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Zoogeography of Cetaceans off Puerto Rico and the Virgin Islands

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ABSTRACT.—A zoogeographical analysis of cetaceans in the waters of Puerto Rico, US Virgin Islands, and British Virgin Islands was conducted to document the different species found, and to relate their occurrences to patterns of ocean floor topography. A total of 2,016 sighting records was entered into a specially formatted database system, and analyzed for distributional and temporal patterns. Species included 13 odontocetes and four mysticetes. The hypothesis that the spatial distribution of cetaceans is highly correlated to the area's bathymetric relief, whether high or low, was generally supported. Through the use of a relative slope index measure, each sighting was characterized by depth classes (shelf, shelf edge, or offshore), and by sea floor relief.

RESUMEN.—Para documentar la presencia de las distintas especies de cetáceos y relacionar la misma con patrones de topografía del fondo marino, se llevó a cabo un análisis zoogeográfico de los cetáceos de Puerto Rico, Islas Vírgenes Estadounidenses e Islas Vírgenes Británicas. Un total de 2,016 avistamientos fueron anotados en una base de datos con formato específico para avistamientos, y los datos fueron analizados en busqueda de patrones de distribución espacial y temporal. Las especies estudiadas incluyeron 13 odontocetos y cuatro misticetos. La hipótesis de que la distribución espacial de los cetáceos está estrechamente relacionada con el relieve batimétrico del área, ya sea alto o bajo, fue apoyada generalmente. A través de una medida de índice de pendiente relativa, cada avistamiento fue caracterizado por categoría de profundidad (de plataforma, borde de plataforma o mar afuera) y por relieve del fondo marino.

INTRODUCTION

Whales and dolphins are an intricate part of the marine and coastal fauna of the northeastern Caribbean Sea, with some of the islands serving as primary habitat for the mating and calving of endangered species. Although the presence of these creatures has been documented (Erdman, 1970; Erdman et al., 1973; Taruski and Winn, 1976; Mattila and Clapham, 1989), there is still a lack of information on the basic biology, life history and distribution of the species in the northeastern Caribbean. Two basic questions remain: where and when are each of the cetacean species found, and which factors affect their distribution in the northeastern Caribbean.

Cetacean distribution may be determined by factors which enhance the availability of food and the suitable conditions required for reproduction (Townsend, 1935), including water temperature, bottom depth, tidal flow, currents, areas of upwelling or areas of convergence and divergence, prey movements or concentrations, and sea floor relief. Of these conditions, water temperature seems to be the most important factor in determining breeding and calving grounds, at least in large whales (Gaskin, 1982). In contrast, whale and dolphin congregations in high latitude feeding grounds appear to be more related to phenomena such as ocean fronts, eddies and areas of upwelling which concentrate prey. These three features can be of either of a dynamic or topographic nature, with the latter highly induced by surface land masses or underwater sea floor relief (i.e. sea mounts, subsurface ridges and edges of the continental shelf) (Gaskin, 1982).

There is a direct relationship between cetacean distribution and bottom topogra-

phy in some areas (Hui, 1985; Kenney and Winn, 1987; Selzer and Payne, 1988). In many instances, sea floor contour appears to be the limiting factor affecting species aggregations (Gaskin, 1971). Probably as bottom topography increases in complexity, so does the complexity of the total aquatic environment (Hui, 1979). This complexity is characterized by seasonal areas of upwelling, bringing high levels of nutrients which enhance primary productivity, and therefore facilitating the build up of primary and secondary consumers such as zooplankton, cephalopods and fish (Hui, 1979; Gaskin, 1982). Consequently, opportunistic apex predators such as whales and dolphins appear. The assumption that complex sea floor relief enhances food availability has been well documented in the western North Atlantic, especially for the area off the northeastern coast of the United States (Kenney, 1984; Kenney and Winn, 1986; Hain et al., 1985), where most large species of cetaceans migrate to feed. Only Wells et al. (1980), Dorf (1982) and Baumgartner (1997), have examined underwater topography as a factor affecting cetacean distribution in tropical or subtropical areas of the western North Atlantic. Relationships between underwater topography and areas of breeding and calving have not been analyzed.

The waters of the northeastern Caribbean are feeding grounds for some species, and reproductive grounds for others at different times of the year. Some species do not migrate, utilizing these waters for feeding and reproduction throughout the year. Given the presence of whales and dolphins off Puerto Rico and the Virgin Islands, it is hypothesized that their spatial distribution is correlated with the area's bottom topography. Some cetaceans are expected to be distributed in relation to areas of high sea floor relief, while in other species the factor affecting distribution may be a low-complexity level in bottom topography.

Materials and Methods

Sighting data were obtained from published and unpublished records collected in the study area up to 1989. In 1985, and between 1987 and 1989, 18 fishing villages were visited throughout Puerto Rico, and locals were interviewed on the occurrence of all species of marine mammals in the area. State and federal government officials and previous researchers (H. E. Winn, D. K. Mattila, J. C. Jiménez and D. S. Erdman) were also interviewed, and their marine mammal data files kindly made available for analysis.

By its nature, most of the data presented here are non-random and biased in a variety of ways, mainly by observational chance and effort. The location of some of the occurrences may relate more to the distribution of human populations or activities, and not necessarily to the distribution of the animals. Therefore, conclusions based on the statistical analysis must be treated with caution. However, since this is the only available information, it serves as a general overview of expected patterns of aggregation, spatial distribution, and seasonality of the species.

A database management system was established to file sighting records for each species in the study area. Opportunistic sightings were included after they proved to be reliable in terms of species identification, date, and event location. A serial number (NEPSGXXXX) and a quadrant number were assigned to each sighting in the database.

The study area included the insular shelf waters of Puerto Rico, the US Virgin Islands, and the British Virgin Islands (Fig. 1). The area was partitioned into 864 quadrants, each measuring five minutes of latitude by five minutes of longitude, and with an area of approximately 68 km^2. The bathymetry of the study area was analyzed by calculating a Slope Index (SI) for each quadrant, following Kenney's (1984) technique for measuring absolute bottom slope, and adapted from Evans' (1975) Depth Index (DI) and Hui's (1979; 1985) Contour Index (CI) formulas. These formulas characterize sea floor relief as a percentage of maximum depth change for a given section of the study area. Evans' DI and Hui's CI measure this change as a percentage of the maximum depth in that section, while the SI developed by Kenney (1984) incorpo-

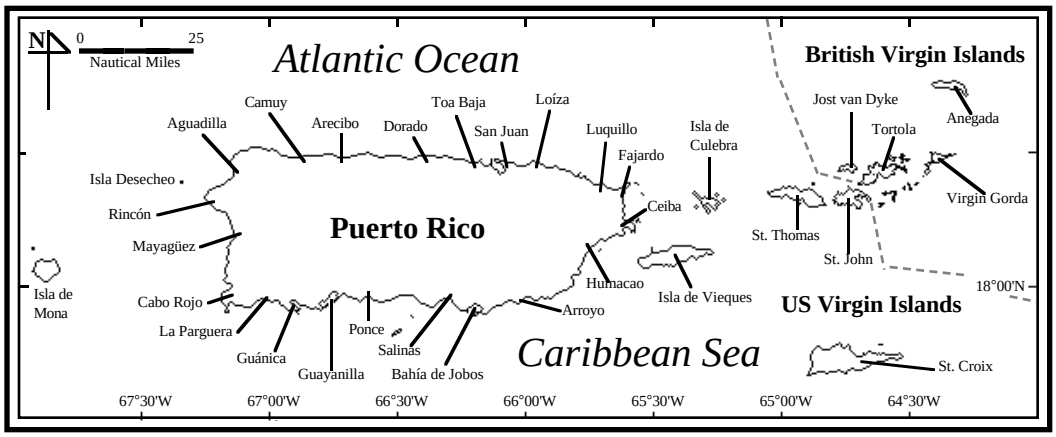

FIG. 1. Study area and localities referred to in the text.

rates into a single number the slope of a specific quadrant as a percentage of change of the bottom topography to the whole study area. The SI appears as a dimensionless formula defined as:

$$SI = 100\left(\frac{M - m}{M_{sa}}\right)$$

where M and m is the maximum and minimum depth, respectively, within each quadrant, and M_{sa} is the maximum depth in the entire study area (6,373 m). Quadrants which border the shoreline were assigned a minimum depth of 1.0 m. Strandings and mortality records were not included in the spatial distribution analysis because it is impossible to determine the origin of the animals.

Slope indices (SI) were grouped into categories or classes using a cluster analysis together with a discriminative procedure. The cluster analysis created six distinct classes of the SI distribution, and the discriminative analysis provided the ranges for each of the six classes. Class 1 characterized areas with very small sea floor relief (up to 4.1%), while Class 6 characterized areas with the highest percentage of underwater relief (as much as 65.3%).

To test for a significant relationship between species sightings and bottom topography, the observed sighting frequency of each species relative to bottom topography was compared to an estimate of expected frequency of sightings using a chi-square (χ^2) one-sample test of independence (as in Evans, 1975; Hui, 1979; Selzer and Payne, 1988). The null hypothesis (H_o) was: the spatial distribution, represented by the location of sightings of a given species of cetacean in the study area, is random and proportional to the number of quadrants in each SI class. The expected frequency of sightings in SI class *i* (E_i) was calculated following Evans (1975), and defined as:

$$E_i = O_t\left(\frac{L_i}{L_t}\right)$$

where O_t is the total number of sighting occurrences for a species in the study area, L_i is the number of quadrants in SI class *i*, and L_t is the total number of water quadrants in the study area (762). The E_i is then an estimate of the expected number of sightings for a species if their spatial distribution is random or proportional to the number of water quadrants in the study area. The α level for all tests was 0.05 or lower, thus avoiding a Type II Error (accepting the hypothesis when it is false). Only species with more than eight occurrences were included in this analysis.

RESULTS AND DISCUSSION

Diversity

The total number of sighting records catalogued was 2,016. Seventeen species of

TABLE 1. Cetacean fauna and summary of sighting records catalogued for Puerto Rico and the Virgin Islands up to 1989 (UNE = unknown status but probably non endangered, V = vulnerable, EBR = endangered but probably recovered).

Taxonomic grouping Species	Total no. sightings	Percent of all records	Earliest/latest record	Status
Suborder Odontoceti				
Family Delphinidae				
Delphinus spp.	13	0.64	1971/1986	UNE
Globicephala macrorhynchus	69	3.42	1958/1988	UNE
Grampus griseus	2	0.10	1957/1967	UNE
Orcinus orca	13	0.64	1960s/1988	UNE
Pseudorca crassidens	1	0.05	1988/1988	UNE
Stenella coeruleoalba	0[a]			UNE
Stenella frontalis	31	1.54	1958/1987	UNE
Stenella longirostris	41	2.03	1956/1988	UNE
Steno bredanensis	9	0.45	1980/1986	UNE
Tursiops truncatus	151	7.49	1966/1989	UNE
Unidentified Delphinidae	11	0.55	1969/1985	
Family Physeteridae				
Kogia breviceps	0[b]			UNE
Physeter macrocephalus	43	2.13	1952/1986	EBR
Family Ziphiidae				
Ziphius cavirostris	8	0.40	1954/1986	UNE
Unidentified small odontocete	2	0.10	1968/1984	
Unidentified large odontocete	3	0.15	1960s/1989	
Suborder Mysticeti				
Family Balaenopteridae				
Balaenoptera acutorostrata	3	0.15	1971/1973	UNE
Balaenoptera borealis	2	0.10	1967/1982	V
Balaenoptera physalus	3	0.15	1975/1982	V
Balaenoptera spp.	14	0.69	1964/1981	V
Megaptera novaeangliae	1,597	79.22	1957/1989	EBR

[a]A stranding of a striped dolphin was recorded for the Virgin Islands in 1982.
[b]Five strandings of a pygmy sperm whales were recorded for Puerto Rico and the Virgin Islands between 1976 and 1989.

whales and dolphins were identified (Table 1), including two species, the striped dolphins (*Stenella coeruleoalba* [Meyen]) and the pygmy sperm whale (*Kogia breviceps* [de Blainville]), which are only known from strandings. The earliest sighting record dates to 1952 and consists of three sperm whales (*Physeter macrocephalus* Linnaeus) sighted on 5 July at the edge of the drop-off south of Isla de Vieques. The latest record, 16 April 1989, is of a humpback whale (*Megaptera novaeangliae* [Borowski]) sighted at the shelf edge south of Bahía de Guánica.

Toothed whales (odontocetes) were reported 397 times (19.7% of all occurrences). Of the total number of odontocete sightings, 16 (4.0%) were of unidentified species. Three families and thirteen species of odontocetes were present at one time or another throughout the year. The oceanic dolphin family Delphinidae is represented in the area by eight genera, and ten species (Table 1). Other species of delphinids which may be present, but so far not reported in the study area include: pygmy killer whales (*Feresa attenuata* Gray), Fraser's dolphins (*Lagenodelphis hosei* Fraser), melonhead whales (*Peponocephala electra* [Gray]), pantropical spotted dolphins (*Stenella attenuata* [Gray]), and clymene dolphins (*Stenella clymene* [Gray]). These have been observed in other areas of the Caribbean (Mignucci-Giannoni, 1989), but as of 1989, not in Puerto Rico and the Virgin Islands.

The sperm whale family Physeteridae is present, with two out of its three known species (Table 1). The dwarf sperm whale (*Kogia simus* Owen), although it may be present as evidenced by records from St. Vincent (Caldwell et al., 1973), has not been reported for the study area. The beaked whale family Ziphiidae, probably the least known of all the Cetacea, is represented in the study area only by the goosebeak whale (*Ziphius cavirostris* Cuvier) (Table 1). Tropical species of the genus *Mesoplodon*, including the Antillean beaked whale (*M. europaeus* Gervais), densebeak whale (*M. densirostris* [de Blainville]) and True's beaked whale (*M. mirus* True), may be present, but have not been reported as of 1989. Mattila and Clapham (1989) reported the sighting of a *Mesoplodon* sp. east of the Virgin Islands, but could not ascertain the species identity.

Baleen whales (mysticetes) were reported 1,619 times (80.3% of all occurrences). The rorqual family Balaenopteridae is the only one represented in the area with two genera, and four species (Table 1). Since it is difficult to distinguish at sea between fin whales (*Balaenoptera physalus* [Linnaeus]) and sei whales (*B. borealis* Lesson), and most occurrences of large balaenopterids in the study area did not specify which of the two species was sighted, the two are treated here as a group. Two balaenopterid whales were not reported in the study area: blue whales (*B. musculus* [Linnaeus]) and Bryde's whales (*B. edeni* Anderson). Of these, only the latter may be present as it is well known from the southeastern Caribbean. The only Caribbean record for a blue whale is from a cervical vertebrae encountered at San Cristobal in Panamá in 1922 (Harmer, 1923).

Species accounts

Delphinus spp.—Saddleback or common dolphins have been reported 13 times. Based on the sighting records, no clear indication exist to assign the species sighted to the shortsnout saddleback dolphin (*D. delphis* Linnaeus) or to the longsnout saddleback dolphin (*D. capensis* [Gray]); therefore, they are described here as *Delphinus* spp. These dolphins are highly gregarious, at times in groups of thousands, probably segregated by sex and age (Schmidly, 1981). In the study area they were observed singly or in groups of up to 50 animals. Their mean group size was 9.2 (n = 12), and four types of aggregations were observed: 1-3 animals (66.8%), 7-15 animals (6.9%), 25-29 animals (6.9%), and 30-50 animals (19.4%). Saddlebacks are notably acrobatic, and they were reported jumping clear out the water, porpoising, and frequently riding bow waves.

In the western North Atlantic, the species is widely distributed from Newfoundland south to Venezuela, including the Gulf of Mexico (Leatherwood et al., 1976). In the Caribbean, sightings of saddleback dolphins have been reported from Antigua, Cuba, Dominican Republic, St. Lucia, St. Vincent, and the Grenadines (Mignucci-Giannoni, 1989).

Saddlebacks are an offshore species found over the continental slope and in proximity to ocean ridges (Winn et al., 1979). Their distribution has been associated with rich areas of convergence and divergence, and with areas of intrusion of warm water into cooler regions (Gaskin, 1968; Au et al., 1979). Evans (1975) and Hui (1979) showed that saddleback dolphins in southern California are found in areas of high sea floor relief. Selzer and Payne (1988) and Dorf (1982) came to the same conclusion for the Gulf of Maine and Gulf of Mexico, respectively, describing the areas as of moderate to high bathymetric slope. Saddlebacks in the study area showed no higher than expected occurrences for any specific slope class ($n = 13$, $p > 0.70$). The average SI was 7.2 ($n = 13$, max = 40.6, min = 0.3, $\sigma = 10.7$, SI class = 2). Of all sightings, 69.2% were well within the continental shelf, while 30.8% were near the shelf edge. These dolphins have been observed off Isla de Mona, northwest of Bajo Gallardo in the Mona Passage, off Isabela, north of Manatí, east of Luquillo, at Bahía de Guánica and Bahía de Jobos, off Salinas, north of St. Croix, and near Tortola. The species was reported throughout the year, except in May and from August to

October. The only record describing the presence of calves was on early June.

Globicephala macrorhynchus Gray—Sixty-nine sightings of shortfin pilot whales have been reported. This species has a strong herding behavior (Nature Conservancy Council, 1980), including epimeletic behavior (group cohesiveness in stressful or life-threatening situations). In the study area, they have been observed in groups of up to 100 animals. The mean group size was 11.1 (n = 66), and four types of aggregations were observed: 1-3 animals (50.0%), 4-7 animals (19.6%), 8-20 animals (15.2%), and 25-100 animals (15.2%). They were sometimes observed logging stationary at the surface or leisurely swimming.

Shortfin pilot whales are cosmopolitan, found in tropical and warm temperate waters of all oceans (Rice, 1977). In the western North Atlantic, they have been reported as far north as Delaware Bay and Virginia in the summer, but are most commonly found from Cape Hatteras and Bermuda, south to Venezuela, including the Gulf of Mexico (Leatherwood et al., 1976). In the Caribbean, sightings of shortfin pilot whales have been reported from Anegada Passage, Bequia, Cuba, Dominica, Dominican Republic, Haiti, Martinique, Petit Nives, St. Lucia, St. Vincent, and Venezuela (Mignucci-Giannoni, 1989).

Pilot whales were observed 45.3% of the time over the shelf, 26.6% offshore, and 28.1% near the shelf edge. Hui (1985) and Dorf (1982) showed a significant relationship between their distribution and areas of high sea floor relief in other areas. Data for Puerto Rico and the Virgin Islands does not show a clear relation to bottom topography ($n = 64$, $p > 0.20$). The average SI was 11.6 ($n = 64$, max = 52.6, min = 0.3, $\sigma = 11.5$, SI class = 3). They have been observed scattered throughout the study area, particularly near Isla Desecheo and Isla de Mona, off San Juan, south of Salinas, southwest of Cabo Rojo, off Mayagüez, off Rincón and Aguadilla, north of Hatillo, offshore from Loíza, north of Luquillo, off Guánica and Ponce, south of Juana Díaz, off Yabucoa, throughout the Virgin Bank, northwest of Anegada, northwest and south of St. John, south of St. Thomas, between Tortola and Virgin Gorda, south of Horseshoe Reef (northeast of Virgin Gorda), between St. John and St. Croix and north, northwest and southwest of St. Croix.

Shortfin pilot whales have been observed during all months of the year, more commonly during winter and spring. Pilot whales in the northeastern Caribbean were initially characterized as a summer, warm month species, seen from May through October, and absent from November through April (Caldwell and Erdman, 1963; Erdman, 1970; Erdman et al., 1973). However, Taruski and Winn (1976) documented winter sightings. The cumulative analysis of all occurrences indicates that *G. macrorhynchus* is present in the study area throughout the year, but its appearance, compared to the summer and fall months, more than doubles during the winter and spring months. This seasonal pattern is in accord with those described for pilot whales between Cape Hatteras and northern Florida, and in the Lesser Antilles (Caldwell and Erdman, 1963). Their occurrence in the Gulf of Mexico seems to be extended as well, but in contrast, with an increase in sightings during the spring and summer (Moore, 1953; Dorf, 1982). The only record indicating the presence of calves was in late December.

There is little information on migration or movements of this species for the study area. Taruski and Winn (1976) suggested the occurrence of a slight seasonal inshore-offshore movement probably related to prey habits. This type of movement has been documented for shortfin pilot whales in southern California and Japan, where the species comes fairly close to shore in the early spring, coinciding with the spawning of squid (Leatherwood and Reeves, 1983b). In the northeastern Caribbean, the seasonal appearance of pilot whales could coincide with the inshore movement of spawning octopus described by Voss (1960). Although several species of squid are present in the study area, their spawning habits are unknown.

Grampus griseus (Cuvier)—Two sightings of Risso's dolphins have been recorded. One of the sightings reported in Erdman et al. (1973) as an unidentified dol-

phin, is classified here as *G. griseus*. Risso's dolphins, were observed once singly and in a group of 18-20 individuals. The latter agrees with herding behavior described for other areas (Leatherwood and Reeves 1983b).

Grampus in the western North Atlantic has been reported from eastern Newfoundland south to St. Vincent, including the eastern and northern Gulf of Mexico (Leatherwood et al., 1976). It is generally restricted to offshore areas deeper than 200 m (Mitchell, 1975). Caribbean records included only specimens caught from St. Vincent (Caldwell et al., 1971). In the study area, Risso's dolphins have been observed north of St. Croix, and offshore northwest of Whale Banks. Both locations are areas of high underwater relief, with an average SI of 35.1 ($n = 2$, max = 40.4, min = 29.9, $\sigma = 5.3$, SI class = 5). Dorf (1982) also found Risso's dolphin in the Gulf of Mexico distributed in areas of steep bathymetric slope. The two sightings reported were for the months of April and September. In the western North Atlantic, a north-south, summer-winter migration has been suggested (Schmidly, 1981).

Orcinus orca (Linnaeus)—Thirteen sightings of killer whales has been reported. Killer whales were observed singly or in herds of up to 25 animals, with a mean group size of 7.7 ($n = 6$). Two types of aggregations were observed: 1-3 animals (67%), and 12-25 animals (33%). This group composition agrees with reports, in which killer whales were frequently observed in pairs or trios, but at times up to 40 individuals (Minasian et al., 1984). In the study area, killer whale attacks on larger whales have been observed twice: first on an unidentified species of whale south of Isla de Culebra, and second, on a pod of sperm whales between St. Thomas and St. Croix.

Killer whales in the western North Atlantic, have been reported from Greenland and Iceland, south to St. Vincent, including the Gulf of Mexico (Leatherwood et al., 1976). In the Caribbean, sightings of killer whales have been reported from Cayman Islands, Cuba, Dominican Republic, St. Lucia, Vincent, and Trinidad and Tobago (Mignucci-Giannoni, 1989). The species seems to be pelagic in some areas, and coastal in others. Killer whales in the study area were observed 53.5% of the time over the continental shelf, 36.4% offshore, and only 0.1% near the shelf edge. No relationship was evident to bottom topography ($n = 10$, $p > 0.3$), although the average SI was 7.3 ($n = 9$, max = 20.6, min = 0.3, $\sigma = 8.2$, SI class = 2). Killer whales have been observed in the Mona Channel, near Isla de Mona, near Rincón, west of Puerto Real in Cabo Rojo, off Isla de Culebra, off Luquillo, east of St. Thomas, near St. John, in the Sir Francis Drake Channel, and between St. Thomas and St. Croix.

Killer whales were sighted most frequently during the winter and early spring months of December, February and March, but also in June. In contrast, killer whales in the Lesser Antilles were most often captured within sight of land during the summer (Winn et al., 1979). Killer whales appear to follow the seasonal movements of their prey (Leatherwood et al., 1976), but no information is available for the study area. It has been suggested that killer whales move toward the equator during the winter and away from it during the summer (Minasian et al., 1984).

Pseudorca crassidens (Owen)—False killer whales were observed only once in the study area, on March 1988 at Reef Bay in St. John. The animals were in a group of 15-20 individuals. In the western North Atlantic, false killer whales are found in tropical and warm temperate waters from Maryland south to Venezuela, and in the Gulf of Mexico (Leatherwood et al., 1976). They are mainly pelagic, but at times may venture inshore (Winn et al., 1979). In the Caribbean, false killer whales has been reported from Cuba, St. Vincent, and Tobago (Mignucci-Giannoni, 1989). No information can be ascertained in relation to bottom topography from the single sighting.

Stenella coeruleoalba—The only record of the striped dolphin is of a skull found in St. Croix in 1982. In the western North Atlantic the species is restricted to warmer waters from Nova Scotia south to Venezuela, including the Gulf of Mexico (Leatherwood et al., 1976). In the Caribbean, sightings of striped dolphins have been reported for

Bonaire, Curaçao, and Venezuela (Mignucci-Giannoni, 1989). Dorf (1982) found striped dolphins in the Gulf of Mexico to be distributed in areas of low bathymetric slope.

Stenella frontalis (Cuvier)—Thirty-one sightings of Atlantic spotted dolphins have been reported. They were observed singly or in groups of up to 50 animals. The mean group size was 14.2 (n = 26), and four types of aggregations were observed: 1-4 animals (30.8%), 5-10 animals (34.6%), 11-29 animals (15.4%), and 30-50 animals (19.2%). This agrees with Perrin et al. (1987), who suggested that pods are usually of fewer than 50 animals and most typically of 5 to 15 individuals in coastal waters.

Atlantic spotted dolphins in the Caribbean constitute one of the six geographical populations endemic to the Atlantic Ocean (Perrin et al., 1987). In the Caribbean, sightings of these dolphins have been reported from the Colombia, Cuba, Dominican Republic, Panamá, St. Vincent, and Venezuela (Mignucci-Giannoni, 1989). Of all sightings in the study area, 85.0% were within the shelf. Dorf (1982) found Atlantic spotted dolphins in the Gulf of Mexico to be distributed in areas of low bathymetric slope. In the study area they showed higher than expected frequencies for areas of low sea floor relief ($n = 27$, $p > 0.001$), with an average SI of 3.4 ($n = 27$, max = 28.6, min = 0.1, $\sigma = 6.5$, SI class = 1). They were observed off Mona Island, south of La Parguera, southwest of Cabo Rojo, west and northwest of Mayagüez, off Punta Borinquen in Aguadilla, near Ceiba, south of Vieques Island, across the Virgin Bank, west of Anegada, and most commonly near Jost Van Dyke and Tortola. In the study area, these dolphins seem to be restricted to the shelf areas of low sea floor relief, at times moving to the shelf edge, and rarely offshore.

Atlantic spotted dolphins were sighted throughout the year, with the exception of July, December and April. Their seasonality seems to be bimodal, peaking in August, decreasing gradually until November, peaking again in January and February, and then rarely seen in the spring and summer. The seasonality in Puerto Rico and the Virgin Islands contradicts the patterns observed in Florida and the Gulf of Mexico, where they move inshore in late spring and summer (Caldwell and Caldwell, 1966). It has been suggested that this movement may be related to fish movements, in particular that of the pelagic blue runner (*Caranx crysos* [Mitchill]), but the relationship may be more coincidental than associative (Caldwell and Caldwell, 1966). The blue runner, although present in the study area, is not particularly abundant (Erdman et al., 1988). While no information is available for the study area, given their deep water distribution elsewhere, and their seasonal occurrence over the shelf and shelf edge in the study area, an inshore-offshore seasonal movement is suspected.

Stenella longirostris (Gray)—Spinner dolphins were recorded 41 times. Individuals have been observed singly or in groups of up to 500 animals. The mean group size was 53.7 (n = 37), and six types of aggregations were observed: 1-5 animals (32.5%), 6-10 animals (18.9%), 11-30 animals (18.9%), 31-100 animals (18.9%), 200 animals (5.4%), and 500 animals (5.4%). They were frequently seen jumping clear out of the water, spinning in mid-air, and riding bow waves. Spinner dolphins also were seen in association with humpback whales, even riding the whale's bow wave.

Spinner dolphins are found in pelagic and neritic tropical waters (Schmidly, 1981). In the western North Atlantic, they range from Cape Hatteras, throughout the Gulf of Mexico and the Caribbean, south to Venezuela. In the Caribbean, sightings of spinner dolphins have been reported from Bequia, the Grenadines, St. Vincent, and Tobago (Mignucci-Giannoni, 1989).

Although in the southeastern United States they have been characterized as an offshore, deep water species (Winn et al., 1979), spinner dolphins in the study area were observed 72.5% of the time over the continental shelf, 22.5% near the shelf edge, and only 5.0% offshore. Dorf (1982) found spinner dolphins in the Gulf of Mexico to be distributed in areas of low bathymetric slope. In the study area, spinner dolphins showed higher than expected occurrences in areas of low sea floor relief ($n = 40$, $p >$

0.05). The average SI was 6.2 (n = 40, max = 40.6, min = 0.3, σ = 8.3, SI class = 2). They were observed off Isla de Mona, east of Isla de Desecheo, from Rincón to Aguadilla, near Banco de Esponja west of Mayagüez, southwest of Cabo Rojo, off Toa Baja, north of Luquillo, near Fajardo, throughout the Virgin Bank, east of Virgin Gorda, north and east of St. Croix, and most frequently off Punta Higüero in Rincón, and close to the islands of St. Thomas, St. John and Jost Van Dyke.

Spinner dolphins were observed throughout the year, except in May and August. They are seldom seen in the summer and fall, but sightings increase steadily from November through January, peaking in February, and decreasing in March and April. No information is available for the study area on migration or movements, but given their deep water distribution elsewhere, and their seasonal occurrence inside the shelf near the islands of the study area, an inshore-offshore seasonal movement is suspected.

Steno bredanensis (Lesson)—Nine sightings of roughtooth dolphins have been recorded. The species congregated in small groups of 3 to 30 animals. The mean group size was 9.9 (n = 8). Three types of aggregations were observed: 3-4 animals (25%), 5-10 animals (50%), and 15-30 animals (25%). They were observed on four occasions in association with humpback whales, once riding the bow wave of a whale.

Leatherwood et al. (1976) described the distribution of these dolphins in the North Atlantic as deep tropical and warm temperate waters. Winn et al. (1979) confirmed this for the West Indies, but added that they also occur near the islands. In the Caribbean, sightings of roughtooth dolphins have been reported from Cuba, Haiti and St. Vincent (Mignucci-Giannoni, 1989). In contrast to the generally suggested pelagic distribution, all sightings in the study area were within the continental shelf. Furthermore, roughtooth dolphins showed higher than expected values for areas of low sea floor relief (n = 9, $p > 0.01$), with an average SI of 2.4 (n = 8, max = 10.6, min = 0.2, σ = 3.3, SI Class = 1). They were observed off Aguadilla, Rincón, Aguada, Fajardo, on the Virgin Bank, and off St. John and Virgin Gorda.

The species only has been sighted during February and March. Although the data may indicate a seasonal presence during late winter and early spring, this is inconclusive. No information is available on migration or movements, but given their deep water distribution elsewhere, and their seasonal occurrence inside the shelf near the islands in the study area, an inshore-offshore seasonal movement is suspected.

Tursiops truncatus (Montagu)—Bottlenose dolphins were sighted on 151 occasions. They were observed singly or in groups of up to 50 animals. The mean group size was 7.8 (n = 147), and six types of aggregations were observed: single animals (24.9%), 2-4 animals (31.0%), 5-10 animals (18.6%), 11-19 animals (14.5%), 20-39 animals (7.6%), and 40-50 animals (3.4%). In the Gulf of Mexico, Leatherwood and Reeves (1983a) found that most groups averaged 5-6 animals. Group size in this species seems to increase in open water, with depth and during different seasons (Shane et al., 1986; Würsig, 1978; Odell and Reynolds, 1980). In the study area, while group sizes in the summer and fall averaged 5.5, spring and winter groups averaged between 8.4 animals. Bottlenose dolphins were observed feeding off Ponce by circling and charging toward the shore as if they were going to strand, a commonly reported behavior of the species (Leatherwood, 1975). They were observed traveling in association with humpback whales off Rincón and some dolphins have been observed interacting with humans, some even approaching divers and swimmers, and at times allowing themselves to be stroked or petted.

In the Caribbean, sightings of bottlenose dolphins have been reported from Cuba, Dominican Republic, Grenada and the Grenadines, Trinidad and St. Vincent (Mignucci-Giannoni, 1989). Bottlenose dolphins were observed throughout the study area, but were commonly recorded for Isleta de San Juan, including inside the San Juan Bay, and between the Virgin Islands. Sightings were recorded for San Juan, Rio Grande, Fajardo, Isla de Culebra, Vieques, Arroyo,

Salinas, Ponce, La Parguera, Rincón, Aguada, Aguadilla, St. Croix, St. Thomas, St. John, Tortola, Virgin Gorda and Anegada.

Bottlenose were observed more often over the shelf (85.2%), occasionally near the shelf edge (7.5%), and in offshore waters (6.9%). They showed higher than expected frequencies for areas of low sea floor relief ($n = 151$, $p > 0.001$), with an average SI of 4.6 ($n = 151$, max = 40.6, min = 0.1, $\sigma = 6.6$, SI class = 2). Dorf (1982) found bottlenose dolphins in the Gulf of Mexico with similar distributional and bathymetry patterns. Bottlenose from Florida to Cape Hatteras exhibit the same distribution pattern, with animals not extending beyond the continental shelf (Caldwell and Caldwell, 1973), and most being found close to shore, sometimes in bays, lagoons and even venturing into rivers (Leatherwood et al., 1976). From Cape Hatteras to Georges Bank, bottlenose dolphins are found on the shelf edge, in areas of high bathymetry (Kenney 1984).

Although bottlenose dolphins were observed during all months of the year, they were more often seen between December and April. Dorf (1982) found a similar seasonal pattern for bottlenose dolphins in the Gulf of Mexico. The statement by Erdman (1970) of the great number of *Tursiops* during the summer as a characterization of their seasonality is unsupported.

Seasonal inshore (during winter) and offshore (during summer) movements for the Gulf of Mexico are described by Shane and Schmidly (1978), Shane (1980), and Dorf (1982), these related to prey concentration (Wells et al., 1980). Given the seasonal pattern observed in the study area, a similar movement pattern is expected for this region. In addition to regional movements, short-term movements dependent on floods, ebb tides, and probably diurnal patterns are also expected.

Kogia breviceps—Pygmy sperm whales stranded on five occasions between, 1976 and 1989. These whales are found in temperate, subtropical and tropical oceanic waters of the western North Atlantic, from Nova Scotia to the Virgin Islands and in the Gulf of Mexico. They stranded in Aguadilla, Mayagüez, Punta Pitahaya in Cabo Rojo, and St. Croix. Pygmy sperm whales stranded in January, April, May and December. A winter and spring seasonality similar to that of the sperm whale is expected.

Physeter macrocephalus—Sperm whales have been sighted on 43 occasions. They have been observed singly or in groups of up to 30 animals. The mean group size was 4.1 ($n = 32$), and three main types of aggregations were observed: 1-3 animals (65.5%), 4-10 animals (31.2%), and 30 animals (3.3%). In the Lesser Antilles they have been found in less coherent groups, scattered over many miles (Watkins et al., 1985). Watkins and Moore (1982) found that Caribbean breeding groups usually comprised 1 to 3 calves, 8 or more medium whales, and 1 or 2 large whales.

Sperm whales are found in deep waters throughout the world (Rice, 1989). Their distribution is clumped into "grounds" and dependent on food source and breeding, varying with sex and age (Gosho et al., 1984). They are most often found along the edge of the continental shelf and along ocean trenches (Watson, 1981), seldom inside the 200 m isobath (Leatherwood et al., 1976). Whales in the southeastern Caribbean have been observed to be attracted to some areas where sound scattering organisms concentrate just above the 80 to 90 m thermocline (Watkins et al., 1985). At times, they appear close to land, in association with areas of upwelling, but they also occur in deep waters, where they search for large species of cephalopods. Females are more restricted to the tropical and subtropical zones, up to the 54°N mark, while males may inhabit waters further north (Gosho et al., 1984).

In the western North Atlantic, they have been reported from southeastern Greenland and Iceland, southward to the Lesser Antilles, including the Gulf of Mexico (Leatherwood et al., 1976). In the Caribbean, sightings of sperm whales have been reported from Anegada, Bequia, Canovan, Cuba, Grenada, Grenadines, Guadeloupe, Martinique, St. Lucia, and St. Vincent (Mignucci-Giannoni, 1989). Most sightings in the northeastern and southeastern Caribbean appear to be on the leeward side of the islands.

In the study area, sperm whales were observed 64.2% of the time near the shelf edge, 26.4% offshore, and 9.4% over the continental shelf. Sightings were recorded for Isla de Mona, Mona Passage, off Rincón, off San Juan and Loíza, south of Ponce, south of Isla de Vieques, north of St. Croix, along the southern shelf edge of the northern Virgin Islands, between St. Thomas and St. Croix, and off Anegada. Sperm whales showed higher than expected occurrences in areas of high bottom relief ($n = 32$, $p > 0.05$), with an average SI of 14.0 ($n = 32$, max = 65.3, min = 0.1, $\sigma = 14.0$, SI class = 3).

Although older data suggested that sperm whales were less seasonal in their appearance than humpback whales (Erdman et al., 1973), the present summary of occurrences shows a similar seasonal pattern for both species. Nonetheless, the sperm whale season is more extended than that of the humpback, and the bimodal seasonality suggested by Mignucci-Giannoni (1988) seems to be more continuous than two distinct seasons. Sperm whales occur in the northeastern Caribbean from the late fall, throughout the winter and early spring, as early as October, increasing in November through January, peaking in February, declining in March and are rarely seen, from April through September. The only two records of whales with calves were in late December and early January. Their temporal distribution is related to migratory movements, which varies between bachelor and breeding groups (Leatherwood et al., 1976).

Ziphius cavirostris—Goosebeak whales or Cuvier's beaked whales, have been sighted eight times. They were observed singly or in groups of 2 or 3 animals. The mean group size was 1.5 ($n = 8$), and most sightings were of single animals (62.5%). At other locations, *Ziphius* have been observed in groups of up to 25 animals (Leatherwood et al., 1976; Leatherwood and Reeves, 1983b; Minasian et al., 1984).

In the western North Atlantic, goosebeak whales are found in tropical and temperate waters, from Cape Cod to the Lesser Antilles, and in the Gulf of Mexico (Winn et al., 1979). *Ziphius* appears to be found primarily in tropical pelagic waters, especially in the vicinity of sea canyons and escarpments (Minasian et al., 1984). Caribbean records include Barbados, Bonaire, Curaçao, and St. Martin (Mignucci-Giannoni, 1989).

This species has been observed off Ramey in Aguadilla, near Isla de Caja de Muertos, south of Bahía de Guánica, in the vicinity of La Parguera, and between St. Thomas and St. Croix. Goosebeak whales did not show a relationship to bottom topography ($n = 8$, $p > 0.5$). The average SI was 6.6 ($n = 7$, max = 28.1, min = 0.1, $\sigma = 4.8$, SI class = 2). *Ziphius* was recorded during all months of the year, except July and October, with most occurrences during the winter and early spring. A mother and calf sighting occurred during November.

Balaenoptera acutorostrata Lacépède—Minke whales were sighted on three occasions. A sighting described by Erdman et al. (1973) and Winn and Perkins (1976) between the northeast corner of Puerto Rico and San Juan on 15 February 1965, was found to be, from the coordinates given, considerably far from the study area and not considered in the analysis of records. Ten additional sightings were reported by Winn and Perkins (1976), Taruski and Winn (1976) and by Mattila and Clapham (1989) in nearby Anguilla and in the Anegada Passage. Minke whales congregated in small groups of 1 to 3 animals. Similarly, the mean group size of the minkes sighted in Anguilla and Anegada Passage was 2.4, with most animals found in pairs or trios and to a lesser extent, singly. Although they were reported to apparently not feed while in tropical waters (Williamson, 1975), Winn and Perkins (1976) observed minke whales near Anguilla in association with a large group of shortfin pilot whales and sperm whales feeding.

In the western North Atlantic, minke whales are distributed from Baffin Bay in Canada, south to Florida, in the Gulf of Mexico (Winn et al., 1979), and southeast through the West Indies, at least to Anguilla Bank in the northern part of the Lesser Antilles. Additional records of minke whales in the Caribbean include animals sighted off the Bahamas, and near

Turk and Caicos (Winn and Perkins, 1976). In the study area, they have been observed near Isla de Mona, off Banco Los Placeres southwest of Isla Desecheo, and east of Beef Island near Tortola.

Minke whales are supposedly limited to shelf waters (Schmidly, 1981) and are mostly found inshore, or even entering bays. Records in the northeastern Caribbean, were observed equally over the shelf and near the shelf edge, but less frequently offshore. The average SI for the study area was 3.9 ($n = 3$, max = 6.3, min = 0.4, $\sigma = 2.5$, SI class = 1). Not enough data are available to make inferences on bathymetry.

Taking into account, in addition, the sightings of the nearby Anguilla Bank and Anegada Passage, minke whales have been reported equally in January and February, and only once in May. Other sightings west of the study area indicate that they may appear in Caribbean waters as early as December (Winn and Perkins, 1976). Calf sightings were reported in the study area in February and May. The species is known to be migratory (Seargent, 1963). It is almost absent from the New England region in the winter, when it is in its southern range. In the spring they migrate north towards their summer feeding grounds, with males reaching farther north, and females staying near coastal and more southern areas (Stewart and Leatherwood, 1985).

Balaenoptera spp., *B. borealis*, and *B. physalus*—Large rorquals, other than the humpback whale, were observed 19 times, including two sightings of sei whales (*B. borelis*) and three of fin whales (*B. physalus*). These congregated in small groups of up to 5 animals. Mean group size was 1.8 ($n = 12$) and the animals were most often sighted singly (50%) or in pairs (42%). One group of five animals was reported. The observed group composition of both fin and sei whale herds is in agreement to those described at other locations (Leatherwood et al., 1976; Nature Conservancy Council, 1980; Gambell, 1985a; Gambell 1985b).

In the western North Atlantic, fin and sei whales are found from Greenland south to Florida, in the Gulf of Mexico and the West Indies. Sei whales are more tropical (Schmidly, 1981) and may be found as far south as the northeastern coast of Venezuela (Leatherwood et al., 1976; Mitchell and Kozicky, 1974). While fin whales in the northeastern United States are found more often over the shelf, sei whales are found inshore as well as offshore, frequently near the shelf edge. For both species, a separate Caribbean and Gulf of Mexico population has been suggested (Mitchell and Kozicky, 1974; Mead, 1975; Schmidly, 1981). Large rorquals in Puerto Rico have been observed only north of Isla de Mona, and south of Cayo Ratones in Salinas. Most sightings of *Balaenoptera* spp. have been from the Virgin Islands: north of Whale Banks, off Anegada, Virgin Gorda, Tortola, south of St. John and St. Thomas, and west and east of St. Croix. In the study area, rorquals were equally distributed over the shelf (30.8%), near the shelf edge (30.8%) and in offshore waters (38.4%). The average SI was 3.7 ($n = 12$, max = 9.4, min = 0.3, $\sigma = 3.4$, SI class = 1), and no relationship to bottom topography was evident ($n = 12$, $p > 0.2$).

Rorquals have been sighted at different months during all seasons, but the majority of sightings (66.7%) occurred during the winter or early spring. This partially agrees with what Mitchell and Kozicky (1974) found for sei whales in the southern portions of the western North Atlantic of a bimodal seasonality of February-March, and July-October, and what Gambell (1985b) described for fin whales, of a breeding season from December-January. Fin whales in the western North Atlantic have been reported to move south towards Florida, the Gulf of Mexico and the West Indies after October, where supposedly they spend their winter in offshore waters (Leatherwood et al., 1976; Mizroch et al., 1984; Gambell, 1985b). During the spring, they travel north toward their feeding grounds north of Long Island. Movements patterns of sei whales are less apparent that those of fin whales, closely following the movements of their prey.

Megaptera novaeangliae—A total of 1,597 sightings have been recorded, most obtained from unpublished studies by D. K. Mattila and his colleagues between 1978 and 1984. Humpback whales usually congregated in small groups, with a mean size

of 2.0 animals (n = 1,293). They were often found singly (43.2%), in pairs (37.5%), in trios (9.2%), or groups of four or more animals (10.1%). These values are generally in agreement with those reported for the Virgin Islands by Mattila and Clapham (1989), with the exception of their lower values (less than 2.9%) for groups of four or more individuals. Mattila and Clapham (1989) reported that singers, always lone individuals, composed 24.7% of the sightings in the Virgin Islands and 11.3% of those in Puerto Rico. Mother-calf aggregations constituted 11.9% of sightings in the overall study area, but differed considerably between Puerto Rico (6.8%) and the Virgin Islands (17.1%) (Mattila and Clapham, 1989). Balcomb and Nichols (1978) reported similar mother-calf ratios to that of the overall study area in Banco de la Plata in the Dominican Republic. Mattila and Clapham (1989) also noticed that mother and calf groups were commonly escorted by a third adult-size animal, supposedly a mature male waiting to mate with the female, but indicated that as the season progressed, less mother and calf groups were observed in association with a third individual.

In the western North Atlantic, humpback whales breed mainly along the Antillean chain (Winn and Winn, 1978; Whitehead, 1982). Although the Caribbean distribution of humpbacks extends from Venezuela to Grand Turks, it is clearly concentrated in the north-central and northeastern Caribbean, in areas less than 200 m deep (Winn et al., 1975). The total area inhabited by whales was estimated as 64,752 km^2, but the major breeding and calving grounds are restricted to two relatively small banks north of the Dominican Republic: Banco de la Plata and Banco de Navidad (Winn et al., 1975). Other Caribbean localities were humpback whale sightings have been reported include Anegada Passage, Anguilla Bank, Antigua, Barbuda, Belize, Cuba, Curaçao, Dominica, Dominican Republic, Grand Turks, the Grenadines, Guadeloupe, Isla de Aves, Monseratt, St. Eugtaius, St. Kitts, and St. Martin (Mignucci-Giannoni, 1989).

Humpback whales were observed throughout the study area, with two major areas of concentration; one along the northwestern coast of Puerto Rico, and the second widely spread around the northern Virgin Islands. Scattered sightings, both on the Atlantic and Caribbean sides of the islands, occurred at other locations, but with less frequency. Of interest is the sporadic occurrence of humpbacks between St. Thomas and St. Croix, off St. Croix itself, and on the southern coast of Puerto Rico. Humpbacks were also reported near Isla de Mona, Isla Desecheo, and along the north coast of Puerto Rico, at times close to San Juan and Arecibo. Off the northwestern coast of Puerto Rico, humpbacks aggregated more often in two areas, off Punta Higüero in Rincón, and off Punta Agujereada (near Punta Borinquen) in Aguadilla. In the Virgin Islands, the largest concentration of humpbacks occurs along the northern coast of the islands, from St. Thomas to Tortola, and within these, most sightings were reported off the northeastern coast of St. John.

Most of the sightings were close to shore, or at least over the continental shelf. In very few instances were humpbacks seen on the shelf edge or offshore, and in those cases, they were traveling. Mother and calf groups where observed closer inshore. In addition, humpbacks showed higher than expected frequencies for areas of low sea floor relief ($n = 1{,}558$, $p > 0.001$), with an average SI in the study area of 5.4 ($n = 1{,}558$, max = 40.4, min = 0.03, $\sigma = 6.7$, SI class = 2). The SI was slightly higher in Puerto Rico than in the northern Virgin Islands (Puerto Rico: mean SI = 7.1, n = 923, max = 33.3, min = 0.3, $\sigma = 4.8$, SI class = 2; Virgin Islands: mean SI = 1.8, n = 620, max = 39.5, min = 0.3, $\sigma = 5.7$, SI class = 1). The higher SI in Puerto Rico is due to the narrower nature of its continental shelf. Both areas were highly correlated with areas of low bathymetric relief.

The distribution of humpback whales in the study area appears to be determined by conditions necessary for breeding and calving: warm waters, protection from heavy sea action, and relatively shallow banks. It seems now that areas with low bathymetry may play, in addition, a role in enhancing the conditions needed for reproduction.

Puerto Rico and the Virgin Islands provide these suitable conditions, with as many as 6,183 km^2 of habitable banks (Winn et al., 1975), although the whales are concentrated in smaller specific areas. A density of 0.044 humpback whales per nautical mile^2 has been reported for the Virgin Islands (Mattila and Clapham, 1989), and is expected to be similar in Puerto Rico.

Humpback whales have a marked seasonality in the northeastern Caribbean, being reported in the tropical waters between November and May. In the northeastern United States, 95% of the humpback whale sightings occur between April and October (Kenney, 1984). The earliest record of the season in the study area is of 10 November, and the latest is of 30 May. Most individuals were seen after 15 January, with 3.5% of the sightings occurring before that date. The peak of the season occurred by the first two weeks of February and through the middle of March. The last two weeks in March were characterized by a steep decline in sighting frequency, and whales were rarely seen after the beginning of April (<3.0%). An analysis by Mattila and Clapham (1989) of the whales sighted per hour surveyed supports this seasonal pattern. Their analysis also showed a difference in the peak seasonal abundance between the Virgin Islands and Puerto Rico, with the latter occurring slightly later. Mother and calf groups have been reported as early as the first two weeks of December, through the last two weeks in May.

Through the use of photographic individual identification, animals from the four major North Atlantic feeding grounds have been identified migrating to Puerto Rico and the Virgin Islands. Most of the animals photo-identified in the study area have been photographed in the Newfoundland/Labrador grounds (44.6%) and in the Gulf of Maine (10.8%) (Mattila and Clapham, 1989). Matches between the study area and Greenland and Iceland were uncommon (2.3% and 3.1%, respectively). The photomatches between Puerto Rico and Iceland document a great circle distance of 5,982 km, probably one of the longest recorded traveling distances of any marine mammal (Martin et al., 1984). Mattila and Clapham (1989) classified the whales in Puerto Rico as a transient population, since most individuals, except mother-calf groups, were not usually resighted within the same season. This transient nature also seems be true for the Virgin Islands, given that the longest period between resightings was 13 days (Mattila and Clapham, 1989).

Spatial distribution

Whales and dolphins were reported more often near land masses or within the insular shelf (Fig. 2). Each species can be grouped zoogeographically into different habitats, either by depth classes (shelf, shelf edge, or offshore), or by sea floor relief (using contour or slope indices). Most cetaceans were found within the continental shelf, although sightings of some species extended into the shelf edge or offshore. Sperm whales predominated near the shelf edge and Risso's dolphins were most common offshore.

Relative bottom topography, measured by Contour Index (CI) and Slope Index (SI), have been used successfully elsewhere to characterize geographic areas in which sea floor relief enhances primary productivity, the availability of food prey, and consequently, the concentration of cetacean species. The bathymetric analysis of the study area showed distinct areas of high and low sea floor relief. Areas of low bathymetry were found in coastal waters and on the wide eastern shelf, while areas of high sea floor relief were evident west and northwest of Aguadilla, and along the shelf edge and offshore on the south side of the insular shelf. The high productivity of these areas is evidenced by their continuous use for sport and commercial fishing.

The hypothesis that the spatial distribution of a given species of cetacean is highly correlated to the area's bathymetric relief is generally supported, although for some species the relationship was not as clear. Nonetheless, by using the measurement of higher than expected occurrences of each species per SI class, the species in the study area can be more reliably characterized into distinct bathymetrical SI habitats, whether of a low, medium or high sea floor relief (Table 2).

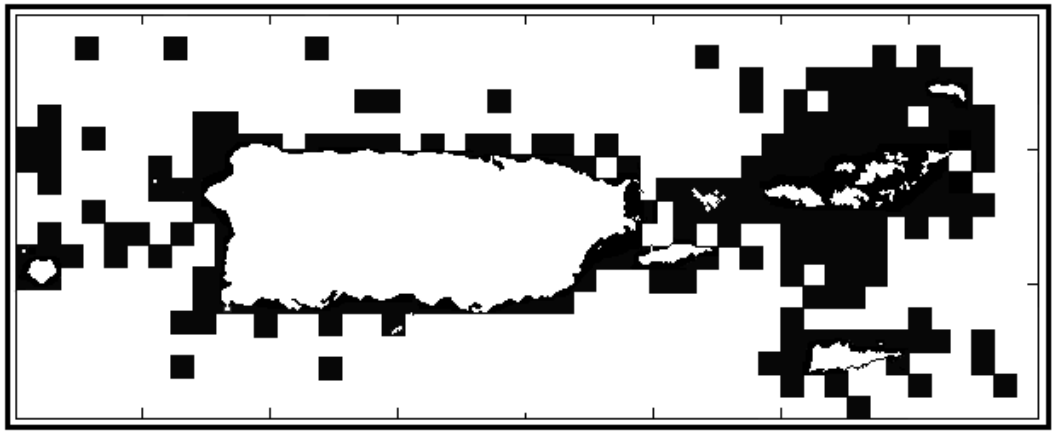

FIG. 2. Spatial distribution of all cetaceans from the study area.

Other factors play important roles in the distribution of whales and dolphins in the study area. This is clearly the case of the humpback whale. Humpback whale distribution seems to be concentrated on the windward side of land masses, in banks of enough width, as is the case of Banco Borinquen and Virgin Bank. Humpback whales observed elsewhere appear to be simply passing through. The degree of protection from rough weather also comes into play in the case of birthing and calving mothers, with most of them distributed close to shore.

Temporal distribution

Most species were sighted during the winter and early spring, in a similar seasonal pattern to the one well documented for humpback whales. This seasonality is clearly seen in most odontocetes, even in previously considered summer species like bottlenose dolphins and pilot whales. The increase in sightings begins in December, peaks in February, and gradually decreases in March and April. The rate of sightings from May through November is similar every month, averaging 4.0% of all sightings.

The winter and early spring seasonality of odontocetes coincides with the known spawning, inshore-movement of octopus in Puerto Rico. Little is known about the life histories of cephalopods in the northeastern Caribbean, although a number of species of octopus and squid have been reported (Voss, 1960). Some of these species are known as prey items for odontocetes, however, it is impossible to assess from the data, whether the inshore movement of octopi and the near shore seasonality of odontocetes are related. It is reasonable to hypothesize that the same conditions which drive some species of octopi to spawn inshore in the winter and spring months, could drive similar tropical species of cephalopods, particularly squid, to do likewise. The higher number of odontocete

TABLE 2. Characterization of cetaceans by bathymetric slope index (SI) habitats in Puerto Rico and the Virgin Islands.

Sea floor characterization	Species
Low sea floor relief (SI Classes 1 and 2)	*Balaenoptera acutorostrata* *Balaenoptera* spp. *Delphinus* spp. *Megaptera novaeangliae* *Orcinus orca* *Stenella frontalis* *Stenella longirostris* *Steno bredanensis* *Tursiops truncatus* *Ziphius cavirostris*
Medium sea floor relief (SI Classes 3 and 4)	*Globicephala macrorhynchus* *Physeter macrocephalus*
High sea floor relief (SI Classes 5 and 6)	*Globicephala macrorhynchus* *Physeter macrocephalus*
Not analyzed	*Kogia breviceps* *Pseudorca crassidens* *Stenella coeruleoalba*

sightings near shore from December through April would tend to indicate this, but concrete evidence is needed to support this hypothesis.

Whales and dolphins are an integral part of the Caribbean fauna. Four endangered cetaceans are found off Puerto Rico and the Virgin Islands, with two of these, fin and sei whales, considered vulnerable, and the sperm whales and humpback whales to some extent recovered. Through the efforts of dedicated researchers, the basis for understanding the composition of the cetacean fauna of the northeastern Caribbean has expanded. These data must be supplemented with additional research on the life history, stranding and mortality, general biology, and zoogeography of the species in order to provide important information for the management and conservation of the whale and dolphin species in the area.

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