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DISTRIBUTION OF PANTROPICAL SPOTTED DOLPHINS IN PACIFIC COASTAL WATERS OF PANAMA

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Abstract - Spotted dolphins (*Stenella attenuata*) have been subjected to large removals as bycatch in the purse-seine tuna fishery. While pelagic stocks are relatively well known, information on coastal populations is scarce. This study attempted to quantify seasonal differences in the distribution of a coastal population in Bahía Honda, on the Pacific coast of Panama (7°50'N, 81°35'W). Field work (117 days) was conducted from January to June 2002. To analyse distribution, the study area was divided into a grid of 4.84km^2 squares. Survey effort was logged by recording a GPS position every two minutes. Number of sightings in each square was divided by effort and corrected according to the proportion of sea/land. Dolphin presence and group size distribution were analysed using geostatistics and density contours were created through kriging. Only slight differences in distribution were detected between dry (Jan-Mar) and rainy (Apr-Jun) seasons. Dolphins preferred the area around Cativo bay, with a secondary core area next to Canales de Tierra Island. Encounters were rare towards Rosario bay. In general, sightings per unit effort seemed to be higher during the rainy season, although this may be a result of the dolphins getting used to the boat and improved observer experience. Group size was very variable, ranging from solitary animals to around 50 individuals with a median of 12 with no seasonal difference (U= 7142, p = 0.83). Most groups found in Bahía Honda (83.4%) contained fewer than ten individuals. This study, in conjunction with those elsewhere along the coastal eastern Pacific suggests that group size could be related to depth and/or to the presence/absence of the sympatric bottlenose dolphin, *Tursiops truncatus*. Further studies on biotic and abiotic correlates of dolphin distribution are needed, and information on potential prey, diet and feeding habits would help clarify the interspecific relationship with bottlenose dolphins.

Resumen - El delfín manchado pantropical (*Stenella attenuata*) ha sido sujeto a importantes capturas involutarias en la pesquería de red de cerco de atún. Aunque las subpoblaciones pelágicas han sido ampliamente estudiadas en el Pacífico Oriental, la subespecie costera (*S. a. graffmani*) es aún poco conocida. Este trabajo se enfocó en entender las diferencias estacionales en la distribución del delfín manchado en la zona de Bahía Honda, Panamá (7°50'N, 81°35'W). El estudio fue realizado de enero a junio 2002 llevando a cabo 117 días de observaciones. Un GPS grabó la posición de la embarcación cada dos minutos para cuantificar el esfuerzo de muestreo. El área de estudio fue dividida en una grilla de 4.84km^2. La cantidad de avistamientos en cada celda fue dividida por el esfuerzo y corregida de acuerdo a la proporción de mar/tierra firme. La presencia de individuos y la distribución del tamaño de grupos fueron analizadas mediante método geoestadístico con lo cual se generaron contornos de distribución. El patrón espacial de los avistamientos no mostró diferencias marcadas entre la estación seca (enero-marzo) y la lluviosa (abril-junio), siendo la bahía de Cativo la zona de mayor preferencia, seguida por el área al occidente de Isla Canales de Tierra durante el verano. La región de la bahía de Rosario fue poco frecuentada. Durante el invierno se realizaron más avistamientos por unidad de esfuerzo; esto puede ser resultado de una mayor cantidad de delfines en el área, de la habituación de los delfines al bote o una mayor experiencia de observación a lo largo del estudio. El tamaño de grupo fue muy variable, desde animales solitarios hasta grupos de 50 individuos, con una mediana de 12. El tamaño grupal no mostró diferencias estacionales (U= 7142, p = 0,83). La mayoría de los grupos en el interior de la bahía (83,4%) fueron menores de diez individuos. En comparación con otros estudios de la costa este de Sur y Centro América, el tamaño grupal típico puede estar relacionado a la profundidad y/o a la presencia/ausencia del bufeo (*Tursiops truncatus*). Para entender más clararamente la distribución de los delfines manchados, es necesario investigar otros aspectos bióticos y abióticos del ecosistema. Información sobre patrones espaciales y temporales de potenciales presas, dieta y hábitos alimentarios de los delfines es esencial para entender las relaciones interespecíficas.

Keywords: Pantropical spotted dolphin, *Stenella attenuata graffmani*, distribution, geostatistics, Panama

Introduction

Pantropical spotted dolphins (*Stenella attenuata*) are widely distributed in the tropical and subtropical oceans of the world. In the Eastern tropical Pacific (ETP), the species shows strong geographic variation. Two pelagic stocks are known as northeastern and western/southern (Perrin and Hohn, 1994). A coastal form has been classified as a separate subspecies, *S. a. graffmani*, occurring from the Gulf of Mexico to Perú within 185 km off the coast (Wade and Gerrodette, 1993). This form is larger, stockier, and has heavier spotting than its offshore counterpart (Perrin and Hohn, 1994).

In the ETP, spotted dolphins have been severely affected by bycatch in tuna fisheries (Hall, 1996: Wade, 1995). Since the late 1950s, an estimated six million dolphins (mostly spotted and spinner dolphins) have died in this fishery. The current abundance of the northeastern offshore stock of spotted dolphins is considered to be about a 15% of its original population size (Gerrodette, 2002). Not surprisingly, this problem has prompted extensive research on the biology, distribution and abundance of the species in the ETP (*e.g.* Reilly and Fiedler, 1994; Gerrodette and Palacios, 1996).

While these studies have been focused mainly on the pelagic stocks, the coastal subspecies still remains poorly understood. The current impact of the tuna fishery on them is unknown, but in 1979, when fishing effort was concentrated in coastal areas, the population was estimated to be at 42% of its original size (NOAA, 1999). Large-scale estimates are regularly calculated (Wade and Gerrodette, 1993; Gerrodette and Palacios, 1996;

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Gerrodette, 2000), but genetic studies suggest that the coastal subspecies is comprised of several stocks (Escorza-Trevino *et al.*, 2002). There are only few studies focusing on specific stocks (Suárez, 1994; Acevedo and Burkhart, 1998; Pardo, 1998; May, 2001), hence, in general, subpopulation sizes, spatial distributions and movements are poorly known.

Data on the distribution of a species in space and time are crucial in reaching an understanding of the critical habitat requirements, highlighting the conservation actions most urgently needed and guiding the design of management tools (*e.g.* reserves, time area closures). In this study geostatistical analyses were used to model the seasonal distribution of a coastal population of pantropical spotted dolphins in the surrounding area of Bahía Honda, an embayment on the Pacific Coast of Panama (figure 1).

Material and Methods

The Bahía Honda (7°50'N, 81°35'W) lies on the Pacific coast of Panama, Central America (figure 1). The study area, approximately 178km^2, comprises mostly open areas partly protected by an island system, as well as some more sheltered bays. The various habitats include tidal banks, mangroves, coral and rocky reefs, and areas with sandy or muddy bottoms. The maximum depth in the study area is approximately 80m, but most of the work was conducted

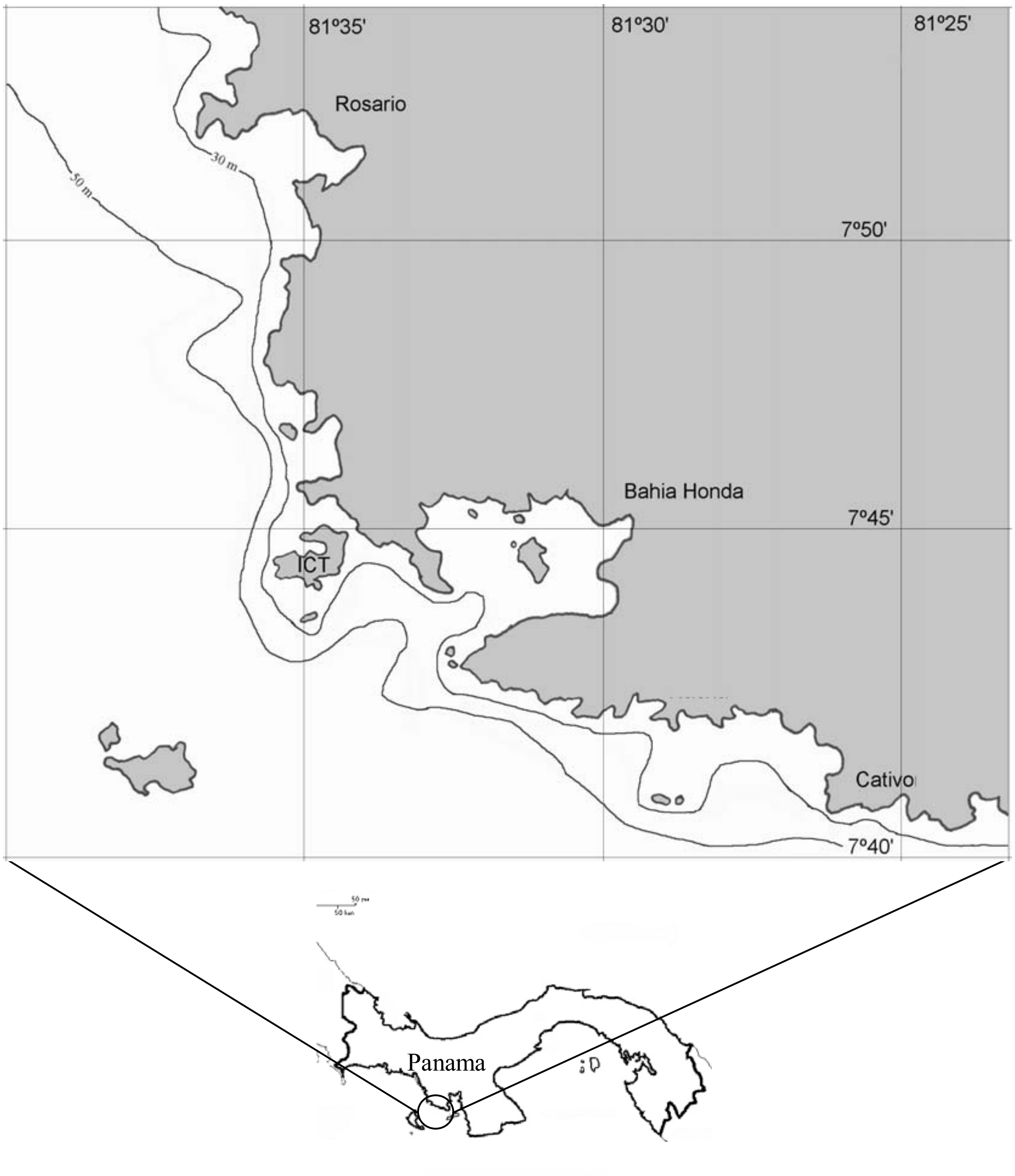

Figure 1. Bahía Honda (Panama) study area showing 30 m and 50 m contours. Dashed lines show systematic survey transects.

within the 50m contour. The dry season extends from late December until the beginning of April; the rest of the year is considered the rainy season. Average air temperature throughout the year is 25.9°C (Cardiel *et al.*, 1997).

Survey methods

Fieldwork was divided into two different sampling periods to cover the dry season (Jan-Mar 2002) and the rainy season (Apr-Jun 2002). Surveys were conducted at approximately 10 knots in a 3.7m fibreglass boat powered with a 15 hp outboard motor. At least once a week, two systematic transects were followed, one within 500-800m from shore and a second one approximately two km from shore (see figure 1). On these surveys, less than half an hour was spent with each group so that all of the study area could be covered. On other days, or when transects had been completed, we continued searching the study area, following dolphins for as long as possible to photo-identify individuals and sample group behaviour. When dolphins were found, time, group size and behavioural state were recorded. A Garmin 12XL GPS recorded location every two minutes thus logging search effort, initial and final locations and movement of the group. Observations were made only in wind/sea conditions of Beaufort two or less.

Spotted dolphins in this area seemed to avoid close approach by boats. For this reason, to sample behaviour, groups were followed at idle speed at a distance of >30 metres (unless the dolphins approached the boat). If the group was stationary, the boat's motor was turned off in order to minimise disturbance to the dolphins.

Analysis of distribution

The study area was divided into a 10 x 10 grid, each grid square approximately 2.2km x 2.2km. Grid size was chosen as a compromise between maximising resolution while ensuring that not too many grid squares had zero sightings. Sighting effort, calculated as number of 2-min sampling points, was calculated for each grid square. Only squares with more than 15 sampling points were considered in the analysis. The number of sightings in each square was divided by effort, and for inshore squares, corrected according to the proportion of sea in that square. The resulting number is here onwards referred to as SPUE (sightings per unit effort).

A geostatistical approach allowed us to model and interpolate samples to create a contoured distribution of spotted dolphins in the area. VARIOWIN 2.21 (Pannatier, 1996) software was used to estimate experimental standard variograms and to explore different variogram models. Directional and omnidirectional variograms were computed and variogram parameters were calculated for gaussian, exponential, spherical and linear fits. The weighted least squares formula described by Cressie (1993) was used to choose the best parameters. Resulting models were then used to contour the estimated distribution via ordinary kriging with SURFER 6.01 (Smith *et al.*, 1995). Data were log-transformed before analysis.

Analysis of behaviour

During the first two weeks, *ad libitum* observations on behaviour were conducted in order to learn their behavioural range and to build the categories and behavioural key (appendix A). The focal group was defined after Schneider (1999), as individuals engaged in the same general activity, scattered over no more than one km^2. After the first two weeks, behaviour was scan-sampled (Altmann, 1974) for a two-minute period every five minutes. Following Schneider's attempt to reduce bias in behavioural studies (Schneider, 1999), we modified his key to assign minor categories of behaviour (see appendix A). Minor categories were then grouped into one of each of the following categories: Feed (F): individual, group and co-operative feeding; Travel (T): travel and fast travel; Mill (M): mill and erratic; Dive (D); and Social (S).

Markov chain analysis was chosen to examine behavioural data, thus accounting for the temporal dynamics of behaviour (Lusseau, in press). The highest Bayes Information Criterion (BIC) was used to determine which order chain best described the data (Guttorp, 1995). PopTools 2.3 (http://www.cse.csiro.au/CDG/poptools) were used to perform the eigenanalyses of the transition probabilities matrixes. With this analysis, it is possible to obtain the behavioural budget. Readers are referred to Lusseau (in press) for a detailed description of the method.

Results

Field effort comprised 117 sampling days with a total of 630 effort hours, 366 during the dry season and 264 during the rainy season. Two hundred and sixty nine dolphin groups were encountered (figure 2), 130 during the dry season and 139 during the rainy season. In contrast, only eight groups of bottlenose dolphins were sighted during this period.

For dolphin presence, omnidirectional standard variograms were chosen to calculate a variogram model (figure 3). Gaussian and spherical models best fitted dry and rainy season experimental variograms respectively (table 1).

For both seasons, the Cativo bay area had the highest dolphin density while sightings in the Rosario bay area were rare. There was a second area of high density around Canales de Tierra Island (ICT). SPUE values are slightly higher overall during the rainy season (figure 4).

Group size varied from one to 50, with a median of 12 (25^{th}–75^{th}percentiles: 5-23), with no significant seasonal difference (U = 7142, p. = 0.83). Non-parametric descriptors and tests were chosen because data could not be transformed to normality. Within the Bahía Honda, groups of more than ten individuals were unusual (16.6%, n=24). In contrast, outside the bay about half of the groups contained more than ten individuals.

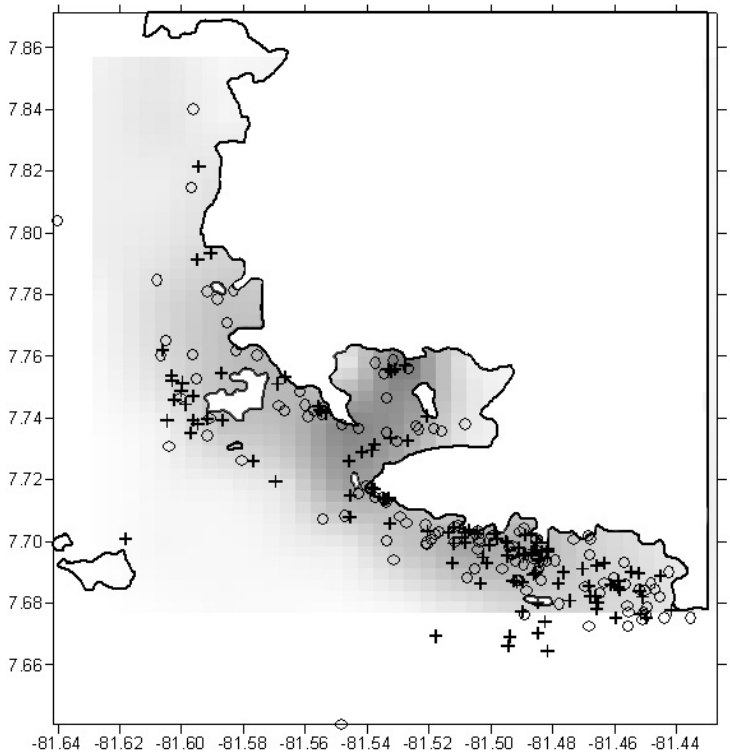

Figure 2. *S. attenuata* sighting locations (+ are dry season sightings, O are rainy season sightings), and search effort. Zones with more search effort are shown in darker shades of gray.

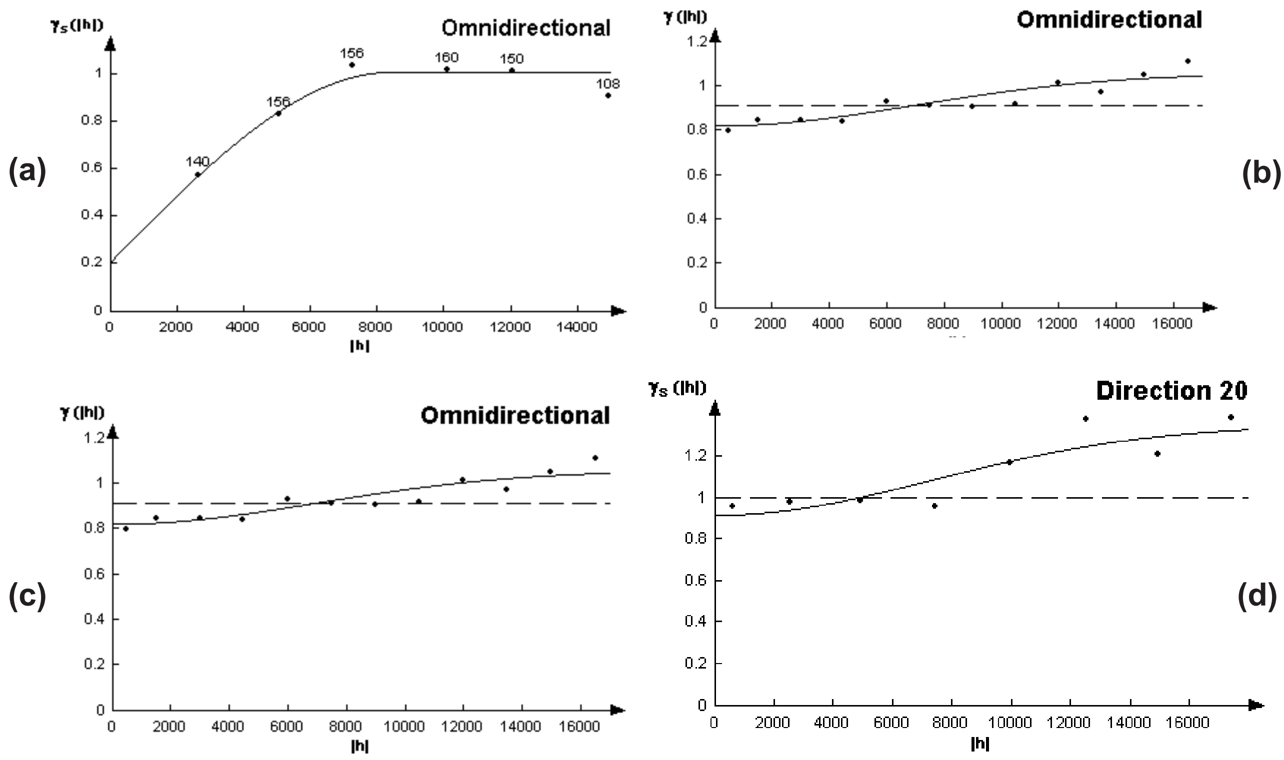

Figure 3. Experimental standard variograms and fitted models for the distribution of *S. a. graffmani* in Bahía Honda, Panama. |h| values are in meters. a) Omnidirectional standard variogram for dry season SPUE. b) Omnidirectional standard variogram for rainy season SPUE. c) Omnidirectional standard variogram for log-transformed group size. d) Directional standard variogram for log-transformed group size.

Table 1. Results from goestatistical analyses. Parameter values for the models fitted to the omnidirectional standard variograms for the dry and rainy seasons and to the 20° log-transformed group size distribution of *S. a. graffmani* in Bahía Honda, Panama.

	Model	Nugget	Range (m)	Sill	Anisotropy
Dry season	Gaussian	0.58	8000	0.46	-
Rainy season	Spherical	0.21	8400	0.80	-
Group size	Gaussian	0.95	21000	0.36	8

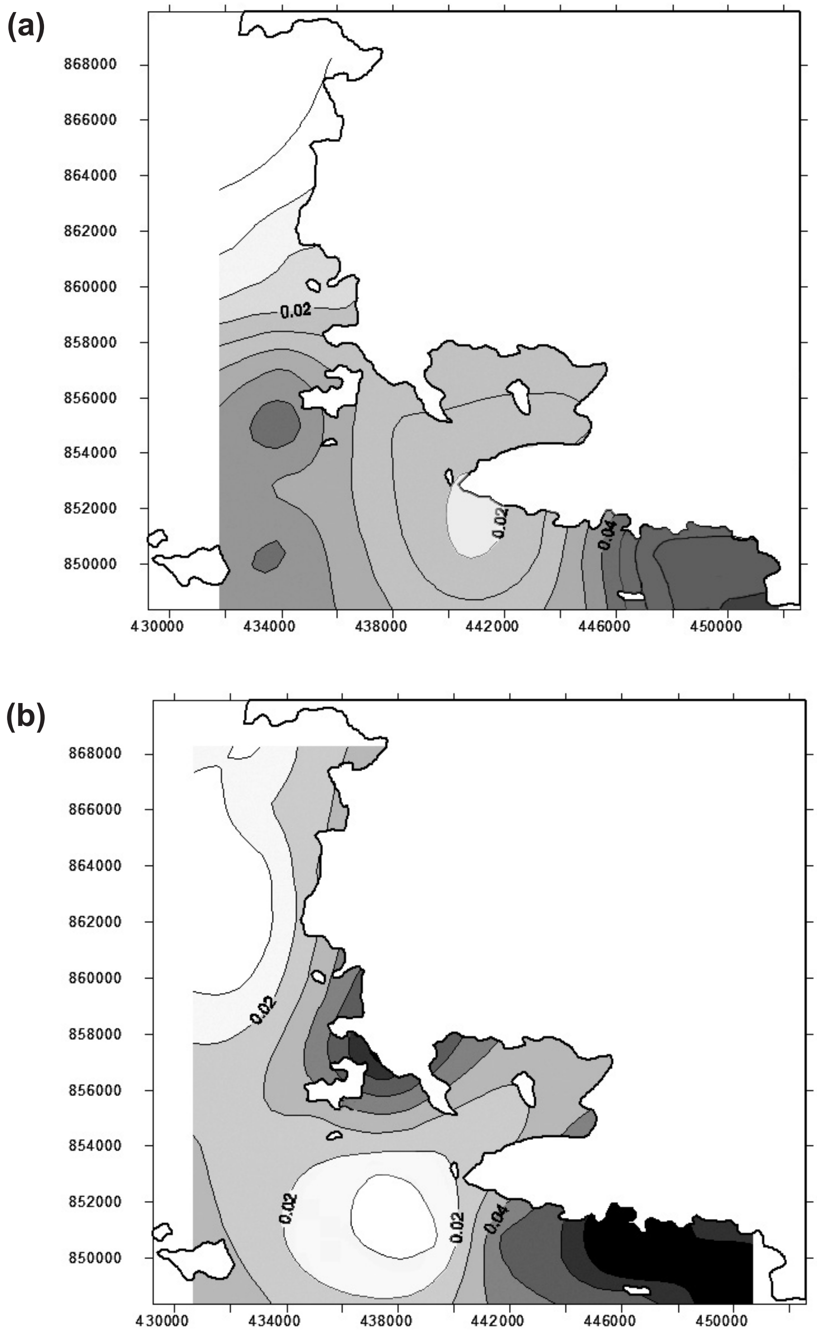

Figure 4. Contoured distribution of *S. a. graffmani* for a) dry and b) rainy seasons in Bahía Honda, Panama. Values are an arbitrary measure of relative abundance, SPUE. Coordinates are UTM (units in metres).

The largest groups were seen during the wet season (figure 5). However, because there was no significant difference in average group size between seasons, data were pooled for analysis of spatial distribution. The omnidirectional variogram showed that group size was variable but without a strong spatial relationship. The variogram showing the clearest structure was in the 20° direction (figure 3), an angle almost perpendicular to the coast direction and in particular similar to the layout of the entrance to Bahía Honda. We suggest that the directional variogram shows a better spatial structure as it might be related to the prevalence of small groups inside Bahía Honda, as suggested by the contoured distribution of this aspect (figure 6). Spatial patterns of group size further offshore from the regularly surveyed area (see figure 1) are unreliable, due to paucity of data.

Insufficient data were available to make robust behavioural comparisons between seasons or zones. A first-order Markov chain described the whole data set better than a 0-order chain, meaning that a behavioural state depended on the previous behaviour (0-order, BIC = -732; 1-order, BIC = -620). Eigenanalysis results showed that the most frequent behaviour was feeding, while social bouts were scarce (figure 7).

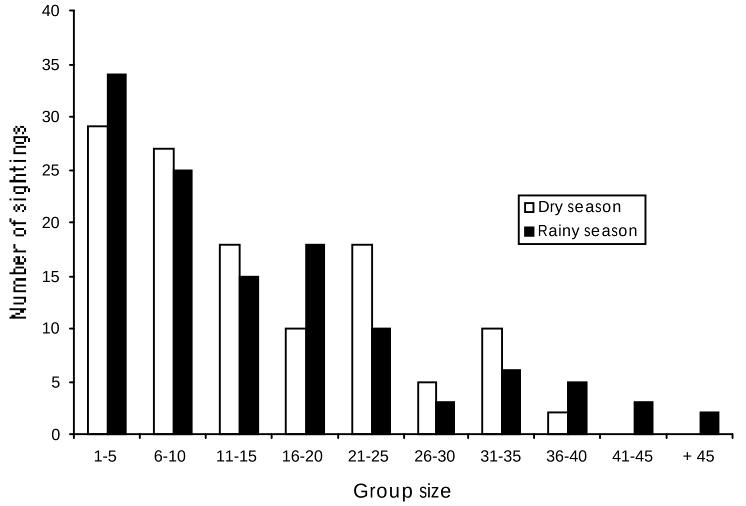

Figure 5. Group size frequency of *S. a. graffmani* in Bahía Honda, Panama. n = 119 (dry season), 121 (rainy season).

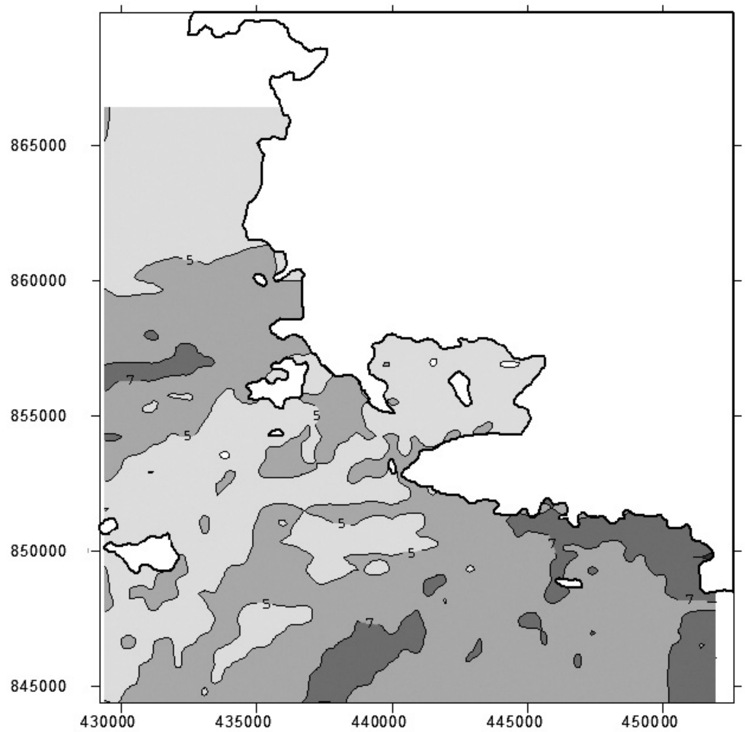

Figure 6. Group size distribution of *S. a. graffmani* in Bahía Honda, Panama. Contour line values are the back transformed group size values, but are much smaller than the original numbers. Coordinates are UTM (units in metres).

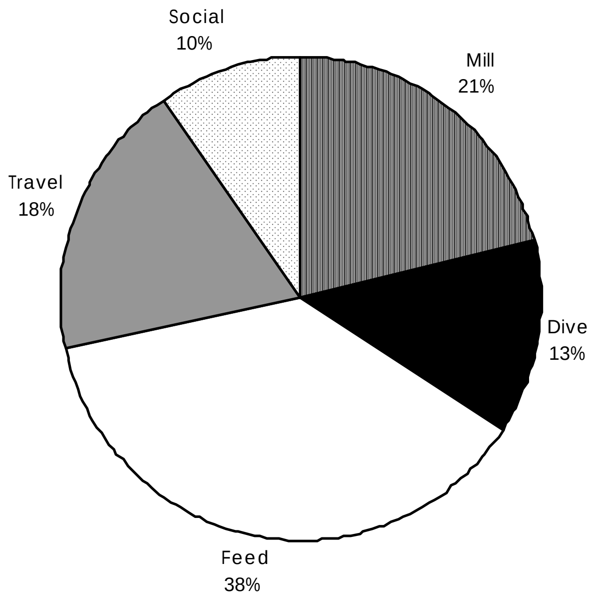

Figure 7. Time budget of *S. a. graffmani* in Bahía Honda, Panama. n = 475.

Discussion

Geostatistics were originally developed to analyse continuous variables in geology (Webster and Oliver, 2001). In more recent years, this method has been applied to discontinuous data to understand wildlife distributions (*e.g.* Petitgas, 1998; Linder *et al.*, 2000), locate nursery areas (*e.g.* Lembo *et al.*, 2000; Roa and Tapia, 2000) estimate fish biomass and assess fisheries status (*e.g.* Rueda and Defeo, 2001). In this study, geostatistics proved to be a useful tool to visualise a pattern of distribution of spotted dolphins in spite of their mobile nature. For both seasons, spotted dolphins seemed to prefer some zones within the study area, namely around the Cativo bay area and secondarily, around ICT. On the other hand, Rosario showed the lowest dolphin presence during both seasons. The lack of a seasonal pattern might have been an artefact of our study period, which covered a small fraction of the rainy season and may have been too close in time to the dry season for differences to be clear.

Photo-identification data suggest that the two zones of higher dolphin density could be due to movements of two different dolphin communities in the study area (García, unpublished data), but this needs confirmation. The factors driving for the spatial pattern are not understood, but it is possible that patches of rocky and coral reefs, both around Cativo and ICT, might be areas of higher prey abundance. Factors that influence cetacean distribution in other places, such as sea bottom slope (*e.g.* Selzer and Paine, 1988) and depth (*e.g.* Davis *et al.*, 1998), did not seem to influence dolphin presence in Bahía Honda. While the sea bottom is steepest to the west of ICT, the region of highest presence, Cativo, does not show a particularly steep slope. Dolphins were found over a wide range of depths, with no clear preferences. Since behaviours indicative of feeding were the most common behaviours observed, prey distribution might strongly influence dolphin distribution. However, if nocturnal feeding is more important, as reported for oceanic (Robertson and Chivers, 1997; Scott and Cattanach, 1998) and Hawaiian spotted dolphins (Baird *et al.*, 2001), the observed daytime distribution might not indicate the most important relationship between environmental features and dolphin distribution.

Spotted dolphins showed clear seasonal differences in distribution or relative abundance in all other studies on the Pacific coast of South and Central America. All authors suggested that these changes could have been related to prey presence (Suárez, 1994; Acevedo and Burkhart, 1998; Pardo, 1998; May, 2001). In Golfo Dulce, these differences were not consistent between years (Acevedo and Burkhart, 1998; Pardo, 1998). The reasons for the shift in the distribution pattern were not clear, but offshore movements might explain part of the seasonal differences in dolphin density (Pardo, 1998). Though these animals do not prey on zooplankton, relative abundance of spotted dolphins correlates with zooplankton presence in the Murciélago Islands, north of Costa Rica (May, 2001). The relationship between them was supported by the fact that *dorado* (*Coryphaena hippurus*), which might share some prey items with the dolphins (such as flying fish and squid), shows a similar pattern of relative abundance. Zooplankton, therefore, probably dictate the distribution of the prey items of both species (May, 2001). Davis *et al.* (2002) also found that cetacean presence was related to zooplankton biomass, which in turn was related to biomass of cetacean prey. In other studies, zooplankton diversity, rather than abundance, had a positive relationship with dolphin presence (Griffin, 1997) and therefore we suggest that future studies in the area consider composition and seasonality of zooplankton and prey species.

Even though a seasonal change in distribution was not detected, inshore-offshore or along-shore movements might explain a higher SPUE during the second part of the study. Inshore-offshore movements apparently explained the seasonal differences in dolphin density in Golfo Dulce (Pardo, 1998). Documenting movements of individual dolphins, through photo-identification methods, could help explain an apparent increase in the encounter rates during the rainy season. However, a higher encounter rate could also be related to increased observer experience and/or dolphins habituating to the research vessel. In contrast to relatively higher SPUE during the rainy season, May (2001) discovered that relative abundance increased during the dry season in her study area. She associated this seasonal pattern with movements from oceanic waters into more coastal areas during the same season (Reilly and Fiedler, 1994).

An interesting aspect of the distribution of this species in the present study area is their proximity to the shore and the utilisation of sheltered areas such as bays and in particular, the Bahía Honda embayment. When compared with other study sites, this is relatively unusual and it seems related to the presence/absence of bottlenose dolphins (*Tursiops truncatus*). In Golfo Dulce, Costa Rica, in addition to spotted dolphins, bottlenose dolphins inhabit the area but were found closer to shore in steep, shallow (around 35m) and less saline waters, whereas spotted dolphins preferred deeper (around 90m), further offshore, more saline waters (Acevedo and Burkhart, 1998; Pardo, 1998). A similar pattern was reported by Suárez (1994) and Rengifo *et al.* (1995) for two locations on the Pacific coast of Colombia, where spotted dolphins used more open habitats further from shore, while bottlenose dolphins were usually found close inshore in more sheltered areas, such as mangrove areas. In contrast, where bottlenose dolphins are seldom present, such as in the Murciélago Islands in Costa Rica (May, 2001) and in the present study, spotted dolphins were found in a larger range of depths and habitats, including those inshore habitats favoured by bottlenose dolphins in the above mentioned studies.

This apparent difference in habitat use and distribution between localities also seems to be related to group size. The present study was mostly confined to depths of less than 50m and most groups contained fewer than ten individuals. The dolphins at this site do use deeper waters, but they were beyond the practical range of the research boat. Larger groups of up to 300 individuals have been sighted to the Southwest of the nearby Coiba Island, in waters around 200m deep (Aguilar *et al.*, 1997). In the northern part of Costa Rica, where depth ranged between 20 and 80m, most groups numbered one to five individuals (May, 2001). On the other hand, In Golfo Dulce, where depth reaches a maximum of 215m, the most common group size for spotted dolphins was larger than 80, while bottlenose dolphins moved in groups of fewer than 10 individuals (Pardo, 1998). Likewise, off Colombia's Pacific coast, groups observed by Suárez (1994) were typically between 20 and 100 animals for spotted dolphins and fewer than 10 for bottlenose dolphins.

In the present study area, dolphins entering the bay, which is relatively shallow and sheltered from offshore conditions, usually moved in groups of fewer than ten. Although these small groups were common throughout the study area, larger groups were seen inside the bay on only a few occasions. This result was supported by the geostatistical analysis of group size distribution. Omnidirectional variograms showed that group size variability is high without a clear spatial pattern. However, variograms on an angle perpendicular to the coast, in particular 20°, showed a clearer structure, still with a high so-called nugget effect. Although this high variability obscures the contour maps generated and actual values tend to be smoothed down by the gaussian model that we chose, it is still possible to visualise a pattern of mainly small groups using the bay. Several authors have discussed how the degree of shelter from predators and feeding efficiency might determine the group size relationship with depth and distance to shore (*e.g.* Norris and Shilt, 1988; Scott and Cattanach, 1998).

Of particular interest is that spotted dolphins from the Pacific coast of South and Central America appear to expand their niche in places where bottlenose dolphins are absent or rare, ranging over depths and habitats otherwise not used. Potentially, it implies competitive exclusion or that the areas are not favourable bottlenose dolphin habitat. In Colombia and Golfo Dulce, the two species probably consume different prey (Suárez, 1994; Acevedo and Bulkhart, 1998). Pardo (1998) suggests that they might actively avoid each other in Golfo Dulce, based on the low spatial and temporal overlap.

The coastal pantropical spotted dolphin has been studied in only a few locations, including off the coasts of Colombia, Panama and Costa Rica. Differences in habitat use and community structure, as well as genetic differences between populations along the Central and South American Pacific (Escorza-Trevino *et al*, 2002), prevent generalisations on either ecological aspects or conservation needs. Therefore, we suggest that studies on this subspecies should be continued to expand our knowledge and determine the need and design of conservation efforts. In particular, aspects of their ecology that might explain the results found so far and studies of abundance are a priority.

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APPENDIX A

Behaviour sampling key

1)
The group is spread apart (more than 10 dolphin lengths between individuals) .... 2)
The group is loose or tight (less than 5 dolphin lengths between individuals) .... 3)

2)
Fish spotted and/or birds associated .... Individual feeding
No fish or birds associated .... Milling

3)
Fish spotted and/or birds associated .... 4)
No fish spotted and/or birds associated .... 5)

4)
Circle swimming or fronts swimming towards each other .... Cooperative feeding
None of the above formations .... Group feeding

5)
Steady direction of movement (over a period of two minutes) .... 6)
No steady direction of movement .... 7)

6)
Porpoising .... Fast travel
No porpoising .... Travel

7)
Physical contact. Optionally, aerial behaviour such as spy-hoping, belly-up or lateral swimming, subsurface swimming, eye out .... Social
No apparent physical contact or any of the above mentioned aerial behaviours .... 8)

8)
Fluke out diving .... Dive
No fluke out when diving .... Erratic

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