Effects of nature-based tourism and environmental drivers on the demography of a small dolphin population

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Sergi Pérez-Jorge [a,b,*], Inês Gomes [a,c], Kirsty Hayes [a], Graham Corti [a], Maite Louzao [d], Meritxell Genovart [b], Daniel Oro [b]

[a] *Global Vision International (GVI) 7 The Space, Stibitz Road, Westlake, 7945 Cape Town, South Africa*
[b] *Population Ecology Group, IMEDEA (UIB-CSIC), Miquel Marques 21, 07190 Esporles, (Balearic Islands), Spain*
[c] *Departmento de Biologia & CESAM, Universidade de Aveiro, Campus Universitario de Santiago, Aveiro, Portugal*
[d] *AZTI, Herrera Kaia, Portualdea z/g, 20110 Pasaia, Spain*

ABSTRACT

Many marine top predators are experiencing significant declines due to anthropogenic impacts, and therefore reliable monitoring is essential to understand their population dynamics. We used Pollock's robust design capture–recapture modelling to assess the influence of oceanographic variables, artisanal fisheries and human disturbance on several demographic parameters (abundance, temporary emigration and survival) of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), using long-term data on marked individuals from East Africa. Photo-identification data was collected over 551 boat-based surveys between 2006 and 2009, with 137 individuals identified. Our best fitting model indicated that exposure to tourism (represented by the number of tourist boats) increased the probability of dolphins seasonally emigrating from the study area. The return rate of temporary emigrants was negatively linked to the seasonal sea surface temperature, probably associated with food availability. That model supported the existence of heterogeneity in annual local survival estimates, with transient dolphins showing a lower value than resident individuals (0.78 and 0.98, respectively). Furthermore, abundance estimates showed a small population size ranging from 19 individuals (95% CI: 11–33) to a maximum of 104 dolphins (95% CI: 78–139). This small population, together with their high site fidelity and coastal distribution, might be particularly vulnerable to human disturbances. This study highlights the influence of environmental and anthropogenic factors on dolphin demography and population dynamics and the need to integrate these drivers to provide robust evidences for conservation stakeholders in an adaptive management framework.

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1. Introduction

As populations of marine top predators decline worldwide (Pauly et al., 1998), there is an urgent need to estimate robust demographic parameters to accurately inform and assess management decisions. Assessing population dynamics for long-lived and highly migratory marine species is complex but an essential component for managing populations. Marine top predators play a major role on the structure and functioning of marine ecosystems, and are dependent upon a broad range of trophic links within the marine food web (Heithaus et al., 2008). As a result, these species are vulnerable to anthropogenic pressures, climate variability and subsequent habitat alterations (Barbraud and Weimerskirch, 2001), fisheries interactions (Lewison et al., 2004), and overfishing among others. Thus, understanding the effects of biotic and abiotic factors on demographic parameters can provide valuable

information to evaluate changes in these populations (Weimerskirch et al., 2003).

Mark-recapture modelling techniques have been widely used to estimate population dynamics and demographic parameters (Oro et al., 2004). These methods have traditionally been developed from either closed population models, where no population losses (through emigration or death) occur along the sampling period, or open, which rely on the assumption that all emigration is permanent. Consequently, animal population studies can introduce bias into demographic parameters if temporary emigration is not correctly accounted for (Fujiwara and Caswell, 2002). Pollock's robust design, which combines close and open population models under a nested sampling framework, brings a more biologically realistic approach into the analysis by allowing animals to temporarily emigrate and return to the study area (Kendall et al., 1997; Pollock et al., 1990). The significance of estimating the probability of temporary emigration has been proved in multiple taxa: amphibians (Muths et al., 2006), bats (Frick et al., 2010), voles (Kendall et al., 1997), and marine top predators (Kendall and Bjorkland, 2001), including marine mammals (Smith et al., 2013). In fact, many studies have recognized that temporary emigration fluctuates due to temporal

components that may reveal changes on environmental conditions or seasonal behavioural patterns (Dwyer et al., 2014; Smith et al., 2013). This temporal variation has also been reported in capture probability (Silva et al., 2009), which has been suggested to be partially linked to temporary emigration (Muths et al., 2006). However, to our knowledge, temporary emigration parameters modelled as a function of candidate biotic or abiotic covariates has received little quantitative attention in cetacean demographic studies.

Investigating how environmental variations shape the dynamics of animal populations is of paramount importance in an increasingly changing world (Barbraud and Weimerskirch, 2001). Recent studies have evidenced the effect of climate change and anthropogenic activities on local fish stocks, and how changes in prey availability can impact on marine top predator populations (Ford et al., 2010). In the case of cetaceans, exposure to human disturbance, through dolphin-watching, can caused short term changes on individuals activity such as: breathing rates (Janik and Thompson, 1996); diving times (Ng and Leung, 2003); swimming directions (Lemon et al., 2006) or specific behavioural states (Christiansen et al., 2010). In addition, it can cause long-term effects on cetacean vital rates, such as a decrease in female reproductive success (Lusseau et al., 2006) or a decline in relative abundance (Bejder et al., 2006). At the population level, consequences depend upon the proportion of the population exposed to different levels of human interactions. Moreover, repeated human disturbance is significantly more important if it occurs within the core habitat of the species, or is concentrated during critical periods, which can affect the viability of the population (Bejder et al., 2006; Williams et al., 2006). As a result, the estimation of demographic parameters is considered a crucial step for identifying negative impacts on animal populations (Gormley et al., 2012).

Particularly, demographic studies on cetacean populations are urgently needed in the Western Indian Ocean (WIO) due to the increase of potential anthropogenic threats in the area (e.g., overfishing, dolphin-watching, seismic exploration)(Kenya Wildlife Service, 2011). Based on demographic modelling, we studied the population dynamics of the IUCN data deficient Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in southern Kenya at the Kisite-Mpunguti Marine Protected Area (KMMPA). Specifically, we assessed four years of mark-recapture data to fit multiple competing models to investigate a set of hypothesis about dolphin population parameters within the Information Theoretic Approach. We considered the effect of natural factors (oceanographic conditions and prey availability) and human disturbance. Regarding the latter, artisanal fishing and tourism are the main economic activities for local communities, and dolphins are considered flagship species and the main attraction for the 60,000 yearly park visitors (Emerton and Tessema, 2001). We estimate seasonal temporary emigration movements influenced by environmental, human disturbance or fisheries covariates. Finally, we estimated seasonal population abundances across the study period. This study overcomes the challenge of integrating multiple data sources to study the effect of natural and human-related pressures on the population dynamics of a highly mobile predator.

2. Material and methods

2.1. Study area

Kisite-Mpunguti Marine Protected Area (KMMPA, 04°04′S–39°02′E), located on the southern coast of Kenya, lies south of Wasini Island and incorporates the Kisite Marine Park, the largest no-take area in Kenya (28 km²), and the adjacent Mpunguti Marine Reserve, Kenya's smallest reserve, where traditional fishing is allowed (11 km²) (Fig. 1). This MPA was established in 1978 and it has been under the administration of the Kenya Wildlife Service (KWS) since 1988. KMMPA covers shallow waters (<20 m depth) and supports a high marine biodiversity from corals to marine mammals and sea turtles.

2.2. Sampling methods

Boat-based surveys were conducted on a monthly basis all year around between January 2006 and December 2009 off the south coast of Kenya (with the exception of the period comprised between January and June 2008 due to national political instability). Searching effort was carried out with Beaufort sea states ≤3, low swells and good visibility (≥1 km), reducing the probability of missing dolphins. When a group was sighted, we recorded on location and time of the sighting, group size and group composition. A group was defined as the total number of individuals encountered, moving in the same direction or engaged in the same activity, within 100 m of each other (Wells et al., 1987).

2.3. Data analysis

2.3.1. Photo-identification process

Photo-identification was performed following standard cetacean protocols (Würsig and Jefferson, 1990). Dolphins within photographic range were photographed irrespective of their level of marking in order to have an unbiased estimation of the number of animals with marks in each mark class (Wilson et al., 1999). Because several pictures contain more than one individual, the term "fin image" was used to refer to a single dorsal fin in a picture (Verborgh et al., 2009). Each fin image was given information on sighting number, frame number, date, flank, angle (every 30° starting from 0° when the dolphin was facing the camera), individual fin image quality "Q" and code of the individual in the photo-identification catalogue. The quality rating (Q) was assigned on a scale of 0 to 2 (poor to excellent) considering four characteristics: exposure, focus, size and orientation. Every individual dorsal fin image was compared to a photo-identification catalogue, which included left and right dorsal fins from previously identified animals. This process was verified by two independent researchers to minimize misidentifications. Nicks and marks on the leading and trailing edges of the dorsal fin were used to identify individual Indo-Pacific bottlenose dolphins (Wilson et al., 1999). A quality marking level (M) was given to each animal in the catalogue ranging from 1 (few nicks/marks) to 3 (highly marked). Individuals showing light marks were assigned to M_1 were lightly marked and those with conspicuous marks to levels M_2 and M_3 (Verborgh et al., 2009). To minimize heterogeneity resulting from mark distinctiveness, only dorsal fin images with Q1 and Q2 and well-marked individuals were used on the analysis. Our analysis did not include calves, as they were not enough marked for identification and recapture. For more details see 'Robust design assumptions' section in Supporting material.

2.3.2. Covariates description

Covariates were selected based on their potential influence on dolphin demography: anthropogenic factors such as tourist boats and swimmers numbers, oceanographic variables or prey availability (Table A1). Previous studies have shown that tourist boats can have negative impacts on dolphin populations, especially when dolphin-watching activities are not monitored or sustainably managed (Christiansen et al., 2010). Impacts may be long-term and life-threatening; both at the individual and population level (Bejder et al., 2006). We predicted that the number of tourist boats operating around the MPA could influence the presence of dolphins in the area. Specifically, we hypothesised that spring months (April–June) would have the largest number of dolphins, as this is the season with the lowest number of tourist boats. We also predicted that a higher number of swimmers would negatively affect the probability of dolphin encounters, as tourists snorkel during their trips around Kisite Island, which is the core habitat for the Indo-Pacific bottlenose dolphin (Pérez-Jorge et al., 2015). We obtained 4 variables to assess the possible impact of the dolphin-watching tourism: number of tourist boats (BOATS) and swimmers (SWIMMERS) having access to the MPA on a given month. We also considered both covariates of the previous month (BOATS_1 and
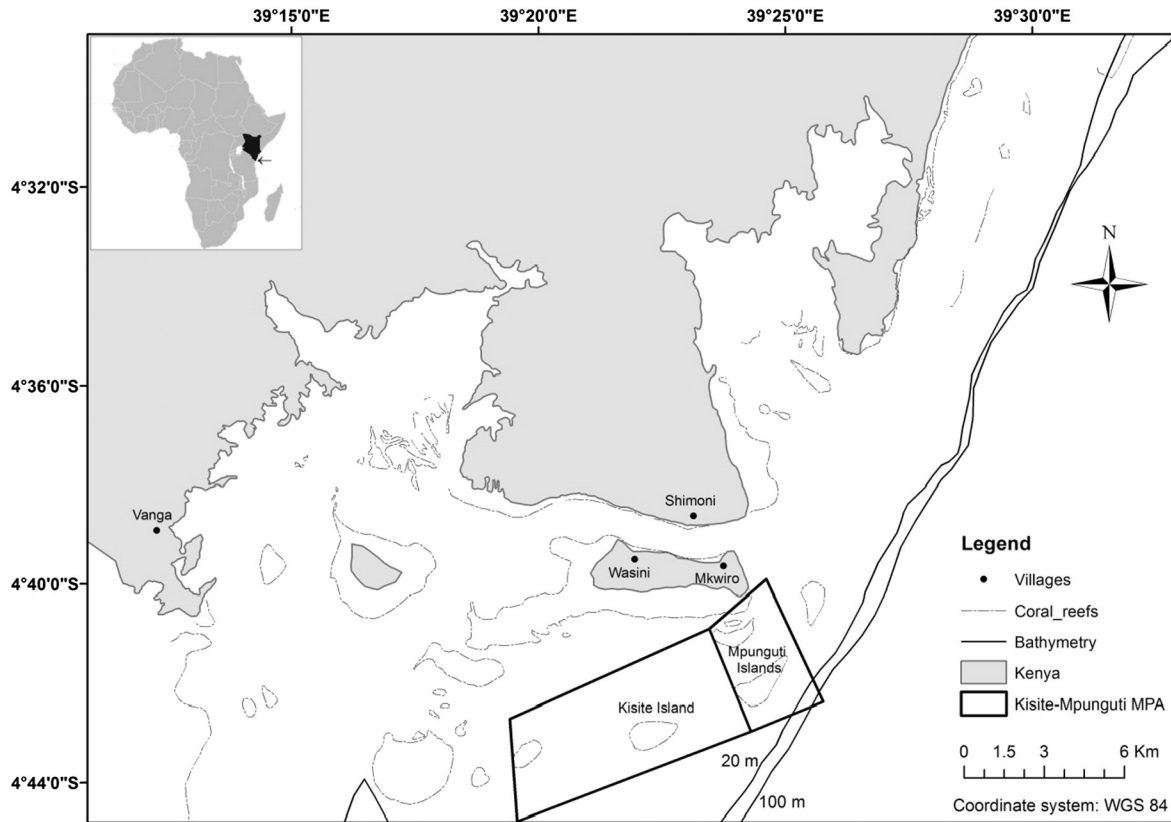
Fig. 1. General map of the study area, Kisite-Mpunguti Marine Protected Area, southern Kenya.

SWIMMERS_1) in order to account for time-lag effects. Kenya Wildlife Service collected these data through the number of tourists and boats paying park fees to enter Kisite-Mpunguti MPA (KWS, unpublished data).

We predicted that monthly differences on sea surface temperature (SST) and chlorophyll (CHL) could critically influence dolphin's seasonal movement (e.g., temporary emigration), since they can adapt to specific temperature regimes and associate with highly productive areas (e.g., high chlorophyll a values)(Redfern et al., 2006; Stevick et al., 2002). In fact, both variables have been recently shown to be crucial in determining the habitat preferences and abundances of this Indo-Pacific bottlenose dolphin population, with CHL and SST negatively related to sightings and group size data (Pérez-Jorge et al., 2015). Monthly composite for SST and CHL were derived from aqua-MODIS sensor and converted with the Marine Geospatial Ecology Tool (MGET, Roberts et al., 2010) from their original formats to raster formats compatible with ArcGIS. SST and CHL were averaged across the study area per month (SST and CHL) and season (three months; SST_3 and CHL_3). Marine top predators are associated with oceanographic fronts as they find favourable feeding conditions and this will likely influence their distribution and abundance (Worm et al., 2005). The spatial ecology of our targeted species has been described to be strongly influenced by oceanographic fronts, showing the highest occurrence and abundance probabilities when the fronts are close to the study area (Pérez-Jorge et al., 2015). Thus, MGET's Cayula–Cornillon Fronts tool was used to identify these fronts by detecting the edge of adjacent water masses of different SST with the Cayula–Cornillon algorithm, using the SST images from AVHRR Pathfinder SST dataset. Then the distance to the front was averaged for the study area per month (FRONT) and season (FRONT_3).

The distribution of dolphins is strongly influenced by the abundance and distribution of its prey (Sveegaard et al., 2012). For our study region, Indo-Pacific bottlenose dolphins feed upon inshore and reef fish and cephalopods (Amir et al., 2005). In addition to reef prey, species comprised within the *Tursiops* genera feed upon alternative prey such as bathydemersal fish and cephalopods in offshore waters along the WIO (Cockcroft and Ross, 1990). We then forecast a positive relationship between prey and dolphin abundance. We acquired monthly fisheries data on total amount of prey landed (TOTAL_PREY) (i.e. as an index of prey availability), pelagic species catch (PELAGIC), demersal species (DEMERSAL) and cephalopod species (CEPHALOPOD). Data was prepared by the Fisheries department of the Kenyan Ministry of Fisheries Development, from the closest harbour to our study area (Shimoni). Fishing effort was conducted by small-scale artisanal fishermen that operate near shore (Gomes et al., 2014).

Finally, photo-identification effort has been shown to influence cetacean's capture probability (Verborgh et al., 2009). We used the number of survey hours (corresponding to each primary sampling occasion) and photos analysed (dorsal fin images with Q1 and Q2), to test the hypothesis of an effort-dependent capture probability.

We investigated the collinearity between predictors by calculating pairwise Spearman-rank correlation coefficient, which identified highly correlated variables ($|rs| \geq 0.7$) (Table A2). This led to the removal of SST, CHL_3, SWIMMERS and BOATS_1.

2.3.3. Demographic parameters

We used the full-likelihood approach of the Pollock's closed robust design, which combines open and closed capture-recapture models to estimate annual apparent survival, temporary emigration, capture and recapture probabilities, and population size (Kendall et al., 1997). This methodology incorporates open sampling events called "primary periods", within which there are a number of closed "secondary periods". Primary periods allow population gains and losses between them, and temporal closure is assumed between secondary periods. Our primary periods were based on the following seasons: summer (January–March), autumn (April–June), winter (July–September), and spring (October–December). The time interval between primary periods was two and a half months (mean: 76.3 days; SD: 0.86), except for the periods of Winter 2007–Spring 2008 and Autumn 2009–Spring 2009

that was 11.5 and 5.5 months, respectively, due to political instability and inability to perform fieldwork. Capture probabilities were fixed to 0 for those periods separated by more than 2.5 months, as robust design analysis cannot estimate temporary emigration parameters when time intervals are unequal between primary periods. Secondary sampling occasions' data was collected within 15 day periods to fulfil the assumption of temporal closure within primary periods, to minimize the probability of dolphin movements in and out of the study area. To identify these 15 day periods, we calculated the daily number of individual dolphins identified on each period within each season, and choose those same periods within each season that had the highest count across the study. In total, we had 16 primary periods (seasons) and 53 secondary periods during the four years of the study (Table A3). The assumption of closure over primary periods was tested with the programme CAPTURE (Rexstad and Burnham, 1991). For more details see 'Robust design assumptions section in Supporting material.

Pollock's closed robust design models do not have a goodness-of-fit (GOF) test to validate the assumptions of equal probabilities of capture and survival between individuals. We used the programme U-CARE (Choquet et al., 2009) to test the fit of our data to the Cormack–Jolly–Seber model, previously pooled into primary sessions. We paid special attention to the Test 3.SR component that detects the presence of transients (Pradel et al., 1997). Transients are individuals that enter only once into the study area and are never seen again. Based on the U-CARE results, we included a transient effect on our models and calculated a variance inflation factor ($\hat{c}$) to be used in the models (see below) to account for the remaining overdispersion (Hurvich and Tsai, 1989). To include transients in our models, we estimated separately the survival probabilities of newly marked individuals (ϕ') from those individuals previously encountered (ϕ). We also calculated the proportion of transients as $1 - \phi'/\phi$, and estimated the 95% CI of this proportion using the Delta method (see for instance, Morgan, 2000).

Two general parameters were used to describe the process of temporary emigration: Υ' and Υ'' (Kendall et al., 1997). Υ' determines the probability that an individual dolphin not present in the study area in a given time (t_i) remains outside the study area and is unavailable for capture in the next time unit (t_{i+1}). Thus, ($1-\Upsilon'$) is the probability of not being present in the study area at time i (t_i) and moving into the study area and being available for capture at time $i + 1$ — i.e., return rate of temporary emigrants. Υ'' determines the probability that an individual dolphin present in the study area at time i (t_i) temporarily emigrates of the study area and is unavailable for capture at time $i + 1$. Thus, ($1-\Upsilon''$) is the probability of remaining in the study area between time i and $i + 1$. We combined these parameters to explore different models of temporary emigration: Markovian ($\Upsilon'' \neq \Upsilon'$), where the probability of an individual is present at time $i + 1$ depends on whether or not it was present at time t, random ($\Upsilon'' = \Upsilon'$) and no movement ($\Upsilon'' = \Upsilon' = 0$). Capture and recapture probabilities (p and c) were set equal on all fitted models, as photo-identification protocols should not affect the recapture probabilities because they do not require capture and/or handling of animals (Parra et al., 2006).

2.3.4. Model selection

We followed a step-down model selection procedure (Lebreton et al., 1992) to estimate each one of the demographic parameters. In the first step, we modelled p (testing whether it was constant, variable between seasons, between years, or a combination of season and year) and kept the remaining structure constant and very simple: no movement ($\Upsilon'' = \Upsilon' = 0$) and constant survival for transients and residents, because as expected for a long-lived species, adult survival is expected to be constant over time. We also allowed p to vary within primary periods, and between primary periods, as well as a combination of both. In addition, we integrated factors related to survey effort (the number of survey hours and photos analysed) to investigate the effect of these on capture probabilities. In the second step, we modelled survival by testing whether survival changed seasonally and yearly and by their

interaction; in this step, we also kept no movement model structure and the best fitting capture probability models from the previous model procedure step. In the third step, we modelled temporary emigration parameters by incorporating random and Markovian models, including constant and temporal effects with the best fitting models of survival and capture probability from the precedent steps. Moreover, these emigration parameters were also modelled as a function of the previously described covariates (environmental, fisheries and human disturbance variables). Finally, we estimated the population size of well-marked individuals (M_2 and M_3) across primary sampling periods.

Our modelling approach allowed us to estimate the population of marked animals, as it relies on individuals identified through natural marks. To obtain the total population size, we need to adjust our estimates to incorporate the proportion of unmarked and slightly marked individuals (M_1), as follows:

$$\hat{N}_{total} = \hat{N}_m / \hat{\theta}.$$

Where $\hat{N}_{total}$ is the estimated total population size, $\hat{N}_m$ the estimated well-marked population size and $\hat{\theta}$ the estimated proportion of well-marked individuals in the population. We calculated the correction factor ($\hat{\theta}$) as the total number of well-marked individuals (M_2 and M_3) divided by the estimated group size on each secondary sampling occasion (Daura-Jorge et al., 2013). We estimated a single correction factor for each primary sampling occasion averaging all correction factors within each primary period. The total population size includes calves, juveniles, and adults of both sexes combined.

The standard errors (SE) for the estimated total population size were derived from the following formula of approximate variance of $\hat{N}_{total}$, using the delta methods (Williams et al., 2002):

$$SE\left(\hat{N}_{total}\right) = \sqrt{\hat{N}_{total}^2 \left(\frac{SE\left(\hat{N}_m\right)^2}{\hat{N}_m^2} + \frac{1-\hat{\theta}}{n\hat{\theta}} \right)},$$

Log-normal 95% confidence intervals were calculated, with a lower limit of $\hat{N}_{total}^L = \hat{N}_{total}/C$ and upper limit of $\hat{N}_{total}^U = \hat{N}_{total}/C$ where (Burnham et al., 1987)

$$C = \exp\left(1.96\sqrt{\ln\left(1 + \left(\frac{SE\left(\hat{N}_{total}\right)}{\hat{N}_{total}}\right)^2\right)} \right)$$

Model selection relied on the Quasi-Akaike Information Criterion corrected for overdispersion and small samples sizes (QAICc, Burnham and Anderson, 2002), using the lowest QAICc to identify the most parsimonious model. Models were built within the R environment (version 2.15.3; R Development Core Team, 2013) using 'RMark' (Laake, 2013), which uses custom scripts to call programme MARK (White and Burnham, 1999).

3. Results

We conducted 551 dedicated vessel-based surveys between 2006 and 2009, resulting in 13,850 km of survey effort. A total of 367 photo-identification sessions were performed and 28,601 photos were taken, resulting in 137 individuals identified. Among these, 20% were classified as slightly marked individuals (M_1) and 80% as well-marked (M_2 and M_3). The individual recapture rate ranged from 1 to 75 with an average of 19 (SD: 19.76) recaptures along the study period. From these data, the 15 days period with the maximum number of well-marked identifications was the fifth period of each season (first and second week of March, June, September and December), with 302 of the total 1319 identifications (23%). Using these data, the number of

individual dolphins identified within primary periods was 85 well-marked individuals, ranging from 1 to 29 on each secondary sampling period. A total of 66% of the bottlenose dolphins were identified over two years and 40% of them were present over three years. The proportion of well-marked individuals using the study area was calculated to be 0.65 (SD: 0.16).

The closure test was performed in twelve of the sixteen primary periods, as there were four that did not have data (Section 2.3.3 Demographic parameters). The results from programme CAPTURE indicated that the population was closed over nine of the twelve primary periods, assuming the closure on the majority of the sampling period (Table A4).

The goodness-of-fit test run in U-CARE indicated a reasonable overdispersion in our data (Global Test: $\chi^2 = 72.501$, df = 33, $\hat{c} = 2.2$), showing the presence of transients (TEST 3. SR, p = 0.018) and trap-dependence (TEST 2. CT; p = 0.001). We corrected for the presence of transients in our data by including a transient effect in all our models. We corrected for the remaining overdispersion due to trap heterogeneity adjusting the QAICc by a $\hat{c} = 2.13$ (Global Test: $\chi^2 = 55.577$, df = 26). We acknowledge that this moderate extra-binomial variation may exist likely due to heterogeneity of capture caused by factors such as age, sex or willingness to approach vessels.

3.1. Model selection

After the first step of the model selection approach, the best ranked model considered that capture probability was dependent on season (51% of QAICc weight; Model 1 in Table A5). The model with capture probability dependent on the number of photos analysed had the second lowest QAICc and also fitted the data adequately (ΔQAICc < 2, 19% of QAICc weight). These two capture probabilities were incorporated into the second model selection step to determine the best survival probabilities. Models where survival was constant, with one survival for transients and one for residents, received the highest support (64% of the QAICc weight; Model 1 and 2 in Table A6). These survival probability structure and the two previous capture probabilities were integrated into the last step of the modelling procedure. In this final step, where we also modelled gamma probabilities, the best fitting model identified a Markovian emigration with Υ'' depending on the number of boats, and Υ' depending on the seasonal temperature, with one survival for transients and another for residents, and a capture probability dependent on the number of photos analysed. Based on the weights, this model received 4 times more support than the following most likely model (36% of QAICc weight; Model 1 in Table 1). In contrast, the second model with the lowest QAICc was similar to the best fitting model except temporary emigration was random depending on the seasonal temperature. Markovian emigration models were supported by 81% of all models, showing a greater support for this population structure.

3.2. Parameters estimates

Our best fitting model includes the transient effect and estimated apparent seasonal survival probability of 0.941 (0.891-0.968) for transients and 0.996 (0.989-0.998) for residents. Thus, our annual survival was 0.784 (0.661-0.907) for transients and 0.985 (0.969-1.00) for residents. The proportion of transient individuals in the population was estimated at 0.056 (95% CI: 0.053–0.059). Capture probabilities were dependent on the number of photos analysed ranging from 0.18 to 0.21, with a mean value of 0.19 (SE: 0.007).

The best fitting model estimated the probability that an individual available for capture on previous occasions temporarily emigrated from the study area (Υ'') depend upon the number of tourist boats, and ranged from 0.11 (95% CI: 0.06–0.36) to 0.78 (95% CI: 0.56–0.91) (Fig. 2). This matches our predictions, indicating that as the number of tourist boats operating in the MPA increases, the probability of temporary emigration increases. For example, due to the high number of boats in March 2006, the probability of temporary emigration from the study area increased to the relatively high values of 0.78 (95% CI: 0.56–0.91). The probability that an individual that was outside the study area on a previous occasion remained outside it (Υ'), relied on the seasonal temperature, ranging from 0.01 (95% CI: 0.00–0.30) to 0.81 (95% CI: 0.64–0.91). Thus, the return rate of temporary emigrants to the study area (1-Υ') was linked to the sea surface temperature, suggesting that warmer periods had a lower probability of animals returning to the study area in the following months (Fig. 3). However, our second best model described a random temporary emigration structure, in which the probability of any dolphin being present in our study area in a given study period is independent on whether or not it was present in the study area in the previous sampling occasion. This ranged from 0.03 (95% CI: 0.00–0.39) to 0.61 (95% CI: 0.46–0.75). The models including the impact of tourism exposure explain an important part of our Υ'' variability; nevertheless we cannot discard that this variability is seasonally-dependent, through a temperature effect. Model 3 and 4 also showed the effect of season explaining 9% and 9% of the variance respectively (Table A7). None of the effects of the fisheries covariates tested on temporary emigration were retained in the best models (Table 1).

The total number of individuals using the study area varied along the four study years, ranging from 19 (SE: 5.51, 95% CI: 11–33) in June 2007 to 104 (SE: 15.36, 95% CI: 74–139) in December 2009 (Fig. 4). These abundance estimates were roughly stable from 2006 to 2009, with a mean of 62 dolphins (SE: 6.66). Heterogeneity models using two point finite mixtures (different capture probabilities among individuals) (Pledger, 2000) resulted in overparameterised models and led to non-identifiability of several parameters due to small population size and low capture probabilities.

Table 1

Summary of the best 12 models from model selection results. Parameters: S denotes survival, Υ' and Υ'' denote temporary emigration (Markovian ($\Upsilon'' \neq \Upsilon'$), random ($\Upsilon'' = \Upsilon'$)), p denotes capture probability, c denotes recapture probability, Nm denotes number of marked individuals and session denotes time varying between primary occasions. Capture and recapture probabilities were set equal on all fitted models. Quasi-Akaike information criterion corrected for small sample size (QAICc).

| ID	Model	Npar	QAICc	DeltaQAICc	Weight	QDeviance
1	S(~transients)Υ''(~BOAT)Υ'(~SST_3)p(~photosanalysed) = c(~photosanalysed)Nm(~session)	20	466.44	0.00	0.36	782.49
2	S(~transients)Υ''(~SST_3)Υ'()p(~photosanalysed) = c(~photosanalysed)Nm(~session)	18	469.12	2.68	0.09	789.56
3	S(~transients)Υ''(~season)Υ'()p(~season) = c(~season)Nm(~session)	18	469.21	2.77	0.09	789.64
4	S(~transients)Υ''(~season)Υ'(~SST_3)p(~season) = c(~season)Nm(~session)	20	469.32	2.88	0.09	785.37
5	S(~transients)Υ''(~BOAT)Υ'(~CEPHALOPODS)p(~photosanalysed) = c(~photosanalysed)Nm(~session)	20	469.42	2.98	0.08	785.47
6	S(~transients)Υ''(~SST_3)Υ'(~photosanalysed)p(~photosanalysed) = c(~photosanalysed)Nm(~session)	19	469.46	3.02	0.08	787.71
7	S(~transients)Υ''(~TOTALPREY)Υ'(~SST_3)p(~season) = c(~season)Nm(~session)	19	469.78	3.35	0.07	788.03
8	S(~transients)Υ''(~Year)Υ'(~SST_3)p(~season) = c(~season)Nm(~session)	20	470.07	3.64	0.06	786.12
9	S(~transients)Υ''(~SWIMMERS_1)Υ'(~SST_3)p(~photosanalysed) = c(~photosanalysed)Nm(~session)	20	470.18	3.75	0.06	786.23
10	S(~transients)Υ''(~SWIMMERS_1)Υ'(~CEPHALOPODS)p(~photosanalysed) = c(~photosanalysed)Nm(~session)	20	471.87	5.43	0.02	787.92
11	S(~transients)Υ''(~1)Υ'(~1)p(~season) = c(~season)Nm(~session)	16	481.77	15.33	0.00	806.55
12	S(~transients)Υ''(~1)Υ'(~1)p(~photosanalysed) = c(~photosanalysed)Nm(~session)	16	483.75	17.31	0.00	808.55
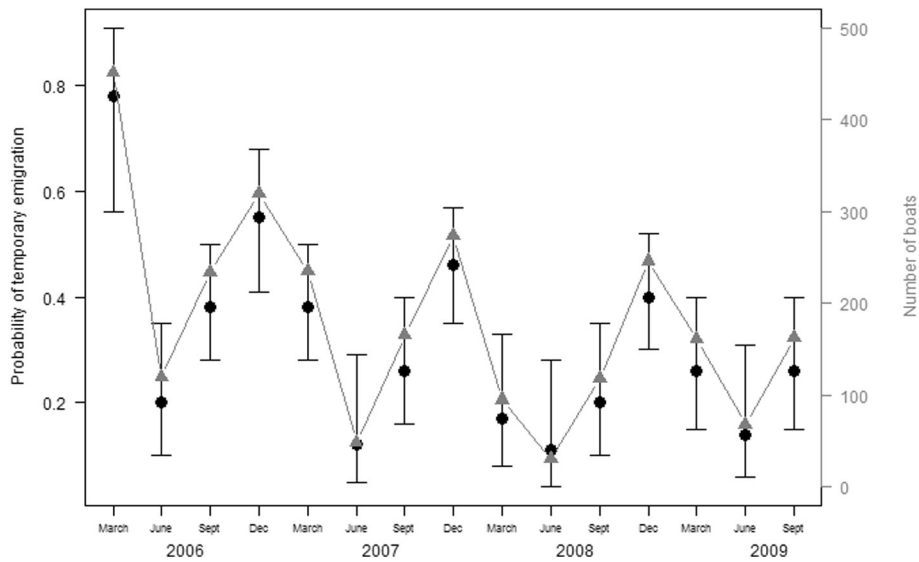
Fig. 2. Relationship between the probability of temporary emigration (γ'') and the number of boats between 2006 and 2009 around Kisite-Mpunguti Marine Protected Area (KMMPA). Vertical bars represent 95% confidence intervals.

4. Discussion

Our results demonstrate the importance of understanding temporary emigration movements in cetacean populations, due to the effect of multiple pressures. Importantly, we found that human disturbance and seasonal temperature influence the probability of animals leaving and entering the study area. These emigration parameters have seldom been addressed, and temporary emigration movements have often been identified as time-dependent (e.g., varying by season or year), independently of being random or Markovian (Nicholson et al., 2012; Smith et al., 2013).

4.1. Tourism impact on dolphins leaving the study area

Our best fitting Markovian model determines a positive correlation between the probability of animals temporarily leaving the study area and the number of boats present. Our results indicated that up to 78% of the population left the study area in March 2006, which recorded the highest number of boats entering Kisite-Mpunguti MPA since its

implementation in 1978 (Ministry of Tourism, 2010), with 451 boats and 6246 tourists present. It is important to notice that no code of conduct was present and swimming with dolphin was frequent in the area. However, in 2007, a code of conduct was drawn and started to be implemented, which prohibited swim-with dolphins and limited the distance and number of boats around them, as major changes for the dolphin-watching activity. In 2008, a significant drop in tourism (40% of the 2006 tourism), along with the swimming with dolphin prohibition, resulted in few animals leaving temporally the area during the month of June (49 boats and 1555 tourists). This temporal area avoidance means that dolphins inhabiting the MPA, the most critical core habitat for the species (Pérez-Jorge et al., 2015), temporarily move away when tourism intensity increase (i.e., number of swimmers and tourist boats). Additionally, groups of females with calves are common (authors' personal observation), and these groups are known to be negatively affected by high levels of tourism (Stensland and Berggren, 2007). In New Zealand, it has been reported that an increase in swim-with dolphins' attempts led to higher levels of swimmers avoidance, suggesting that animals became more sensitive to swimmers (Constantine, 2001). The
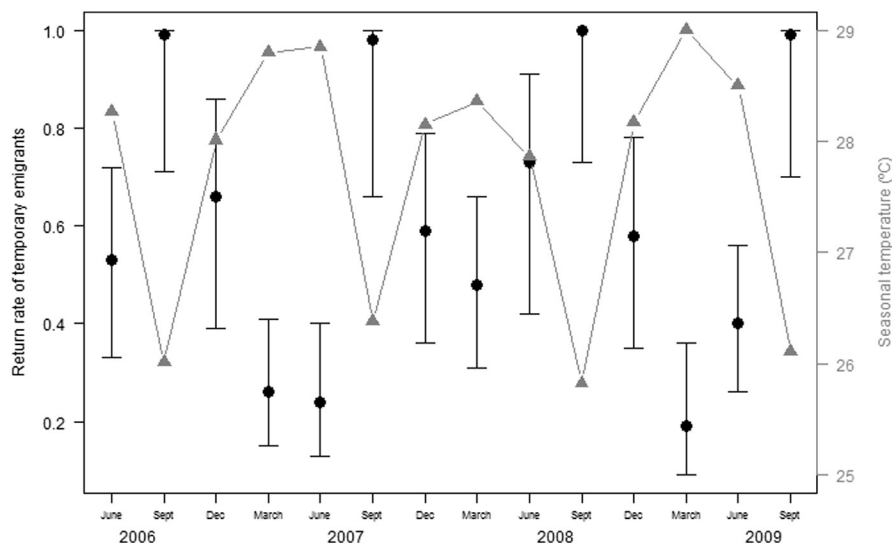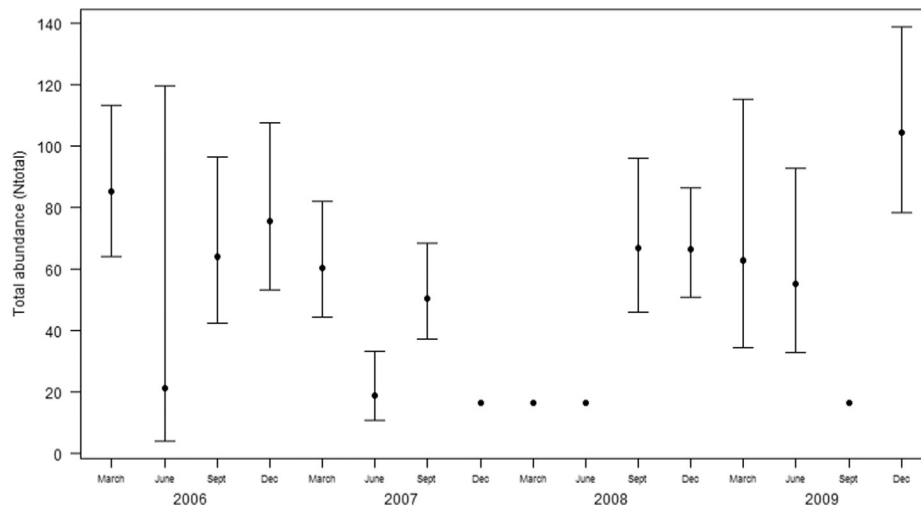

Fig. 3. Negative association between the return probability of temporary emigrants ($1-\gamma''$) and seasonal temperature (°C) between 2006 and 2009 around Kisite-Mpunguti Marine Protected Area (KMMPA). Vertical bars represent 95% confidence intervals.

Fig. 4. Seasonal abundance estimates (N_{total}) of the Indo-Pacific bottlenose dolphins between 2006 and 2009 around Kisite-Mpunguti Marine Protected Area (KMMPA). Vertical bars represent 95% confidence intervals.

likelihood that human disturbance leads to population-level consequences relies on its potential to impact on life-history traits, as well as on the proportion of the population subjected to these perturbations, which can also modify their life-history traits (Currey et al., 2009). Based on the above, our results may indicate that the number of temporary emigrants is likely related to the displacement of more sensitive individuals away from the perturbation area (Bejder et al., 2006; Lusseau et al., 2009). This provides strong evidence on the impact of tourism in local cetacean demography and the importance of regulating dolphin-watching tourism, specifically the presence of boats and swimming with dolphins.

In addition to the nature-based tourism influence, we should also take into account that this variability on the probability of dolphins temporarily emigrating from the study area is seasonally-dependent, as it was identified among the best four models with higher explanatory power. Previous studies have described this time-dependent effect, suggesting that some individual dolphins leave the study area for various seasons or years but subsequently return (Silva et al., 2009; Smith et al., 2013).

4.2. Influence of seasonal temperature on the return rate of temporary emigrants

We found a negative correlation between the probability of temporary emigrants returning to the study area and seasonal SST. The high variability of temporary emigration was likely due to seasonal movements and behavioural aspects of the species ecology driven by environmental conditions. Dolphins had a higher return rate during winter months, not supporting the hypothesis of temporary emigrants entering the study area seeking for mating opportunities during the peak-breeding season of spring and summer as previously described in other studies (Fury et al., 2013; Smith et al., 2013). Positive relationship between lower temperatures and increased cetacean occurrence seems to be related with higher abundance of prey items (Smith and Whitehead, 1996). In this regard, Kisite-Mpunguti MPA has one of the highest fish species abundance and biomass along the Kenyan coast (McClanahan et al., 2010; McClanahan et al., 2006). However, in our study, prey availability did not show a significant effect on the temporary emigration models which can be related with anon-linear relationship among prey catch and prey abundance and availability (Pauly et al., 2013), and therefore, landing data might not be reflecting dolphin prey availability. In addition, there is a lack of studies on the local diet composition of Indo-Pacific bottlenose dolphins, which might not be fully represented on the prey landing data. Although catch-per-unit-effort

(CPUE) data was not available for the study area during the sampling period, we think that it would have been a better proxy for prey availability (Smout et al., 2014). For these reasons, further investigations are needed to uncover the causes behind the temporary emigration movements.

4.3. Survival rates and population size

Life-history theory predicts high survival in marine mammals, given their low reproductive rate and long life spans (Wells, 1991). In this study, apparent survival rates were fairly high and consistent with known survival rates for *Tursiops* sp. (Nicholson et al., 2012; Silva et al., 2009). However, our results showed that our population had a difference in apparent survival rate dependent on whether or not dolphins had been captured before (i.e., transient effect models). This corresponds to the presence of a low proportion of transients in the population, likely caused by animals that are either passing through the study area only once (such as migrants) or animals that leave the area to join other groups (such as dolphins performing permanent dispersal) and are never recaptured, in contrast to resident dolphins.

Our findings provide the first robust abundance estimates for the Indo-Pacific bottlenose dolphin in Kenya. This study highlights the small population size and its seasonal fluctuations, ranging from 19 to 104 individuals, similar to previous studies for this species (Fury and Harrison, 2008; Möller et al., 2002; Smith et al., 2013). It has been considered that populations with less than 100 dolphins had a higher extinction risk, regardless of conservation measures adopted (Thompson et al., 2000). Additionally, small populations might be particularly vulnerable to human disturbances due to their high site fidelity and coastal distribution. In the Western Indian Ocean, a population of bottlenose dolphins has already been classified, and another one is proposed to be classified as endangered under the IUCN Red List criteria (IUCN and MNHM, 2012; Pusineri et al., 2014). Moreover unsustainable levels of dolphins' bycatch have been reported in Zanzibar, about 100 km south from our study area, where an adjacent community of Indo-Pacific bottlenose dolphin is resident (Amir et al., 2002). Despite the high survival rates estimated in this study, bycatch could represent a concern for the dolphin population inhabiting around Kisite-Mpunguti MPA, since known individuals have been already identified in other locations, like Watamu, which lies 140 km north (authors, unpublished data).

The overdispersion or extra-binomial variation detected through our model selection was likely caused by lack of independence in our data, e.g. preferred association among dolphins, and heterogeneity in capture probability and/or survival. These factors are likely to be important on

this study, as bottlenose dolphins often have social structure in their societies, which violates the assumptions of equal capture probability and survival among individuals (Durban and Elston, 2005; Hammond, 1986). We addressed these violations adjusting our models using the variance inflation factor, and incorporating the transient effect models. However, we are aware that our parameter estimates can still be biased due to the violation of these assumptions, and therefore, the population size given by our best fitting model may be underestimated (Pollock et al., 1990; Williams et al., 2002).

5. Conclusions

Our modelling approach highlights the importance to incorporate biotic and abiotic variables to study temporary emigration movements, which have been poorly described in cetacean species. Emigration movements are crucial in the dynamics of spatially structure populations, and have the potential to act as key aspects to determine management strategies for endangered or threatened populations. Moreover, these movements may be a resilient strategy that allows cetaceans to mitigate impacts under unfavourable situations. Our results show that seasonal SST and exposure to tourism influence temporary emigration. Understanding the effect of sea temperature variations on demographic parameters may help to predict how global change could affect local dolphin populations. Furthermore, investigating the impact of anthropogenic activities is crucial for the sustainable management of any nature-based tourism activity. The impact of tourist boats on the dolphin's temporary emigration seems to have been reduced after the suitable implementation of a new code of conduct. Other management actions, such as area or time closures, have been successfully implemented when unregulated and unmanaged cetacean-watching tourism has been identified as a potential threat to cetacean populations (Constantine et al., 2004; Notarbartolo-di-Sciara, 2009). Finally, it is important to maintain the long-term monitoring of this dolphin population, to be able to document tourism fluctuations, their consequences and to apply adaptive management strategies (Lahoz-Monfort et al., 2014).

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.03.006.

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