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Intertidal habitat use of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Argentina

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*Very little information is available on bottlenose dolphin (*Tursiops truncatus*) habitat use in the South-western Atlantic. It is, however, essential in understanding their ecology and to improve conservation management. In this study, habitat use of bottlenose dolphins was examined in Bahía San Antonio, an area frequented by the species. Given the large tidal amplitude and extended intertidal zone in this bay, special focus was given to the intertidal* vs *subtidal habitat use patterns. Bottlenose dolphins were observed in only half of the surveyed area, with on average 1 dolphin group encountered per 100 km surveyed. All dolphin groups were seen in shallow waters <10 m deep. GLM analyses showed that especially during high tide, depth had an important effect on the dolphin encounter rate, with most dolphin groups encountered in the intertidal zone. While in the intertidal zone, most dolphin groups were observed to be engaged in surface feeding activities. The presented data indicate dolphins remained in shallow waters, and moved to the intertidal zone during high tide where they appear to find feeding opportunities. This information is believed to be of high value in understanding this population's ecological needs, and essential when aiming to improve marine conservation efforts at times of increased anthropogenic pressures in the area.*

Keywords: bottlenose dolphin, coastal habitat, environmental variables, habitat use, intertidal zone

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INTRODUCTION

Cetaceans, including bottlenose dolphins (*Tursiops truncatus*), live in complex habitats with a dynamic regime of physical and chemical properties (Bräger *et al.*, 2003). The relationship between coastal bottlenose dolphins and their habitat differs largely among regions. Some coastal populations were shown to perform seasonal movements from deeper channels to shallow waters (e.g. Waples, 1995), whereas others indicated preferences for estuarine habitats (e.g. Shane, 1990; Ballance, 1992; Hanson & Defran, 1993; Scott *et al.*, 1996). Other studies indicated a high correlation between dolphin occurrence and water depth, often with a preference for shallow waters (e.g. Cañadas *et al.*, 2002; Bearzi, 2005; Blasi & Boitani, 2012). An increased use of steep slopes has also been documented, suggested to facilitate the dolphins' feeding activities (Ingram & Rogan, 2002; Cañadas *et al.*, 2005). Overall, most studies indicated habitat use of bottlenose dolphins is mainly driven by prey distribution and abundance, sometimes in combination with predation risk (e.g. Shane, 1990; Ballance, 1992; Hanson & Defran, 1993; Waples, 1995; Scott *et al.*, 1996).

To date, only one study has assessed bottlenose dolphin habitat use in Argentina (Würsig & Würsig, 1979). According to the authors, bottlenose dolphin movements in Golfo San José were related to the tide. Dolphins seemed to stay in shallower water as the tide retreated, until they needed to go to deeper waters when the tide was too low. Another community of bottlenose dolphins is known to range further up north, with a core area in Bahía San Antonio (BSA) (Vermeulen & Cammareri, 2009; Vermeulen *et al.*, 2016). This population was reported to be small and declining (Vermeulen & Bräger, 2015).

In general, BSA is of great ecological value due to its high biodiversity, not only harbouring a community of resident bottlenose dolphins (Vermeulen *et al.*, 2016) but also being an important spawning and nursing area for many fish species (Perier, 1994), and one of the most important resting and feeding sites of the South-western Atlantic Ocean for several migratory bird species (González *et al.*, 1996). However, although the area was declared a 'Natural Reserve' in Argentina by provincial law 2670 of June 1993, the area is still designated for 'multiple use' and includes one of the largest ports of Argentina, a chemical plant producing sodium carbonate, as well as artisanal and recreational fishing activities, and whale- and dolphin-watching activities (Giaccardi & Reyes, 2012). Additionally, BSA is the most important touristic destination along the coast of North-east Patagonia, with three expanding towns under the municipality of San Antonio: (1) San Antonio Oeste, (2) San Antonio Este and (3) Las Grutas.

In general, various authors have stated that the rapid demographic and industrial growth along the Patagonian coast is resulting in increased pressures on the natural resources (Peralta, 1998; Boltovskoy, 2009; González &

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Benseny, 2013). In view of this, the present study aims to investigate the habitat use patterns of the local declining bottlenose dolphin population in BSA. As the area is known for its large tidal amplitude and extended intertidal zone, special focus was placed on the dolphins' intertidal *vs* subtidal habitat use. The information presented here is believed to be highly valuable for understanding the ecological needs of this population of dolphins, and essential for improved conservation management in the area in times of increased coastal urban and industrial developments.

MATERIALS AND METHODS

Study area

The study area, Bahía San Antonio (BSA, 40°45′S 64°54′W; Figure 1) is a shallow bay with a length of 20 km in the east–west direction, a width of 10 km north–south, an average depth of 6 m and a maximum depth not exceeding 30 m (SHN, 2000). With a surface area of ~655 km², the bay is known for its large tidal differences (Perier, 1994; SHN, 2000). The tidal regime is semidiurnal and the tidal amplitude varies between 6.5 m at neap and 9.3 m at spring tide (average ± 8.3 m), leaving up to 86% of the total surface of the bay exposed during low tide (Perier, 1994; SHN, 2000). The region is characterized by different types of intertidal habitat, with sandy beaches and rocky flats (up to 800 m wide) covering the majority of the area (González *et al.*, 1996).

Fieldwork

Between August 2008 and December 2011, boat-based surveys were conducted from a small outboard-powered inflatable boat. All survey effort was restricted to calm seas of Beaufort state ≤3, periods of no precipitation and good visibility. During each survey, the boat was maintained at a steady speed of 4–5 knots. This slow speed was possible due to the environmental conditions in the area (lack of a large swell, often flat sea conditions) and the relatively small size of the study area; i.e. it improved the chances to spot dolphins while having enough time to sample large portions of the study area. During the surveys, the same 2–3 observers maintained a continuous visual search for dolphins. Due to logistical limitations, the course of the survey could not be standardized; the area was surveyed non-systematically until a dolphin group was found. Effort was logged using the automatic tracking system of a hand-held Geographical Positioning System (GPS) Garmin Etrex and GPSmap 62s.

Once a bottlenose dolphin group was encountered, the speed of the vessel was changed to match the pace of the group. A bottlenose dolphin group was defined as a collection of dolphins within a 100 m radius of each other that operated in a coordinated way (Lusseau *et al.*, 2003), interacting or engaged in similar activities (Irvine *et al.*, 1981; Wells *et al.*, 1987; Wilson, 1995; Connor *et al.*, 2000; Lusseau *et al.*, 2006). Once a bottlenose dolphin group was encountered, group composition was determined; groups were classified as either 'groups with calves' or 'groups without calves'. Calves were defined as being up to 2/3 the length of an adult, with or without foetal folds (Mann & Smuts, 1999) and commonly swimming in close association with an adult (Shane, 1990). A dolphin group was followed until it was out of sight. When a dolphin group split up, a sub-group was arbitrarily chosen and followed based on a variety of factors such as e.g. direction of travel, weather conditions, presence of interesting individuals (e.g. a newborn calf), etc.

Data on the behaviour of dolphin groups were gathered using a focal group 5-min point sampling mode (Altmann, 1974; Mann, 1999). For each sample, the predominant activity of the majority of the group (>50%) was recorded. The behavioural categories used are summarized in Table 1. Along with behavioural data, *in situ* GPS positions and depths (when an echo-sounder was available) were recorded every 5 min in the presence of dolphins using a hand-held GPS Garmin Etrex and GPSmap 62s, and the vessel's echo-sounder respectively.

Analyses

ESRI ArcGIS version 10.1 was used to subdivide the study area into grid cells of 1 km² (1 km × 1 km). Due to the relative homogeneity in the area this was believed to give sufficient detail for this study. Cells with a total survey effort lower than a cell's diagonal (1414 m) were excluded from analysis.

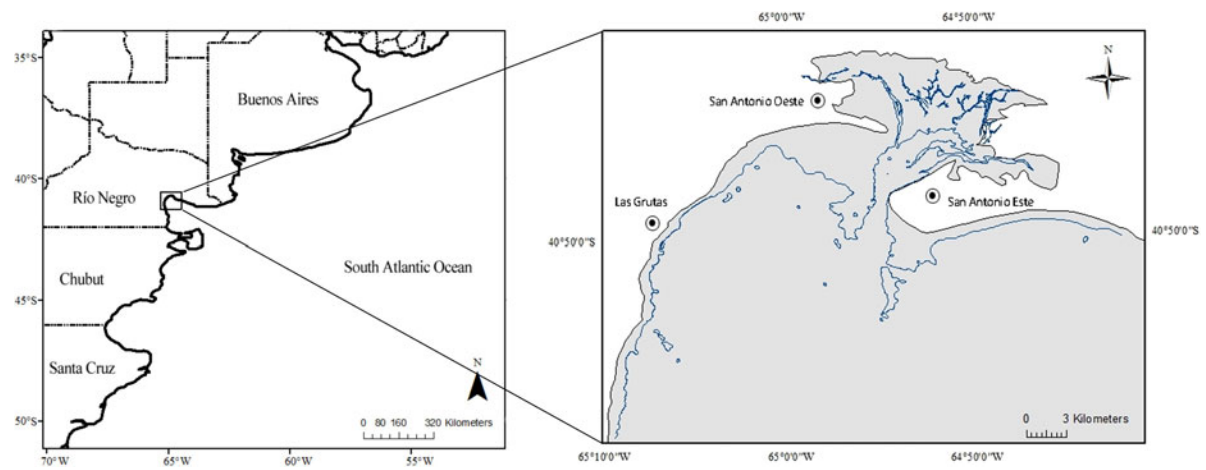

Fig. 1. Left: Map of Argentina indicating the location of the study area, Bahía San Antonio (BSA). Provinces are also indicated. Right: Map of BSA indicating the three urbanized areas. Contour line of the bay indicates the shoreline at high tide, the isobath indicates the shoreline at low tide.

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Table 1. Definitions of behavioural categories used in this study (adapted from Shane, 1990; Bearzi *et al.*, 1999; Bearzi, 2005).

Travel	**Moving steadily in one direction**
Surface-feeding	Feeding activities performed close to water surface, typical fast moving in circles at the surface. Fish are seen to jump out of the water (birds concentrating over the dolphins). No physical contact between individuals can be observed
Diving	Tail-out dives longer than 30 s occurring during the 5 min sample. The 30 s cut off was chosen as it was longer than the mean dive duration of 21.8 s measured for coastal bottlenose dolphins in Argentine waters (Würsig, 1978). No horizontal movements, direction of surfacing irregular. Typically followed by two/three breaths after which the next dive commences
Socializing	Group members are in frequent physical contact, no steady directional movement, displaying surface behaviours (e.g. rolling over each other, jumping towards each other). Playful behaviour, defined as any activity involving a foreign object e.g. kelp tossing was included in this category (Shane *et al.*, 1986)
Milling	Moving in varying directions in one general location, no surface behaviours, no physical contact can be observed
Resting	Lying motionless at the surface
Not classified	When none of the above categories could be assigned correctly

WGS 1984 UTM zone 20S was used as the projected coordinate system.

Subsequently, each cell was attributed a value of three environmental variables: depth, slope and substrate. The mean depth (hereafter *MD*) and substrate type were extracted from an electronic bathymetric chart obtained from the Naval Hydrographical Service of Argentina.

(1) *Depth*: The *MD* value for each cell was obtained by averaging the *MD* values marked on the chart within each cell (Cañadas *et al.*, 2002). The *MD* value reflects a depth range ± 4.15 m depending on tide (considering the mean tidal amplitude of 8.3 m in the study area). Therefore, the intertidal zone was defined as all cells with a $MD < 4$ m, whereas cells with $MD \geq 4$ m were defined as the subtidal zone. Additionally, exact depth measurements recorded in the field were analysed to assess exact depths at which dolphins were encountered. Due to logistical limitations this could only be done for 41 dolphin groups. In order to check for the reliability of *MD* data, a Pearson's correlation coefficient was calculated between *MD* and the measured depth values in the corresponding grid cells.
(2) *Slope*: Slope, expressed in degrees, was calculated as $(D_{max} - D_{min})/\mathrm{DI}$ where D_{max} is the maximum depth of the cell, D_{min} is the minimum depth of the cell and DI the distance between the points of maximum and minimum depth of the cell (Cañadas *et al.*, 2002; Garaffo *et al.*, 2007).
(3) *Substrate*: Substrate type (sand, rocky flats, gravel or shells) was attributed to each cell according to the substrate most commonly found in each cell.

To test whether variables in the cells were spatially autocorrelated, and thus not independent, Moran's I index was calculated for the encounter rate of dolphin groups using the Spatial Statistics Tool in ArcGIS. To correct for the potential bias of non-systematic surveys, an encounter rate of dolphin groups was calculated as n/L where n is the number of dolphin groups encountered in each grid cell (i.e. first sighting of each dolphin group) and L the total number of kilometres spent on effort in each cell (Bearzi, 2005; Bearzi *et al.*, 2008). To investigate any temporal variation in the encounter rate, Kruskal–Wallis and Mann–Whitney *U* tests were used to test for differences between survey years, seasons and tidal state. For analysis, each survey year was divided into four seasons: summer (January–March), autumn (April–June), winter (July–September), spring (October–December). High tide was defined as a 3 h period including the hour of high tide plus the hour prior and subsequent to it. Accordingly the other tidal phases were defined as follows: low tide is the hour of low tide and the hour prior and subsequent, ebb tide is a 3 h time period between high and low tide and flood tide is a 3 h time period between low and high tide.

The influence of the environmental variables *MD*, slope and substrate on the encounter rate of dolphin groups was investigated using a Generalized Linear Model (GLM) in the program R (R core team, 2016). The number of dolphin groups encountered in each grid cell was set as the response variable with effort in each grid cell (number of km surveyed) as an offset. Given the characteristics of the response variable (counts of dolphin groups), the Poisson distribution and the log-link function were used. Stepwise model selection was performed and the AIC (Akaike Information Criterion) was used as a selection criterion for the best model. A quasi-Poisson GLM model was used to check for over-dispersion of the data (dispersion parameter $\phi > 1$), whereas model validation was achieved by examining the plotted scaled Pearson residuals, and examining the mean-variance relationship and (non-)independence of model residuals.

Considering the large tidal amplitude in the study area, a second GLM was used to investigate the influence of the environmental variables *MD*, slope and substrate on the encounter rate of dolphin groups only during high tide (as it was the only time when both intertidal and subtidal zones were simultaneously available). For this, the number of dolphin groups encountered during high tide was set as the response variable with effort during high tide (number of km surveyed during high tide) as an offset. Model construction, selection and validation was done in the same way as described above.

Further analysis was conducted to verify if the environmental variables (*MD*, slope and substrate) varied with group composition (groups with calves *vs* groups without calves) and behaviour. To account for non-independence of 5-min behavioural samples, only the first behavioural sample of each group was used in analysis. Kruskal–Wallis and Mann–Whitney *U* tests were employed to assess whether different group compositions and behaviours were observed in areas with different *MD* and slopes. A χ^2

Table 2. Hours of boat-based survey effort over the different seasons.

	Summer	Autumn	Winter	Spring
2008	–	–	30.9	52.6
2009	67.3	40.3	36.8	17.6
2010	31.0	14.0	143.1	21.8
2011	77.9	32.6	19.6	–
Total	176	87	230	92

of independence was used to test whether different group compositions and behaviours were observed in areas with different types of substrate. In order to investigate the difference in behaviour observed in the intertidal *vs* subtidal zone, a contingency table was created for the initial behaviour observed for each dolphin group, considering only those groups observed during high tide (when both intertidal and subtidal areas were available simultaneously). A Pearson's χ^2 test was then used as the test statistic.

RESULTS

Effort

A total of 129 non-systematic boat-based surveys were conducted between 2008 and 2011, resulting in 586 h of survey effort during which 155 dolphin groups (DG) were observed (Table 2).

In total, 245 grid cells were used in analysis (or 233 km^2 excluding surface of grids overlapping land; Figure 2A). Of these grid cells, 102 were located in the intertidal zone whereas the other 143 were located in the subtidal region.

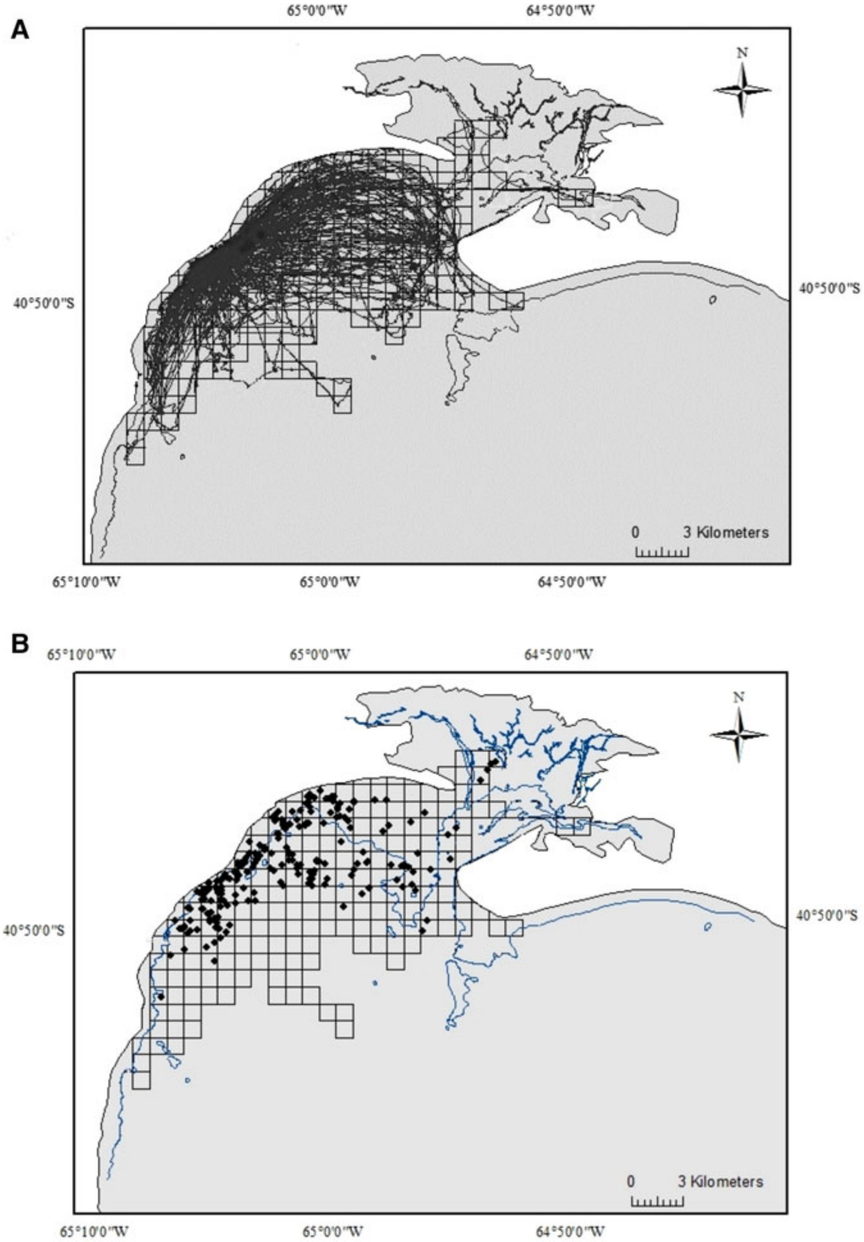

Fig. 2. (A) Survey effort tracks in Bahía San Antonio, indicating the 245 grid cells covered. (B) Geographic positions of initial sightings of 155 bottlenose dolphin groups within 66 of the surveyed grid cells. Contour line delineates the intertidal area.

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Table 3. The number of grid cells covered by the survey effort and dolphin groups (DG) encounters.

	Total # grid cells	# grid cells intertidal zone	# grid cells subtidal zone
Total effort	245	102	143
DG encounters	66	21	45
Effort high tide	175	72	103
DG encounters high tide	13	10	3

Bottlenose dolphin groups were initially sighted in 66 of these grid cells (Figure 2B) and were followed over a total of 127 grid cells or 121 km^2 (51% of surveyed area). Of these 66 grid cells, 21 were in the intertidal zone whereas the other 45 were located in the subtidal zone.

Survey effort during high tide only (61 surveys) covered a total of 175 grid cells, of which 72 and 103 were located in the intertidal and subtidal zone respectively. During these surveys, 28 dolphin groups were encountered in 13 grid cells, of which 10 were located in the intertidal zone and 3 in the subtidal region. Table 3 provides an overview.

Encounter rate

The median encounter rate was 0.02 or two dolphin groups encountered every 100 km surveyed (average = 0.01; quantile values Q1 = 1.3; Q3 = 2.8). Moran's I index calculated for the encounter rates was not significantly different from zero ($z = 0.12$; $P > 0.05$) indicating that cells were not spatially auto-correlated. No significant variations in encounter rate were found across the different study years (H = 3.2, $P = 0.36$), seasons (H = 4.13; $P = 0.24$) or tidal states (H = 0.46, $P = 0.93$).

Data were not over-dispersed (dispersion parameter $\phi = 0.54$). The best fitting model of the Poisson GLM analysis indicated an importance of the variable substrate on the overall dolphin encounter rate (Table 4A). As such, dolphins were encountered more often over sandy substrates. However, AIC values did not differ greatly when removing all variables from the model, suggesting a relatively low influence of any environmental variable on the overall dolphin encounter rate. On the other hand, the GLM analysis of the data collected during high tide showed an importance of *MD* on the dolphin encounter rate (Table 4B). As such, models excluding *MD* had substantially larger AIC values. Model validation was performed in both GLM analyses and indicated the models were deemed appropriate.

Investigating further the relation between encounter rates and the *MD*, it was notable that overall encounter rates dropped substantially at $MD > 9$ m deep, equalling 0 at $MD \geq 13$ m deep (Figure 3A). During high tide, encounter rate were significantly higher in the intertidal zone ($MD < 4$ m deep) than in the subtidal region ($MD \geq 4$ m deep; Figure 3B; $U = 1548$, $P < 0.01$). Accordingly, specific depth values measured in the field in the presence of dolphins (N = 41 groups) never exceeded 10 m (median depth = 5.8 m; quantile values Q1 = 4.1 m; Q3 = 7.2 m; range: 0.8 to 10 m). These measured depth values were positively correlated to the *MD* of the corresponding grid cells ($r^2 = 0.51$, $P < 0.01$) indicating the reliability of *MD* values. Slope and *MD* were weakly correlated in the grid cells ($r^2 = 0.25$, $P < 0.05$).

Group composition and behaviour

In total, 61% of the encountered groups contained calves (N = 95 groups). No significant variation could be found in the environmental variables of where these groups were encountered, when compared with groups without calves (*MD* $U = 3800$, $P = 0.73$; slope $U = 3622$, $P = 0.44$; substrate $\chi^2 = 0.28$, $P = 0.96$). Similarly, depth values measured in the field did not vary between groups with calves (N = 27) and groups without calves (N = 14; $U = 1.31$, $P = 0.19$).

Table 4. Ranked Generalized Linear Models assessing the relationship between the environmental variables *MD*, slope and substrate on the encounter rate of dolphin groups (DG)

A				
Total	***df***	**AICc**	**ΔAIC**	**Weight**
DG ~ substrate + offset (log(effort))	3	244.2	0.00	0.32
DG ~ offset (log(effort))	1	245.1	0.89	0.20
DG ~ MD + substrate + offset (log(effort))	4	245.8	1.62	0.14
DG ~ slope + substrate + offset (log(effort))	4	246.3	2.09	0.11
DG ~ slope + offset (log(effort))	2	247.1	2.88	0.08
DG ~ MD + offset (log(effort))	2	247.1	2.91	0.07
DG ~ MD + slope + substrate + offset (log(Effort))	5	248.0	3.74	0.05
DG ~ MD + slope + offset (log(effort))	2	249.1	4.93	0.03
B				
High tide	*df*	AICc	ΔAIC	Weight
DG ~ MD + offset(log(effort))	2	85.0	0.00	0.57
DG ~ MD + slope + offset(log(effort))	3	86.9	1.88	0.22
DG ~ MD + substrate + offset(log(effort))	4	87.8	2.80	0.14
DG ~ MD + slope + substrate + offset(log(Effort))	5	90.2	5.15	0.04
DG ~ slope + offset(log(effort))	2	99.2	14.17	0.00
DG ~ slope + substrate + offset(log(effort))	4	103.1	18.10	0.00
DG ~ substrate + offset(log(effort))	3	103.5	18.43	0.00

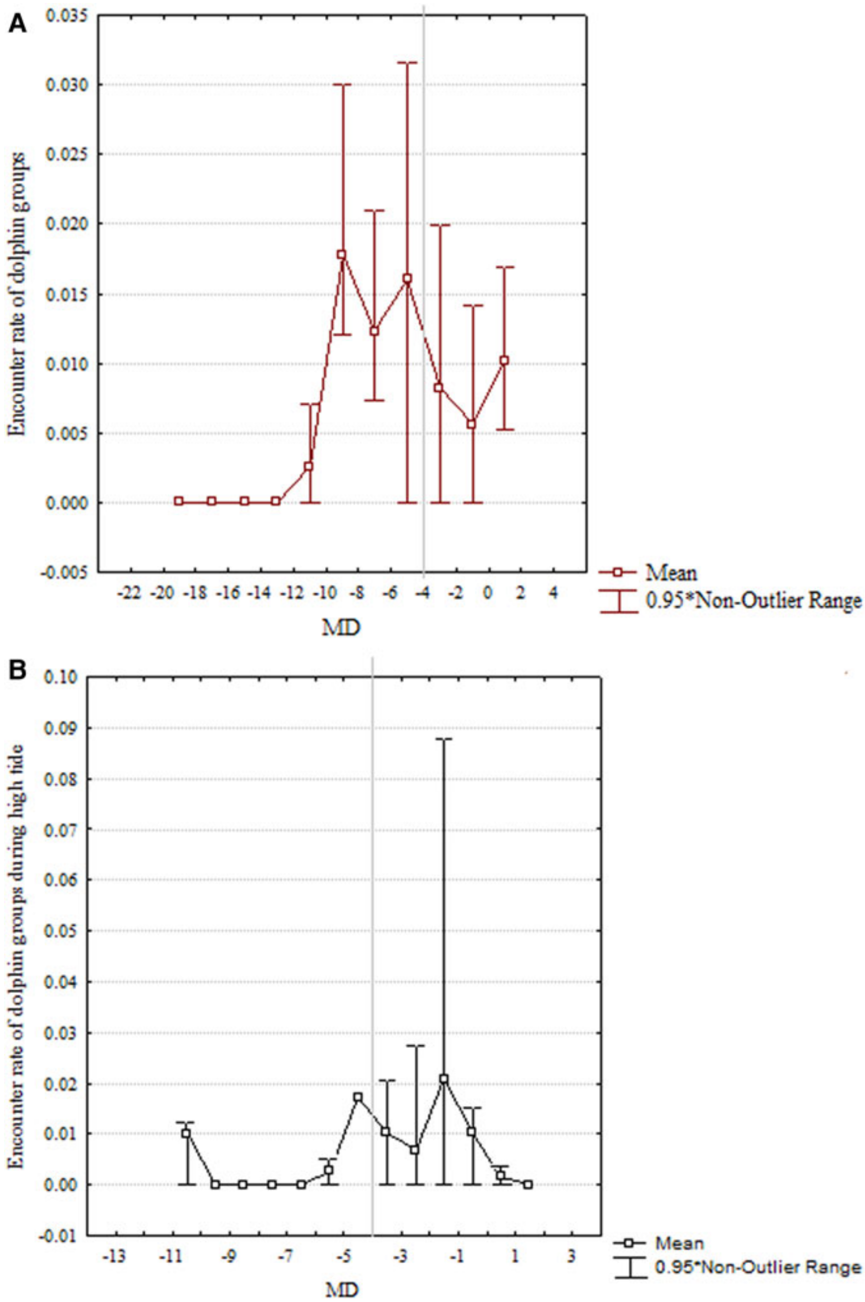

Fig. 3. Variation in encounter rate of dolphin groups according to the *MD* of surveyed cells. The line indicates the transition from intertidal to subtidal zone. (A) In general, (B) During high tide.

However, depth changed significantly with the behaviour of dolphins (*MD*: $H = 26.3$, $P < 0.01$; measured depths: $H = 61.9$, $P < 0.01$; Figure 4). Additional Mann–Whitney *U* tests showed that diving, feeding and travelling behaviour occurred in deeper areas, whereas resting, milling and socializing were observed in significantly shallower regions.

Diving occurred over steeper slopes than all other behaviours ($H = 17.6$, $P < 0.01$). There was no significant variation in substrate for the different behaviours ($\chi^2 = 17.3$, $P = 0.50$). During high tide, most dolphins groups encountered in the intertidal zone were surface feeding, whereas in the subtidal region most were diving ($\chi^2 = 14.4$, $P < 0.05$; Figure 5).

DISCUSSION

Due to the large tidal amplitude and the extended intertidal habitat in the study area, the region offers an ideal scenario to study the use of intertidal habitat by bottlenose dolphins. However, although data were carefully selected to account for possible bias, data were collected during a photo-identification study and therefore may have limitations. Results should therefore be interpreted with care.

Overall, bottlenose dolphins were observed in only half of the surveyed area, and remained in relatively shallow waters. During high tide, depth appeared to be an important factor affecting the dolphins' habitat use patterns. As such, when the intertidal zone was immersed during high tide, dolphins

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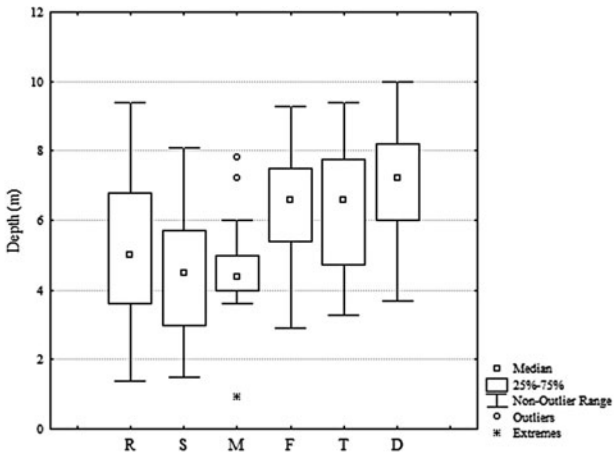

Fig. 4. Depth values measured in the field (N = 41 dolphin groups) for different behavioural states: R, resting; S, socializing; M, milling; F, surface feeding; T, travel; D, diving.

clearly moved to this area. The only other study conducted in Argentina on the topic indicated similar movements of bottlenose dolphins related to the tide (Würsig & Würsig, 1979). In general, tidal flow is known to affect short-term movement in coastal bottlenose dolphins (e.g. Irvine & Wells, 1972; Shane *et al.*, 1986; Shane, 1990; Acevedo, 1991; Hanson & Defran, 1993; Chilvers *et al.*, 2003). As such, the species is commonly present in very shallow waters (e.g. Würsig & Würsig, 1979; Leatherwood & Reeves, 1983; dos Santos & Lacerda, 1987; Ballance, 1992; Wilson *et al.*, 1997; Defran & Weller, 1999; Ingram & Rogan, 2002). This has often been related to a trade-off between food availability and predation risk (Heithaus & Dill, 2002). Predation risk was reported to be low in the study area (Vermeulen & Bräger, 2015). Therefore food availability is hypothesized to be one of the main driving factors behind the observed use of the intertidal zone, an idea supported by the large number of dolphin groups engaged in foraging activities in this part of their habitat.

Although intertidal habitats generally represent only a small proportion of the marine environment, they often sustain a high biodiversity of organisms. Due to the large extension of BSA's intertidal zone, it has already been nationally and internationally recognized for its high value as a feeding ground for migrating shore birds (e.g. González *et al.*, 1996; DiGiacomo, 2005). Similarly, Perier (1994) reported on the importance of BSA's intertidal zone as a foraging (and spawning) ground for multiple fish species. The presented study indicates a similar significance of this intertidal habitat for the bottlenose dolphins, suggesting they are an integral part of the intertidal food web. Indeed, it was previously reported that the many invertebrate species inhabiting an intertidal zone may serve as an important food source attracting predators up the food chain (e.g. Perier, 1994; García *et al.*, 2010). Such an exploitation of resources in the intertidal zone during its immersion at high tide has also been recorded for several other coastal marine mammal species around the world, including for example Indo-Pacific humpback dolphins (*Sousa chinensis*, Lin *et al.*, 2013), marine tucuxi (*Sotalia fluviatilis*, Gurjão *et al.*, 2003), finless porpoises (*Neophocaena phocaenoides*, Singh, 2003), marine otters (*Lutra felina*, Medina-Vogel *et al.*, 2006), dugongs (*Dugong dugong*) and manatees (*Trichechus* sp.) (Gibson *et al.*, 2003).

However, humans are often also highly dependent on intertidal habitats. This frequently leads to strong environmental pressures and conservation related issues (e.g. Litler, 1980; Keough *et al.*, 1993; Brosnan & Crumrine, 1994; Addessi, 1995; Thompson *et al.*, 2002). Specifically in BSA, continued anthropogenic activities have shown to affect the invertebrate community of the local intertidal habitat through eutrophication (García *et al.*, 2010), pollution (Gil *et al.*, 1996, 1999, 2006; Bonuccelli *et al.*, 2004; Vázquez *et al.*, 2007) and habitat degradation (Gil *et al.*, 2006; Carbone *et al.*, 2011). How this affects predators up the food chain remains unknown. However, as large marine predators are often good indicators for ecosystem health (e.g. Agrawal, 2011), understanding the ecological importance of the intertidal habitat for bottlenose dolphins is of great value for further in depth research and enhanced impact assessments. This in turn will be essential to ensure accurate conservation

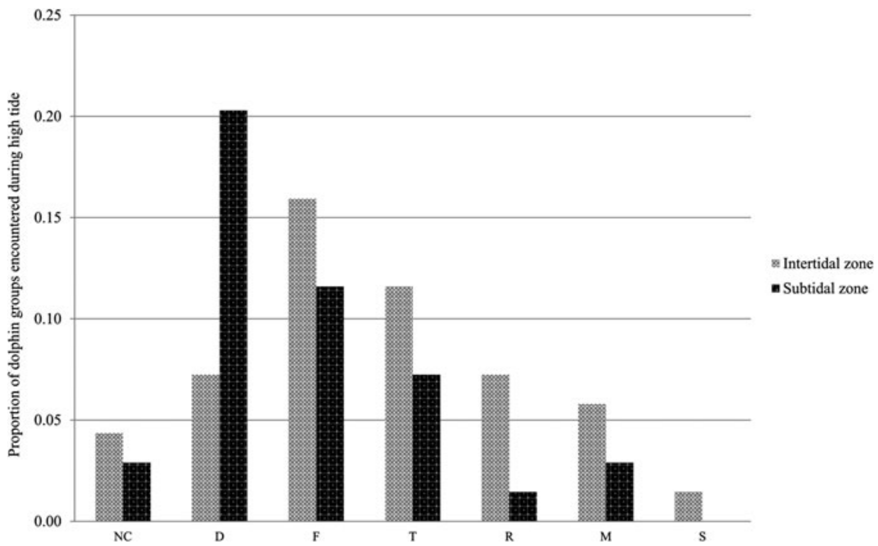

Fig. 5. Proportion of dolphin groups encountered during high tide and their respective behaviours in the intertidal *vs* subtidal zone: NC, not classified; D, diving; F, surface feeding; T, travelling; R, resting; M, milling; S, socializing.

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management in the area, not only positively affecting this vulnerable population of bottlenose dolphins but also a wide range of other marine and coastal (often less charismatic) species under its shadow. In the end, management of intertidal habitat may arguably be easier than of open sea, as access can be restricted and implementation of regulations more strictly controlled (Thompson *et al*., 2002).

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