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Sixteen years later: Occurrence, group size, and habitat use of humpback dolphins (*Sousa plumbea*) in Algoa Bay, South Africa

Renée P. Koper,[1] University of Groningen, Department of Ocean Ecosystems, PO Box 11103, 9700 CC, Groningen, The Netherlands; **Leszek Karczmarski,**[2] The Swire Institute of Marine Science and School of Biological Sciences, The University of Hong Kong, Cape d'Aguilar, Shek O, Hong Kong; **Derek du Preez,** Nelson Mandela Metropolitan University, Coastal and Marine Research Institute, PO Box 77000, Port Elizabeth, 6031, South Africa; **Stephanie Plön,**[2, 3] South African Institute for Aquatic Biodiversity (SAIAB) and South African Environmental Observation Network (SAEON), Grahamstown, 6140, South Africa.

Abstract

Coastal dolphins are more prone to cumulative impacts of environmental and anthropogenic changes than pelagic species. However, few studies use historical comparisons to evaluate those impacts across a temporal scale. The study presented here describes the pattern of occurrence, group size, behavior, and habitat use of humpback dolphins in Algoa Bay and compares these to a similar study conducted in the early 1990s. Results indicate a considerable change in the frequency of occurrence. Furthermore, the mean group size has decreased from six to three individuals, mainly due to an increase in occurrence of solitary individuals (36.3% *vs.* 15.4%). Foraging, which was previously the predominant activity (64%), has now been replaced by traveling (49%). Moreover, dolphins showed a negative reaction towards a variety of watercrafts and swimmers. These observed differences could be due to a change in prey abundance, direct anthropogenic disturbance, and/or population decline. We emphasize the need for long-term environmental and biological data series and long-term monitoring of the demographics of this population to accurately assess any changes observed in future.

Key words: *Sousa plumbea*, group size, occurrence, behavior, habitat use, anthropogenic disturbance, environmental change, South Africa, Algoa Bay.

Coastal dolphins are considered more prone to disturbance caused by a cumulative effect of environmental changes, coastal infrastructure developments, and various direct anthropogenic disturbances than more offshore, pelagic species (Thompson *et al.* 2000, Stockin *et al.* 2008). One such species highly susceptible to environmental and anthropogenic impacts is the humpback dolphin, genus *Sousa* (*e.g.*, Ross *et al.*

[1,3]Current address: Nelson Mandela Metropolitan University, Coastal and Marine Research Institute, PO Box 77000, Port Elizabeth, 6031, South Africa.

[2]Corresponding authors: (e-mail: leszek@hku.hk, stephanie.plon@nmmu.ac.za).

1994, Karczmarski 2000, Van Parijs and Corkeron 2001, Ng and Leung 2003, Stensland *et al.* 2006).

Globally, humpback dolphins are listed as "Near Threatened" by the International Union for the Conservation of Nature (IUCN) (Reeves *et al.* 2008), although there are calls for this status to be revised (Huang and Karczmarski 2014). This genus inhabits shallow coastal waters within the eastern Atlantic and throughout the Indo-Pacific. The taxonomy has long been debated, but at present the Society for Marine Mammalogy recognizes four species following Mendez *et al.* (2013). These four species are described in detail by Jefferson and Rosenbaum (2014) as *S. teuszii* (Atlantic), *S. plumbea* (western Indian Ocean), *S. chinensis* (northeastern Indian Ocean and northwestern Pacific), and *S. sahulensis* (southeastern Indian Ocean and southwestern Pacific).

Small population sizes and high mortality throughout their range have raised concern about the conservation of all four species (*e.g.,* Cockcroft 1990, 1999; Karczmarski 1996, 2000; Jefferson *et al.* 2006; Wang *et al.* 2007; Guissamulo 2008; Bejder *et al.* 2012; Huang *et al.* 2012; Atkins *et al.* 2013). Few studies, however, have considered a comparison between historic and recent data from the same population, to evaluate potential impacts of environmental or anthropogenic changes. Humpback dolphins found in Algoa Bay (Eastern Cape), thought to be part of the largest population of this species off the South African coast, provided an opportunity for such a comparison as the most recent study of this population was conducted well over a decade ago (*i.e.,* from 1991 to 1994) (Karczmarski 1996). This study estimated a minimum population size of 466 animals (95% CI 447–485) (Karczmarski *et al.* 1999*a*) that form small groups (mean group size of six; Karczmarski 1999, Karczmarski *et al.* 1999*b*), occur mostly within 500 m off the shore, in waters <20 m deep, and have a preference for shallow rocky reefs (Karczmarski *et al.* 2000).

The present study was undertaken to evaluate the current pattern of occurrence, habitat use, group size, and behavior of humpback dolphins in Algoa Bay to determine whether these have changed in comparison to the earlier study (Karczmarski 1996). The field methods applied during the current study followed closely and as feasibly as possible on the previous study (Karczmarski 1996) to facilitate a meaningful comparison of data collected 16 yr apart. In addition, the current study includes an assessment of dolphin reactions to human recreational activities.

We follow the latest taxonomic revision as suggested by Mendez *et al.* (2013) and refer to our study animals as *S. plumbea*, hereafter the "humpback dolphin," although earlier published work has usually referred to these animals as *S. chinensis* (*e.g.*, Cockcroft 1990; Jefferson and Karczmarski 2001; Atkins *et al.* 2004; Guissamulo and Cockcroft 2004; Stensland *et al.* 2006, and the series of articles by LK cited throughout this manuscript).

Materials and Methods

Survey Area

Algoa Bay is situated on the southeast coast of South Africa between Cape Recife (34°02′S, 25°42′E) in the west and Cape Padrone (33°46′S, 26°28′E) in the east (Fig. 1). Our shore-based surveys were conducted in the southwest of the bay, consistent with the previous study by Karczmarski (1996), along a 10 km stretch of coast that has previously been identified as "preferred habitat" for humpback dolphins in

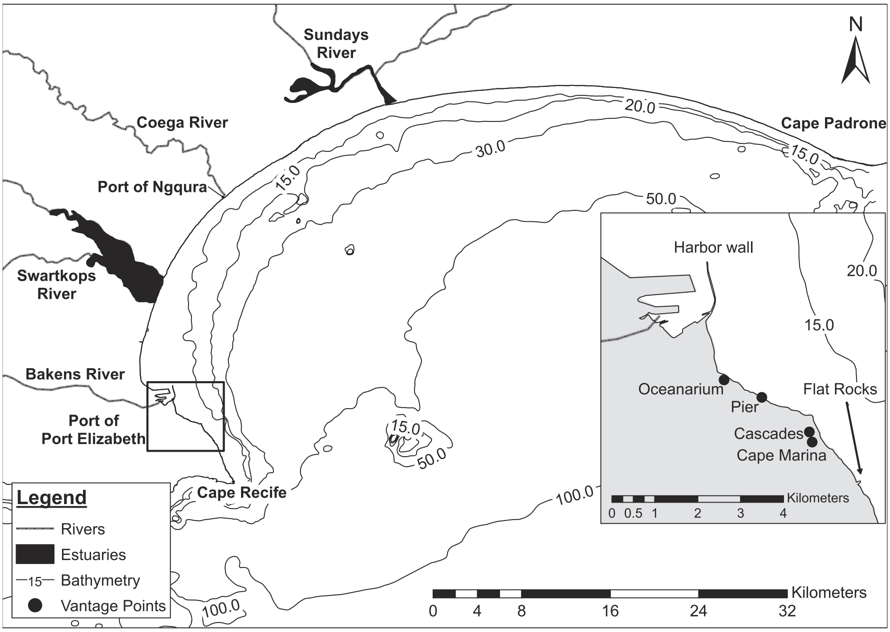

Figure 1. Map of Algoa Bay showing the survey area in the western-most part of the bay. The survey area extends from the Port of Port Elizabeth harbor wall in the north to "Flat Rocks" in the south. Observations were made from a total of four different vantage points throughout the study period (see insert).

Algoa Bay (Karczmarski *et al.* 2000); a pattern that was recently supported by a 3 yr study conducted from 2008 to 2011 (SP, unpublished data). In this southwest section of Algoa Bay, waters <15 m deep extend up to 1,300 m offshore. The sediment is comprised of mud and sand near the harbor wall, while shallow rocky reefs increasingly dominate towards the south (Beckley and Buxton 1989). The mean maximum sea surface temperatures (SST) in summer (November–April) ranges from 20°C to 22°C in the inshore areas, whereas the mean minimum temperatures in winter (May–October) are 14°C to 15°C (Schumann *et al.* 2005). The tidal range is approximately 2.0 m and 0.5 m for spring and neap tides, respectively (Schumann *et al.* 2005).

General Survey Procedure

Daily land-based surveys were conducted between 19 May 2010 and 18 May 2011, weather permitting. Surveys were carried out from four elevated vantage points along the coast with overlapping visual ranges: the Oceanarium of the Port Elizabeth Museum (PEM) (33°58′36.8″S, 25°38′56.0″E; elevation: 10.5 m), the pier (33°58′48.6″S, 25°39′30.9E; elevation: 3 m), and the roofs of the apartment complexes "Cascades" (33°59′13.1″S, 25°40′15.4″E; elevation: 20 m) and "Cape Marina" (33°59′20.7″S, 25°40′18.3″E; elevation: 51 m) (Fig. 1). The Oceanarium of the PEM and the pier were also used as vantage points during the study in the early 1990s (Karczmarski 1996). Each vantage point covered an individual survey area, marked by natural and man-made boundaries, such as reefs, the pier, the harbor wall, *etc.*

Surveys were conducted during daylight hours, ranging from 30 min after sunrise until 30 min before sunset. Daylight hours ranged from approximately 0730 to 1700 in winter and 0500 to 1930 in summer. Consequently, the daylight period was divided into four time slots of 2–2.5 h and five time slots of 2.5 h per day in winter and summer, respectively. A minimum of two time slots were completed per survey day, but surveys were never longer than six consecutive hours to not overexert observers' fatigue. No surveys were conducted at Beaufort sea states >3 or during poor visibility. The survey schedule was designed to allow equal amount of effort per vantage point (*i.e.*, equal amount of time spent either searching for or observing a group of dolphins). All surveys were conducted using a pair of 7 × 50 Fujinon FMTRC-SX binoculars with a build-in compass and reticule with a scale in angular mils (De Boer *et al.* 2014). This method was chosen over the use of a theodolite for financial and security considerations. During each survey, the coastal zone was scanned for 10 min (*i.e.*, search effort) every 15 min with both the unaided eye and the binoculars. The individual survey area was scanned from left to right with an equal level of search effort allocated to "inshore" (≤500 m offshore) and "offshore" (≥500 m to approximately 1 km offshore) sections of the coastal waters, similarly as in Karczmarski (1996), with no survey effort beyond 1 km offshore.

All surveys were conducted by the same observer, with the only exception of a 4 wk period in December 2010, when it was done by a secondary observer who received an extensive 2 wk prior training to ensure consistency of individual survey areas, environmental parameters, group compositions, and behavioral states.

Environmental Variables

Environmental variables such as Beaufort sea state, swell height, cloud cover, glare, rain, and haze were recorded every 30 min (unless conditions changed considerably within a shorter time frame) in order to assess the searching and tracking conditions. A "visibility index" was assigned to each survey period, which is a subjective index on a scale of 1–5 (1 = very poor, 5 = very good) (following Barendse *et al.* 2010). All observations conducted under a visibility index below 3 were not considered for further data analyses.

Spatial Data

When a solitary individual or group of dolphins was sighted, the time of day, direction of sighting, and distance from vantage point were recorded (calculations following Lerczak and Hobbs 1998). The ability of an observer to sight an animal is negatively affected by an increasing distance between the animal and the observer (De Boer *et al.* 2014). When analyzing spatial data, it is assumed that spatial variations in sighting density are the result of differences in habitat use rather than of the effect of the distance from the observer (De Boer *et al.* 2014). To minimize distance-related bias in our study, the percentage of total sightings from a vantage point was plotted against the distance from that vantage point (after De Boer *et al.* 2014). These plots allowed for the calculation of an effective sighting distance (*i.e.*, the distance at which the increase in percentage of total sightings changed from a constant to a more stagnant increase), which differed for each individual vantage point. All sightings beyond the calculated effective sighting distances were removed from any subsequent spatial analysis.

Direction and distance of all sightings that fell within the effective sighting distances were converted into geographic coordinates and plotted in ArcGIS version 9.3.1[4] as a Global Positioning System (GPS) position. The habitat preference of dolphins was determined with a kernel density analysis of sightings with localized behavior, which includes foraging, socializing, milling, and resting (see *Behavior* below). We obtained the number of sightings per square kilometer with the output raster cell size set at 17.5 m and the search radius set at 250 m.

Annual and Diurnal Sighting Frequency

Statistical analyses of the annual and diurnal sighting frequency were performed with RStudio version 0.98.1028[5] with the use of the packages "pscl" (Zeileis *et al.* 2008) and "lmtest" (Zeileis and Hothorn 2002). A single full (*i.e.*, including all explanatory variables) zero inflated poisson (ZIP) model with a Poisson distribution and an offset for search effort, tested for significant variation in the number of sightings per day per hour of search effort (*i.e.*, Sighting Index, SI) (Whittingham *et al.* 2006, Zuur *et al.* 2009*a*). Both the variables month and visibility index were included in the model to test their effect on the count process, whereas only visibility index was included to test its effect on the generation of false zeros. An autocorrelation function (ACF) plot, supported by a Ljung-Box test, assessed the presence of temporal dependence in the model residuals (Zuur *et al.* 2009*b*).

A two-way ANOVA was performed to test whether the SI was significantly related to the tidal cycle or the time of day. The covariate "time of day" consisted of six time slots (*i.e.*, A–F). Time slots A–C comprised the hours after sunrise, while the time slots D–F comprised the hours before sunset.

Group Size

When a solitary individual or a group of dolphins was sighted, search effort changed to behavioral observation effort which lasted until (1) animals left the individual survey area, (2) a maximum of 1 h of behavioral observation effort was reached, or (3) environmental conditions deteriorated. For each sighting, the group size was recorded at 5 min intervals. A minimum observation effort of 5 min was set to obtain a reliable estimate of group size. Consequently, data gathered during less than 5 min of observation were excluded from the analysis.

A statistical analysis on the group sizes was performed with RStudio version 0.98.1028, with the use of the package "geepack" (Yan 2002, Yan and Fine 2004, Højsgaard *et al.* 2006). Group size was analyzed with a generalized linear model (GLM) fitted by a generalized estimation equation (GEE) with an "Ar1" correlation structure, assuming that two observations close in time are more highly correlated than two observations further away in time (Zuur *et al.* 2009*a*). The GLM model tested for a significant effect of season, tidal cycle, time of day, and behavior. An ACF plot, supported by a Ljung-Box test, assessed the presence of temporal dependence in the model residuals (Zuur *et al.* 2009*b*). The covariate "season" consisted of summer and winter, after Karczmarski *et al.* (1999*b*) (*i.e.*, summer from November to April

[4]ESRI. 2009. ArcGIS 9.3.1 Geographical Information System computer program. Environmental Systems Research Institute (ESRI). Available at http://www.esri.com/contact.

[5]R Core Team. 2014. R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. Available at http://www.R-project.org/.

when SST ≥ 18°C and winter from May to October when SST ≤ 18°C), for consistency with the previous study.

Behavior

For each sighting the behavioral states were recorded at 5 min intervals, using the definitions from Karczmarski and Cockcroft (1999). These were "foraging," "traveling," "socializing and playing," and "resting." The activity defined as "opportunistic foraging" by Karczmarski and Cockcroft (1999) was included under "foraging" in the current study. In addition, the current study includes the state of "milling," which was defined as localized movements of individuals with relaxed asynchronous surfacing in relatively close proximity of one another. Milling behavior was not identified as a separate behavioral state in Karczmarski's study in the early 1990s and therefore not included in the definitions of behaviors by Karczmarski and Cockcroft (1999).

A minimum behavioral observation effort of 5 min was set to obtain a reliable assessment of observed behavior. Consequently, data gained during less than 5 min of observation were excluded from the analysis. A statistical analysis of the percentage of observation time engaged in each of the behavioral categories was performed with RStudio version 0.98.1028 with the use of the package "mlogit."[6] A multinomial logistic regression analysis was performed to detect significant effects of season, time of day, and tidal cycle.

Human Activities

Human activities as defined in Table 1, occurring within an individual survey area, were recorded during each survey to measure the general level of potential disturbance within each survey area. During each sighting, the individual observation area was monitored for the presence of human activities. Each activity was recorded, including the type of activity (*e.g.*, swimmers, paddle skiers, high-speed vessels, *etc.*), quantity, the direction from which the activity approached the dolphins (*i.e.*, front, back, side, alongside), and the distance between the human activity and the sighted animals. When an "activity" passed the animal(s) parallel to their travel path, the distance to the dolphin(s) was measured when the activity was in perpendicular position by measuring the vertical angular scale reading to the horizon for both the dolphin(s) and the activity (following Lerczak and Hobbs 1998). For any other direction of approach, the direction and distance from vantage point to the dolphin(s) as well as the activity were measured with the binoculars and converted into GPS positions in ArcGIS version 9.3.1. Subsequently, the distance between the dolphin(s) and the activity could be extrapolated in ArcGIS. When human activities approached the dolphin(s) to an extent that they seemed to move exactly over the animal(s), the distance was recorded as 0.5 m. The sighted animals were continuously observed to assess their response to the activity, which was either assigned to be positive, negative, neutral, or undetermined (following definitions of reactions in Ng and Leung 2003).

Statistical analyses on the type of response towards human activities were performed with RStudio version 0.98.1028 with the use of the package "mlogit." A multinomial logistic regression analysis was performed with the type of response as the response variable, and the type of activity, group size, and distance to specific

[6]Croissant, Y. 2013. Mlogit: multinomial logit model. R package version 0.2-4. Available at http://CRAN.R-project.org/package=mlogit.

Table 1. Definitions of human activities.

Type	Definition
Swimmers/surfers	People lying in the water with their full bodies, with or without surfboards.
Surf skier	A surf ski is a light, long, and narrow nonmotorized water craft frequently used for racing. In contrast to kayaks, they are suitable to ride waves and to make quick turns. Surf skis are propelled with a two-ended paddle by one or two persons on top of the watercraft (*i.e.*, not inside the hull as in a kayak).
Personal water craft (PWC) (*i.e.*, jet ski)	Plastic boats (2–4.5 m long) powered by an inboard engine driving a pump jet, comprising both smaller, one person "stand-ups" and the bigger "sit-down" models for up to four riders (Koschinski 2008).
High speed vessel	Vessels traveling at high speed, including speed boats, inflatable boats (so-called rubber ducks, RIB's), recreational fishing boats, and pleasure boats (Ng and Leung 2003).
Fishing vessel	Vessels used to catch fish and squid (*e.g.*, chokka squid, *Loligo vulgaris*) for commercial purposes (FAO 1996).
Sailing boat	A boat driven by sails.
Other	Any other activity that could not be assigned to one of the above mentioned categories, such as high speed vessels at low speed, cargo ships, and tug boats.

activity as the explanatory variables. An ANOVA was performed to analyze whether there was a significant difference in the average distance during negative reactions between the different types of activity.

Results

Whenever possible, figures generated with the data gathered in the present study are depicted alongside with figures published by LK on data gathered during 1991–1994.

Observation Effort

A total of 512 h of search effort was reached, resulting in 185 independent sightings and 29 h of behavioral observation effort. In summer, the field effort was higher in the morning (290.25 h) compared to late afternoon (146 h) due to the weather pattern in Algoa Bay. In winter, a similar amount of field hours was spent at each vantage point for each time slot.

Spatial Distribution of Sightings

The sighting accumulation curves indicated effective sighting distances of 1,300 m, 550 m, and 1,500 m for the Oceanarium, "Cascades," and "Cape Marina," respectively. The accumulation curve for the Pier revealed a constant detection rate up to 600 m, beyond which no sightings were reported. Twenty-eight sightings fell beyond the effective sighting radii and were thus removed from the spatial distribution analysis. Of the remaining 157 sightings, 89.2% (n = 140) occurred within 500 m from the shore in water <15 m deep (Fig. 2). A kernel density analysis of sightings with localized behavior depicted four favored areas (Fig. 2); all of these areas are characterized by shallow rocky reefs or man-made structures (*i.e.*, the pier). However, the sample size of localized behavior was insufficient to identify the predominant activities within these areas.

Seasonal and Diurnal Sighting Frequency

Analyses of annual sighting frequencies based on the full data set (n = 207 d) revealed autocorrelation in the model residuals. Therefore, data was subsampled so that no data was gathered on two consecutive days (n = 132) (Mattson *et al.* 2005).

Humpback dolphins were seen throughout the year. There was no significant effect of visibility index or time of year on the daily SI, although a higher SI was reached in September (SI = 1.1), October (SI = 0.98), and February (SI = 0.68) in comparison to the rest of the year (average SI = 0.31) (Fig. 3). The ANOVA analysis indicated that the SI was not significantly affected by the tidal cycle (F-test, n = 24, F = 0.119, P = 0.95). There was, however, a significant effect of time of day (F-test, n = 24, F = 4.813, P < 0.01), with a higher SI reached within three hours after sunrise in comparison to late afternoon (Tukey test, P = 0.01 and P < 0.05 for A *vs.* E and A *vs.* F, respectively). The amount of data represented by SI in relation to time of day for summer and winter separately was insufficient to test whether the effect of time of day differed between seasons.

Group Size

Of the 185 sightings, 157 met the minimum observation effort of 5 min. The dolphin group size during those sightings ranged from 1 to 13, with a mean of three individuals (SD = 2.35, median = 2). Solitary individuals were most frequent (36.3%) (Fig. 4).

The GLM model indicated that the group size was not affected by the season (χ^2 = 0.1, df = 1, P = 0.71) or tidal cycle (χ^2 = 1.4, df = 3, P = 0.71). Time of day had a significant effect (χ^2 = 15.9, df = 5, P < 0.01), but only indicated smaller group sizes just prior to midday in comparison to the early morning (*i.e.*, A *vs.* C, W = 4.21, P < 0.05). Behavior had a more prominent effect on the group size (χ^2 = 85.2, df = 4, P < 0.001), with significantly smaller groups during "traveling" and "resting" in comparison to "foraging" (W = 30.67, P < 0.001 and W = 21.85, P < 0.001, respectively), "milling" (W = 16.76, P < 0.01 and W = 9.12, P < 0.001, respectively), and "socializing" (W = 8.59, P < 0.01 and W = 11.43, P < 0.001, respectively).

Behavior

Humpback dolphin behavior was dominated by "traveling" (49%), followed by "milling" (23%) and "foraging" (18%), while "resting" and "socializing" were only infrequently observed (*i.e.*, <7%) (Fig. 5). "Traveling" was particularly prevalent in solitary individuals (76%), while "milling" was more frequently displayed by groups (29%).

A multinomial logistic regression analysis indicated that the percentage of time engaged in each of the behavioral categories did not vary with the tidal cycle. There was a significant effect of season and time of day, however. In winter, humpback dolphins were less likely to "socialize" and more likely to "mill" (t = –2.17, P < 0.05)

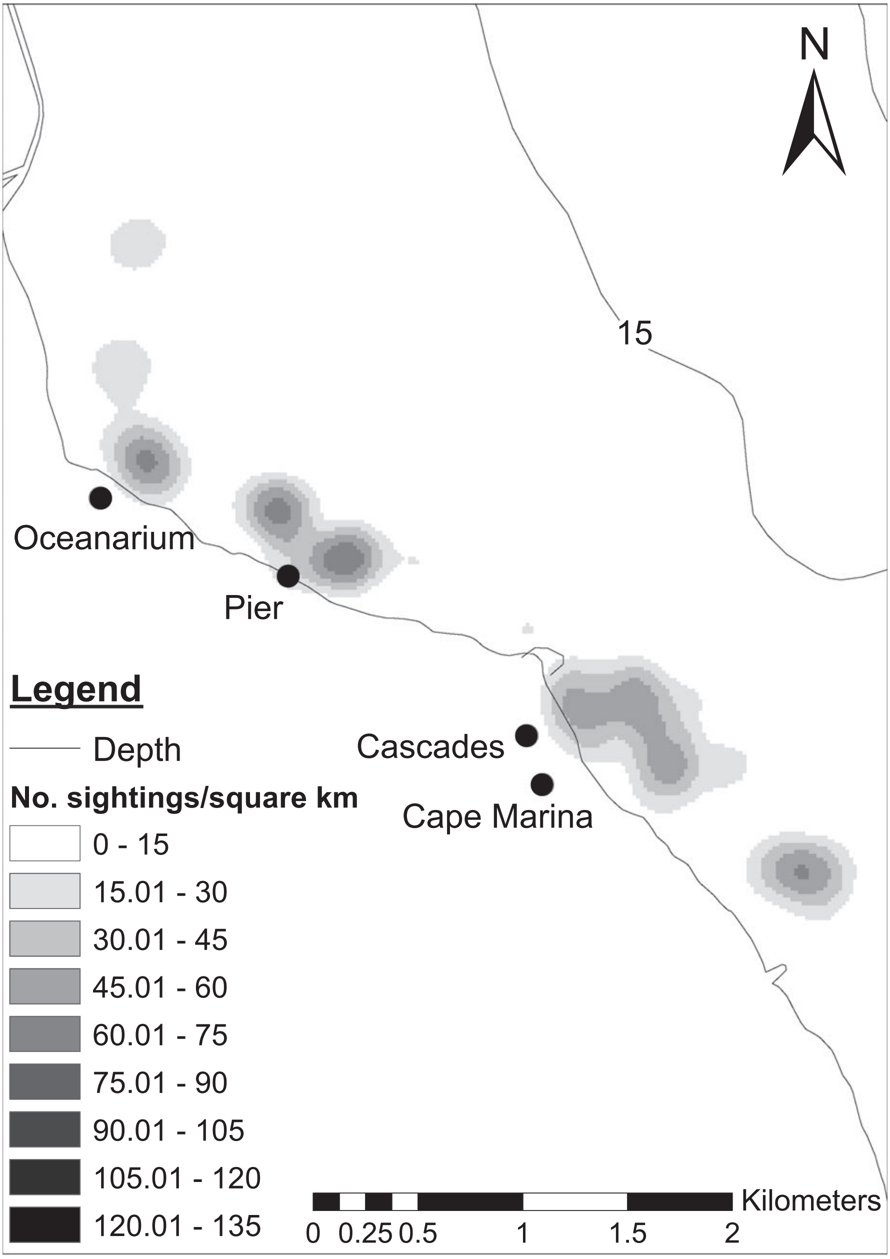

Figure 2. Kernel density map of sightings of humpback dolphins engaged in localized behavior (foraging, socializing, milling, and resting) between May 2010 and May 2011. Density analysis was performed with a chosen radius of 250 m and an output raster cell size of 17.5 m. Density values represent the amount of sightings per square kilometer.

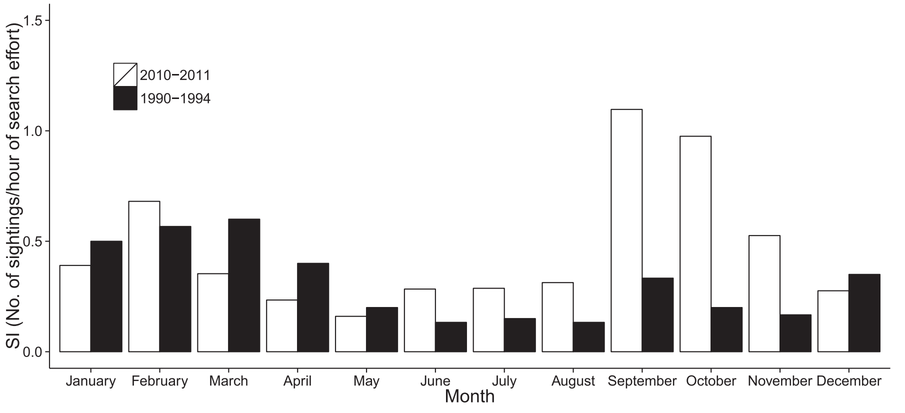

Figure 3. The number of sightings of humpback dolphins, both solitary animals and groups, per hour of search effort per month, observed in Algoa Bay between 2010 and 2011 (open bars) as well as between 1991 and 1994 (black bars, modified from Karczmarski *et al.* 1999*b*).

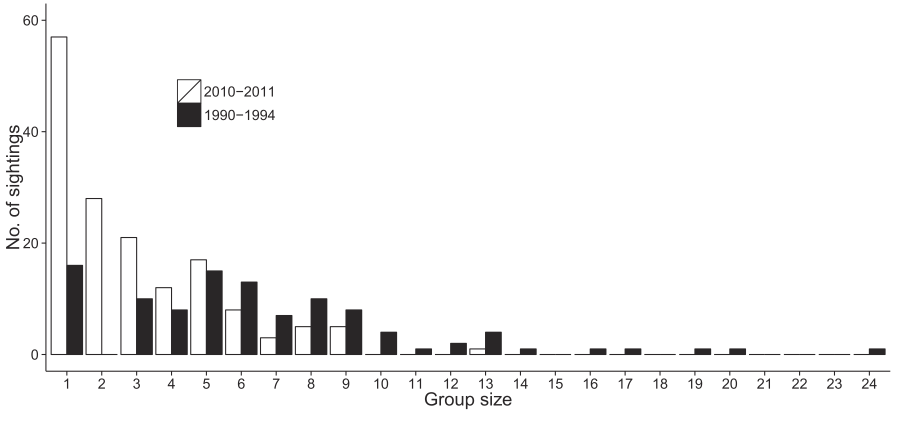

Figure 4. Group size frequency distribution for 157 sightings of humpback dolphins recorded in Algoa Bay between 2010 and 2011 (open bars) as well as for 104 sightings recorded between 1991 and 1994 (black bars, modified from Karczmarski *et al.* 1999*b*).

than in summer, and significantly less "foraging" and more "milling" was observed around midday ($t = 2.36$, $P < 0.05$) than at any other time of day.

Reactions Towards Human Activities

A total of 92 independent reactions of humpback dolphins towards human activities were recorded (Table 2). None of the recorded reactions were positive, the majority (65.2%) were neutral. Twenty reactions (22.8%) were negative, as defined by increased dive duration (33.3%), a change from localized behavior (socializing, foraging, milling, or resting) to directional behavior (traveling) in tight cohesion (23.8%),

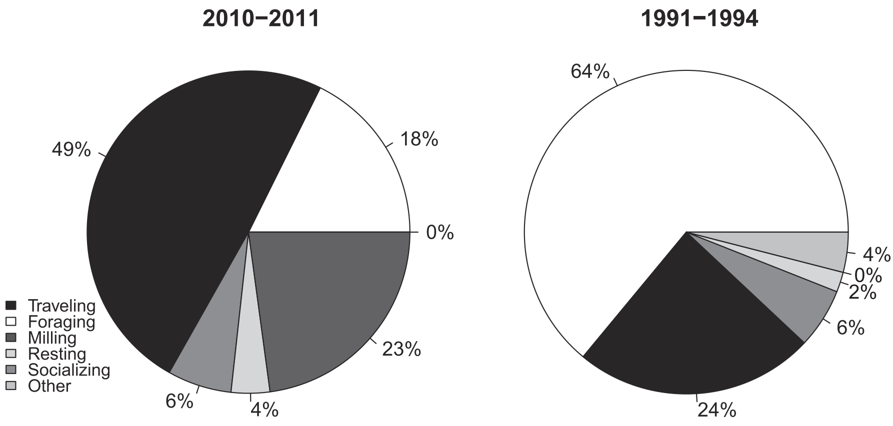

Figure 5. The mean percentage of time spent by humpback dolphins in each of the behavioral states observed in Algoa Bay between 2010 and 2011 (left graph) as well as between 1991 and 1994 (right graph, modified from Karczmarski and Cockcroft 1999).

a change in direction of movement (19.0%), a group split (9.5%), or a combination of the above, which often resulted in disappearance of the sighted animal(s) (14.3%).

Although only two reactions to personal water crafts (PWCs) were seen, both were negative. In general there was no effect of the type of activity or group size on the type of reaction. Furthermore, for each activity, distance did not affect the type of reaction. However, a comparison of the average distance revealed that negative responses to high speed vessels were evident at a significantly larger distance from the vessel (175.4 m) than from surf skiers (16.9 m) (Tukey test, $P < 0.05$). Similarly, negative reactions towards fishing vessels occurred on average at 551.8 m, which was significantly further than for high speed vessels (Tukey test, $P = 0.001$), paddle skiers (Tukey test, $P < 0.001$), and swimmers (Tukey test, $P = 0.001$).

Discussion

Direct comparisons between historical and current data can be a challenge due to the continuous development of advanced research equipment (*e.g.*, GPS, binoculars with built-in compass and scale, *etc.*), analytical tools (*e.g.*, ArcGIS, ecological modeling, statistical packages, *etc.*), and potential differences in research methodology. Similarly, the identification of drivers behind observed changes in animal distribution and/or behavior can be a challenge due to the lack of environmental and biological long time-series data (Moloney *et al.* 2013). Nevertheless, whenever possible we made a comparison between our data and the data collected during the early 1990s (Karczmarski 1996) in order to document changes in humpback dolphin distribution and behavior and to infer possible causal processes.

Our spatial distribution data indicate that the majority of humpback dolphin sightings in Algoa Bay (89.2%) occur within 500 m from the shore in waters <15 m deep. Humpback dolphins preferred areas with rocky reefs for localized behaviors whereas traveling occurred over sandy areas.

Data from land-based observations can be subject to distance related bias, resulting in an unreliable quantification of dolphin distribution (De Boer *et al.* 2014).

Table 2. Percentage of negative, neutral, and undetermined responses of humpback dolphins towards each type of human activity observed in Algoa Bay between May 2010 and May 2011.

Activity	Negative	Neutral	Undetermined
Swimmers (n = 33)	6.1%	81.8%	12.1%
Surf skier (n = 26)	34.6%	53.9%	11.5%
High speed vessels (n = 17)	29.4%	58.8%	11.8%
Fishing vessels (n = 13)	15.4%	15.4%	69.2%
Personal water crafts (n = 2)	100.0%	0.0%	0.0%

However, the effective sighting distances for the Oceanarium (1,300 m) and the apartment complex "Cape Marina" (1,500 m) extended well beyond the dolphin's apparent preferred distance from shore. Furthermore the effective sighting distance of 550 m for the 20 m elevated apartment complex "Cascades" was considerably lower than the effective sighting distance for the 10.5 m elevated Oceanarium, whereas the effective sighting distance for the Pier was undetermined as the rate of detection remained constant up to a distance of 600 m. These findings suggest that the dolphin preference for inshore shallow waters was due to their habitat use pattern and not a distance related bias (De Boer *et al.* 2014). The predominantly inshore distribution as well as the animals' preference for shallow waters has previously been indicated for humpback dolphins in Algoa Bay (Karczmarski *et al.* 2000) as well as elsewhere in South Africa (Saayman *et al.* 1972, Saayman and Tayler 1979, Findlay *et al.* 1992, Atkins *et al.* 2004, Keith *et al.* 2013), Mozambique (Guissamulo 2008), Zanzibar (Stensland *et al.* 2006), Australia (Corkeron 1990, Parra *et al.* 2006), Taiwan (Wang *et al.* 2007, Huang *et al.* 2014) and China (Parsons 1998, Jefferson 2000, Hung 2008, Huang and Karczmarski 2014), with water depth representing the main factor limiting their long-range as well as offshore distribution (*e.g.*, Karczmarski *et al.* 2000, Parra *et al.* 2006, Guissamulo 2008, Hung 2008). Furthermore, a boat-based study conducted in Algoa Bay between 2008 and 2011 confirmed a mean water depth of 6.6 m (range = 2.5–12.5 m, SD = 2.24) for 50 sightings of this species (SP, unpublished data), supporting their preference for shallow-water in Algoa Bay.

The observed preference for areas with rocky reefs corresponds to previous findings for humpback dolphins in Plettenberg Bay (Saayman and Tayler 1979) and Algoa Bay (Karczmarski *et al.* 2000) and is most likely related to the species' prey distribution (*e.g.*, Karczmarski and Cockcroft 1999, Jefferson 2000, Karczmarski *et al.* 2000, Parra *et al.* 2006, Guissamulo 2008, Hung 2008).

In comparison to Karczmarski's study from 1991 to 1994, our data indicate that humpback dolphins in Algoa Bay are still seen throughout the year, but the annual pattern of occurrence has changed from a primary peak during mid-summer to a primary peak in late winter (Fig. 3). In general, the monthly SI has decreased in summer, but more than doubled in late winter. The annual mean group size was half that of the previous mean of six individuals reported for humpback dolphins in Algoa Bay by Karczmarski *et al.* (1999*b*) and smaller than observed elsewhere (Guissamulo 2008, Parsons 1998, Baldwin *et al.* 2004). The mean monthly group size did not vary significantly between seasons, which also differs from findings by Karczmarski *et al.* (1999*b*) who described that the mean group size increased significantly during summer and late winter, apparently corresponding to an increase in availability of prey. Furthermore, the dominant behavior has shifted from "foraging" in 1991–1994 to "traveling" in 2010–2011 (Fig. 5).

A recent 3 yr boat-based survey in Algoa Bay (2008–2011; SP, unpublished data) also noted a mean group size of three (range = 1–23; SD = 3.68), which supports our findings and does not support a possibility of interannual variability in group sizes.

The observed changes may indicate a decreased prey abundance (*i.e.*, distribution shift or decline of prey), which could result in smaller food patches. When food patches are small, the costs associated with increased competition among group members may outweigh the advantages of group living, leading to smaller group sizes (Gowans *et al*. 2008, Gomez-Salazar *et al*. 2012). When prey is scarce, seasonal fluctuations in prey abundance may be less discernible, which would explain the absence of a seasonal increase in average group size as observed by Karczmarski *et al.* (1999*b*). In addition to smaller group sizes, animals can be expected to spend more time traveling between multiple smaller food patches, whereas the amount of time spent resting and socializing remains the same or decreases (Herbers 1981). This corresponds to the differences in daily activity budget of humpback dolphins observed in Algoa Bay in 1991–1994 and 2010–2011.

Both commercial and recreational fishermen in Algoa Bay have reported a decline in catch per unit effort (cpue), change in catch composition, and/or change in fishing pattern as a consequence of overfishing (Brouwer and Buxton 2002, Dicken *et al.* 2012). In addition, a recent study by Rishworth *et al.* (2014) indicated a significant shift in the composition of the surf-zone fish community within our study area between 1982 and 2011 as a consequence of the line-fish stock collapse. It is, however, unknown whether these changes have affected humpback dolphin prey abundance.

The observed changes may also be attributed to an increased disturbance caused by human activities. Humpback dolphins in Algoa Bay displayed a number of behavioral responses to surf skis, high speed vessels and PWCs and, to a lesser degree, to swimmers, surfers, and fishing vessels (Table 2); broadly similar to what has been reported for some large whales (*e.g.,* humpback whales, *Megaptera novaeangliae*, in Stamation *et al.* 2010) and small cetaceans (*e.g.*, humpback dolphins in Hong Kong in Ng and Leung 2003). The overall increase in traveling and milling with a decrease in foraging seen in Algoa Bay resembles the behavioral responses to marine traffic by killer whales (*Orcinus orca*) (Lusseau *et al.* 2009), bottlenose dolphins (*Tursiops* spp.) (Arcangeli and Crosti 2009, Christiansen *et al.* 2010), dusky dolphins (*Lagenorhynchus obscurus*) (Dans *et al.* 2008), and common dolphins (*Delphinus delphis*) (Stockin *et al.* 2008). Humpback dolphins in Algoa Bay thus seem prone to disturbance from vessel traffic, as first noted by Karczmarski *et al*. (1997), which may have caused a change in grouping pattern (Arcangeli and Crosti 2009, Pikesley *et al.* 2012) and displacement of individuals from the study area over time, as suggested earlier by Karczmarski *et al*. (1998) and as seen in bottlenose dolphins off western Australia (Bejder *et al.* 2006). Increased anthropogenic disturbance in summer may have also contributed to a shift in occurrence for winter months when human coastal activities are generally low, as previously suggested for Algoa Bay (Karczmarski *et al.* 1998) as well as elsewhere (Lusseau 2005).

Increased anthropogenic disturbance can be inferred from the considerable development of the coastal zone of Algoa Bay over the past 20 yr, including the establishment of the deep water Port of Ngqura and the recurrence of at least six annual water sport events with the number of participants increasing annually,[7, 8]

[7]Personal communication from Michael Flanigan, Triangle Events South Africa, e-mail: mike@triangle.cc, April 2011.

[8]Personal communication from Sharon Talbot, Ironman South Africa, e-mail: sharon.talbot@ironman.com, January 2015.

(*e.g.*, participation in the Iron Man event increased from 751 in 2005 to 1,840 in 2010). These water sport events have led to a substantial increase in recreational coastal activities, especially in summer (*i.e.*, motorized vessels as well as swimmers and surf skiers).

A third possible driver behind the changes observed is a population decline, which may lead to smaller group sizes (Bearzi *et al.* 2005). However, under a declining population size alone, it can be expected that the overall frequency of occurrence decreases (Maynou *et al.* 2011), while prey availability per individual increases, resulting in more time spent resting (Herbers 1981) and/or socializing (Neumann 2001, Guilherme-Silveira and Silva 2009). This was not the case in the present study.

Finally, both decrease in prey abundance and increased anthropogenic disturbance can in the long-term contribute to population decline (Adams *et al.* 1982, Chapman *et al.* 2000). Hence, all three drivers mentioned above may in fact act synergistically on humpback dolphins in Algoa Bay.

At present, there is insufficient evidence to determine the exact drivers behind the changes in occurrence, group size, and behavior pattern of humpback dolphins in Algoa Bay. Further quantitative evaluation of the processes involved is much needed before conclusive comments can be reached. A series of long-term targeted data sets on environmental (*e.g.*, SST, wind, pollution, *etc.*), biological (*e.g.*, long-term monitoring of humpback dolphin population, rocky reef fish stocks, *etc.*), and anthropogenic (*e.g.*, fish catches, disturbance, *etc.*) data is needed to accurately assess the long-term effects of the environment on humpback dolphins and their prey. However, a first step towards understanding the changes observed, should be a new population size estimate to assess the current population status.

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