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Seasonal distribution of bottlenose (*Tursiops truncatus*) and pan-tropical spotted (*Stenella attenuata*) dolphins (Cetacea: Delphinidae) in Golfo Dulce, Costa Rica

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Abstract: There are no detailed studies on the sympatric dolphin species of Golfo Dulce. Studies in other areas have indicated that the presence of sympatric dolphins is maintained by each species using different habitats. This study describes the distribution of bottlenose (*Tursiops truncatus)* and pan-tropical spotted (*Stenella attenuata*) dolphins in Golfo Dulce and its relation to habitat. A total of 428 boat surveys were conducted from September 1991 through December 1992. There were 529 bottlenose dolphin sightings and 200 spotted dolphin sightings. The two species were only once observed in mixed aggregations. There were differences in relative abundance and group size between both dolphin species. Bottlenose dolphins were found mostly in shallow waters, close to shore, near rivers, and along steep marine slopes. Spotted dolphins were associated with deeper waters and increased distance from shore. Despite apparent differences in habitat preferences, the two dolphin species were commonly observed in the same areas, albeit at different times, due in part to seasonal variations in dolphin distribution and habitat preference. Most notably, during the Late Wet season of 1991 bottlenose dolphins were found in the middle and spotted dolphins at both ends of the Gulf. This pattern was almost reversed during the Late Wet season of 1992. The observed seasonal variation patterns are inadequately explained by habitat-preference arguments alone.

Key words: Golfo Dulce, Costa Rica, *Tursiops truncatus*, *Stenella attenuata*, distribution.

Golfo Dulce, Costa Rica, has been recognized as a unique oceanographic environment since the early 70's (Richards *et al.* 1971). Research to date has focused primarily on its geology (Obando 1986, Berrangé 1987), benthos (Nichols-Driscoll 1976, León-Morales and Vargas 1998), coral reefs (Cortés 1990, 1991, 1992), and fisheries (Segura and Campos 1990). More recently, a survey of various physical and biological attributes of the Gulf has been completed (Wolff and Vargas 1994). Despite these efforts, no detailed studies on marine mammals, a conspicuous biological component of Golfo Dulce, had been conducted.

While the presence of marine mammals in Golfo Dulce has been long recognized by local people, their occurrence was not systematically documented until recently (Acevedo and Smultea 1995, Acevedo 1996). Five cetacean species have been recorded in the Gulf; however, only the bottlenose (*Tursiops truncatus* Montagu 1821) and the pan-tropical spotted (*Stenella attenuata* Gray 1846) dolphins are sighted frequently, being considered resident species (Acevedo 1996). Thus, Golfo Dulce provides a unique opportunity to study year around the distribution of sympatric dolphin species.

Several studies have described a correlation between environmental variables and the non-overlapping distribution of sympatric dolphin species (Saayman and Tayler 1973; Würsig and Würsig 1980; Reilly and Fiedler 1994; Silber *et al.* 1994). In most cases, differences in preferred depth and distance from shore explain this non-overlapping dolphin distribution. In contrast, changes in distribution of presumed prey have been presented to explain the seasonal variation in dolphin distribution. The objectives of this study were to describe the distribution of bottlenose and pan-tropical spotted dolphins in Golfo Dulce, its seasonal variation, and its relationship to the environment.

MATERIALS AND METHODS

Study area: Golfo Dulce is a semi-enclosed tropical embayment of the eastern tropical Pacific, located on the southwest coast of Costa Rica and centered around 08°30'N and 83°16'W. The Gulf is approximately 50 km long and 10 to 15 km wide, with a surface area of 750 km^2. The study area is constituted by a deep inner basin with a maximum depth of 215 m and a shallow outer basin with a sill depth of 70 m. The two largest rivers draining into the Gulf are the Coto-Colorado and the Tigre, both draining close to the region where the inner and outer basins meet.

Survey procedure: Non-random boat surveys were conducted on board two inflatable boats (<5 m long) each powered by a 25 Hp outboard engine. Surveys were conducted an average of 5 days per week and effort was made to cover the entire study area each week. On all surveys at least two observers simultaneously watched with the naked eye for dolphins on each side and in front of the boat. Vessel speed was kept at approximately 20 km/hr by monitoring travel time between landmarks of known distance. Once a dolphin group was sighted, it was followed to record location, identify the species, and, when possible, estimate group size and describe their behavior. Sightings of other dolphins made while following a group were not included in the analysis because such sightings were made at a different survey speed. Based on Shane (1990), a group was defined as any number of dolphins behaving in a similar manner or moving in the same direction, regardless of distance between dolphins. The occurrence of debris lines (lines of floating material such as plants, logs, and garbage brought into the area by rivers) was also recorded.

The study was conducted from September 1991 through December 1992; covering the Late Wet season of 1991, and Dry, Early Wet and Late Wet seasons of 1992. A total of 428 surveys were conducted, covering 29 711.5 km in good sighting conditions.

Treatment of data followed in general that of other studies relying on non-random surveys (Polacheck 1987, Reilly 1990, Reilly & Fiedler 1994). Only surveys conducted during good sighting conditions (Beaufort 3 or less and swell 0.5 m or less) were considered for analysis. The study area was divided into 3 X 3 km grids to analyze spatial distribution. Polacheck (1983) suggested to analyze only grids for which there was an effort equal or greater than the size of the grid. Therefore, only grids with at least 9 km of effort were included in the analysis and dolphin distribution was analyzed as number of sightings/9 km and number of dolphins/9 km. Results derived from both estimates were similar, thus only analyses based on number of sightings/9 km are included. However, for comparison with other studies on bottlenose dolphins in coastal areas (Silber *et al.* 1994), results are reported as number of sightings/100 km or number of dolphins/100 km.

Coastal and bathymetric contours of the study site (taken from nautical chart No. 21562), and dolphin locations were digitized in Mappix, a Geographical Information System software. Contour plots of dolphin distribution in each grid were estimated for the most frequent sightings (>0.44 sightings/9 km) and subsequently smoothed by hand. To describe temporal distribution the year was divided into three seasons based on historical pluviometric records in the city of Golfito (IMN 1988): Dry (January through April); Early Wet (May through August); and Late Wet (September through December) (Fig. 1).

Canonical Correspondence Analysis (CCA; Ter Braak 1986) was used to relate dolphin distribution to environmental variables. In this paper results are presented in a Table format to avoid confusion. Environmental and species variables that have the same sign are positively

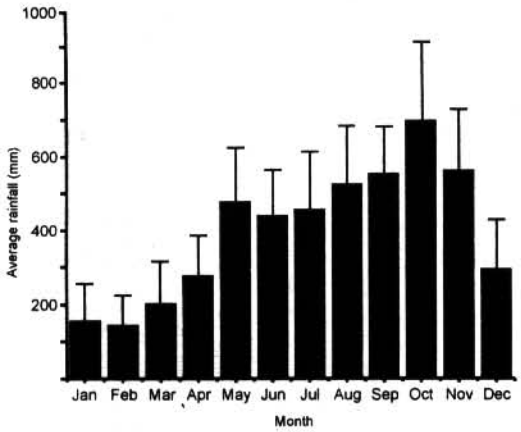

Fig. 1. Monthly average rainfall in Golfito (1941 - 1984).

correlated, environmental and species variables that have a different sign are negatively correlated. Environmental scores close in value to the score of a species are important in explaining the distribution of that species. Seven environmental variables were defined for each grid: predominant depth, distance to closest shore from center of grid, number of isobaths as a measure of slope steepness, number of rivers, number of debris lines/100 km, latitude, and longitude. Skewed data were transformed taking either natural logarithms (depth, latitude and longitude) or square roots (distance to shore).

RESULTS

There were 529 bottlenose dolphin sightings and 200 spotted dolphin sightings; however, the two species were only once observed in mixed aggregations. Since some sightings were made while following dolphins, only 466 sightings of bottlenose dolphins and 195 sightings of spotted dolphins were analyzed. There was no significant difference in the sighting conditions (a combination of Beaufort, swell, and cloud cover) under which the two dolphin species were observed (Mann-Whitney U=170,922.5, n_1=1066, n_2=336, p>0.05). However, relative abundance and group size were different between both dolphin species (Table 1).

Using values from all seasons both dolphin species preferred different areas of Golfo Dulce. Bottlenose dolphins were more frequently seen in Bahía Pavón, along the coastline from Bahía Rincón to Río Tigre, in the nearshore area around Río Esquinas, and in the mid-Gulf between Puerto Jiménez and Bahía Golfito. They were never observed in the outer edge of the sill or along the SW coast (Cabo Matapalo to Punta Tigre, characterized by rocky shores and strong surf). In contrast, spotted dolphins were more frequently found in the deep waters of the inner basin and on the outer edge of the sill. They were never observed in Bahía Pavón, inside most small embayments (including Bahía Golfito), or near the SW coast (Figs. 2, 3, 4, 5). Overall, bottlenose dolphins were mostly associated with shallow waters, close to shore, near rivers, and with steep marine slopes. Whereas spotted dolphins were associated with deep waters and increased distance from shore (Table 2).

TABLE 1

Relative abundance and group size of dolphins in Golfo Dulce

	Sightings/ 100 km	Number of dolphins/ 100 km	Group Size
T. truncatus	1.57	8.22	x=5.8 s=4.17 range=1-25 median=5 n=463
S. attenuata	0.66	21.4	x= 37.6 s=49.54 range=1-300 median=15 n=171
Mann-Whitney			U=12 752.5 p<0.001

Seasonal findings: Late Wet season of 1991 (Fig. 2, Table 2). Bottlenose dolphins were more frequently observed in the middle of the Gulf, between the mouths of the Tigre and Coto-Colorado rivers. The distribution of the species was mostly related to the presence of debris lines. In contrast, spotted dolphins were preferably found in the inner basin and on the outer edge of the sill, essentially distributed to

TABLE 2

Results of Canonical Correspondence Analysis. (Based on sightings/9km)

	Ordination Axis per Season				
	Late Wet season 1991	Dry season 1992	Early Wet season 1992	Late Wet season 1992	Overall
Species scores:					
T. truncatus	0.7677	-0.3423	-0.4282	-0.5709	-0.3900
S. attenuata	-0.7489	1.1306	1.0714	0.6873	0.6953
Environmental scores:					
1-Rivers	0.1253	-0.3073	-0.3862	-0.3997	-0.4328
2-Isobath	0.0573	-0.2898	-0.3132	-0.5089	-0.3402
3-Debris	0.6279	-0.2721	-0.2242	0.5527	-0.0745
4-Depth	-0.0972	0.5134	0.7036	0.6182	0.6968
5-Distance	0.0867	0.7454	0.5180	0.4639	0.6191
6-Latitude	-0.1558	-0.3663	0.0844	-0.1594	-0.0688
7-Longitude	-0.6949	-0.1222	0.3075	-0.3396	0.1722
Eigenvalue	0.5749	0.3870	0.4588	0.3924	0.2712
Monte Carlo	F=91.35 p<0.001	F=90.98 p<0.001	F=129.12 p<0.001	F=60.37 p<0.001	F=140.68 p<0.001

the sides of the distribution of bottlenose dolphins. The distribution of spotted dolphins was related to high values of longitude (i.e. northern end of inner basin) and areas without debris lines.

Dry season of 1992 (Fig. 3, Table 2). Bottlenose dolphins were found along the coast, particularly on the North and West shores (Río Esquinas to Río Tigre) and in Bahía Pavón. Their distribution was mostly related to presence of rivers, high values of latitude (i.e. North shore), shallow waters, and close distance to shore. Spotted dolphins moved into the area occupied by bottlenose dolphins during the previous season, although it their were still found on the outer edge of the sill. The distribution of spotted dolphins was in part related to deep water, and increased distance from shore.

Early Wet season of 1992 (Fig. 4, Table 2). Bottlenose dolphins were still observed along the coast; however, the preferred shores were the Northeast (Río Esquinas to Punta Gallardo) and the West (Río Tigre to Playa Platanares) shores. The species was also frequently found on the inner edge of the sill and along the northern end of Bahía Pavón. The distribution of bottlenose dolphins was related to the presence of rivers and steep slopes, as well as shallow waters and close distance from shore. Spotted dolphins were preferably found in the inner basin and on the outer edge of the sill. Their distribution was partly related to deep waters and increased distance from shore.

Late Wet season of 1992 (Fig. 5, Table 2). Dolphin distribution was almost reversed from that recorded during the Wet season of 1991. Bottlenose dolphins were observed preferably in the northern end of the inner basin, mostly close to shore. They were also frequently found along the northern end of Bahía Pavón. The distribution of bottlenose dolphins was mostly related to steep slopes. In contrast, spotted dolphins were more frecuently found in the middle of the Gulf, in most of the area occupied bottlenose dolphins during the late wet season of 1991. The distribution of spotted dolphins was related to deep waters and the presence of debris lines.

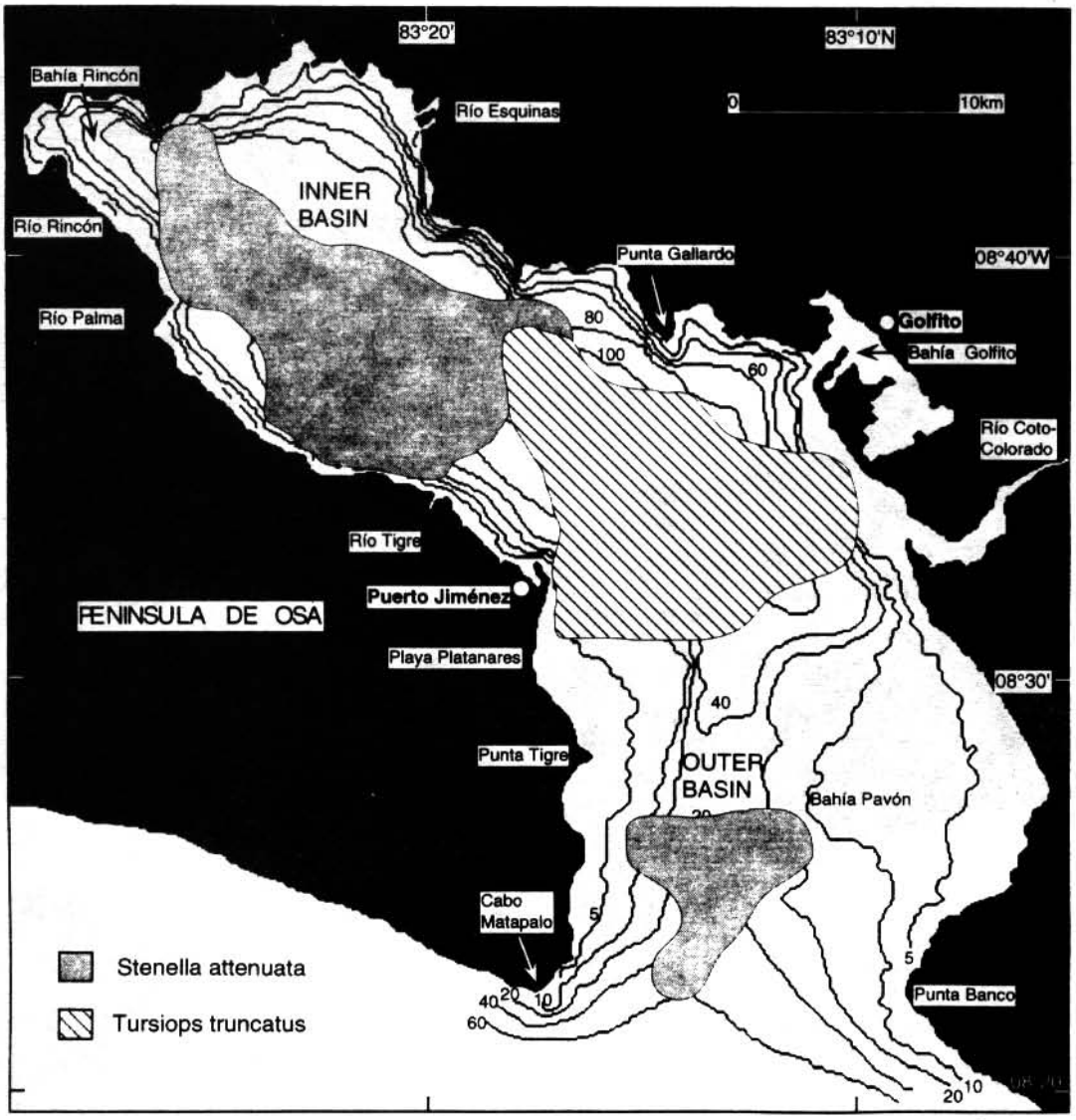

Fig. 2. Regions of high dolphin frequency during Late Wet season 1991. (More than 0.44 sightings/9 km).

DISCUSSION

The similarity in sighting conditions for both bottlenose and spotted dolphins suggests that each species was equally likely to be detected despite differences in their group sizes. High frequency of sightings for bottlenose dolphins indicate that the species remained most of the time in Golfo Dulce. In contrast, the relatively low sighting frequency of spotted dolphins and their preference for the outer edge of the sill suggest that the species may move into the Pacific Ocean. Relative abundance of spotted dolphins was larger than that of bottlenose dolphins apparently due to its significantly larger group sizes, which in turn may be related to habitat preferences. In general, dolphins using deep-water habitat have larger group sizes than

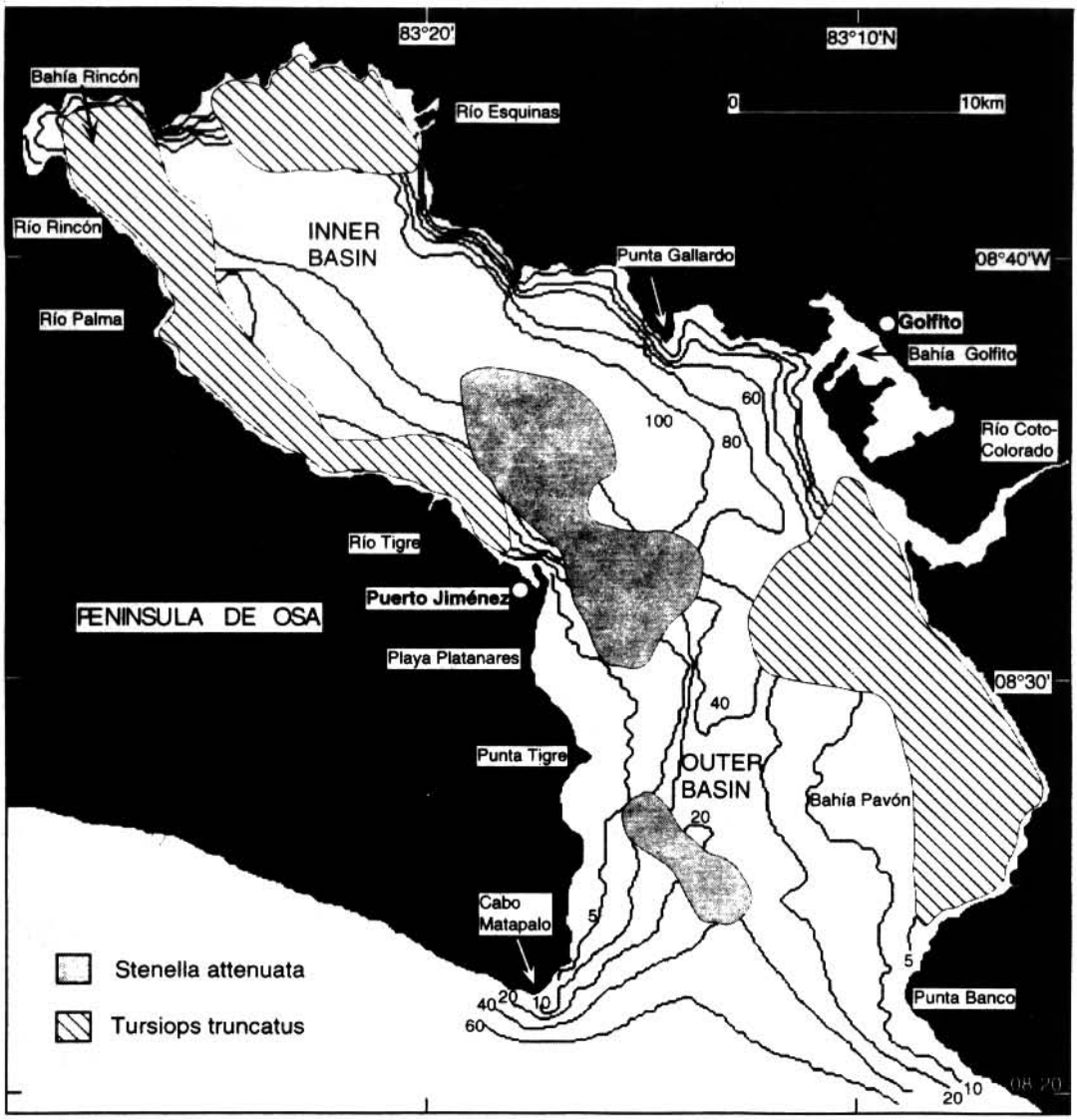

Fig. 3. Regions of high dolphin frequency during Dry season 1992. (More than 0.44 sightings/9 km).

dolphins using shallow-water habitat (reviewed by Wells *et al.* 1980, Würsig 1986).

Overall preference of bottlenose dolphins for shallow waters close to shore, and of spotted dolphins for deeper waters away from shore agrees with results from other studies on habitat preferences. In a Colombian bay, Suárez *et al.* (1994) observed bottlenose dolphins in nearshore, semi-enclosed waters and spotted dolphins in open waters, farther from shore. In the Gulf of San José, Argentina, bottlenose dolphins used preferably the shallow, nearshore waters; whereas dusky dolphins (*Lagenorhynchus obscurus*) used the deeper waters away from shore, with some overlap in area covered by both species (Würsig and Würsig 1980). In the northern Gulf of California, bottlenose dolphins also preferred nearshore, shallow waters;

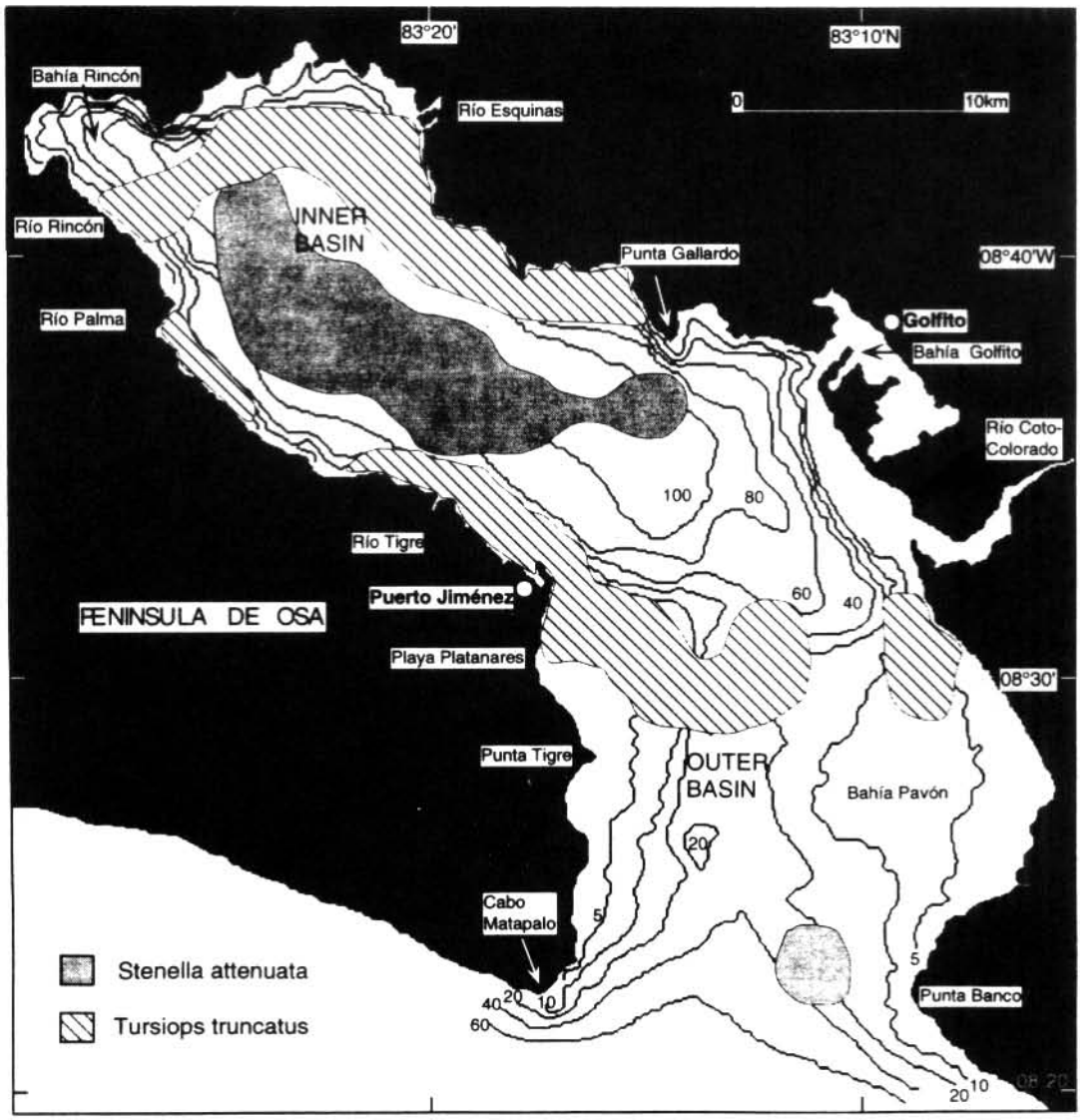

Fig. 4. Regions of high dolphin frequency during Early Wet season 1992. (More than 0.44 sightings/9 km).

in contrast, common dolphins (*Delphinus delphis*) preferred offshore, deep waters, with little spatial overlap (Silber *et al.* 1994). In South Africa, there was separation among humpback (*Sousa* sp.), striped (*Stenella coeruloalba*), and bottlenose dolphins into nearshore, offshore and intermediate habitats, respectively (Saayman *et al.* 1972, Saayman and Tayler 1973). In all these studies, each dolphin species preferred a different habitat, usually shallower, closer to shore areas versus deeper, farther from shore regions.

In Golfo Dulce there were intra-specific variations in dolphin distribution and habitat use, as indicated by the lower overall eigenvalue compared to any of the seasonal eigenvalues. The observed seasonal variations resulted in use of the same areas by both dolphin

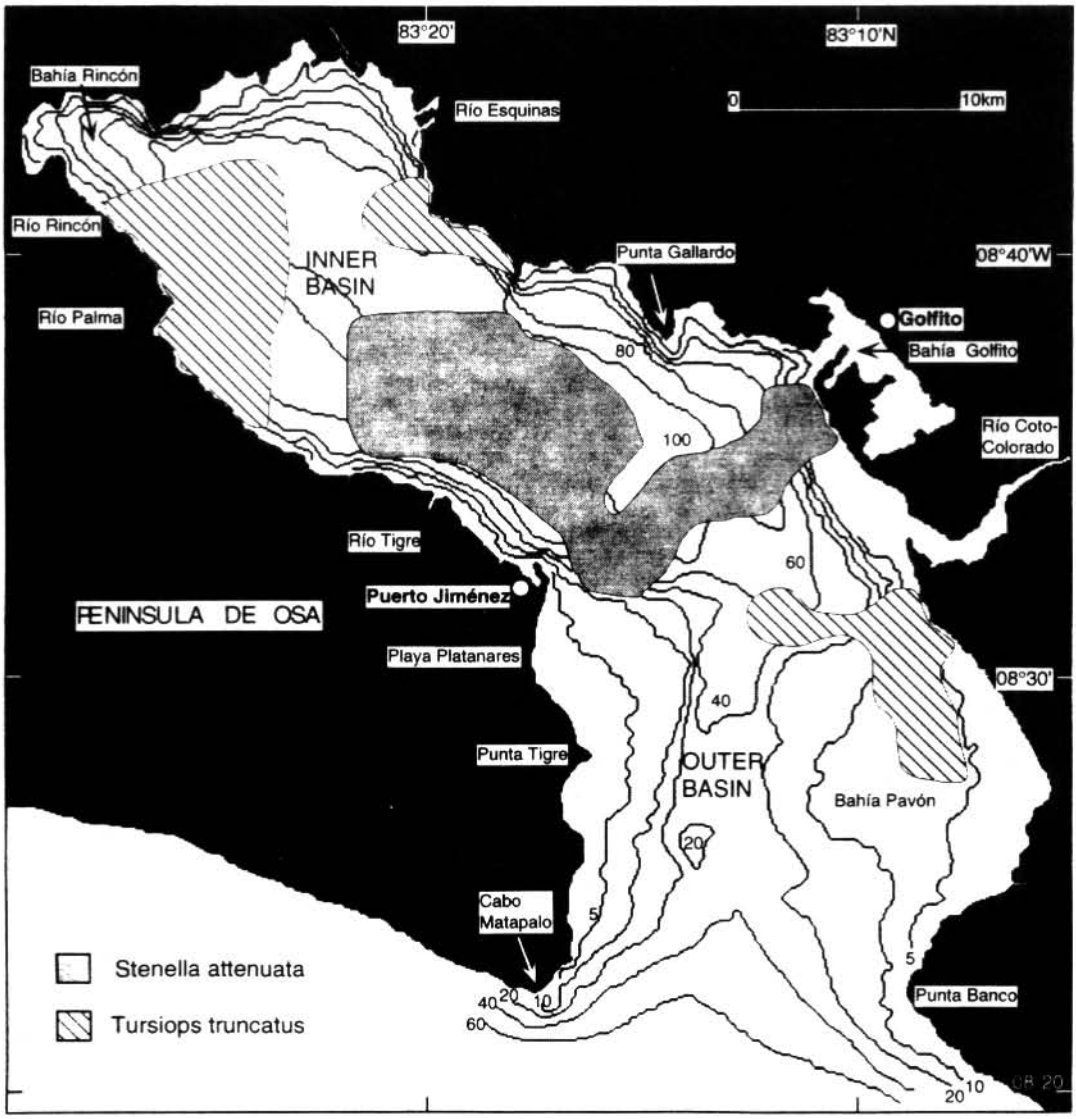

Fig. 5. Regions of high dolphin frequency during Late Wet season 1992. (More than 0.44 sightings/9 km).

species during different seasons while maintaining separate distributions within each season. Thus, the argument that bottlenose and spotted dolphins are separated by depth, distance to shore or any of the other environmental variables measured, leaves unexplained the seasonal overlaps in dolphin distribution. One possible explanation for this seasonal variation is that dolphin distribution was related to an unmeasured component of the habitat. For instance, although dolphin species in the eastern tropical Pacific showed annual variations in distribution, their preferred habitat, as defined by several oceanographic variables, remained the same (Reilly and Fiedler 1994). Nonetheless, oceanographic data indicated no difference in four surface water parameters under which spotted and bottlenose dolphins were

sighted (Acevedo, unpublished). It seems necessary then to present a different argument to explain the results herein presented.

In other areas, differences in habitat preferences among dolphin species have been related to their food habits. In Argentina, bottlenose dolphins preyed on nearshore prey, while dusky dolphins fed mostly on pelagic schooling fish with seasonal switches to nearshore prey (Würsig and Würsig 1980). In South Africa, humpback dolphins preyed on nearshore prey, striped dolphins on pelagic fish, and bottlenose dolphins on both types of prey (Saayman *et al.* 1972, Saayman and Tayler 1973). In the eastern tropical Pacific, nearshore bottlenose dolphins feed on nearshore fishes (Walker 1981), whereas spotted dolphins feed on epipelagic fish and squid (Perrin *et al.* 1973). Food habits of both dolphin species in Golfo Dulce are unknown; however, field observations suggest that spotted dolphins preyed on pelagic schooling fish and bottlenose dolphins mostly on nearshore fish with seasonal feeding on pelagic schooling fish (Acevedo-Gutiérrez & Burkhart 1995). The distribution and habitat use of both dolphin species in Golfo Dulce may be also related to their presumed food habits. Bottlenose dolphins favored the coastal areas where nearshore fishes live and spotted dolphins preferred deep-water and open areas traditionally associated with pelagic schooling fish. However, this food habit argument is insufficient to explain the seasonal feeding on pelagic schooling fish by bottlenose dolphins.

Neither differences in habitat nor differences in food habits can solely explain the observed results: a non-overlapping distribution with seasonal variations in which both dolphin species used the same habitats and fed in part on the same type of prey. A third possible explanation for these variations is that there was avoidance between both dolphin species, either one species avoiding the areas occupied by the other or both species avoiding each other. A non-random distribution between spotted and bottlenose dolphins in Golfo Dulce supports this argument (Acevedo-Gutiérrez & Burkhart 1995).

A combination of the three arguments herein presented provides the most satisfactory explanation for the distribution of bottlenose and spotted dolphins in Golfo Dulce. In general, bottlenose dolphins preferred shallower waters, closer to shore; whereas spotted dolphins preferred deeper waters, farther from shore. Presmably this distribution was related to their food habits. Variations from this general pattern were apparently indicative of inter-specific avoidance.

The unique physiography of Golfo Dulce (Richards *et al.* 1971) has without a doubt permitted the apparent residency of bottlenose and spotted dolphins. In other areas, the presence of sympatric dolphin species has been explained by differences in habitat preferences. In Golfo Dulce, however, this argument alone is inadequate to explain the observed results. Rather, it seems that a combination of habitat preferences, feeding habits and inter-specific avoidance has allowed both dolphin species to share this tropical embayment. Further studies on dolphin food habits and prey distribution are necessary to describe in detail seasonal variations in dolphin distribution and habitat use in Golfo Dulce. It is possible that arguments besides habitat-preferences are also necessary to explicate the distribution of sympatric dolphin species in other areas.

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RESUMEN

No existen estudios detallados sobre las especies simpátricas de delfines en Golfo Dulce. En otras áreas se ha reportado que la presencia de especies simpátricas de delfines está rela-

cionada a la preferencia de cada especie por diferentes habitats. Los objetivos de este trabajo fueron describir la distribución de la tonina (*Tursiops truncatus)* y del delfín manchado tropical (*Stenella attenuata*) en Golfo Dulce y su relación con el hábitat. Un total de 428 censos se condujeron de septiembre de 1991 a diciembre de 1992. Se registraron 529 avistamientos de toninas y 200 avistamientos de delfines manchados. En ninguna ocasión se observaron ambas especies en agregaciones mixtas. Hubo diferencias en la abundancia relativa y el tamaño de grupo entre ambas especies. Las toninas se observaron principalmente en aguas someras, cerca de la costa, cerca de la desembocadura de ríos y a lo largo de pendientes submarinas empinadas. Los delfines manchados se observaron la mayor parte del tiempo en aguas profundas y lejos de la costa. A pesar de las aparentes diferencias en preferencia del hábitat, ambas especies fueron comúnmente observadas en las mismas áreas, aunque en diferentes temporadas, debido en parte a variaciones estacionales en la distribución y preferencia del hábitat de cada especie. Durante la temporada tardía de lluvias en 1991, las toninas se observaron en el centro del Golfo mientras que los delfines manchados se observaron en ambos extremos del mismo. Esta situación cambió casi por completo durante la temporada tardía de lluvias en 1992. Las variaciones estacionales detectadas no pueden ser explicadas únicamente con el argumento de diferencias en la preferencia del hábitat por parte de cada especie.

REFERENCES

Acevedo, A. 1996. Lista de mamíferos marinos en Golfo Dulce e Isla del Coco, Costa Rica. Rev. Biol. Trop. 44: 933-934.

Acevedo, A. & M. Smultea. 1995. First records of humpback whales including calves at Golfo Dulce and Isla del Coco, Costa Rica, suggesting geographical overlap of northern and southern hemisphere populations. Mar. Mamm. Sci. 11: 554-559.

Acevedo-Gutiérrez, A. & S. Burkhart. 1995. Distribution of bottlenose and spotted dolphins in a tropical embayment: habitat preferences and competitive exclusion?. Abstracts XI Biennial Conference on the Biology of Marine Mammals, Orlando, Florida.

Berrangé, J. P. 1987. Gas seeps on the margins of the Golfo Dulce pull-apart basin, southern Costa Rica. Rev. Geol. Amer. Central 6: 103-111.

Cortés, J. 1990. The coral reefs of Golfo Dulce, Costa Rica: distribution and community structure. Atoll. Res. Bull. 344: 1-37.

Cortés, J. 1991. Los arrecifes coralinos del Golfo Dulce, Costa Rica: aspectos geológicos. Rev. Geol. Amer. Central. 13: 15-24.

Cortés, J. 1992. Los arrecifes coralinos del Golfo Dulce, Costa Rica: aspectos ecológicos. Rev. Biol. Trop. 40: 19-26.

Instituto Meteorológico Nacional (IMN). 1988. Catastro de las series de precipitaciones medidas en Costa Rica. Ministerio de Recursos Naturales, Energía y Minas, San José, Costa Rica. 364 p.

León-Morales, R. & J. A. Vargas. 1998. Macroinfauna of a tropical fjord-like embayment: Golfo Dulce, Costa Rica. Rev. Biol. Trop. 46. Supl. 6: 81-90.

Nichols-Driscoll, J. 1976. Benthic invertebrate communities in Golfo Dulce, Costa Rica, an anoxic basin. Rev. Biol. Trop. 24: 281-297.

Obando, J. A. 1986. Sedimentología y tectónica del Cretácico y Paleogéno de la región de Golfito, Península de Burica y Península de Osa, Puntarenas, Costa Rica. Tesis de Licenciatura, Universidad de Costa Rica, San José. 211p.

Perrin, W. F., R. R. Warner, C. H. Fiscus & D. B. Holts. 1973. Stomach contents of porpoise, *Stenella* spp. and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull. 71: 1077-1092.

Polacheck, T. W. 1983. The relative abundance of dolphins in the eastern tropical Pacific based on encounter rates with tuna purse seiners. Ph. D. diss. University of Oregon, Eugene. 444p.

Polacheck, T. W. 1987. Relative abundance, distribution and inter-specific relationships of cetacean schools in the eastern tropical Pacific. Mar. Mamm. Sci. 3: 54-77.

Reilly, S. B. 1990. Seasonal changes in distribution and habitat differences among dolphin in the eastern tropical Pacific. Mar. Ecol. Prog. Ser. 66: 1-11.

Reilly, S. B. & P. C. Fiedler. 1994. Interannual variability of dolphin habitats in the eastern tropical Pacific. I. Research vessel surveys, 1986-1990. Fish. Bull. 92: 434-450.

Richards, F. A., J. A. Anderson & J. D. Cline. 1971. Chemical and physical observations in Golfo Dulce, an anoxic basin in the Pacific coast of Costa Rica. Limnol. Oceanogr. 16: 43-50.

Saayman, G. S. & C. K. Tayler. 1973. Social organisation of inshore dolphins (*Tursiops aduncus* and *Sousa*) in the Indian Ocean. J. Mammal. 54: 993-996.

Saayman, G., S. D. Bower & C. K. Tayler. 1972. Observations on inshore and pelagic dolphins on the southeastern Cape Coast of South Africa. Koedoe 15: 1-24.

Segura, A. & J. A. Campos. 1990. Pérdidas poscaptura en la pesquería artesanal del Golfo Dulce y su proyección al Pacífico de Costa Rica. Rev. Biol. Trop. 38: 425-429.

Shane, S. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida, p. 245-265. *In* S. Leatherwood & R. R. Reeves (eds.). The bottlenose dolphin. Academic, San Diego, California.

Silber, G. K., M. W. Newcomer, P. Silber, H. Pérez-Cortés & G. M. Ellis. 1994. Cetaceans of the northern Gulf of California: distribution, occurrence, and relative abundance. Mar. Mamm. Sci. 10: 283-298.

Suárez, C. L., Martha, F. Trujillo & A. Cadena. 1994. Distribución espacio-temporal y aspectos del comportamiento y de la interacción con la pesquería artesanal de *Tursiops truncatus* y *Stenella attenuata* en el Parque Nacional Uria, Choco, Colombia. Resúmenes del IX Seminario Nacional de Ciencias y Tecnologías del Mar y Congreso Latinoamericano en Ciencias del Mar, Medellín, Colombia.

Ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

Walker, W. A. 1981. Geographical variation in morphology and biology of bottlenose dolphins (*Tursiops*) in the eastern north Pacific. NOAA Admn. Rept. NMFS LJ-81-03C, La Jolla. 54p.

Wells, R. S., A. B. Irvine & M. D. Scott. 1980. The social ecology of inshore odontocetes, p. 263-317. *In* L. M. Herman (ed.). Cetacean behavior: mechanisms and functions. Wiley, New York.

Wolff, M. & J. Vargas (eds.) 1994. Cruise Report of the R/V *Victor Hensen* Costa Rica Expedition 1993/1994. Center for Tropical Marine Ecology Contribution 2, Bremen. 109 p.

Würsig, B. 1986. Delphinid foraging strategies, p. 347-359. *In* R. J. Schusterman, J. A. Thomas & F. G. Wood (eds.). Dolphin cognition and behavior: a comparative approach. L. Erlbaum, Hillsdale, New Jersey.

Würsig, B. & M. Würsig. 1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the south Atlantic. Fish. Bull. 77: 871-890.