Population dynamics of killer whales (*Orcinus orca*) in the Crozet Archipelago, southern Indian Ocean: a mark-recapture study from 1977 to 2002

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ABSTRACT

Population size and annual survival probabilities for the killer whales (*Orcinus orca*) inhabiting the inshore waters of Possession Island, Crozet Archipelago, southern Indian Ocean, were estimated through mark-recapture modelling. Capture histories were generated from a set of photographs taken under a photo-identification protocol and a set of photographs taken opportunistically, between 1964 and 2002. Photographs were selected according to their intrinsic quality and the degree of natural marking of individuals. Under those conditions, only well-marked individuals were considered as 'marked' from a capture-recapture perspective. The purpose of this double selection was to minimise identification errors and reduce the heterogeneity of capture probabilities. Abundance estimates were derived from the M_{th} sequential model for closed populations and adjusted for the proportion of well-marked individuals in the study population and for the number of photo-identified individuals. Under this framework, estimates of 98 (95% CI 70-156) individuals in 1988-89, and 37 (95% CI 32-62) individuals in 1998-2000 are proposed. After a weighted model averaging, the Cormack-Jolly-Seber models with the strongest support from the data produced low survival probability estimates, decreasing from 0.935 (95% CI 0.817-0.979) to 0.895 (95% CI 0.746-0.961) for males, and from 0.942 (95% CI 0.844-0.980) to 0.901 (95% CI 0.742-0.966) for females over the period 1977-2002. A Jolly-Seber model was used as a 'second opinion' model. It confirmed the worrying status of the population with a constant survival probability estimated at 0.89 (95% CI 0.84-0.93) and a constant rate of increase (applying to the well-marked fraction of the population) estimated at 0.94 (95% CI 0.90-0.99) for the period 1987-2000. This rate of increase is consistent with the abundance estimates presented here. Possible violations of the underlying model assumptions were investigated and it was concluded that the abundance estimates for the period 1988-89 and the CJS survival estimates should be the most reliable results. It is feared that the killer whales around Possession Island are in sharp decline, as may be true for the whole Crozet Archipelago. The effect of low prey stocks and lethal interactions with fisheries as the most likely causes of this decline are discussed.

KEYWORDS: KILLER WHALE; INDIAN OCEAN; PHOTO-ID; MARK-RECAPTURE; ABUNDANCE; SURVIVAL; FISHERIES

INTRODUCTION

Top predators are dependent upon an extensive set of trophic links within the marine food web. Consequently, they are directly or indirectly affected by human activities and changes in environmental conditions such as climatic and subsequent habitat changes (Barbraud and Weimerskirch, 2001), concentration of pollutants in the food web (Ylitalo *et al.*, 2001), interactions with fisheries (Lewison *et al.*, 2004), or depletion of prey stocks. Top predators are thus conveying a range of information on the marine environment and are often considered as biological indicators of the changes in their ecosystems (Boyd *et al.*, 2006; Sergio *et al.*, 2005).

Around the southern Indian Ocean Subantarctic islands, the killer whale (*Orcinus orca*) can be considered as a biological indicator of choice because of its eclectic diet (elephant seals, penguins, cetaceans, fish; Guinet, 1991). The first documented sighting in the Crozet Islands occurred in 1825 (Lesquin, 1840) and in the 1970s the first studies focused on their behaviour (Voisin, 1976). The first demographic parameters were estimated by Guinet (1991), who pointed out a low fecundity and a decrease in the number of individuals observed from the coasts of Possession Island (one of the main islands in the archipelago). This paper focuses on these individuals, whose status is still unknown from a population biology point of view. However, for the sake of simplicity, they are hereafter referred to as a 'population'.

Initially developed to model physical recaptures and derive population parameters, capture-recapture models are now widely applied to capture histories generated from photographic observations (Hammond, 1986; Karanth and

Nichols, 1998). Since part of the Crozet population can be reliably identified from natural marks (Guinet, 1991), mark-recapture models were used to estimate some population parameters (annual adult survival probabilities, population size and population growth rate).

Today, only northeastern Pacific resident killer whales have been studied using advanced population dynamics methods leading notably in survival estimates (Olesiuk *et al.*, 1990). The results presented have been compared to the parameters of this, at least at that time, healthy growing population.

METHODS

The photographic collection
A pool of photographs taken between 1964 and 2002 by land-based observers from various places along the shore of Possession Island (46°25'S, 51°40'E) in the Crozet Archipelago was used for this study. Most photographs were taken according to a protocol aiming at getting the completely exposed dorsal fins of all the individuals surfacing in the study area with the best possible magnification. The rest of the photographs were taken opportunistically without any special protocol.

Selection and analysis of photographs
The photographs were given a 'Q' (quality) value between 0 and 3. Q=3 when individuals were very well represented with fully visible dorsal fins on close-up and when the shooting angle was 90°. Q=2 when dorsal fins were fully visible, but not on close-up or with an angle slightly different from 90°. Q=1 when dorsal fins were partially visible on exploitable photographs. Q=0 for unusable
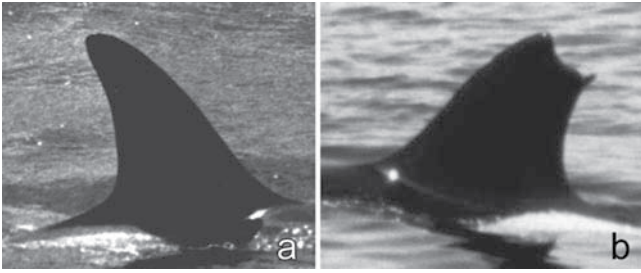
Fig. 1. a. Individual without any significant natural mark ('*M*' quality value = 0; photo C. Guinet). b. Individual with a significant natural mark (amputation; '*M*' quality value = 2; photo E. Fernandez).

photographs (e.g. subject blurred or too far, shooting angle very different from 90°).

The whales were identified by the natural marks on their dorsal fins (Bigg, 1982). A photo-identification catalogue was created and each occurrence of identified whales was recorded in a database with date and location details to produce sighting histories.

The quality of marking of each photographed whale was given an '*M*' quality value between 0 and 2. $M=0$ for individuals with dorsal fins bearing no significant mark (Fig. 1a). $M=1$ for individuals with dorsal fins bearing temporary marks (e.g. scars, desquamation), non symmetric marks, or marks that are hardly visible on photograph with $Q \geq 2$. $M=2$ for well-marked physically mature individuals with dorsal fins bearing symmetric marks that are assumed to remain unchanged, or almost unchanged, for the study duration (e.g. notches, amputations, Fig. 1b) and that are easily visible on photographs with $Q \geq 2$.

Estimating demographic parameters
Only photographs with $Q \geq 2$ of individuals with $M=2$ were considered. Thus, only well-marked individuals were considered as 'marked' from a capture-recapture perspective. This double selection aimed at minimising identification errors and reducing the influence of the quality of natural marks on capture probabilities, in other words, reducing the heterogeneity in capture probabilities (Hammond, 1986).

Abundance
The best documented periods of the study were focussed on, i.e. 1988-89 (Table 1) and 1998-2000 (Table 2), to estimate the number of killer whales frequenting the coasts of Possession Island. Among the classical sequential mark-recapture models for closed populations (Otis *et al.*, 1978; Pollock *et al.*, 1990), model M_{th} was chosen for the consistency of its underlying assumptions with the study conditions. These assumptions are: (1) the population is closed demographically (no deaths or births) and geographically (no emigration or immigration) for the duration of the study; (2) all marks are correctly read and recorded on each capture occasion; (3) marks are not lost nor overlooked; (4) individual capture probabilities are heterogeneous; and (5) capture probabilities can vary with time.

The closure assumption could not be tested because the data were too sparse for the closure tests of Otis *et al.* (1978) and Stanley and Kenneth (1999). The possible violations of this assumption and their consequences are discussed later. Assumptions (2) and (3) were considered to be fulfilled thanks to the selection procedure used for photographs and marks. A model with assumptions (4) and (5) was needed because many parameters affected capture probabilities during the study (behavioural heterogeneity among individuals, diversity of natural marks, photographers and capture sites, varying effort of observation, etc.).

As the photographic material was initially intended for simple photo-identification analyses, the sampling occasions were not planned 'by the rule book' for mark-recapture modelling. Therefore capture occasions were defined *a posteriori* in such a way that the time intervals between them were supposedly long enough (at least two months) to allow mixing between individuals.

For choosing among the various estimators for model M_{th}, Chao *et al.* (1992) recommend examining the sample coverage (*C*) defined as 'the proportion of the total individual capture probabilities of the captured animals' and the coefficient of variation of individual capture probabilities (γ, a measure of the heterogeneity mentioned in assumption (iv)). *C* can be estimated by the mean of estimators $\hat{C}_1$ and $\hat{C}_2$ (see Chao *et al.*, 1992 for details):

$$\hat{C} = 1 - \frac{f_1 - f_2 /(t-1)}{\sum_{k=1}^{t} k f_k}$$

where f_k is the number of animals captured k times in t samples. $\hat{\gamma}^2$, the estimation of the square of γ, and the abundance were estimated by the program *CAPTURE* (Otis *et al.*, 1978).

Since only well-marked individuals (with $M=2$) were regarded as 'marked' in the analyses, the models estimated the abundance of this fraction of the population ($\hat{N}$). To estimate the abundance of the whole population, the proportion of well-marked individuals was estimated, denoted θ, in the population. This proportion was estimated for the periods 1987-90 (corresponding to 1988-89 plus two years of extension in order to increase the sample size) and 1998-2000. For each period, photographs were selected with $Q \geq 2$, taken according to the protocol and showing at least two individuals to avoid over-representation of well-marked animals. Standard errors were estimated using the binomial theory of probability.

The size of the whole population (N') was estimated by adjusting $\hat{N}$ for $\hat{\theta}$ with $\hat{N}' = \hat{N} / \hat{\theta}$.

To maintain the asymmetry in the confidence interval of computed by *CAPTURE* (has a non-normal distribution so *CAPTURE* assumes a log-normal distribution or exploits the likelihood principle), the limits of this interval were adjusted for the coefficient of variation (CV) of $\hat{\theta}$, according to formulas derived from Whitehead *et al.* (1997):

$$\text{l.b.}(\hat{N}') = \frac{\hat{N}}{\hat{\theta}} \cdot \left(1 - 2 \cdot \sqrt{\left(\frac{\hat{N} - \text{l.b.}(\hat{N})}{2 \cdot \hat{N}} \right)^2 + \text{CV}(\hat{\theta})^2} \right)$$

$$\text{u.b.}(\hat{N}') = \frac{\hat{N}}{\hat{\theta}} \cdot \left(1 + 2 \cdot \sqrt{\left(\frac{\text{u.b.}(\hat{N}) - \hat{N}}{2 \cdot \hat{N}} \right)^2 + \text{CV}(\hat{\theta})^2} \right)$$

where l.b.(*X*) and u.b.(*X*) are respectively the lower and upper bounds of the 95% confidence interval of the variable *X*.

Analysis of the apparent annual survival and rate of increase of the population
The annual capture-recapture data (see Tables 1, 2 and 3) were analysed with the Cormack (1964), Jolly (1965) and Seber (1965) model (referred to as the 'CJS model' hereafter) to estimate the apparent survival probabilities and the capture probabilities for adults (physically mature individuals) over the study period. The underlying assumptions for this model are: (1) capture probabilities (*p*) are homogeneous among marked individuals at each

occasion *t*; (2) survival probabilities (*Φ*) are homogeneous among marked animals between each occasion; (3) marks are not lost nor overlooked; (4) capture occasions are short in comparison to the time interval between successive occasions; (5) emigration is permanent; and (6) animals are independent regarding capturability and survival (Williams *et al.*, 2002).

Table 1

Capture-recapture summary statistics for the period 1988-89. *i* is the capture occasion number, C_j the number of individuals captured at occasion *j*, R_j the number of individuals recaptured among C_j, N_j the number of newly captured individuals during occasion *j* and M_j the cumulated number of marked individuals in the population at the end of occasion *j*.

j	Date	Effort	C_j	R_j	N_j	M_j
1	April 11 1988	6	3	0	3	3
2	November-December 1988	102	14	0	14	17
3	November-December 1989	57	19	11	8	25

Table 2

Capture-recapture summary statistics for the period 1998-2000. *j* is the capture occasion number, C_j the number of individuals captured at occasion *j*, R_j the number of individuals recaptured among C_j, N_j number of newly captured individuals during occasion *j* and M_j the cumulated number of marked individuals in the population at the end of occasion *j*.

j	Date	Effort	C_j	R_j	N_j	M_j
1	April 1998	1	1	0	1	1
2	November-December 1998	141	13	0	13	14
3	December 1999-January 2000	40	3	3	0	14
4	April 15 2000	2	2	2	0	14
5	June 21-29 2000	26	3	3	0	14
6	October-December 2000	175	11	10	1	15

Table 3

Capture-recapture summary statistics for the period 1977-2002. *j* is the capture occasion number, C_j the number of individuals captured at occasion *j*, R_j the number of individuals recaptured among C_j, N_j the number of newly captured individuals during occasion *j* and M_j the cumulated number of marked individuals in the population at the end of occasion *j*.

i	Year	Effort	C_j	R_j	N_j	M_j
1	1977	44	2	0	2	2
2	1978	2	1	1	0	2
3	1979	3	1	0	1	3
4	1980	60	5	1	4	7
5	1981	8	1	1	0	7
6	1982	27	1	1	0	7
7	1984	3	1	0	1	8
8	1985	40	4	2	2	10
9	1986	38	1	1	0	10
10	1987	443	9	3	6	16
11	1988	399	17	10	7	23
12	1989	321	19	13	6	29
13	1990	26	2	2	0	29
14	1993	1	1	1	0	29
15	1996	108	4	3	1	30
16	1997	7	3	3	0	30
17	1998	402	14	10	4	34
18	1999	90	3	3	0	34
19	2000	796	12	11	1	35
20	2001	10	1	1	0	35
21	2002	61	6	6	0	35

In the standard parameterisation of the CJS model, denoted [$\Phi_t\ p_t$], time is regarded as a source of variation in *Φ* and *p*. More general variants of this model allow the consideration of extra sources that are regarded alone or combined, with or without interaction (see Lebreton *et al.*, 1992 for details). The effect of time (t) and sex (s) on parameters *Φ* and *p* were studied with the general starting model [$\Phi_{s*t}\ p_{s*t}$]. The notation s*t, represents the cumulated effect of time and sex and their interaction on the considered parameter. The notation s+t represents the additive model without interaction.

Assumptions (3) and (4) were considered met thanks to the study design. Assumption (6) could not be met; the consequences of this violation will be discussed at the end of the study. The goodness-of-fit of the starting model [$\Phi_{s*t}\ p_{s*t}$] for the remaining assumptions was tested with the program *U-CARE* (Choquet *et al.*, 2003). Variants of this model were fitted in two steps, first focusing on the modelling of capture probabilities with increasing constraints while keeping the full variability in survival probabilities. The annual photographic effort was used as a covariate to test the hypothesis of an effort-dependent capture probability (notation p_{effort}). The best model from the first step to model survival probabilities was then used. Survival probabilities were progressively constrained and tested for a trend over the study period (denoted Φ_{trend}) as well as the influence of the beginning of Patagonian toothfish (*Dissostichus eleginoides*) poaching in 1996 (denoted $\Phi_{poaching}$).

To compare the survival estimations produced by the CJS models to another source of estimation, a set of Jolly-Seber models was fitted with the Pradel-λ parameterisation (hereafter referred to as 'JS models'; Pradel, 1996). Jolly-Seber models have an extra assumption compared to CJS models; unmarked animals in the population have the same probability of capture as marked animals in the population. This assumption was considered to be met (well-marked photo-identified individuals have the same probability of capture as well-marked individuals that have not been photo-identified yet). A sex effect could not be included in the JS candidate models because our data were too sparse to allow goodness-of-fit testing. Consequently, the starting model was the fully time dependant model [$\Phi_t\ p_t\ \lambda_t$], where λ denotes the apparent rate of increase of the adult population. The goodness-of-fit of this starting model was tested with the program *JOLLY* (Pollock *et al.*, 1990). All possible candidate models were designed to include a trend over time on *Φ* and λ, and the effects of the photographic effort on *p*. λ is the sum of *Φ* and the apparent fecundity, which is small compared to *Φ* in large-mammal populations, especially in the study population (Guinet, 1991). As *Φ* is approximately equal to λ, models were designed with the same effects on these parameters. Due to the complexity of the JS models compared to the small size of the data set, the candidate models were applied only to the years with high photographic effort (i.e. 1987, 1988, 1989, 1998, 1999 and 2000) to avoid numerical convergence problems in the computing process.

The selection among CJS and JS model sets was achieved following the information-theoretic approach (Burnham and Anderson, 2002). The Akaike's information criterion adjusted to the size of the sample (AIC_c) was used to measure the parsimony of candidate models (Hurvich and Tsai, 1989). Differences of AIC_c (ΔAIC_c) were used to measure the plausibility of a given model compared to the model with the lowest AIC_c. In the case of selection uncertainty, i.e. when several models had $\Delta AIC_c < 2$ (Burnham and Anderson, 2002), a model averaging was performed with the best candidate models. This procedure yields a weighted average of the estimates produced by these models, using Akaike weights (w_i, a normalised measure of the relative support for

model i in a set of models; Burnham and Anderson, 2002). All computations (model fitting, parameter estimation, AIC_c and w_i computation and model averaging) were carried out using the program *MARK* (White and Burnham, 1999).

RESULTS

Photo-identification
A total of 2,329 photographs were examined, including 1,812 taken according to the photo-identification protocol and 517 opportunistically. There were on average 1.26 individuals per photograph (2,930 killer whales were represented on the photographs). Each representation of a whale was treated as a photograph. The following totals were obtained for each 'Quality' category: $Q = 0$ (498 photographs); $Q = 1$ (582 photographs); $Q = 2$ (1,612 photographs); and $Q = 3$ (238).

All values of Q and M confounded, 70 different killer whales were photo-identified in the study area for the period 1988-89, and 32 for the period 1998-2000. These values represent minimum abundance estimates. Photographic effort for 1964-2002 is illustrated in Fig. 2.

Opportunistic photographs were of significant importance in our study. For the two abundance analyses (periods 1988-89 and 1998-2000) and for the survival analysis (period 1977-2002), respectively 16.2%, 5.7% and 31.5% of the captures were opportunistic.

Estimation of the number of individuals frequenting the coast of Possession Island
For the period 1988-89, the estimated sample coverage was high ($\hat{C} = 0.76$) and the estimated heterogeneity in individual capture probabilities was low ($\hat{\gamma} = 0.24$). With $\hat{C} > 50\%$ and $\hat{\gamma} < 0.4$, Chao *et al.* (1992) recommend using Darroch's estimator (Darroch, 1958) for model M_t instead of their estimator for model M_{th} (it performs better with this level of heterogeneity). Thus, under model M_{th} and with Darroch's estimator, the estimated number of the well-marked individuals was $\hat{N} = 30$ (95%CI 25-42) for the period. After adjustment for $\hat{\theta}_{87-90} = 30.6\%$ (sample size: 49, SE 6.6%), the estimated total number of individuals was $\hat{N}' = 98$ (95% CI 53-156). If the number of photo-identified whales for the period is considered as the lower bound of the confidence

interval, the 95% CI can be crudely adjusted to [70, 156].

For the period 1998-2000, the estimated sample coverage was very high ($\hat{C} = 0.92$) and a high level of heterogeneity in individual capture probabilities was detected ($\hat{\gamma} = 0.43$). With >50% and $0.4 \leq \hat{\gamma} < 0.8$, Chao *et al.* (1992) recommend using their estimator for model M_{th}. Under these conditions, the estimated number of the well-marked individuals was $\hat{N} = 17$ (95% CI 16-28) for the period. After adjustment for $\hat{\theta}_{98-00} = 45.9\%$ (sample size: 98, SE 5.0%), the estimated total number of killer whales was $\hat{N}' = 37$ (95% CI 29-62). If the number of photo-identified whales for the period is considered as the lower bound of the confidence interval, the 95% CI can be crudely adjusted to [32, 62].

From these two abundance estimates, the corresponding geometric rate of increase of the population is $(37/98)^{1/10} = 0.907$. The associated standard error estimated with the Delta method (Oehlert, 1992) is 0.027, hence a 95% confidence interval (assuming a Normal distribution) of [0.854, 0.961].

Analysis of apparent survival and rate of increase of the population
The overall goodness-of-fit test did not detect any significant lack of fit to the CJS starting model [$\Phi_{t*s}\ p_{t*s}$] (see Table 4). However, most component tests for males could not be carried out due to sparse data. Possible violations of the model assumptions are discussed later. Table 5 summarises the details of the candidate CJS models fitted to the observed data. Starting from model 1, capture probabilities were constrained in models 2 to 6. Model 6 [$\Phi_{s*t}\ p_{effort}$] had the highest empirical support from the data with the lowest AIC_c to this point. Models 6 to 16 were pursued, constraining survival probabilities. Finally, having the lowest AIC_c, model 10 [$\Phi\ p_{effort}$] was designated as the most adequate model to the data. However models 9 [$\Phi_s\ p_{effort}$], 13 [$\Phi_{trend}\ p_{effort}$] and 16 [$\Phi_{poaching96}\ p_{effort}$] had also strong empirical support from the data, with ΔAIC_c-values < 2 (Burnham and Anderson, 2002). The evidence ratios of these models ranged from 1.3 to 2.2, indicating a likely high uncertainty on the selection of the best model. To account for this uncertainty, a weighted model averaging was performed over models 9, 10, 13 and 16 to obtain survival probability estimates that
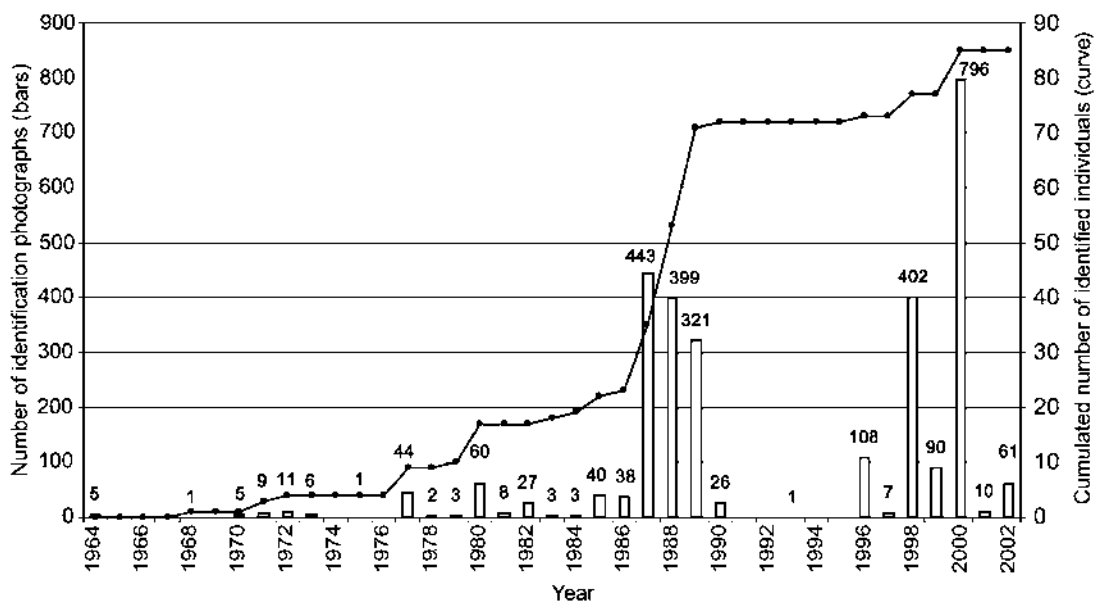

Fig. 2. Annual photographic effort (labelled histogram) and cumulative number of identified individuals ('discovery curve').

are unconditional to any model or sample. The estimated apparent survival probabilities decreased between 1977 and 2002, from 0.935 (95%CI 0.817-0.979) to 0.895 (95%CI 0.746-0.961) for males, and from 0.942 (95%CI 0.844-0.980) to 0.901 (95%CI 0.742-0.966) for females (Fig. 3).
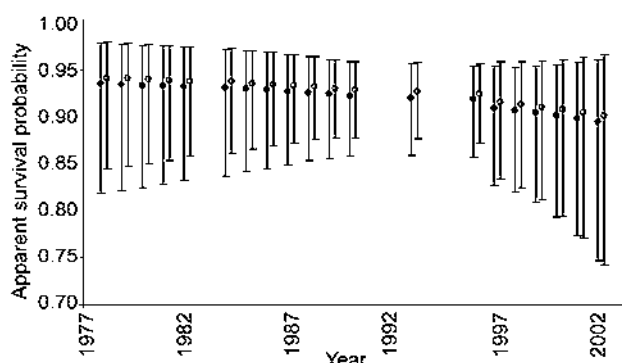

Fig. 3. Unconditional estimates of survival probabilities for male and female killer whales, obtained from a weighted model averaging procedure over the most adequate fitted models (error bars represent the 95% confidence intervals). ● = male; ○ = female.

Under the JS model framework, the goodness-of-fit test did not detect any significant lack of fit to the data for the starting model $[\Phi_t\, p_t\, \lambda_t]$ ($\chi^2_1 = 0.780$, $P = 0.377$). However, due to sparse data again, most component tests could not be carried out. Possible violations of the model assumptions are discussed later. For the most adequate models in the set of candidate models, most parameters were not estimable: the program *MARK* returned invalid estimates of Φ and λ (i.e. with standard errors tending to 0). The next most adequate model producing valid estimates was the model $[\Phi\, p_t\, \lambda]$. Under this model, Φ was constant and estimated at 0.894 (95% CI 0.835-0.934) for the period 1987-2000. The rate of increase (applying to the well-marked fraction of the population) was estimated 0.940 (95% CI 0.895-0.987) for this period.

DISCUSSION

Due to the sparseness of the data, the classical tests aiming at investigating the validity of the underlying assumptions could not be undertaken for the models used. Consequently, in the first part of this discussion, the possible violations and their consequences are reviewed.

Possible violations of the closure assumption while estimating abundance

Mortality, births, permanent migrations, temporary emigration and transience are the modalities of violation of the closure assumption.

Regarding mortality, had some deaths occurred during the assessment periods, they are expected to be rare since the sampling periods were short (1.75 and 2.75 years) relative to the life expectancy of an adult individual. Moreover, these hypothetical deaths would have occurred during the longest period, i.e. 1998-2000, which is the period with the lowest estimated survival.

Since the observed fecundity rate was extremely low (of the order of 0.02 neonates per year per killer whale over one-year old; Poncelet, unpublished), the recruitment of juveniles into the adult study population was probably negligible.

Since 1997, fishery controllers have been conducting a photo-identification programme on killer whales observed off the Crozet Islands and interacting with fishing vessels.

An analysis of over 1,600 opportunistic photographs taken in this area indicated that eight killer whales, initially identified along the coasts of Possession Island, temporarily joined other individuals offshore. In 2004, these eight whales were still occurring mainly in the coastal waters (Guinet, unpublished data). In addition, none of the easily identifiable individuals initially photo-identified offshore have ever been observed in the coastal waters of Possession Island. These facts highlight the existence of temporary emigrations out of the study area and support the hypothesis that permanent migrations and transience are non-existent or anecdotal in this coastal killer whale population. The social cohesion in this population of killer whales (Guinet, 1991) is another argument against permanent emigration. Temporary emigration episodes were most probably short relative to the time intervals (at least 2 months, Tables 1 and 2) separating capture occasions. It therefore seems reasonable to assume that temporary emigration movements can be considered as random for our sampling scheme.

Table 4

Results of the goodness-of-fit tests for the CJS starting model $[\Phi_{t*s}\, p_{t*s}]$.

Test	Chi-square value	*df*	*p*-value
Males			
TEST 2.*Ct*	-	-	-
TEST 2.*Cl*	0.000	1	1.000
TEST 3.*SR*	0.455	1	0.884
TEST 3.*Sm*	0.000	2	1.000
Females			
TEST 2.*Ct*	4.327	9	0.889
TEST 2.*Cl*	1.872	7	0.967
TEST 3.*SR*	1.162	4	0.844
TEST 3.*Sm*	0.000	4	1.000
Both sexes			
Overall test	7.816	28	1.000

Based on the above, the following violations may have occurred during the study: temporary emigration for both assessment periods, plus mortality for the period 1998-2000. Consequently, and also because the sample size was larger for the period 1988-1989, the abundance estimate for 1988-89 appears to be the most reliable.

According to Kendall (1999), whichever closed model is selected, temporary emigration with random movements result in accurate but less precise estimations. If mortality occurred during the study, then the estimates presented here would be upwardly biased.

Possible violations of the model assumptions while estimating survival

Selection of high quality photographs and well-marked individuals was undertaken to reduce the heterogeneity of capture probabilities generated by the photo-identification process. Nevertheless, some level of heterogeneity must persist due to the existence of opportunistic sightings in the samples and to the behavioural variability among individuals. The bias induced by such heterogeneity is negligible when capture probabilities are high enough (Carothers, 1973), and in this respect Buckland (1990) recommends to plan at least 10 capture occasions and to achieve a minimum capture probability of *ca.* 0.2. With 20 capture occasions and an average capture probability of 0.343 from the CJS survival analysis, the above recommendations have been met and thus the residual heterogeneity should not significantly bias survival estimates. With regards to the JS analysis, the

Table 5

Candidate Cormack-Jolly-Seber models for killer whales occurring in inshore waters of Possession Island from 1977 to 2002. ΔAIC_c indicate the AIC_c difference with the most parsimonious model, ER is the evidence ratios and NP indicates the number of parameters in each model.

No.	Model	AIC_c	ΔAIC_c	w_i	ER	NP	Deviance
Modelling capture probabilities							
1	$\Phi_{s*t}\, p_{s*t}$	967.328	723.353	0.000	-	74	124.292
2	$\Phi_{s*t}\, p_{s+t}$	487.201	243.226	0.000	-	57	136.636
3	$\Phi_{s*t}\, p_t$	475.874	231.899	0.000	-	56	139.380
4	$\Phi_{s*t}\, p_s$	406.120	162.145	0.000	-	40	219.712
5	$\Phi_{s*t}\, p$	403.175	159.200	0.000	-	39	223.081
6	$\Phi_{s*t}\, p_{effort}$	351.967	107.992	0.000	-	40	165.559
Modelling survival probabilities							
6	$\Phi_{s*t}\, p_{effort}$	351.967	107.992	0.000	-	40	165.559
7	$\Phi_{s+t}\, p_{effort}$	287.534	43.559	0.000	-	23	183.205
8	$\Phi_t\, p_{effort}$	280.674	36.700	0.000	-	21	183.380
9	$\Phi_s\, p_{effort}$	245.314	1.339	0.143	1.953	4	194.760
10	$\Phi\, p_{effort}$	243.975	0.000	0.280	1.000	3	195.608
11	$\Phi_{s*trend}\, p_{effort}$	247.783	3.808	0.042	6.711	6	192.700
12	$\Phi_{s+trend}\, p_{effort}$	246.058	2.084	0.099	2.834	5	193.267
13	$\Phi_{trend}\, p_{effort}$	244.424	0.449	0.224	1.251	4	193.870
14	$\Phi_{s*poaching96}\, p_{effort}$	248.670	4.695	0.027	10.457	6	193.587
15	$\Phi_{s+poaching96}\, p_{effort}$	247.038	3.063	0.060	4.626	5	194.246
16	$\Phi_{poaching96}\, p_{effort}$	245.571	1.596	0.126	2.222	4	195.017

number of capture occasions was only six, but the estimated capture probabilities were high (≥ 0.698) suggesting that survival estimates should not be substantially biased.

As stated previously, temporary emigration from the study site has been documented. Emigration episodes are believed to be short compared to the intervals between capture occasions, and temporary emigration movements can thus be considered as random for the sampling scheme. In this context, survival estimates are assumed to be unbiased (Burnham, 1993) although their precision is reduced. As also stated previously, transience is considered non-existent or anecdotal in the study population.

Effect of social grouping

Social grouping results in non-random associations of individuals that violate the (often implicit) assumption of independence of capture histories underlying mark-recapture models. Although this should not result in biased estimates, the precision may be overestimated in an extent depending on the fluidity of the associations and the proportion of the population captured at each sampling occasion (Anderson *et al.*, 1995; Wilson *et al.*, 1999).

Identity of the study animals

In addition to respecting the underlying assumptions of the models, it is imperative to clearly define the population under study (Cormack, 2001). The abundance analysis is based on observations conducted in the very inshore waters of Possession Island. Consequently, the estimates only describe what are referred to as 'Possession killer whales' hereafter. Considering the temporary emigration of Possession killer whales to offshore waters, an area that is predominantly exploited by individuals that have never been observed along the coasts of Possession Island, Possession killer whales must be regarded as as a fraction of a group of individuals whose home range is unknown.

The killer whale is widely distributed in the Indian Ocean (Leatherwood *et al.*, 1991), inhabiting the waters of Prince Edward, Kerguelen, Amsterdam and St-Paul Islands among others. In the north-eastern Pacific, two very distant populations in terms of phylogeny and behaviour live in sympatry (Barrett-Lennard, 2000). Such a segregation has not been suggested in the Indian Ocean yet. The high

mobility of the species, 2,400km (Matkin *et al.*, 1999) or perhaps even 4,000km (Visser, 1999), raises the question of which status should be granted to the individuals observed in Crozet Islands. No mixing with well known Marion Island individuals (Prince Edward Islands; Keith *et al.*, 2001), located a thousand kilometres away from Crozet Islands, has been documented as yet (Guinet, unpublished data). In addition, no type B or C individuals (Pitman and Ensor, 2003) have been observed in the Crozet Islands. If there is no gene flow between Crozet killer whales and other adjacent groups, they could be regarded as a distinct population.

A declining concentration?

The estimates of the number of Possession killer whales suggest a sharp decline of the order of 60% between 1988 and 2000, although the slight overlap in the confidence intervals does not entirely rule out the possibility of stable numbers. This decline was previously suggested by Guinet (1991) for the period 1987-1990. Other results also support the decline hypothesis; abundance estimates and the JS model yielded similar growth rates that are substantially lower than one for the period 1987-2000.

The abundance estimates are strongly bound to the estimates of the proportion of well-marked individuals in the population. Although many precautions were taken to estimate this proportion as precisely as possible with the available data, the sensible difference (about +15%) in this proportion between 1987-1990 and 1998-2000 could result from a difference in the implementation of the photo-ID protocol or be the consequence of the violent interactions between poachers and killer whales in the latter period.

The apparent survival estimated from the CJS models for well-marked individuals, which were mostly mature during the study according to their size, decreased approximately from 0.94 in 1977 to 0.90 in 2002 (it should be emphasised that the JS model produced consistent estimates for the period 1987-2000). When compared to other well-studied killer whale populations such as the so-called 'residents' of the coastal waters British Columbia and Washington State (which had survival rates of 0.961 and 0.989 in males and mature females respectively for the period 1973-87; Olesiuk *et al.*, 1990), the apparent survival rate of the Crozet

killer whales was strikingly low, both sexes having similar survival rates and undergoing a similar declining rate.

As stated previously, the social cohesion of Possession killer whale groups makes the dispersion hypothesis highly unlikely as an explanation for the decrease in their numbers, and supports the hypothesis of a high mortality. It is feared that these killer whales, which have developed a unique culture of hunting and social interactions transmitted to the young individuals by the most skilled females (Guinet and Bouvier, 1995) are disappearing. The scarcity of their prey in the region is a possible cause. The elephant seal population in the Crozet Islands declined by 70% from 1970 to 1990, falling to its lowest documented numbers until 1997 (Guinet *et al.*, 1999). The whaling industry exploited large-whale populations in the south-western Indian Ocean (among other areas) until 1979 (IWC, 1983) and again may have impacted the local killer whales by lowering the abundance of some of their prey species. In addition to these possible causes which would have long term consequences, more recently, Patagonian toothfish (*Dissostichus eleginoides*) poachers were a new immediate threat to killer whales. Witnesses reported that they use explosives to repel killer whales that come to the longlines to feed on the hooked fishes. As suggested in our modelling approach, these sometimes lethal interactions may increase the decline of Possession killer whales, some of which are known to take part in these interactions.

The population status of both Possession killer whales and Crozet killer whales are of concern. Unfortunately there are insufficient data regarding strictly offshore individuals to describe their demography and feeding ecology. Research is needed to investigate a potential segregation in the diet of inshore and offshore killer whales. In order to better understand the ecology of this top predator in the region, complementary observations throughout the archipelago, and if possible, from adjacent archipelagos, either by increased information from fishery controllers or by running a specific research programme, are needed. The use of satellite tags and activity recorders can yield important information about movements, feeding areas and prey types. Finally, collection of DNA samples from killer whales in the Indian and Antarctic Oceans would increase the understanding of their population biology and help to define priorities for the conservation of populations.

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REFERENCES

Anderson, D.R., White, G.C. and Burnham, K.P. 1995. Some specialized risk assessment methodologies for vertebrate populations. *Environmental and Ecological Statistics* 2(2): 91-115.

Barbraud, C. and Weimerskirch, H. 2001. Emperor penguins and climate change. *Nature 411*(6834): 183-86.

Barrett-Lennard, L.G. 2000. Population stucture and mating patterns of killer whales as revealed by DNA analysis. PhD thesis, University of British Columbia, Vancouver, BC. 97pp.

Bigg, M. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Rep. int. Whal. Commn* 32: 655-66.

Boyd, I.L., Wanless, S. and Camphuysen, C. 2006. *Top Predators in Marine Ecosystems: their role in monitoring and management*. Cambridge University Press, Cambridge, UK.

Buckland, S.T. 1990. Estimation of survival rates from sightings of individually identifiable whales. *Rep. int. Whal. Commn (special issue)* 12: 149-53.

Burnham, K.P. 1993. A theory for combined analysis of ring recovery and recapture data. pp.199-213. *In*: Lebreton, J.D. and North, P.M. (eds). *Marked Individuals in the Study of Bird Population*. Birkhäuser Verlag, Basel, Switzerland.

Burnham, K.P. and Anderson, D.R. 2002. *Model Selection and Multimodel Inference: a Practical Information-theoretic Approach*. 2nd ed. Springer-Verlag, New York. 488pp.

Carothers, A.D. 1973. The effects of unequal catchability on Jolly-Seber estimates. *Biometrics* 29: 79-100.

Chao, A., Lee, S.M. and Jeng, S.L. 1992. Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. *Biometrics* 48: 201-16.

Choquet, R., Reboulet, A.M., Pradel, R., Gimenez, O. and Lebreton, J.D. 2003. *U-CARE version 2.0 user's guide*. CEFE/CNRS, Montpellier.

Cormack, R.M. 1964. Estimates of the survival from the sightings of marked animals. *Biometrika* 51(3-4): 429-38.

Cormack, R.M. 2001. Population size estimation and capture-recapture methods. pp.11809-13. In: Smelser, N.J. and Baltes, P.B. (eds). *International Encyclopedia of the Social and Behavioural Sciences*. Elsevier.

Darroch, J.N. 1958. The multiple-recapture census. I: Estimation of a closed population. *Biometrika* 45: 343-59.

Guinet, C. 1991. L'Orque autour de l'archipel Crozet. Comparaison avec d'autres localités. *Rev. Ecol. Terre Vie* 46(4): 321-37. [In French].

Guinet, C. and Bouvier, J. 1995. Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Can. J. Zool.* 73(1): 27-33.

Guinet, C., Jouventin, P. and Weimerskirch, H. 1999. Recent population change of the southern elephant seal at Iles Crozet and Iles Kerguelen: the end of the decrease? *Antarct.* Sci. 11(2): 193-95.

Hammond, P.S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. *Rep. int. Whal. Commn (special issue)* 8: 253-82.

Hurvich, C.M. and Tsai, C.L. 1989. Regression and time series model selection in small samples. *Biometrika* 76: 297-307.

International Whaling Commission. 1983. Chairman's Report of the Thirty-Fourth Annual Meeting. *Rep. int. Whal. Commn* 33:20-42.

Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration - a stochastic model. *Biometrika* 52: 225-47.

Karanth, K.U. and Nichols, J.D. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79(8): 2852-62.

Keith, M., Bester, M.N., Bartlett, P.A. and Baker, D. 2001. Killer whales (*Orcinus orca*) at Marion Island, Southern Ocean. *African Zoology* 36(2): 163-75.

Kendall, W.L. 1999. Robustness of closed capture-recpature methods to violations of the closure assumption. *Ecology* 80(8): 2517-25.

Leatherwood, S., McDonald, D., Prematunga, W.P., Girton, P., Ilangakoon, A. and McBrearty, D. 1991. Records of the 'Blackfish' (killer, false killer, pilot, pygmy killer and melon-headed whales) in the Indian Ocean, 1772-1986. pp.33-65. In: Leatherwood, S. and Donovan, G.P. (eds). *Cetaceans and cetacean research in the Indian Ocean Sanctuary*. United Nations Environment Programme Marine Mammal Technical Report, Nairobi, Kenya. 287pp.

Lebreton, J.D., Burnham, K.P., Clobert, J. and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62(1): 67-118.

Lesquin, W. 1840. Voyage aux Iles Marion et Crozet. pp.125-85. *In*: Denis, F. (eds). *André le voyager, avec des notes nouvelles comprenant le naufrage aux Iles Crozet suivi du Brahme*. L'Editeur, Paris. [In French].

Lewison, R.L., Crowder, L.B., Read, A.J. and Freeman, S.A. 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol. Evol.* 19: 598-604.

Matkin, C.O., Ellis, G.M., Barrett-Lennard, L., Jurk, H., Scheel, D. and Saulitis, E.L. 1999. Comprehensive killer whale investigation, *Exxon Valdez* oil spill restoration annual project. pp.1-52. *Restoration Project 98012 Annual Report*. North Gulf Oceanic Society, Homer, AK.

Oehlert, G.W. 1992. A note of the Delta method. *Am. Stat.* 46(1): 27-29.

Olesiuk, P., Bigg, M.A. and Ellis, G.M. 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep. int. Whal. Commn (special issue)* 12: 209-43.

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

Pitman, R.L. and Ensor, P. 2003. Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *J. Cetacean Res. Manage.* 5(2): 131-39.

Pollock, K.P., Nichols, J.D., Brownie, C. and Hines, J.E. 1990. Statistical inference for capture-recapture experiments. *Wildl. Monogr.* 107: 1-97.

Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52: 703-09.

Seber, G.A.F. 1965. A note on multiple recapture census. *Biometrika* 52: 249-59.

Sergio, F., Newton, I. and Marchesi, L. 2005. Top predators and biodiversity. *Nature* 436(7048): 192.

Stanley, T.R. and Kenneth, P.B. 1999. A closure test for time-specific capture-recapture data. *Environmental and Ecological Statistics* 6(2): 197-209.

Visser, I.N. 1999. Antarctic orca in New Zealand waters? *NZ J. Mar. Freshwater Res.* 33: 515-20.

Voisin, J.F. 1976. On the behaviour of the killer whale, *Orcinus orca* (L.). *Norw. J. Zool.* 24: 69-71.

White, G.C. and Burnham, K.P. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46(Supplement): 120-38.

Whitehead, H., Gowans, S., Faucher, A. and McCarrey, S. 1997. Population analysis of northern bottlenose whales in the Gully, Nova Scotia. *Mar. Mammal Sci.* 13(2): 173-85.

Williams, B.K., Nichols, J.D. and Conroy, M.J. 2002. *Analysis and Management of Animal Populations*. Academic Press, San Diego, CA. 815pp.

Wilson, B., Hammond, P.S. and Thompson, P.M. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecol. Appl.* 9: 288-300.

Ylitalo, G.M., Matkin, C.O., Buzitis, J., Krahn, M.M., Jones, L.L., Rowles, T. and Stein, J.E. 2001. Influence of life-history parameters on organochlorine concentrations in free-ranging killer whales (*Orcinus orca*) from Prince William Sound, AK. *Sci. Total Environ.* 281: 183-203.