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Report of the Working Group on the Behavioral Ecology of bottlenose dolphins in the Southwest Atlantic Ocean

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Introduction

The cetacean brain accommodates an intricate neurological system that supports processing information to function effectively in a complex society, facilitating adaptive behavioral flexibility throughout social and ecological shifts (Marino *et al.,* 2007). In this context, behavior can vary according to specific environmental conditions, changing during the lifetime of an individual, or even during a single day (Reynolds *et al.,* 2000).

Such behavioral diversity has been ascribed to many cetaceans around the world, but especially to the common bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), hereafter bottlenose dolphin (Würsig, 1986; Wells *et al.,* 1999; Connor *et al.,* 2000; Marino *et al.,* 2007). This species displays a wide range of behaviors according to both external constraints (environmental conditions) and internal traits (morphological, anatomical or physiological). The behavioral flexibility of the bottlenose dolphin is evidenced by the wide variety of foraging techniques, social systems and communication patterns, including cultural transmission (Shane *et al.,* 1986; Barros and Odell, 1990; Barros and Wells, 1998; Connor *et al.,* 1998; 2000; Connor, 1999; Wells *et al.,* 1999; Nowacek, 1999; 2002).

It is important to understand the ecology and behavioral plasticity of bottlenose dolphins inhabiting different habitats. This information contributes to a better understanding of the species ecological adaptations and may assist in diagnosing responses to environmental change and anthropogenic disturbances (Sutherland, 1998). While numerous studies have specifically assessed the behavioral ecology and social structure of bottlenose dolphins throughout world, most of the available literature in the Southwest Atlantic Ocean (SWAO; 4°N-56°S, 25°-67°W) is based on opportunistic sampling of small and highly localized populations. For example, some behavioral observations conducted off northeastern, southeastern and southern Brazil (Simões-Lopes, 1998; Mattos *et al.,* 2007; Barbosa *et al.,* 2008; Hoffmann *et al.,* 2008; Wedekin *et al.,* 2008; Lodi, 2009; Lodi and Monteiro-Neto, 2012; Lodi *et al.,* 2014). Relevant data from the northern region are scarce (Baracho *et al.,* 2007; Caon *et al.,* 2009; Moreno *et al.,* 2009; Ott *et al.,* 2009). Studies conducted in Uruguay and Argentina are also quite

limited. In Uruguay, most research has concentrated around Cabo Polonio and La Coronilla (Laporta, 2004), while in Argentina most research has focused around Samborombón Bay (Province of Buenos Aires), Bahia Engaño and San Antônio Bay (Vermeulen and Cammareri, 2009), and in Rio Negro in Patagonia (Failla *et al.,* 2016 this volume). For areas of bottlenose dolphin occurrence, see the report of working group on distribution (Lodi *et al*., 2016 this volume).

Despite the absence of directed research, the various regional studies conducted so far provide relevant information, especially when combined and examined jointly. In this report, we present a compilation of the behavioral patterns of bottlenose dolphins and social structure throughout the SWAO. We have compiled and summarized available data concerning: (i) behavioral activities (states and events), (ii) social structures (group size and composition), (iii) acoustic behavior, and (iv) intra and interspecific interactions of bottlenose dolphin populations throughout the SWAO, from north of Brazil to south of Argentina.

Materials and methods

In order to standardize geographic information, we adopted the division proposed at the *First Workshop on the Research and Conservation of* Tursiops truncatus*: Integrating knowledge about the species in the Southwest Atlantic Ocean*, carried out in Rio Grande, Brazil in 21-23 May 2010. The geographic areas were divided into i) insular and oceanic and ii) coastal. Further, the coastal zone was divided into five regions: 1) northern Brazil; 2) northeastern Brazil; 3) southeastern Brazil; 4) southern Brazil and Uruguay and 5) Argentina (see more details of geographical division criteria in Fruet *et al.*, 2016 this volume).

Data sources

This review compiles information of bottlenose dolphins in the SWAO based on 36 articles in peer-reviewed journals, four undergraduate monographs, three master's and two doctoral theses, five book chapters, one technical report, one conference abstract and three working papers. Working papers cited in this report were presented at the above-mentioned *Tursiops* workshop. In addition, thirteen personal communications with specialists are included as supplementary material.

Adopted definitions about behavior sampling

Behavior encompasses everything that animals do to interact with, respond to, and adapt to their environment. Consequently, careful observations of behavior can provide us with a great deal of information about the animals' requirements, preferences and their internal states (Mench and Mason, 1997). In general, behavior is described as states and events (Shane, 1990*a*, *b*). Behavioral states are general categories describing what an animal is doing at any point in time (*i.e.* feeding, resting, socializing and traveling). Behavioral events comprise functional movements performed as a unit; they are relatively short in duration (as opposed to states). Behavioral states can be analyzed to evaluate how dolphins use different areas and to estimate behavioral budgets (the amount of time that an animal spends conducting different activities), as well as evaluating anthropogenic impact (Mench, 1998; Sutherland, 1998). Probably because it is easier and faster to identify and record behavioral states in the field, this is the most common parameter measured. Observing the behavioral events performed by individuals allows understanding fine-scale patterns of habitat use and social interactions that can provide valuable information to evaluate potential short-term reactions elicited by anthropogenic activities (*i.e.* boat traffic; Lusseau, 2006). These short-term reactions in some cases can lead to longer-term impacts such as area avoidance or alteration of the population's behavioral budget (Lusseau, 2004; 2006). Events are usually recorded as a frequency (number of times the event occurred over a standard period of time the animals were observed).

Several observational techniques and sampling methods are described to study cetacean behavior (Mann, 1999*a*). The use of a specific technique/method should be driven by the species access, habitat characteristics and especially by the scientific question being posed. Behavioral data can be obtained using surveys and convenience sampling method (*e.g. ad libitum*) typically to gather punctual information, such as group size and composition. However, a 'follow' protocol (*e.g.* individual or group follow) and some specific protocols/sampling methods (principal activity, scan, continuous sampling) will be better approaches to understand the adaptive function of some complex behaviors and the social dynamics. Despite the large range of behavioral methods available, some important criteria should be followed to achieve different approaches.

Results

Behavior

No set of behavioral terms has been used consistently, although the same range of activities were analyzed. Behavioral states among bottlenose dolphins are usually described as: foraging (or feeding), social interactions (socializing), milling, traveling and resting (*e.g.* Shane *et al.,* 1986; Shane, 1990*b*; Reynolds *et al.,* 2000; Lusseau, 2006; Table 1). However, some recent publications use a combination of these behavioral states (Cruz, 2005), and other categories such as playing, idling, aerial and associative behavior (Reynolds *et al.,* 2000).

In the SWAO, behavioral states have been used by different studies incorporating different descriptions and/or definitions (Möller, 1993; Simões-Lopes *et al.,* 1998; Laporta, 2004; Cruz, 2005; Mattos *et al.,* 2007; Barbosa *et al.,* 2008; Hoffmann *et al.,* 2008; Wedekin *et al.,* 2008). For example, several studies (n = 6) used a focal-group sampling method associated with the scan technique (instantaneous sampling), while a few others used continuous sampling (for methods definition see Altmann, 1974; Lehner, 1996; Mann, 1999*a*). However, almost all approaches were opportunistic.

Table 1. Definitions of behavioral states of bottlenose dolphins. NA = not available.

Behavioral state	General definition	Related states	References
Feeding (foraging)	Dolphins are involved in any effort to capture and consume prey as evidenced by chasing fish on the surface, pursuing them parallel to the water surface or moving in circles and/or coordinating deep diving in the same area. Individuals are often observed interacting with each other, but usually there is no direct contact between them (not as often as in socializing). Prey is sometimes observed in the dolphin's mouth and during the foraging bout. Birds may concentrate over the dolphins' group.	NA	Shane *et al.* (1986); Shane (1990*b*); Reynolds *et al.* (2000); Constantine *et al.* (2004)
Traveling	Dolphins are involved in persistent, directional movement. Swimming with short and relatively constant dive intervals. The group spacing varies. Leaps can be observed when the speed is increased.	NA	Shane *et al.* (1986); Shane (1990*b*); Lusseau (2006)
Milling	Dolphins moving within a given area but with frequent changes in heading and direction. Dive intervals are variable, but mostly short. The group spacing varies. Sometimes it presents as a transitional behavior.	Many studies associated with other behaviors such as feeding, socializing and playing.	Shane *et al.* (1986); Shane (1990*b*); Reynolds *et al.* (2000); Constantine *et al.* (2004); Lusseau (2006)
Socializing	Diverse interactive behavioral events, such as body contact, pouncing, leap, chase, and tail slaps. Individuals often change their position in the group which may be split in small subgroups that are spread over a large area. Includes aspects of play and sexual behavior, involving the 'mating' and 'rubbing' behavior.	Many studies associated with other behavior such as 'play'.	Shane *et al.* (1986); Shane (1990*b*); Constantine *et al.* (2004); Lusseau (2006)
Resting	Dolphins engaged in slow movements generally lacking the activity components of the other types of behavior. Swimming with short, relatively constant, synchronous dive intervals. Individuals are tightly grouped.	Some studies associated this behavior with 'idling'.	Shane *et al.* (1986); Shane (1990*b*); Lusseau (2006)

Behavioral studies off northeastern Brazil were carried out predominantly off oceanic islands (deeper than 100m). In Rocas Atoll (03°50'S, 33°39'W), only two groups containing three and 15 individuals respectively, were observed. At both encounters, dolphins displayed intense physical contact, and mother-calf associations were present (Baracho *et al.,* 2007). At the São Pedro and São Paulo Archipelago (SPSPA) (00°56'N, 29°22'W), groups of resident bottlenose dolphin were observed foraging during the day (Moreno *et al.,* 2009; Ott *et al.,* 2009). No behavioral information was recorded for coastal areas of northern and northeastern Brazil.

Off southeastern Brazil, studies of behavioral activities of bottlenose dolphins are limited to a coastal group of islands, the Cagarras Archipelago, Rio de Janeiro (RJ). The ethogram, elaborated over two years of study, includes six behavioral states: explore, play, social and/or foraging, social, agonistic and foraging; and 43 behavioral events (Cruz, 2005). Social and/or foraging activities presented a greater number of associated behavioral events (34.9%). Environmental conditions (*e.g.* depth and tide) and diurnal periods did not affect the frequency of behavioral states (Cruz, 2005).

In the same area, using focal group and instant sampling methods (Altmann, 1974), Barbosa *et al.* (2008) investigated the influence of group size and geometry on the frequency of behavioral activities. Geometry is a dimensional analysis of an individual's position within a group of bottlenose dolphins and it is described as 'tight' (dolphins spaced less than one body length apart), 'loose' (dolphins separated greater than one and less than five body lengths), 'widely dispersed' (group members spread more than five body lengths apart), and 'mixed' (when the group members are irregularly spaced) (Shane *et al*., 1990*a*). Behavioral states defined in this study included traveling, foraging, socializing, resting and some combinations of categories (*i.e.* mixed behaviors). Foraging and traveling were predominant behaviors reported and did not vary diurnally or according to group size and geometry. Foraging activities were most frequently associated with large groups (> 13 individuals) and were found in both cohesive and dispersive group geometries, which were interpreted as cooperative foraging strategies.

Off southern Brazil and Uruguay, some resident bottlenose dolphins were recorded as being associated with the mouths of estuaries and lagoons, as well as bays, coastal islands and exposed beaches (*e.g.* Castello and Pinedo, 1977; Simões-Lopes and Fabian, 1999; Wedekin *et al.,* 2008; Laporta, 2009; Di Tullio *et al*., 2015; Lodi *et al*., 2016 this volume). Owing to the proximity of such populations to coastal areas and the inherent ease of observation, substantial data have been collected.

Off Florianópolis Island (Santa Catarina - SC), a study conducted between 1989 and 2005 recorded 71 groups of bottlenose dolphins (Wedekin *et al.,* 2008). The most common behavioral state observed was identified as foraging, and included events such as leaping, tail slapping, rapid movements across the surface, pursuits, and prey captured at the surface. These events were observed among groups of dolphins and also performed by solitary individuals across different habitats: surf zones, next to rocky shores, close to physical barriers (to catch fish), and also in open areas shallower than 30m (Wedekin *et al.,* 2008).

A separate, systematic study was conducted to record behavioral data in the Itajaí River (SC)[1] between 2001 and 2003. The most common behavioral state was diving and foraging, mainly near the river mouth. This area is subject to various fishing and port activities (*e.g.* movements of fishing boats, merchant ships and dredging) which affect how bottlenose dolphins use the area and the frequency of their behavioral states. An example given by the authors refers to dredging work, during which the dolphins reduced their frequency of foraging behavior and abandoned the area for short periods.

A longer-term study conducted over 30 years on a resident population of bottlenose dolphins at Laguna (SC) provided a comprehensive set of behavioral data, especially about foraging (Simões-Lopes 1991; Simões-Lopes *et al.,* 1998; Simões-Lopes and Fabian, 1999; Daura-Jorge *et al.,* 2012). In this region, the association of bottlenose dolphins with artisanal fishermen appeared to play an important role in their behavior, social organization and habitat use (Peterson *et al.,* 2008; Daura-Jorge *et al.,* 2012). A group of bottlenose dolphins developed specific strategies to catch fish (specially *Mugil* sp.) using the nets as a barrier in some areas of the lagoon (Simões-Lopes *et al.,* 1998; Daura-Jorge *et al.,* 2012). This is a complex, cooperative strategy between dolphins and the artisanal fishermen from which both have benefited. Specifically, the dolphins acquire food, while the fishermen increase their harvest (Simões-Lopes, 1991).

A similar association with artisanal fishermen was observed in the Tramandaí and Mampituba rivers in Rio Grande do Sul (RS) (Simões-Lopes, 1991; Simões-Lopes *et al.,* 1998; Simões-Lopes and Fabian, 1999; Hoffmann *et al.,* 2008; Zappes *et al.,* 2011), where foraging activities and social behaviors were recorded. Such associations were stronger during autumn and winter owing to the great availability of mullet (*Mugil* spp), which affected the frequency and type of bottlenose dolphins foraging behavior. Specifically, during summer, when interactions with fishermen were less intense, dolphins fed inside the rivers across shallower waters (up to 2.5m depth) (Simões-Lopes, 1991; Simões-Lopes *et al.,* 1998; Simões-Lopes and Fabian, 1999). In Laguna (SC) and Tramandaí (RS), social behaviors were more frequent during autumn and summer (Simões-Lopes *et al.,* 1998; Hoffmann *et al.,* 2008).

The resident population of bottlenose dolphins inhabiting the Patos Lagoon Estuary (PLE, RS) was studied during 1991–1993 and also 2001–2003 to investigate behavioral activities via focal-group sampling (Möller, 1993; Mattos *et al.,* 2007). The most common activities were foraging (60 and 37.6%, respectively for the both studies), with behavioral frequencies varying temporally and spatially. The feeding activity of the bottlenose dolphins was concentrated at the estuary mouth, which comprised a narrow and deep channel with fast currents, acting as a bottleneck for fish moving through the area and helping dolphins to take advantage of prey concentration, improving their foraging efficiencies (Hastie *et al.,* 2004; Mattos *et al.,* 2007). A greater frequency of feeding in winter was observed during the two studies. Mattos *et al.* (2007) observed a predominance of travel-feeding in autumn, suggesting this might be related to increased energy requirements in cooler waters combined with lower prey densities, or even may be a change in diet. Both studies observed an increase in social-reproductive interactions and mother-calf associations during spring and summer. Overall, the studies conducted in Laguna (SC), Mampituba River, Tramandaí River and the PLE (all in RS, southern Brazil) indicate these are areas of great importance for the resident populations of bottlenose dolphins.

[1]Britto, M.K. and Barreto, A.S. (2010) Effects of human activities on the behavior of bottlenose dolphins (*Tursiops truncatus*) in the Itajaí river mouth. Paper 39 presented during the *First Workshop on the Research and Conservation of* Tursiops truncatus *in SWAO*, 21-23 May 2010, Rio Grande, RS, Brazil.

In Uruguay, the first study aiming to describe and quantify the activity patterns of bottlenose dolphins along the Atlantic coast was carried out at La Coronilla-Cerro Verde, between 2002 and 2004 (Laporta, 2004). The behavioral data were collected by focal-group sampling during surveys from fixed points on coastal rocky areas (Laporta, 2004). Traveling was the predominant state observed (51%), followed by milling (31%), foraging (12%) and socializing (6%). Milling was most frequently observed in the mornings, while socializing was predominant during the afternoons. No differences were found in the seasonal frequency of behaviors.

In Argentina, a systematic study describing the presence of bottlenose dolphins in the Río Negro Estuary (RNE), Patagonia, was carried out between March and July each year from 2008 to 2011. Data on the dolphins' activity patterns were gathered via an *ad libitum* focal-group sampling technique (*e.g.* Altmann, 1974; Lehner, 1996). Data analyses showed that two main behavioral states were observed, including traveling (65%) and foraging (26%). The remaining groups (9%) were involved in other activities (Failla *et al.,* 2016 this volume).

Social Structure

Social structure encompasses social affiliation, group size and composition (*e.g.* Whitehead, 1997; 2008). Below we summarize available information on each of these topics for the SWAO.

Group size

Bottlenose dolphin group size and composition in the SWAO are relatively well known, except along the northern and northeastern Brazilian coast, where information is recent and restricted to offshore populations (Table 2).

Off northeastern Brazil, oceanic populations seem to comprise small groups (average of eight individuals) around key geographical features, like the Abrolhos Bank (Rossi-Santos *et al.,* 2006), Rocas Atoll (Baracho *et al.,* 2007) and Trindade Island (Carvalho and Rossi-Santos, 2011). At the SPSPA, groups of one to 18 bottlenose dolphins have been observed[2] (Caon *et al.*, 2009; Ott *et al.,* 2009). Larger groups (≥ 50 individuals) have been reported at the Fernando de Noronha Archipelago[3]. In each of these regions, groups contained newborns and calves. Except for the SPSPA, where data have been systematically collected, all other studies were based on opportunistic sightings and therefore it is not possible to draw robust conclusions concerning the group size of these populations.

For the southeastern Brazilian region, long-term research focusing on bottlenose dolphins has been restricted to RJ, especially at the Cagarras Archipelago, where the average group size (mean = 14; SD = 7; Lodi and Monteiro-Neto, 2012) was greater than values reported for other coastal populations in the region (Table 2). A similar case was described for southern Brazil, at Arvoredo Reserve (SC), where larger group sizes have been reported opportunistically, reaching up to 200 dolphins[5] (Wedekin *et al.,* 2008). However, for coastal islands (Arvoredo and Deserta Islands) in SC, the coloration and morphological characteristics of dolphins suggest they may belong to the oceanic population (see Ott *et al.*, 2016 this volume).

The maximum group size reported for coastal areas of RJ was more than 50 individuals (Ilha Grande Bay, Redonda and Cagarras Islands, Ipanema Beach and Arraial do Cabo) with calves present during all sightings (Lodi*,* 2016 this volume). Larger aggregations (up to 100 individuals) were observed offshore from Campos Basin[5]. However, Zerbini *et al.* (2004) reported small group sizes (mean = 4.5) from six encounters of bottlenose dolphins in depths ranging from 105 to 250m between RJ and SC. Calves were only observed during summer at this location.

Information regarding group composition is relatively scarce in the scientific literature. At the Cagarras Archipelago, the average group size was 14 individuals with 81% of records comprising of groups smaller than 20 dolphins, including immature individuals (Barbosa *et al.,* 2008; Lodi and Monteiro-Neto, 2012; Lodi *et al.,* 2016 this volume).

For all other coastal bottlenose dolphin populations (southern Brazil, Uruguay and Argentina), very similar group sizes were reported, averaging between three and six individuals, with a maximum of approximately 20 to 30 animals. Larger aggregations were less common. Group sizes seemed stable in populations studied over long-term periods (*i.e.* more than one decade in Laguna: Simões-Lopes, 1991; Daura-Jorge *et al.*, 2013; and Tramandaí River: Simões-Lopes, 1991; Hoffmann *et al.,* 2008; Giacomo and Ott, 2016 this volume; and more than two decades in the PLE: Möller, 1993; Dalla Rosa, 1999; Mattos *et al.,* 2007; Fruet *et al.,* 2011; 2015).

Regarding group composition, Mattos *et al.* (2007) reported the PLE population group size frequencies as: 11% for solitary individuals, 26% for pairs, 21% for trios, 31% for groups of four to six, 10% for seven to 10, and 2% for larger groups. Seasonal variation in group size was also observed: larger groups (>4) were most common during spring and summer (44 and 37%, respectively); pairs were more dominant during autumn (33%); and trios during winter (36%). Mattos *et al.* (2007) further observed that different groups used different areas. Specifically, larger groups were more commonly reported in the outer area of the lagoon, while trios and pairs were more common in the inner lagoon. Typically, pairs included a mother and calf, while trios included a mother-calf pair accompanied by another adult. During summer, large aggregations of mother-calf pairs were commonly encountered inside the lagoon (P.F. Fruet., pers. obs.).

[2]Genoves, R.C., Fruet, P.F., Di Tullio, J.C. and Secchi, E.R. Padrões de associação do boto *Tursiops truncatus* no estuário da Lagoa dos Patos, RS, Brasil. Working Paper 60 presented during the *First Workshop on the Research and Conservation of Tursiops truncatus: Integrating knowledge about the species in the Southwest Atlantic Ocean*, 21-23 May 2010, Rio Grande, Brazil.

Table 2. Summaries of the locations and mean bottlenose dolphin (*Tursiops truncatus*) group sizes estimated during studies in the Southwest Atlantic Ocean.

Country	Location (State)	Latitude	Longitude	Mean group size (Range)	Environment	Source
Brazil	São Pedro and São Paulo Archipelago - SPSPA	00°56'N	29°22'W	6.7 (3–16) 9.1 (3–25)	Oceanic island	Ott *et al.* (2009) Genoves *et al.*[2]
	Fernando de Noronha Archipelago (PE)	03°50'S	32°24'W	50	Oceanic island	Silva Jr. and Silva[3]
	Rocas Atoll (RN)	03°50'S	33°49'W	7.6 (3–15)	Oceanic island	Baracho *et al.* (2007)
	Abrolhos Bank (BA)	16°40'–19°30'S	38°00'–39°30'W	5.4 (1–20)	Oceanic island	Rossi-Santos *et al.* (2006)
	Trindade Island (ES)	20°30'S	29°18'W	5.3 (1–10)	Oceanic island	Carvalho and Rossi-Santos (2011)
	Cagarras Archipelago (RJ)	23°01'S	43°12´W	13 (3–20) 15.4 (3–30)	Coastal island	Barbosa *et al.* (2008) Lodi and Monteiro-Neto (2012)
	Paraty to Arraial do Cabo (RJ)	23°09'S	44°13´W	20.6 (1–50)	Coastal	Lodi *et al.* (2016 this volume)
	Campos Basin (RJ)	21°17'–23°01'S	40°56'–40°59'W	30 (5–100)	Offshore	Siciliano and Moreno[4]
	Rio de Janeiro and Santa Catarina State	21°17'–29°09'S	40°56'–49°34'W	4.5 (2–10)	Offshore	Zerbini *et al.* (2004)
	Itajaí River mouth (SC)	26°54'S	48°37´W	3.6 (1–13)	Coastal	Britto and Barreto[1]
	Norte Bay (SC)	27°30'S	48°31´W	5.4 (1–16)	Coastal	Flores and Fontoura (2006)
	Arvoredo Reserve and North Bay (SC)	27°17'S	48°22'W	8 (up to 200)	Coastal and adjacent islands	Wedekin *et al.* (2008) Simões-Lopes[5]
	Laguna (SC)	28°13'	48°45'W	2.6	Estuary	Daura-Jorge *et al.* (2013)
	Mampituba River (RS)	29°19'S	49°42´W	2.0 (1–8)	Coastal	Bernardi (2000)
	Tramandaí River (RS)	29°58'S	50°07´W	1.2 (1-8) 2.8 (1–7)	Coastal	Hoffmann *et al.* (2008); Giacomo and Ott (2010)[6]
	Patos Lagoon Estuary (RS)	32°09'S	52°05´W	4 (1-23)	Estuary	Möller (1993); Dalla Rosa (1999); Mattos *et al.* (2007); Fruet *et al.* (2011)
Uruguay	La Coronilla/Cabo Polonio	33°56'–34°23'S	53°29'–53°46'W	5 (1–15) 6 (1–25)	Coastal	Laporta (2004; 2009)
Argentina	San Antonio Bay	40°49'S	64°56´W	5.4 (1–30)	Embayment	Vermeulen and Cammareri (2009)

Off La Coronilla, Uruguay, the mean group size reported was five dolphins (SD = 3; range = 1–25). The most frequent groups encountered were those with one to six dolphins, followed by groups of seven and 15 individuals. Most groups (77%) included adults and juveniles, whereas a smaller proportion (21%) included mixed groups containing also calves. Only one group (2%) containing a single mother-calf pair was observed (Laporta, 2004). Two records of more than 25 individuals of mixed-age classes were reported in La Coronilla (Laporta, 2009).

At Samborombón Bay, Argentina, 40 to 50% of the groups sighted during spring and summer contained calves and/or juveniles. This percentage decreased noticeably in Mar del Plata, where the presence of calves and/or juveniles did not exceed 25%[6]. Further south in San Antonio Bay, Patagonia, bottlenose dolphin groups (n = 213) ranged between one and 30 individuals with a mean group size of 5 individuals (SD = 3; Vermeulen and Cammareri, 2009). Group size was significantly larger in winter and spring than during summer and autumn. In this area, 53% of the groups sighted contained calves, which represented 18% of all the

[3]Silva Jr, J.M. and Silva, F.J.L. (2004) Interação agonística de *Stenella longirostris* com *Stenella attenuata* e *Tursiops truncatus* no Arquipélago de Fernando de Noronha, Brasil. Page 32 *in* Abstracts, *11ª Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur*, 11-17 September 2004, Quito, Ecuador.
[4]S. Siciliano and I.B. Moreno, pers. comm., 22 May 2010
[5]P.C. Simões-Lopes, pers. comm., 22 May 2010
[6]R. Bastida, pers. comm., 21 May 2010

dolphins sighted. Juveniles represented 29% of the individuals recorded. The group size seemed to be positively correlated with the presence of calves and increased when the groups were foraging (Vermeulen and Cammareri, 2009). Calves (and most notably newborns) were recorded throughout the year in more than half of the observed groups, suggesting that perhaps San Antonio Bay is a nursing area for this population (Vermeulen and Cammareri, 2009).

In the RNE, 37% of the observed groups contained one to five individuals, although occasional aggregations (2%) of up to 20 dolphins per group were recorded. In total, 31% of the observed groups had calves, but never more than one per group. Nevertheless, in 30% of the sightings, the presence of calves could not be accurately determined (Failla *et al.,* 2016 this volume).

Social structure of identified individuals

Some social analyses are based on indices, which estimate the proportion of time that two individuals are associated (Cairns and Schwager, 1987). For bottlenose dolphin populations, the most common association index used is the 'half-weight' index (HWI). However, prior to wide-scale use of the HWI, other association indices were used, such as the simple ratio (SR) and the twice-weight index (TWI), limiting direct comparisons among studies (Whitehead, 2008). Thus, it was only possible to make general comparisons in relation to the strength of associations between individuals of each population and the consequent social dynamics.

Similar to other populations elsewhere, bottlenose dolphins in the SWAO exhibit a 'fission-fusion' pattern of associations, with spatio-temporal changes in group size and composition (Connor *et al.,* 2000). Studies of the association patterns of individuals are limited to six populations including four in Brazil: the Cagarras Archipelago, Laguna, Tramandaí and the PLE; one in Uruguay at La Coronilla/Cabo Polonio; and one in Argentina at San Antonio Bay (Table 3). The association index reported for each region did not exceed 0.5, indicating weak bonds between individuals (Table 3). Moreover, despite occurrences of non-random and preferred association at Laguna and the association variations at Cagarras Archipelago, most studies concluded that the majority of associations were random (Table 3).

Acoustic behavior

Studies of acoustic behavior may provide important insights into the nature of dolphin associations by identifying intra and interspecific population differences and providing information about individual identification and behavior (May-Collado, 2010). The bottlenose dolphin produces a wide repertoire of complex vocalizations, but the 'whistle' (a narrow band, frequency-modulated sound) is perhaps the category that receives most attention due to the social context in which it occurs (Wang *et al.,* 1995*a*, *b*; Herzing, 1996; Bazúa Durán and Au, 2002; Lammers *et al.,* 2003).

The methods used to describe whistles can be both qualitative and quantitative. Qualitative analyses are based on temporal variation of a whistle's fundamental frequency. These modulation patterns can be classified into six distinct groups, which have been adopted in many studies: ascendant, descendent, ascendant-descendent, descendent-ascendant,

Table 3. Studies in the Southwest Atlantic Ocean that investigated the association patterns of bottlenose dolphins (*Tursiops truncatus*) using an association index (AI, Whitehead, 2008).

Area	Geographic coordinates (lat/long)	Association Index (AI)	Mean of the AI (±SD) or distribution of the AI	References
Brazil				
Cagarras Archipelago (RJ)	23°01'S 43°45'W	Half-weight index	0.38 (± 0.18) 0.0 to 0.86	Lodi *et al.* (2014)
Laguna (SC)	28°13'–28°30'S 48°45'–48°55'W	Half-weight index	0.051 (0.058)	Daura-Jorge *et al.* (2013)
Tramandaí (RS)	29°58'S 50°07'W	Half-weight index	< 0.2	Hoffmann *et al.* (2008)
Patos Lagoon Estuary (RS)	32°09'S 52°05'W	Half-weight index	< 0.4	Dalla Rosa (1999) Genoves (2008)
Uruguay				
La Coronilla/Cabo Polonio	33°56'–34°23'S 53°29'–53°46'W	Simple Ratio	< 0.33	Laporta *et al.*[7]
Argentina				
San Antonio Bay	40°49'S 64°56'W	Half-weight index	0.21 (± 0.07)	Vermeulen and Cammareri, 2009

[7]Laporta, P., Trimble, M. and Zamisch, V. (2007) Management and conservation plan for a bottlenose dolphin (*Tursiops truncatus*) population in the first marine protected area proposed in Uruguay. Report for National Direction of Aquatic Resources (DINARA), Montevideo, Uruguay. July 2007. 14 pp.

multiples and constant (*e.g.* Caldwell *et al.,* 1990; Janik, 1999; Cook *et al.,* 2004; Hoffmann, 2004; Azevedo and Van Sluys, 2005). Quantitative analysis evaluates associated spectral and temporal parameters, including the initial, final, minimum, maximum and range of frequencies and the duration of the signal.

There are few studies related to bottlenose dolphin acoustics in the SWAO. Two independent studies were conducted with resident coastal populations in Brazil at the Tramandaí River mouth (29°58'S, 50°07'W; Hoffmann, 2004) and Patos Lagoon (32°06'S, 052°02'W; Azevedo *et al.,* 2007). These locations are 315km apart; however, it was possible to detect differences among some parameters, including the final, minimum and maximum frequencies, duration, and inflections (Table 4). Whistles from the Tramandaí River presented a maximum frequency of 17.15kHz (mean = 10.37; SD = 2.31), range of 12.62kHz (mean = 5.64; SD = 2.35) and duration of 1.94 second (mean = 0.39; SD = 0.27). In contrast, these same values for Patos Lagoon were 22.3kHz (mean = 12.21; SD = 3.20), 16.6kHz (mean = 6.25; SD = 3.34) and 2.45 seconds (mean = 0.55; SD = 0.39), respectively. In the Tramandaí River, the ascendant class predominated, with 45% of occurrences, followed by the ascendant-descendent class (29%). In the PLE, the predominance of multiples (31.5%) was verified over ascendant whistles (17.3%). The differences in whistle modulation between those two close sites may be useful to discern bottlenose dolphin populations.

The only study specifically designed for comparative purposes (*i.e.* standard method and equipment used for data recording in the areas sampled) involved assessing repertoire differences between resident bottlenose dolphins at the Tramandaí River and those associated with the oceanic SPSPA, off northeastern Brazil (Hoffmann *et al.,* 2012). Significant inter-population differences were found among most whistles parameters, both qualitative and quantitative (modulation classes and ascendant, descendent and ascendant-descendent), except for the final frequency.

Among the three bottlenose dolphin populations studied in Brazilian waters (Table 4) the average acoustic values ascribed to individuals from PLE (*e.g.* maximum frequency, duration and frequency range) were different from those described for the coastal group at the Tramandaí River mouth, and the oceanic group of SPSPA. The three populations also differed in relation to the modulation patterns. According to the tendency of the geographic distance/isolation of the populations, greater similarities were expected between the coastal groups, as well as both coastal groups equally differing from the SPSPA population. But the observed data did not support this hypothesis. Preliminary analyses suggested that each population presents its own unique acoustic characteristics. However, further studies should be conducted to obtain more data and examine the impact of habitat characteristics and environmental conditions on the acoustic repertoire of bottlenose dolphins in Brazil.

Acoustic information was also collected from five locations along the coast of Uruguay using passive acoustic monitoring (PAM) buoys: a total of 4152 whistles and 409 clicks were recorded from free-ranging bottlenose dolphins (Tellechea *et al.,* 2014). The various whistle repertoires were categorized, ascending was the most common pattern recorded and corresponded to 44% of all whistles. Multi-looped (more than one inflection point) represented 23% of the total. Ascending-descending (12%) and descending (8.1%) whistles were also documented, while descending-ascending (7.5%) and constant (5.5%) whistles were less frequent. Whistle ranges varied between 1.6 and 22.4kHz, and whistle duration was 628 ± 293ms. Click train duration had a mean of 1105 ± 59.6ms, and the mean click number per train was 11.4 ± 1.64. Mean click duration was 63.2 ± 4.06ms, and the inter-click interval was 129.4 ± 3.94ms. Click trains had a mean peak frequency of 52.02 ± 12.09kHz. Overall, bottlenose dolphins seemed to be more vocal during summer and less so during winter. Whistles showed strong seasonal variability associated with fluctuations in sea surface temperatures (SST). During winter and early

Table 4. Means and standard deviations of some bottlenose dolphin (*Tursiops truncatus*) whistle parameters from previous studies in the Southwest Atlantic Ocean. *Sf* = starting frequency; *Ef* = ending frequency; *MinF* = minimum frequency; *MaxF* = maximum frequency; *Dur* = duration; *Inf* = inflections; *n* = sample size. The frequency variables were measured in kHz and the duration in seconds.

Country	Location	*Sf* (±SD)	*Ef* (±SD)	*MinF* (±SD)	*MaxF* (±SD)	*Dur* (±SD)	*Inf* (±SD)	*n*	Source
Brazil	Tramandaí River (RS)	5.64 (±1.78)	8.59 (±2.81)	4.73 (±1.09)	10.38 (±2.31)	0.39 (±0.26)	1.28 (±0.64)	1768	Hoffmann (2004)
	Patos Lagoon Estuary (RS)	8.28 (±3.11)	8.37 (±3.70)	5.96 (±2.15)	12.21 (±3.20)	0.55 (±0.39)	1.42 (±1.85)	788	Azevedo *et al.* (2007)
Argentina	Gulf of San Jose	9.24 (±2.74)	6.63 (±2.29)	5.91 (±1.50)	13.65 (±1.54)	1.14 (±0.49)	1.58 (±1.24)	110	Wang *et al.* (1995)

spring (SST < 15°C), the average number of whistles was low, increasing in mid-spring and early summer (SST 16°-20°C) to reach maximum values in summer. Meanwhile, a decreasing trend in whistle numbers was found in late summer and early autumn. In autumn, the SST and the average number of whistles dropped sharply (Tellechea *et al.,* 2014).

The first acoustic study in SWAO was conducted by Wang *et al.* (1995*a*) who compared the whistles of *Tursiops* spp. from different geographical regions, including the North Atlantic (Gulf of Mexico/USA and Gulf of California/México), Pacific (Taiji/Japan) and Indian oceans (Shark Bay/Australia) and the Gulf of San Jose, Argentina. The authors found that groups from adjacent areas presented similar whistle structures; albeit with slight differences. Conversely, bottlenose dolphins living in non-adjacent areas presented distinct and unique acoustic characteristics; probably owing to their geographic isolation and the fact that the bottlenose dolphin from Indian Ocean was defined as a different species (*e.g.* Wells and Scott, 2002; Hammond *et al.*, 2012). The whistle data from bottlenose dolphins off Argentina (collected by Wang *et al.*, 1995*a*) suggested values of 17kHz as the maximum frequency (mean = 13.65; SD = 1.54). Nevertheless, the variation in frequency values and modulation classes were not presented, which precludes accurate comparisons with whistles parameters from others populations along the SWAO.

Interspecific interactions

Several interspecific interaction categories among bottlenose dolphin and other species had been opportunistically observed throughout the SWAO. Interactions or aggregations among bottlenose dolphins and other cetacean species were frequently recorded; however, interactions varied among species and contexts, and sometimes it was not possible to determine the nature of the interaction (Table 5). Interactions between bottlenose dolphins and other taxonomic groups, such as pinnipeds and seabirds during foraging were commonly reported in the SWAO, in Uruguay and southeastern and southern Brazil (Martin, 1986; Wedekin *et al.,* 2008).

Conclusions

Most regional studies have not considered behavioral sampling as their main objective. Consequently, there is a lack of consistency in terms of sampling design, methods for data collection and analyses. It is essential to standardize behavioral categories, improve sampling design to better understand the behavioral ecology of bottlenose dolphins in the SWAO. A standardized description of behavioral states is important to facilitate comparisons among populations, across potentially different environmental and temporal conditions, while evaluating responses to anthropogenic effects.

Nevertheless, available information suggests that the studied bottlenose dolphin populations in the SWAO presented weak intra-population associations, which are characteristic of fission-fusion societies. Information regarding the size and composition of bottlenose groups indicates that coastal individuals tend to form smaller groups than their oceanic counterparts. Despite the available data on social affiliation, group size and composition, assessing spatial and temporal variability in social structures and dynamic patterns is necessary to better understand regional bottlenose dolphin area preferences, habitats, social structures and population dynamics.

In terms of bottlenose dolphin acoustics, studies remain scarce and preliminary in the SWAO. Off Rio Grande do Sul and Uruguay, bottlenose dolphins emitted a varied repertoire of whistles, in which those with more than one inflection point were frequent. Bottlenose dolphins also emitted repeated whistle contours. However, no singular method has been applied to evaluate the signature whistle hypothesis in bottlenose dolphins in the SWAO. Also, few researchers have focused on whistle-parameter characteristics, and only the study developed in Uruguay has provided information about pulses.

Bottlenose dolphins from Brazilian, Uruguayan and Argentinean waters produce stylized whistles in which the acoustic parameters are similar to published ranges around the world, but there is no information about their functions. Some results indicate significant local inter-population variation in the acoustic parameters of the whistles. Future studies including more populations along the SWAO would help to improve our understanding of the natural variation of the animals' vocalizations, as well as their relation to processes of geographic isolation and adaptations to environmental conditions.

In summary, the studies describing the various intra and interspecific interactions of bottlenose dolphins in the SWAO mostly have been opportunistic and therefore do not fully allow a comprehensive analysis of the situational contexts. Ongoing descriptions of behaviors executed during interactions, time durations and the relationships between these activities and environmental conditions could provide the basis for an ecological analysis, and also the assessment of habitat importance; which ultimately could facilitate planning conservation actions.

Recommendations

To further improve our understanding of the behavioral ecology and social organization of bottlenose dolphins in the SWAO, we recommend the following actions:

1. It is strongly recommend for students and researchers interested in behavior to find a suitable method in the available literature (*e.g. Cetacean Societies* - Mann*,* 1999*b*; and *Handbook of Ethological Methods* - Lehner, 1996).

2. Behavioral data (events and states) should be described from bottlenose dolphins in different areas using standard definitions, implementing focal-sampling protocols (group and/or individuals) to evaluate: (i) behavioral patterns and budgets and their variations in response to different environmental parameters, and so facilitate analysis about

habitat use; and (ii) spatio-temporal behavioral changes and their relationship with anthropogenic activities. Behavioral data should be collected following the sampling methods defined by Shane (1990*b*) and Mann (1999*a, b*). In addition, behavioral events should be sampled to assess the influences of extrinsic factors on their frequency and context, and to evaluate potential effects of anthropogenic activities;

3. Evaluate association patterns of individuals, including sex ratios and age classes (adults, juveniles, and calves) per group and populations, and also any spatio-temporal variability in social structures and dynamics;

4. Expand acoustic data sampling from different populations of bottlenose dolphins using standardized definitions (modulation patterns and spectral and temporal parameters) and appropriate equipment to describe the bioacoustics physical parameters and environmental noises;

Table 5. Interspecific interactions between bottlenose dolphins and other cetaceans, pinnipeds, seabirds and elasmobranchs reported in the Southwest Atlantic Ocean and off north Brazil.

Common name	Scientific name	Region	Location	Observations	References
Cetacean interactions					
Humpback whale	*Megaptera novaeangliae*	Northeastern Brazil	Bahia	Dolphins leapt and surfaced very close to the whales, producing highly audible whistles while the humpback whales were breaching and tail slapping. No direct contact between the species, nor obvious fresh scars, bite marks or even blood in the water were observed.	Rossi-Santos *et al.* (2009)
Spinner dolphin	*Stenella longirostris*	Northeastern Brazil	Fernando de Noronha Archipelago	Spinner dolphins were traveling and they markedly changed direction and departed from the site in response to a group of ~50 bottlenose dolphins.	Silva Jr. and Silva[3]
Rough-toothed dolphin	*Steno bredanensis*	Southeastern Brazil	Ilha Grande Bay	Interspecific feeding aggregation between a group of ~20 bottlenose and rough-toothed dolphins and brown booby (*Sula leucogaster*) and magnificent frigatebirds (*Fregata magnificens*).	L. Lodi, unpub. data
Guiana dolphin	*Sotalia guianensis*	Southeastern Brazil	Guaratuba Bay, Paraná	Interaction between three bottlenose dolphins and one Guiana dolphin during feeding activities (commensalism).	Monteiro-Filho *et al.* (1999)
Common minke whale	*Balaenoptera acuturostrata*	Southeastern Brazil	Continental slope	Bottlenose dolphins interacted aggressively several times with a common minke whale until it left the area.	Cremer *et al.* (2009)
Atlantic-spotted dolphins	*Stenella frontalis*	Southern Brazil	Guaratuba Bay, Paraná	Four bottlenose and two Atlantic-spotted dolphins traveling together.	C. Domit, pers. obs.
Guiana dolphin	*Sotalia guianensis*	Southern Brazil	North Bay	Event 1: a bottlenose dolphin avoided an area occupied by a group of Guiana dolphins. Event 2: the arrival of up to 16 bottlenose dolphins in an area regularly occupied by Guiana dolphins resulted in the latter abandoning the area.	Flores and Fontoura (2006)
				Aggressive behavior by a group of bottlenose dolphins towards to a Guiana dolphin.	Wedekin *et al.* (2004)
Southern right whale	*Eubalaena australis*	Southern Brazil	Open coastal waters, close to the Patos Lagoon Estuary	A group of ~20 bottlenose dolphins were observed swimming around and following an adult whale. Neither aggression by the dolphins nor any change in the whale's behavior was observed.	P.F. Fruet, pers. obs.
False killer whale	*Pseudorca crassidens*	Southern Brazil	Oceanic waters	Traveling in the same group of each of those species.	E.R. Secchi[8]
Atlantic spotted dolphin	*Stenella frontalis*				
Common dolphin	*Delphinus delphis*				
Long-finned pilot whale	*Globicephala melas*				
Southern right whale	*Eubalaena australis*	Uruguay	Cabo Polonio	Dolphins swimming around a whale without any observed contact between them.	P. Laporta, pers. obs.

Killer whale	*Orcinus orca*	Argentina	Samborombón Bay	Attacking a bottlenose dolphin.	J.D. Loureiro[9]
Southern right whale	*Eubalaena australis*	Argentina	San Antonio Bay, north Patagonia	Interactions between bottlenose dolphins and southern right whales and associations with pinnipeds during feeding strategies.	E. Vermeulen[10]
Commerson's dolphins	*Cephalorynchus commersonii*	Argentina	Engaño Bay	Distinct aggressive situations and feeding interactions.	Coscarella and Crespo (2010)
Pinniped interactions					
South American fur seal	*Arctocephalus australis*	Uruguay	Cabo Polonio and La Coronilla	Pinnipeds and dolphins interacting during feeding activities.	P. Laporta, pers. obs.
South American sea lion	*Otaria flavescens*				
Seabird interactions					
Magnificent frigatebird	*Fregata magnificens*	Southeastern Brazil	Cagarras Archipelago	Interacting with the bottlenose dolphins, mainly during feeding activities. Seabirds benefited from school fish concentrated by the dolphins.	Lodi (2009)
Brown booby	*Sula leucogaster*				
Magnificent frigatebird	*Fregata magnificens*	Southern Brazil	Florianópolis Island		Wedekin *et al.* (2008)
Brown booby	*Sula leucogaster*				
Kelp gull	*Larus dominicanus*				
Magnificent frigatebird	*Fregata magnificens*	Southern Brazil	Patos Lagoon Estuary	Feeding on a shoal of fish surrounded by resident bottlenose dolphins.	P.F. Fruet, pers. obs.
Elasmobrachii interactions					
Manta ray	*Manta birostris*	Southern Brazil	North Bay	Observed jumping in the middle of a bottlenose dolphins group.	P.A. Flores[11]

5. Combine different sources of information from behavior, bioacoustics, genetics and social organization to determine priority areas for species conservation (foraging, breeding and care of calf areas) and ultimately, manage impacting anthropogenic activities.

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[8]E.R. Secchi, pers. comm., 22 May 2010
[9]J.D. Loureiro, pers. comm., 22 May 2010
[10]E. Vermeulen, pers. comm., 22 May 2010
[11]P.A. Flores, pers. comm., 22 May 2010

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