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Largest reported groups for the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) found in Algoa Bay, South Africa: Trends and potential drivers

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ABSTRACT

This study investigates how group size of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) changes temporally, spatially, and/or with predominant behavior at two discreet sites along the Eastern Cape coastline of South Africa: Algoa Bay and the Wild Coast. The mean group size of bottlenose dolphins was large with an average of 52 animals. Significantly larger groups were observed in Algoa Bay ($\bar{x} = 60$, range = 1–600) than off the Wild Coast ($\bar{x} = 32.9$, range = 1–250). In Algoa Bay, the mean group size increased significantly over the study period, from an average 18 animals in 2008 to 76 animals in 2016. Additionally, the largest average and maximum group sizes ever reported both in South Africa and worldwide, were recorded in Algoa Bay (maximum group size = 600). Neither season nor behavior had a significant effect on mean group size at both sites. Similarly environmental variables such as the depth and substrate type also had no influence on group size. It remains unclear which ecological drivers, such as predation risk and food availability, are leading to the large groups observed in this area, and further research on abundance and distribution of both predators and prey is necessary.

Key words: group size, behavioral strategy, predation risk, food availability, zero-truncated negative binomial regression, Indian Ocean, Algoa Bay, Wild Coast, South Africa.

In social animals, variation in group size reflects adaptations to the local environment resulting in cost-benefit trade-offs in behavioral strategies of grouping patterns (Gyax 2002, Silk 2007, Wey *et al.* 2008, Ebensperger *et al.* 2012). In various taxa (*e.g.*, insects, fish, birds, and mammals), group size may increase for protection from predators to reduce the amount of time spent on predator vigilance, as described in the “many-eyes hypothesis” (Pulliam 1973, Robinette and Ha 2001, Creel *et al.* 2014). Living in a group may either increase the likelihood of detecting a predator

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(Elgar 1989, Fitzgibbon and Lazarus 1995, Creel and Winnie 2005, Silk 2007), or create a dilution strategy for individuals (Wolf 1985, Magurran 1990, Roberts 1996). Some animal groups show a positive correlation between group size and prey availability (Langen and Vehrencamp 1998, Gillespie and Chapman 2001, Heithaus 2005, Vaughn *et al.* 2010) due to the greater effectiveness of cooperative hunting and prey detection (Gygax 2002). However, large group size may also generate competition for resources, especially in food-limited environments (Lima *et al.* 1999, Steenbeek and van Schaik 2000, Beauchamp 2014) and reflects the capacity of an ecosystem to sustainably support many apex predators, including in several cetacean species (Wells *et al.* 2004).

In dolphins, group size is largely determined by predation pressure (Wells *et al.* 1980, 1987; Heithaus and Dill 2002) and prey availability (Wells and Scott 1999; Heithaus 2001*a, b*; Heithaus and Dill 2002), or a trade-off between these two factors (Heithaus and Dill 2002). When group size increases for protection of individuals, especially young animals (Baird and Dill 1996, Mann *et al.* 2000, Stanton and Mann 2012, Smith *et al.* 2016) or females against males (Connor 2000, Connor *et al.* 2001), it may also increase the competition for resources within the group (Heithaus and Dill 2002, Lodi and Monteiro-Neto 2012). However, energetic gains during cooperative feeding in larger groups have been described in many delphinid species, such as killer whales (*Orcinus orca*), common dolphins (*Delphinus delphis*), and spotted dolphins (*Stenella frontalis*) (Baird and Dill 1996, Clua and Grosvalet 2001, Gygax 2002).

Although there are ecological and behavioral benefits of living in groups for dolphin populations, potential costs are also reported. As previously mentioned, aggregations may lead to competition for food resources (Heithaus and Dill 2002, Lodi and Monteiro-Neto 2012), but also to transfer of pathogens and ectoparasites between individuals potentially leading to epizootics (Connor 2000, Van Bresseem *et al.* 2009, Ebensperger *et al.* 2012), dominance and competition between males for access to reproductive females (Le Boeuf 1974, Connor and Krützen 2015) or a higher probability of being detected by predators (Hebblewhite and Pletscher 2002).

In bottlenose dolphins (*Tursiops* spp.), group size varies daily (Shane *et al.* 1986) and exhibits a fission-fusion grouping pattern, where associations between individuals vary in space and time to maximize their fitness (Smolker *et al.* 1992; Connor *et al.* 2000, 2011; Mann *et al.* 2000; Möller *et al.* 2002; Connor and Krützen 2015). Associations between individuals have been observed to improve the communication and social learning between animals (Gygax 2002, Krützen *et al.* 2005), mating success of adult males (Mann *et al.* 2000, Krützen *et al.* 2004), and increase calving rates (Frère *et al.* 2010). In some populations, bottlenose dolphins preferentially associate with members of the same sex, which likely reflects different reproductive strategies between males and females (Wells *et al.* 1987, Connor *et al.* 2000, Krützen *et al.* 2004). However, the specific way these groupings benefit the reproductive success of females is unclear as it varies between areas (Mann *et al.* 2000, Wells 2003, Gibson and Mann 2008).

Bottlenose dolphins and other apex predators are considered sentinels of the health of marine ecosystems (Wells *et al.* 2004). As apex predators, they provide a good indication of the health and richness of habitats and may also reflect the effects of global change (Bowen 1997). Their distribution and abundance are often linked to the distribution and abundance of their prey and predators (Bowen 1997, Peddemors and Cockcroft 1997, Jefferson *et al.* 2008, Heithaus and Dill 2009, Rosel *et al.* 2009, Möller *et al.* 2010). As such, investigations of bottlenose dolphin group dynamics

may provide key information on ecosystem health given that they would need to have abundant and rich prey resources to sustain large groups of dolphins and/or large population size (Wells *et al.* 2004). Studying group size in animal societies may also provide significant information on the ecosystem in terms of perceived safety (predation pressure) and richness of food resources, and may reflect how animals respond and adapt to changes in their environment (Heithaus and Dill 2002).

In this study, we investigated the effect of temporal, environmental, and behavioral variables on group size of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) and determined the spatial distribution of groups at two discrete regions, Algoa Bay and the Wild Coast, along the Eastern Cape coastline of South Africa. In any habitat, there should be an optimum group size, which maximizes the fitness of individuals (Silk 2007). In general, protected habitats such as coastal areas of small, shallow bays, lagoons and estuaries, host small groups of bottlenose dolphins (Shane *et al.* 1986, Wells *et al.* 1987, Möller *et al.* 2002, Kiszka *et al.* 2007, Stensland and Berggren 2007, Fury and Harrison 2008), while in open habitats such as deep open bays or pelagic waters, they are usually found in larger groups (Würsig 1978, Balance 1992, Defran and Weller 1999, Bearzi 2005). Therefore, we tested the hypothesis that smaller group size would be expected in Algoa Bay than along the Wild Coast, as it represents a more protected habitat, occurring closer to shore and in shallower waters, and therefore larger groups would be found further offshore in both areas.

MATERIALS AND METHODS

Study Areas

Boat-based surveys were conducted along the Eastern Cape coastline (South Africa), in Algoa Bay and at three study sites off the Wild Coast: Kei Mouth, Hluleka, and Mkambati (Fig. 1). The Eastern Cape coastline is strongly influenced by the warm, southward flowing Agulhas Current (Shannon 1989, Roberts *et al.* 2010). Algoa Bay is the largest and eastern-most bay on the south coast of South Africa, with approximately 90 km of coastline (Karczmarski 1999). The Bay is relatively shallow with a maximum depth of about 70 m (Goschen and Schumann 2011, Dicken and Booth 2013), and is flanked on the west side by Cape Recife and on the east side by Cape Padrone (Fig. 1). Surface water temperatures generally range between 16°C and 21°C (Schumann *et al.* 2005); however, the Bay is subject to intermittent wind-induced coastal upwelling, which can reduce water temperatures to below 13°C (Schumann 1982, Lutjeharms 2006). The Wild Coast (former Transkei; Fig. 1) is characterized by a rugged and exposed coastline. Boat-based surveys are difficult in this region due to the absence of harbors or launch sites, and inclement weather (strong winds and big swell). In this area, the continental shelf is at its narrowest, bringing the Agulhas Current closer inshore, which increases its influence along this stretch of coastline (Roberts *et al.* 2010). During the austral winter (June–July), large aggregations of shoaling sardines (*Sardinops sagax*) known as *the Sardine Run*, appear and move northwards along the continental shelf from Port Elizabeth to Durban, following the penetration of inshore cool waters (O'Donoghue *et al.* 2010a, b, c; Roberts *et al.* 2010; van der Lingen *et al.* 2010). The narrow continental shelf in the Wild Coast area concentrates the sardines and their predators (*e.g.*, common dolphins, *Delphinus capensis*; Cape gannets, *Morus capensis*; ragged-tooth sharks, *Carcharhinus taurus*; dusky sharks,

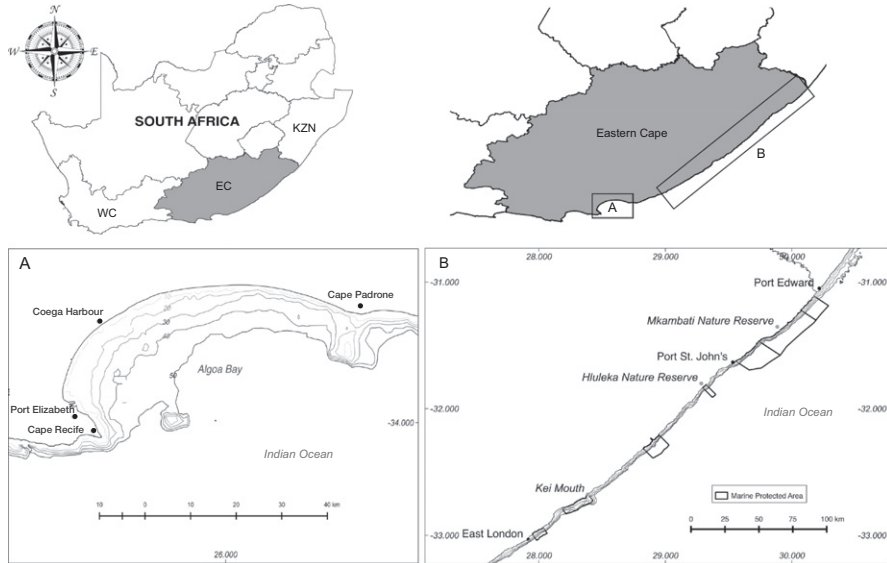


Figure 1. Study areas of (A) Algoa Bay and the (B) Wild Coast, showing the three Marine Protected Areas surveyed: Kei Mouth, Hluleka and Mkambati. WC: Western Cape; EC: Eastern Cape; KZN: KwaZulu-Natal.

Carcharbinus obscurus) near to the coastline (Roberts *et al.* 2010; O'Donoghue *et al.* 2010a, b, c).

Data Collection

Data were collected using semirigid boats following predetermined coastal routes at a constant speed of 6–9 knots and in wind conditions of less than Beaufort 4. Surveys were conducted from June 2008 to May 2011 and from July 2015 to August 2016 in Algoa Bay. Along the Wild Coast, surveys were conducted over 3 wk per field trip in June and December 2014; February, June, and December 2015; March, June, and December 2016 at the three different sites (Kei Mouth, Hluleka, and Mkambati). The surveys conducted in Algoa Bay covered the entire coastline at ~500 m from shore along the 10 m depth contour in three survey days every month. Opportunistic offshore legs conducted at higher speed were used to join the starting waypoints of surveys. On the Wild Coast, surveys were conducted along the 15 m depth contour, returning along the 30 m depth contour (or *vice versa*) to avoid sampling the same group twice (Fig. 2).

Since group size was typically large, for the purposes of this study, a group of dolphins was defined as any individuals in close proximity (<10 m) to one another, usually but not always, moving in the same direction and engaged in similar predominant behaviors (adapted from Irvine *et al.* 1981, Smolker *et al.* 1992, Toth *et al.* 2011). In both study areas, data were collected by two experienced observers (excluding the skipper) who continuously scanned an estimated strip of ~500 m 180° ahead (90° for each observer) to detect dolphins with the naked eye. To limit biases in group size estimation, at least one of the two researchers was present on the boat in

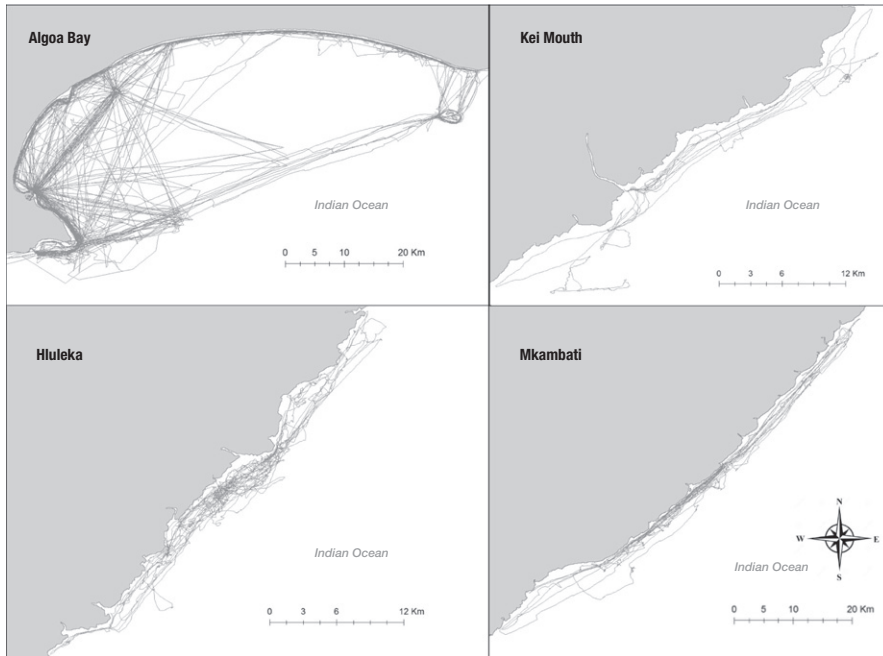


Figure 2. Outline of the survey track lines conducted in Algoa Bay between 2008–2011 and 2015–2016, and the Wild Coast (Kei Mouth, Hluleka, Mkambati) between 2014 and 2016.

both research areas when collecting data. When a group of dolphins was sighted, the survey vessel slowly approached the group and ran parallel to their course. When animals could not be approached closer for safety reasons of the crew (*i.e.*, when animals were too close to shore or swimming in the waves), time dedicated for data recording was increased to ensure accuracy. At the beginning of each sighting, the time of the sighting, number of animals present in the group based on multiple visual counts (best, minimum, and maximum), group composition (number of adults, juveniles, and calves) based on the total body length of individuals (following Smolker *et al.* 1992), location of the sighting (using a hand-held Global Positioning System) and predominant group activities were recorded. Environmental parameters including, sea surface temperature (SST) and depth (using a depth sounder), wind direction and strength, and Beaufort Sea State were also recorded. In cases of large groups or when animals were swimming in the waves, group size was estimated using a minimum and maximum group size, then rounding of estimates to the nearest 5 or 10 animals was applied (Gerrodette *et al.* 2002). For these sightings, data on group composition could not be recorded. When possible, predominant group activities (*i.e.*, >50% of the individuals engaged in the same behavior, see Mann 1999) were continuously assessed during the observation and then defined as one of five behavioral categories (following Shane 1990): *foraging* (see Nowacek 2002), *milling*, *socializing*, *resting*, and *traveling*. Changes in group size, with dolphins joining or leaving a group, and/or any change of the predominant behavior recorded were considered as a new sighting.

Data Analysis

To determine variations in group size, we analyzed positive count data for dolphin according to the framework outlined by Zuur *et al.* (2009) employing R v 3.4 software (R Core Team 2017). Explanatory variables were assessed for collinearity. No variables were considered strongly collinear (Pearson coefficient >0.7); however, depth and distance to shore were moderately collinear in Algoa Bay (Pearson coefficient = 0.54) and approaching collinearity in the Wild Coast (Pearson coefficient = 0.68). Following data exploration, differences in group size of dolphins was assessed against covariates using a zero-truncated negative binomial (ZTNB) generalized linear model (GLM), which was fit using the *zerotrunc* function in the *countreg* package (Zeileis and Kleib 2017). Separate models were constructed where necessary to preserve sample size as logistical constraints did not warrant a balanced data set. We used likelihood ratio tests (LRT) to test specific biological hypotheses between nested models. For multivariate models, we fitted global models and then followed a backward stepwise deletion process, using the *step* function, to determine the optimal model by selecting that which minimized the Akaike information criterion (AIC), and with a $\Delta\text{AIC} < 2$ (see Table 1). Model validation was performed *via* assessment for normal distribution of residuals, equality of variance and that no excessively influential observations were present. We first assessed whether site (2015–2016 data, Algoa Bay *vs.* Wild Coast) influenced group size. Then, using the larger data set (2008–2016 data) collected in Algoa Bay and the Wild Coast combined, we assessed the influence of year, austral season, predominant behavioral activity, and environmental variables (depth, SST, distance from shore, and sea-bottom substrate) on dolphin group size. Variations in the frequency of the different behaviors (*i.e.*, % of time in each predominant behavior) between Algoa Bay and the Wild Coast were investigated using a chi-square test.

To investigate how group size varies spatially we used the conversion tool *point to raster* in ArcMap 10.² Grids cells of 1×1 km were created and the maximum mean group size observed within each cell was calculated within the two study areas (equivalent to the estimated strip scanned with the naked eye). The closest distance between each sighting and the shore was calculated using a spatial junction between the data shapefile and the coastline shapefile. The sea-bottom substrate (sandy, rocky mixed, muddy) under which dolphins were observed was also obtained using a spatial junction between the data shapefile and the benthic and coastal habitat classification shapefile, provided by the South African National Biodiversity Institute (SANBI, Sink *et al.* 2012).

RESULTS

During the study period, 133 surveys were conducted in Algoa Bay and 47 along the Wild Coast. A total of 325 sightings and an estimated 19,694 dolphins were recorded in Algoa Bay, while along the Wild Coast, 135 sightings comprising an estimated 4,444 dolphins were observed (Table 2). In both study areas, sightings were recorded at an average distance of about 925 m ($\bar{x} = 924.6 \text{ m} \pm \text{SE} = 56.9$, median = 376.1, range = 38.5–7,761.4 m) from shore. In Algoa Bay, the bottlenose dolphins were generally observed in shallow waters of 9 m depth on average ($\bar{x} =$

²ArcGIS 10.2.2 for desktop (advanced). Esri Inc., Redlands, CA.

Table 1. Model selection using backwards stepwise selection using GLMs that were tested and selected for statics analysis on the group size of dolphins. Models having the lowest AIC and a $\Delta AIC < 2$ were the best models with the highest Akaike weights (w) values (in bold). Dist = distance to shore, SST = sea surface temperature.

Subset	Candidate models	AIC	ΔAIC	w
All data ($n = 460$)	Site	909.91	0.00	1
Algoa Bay				
Temporal effects ($n = 325$)	Year	3,267.2	0.00	0.57
	Year + Season	3,267.8	0.60	0.43
Behavioral effects ($n = 320$)	Year	3,230.1	0.00	0.96
	Year + Behavior	3,236.4	6.30	0.04
	Behavior	3,241.1	11.00	0.004
Environmental effects ($n = 280$)	Year + Dist	2,813.8	0.00	0.42
	Year + Dist + Depth	2,814.0	0.22	0.37
	Year + Dist + Depth + SST	2,816.0	2.08	0.15
	Year	2,818.4	4.60	0.04
	Year + Dist + Depth + Substrate + SST	2,819.8	5.98	0.02
	Dist	2,823.6	9.80	0.003
	Dist + Depth + Substrate + SST	2,826.9	13.1	0.0006
Wild Coast				
Temporal effects ($n = 135$)	Year	1,197.5	0.00	0.99
	Season	1,213.7	16.2	0.0003
	Year + Season	1,221.3	23.8	<0.0001
Behavioral effects ($n = 135$)	Behavior	1,213.00	0.00	0.58
	Year + Behavior	1,213.68	0.68	0.42
Environmental effects ($n = 78$)	SST + Depth	705.9	0.00	0.45
	SST	707.0	1.16	0.25
	SST + Depth + Substrate	707.7	1.80	0.18
	SST + Depth + Dist + Substrate	709.1	3.20	0.09
	Year + SST + Depth + Dist + Substrate	712.8	6.90	0.01
	SST + Depth + Dist	714.8	8.97	0.005

8.9m \pm SE = 0.3, median = 6.5, range = 2.3–38 m) and in SST ranging from 11.8°C to 23.6°C. Along the Wild Coast, dolphins were observed in deeper waters of about 20 m depth on average (\bar{x} = 19.77 m \pm SE = 0.9, median = 19.1, range = 3–61.7 m) and in SST ranging from 16.9°C to 25.4°C.

Group Size

The combined mean group size of bottlenose dolphins observed in the Eastern Cape was 52 ($n = 460$, \bar{x} = 51.78 \pm SE = 3.59, median = 25), ranging from 1 to 600 animals. However, in Algoa Bay, group size was significantly larger ($n = 325$, \bar{x} = 59.8 \pm SE = 4.67, median = 25, range = 1–600) than along the Wild Coast over the entire study period ($n = 135$, \bar{x} = 32.92 \pm SE = 3.29, median = 19, range = 1–250) (df = 1, likelihood ratio test (LRT) = 21.95, $P < 0.001$). Forty percent (39.3%) of the observed groups comprised more than 50 individuals in Algoa Bay, and 17.8% along the Wild Coast. As group size did not differ between seasons (Algoa Bay: df = 3, LRT = 5.41, $P = 0.144$; see Table 1) we pooled the data for all years. Results indicate

Table 2. Summary of survey effort for Algoa Bay and the Wild Coast, including mean group size, number of sightings and dolphins observed, and encounter rates.

Study area	No. days	No. Surveys/seasons	Mean group size (\pm SE)	Median	No. hours	No. sightings	No. animals	No. sightings/hour	No. animals/hour
Algoa Bay									
2008	21	Summer = 3, Autumn = 0, Winter = 11, Spring = 7	18.4 (4.77)	15	100.75	15	276	0.15	2.74
2009	44	Summer = 10, Autumn = 12, Winter = 12, Spring = 10	44.16 (5.94)	20	221.9	95	4,294	0.43	19.35
2010	31	Summer = 7, Autumn = 8, Winter = 10, Spring = 6	65.73 (10.07)	28	147.33	101	6,622	0.68	44.95
2011	10	Summer = 5, Autumn = 5, Winter = 0, Spring = 0	63.47 (15.38)	37	54.36	15	952	0.28	17.51
2015	11	Summer = 0, Autumn = 0, Winter = 7, Spring = 4	75.60 (16.26)	30	90.6	43	3,251	0.47	35.88
2016	16	Summer = 5, Autumn = 6, Winter = 5, Spring = 0	76.76 (13.19)	52.5	120.5	56	4,299	0.46	35.67
Total	133		—		535.73	325	19,694	—	—
Wild Coast									
2014	10	Summer = 1, Autumn = 0, Winter = 5, Spring = 4	30.06 (8.39)	19.5	32.28	18	507	0.56	15.52
2015	16	Summer = 4, Autumn = 3, Winter = 7, Spring = 2	30.12 (4.52)	19	71.75	51	1,536	0.71	21.41
2016	21	Summer = 6, Autumn = 4, Winter = 9, Spring = 2	36.38 (5.39)	22.5	77.21	66	2,401	0.85	31.10
Total	47		—		181.24	135	4,444	—	—

that in Algoa Bay, both the mean and the median group size increased significantly over the study period ($df = 5$, $LRT = 24.23$, $P = 0.0002$), from an average of 18 individuals per group in 2008 ($\bar{x} = 18.4 \pm SE = 4.77$, median = 15, range = 1–65) to 76 individuals per group in 2016 ($\bar{x} = 76.7 \pm SE = 13.19$, median = 52.5, range = 1–600; Fig. 3, Table 2). Along the Wild Coast, group size did not increase significantly over the study period ($df = 2$, $LRT = 1.15$, $P = 0.4849$).

In both areas, predominant behavior had no significant effect on group size (Algoa Bay: $df = 5$, $LRT = 2.61$, $P = 0.7595$; Wild Coast: $df = 4$, $LRT = 9.83$, $P = 0.04344$; Fig. 4). The behavioral patterns of the dolphins were broadly similar in the two regions although the frequency of each behavior recorded was significantly different (χ^2 : $df = 4$, $P < 0.0001$). Dolphins in both areas were predominantly travelling (60% and 58.5% of the sightings, respectively for Algoa Bay and the Wild Coast) and were foraging in about 20% of the sightings (20.6% and 25.2%, respectively for Algoa Bay and the Wild Coast).

Finally, over the observed range of environmental variables recorded in Algoa Bay, group size did not vary significantly with depth ($df = 1$, $LRT = 2.021$, $P = 0.155$) or distance from shore ($df = 1$, $LRT = 3.316$, $P = 0.0686$; see Table 1). Along the Wild Coast, only the SST had a significant effect on group size (SST: $df = 1$, $LRT = 5.936$, $P = 0.01483$; depth: $df = 1$, $LRT = 3.2301$, $P = 0.0723$; substrate: $df = 1$, $LRT = 0.1879$, $P = 0.6647$; see Table 1).

Spatial Distribution of Group Size

In Algoa Bay, animals were observed along the entire coastline; however, the majority of large groups (*i.e.*, >200 animals) were recorded in the northern sector of the bay, between Sundays River and Cape Padrone, with groups of up to 600 animals

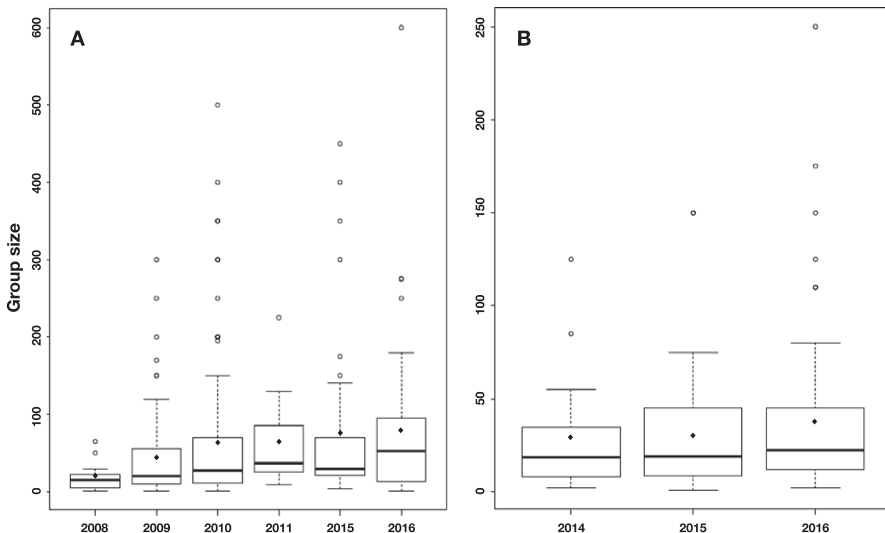


Figure 3. Box-plot graphs of the annual variation of the mean group size (diamond) of bottlenose dolphins in (A) Algoa Bay ($n = 325$) and (B) the Wild Coast ($n = 135$), including the median (black horizontal line), the lower (25%) and upper (75%) quartiles, and outlier values (open circles). Years between 2012 and 2014 are missing due to no survey effort in Algoa Bay.

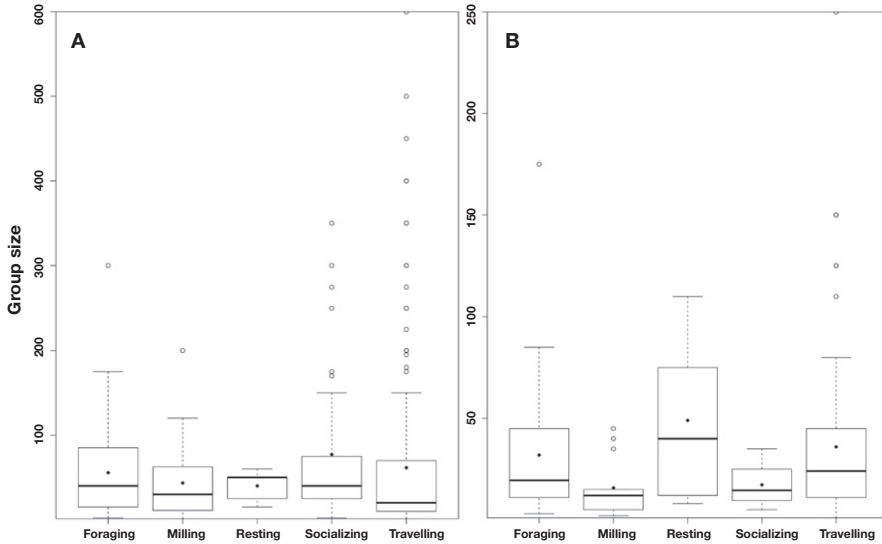


Figure 4. Box-plot graphs of the mean group size (diamond) of bottlenose dolphins according to behavior in (A) Algoa Bay ($n = 320$) and the (B) Wild Coast ($n = 135$). The median (black horizontal line), the lower (25%) and upper (75%) quartiles, and outlier values (open circles) are also illustrated.

recorded (Fig. 5). Around Bird Island, groups of up to 250 animals ($n = 3$) were observed. Large groups were also recorded around St. Croix Island (maximum group size ranging between 275 and 300 animals, $n = 19$) and near the Coega Harbour (maximum group size of 110 animals, $n = 6$). Few sightings of large groups were observed between Port Elizabeth Harbour and Cape Recife, with the maximum group size ranging between 120 and 175 animals ($n = 36$), although most groups comprised less than 50 animals (Fig. 6).

Along the Wild Coast, the distribution of the largest groups revealed no visible spatial pattern. The largest group size recorded along the Wild Coast was smaller than the largest group in Algoa Bay (maximum 600), with a maximum of 150 animals recorded at Kei Mouth ($n = 10$, $\bar{x} = 27.7 \pm \text{SE} = 10.12$), 250 animals in Hlu-leka ($n = 64$, $\bar{x} = 36.9 \pm \text{SE} = 5.07$) and 150 animals in Mkambati ($n = 61$, $\bar{x} = 29.5 \pm \text{SE} = 5.01$) (Fig. 6).

DISCUSSION

Our data indicate that Algoa Bay hosts the largest groups of bottlenose dolphins reported both in South Africa and globally (Möller *et al.* 2002, Stensland *et al.* 2006, Stensland and Berggren 2007, Fury and Harrison 2008, Guissamulo 2008, James 2014, Sprogis *et al.* 2016, Vinding 2016), with a significant increase in group size throughout the study period (from 18 to 76 animals on average). Groups off the Wild Coast were also relatively large, but significantly smaller than in Algoa Bay. The largest groups in Algoa Bay were recorded along the northern part of the Bay, with no spatial pattern evident along the Wild Coast. In both study sites, group size did not

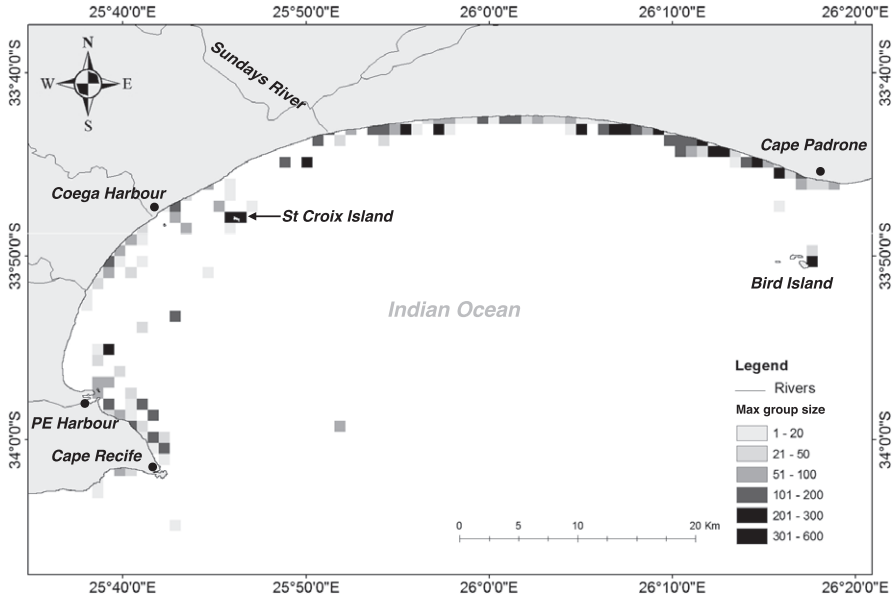


Figure 5. Spatial distribution of the maximum group size of bottlenose dolphins recorded in Algoa Bay from 2008 to 2011 and 2015 to 2016 (not weighted by effort).

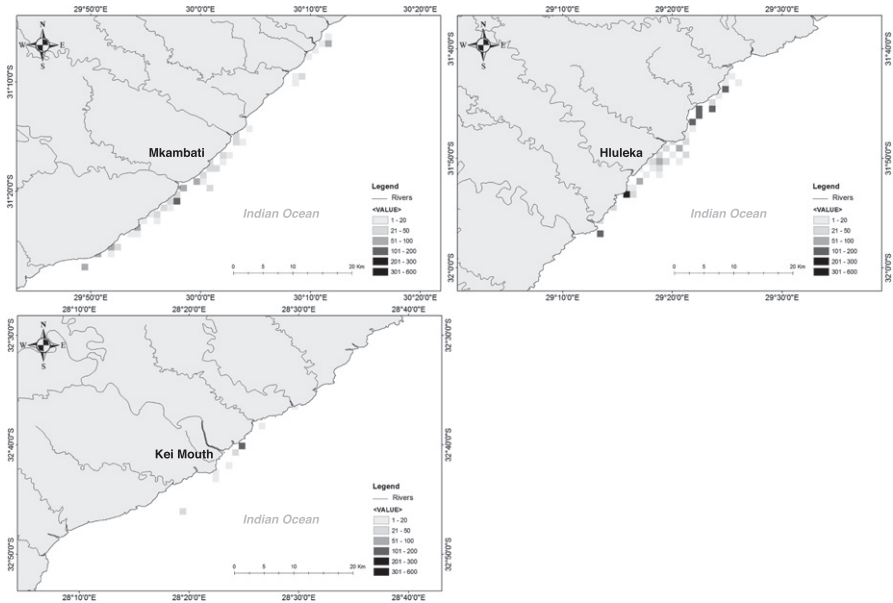


Figure 6. Spatial distribution of the maximum group size of bottlenose dolphins recorded along the Wild Coast. From north to south of the Wild Coast are Mkambati, Hluleka, and Kei Mouth (not weighted by effort).

change seasonally or with behavior. Distance to shore was the only environmental variable that produced an effect on group size in Algoa Bay, rejecting our hypothesis that larger groups would be found further offshore, as these were actually observed closer to shore. The lack of seasonal or environmental effects suggests that other mechanisms are causing animals to group, but also indicates that these areas are rich enough to support such large groups of dolphins year-round.

To investigate the behavioral ecology of dolphins, determining an accurate group size and composition are essential. When the group size is large, accurate counts and group characterization (*i.e.*, number of calves, juveniles and adults) is often difficult to record and can vary considerably between observers (Gerrodette *et al.* 2002). In addition, the reliability of the counts is also dependent on the distance from which the animals are observed, the sea state and the behavior of the animals (Buckland *et al.* 1998, Thomas *et al.* 2010, Keeping and Pelletier 2014), becoming especially challenging when animals are dispersed and/or when feeding. Despite these limitations, our group size estimates far exceeds those reported in other studies, both within the same region and worldwide (Wang and Yang 2009, James 2014, Vinding 2016).

Coastal populations of *Tursiops aduncus* are generally observed in groups of 6–60 animals (Möller *et al.* 2002, Stensland and Berggren 2007, Fury and Harrison 2008, Guissamulo 2008, Wang and Yang 2009, Oremus *et al.* 2013, James 2014, Sprogis *et al.* 2016, Vinding 2016). In South African waters, large groups of *T. aduncus* have occasionally been reported in other locations in the Western Cape, with a maximum group size of 140 individuals recorded in Plettenberg Bay (Saayman and Tayler 1973, Ross 1984), over 200 individuals in Mossel Bay (only 1.7% of the sightings; James 2014), 200 in Kleinbaai (Vinding 2016) and a maximum 300 off the Natal coast (Ross *et al.* 1987). Although groups composed of more than 100 animals are commonly observed in Japanese (Shirakihara *et al.* 2002) and South African waters (Ross 1984), groups larger than 300 animals have only been reported in Algoa Bay and occasionally in nearby Mossel Bay (maximum recorded group of 500 individuals; see James 2014). Previous studies conducted in Algoa Bay reported groups of between 20 and 50 animals on average, ranging from 25 to over 500 individuals, with 52% of the observed groups larger than 100 individuals and groups >300 dolphins sighted frequently (Ross 1984, Reisinger and Karczmarski 2010). Groups up to 2,000 animals have also been documented, but in these instances they were comprised of several smaller groups (Ross 1984, Findlay *et al.* 1992).

Despite many possible mechanisms causing the largest groups reported in this study, determining the main factors influencing grouping patterns is difficult and requires more data on abundance and distribution of both predators and prey in the area. One possible driver of large group size in Algoa Bay is predation pressure. Previous studies conducted on white sharks (*Carcharodon carcharias*) reveal a partial overlap in the spatial distribution between large dolphin groups (up to 600 individuals) and white sharks in the northern and central sectors of the bay (Dicken and Booth 2013). Indeed, the coastal waters of Algoa Bay have been suggested as a nursery ground for white sharks with a feeding area centered around Bird Island (Dicken 2008, Dicken *et al.* 2013*b*). In this area, white sharks are mainly present between April and November with 72% of animals larger than 2.5 m in length (with a maximum estimated size of 4.5 m; Dicken *et al.* 2013*a, b*). Our study, however, did not reveal any temporal shifts in dolphin group size, which would be expected as more sharks migrate into the area between April and November, contrary to what is observed in Mossel Bay for example (James 2014).

Previous research conducted in South African waters on shark predation has provided evidence of shark attacks and bites on bottlenose and Indian Ocean humpback dolphins, *Sousa plumbea* (Cockroft *et al.* 1989, Cockroft 1991). In KwaZulu-Natal, marine mammals, especially delphinids, are the primary prey of large sharks (>2.5 m total length; Cliff *et al.* 1989). In Algoa Bay, several bottlenose and humpback dolphins show severe lesions of shark bites on their body, providing evidence that shark attacks on dolphins occur in this area (TB, unpublished data). Other studies showed that bottlenose dolphins in the coastal waters of southern Africa display lower shark-inflicted scar rates (10%–20%, see Cockroft *et al.* 1989) than other areas, such as Shark Bay (74%), Moreton Bay, Australia (37%), or Sarasota (31%; see Heithaus 2001a). The reduced incidence of shark related injuries may reflect the larger group sizes. When present, white sharks are commonly observed in the surf zone between 20 m and 500 m from shore (Dicken and Booth 2013), overlapping with the sightings of large dolphins groups recorded in this study. The northern sector of Algoa Bay, where the largest dolphin groups were observed is shallow with a sandy bottom, and is an area where we would have expected to see smaller groups, since it represents a safer habitat in term of predation risk (Heithaus 2001b). Therefore, we hypothesize that the large groups of dolphins observed in this area could be gathering for protection against shark predation (Dicken and Booth 2013). To reduce the potential risk of shark attacks, dolphins may form larger and tighter groups, traveling more along sandy substrates (presumably due to the greater possibility of shark attacks in more complex substrata) and/or stay in the shallow waters of the surf zone for hiding (Würsig *et al.* 1994). Whether predation pressure has increased or is sufficiently high enough year-round to drive large group sizes, and how these two apex predators interact in the study area remains unclear.

Given that bottlenose dolphins are considered sentinels of global change (Wells *et al.* 2004), the large groups found in Algoa Bay, and to a lesser extent the Wild Coast, provide evidence that these two regions are sufficiently productive to support large apex predator populations. Being in a large group increases intraspecific competition for food resources, which in a prey-limited environment should shape the group dynamics of dolphins (Lima *et al.* 1999, Beauchamp 2014). In Algoa Bay, a significant increase in group size is observed, including large groups of over 100 dolphins, with an estimated population size of 28,482 animals (see Reisinger and Karczmarski 2010). In addition, the large groups of schooling sardines occurring during the austral winter along the Eastern Cape coastline may provide sufficient prey in our study sites. Therefore, high prey availability in this area could be another potential driver to large group size. Aerial surveys conducted along the Eastern Cape and KwaZulu-Natal coastlines during the austral winter found bottlenose dolphins in shallow waters (<30 m) (O'Donoghue *et al.* 2010a, b), and in large groups of over 100 individuals (O'Donoghue *et al.* 2010a, c), which seems to indicate that these animals may be feeding cooperatively (Heithaus and Dill 2009, Vaughn *et al.* 2010). However, our study showed no seasonal change in group size which suggests that the influx of additional prey did not affect group size, potentially because prey availability is high enough year-round.

Although a significant increase in the abundance of sardines is observed between May and August in Algoa Bay (Pichegru *et al.* 2009), little is known of how changes in oceanographic conditions affect prey abundance and distribution within the region (van Eeden *et al.* 2016), which confined our study to drawing on specific predator-prey interactions. However, studies conducted on patterns in the abundance and foraging effort of African penguins (*Spheniscus demersus*) suggest that coastal prey

availability is higher in the northern part of Algoa Bay and around Bird Island and moderate to low in the western sector (Pichegru *et al.* 2012, van Eeden *et al.* 2016), which corresponds to areas with larger groups of dolphins. Nevertheless, from 2001 to 2009, the commercial catch of sardines in and around Algoa Bay increased substantially, leading to lower fish stocks (Crawford *et al.* 2009, Pichegru *et al.* 2012). Subsequently, in 2009, a 20 km radius experimental purse-seine fishing exclusion zone was established around St Croix Island, resulting in an increase of prey abundance (Pichegru *et al.* 2010, 2012). At the same time, prey availability decreased around Bird Island. Despite evidence of a decrease in prey availability during some of our study period, a steady increase in the group size of bottlenose dolphins in Algoa Bay, from 18 animals in 2008, 44 in 2009, 65 in 2010 and up to 76 animals on average in 2016 was observed. These data therefore suggest that factors other than food availability account for the large group sizes of bottlenose dolphins in Algoa Bay. Further research is needed into prey availability, with specific focus on spatio-temporal shifts in dolphin-specific prey.

Determining social structure in large groups of dolphins is logistically challenging. New technology, such as unmanned aerial vehicles, may provide useful information on the spatial distribution and density of these animals, their predators and prey in shallow coastal waters along the Eastern Cape coastline. This technology will greatly enhance our ability to characterize group composition in terms of adults, juveniles, and calves, and to investigate mother-calf strategies in grouping patterns as well as the reproductive success of dolphins. The social organization of *Tursiops* spp. has been described in several locations globally, having significantly smaller group sizes of dolphins than found in Algoa Bay (Smolker *et al.* 1992, Connor *et al.* 2000, Lusseau *et al.* 2003, Bouveroux and Mallefet 2010, Louis *et al.* 2015, Smith *et al.* 2016). Social structure studies in Algoa Bay would allow the determination of social units and characterization of their organization within the population, as well as determination of the main ecological factors leading the different social units to merge or split in space and time. This would help to elucidate the main mechanisms underpinning the large groups of bottlenose dolphins in this area.

In conclusion, these large group sizes of bottlenose dolphins frequently observed in Algoa Bay are unique and provide much insight into the health and richness of the Eastern Cape coastal waters. The lack of seasonal, behavioral, and environmental trends in their grouping strategies suggests that this area can sustain large numbers of apex predators year round, with a significant increase in group size of dolphins in Algoa Bay during the study period. Determining the function for these large groups remains difficult, as we have insufficient data on predators and prey in this region. However, there is some evidence that both predation risk and prey availability may play important roles in grouping patterns. To pinpoint the main factor or combined factors influencing the behavioral strategies of bottlenose dolphins in grouping patterns, further research using novel techniques and a collaborative approach is needed for this region. As these animals may tell us a great deal about the environment they inhabit, ongoing research and monitoring of these groups is important for the conservation of ecosystems, as well as monitoring the impact of human activities on prey-predator relationships.

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