

# Estimating survival and abundance in a bottlenose dolphin population taking into account transience and temporary emigration

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**ABSTRACT:** Knowledge of demographic parameters of most cetacean populations is scarce because of problems associated with sampling open populations of wide-ranging animals. In recent years, capture–recapture models have been developed to address these problems. We used a photo-identification dataset collected from a population of bottlenose dolphins *Tursiops truncatus* between 1999 and 2004 around 2 islands of the Azores archipelago, to demonstrate the use of some of these methods. A variety of open models and Pollock’s robust design were applied to estimate population size, survival probability and emigration rates. Using only the estimates with the lowest coefficients of variation, the annual abundance of adult dolphins varied between 202 (95% CI: 148 to 277) and 334 (95% CI: 237 to 469), according to the Jolly-Seber method, and between 114 (95% CI: 85 to 152) and 288 (95% CI: 196 to 423), according to the robust design. The number of subadult individuals varied from 300 (95% CI: 232 to 387) to 434 (95% CI: 316 to 597) based on the Jolly-Seber method. The open models yielded estimates of adult survival ( $0.970 \pm 0.029$  SE) that were significantly higher than those for subadults ( $0.815 \pm 0.083$  SE). Movement patterns of dolphins in the Azores seem to follow a Markovian model, in which dolphins seen in the study area in 1 yr show higher probability of emigrating in the following year. Despite some limitations, this is the first study to model transience and temporary emigration in a dolphin population.

**KEY WORDS:** Pollock’s robust design · Open models · Abundance · Survival · Transience · Temporary emigration · Capture–recapture data · Bottlenose dolphins

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## INTRODUCTION

To understand the dynamics of a natural population, it is essential to have information about its population size, recruitment and survival. Understanding the factors that influence these processes increases knowledge of evolutionary, population and behavioural ecology and helps in the formulation of effective conservation measures.

Capture–recapture methods provide a way of estimating demographic parameters and have been used extensively for estimating abundance, survival proba-

bility, population growth rates and recruitment of several species of birds, reptiles and mammals (reviewed by Schwarz & Seber 1999). The ability to recognize individual whales and dolphins from natural markings and the relative ease of obtaining photo-identification data have encouraged the application of capture–recapture methods to cetacean populations (e.g. Hammond et al. 1990). Typically, estimation of population size has been based on closed-population models, including series of 2-sample Peterson estimates (e.g. Stevick et al. 2003) or multi-sample estimators allow-

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ing for time variation, behavioural response and individual heterogeneity in capture probabilities (e.g. Cerchio 1998, Wilson et al. 1999). Open-population models have also been used to estimate abundance (e.g. Gormley et al. 2005) and survival rates (e.g. Zeh et al. 2002).

Conventional capture–recapture models do not explicitly separate survival from permanent or temporary emigration of individuals. Closed models (Otis et al. 1978) assume a static population for the duration of the study. Open models assume that all animals that are alive on a given sampling occasion have the same probability of surviving and remaining in the population, and of being captured, given that they are alive and in the population (Lebreton et al. 1992). Apparent permanent emigration in capture–recapture data can occur when individuals passing through the study area are sampled together with resident animals. Such transient individuals do not remain in the study area and have zero probability of being recaptured. Because open models do not distinguish between permanent emigration and death, failure to account for transients leads to survival rate estimates that are negatively biased (Pradel et al. 1997). Apparent temporary emigration occurs when members of the population are available for capture on some sampling occasions but not on others. The study area may not encompass the whole range of the population and some individuals may be outside the area during certain sampling sessions. For example, animals may not use the same foraging grounds every year, or nonbreeders may be absent from breeding areas in some years. When temporary emigration is random, i.e. all individuals have the same probability of being unavailable for capture on a given occasion, open models produce biased estimates of population size, recruitment and capture rates, but unbiased estimates of survival (Kendall et al. 1997). If the probability of being unavailable depends on whether or not the individual was absent during the previous occasion, temporary emigration is Markovian and all estimators provided by open models can be biased (Kendall et al. 1997).

Modelling approaches have been developed to account for transience and temporary emigration and to produce estimates that are unbiased by such movement. By definition, transients leave the area after their first sampling occasion and the negative bias will only be evident in the first survival estimate. Thus, one way to account for transience is to use an age (or time-since marking) model in which the probability of survival over the first interval after marking is allowed to differ from that of following intervals (Pradel et al. 1997).

The robust design, a method that combines both open and closed models, consists of a long-term capture–recapture experiment with a number of primary

periods, each of which is composed of several secondary sampling periods (Pollock 1982). Consecutive primary sampling occasions should be sufficiently separated in time to allow the population to change. Conversely, the time interval between secondary sampling occasions must be sufficiently short so that the population can be assumed to be closed, yet allow sufficient time for mixing. Data from secondary samples within each primary period are analysed using closed models to derive estimates of capture probability and population size. Survival is estimated using open models by collapsing data from the secondary periods into a single instance of being captured or not captured. Using Pollock's robust design general framework, Kendall et al. (1997) developed models and estimators that incorporate temporary emigration and provide estimates of the probability of temporary emigration.

Models incorporating transience and temporary emigration are used routinely in the analysis of capture–recapture data from various taxa (e.g. Julliard et al. 1999, Perret et al. 2003, Sasso et al. 2006). Some of these methods have also been employed in studies of migratory whales to account for the fact that sampling often takes place annually at breeding or feeding locations where whales may not return every year (e.g. Chaloupka et al. 1999, Bradford et al. 2006, 2008, Ramp et al. 2006). In contrast, studies of dolphins often ignore the possibility that some members of the population may emigrate permanently or temporarily from the study area. In this study, we used some of these models to analyse data from a population of bottlenose dolphins *Tursiops truncatus* with pronounced transience and temporary emigration. Specifically, we developed models to estimate annual abundance, survival and temporary emigration, while accounting for aspects of dolphin behavior and movement patterns that likely affect model results.

Photo-identification and genetic data indicate that bottlenose dolphins in the Azores constitute a single, open population composed of several geographic communities that interact with neighbouring communities and with dolphins from outside the archipelago (Quérrouil et al. 2007, Silva et al. 2009). Previous work conducted in the same study area showed that only 44 out of 611 identified dolphins were frequently sighted within and between years and showed strong site fidelity. The remaining individuals, which were classified as non-residents, showed varying patterns of occurrence. Fifty-seven percent of the dolphins were seen in a single year. Most of these individuals may have been just passing through the study area. A few dolphins, however, were also encountered at islands outside the study area and may have been residents there. Other dolphins were seen frequently but in non-consecutive years, suggesting that the study area did

not encompass the whole range of these animals. When visiting the study area, non-resident dolphins used the same areas as the resident individuals and interacted frequently with them (Silva et al. 2009).

The present study used photo-identification data collected over a 6 yr period in an area of ~5400 km<sup>2</sup> around the islands of Faial and Pico and in the channel between Pico and S. Jorge, Archipelago of the Azores (Portugal) (Fig. 1). First, we investigated the existence of transience and temporary emigration in the population by developing and testing appropriate models. We then used open-population models and Pollock's robust design to derive estimates of population size, survival and temporary emigration rates, taking transience into account. Finally, we used these models to address specific hypotheses regarding variations in survivorship and the type of emigration process. This is the first study that attempts to model transience and temporary emigration simultaneously in a dolphin population.

## MATERIALS AND METHODS

**Field methods and dataset.** From 1999 to 2004, 120 photo-identification surveys were conducted in the study area. Surveys followed a predetermined track that was either alongshore at 1 km from the coast or in a zigzag pattern up to 8 km from the islands, and were designed to ensure consistent coverage within the area (Fig. 1). The alongshore track totalled 352 km while the zigzag track totalled 498 km; thus, it was impossible to survey the whole area in 1 d. The survey area and track were selected based on sea conditions and time constraints on each day. Data from incomplete surveys were not included in the analysis. A summary of the annual sampling effort and number of dolphins identified is presented in Table 1.

Surveys were conducted from a 5.5 m rigid inflatable boat or from a 12 m fibreglass boat. During surveys, a steady speed of 16 to 22 km h<sup>-1</sup> was maintained, while a minimum of 3 observers searched for

dolphins and collected data on observation effort and weather and sea conditions. Surveys were conducted in Beaufort sea states  $\leq 3$ . When dolphins were encountered, the initial time and location, and the school size and composition were recorded. A 'school' was defined as all individuals within 100 m radius of each other. We attempted to obtain several photographs of both sides of every dolphin in the school, irrespective of the degree of marking, age class or behaviour of the individual towards the boat. Dolphins were classified into broad categories (adults, subadults or calves) according to their size and colour. This classification was performed in the field while the individual was being photographed, and confirmed in the laboratory via examination of the pictures taken. Once photographic data had been collected, the dolphin school was abandoned and the survey resumed from that location.

Photographs were graded 'good', 'fair' and 'poor' according to their sharpness, exposure, contrast and the size of the dorsal fin relative to the frame and angle of the dorsal fin. Only 'good' quality photographs were used in this study. Individual animals were identified based primarily on the number and location of nicks and scars on their dorsal fins, but also on the scars and pigmentation pattern along the flanks. Individuals with few distinct marks or those bearing marks that were judged to be only temporary were not included in the analysis but were used to estimate the proportion of well-marked individuals in a school (see details below). Calves were excluded from all analyses because they usually do not possess sufficient markings to ensure their future recognition without error.

The catalogue analysed included 611 well-marked adult and subadult dolphins. In the sixth year of this study, 16 new adults and 52 new subadult dolphins were identified, which corresponded to 18 and 37% of the catalogue size, respectively (Table 1). The high and continuous recruitment of new individuals to the catalogue cannot be explained by dolphins acquiring new marks and strongly suggests temporary immigration of previously unknown individuals into the study area.

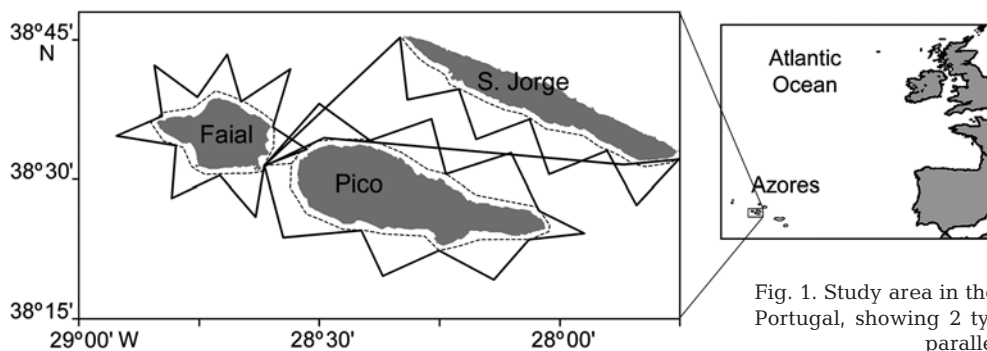


Fig. 1. Study area in the central group of islands, Azores, Portugal, showing 2 types of survey tracks (zigzag and parallel to the coastline)

Table 1. Summary of annual sampling effort and photo-identification of well-marked adult and subadult dolphins. Only complete surveys were included in the analysis. Effort was calculated by adding the number of hours spent surveying for dolphins and the number of hours spent photographing each school

Year	No. of months	No. of surveys	Effort (h)	Adults/sub-adults identified	Adults/subadults in the catalog
1999	7	11	92	15/32	15/32
2000	10	19	141	23/29	27/54
2001	6	15	159	37/98	45/144
2002	8	26	227	120/195	132/287
2003	7	29	238	133/135	208/335
2004	7	20	185	89/142	224/387

Thus, unless the time period considered is short, this population cannot be assumed to be geographically closed.

**Open models: survival, capture probability and population size.** We analysed the sighting histories of 224 adult and 387 subadult dolphins. Sightings of individual dolphins made during the same year were pooled and each year was treated as a sampling occasion. We used Cormack-Jolly-Seber (CJS) models (Cormack 1964, Jolly 1965, Seber 1965) to estimate survival ( $\phi$ ) between years and capture probability ( $p$ ) for each year (Lebreton et al. 1992). Population size ( $N$ ) for each year of the study was estimated using the Schwarz & Arnason (1996) parameterisation of the Jolly-Seber (JS) model.

Open models make several assumptions: (1) marks are not lost or missed, (2) individuals are immediately released after being sampled, and samples are instantaneous relative to the intervals between sampling occasions, (3) all marked individuals that are present on a given sampling occasion have the same probability of capture, and (4) all marked individuals in the population that are alive on a given sampling occasion have the same probability of surviving to the next sampling occasion.

Errors in the identification of individuals leading to violation of the first assumption may result from poor quality of photographs used, indistinctiveness of individual markings and instability of markings through time (Hammond 1986, Stevick et al. 2001). To reduce the chances of missing or misidentifying marks, the dataset analysed in this study only included well-marked individuals and high-quality photographs. The second assumption should have been easily met because the length of the photo-identification sessions was negligible compared to the interval between sampling occasions, and because individuals were not removed from the population during the sampling process. Departure from the assumptions of equal probabilities of capture and survival was specifically assessed through goodness-of-fit tests (GOF) provided

in the program U-CARE (Choquet et al. 2003) and is addressed in the 'Discussion'.

**Open models: modelling procedures and model selection.** Data analysis and model selection procedures were carried out using the program MARK (White & Burnham 1999). A set of candidate models was developed, including a general model containing all potentially important effects on survival and capture probabilities: no variation ( $\cdot$ ), time variation ('t'), cohort ('cohort'), age class ('g') and

time-since marking (hereafter referred to as age dependence) ('a2'). Cohort refers to the dolphins identified (marked) for the first time on a given sampling occasion (Lebreton et al. 1992). Age class was incorporated in the models as a group effect to (1) investigate if there were differences in survival and capture probabilities between subadults and adults, and (2) control for some of the heterogeneity in capture probabilities, thus, increasing the precision of the estimates by obtaining separate parameters for each age class. This general model was used to evaluate how well each candidate model fitted the data, using GOF tests. We used the program U-CARE to test for transience (Pradel et al. 1997) and trap dependence (Choquet et al. 2003). After finding an adequate general model, we fitted progressively simpler models, i.e. models with fewer parameters, which were derived as special cases of the global model. Sampling effort (calculated as the time spent looking for dolphins plus the time spent photographing each school) varied during the study period. Its effect on capture probabilities was tested by introducing sampling effort in the model as an external covariate ('effort') and by forcing time ('effort time') or cohort-dependent ('effort cohort') capture probabilities to be estimated as a linear function of effort. A special case of linear models was developed to test for the significance of a linear trend ('trend') in capture probabilities across cohorts. The combined effect of 2 or more parameters was tested by developing interaction ( $\times$ ) and additive (+) models.

Overdispersion is common in cetacean capture-recapture data because the fate (seen versus not seen) of each individual within the school is not independent on the fate of the others (Anderson et al. 1994). Data were examined for overdispersion by calculating the variance inflation factor,  $\hat{c}$ . There are several ways of estimating  $\hat{c}$  in CJS models. We followed a conservative approach by using all the available methods in the programs MARK (White & Burnham 1999) and RELEASE (Burnham et al. 1987) and selecting the highest estimate of  $\hat{c}$  to measure and adjust for the lack

of fit of the models. For JS models,  $\hat{c}$  was estimated by dividing the chi-square statistics of GOF tests by the number of degrees of freedom. We used a parametric bootstrap to simulate capture histories that met the assumptions of no overdispersion and independence among individuals. The deviance of the model being evaluated was compared with the distribution of simulated deviances to calculate the probability of obtaining a deviance as large as the one obtained.

We used likelihood ratio tests (LRT) to test specific biological hypotheses between nested models and Quasi-likelihood Akaike Information Criteria (QAIC<sub>c</sub>) to select the best model. The LRT is a chi-square test of the difference between the maximum log-likelihood of the general model and that of a reduced model. QAIC<sub>c</sub> provides a convenient way to deal with overdispersed data (Seber 1992, Anderson et al. 1994) and also takes into account differences in effective sample size between models (Burnham & Anderson 2002). The model with the lowest QAIC<sub>c</sub> value was selected as the best fitting model. The normalized QAIC<sub>c</sub> weights were used to measure the strength of evidence for a given model relative to others. Parameter estimates and respective SEs were averaged across all models in the candidate set based on the normalized Akaike weights, to account for model uncertainty (Burnham & Anderson 2002).

**Robust design: survival, temporary emigration and population size.** Pollock's robust design (Pollock 1982, Kendall et al. 1995, 1997) was used to analyse a subset of the data that was analysed with open models: the sighting histories of 162 adult dolphins generated from data collected in 2 mo periods during the summers of 2001 to 2004 (Table 2). Data from 1999 and 2000 and from subadult dolphins were excluded because the number of within-season recaptures was too small to provide reliable parameter estimates. Each 2 mo period represented a secondary sampling occasion in which the population was assumed to be closed. Information from each 2 mo period was then collapsed into a single primary period corresponding to 1 yr. We estimated the following parameters:  $\phi_t$  = the probability that a dolphin survives from primary period  $t$  to period  $t+1$ ;  $p_{ts}$  = the probability that a dolphin is captured in

secondary sample  $s$  of primary period  $t$ , given that it is alive and in the sampled area during period  $t$ ;  $\gamma''_t, \gamma'_t$  = the probability that a dolphin is unavailable for capture during primary period  $t$ , given that it was available or unavailable, respectively, for capture in period  $t-1$  (i.e. the probability of temporary emigration under the Markovian emigration model). When emigration is completely random,  $\gamma''_t = \gamma'_t$ . Population size (N) was estimated using the full-likelihood parameterization available in MARK (White & Burnham 1999).

In addition to the assumptions of open models outlined earlier, the robust design also includes the assumptions of closed-population models for the secondary periods (Kendall et al. 1995). The latter assumptions were not investigated prior to data analysis; possible violations are considered in the discussion.

**Robust design: modelling procedures and model selection.** The robust design module in MARK (White & Burnham 1999) includes the 8 classical closed-population models (Otis et al. 1978). Models with a behavioural response were not fitted to the data because there was no evidence of trap dependence in the sample. Thus, recapture probability ( $c$ ) was set to equal capture probability ( $p$ ) in all the models. Heterogeneity in capture probabilities was modelled using Pledger's (2000) mixture models. We used a maximum of 2 mixtures of capture probabilities because models with 3 mixtures led to non-identifiability of the parameters. Heterogeneity in capture probabilities was not included in models that incorporated temporary emigration because full-likelihood estimators have not yet been developed for these models and the performance of existing ad hoc estimators for the completely random emigration model has not been studied in detail (Kendall et al. 1997).

The model with no emigration ( $\gamma'' = \gamma' = 0$ ) was used to assess the effects of time (' $t$ ') and age dependence (' $a_2$ ') on survival, and of heterogeneity ( $\pi_i$ ), session (variation in capture probabilities among secondary periods  $s$ ) and the interaction between session and time on capture probabilities. Heterogeneity could not be included in models that allowed a separate parameter for each capture occasion because it resulted in overparameterised models and led to non-identifiability of several parameters. After selecting the most parsimonious model based solely on survival and capture parameters, models that incorporated constant and time-specific random and Markovian emigration were fitted to the data.

There is no GOF test available in MARK (White & Burnham 1999) for robust design models so the overall model fit could not be evaluated. This

Table 2. Data used in the robust design analysis: number of adult dolphins marked and recaptured within each primary period

Primary period	Secondary period	Sampling occasions	Individuals marked	Individuals recaptured			Total recaptured
				2002	2003	2004	
2001	11 Jul–25 Sep	4	24	10	11	2	24
2002	01 Jul–27 Aug	8	84		15	20	35
2003	04 Jul–09 Sep	11	73			36	36
2004	01 Jul–14 Sep	9	76			–	–

means that the variance inflation factor could not be estimated and the models were not adjusted for overdispersion. Hence, the  $AIC_c$  was used to assess the relative model fit and the model with the lowest  $AIC_c$  was selected as the most parsimonious. Model averaging was performed to obtain more precise estimates of parameters. LRTs were used to test hypotheses of biological interest between nested models.

**Total population size.** Abundance estimates obtained from the JS and robust design models pertain only to the population of identifiable individuals. Total population size ( $\hat{N}_{total}$ ) of bottlenose dolphins occurring in the study area was calculated by dividing the population estimate provided by these models ( $\hat{N}$ ) by the proportion of identifiable individuals ( $\hat{\theta}$ ) in the schools encountered. The proportion of identifiable individuals was estimated as the number of individuals with recognizable marks divided by the total number of individuals observed in each encounter, averaged over all encounters. The variance of total population size was estimated following Wilson et al. (1999) as:

$$\text{var}(\hat{N}_{total}) = \hat{N}_{total}^2 \times \left( \frac{\text{var}(\hat{N})}{\hat{N}^2} + \frac{1 - \hat{\theta}}{n\hat{\theta}} \right) \quad (1)$$

where  $n$  is the total number of dolphins from which  $\theta$  was estimated. Log-normal CIs for total population size were calculated according to Burnham et al. (1987), with a lower limit of  $\hat{N}_{total}^L = \hat{N}_{total}/C$  and an upper limit of  $\hat{N}_{total}^U = \hat{N}_{total} \times C$ , where

$$C = \exp \left[ z_{\alpha} \times \sqrt{\ln \left( 1 + [CV(\hat{N}_{total})]^2 \right)} \right] \quad (2)$$

in which  $z$  is the normal deviate,  $CV$  is coefficient of variation, and  $\alpha = 0.05$ . When appropriate, the parameters that resulted from model averaging were averaged again within a single group, time interval or cohort, to provide a unique estimate and to facilitate statistical comparisons. The new averaged parameters ( $\hat{\delta}$ ) could then be compared using the following test statistic

$$z = \frac{\hat{\delta}_1 + \hat{\delta}_2}{\sqrt{\text{var}(\hat{\delta}_1) + \text{var}(\hat{\delta}_2) - 2\text{cov}(\hat{\delta}_1, \hat{\delta}_2)}} \quad (3)$$

where  $z \approx N(0,1)$  under the null hypothesis (Lebreton et al. 1992).

## RESULTS

### Open models

The full time-dependent model with group effect (Model 19,  $QAIC_c = 1167$ ) provided a poor fit to the data ( $\chi^2 = 78.719$ ,  $p < 0.0001$ ,  $df = 22$ ) (Table 3). The directional test for transience was highly significant for adults ( $p < 0.0001$ ) and moderately significant for subadults ( $p = 0.039$ ). There was no significant evidence of a behavioural response in either age class (adults:  $p = 0.495$ , subadults:  $p = 0.884$ ). The global model with age dependence on survival (Model 16) represented a considerable improvement ( $\Delta QAIC_c = 26$ ) over the full time-dependent model but still fitted

Table 3. Model selection details for a subset of Cormack-Jolly-Seber (CJS) candidate models of survival ( $\phi$ ) and capture ( $p$ ) probabilities. Models are in decreasing order of the Quasi Akaike Information Criterion ( $QAIC_c$ ).  $\Delta QAIC_c$ : the difference in the  $QAIC_c$  of a model from that of the minimum  $QAIC_c$  model. <sup>a</sup>/<sub>1</sub>' is used to distinguish models that were fitted separately for adults/subadults, <sup>b</sup>number used as suffix corresponds to the number of parameters fixed

#	Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	Likelihood	No. parameters	Deviance
1	$\phi(g+a2) p(g \times \text{cohort})$	1092.7	0	0.426	1	13	78.4
2	$\phi(g \times a2) p(g \times \text{cohort})$	1093.7	1.0	0.257	0.603	14	77.4
3	$\phi(g \times a2) p(g \times \text{trend+/-})^a$	1095.1	2.4	0.127	0.298	8	91.1
4	$\phi(g) p(g \times \text{cohort})$	1096.2	3.5	0.075	0.177	12	84.0
5	$\phi(g \times a2) p(g \times \text{cohort} \times t)$	1096.3	3.6	0.072	0.170	29	48.2
6	$\phi(g \times a2 \times -t) p(g \times \text{cohort})$	1099.6	6.9	0.014	0.032	20	70.7
7	$\phi(g \times a2) p(g \times \text{effort cohort})$	1100.0	7.3	0.011	0.027	8	96.0
8	$\phi(g \times a2) p(g \times \text{trend3-+})^{a,b}$	1100.4	7.6	0.009	0.022	8	96.4
9	$\phi(g \times a2) p(g \times \text{cohort3})^b$	1101.3	8.6	0.006	0.014	10	93.2
10	$\phi(g \times a2 \times t-) p(g \times \text{cohort})$	1103.0	10.3	0.003	0.006	20	74.1
11	$\phi(g \times a2) p(g \times \text{cohort3/cohort} \times t)^{a,b}$	1106.8	14.1	<0.001	<0.001	22	73.7
12	$\phi(g \times a2 \times t-t) p(g \times \text{cohort})$	1108.6	15.8	<0.001	<0.001	26	67.0
13	$\phi(g \times a2) p(g \times \text{cohort3} \times t.)^{a,b}$	1109.3	16.6	<0.001	<0.001	16	88.8
14	$\phi(g \times a2) p(g \times \text{trend-/+})^a$	1111.9	19.2	<0.001	<0.001	7	109.9
15	$\phi(a2) p(g \times \text{cohort})$	1114.9	22.2	<0.001	0	12	102.7
16	$\phi(g \times a2 \times t-t) p(g \times t)$	1140.2	47.5	0	0	26	98.6
17	$\phi(g \times a2) p(g \times t)$	1153.0	60.3	0	0	14	136.6
18	$\phi(g \times a2) p(g \times \text{effort time})$	1154.3	61.6	0	0	8	150.4
19	$\phi(g \times t) p(g \times t)$	1166.7	74.0	0	0	18	142.1

the data poorly ( $\chi^2 = 24.435$ ,  $p = 0.041$ ,  $df = 14$ ). The lack of fit resulted from the rejection of Test 3.Sm (one of the components of the GOF test in program U-care) among adults ( $\chi^2 = 18.316$ ,  $p = 0.0004$ ,  $df = 3$ ), implying that newly and previously marked individuals differed on when they were re-encountered. The model with age dependence was used as a starting point to find more parsimonious models.

The model with a capture probability constrained as a linear function of the observation effort (Model 18,  $QAIC_c = 1154$ ) provided a slightly worse fit to the data than the model with time variation and group effect (Model 17,  $QAIC_c = 1153$ ). When cohort dependence was introduced as an effect to model capture rates (Model 2), there was a substantial improvement in model fit ( $QAIC_c = 1094$ ). We attempted to model the effect of sampling effort by forcing cohorts with similar amounts of effort to have equal capture parameters (Model 9), constraining capture probabilities to be a function of the sampling effort by cohort (Model 7), or imposing a linear trend over cohorts on capture probabilities (Model 3). None of these models provided a better fit to the data than the global model (Model 2), with the exception of the model with an additive effect between group and age dependence on survival (Model 1,  $QAIC_c = 1093$ ).

The variance inflation factor of the best fitting model ranged from 0.95 to 1.31, as estimated by the median  $\hat{c}$  and the bootstrap approaches, respectively. These values were not substantially different from 1 (model with perfect fit). In addition, the results of the bootstrap indicated that the deviance of the model was reasonably likely to be observed ( $p = 0.338$ ).

Both group and age dependence had a significant effect on annual survival rates (group:  $\chi^2 = 24.269$ ,  $p < 0.001$ ,  $df = 1$ ; age:  $\chi^2 = 5.525$ ,  $p = 0.019$ ,  $df = 1$ ) but the interaction between the 2 effects was not significant ( $\chi^2 = 1.058$ ,  $p = 0.304$ ,  $df = 1$ ) implying that the effect of age dependence was similar in adults and subadults. The model with constant capture probability per group cohort was almost 4× better supported by the data than the model where cohort capture probabilities varied across years ( $QAIC_c = 1096$ ). Despite this, the results of the LRT showed that there was a significant effect of year on capture probability ( $\chi^2 = 29.153$ ,  $p = 0.015$ ,  $df = 15$ ) but not on survival ( $\chi^2 = 10.425$ ,  $p = 0.579$ ,  $df = 12$ ). There was a significant linear trend in the capture probability along the cohorts, with opposite effects in each age class ( $\chi^2 = 13.754$ ,  $p = 0.033$ ,  $df = 6$ ).

Although two of the models included a time effect, annual differences in survival rate were negligible. Similarly, there was no variation in survival rate within each cohort. As expected, survival rate over the first time interval ( $\phi_1$ ) was lower than for subsequent intervals ( $\phi_{2+}$ ) in both age classes, although the difference was small among adults ( $\phi_1 = 0.960 \pm 0.049$  SE;  $\phi_{2+} = 0.970 \pm 0.029$  SE). Subadult survival rate over the first time interval was considerably lower ( $\phi_1 = 0.623 \pm 0.080$  SE) than for subsequent intervals ( $\phi_{2+} = 0.815 \pm 0.083$  SE). Average adult survival following the first interval after marking was significantly higher than subadult survival across all years and within all cohorts ( $z = 1.762$ ,  $p = 0.039$ ).

Capture probability was much higher in adults than in subadults for dolphins photo-identified in 1999 and 2000 (Fig. 2). It was similar among adult and subadult

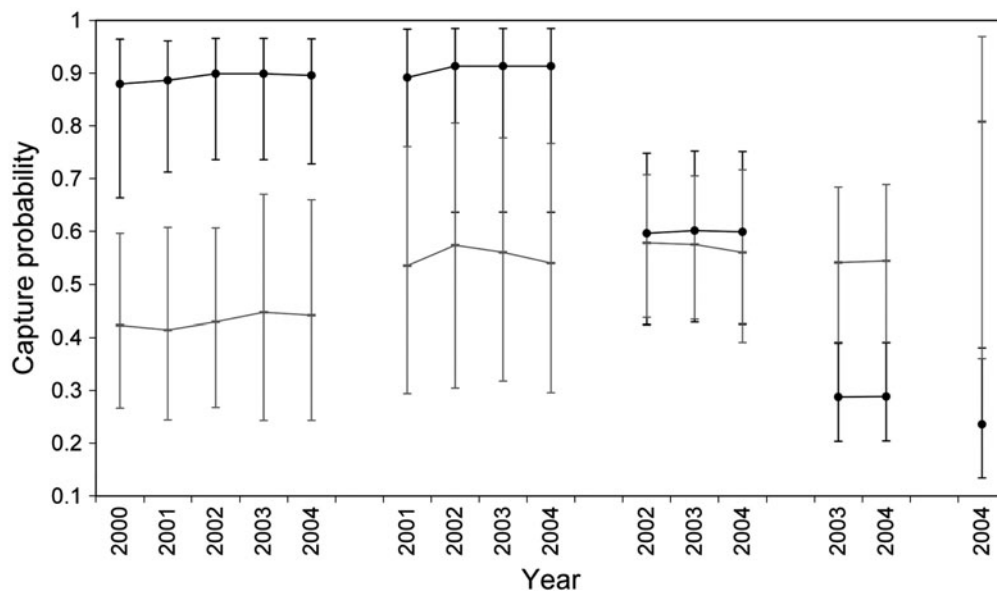


Fig. 2. Estimates of capture probability for adult (black) and subadult (gray) dolphins based on the weighted averages of the 15 best Cormack-Jolly-Seber (CJS) models (95% profile confidence interval, CI). Each grouping represents the estimates of a given cohort

individuals from the 2001 cohort, but was lower in adults identified in the last 2 cohorts. Overall, there was a marked negative trend in adult and a slight positive trend in subadult capture probabilities. Within each cohort, capture probability showed only minor fluctuations for both adult and subadult dolphins. Adult individuals photo-identified in the 2003 cohort showed the lowest capture probability ( $0.236 \pm 0.063$  SE), whereas the highest values were found in the 2000 cohort ( $0.908 \pm 0.090$  SE). Subadult capture probability varied between  $0.808 (\pm 0.159$  SE) in 2003 and  $0.431 (\pm 0.107$  SE) in 1999.

Since cohort effects cannot be tested with JS models, the final results differed from those obtained from the CJS models. Only 2 models—those with group specific survival or group and age-dependent survival, and with group and time variation in capture and entrance probabilities—received support from the data (Table 4). Thus, parameter inference was made using only these models.

There were considerable variations in the annual estimates of abundance for both age classes, with higher numbers of subadults in all but two years (Table 5). The estimate of the proportion of identifiable individuals in a school ( $\hat{\theta}$ ) varied substantially between

years, so we used annual values of  $\hat{\theta}$  to estimate total population size for that year (Table 5). The total number of adult bottlenose dolphins in the main area ranged from 28 (95% CI: 11 to 67) in 1999 to 334 (95% CI: 237 to 469) in 2004. Estimates of subadults using the area varied from 55 (95% CI: 28 to 107) to 591 ind. (95% CI: 279 to 1251) (Table 6).

### Robust design

The model with time variation in survival probabilities and a separate parameter for each capture occasion ( $s \times t$ ) was the best fitting model in the first modelling round (Model 11,  $AIC_c = 333$ ) and was used to investigate a suitable emigration model (Table 6). This model fitted the data much better than the model with constant capture probability (Model 18,  $AIC_c = 452$ ) or the models with heterogeneity with 2 mixtures (Model 17,  $AIC_c = 419$ ; Model 16,  $AIC_c = 409$ ). At this stage, models where survival was kept constant (Model 15,  $AIC_c = 350$ ) or was varied as a function of age dependence (Model 12,  $AIC_c = 337$ ) also received less support from the data than the model with time variation in survival.

Table 4. Model selection details for a subset of Jolly-Seber (JS) candidate models of survival ( $\phi$ ), capture ( $p$ ) and entrance (pent) probabilities. Models are in decreasing order of the Quasi Akaike Information Criterion (QAIC<sub>c</sub>).  $\Delta QAIC_c$ : the difference in the QAIC<sub>c</sub> of a model from that of the minimum QAIC<sub>c</sub> model

Model	QAIC <sub>c</sub>	$\Delta QAIC_c$	QAIC <sub>c</sub> weight	Likelihood	No. parameters
$\phi(g) p(g \times t) pent(g \times t)$	1231.6	0	0.576	1	22
$\phi(g \times a2) p(g \times t) pent(g \times t)$	1232.2	0.6	0.423	0.735	23
$\phi(g \times t) p(g \times t) pent(g \times t)$	1246.4	14.8	<0.001	<0.001	24
$\phi(g \times a2) p(g) pent(g \times t)$	1247.1	15.5	<0.001	<0.001	15
$\phi(a2) p(g \times t) pent(g \times t)$	1247.3	15.8	<0.001	<0.001	22
$\phi(.) p(g \times t) pent(g \times t)$	1249.2	17.7	<0.001	<0.001	22
$\phi(g \times a2) p(.) pent(g \times t)$	1249.9	18.3	<0.001	<0.001	15
$\phi(g \times a2) p(t) pent(g \times t)$	1250.9	19.3	<0.001	<0.001	19
$\phi(g \times a2) p(g \times t) pent(t)$	1271.3	39.7	0	0	21
$\phi(t) p(g \times t) pent(g \times t)$	1352.0	120.5	0	0	23

Table 5. Estimates of the proportion of identifiable dolphins in a school ( $\hat{\theta}$ ) and population size (N) from the Jolly-Seber (JS) models that were used to estimate total population size ( $\hat{N}_{total}$ ) of adult and subadult dolphins. Estimates are presented with SEs, CVs and log-normal 95% lower ( $\hat{N}_{total}^L$ ) and upper confidence limits ( $\hat{N}_{total}^U$ )

Year	$\hat{\theta}$	SE	Adults					Subadults				
			— Model —		Total	—		— Model —		Total	—	
N	CV	N <sub>tot</sub>	$\hat{N}_{total}^L$	$\hat{N}_{total}^U$		N	CV	N <sub>tot</sub>	$\hat{N}_{total}^L$		$\hat{N}_{total}^U$	
1999	0.59	0.06	16	0.41	28	11	67	32	0.26	55	28	107
2000	0.40	0.06	31	0.23	78	37	161	97	0.37	243	99	596
2001	0.66	0.07	49	0.17	74	45	122	389	0.35	591	279	1251
2002	0.74	0.04	150	0.11	202	148	277	323	0.11	434	316	597
2003	0.81	0.03	253	0.06	312	254	384	242	0.10	300	232	387
2004	0.72	0.06	239	0.10	334	237	469	222	0.13	311	212	456



Table 6. Model selection details for a subset of robust design candidate models of survival ( $\phi$ ), capture ( $p$ ), recapture ( $c$ ) and emigration ( $\gamma$ ) probabilities. Models are in decreasing order of the Akaike Information Criterion ( $AIC_c$ ).  $\Delta AIC_c$ : the difference in the  $AIC_c$  of a model from that of the minimum  $AIC_c$  model. Model notation follows Kendall et al. (1997):  $\gamma'' = \gamma' = 0$  = no emigration model;  $\gamma'' = \gamma' = \gamma'$  = random emigration model;  $\gamma''(x) \gamma'(x)$  = Markovian emigration model;  $\pi$  = mixture proportion;  $p(x) = c(x)$  = no behaviour effect. In models marked †, the last and penultimate emigration probabilities were set to be equal to allow identifiability of the parameters (Kendall et al. 1997)

#	Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight	Likelihood	No. parameters	Deviance
1	$\phi(.) \gamma''(t) \gamma'(. ) p(s \times t) = c(s \times t)$	298.83	0	0.579	1	41	598.4
2	$\phi(.) \gamma''(t) \gamma'(t) p(s \times t) = c(s \times t)$	300.07	1.25	0.310	0.536	42	597.1
3	$\phi(a2) \gamma''(t) \gamma'(t) p(s \times t) = c(s \times t)$	302.66	3.83	0.085	0.147	43	597.1
4	$\phi(t) \gamma''(t) \gamma'(t) p(s \times t) = c(s \times t)$	305.27	6.44	0.023	0.04	44	597.1
5	$\phi(.) \gamma''(t) = \gamma'(t) p(s \times t) = c(s \times t)$	310.39	11.56	0.002	0.003	40	612.5
6	$\phi(a2) \gamma''(t) = \gamma'(t) p(s \times t) = c(s \times t)$	312.94	14.12	<0.001	<0.001	41	612.5
7	$\phi(t) \gamma''(t) = \gamma'(t) p(s \times t) = c(s \times t)$	314.47	15.65	<0.001	<0.001	42	611.5
8	$\phi(t) \gamma''(. ) \gamma'(. ) p(s \times t) = c(s \times t)$	329.62	30.79	0	0	41	629.2
9	$\phi(t) \gamma''(t) \gamma'(t) p(s \times t) = c(s \times t) \dagger$	331.84	33.01	0	0	42	628.8
10	$\phi(t) \gamma'' = \gamma' p(s \times t) = c(s \times t)$	332.29	33.46	0	0	40	634.4
11	$\phi(t) \gamma'' = \gamma' = 0 p(s \times t) = c(s \times t)$	332.68	33.85	0	0	39	637.4
12	$\phi(a2) \gamma'' = \gamma' = 0 p(s \times t) = c(s \times t)$	337.13	38.31	0	0	38	644.3
13	$\phi(.) \gamma''(t) = \gamma'(t) p(s \times t) = c(s \times t) \dagger$	337.19	38.37	0	0	39	641.9
14	$\phi(.) \gamma''(t) \gamma'(t) p(s \times t) = c(s \times t) \dagger$	337.58	38.75	0	0	40	639.7
15	$\phi(.) \gamma'' = \gamma' = 0 p(s \times t) = c(s \times t)$	350.21	51.39	0	0	37	659.9
16	$\phi(t) \gamma'' = \gamma' = 0 \pi(s) p(s)$	409.47	110.64	0	0	17	766.2
17	$\phi(t) \gamma'' = \gamma' = 0 \pi(. ) p(s)$	419.45	120.62	0	0	15	780.6
18	$\phi(t) \gamma'' = \gamma' = 0 p(. ) = c(. )$	452.14	153.31	0	0	8	828.3

In the second round of modelling, constant and time-specific random and Markovian emigration models were fitted to the data, and the survival parameter was modelled again in the third round to look for a more parsimonious model. Overall, the best fitting model had constant survival, Markovian emigration (with time variation in  $\gamma''$  and constant  $\gamma'$ ) and a different capture probability for each sampling occasion. This model fitted the data almost twice as well as Model 2 (with time variation in  $\gamma'$ ) and almost 7× better than Model 3 (with age dependence on survival) (Table 6).

The LRT rejected the models with no emigration and random emigration in favour of the models with a Markovian emigration process (no emigration:  $\chi^2 = 8.155$ ,  $p = 0.017$ ,  $df = 2$ ; random emigration:  $\chi^2 = 5.227$ ,  $p = 0.022$ ,  $df = 1$ ). There was strong evidence of annual variations in the probability of emigration for dolphins that were in the sampled area in the previous year ( $\chi^2 = 32.115$ ,  $p < 0.001$ ,  $df = 3$ ) but not for dolphins that were outside the area ( $\chi^2 = 1.325$ ,  $p = 0.250$ ,  $df = 1$ ).

Survival probability was equal or very close to unity in all the candidate models and the resulting averaged survival rate (weighted over the 7 best models) varied between 0.999 ( $\pm 0.003$  SE) and 1 ( $\pm 0.000$  SE). The probability of temporary emigration for animals that were in the sampled area in the previous period was 0.421 ( $\pm 0.124$  SE) for the first time interval (2001–2002), and 0.760 ( $\pm 0.057$  SE) for the second interval (2002–2003). For animals that were emigrants during

the previous year, the emigration probability in the interval 2003–2004 was 0.097 ( $\pm 0.164$  SE). The remaining emigration parameters could not be estimated. Capture probabilities varied greatly between and within primary periods but were usually very low, ranging from 0.590 to 0.017.

The number of dolphins using the area varied considerably between years, reaching the lowest value of 41 adult dolphins (95% CI: 26 to 65) in 2001 and the highest value of 288 animals (95% CI: 196 to 423) in 2004 (Table 7).

To determine if the upward bias in survival was due to models overestimating emigration rates and thus interpreting all absences of individuals as temporary emigration, survival probability was calculated using best fitting models with no emigration. Survival was

Table 7. Estimates of population size ( $N$ ) from the robust design that was used to estimate total population size ( $N_{total}$ ) of adult dolphins. Estimates are presented with CVs and log-normal 95% lower ( $\hat{N}_{total}^L$ ) and upper confidence limits ( $\hat{N}_{total}^U$ )

Year	Model		$N_{tot}$	Total	
	N	CV		$\hat{N}_{total}^L$	$\hat{N}_{total}^U$
2001	27	0.10	41	26	65
2002	159	0.14	213	145	315
2003	92	0.07	114	85	152
2004	206	0.15	288	196	423

estimated as 0.969 ( $\pm 0.097$  SE), 0.657 ( $\pm 0.130$  SE) and 0.999 ( $\pm 0.001$  SE) for the time intervals 2001–2002, 2002–2003 and 2003–2004, respectively.

## DISCUSSION

### Analysis of model assumptions

Capture–recapture models assume that individual marks are not lost or missed. In small cetaceans, the acquisition of permanent or long-lasting marks is cumulative (Würsig & Jefferson 1990) and young dolphins are usually less distinctively marked than adult individuals. Failure to recognize previously marked dolphins due to changes in the pattern of marking was therefore more likely to occur among subadults, resulting in a downward bias in capture and survival rates and an upward bias in abundance estimates.

Perhaps the most difficult assumption to satisfy in capture–recapture studies is that of equal catchability among individuals at any sampling occasion. By stratifying the sample analysed with open models by age class, we were able to control for heterogeneity arising from differences in distinctiveness of natural markings and behaviour between adult and subadult dolphins. Yet, the results of the GOF tests suggested that there was still a considerable amount of heterogeneity, especially among adults. Fitting an age-dependent model enabled us to deal with the problem of transient dolphins and avoid the consequent downward bias in survival estimates. However, the age-dependent model still fitted the data poorly, suggesting that there were further problems. More than 17% (36 adults, 70 subadults) of the dolphins used in the analysis with open models showed a form of capture history that was consistent with temporary emigration, which likely resulted in negatively biased capture probabilities for both age classes. Additionally, both the AIC and the LRT results of the robust design models indicated that the emigration model in adult dolphins is Markovian. When the probability of temporary emigration is higher for animals that were not emigrants in the previous year, such as in the present study, survival probabilities estimated with open models could suffer from a slight upward bias (Kendall et al. 1997).

Even if some of the assumptions of open models may have been violated, results from the GOF tests indicate that model structure was correct and the small variance inflation factor indicates that the excess variation was within acceptable limits. Moreover, by incorporating a measure of overdispersion in model selection and parameter inference, the precision of the estimates presented here reflects the extra amount of variance in the data.

Besides some of the general assumptions of capture–recapture models discussed earlier, Pollock's robust design also assumes population closure within primary periods. In this study, the secondary periods spanned over 2 mo as this was the minimum interval with enough recaptures to allow reliable parameter estimation. The assumption of demographic closure within these 2 mo periods seems reasonable. We have no way of determining if dolphins moved in and out of the study area during the secondary periods; however, given the degree of mobility recorded for this population (Silva et al. 2009), it is unlikely that the assumption held. Under the Markovian movement model, violation of the closure assumption will bias capture probabilities and population size but the magnitude and direction of the bias cannot be predicted (Kendall 1999). One implicit assumption in the robust design is that survival probability is not affected by the emigration status. Although this assumption is difficult to test, we suspect that its influence on the results was negligible.

### Capture probabilities

As expected, capture probabilities varied between adult and subadult dolphins and all the best fitting open models included group effect on capture probabilities. More surprising was the decreasing trend in adult capture probabilities across cohorts. This pattern likely resulted from an increase in the proportion of sampled dolphins with lower site fidelity to the area (and thus, with higher probability of being unavailable for capture on subsequent occasions), which in turn was induced by variations in sampling effort. The number of hours spent searching for and photographing schools of bottlenose dolphins almost doubled from 1999 to 2000–2001, and almost tripled from 1999 to 2002–2004. It was reasonable to expect that the variation in sampling effort strongly influenced capture probabilities, but all attempts to model it directly were unsuccessful. It is possible that the chosen variable was not a good proxy or, most likely, failed to tease apart the simultaneous effect of the increase in the number of new dolphins identified and the probability of recognizing previously photographed dolphins with time, but more importantly, across cohorts.

Sampling effort influenced the number of dolphins identified each year and, consequently, the relative proportion of individuals with different probabilities of remaining in the population. Based on their long-term and year-round site fidelity, 44 resident dolphins were identified in the study area by Silva et al. (2009). Nearly all the adult dolphins photographed in the first 2 yr of this study belonged to the resident group and were seen again in the following years. As a result, in

the 1999 and 2000 cohorts, adult survival rate was close to unity and capture probabilities approached 90%. In 2001, the proportion of residents in the sample dropped to 50%. The increase in sampling effort in 2002 and 2003 resulted in a substantial increase in the number of non-residents, which represented 80 and 90% of the dolphins identified, respectively. Non-resident dolphins showed lower site fidelity to the area; consequently, capture probabilities of the last cohorts dropped. We suspect that this decrease was exaggerated because data for adult dolphins were best explained by a Markovian emigration model. Under this form of emigration, the negative bias in capture probabilities that were estimated with open models may reach 30% (Kendall et al. 1997).

Subadult dolphins were generally less distinctively marked than adult animals, increasing the chances of missing some matches. During the first years of the study, the sampling effort may have been insufficient to ensure that enough good-quality photographs were obtained to allow recognition of subadults, resulting in slightly lower capture rates. With more effort having been put into photographing the schools in later stages of the study, individuals from the first cohorts continued to be identified and a greater proportion of newly marked subadults was recognized on the year following release. Improvement in photographic efficiency is supported by data on the proportion of identifiable dolphins in the schools, which increased from <60% in the first 2 yr of the study to >72% in the last 3 yr. Therefore, the combined effect of sampling effort, and photographic and identification efficiency may explain the slight increase in subadult capture probabilities across cohorts and the larger difference in survival probabilities between the first and the succeeding time interval.

Silva (2007) analysed data from dedicated and opportunistic sighting surveys conducted in the study area from 1999 to 2004. Encounter rate of bottlenose dolphins varied between years but there was no evidence of an increasing trend in the number of dolphins using the area. Although annual fluctuations in dolphin abundance might have contributed to variations in capture probabilities across years, they could not explain the opposite trends observed for adults and subadults.

Although we were unable to model the variation in sampling effort directly, bias resulting from differences in sampling effort was minimized by allowing capture probability to vary by cohort in both open and robust design models. As anticipated, capture probabilities also varied with time within a cohort, although the temporal effect was less influential than the cohort effect, as indicated by the poorest fit to the data of the models with only time effect.

We tried to control for some heterogeneity in capture probabilities by using robust design models with 2 mixtures, which correspond to resident and non-resident dolphins. However, these models provided a poor fit to the data, possibly because 2 mixtures were insufficient to accommodate the full spectrum of residence patterns in the population.

## Survival

Incorporating age dependence on survival probability significantly improved the fit of the CJS models, confirming the existence of transient dolphins in the population sampled. In addition, transience affected adult and subadult survival probabilities in a similar way, as indicated by the better fit of the model with additive effects between group and age dependence. In contrast, robust design models provided no evidence of age dependence in survival rates in adult dolphins, after the models have accounted for temporary emigration. This is certainly explained by the lower number of transient dolphins encountered in each 2 mo period considered in the robust design analysis.

As anticipated, models accounting for differences in survival between the 2 age classes provided the best fit to the data and the LRT showed that age class had a significant effect on survival probabilities. Both CJS and robust design methods failed to provide any evidence of temporal variability in survival probabilities.

Adult survival given by the robust models was undoubtedly overestimated. Survival estimates provided by the models with no emigration were lower, which may suggest that part of the upward bias in survival occurred because the models interpreted all absences from the study area as emigration. We suspect that the time span of this study was insufficient to model survival correctly under more complex designs, and that a larger number of primary periods are required to estimate all the parameters accurately.

Survival estimates from open models should not have been greatly affected by Markovian emigration although the precision of the estimates might have been reduced. The survival estimate of adult bottlenose dolphins given by the CJS models (0.97) is higher than the estimates reported for the same species in Kvarneric, Croatia (range:  $0.825 \pm 0.054$  to  $0.938 \pm 0.042$  SE; Fortuna 2006) and Doubtful Sound, New Zealand (0.937, 95% CI: 0.917 to 0.953; Currey et al. 2008), but similar to estimates obtained in Sado Estuary, Portugal (range:  $0.953 \pm 0.015$  to  $0.995 \pm 0.008$  SE; Gaspar 2003) and Sarasota Bay, USA (range: 0.920 to 0.988, mean:  $0.962 \pm 0.008$  SD; Wells & Scott 1990). These differences in survival estimates may be related to ecological differences between study sites (Currey

et al. 2008) or to different levels of natural or human-induced impacts.

Although the estimates of subadult survival reported here may be negatively biased, the pattern of lower survival in subadults agrees with reports for other populations (Gaspar 2003, Stolen & Barlow 2003).

### Temporary emigration

As expected, we found clear evidence of temporary emigration of the population from the study area. Movement patterns of adult bottlenose dolphins seem to follow a Markovian model. The probability of temporary emigration for dolphins seen in the study area in the preceding year ranged from 42 to 76%. Between-year variation in emigration rates likely reflects the heterogeneity in capture probabilities that was caused by sampling effort and was probably exaggerated by the small sample sizes. Interestingly, the probability that these dolphins would return to the study area in the subsequent year approached 90%. Unfortunately, immigration rates could only be calculated for a single year, which limits the interpretation of the results.

Care should be taken when interpreting our results, as the number of surveys conducted in each primary period was probably insufficient to sample all dolphins present in the area, given the size of the area and the extensive ranging behaviour of some individuals. In fact, precision of the estimates was generally low, which likely reflects the small sample size considering the number of parameters required under the more complex Markovian model. On the other hand, estimated temporary emigration probabilities approached zero in some years, which may have been caused by sampling variation (Kendall et al. 1997). Thus, the estimates of emigration probability reported in this study are likely to be overestimated. However, high levels of emigration followed by immigration back to the original area is consistent with the extensive ranging behaviour that has been reported for this population and further indicates that the study area did not encompass the whole range of several dolphins sampled (Silva et al. 2009).

### Population size

Estimates of bottlenose dolphin population size varied greatly between years. In the first years of the study, effort was insufficient to obtain a representative sample of all dolphins using the study area; therefore, these dolphins were simply excluded from the estimates. The annual differences in abundance that were

found in later years do not appear to be related to methodological issues and may reflect natural fluctuations in the overall distribution and abundance of dolphins in the area, which may have resulted from temporal changes in prey density and availability.

The pattern of temporal variability in the estimates of population size was not always consistent between the JS and robust design methods. This is expected since both methods used different datasets. In addition, the short secondary sampling periods of the robust design model resulted in low capture probabilities for some periods, ultimately leading to poorer precision of the abundance estimates.

As described earlier, possible violation of the respective assumptions of homogeneity of capture probabilities and of geographic closure under the JS and robust designs may have biased the estimates of population size to an unknown degree. Despite this, if we consider the estimates with the lowest CV, which also corresponded to the years with greater sampling effort, then the number of adult dolphins using the study area varied from 202 (95% CI: 148 to 277) to 334 (95% CI: 237 to 469), according to the JS method, and from 114 (95% CI: 85 to 152) to 288 (95% CI: 196 to 423), according to the robust design. The number of subadult individuals that frequented the area varied from 300 (95% CI: 232 to 387) to 434 (95% CI: 316 to 597) based on the JS method.

These estimates fall outside the range of population sizes that are typically reported for coastal and estuarine areas, which are usually a little over 100 ind. (Wells et al. 1980, Wilson et al. 1999, Ingram & Rogan 2002), and even for other oceanic islands such as Hawaii (134 dolphins, 95% CI: 107 to 179; Baird et al. 2001). However, our estimates pertain to an area that is 2 to 20× larger than the areas in the aforementioned studies. In addition, these studies were focused on areas that were inhabited by populations of dolphins with a high degree of site fidelity to a well-defined and restricted range. Although the ranges of these populations were sometimes visited by dolphins living in neighbouring areas, none of these studies documented levels of emigration and immigration as high as the ones observed in the Azores (Wells et al. 1980, Baird et al. 2001). Finally, both the JS and robust design methods presume the existence of a 'superpopulation' in the area. At any instance, animals from this 'superpopulation' may 'enter' or 'leave' the sampled area, either by demographic or movement processes. In this case, the 'superpopulation' does not include the whole population of bottlenose dolphins living in the archipelago, as there is some suspicion of the existence of resident dolphins in other islands (Silva et al. 2009). If the behaviour of these 'other dolphins' is similar to that reported for the group residing in our study area, then

they will probably show a restricted range. This implies that these animals are excluded from the abundance estimates presented here.

## CONCLUSIONS

This study illustrates how modelling transience and temporary emigration in cetacean populations, while challenging because of the problems associated with sampling wide-ranging animals at the required temporal and spatial scales, can improve the precision of estimated population parameters. Estimation of population parameters that consider emigration usually implies fitting complex models with a large number of parameters that may require large sample sizes to be estimated accurately. Thus, it is necessary to introduce constraints to reduce the number of parameters that need to be estimated. Care must be taken to ensure that constraints introduced are reasonable and do not conflict with knowledge of the ecology of the population under study. This work also shows the importance of adapting sampling effort to the study area and to the degree of mobility of the population. Sampling effort in the early stages of this work was enough to estimate size and survival of the resident group but was clearly insufficient to obtain reliable estimates for the whole population using the area.

Despite suffering from an unknown degree of bias, this study provided the first estimates of survival, temporary emigration and population size for bottlenose dolphins occurring in the Azores. Rates of temporary emigration of adult dolphins may be biased upwards, even though they confirm initial expectations, given the extensive ranging behaviour previously documented for this population. At present, our study area is the only region within the Archipelago with enough data to allow estimation of population parameters. Capture–recapture data from the other islands are urgently needed to produce reliable estimates for the total population of the Azores. If data are collected simultaneously, multi-state models could be employed to provide population parameters and at the same time estimate movement probabilities between the different groups of islands (Brownie et al. 1993).

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