Residency Patterns, Abundance, and Social Composition of Bottlenose Dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina

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Abstract

Residency patterns, abundance, and social composition of bottlenose dolphins (Tursiops truncatus) were assessed from 2006 to 2008 in Bahía San Antonio (BSA), Patagonia, Argentina. A total of 714 survey hours resulted in 132 contact hours with 224 bottlenose dolphin groups. Results indicated that dolphins can be seen year-round on average every 4 h, with sighting periods lasting an average of 45 min. A total of 57 bottlenose dolphins were positively identified in the bay, of which 56% showed a degree of residency, including almost all mother and calf pairs. Using the closed time heterogeneity model (Mth), and accounting for the proportion of unidentifiable individuals, calculations resulted in a corrected abundance estimate of 83 individuals for the study area. Further analysis revealed that individual dolphins associated at random and that the entire community exhibits rapid disassociations and two levels of casual acquaintances.

Data suggest that the shallow waters of BSA support a relatively resident community of bottlenose dolphins, living in a fission-fusion society in which companionships frequently change. The relative constant presence of calves in more than 50% of the dolphin groups and the observed presence of neonates might furthermore indicate that dolphins specifically use this area, among others, to give birth and nurse their young. In addition, a reported decline in bottlenose dolphin sightings in the larger area of the Argentinean coast might indicate that BSA is one of the last remaining refuges of the species in the country. Further research seems vital for their conservation.

Key Words: bottlenose dolphins, *Tursiops truncatus*, photo-identification, residency, abundance, social composition, Patagonia, Argentina

Introduction

Populations of bottlenose dolphins (*Tursiops truncatus*) are known to inhabit coastal areas,

including bays and tidal creeks (Leatherwood et al., 1983), and their frequent presence along coastlines has made them one of the best-studied cetacean species in the world (Bearzi, 2005). In Argentina, bottlenose dolphins can be seen from the Bay of Samborombón (province of Buenos Aires) south to the province of Chubut, although some records have been made as far south as the province of Santa Cruz and Tierra del Fuego (Perrin et al., 2002; Bastida & Rodríguez, 2003). In general, very little is known about the species in this country. First research efforts on bottlenose dolphins in Argentinean waters were made from 1970 to 1980 (Würsig, 1978; Würsig & Würsig, 1979; Bastida & Rodríguez, 2003) but were discontinued. Consequently, today, no clear explanation can be given on the reported decrease of bottlenose dolphin sightings along coasts where they used to be seen frequently (Bastida & Rodríguez, 2003). Hence, no adequate conservation attempts can be taken to prevent a continued decrease.

As reported previously, the shallow bay of San Antonio may represent one of the last remaining areas in Argentina where bottlenose dolphins are resident (Holsbeek et al., 2008; Vermeulen et al., 2008). As a result of the high frequency of bottlenose dolphin observations in this area, it seems a very suitable location for long-term research of ecological and behavioural aspects of this species. This study's aim was to obtain more data on the bottlenose dolphin residency patterns in this region and to obtain the first recent estimates on the local abundance and social composition, information needed to improve the conservation of the species in Argentina.

Materials and Methods

Study Area

The study area Bahía San Antonio (BSA) is a shallow bay (maximum depth not reaching more than 30 m) located to the north of the San Matías Gulf (40° 50' S, 64° 50' W), Patagonia, Argentina. The region is known for its large fluctuations in sea surface temperature (difference between summer and winter reaching up to $\pm 16^{\circ}$ C) and relative high salinity compared to the more southern waters of the gulf (Gagliardini & Rivas, 2004).

Field Work and Analysis

Land-based surveys were conducted between August 2006 and December 2008, the majority of which were conducted in good weather conditions (< 3 Beaufort: a "calm" sea state). A bottlenose dolphin group was defined as all individuals within a 100-m radius of each other, interacting or engaged in similar activities (Irvine et al., 1981; Wells et al., 1987; Wilson, 1995; Lusseau et al., 2005). When dolphins were seen, group size was determined and groups were labelled as "groups with calves" and "groups without calves." Calves were categorized as being $\frac{2}{3}$ or less the length of an adult and mostly swimming in close association with an adult. Neonates were defined by their very small size (less than ¹/₃ the length of an adult), their fetal folds, and their very close association with an adult (Shane, 1990). Dolphins identified closely accompanied by a calf or neonate in at least two different occasions were assumed to be females (Mann & Smuts, 1999; Grellier et al., 2003). Data on behaviour were recorded following the definitions of Bearzi (2005), using a focal group 5-min point sampling mode (Altmann, 1974; Mann, 1999). Dorsal fins of all individuals in the group were photographed regardless of the presence of clear marks. The number of bottlenose dolphins and size classes were verified later through photoidentification analyses. The observation of different groups of dolphins had to be separated by at least half an hour to be categorized as a different sighting period and, thus, one sighting period could contain several dolphin groups. The sighting frequency (SF) was further determined as the number of sighting periods per hour. The distance from the coast was estimated (when possible) by eye using various reference points (buoys) at known distances. Four categories are used in analysis: (1) \leq 100 m, (2) 100 to 500 m, (3) 500 to 1,000 m, and (4) > 1,000 m.

Additionally, intensive boat-based surveys were made between August and November 2008 from a 5-m vessel (outboard motor Suzuki 40 HP) with the aim of completing photo-identification of bottlenose dolphins in the bay. Data from these surveys were used solely for estimations of residency and abundance.

All clear photographs of dorsal fins were analysed using the computer-assisted identification systems *FinEx* and *FinMatch* (EC EuroPhlukes Initiative, University of Leiden, The Netherlands). Residency patterns were analysed regarding the presence or absence of dolphins in four different seasons: (1) summer = January-February-March; (2) autumn = April-May-June; (3) winter = July-August-September; and (4) spring = October-November-December. Dolphins re-identified during all four seasons (regardless of year) were defined as "year-round" residents, while those re-identified only in specific seasons in two consecutive years were defined as "seasonal" residents (Zolman, 2002).

The Capture software application of the program MARK (White & Burnham, 1999) was used to estimate the abundance of bottlenose dolphins in BSA. Because variations in captures (defined as re-identifications) among different periods were strongly evident in our data, the time model Mt (Darroch, 1958) was selected as a qualification for modelling this population. Furthermore, the time heterogeneity model (M_{th}) (Chao et al., 1992) was also applied to test whether the capture probabilities of individuals varied over time. Both the null model (M_o) and the behavioural models (M_b) were largely ignored, the reasons being that the M₀ is unlikely to occur under natural circumstances, and the M_b were simply not applicable to these data (i.e., photo-identification is unlikely to result in a subject becoming "trap happy" or "trap shy"). Calves were excluded from this part of the analyses because their probability of capture was highly related to that of their mothers (Wells & Scott, 1990). To minimize the probability of changes in the population size, a sampling period of 30 d (September 2008) (including 11 positive encounters, 44 individuals) with high boat-based photo-identification effort was selected for analysis. Furthermore, to avoid an overestimation of capture probability of highly marked individuals and a consequent underestimation of the population size, only clear and highly distinctive pictures were selected for analysis. Image quality classification was therefore independent of the presence or extent of natural markings present on the individual (Friday et al., 2000). In addition, these obtained data were corrected for the proportion of "uncatchable" individuals in the population (noncalves) by dividing the total number of unmarked individuals by the total number of identified dolphins per survey, following Stensland et al. (2006). To calculate the proportion of calves in the population, the total number of identified calves (through the mother) was divided by the total number of marked dolphins.

Association indices were calculated using *SocProg 1.3*, a program developed for *Matlab* to analyze the social organization of animal communities (Whitehead, 1999). To accurately estimate the association indices of identified animals, a total of 37 encounters were selected during which more than 50% of the individuals in the group could be positively identified. From these

encounters, 38 individuals that were seen ≥ 5 times were selected for social association analysis. All individuals within a group were considered to be associated with each other, a definition of association commonly used in studies of dolphin structure (Whitehead & Dufault, 1999). The more frequent a dolphin pair was sighted together in the same group, the closer they were associated (Lott, 2004). The half-weight index (HWI) was chosen as a measure of association because it introduces a bias to correct for missed identifications of one member of a pair, which is inherent in photo-identification techniques (Cairns & Schwager, 1987, following Smolker et al., 1992).

All statistical analyses were conducted using *STATISTICA*, Version 6.0, and Zar (1996).

Results

Field Effort and Occurrence

A total of 218 land-based observation sessions were conducted in the period of 2006 to 2008, accounting for a total observation effort of 714 h (average 3.3 h/survey; min = 42 min; max = 7.25 h; Table 1), resulting in 132 contact hours with a total of 224 bottlenose dolphin groups (DGs) over 180 sighting periods (SP). In addition, 19 boat-based observations were conducted with a total survey effort of 83 h (average 4.3 h/survey; min = 2 h; max = 6.3 h) of which 10 h were spent actively with 14 DGs.

From land-based observations, bottlenose dolphins could be observed every 4 h (SF = 0.24/h; SD = 0.11); this frequency stayed relatively constant over the different seasons (Table 1). Sighting periods lasted on average 45 min, ranging between 5 min to 4 h (Quartile values: Q1 = 15 min; Q2 = 30 min; Q3 = 55 min), whereas the observation of a DG had an average duration of 35 min, ranging between 5 min to 4 h (Q1 = 15 min; Q2 = 25 min; Q3 = 45 min). A Kruskal-Wallis test indicated that these durations did not fluctuate significantly among the different seasons (SP: p = 0.06; DG: p = 0.07). A SP had on average 1.3 DGs (SD = 0.4), which stayed relatively constant over the different seasons.

Residency and Abundance Estimates

Of over 15,000 photo-identification photographs, a total of 57 bottlenose dolphins were individually identified inside BSA and re-identified up to 18 times (average = 7). Up to 45 individuals were identified in 2006-2007 after which the rate of new identifications levelled off (Figure 1).

Out of 57 photo-identified bottlenose dolphins, 10 were classified as year-round residents in the bay and 22 as seasonal residents of which three individuals were identified for the period winter/ spring, three individuals for autumn/winter, and the remaining 16 individuals only during the winter months. A total of 13 females were sexed through their close association with a calf. Eight of these females were year-round residents, whereas three were seasonal residents during the winter months. Three of the year-round resident females could be identified with a calf in 2006 and again with a newborn in 2008.

Mark-recapture analyses based on closed population models (30-d sample) resulted in an abundance estimate for the M_{th} model of 55 individuals (CI 95%



Figure 1. Cumulative number of photo-identifications of individual bottlenose dolphins in BSA (2006 to 2008) with polynomial trendline

Table 1. Land-based observation effort, sighting frequency (SP/h), average and median (Q2) duration of sighting periods (SP), and number of dolphin groups (DG) of bottlenose dolphins per season (2006 to 2008), including quartile values Q1 and Q3

Season	Effort (h)	SP/h (SF)	SD	Average duration SP (min)	Median (Q2) (min)	Q1 (min)	Q3 (min)	Average duration DG (min)	Median (Q2) (min)	Q1 (min)	Q3 (min)
Summer	202	0.20	0.08	48	35	20	60	35	28	15	47
Autumn	220	0.24	0.08	38	25	15	45	32	20	10	35
Winter	238	0.24	0.09	52	35	20	60	40	28	15	50
Spring	54	0.26	0.17	40	30	20	40	27	20	15	30
Total	714	0.24	0.11	45	30	15	55	35	25	15	45

= 48 to 74) and for the alternative M_t model of 50 individuals (CI 95% = 46 to 64). Estimates based on the M_{th} model were larger than the equivalent estimates based on the Mt model, further confirming that there was heterogeneity of capture probabilities within these data (Williams et al., 1993; Wilson et al., 1999), therefore population estimates obtained through the Mth model were considered to be the most reliable in this study. Based on the number of unmarked animals per identifiable individual, the proportion of uncatchable individuals (non-photo-identifiable individuals, mostly juveniles) was estimated to be 29%. By dividing the number of identified calves (through the mother) by the total number of marked dolphins, the proportion of calves in the population was estimated to be 18%. The adjusted population estimates, including unmarked bottlenose dolphins and calves, was 83 individuals (CI 95% = 73 to 112; Table 2) for September 2008.

Group Size and Social Composition

Dolphin groups consisted of 5.4 animals on average (n = 213; median = 4), ranging between 1 and 30 individuals. Group size (GS) did not vary with distance from the coast (K-W: p = 0.46) but varied among months (K-W: p < 0.05). Separate Mann-Whitney tests indicated the strongest difference in GS between winter (GS = 7) and autumn (GS = 4) (p < 0.01; summer GS = 5; spring GS = 6).Furthermore, GS seemed to vary with behaviour (K-W: p < 0.05), with feeding groups being considerably larger (GS = 14) than groups displaying behavioural states other than socializing (GS = 8)(i.e., resting: GS = 5; travelling: GS = 6; milling: GS = 4). Socializing groups were not significantly larger than groups involved in resting, travelling, or milling, however (K-W: p = 0.2).

Group size seemed positively correlated with the presence of mother and calf pairs ($R^2 = 0.72$; n = 93; p < 0.05). Groups containing calves, excluding mothers and calves from analysis (GS = 6; n = 62), were significantly larger than groups without calves (GS = 3; n = 31) (M-W: p < 0.05; n = 93). In general, calves were seen in 53% of the groups encountered with a range of 1 to 5 calves per group, not varying significantly among seasons (one-way ANOVA: F = 0.72; df = 9; p = 0.62). Neonates were observed in all seasons except winter.

Analyzing social composition, the distribution of coefficient of associations (CoAs) for all sighted individuals (n = 1,444) leaned towards relatively low values (Figure 2) with most bottlenose dolphins showing low or no associations at all; only a few dolphin pairs had relatively high CoAs. The CoAs ranged from 0.0 (never seen together) to 0.8 with a mean of 0.21 (SD = 0.07). The sum of associations per individual averaged 7.9 (SD = 2.4), and the maximum associations per individual averaged 0.57 (SD = 0.12). Of a total of 1,444 pairs, 39 pairs (3%) associated at a level of 0.5 or higher, which indicates they spent at least half of their time together.

The association dataset was further permuted randomly 10,000 times (groups within samples), and the permuted CoAs were not significantly different from the observed mean (real mean = 0.21, random mean = 0.21, p = 0.18). Also, the observed SD (0.17) did not vary with the random SD (0.17; p = 0.85). In addition, no evidence could be found for individuals actively avoiding each other (real non-zero associates = 0.71, random non-zero



Figure 2. Association index values for all pair-wise comparisons of 38 individual bottlenose dolphin identified five or more times (n = 1,444) in BSA

Table 2. Abundance estimates of bottlenose dolphins in BSA during September 2008 using the time-dependency model and the time-dependent heterogeneity model; n = the number of individuals, p = the mean probability of recapture, N-hat = adult population estimate, SE = standard error of the population estimate, CV (%) = the coefficient of variation, CI 95% = the 95% confidence intervals, and Corrected N-hat = total abundance estimate.

	n	р	N-hat	SE	CV (%)	CI 95%	Corrected N-hat	CI 95%
Mt (Darroch, 1958)	44	0.13	50	4.17	8.33	46-64	76	70-97
Mth (Chao et al., 1992)	44	0.12	55	6.17	11.20	48-74	83	73-112

associates = 0.71, p = 0.4). Known females were analysed separately and were equally associated at random (10,000 permutations: real mean = 0.17, random mean = 0.16, p = 0.83; observed SD = 0.15, random SD = 15, p = 0.54; non-zero associates = 0.69, random non-zero associates = 0.66, p = 0.75).

The lagged association rate nearly equalised the null association rate, moreover suggesting that there was no preferred association over the time lags. The best-fit model suggests that the population of bottlenose dolphins in BSA exhibits rapid dissociations and two levels of casual acquaintances, this latter indicating that dolphins may associate for some time, dissociate, and re-associate afterwards (Figure 3). All results indicated that associations between dolphins were almost fully at random and unstable over time.

Discussion

Data presented herein indicated that bottlenose dolphins can be seen from the shore of Bahía San Antonio on average every 4 h, and that sighting periods lasted approximately 45 min. This relatively high SF, considering that observations were land-based, confirms that the area is highly suitable for a long-term study on this species. In addition, up to 56% of the identified dolphins show some degree of residency within the bay, with the highest re-identification rates during the winter months.

Of the identified mother-calf pairs, 85% showed a yearlong or seasonal residency in the bay. Around 53% of the dolphin groups contained calves, and neonates were observed on several occasions, indicating that the shallow waters of the study area form a favourable place for the dolphins to give birth and nurse their young. Moreover, it was assumed that up to 47% of the bottlenose dolphins in the study area were unidentifiable due to the lack of marks, possibly indicating a large proportion of juveniles and calves. No clear indication could be found regarding seasonality of births because groups containing calves did not vary among seasons, and neonates were observed and photographed during all seasons except winter. The presence of seasonal birthing in bottlenose dolphins has been reported before, with birth peaks probably depending on thermal efficiency, food availability, and predator density (Mann et al., 1999), suggesting that in areas with large temperature fluctuations, such as BSA, peaks in births should be found during the warmer months. In any case, results obtained from landbased observations should be interpreted carefully. Winter sea surface temperatures decreased to nearly 6° C, and although this did not seem to influence the land-based sighting frequency of dolphins in the larger area, these temperatures



Figure 3. Association rates for pairs of bottlenose dolphins associated within groups in BSA; the plot shows the probability of associations persisting after increasing lags in time between observations (lagged). The null rate (null) represents the association rate if dolphins associated at random. The best-fit curve (represented by a3*exp(-a1*td)+a4*exp(-a2*td)) represents a population of rapid disassociations and two levels of casual acquaintances.

may influence directly or indirectly (e.g., prey availability) the occurrence of dolphins in even more shallow coastal water.

Intensive boat-based surveys resulted in the first abundance estimate of bottlenose dolphins in BSA, varying between 73 and 112 animals during September 2008. The discovery rate of newly marked (adult) individuals levelled-off by the end of the study period at 57, possibly indicating that the community of bottlenose dolphins in BSA is relatively closed and that the majority of adults have been identified. On the other hand, it has been confirmed that the BSA is only part of the total home range of at least 12% of the catalogued individuals (Vemeulen et al., 2008), therefore making the study area not geographically closed. Nonetheless, as was expressed by several authors, only more time in the field will allow these trends to be clarified and confirmed (Shane, 1987; Ballance, 1990).

By analysing social associations between identified individuals, it was estimated that the population of bottlenose dolphins in BSA exhibits rapid dissociations and two levels of casual acquaintances. Although association rates were up to 0.8, the entire group associated in a random pattern. Long-term studies of bottlenose dolphins in Sarasota Bay, Florida, and Sharks Bay, Australia, have shown that strong associations exist between females and their dependent calves, and in alliances between pairs of sexually reproductive males (Scott et al., 1990; Wells, 1991; Connor et al., 1992). In contrast to these findings, bottlenose dolphin populations of the Moray Firth, Scotland, and the Shannon Estuary, Ireland, have strong bonds only between mother and calf, with little evidence for male alliances in resident dolphins (Wilson et al., 1999). Likewise, even with a lack of positive identifications of males in this study, overall, almost no associations were found in the bottlenose dolphin population of BSA.

Average group size of bottlenose dolphins in BSA seemed positively correlated with the presence of calves and increased during foraging behaviour. This first tendency has been reported before in other bottlenose dolphin populations (dos Santos & Lacerda, 1987; Wells et al., 1987; Weigle, 1990; Weller, 1991; Bearzi et al., 1997) and was associated with the improved calf assistance and protection, a reduced maternal investment, and the benefits of learning (Norris & Dohl, 1980; Johnson & Norris, 1986). The second tendency may be related to increased food capture efficiencies where prey is abundant. It has been previously described that coastal communities of bottlenose dolphins feed primarily on shoaling fish species (Wells et al., 1980) and, therefore, cooperative feeding may improve individual fitness. The additionally large variation in observed group sizes could further suggest that the dolphins in BSA fall under the definition of a fission-fusion society as proposed by Clapham (1993) in which the associates of an individual frequently change. As expressed by Lehmann & Boesch (2004), "[In] populations with long-lived animals in which social organisation is based on individual recognition, maintaining optimal group size might be difficult. When optimal group size varies largely over short periods of time, individuals could benefit from a fission-fusion social organization, in which members of a stable community form frequently changing subgroups. This can allow regulation of feeding competition, offer greater flexibility in exploiting resources or allow males to maximise monitoring of reproductive females" (p. 1). Fission-fusion societies exhibiting a fluid and dynamic social structure have been described in many bottlenose dolphin communities before (Würsig & Würsig, 1977; Wells et al., 1987; Smolker et al., 1992; Connor et al., 2000). Generally, living in groups includes a wide range of benefits and costs; fission-fusion societies present the opportunity to examine these costs and benefits and adapt their associations.

Furthermore, it seems worth mentioning that out of a total of 10 year-round resident individuals, three are morphologically distinct in dorsal fin shape, coloration, and size. Bastida & Rodríguez (2003) have described two geographic variations in bottlenose dolphin morphology in Argentina. The bottlenose dolphins living along the coasts of the province Buenos Aires are characterized by their triangular dorsal fin shape, whereas bottlenose dolphins living further south along the coasts of the province of Chubut are characterized by their falcate dorsal fin shape. Bastida & Rodríguez stated in addition that "their clear difference would indicate that both populations are completely isolated" (p. 137). The association of these individuals with other identified individuals in combination with the highly discussed taxonomy of bottlenose dolphins in South America indicates the urgent need for deeper taxonomic investigation in the region.

Overall, data suggest that the shallow waters of BSA support a relatively resident community of around 100 bottlenose dolphins, living in a fission-fusion society in which companionships frequently change. Data furthermore indicate that these dolphins use this area, among others, to give birth and nurse their young. These results, in combination with a reported decline in bottlenose dolphin sightings in the larger area of the Argentinean coast, might indicate the importance of BSA for this species in the country. Further research seems crucial for their conservation.

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