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POPULATION SIZE, DISTRIBUTION, AND BEHAVIOR OF INDO-PACIFIC BOTTLENOSE (*TURSIOPS ADUNCUS*) AND HUMPBACK (*SOUSA CHINENSIS*) DOLPHINS OFF THE SOUTH COAST OF ZANZIBAR

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ABSTRACT

Indo-Pacific bottlenose (*Tursiops aduncus*) and humpback dolphins (*Sousa chinensis*) off the south coast of Zanzibar, East Africa, have been subject to both direct and indirect takes as well as disturbance from local dolphin tourism during the last decade. Meanwhile, little or no information on population parameters exists for these animals. In order to assess the anthropogenic threats, a study was conducted between 1999 and 2002 to determine population sizes, distribution, and behavior of these animals. Population sizes were calculated for each year using mark-recapture methods applied to photo-identification data. The estimates ranged between 136 and 179 for the bottlenose dolphins and between 58 and 65 for the humpback dolphins in the calculated 26 km^2 study area. Patterns in distribution and behavior were investigated using image and spatial statistic software on data from boat surveys. Analyses of spatial densities showed that both species concentrated their activities to smaller areas (2%–11.5%) within the study area. When the study results were considered in light of the anthropogenic threats, it was clear that immediate conservation measures were needed. This is critical if the negative impact

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on the species is to be minimized and the dolphins are to continue to represent a socioeconomic resource in the region.

Key words: mark–recapture, photo-identification, population size, distribution, behavioral ecology, hunt, bycatch, dolphin tourism, critical areas, TISS.

There are about 25 species of marine mammals in the East African region, many of which are subject to both direct (hunt) and indirect takes (bycatch in fisheries) as well as habitat degradation due to anthropogenic activities (Borobia 1997). There is a recognized need for better information on population parameters such as population size, distribution, stock structure, behavior, and survival to allow status assessment of those species present in the East African region (Anonymous 1998). This is true for the subjects of this paper—the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) and the humpback dolphin (*Sousa chinensis*) found off the south coast of Zanzibar.

Dolphins are still actively hunted in some areas of eastern Africa where they are used for bait and human consumption (Stensland *et al.* 1998). Off the south coast of Zanzibar, dolphins were hunted until 1996 when 23 animals were taken during one season.[2] Bycatch in fishing gear has been recognized as the most serious threat to small cetaceans world wide (Read *et al*. 2006) and in eastern Africa (Anonymous 1998). Six dolphin and three whale species have been recorded as bycatch in drift- and bottom-set gill nets around Zanzibar alone (Amir *et al.* 2002). Dolphin tourism is a growing industry worldwide, which in many areas can be an alternative to the direct utilization of dolphins and in some cases also to the fishing activities that cause indirect mortalities. Dolphin tourism has been conducted off the south coast of Zanzibar, Tanzania, since 1992 and in 2001 there were about 35 local boats that took tourists out to watch and swim with the dolphins. This is one of only a few areas where a cetacean hunt has been directly replaced by cetacean tourism which now forms a socioeconomic alternative. However, it has been shown that tourism activities also pose a potential threat to dolphins under certain circumstances (*e.g.*, Lusseau 2003, Constantine *et al.* 2004). A study comparing dolphin behavior when proposed guidelines for the dolphin tourism off the south coast of Zanzibar were either followed or violated, showed that violation of the guidelines caused changes in behavioral activity and in particular increased frequency of stress-related behaviors (Englund and Berggren 2002). Further research has also shown that tourism affects the behavior, movement, and dive patterns of nursing female bottlenose dolphins in the area (Stensland 2004).

Mark–recapture methods have been used successfully to estimate population sizes for a diverse range of terrestrial and marine mammals (*e.g.*, Otis *et al.* 1978, Hammond 1986). The basic method uses data on marked individuals and their proportion in subsequent samples to estimate population size and other population parameters (Seber 1982). In cetacean research photo-identification has been widely used to estimate population sizes (see *e.g.*, Hammond 1986, 1990; Williams *et al.* 1993; Read *et al.* 2003).

In order to study dolphin distribution and habitat preferences, information on sighting locations, relative abundance, and behavior has been utilized to good effect (see *e.g.*, Wilson *et al.* 1997, Ingram and Rogan 2002, Bräger *et al.* 2003, Torres *et al.* 2003). Analytical tools such as Geographic Information Systems (GIS) are available to overlay dolphin locations on habitat maps where patterns of distribution and habitat

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use can be plotted and investigated (Allen *et al.* 2001). Heterogeneity in distribution and varied use of patches within a habitat may indicate where important key habitats (critical areas) are situated for a population or a species.

To address the lack of information on population parameters of Indo-Pacific bottlenose and humpback dolphins off the south coast of Zanzibar and to assess the extent of anthropogenic threats, a study was conducted between 1999 and 2002. This study investigates the population sizes, patterns of distribution, and habitat preferences of dolphins using mark–recapture methods and novel spatial analyses techniques.

METHODS

Data Collection

Surveys were conducted between January and March 1999–2002 off the south coast of Zanzibar, East Africa (Fig. 1). During this time of the year the northeast monsoon prevails with light winds and minimum rainfall. A 5-m outboard powered boat was used to survey the study area (for a definition of the study area see below) at a speed of about 10 km/h. All surveys were conducted in Beaufort Sea State 0–3 in clear weather. Starting at right angles to the boat, two researchers scanned through 100° on each side of the boat. Information on boat position and water depth was logged every 30 s with a GPS/echo sounder (Garmin GPSMAP 185 Sounder, Garmin International Inc., Olathe, KS) connected to a laptop computer using custom-developed logging software (for information contact: info@pihldata.com). The number of survey days during each field season was 11 in 1999, 44 in 2000, 45 in 2001, and 31 in 2002. The total logged distance surveyed was 4,037 km (excluding distances while observing encountered dolphins). When a group of dolphins was sighted, the boat slowed to idling speed while one researcher photographed the individuals in the group (see below) and the other recorded position, depth, group size, group composition, and predominant behavior. The predominant behavior was recorded as the activity displayed by the majority of the animals in the group during the first 5–10 min. These data were collected by scan sampling of the group (Mann 1999) using four different behavioral categories: resting, traveling, foraging, and socializing (similar to those used by Mann and Smuts 1999 and Connor *et al*. 2000; for detailed definitions of behavioral categories see Table 1). The dolphins were considered to associate in a group when any individual occurred within 10 m of another individual. No groups were sampled more than once each day, however because both species live in non-stable groups (Würsig and Würsig 1977, Smolker *et al.* 1992, Karczmarski 1999, Jefferson 2000), some individuals could occur in more than one group in a single day.

Photo-identification

We attempted to photograph the dorsal fin of all dolphins in the groups using a 35-mm camera with a 75–300-mm zoom lens and color slide film (100 ISO). Individual dolphins were identified from nicks and marks in the dorsal fin (Wells and Scott 1990, Würsig and Jefferson 1990). The best pictures of the identified dolphins were compiled into a catalog of all identified dolphins in the study area. All pictures were analyzed regarding photographic quality; good photos had dorsal fins in focus and perpendicular to the photographer. The photographs were ranked according to photographic quality (0–4) and only qualities 2–4 were retained in the catalog to reduce false identification. Pictures of new individuals were added to the

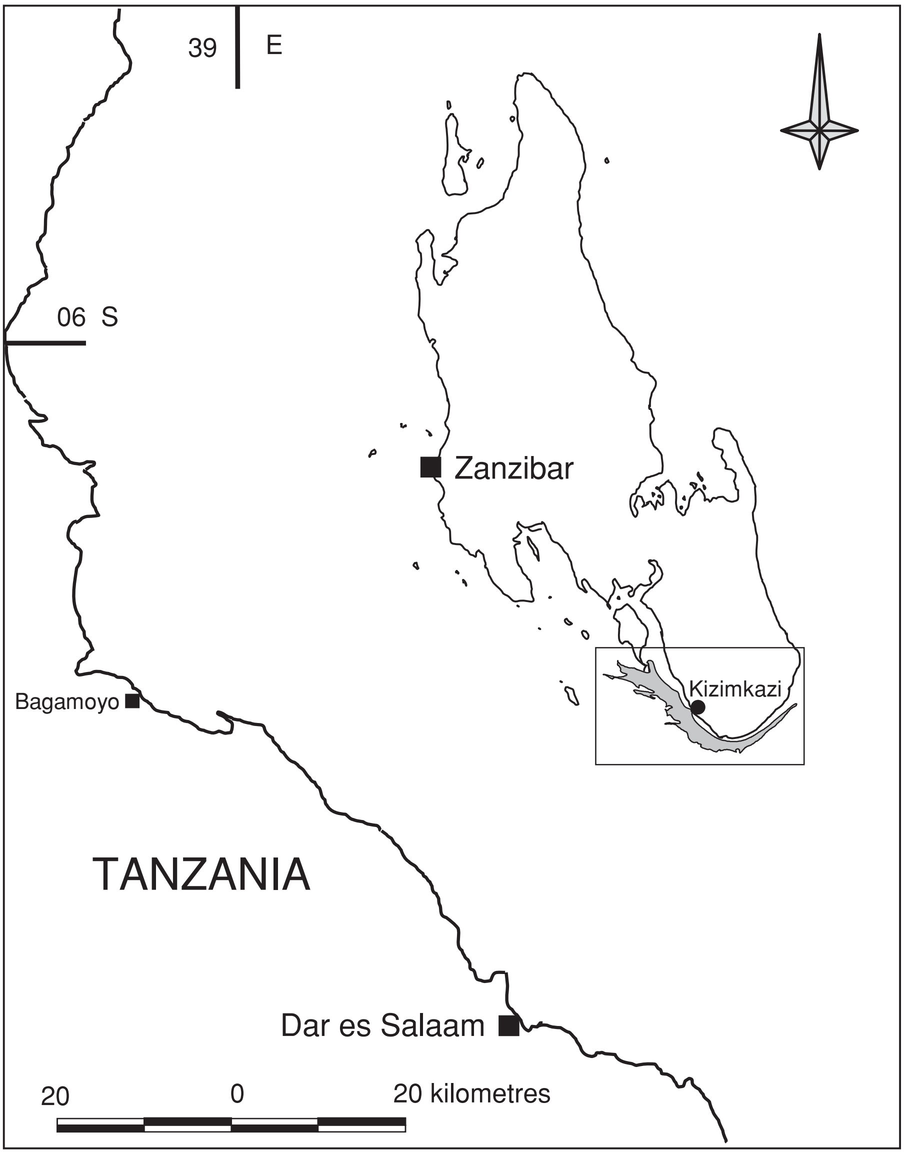


Figure 1. Map of the study area off the south coast of Zanzibar, East Africa. The gray area within the rectangle represents the calculated 26 km^2 study area.

catalog if the pictures fulfilled the quality criteria. Both left- and right-side pictures of the dorsal fin were used to identify individuals.

Mark–Recapture

We used the software MARK (White and Burnham 1999) to estimate the population sizes of the bottlenose and humpback dolphins in the study area. Photo-identification data from four field seasons 1999, 2000, 2001, and 2002 were used for

Table 1. Definition of behavioral categories.

Behavior	Definition
Rest	Low level of activity, dolphins moving slowly (speed <2 knots). Slow surfacings 3–4 times before diving for an extended period of time.
Travel	Persistent and directional movement (speed >2 knots). Dolphins could be meandering but still moving in a general direction.
Forage	Rapid energetic surfacings, frequent directional changes, fish chases, and observations of dolphins with fish in mouth. Peduncle and tail-out dives common.
Social	Petting, rubbing, mounting, chasing, genital inspections, play and displays, and other physical contact between individuals.

the mark–recapture analysis. Only individuals with distinct marks in the dorsal fin (large marks or several smaller nicks) were used in the mark–recapture analyses. A total of 129 bottlenose dolphins and 27 humpback dolphins met the criteria as marked animals and were used in the analyses but not all marked individuals were sighted each year. Calves were excluded from the mark–recapture analysis as their probability of capture is not independent from that of their mothers (Wells and Scott 1990). Individuals with small nicks or no marks were classified as unmarked dolphins. We calculated the proportion of unmarked individuals (non-calves) in the population as the total number of unmarked individuals identified (in pictures of quality 2–4) divided by the total number of individuals identified in all sightings. To calculate the proportion of calves in the population we pooled the average number of calves estimated in the field from all field seasons compared to the average group size estimated in the field from all field seasons.

We grouped the identification data of all marked individuals within each year to maximize the capture probability. The populations were considered closed within each field season. We constructed and compared models in MARK, for estimation of population sizes following standard models (Otis *et al.* 1978). For our estimates we used the models that were found to be most appropriate based on the AIC-criterion (Burnham *et al.* 1995).

As we only used marked non-calf individuals for the mark–recapture analysis we recalculated the population estimates derived by MARK and adjusted the estimates (following the equation used by Williams *et al.* 1993) with the proportion of unmarked individuals (non-calves) and the proportion of calves in the population to calculate $\hat{N}_{total}$ as:

$$\hat{N}_{total} = \frac{\overline{N}}{\hat{\theta}} / \hat{\phi}$$

where $\hat{\theta}$ is the proportion of marked individuals in the population (1 minus the proportion of unmarked non-calves) and $\hat{\phi}$ is the proportion non-calves (1 minus the proportion of calves in the population). The confidence intervals were adjusted correspondingly.

Residency

We calculated the cumulative number of identified dolphins over the four field seasons to investigate if the rate of newly identified dolphins decreased over time, which would indicate that most of the marked dolphins had been identified. We used two measures to investigate the residency of the marked animals in the study area. First we counted the number of days each marked individual had been identified (Chilvers and Corkeron 2003) and secondly we calculated the resighting frequency of marked individuals in subsequent years. The photo-identification data from 1999 to 2002 were collected during the same season every year (December–March) and for comparison we also included an additional data set, from a pilot-study for a biopsy sampling program conducted in September 2002. We investigated how many of the known marked individuals were found in the area during this time of the year, indicating potential year round residents.

Study Area and Patterns of Distribution

The size of the study area was calculated using the Thematic Images and Spatial Statistics (TISS) software package (version TISS, 02-05-17) developed by A. Bignert. TISS presents spatial information on maps where patterns of distributions can be investigated and described by different statistical parameters. The points on the resulting maps may be transformed to surfaces using several approaches such as placing the points into a matrix or grid where they can be generalized to a layer through interpolation. We calculated the size of our study area from the survey data, excluding the time and positions when the boat approached dolphin groups. We laid a grid with a cell size of 100 × 100 m over the entire area and for every grid cell calculated time spent searching for dolphins in each cell. The study area was then defined as the smoothed polygon enclosing all neighboring cells that were visited for at least 1 min during the study period. The TISS software package was also used to investigate distribution patterns. A total of 184 Indo-Pacific bottlenose and 53 humpback dolphin group sightings were available for analyses. Given that tourist boats may affect the dolphin distribution, we excluded sightings of dolphin groups with tourist boats when investigating patterns in dolphin distribution. This left 128 bottlenose and 50 humpback group sightings for analyses. Maps of dolphin distribution were constructed in a similar way as when calculating the size of study area (see above). For every 100 × 100 m grid cell a dolphin group density value was calculated by drawing a circle with a 150-m diameter around the center of each cell and counting the number of dolphin group sightings inside the circle. The given value was then applied to the grid cell in question. This approach gives smoothed density maps of observed dolphin groups. Density values were then adjusted for survey effort to account for uneven search effort in the study area using the following equation:

$$\hat{y} = y_i + (x_m - x_i)b,$$

where $\hat{y}$ equals the weighted (adjusted) value of density in each specific grid cell, y_i is the observed density in the cell, x_m is the mean value of time spent in each grid cell, x_i is the observed time spent in the specific cell, and b is the slope of the regression line (the number of sightings to survey effort). The regression was highly significant ($r^2 = 0.432$, $F = 714.8$, df $= 940$, $P < 0.001$). The adjustment was carried out with the same smoothing as described in the density maps above.

We created distribution maps of the adjusted bottlenose and humpback dolphin group sighting densities. The maps show areas with densities of 1–24 and 25 or more dolphin group sightings per km^2. We also plotted the adjusted density of tourist boat sightings (*i.e.*, dolphin groups with tourist boats present) in the same way as the dolphin group distributions. We then calculated the spatial overlap (percentage) between distributions of bottlenose and humpback dolphin groups, and between the tourist boats and the two species of dolphins, respectively.

We further investigated the distribution of bottlenose and humpback dolphin sighting locations relative to depth and distance to shore. A non-parametric Mann-Whitney *U* test was used to test for differences in depth and distance to shore between bottlenose and humpback dolphin group locations. Statistical tests were performed in Statistica (StatSoft 1999) and the significance level for tests was set at $\alpha = 0.05$.

Behavior

To investigate the significance of areas with high group density ($\geq$25 dolphin group sightings per km^2) behavioral activity budgets (the proportion of groups that were traveling, resting, foraging, or socializing) were calculated for both dolphin species. The predominant behavior of the groups (groups with tourist boats present excluded) was used for this analysis. For each dolphin species we tested if the proportion of behavioral activities was different between high group density areas and the remaining study area in a contingency table analysis (Siegel and Castellan 1988). The standardized residuals were examined to reveal differences (Siegel and Castellan 1988).

RESULTS

Population Estimates

Dolphins were encountered in the study area on 122 of the 131 d that were spent at sea throughout the study. In total we encountered 186 bottlenose dolphin groups and 56 humpback dolphin groups during this study. The latest population estimates (from 2002) based on the mark–recapture analyses were 136 (log-normal 95% CI 124–172) for the Indo-Pacific bottlenose dolphins and 63 (log-normal 95% CI 57–95) for the humpback dolphins, in the 26 km^2 study area. Table 2 shows the adjusted population estimates and the model used for each year between 1999 and 2002 as derived from MARK.

Table 2. Adjusted estimates for total population size. Models used were Mt, time- Mh, heterogeneity-, and Mth, time-, and heterogeneity-dependant capture probabilities. "No estimate" indicates that there were not enough data available to calculate estimates.

Species	Year	Model	Adjusted estimate	95% log-normal CI
Bottlenose	1999	Mth	150	142–172
	2000	Mth	153	142–183
	2001	Mh	179	167–212
	2002	Mth	136	124–172
Humpback	1999	Mt	58	56–79
	2000		No estimate	
	2001	Mh	65	62–102
	2002	Mh	63	57–95

The median group size of bottlenose dolphins in the study area varied between 8 and 21 for the different survey years. The humpback dolphin groups were smaller with a median group size between 5 and 9.

Residency

The cumulative curve of identified marked dolphins indicated that the total available number of identifiable animals in the study area were identified during each field season and that the number of additional animals identified in subsequent years were few (Fig. 2). A large number of the identified dolphins were resighted between years. Of the 91 marked bottlenose dolphins identified in 1999, 80% were sighted in 2000, 77% in 2001, and 60% in 2002. Of the 19 humpback dolphins identified in 1999, 42% were re-identified in 2000, 94% in 2001, and 68% in 2002. The number of days that an individual dolphin was sighted during the study varied from 1 to 57 for the bottlenose dolphins and 1 to 19 for the humpback dolphins (Fig. 3). Further, 46 marked bottlenose dolphins were identified in September 2002 of which 41 were recaptures of previously known individuals. The remaining five marked individuals had not been identified previously.

Study Area and Patterns of Distribution

The calculated 26 km^2 study area and its location is shown in Figure 1. Analyses of spatial densities, corrected for survey effort, showed that bottlenose dolphin groups utilized 8% (1.7 km^2) and humpback dolphins about 2% (0.5 km^2) of the 26 km^2 study area, at the high spatial density level ($\geq$25 dolphin group sightings per km^2) (Fig. 4a, b). Including also a low spatial density level (1–24 dolphin groups sighting

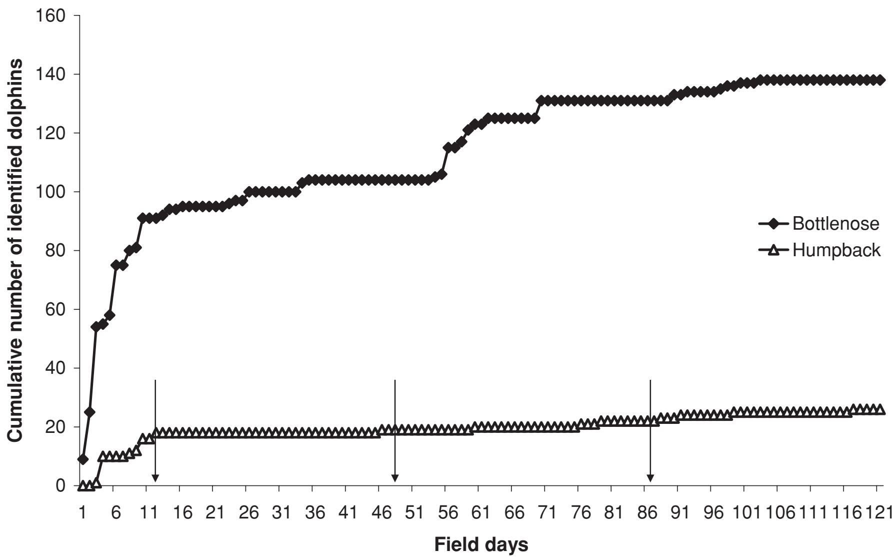


Figure 2. Cumulative discovery curve for the marked dolphins. Arrows on the x-axis indicate the start of the year 2000, 2001, and 2002 field seasons, respectively.

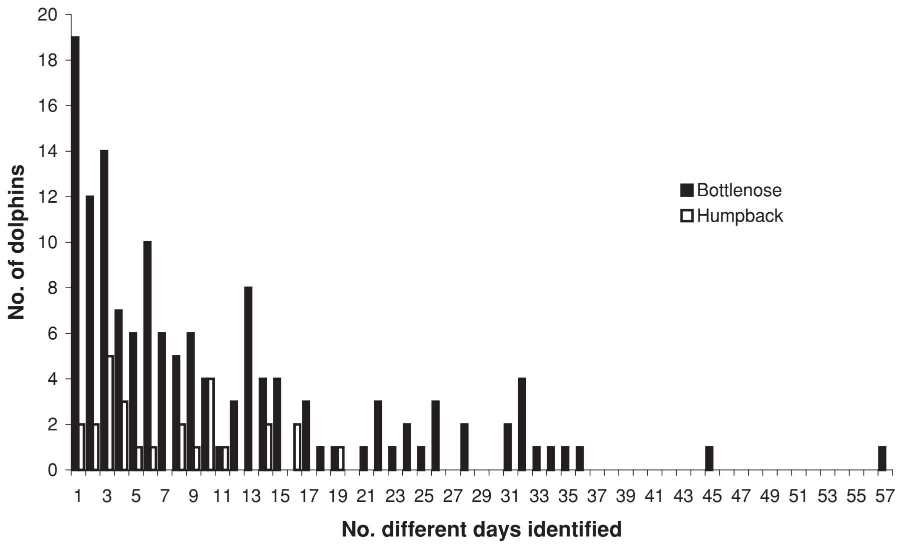


Figure 3. Frequency distribution of the number of times individual Indo-Pacific bottlenose and humpback dolphins were identified during 1999–2002.

per km^2) the bottlenose dolphins used 11.5% (3.0 km^2) and humpback dolphins about 6% (1.6 km^2) of the study area (Fig. 4a, b).

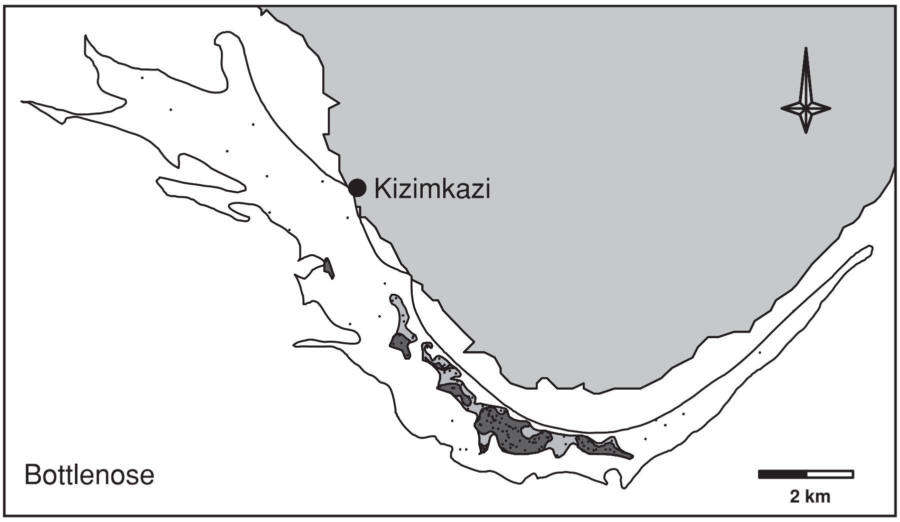
Bottlenose dolphin groups were found significantly further from shore (Mann-Whitney $U = 2{,}112$, bottlenose $n = 186$ and humpback $n = 56$, $P < 0.0001$) and at greater depths (Mann-Whitney $U = 2{,}837$, bottlenose $n = 169$ and humpback $n = 56$, $P < 0.001$) than humpback dolphin groups. The bottlenose dolphins were encountered throughout the study area (median depth 14 m, min–max: 4–52 m, median distance from shore 1,120 m, min–max: 490–3,300 m) whereas the distribution of the humpback dolphin groups was restricted to a median distance of 830 m (min–max: 200–1,550 m) from the shore line and a median water depth of 11 m (min–max: 2–26 m). The two species' distributions had a 35% overlap (at the low spatial density level).

The dolphin tourism activities were concentrated to a 1.9 km^2 area, of these 1.2 km^2 constituted a high spatial density level ($\geq$25 dolphin group sightings with tourism per km^2) (Fig. 4c). The tourism activities overlapped with the areas used by bottlenose and humpback dolphins by 44% and 27%, respectively.

Behavior

The bottlenose dolphin groups were traveling less and socializing more frequently within the high-density area than in the rest of the study area (contingency table analysis $\chi^2 = 9.68$, df = 3, $P = 0.02$) (Fig. 5a). Outside the high-density area ($n = 42$), 40% of the groups were traveling, 38% resting, 17% foraging, and 5% socializing. In the high-density area ($n = 76$) fewer dolphin groups were traveling and instead more groups were socializing (21% traveling, 30% resting, 32% foraging, and 17% socializing) (Fig. 5a). The proportion of groups foraging was higher within

(a)



(b)

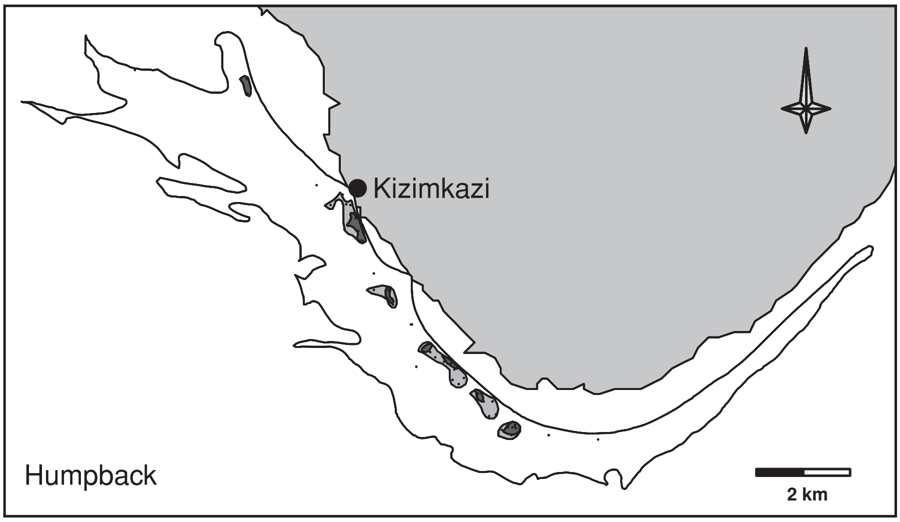


Figure 4. Dolphin group density distribution maps (adjusted for effort) of (a) Indo-Pacific bottlenose dolphin groups, (b) Indo-Pacific humpback dolphin groups, and (c) tourist boats in the 26 km^2 study area off the south coast of Zanzibar, East Africa. For (a) and (b), the lighter-shaded grey areas represent 1–24 dolphin group sightings per km^2 throughout the study and the darker grey $\geq$25 dolphin group sightings per km^2, respectively. For (c), the lighter and darker grey areas represent 1–24 and $\geq$25 dolphin groups with tourist boats per km^2, respectively. The small black dots indicate sighting locations of dolphin groups in (a) and (b), and dolphin groups with tourist boats (c).

(c)

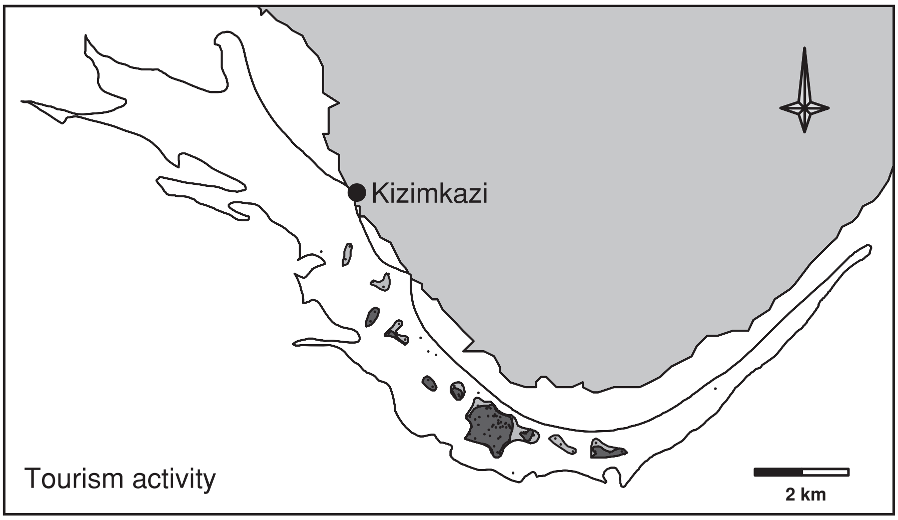


Figure 4. Continued.

the high-density area although the difference was not significant. There was no significant difference (contingency table analysis $\chi^2 = 0.92$, df $= 3$, $P = 0.82$) between the activity budgets for the humpback dolphins within ($n = 22$) or outside the high-density areas ($n = 19$) (Fig. 5b). However, the proportion of groups resting was higher (27% compared to 16%) within the high-density areas, although this could not be shown statistically.

Discussion

This study has supplied some of the first estimates of population size for east African dolphin populations. Off the south coast of Zanzibar, the populations of Indo-Pacific bottlenose and humpback dolphins are small and resident (Table 2). The results show that both species actively use only small parts of their coastal habitat and that the bottlenose dolphins were socializing and foraging to a larger extent in particular areas. This is important information for understanding the ecology of the species and for guiding management decisions necessary for the conservation of the dolphins off the south coast of Zanzibar.

Without more detailed information on individual animals' ranging patterns it is unclear how the study area relates to the animals' home ranges. Of the total 173 dolphin groups used in the population size estimates, only four were encountered outside the study area. However, the animals in these groups had previously been identified within the study area. This indicates that the estimates for the two dolphin populations relate to the calculated study area and further that the study area underestimates the home range of some individuals in the populations. The photo-identification data support the hypothesis that dolphins of both species were resident

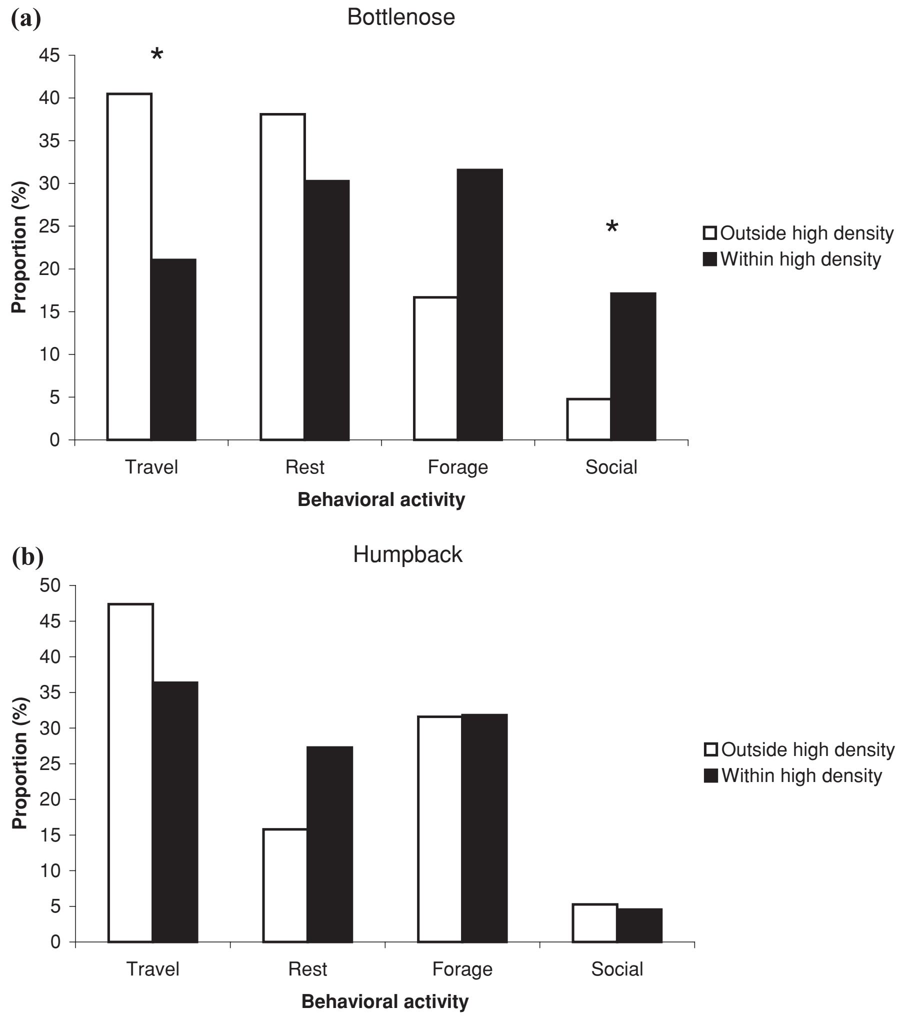


Figure 5. Behavioral activity budgets for (a) bottlenose dolphin groups and (b) humpback dolphin groups based on the proportion of sighted dolphin groups engaged in respective behavioral activity (travel, rest, forage, and social) in the high-density areas ($\geq$25 groups per km^2) compared to the rest of the study area. Significant differences are indicated with*.

in the study area both between and within years. Further, during the field trip in September 2002, all but five marked bottlenose dolphins were previously known individuals, indicating that some of the animals may be year round residents in the area.

Both bottlenose and humpback dolphins preferred smaller areas within their coastal habitat. A higher proportion of bottlenose dolphin groups were socializing and foraging in the high-density areas than outside these areas. This indicates that these high-density areas may be important to the population, particularly for breeding and foraging activities. Areas outside the high-density areas should however not be regarded as insignificant because a high proportion of bottlenose dolphin groups rested both outside and within the high-density areas. By using a different approach (harmonic mean transformation) Ingram and Rogan (2002) identified two potential critical areas for a population of common bottlenose dolphins (*Tursiops truncatus*) in a 150 km^2 area off the west coast of Ireland. Similar to our study, Ingram and Rogan (2002) concluded that the identified areas were primarily used by the dolphins for foraging-related activities.

The humpback dolphins were found closer to shore and in shallower water than the bottlenose dolphins indicating spatial separation between the species in the study area. This distribution of humpback dolphins is similar to that described in other areas such as Algoa Bay, South Africa, where the humpback dolphins seldom venture further than 500 m from shore (Karczmarski *et al.* 2000).

Hunting marine mammals is illegal in Tanzania and no hunt has officially been conducted off the south coast of Zanzibar since 1996. There are no records of the magnitude of this hunt or for how many years it had been carried out but the last hunt in 1996 took 23 specimens in one season. This would represent an annual mortality close to 12% for a combined population estimate of 199 animals for the two dolphin species in the area. This is much higher than the 2% anthropogenic removal that the Scientific Committee of the International Whaling Commission (IWC) considers to be unsustainable for small cetacean populations (IWC 1996). It is therefore likely that the hunt has had a significant negative impact on the status of the dolphins off the south coast of Zanzibar.

Bycatch in fishing gear has been recognized as the most serious threat to small cetaceans world wide and in the east African region (Anonymous 1998, Read *et al.* 2006). Incidental catch of both Indo-Pacific bottlenose and humpback dolphins has been documented in gillnets off the south coast of Zanzibar (Amir *et al.* 2002). There are currently no estimates of the magnitude of this bycatch, but given that even three bottlenose and two humpback dolphins taken per year would exceed 2% of the respective population estimates, it is very likely that bycatch represents a threat to the dolphins in the area.

Dolphin tourism is an additional threat facing the dolphin populations off the south coast of Zanzibar. These activities, which mainly target the bottlenose dolphins, have been shown to affect dolphin behavior in this area (Englund and Berggren 2002, Stensland 2004) as well as in other regions (see *e.g.*, Lusseau 2003, Constantine *et al.* 2004). The tourism activities in our study area overlap geographically with the distribution areas of bottlenose and humpback dolphins by 44% and 27%, respectively. Tourist boats focus their activities in the high-density areas where a high proportion of dolphins forage and socialize (Fig. 5a). Due to this spatial overlap between tourist activities and areas where animals are foraging and socializing, the dolphins may be subject to disturbance that can have negative effects on both individual and population level. If foraging individuals are repeatedly interrupted by tourism activities it is possible that this may compromise survival of the affected individuals. Interruption by boats and swimmers during sexual activities, which is often included in socializing, may lower the rate of successful mating attempts which can have a long-term effect on populations.

On a positive note the dolphin tourism off southern Zanzibar has directly replaced an unsustainable hunt for dolphins in the area and now forms a socioeconomic alternative. This is something which has been rarely observed elsewhere. The research conducted in the area has increased the knowledge on the population parameters such as population size, distribution, behavior, demography, and stock structure. It has also succeeded in raising the local people's awareness of the dolphins and we are hopeful that this bodes well for a sustainable future for these animals.

In conclusion, given the relatively small population sizes, limited distribution ranges, and the magnitude of anthropogenic threats facing the Indo-Pacific bottlenose and humpback dolphins in the area, it is clear that immediate conservation measures are needed such as mitigation of the bycatch and implementation of tourism guidelines. This is critical if the negative impact on the species is to be minimized and the dolphins are to continue to represent a socioeconomic resource in the region.

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Literature Cited

Allen, M. C., A. J. Read, J. Gaudet and L. S. Sayigh. 2001. Fine-scale habitat selection of foraging bottlenose dolphins *Tursiops truncatus* near Clearwater, Florida. Marine Ecology Progress Series 222:253–264.

Amir, O. A., P. Berggren and N. S. Jiddawi. 2002. The incidental catch of dolphins in gillnet fisheries in Zanzibar, Tanzania. Western Indian Ocean Journal of Marine Science 1:155–162.

Anonymous. 1998. Report of the 49th meeting of scientific committee of the International Whaling Commission (IWC) in Bournemouth, United Kingdom. Report of the International Whaling Commission 48:53–118.

Borobia, M. 1997. Small cetaceans of eastern, western and central Africa regions: A summary report. Paper SC/49/SM48 available from the Secretariat of the International Whaling Commission.

Bräger, S., J. A. Harraway and B. F. J. Manly. 2003. Habitat selection in a coastal dolphin species (*Cephalorhynchus hectori*). Marine Biology 143:233–244.

Burnham, K. P., D. R. Anderson and G. C. White. 1995. Selection among open population capture-recapture models when capture probabilities are heterogeneous. Journal of Applied Statistics 22:611–624.

Chilvers, B. L., and P. J. Corkeron. 2003. Abundance of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, off Point Lookout, Queensland, Australia. Marine Mammal Science 19:85–95.

Connor, R. C., R. S. Wells, J. Mann and A. J. Read. 2000. The bottlenose dolphin. Pages 91–126 *in* J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead, eds. Cetacean societies: Field studies of dolphins and whales. The University of Chicago Press, Chicago, IL.

Constantine, R., D. H. Brunton and T. Dennis. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. Biological Conservation 117:299–307.

ENGLUND, A., AND P. BERGGREN. 2002. The impact of tourism on Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Menai Bay, Zanzibar. Paper SC/54/WW1 available from the Secretariat of the International Whaling Commission.

HAMMOND, P. S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. Report of the International Whaling Commission (Special Issue 8):253–282.

HAMMOND, P. S. 1990. Capturing whales on film—estimating cetacean population parameters from individual recognition data. Mammal Review 20:17–22.

INGRAM, S. N., AND E. ROGAN. 2002. Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. Marine Ecology Progress Series 244:247–255.

IWC. 1996. Report of the1995 Scientific International Whaling Commission. Report of the International Whaling Commission 46:49–97 + Annex H.

JEFFERSON, T. A. 2000. Population biology of the Indo-Pacific hump-backed dolphin in Hong Kong waters. Wildlife Monographs 144:1–65.

KARCZMARSKI, L. 1999. Group dynamics of humpback dolphins (*Sousa chinensis*) in the Algoa Bay region, South Africa. Journal of Zoology 249:283–293.

KARCZMARSKI, L., V. G. COCKCROFT AND A. MCLACHLAN. 2000. Habitat use and preferences of Indo-Pacific humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. Marine Mammal Science 16:65–79.

LUSSEAU, D. 2003. Effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. Conservation Biology 17:1785–1793.

MANN, J. 1999. Behavioral sampling methods for cetaceans: A review and critique. Marine Mammal Science 15:102–122.

MANN, J., AND B. SMUTS. 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). Behaviour 136:529–566.

OTIS, D. L., K. P. BURNHAM, G. C. WHITE AND D. R. ANDERSON. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:1–135.

READ, A. J., K. W. URIAN, B. WILSON AND D. M. WAPLES. 2003. Abundance of bottlenose dolphins in the bays, sounds, and estuaries of North Carolina. Marine Mammal Science 19:59–73.

READ, A. J., P. B. DRINKER AND S. P. NORTHRIDGE. 2006. Bycatch of marine mammals in U.S. and global fisheries. Conservation Biology 20:163–169.

SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd edition. Charles Griffin & Co., London, U.K.

SIEGEL, S., AND N. J. CASTELLAN. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, NY.

SMOLKER, R. A., A. F. RICHARDS, R. C. CONNOR AND J. W. PEPPER. 1992. Sex differences in patterns of association among Indian-Ocean bottlenose dolphins. Behaviour 123:38–69.

STATSOFT. 1999. STATISTICA 5.5 for Windows computer program manual. StatSoft Inc., Tulsa, AZ.

STENSLAND, E. 2004. Behavioural ecology of Indo-Pacific bottlenose and humpback dolphins. Doctoral thesis, Department of Zoology, Stockholm University, Sweden. 117. pp.

STENSLAND, E., P. BERGGREN, R. JOHNSTONE AND N. JIDDAWI. 1998. Marine mammals in Tanzanian waters: Urgent need for status assessment. Ambio 27:771–774.

TORRES, L. G., P. E. ROSEL, C. D'AGROSA AND A. J. READ. 2003. Improving management of overlapping bottlenose dolphin ecotypes through spatial analysis and genetics. Marine Mammal Science 19:502–514.

WELLS, R. S., AND M. D. SCOTT. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-recapture techniques. Report of the International Whaling Commission (Special Issue 12):407–415.

WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Suppl.:120–138.

WILLIAMS, J. A., S. M. DAWSON AND E. SLOOTEN. 1993. The abundance and distribution of bottlenosed dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. Canadian Journal of Zoology 71:2080–2088.

WILSON, B., P. M. THOMPSON AND P. S. HAMMOND. 1997. Habitat use by bottlenose dolphins: Seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. Journal of Applied Ecology 34:1365–1374.

WÜRSIG, B., AND M. WÜRSIG. 1977. The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). Science 198:755–756.

WÜRSIG, B., AND T. A. JEFFERSON. 1990. Methods of photo-identification for small cetaceans. Report of the International Whaling Commission (Special Issue 12):43–52.

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