and 73% (aerial) were encountered within 5 km of it. Since it is unlikely that the physiography alone can attract dolphins, oceanographic mechanisms that may concentrate prey along the steep upper continental slope are discussed. The implications of this distribution, including potential prey species, foraging strategies, and impacts of proposed mineral exploration and development, are also considered.

Key words: Risso's dolphin, *Grampus griseus,* Gulf of Mexico, habitat, physiography, depth, depth gradient.

Relationships between the distribution of cetaceans and physiographic features have been demonstrated for several species, including common dolphins (*Delphinus delphis*) (Evans 1975; Hui 1979, 1985; Selzer and Payne 1988), short-finned pilot whales (*Globicephala macrorhynchus*) (Hui 1985), Atlantic white-sided dolphins (*Lagenorhynchus acutus*) (Selzer and Payne 1988), and

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humpback whales (*Megaptera novaeangliae*) (Sutcliffe and Brodie 1977, Payne *et al.* 1986). These relationships suggest that complex seafloor relief can concentrate prey species through oceanographic mechanisms such as topographically-induced upwelling of nutrients, increased primary productivity, and aggregation of zooplankton due to enhanced secondary production or convergence of surface waters. Cetacean habitat can be defined in terms of these relationships to physiography or other physical parameters with the underlying assumption that the physical environment is not directly significant. Instead, the primary influence over cetacean distribution is the aggregation of prey species promoted by the physical environment.

The northern Gulf of Mexico contains very diverse physiographic regimes, including a broad, flat continental shelf along the west Florida and Texan coasts, a very narrow and steep shelf and slope off the Mississippi delta, two major canyon systems imbedded in the continental slope and shelf edge (the Mississippi and DeSoto canyons), a complex topography of salt domes and basins on the northwestern continental slope, a very steep escarpment off the west Florida shelf, a variably sloping continental slope and rise, and flat abyssal plains. The oceanography of the Gulf is also diverse, both temporally and spatially. The dominant feature of the eastern Gulf of Mexico is the Loop Current, a significant part of the Gulf Stream system which enters the Gulf from the Yucatan Strait, turns anticyclonically, and exits *via* the Straits of Florida. The Loop Current penetrates northward into the Gulf on a quasi-annual cycle (Sturges and Evans 1983), extending as far north as the Mississippi/Alabama/Florida continental shelf (Huh *et al.* 1981). The western Gulf is characterized by a large anticyclonic gyre (Nowlin and McLellan 1967) which is occasionally impacted and probably forced by warm-core eddies that are shed by the Loop Current in the east (Elliot 1982). Continental shelf waters are greatly influenced by river runoff, and frequently an oceanic front on the outer shelf and upper slope separates the cooler, fresh shelf waters from the warmer, salty oceanic waters.

The complex physiographic and oceanographic environment of the northern Gulf of Mexico may promote the concentration of prey for some cetaceans. The Risso's dolphin or gray grampus (*Grampus griseus*) has been recognized as an inhabitant of the Gulf of Mexico since 1968 (Paul 1968) and has been observed on the upper continental slope of the northern Gulf in previous studies (Jennings 1982, Mullin *et al.* 1994, Davis *et al.* 1995). Leatherwood *et al.* (1980) described the distribution of Risso's dolphin in the eastern north Pacific as oceanic, occurring mostly seaward of the 100-fathom curve, although several sightings of this species were over the continental shelf. Some anecdotal evidence of this species' relationship to steep topography exists (Würtz *et al.* 1992, Davis *et al.* 1995), suggesting that it may be possible to define a habitat for Risso's dolphins in terms of physiography.

This paper examines the distribution of Risso's dolphins with respect to the physiography of the northern Gulf of Mexico based on shipboard and aerial surveys conducted by the National Marine Fisheries Service. Two physiographic variables were considered, water depth and depth gradient (seafloor slope), to specifically explore the possible relationships between Risso's dolphins and the upper continental slope and steep topography. The shipboard and aerial data were analyzed separately due to significant differences in survey capabilities associated with each platform, such as vessel speed and detection range. While the shipboard surveys were conducted during only the spring seasons, the aerial surveys were conducted throughout the year.

Methods

Data Collection

Shipboard surveys were conducted from the NOAA Ship *Oregon II* in the oceanic (> 200 m) northern Gulf of Mexico (the area approximately north of a line from Key West, Florida, to Brownsville, Texas) in the spring seasons of 1992, 1993, and 1994. The survey transects were generally conducted perpendicular to the local topography and sampled the entire study area at least once per cruise (Fig. 1a). Cetacean sighting data were collected visually during daylight hours using two 25× 'big eye' binoculars mounted atop the flying bridge, as well as hand-held binoculars and the naked eye (see Holt and Sexton 1990). The time, position, species, and group size of all cetaceans encountered were recorded digitally with a laptop computer. When necessary, the ship was diverted from the transect to approach a group in order to estimate group size and identify the species. Ancillary data, including sighting conditions, sea state, and effort status were recorded by the observers. Position and time data were recorded automatically at regular intervals *via* a LORAN-C positioning receiver interfaced with the computer.

Aerial surveys were conducted from a NOAA-operated DeHavilland Twin Otter aircraft modified with concave 'bubble' windows on each side for improved monitoring of the track line. Similar data were collected as in the shipboard survey (*i.e.*, species, position, time, *etc.*). Data from two aerial survey programs were used in this study. The Gulf of Mexico regional survey program (hereafter referred to as the GOMEX survey) was conducted between 1992 and 1994 and covered a coastal stratum from the shoreline to the 18.3-m isobath and an outer continental shelf stratum from the 18.3-m isobath to 9.3 km past the 183-m isobath (Blaylock and Hoggard 1994). Aerial surveys conducted during the GulfCet Program between 1992 and 1994 concentrated on the waters of the continental slope between the 100-m and 1,000-m isobaths from the Texas/Mexico border to the Mississippi/Alabama border (Davis *et al.* 1995). Both surveys were conducted at an altitude of 229 m (750 ft), and transects were generally perpendicular to the local bathymetry (Fig. 1b).

The physiographic data were not collected during the surveys but were derived from a U.S. Minerals Management Service digital bathymetry dataset compiled by Dynalysis of Princeton for the Gulf of Mexico (Herring 1993). This dataset was compiled from three separate data sources: NAVOCEANO's DBDB5 5-min-by-5-min gridded bathymetry, National Ocean Service's high resolution coastal bathymetric dataset, and Texas A&M's digitized bathymetric

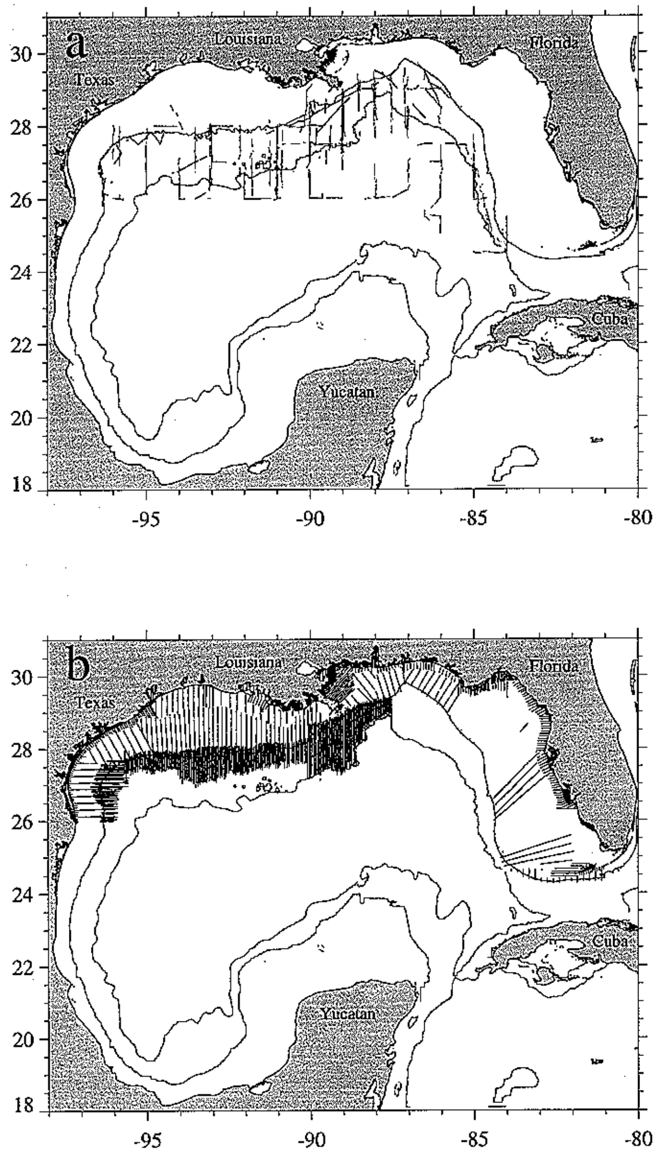

Figure 1. (a) Shipboard survey transects conducted by the NOAA Ship *Oregon II* in the spring seasons of 1992, 1993, and 1994. (b) Aerial survey transects conducted during the GOMEX (inshore and continental shelf) and GulfCet (continental slope) programs. The 200 m and 2,000 m isobaths are shown.

charts. These independent sources were merged and interpolated on a gridded field having a cell resolution of 0.01° latitude by 0.01° longitude. The digital dataset provided a depth for every 1.2 km² area in the Gulf of Mexico. I derived the depth gradient from this base bathymetric dataset using digital image processing (specifically, an image gradient computation employing vertical and horizontal Sobel operators). The depth gradient dataset had the same base resolution and aerial coverage of the original bathymetry dataset and yielded the slope of the sea floor in units of meters per 1.1 km for every 1.2 km^2 area of the Gulf of Mexico.

Data Treatment and Statistical Methods

The effort and cetacean sighting datasets were initially treated separately. The effort data consisted of a set of position/time records for each contiguous transect (one day of survey effort). These records were collected at one- to two-minute intervals *via* the LORAN-C/computer system described above. The physiographic data were extracted from the digital depth and depth gradient datasets at each survey position and included in the position/time records. Each contiguous transect was then broken into 1-km (shipboard) or 3-km (aerial) linear sections which were considered the base unit of effort. The physiographic data were averaged over these linear sections so that each section or unit of effort had only one representative depth or depth gradient. Only those units of effort that were actively surveyed during adequate sighting conditions (sea state of Beaufort 3 or less for the shipboard and Beaufort 4 or less for the aerial surveys) were used in the subsequent analyses. These sighting requirements guaranteed that the analyses would include only those transect sections where cetaceans could be sighted with a reasonable probability if they were present.

The cetacean sighting dataset consisted of one record for each group observed while actively searching and during adequate sighting conditions. Each sighting record contained the species, group size, time, and position of the encounter, as well as the depth and depth gradient extracted from the digital datasets for the location of the sighting.

The analysis of the sighting and effort datasets relied on the use of a simple chi-square (χ^2) test to determine if the Risso's dolphin groups were distributed non-uniformly with respect to the physiographic variables. Both univariate and bivariate forms of the χ^2 test were employed by determining a predicted, uniform distribution of dolphin groups from the effort dataset with respect to one or both of the physiographic variables. The observed distribution of Risso's dolphins with respect to the same physiographic variable or variables was compared to this expected distribution using the χ^2 statistic. The univariate χ^2 analysis has been applied successfully in previous studies of cetacean distribution (Hui 1979, 1985; Smith *et al.* 1986; Selzer and Payne 1988 [using the G rather than χ^2 statistic]). The bivariate test is a simple extension of the univariate form and was used to investigate the distribution of Risso's dolphins with respect to both depth and depth gradient simultaneously.

The predicted, uniform distribution or frequency histogram in the univariate χ^2 test was determined from the effort dataset by classifying the values of the physiographic variable such that each class contained an equal amount of effort. Using an equal amount of effort in each class is a departure from the conventional frequency histogram (Kendall and Stuart 1967) and was used to 'normalize' the effort by creating class sizes of equal probability, not equal intervals (*i.e.,* each class will predict the same number of sightings for a uniform distribution). This approach avoided the distortion of the predicted uniform distribution due to classes with unusually low or high amounts of effort. The histogram of the effort was then converted to an expected uniform distribution using the following equation (after Hui 1979):

$$E_i = n\frac{L_i}{L_T} \tag{1}$$

where E_i is the expected number of sightings in class i, n is the total number of group sightings, L_i is the amount of effort in class i, and L_T is the total amount of effort. The actual or observed distribution of dolphins with respect to the physiographic variable was then determined using the same class intervals and quantitatively compared to this expected uniform distribution using the χ^2 statistic. All statistics were considered significant at $\alpha = 0.05$. The sighting rate (R_i) in each class was then computed as

$$R_i = \frac{n_i}{DL_i} \tag{2}$$

where n_i is the number of sightings in class i, L_i is as above, and D is the number of kilometers in a unit of effort (1 km for shipboard surveys, 3 km for aerial surveys). Sighting rates are expressed as the number of sightings per 100 km for shipboard surveys and the number of sightings per 1,000 km for aerial surveys.

Note that Equation 1 can be rearranged so that L_i can be computed given an expected number of sightings (E_i) in each class. Since a conservative application of the χ^2 statistic requires that each class contain at least five expected sightings, the rearranged equation was used to compute the amount of effort required to predict at least five expected sightings in each class. This procedure was used to determine how much effort should be included in each class when computing the original histogram of the effort. For example, if 100 groups of dolphins (n) were sighted during 8,000 total units of survey effort (L_T), selecting five expected sightings per class ($E_i = 5$) would yield 400 units of effort in each class (L_i).

The expected uniform distribution with respect to both depth and depth gradient in the bivariate χ^2 test was determined by first classifying each of the variables independently as described above to determine the class intervals. Both the effort and the sightings were then classified by the joint class intervals to create the bivariate contingency table. The expected number of sightings is

$$E_{ij} = n\frac{L_{ij}}{L_T} \tag{3}$$

where E_{ij} is the expected number of sightings that fall into both depth class i and depth gradient class j, n is the total number of sightings, L_{ij} is the total

Table 1. Dates, duration, and total distance traveled for all shipboard and aerial surveys.

Survey	Start date	End date	Duration (days)	Distance (km)
Shipboard				
Cruise 199	Apr 22 92	Jun 07 92	38	3,453
Cruise 204	May 04 93	Jun 15 93	39	2,374
Cruise 209	Apr 16 94	Jun 09 94	36	3,275
			113	9,102
Aerial				
GulfCet 1	Aug 12 92	Sep 18 92	15	7,353
GOMEX 1	Sep 16 92	Oct 24 92	20	10,092
GulfCet 2	Nov 14 92	Dec 13 92	9	5,598
GulfCet 3	Feb 07 93	Mar 21 93	11	6,501
GulfCet 4	Apr 27 93	May 31 93	16	7,611
GulfCet 5	Aug 03 93	Aug 20 93	14	6,675
GOMEX 2	Sep 17 93	Oct 19 93	18	9,573
GulfCet 6	Nov 11 93	Dec 16 93	12	6,492
GulfCet 7	Feb 06 94	Mar 15 94	13	6,726
GOMEX 3	Sep 28 94	Oct 15 94	11	5,679
			139	72,300

amount of effort in depth class i and depth gradient class j, and L_T is the total amount of effort. The actual number of sightings in each class was compared to the expected number using the χ^2 statistic.

Results

The shipboard surveys completed 9,102 km of effort during adequate sighting conditions in 113 d over the three spring cruises (Table 1). The GulfCet aerial surveys completed 46,956 km in 90 d of survey effort and the GOMEX surveys 25,344 km in 49 d of survey effort. Sixty-seven and 25 groups of Risso's dolphins were sighted during shipboard and aerial surveys, respectively, while actively surveying during acceptable sighting conditions. Average sighting rates were 0.74 group sightings per 100 km (shipboard) and 0.35 per 1,000 km (aerial).

The results of the univariate χ^2 analysis of the shipboard survey data with respect to depth are presented in Table 2. The distribution of Risso's dolphins was significantly different from an expected, uniform distribution with respect to depth (χ^2 = 53.9, df = 12, $P \ll 0.001$). The sighting rate distribution is shown in Figure 2a. The overall distribution of the shipboard effort with respect to depth is shown in Figure 2b. The sighting rate distribution is modal about the upper continental slope (*ca.* 200–1000 m).

The distribution of Risso's dolphins with respect to depth gradient was also significantly different from an expected uniform distribution (χ^2 = 57.2, df = 12, $P \ll 0.001$; Table 3). The sighting rate distribution with respect to

Table 2. Contingency table of shipboard survey results with respect to depth. The range, mean, and standard deviation of the depth as well as the effort (L), number of group sightings (n), expected number of sightings (E), χ^2 contribution ($[E - n]^2 E^{-1}$), and sighting rate in each class are reported. Effort is in units of effort, depth is in meters, and sighting rates are the number of group sightings per 100 km searched.

	Class statistics				χ^2 analysis				
Class	Min	Max	Mean	SD	L	n	E	$\frac{(E-n)^2}{E}$	Sighting rate
1	16≤	<117	80	26	700	0	5.2	5.2	0.00
2	117≤	<257	181	41	700	1	5.2	3.3	0.14
3	257≤	<470	352	54	700	12	5.2	9.1	1.71
4	470≤	<747	616	82	700	17	5.2	27.2	2.43
5	747≤	<936	830	54	700	8	5.2	1.6	1.14
6	936≤	<1,162	1,035	60	700	6	5.2	0.1	0.86
7	1,162≤	<1,416	1,295	73	701	3	5.2	0.9	0.43
8	1,416≤	<1,717	1,566	96	700	4	5.2	0.3	0.57
9	1,717≤	<2,045	1,874	105	700	3	5.2	0.9	0.43
10	2,045≤	<2,372	2,181	96	700	3	5.2	0.9	0.43
11	2,372≤	<2,903	2,659	149	700	3	5.2	0.9	0.43
12	2,903≤	<3,242	3,089	100	700	6	5.2	0.1	0.86
13	3,242≤	≤3,510	3,309	74	701	1	5.2	3.4	0.14
					9,102	67	67.0	53.9	(df = 12, $P \ll 0.001$)

depth gradient and the overall distribution of shipboard effort are presented in Figure 3. Linear correlation analysis of the average depth gradients and the sighting rates in each class reveals a strong relationship between groups of Risso's dolphins and depth gradient ($r = 0.978$, $t = 15.5$, df = 11, $P \ll 0.001$). Caution must be exercised in interpreting this linear relationship, however, since the final point in the correlation (class 13 in Table 3) represents a very large range of high depth gradients. The use of linear regression analysis to predict sighting rates based on this apparent linear relationship is inappropriate for two reasons. The actual relationship would more likely be asymptotic instead of linear, with the distribution tailing off over large depth gradients to an asymptote close to the sighting rate in class 13. More importantly, the distribution of Risso's dolphins is not solely related to depth gradient, but also to water depth as was demonstrated above. The bivariate analysis resolved the distribution of these dolphins with respect to the observed physiography more effectively than the independent univariate tests alone.

The distribution of Risso's dolphins with respect to both depth and depth gradient (Table 4) is significantly different than a uniform distribution predicted from the effort ($\chi^2 = 91.7$, df = 16, $P \ll 0.001$). Note, however, that three of the classes in the bivariate contingency table contain an expected number of sightings of less than one (Table 4c). Although this violates the most basic, non-conservative requirements of the χ^2 test, the contingency table itself contains results that are quite significant. The class bounded by the

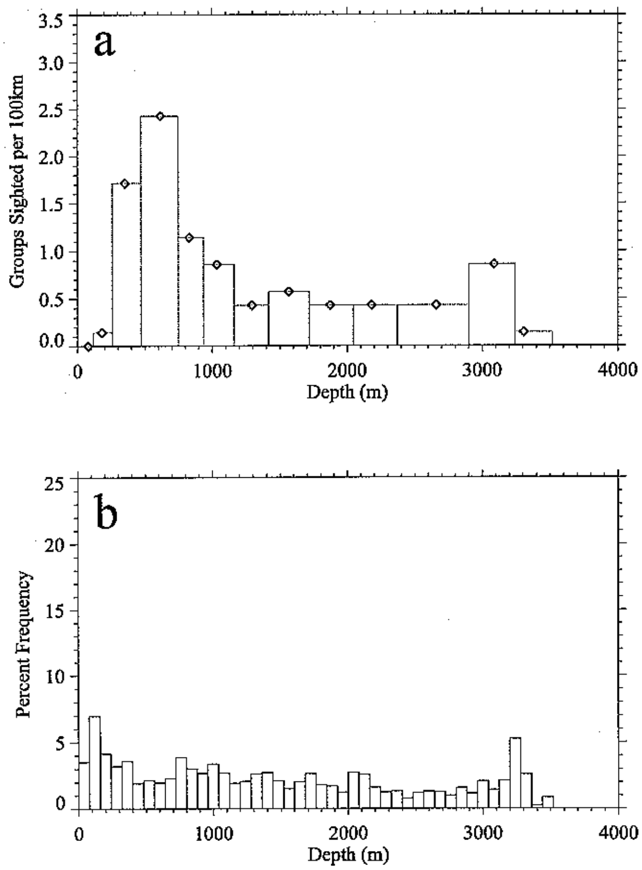

Figure 2. (a) Sighting rate distribution of Risso's dolphin with respect to depth from shipboard surveys. (b) Overall distribution of effort with respect to depth from shipboard surveys.

359-m and 976-m isobaths with depth gradients 23.8 m 1.1 km^{-1} or greater accounts for 66% of the total χ^2 statistic and alone is sufficient to make the bivariate χ^2 test significant ($\chi^2_{0.001}$ = 39.3, df = 16). Thirty percent of the sightings (20 of 67) are found in this class while only 6% of the effort was expended in the class, yielding a sighting rate almost five times the average. Figure 4a shows the regions of the Gulf of Mexico where the water depth is between 350 m and 975 m and the depth gradient is 24 m 1.1 km^{-1} or greater. Of the remaining dolphin sightings, 40% (19 of 47) were encountered within 5 km of this area. Due to the disproportionate number of sightings close to and inside this area, the steep sections of the upper continental slope are considered significant in the distribution of Risso's dolphins.

Class limits were selected arbitrarily in the bivariate analysis, so it would seem quite fortuitous if the analysis selected the exact limits of Risso's dolphin habitat based on depth and depth gradient. The identified area can be

Table 3. Contingency table of shipboard survey results with respect to depth gradient. Effort is in units of effort, depth gradient in m 1.1 km^{-1}, and sighting rates are the number of group sightings per 100 km searched.

	Class statistics				χ^2 analysis				
Class	Min	Max	Mean	SD	L	n	E	$\frac{(E-n)^2}{E}$	Sighting rate
1	0.0≤	<1.6	0.9	0.4	700	2	5.2	1.9	0.29
2	1.6≤	<2.5	2.0	0.3	700	3	5.2	0.9	0.43
3	2.5≤	<3.3	2.9	0.3	700	3	5.2	0.9	0.43
4	3.3≤	<4.8	4.0	0.4	700	2	5.2	1.9	0.29
5	4.8≤	<6.6	5.7	0.5	700	2	5.2	1.9	0.29
6	6.6≤	<8.6	7.6	0.6	700	1	5.2	3.3	0.14
7	8.6≤	<10.8	9.7	0.7	700	4	5.2	0.3	0.57
8	10.8≤	<13.6	12.2	0.8	700	5	5.2	0.0	0.71
9	13.6≤	<16.7	15.1	0.9	700	4	5.2	0.3	0.57
10	16.7≤	<21.2	18.8	1.3	700	5	5.2	0.0	0.71
11	21.2≤	<28.1	24.4	2.0	700	8	5.2	1.6	1.14
12	28.1≤	<41.6	33.8	3.8	700	8	5.2	1.6	1.14
13	41.6≤	≤402.5	75.7	46.5	702	20	5.2	42.6	2.85
					9,102	67	67.0	57.2	(df = 12, $P \ll 0.001$)

considered a core of the habitat, though, since the depth and depth gradient classes in the immediate vicinity of the steep upper continental slope class in Table 4 still have a larger number of sightings than expected. The class bounded by 359–976 m, 13.1–23.8 m 1.1 km^{-1} and the deeper class bounded by 976–1669 m, 23.8–402.5 m 1.1 km^{-1} both have sighting rates roughly twice the average, while the shallower class bounded by 16–359 m, 23.8–402.5 m 1.1 km^{-1} has a sighting rate about three times the average (although this sighting rate may be inflated due to low effort in this class). These classes, combined with the core class bounded by 359–976 m, 23.8–402.5 m 1.1 km^{-1}, account for 55% of the sightings with only 19% of the effort being expended in these classes, yielding a sighting rate roughly three times the average. The 'rolloff' of elevated sighting rates in classes adjacent to the steep upper continental slope class in Table 4, as well as the high number of sightings in spatial proximity to the area represented by this class (Fig. 4a), support its designation as a core region of Risso's dolphin habitat.

The univariate analysis of the aerial survey data provides complementary results when compared to the shipboard survey analyses. The distribution of Risso's dolphins was found to be significantly different from expected uniform distributions with respect to both depth (χ^2 = 25.6, df = 4, $P \ll$ 0.001; Table 5) and depth gradient (χ^2 = 31.6, df = 4, $P \ll 0.001$; Table 6). A similar modal relationship about the upper continental slope is evident in the sighting rate distribution with respect to depth (Fig. 5a) when compared to the shipboard survey results (Fig. 2a). Although inappropriate for

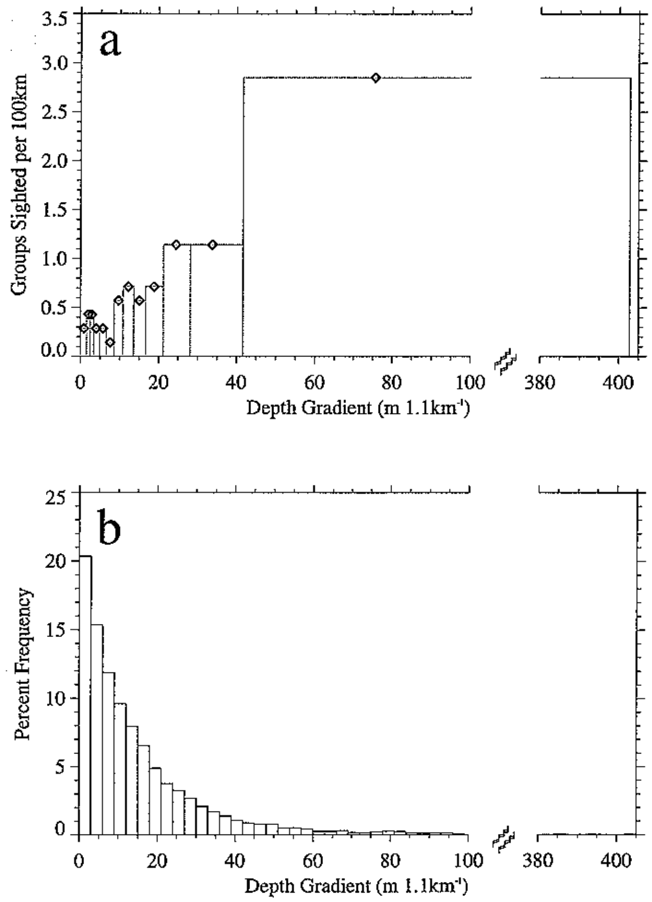

Figure 3. (a) Sighting rate distribution with respect to depth gradient from the shipboard surveys. Note that the abscissa axis is not continuous between 100 and 380 m 1.1 km^{-1}. (b) Overall distribution of effort with respect to depth gradient from the shipboard surveys. The amount of effort in waters with depth gradients greater than 100 m 1.1 km^{-1} was 1.3% of the total effort.

the conservative χ^2 test, the sighting rate distribution was computed with less effort in each class to better resolve the distribution of dolphins about the upper continental slope (Fig. 7a). Linear correlation analysis of the average depth gradients and sighting rates in each class of Table 6 ($r = 0.998$, $t = 28.0$, df = 3, $P \ll 0.01$) give results very similar to the shipboard survey results. The sighting rate distribution with respect to depth gradient is presented in Figure 6a, and the distribution computed with lower effort in each class in Figure 7b. While the distributions of Risso's dolphins from the shipboard and aerial surveys were similar, the differences in sighting rates are attributable to the relative detection capabilities of the two survey platforms.

The sightings from the aerial surveys provide an opportunity to indepen-

Table 4. Bivariate contingency table of shipboard survey results with respect to depth (m) and depth gradient (m 1.1 km^{-1}). (a) Effort (L), (b) observed (n), (c) expected (E), and (d) χ^2 contribution ($[E - n]^2 E^{-1}$) are shown. The χ^2 value of 91.7 is highly significant (df = 16, $P \ll 0.001$).

a

	Depth					
Depth gradient	16–359	359–976	976–1669	1669–2614	2614–3510	Total
0.0–3.0	801	67	68	153	731	1820
3.0–7.0	470	190	251	344	565	1820
7.0–13.1	229	482	417	455	237	1820
13.1–23.8	238	518	484	445	135	1820
23.8–402.5	82	563	600	423	154	1822
Total	1820	1820	1820	1820	1822	9102

b

	Depth					
Depth gradient	16–359	359–976	976–1669	1669–2614	2614–3510	Total
0.0–3.0	2	1	0	2	2	7
3.0–7.0	0	0	1	2	2	5
7.0–13.1	1	5	2	0	2	10
13.1–23.8	1	7	1	2	1	12
23.8–402.5	2	20	8	1	2	33
Total	6	33	12	7	9	67

c

	Depth					
Depth gradient	16–359	359–976	976–1669	1669–2614	2614–3510	Total
0.0–3.0	5.9	0.5	0.5	1.1	5.4	13.4
3.0–7.0	3.5	1.4	1.8	2.5	4.2	13.4
7.0–13.1	1.7	3.5	3.1	3.3	1.7	13.3
13.1–23.8	1.8	3.8	3.6	3.3	1.0	13.5
23.8–402.5	0.6	4.1	4.4	3.1	1.1	13.3
Total	13.5	13.3	13.4	13.3	13.4	66.9

d

	Depth					
Depth gradient	16–359	359–976	976–1669	1669–2614	2614–3510	Total
0.0–3.0	2.6	0.5	0.5	0.7	2.1	6.4
3.0–7.0	3.5	1.4	0.4	0.1	1.1	6.5
7.0–13.1	0.3	0.6	0.4	3.3	0.1	4.6
13.1–23.8	0.3	2.7	1.8	0.5	0.1	5.3
23.8–402.5	3.2	60.7	2.9	1.4	0.7	68.9
Total	9.9	65.9	6.0	6.0	3.9	91.7

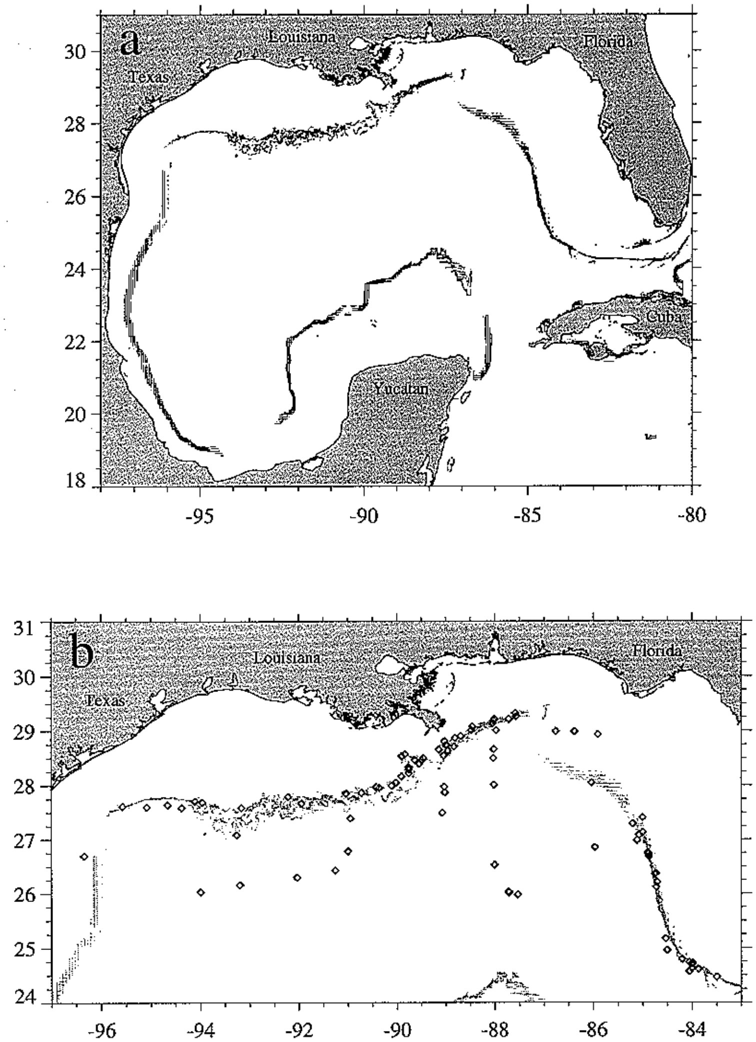

Figure 4. (a) Area of the Gulf of Mexico bounded by the 350-m and 975-m isobaths with depth gradients greater than 24 m 1.1 km^{-1}. (b) Sightings of Risso's dolphin groups from both shipboard and aerial surveys. Area shaded in gray is the identified habitat depicted in (a).

dently test the fidelity of Risso's dolphins to the core region identified in the bivariate analysis (Fig. 4a). Forty percent of the groups sighted during the aerial surveys (10 of 25) were found in water depths between 350 and 975 m and depth gradients of 24 m 1.1 km^{-1} or greater while only 7% of the effort was expended in this region, yielding a sighting rate nearly 6 times the average. Of the 15 remaining groups, 73% (11 of 15) were sighted within 5 km of the area depicted in Figure 4a. All of the sightings for the shipboard

Table 5. Contingency table of aerial survey results with respect to depth. Effort is in units of effort, depth is in meters, and sighting rates are the number of group sightings per 1,000 km searched.

	Class statistics				χ^2 analysis				
Class	Min	Max	Mean	SD	L	n	E	$\frac{(E-n)^2}{E}$	Sighting rate
1	0≤	<21	7	6	4,825	0	5.0	5.0	0.00
2	21≤	<127	72	34	4,822	0	5.0	5.0	0.00
3	127≤	<470	252	97	4,820	10	5.0	5.0	0.69
4	470≤	<955	739	138	4,821	12	5.0	9.8	0.83
5	955≤	≤2,428	1,337	315	4,812	3	5.0	0.8	0.21
					24,100	25	25.0	25.6	(df = 4, $P \ll 0.001$)

and aerial surveys combined are shown in relation to the identified habitat in Figure 4b.

Since several investigators have used contour index to describe physiography (Evans 1975; Hui 1979, 1985; Selzer and Payne 1988), it is useful to compare the results obtained in the above analyses to a description of the distribution of Risso's dolphins with respect to contour index. Contour index (after Evans 1975) was derived from the original bathymetry dataset (Herring 1993) as

$$CI = 100\frac{D_{max} - D_{min}}{D_{max}} \tag{4}$$

where CI is the contour index and D_{min} and D_{max} are the minimum and maximum depths, respectively, of each 13 km^2 area of the Gulf. The contour index dataset had the same base resolution and aerial coverage of the original bathymetry dataset. A univariate analysis was conducted in the same manner

Table 6. Contingency table of aerial survey results with respect to depth gradient. Effort is in units of effort, depth gradient is in m 1.1 km^{-1}, and sighting rates are the number of group sightings per 1,000 km searched.

	Class statistics				χ^2 analysis				
Class	Min	Max	Mean	SD	L	n	E	$\frac{(E-n)^2}{E}$	Sighting rate
1	0.0≤	<0.6	0.3	0.2	4,821	0	5.0	5.0	0.00
2	0.6≤	<4.3	2.0	1.1	4,820	0	5.0	5.0	0.00
3	4.3≤	<10.4	7.2	1.8	4,820	3	5.0	0.8	0.21
4	10.4≤	<18.9	14.2	2.4	4,820	7	5.0	0.8	0.48
5	18.9≤	≤158.0	31.5	14.1	4,819	15	5.0	20.0	1.04
					24,100	25	25.0	31.6	(df = 4, $P \ll 0.001$)

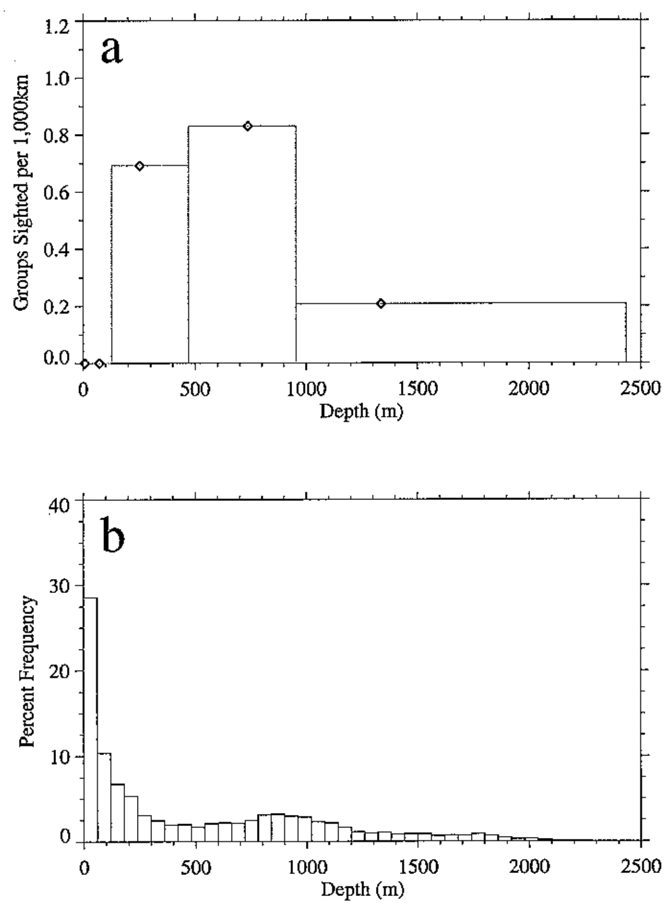

Figure 5. (a) Sighting rate distribution of Risso's dolphin with respect to depth from aerial surveys. (b) Overall distribution of effort with respect to depth from aerial surveys.

as described above for depth and depth gradient. Since contour index is proportional to the ratio of depth gradient to depth, it should incorporate the effects of both. Hence, the core region identified in the bivariate analysis may be more simply represented by contour index alone.

The results of the univariate χ^2 analysis of the shipboard survey data with respect to contour index are presented in Table 7, and the sighting rate distribution is shown in Figure 8a. The distribution of Risso's dolphins was significantly different from an expected uniform distribution with respect to contour index (χ^2 = 71.8, df = 12, $P \ll 0.001$). Class 13 (Table 7) was selected as a potential habitat since this class contains 33% (22 of 67) of the sightings and only 8% of the effort or a sighting rate 4 times the average. Figure 9 shows all sightings from the shipboard and aerial surveys combined in relation to waters with contour indices of 21% or greater.

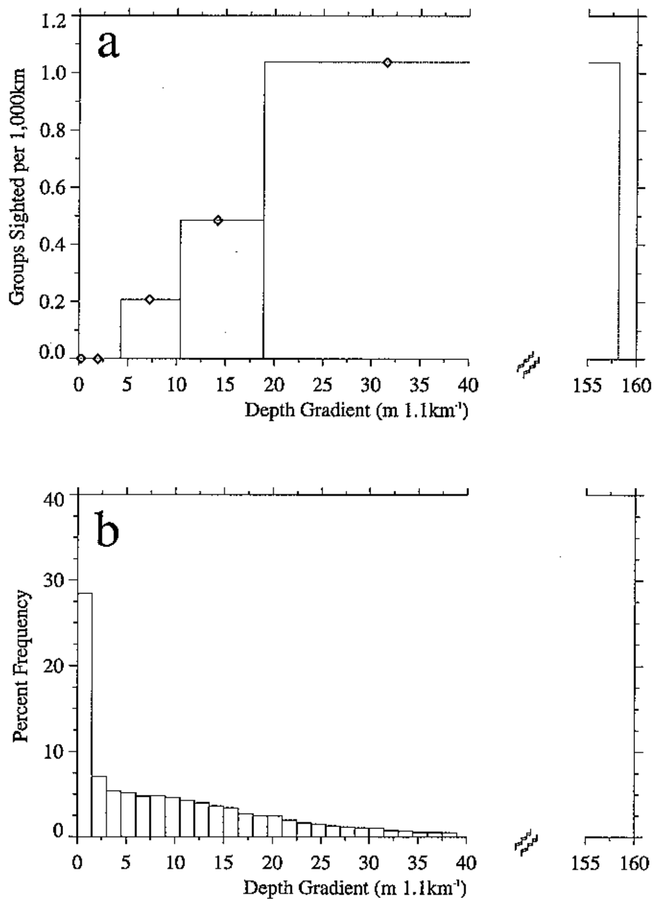

Figure 6. (a) Sighting rate distribution with respect to depth gradient from aerial surveys. Note that the abscissa axis is not continuous between 40 and 155 m 1.1 km^{-1}. (b) Overall distribution of effort with respect to depth gradient from aerial surveys. The amount of effort in waters with depth gradients greater than 40 m 1.1 km^{-1} was 3.8% of the total effort.

From this figure it is clear that contour index alone is inadequate as an indicator of Risso's dolphin habitat. Many areas on the continental shelf are included in this contour index class; however, Risso's dolphins were never observed landward of the 225-m isobath in any of the shipboard or aerial surveys. The inclusion of the upper continental slope in this high-contour index class is primarily due to the high depth gradients of the slope. While contour index is adept at identifying complex seafloor relief, it is unable to distinguish between distinctly different features that may have the same contour index value, such as a smooth, inclining continental slope, a submarine canyon, the shelf break, significant topographic features on the relatively flat continental shelf, or subtle features very close to shore. Distin-

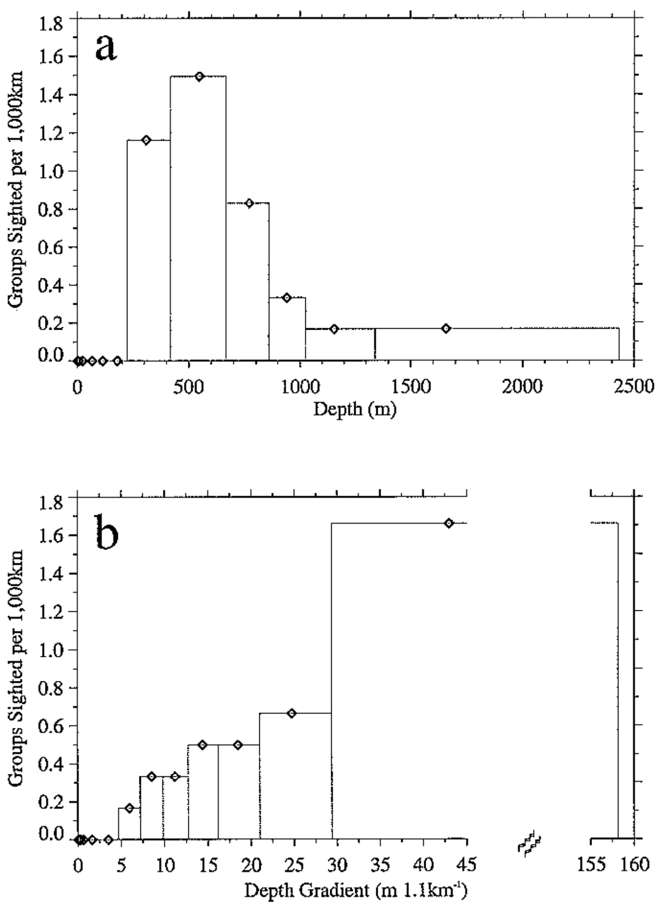

Figure 7. (a) Sighting rate distribution of Risso's dolphin with respect to depth from aerial surveys. Computation of sighting rates is the same as in Table 5 (Fig. 5) but with $L_i \approx 2{,}008$ (6,024 km). (b) Sighting rate distribution of Risso's dolphin with respect to depth gradient from the aerial surveys. Computation of sighting rates is the same as in Table 6 (Fig. 6) but with $L_i \approx 2{,}008$. Note that the abscissa axis is not continuous between 45 and 155 m 1.1 km^{-1}. Effort in waters with depth gradients greater than 45 m 1.1 km^{-1} was 2.4% of the total effort.

guishing between these features is vital to understanding what topographically influenced oceanographic processes are important in determining the distribution of cetaceans.

Discussion

The narrow region of the northern Gulf of Mexico bounded by the 350-m and 975-m isobaths with seafloor slopes greater than 24 m 1.1 km^{-1} is considered a core habitat of Risso's dolphins, since sighting rates within this region were almost five times the average sighting rates for the shipboard

Table 7. Contingency table of shipboard survey results with respect to contour index. Effort is in units of effort, contour index is in percent, and sighting rates are the number of group sightings per 100 km searched.

	Class statistics				χ^2 analysis				
Class	Min	Max	Mean	SD	L	n	E	$\frac{(E-n)^2}{E}$	Sighting rate
1	0.0≤	<0.3	0.2	0.1	700	2	5.2	1.9	0.29
2	0.3≤	<0.7	0.5	0.1	700	4	5.2	0.3	0.57
3	0.7≤	<1.3	1.0	0.2	700	4	5.2	0.3	0.57
4	1.3≤	<2.0	1.7	0.2	700	3	5.2	0.9	0.43
5	2.0≤	<2.9	2.4	0.2	700	4	5.2	0.3	0.57
6	2.9≤	<3.7	3.3	0.3	700	0	5.2	5.2	0.00
7	3.7≤	<5.0	4.3	0.4	700	1	5.2	3.3	0.14
8	5.0≤	<6.5	5.7	0.4	701	4	5.2	0.3	0.57
9	6.5≤	<8.4	7.4	0.5	700	3	5.2	0.9	0.43
10	8.4≤	<10.7	9.5	0.7	701	4	5.2	0.3	0.57
11	10.7≤	<14.5	12.5	1.1	700	8	5.2	1.6	1.14
12	14.5≤	<21.0	17.4	1.9	700	8	5.2	1.6	1.14
13	21.0≤	≤54.9	28.8	6.9	700	22	5.2	55.1	3.14
					9,102	67	67.0	71.8	(df = 12, $P \ll 0.001$)

surveys and nearly six times the average for the aerial surveys. Forty and 73% of the groups not encountered in this region during the shipboard and aerial surveys, respectively, were within 5 km of it. It is unlikely, however, that the physiography alone attracts dolphins. The shelf edge and upper continental slope are frequently sites of increased biological activity due to the formation of oceanic fronts along the shelf break. These fronts generally separate cooler, fresher shelf waters from warmer, saltier slope waters, and aggregations of prey species along these fronts may be the primary influence on the distribution of Risso's dolphins.

Higher concentrations of phytoplankton (Fournier *et al.* 1979, Herman and Denman 1979, Herman *et al.* 1981, Holligan and Groom 1986, Marra *et al.* 1990), zooplankton (Herman *et al.* 1981), fish (Maul *et al.* 1984, Herron *et al.* 1989, Podestá *et al.* 1993), seabirds (Kinder *et al.* 1983), and cetaceans (Brown and Winn 1989) have been observed within or in close proximity to frontal systems near the shelf break. In general, physical mechanisms such as tidal stirring, dissipation of internal waves, or eddy/slope interaction at the shelf break can promote lateral and vertical mixing. The amplitudes of these physical processes can be enhanced along steeper sections of the slope or near irregular topography, such as shelf-edge canyons (Huthnance 1981). Upwelling introduces nutrients from deeper shelf or slope waters into the euphotic zone, which stimulates increased rates of primary productivity (Fournier *et al.* 1979, Marra *et al.* 1990). Increased phytoplankton biomass at the front can then support secondary production if the front is stable and long-lived. Zooplankton

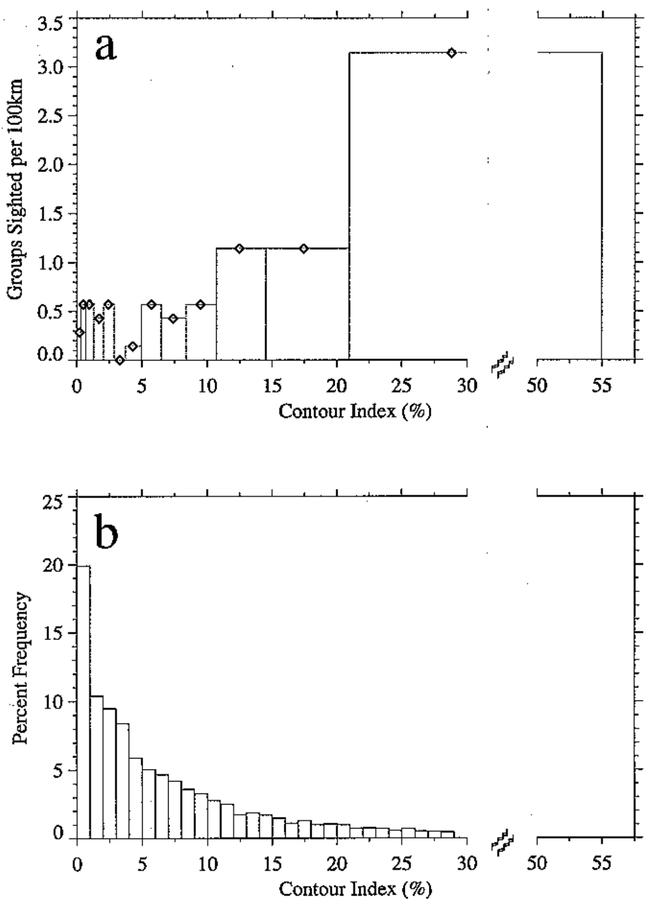

Figure 8. (a) Sighting rate distribution of Risso's dolphins with respect to contour index from shipboard surveys. (b) Overall distribution of effort with respect to contour index from shipboard surveys. Note that the abscissa axis is not continuous between 30% and 50%. The amount of effort in classes with contour indices greater than 30% was 2.5% of the total effort.

maintain their position within the front by swimming vertically against upwelling or downwelling currents (Olson and Backus 1985) and, hence, aggregate at the frontal interface. Higher trophic consumers, including cetaceans, can then take advantage of the higher concentrations of zooplankton at the front either directly (Brown and Winn 1989) or through the aggregation of prey species.

The distribution of Risso's dolphins along the steeper sections of the upper continental slope of the northern Gulf of Mexico is probably associated with the physical/biological interactions just described. Documented interactions between shelf waters and the Loop Current in the northeastern and eastern Gulf (Maul 1977, Huh *et al.* 1981, Molinari and Mayer 1982, Schroeder *et al.* 1987) suggest that the Loop Current may influence physical and biological

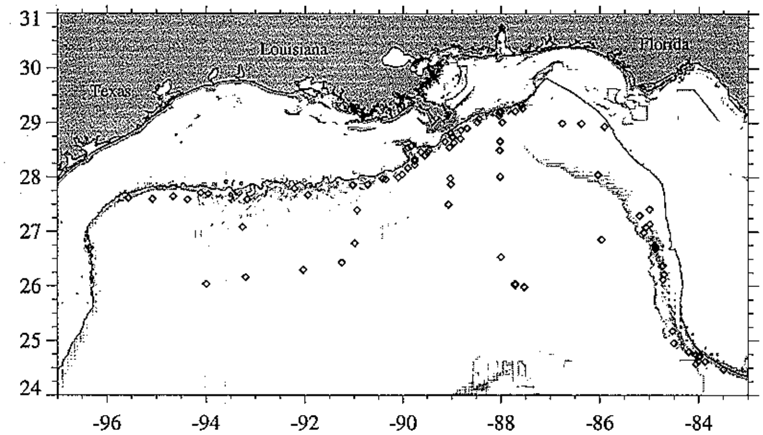

Figure 9. Sightings of Risso's dolphin groups from both shipboard and aerial surveys in relation to waters with contour indices of 21% or greater. The 200-m isobath is shown.

processes at the shelf break. Herron *et al.* (1989) found that high catch rates of demersal butterfish (*Perprilus burti*) in the northeastern Gulf were strongly associated with a shelf break front between shelf waters and a northerly extension of the Loop Current. They described the front as a recurrent feature over the three years of their study, indicating that shelf break fronts may be common in this region. Maul *et al.* (1984) described an association of high catch rates for Atlantic bluefin tuna (*Thunnus thynnus thynnus*) with proximity to the edge of the Loop Current along the Florida Escarpment near the Dry Tortugas (24°36′N, 82°54′W). This region of high tuna catches was later determined to be an active upwelling system caused by a cyclonic Loop Current meander over the continental slope (Vukovich and Maul 1985). The association of apex predators such as the Atlantic bluefin tuna with fronts suggests that enhanced primary production and aggregation of zooplankton at the frontal interface can attract predators throughout the food chain. There is no reason to suspect that Risso's dolphins do not also take advantage of higher concentrations of prey species along the upper continental slope in response to shelf break fronts.

Risso's dolphins prey almost exclusively on cephalopods (Clarke and Pascoe 1985, Würtz *et al.* 1992). While little is known of cephalopod distributions in the Gulf of Mexico, Voss (1971) characterized one species, the shortfin squid (*Illex illecebrosus*), as having a distribution along the continental slope in such abundance as to warrant the proposal of a commercial fishery. This squid is also concentrated about the shelf break and continental slope in the Middle Atlantic Bight (Wilk *et al.* 1988) and is associated with upwelling regions along the slope (O'Dor 1983). Due to its overlap in distribution with Risso's dolphin, this species of squid seems a likely candidate as a primary prey species of Risso's dolphins within, and possibly outside, the Gulf of Mexico. Other predators that have been associated with shelf break fronts also prey on shortfin

Table 8. Areas of various depth strata in the Gulf of Mexico, including the identified Risso's dolphin habitat between the 350-m and 975-m isobaths with depth gradients larger than 24 m 1.1 km^{-1}.

Region	Area (km^2)	Percentage of Gulf
Gulf of Mexico	1,718,482	100
Continental shelf (< 200 m)	623,444	36
Upper continental slope (≥ 200 m and < 1000 m)	200,441	12
Lower continental slope (≥ 1000 m and < 2000 m)	237,691	14
Oceanic waters (≥ 2000 m)	656,905	38
Between 350-m and 975-m isobaths	135,697	8
Identified habitat	36,921	2

squid, including swordfish (*Xiphias gladius*) (Podestá *et al.* 1993) and bluefin tuna (*Thunnus thynnus*) (Lange and Sissenwine 1980, Maul *et al.* 1984). Kenney and Winn (1986) found that teuthivorous cetaceans, including Risso's dolphins, were concentrated near the shelf break and upper continental slope in the Mid Atlantic Bight during the CeTAP study (CeTAP 1982, Hain *et al.* 1985). Also included in this group of teuthivorous cetaceans was a known predator of shortfin squid, pilot whales (*Globicephala melaena*) (Sergeant 1962, Mercer 1975). Only direct observations of feeding or stomach content analyses, however, can confirm this hypothesis.

It is also plausible that Risso's dolphins take advantage of a wide variety of cephalopod prey, since the upper continental slope and shelf break region is a transition zone between two distinct ecosystems, the continental shelf and oceanic waters. These dolphins have been known to take neritic cephalopods in addition to oceanic species (Clarke and Pascoe 1985, Würtz *et al.* 1992) and have been encountered on the shelf in the northeastern Pacific (Leatherwood *et al.* 1980). A physical mechanism that may explain this diet is shelf/oceanic water exchange at the upper continental slope and shelf break. As mentioned above, mesoscale oceanographic features such as the Loop Current can transport water from the shelf to the upper slope (Maul 1977, Schroeder *et al.* 1987), providing a windfall of shelf species for oceanic predators. Likewise, similar physical features can push more oceanic waters onto the shelf (Huh *et al.* 1981). A predator situated along the boundary of shelf and oceanic waters is in a strategic position to benefit from advection of prey species in and out of its vicinity. Movements onto the shelf, such as those documented by Leatherwood *et al.* (1980), or to deep waters (Fig. 4b), may be related to this foraging strategy. As fronts move on or off the shelf and upper continental slope, Risso's dolphins may move with them to continue to take advantage of prey aggregations. Once these fronts dissipate, the dolphins move back to the core habitat at the upper continental slope, possibly to meet the next shelf break front.

A significant portion of the identified habitat in the northern Gulf of Mexico (Fig. 4b) is presently a proposed region for large-scale mineral exploration and development. Recognition of the Risso's dolphin as a potentially affected species in this endeavor is not only vital to the long-term health of the Gulf of Mexico population but is also required by the U.S. Marine Mammal Protection Act. Should industrial activity commence within this region, Risso's dolphins must be carefully monitored for changes in distribution. The core habitat for this species is quite narrow, representing only 2% of the total area of the Gulf (Table 8). Outside this core habitat, a much more conservative estimate of the area used by Risso's dolphins would be the entire upper continental slope, which still makes up only 12% of the total area of the Gulf. Any disruptions of this dolphin's distribution along the upper continental slope by forcing movement onto the shelf or to deeper waters may have serious implications for the long-term survival of this species in the Gulf of Mexico.

Although this study has identified a close association of Risso's dolphins with the steeper sections of the upper continental slope, the discussed mechanisms which might attract dolphins to this region are only hypotheses. Demonstrating causal links between increased primary productivity, aggregations of zooplankton, concentration of prey species, and high encounter rates of dolphins at oceanic fronts is difficult unless high resolution or synoptic environmental monitoring is utilized. All of the shelf break studies cited here used rapid sampling schemes to sample the water column across a front (*e.g.*, to-yo'ed CTD or instrumented Batfish or Seasoar vehicles) or synoptic satellite data to determine large-scale frontal features with surface signatures (*e.g.*, AVHRR or CZCS). While some hydrographic measurements were obtained during the shipboard surveys in this study, the spatial scales were inadequate to accurately resolve shelf break fronts. Continuous measurements of surface properties from a flow-through shipboard system are often also inadequate, since surface properties may not always be correlated with subsurface structure (especially near a front), biological activity may be offset from the surface signature of a front (Brown and Winn 1989, Podestá *et al.* 1993), or important along-front horizontal variability may not be sampled at all over a single transect through the frontal region. Smaller scale studies with higher environmental sampling rates are required to resolve the precise physical and biological interactions that influence cetacean distribution along the shelf break and upper continental slope.

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