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An abundance estimate for humpback whales *Megaptera novaeangliae* breeding around Boa Vista, Cape Verde Islands

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ABSTRACT

The abundance of humpback whales occurring around Boa Vista, Cape Verde Islands, was estimated by mark-recapture modelling. Photographs of markings on tail flukes of individual whales were collected during the breeding season. Sighting histories were constructed for each individual and an abundance of 171 animals was estimated using a Jolly-Seber mark-recapture model. Correcting for known biases arising due to sex-specific behaviour and temporary emigration insofar as possible, an estimate of 260 whales was obtained. This is significantly higher than the previous estimate of 99 humpback whales from this region. Due to limited survey effort it is not known how representative the study area is of the entire Cape Verde archipelago and this estimate may be considered to be biased low and serves as a minimum estimate. The high recapture probability (0.37) coupled with the low abundance is consistent with a small local population. The low survival rate (0.86) suggests possible emigration and further studies are needed to assess connectivity between humpback whales breeding in Cape Verde and other breeding locations. The amount of exchange between groups of whales breeding in Cape Verde and adjacent areas remains unknown. It is unclear whether the abundance estimate herein applies to part of an isolated population or part of a larger and continuous one.

RESUMO

Apresenta-se uma estimativa da abundância de baleias-de-bossa na ilha da Boa Vista, Cabo Verde, realizada através de modelação por marcação e recaptura. Durante o período de reprodução, foram fotografadas marcas nas barbatanas caudais de indivíduos, tendo sido também construídos historiais de avistamentos. Aplicando o modelo de marcação e recaptura de Jolly-Seber chegou-se a uma estimativa de 171 baleias-de-bossa. Após correcção, tanto quanto possível, de desvios relacionados com comportamentos sexuais específicos e migração temporária, a estimativa foi alterada para 260 indivíduos. Este valor é consideravelmente maior do que a anterior estimativa para a mesma área, que identifica 99 indivíduos. Sendo os estudos ainda escassos, desconhece-se a representatividade da área de estudo face ao arquipélago de Cabo Verde no seu conjunto, pelo que esta estimativa deve estar enviesada negativamente e deve ser tomada como valor mínimo. A alta probabilidade de recaptura (0.37) e reduzida abundância são consistentes com uma população local e pequena. A baixa taxa de sobrevivência (0.86) sugere uma possível migração, pelo que devem ser realizados mais estudos no sentido de analisar a relação entre a reprodução das baleias-de-bossa em Cabo Verde e noutros locais. A frequência de mistura entre grupos de baleias que se reproduzem em Cabo Verde e em áreas adjacentes permanece desconhecida. Não é claro se a abundância aqui estimada se aplica a parte de uma população isolada ou a parte de uma população mais vasta e contínua.

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INTRODUCTION

Humpback whales *Megaptera novaeangliae* migrate from northern feeding areas to the Cape Verde Islands during winter to breed and give birth. This species is typically found from February to late May in sheltered waters in the lee of islands. Although likely biased by search effort, humpback whales are chiefly found off Boa Vista, Sal and Maio, but occasionally around the other islands of the Cape Verde archipelago (Hazevoet & Wenzel 2000, Wenzel *et al.* 2009, Ryan *et al.* 2013a). Based on whaling records, it has been suggested that these humpbacks are a separate population to that in the West Indies (Townsend 1935, Smith & Reeves 2003). Molecular genetic analysis and photo-identification matching studies are currently underway to investigate if Cape Verde humpbacks are reproductively isolated from those breeding elsewhere in the North Atlantic. Preliminary genetic results suggest that this may indeed be the case (Bérubé *et al.* 2012).

Analysis of whaling ship logbook records indicate that *ca.* 5000 individuals occurred in the waters around Cape Verde prior to over-exploitation during the 18th Century (Smith & Reeves 2003, Punt *et al.* 2006). The only available modern-day abundance estimate for the archipelago is 99 (CV = 0.23), however the authors cautioned that it may be unreliable due to limited data available at that time (Punt *et al.* 2006). Furthermore, whether the abundance estimates presented both herein and by Punt *et al.* (2006) apply to a discreet population of whales is uncertain. Nonetheless, a local abundance estimate is important to monitor trends in the number of humpback whales breeding around Boa Vista in light of rapid development of the coastal environment (Ryan *et al.* 2013a). In the western North Atlantic Ocean, there has been an increase in humpback whale abundance at a rate of 0.031 yr^{-1} (Stevick *et al.* 2003). In contrast, on the eastern side of the Atlantic, a general lack of data available on humpback whales means that the species status is not known.

In this brief study, an updated abundance estimate is presented for humpback whales around Boa Vista, one of the three eastern Cape Verde Islands, using mark-recapture analysis of natural markings from tail fluke images (i.e. photo-identification). These techniques can be used to derive estimates of abundance for cetaceans (Hammond 1986), however the underlying assumptions can be difficult to satisfy (Hammond 1990, Hammond *et al.* 1990). The greatest challenge in this regard is accounting for heterogeneous 'catchability' (i.e. heterogeneity in the probability of recapture) and differentiating between temporary emigrations (Hammond 1990, Kendall *et al.* 1997). Using open-population models, permanent emigration or death can be accounted for, but temporary emigration presents challenges that are difficult to address using small datasets (Hammond 1990, Fujiwara & Caswell 2002). For a scenario such as that in Cape Verde, where population structure is unclear and movements between breeding areas cannot be discounted, open-population models such as the Jolly-Seber and Cormack Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) models are therefore appropriate. However, heterogeneity still remains an issue, which usually results in downward biased abundance estimates (Hammond 1990).

MATERIALS AND METHODS

Between March and May each year from 2010 to 2013, boat-based searches were carried out for humpback whales in inshore waters to the northwest of Boa Vista, Cape Verde Islands (Fig. 1). A total of 385 surveys were carried out from Sal-Rei, the main town in Boa Vista, both opportunistically from whale-watching vessels and on a dedicated basis from a 5 m rigid-hulled inflatable (see Ryan *et al.* 2013a for details). Although different platforms were used, the survey methodology was similar in that vessels left the port of Sal-Rei and carried out searches of the study area *ad hoc* (Fig. 1). The route taken was dictated by the weather and sea conditions and once whales were sighted, efforts were made to photograph the underside of the tail fluke of each whale present by approaching slowly from behind. Photographs taken using digital SLR cameras with telephoto lenses were submitted to the North Atlantic Humpback Whale Catalogue (NAHWC) which was searched for matches based on markings, namely natural variation in pigments and scars. The NAHWC is curated by Allied Whale, College of the Atlantic, 105 Eden

Street, Bar Harbor, Maine 04609, USA (www.coa.edu/ html/alliedwhale.htm). New and recognizable individuals were then included in the catalogue. Images were graded according to photograph quality following criteria outlined by Friday *et al.* (2000) and the lowest quality images on a three level scale were excluded from this study. Due to changes known to occur over time in the pigmentation patterns observed on calf flukes (Carlson *et al.* 1990), all calf fluke photos are retained, but not included in the catalogue or used in this mark-recapture estimate. Following these matching and grading processes, an annual recapture history was constructed for each recognizable individual whale photographed in the study area.

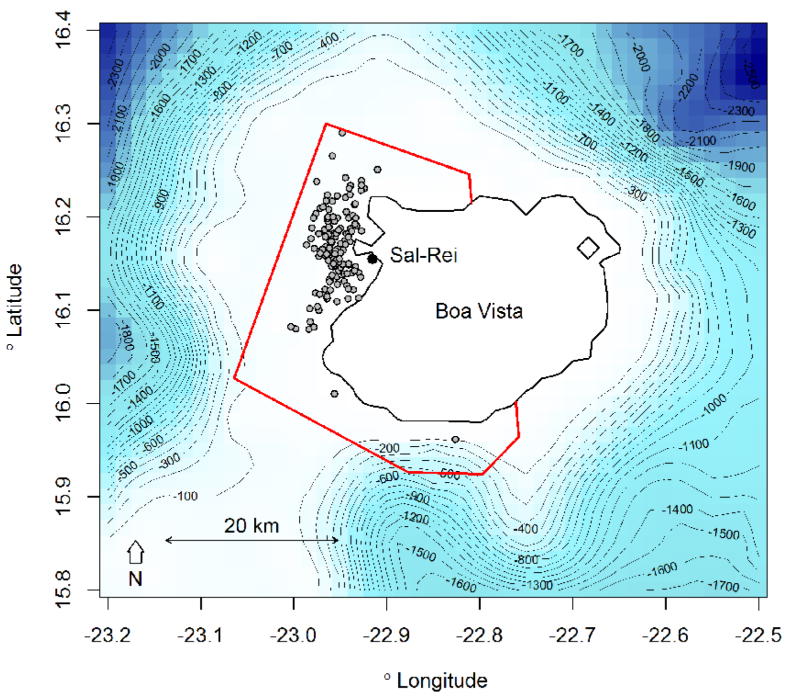

Fig. 1. Map of Boa Vista showing the study area where search effort was conducted and the locations in which photo-identification images were collected during February to May each year between 2010 and 2013.

Abundance was estimated using an open-population mark-recapture approach in R (R Development Core Team 2008). The *Rcapture* package was used to fit both log-linear Jolly-Seber (JS) and Cormack-Jolly-Seber (CJS) models to derive estimates of abundance N, apparent survival ρ and probability of recapture φ. For each annual capture period t ranging from 1 to t, the population size N_1 to N_t were estimated. Given that this study was conducted over a short timescale in comparison to the life-expectancy of a humpback whale, the total number of visitors to the study site N_{total} is the value of interest. However, the N_t values for each year were also considered to examine variability in the number of whales visiting this location between years. The JS model assumes:

1. that 'marked' individuals (i.e. individually recognizable whales) are representative of the population;
2. that individuals do not lose their marks (or remain 'identifiable' between years);
3. that identified (i.e. 'marked' and 'released') whales have the same probability of capture following 'release';
4. that survival probability is equal for all whales during a given sampling period.

As calf pigmentation patterns change during the first couple of years after birth and calves have lower probability of survival, they were removed to ensure that assumption 2 and 4 were not violated (Carlson *et al.* 1990, Blackmer *et al.* 2000). The only available evidence of differential sex-specific survival probabilities in humpback whales is from the Gulf of St. Lawrence, where females have a higher survival rate (0.992) than males (0.971) (Ramp *et al.* 2010). No sex-biased survival rate is available for the population in the present study, although if it is similar to that of Ramp *et al.* (2010), the effect on the population estimate is likely to be minor.

In its simplest form, the JS model which estimates the total abundance $\widehat{N}_t$ is defined as:

$$\widehat{N}_t = \frac{\widehat{M}_t}{\hat{\alpha}_t}$$

Where $\hat{\alpha}_t$, the proportion of marked whales is defined by:

$$\hat{\alpha}_t = \frac{m_t + 1}{n_t + 1}$$

(where m_t is the number of uniquely identifiable whales photographed for time period *t* and n_t is the total number of identifiable and unidentifiable (unmarked) whales captured in *t*). $\widehat{M}_t$, the abundance of the identifiable whales at *t,* is defined as:

$$\widehat{M}_t = \frac{(s_t + 1)Z_t}{R_t + 1} + m_{t-1}$$

(where s_t is the total number of whales 'released' (i.e. photographed and survived); Z_t is the total number of whales photographed previously (i.e. < *t* -1); R_t is the number of $s_t$whales surviving after *t*; and m_{t-1} is the total number of uniquely identifiable whales caught in both *t* and prior to *t*).

For model validation, Pearson's residuals from the fitted models were plotted against the frequency of capture. This method is appropriate for log-linear models such as the JS model (Krebs 1999), permitting assessment of a key assumption of the JS model, that recapture probabilities are homogenous among individuals. Model choice was based on the goodness of fit using Akaike Information Criterion (AIC). The 95 % confidence intervals were estimated using the equation provided by Krebs (1999) for JS models, which uses the variance of the estimate.

Explicitly accounting for the effects of temporary emigration can be challenging, however Kendall *et al.* (1997) provided a means to estimate the rate of temporary migration. This is determined by dividing the capture probability from the JS open population model by that from a closed population model (Kendall *et al.* 1997). For the purpose of estimating the rate of temporary emigration, a closed-population model was applied to our data using *closedp* command in the *Rcapture* package. This routine attempts to fit 12 different log-linear models (see Baillargeon & Rivest 2007 for details). The model with the lowest AIC value was chosen, from which the estimated capture probability was used to estimate the rate of temporary emigration as described above. Kendall *et al.* (1997) also presented a modified model to account for scenarios where temporary emigration occurs in a predictable manner, e.g. Markovian emigration, where the probability that an animal is not available for recapture in period *i* is dependent on whether or not it was available for capture in period *i* – 1. Accounting for Markovian temporary emigration might appear to be appropriate in the case of female humpback whales which have a two year breeding cycle due to their 11 month gestation period. However, our data indicate that some males (as determined by 'singing' and genetic biopsy sampling) returned to the study area each year. As the sex of each whale was not known, we could not implement routine Markovian temporary emigration type models.

RESULTS

Between 2010 and 2013, a total of 119 individually recognizable adult humpback whales were photographed in coastal waters to the west of Boa Vista with image quality sufficient for inclusion in this study. A summary of the number of recaptures per year is presented in Table 1. The simple JS model was selected as it had a lower AIC (83.5) compared to the CJS model (221.5). A Pearson's residual plot exhibited good dispersion of indicating low heterogeneity in the data (Fig. 2). The abundance estimate for the total study period (2010–2013) was 171 and the model parameters are presented in Table 2. It was also possible to derive inter-annual abundance estimates for some periods: 100 ± 8 from 2011 to 2012 and 131 ± 12 from 2012 to 2013. Estimations for the first period (2010–2011) are not possible as there are no appropriate prior data from which to estimate recaptures. The rate at which new individuals are being recorded in the study area is declining, showing that the humpback whales occurring around Boa Vista are well represented in the sample (Fig. 3).

The rate of temporary emigration was found to range from 0.45 to 0.52 for the duration of the study. Therefore temporary emigration appears to be an important source of bias in the probability of recapture in the present study. At this rate of temporary emigration, the resulting negative bias on the abundance estimate is 31% (Kendall *et al.* 1997). The net known bias arising due to both sex-specific behavior and temporary emigration is therefore 52%, giving a final abundance estimate of 260 humpback whales.

Year	2010	2011	2012	2013
Whales identified m_t	31	40	22	26
Whales recaptured R_t	-	23	21	23

Table 1. Number of whales identified and subsequently recaptured during the study.

Parameter	Estimate	CV	95 % CI
$\widehat{N}$	171	0.02	163-179
φ	0.37	0.75	0.23-0.53
ρ	0.86	0.37	0.52-0.97

Table 2. Mark-recapture Jolly-Seber model estimates including the absolute abundance ($\widehat{N}$), capture probability (φ) and survival rate (ρ). NB, the estimate presented here is not corrected for known biases. See results section for further details.

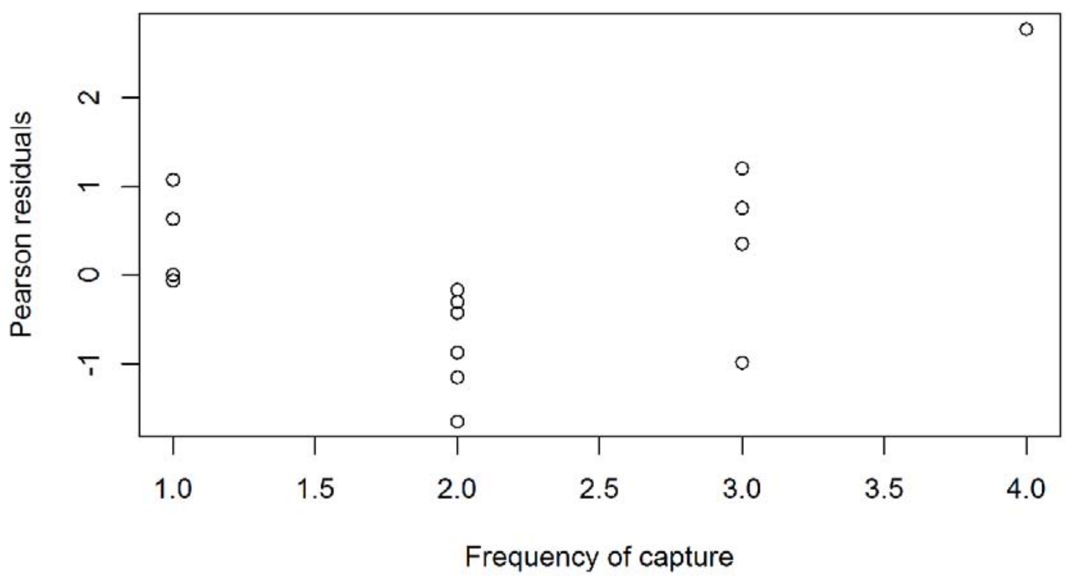

Fig. 2. Scatter-plot of Pearson residuals versus frequency of capture for the fitted data from the chosen (Jolly-Seber) mark-recapture model, showing dispersion which indicates low heterogeneity in the data.

DISCUSSION

Humpback whale research in the Cape Verde Archipelago began in the early 1990s (see Reiner *et al.* 1996, Hazevoet & Wenzel 2000, Jann *et al.* 2003, Wenzel *et al.* 2009). Unfortunately, these research efforts were not spatially or temporally comparable for the purpose of this mark-recapture population estimate. These initial dedicated surveys aimed to determine the distribution and relative abundance of humpbacks around the archipelago, which led researchers to focus their future efforts on Boa Vista. Although still an emerging industry in

Cape Verde, whale-watching activities in Boa Vista have been consistent since 2010. Whale-watch vessels have proved to be a useful platform from which to carry out photo-identification research to facilitate this mark-recapture analysis.

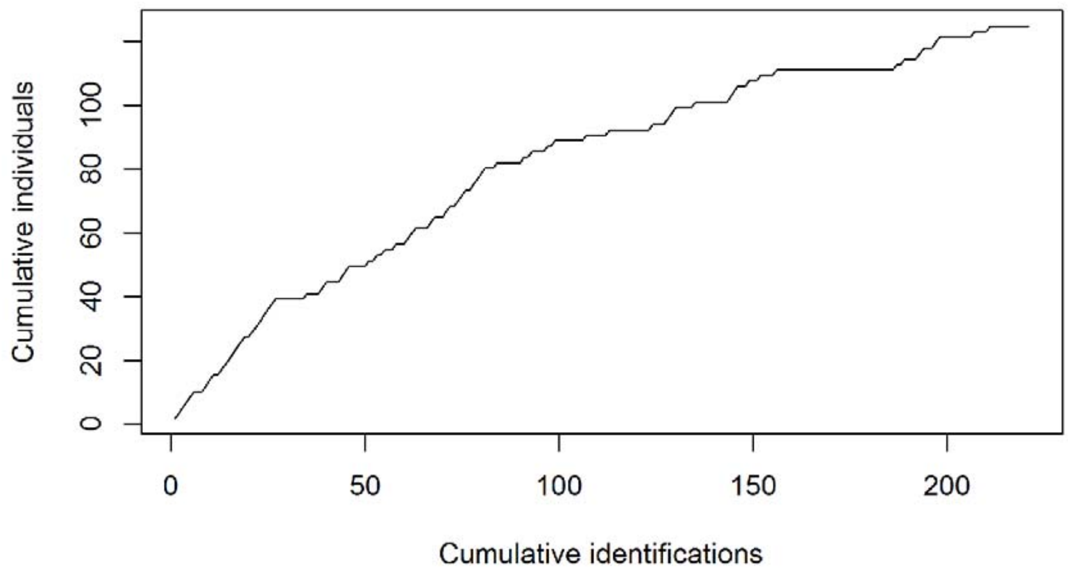

Figure 3. Rate of discovery of individually recognizable whales.

The geographic range of humpback whales found breeding around Cape Verde today is not yet known and this prevents a clear interpretation of our findings. Furthermore, whether this group is isolated or forms part of a continuous population remains to be determined. Nevertheless, one advantage of the JS model is that it does not assume a closed population, i.e. it allows for the possibility of inward or outward migration. The abovementioned assumptions of the JS mark-recapture approach have been satisfied as far as possible, albeit without accounting for the possible sex-biases arising from differential survival rates and capture probabilities. Regarding assumption 1, it has been demonstrated that the distinctiveness of humpback whale fluke patterns has no measurable effect on abundance estimation using comparable mark-recapture methods (Friday *et al.* 2008). Removal of calves from the analysis ensured that assumption 2 was not violated, as fluke pigment undergoes significant changes in young animals, but not so much in older animals over short timescales (Carlson *et al.* 1990, Blackmer *et al.* 2000). Furthermore, calves were not considered because potentially they have a higher rate of natural mortality, violating assumption 4.

Finally, one unavoidable caveat exists in relation to assumption 3 – females with calves in attendance appear to prefer shallow waters (Ryan *et al.* 2013a) where they are less likely to fluke-up (and therefore be ‘captured’ for photo-identification purposes). This results in females with calves being under-represented, resulting in a low biased abundance estimate (Smith *et al.* 1999). Furthermore, differential timing of migrations according to sex and overwintering of females at higher latitudes may exacerbate this bias (Smith *et al.*1999). Such bias can be largely overcome by sampling whales on both their feeding and breeding grounds, but this was not feasible in the present study. A parallel study found that females were significantly under-represented in a sample of biopsied whales from Boa Vista (Ryan *et al.* 2013b). However, it is not known whether sampling effects arising during both biopsy sampling and photo-identification result in comparable sex bias. The net effect of sex bias in humpback whale photo-identification mark-recapture analysis is that abundance estimates are negatively biased by up to 21% (Smith *et al.* 1999). Further bias in the estimate presented herein arises from temporary emigration, estimated to be 31%. Therefore, accounting for a net negative bias of 52%, the best estimate for humpback whales in the study area is 260 individuals. Finally, as the means of 'capture' were non-invasive and were unlikely to result in long-term disturbance, sampling methods did not result in a violation of assumption 3.

The abundance estimate of 171 to 260 individuals is low, but higher than that previously reported by Punt *et al.* (2006) from this region (99 individuals). Given the challenges arising from unavoidable heterogenity in capture probabilities (Hammond 1990, Smith *et al.* 1999), there may be further negative bias in our estimate (in addition to that arising from sex-bias and temporary emigration dealt with above). The coefficient of variation on the estimate presented here is an order of magnitude lower given that more data are now available (0.02 compared to 0.23). It is not known how representative the study area (northwest Boa Vista) is of the total Cape Verde archipelago. This area is the most important known nursing location for this species in the eastern North Atlantic (Wenzel *et al.* 2009, Ryan *et al.* 2013a). However, this may reflect sampling bias given a lack of comparable research effort in adjacent areas. As such, a systematic archipelago-wide survey for humpback whales in Cape Verde is required to determine if the abundance estimate presented here is conservative. The high probability of recapture reported here is consistent with a small and potentially isolated population, with strong fidelity to the area studied off Boa Vista. The low survival rate (0.86), albeit with wide 95% CIs, may indicate some outward migration and would benefit from further investigation.

Photo-identification and molecular genetic studies are underway in order to assess connectivity between humpback whales breeding in Cape Verde and other breeding locations such as the West Indies (Per Palsbøll pers. comm.). It is hoped that these studies may serve to address some of the aforementioned caveats in the present study. The most recent abundance estimate (calculated from data collected only on the high latitude feeding grounds) for the entire North Atlantic Ocean is 11,570, although this estimate is believed to be downwardly biased (Stevick *et al.* 2003). Therefore, assuming the estimate of 260 presented here is representative, the breeding group of humpback whales around Boa Vista might constitute only *ca.* 1.8% of the total North Atlantic population. The aforementioned sampling bias makes it difficult to determine whether our estimate for Boa Vista is representative for the archipelago. During the 1800s, some shore-based whaling was carried out from Boa Vista although the details are lacking (Cabral & Hazevoet 2011). According to available evidence however, shore-based whaling centred around the island of São Nicolão, where an estimated 105 whales were landed between 1874 and 1918 (Cabral & Hazevoet 2011). In addition, *ca.* 200 whales were killed per annum in Cape Verdean waters during peak activity by foreign whalers in the late 1800s (Smith & Reeves 2003). To apply the precautionary principle (i.e. a worst case scenario whereby the abundances estimate presented herein is representative of the entire archipelago), this population may be precariously small and therefore threatened by stochastic effects and anthropogenic impacts. Furthermore, unlike the humpback whale population of the western North Atlantic (Stevick *et al.* 2003), this population may be failing to recover from over-exploitation despite commercial whaling ending in Cape Verde in the 1920s (Cabral & Hazevoet 2011) and in the entire North Atlantic by 1955 (Smith & Reeves 2003). However local site fidelity, a spatially structured population, or even a distribution change cannot be discounted. Therefore, an archipelago-wide abundance estimate, coupled with a clearer understanding of population structure of humpback whales in the North Atlantic is needed. Future research may serve to shed further light on the unknowns regarding site fidelity and movements between adjacent areas. However, until this time, and in the absence of such information, the precautionary principle invokes that strict protection and clear conservation goals should to be established for the estimated 171-260 (minimum estimate) humpback whales remaining in Cape Verde, currently the only known breeding ground for eastern North Atlantic humpback whales.

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