Net loss of endangered humpback dolphins: integrating residency, site fidelity and bycatch in shark nets

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Abstract

Fisheries bycatch—the incidental catch of non-target species during fishing—is problematic for large marine vertebrates. Bather protection programmes that use gillnets to kill sharks cause the incidental mortality of humpback dolphins (*Sousa* spp.) potentially impacting the long-term survival of these threatened species. Understanding dolphins' spatial and temporal use of gillnetted areas is critical for designing effective mitigation strategies. We photo-identified dolphins over eight years in a high-bycatch area (Richards Bay, South Africa) to assess the residency, site fidelity, and movement patterns of Indian Ocean humpback dolphins *S. plumbea* and evaluate how emigration, immigration and mortality rates influence the use of Richards Bay at various temporal scales. Overall, residency was low but site fidelity was high, leading to high population turnover in the short term but low turnover over six months and longer. There was clear individual variation in visitation but no evidence of seasonality. By considering such movements, the net loss of dolphins from the area became evident. While dolphins naturally emigrate from the area, the recognition of several catalogued individuals among the bycaught dolphins indicated that mortality in the shark nets contributes to the permanent loss of both residents and transients. Richards Bay may represent an ecological trap: high site fidelity indicates dolphins perceived the area as ecologically attractive, but high mortality due to shark nets makes it risky. We examined these results relative to gillnet bycatch mitigation methods and recommend that stakeholders collaborate as a mitigation team to prioritise management actions to reduce bycatch without compromising bather safety.

Key-words: bycatch mitigation, incidental catch, gillnets, residency, site fidelity, cetaceans, bather protection, South Africa

Introduction

Fisheries' incidental catch (bycatch) of large marine vertebrates is a pressing marine conservation issue, with many information gaps (Lewison et al. 2004). Examples span the globe and include some of the world's most endangered taxa (Lewison et al. 2014, Reeves et al. 2013). Bycatch in gillnets is particularly high: two orders of magnitude higher than trawls and other types of gear (Lewison et al. 2014, Read et al. 2006). One rather unusual use of gillnets is in the Australian and South African bather protection programmes, where nets are permanently set to catch and kill large sharks to reduce local population sizes, thereby reducing the probability of shark attacks on bathers (Dudley 1997). In addition to the target sharks, other large animals (e.g. cetaceans, chelonids, other elasmobranchs) are caught incidentally (Cliff & Dudley 2011, Gribble et al. 1998, Paterson 1990). Among the species of greatest concern are the threatened humpback dolphins *Sousa* spp. (Braulik et al. 2015, Parra & Cagnazzi 2016).

The taxonomy of the genus *Sousa* was recently revised (Jefferson & Rosenbaum 2014) and the constituent species are being assessed using the IUCN Red List Categories and Criteria. The recommended status of Indian Ocean humpback dolphins *Sousa plumbea* (inhabiting coastal waters from South Africa to the Bay of Bengal) was endangered based on their limited near-shore distribution, continuing decline in habitat quality, likely fragmentation of subpopulations and anthropogenic related mortality (Braulik et al. 2015, Plön et al. 2015). The most pervasive threats are fisheries bycatch and habitat loss/degradation. In South Africa, humpback dolphin bycatch occurs in the shark nets (Cockcroft 1994, Cockcroft 1990). Thirty-seven beaches in the KwaZulu-Natal province use shark nets but most (60%) of the humpback dolphin bycatch occurs at one beach, Richards Bay, which constitutes only 5% of the netting effort (Atkins et al. 2013).

Given the threatened status and strong spatial bias in bycatch, studying how humpback dolphins use the Richards Bay area is necessary. Investigating the length of time individuals spend in an area (i.e. residency) and their tendency to return to that area (i.e. site fidelity) can provide the context for understanding bycatch in shark nets and the magnitude of the effect of the nets on the population, thereby informing effective management strategies (Chapman et al. 2015).

Here, we analyse the residency, site fidelity and movement patterns of humpback dolphins at Richards Bay, where a high density of humpback dolphins and threats overlap. We quantify the dolphins' use of Richards Bay at multiple temporal scales and relate it to demographic processes (emigration, immigration and mortality) and assess which of these processes predominate. We examine bycaught individuals and explore options to mitigate the shark net bycatch of this endangered population.

Materials and methods

Study area and data sampling

Boat-based surveys were conducted over a 100km^2 area at Richards Bay (an estuary modified in 1976 to form a commercial port) (Fig. 1) in good weather (< Beaufort 3). Field seasons ran from the beginning of April and to the end of March of the following year, from April 1998 until March 2006. Surveys followed a regular route parallel to the coastline between 0.5km and 2km offshore at 10km/hr, with 1-3 observers searching for humpback dolphins with the naked eye. When encountered, a dolphin or a group of dolphins was slowly approached, counted and followed until it was lost or weather conditions deteriorated. We defined a group as two or more individuals in close proximity engaged in similar behaviour and moving in the same general direction (Irvine et al. 1981). We photographed the dorsal fins of as many dolphins as possible with no individual preferences. We initially used SLR cameras with 70-300mm zoom lens, changed to a digital video camera (640 x 480 pixels) with equivalent 400mm zoom in January 2000 and to a digital SLR with 70-300mm zoom lens in January 2004.

Individual identification

Individual dolphins were identified using natural permanent marks on its dorsal fin (e.g. notches, scars), using standard photo-identification protocols (Hammond et al. 1990). The quality of each image was scored for sharpness, contrast, proportion of fin visible, relative fin size and relative angle (Urian et al. 1999) and summed (from 5, poor, to 17, excellent); only images scoring >12 were used. We quantified distinctiveness using the best image of each catalogued individual and made it incrementally smaller (20%) until distinguishing features were invisible; the number of steps of size reduction was counted and corrected for original image size. Individuals scored a distinctiveness value between 2 (hardly distinctive) and 14 (extremely distinctive); only individuals scoring >5 were used. We excluded dependent juveniles from the analyses. Finally, we opportunistically photographed dorsal fins of humpback dolphins retrieved from shark nets by the KwaZulu-Natal Sharks Board (hereafter Sharks Board). We rated fin distinctiveness from 1 (indistinct) to 4 (very distinct) using natural marks, and we compared individuals scoring ≥3 with catalogued individuals. Body length and sex data were collected by the Sharks Board (Atkins et al. 2013). All photo-identification analyses were done by one of us (S. Atkins) and the data are available upon request.

Sampling effort

We plotted discovery curves to ascertain whether the sampling effort sufficed to sight most of the individual humpback dolphins using Richards Bay. To determine whether the final estimated number of marked individuals lay near the asymptote of the discovery curve (Work et al. 2005), we calculated sample-based rarefaction curves with 95% confidence intervals (CI) using the estimator “S(est)” which estimate the expected number of individuals in t pooled samples, against the reference sample (Colwell et al. 2004). On the discovery plot, we overlapped the cumulative number of photographs catalogued and the total survey effort (hours) for each field season (April-March). As the annual effort was heterogeneous (decreased during the study), we excluded the possibility that reduced effort decreased the discovery rate by evaluating discovery curves for each year separately.

Site fidelity and residency patterns

We used mean annual number of months with sightings (M_m) and the proportion of years with sightings (P_y) to quantify sighting rates, characterise the use of the area and further classify individuals according to degree of residency. To classify individuals’ residency, we first employed a hierarchical clustering analysis (average linkage method) based on an Euclidean distance matrix considering both M_m and P_y (see Daly et al. 2014). We evaluated the dendrogram accuracy with the Cophenetic Correlation Coefficient (CCC), where CCC>0.8 indicated a reliable representation (Bridge 1993). We used the resultant clusters in the dendrogram to classify individuals into residency categories (see Results). We cross-validated the resulting dendrogram partition into clusters using Similarity Profile Analysis (SIMPROF), testing the null hypothesis that distances within clusters of dolphins were not different from expected by chance using a null model based on iterative permutations (Clarke et al. 2008).

Site fidelity and residency of bycatch

The bycaught individuals that had been catalogued were classified into the same residency categories delineated by the hierarchical clustering analysis using two approaches: clustering snapshots and discriminant analysis. First, we calculated the Euclidean distances between all individuals (bycaught and non-bycaught) based on sighting rates (M_m and P_y) until the date that each bycaught individual was found dead and built hierarchical clustering dendrograms. With such residency snapshots, we evaluated which dendrogram branch (i.e. residency category) the bycaught dolphins clustered with, but considered only the period they were known to be alive, thus controlling for the bias of reduced sighting rates due to mortality as opposed to emigration.

Second, to cross-validate the clustering snapshot classification we employed a linear discriminant analysis (LDA). We expressed the differences in residency patterns among non-bycaught dolphins from each residency category as a linear function of three variables: mean annual number of months (M_m), proportion of months (P_m), and proportion of years with sightings (P_y). We departed from the saturated LDA model and used back and forward stepwise leave-one-out cross-validation procedure to find the best combination of the three variables that separates the residency classes. We then compared it to an LDA model that used the same two variables in the hierarchical cluster analysis (M_m, P_y). The best model was the one with the highest accuracy, given by the proportion of correct assignment of individuals to the residency categories defined previously in the hierarchical clustering. We then used this best LDA model to classify the bycaught dolphins into the residency classes, and finally compared the two—clustering and LDA model—classifications.

Population turnover

We tested whether the population composition (i.e. presence/absence of individuals) changed during the study by estimating the average population turnover at various time scales. We divided the total study length (96 months) into integer periods of months (3, 4, 6, 8, 12, 16, 32 and 48 months) and compared the average Whittaker's dissimilarity between periods based on the presence of individuals in the population (Cantor et al. 2012). The significance of the population turnover was assessed by generating benchmark distributions for each time period with a null model that randomized individuals among periods but constrained their empirical sighting frequency (Cantor et al. 2012). If the observed dissimilarity values were >97.5% CI the population turnover was higher than expected by chance, while values <2.5% CI indicated turnover lower than expected by chance.

Lagged identification rates

To infer movements of individuals, we modelled the probability of resighting individuals over time using lagged identification rates (LIR, Whitehead 2001). The LIR is the probability that an individual identified in the study area at time t would be identified again at a later time. To infer the demographic processes leading to the decay of LIR over time, we fitted eight theoretical exponential models using maximum likelihood and binomial loss (Whitehead 2001). Candidate demographic processes included population closure, permanent exit from the area (emigration and/or mortality), temporary emigration and reimmigration, and combinations of these (Table S1). We selected the most parsimonious model as the one with lowest Quasi-Akaike Information Criterion (QAIC) due to overdispersion in the data (Whitehead 2007). The degree of support for the models was inferred with differences in the QAIC with the best fit models (ΔQAIC; $\Delta<2$ suggests substantial support), relative and standardized QAIC weights (Whitehead 2007). A bootstrap procedure yielded standard errors for the observed LIR and model parameters.

Seasonality

To test whether sightings were seasonal, we employed a circular regression on sightings per unit effort (SPUE; sum of good quality photographs/sum of survey effort) for each month (Vianna et al. 2013, DeBruyn & Meeuwig 2001). To cross-validate the seasonal patterns, we identified one survey in each month that was closest in duration to three hours (the modal survey duration) and used the circular regression on the number of sighted dolphins (boat-based estimate of group size, summed if >1 group was observed); and on photographed dolphins during that survey.

Results

Sampling effort and photo-identification

We conducted 417 surveys (mean ± SD survey effort = 9.88 ± 0.5 months/year; range 8-12 months) and sighted 384 groups of humpback dolphins in 272 surveys. A total of 945 good quality photographs revealed 109 distinctive individuals (Table S1). Sampling effort sufficed; the initial high rate of discovery stabilised around the third sampling year (Fig. 2) and although the curve was not quite asymptotic, we clearly sampled a large portion of the population. The survey effort decreased over time, but photographic effort did not (digital equipment was more efficient). Therefore, the reduced survey effort later in the study probably did not cause the decrease in the rate of discovery.

Variance in the probability of sighting an individual was likely a result of individual variation in attendance at Richards Bay rather than variation in survey effort. When we deconstructed the discovery curve into years the final number of marked individuals did not lie near the rarefaction asymptote for most of the years (Fig. S1). The years with the highest effort (Years 1, 2) were not the ones that stabilised, so greater effort did not necessarily yield more individuals, and effort and cataloguing rate were similar in years 2 & 3 but number of individuals was not (Fig. S1, Table S1).

Photo-identification of bycatch

At least 35 humpback dolphins were retrieved from the Richards Bay shark nets during the study (25 males, 9 females, and 1 sex unknown). Of the 23 individuals we photographed, 16 had distinctive fins: nine had been catalogued (7 males, 1 female, 1 sex unknown), and the others were males that had not been catalogued and dependent juveniles (Table S3). Sighting rates of bycaught individuals varied from 0 months/year (not previously sighted) to 5.6 months/year (the most frequently-sighted individual) (Table 2).

Site fidelity and residency

Humpback dolphins at Richards Bay exhibited variable patterns of site fidelity with monthly sighting rates ranging from 0.13-5.25 months/year (0.91±1.14) and yearly sighting frequency of 1-8 years (3.26±2.37) (Fig. S2). Variation in the residence patterns was also apparent: the hierarchical cluster analysis (CCC=0.94) contained distinct clusters of individuals based on the average and proportion of time spent in the area (Fig. 3). The SIMPROF test indicated seven clusters, which we categorized into three residency categories: 1) "Residents" comprised a single cluster of five dolphins seen ≥4 months/year, in 7-8 years; 2) "Intermediates" contained a single cluster of 14 individuals seen 1-3 months/year in 5-8 years; and 3) "Transients" included five clusters (due to the few observations of these individuals) totalling 81 dolphins seen during ≤1 month/year in 1-6 years.

Site fidelity and residency of bycatch

The two methods of classifying catalogued bycaught individuals into residency categories yielded the same result in 78% (n=9) of the cases; the two that differed were dolphins that died early in the study. LDA models had very high accuracy (correctness rate >98%; Table S3), but since the snapshot method accounted for an important bias (a bycaught dolphin did not have the same sighting opportunities as other dolphins in the year it died) we focused on its results. Therefore, three bycaught dolphins were considered Residents, five were Transients and one was Intermediate (Table 2).

Population turnover

The composition of the population changed over short, but not long, periods of time. Population turnover was significantly greater than expected by chance during 3 and 4 month periods, while for periods ≥6 months, turnover was lower than expected (Fig. 4). Short-term changes reflected a dynamic population, characterized by frequent movements of individuals through the area, while the long-term stability reflected return to the area and site fidelity.

Lagged identification rates

The lagged identification rate was highest within one day and dropped by half 2-3 days later but rose within a week where it remained stable for about a year before it dropped again without recovering (Fig. 5). The two best fitted models (ΔQAIC=0) described variations in LIR as the result of permanent emigration and/or mortality (Models 1,2; Table 1). These two models are equivalent, just parameterised differently. A third well-supported model (ΔQAIC <2) reinforced the influence of emigration and mortality and suggested that reimmigration also contributed to the variation of LIR and movement patterns in this population (Model 3,

Table 1). LIR for each residency category further indicated intrapopulation variation in the residence patterns and use of the area (Figure S3, Table S2).

Seasonality

There was no evidence of seasonality in the presence of humpback dolphins at Richards Bay. SPUE did not vary predictably with season (Multiple R^2=0.03; F_{76}=1.04; p=0.36) (Fig. 6), nor did number of sighted dolphins (Multiple R^2=0.02; F_{76}=0.56; p=0.58), nor number of photo-identified dolphins (Multiple R^2=0.01; F_{76}=0.21; p=0.81) when controlling for survey effort.

Discussion

Our findings reveal how Indian Ocean humpback dolphins use the coastal waters of Richards Bay repeatedly over multiple temporal scales. Residency was low, with reduced individual resighting probabilities—dolphins were only present for a day or two before leaving the area—yielding high population turnover over short periods. However, there was high site fidelity leading to low population turnover over longer periods. Movement patterns clearly varied among individuals: the population using Richards Bay comprised a small core of residents (5%) along with many transients (81%) passing through the area. While our results show that individuals naturally emigrate from the area, they also point to mortality in shark nets as a driver of the permanent loss of individuals. The strong site fidelity indicates that Richards Bay is an attractive area for humpback dolphins and yet imposes a high mortality risk. Coupled with the low abundance of humpback dolphins in Richards Bay (74 individuals, 95% CI = 60-88; Keith et al. 2002), this scenario begs for mitigation initiatives to reduce mortality in the area.

The low residency, high proportion of transients and short duration of visits suggest that the dolphins are moving through Richards Bay. Our study area is relatively small and it is likely that we only covered a portion of the range of this population since humpback dolphins can move distances of 70 to 150km (James et al. 2015, Keith et al. 2002, Karczmarski et al. 1999) and the ranges of individual Indo-Pacific humpback dolphins *Sousa chinensis* average 100 km^2 (Hung & Jefferson 2004). Humpback dolphins using Richards Bay probably form part of a larger population using the KwaZulu-Natal coast.

The long-term site fidelity at Richards Bay suggests the area is part of a key habitat for humpback dolphins. They are possibly attracted by prey availability: feeding is the most frequently observed behaviour (Keith et al. 2013, Atkins et al. 2004) and there is a persistent upwelling cell at Richards Bay enriching biological production (Lutjeharms et al. 2000). Similarly, Australian humpback dolphins *S. sahulensis* exhibit long-term site-fidelity hypothesised to be driven by foraging and mating opportunities (Parra et al. 2006).

The combination of low residency and high site fidelity suggest much movement in and out of Richards Bay. Therefore, temporary emigration and reimmigration are important demographic processes, which have been observed for humpback dolphins in South Africa and Australia (Parra et al. 2006, Karczmarski et al. 1999). However, at Richards Bay the movements were not predictable since no seasonality was evident; bycatch too lacked seasonality (Atkins et al. 2013). Although there is seasonal variation in environmental conditions in the area, short term fluctuations due to upwelling processes may mask or exceed seasonal variation (Lutjeharms et al. 2000). Visiting patterns varied individually which could lead to varying numbers of individuals using the Richards Bay area each year, potentially explaining the marked fluctuations in annual bycatch (Atkins et al. 2013).

We documented a net loss of dolphins, with clear changes in individual re-sighting probabilities partially explained by mortality. Despite the natural emigration and reimmigration at Richards Bay, mortality of humpback dolphins due to bycatch in shark nets is evident. We showed that our sampling efficacy is probably not responsible for the decay in resightings, and that at least 8% of the catalogued individuals were retrieved from shark nets. Since the catalogued dolphins were predominantly transients, one might expect more transients to make up the bycatch. While transient dolphins could be naïve to the threat of the nets and so more likely to be entangled (Keith et al. 2002), our results indicate that individuals with different levels of residency are bycaught and thus naïveté does not necessarily explain entanglement.

Conservation implications

Richards Bay is an important area for humpback dolphins and is used frequently by some residents along with many transient individuals. The repeated selection of this area and the elevated mortality risk suggest that Richards Bay is an attractive sink or ecological trap (Battin 2004): an area of high habitat suitability and high anthropogenic mortality. Populations that overlap with ecological traps might appear stable (even growing) through immigration from adjacent habitats (sources); but theoretical and empirical studies show such traps affect the demography in source habitats, and can drive local populations to extinction (Delibes et al. 2001, Gundersen et al. 2001, Whitehead & Gero 2015). Bycatch rates at Richards Bay were variable and did not decline linearly over time (Atkins et al. 2013). Such a lack of decline in the catch rate is usually interpreted as a sign that the shark nets are not affecting the size of the population (Dudley & Gribble 1999, Dudley & Simpfendorfer 2006). The high short-term population turnover detected in Richards Bay and the immigration of transients from adjacent areas could mask a local population decline. Therefore, even though the bycatch rate did not decline over time, the shark nets could be affecting the population at Richards Bay and further afield.

Most dolphins bycaught at Richards Bay were adolescents (Atkins et al. 2013), yet most of the bycaught dolphins that were catalogued were adults, probably because mark accumulation (and therefore chances of being catalogued) increases over time (Urian et al. 2014). Although they are not the most susceptible age class, mitigating adult bycatch is still valuable given the importance of adult survival to population persistence in dolphins (Reilly & Barlow 1986). The bycatch at Richards Bay is male-biased (2:1 (Atkins et al. 2013); yet for those bycaught dolphins that had been catalogued in this study, the male bias was even more exaggerated at 7:1. We do not know whether males are more prone to be bycaught, or are more easily identified, given that most of the photographed dorsal fins of bycaught humpback dolphin females were not distinctive, as also seen for bottlenose dolphins (Scott et al. 2005).

The shark netting operation does not constitute a conventional fishery but, since nets are used to catch and kill sharks, it can be thought of as a shark fishery. We therefore use a fishery framework to explore bycatch mitigation options which are usually classified into four types of strategies: 1) reducing fishing effort, permanently or temporarily; 2) relocating nets; 3) introducing mitigation technologies; and 4) changing fishing methods. First, although the Richards Bay installation has been reduced from 2.8km in 1989 to the present 1.2km, it is larger than 90% of the other installations. If 2 of the 6 nets were removed, it would still be larger than 80% of the installations. Therefore, permanently reducing fishing effort may be an option, as well as temporary closures. Lack of dolphin bycatch seasonality means that other considerations could determine temporary closure times, e.g. during winter when bather numbers and shark catches are lower (Cliff & Dudley 1992). Second, relocating the nets away from the harbour entrance and away from the dolphins' core feeding area could mitigate bycatch (Keith et al. 2013). But beach infrastructure (facilities, parking) is fixed and determines the required position of the nets, thereby nullifying this option. Third, we used

Werner et al.'s (2006) framework to identify mitigation technologies that have been used successfully to mitigate cetacean bycatch in gillnets; there are two acoustic alarms (pingers) and stiffened nets. Pingers of 10kHz and 3kHz were tested in the Richards Bay shark nets but did not reduce humpback dolphin bycatch (Cliff & Dudley 2011, KwaZulu-Natal Sharks Board unpublished data), indeed many of the dolphins reported here died in nets with 10kHz pingers. Similar pingers changed Australian humpback dolphin *S. sahulensis* behaviour only subtly and were not recommended for use in the Queensland bather protection programme and gillnet fisheries (Berg Soto et al. 2013). There are other pingers with different signals that could be tested but the humpback dolphin, a delphinid with a coastal distribution and high site fidelity, is an unlikely candidate for successful pinger use (Dawson et al. 2013). Gillnets stiffened with metal oxides have reduced small cetacean bycatch in some (Larsen et al. 2007, Trippel et al. 2003) but not all instances (Bordino et al. 2013), either due to increased detectability or decreased chance of entanglement. However, stiffness is lost within 24 hours (Mooney et al. 2007). Shark nets are deployed continuously and each net remains in the water for 10 days before being changed (Dudley 1997), negating this option. Finally, one could change the fishing method. Other types of fishing gear have lower rates of megafauna bycatch than gillnets (Lewison et al. 2014, Read et al. 2006), so changing fishing methods would probably reduce humpback dolphin mortality. Baited hooks have been used successfully to prevent shark attacks in Australia and Brazil and have a reduced bycatch compared to nets (Hazin & Afonso 2014, Cliff & Dudley 2011, Dudley et al. 1998). In the past decade, the Sharks Board has replaced some gillnets with baited hooks (called drumlines), including half of a net at Richards Bay that had a high bycatch of humpback dolphins (Cliff & Dudley 2011). Further replacements of the Richards Bay nets with hooks could be feasible.

Killing sharks is not the only way to prevent shark attacks. More benign methods do exist and are of two types: shark deterrents and shark detection (McPhee et al. 2015). The first type works to deter or repel sharks from an area; examples include physical barriers and electrosensory shark deterrents and the Sharks Board is actively investigating the use of an electrical cable (O'Connell et al. 2012, Cliff & Dudley 2011). The second type alerts bathers to the presence of sharks in an area; a successful example of a shark detection programme is Shark Spotters in Cape Town, South Africa (Kock et al. 2012). However, various factors make the potential implementation of these strategies difficult in KwaZulu-Natal. Examples include the large (average 1.6m) and variable waves (Corbella & Stretch 2012) that makes it impractical to anchor devices and structures in the wave zone; turbid coastal water may make shark spotting difficult; and monetary costs that are a perennial issue. These are some of the problems that render benign methods of bather protection not immediately feasible. We suggest bycatch mitigation should include both short-term and longer-term (non-lethal) strategies.

We conclude that bycatch of Indian Ocean humpback dolphins in shark nets at Richards Bay may be negatively affecting the wider population and continued efforts to mitigate the loss are vital. Conservation resources could be maximised by initially focussing efforts in one small area, Richards Bay, which could have a positive effect on the broader population of this endangered species. Gillnets should be removed from the area and there are options, as explored above, but unfortunately no easy solutions. Bycatch mitigation is most likely to be effective when stakeholders collaborate to find solutions (Knight et al. 2006, Cox et al. 2007) and therefore, we recommend that a "mitigation team" be established urgently to consider in detail the risks, costs and benefits of these potential conservation actions to sharks and bathers as well as dolphins. This mitigation team should prepare a costed and prioritised set of management actions (Carwardine et al. 2012) and should monitor the results of the decisions that are made. Management action must not be delayed and the resultant set of proposed actions should be phased such that a feasible, interim strategy is designed while concomitantly long-term, non-lethal alternatives to the present, outmoded bather protection programme are found.

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Table 1. Candidate exponential decay models ranked by lowest quasi-Akaike Information Criterion (QAICc) for lagged identification rates (LIR) of Indian Ocean humpback dolphins at Richards Bay, 1998-2006. Identification rates of individuals (*R*) is given as a function of time lag (*d*). The ΔQAIC, QAIC weight and model likelihood indicate the relative support for each model.

	LIR models	Biological interpretation	QAIC	ΔQAIC	QAIC weight	Likelihood
1	$R(d) = \left(\frac{1}{28.34}\right) \cdot e^{\left(-\frac{d}{33.37 \cdot 10^{2}}\right)}$	Emigration or mortality	107494	0	0.35	1.00
2	$R(d) = 0.04 \cdot e^{\left(-\left(0.03 \cdot 10^{-1}\right) \cdot d\right)}$	Emigration or mortality	107494	0	0.35	1.00
3	$R(d) = 2.93 \cdot e^{(-5.49 \cdot d)} + 0.04 \cdot e^{\left(-\left(2.98 \cdot 10^{-4}\right) \cdot d\right)}$	Emigration + reimmigration + mortality	107496	1.4	0.13	0.37
4	$R(d) = \left(\frac{1}{28.34}\right) \cdot \left(\frac{\frac{1}{1.46 \cdot 10^{13}} + \frac{1}{33.37 \cdot 10^{2}} \cdot e^{(-(\frac{1}{1.46 \cdot 10^{13}} + \frac{1}{33.37 \cdot 1}}}{\frac{1}{1.46 \cdot 10^{13}} + \frac{1}{33.37 \cdot 10^{2}}}\right.$	Closed: emigration + reimmigration	107496	2	0.13	0.37
5	$R(d) = \left(\frac{e^{\left(-\left(2.99 \cdot 10^{-4}\right) \cdot d\right)}}{26.96}\right) \cdot \frac{\left(\frac{1}{2.02}\right) + \left(\frac{1}{39.38}\right) \cdot e^{\left(-\left(\frac{1}{2.02} + \frac{1}{39.38}\right) \cdot d\right)}}{\frac{1}{2.02} + \frac{1}{39.38}}$	Emigration + reimmigration + mortality	107498	3.8	0.05	0.14
6	$R(d) = 0.03 + 0.07 \cdot e^{(-1.21 \cdot d)}$	Closed: emigration + reimmigration	108035	541.4	0.00	0.00
7	$R(d) = 0.03$	Closed population	108040	546.4	0.00	0.00
8	$R(d) = \frac{1}{37.64}$	Closed population	108040	546.4	0.00	0.00

Table 2. Distinctive humpback dolphins caught in the shark nets. ID: photo-identification label (missing data indicate distinctive individuals not present in the catalogue); Sex (M=male, F=female); Length: body length (m); Age class: Adults and Adolescents (as classified in Atkins et al. (2013)); M_m: mean annual number of months with sightings; P_y: proportion of years with sightings; and residency classifications by two methods, hierarchical clustering analysis (HCA) and linear discriminant analysis (LDA). Missing data is indicated by "-".

Date of retrieval from nets	ID	Sex	Length	Age class	M_m	P_y	Residency by HCA	Residency by LDA
98-06-18	-	M	2.6	Adult	-	-	-	-
98-09-22	139	M	2.3	Adult	1.0	1.0	Transient	Intermediate
99-05-22	134	M	2.6	Adult	3.5	0.5	Resident	Resident
99-06-18	-	M	2.0	Adolescent	-	-	-	-
99-07-21	54	M	2.3	Adult	3.0	1.0	Resident	Intermediate
00-02-07	137	M	2.7	Adult	0.5	0.5	Transient	Transient
01-06-01	59	-	-	-	0.8	0.5	Transient	Transient
02-03-30	81	M	-	-	0.3	0.3	Transient	Transient
02-04-02	-	M	-	-	-	-	-	-
02-10-28	101	M	2.2	Adolescent	0.4	0.4	Transient	Transient
02-11-01	75	F	2.3	Adult	5.6	1.0	Resident	Resident
03-03-24	40	M	2.3	Adult	2.4	1.0	Intermediate	Intermediate

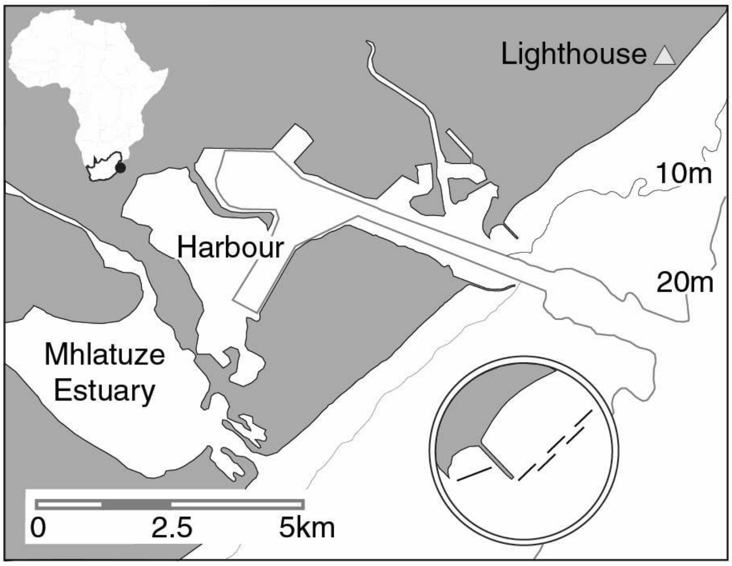

Figure 1. The Richards Bay (28.80873°S, 032.089663°E) study area, from the Mhlatuze Estuary mouth to the lighthouse and including the dredged harbour, with bathymetry indicated; South African Navy Chart SAN1032, 1997. The inset shows the shark nets which are set near the harbour entrance.

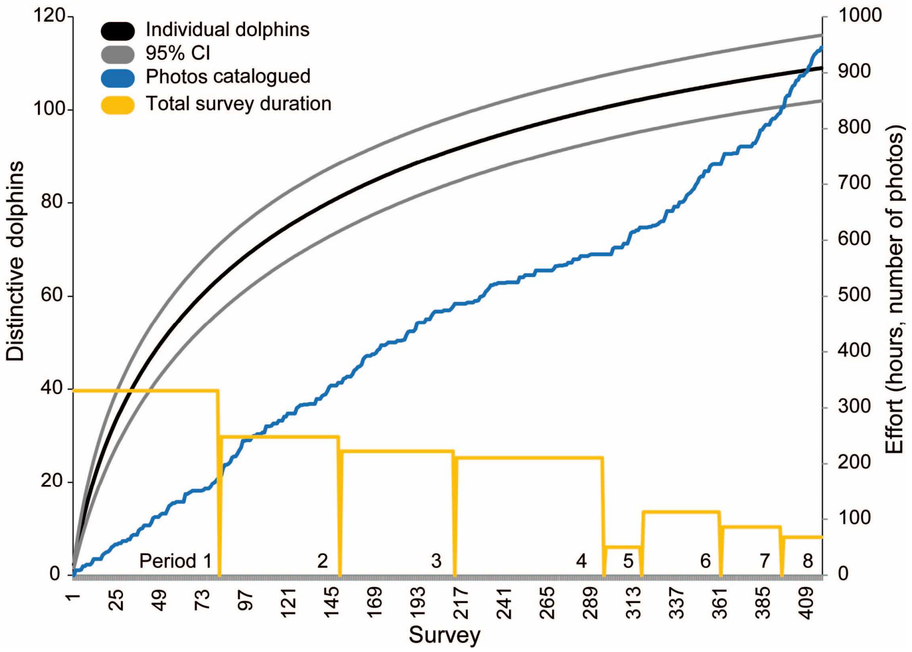

Figure 2. Discovery curve with 95% confidence intervals (CI) of distinctive humpback dolphins and effort expressed as total survey duration (hours) for each field season and the cumulative number of photographs catalogued at Richards Bay, April 1998-March 2006. The yellow lines represent the survey periods indicated in Table S1.

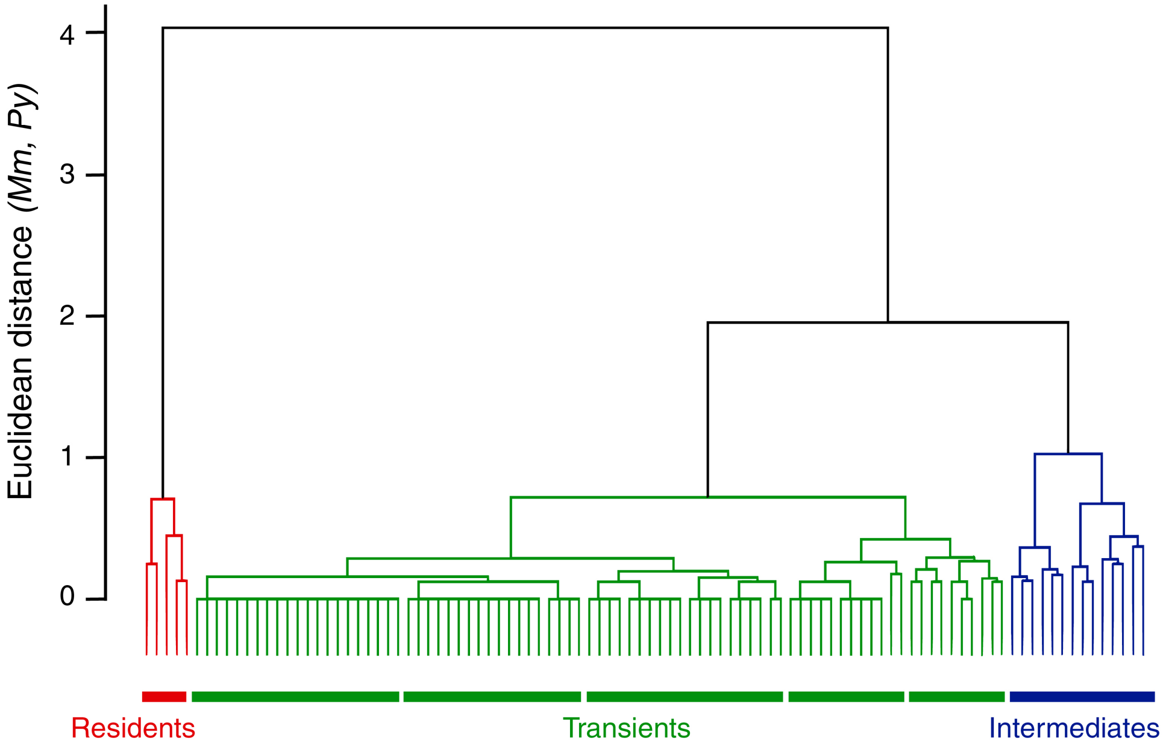

Figure 3: Hierarchical clustering dendrogram of individual humpback dolphins (excluding bycatch) based on residency rates (Euclidean distances based on mean annual number of months, *Mm*, and the proportion of years with sightings, Py). Significant clusters (horizontal bars) defined three residency categories (colour coded): Residents, Intermediates and Transients (note that 5 Transient clusters are combined for further analyses).

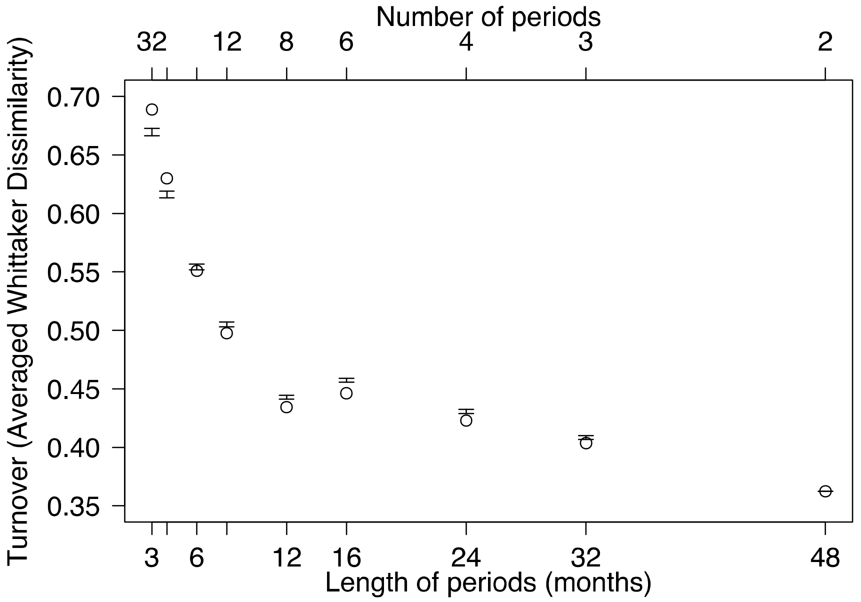

Figure 4. Differences in individual humpback dolphins composing the population (turnover) over various time periods. Top axis gives the number periods in which the total study was divided into; x-axis gives the length of such periods; y-axis gives our measure of population turnover, the average Whittaker dissimilarity index between periods. Whiskers represent 95% confidence intervals generated by a null model.

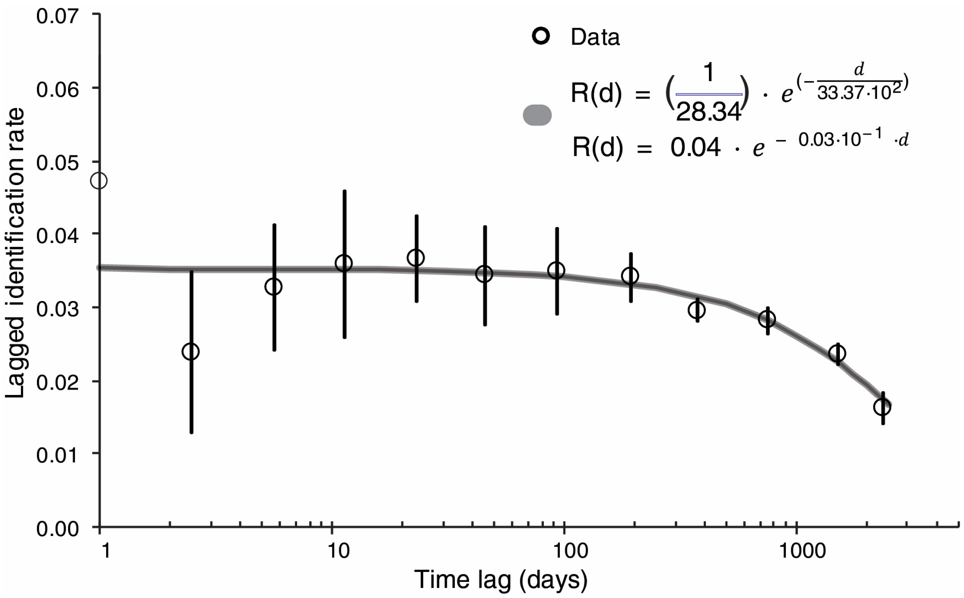

Figure 5. Lagged identification rates (LIR) for humpback dolphins photo-identified at Richards Bay and the best fit models (see Table 1). Open circles represent observed LIR; the solid grey line represents the best fit model; whiskers represent bootstrap-estimated standard errors

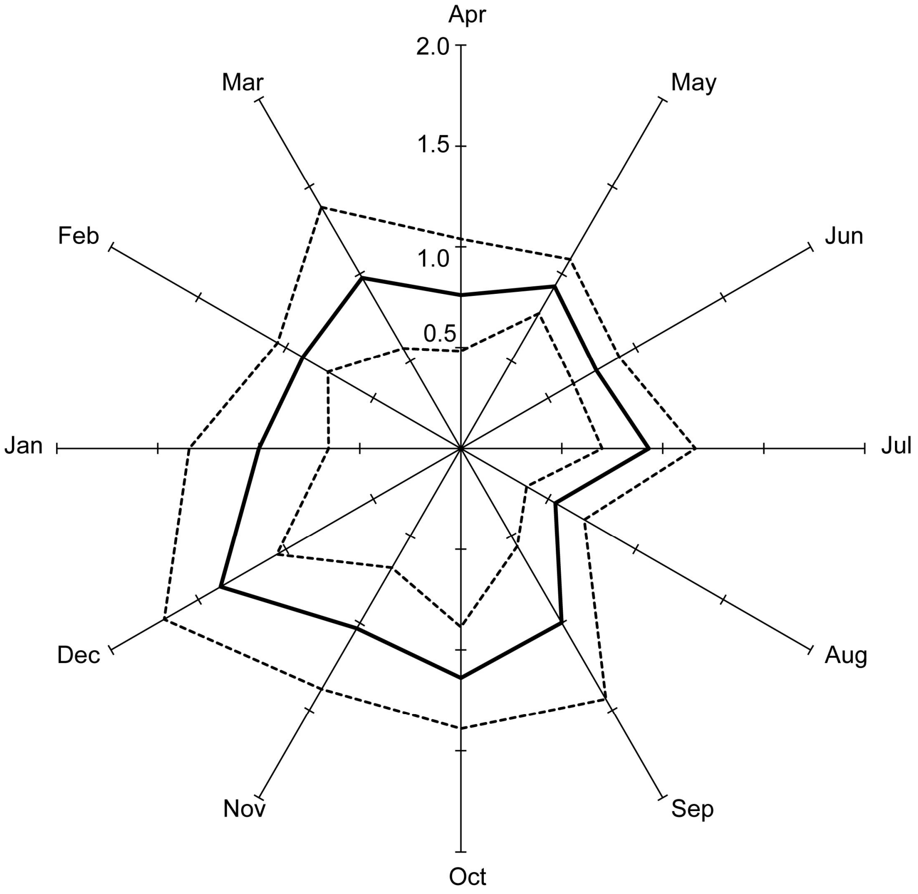

Figure 6. Monthly sightings of humpback dolphins per unit effort (sum of good quality photographs/ sum of hours of survey effort). Solid line represent mean values; dashed lines represent standard errors.