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Differences in the whistle characteristics and repertoire of Bottlenose and Spinner Dolphins

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ABSTRACT
Several methods have been used to compare the whistles produced by dolphins. The two methods used in this study are: (1) a classification of whistle contours in six categories (i.e. constant frequency, upsweep, downsweep, concave, convex, and sine) and (2) the extraction of frequency and time parameters from each whistle contour. Bottlenose Dolphin *Tursiops truncatus* whistles are described in the same way when comparing whistle contour distributions in each of the six categories and whistle frequency and time parameters using Discriminant Function Analysis. For Spinner Dolphin *Stenella longirostris* whistles, each method describes whistles differently. Several facts may explain these differences in describing dolphin whistles, such as a greater fluidity of Spinner Dolphin groups when compared to Bottlenose Dolphin groups, greater geographic variation in the whistles of Bottlenose Dolphins than in those of Spinner Dolphins, an average beginning frequency 16% lower than the average ending frequency in Spinner Dolphin whistles compared to a varied relationship for Bottlenose Dolphins, and stricter criteria used to define whistle contour categories in the study of Spinner Dolphin whistles than in the Bottlenose Dolphin whistle study.

Key words: whistle characteristics, classification methods, whistle comparison, geographic variations, Delphinidae.

INTRODUCTION
Bottlenose *Tursiops truncatus* and Spinner *Stenella longirostris* Dolphins live in fission-fusion societies in coastal and oceanic waters of the world’s oceans (Norris et al. 1994, Wells and Scott 2002). Bottlenose Dolphins inhabit tropical and temperate zones (60°N—50°S) with herd sizes that range from 1 to 30 animals in coastal areas and up to hundreds in oceanic waters (Jefferson et al. 1993). Spinner Dolphins inhabit tropical and subtropical zones (40°N—30°S) (Jefferson et al. 1993) with herd sizes that range from 2 to 300 in coastal areas (Bazúa Durán 2001) and up to thousands in oceanic waters (Scott and Cattanach 1998). Spinner Dolphins rest and socialize during the day, feeding at night on mesopelagic prey (Norris et al. 1994), while Bottlenose Dolphins rest, socialize, and feed both during the day and night (Wells and Scott 2002).

Bottlenose and Spinner Dolphin acoustic emissions or phonations can be classified into two general categories: a) tonal whistles, and b) pulsed sounds or clicks (Herman and Tavolga 1980). Dolphin whistles have typically been characterized in terms of their frequency as a function of time (spectrograms) (see Fig. 1), which is also referred to as ‘whistle contour’ (Dreher 1961). Whistles are frequency-modulated sounds with a fundamental frequency...
Fig. 1 – Spinner Dolphin whistle showing the fundamental frequency or whistle contour and two harmonics (H2 and H3). The 10 whistle parameters extracted are also shown.

usually below 20 kHz and harmonics up to 100 kHz (Lammers et al. 2003), and durations between 0.05 and 3.2 s (Wang et al. 1995a, Bazúa-Durán and Au 2002). Whistles are considered signals used to regulate group organization and function (Norris et al. 1994, Janik and Slater 1998).

The study of dolphin whistles has included the categorization of whistle contours into classes (e.g. Janik 1999, Bazúa-Durán and Au 2002) and the extraction of acoustic parameters from each whistle contour (e.g. Wang et al. 1995a, Bazúa-Durán 2001). When comparing different categorization methods it has been shown that there are discrepancies in the methods (Janik 1999, Bazúa-Durán and Au 2002), therefore, the use of an external validation is crucial. It is not known how the categorization method compares to the extraction of acoustic parameters. In this study, the categorization of whistle contours in six classes was compared to the extraction of acoustic parameters from each whistle contour by looking at geographic variations in the whistles of Spinner and Bottlenose Dolphins.

MATERIALS AND METHODS

Bottlenose Dolphins were recorded in the Gulf of Mexico from coastal locations in Galveston and Corpus Christi Bays and Lagunas Madre and Términos from 1991 to 1996, whereas Spinner Dolphin whistles were recorded from 1998 to 2000 from coastal locations in the Pacific Ocean: Midway Atoll (Northwestern Hawaiian Islands), the island of Oahu (main Hawaiian Islands), and Moorea (French Polynesia).

Bottlenose Dolphin recordings were made using a spherical hydrophone and an analog portable Marantz recorder (frequency response of the recording system was flat to 15 kHz), a system that can record the complete fundamental frequency of approximately 90% of Bottlenose Dolphin whistles. Spinner Dolphin recordings were made using a spherical hydrophone and a portable DAT recorder (frequency response of the recording system was flat to 24 kHz), a system that can record the complete fundamental frequency of 98% of Spinner whistles (Bazúa-Durán and Au 2002). The Canary© software 1.2.4 was used to generate the spectrogram of each whistle and to extract 10 whistle parameters: beginning, ending, peak, maximum, and minimum frequencies, peak and center times, duration, and number of turns and steps (Fig. 1). These parameters were used in a Discriminant Function Analysis (DFA) to evaluate differences. Canonical correlation was also calculated to obtain the relative degree of distances between groups. The Mahalanobis distance ($D^2$) between each pair of areas was used.
to evaluate the differences in the whistles of several areas. The larger the $D^2$ value the more different the groups were. Each whistle contour was also ascribed to one of six categories: upsweep, downsweep, concave, convex, constant frequency, and sine (Bazúa Durán 1997, Bazúa-Durán and Au 2002). The occurrence of whistles in each category was compared between areas using chi-squared tests ($X^2$). The larger the $X^2$ value the greater the difference between groups. Whistles used represent the different whistle contour types and their usage.

RESULTS AND DISCUSSION

A total of 1226 Bottlenose Dolphin whistles: 359 from Galveston Bay, 390 from Corpus Christi Bay, 395 from Laguna Madre and 182 from Laguna de Términos, and of 4168 Spinner whistles: 925 from Midway, 2646 from Oahu and 597 from Moorea, were selected for analysis.

Bottlenose whistles were described in the same way when comparing whistle contour distributions in each of the six categories and whistle frequency and time parameters using Discriminant Function Analysis (Tables Ia, IIa). Along the Texas coast, Galveston was closer to Corpus Christi than to Laguna Madre, whereas Corpus Christi was closest to Laguna Madre (Fig. 2a, Table Ia). These differences found in the whistles of Bottlenose Dolphins agree with the degree of movement of animals between areas. There is more mixing between Corpus Christi and Laguna Madre than between Galveston and Corpus Christi (B. Würsig pers. comm.). Galve-
TABLE I

Mahalanobis distances ($D^2$) and chi-squared values ($X^2$) for the between-group pairwise comparison of (a) Bottlenose and (b) Spinner Dolphin whistles. $X^2_{0.95} = 16.75$ with d.f. = 5. Localities: a) G = Galveston, CC = Corpus Christi, LM = Laguna Madre, LT = Laguna Términos; b) M = Midway, O = Oahu, Mo = Moorea.

<table>
<thead>
<tr>
<th></th>
<th>a) $D^2$</th>
<th></th>
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<th>b) $D^2$</th>
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<tr>
<td></td>
<td>CC</td>
<td>CC</td>
<td>LM</td>
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<td>Mo</td>
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<td>CC</td>
<td>0.850</td>
<td></td>
<td></td>
<td>0.693</td>
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<tr>
<td>LM</td>
<td>1.910</td>
<td>0.687</td>
<td>3.299</td>
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</tr>
<tr>
<td>LT</td>
<td>0.684</td>
<td>1.637</td>
<td></td>
<td>Mo</td>
<td>0.520</td>
</tr>
<tr>
<td>$X^2$</td>
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<td></td>
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<tr>
<td>CC</td>
<td>72.01</td>
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<td></td>
<td>O</td>
<td>106.51</td>
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<tr>
<td>LM</td>
<td>115.56</td>
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<td>Mo</td>
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<tr>
<td>LT</td>
<td>19.27</td>
<td>48.31</td>
<td>79.90</td>
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TABLE II

Chi-squared values ($X^2$) for the between-group comparison of (a) Bottlenose and (b) Spinner Dolphin whistles.

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<tr>
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<tr>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Galveston</td>
<td>63.88</td>
<td></td>
<td>Midway</td>
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<tr>
<td></td>
<td>Corpus Christi</td>
<td>25.96</td>
<td></td>
<td>Oahu</td>
</tr>
<tr>
<td></td>
<td>Laguna Madre</td>
<td>59.49</td>
<td></td>
<td>Moorea</td>
</tr>
<tr>
<td></td>
<td>Lag. Términos</td>
<td>30.60</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>179.93</td>
<td></td>
<td>$X^2_{0.95}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>25.00</td>
<td></td>
<td>d.f.</td>
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An Acad Bras Cienc (2004) 76 (2)
1998) and Spinner Dolphins are mainly pelagic whereas Bottlenose Dolphins are mainly neritic (Jefferson et al. 1993).

Acoustical reasons may include: (1) differences in the criteria used to define whistle contour categories in the studies of these two species, (2) differences in the magnitude of the geographic variations in the whistles of these two species, and (3) differences in the relationship between the average beginning and ending frequencies of the whistles from these two species.

There may be variations due to the classification limits used in the studies of both species. Spinner Dolphin whistle classification had stricter limits to define whistle contour categories than Bottlenose Dolphin whistle classification. Bottlenose Dolphin whistles will be reclassified using the stricter limits of the Spinner Dolphin whistle classification to determine the influence of stricter classification limits. In addition, there may also be measurement bias by the observer (Bazúa-Durán and Au 2002), which has not been quantified.

Microgeographic variations in the whistles of Bottlenose Dolphins (MiGV, i.e. among areas in which animals have the possibility of intermixing) were larger than macrogeographic variations in Spinner Dolphin whistles (MaGV, i.e. between areas separated by large distances) (Fig. 3). Mahalanobis distances were larger (Table I) and the means of canonical variate 1 were more separated (Figs. 2 and 3) for Bottlenose MaGV than for Spinner Dolphin MiGV.

There is an average beginning frequency (BF) 16% lower than the average ending frequency (EF) (0.84 BF = EF relationship) in Spinner Dolphin whistles (Bazúa-Durán and Au 2002) compared to a varied relationship for Bottlenose Dolphin whistles (Bazúa Durán 1997). Spinner Dolphins produce mainly upsweep whistles (47%) (Bazúa-Durán and Au 2002), whereas the whistle contour produced
most often by Bottlenose Dolphins varies with location (Bazúa Durán 1997, Janik 2003).

CONCLUDING HYPOTHESES

It is possible that the differences found in the two methods used in this study to describe geographic variations in the whistles of two different species of dolphins are because dolphin species that differ considerably in their ecology will have larger differences in the characteristics and use of their whistles. If this is true, it is possible that species such as the pantropical Spotted Dolphin *Stenella attenuata*, the Clymene Dolphin *Stenella clymene*, the Tucuxi *Sotalia fluviatilis*, the Common Dolphin *Delphinus delphis*, and the White-beaked Dolphin *Lagenorhynchus albirostris* will have a similar whistle system to that of Spinner Dolphins. Likewise, species such as the Pilot Whale *Globicephala macrorhynchus*, the Fraser’s Dolphin *Lagenodelphis hosei*, the Striped Dolphin *Stenella coerulealba*, and the Atlantic Spotted Dolphin *Stenella frontalis* will have a similar whistle system to that of Bottlenose Dolphins.

Additionally, the results of this study suggest that geographic differences may not occur solely due to geographic isolation. Other factors, such as differences in the fluidity of Spinner Dolphin groups (population structure characteristics) may be more important when looking at geographic differences in the whistles of dolphins.

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RESUMO

Vários métodos foram usados para comparar assobios produzidos por golfinhos. Os dois métodos usados no presente estudo são: (1) uma classificação dos contornos do assobio em seis categorias (frequência constante, modulação ascendente, modulação descendente, côncavo, convexo e senóide) e (2) a extração dos parâmetros de frequência e tempo de cada contorno de assobio. Os assobios do Golfinho-nariz-de-garrafa ou Golfinho-fliper *Tursiops truncatus* são definidos da mesma maneira quando se compara, por análise de função discriminatória, a distribuição dos contornos de assobios nas seis categorias e os parâmetros tonais e temporais dos assobios. Os assobios do Golfinho-saltador *Stenella longirostris* são caracterizados de maneira diferente por cada método. Vários fatos podem explicar essas diferenças na classificação dos assobios de golfinhos, tais como a maior fluidez dos grupos do Golfinho-saltador em comparação aos grupos do Golfinho-nariz-de-garrafa, uma variação geográfica mais ampla dos assobios nessa última espécie de que na primeira, uma frequência inicial média 16% mais baixa de que a frequência final média nos assobios do Golfinho-saltador contra diferenças variadas no Golfinho-nariz-de-garrafa, e o uso de critérios mais estritos para definir as categorias de contornos de assobios no Golfinho-saltador do que os usados no Golfinho-nariz-de-garrafa.

Palavras-chave: características de assobio, métodos de classificação, comparação entre assobios, variações geográficas, Delphinidae.

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