

## Delphinid Mixed-Species Associations in the Oceanic Waters of the Western South Atlantic

Renan C. de Lima,<sup>1,2</sup> Juliana C. Di Tullio,<sup>2</sup> Eduardo R. Secchi,<sup>2</sup>  
Franciele R. Castro,<sup>3</sup> and Genyffer C. Troina<sup>2</sup>

<sup>1</sup>Programa de Pós-Graduação em Oceanografia Biológica, Instituto de Oceanografia, Universidade Federal do Rio Grande-FURG, Rio Grande/RS, CEP 96203-900, Brazil

<sup>2</sup>Laboratório de Ecologia e Conservação da Megafauna Marinha (ECOMEGA), Instituto de Oceanografia, Universidade Federal do Rio Grande-FURG, Rio Grande/RS, CEP 96203-900, Brazil

E-mail: renandl@gmail.com

<sup>3</sup>Instituto Aqualie, Avenida Doutor Paulo Japiassú Coelho, 714 Salas 201 e 202, Cascatinha, Juiz de Fora/MG, CEP 36033-310, Brazil

### Abstract

Dolphins are highly social animals usually reported in large groups comprised of individuals of a single species, although they are often reported associating with other species as well. The drivers for the formation of these mixed-species associations (MSAs) are poorly understood, and records in Brazilian waters are scarce. To better understand their occurrence in the region, we assessed seasonal and spatial distribution of MSAs in waters over the outer continental shelf and slope off Brazil (22° to 33° S). Data were collected during spring and autumn between 2009 and 2014. From a total of 187 Delphinidae sightings, 28 consisted of MSAs. *Tursiops truncatus* was the most frequently sighted species in an MSA ( $n = 22$  sightings) and was mostly found in lower numbers than its associated counterparts: *Globicephala melas*, *Stenella frontalis*, *Grampus griseus*, and *Pseudorca crassidens*. MSAs between *Stenella attenuata* and *Stenella longirostris* or *Delphinus delphis* and *S. frontalis* were also reported. Our data did not show any seasonal or spatial trends in overall MSA frequency; nevertheless, the widely distributed *T. truncatus* appears to shift its associates according to their local abundance (e.g., associating with *G. melas* in the southern region of the study area and with *S. frontalis* in the southeastern region). Although a lot remains to be investigated regarding the ecological drivers for such associations between sympatric dolphins in Brazilian waters, this was the first effort to describe their occurrence and distribution patterns using cetacean dedicated surveys.

**Key Words:** Brazil, odontocetes, distribution, interspecific associations, cetaceans

### Introduction

*Mixed-species association* (MSA) is a term applied to associations involving individuals from two or more species presenting similar behaviours (Stensland et al., 2003). Such associations may occur over variable time periods—from minutes or hours to even years (Clua & Grosvalet, 2001). The attraction between species can be either mutual or unidirectional as long as the approaching species is tolerated by the other species (Stensland et al., 2003). The MSA concept should not be confused with that of aggregations in which individuals do not belong to the same group but are rather independently converged towards the same specific resource or area (e.g., in highly productive upwelling zones; Powell, 1985). Interspecific associations have been reported for several vertebrate taxa (Terborgh, 1990). Among mammals, associations including more than one species are likely to involve taxa that exhibit naturally gregarious behaviours such as primates and dolphins (Cords & Würsig, 2014).

Dolphins live in groups whose size can range from a few individuals to thousands, depending on the species and the area they inhabit (LeDuc, 2009). Gregarious dolphin species usually live under fluid and complex associations of a fission-fusion nature (Cords & Würsig, 2014). MSAs of dolphins have been reported in waters all around the world, from tropical to temperate seas (Frantzis & Herzog, 2002; Quérouil et al., 2008; Rossi-Santos et al., 2009; Zaeschmar et al., 2014; Elliser & Herzog, 2015; Svendsen et al., 2016), but dedicated studies remain scarce.

The ecological drivers for associations between different species are not well understood, but they may include foraging and social advantage, and/

or protection against predators (Stensland et al., 2003; Cords & Würsig, 2014). For instance, individuals of different species may cooperate in searching for food sources or use one another to practice social and/or reproductive behaviours and, thus, gain social advantage within its own species in the future. Population abundance may also play a role in the mixing of different species in certain areas (Baraff & Asmutis-Silvia, 1998; Frantzis & Herzing, 2002; Quérouil et al., 2008) as the less abundant species are usually seen in association with heterospecifics more frequently than others. In that case, the antipredator advantage should be of particular importance as larger groups may increase chances of earlier detection of potential predators, allowing individuals to spend less time being vigilant, with a lower probability of becoming a target.

The diversity of delphinids in Brazilian waters is high (Zerbini et al., 2004; Di Tullio et al., 2016; Bastida et al., 2018), yet little is known about the associations between species in the region or about their ecological significance. A few reports include associations between coastal common bottlenose (*Tursiops truncatus*) and Guiana (*Sotalia guianensis*) dolphins, and between spinner (*Stenella longirostris*) and Atlantic spotted (*Stenella frontalis*) dolphins (Monteiro-Filho et al., 1999; Zerbini et al., 2004) in southeastern Brazil. In northeastern Brazil, there have also been records of *T. truncatus* associating with rough-toothed dolphins (*Steno bredanensis*) and melon-headed whales (*Peponocephala electra*), as well as mixed-groups of pantropical spotted (*Stenella attenuata*) and Clymene (*Stenella clymene*) dolphins (Rossi-Santos et al., 2009). A better understanding of such associations in Brazilian waters would shed light on the possible ecological triggers involved and how they could ultimately affect population dynamics.

Herein, we report MSAs involving seven Delphinidae species sighted in Brazilian offshore waters. Our purpose was to describe the structure (i.e., specific composition and relative abundance) of these groups and to identify spatial and seasonal patterns, if any, in their frequency of occurrence throughout the study area.

## Methods

### Study Area

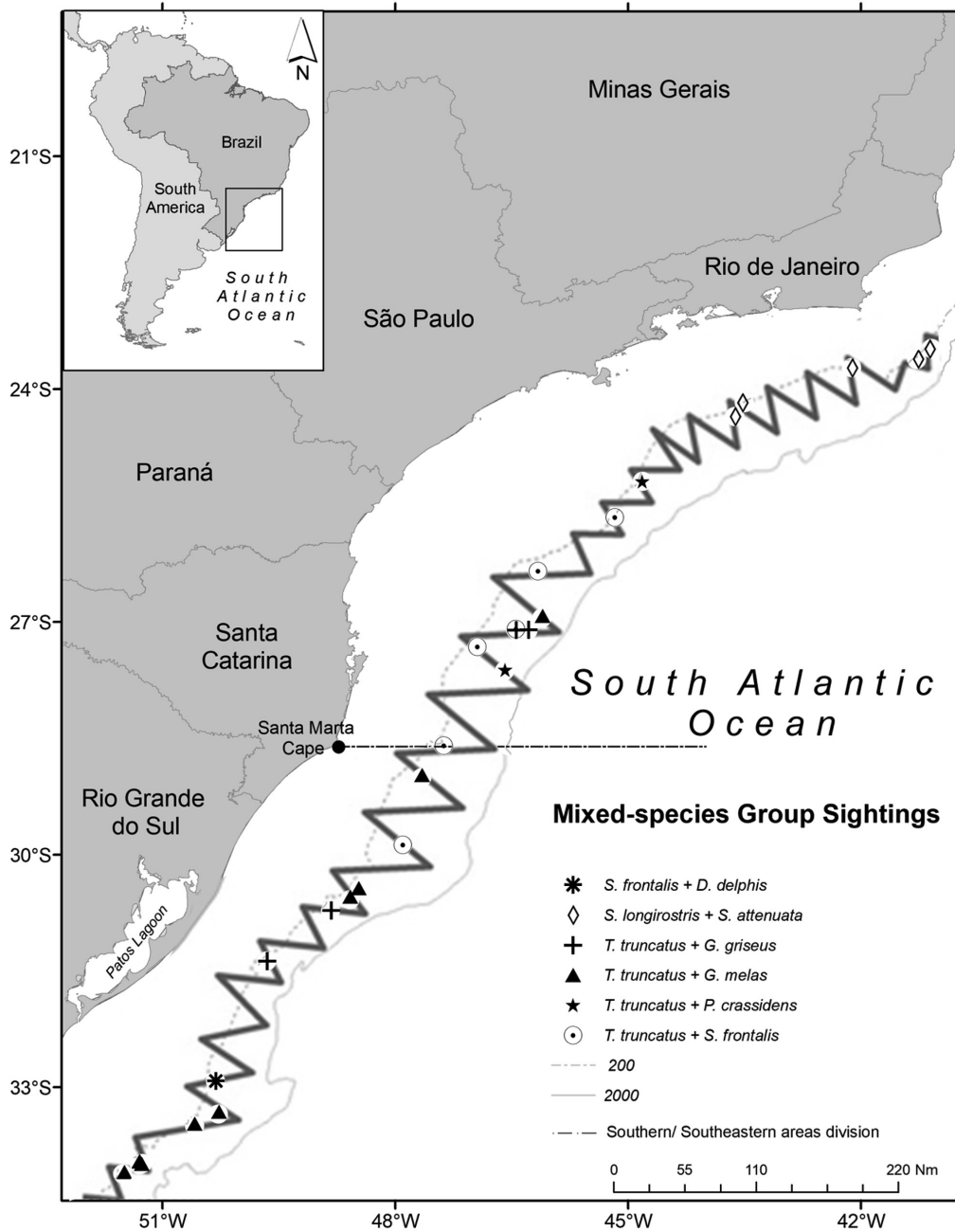
The surveys were carried out within the Brazilian southeastern (24° to 28° S) and southern (28° to 34° S) oceanic waters, which consist of the outer continental shelf and slope (Figure 1). The region is seasonally influenced by dynamic oceanographic processes driven by distinct water masses (Knoppers et al., 2010). These two areas are separated by the Santa Marta Cape (28° 30' S), which

is an area where upwellings occur frequently, allowing for the ascension of nutrient rich waters of the South Atlantic Central Waters (Castello & Möller, 1977; Matsuura, 1986). The southeastern area is mainly under the influence of the Brazil Current (BC), which transports warm and oligotrophic waters southward (Silveira et al., 2000). Seasonal upwellings are important in this area as they fertilize superficial waters, enhancing phytoplankton and zooplankton density (Braga et al., 2008; Muelbert et al., 2008). Additionally, cyclonic meanders of the BC, wind, and shelf break steep topography may trigger upwellings during winter and summer, respectively (Campos et al., 2000; Mahiques et al., 2004). The southern area is influenced by the BC and continental discharge of the Río de La Plata and Patos Lagoon, as well as the subantarctic waters transported by the Malvinas (Falklands) Current. The mixing intersection of these water masses and the BC form the Subtropical Shelf Front, which is the subject of local seasonal wind regimes, changing its strength and location from the shelf to beyond the continental slope (Möller et al., 2008; Piola et al., 2008; Figure 1).

### Survey Design and Data Collection

Data were collected during eight ~30 day-long cetacean visual monitoring surveys conducted in the austral spring ( $n = 4$ ) and autumn ( $n = 4$ ) on board the *R/V Atlântico Sul* of the Federal University of Rio Grande (FURG) between 2009 and 2014. Effort occurred following previously designed transect lines between the 150 and 1,500 m isobaths (Figure 1) using the distance sampling method (Buckland et al., 2001). Trained observers positioned in the upper deck of the research vessel independently searched for cetaceans from the bow to 90°, one to port and one to the starboard side of the vessel, using reticulated binoculars (7 × 50). Data were recorded on a computer connected to the vessel's navigation system using *WinCruz* software (<http://swfsc.noaa.gov/textblock.aspx?Division=PRD&ParentMenuId=147&id=1446>). Survey effort always happened during sunlight and with ideal sea conditions (Beaufort Sea State < 5). When a dolphin (or group) was sighted, the following data were recorded: number of individuals and species composition, date, time, geographical position, local depth, type of behaviour, and presence of calves.

Due to logistical reasons, weather conditions, and ship schedule, the surveys started at the southernmost transect line on different dates, and the effort varied along the study area (Table 1). All cetacean sightings were recorded (Di Tullio et al., 2016); however, only delphinid MSA data were analysed in this study. Since the study area presents



**Figure 1.** Sightings distribution of delphinid mixed-species associations (MSAs) in the outer continental shelf and slope in southern-southeastern Brazil between 2009 and 2014; the dark continuous line represents the previously designed transects followed by the vessel.

**Table 1.** Survey effort (expressed in nautical miles [nmi]) and encounter rate (highlighted in bold) for mixed-species groups for each research cruise, and within each area along the southern-southeastern Brazilian outer continental shelf and slope, between 2009 and 2014

Survey	Season	Year	Total effort (nmi)	Southeastern area effort (nmi)	Southern area effort (nmi)
#1	Spring <b>(0.0008)</b>	2009	1,210	553 <b>(0.001)</b>	657 <b>(0)</b>
#2	Autumn <b>(0.002)</b>	2010	1,230	312 <b>(0.003)</b>	918 <b>(0.001)</b>
#3	Spring <b>(0.005)</b>	2010	1,904	1,061 <b>(0.005)</b>	843 <b>(0.003)</b>
#4	Autumn <b>(0.002)</b>	2011	1,818	887 <b>(0.001)</b>	931 <b>(0.003)</b>
#5	Spring <b>(0.003)</b>	2012	1,769	778 <b>(0.002)</b>	991 <b>(0.004)</b>
#6	Autumn <b>(0.004)</b>	2013	1,681	721 <b>(0.005)</b>	960 <b>(0.003)</b>
#7	Autumn <b>(0.002)</b>	2014	1,238	500 <b>(0.002)</b>	738 <b>(0.001)</b>
#8	Spring <b>(0.001)</b>	2014	1,360	813 <b>(0.001)</b>	547 <b>(0.002)</b>
		Σ:	12,210	5,625	6,585

distinct oceanographic features (see above), it was divided into the north and south portion in regard to the Santa Marta Cape (28.6° S), herein referred to as the southeastern (SE) and southern (S) areas, respectively (Figure 1).

#### Data Analysis

We applied the encounter rate (ER), defined as the number of total MSA sightings within each area (S and SE) per distance surveyed (expressed in nautical miles [nmi]) for each research cruise to statistically compare the seasonal (autumn and spring) and spatial differences in MSA sighting frequency. This is because the survey effort (distance surveyed) differed among cruises and between the two regions (Table 1). The Shapiro-Wilk test was used to evaluate data normality, and the Levene's test was used to evaluate homoscedasticity. As assumptions were rejected, ER data were normalized using a (log + 1) transformation. The differences in ER between the S and SE areas and between the seasons were tested with a two-way ANOVA followed by *post-hoc* Tukey HSD tests. Analyses were performed in R (R Development Core Team, 2016) using the 'MASS' and 'car' packages (Ripley et al., 2015; Fox & Weisberg, 2016).

#### Results

A total of 12,210 nmi were surveyed, along which 187 encounters with delphinids have been registered. MSA sightings represented 15.5% ( $n = 28$ ) of all sightings (Figure 1; Table 2). We could not find significant seasonal (Spring: 14 sightings = 4.5,  $SE = 1.85$ ; Autumn: 14 sightings = 3.75,  $SE = 1.81$ ;  $p = 0.46$ ) or spatial (S area: 14 sightings = 1.75,  $SE = 0.45$ ; SE area: 14 sightings = 1.87,  $SE = 0.74$ ;  $p = 0.81$ ) differences in MSA sighting frequency. *T. truncatus* was the most frequently sighted species in MSAs, being registered in 22 of the 28 MSA sightings. Associations occurred with four different species: *G. melas* (10 sightings), *S. frontalis* (6 sightings), Risso's dolphin (*Grampus griseus*; 4 sightings), and false killer whale (*Pseudorca crassidens*; 2 sightings). The proportional number of individuals of *T. truncatus* was generally lower than that of the associated counterpart. Other MSAs recorded included associations between *S. attenuata* and *S. longirostris* (5 sightings) and one registered association between *S. frontalis* and *D. delphis*. Detailed information regarding these sightings are presented in Table 2.

**Table 2.** Information for each mixed-species association (MSA) sighting recorded along the outer continent shelf and slope in southern-southeastern Brazil. The number of individuals refers to species 1, species 2, and mixed-associations of species 1 and 2 in each encounter. Mean total number of individuals (species 1, species 2, and total) for each group composition and mean depth where the MSA encounters were registered ( $\pm$  standard deviation) are highlighted in bold.

Group composition	Sighting	Season	Year	Area	Number of individuals	Depth	Presence of calves
<i>Tursiops truncatus</i> + <i>Globicephala melas</i>	T3#50	Spring	2010	South	200 + 500 (700)	278	Yes
	T4#2	Autumn	2011	South	35 + 15 (50)	1,122	No
	T5#2	Spring	2012	South	50 + 400 (450)	575	No
	T5#11	Spring	2012	South	5 + 20 (25)	810	No
	T5#13	Spring	2012	South	7 + 20 (27)	810	No
	T5#136	Spring	2012	Southeast	15 + 35 (50)	1,385	Yes
	T6#3	Autumn	2013	South	18 + 30 (48)	240	Yes
	T6#27	Autumn	2013	South	120 + 60 (180)	665	Yes
	T7#6	Autumn	2014	South	70 + 60 (130)	439	Yes
T8#27	Autumn	2014	South	18 + 18 (36)	547	No	
					<b><i>T. t.</i> (54 <math>\pm</math> 62);</b>	<b>715 <math>\pm</math> 106</b>	
					<b><i>G. m.</i> (116 <math>\pm</math> 178);</b>		
					<b>MSA (155 <math>\pm</math> 66)</b>		
<i>T. truncatus</i> + <i>Stenella frontalis</i>	T1#50	Spring	2009	Southeast	40 + 700 (740)	257	Yes
	T3#55	Spring	2010	South	10 + 120 (13)	412	No
	T3#80	Spring	2010	Southeast	20 + 200 (220)	NA	No
	T3#91	Spring	2010	Southeast	5 + 120 (125)	470	Yes
	T5#112	Spring	2012	South	5 + 100 (105)	250	Yes
	T6#46	Autumn	2013	Southeast	15 + 230 (245)	247	Yes
					<b><i>T. t.</i> (16 <math>\pm</math> 13);</b>	<b>260 <math>\pm</math> 98</b>	
					<b><i>G. m.</i> (245 <math>\pm</math> 229);</b>		
					<b>MSA (272 <math>\pm</math> 66)</b>		
<i>T. truncatus</i> + <i>Grampus griseus</i>	T2#20	Autumn	2010	South	100 + 5 (105)	572	No
	T5#16	Autumn	2011	South	10 + 40 (50)	678	Yes
	T6#35	Autumn	2013	Southeast	15 + 230 (245)	745	Yes
	T6#36	Autumn	2013	Southeast	300 + 10 (310)	1,235	No
						<b><i>T. t.</i> (106 <math>\pm</math> 135);</b>	<b>807 <math>\pm</math> 46</b>
					<b><i>G. g.</i> (71 <math>\pm</math> 106);</b>		
					<b>MSA (152 <math>\pm</math> 55)</b>		
<i>T. truncatus</i> + <i>Pseudorca crassidens</i>	T2#32	Autumn	2010	Southeast	3 + 10	340	No
	T6#32	Autumn	2013	Southeast	50 + 30	1,440	Yes
						<b><i>T. t.</i> (26 <math>\pm</math> 33);</b>	<b>152 <math>\pm</math> 55</b>
					<b><i>P. c.</i> (20 <math>\pm</math> 14);</b>		
					<b>MSA (46 <math>\pm</math> 33)</b>		
<i>Delphinus delphis</i> + <i>S. frontalis</i>	T4#7	Autumn	2011	South	<b><i>D. d.</i> (20);</b>	620	Yes
					<b><i>S. f.</i> (80);</b>		
					<b>MSA (100)</b>		
<i>Stenella longirostris</i> + <i>Stenella attenuata</i>	T3#105	Spring	2010	Southeast	30 + 70 (100)	211	Yes
	T3#113	Spring	2010	Southeast	40 + 10 (50)	756	No
	T3 #114	Spring	2010	Southeast	300 + 300 (600)	815	Yes
	T5 #137	Spring	2012	Southeast	230 + 230 (460)	481	Yes
	T7 #43	Autumn	2014	Southeast	400 + 400 (800)	638	Yes
					<b><i>S. l.</i> (200 <math>\pm</math> 162);</b>	<b>580 <math>\pm</math> 108</b>	
					<b><i>S. a.</i> (202 <math>\pm</math> 161);</b>		
					<b>MSA (402 <math>\pm</math> 322)</b>		

## Discussion

The proportion of mixed-species groups in relation to all delphinid sightings (multi- and mono-specific groups) observed here (15.5%) was similar to other studies (Herzing & Johnson, 1997; Herzing et al., 2003) but considerably higher than others (García-Tiscar et al., 2000; Maze-Foley & Mullin, 2006; Quérouil et al., 2008). *T. truncatus* was the most frequently sighted species in MSAs, associating with a variety of other species. This species has been reported in association with over 20 different taxa worldwide (Ballance, 2009). In this study, in addition to being the most common species in MSAs, it was generally the species with lower numbers of individuals as reported for other regions (Ballance & Pitman, 1998; Maze-Foley & Mullin, 2006). As suggested by Quérouil et al. (2008), some species may face a strong constraint to associate with others to maintain a certain group size when their abundance is low. Nevertheless, it is debatable whether this tendency occurs to increase individual protection against predators or to enhance chances of finding resources.

Associations between *T. truncatus* and *G. melas* were the most frequent. The few studies available on the feeding habits of *G. melas* in Brazilian waters have shown that the species preys upon cephalopods (Santos & Haimovici, 2001; Santos et al., 2002). Although *T. truncatus* is considered a generalist species (Wells & Scott, 2009), the diet of offshore populations remains unknown. While it is still possible that these two species mix to gain foraging advantage for one or both species involved, the fact that *G. melas* seems to be a relatively abundant species in the outer continental shelf and slope of southern Brazil (see Di Tullio et al., 2016) would make them attractive for species in lower numbers such as *T. truncatus*. Such associations could be advantageous in terms of enhancing protection against attacks from potential predators such as killer whales (*Orcinus orca*), which are also commonly found in the area (Secchi & Vaske, 1998; Zerbini et al., 2004; Di Tullio et al., 2016). Occasional associations involving these species were reported for northern and western Scotland and New Zealand (Weller et al., 1996; Weir et al., 2001; O'Callaghan & Baker, 2002).

Sightings of *T. truncatus* associated with *S. frontalis* were limited between 25° and 29° S, which mostly includes the SE region. This coincides with a density decrease of *G. melas* within the study area (Di Tullio et al., 2016) and could indicate that *T. truncatus*, in fact, associates with the most abundant and available species. *T. truncatus* and *S. frontalis* MSAs are well known around the Bahamas in the North Atlantic where

a diversity of interactions have been reported, including cooperative feeding and social interactions (Herzing & Johnson, 1997; Herzing et al., 2003; Melillo et al., 2009; Elliser & Herzing, 2015). Based on these reports, we could hypothesize that the association between these species within our study area could also be equally complex, even though we could not record the same types of behaviours.

MSAs involving *T. truncatus* and *G. griseus* or *P. crassidens* were less frequent within the study area. MSAs with such species composition have been widely reported around the globe (Ballance & Pitman, 1998; Hodgins et al., 2004; Roch et al., 2015; Bacon et al., 2017), yet very little is known about their patterns of occurrence. Our data suggest that associations between *T. truncatus* and *P. crassidens* are rare within the study area. *P. crassidens* remains one of the lesser-known dolphin species, especially in Brazilian waters, which makes it even more difficult to understand the drivers for such associations. In New Zealand, in contrast to our observations within Brazilian oceanic waters, MSAs comprised of these two species are frequent, with long-term resightings of individuals and records of feeding behaviour (Zaeschar et al., 2014).

Records of associations between *S. longirostris* and *S. attenuata* had the northernmost and most limited latitudinal range (23 to 24° S), which is consistent with the overlap in distribution range between these species within the study area (Zerbini et al., 2004; Moreno et al., 2005; Amaral et al., 2015; Di Tullio et al., 2016). The number of individuals of each species was very similar in the mixed-species groups recorded herein. An equivalent number of individuals for each species was also observed in MSAs involving *S. longirostris* and *S. attenuata* in the southwestern Indian Ocean where the associations have ultimately been attributed to an antipredatory strategy (Kiszka et al., 2011). Advantage against predator pressure has also been determined as triggering MSAs in the eastern Pacific (Scott & Catanach, 1998). Therefore, considering the even numbers of both species when in association, it is possible that they both simultaneously seek enhanced protection against potential predators. Nevertheless, a foraging advantage could also be involved since a higher number of individuals would increase the chances of prey detection. Isotopic data for individuals of these two species occurring in the same region have indicated large niche overlap (Troina et al., 2020). The use of similar food resources seems a plausible reason for associations involving *S. longirostris* and *S. attenuata* as both species have been reported to consume similar prey, including oceanic squid and mesopelagic fishes (Perrin, 2009a, 2009b).

The single register of association between *D. delphis* and *S. frontalis* indicates that these are rare within the study area. This is consistent with these species' distribution patterns in the region where there is a small overlap in their area of occurrence (Di Tullio et al., 2016). The highest densities of *S. frontalis* in the Brazilian shelf-break and slope region have been observed in the SE portion where the occurrence of *D. delphis* shifts from deeper to inner shelf waters (Tavares et al., 2010; Di Tullio et al., 2016).

Although the formation of an MSA is likely beneficial for at least some individuals, it is important to emphasize its possible drawbacks. For instance, interspecific sexual interactions are more frequent among species that have similar life histories and/or habitat use and, thus, may result in hybridization (Bérubé, 2009). Potential hybrids of *T. truncatus* with other species, such as *S. frontalis* (Herzing et al., 2003) and *G. griseus* (Hodgins et al., 2004), have already been reported in the wild. This phenomenon may have negative impacts on the fitness of parental species and their hybrid offspring (Crossman et al., 2016). Furthermore, the aggregation of different species may also increase the exposure to parasites or diseases (e.g., dolphin morbilliviruses) as seen in aggregations of monospecifics (Côté & Poulinb, 1995; Morris et al., 2015; Balmer et al., 2018).

In the present study, we provide original information about the specific composition of mixed-species groups and their spatiotemporal patterns within the oceanic waters of southeastern and southern Brazil. Nevertheless, attention should be given to the assessment of MSAs within Brazilian coastal waters, as well as to the oceanic region during other seasonal periods not covered by our surveys (e.g., summer and winter). It is very difficult to know the factors triggering these associations since feeding observations in this environment are rare, and chemical tracers such as stable isotopes in skin biopsies would not necessarily be representative of the period these associations take place. Apart from trophic interactions, MSAs may play an important role in protection against predators (Cords & Würsig, 2014). As in monospecific groups, the predation pressure is a major factor leading to aggregation of dolphins (Norris & Dohl, 1980). Even though we could not properly evaluate latitudinal patterns in group composition due to the limited number of observations, we could suggest that the widely distributed *T. truncatus* associates change depending on their abundance. This assumption, however, needs further investigation since abundance estimates for offshore dolphins in this area are still not available. As we deal with very socially complex animals, we recognize that there is still plenty to be

investigated. This is just the first step towards a better understanding of dolphins' interspecific interactions in Brazilian waters and their ecological significance at an ecosystem level.

### Acknowledgments

We would like to thank all of the researchers and students from Federal University of Rio Grande (FURG), Instituto Aqualie, and other institutions who helped collect data during the eight research cruises. We also thank the crew of the *R/V Atlântico Sul* for all the logistical support and onboard activities, and Chevron Brasil Upstream Ltda., BG Group, and Cetacean Society International for financial support. We are especially grateful to E. Seyboth, three anonymous reviewers, and Dr. K. Biolsi for their constructive comments on earlier drafts of the manuscript. The National Council for Research and Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq Grant Number 407889/2013-2) of the Brazilian Ministry of Science, Technology, Innovation and Communication (MCTIC) provided a research fellowship to ERS (PQ 310597/2018-8) and a doctoral fellowship to RCL (PQ 140907/2018-1). The Coordination for the Improvement of Higher Education Personnel (CAPES) provided a post-doctoral research fellowship (88887.314453/2019-00 – PROANTAR) to GCT. The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) provided access to the Portal de Periódicos. This is a contribution of the Research Group “Ecologia e Conservação da Megafauna Marinha – EcoMega/CNPq.”

### Literature Cited

- Amaral, K. B., Alvares, D. J., Heinzmann, L., Borges-Martins, M., Siciliano, S., & Moreno, I. B. (2015). Ecological niche modeling of *Stenella* dolphins (Cetartiodactyla: Delphinidae) in the southwestern Atlantic Ocean. *Journal of Experimental Marine Biology and Ecology*, 472, 166-179. <https://doi.org/10.1016/j.jembe.2015.07.013>
- Bacon, C. E., Smultea, M. A., Fertl, D., Würsig, B., Burgess, E. A., & Hawks-Johnson, S. (2017). Mixed-species associations of marine mammals in the Southern California Bight, with emphasis on Risso's dolphins (*Grampus griseus*). *Aquatic Mammals*, 43(2), 177-184. <https://doi.org/10.1578/AM.43.2.2017.177>
- Ballance, L. T. (2009). Cetacean ecology. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 196-201). Academic Press. <https://doi.org/10.1016/B978-0-12-373553-9.00052-3>
- Ballance, L. T., & Pitman, R. L. (1998). Cetaceans of the western tropical Indian Ocean: Distribution, relative abundance, and comparisons with cetacean communities of

- two other tropical ecosystems. *Marine Mammal Science*, *14*, 429-459. <https://doi.org/10.1111/j.1748-7692.1998.tb00736.x>
- Balmer, B., Zolman, E., Rowles, T., Smith, C., Townsend, F., Fauquier, D., George, C., Goldstein, T., Hansen, L., Quigley, B., McFee, W., Morey, J., Rosel, P., Saliki, J., Speakman, T., & Schwacke, L. (2018). Ranging patterns, spatial overlap, and association with dolphin morbillivirus exposure in common bottlenose dolphins (*Tursiops truncatus*) along the Georgia, USA coast. *Ecology and Evolution*, *8*, 12890-12904. <https://doi.org/10.1002/ece3.4727>
- Baraff, L. S., & Asmutis-Silvia, R. A. (1998). Long-term association of an individual long-finned pilot whale and Atlantic white-sided dolphins. *Marine Mammal Science*, *14*, 155-161. <https://doi.org/10.1111/j.1748-7692.1998.tb00700.x>
- Bastida, R., Rodríguez, D., Secchi, E. R., & Silva, V. (2018). *Mamíferos acuáticos de Sudamérica y Antártida* [Marine mammals of South America and Antarctica]. Vázquez Mazzini Editores.
- Bérubé, M. (2009). Hybridism. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 588-592). Academic Press. <https://doi.org/10.1016/B978-0-12-373553-9.00137-1>
- Braga, E. S., Chiozzini, V. C., Berbel, G. B. B., Maluf, J. C. C., Aguiar, V. M. C., Charo, M., Molina, D., Romero, S. I., & Eichler, B. B. (2008). Nutrient distributions over the southwestern South Atlantic continental shelf from Mar del Plata (Argentina) to Itajaí (Brazil): Winter-summer aspects. *Continental Shelf Research*, *28*, 1649-1661. <https://doi.org/10.1016/j.csr.2007.06.018>
- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: Estimating abundance of biological populations*. Oxford University Press.
- Campos, E. J. D., Velhote, D., & Silveira, I. C. A. (2000). Shelf break upwelling driven by Brazil Current cyclonic meanders. *Geophysical Research Letters*, *27*, 751-754. <https://doi.org/10.1029/1999GL010502>
- Castello, J. P., & Möller, O. O. (1978). On the relationship between rainfall and shrimp production in the estuary of the Patos Lagoon (Rio Grande do Sul, Brazil). *Atlântica*, *3*, 67-74.
- Clua, E., & Grosvalet, F. (2001). Mixed-species feeding aggregation of dolphins, large tunas and seabirds in the Azores. *Aquatic Living Resources*, *14*, 11-18. [https://doi.org/10.1016/S0990-7440\(00\)01097-4](https://doi.org/10.1016/S0990-7440(00)01097-4)
- Cords, M., & Würsig, B. (2014). A mix of species: Associations of heterospecifics among primates and dolphins. In J. Yamagiwa & L. Karczmarski (Eds.), *Primates and cetaceans: Field research and conservation of complex mammalian societies* (pp. 409-431). Springer. [https://doi.org/10.1007/978-4-431-54523-1\\_21](https://doi.org/10.1007/978-4-431-54523-1_21)
- Côté, I. M., & Poulinb, R. (1995). Parasitism and group size in social animals: A meta-analysis. *Behavioural Ecology*, *6*, 159-165. <https://doi.org/10.1093/beheco/6.2.159>
- Crossman, C. A., Taylor, E. B., & Barrett-Lennard, L. G. (2016). Hybridization in the Cetacea: Widespread occurrence and associated morphological, behavioural, and ecological factors. *Ecology and Evolution*, *6*, 1293-1303. <https://doi.org/10.1002/ece3.1913>
- Di Tullio, J. C., Gandra, T. R. B., Zerbini, A. N., & Secchi, E. R. (2016). Diversity and distribution patterns of cetaceans in the subtropical southwestern Atlantic outer continental shelf and slope. *PLOS ONE*, *11*, e0155841. <https://doi.org/10.1371/journal.pone.0155841>
- Elliser, C. R., & Herzog, D. L. (2015). Long-term inter-species association patterns of Atlantic bottlenose dolphins, *Tursiops truncatus*, and Atlantic spotted dolphins, *Stenella frontalis*, in the Bahamas. *Marine Mammal Science*, *32*, 38-56. <https://doi.org/10.1111/mms.12242>
- Fox, J., & Weisberg, S. (2016). *Companion to applied regression*. <https://r-forge.r-project.org/projects/car>
- Frantzis, A., & Herzog, D. L. (2002). Mixed-species associations of striped dolphins (*Stenella coeruleoalba*), short-beaked common dolphins (*Delphinus delphis*), and Risso's dolphins (*Grampus griseus*) in the Gulf of Corinth (Greece, Mediterranean Sea). *Aquatic Mammals*, *28*(2), 188-197.
- García-Tiscar, S., Knouse, D., Sagarminaga, R., & Cañadas, A. (2000). An insight on the biological significance of mixed groups of common dolphins (*Delphinus delphis*) and striped dolphins (*Stenella coeruleoalba*) in the Alboran Sea. *European Research on Cetaceans*, *14*, 135-137.
- Herzog, D. L., & Johnson, C. M. (1997). Interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas, 1985-1995. *Aquatic Mammals*, *23*(2), 85-99.
- Herzog, D. L., Moewe, K., & Brunnick, B. J. (2003). Interspecific interactions between Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*, on Great Bahama Bank, Bahamas. *Aquatic Mammals*, *29*(3), 335-341.
- Hodgins, N. K., Dolman, S. J., & Weir, S. J. (2014). Potential hybridism between free-ranging Risso's dolphins (*Grampus griseus*) and bottlenose dolphins (*Tursiops truncatus*) off north-east Lewis (Hebrides, UK). *Marine Biodiversity Records*, *7*, 1-7. <https://doi.org/10.1017/S175526721400089X>
- Kiszka, J., Perrin, W. F., Pusineri, C., & Ridoux, V. (2011). What drives island-associated tropical dolphins to form mixed-species associations in the southwest Indian Ocean? *Journal of Mammalogy*, *92*(5), 1105-1111. <https://doi.org/10.1644/10-MAMM-A-376.1>
- Knoppers, B., Souza, W. F. L., Ekau, W., Figueiredo, A. G., & Soares-Gomes, A. (2010). Interface Terra-Mar do Brasil [Land-sea interface of Brazil]. In R. C. Pereira & A. Soares-Gomes (Eds.), *Biologia marinha* [Marine biology] (pp. 529-552). Editora Interciência.
- LeDuc, R. (2009). Distribution. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 298-302). Academic Press.
- Mahiques, M. M., Tessler, M. G., Ciotti, A. M., Silveira, I. C. A., Sousa, S. H. M., Figueira, R. C. L., Tassinari,



- C. C. G., Furtado, V. V., & Passos, R. F. (2004). Hydrodynamically driven patterns of recent sedimentation in the shelf and upper slope off southeast Brazil. *Continental Shelf Research*, 24, 1685-1697. <https://doi.org/10.1016/j.csr.2004.05.013>
- Matsuura, Y. (1986). Contribuição ao estudo da estrutura oceanográfica da região sudeste entre Cabo Frio (RJ) e Cabo de Santa Marta Grande (SC) [Contribution to the study of the oceanographic structure of the southeast region between Cabo Frio (RJ) and Cabo de Santa Marta Grande (SC)]. *Ciência e Cultura*, 38, 1439-1450.
- Maze-Foley, K., & Mullin, K. D. (2006). Cetaceans of the oceanic northern Gulf of Mexico: Distributions, group sizes and interspecific associations. *Journal of Cetacean Research and Management*, 8, 203-213.
- Melillo, K. E., Dudzinski, K. M., & Cornick, L. A. (2009). Interactions between Atlantic spotted (*Stenella frontalis*) and bottlenose (*Tursiops truncatus*) dolphins off Bimini, The Bahamas, 2003-2007. *Aquatic Mammals*, 35(2), 281-291. <https://doi.org/10.1578/am.35.2.2009.281>
- Möller, O. O., Piola, A. R., Freitas, A. C., & Campos, E. J. D. (2008). The effects of river discharge and seasonal winds on the shelf off southeastern South America. *Continental Shelf Research*, 28, 1607-1624. <https://doi.org/10.1016/j.csr.2008.03.012>
- Monteiro-Filho, E. L. A., Bonin, C. A., & Rautenberg, M. (1999). Interações interespecíficas dos mamíferos marinhos na região da Baía de Guaratuba, litoral sul do Estado do Paraná [Interspecific interactions among marine mammals of the Guaratuba Bay region, southern coast of Paraná Estate]. *Biotemas*, 12, 119-132.
- Moreno, I. B., Zerbini, A. N., Danilewicz, D., Santos, M. C. O., Simões-Lopes, P. C., Lailson-Brito, J., Jr., & Azevedo, A. F. (2005). Distribution and habitat characteristics of dolphins of the genus *Stenella* (Cetacea: Delphinidae) in the southwest Atlantic Ocean. *Marine Ecology Progress Series*, 300, 229-240. <https://doi.org/10.3354/meps300229>
- Morris, S. E., Zelnor, J. L., Fauquier, D. A., Rowles, T. K., Rosel, P. E., Gulland, F., & Grenfell, B. T. (2015). Partially observed epidemics in wildlife hosts: Modelling an outbreak of dolphin morbillivirus in the northwestern Atlantic, June 2013-2014. *Journal of the Royal Society Interface*, 12, 20150676. <https://doi.org/10.1098/rsif.2015.0676>
- Müelbert, J. H., Acha, M., Mianzan, H., Guerrero, R. A., Reta, R., Braga, E. S., Garcia, V. M. T., Berasategui, A., Gomez-Erache, M., & Ramirez, F. (2008). Biological, physical and chemical properties at the Subtropical Shelf Front Zone in the SW Atlantic Continental Shelf. *Continental Shelf Research*, 28, 1662-1673. <https://doi.org/10.1016/j.csr.2007.08.011>
- Norris, K. S., & Dohl, T. P. (1980). The structure and functions of cetacean schools. In L. M. Herman (Ed.), *Cetacean behaviour: Mechanisms and functions* (pp. 211-261). Wiley-Interscience.
- O'Callaghan, T. M., & Baker, C. S. (2002). *Summer cetacean community, with particular reference to Bryde's whales, in the Hauraki Gulf, New Zealand*. Department of Conservation.
- Perrin, W. F. (2009a). Pantropical spotted dolphin *Stenella attenuata*. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 819-821). Academic Press. <https://doi.org/10.1016/B978-0-12-373553-9.00192-9>
- Perrin, W. F. (2009b). Spinner dolphin *Stenella longirostris*. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 1100-1103). Academic Press. <https://doi.org/10.1016/B978-0-12-373553-9.00251-0>
- Piola, A. R., Möller, O. O., Jr., Guerrero, R. A., & Campos, E. J. D. (2008). Variability of the subtropical shelf front off eastern South America: Winter 2003 and summer 2004. *Continental Shelf Research*, 28, 1639-1648. <https://doi.org/10.1016/j.csr.2008.03.013>
- Powell, G. V. N. (1985). Sociobiology and adaptive significance of interspecific foraging flocks in the neotropics. *Ornithological Monographs*, 36, 713-732. <https://doi.org/10.2307/40168313>
- Quérouil, S., Silva, M. A., Cascão, I., Magalhães, S., Seabra, M. I., Machete, M. A., & Santos, R. S. (2008). Why do dolphins form mixed-species associations in the Azores? *Ethology*, 114, 1183-1194.
- R Development Core Team. (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Ripley, B., Venables, B., Bates, D. M., Hornik, H., Gebhardt, A., & Firth, D. (2015). *Support functions and datasets for Venables and Ripley's MASS*. <https://r-forge.r-project.org/projects/car>
- Roch, M. A., Stinner-Sloan, J., Baumann-Pickering, S., & Wiggins, S. M. (2015). Compensating for the effects of site and equipment variation on delphinid species identification from their echolocation clicks. *The Journal of the Acoustical Society of America*, 137, 22-29. <https://doi.org/10.1121/1.4904507>
- Rossi-Santos, M. R., Neto, E. S., & Baracho, C. G. (2009). Interspecific cetacean interactions during the breeding season of humpback whales (*Megaptera novaeangliae*) on the north coast of Bahia State, Brazil. *Journal of the Marine Biological Association of the United Kingdom*, 89, 961-966. <https://doi.org/10.1017/S0025315409000897>
- Santos, M. C. O., Rosso, S., Santos, R. A., Lucato, S. H. B., & Bassoi, M. (2002). Insights on small cetacean feeding habits in southeastern Brazil. *Aquatic Mammals*, 28(1), 38-45.
- Santos, R. A., & Haimovici, M. (2001). Cephalopods in the diet of marine mammals stranded or incidentally caught along southeastern and southern Brazil (21-34°). *Fisheries Research*, 52, 99-112. [https://doi.org/10.1016/S0165-7836\(01\)00234-X](https://doi.org/10.1016/S0165-7836(01)00234-X)
- Scott, M. D., & Cattanch, K. L. (1998). Diel patterns in aggregations of pelagic dolphins and tunas in the eastern Pacific. *Marine Mammal Science*, 14, 401-428. <https://doi.org/10.1111/j.1748-7692.1998.tb00735.x>

- Secchi, E. R., & Vaske, T., Jr. (1998). Killer whale, *Orcinus orca*, sightings and depredation on tuna and swordfish longline catches in southern Brazil. *Aquatic Mammals*, 24(2), 117-122.
- Silveira, I. C. A., Schmidt, A. C. K., Campos, E. J. D., Godoi, S. S., & Ikeda, Y. (2000). The Brazil Current off the eastern Brazilian Coast. *Revista Brasileira de Oceanografia*, 48, 171-183. <https://doi.org/10.1590/S1413-77392000000200008>
- Stensland, E., Angerbjorn, A., & Berggren, P. (2003). Mixed species groups in mammals. *Mammal Review*, 33, 205-223. <https://doi.org/10.1046/j.1365-2907.2003.00022.x>
- Svendsen, G. M., Romero, M. A., Williams, G. N., Gagliardini, D. A., Crespo, E. A., Dans, S. L., & González, A. (2016). Environmental niche overlap between common and dusky dolphins in North Patagonia, Argentina. *PLOS ONE*, 10, e0126182. <https://doi.org/10.1371/journal.pone.0126182>
- Tavares, M., Moreno, I. B., Siciliano, S., Rodríguez, D., Santos, M. C. O., Lailson-Brito, J., Jr., & Fabián, M. E. (2010). Biogeography of common dolphins (genus *Delphinus*) in the southwestern Atlantic Ocean. *Mammal Review*, 40, 40-64. <https://doi.org/10.1111/j.1365-2907.2009.00154.x>
- Terborgh, J. (1990). Mixed flocks and polyspecific associations: Costs and benefits of mixed groups to birds and monkeys. *American Journal of Primatology*, 21, 87-100. <https://doi.org/10.1002/ajp.1350210203>
- Troina, G. C., Botta, S., Dehairs, F., Di Tullio, J. C., Elskens, M., & Secchi, E. R. (2020). Skin  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  reveal spatial and temporal patterns of habitat and resource use by free-ranging odontocetes from the southwestern Atlantic Ocean. *Marine Biology*, 167, 186. <https://doi.org/10.1007/s00227-020-03805-8>
- Weir, C. R., Pollock, C., Cronin, C., & Taylor, S. (2001). Cetaceans of the Atlantic frontier north and west of Scotland. *Continental Shelf Research*, 21, 1047-1071. [https://doi.org/10.1016/S0278-4343\(00\)00124-2](https://doi.org/10.1016/S0278-4343(00)00124-2)
- Weller, D. W., Würsig, B., Whitehead, H., Norris, J. C., Lynn, S. K., Davis, R. W., Clauss, N., & Brown, P. (1996). Observations of an interaction between sperm whales and short-finned pilot whales in the Gulf of Mexico. *Marine Mammal Science*, 12, 588-594.
- Wells, R. S., & Scott, M. D. (2009). Common bottlenose dolphin (*Tursiops truncatus*). In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 249-255). Academic Press. <https://doi.org/10.1016/B978-0-12-373553-9.00062-6>
- Zaeschmar, J. R., Visser, I. N., Fertl, D., Dwyer, S. L., Meissner, A. M., Halliday, J., Berghan, J., Donnelly, D., & Stockin, K. A. (2014). Occurrence of false killer whales (*Pseudorca crassidens*) and their association with common bottlenose dolphins (*Tursiops truncatus*) off northeastern New Zealand. *Marine Mammal Science*, 30(2), 594-608. <https://doi.org/10.1111/mms.12065>
- Zerbini, A. N., Secchi, E. R., Bassoi, M., Dalla Rosa, L., Higa, A., de Sousa, L., Moreno, I. B., Möller, L. M., & Caon, G. (2004). Distribuição e abundância relativa de cetáceos na Zona Econômica Exclusiva da região sudeste-sul do Brasil [Distribution and relative abundance of cetaceans in the Exclusive Economic Zone of the southeast region—south of Brazil]. *Série de Documentos Revizee-Score Sul*. Instituto Oceanográfico da USP. 40 pp.