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Multi-state open robust design applied to opportunistic data reveals dynamics of wide-ranging taxa: the sperm whale case

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Abstract. Capture–mark–recapture methods have been extensively used to estimate abundance, demography, and life history parameters of populations of several taxa. However, the high mobility of many species means that dedicated surveys are logistically complicated and expensive. Use of opportunistic data may be an alternative, if modeling takes into account the inevitable heterogeneity in capture probability from imperfect detection and incomplete sampling, which can produce significant bias in parameter estimates. Here, we compare covariate-based open Jolly-Seber models (POPAN) and multi-state open robust design (MSORD) models to estimate demographic parameters of the sperm whale population summering in the Azores, from photo-identification data collected opportunistically by whale-watching operators and researchers. The structure of the MSORD also allows for extra information to be obtained, estimating temporary emigration and improving precision of estimated parameters. Estimates of survival from both POPAN and MSORD were high, constant, and very similar. The POPAN model, which partially accounted for heterogeneity in capture probabilities, estimated an unbiased super-population of ~1470 whales, with annual abundance showing a positive trend from 351 individuals (95% CI: 234–526) in 2010 to 718 (95% CI: 477–1082) in 2015. In contrast, estimates of abundance from MSORD models that explicitly incorporated imperfect detection due to temporary emigration were less biased, more precise, and showed no trend over years, from 275 individuals (95% CI: 188–404) in 2014 to 367 (95% CI: 248–542) in 2012. The MSORD estimated short residence time and an even-flow temporary emigration, meaning that the probability of whales emigrating from and immigrating to the area was equal. Our results illustrate how failure to account for transience and temporary emigration can lead to biased estimates and trends in abundance, compromising our ability to detect true population changes. MSORD models should improve inferences of population dynamics, especially when capture probability is low and highly variable, due to wide-ranging behavior of individuals or to non-standardized sampling. Therefore, these models should provide less biased estimates and more accurate assessments of uncertainty that can inform management and conservation measures.

Key words: abundance; capture–mark–recapture; mobile taxa; multi-state open robust design model; opportunistic data; photo-identification; POPAN model; population dynamics; sperm whales (*Physeter macrocephalus*); survival; temporary emigration; transients.

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INTRODUCTION

Application of capture–mark–recapture (CMR) methods to estimate life history parameters from photo-identification data of naturally marked individuals has been extensively used on several taxa, such as cetaceans (Hammond et al. 1990), manatees (Langtimm et al. 2004), sharks (Arzoumanian et al. 2005), and a variety of felids (Broekhuis and Gopalaswamy 2016). Ideally, CMR studies would involve extensive sampling effort across the geographic range of the target population (Kendall and Nichols 2004). In addition, in the case of long-lived species, sampling over multiple years is usually required to efficiently estimate survival or recruitment. However, such effort is expensive and logistically demanding. A cost-effective approach could be the use of individual-identification data that are opportunistically collected (Tezanos-Pinto et al. 2013, Strandbråten Rødland and Bjorge 2015, Bertulli et al. 2017).

The application of CMR methods to highly mobile species can be challenging though. Differences in movement patterns and site fidelity among individual animals over time can lead to heterogeneous capture probabilities, violating the standard assumptions of conventional models (Kendall et al. 1997). Heterogeneity may also arise from the uneven distribution of survey effort, if individuals are more likely to be detected at some locations and times than others which may be exacerbated in opportunistic sampling. Ignoring individual heterogeneity in capture probability can affect accuracy and precision of CMR estimates and may result in false trends being observed (Pfaller et al. 2013, Sanders and Trost 2013).

The most commonly used modeling approaches to deal with individual heterogeneity and imperfect detection are random-effects, finite-mixture, and models with individual covariates. Random-effects (Gimenez and Choquet 2010) and finite-mixture (Pledger et al. 2010) models are especially appropriate when heterogeneity cannot be measured or when individual covariates are not applicable (Gimenez et al. 2017). When heterogeneity is adequately explained by individual covariates, capture and survival probabilities can be modeled as a function of these covariates (Pollock 2002). Continuous time-varying individual covariates can be observable attributes of individuals (e.g., age class or body mass) or variables that allow inference about hidden states (e.g., capture frequency data from previous sampling periods; Pollock 2002). Continuous time-varying covariates are challenging to model, but discrete time-varying individual covariates, known as states (Gimenez et al. 2017), can be analyzed with multi-state models. In essence, multi-state CMR models assume that animals may be in a discrete set of states (defined by geographic location, reproductive status, age, etc.), some of which may be observable and others unobservable, and individuals may transition between states over time (Schwarz et al. 1993, Lebreton and Pradel 2002).

Therefore, multi-state models provide a convenient way of modeling heterogeneity caused by temporary emigration, by implicitly assuming that animals present in the study area are observable, whereas unobservable individuals are those temporary emigrants, absent from the study area during a given period. These models can produce unbiased estimates of state-specific parameters (abundance, apparent survival, capture probability) and of the probability of animals changing between states. A special case of these models is the multi-state open robust design (MSORD) that combines features of multi-state models with Pollock's robust design sampling strategy and implicitly accounts for imperfect detection probability (Kendall et al. 1997, 2018, Schwarz and Stobo 1997, Kendall and Bjorkland 2001, Ruiz-Gutierrez et al. 2016). Pollock's robust design (Pollock 1982) consists of two or more secondary samples over relatively short intervals (days to weeks) within each primary period (usually seasons or years). Multi-state open robust design models benefit from the extra information in the secondary occasions to estimate abundance for each state within each primary period and to improve precision of survival and transition probabilities (Kendall and Bjorkland 2001). An important assumption of MSORD models is that animals may enter and exit the study area once during each primary period (Kendall and Bjorkland 2001), allowing the population to be geographically open. Therefore, MSORD models permit animals to arrive and depart the study area at different times within a primary period, accounting for transience and temporary emigration, and only assume equal capturability among those individuals present in the area during a primary period.

Multi-state open robust design models can be more complex and data-hungry than open models incorporating individual covariates but offer greater flexibility in modeling heterogeneity in capture probabilities. Here, we apply both methods to a large sperm whale (*Physeter macrocephalus*) photo-identification dataset collected opportunistically by whale-watching operators and researchers around Faial and Pico islands, in the Azores. Our aim was to examine the ability of these methods to handle strong individual heterogeneity and estimate the abundance and demographic parameters of highly mobile taxa from data collected opportunistically.

Sperm whales are widely distributed from the tropics to near the ice edges in both hemispheres, but males and females occupy distinct parts of this range (Whitehead 2003). Females stay in tropical and subtropical waters year-round where they live in long-term social groups with their immature offspring (Lyrholm and Gyllesten 1998, Whitehead 2003). Males disperse from their natal group as they approach puberty and gradually move to higher latitudes reaching as far as polar waters (Whitehead 2003). In their late twenties, males start migrating periodically to the warm waters inhabited by females to mate (Rice 1989). The Azores is an important feeding, calving and possibly mating ground for sperm whales in the North Atlantic (Clarke 1981). Whales of both sexes and all age classes use the area year-round, but the majority of the observations consist of social groups in late spring and summer (Silva et al. 2014). Sperm whale social groups are nomadic (Whitehead et al. 2008), and the Azores encompasses only a part of their range. Although a few groups appear to regularly use the area, none permanently remain there (Silva et al. 2006, 2014; Appendix S1: Fig. S3).

Photo-identification of sperm whales in the Azores began in 1987, and since then, photo-identification data are regularly collected by whale-watching operators and researchers. So far, there has been a single study applying CMR methods to these data (Matthews et al. 2001), using a two-sample closed model to estimate annual abundance during summer (May–September), and an open model to estimate survival and birth rates. Unfortunately, these estimates are likely biased because such classical closed and open population models cannot adequately account for the inevitable heterogeneity in capture probabilities resulting from differences in sperm whale movements and uneven sampling effort in space and time (Otis et al. 1978, Kendall et al. 1997).

In the present study, we investigate alternative CMR methods that incorporate individual heterogeneity and imperfect detection. We applied the Schwarz and Arnason (1996) parameterization of the open Jolly-Seber model with an individual covariate (hereafter called POPAN) and MSORD models to the sperm whale photo-identification catalogue collected opportunistically. We explored the potential of POPAN models to account for transience and temporary emigration by modeling survival and capture probabilities as a function of previous capture histories (PriorCapL; Cooch and White 2017). We also applied the MSORD approach that explicitly accounts for heterogeneity in capture probabilities due to movement, using a model with one observable state (*P*, *present* in the study area) and one unobservable state (*E*, *temporary emigrant*), to estimate population size, survival, average residence time, and temporary emigration.

METHODS

Study area and data collection

We analyzed 28 yr (1987–2015) of photo-identification data collected in the Azores (37°–41° N, 25°–31° W) by three main contributors: a whale-watching operator, a research institution, and a non-governmental organization (Appendix S1: Table S1). Survey platforms, photographic equipment, and data collection procedures differed among data contributors and throughout the study period (Appendix S1: Table S1; see Matthews et al. 2001, Steiner et al. 2012, Silva et al. 2014 for further details), though most data were obtained during 6- to 8-h daily trips. We restricted the study area to the waters around the islands of Faial and Pico (Fig. 1) where most sampling effort was undertaken and discarded photographs taken outside this area. Still, because photo-identification data were not obtained during random or systematic surveys, sampling effort was unevenly distributed across the study area.

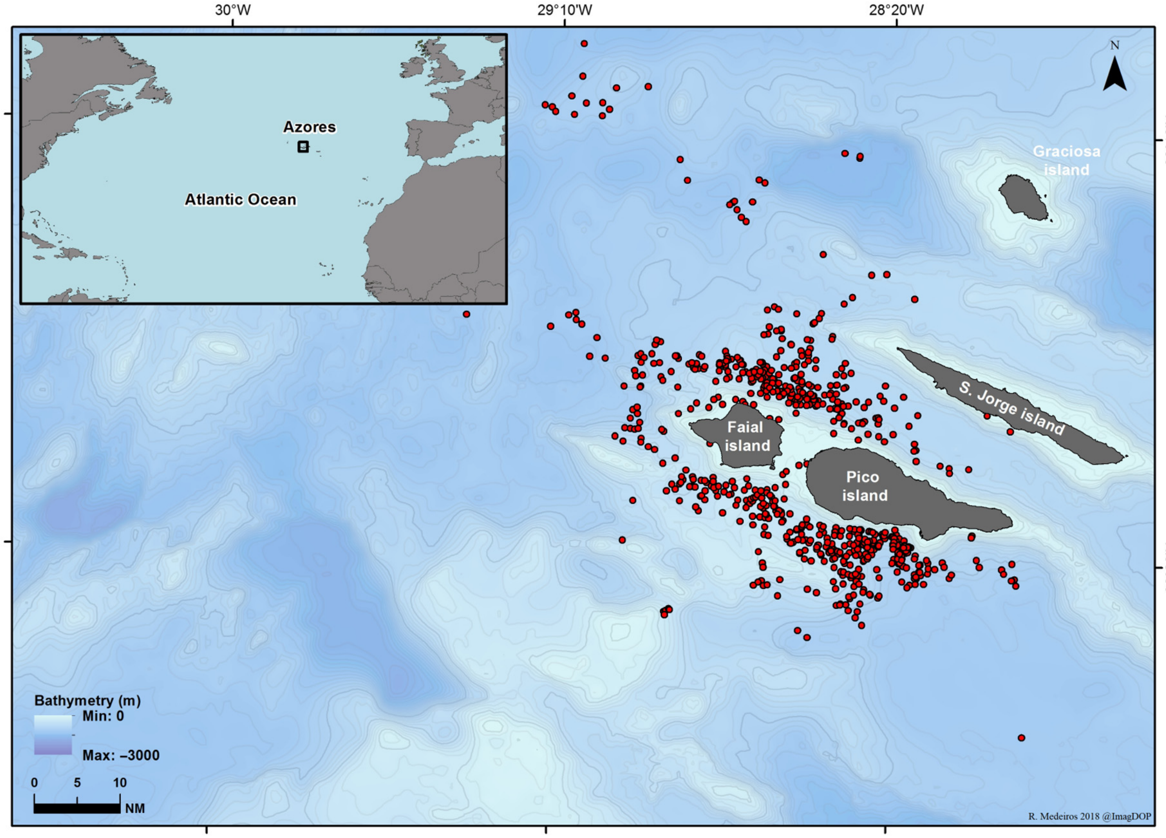

Fig. 1. Location of Azores and of sperm whales identified in the study area from 2009 to 2015.

Photographic processing and matching

Sperm whales were individually identified from photographs of the ventral side of the fluke, based on natural markings on the trailing edge. Photographs were graded for quality based on Arnbom (1987; ranges from Q1 = bad quality to Q5 = excellent quality), irrespective of distinctiveness of fluke markings. Each whale was assigned a distinctiveness value that ranged from D0 = no markings to D5 = missing portion of fluke, based on certainty of future re-identification using the shape and marks on the trailing edge of the fluke (Dufault and Whitehead 1995, Childerhouse et al. 1996). To minimize heterogeneity in captures due to misidentification of non-distinctive flukes, only high-quality photographs ($Q \geq 3$) of large sub-adult and adult whales with distinct flukes ($D \geq 3$) were used in this study, as calves usually bear few distinct marks. Potential matches were found using Match and Phlex 1.3 software (Beekmans et al. 2005), and these probable matches were checked visually by two independent observers. Adult males, females, and sub-adults have not been analyzed separately as they are indistinguishable from fluke photographs.

CMR dataset

The full dataset consisted of 4815 high-quality photographs of 2342 distinctive individuals collected on 1188 survey days between 1987 and 2015 (Appendix S1: Fig. S1). In our study, a capture event represents the photographic record of an individually identified sperm whale. Analysis of the encounter histories built from this dataset showed that 76% of the whales identified were only captured once (i.e., *transients* according to Pradel et al. 1997), and the average number of captures of the remaining whales was low (3.97). As a result, capture probability (p) over the study period was low (p = 0.108, SD = 0.02) and all models tested provided a poor fit to the data and few identifiable parameters (not shown here). Therefore, we discarded data from years and months with lower sampling effort and models were fit to a subset of data collected for approximately 2 months (July–early September) from 2009 to 2015.

Statistical modeling

As expected, results from the program CloseTest (Stanley and Burnham 1999) indicated that the sperm whale population was not closed ($P \leq 0.001$) within each 2-month sampling period (Appendix S1: Table S2), likely, and at least partially, due to the high proportion of transients. Therefore, we used two different classes of open models: the POPAN model (i.e., the Schwarz and Arnason (1996) parameterization of the Jolly-Seber model) with an individual covariate and a MSORD model (Schwarz and Stobo 1997). All models were fitted in program MARK version 8.0 (Cooch and White 2017).

Transient animals were defined as those that permanently emigrated from the study area after initial capture, such that they were not available to be encountered in the future (Pradel et al. 1997). However, models including only live captures cannot distinguish between death and permanent emigration, meaning that a transient individual will appear to have died after first capture. If this is not accounted for, then survival estimates will be negatively biased for those animals that remain in the study area (Pradel et al. 1997). Nevertheless, since transients are not captured again after the first capture, the negative bias on survival will only affect the first occasion. Therefore, a common way to account for transience is to use a model that allows for the estimate of survival from the first occasion to be different from the following occasions. This can be done using time since marking (TSM) models which generally provide satisfactory results (Pradel et al. 1997, Cooch and White 2017). Since TSM models are not applicable in POPAN due to the model structure, we used the PriorCapL covariate function instead. Similarly to TSM, this function distinguishes individuals based on whether they have been captured before or not, and estimates survival separately for the interval after first capture and for subsequent intervals (Cooch and White 2017).

POPAN models

POPAN models were used to estimate the following parameters: (1) abundance of the super-population (N_{super}), which is the total number of sperm whales using the study area in the summers of 2009–2015; (2) annual abundance (N_t), the abundance of sperm whales summering in the study area in sampling year t; (3) apparent survival probability (ϕ_t), hereafter survival, which is the probability of whales surviving and returning to the study area between sampling years t and $t + 1$; and (4) the probability that a sperm whale from the super-population entered the study area between years t and $t + 1$ ($pent_t$).

Captures of individual sperm whales made during the same year were pooled, and each year was treated as a sampling occasion. Models were built with the capture (p) and survival (ϕ) probabilities set as constant (.), time-dependent (t), or varying as a function of prior capture. The individual covariate function PriorCapL was applied to indicate whether a whale was observed or not on specified sampling occasions (Cooch and White 2017). Here, PriorCapL was incorporated in the models to enable survival (ϕ) to be estimated separately for transients and those whales seen twice or more, thus avoiding the negative bias on survival from transient individuals. PriorCapL (t, j) applied to ϕ took the value 1 if the whale was captured on any previous occasion t, $t + 1, \ldots, j$ and 0 otherwise. PriorCapL was also applied to the capture probability (p) to account for some heterogeneity from temporary emigration. In this case, PriorCapL(t) was 1 for whales seen on the preceding occasion $t-1$ and 0 for whales not seen on that occasion. Finally, *pent* was modeled as constant or varying over sampling years.

MSORD models

Multi-state open robust design models are based on observations from multiple secondary (typically within-season) sampling occasions over multiple primary occasions (typically years). The extra information on capture probabilities from secondary periods allows estimation of movement in and out of the study area, as well as achieving unbiased and more precise parameter estimates (Kendall and Bjorkland 2001). However, MSORD models require large amounts of data to obtain estimates for additional within-primary period parameters. Consequently, MSORD models could only be fit to a subset of data of the same 2 months from 2011 to 2015. We modeled these data as five primary periods, corresponding to the years 2011–2015, where each primary period was composed of three secondary occasions of 3 weeks (Appendix S1: Table S4). The 3-week secondary occasions were chosen to ensure sufficient captures and because 3 weeks is a compromise between the average residence time estimated from a preliminary analysis of the 2011–2015 dataset (33.1 d) and residency estimated using the emigration and re-immigration model with lagged identification rates (Whitehead 2007) on the 1997–2004 dataset (14.9 d; Silva et al. 2006). Similarly to the POPAN models, the MSORD method also assumes a super-population of individuals, part of which may be *present* (P) in the study area and available for detection (observable state) on a given sampling occasion, while others may be outside the area (*temporary emigrants,* E) and therefore be unobservable. Using a two-state model structure, we estimated the following parameters describing the annual dynamics of the sperm whale population: (1) the apparent survival (S_t) hereafter survival, the probability of whales surviving between sampling years t and $t + 1$ for those occupying state P; (2) the transition probabilities (ψ_t^{P-E}) and (ψ_t^{E-P}), which indicate the probability of whales transitioning from being present (P) in the study area to being temporary emigrants (E), and vice-versa, between years t and $t + 1$, conditional on survival. Because of the multinomial nature of transition probabilities, the probability that a whale remains in the original state is simply derived by subtraction; that is, $\psi_t^{P-P} = 1 - \psi_t^{P-E}$. In addition, we modeled the movement dynamics and detectability of sperm whales present in the area in each year: (3) the entry or arrival probability ($pent_j$), the probability that a whale arrives to the study area in secondary period j; (4) the persistence probability (φ_j), the probability of being present in the study area at occasion j, given it was present at occasion $j-1$ (departure probability = $1-\varphi$); (5) the capture probability (p_j), the probability of being detected at occasion j, given it was present.

MSORD models assume that survival is the same for animals occupying the observable and unobservable state, so S for temporary emigrant whales was set to equal that of whales present in the area. To avoid bias in survival probability from transient whales, S was modeled as a function of time since marking (TSM) to allow a separate survival estimate for newly and previously captured whales (Pradel et al. 1997). The PriorCapL function was also applied to S to understand whether there were differences in estimates based on the function applied. To investigate the pattern of movement of sperm whales, we compared four different emigration models: Markovian ($\psi_t^{P-E} \neq \psi_t^{E-E}$) where the probability of being a temporary emigrant depends on whether or not the individual was present in the previous year, random ($\psi_t^{P-E} = \psi_t^{E-E}$) where the probability of being a temporary emigrant is independent of the individuals' previous availability, even-flow ($\psi_t^{P-E} = \psi_t^{E-P}$) where emigration out of and immigration into the area occur with the same probability, and no movement ($\psi_t^{P-E} = \psi_t^{E-P} = 0$) where there are no transitions into or out of the area. We also modeled ψ as constant (.) and varying across years (t). Arrival (*pent*), persistence (φ), and capture (p) probabilities for temporary emigrants (E) were fixed to 0, since these whales were not available for capture. For whales present in the study area *pent*, φ and p were allowed to vary between years and secondary occasions or were set to constant. In addition, φ was also modeled as a function of TSM to test whether the probability of whales leaving the study area within a year varied as a function of their time since arrival.

Estimates of the total number of sperm whales from the super-population visiting the study area each summer (N_t) and of their residence time (R_t, calculated as the average number of secondary occasions whales remained in the study area) were obtained as derived parameters of the models.

The model with no emigration ($\psi_t^{P-E} = \psi_t^{E-P} = 0$) was deemed biologically unreasonable but was used as a basis to assess the effects of time and TSM dependence on other parameters (S, *pent*, φ, p). Following the selection of the most parsimonious model based on only these parameters, models were then built to incorporate other emigration types. In some models where parameters were time-dependent, the first and second or, ultimate and penultimate occasions were constrained equal to avoid confounding parameters (Kendall et al. 1997).

Model assumptions and selection

Currently, there are no methods to assess goodness of fit (GOF) and estimate overdispersion of models with individual covariates or MSORD models. In the case of POPAN models, a Cormack-Jolly-Seber (CJS) model was built with the same dataset and GOF tests performed on the most general data structure without covariates ($\varphi_t\ p_t\ pent_t$) using program RELEASE (Burnham et al. 1987) in MARK. Model overdispersion was examined by calculating the median $\hat{c}$ for the same CJS global model.

Two different GOF tests were used to assess the MSORD data. The first was constructed as an annual CJS model where secondary occasions were pooled. This allowed for a time-dependent model to be tested in RELEASE to examine capture heterogeneity (Test 2) and heterogeneity in survival, for example, transience (Test 3; Cooch and White 2017). Following this, transience was accounted for in the CJS model and the median $\hat{c}$ approach used to estimate overdispersion. The second GOF test was through the Pearson chi-square test available in program ORDSURV (Hines 2001). This tested whether the data were appropriately structured to be modeled with MSORD. This program also provides an indication of the type of temporary emigration in the data by setting the emigration parameter to different values and comparing model fit. Results from ORDSURV GOF were then used to calculate model overdispersion.

Model selection was based on the Akaike information criterion corrected for the effective sample size (AIC$_c$; Burnham and Anderson 2002) or on the quasi-likelihood AIC (QAIC$_C$; Anderson et al. 1994) where overdispersion and $\hat{c}$ were applied. Models with ΔAIC$_C$ (or ΔQAIC$_C$) <2 were considered to have some support from the data and were used to estimate parameters and respective standard errors (SEs; Burnham and Anderson 2002).

Estimating total population size

Abundance estimates from POPAN and MSORD models only pertain to individuals with sufficient distinct natural markings to allow their identification and must therefore be corrected to include unmarked individuals as well. Total population size (N_{total}) of sperm whales in the area during the sampling years was calculated by dividing model-based abundance estimates (N) by the proportion of marked animals (θ). This was calculated using only photographs of Q ≥ 3, as the number of whales with recognizable marks divided by the total number of whales.

The SEs of the corrected abundance estimates were then calculated as:

$$\mathbf{SE}(\widehat{\boldsymbol{N}}_{\textbf{total}}) = (\widehat{\boldsymbol{N}}_{\textbf{total}})^2 \left[\frac{\mathbf{SE}(\widehat{\boldsymbol{N}})^2}{(\widehat{\boldsymbol{N}})^2} + \frac{\mathbf{1}-\boldsymbol{\theta}}{\boldsymbol{n\theta}} \right]$$

Log-normal confidence intervals were calculated following Burnham et al. (1987), where C is

$$\boldsymbol{C} = \mathbf{exp}\left[\boldsymbol{Z}_{\frac{\alpha}{2}} \times \sqrt{\mathbf{ln}\left[\mathbf{1} + \left\{ \frac{\mathbf{SE}(\widehat{\boldsymbol{N}}_{\textbf{total}})}{\widehat{\boldsymbol{N}}_{\textbf{total}}} \right\}^2 \right]} \right]$$

and the lower confidence limit is $N_{\text{total}}L = N_{\text{total}}/C$ and the upper confidence limit is $N_{\text{total}}U = N_{\text{total}} \times C$.

RESULTS

The majority of photographs were obtained during encounters with social units and likely include both adult females and immatures of both sexes. Although a few adult males may have been mixed with social units, the population estimates presented here should pertain to the female and immature component of the sperm whale population.

POPAN: model assumptions and selection

A total of 539 individual sperm whales were photo-identified during the summer months between 2009 and 2015. The number of whales identified per year ranged between 48 in 2013 and 91 in 2015 (mean = 68.5, SD = 16.32). Only 122 of the 539 individuals had been captured in previous years, meaning that most captures (77%) were of animals seen once.

Not surprisingly, the full time-dependent CJS model fitted the data poorly ($\hat{c} = 3.09; \chi^2 = 49.46$, df = 16, P = 0.001). Lack of fit was due to significant heterogeneity in survival probabilities (Test 3: P = 0.000) in agreement with the high proportion of transients found in the data, but not in capture probabilities (Test 2: P = 0.181). Accounting for the transient effect by stratifying the survival parameter with a TSM model reduced the overdispersion and resulted in a good fitting model ($\hat{c}$ = 1.13; χ^2 = 133.87, df = 118, $P \leq 0.10$). We assumed $\hat{c}$ = 1.13 to be a liberal estimate of the overdispersion value of our POPAN models, since the application of PriorCapL function on survival and capture probabilities is expected to account for part of the excess of variation in the data from transients, as well as temporary emigrants (G. White, Colorado State University, *personal communication*). The most parsimonious model had 86% of the support in the data and was used for parameter inference. This model had apparent survival and capture probabilities varying as a function of whether or not the individual was previously captured (PriorCapL) and constant probability of entry into the study area (Table 1).

POPAN: estimates of abundance and apparent survival

Estimates of the model-based annual abundance of sperm whales summering in the study area varied between 250 and 545 (Appendix S1: Table S5). Abundance for the first year (2009) could not be reliably estimated due to confounding survival and capture parameters. The estimated proportion of identifiable individuals varied between 0.64 and 0.78 (SD = 0.05) per year. The corrected abundance estimates accounting for the unidentifiable sperm whales ranged from 351 (95% CI: 234–526) in 2010 to 718 (95% CI: 477–1082) in 2015 (Fig. 2). These estimates showed an increasing trend until 2013, after which it leveled off.

The POPAN model estimated the total size of the super-population of sperm whales at 1062 individuals (95% CI: 877–1286), which was 1468 (95% CI: 1203–1791) when corrected for the unidentifiable individuals. This abundance estimate represented all sperm whales summering in the study area from 2009 to 2015, including transient individuals and those that may have died. Although calves were not included in the analysis, those that became juveniles during the study period and possessed distinctive marks could also be included in this estimate. The probability that a sperm whale from the super-population entered the study area between years was 0.078 (SE = 0.012).

The mean apparent annual survival probability of sperm whales was 0.95 (SE = 0.07), while the apparent survival for newly captured whales was 0.33 (SE = 0.05). Applying the Pradel et al. (1997) formula to these estimates yields a proportion of transients in the sperm whale population of 66%.

MSORD: model assumptions and selection

A total of 426 individual sperm whales were identified in the summers of 2011–2015. The number of whales captured per secondary occasion ranged between 20 (in the third occasion of 2014) and 46 (in the first occasion of 2014; mean = 34.3, SD = 8.77). The number of recaptured individuals per secondary occasion varied from 1 to 20, and 81% of individuals were only captured once.

The full time-dependent CJS model showed poor fit to the data ($\hat{c}$ = 3.95; χ^2 = 31.62, df = 8, P = 0.00). As with the POPAN results, Test 2 was

Table 1. Summary of best fitting POPAN models fit to sperm whale data ranked by the lowest Akaike information criterion corrected for the effective sample size ($\mathrm{AIC_c}$) values.

Model No	Structure	$\mathrm{AIC_c}$	Delta $\mathrm{AIC_c}$	$\mathrm{AIC_c}$ weight	Model likelihood	No. parameters	Deviance
1	ϕ (PriorCapL) *p* (PriorCapL) *pent* (.)	631.51	0.00	0.86	1.00	6	−1345.63
2	ϕ (PriorCapL) *p* (.) *pent* (t3 = t4)	636.65	5.14	0.07	0.08	9	−1346.69
3	ϕ (PriorCapL) *p* (PriorCapL) *pent* (t1 = t2, t5 = t6)	637.01	5.50	0.06	0.06	9	−1346.33
4	ϕ (PriorCapL) *p* (.) *pent* (.)	640.27	8.76	0.01	0.01	5	−1334.81
5	ϕ (PriorCapL) *p* (.) *pent* (t4 = t5)	640.80	9.29	0.01	0.01	9	−1342.54
6	ϕ (*t*) *p*(.) *pent* (.)	652.50	20.99	0.00	0.00	11	−1335.03
7	ϕ (.) *p* (2a) *pent* (*t*)	652.82	21.31	0.00	0.00	10	−1332.61
8	ϕ (*t*) *p* (*t*) *pent* (*t*)	653.02	21.51	0.00	0.00	20	−1353.78
9	ϕ (.) *p* (.) *pent* (*t*)	653.57	22.06	0.00	0.00	9	−1329.78

Notes: Model parameters are ϕ, apparent survival probability; *p*, capture probability; *pent*, probability of entry; where PriorCapL, previous capture function; *t*, time-dependent; and ., constant.

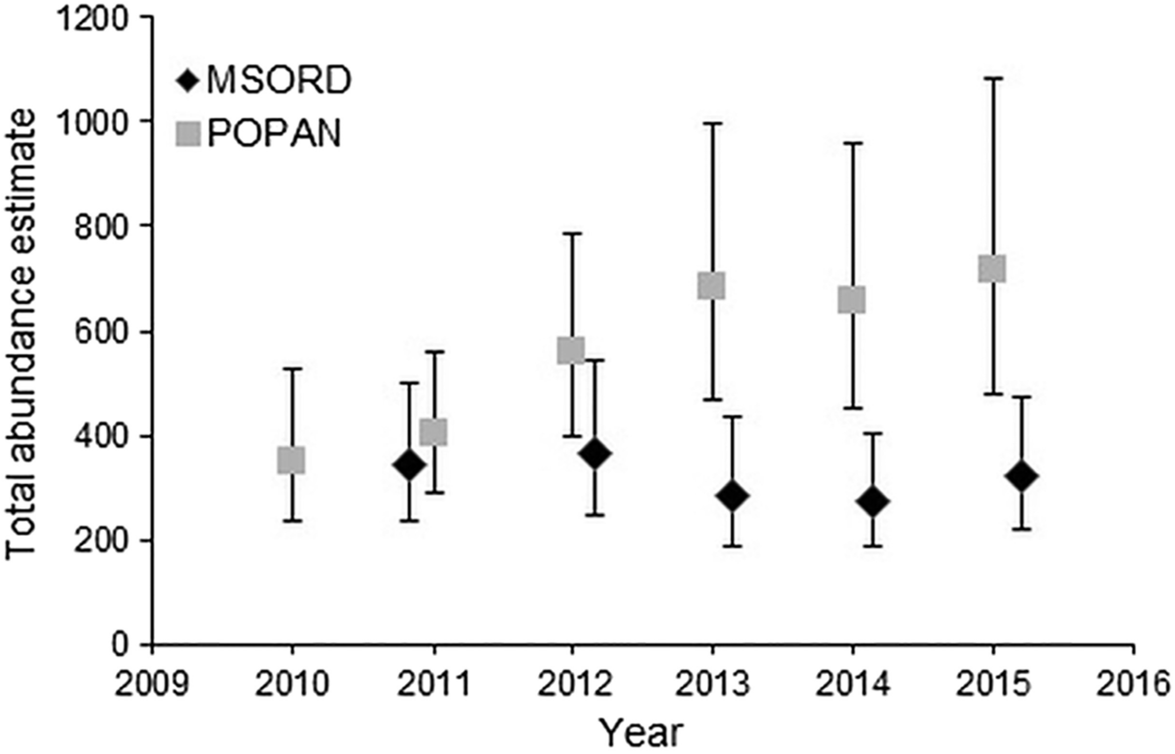

Fig. 2. Estimated total abundance and 95% log-normal confidence intervals based on best fitting POPAN model and multi-state open robust design (MSORD) model.

not significant (P = 0.20), while Test 3 was significant (P = 0.001). Incorporating TSM on survival improved overall model fit and reduced overdispersion ($\hat{c}$ = 0.98; χ^2 = 115.5, df = 118, P ≤ 0.20). Models with TSM and PriorCapL gave similar results, but as models with covariates cannot be adjusted for overdispersion, we decided to model transience with TSM. Also, results from ORDSURV indicated that Markovian emigration poorly fit the data ($\hat{c}$ = 13.09; χ^2 = 549.751, df = 42, P ≤ 0.00), while both constant and random temporary emigration fit reasonably with low overdispersion (constant: $\hat{c}$ = 1.53; χ^2 = 36.814, df = 24, P ≥ 0.05; random: $\hat{c}$ = 1.75; χ^2 = 36.748, df = 21, P = 0.05). Models were adjusted for overdispersion using the constant $\hat{c}$ from ORDSURV.

The best fitting MSORD model had 42% of the support of the data and was only three times better supported than the second and third candidate models (Table 2). The top model included a different survival probability for newly and previously captured whales (TSM effect), even-flow temporary emigration that varied over time, time-dependent probability of whales entering the study area within-primary periods and constant between primary periods. The probability of whales remaining (φ) in the study area and probability of capture (*p*) were constant within and between primary periods. The top model was used for parameter inference (Table 2).

MSORD: estimates of abundance, survival, and temporary emigration

The survival estimate for the whales captured more than once was 0.93 (SE = 0.11). Annual abundance varied from 183 (95% CI: 117–249) in 2013 to 270 (95% CI: 173–368) in 2011 (Appendix S1: Table S6). Model-based abundance estimates were adjusted by the proportion of marked whales from the corresponding years to give total abundances ranging between 275 (95% CI: 188–404) in 2014 and 367 (95% CI: 248–543) in 2012 (Fig. 2).

The top model in the candidate set included time-dependent even-flow temporary emigration.

Table 2. Summary of best fitting multi-state open robust design models fit to sperm whale data ranked by the lowest QAIC_c.

Model No	Model structure	QAIC_c	Delta QAIC_c	QAIC_c weights	Model likelihood	No parameters	QDeviance
1	S (tsm) Ψ (EVENt) *pent* (*t*.) φ (..) *p* (..)	1178.41	0.00	0.42	1.00	10	1157.98
2	S (tsm) Ψ (0) *pent* (*t*.) φ (*t*.) *p* (.t1 = t2 *t*)	1180.61	2.20	0.14	0.33	10	1160.18
3	S (tsm) Ψ (0) *pent* (*t*.) φ (..) *p* (..)	1181.06	2.65	0.11	0.27	6	1168.90
4	S (tsm) Ψ (0) *pent* (..) φ (..) *p* (..)	1181.83	3.42	0.08	0.18	5	1171.71
5	S (tsm) Ψ (0) *pent* (*t*.) φ (.*t*) *p* (.t1 = t2)	1182.46	4.05	0.06	0.13	13	1155.75
6	S (tsm) Ψ (EVEN.) *pent* (*t*.) φ (..) *p* (..)	1182.84	4.43	0.05	0.11	7	1168.63
7	S (tsm) Ψ (0) *pent* (.*t*) φ (..) *p* (..)	1183.46	5.06	0.03	0.08	9	1165.11
8	S (tsm) Ψ (EVEN.) *pent* (*t*.) φ (*t*.) *p* (.*t*)	1184.54	6.13	0.02	0.05	12	1159.93
9	S (tsm) Ψ (RANDOM.) *pent* (*t*.) φ (..) *p* (..)	1184.71	6.30	0.02	0.04	7	1170.49
10	S (tsm) Ψ (MARKOVIAN.) *pent* (*t*.) φ (..) *p* (..)	1184.75	6.34	0.02	0.04	8	1168.47
11	S (tsm) Ψ (0) *pent* (..) φ (.*t*) *p* (.*t*)	1184.86	6.45	0.02	0.04	13	1158.15
12	S (tsm) Ψ (0) *pent* (.*t*) φ (*t*.) *p* (.*t*)	1184.95	6.54	0.02	0.04	14	1156.12
13	S (tsm) Ψ (EVENt) *pent* (*t*.) φ (..) *p* (.*t*)	1185.50	7.09	0.01	0.03	14	1156.67
14	S (tsm) Ψ (EVENt) *pent* (*t*.) φ (*t*.) *p* (.*t*)	1185.68	7.27	0.01	0.03	15	1154.73
15	S (tsm) Ψ (EVENt) *pent* (*t*.) φ (.*t* *p* (.*t*)	1186.32	7.92	0.01	0.02	16	1153.25

Notes: Model parameters are S, survival probability; Ψ, transition probability; *pent*, probability of entry; φ, probability of remaining; *p*, capture probability; tsm, time since marking; Ψ(0), no movement; Ψ(EVEN), even-flow emigration; Ψ(RANDOM), random emigration; Ψ(MARKOVIAN), Markovian emigration; *t*, time-dependent; and ., constant. For *pent*, φ, and *p* parameters, the first annotation in brackets refers to within the primary period and the second annotation to between primary periods.

Models with no emigration also had some support from the data, but we found little support for models with random or Markovian emigration. The probability of emigrating from and immigrating into the study area varied between 0.22 (SE = 0.20) in 2014–2015 and 0.66 (SE = 0.17) in 2013–2014. After applying the Pradel et al. (1997) method, we estimated that 56% of the sperm whale population consisted of transient animals.

MSORD: estimates of within-year dynamics

Within a year, the probability of sperm whales entering the study area between secondary sampling occasions varied from 0.32 (SE = 0.027) to 0.40 (SE = 0.028) and the probability of remaining in the study area was constant at 0.053 (SE = 0.025). The average residence time within a primary period was 1.06 (SE = 0.02), where one unit represented a 3-week period, and the probability of persistence was a function of time since arrival. The capture probability was constant between secondary occasions at 0.44 (SE = 0.10).

DISCUSSION

By combining MSORD models and individual covariates in standard open models, we estimated key parameters of the population dynamics of sperm whales summering in the Azores, which would not be possible with conventional analytical approaches. POPAN estimated a super-population abundance of about 1500 sperm whales using the Azores as part of their summer habitat. However, not all whales visit the area every summer; the MSORD estimates suggest that the annual population comprises about 20% of the super-population. Apparent survival rates from both models were high and constant over time, as expected for a long-lived mammal. The sperm whale population in the study area is characterized by short residence times, with an even-flow of animals entering and leaving the area in consecutive years.

Our results highlight the ability of MSORD models to estimate demographic parameters with reliability and precision, when there is severe heterogeneity in capture probabilities due to non-standardized sampling and wide-ranging behavior of animals. This method could be applicable to CMR studies of wide-ranging taxa and may be especially suited for the analysis of data collected opportunistically.

Comparing modeling approaches: POPAN vs. MSORD

Even if some model assumptions were not fully met, diagnostic tests indicated that both POPAN and MSORD models fitted the data well and variance was within acceptable limits. Nonetheless, there were important differences in the estimates between the two types of models, resulting from their different abilities to handle temporary emigration.

Estimates of annual abundance from the MSORD were lower and had smaller confidence intervals than those based on POPAN. Moreover, POPAN estimates showed an increasing trend over time, whereas those of MSORD varied only slightly between years. The best fitting MSORD model indicated high rates of temporary emigration in the sperm whale population, with an even-flow of animals into and out of the area. MSORD models account for the temporary unavailability of individuals and estimate only the number of animals observable in the study area in a given sampling period. POPAN models ignore temporary emigration and estimate the total abundance of individuals from the super-population found in the study area during at least one sampling period and the probability that an animal from the super-population entered the study area at each sampling occasion (Pollock et al. 1990, Arnason and Schwarz 1995, 1999, Schwarz and Arnason 1996). Thus, in cases of even-flow temporary emigration, we expect capture probabilities from POPAN to be negatively biased and estimates of annual abundance to be positively biased with respect to the number of animals in the sampled area in a given sampling period (Pollock et al. 1990, Arnason and Schwarz 1995, 1999, Schwarz and Arnason 1996). Our attempts to eliminate this bias by modeling capture probabilities as a function of previous capture histories with the PriorCapL function were unsuccessful, and capture probabilities estimated in POPAN models were substantially lower than those of MSORD. Furthermore, capture probabilities decrease with increasing rates of temporary emigration (Kendall et al. 1997), which may explain the increasing trend in abundance in the first years of the study when emigration rates were higher. These results illustrate how failure to explicitly account for imperfect and incomplete detectability can strongly influence population size estimates and eventually lead to detection of false population trends.

An advantage of the POPAN model compared to the MSORD is its ability to provide unbiased estimates of the total number of individuals using the study area throughout the survey period (Arnason and Schwarz 1995, 1999, Schwarz and Arnason 1996). The super-population estimates may be especially useful in studies of migratory animals where the main interest is determining the number of individuals going through a specific area. Apparent survival rates from POPAN and MSORD models were very similar and the difference could simply be due to the different study periods analyzed. Except in the case of Markovian emigration, survival rates from POPAN models are robust to heterogeneity in detection probability (Kendall et al. 1997) and estimates of survival from our models should be unbiased although their precision may be lower. In the case of MSORD, survival would only be affected by temporary emigration if there is more than one entry and exit per primary period (Kendall et al. 2013) which, if occurring, would not be detectable with only three sampling occasions. The presence of transient individuals negatively biases survival estimates (Pradel et al. 1997). Our results indicate that using the PriorCapL function to model survival as a function of previous captures should give reliable estimates of survival probability, providing a suitable alternative to TSM models that can handle transients in POPAN models.

Population size and survival probability

Although true values for this sperm whale population are unknown, the fact that the MSORD model accounts for individual movements, whereas the POPAN model does not, leads us to suggest that the MSORD is more robust (Pfaller et al. 2013, Ruiz-Gutierrez et al. 2016). The MSORD model estimated that 275–367 sperm whales used the area around Faial and Pico islands each summer. This estimate includes all whales that visited the area in a given summer regardless of their residence time, including transiting individuals. Abundance estimates from the MSORD varied slightly between years but showed no annual trend, suggesting a fairly constant number of individuals using the area each summer. The super-population size estimated from POPAN was ~1470 whales, which summered in the area over the 7-year study period. It should be stressed that our study area encompasses a small fraction of the Azorean waters, so the number of sperm whales visiting the archipelago is expected to be greater than the estimates presented here. The assumption of individual capture probabilities being independent is violated in social species, such as the sperm whale (Hammond 1986, Wells et al. 1987). We did not account for this violation, and although the effect on abundance estimates should be negligible, the variance of parameter estimates may be negatively biased, resulting in higher precision than reality (Gupta et al. 2017).

Using a standard POPAN formulation, Matthews et al. (2001) estimated that about 450–900 female and immature whales visited the central islands of the Azores each summer from 1988 to 1990, increasing to 1800–2500 animals in 1991–1994. The two-sample closed estimator used by these authors indicated that 340–900 whales were present at any given time. Compared to our study, Matthews et al. (2001) covered a wider geographic area and slightly longer season (May to mid-September), but >85% of their whale identifications were from the same area and months as ours. Although care should be taken when comparing these results, the POPAN estimates reported by Matthews et al. (2001) point to a much larger population than our MSORD estimates, which could indicate that the number of whales summering in the area declined between study periods. Instead, we believe the difference in the estimates between the two studies reflects the inability of POPAN models to deal with high temporary emigration (Kendall et al. 1997), overestimating population size. Additionally, estimates from the closed models were probably biased by violation of the closure assumption, as acknowledged by the authors (Matthews et al. 2001).

The boundaries of the sperm whale population sighted in the Azores and connectivity to other populations in the North Atlantic are not well known. The information currently available suggests that this population may have its core habitat within Macaronesian waters (Azores, Madeira and Canary Islands; Steiner et al. 2015). The only abundance estimates within this region are from the Canary Islands. An acoustic line-transect survey conducted in autumn and winter in the territorial waters of this archipelago gave an absolute abundance of 224 sperm whales (95% log-normal CIs: 120–418; Fais et al. 2016). These authors suggest that the Canary Islands may be acting as a population sink due to high rates of mortality from ship strikes in the area. Thus, information on the size, structure, and productivity of the population inhabiting Macaronesia is urgently needed. Application of MSORD models to sperm whale photo-identification data from multiple sites could provide information on movement rates of the population and enable estimation of global and site-specific demographic parameters (Nichols et al. 2007, Chabanne et al. 2017).

In our study, models incorporating PriorCapL or TSM effects on survival provided the best fit to data. These models enabled separating transients from temporary emigrants, producing estimates of apparent survival that should approximate well to true survival of whales (Lebreton et al. 1992). All the best fitting POPAN and MSORD models indicated that survival of sperm whales was constant over time, with estimates of 0.95 (95% log-normal CIs: 0.56–0.99) and 0.93 (95% log-normal CIs: 0.74–1), respectively, for POPAN and MSORD. These estimates were higher than previous estimates reported in the study area (Matthews et al. 2001), which we expect were negatively biased by the large percentage of transient whales in the dataset that were not accounted for in the modeling process.

Our estimates are consistent with known adult survival rates of sperm whales in Southern Australia (Evans and Hindell 2004) and in the Eastern Caribbean (Gero and Whitehead 2016), and are considerably higher than those found in Japan, where the population is subject to significant mortality in fishing gear (Evans and Hindell 2004).

Survival rates of mammals tend to be high and constant for most of their adulthood, whereas juvenile survival is usually lower and tends to increase as the animals approach maturity (Gaillard et al. 1998). We could not fit separate models for females and immatures because they were indistinguishable from fluke photographs and the criteria used to identify them in the field were not consistent among data providers. Thus, the survival probabilities reported here may be slightly overestimating the true survival of immature sperm whales and underestimating survival of adult females.

Inter- and intra-annual movement dynamics

POPAN models cannot inform about movements of animals. Conversely, MSORD models enable investigating movement dynamics through the estimation of transition probabilities between states representing the presence or absence of animals in an area. The models that best described the temporary emigration of sperm whales included time-dependent even-flow. This means that the probability of whales temporarily leaving the area between consecutive primary periods was the same as the probability of whales immigrating into the area, but movement rates varied between years. About 41% of the whales encountered in the study area in 2012 were not observed in 2013, the same proportion of individuals not encountered in 2012 but observed the following year. The symmetric flow rate of whales increased to 66% between 2013 and 2014 and decreased to 22% in 2014–2015. However, inter-annual variations in movement rates should be interpreted cautiously because the confidence intervals on the transition parameters were wide.

Temporary emigration meant some individuals were not observable during the two-month sampling period in a given year, either because they were outside the sampled area or because they were present but were not detected. Our study site is relatively small compared to the overall range of the population, which makes it unsurprising that a large proportion of the population is away during a primary period. This is supported by the analysis of the full CMR dataset (Appendix S1: Figs. S2, S3) spanning 28 years and covering most of the spring and summer. Of the 2342 individuals identified, only 34% were captured more than once and most recaptures occurred within the same year and month of the initial capture; only 17% of the whales were captured in four or more years. A few social units, however, seem to return to the area in consecutive years over an extended period (average 8 years), usually in the same month. Interestingly, three of the 15 matches to the Canary Islands were of whales captured in the study site every year between 2009 and 2015, which shows that even whales that exhibited inter-annual fidelity to the study site also used distant habitats. Several individuals (n = 92) were photographically matched between the Azorean islands (Steiner et al. 2015), sometimes within the same year, indicating that some temporary emigrant whales could also have been elsewhere in the archipelago. Nonetheless, some whales could have been present in the study area at the time of sampling but were not captured, overestimating temporary emigration. Foraging sperm whales spend a large proportion of their time submerged and tend to spread out over a large area (Whitehead 2003), which makes it difficult to detect and systematically photograph all members of a group.

Models with no movement that disregard temporary emigration (Cooch and White 2017) also received some support in the data. Lack of temporary emigration in this CMR dataset is highly unlikely, and we suspect this result to be the consequence of low capture probabilities in some sampling periods leading to the confounding of survival and transition parameters (Schaub et al. 2004).

The MSORD is a useful tool to infer intra-annual movement patterns in the absence of direct measurements. The estimated average residence time, of adult females and immatures within the study area, was just over 3 weeks, slightly higher than the 15 d estimated from lagged identification rates (Whitehead 2007) for the 1997–2004 period (Silva et al. 2006). We note that our estimate of residence time is coarse, conditioned by the necessity to aggregate data from multiple sampling occasions to increase capture probability (see *Challenges of modeling opportunistic photoidentification data*).

The distribution of sperm whales in the Azores is strongly correlated with primary productivity, suggesting that prey availability is an important driver of local movements and habitat use (Tobeña et al. 2016). The displacement of sperm whales from the study area may be a direct response to changes in food resources, feeding success, or be mediated by increased density and intraspecific competition (Whitehead and Rendell 2004, Whitehead et al. 2008, Cantor et al. 2017). Other factors may influence the movement dynamics of sperm whales over periods of days to weeks, including occasional presence and harassment by adult males attempting to mate (Sundaresan et al. 2007, Craig et al. 2014) or repeated disturbance from whale-watching boats (Gordon and Steiner 1992, Magalhães et al. 2002, Christiansen et al. 2013). All these factors may affect the estimates of residence time, probability of remaining and temporary emigration patterns.

As intrinsic and extrinsic drivers of movement patterns are expected to vary both within and between years, so should the probability of individuals persisting and entering the area, but this was not observed in our models. In fact, the probability of whales remaining in the study area was low and constant, while the entry probability varied slightly between secondary periods (0.32–0.40) but was constant over years. While these results are consistent with the even-flow of whales into and out of the area, lack of temporal variability in these parameters may be the consequence of an insufficient sample size for modeling parameters describing both the inter- and intra-annual population dynamics (Kendall and Bjorkland 2001, White et al. 2006). Improved estimation of intra-seasonal movements can be achieved in the future by focusing only on those parameters that model dynamics within primary periods (Ruiz-Gutierrez et al. 2016).

Conservation implications

Whale-watching has become an increasingly important economic activity in the Azores. During the summer, 23 boats operate in our study area, each making two daily trips of approximately 3 h (Oliveira et al. 2007). The Azores is an important foraging, calving, and nursing area for sperm whales (Clarke 1981), raising concerns about the detrimental effects of whale-watching on foraging and reproductive success of the population. Females accompanied by calves increased aerial behavior and mean blow interval when approached by whale-watching boats (Magalhães et al. 2002). Such short-term changes in behavior could translate into increased energetic costs and reduced foraging and nursing times (Williams et al. 2006). Negative effects will likely be higher for individuals frequently exposed to whale-watching interactions because repeated behavioral disruption can result in a constant imbalance of bioenergetic budget (Bejder et al. 2006, Christiansen et al. 2013).

Our results indicate that approximately 300 sperm whales summer in the study area every year. Despite a relatively small population, the short residency time and low inter-annual fidelity mean that exposure to whale-watching activities in the area is likely limited within and across years for most individuals. However, cumulative effects due to whale-watching disturbance may occur in some social units that visit the area nearly every year and remain there for a few months. Furthermore, sperm whales may also be exposed to whale-watching activities outside the study area, scaling up potential negative impacts. Finally, even though exposure levels may be low, disturbance from whale-watching may result in behavioral and physiological changes that might affect individuals' health and vital rates, and have implications to the dynamics of this population. As it is yet unknown how this may reflect on the super-population demographics, local dedicated studies are needed to assess potential effects of whale-watching to this population.

Challenges of modeling opportunistic photo-identification data

Data from opportunistic platforms, such as that collected by whale-watching vessels, are often flagged as a panacea for lack of long-term dedicated monitoring programs of animal populations, with the advantage of being low cost. However, application of CMR models to opportunistic data is challenging and our study provides a good example of some of those difficulties.

One problem with opportunistic data is that sampling is often insufficient and detection probabilities are low. When numbers of captures and recaptures are low and vary across sampling occasions, precision and accuracy of CMR estimators are generally poor (Burnham et al. 1987, Pollock et al. 1990, Lebreton et al. 1992). In our case, this led us to discard 21 years of data collected year-round, to restrict the analyses to times with more whale encounters and ensure a sufficient number of captures and recaptures for reliable estimation. Another way to overcome this problem, such as described here for MSORD models, is to aggregate data across sampling occasions to increase the number of captures and recaptures to generate estimates. This solution comes with several costs. First, some information will be lost. In our case, by pooling data into 3-week secondary periods, we were only able to get a coarse estimate of the residency and within-seasonal movements of whales. Second, it may force the combination of data that are more heterogeneous with respect to detection processes, requiring complex models for detection probability and, consequently, more data (Litt and Steidl 2010). The aggregation process should be driven by biological information and weigh the benefit of increased data for modeling against model complexity (Litt and Steidl 2010).

Opportunistic platforms typically do not sample the entire study area at every sampling occasion. If animals remain outside the sampled area during the study, they are simply excluded from all the estimates. Issues arise when animals occupy well-defined home ranges, but these change between primary periods. When this occurs, incomplete surveying can bias estimates of temporary emigration because some individuals may remain unobservable for the duration of a primary period but not in others (Sanders and Trost 2013). In the case of sperm whales, there is no evidence that individuals or groups exhibit fidelity to specific regions within the study area and we expected whales to move randomly in and out of surveyable areas, and, therefore, be exposed to sampling every primary period.

Despite these challenges, our study demonstrates the feasibility and value of opportunistic data to improve demographic estimates when combined with robust statistical models, such as MSORD. The substantial advantage of this method is in its ability to estimate the size and various parameters describing the inter- and intra-annual dynamics of populations with imperfect detectability. We believe MSORD models could provide relevant information on the demography of many wide-ranging species where data are regularly collected by the public through ecotourism activities (Davies et al. 2012, Dennhardt et al. 2015, Bertulli et al. 2017). We do not advocate that opportunistic data could or should replace data collection under well-designed CMR studies. Rather, CMR analyses of opportunistic data may be carried out alongside and complement those based on dedicated monitoring schemes and may be used to investigate specific aspects of the ecology of the target population.

Future work should focus on exploring other methods, such as spatially explicit CMR models, and integrating photo-identification data from other geographic areas and ancillary information (e.g., from telemetry or focal follows) to obtain robust demographic estimates and understand the dynamics of the population. Finally, a possibility could be the use of a custom-built model (e.g., Conn et al. 2011) for this dataset, to specifically model any biases caused by heterogeneity and incorporate in the model likelihood, the unmarked animals and misidentification parameters, which could improve estimates of uncertainty.

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LITERATURE CITED

Anderson, D. R., K. P. Burnham, and G. C. White. 1994. AIC model selection in overdispersed capture-recapture data. Ecology 75:1780–1793.

Arnason, A. N., and C. J. Schwarz. 1995. POPAN-4: enhancements to a system for the analysis of mark-recapture data from open populations. Journal of Applied Statistics 22:785–800.

Arnason, A. N., and C. J. Schwarz. 1999. Using POPAN-5 to analyse banding data. Bird Study 46: S157–S168.

Arnbom, T. 1987. Individual Identification of sperm whales. Report to the International Whaling Commission. Pages 201–204.

Arzoumanian, Z., J. Holmberg, and B. Norman. 2005. An astronomical pattern-matching algorithm for computer-aided identification of whale sharks *Rhincodon typus*. Journal of Applied Ecology 42:999–1011.

Beekmans, B. W. P. M., H. Whitehead, R. Huele, L. Steiner, and A. G. Steenbeek. 2005. Comparison of two computer-assisted photo-identification methods applied to sperm whales (*Physeter macrocephalus*). Aquatic Mammals 31:243–247.

Bejder, L., A. Samuels, H. Whitehead, N. Gales, J. Mann, R. Connor, M. Heithaus, J. Watson-Capps, C. Flaherty, and M. Krutzen. 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology 20:1791–1798.

Bertulli, C. G., L. Guery, N. McGinty, A. Suzuki, N. Brannan, T. Marques, M. H. Rasmussen, and O. Gimenez. 2017. Capture-recapture abundance and survival estimates of three cetacean species in Icelandic coastal waters using trained scientist-volunteers. Journal of Sea Research 131:22–31.

Broekhuis, F., and A. M. Gopalaswamy. 2016. Counting cats: spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. PLoS ONE 11:5.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis of fish survival experiments based on release-recapture data. American Fisheries Society, Bethesda, Maryland, USA.

Cantor, M., A. Eguiguren, G. Merlen, and H. Whitehead. 2017. Galápagos sperm whales (*Physeter macrocephalus*): waxing and waning over three decades. Canadian Journal of Zoology 95:645–652.

Chabanne, D. B. H., K. H. Pollock, H. Finn, and L. Bejder. 2017. Applying the multistate capture-recapture robust design to characterize metapopulation structure. Methods in Ecology and Evolution 8:1547–1557.

Childerhouse, S. J., S. M. Dawson, and E. Slooten. 1996. Stability of fluke marks used in individual photo-identification of sperm whales at Kaikoura, New Zealand. Canadian Journal of Zoology 73: 723–731.

Christiansen, F., M. Rasmussen, and D. Lusseau. 2013. Inferring activity budgets in wild animals to estimate the consequences of disturbances. Behavioural Ecology 24:1415–1425.

Clarke, R. 1981. Whales and dolphins of the Azores and their exploitation. Report of the International Whaling Commission. Volume 31. Pages 607–615.

Conn, P. B., A. M. Gorgone, A. R. Jogovich, B. L. Byrd, and L. J. Hansen. 2011. Accounting for transients when estimating abundance of bottlenose dolphins in Choctawhatchee Bay, Florida. Journal of Wildlife Management 75:569–579.

Cooch, E. G., and G. C. White. 2017. Program MARK: a gentle Introduction. Colorado State University, Fort Collins, Colorado, USA.

Craig, A. S., L. M. Herman, A. A. Pack, and J. O. Waterman. 2014. Habitat segregation by female humpback whales in Hawaiian waters: Avoidance of males? Behaviour 151:613–631.

Davies, T. K., G. Stevens, M. G. Meekan, J. Struve, and J. M. Rowcliffe. 2012. Can citizen science monitor whale-shark aggregations? Investigating bias in mark–recapture modelling using identification photographs sourced from the public. Wildlife Research 39:696–704.

Dennhardt, A. J., A. E. Duerr, D. Brandes, and T. E. Katzner. 2015. Integrating citizen-science data with movement models to estimate the size of a migratory golden eagle population. Biological Conservation 184:68–78.

Dufault, S., and H. Whitehead. 1995. An assessment of changes in time in the marking patterns used for photo identification of individual sperm whales (*Physeter macrocephalus*). Marine Mammal Science 11:335–343.

Evans, K., and M. A. Hindell. 2004. The age structure and growth of female sperm whales (*Physeter macrocephalus*) in southern Australian waters. Journal of Zoology 263:237–250.

Fais, A., T. P. Lewis, D. P. Zitterbart, O. Álvarez, A. Tejedor, and N. Aguilar Soto. 2016. Abundance and distribution of sperm whales in the canary Islands: Can sperm whales in the archipelago sustain the current level of ship-strike mortalities? PLoS ONE 11:5.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

Gero, S., and H. Whitehead. 2016. Critical decline of the eastern Caribbean sperm whale population. PLoS ONE 11:10.

Gimenez, O., E. Cam, and J. Gaillard. 2017. Individual heterogeneity and capture-recapture models: What, why and how? Oikos 127:5.

Gimenez, O., and R. Choquet. 2010. Individual heterogeneity in studies on marked animals using numerical integration: capture-recapture mixed models. Ecology 91:951–957.

Gordon, J., and L. Steiner. 1992. Ventilation and dive patterns in sperm whales, *Physeter macrocephalus*, in the Azores. Report of the International Whaling Commission. Volume 42. Pages 561–565.

Gupta, M., A. Joshi, and T. N. C. Vidya. 2017. Effects of social organization, trap arrangement and density, sampling scale, and population density on bias in population size estimation using some common mark-recapture estimators. PLoS ONE 12:3.

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

Hammond, P. S., S. A. Mizroch, and G. P. Donovan. 1990. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission Special Issue. Page 12.

Hines, J. E. 2001. ORDSRV. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Kendall, W. L., and R. Bjorkland. 2001. Using open robust design models to estimate temporary emigration from capture-recapture data. Biometrics 57:1113–1122.

Kendall, W. L., J. E. Hines, J. D. Nichols, and E. H. C. Grant. 2013. Relaxing the closure-assumption in occupancy models: staggered arrival and departure times. Ecology 94:610–617.

Kendall, W. L., and J. D. Nichols. 2004. On the estimation of dispersal and movement of birds. Condor 106:720–731.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563–578.

Kendall, W. L., S. Stapleton, G. C. White, J. I. Richardson, K. N. Pearson, and P. Mason. 2018. A multistate open robust design: population dynamics, reproductive effort, and phenology of sea turtles from tagging data. Ecological Monographs 89:1–15.

Langtimm, C. A., C. A. Beck, H. H. Edwards, K. J. Fick-Child, B. B. Ackerman, S. L. Barton, and W. C. Hartley. 2004. Survival estimates for Florida manatees from the photo-identification of individuals. Marine Mammal Science 20:438–463.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Lebreton, J. D., and R. Pradel. 2002. Multistate recapture models: modeling incomplete individual histories. Journal of Applied Statistics 29:353–369.

Litt, A. R., and R. J. Steidl. 2010. Improving estimates of abundance by aggregating sparse capture-recapture data. Journal of Agricultural, Biological, and Environmental Statistics 15:228–247.

Lyrholm, T., and U. Gyllesten. 1998. Global matrilineal population structure in sperm whales as indicated by mitochondrial DNA sequences. Proceeding of the Royal Society London Series B 265: 1679–1684.

Magalhães, S., R. Prieto, M. A. Silva, J. M. Gonçalves, M. Afonso-Dias, and R. S. Santos. 2002. Short-term reactions of sperm whales (*Physeter macrocephalus*) to whale-watching vessels in the Azores. Aquatic Mammals 28:267–274.

Matthews, J. N., L. Steiner, and J. Gordon. 2001. Mark-recapture analysis of sperm whale (*Physeter macrocephalus*) photo-id data from the Azores (1987-1995). Journal of Cetacean Research Management 3:219–226.

Nichols, J. D., J. E. Hines, D. I. MacKenzie, M. E. Seamans, and R. J. Gutiérrez. 2007. Occupancy estimation and modeling with multiple states and state uncertainty. Ecology 88:1395–1400.

Oliveira, C., G. Filla, J. Gonçalves, M. A. Silva, R. Prieto, S. Magalhães, and R. S. Santos. 2007. A social economic perspective of the whale watching activity in the Azores. Report of the Scientific Committee of the International Whaling Commission. Volume 59. Page 8.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:1–135.

Pfaller, J. B., K. A. Bjorndal, M. Chaloupka, K. L. Williams, M. G. Frick, and A. B. Bolten. 2013. Accounting for imperfect detection is critical for inferring marine turtle nesting population trends. PLoS ONE 8:4.

Pledger, S., K. H. Pollock, and J. L. Norris. 2010. Open capture-recapture models with heterogeneity: II. Jolly-Seber model. Biometrics 66:883–890.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:757–760.

Pollock, K. H. 2002. The use of auxiliary variables in capture-recapture modelling: An overview. Journal of Applied Statistics 29(1–4):85–102.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 2:3–97.

Pradel, R., J. E. Hines, J. D. Lebreton, and J. D. Nichols. 1997. Capture-recapture survival models taking account of transients. Biometrics 53:60–72.

Rice, D. W. 1989. Sperm whale *Physeter macrocephalus* Linnaeus 1758. Pages 177–233 *in* S. H. Ridgway and R. Harrison, editors. Handbook of marine mammals. Academic Press, London, UK.

Ruiz-Gutierrez, V., W. L. Kendall, J. F. Saracco, and G. C. White. 2016. Overwintering strategies of migratory birds: a novel approach for estimating seasonal movement patterns of residents and transients. Journal of Applied Ecology 53:1035–1045.

Sanders, T. A., and R. E. Trost. 2013. Use of capture–recapture models with mark-resight data to estimate abundance of Aleutian cackling geese. Wildlife Management 77:1937–2817.

Schaub, M., O. Gimenez, B. R. Schmidt, and R. Pradel. 2004. Estimating survival and temporary emigration in the multistate capture-recapture framework. Ecology 85:2107–2113.

Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of open-model capture recapture experiments. Biometrics 52:860–873.

Schwarz, C. J., J. F. Schweigert, and A. N. Arnason. 1993. Estimating migration rates using tag-recovery data. Biometrics 49:177–193.

Schwarz, C. J., and W. T. Stobo. 1997. Estimating temporary migration using the robust design. Biometrics 53:178–194.

Silva, M. A., S. Magalhães, R. Prieto, S. Querouil, A. M. Pinela, and M. I. Seabra. 2006. Ecologia e estrutura populacional de roazes e cachalotes nos Açores: relação com as características do habitat. Report 4, Arquivos DOP Serie Estudos, University of Azores, Horta, Azores, Portugal.

Silva, M. A., R. Prieto, I. Cascão, M. I. Seabra, M. Machete, M. F. Baumgartner, and R. S. Santos. 2014. Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. Marine Biology Research 10:123–137.

Stanley, T., and K. P. Burnham. 1999. A closure test for time-specific capture-recapture data. Environmental and Ecological Statistics 6:197–209.

Steiner, L., L. Lamoni, M. A. Plata, S. K. Jensen, E. Lettevall, and J. Gordon. 2012. A link between male sperm whales, *Physeter macrocephalus*, of the Azores and Norway. Journal of the Marine Biological Association of the United Kingdom 92:1751–1756.

Steiner, L., M. Perez, derVan Linde M., L. Freitas, R. Santos, V. Martins, and J. Gordon. 2015. Long distance movements of female/immature sperm whales in the North Atlantic. Poster, Proceedings of the 21st Biennial Conference of the Society for Marine Mammalogy, San Francisco, December 13-18 2015, USA.

Strandbråten Rødland, E., and A. Bjorge. 2015. Residency and abundance of sperm whales (*Physeter macrocephalus*) in the Bleik Canyon, Norway. Marine Biology Research 11:974–982.

Sundaresan, S. R., I. R. Fischhoff, and D. I. Rubenstein. 2007. Male harassment influences female movements and associations in Grevy's zebra (*Equus grevyi*). Behavioural Ecology 18:860–865.

Tezanos-Pinto, G., R. Constantine, L. Brooks, J. Jackson, F. Mourao, S. Wells, and C. Baker. 2013. Decline in local abundance of bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands, New Zealand. Marine Mammal Science 29:390–410.

Tobeña, M., R. Prieto, M. Machete, and M. A. Silva. 2016. Modeling the potential distribution and richness of cetaceans in the Azores from fisheries observer program data. Frontiers in Marine Science 3:202.

Wells, R. S., M. D. Scott, and A. B. Irvine. 1987. The social structure of free-ranging bottlenose dolphins. Pages 247–305 *in* H. Genoways, editor. Current mammalogy. Plenum, New York, New York, USA.

White, G. C., W. L. Kendall, and R. Barker. 2006. Multistate survival models and their extensions in program MARK. Journal of Wildlife Management 70:1521–1529.

Whitehead, H. 2003. Sperm whales: social evolution in the ocean. The University of Chicago Press, Chicago, Illinois, USA.

Whitehead, H. 2007. Selection of Models of Lagged Identification Rates and Lagged Association Rates Using AIC and QAIC. Communications in Statistics- Simulation and Computation 36:1233–1246.

Whitehead, H., A. Coakes, N. Jaquet, and S. Lusseau. 2008. Movements of sperm whales in the tropical Pacific. Marine Ecology Progress Series 361:291–300.

Whitehead, H., and L. Rendell. 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. Journal of Animal Ecology 73:190–196.

Williams, R., D. Lusseau, and P. S. Hammond. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). Biological Conservation 133:301–311.

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