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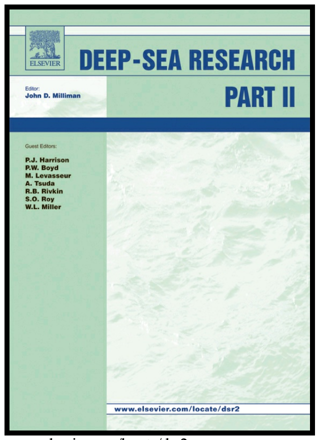

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Estimating the cumulative effects of the nature-based tourism in a coastal dolphin population from southern Kenya

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Abstract

Due to the growth of nature-based tourism worldwide, behavioural studies are needed to assess the impact of this industry on wildlife populations and understand their short-term effect. Tourism impact on dolphin populations remain poorly documented in developing countries. This study investigates the effects of nature-based tourism on the behaviour of the Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in southern Kenya. We used Markov chain models to estimate transition probabilities between behavioural states in the presence and absence of tourist boats, and assess the overall behavioural budgets. Based on these data and the tourism intensity in the area, we quantified the potential tourist boat disturbance over the period 2006-2013. Our results demonstrated that tourist boat interactions affected dolphins' behavioural budgets, with a significant decrease in the overall amount of time travelling and an increase in diving. The average duration of travelling and resting decreased significantly in the presence of boats. Although the cumulative tourism exposure was not significant for the dolphin population at their current levels, these impacts should be taken into consideration with the potential tourism growth in the area. This is particularly important if tourism reaches periods of high intensity, as we have shown that these periods could have a significant impact for the species, particularly where home-range and core areas are highly overlap by this activity. Understanding the effect of human disturbance variations from previous years may help to predict the consequences on dolphin populations, towards achieving a more ecological and economic sustainability of the activity.

Keywords: tourism exposure, marine mammals, behavioural disturbance, Kenya

1 Introduction

Over the last decades, the impact of human disturbance on wildlife populations has increased worldwide due to the growing of nature-based tourism, which involves tours to national parks and wilderness areas where a major percentage of the world's biodiversity is concentrated (Balmford et al., 2009; Olson et al., 2001). Consequently, human-wildlife interactions are becoming more common with potentially severe impacts on the conservation status of targeted species (e.g. Bejder et al., 2006). In marine ecosystems, whale-watching is one of the main drivers of nature-based tourism, and the study of human disturbance on different aspects of the biology and ecology of those species have been the focus of growing attention in the last years (Higham et al., 2014). Indeed, increased exposure to high levels of boat-based tourism has been shown to cause behavioural disturbance, such as changes in breathing rates (Janik and Thompson, 1996), diving times (Ng and Leung, 2003), speed (Nowacek and Wells, 2001), swimming directions (Lemon et al., 2006), group formation (Bejder et al., 1999) and specific behavioural states (Christiansen et al., 2010; Lusseau, 2003). In addition, repeated short-term behavioural impacts can have cumulative negative effects on an animal's behavioural budget, which is directly related to its energy budget (Christiansen et al., 2013). Such cumulative effects can in turn lead to long-term negative effects on individual vital rates, such as decreased female reproductive success (Bejder, 2005; Tezanos-Pinto et al., 2013). At the population-level, negative effects of human disturbance, resulting from changes in vital rates, would depend on the proportion of the population that are subjected to the various levels of disturbance. However, as disturbances are likely to vary across space and time, it might lead to differences in impacts between individuals within a population, and also seasonally (Christiansen et al., 2015; Pirotta et al., 2014).

Whale-watching activities have grown globally at an annual rate of 12% through the 1990s, showing a much higher rate of increase than that of the overall tourism industry (Hoyt, 2001; O'Connor et al., 2009). The whale-watching industry had a total of 13 million whale-watchers globally in 2008, benefiting coastal communities with an estimated $US 2.1 billion, and generating more than 13,000 jobs(O'Connor et al., 2009). The increasing tourists' preference for whale-watching activities around the world suggests the further potential of this industry and the possible benefits for local communities. Indeed, Cisneros-Montemayor et al. (2010) pointed out that an extra $413 million and 5,700 jobs could be generated within the current whale-watching industry, with half of these potential benefits created in developing countries (as defined by the UN; United Nations Development Programme, 2007). In Kenya, the whale-watching industry has grown from 8,300 tourists in 1997 to almost 42,500 in 2013, which equals an annual growth rate in tourist numbers of nearly 11% (Kenya Wildlife Service, unpublished data). The highest number of tourists was recorded in 2006, when more than 60,000 visitors went whale-watching. However, due to political unrest in Kenya the tourism industry suffered multiple drops along the period between 1997 and 2013, with up to a 53% decline on visitors between some years (Kenya Wildlife Service, unpublished data).

A small population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) inhabiting Kisite-Mpunguti Marine Protected Area (KMMPA) is the main focus of the largest dolphin-watching industry in Kenya (Hoyt, 2005; Pérez-Jorge et al., 2015). This MPA attracts the largest number of visitors of all Kenya's marine parks and, in turn, this MPA provides the highest revenue along the Kenyan coast (Kenya Wildlife Service, 2013). Over 50% of these tourists were mainly interested in dolphin-oriented trips, highlighting the importance of dolphin-watching as one of the main economic activities for local communities (unpublished data; Emerton and Tessema, 2001). Dolphin tourism in KMMPA began in the early 1990s and has grown up to a total of 27 tourist boats registered in 2012, with the capacity to carry up to 48 tourists per trip (Kenya Wildlife Service, 2013). The industry has been operating year round, with peak seasons during the months of August and December-January, and a low season during the rainy period of April to June. In the early years of the dolphin-watching industry in KMMPA, the industry was developed with limited management control, as the dolphin-watching activity was perceived to be non-harmful to the animals, and therefore did not require additional regulations (Hoyt, 2008; O'Connor et al., 2009). Due to the rapid growth of the industry between 2004 and 2006, the Kenya Wildlife Service (KWS), in collaboration with international agencies, developed a voluntary code of conduct in 2007 (Convention of Migratory Species, 2007). This code recommended boat operators to keep a minimum distance of 100m from dolphins and suggested a limit of two boats at any given time around the animals. The code of conduct also advised boats to spend no more than 20 minutes with the same dolphin group at a time, and also specified the best manoeuvres to approach the animals. Another major change for the dolphin-watching industry was the prohibition of swimming with dolphins. The code of conduct was implemented to mitigate possible impacts from the dolphin-watching activity. However, it was based on codes for other population from other parts of the world, and lacked scientific information on the targeted population.

We investigated the effects of the nature-based tourism on the behaviour of the Indo-Pacific dolphin population in southern Kenya. Specifically, we firstly used Markov chains analysis to estimate the probability of dolphins changing between different behavioural states (e.g., travelling, diving, socialising and resting) in the presence and absence of tourist boats, from which we estimated changes in the dolphins behavioural budget (Lusseau, 2003). Secondly, we investigated the effect of the current dolphin-watching intensity in KMMPA on the cumulative behavioural budgets of the dolphin population, and quantified the tourism intensity on the area for the 2006-2013 period, to evaluate the potential disturbances caused by this activity these years. Finally, we analysed the spatial overlap of dolphin and tourist boat distribution based on kernel density estimations in order to determine areas where tourist boat impacts could be more significant. Our study aims to assess the impact of nature-based tourism on the behavioural ecology of the Indo-Pacific bottlenose dolphin, and understand which effects must be managed to ensure that the local-dolphin industry is sustainable

2 Material and methods

2.1 Study area

This study was conducted on the International Union for the Conservation of Nature (IUCN) data deficient population of Indo-Pacific bottlenose dolphins inhabiting the Kisite-Mpunguti Marine Protected Area (KMMPA, 04°04'S - 39°02'E), in southern Kenya (Fig. 1). Recent capture-recapture modelling studies estimated a small population size for the area ranging from 20 (95% CI: 11-36) to a maximum of 102 individuals (95% CI: 77-138) (Pérez-Jorge et al., 2016). Abundance estimations remained roughly stable from 2006 to 2009, with a mean of 65 dolphins (SE: 7.06). The presence of this species in the study area is strongly influenced by dynamic (oceanic fronts) and static predictors (shallow areas, distance to reefs, distance to the 100m isobath), with a significantly higher occurrence and abundance of dolphins within the KMMPA (Pérez-Jorge et al., 2015).

2.2 Data collection

Non-systematic boat-based surveys were carried out between the months of October and December 2011, 2012 and 2013. During this part of the year the sea is calm, the wind is light and rainfall is low, which makes the conditions ideal for behavioural surveys, as group-follows can be carried out for extended periods of time. Behavioural data from dolphin groups was collected from a 9.5m dhow, a traditional wooden sailing vessel, with one 15 HP two-stroke outboard engine. A dolphin group was defined as the total number of individuals encountered, moving in the same direction or engaged in the same activity, within 100 metres of each other (Wells et al., 1987). Once a group was sighted, the research vessel was operated in a careful way at slow speed, avoiding changes in gear and staying slightly behind or on the side of the dolphin group to minimise disturbance. Thus, focal groups were followed at a distance ranging from 20 to 100m, both in the presence or absence of tourist boats.

The behaviour of dolphin focal groups was measured using focal-group scan sampling methods (Altmann, 1974). The behavioural state of each focal-group was sampled every 15 minutes and was determined by the activity of the majority (>50%) of the group. We only studied the behaviour of adults and juveniles since calves are dependent on their mothers. The four behavioural states recorded on this study were travelling, socialising, diving and resting (Table 1) (Lusseau, 2003). Behavioural surveys ended when weather conditions deteriorated or the focal-group was lost. Since the distance at which dolphin groups respond to tourist boats was not known, two different threshold values of distance were used to define impact situations: I) when one or more boats approached within 100 meters of the focal group and II) when one or more boats approached within 400 meters of the focal group. The analyses described in the following sections were applied to the data in two separate analyses, based on the two threshold values.

2.3 Behavioural transitions

Markov chains models have been widely used in wildlife ecology, particularly to assess the impact of nature-based tourism on marine mammal populations (Christiansen et al., 2013, 2010; Dans et al., 2012; Lusseau, 2003). Markov chain analysis measures the dependence of the current behavioural state on the preceding behavioural state. We restricted the analysis to include only the previous time step, referred to as a first-order Markov process, since impact interactions lasted on average less time than the 15 minutes scan samples (authors, personal observation; Lusseau, 2003b). To assess the effect of tourist boat interactions on the behaviour of the dolphins, we calculated the probability that a focal-group changed from a preceding to a succeeding behavioural state in the presence (impact) or absence (control) of tourist boats. We first built two-way contingency tables of preceding versus succeeding behavioural states, both for impact and control situations. If no tourist boat was present between two behavioural state samples (either during the first or the second scan sample event), we tallied this transition in a control table. If a tourist boat was present between two samples, this transition was tallied in an impact table. Consistent with other impact studies (Christiansen et al., 2010; Lusseau, 2003; Meissner et al., 2015; Stockin et al., 2008), we used a conservative approach and discarded any behavioural states samples immediately after an impact situation, as the potential impact of the interactions was uncertain and it was not possible to considered the transition as either control or impact. From the contingency tables, the transition probabilities of a dolphin group changing from one behavioural state to another, were calculated for both impact and control contingency tables:

$$p_{ij} = \frac{a_{ij}}{\sum_{j=1}^{n} a_{ij}}, \sum_{j=1}^{n} \mathrm{p_{ij}} = 1,$$

where *i* is the preceding behavioural state, *j* is the succeeding behavioural state, *n* is the total number of behavioural states (i.e. four), a_{ij} is the number of transitions observed from state *i* to *j*, and p_{ij} is the transition probability from state *i* to *j* in the Markov chain. We tested the effect of boat interaction on the transition probability between behavioural states by comparing each control transition to its impact counterpart using a 2-tailed Z-test for proportions (Fleiss et al., 2003).

2.4 Behavioural bout durations

To investigate the effect of tourist boats on the duration of time, in minutes, that dolphins remain in different behavioural states, the average bout length for each behavioural state, t_{ii}, was estimated in the presence and absence of boats from the Markov chains using the mean of the geometric distribution of p_{ii} (Guttorp, 1995; Lusseau, 2003):

$$\mathrm{t}_{ii} = \frac{1}{1 - p_{ii}}$$

with a standard error (SE) of:

$$SE = \sqrt{\frac{p_{ii} \times (1 - p_{ii})}{n_i}}$$

where n_i is the number of samples with *i* as preceding state. We compared the average bout length between control and impact situations using a Student's t-test.

2.5 Behavioural budgets

The proportion of time dolphin groups spent in each behavioural state under both control and impact situations was calculated by Eigen analysis of the two-way contingency tables (Christiansen et al., 2010; Lusseau, 2003; Meissner et al., 2015). Differences between control and impact behavioural budgets were tested using a goodness-of-fit test, and differences in the relative proportion of each state was tested using 2-sample tests for equality of proportions with continuity correction. Finally, 95% confidence intervals were calculated for the estimated proportion of time spent in each behavioural state.

2.6 Cumulative behavioural budget

The impact behavioural budget is an instantaneous measure of the behaviour of dolphin groups during interactions with tourist boats. The proportion of time that dolphin groups spend with tourist boats per day can be added to the previous calculated behavioural budgets to estimate the cumulative diurnal behavioural budget of the dolphin population:

Cumulative budget = (a x impact budget) + (b x control budget)

where *a* is the proportion of time (i.e. daytime hours) that dolphins spend with tourist boats (thus following a behavioural budget similar to the impact budget) and *b* = 1-*a* is the proportion of time that dolphins spend without tourist boats (thus following a behavioural budget similar to control situations) (Christiansen et al., 2010; Meissner et al., 2015). By comparing the cumulative behavioural budget of the dolphins to their control behavioural budgets, we can investigate the effect of tourist boats on the dolphins' diurnal behavioural budgets. By artificially varying the proportion of time per day that dolphins spend with boats (a) from 0 (dolphins spend 0% of their time with boats) to 1 (dolphins spend 100% of their time with boats), we can find out at what boat exposure the dolphins behavioural states are significantly affected. We used a 2-tailed Z-test for proportions for each behavioural state to test the significant differences between the cumulative behavioural budgets and control budgets, assuming that the observed effect size does not vary with daytime exposure rate (Lusseau, 2004).

2.7 Seasonal and yearly effects

To investigate seasonal and yearly variations in the intensity of dolphin-watching tourism in KMMPA and its effect on the dolphins' cumulative behavioural budget, we first estimated the tourist boat intensity during the study period (October to early December). We used the number of boats entering the KMMPA during these months for the period 2011-2013 to calculate a baseline number of boats corresponding to the levels of boat intensity during our study period. We did not include the month of December in the analysis, as behavioural surveys were conducted mainly in the first week of the month and the highest number of boats during this month occurs during the Christmas holiday break.We then used monthly data on the number of tourist boats between 2006 and 2013, provided by the Kenya Wildlife Service (KWS, unpuslibhed data), to calculate dolphins' cumulative behavioural budget for each month and year to assess the seasonal and yearly effects of tourism boats on the behaviour of the dolphins. The estimated exposure of dolphins to tourism interactions during the 2006-2013 period was based on a fixed percentage estimated from the proportion of observed impact transitions relative to the total number of behavioural transitions.. All analyses were performed using R 2.15.3 (R Development Core Team 2013), and the packages 'plyr' (Wickham, 2011), 'reshape2' (Wickham, 2007), 'ggplot2' (Wickham, 2009) and 'markovchain'(Spedicato et al., 2015).

2.8 Spatio-temporal overlap between dolphins and tourist boats

We used a kernel analysis approach to identify spatial overlap areas between dolphins and tourist boats distribution, based on sightings data collected from January 2009 to December 2013 using the survey methodology described by Pérez-Jorge et al., (2015). Kernel density estimators are extensively used to quantify utilization distributions, or home range, for marine and terrestrial animal populations (Kie et al., 2010; Laver and Kelly, 2008). For this, we applied a fixed kernel estimator with contours of 50% and 95% that estimated core and home-range areas respectively (Louzao et al., 2012; Soanes et al., 2013; Worton, 1989). An important decision in home-range analysis is to choose the appropriate smoothing parameter as this could bias the estimate of home-range size. In order to find this value, we sequentially reduced in 0.10 increments the reference bandwidth (*href*) until getting contiguous rather than disjoint 95% kernel polygons (Kie, 2013). We also took into account natural barriers such as islands and mainland, which often prevent dolphins from moving freely in all directions and lead to over-estimation of the core and home ranges areas. We conducted the home-range analysis through ArcMap 10.1 (ESRI, 2011; MacLeod, 2014).

To calculate the proportion of home range overlap between dolphins and tourist boats the following formula was used (Fieberg and Kochanny, 2005; Hauser et al., 2014):

$HR_{i,j} = A_{i,j} / A_i$

where $HR_{i,j}$ is the proportion of population i's (dolphin population) home-range that is overlapped by population j's home-range (tourist boats), such that A_i is the total home-range area of the dolphin population, and $A_{i,j}$ is the area of overlap between the dolphin population and the area used by the tourist boats. We applied the same formula to estimate the proportion of core area (50% contour) overlap. We are aware that the distribution of dolphins and boats may differ temporally, e.g between seasons. However, we could not explore this seasonal effect due to small sample sizes mainly during autumn months (April to June) (Table A1), since 30 sightings is the minimum number suggested to obtain a sufficiently accurate estimate (de Azevedo and Murray, 2007; Seaman et al., 1999). To minimise the effect of sample size, we randomly selected 1,000 times an equal number of dolphin and tourist boat sightings per season to obtain a spatial overlap value for the whole 2009-2013 period. Seasons were defined as: summer (January to March), autumn (April to June), winter (July to September) and spring (October to December). Finally, we tested for differences between seasons using a Kruskal-Wallis (KW) test. Kernel density analyses were performed using the 'sp' (Bivand et al., 2013), 'fields' (Nychka et al., 2015), 'ggplot2' (Wickham, 2009) and 'adehabitatHR' packages (Calenge, 2006) in R.

3 Results

We spent 180 hours over 76 days following a total of 86 focal groups of Indo-Pacific bottlenose dolphins (Fig. 1). After treating the data as described in the methods, we recorded 567 behavioural transitions, of which 204 (36%) and 363 (64%) were considered as impact and control, respectively. During October-December 2011-2013, dolphins spent 30% (54 hours) of the time surrounded by tourist boats within a radius of 400 meters. The number of boats interacting with the same dolphin group varied from one to nine at a time (mean ± SE: 2 ± 0.10).All parameter estimates for impact sequences at 100 and 400 meters were found the same significant differences at both thresholds (Figs 2-5; Figs A1-4), and therefore it is assumed that there were no differences in effect (i.e. effects start when boats were at least 400m from dolphins).

3.1 Behavioural transitions

The presence of tourist boats around dolphins had a significant effect on the behavioural state transitions (χ^2=54.04692, df= 9, $p < 0.001$), but this effect was not uniform throughout all transitions (Fig. 2). The transition probability from the preceding behavioural state travelling to succeeding behavioural state travelling significantly decreased by 12% in the presence of boats

(χ^2=4.9463, df= 1, p = 0.02). In contrast, the transition probability from travelling to diving significantly increased by 8% when interacting with boats (χ^2=3.9819, df= 1, p = 0.04) (Fig. 2).

3.2 Behavioural bout durations

The average bout length for travelling and resting dolphins significantly decreased by 42.8% (37.72 min; t = 47.58, df = 270, p < 0.001) and 15.0% (4.93 min; t = 3.22, df = 96, p = 0.001), respectively, in the presence of tourist boats (Fig. 3).

3.3 Behavioural budgets

The proportion of time spent in each behavioural state changed significantly during boat interactions (χ^2=19.91, df= 3, p < 0.001). Travelling, being the dominant behaviour state both during control and impact situations, was significantly reduced from 61% to 46% in the presence of boats (χ^2=11.5216, df= 1, p < 0.001) (Fig. 4). Conversely, diving increased from 17 to 27% as an effect of boat presence (χ^2=11.5216, df= 1, p < 0.001).

3.4 Cumulative behavioural budget

The dolphins cumulative travelling and diving behaviours were significantly disrupted when dolphins spent 50 and 58% of time with boats, respectively, while socialising and resting were not affected (Fig. 5). During October-December 2011-2013, we observed the tourist boat intensity to be 30% of daytime hours, which falls below the threshold values for travelling and diving. The current boat intensity of 30% corresponded to a median of 160 boats (SE = 8.69) per month (Table A2). Based on this relationship, we identified the month of December and the years 2006 and 2007 as the highest periods of boat intensity, and consequently the periods that had the highest impact on the dolphins' cumulative behavioural budgets (Fig. 6). Along these high intensity intervals, tourist boat exposure was up to 5 times higher than during the low tourist season (May-June) (Fig. 6).

3.5 Spatio-temporal overlap between dolphins and tourist boats

Core and home-range areas of dolphins and tourist boats were calculated based on a total of 775 and 1564 sightings, respectively (Table A1). The dolphins' home-range area (95% of utilization distribution) was estimated without natural barriers to be 68.99 km^2 for the whole period 2009-2013 (Fig. 7). At the 50% of utilization distribution, the core area was estimated to be 11.06 km^2 without natural barriers. For tourist boats, total home-range and core areas were estimated as 44.20 and 13.14 km^2, respectively (Fig. 7). This estimated tourism boat activity varied spatially across the study area, with the highest intensity concentrated within the boundaries of the MPA. The proportion of the dolphins home-range area (95%) that overlapped with the area used by the tourist boats ranged from 0.13 to 0.94 per season, with a mean of 0.46 (SD = 0.25) for the whole year. The core area overlap was very similar, ranging from 0.14 to 0.94 per season, with a mean of 0.44 (SD = 0.18) for the whole year . We found significant differences in the overlapping proportion between seasons, at both 95% (KW = 3195.675, df = 3, p-value < 0.001) and 50% levels (KW = 2951.607, df = 3, p-value < 0.001). The highest overlap values for home-range were encountered during the winter season, whereas the highest overlap for core areas was found during the spring season (Fig. 8). The lowest overlap was during autumn (April to June), at both home-range and core area levels.

4 Discussion

This study provides an assessment of the current, past and also the potential future impact of nature-based tourism on the behaviour of Indo-Pacific bottlenose dolphins in southern Kenya. Our analyses show that tourist boat presence significantly affected the behaviour of the local dolphin population by negative affecting travelling behaviour, while increasing diving behaviour. During spring the intensity of the dolphin tourism was sufficiently high to significantly affect the dolphins' cumulative behavioural budget. Our study, therefore, emphasizes the importance of considering the seasonal and yearly variations when assessing the effect of nature-based tourism on marine mammal populations.

4.1 Behavioural effects of tourism

The significant increase in transition probability from travelling to diving may represent a mitigation strategy by dolphins to avoid tourist boats by altering their diving patterns (Janik and Thompson, 1996; Lusseau, 2003; Nowacek and Wells, 2001; Williams et al., 2002). These behavioural changes following boat interactions affected not only the transition between behavioural states, but also the behavioural budget of the dolphins, with a substantial decrease in the overall amount of time travelling and an increase in diving behaviour. These effects were significant both when considering a threshold of 100 and 400m to define impact situations. This suggests that dolphins responded to approaching boats at least 400m away, which is much further than the recommended minimum distance recommended by the dolphin tourism guidelines in KMMPA (100m). Boat interactions also led to a decrease in the resting bout length of dolphins, which has also been observed in other studies (Lundquist et al., 2012; Lusseau, 2003; Meissner et al., 2015; Stockin et al., 2008). Female dolphins are believed to mainly nurse their calves during resting periods, meaning that a reduction in resting bouts could have serious implications for nursing behaviour (Stensland and Berggren, 2007). To what extent nursing is affected by boat interactions in KMMPA is not known, but should be the focus of future impact studies. Further, it would be worthwhile to extend the study period to also cover other seasons to help determine if dolphins show seasonal variations in behavioural budget which might influence the level of impact that tourism interactions have on their behaviour. It would also be valuable to determine to what extend dolphins are able to compensate from behavioural disturbance at other time periods both diurnally and seasonally.

4.2 Quantifying the spatio-temporal interactions between dolphins and tourist boats

Dolphins are commonly distributed heterogeneously through their main habitats (Sprogis et al., 2015; Stensland et al., 2006), as they tend to aggregate in areas encompassing the resources to survive and reproduce (Gormley et al., 2012). The spatial and temporal variation in human activity can also influence dolphins' habitat use (Chilvers et al., 2003). In southern Kenya, Indo-Pacific bottlenose dolphins experience periods with variable human-disturbance levels due to high heterogeneity in tourism intensity, resulting in different levels of spatial and temporal overlap between tourist boats and dolphins' occurrence. If tourism intensity continues to increase, and as a consequence, the cumulative exposure levels to the population, the most affected individuals could potentially be those dolphins whose habitat preference is situated within and adjacent to the MPA (Christiansen et al., 2015). Although the highest occurrence and abundance of dolphins have been identified within the boundaries of the MPA, this area has shown to be insufficient for the spatial requirement of the species, as important percentage of recurrent and occasional habitats were identified outside the MPA (Pérez-Jorge et al., 2015). Thus, this spatial and temporal variability, both for tourism activity and dolphins occurrence, poses real challenges for mitigation measures aimed at reducing the potential cumulative effects of boat presence on a small dolphin population (Pirotta et al., 2014).

During the study period, dolphins spent around 30% of their time interacting with tourist boats. At this exposure level, there was no significant effect on the cumulative behavioural budget of the dolphins. However, if we consider the tourism intensities during 2006 and 2007, where the highest number of tourists was recorded in Kisite-Mpunguti Marine Protected Area, this population could have been significantly affected. Our results shows that tourism intensity above 180 tourist boats per month can have a significant effect on the cumulative behavioural budget of these animals. The periods of highest intensity were recorded mainly during the holiday breaks of December-January, when tourism numbers are highest, but for 2006 also between January and April, and in August. With the number of tourists in Kenya expected to increase over the coming years, it is likely that the cumulative behavioural budget of the dolphin population will again be significantly affected by tourism boat interactions. Other studies have shown that high exposure to tourism, represented by the number of tourist boats operating in an area, can lead to dolphins seasonally emigrating from an area to avoid interactions (Bejder et al., 2006). In Kisite-Mpunguti MPA, the highest temporary emigration rates of dolphins were recorded in March 2006 (Pérez-Jorge et al., submitted to Biol. Conservation), which corresponded to the period with the highest number of boats entering the MPA since its implementation in 1978 (Ministry of Tourism, 2010). This temporal area avoidance with increased tourism intensity could lead to a decrease of the already small dolphin population size, which in turn could lead to a decrease in the benefits to the local economy (Lusseau et al., 2006; Pérez-Jorge et al., 2016). For these reasons, and aggravated by the small population size, ensuring the sustainability of the dolphin-tourism activity is of paramount importance in both ecological and socio-economic terms (Higham et al., 2015).

4.3 The role of the MPA on the dolphin-watching tourism

In terms of management, both government and community-based organizations should work together to implement different mitigation measures for the dolphin tourism industry in KMMPA. First, an increase in the tour prices could reduce the amount of tourists in the area, and hence the tourism boat pressure on the dolphin population, while still maintaining similar economic benefits for the local community (Curtin, 2003). This strategy has been previously proposed in Zanzibar based on the results from a socio-economic study (Berggren et al., 2007). Second, an increase in the number of tourists per boat would also help to reduce the number of boats interacting with dolphins. Third, by continuing the current tour boat operator training, already conducted in 2011 and 2012, which presents the best ways to approach and interact with dolphins and also highlighting the importance of following the code of conduct, the behavioural impact on dolphin groups during interactions could potentially be reduced. Finally, by improving the quality of the services provided by the boat crew during a trip (e.g., improve guides talk and customers' service towards maximising tourist satisfaction; Lück, 2003), the economic benefits to the boat crew (through tipping; Buultjens et al., 2005; Wunder, 2000), which forms an important part of the employees' salary (authors, unpublished data), could increase. Thus, training tour guides can help to achieve not only the ecological sustainability but also the economic sustainability (Chen, 2011; Weiler and Ham, 2002). To successfully implement all these measures, the involvement of the local communities is fundamental.

This study shows that nature-based tourism could be a serious threat for the dolphin population in the area if this industry is not managed sustainably, especially during periods of high tourism intensity. Thus, a good understanding of how human disturbance affect animal populations is crucial for the development of sustainable management of any nature-based tourism activity (Higham et al., 2009). For these reasons, appropriate conservation measures such as setting limits of acceptable change (LAC), based on the monitoring of demographic parameters of the target population, and establishing operators guidelines, should be implemented by management agencies (Ahn et al., 2002; Higham et al., 2009). Furthermore, incorporating the spatial and temporal extent of the tourist activity into management plans can also help to address this challenge. Future studies should also evaluate the efficiency of the current code of conduct, as our results suggest that the tourist boats' zone of influence exceeds the 100 meters established in the current guidelines. Moreover, with the expected rise in coastal tourism, dolphins are also facing an increase in the number of threats along the Kenyan coast, including overfishing, increased seismic exploration operations, development of coastal infrastructures and maritime traffic (Kenya Wildlife Service, 2011). Recent studies have also shown that coral reefs along the equatorial Western Indian Ocean are subjected to high susceptibility to climate change (Maina et al., 2008). These impacts can affect the distribution and abundance of top marine predators as a result of large scale bleaching events and changes in the distribution and availability of prey (Cheung et al., 2010; Harwood, 2001). Additionally, the loss of coral reef ecosystems may cause tourists to switch from snorkelling or diving excursions towards whale-watching tours, leading to an increase on the tourist boat pressure on the dolphin population, which could have significant impacts on these species. Alter, Simmonds and Brandon (2010) identified that species inhabiting tropical coastal regions, such as the Indo-Pacific bottlenose dolphin, are predicted to suffer the greatest number of climate-driven changes in human behaviour, due to their coastal distribution on densely populated areas. Finally, these issues should be addressed through the implementation of a science-based national conservation policy and management strategy for these species.

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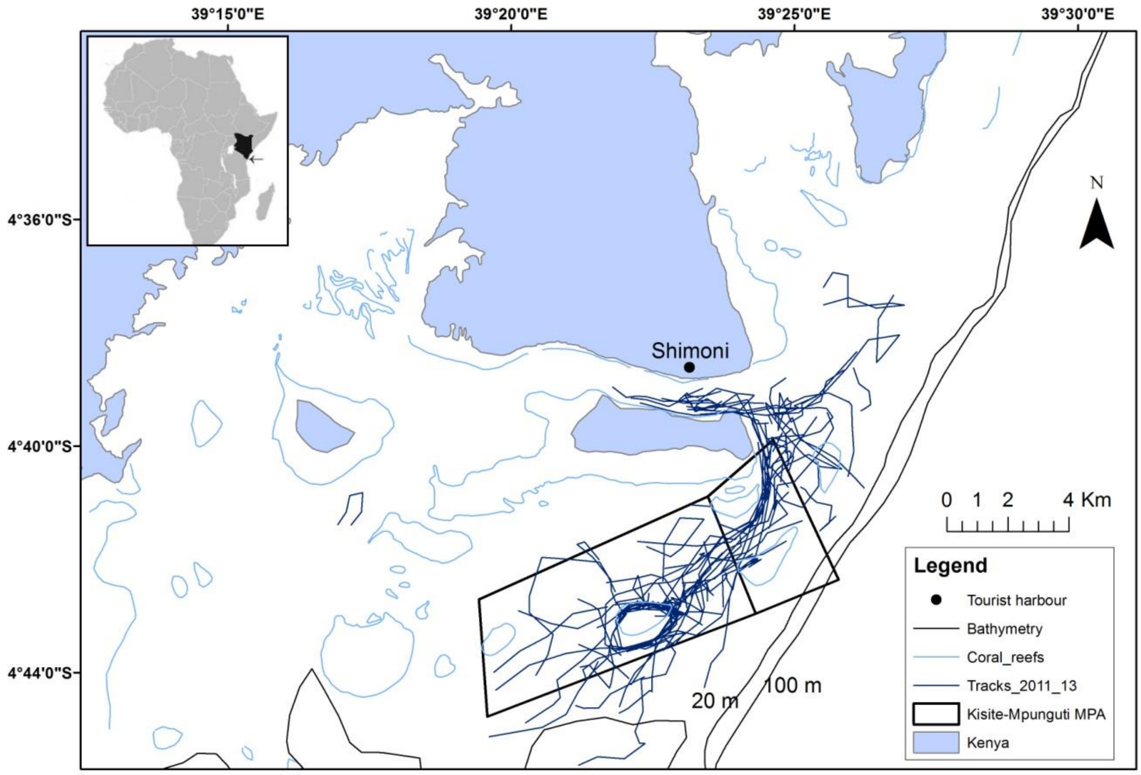

Fig. 1. Map of the study area including the Kisite-Mpunguti Marine Protected Area (KMMPA), Kenya, which contains the Kisite Marine Park (left polygon) and the adjacent Mpunguti Marine Reserve (right polygon). The dark blue lines represent boat tracks from behavioural surveys conducted between 2011 and 2013.

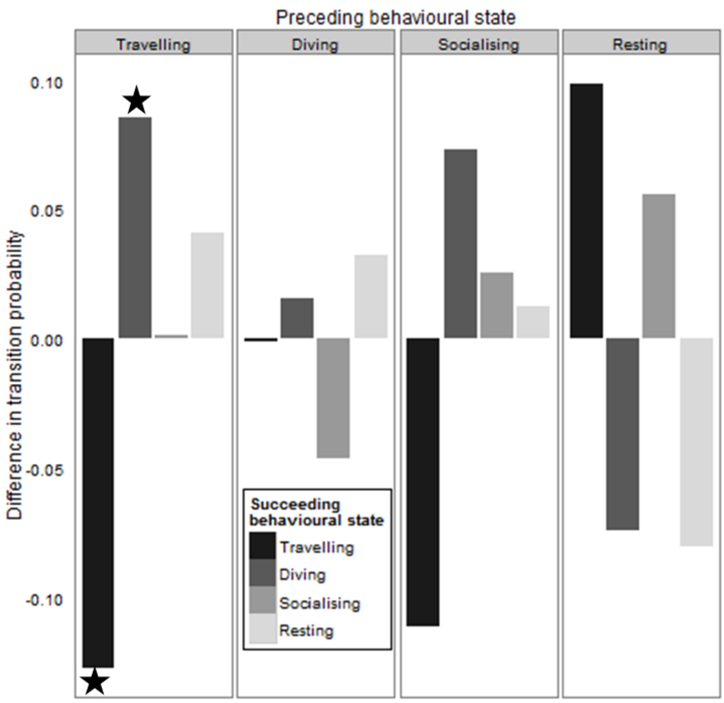

Fig. 2. Differences in transition probability between impact (tourist boat present within 400 meters of the dolphins) and control (tourist boat absent) situations ($p_{ij\ (impact)}-p_{ij(control)}$). The vertical boxes separate each preceding behavioural state, while the bars within each box represent the succeeding behavioural state (see colour legend). Transitions that changed significantly ($p < 0.05$) during boat interactions are marked with a star (★).

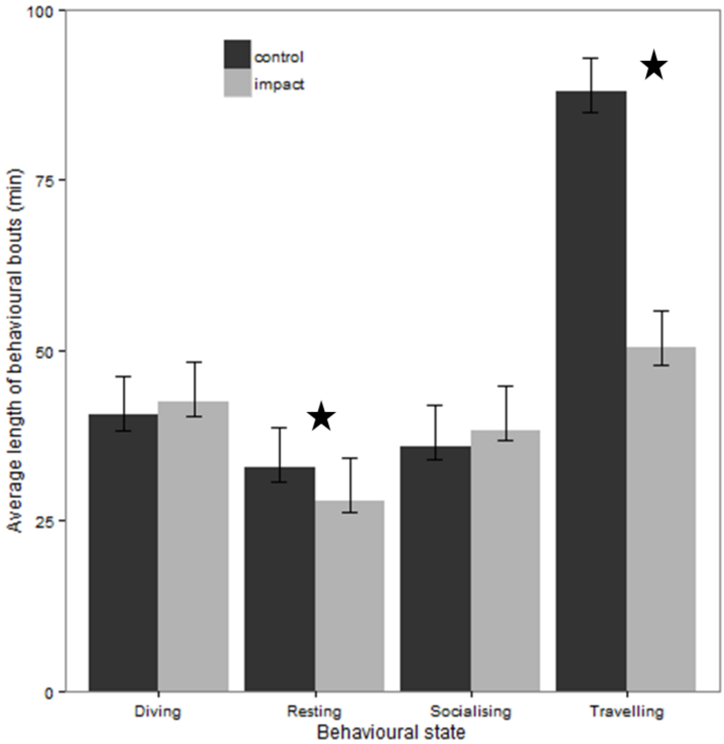

Fig. 3. Average bout length of dolphins represented by the duration of time (minutes) spent on each behavioural state under control (tourist boats absent) and impact (tourist boats present within 400m of the dolphins) situations. The vertical bars represent 95% confidence intervals. Behavioural states with a significant difference ($p < 0.05$) are marked with a star (★).

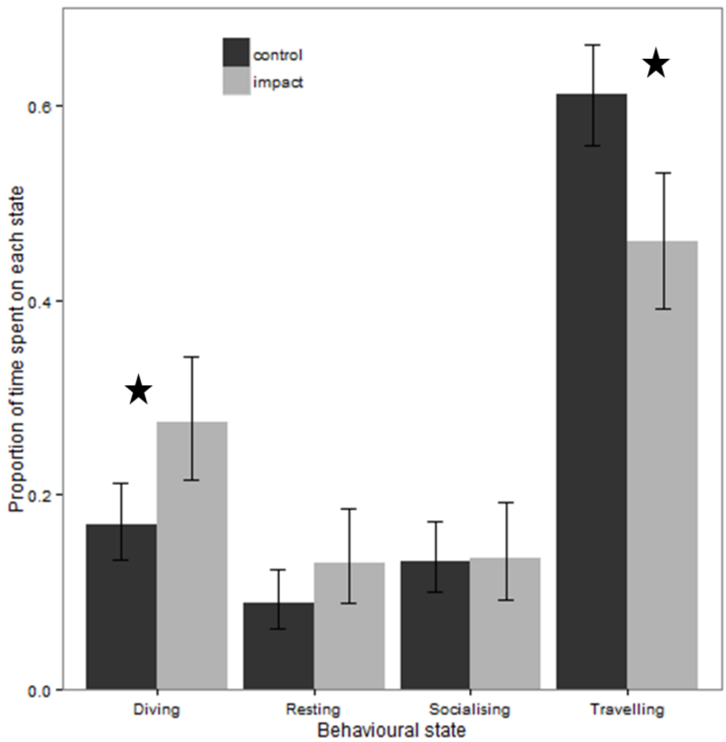

Fig. 4. Dolphin behavioural budgets represented by the proportion of time spent in each behavioural state under control (tourist boats absent) and impact (tourist boats present within 400m of the dolphins) situations. The vertical bars represent 95% confidence intervals. Behavioural states with a significant difference ($p < 0.05$) are marked with a star (★).

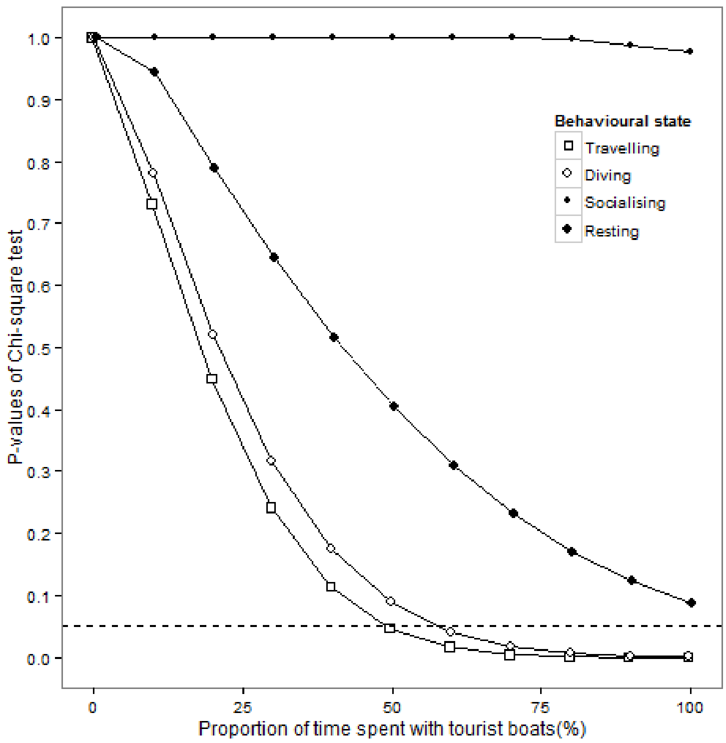

Fig. 5. Effect of tourist boat intensity on cumulative behavioural budget within 400m of the dolphins. P-values of the difference between the cumulative behavioural budget and the control behavioural budget for dolphin activity. The proportion of boat exposure was artificially varied from 0 to 100%. Dashed line represents the statistical level of significance ($p < 0.05$).

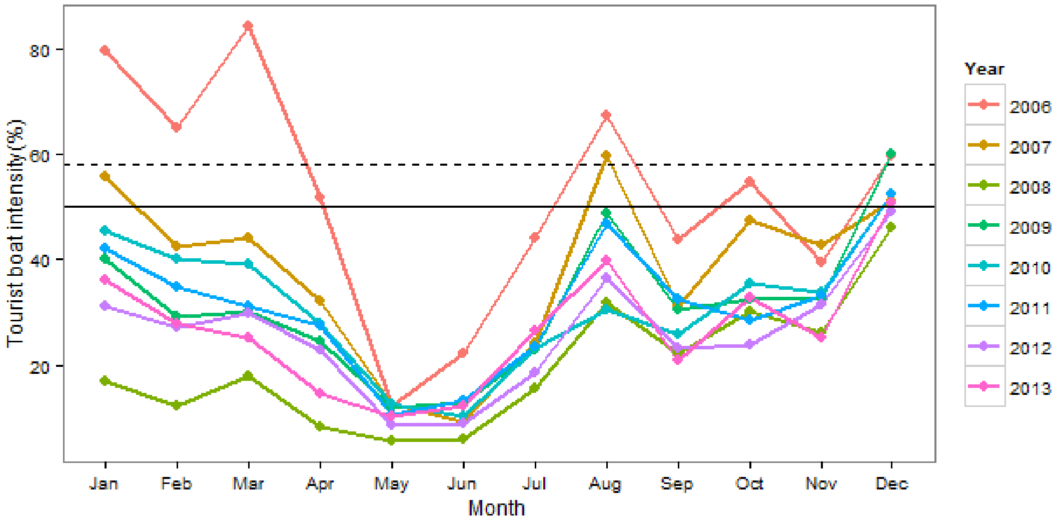

Fig. 6. Monthly tourist boat intensity between 2006 and 2013. The horizontal continuous and dashed lines represent 50 and 58% of tourist boat intensity respectively, which the cumulative travelling and diving behaviours are significantly affected.

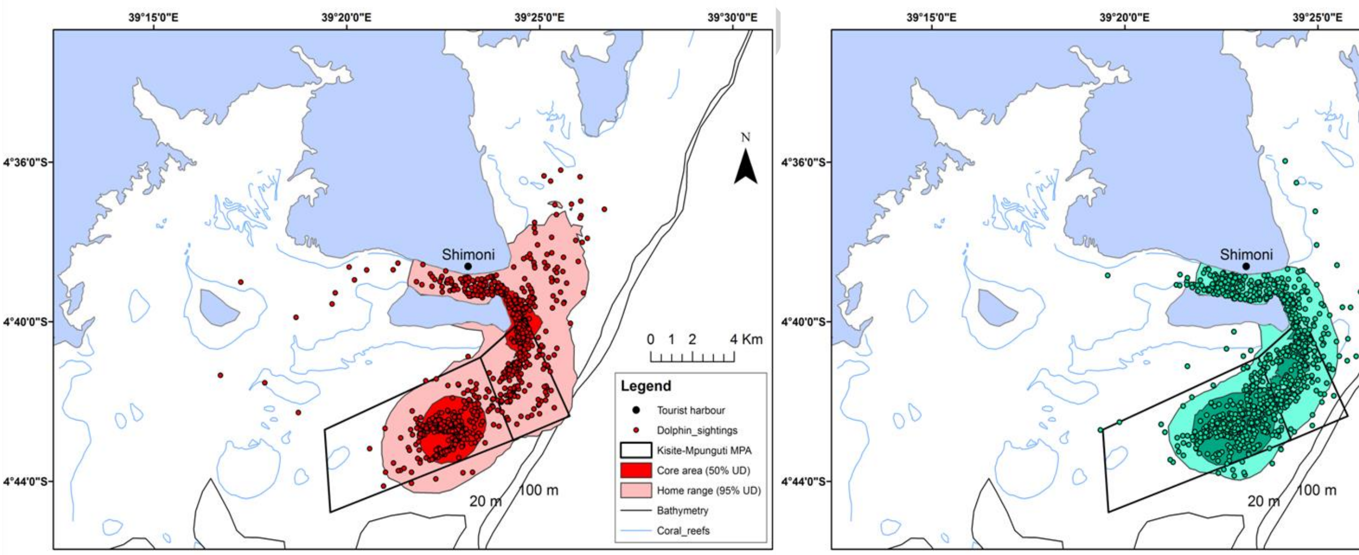

Fig. 7. Locations of dolphins and tourist boat sightings (*n*=775 and 1564, respectively). Shaded polygons represent home-range and core areas (indicated by the utilization distribution contour of 95% and 50%, respectively) (based on Fieberg and Kochanny (2005)).

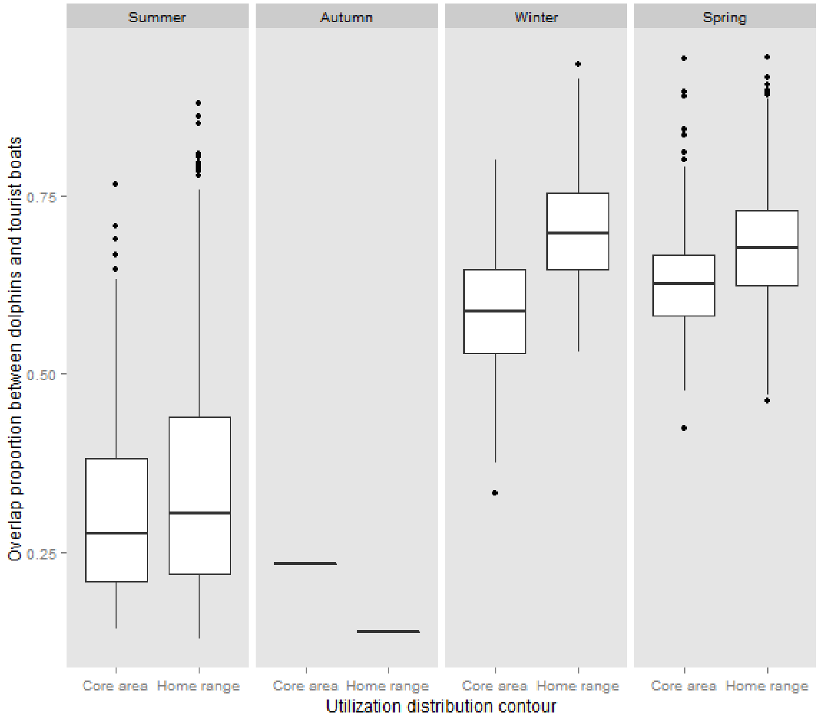

Fig. 8. Proportion of home-range and core areas (indicated by the utilization distribution contour of 95% and 50%, respectively) overlap between dolphins and tourist boats per season (based on Fieberg and Kochanny (2005)). Seasons were defined as: summer (January to March), autumn (April to June), winter (July to September) and spring (October to December).

Behavioural state	Definition
Travelling	Persistent and directional movement (speed >2 knots); short and almost constant dive intervals; individuals could be meandering but still swimming in a constant direction
Resting	Low level of activity, dolphins moving slowly (speed < 2 knots); swimming with short, relatively constant, synchronous dive intervals; individuals tighty grouped
Diving	Frequent changes on direction. Majority of the group performs peduncle and tail out dives. Group spacing varies. Diving most likely represent the "foraging-feeding" category in other studies (Lusseau, 2003b)
Socialising	Various interactive behavioral events: petting, rubbing, mounting, chasing, hitting with tail and other physical contact between individuals. Dive intervals vary

Table 1. Definitions of behavioural states for dolphins in Kisite-Mpunguti MPA.

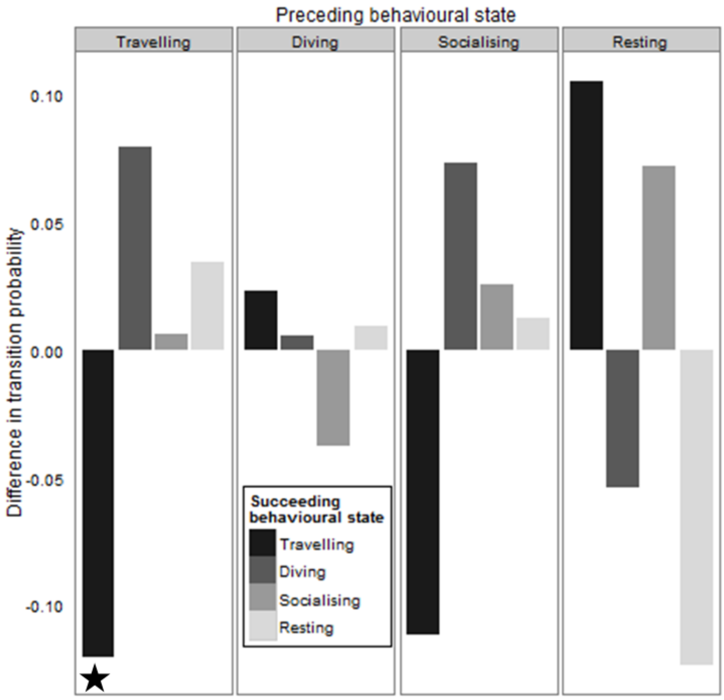

Fig. A1. Differences in transition probability between impact (tourist boat present within 100 meters of the dolphins) and control (tourist boat absent) situations ($p_{ij\ (impact)}$-$p_{ij(control)}$). The vertical boxes separate each preceding behavioural state, while the bars within each box represent the succeeding behavioural state (see colour legend). Transitions that changed significantly ($p < 0.05$) during boat interactions are marked with a star (★)

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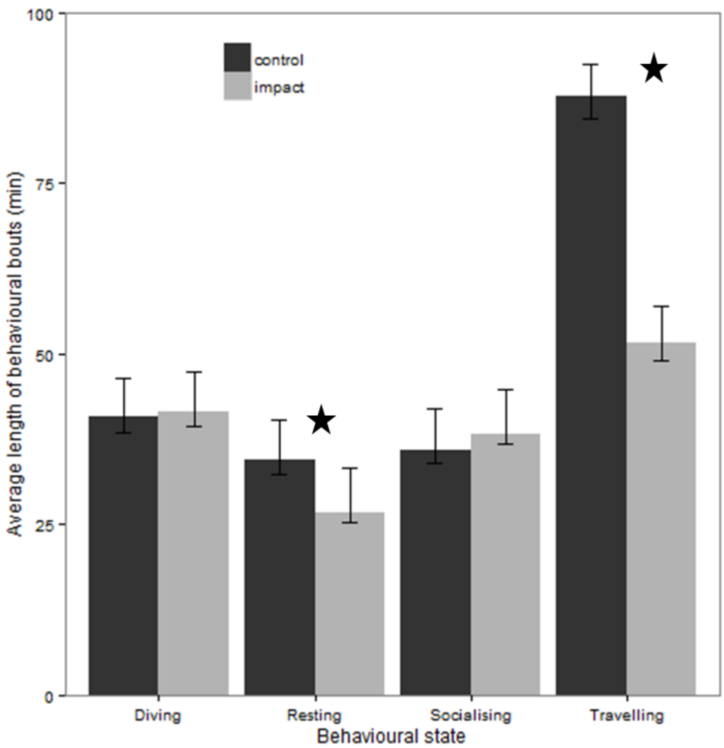

Fig. A2. Average bout length of dolphins represented by the duration of time (minutes) spent on each behavioural state under control (tourist boats absent) and impact (tourist boats present within 100m of the dolphins) situations. The vertical bars represent 95% confidence intervals. Behavioural states with a significant difference ($p < 0.05$) are marked with a star (★).

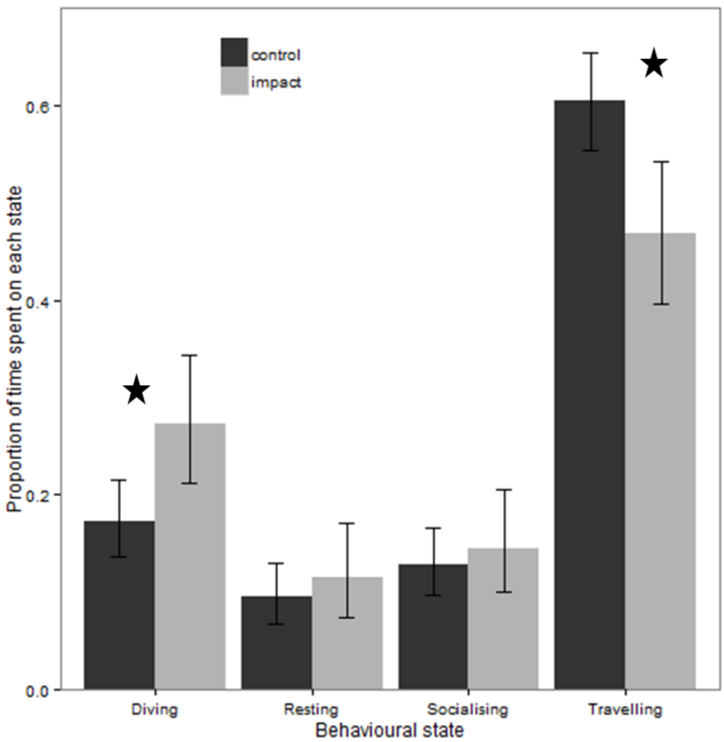

Fig. A3. Dolphin behavioural budgets represented by the proportion of time spent in each behavioural state under control (tourist boats absent) and impact (tourist boats present within 100m of the dolphins) situations. The vertical bars represent 95% confidence intervals. Behavioural states with a significant difference ($p < 0.05$) are marked with a star (★).

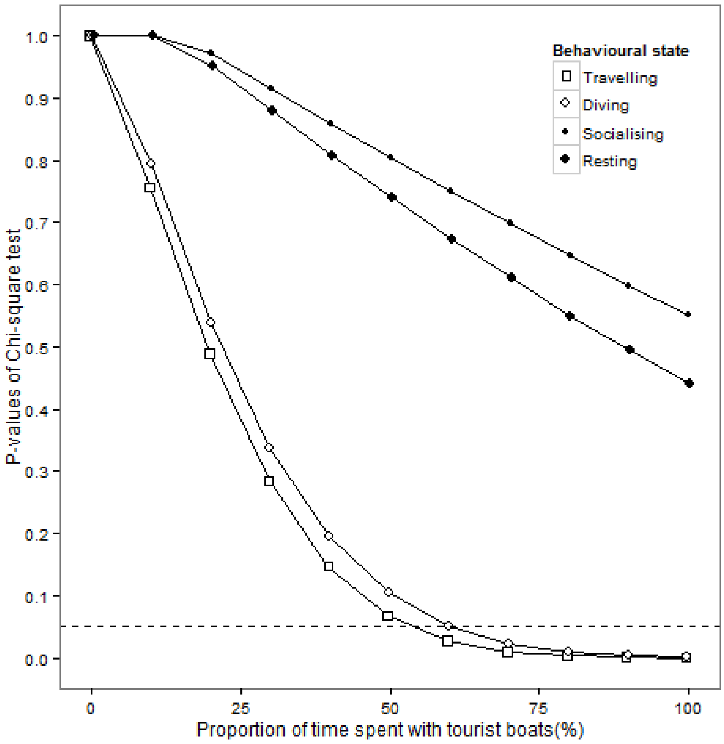

Fig. A4. Effect of tourist boat intensity on cumulative behavioural budget within 100m of the dolphins. P-values of the difference between the cumulative behavioural budget and the control behavioural budget for dolphin activity. The proportion of boat exposure was artificially varied from 0 to 100%. Dashed line represents the statistical level of significance ($p < 0.05$)

	2009	2010	2011	2012	2013	TOTAL
Tourist boat sightings						
Summer	147	81	121	113	20	482
Autumn	51	24	65	64	1	205
Winter	104	184	142	98	98	626
Spring	0	131	77	23	20	251
Dolphin sightings						
Summer	42	46	34	43	34	199
Autumn	22	22	14	23	5	86
Winter	47	57	34	24	45	207
Spring	46	62	61	50	64	283

Table A1. Number of tourist boat and dolphin sightings per season and year. Seasons were divided on the following periods: summer (January to March), autumn (April to June), winter (July to September) and spring (October to December).

Season	Month	2006	2007	2008	2009	2010	2011	2012	2013
Summer	Jan	426	297	90	215	243	224	167	193
	Feb	347	227	65	156	215	185	145	148
	Mar	451	235	95	161	209	167	159	135
Autumn	Apr	277	172	43	130	149	146	122	78
	May	65	67	29	64	67	56	45	55
	Jun	119	49	31	68	54	70	48	65
Winter	Jul	236	129	82	121	124	126	98	141
	Aug	359	319	170	260	162	249	195	213
	Sep	234	166	118	162	138	174	124	111
Spring	Oct	293	254	161	173	189	152	128	176
	Nov	210	228	140	174	180	177	168	134
	Dec	319	273	246	320	280	279	263	271

Table A2. Number of tourist boats entering the Kisite-Mpunguti Marine Protected Area per month and year. Data provided by the Kenya Wildlife Service (KWS, unpublished data)