First demographic insights on historically harvested and poorly known male sperm whale populations off the Crozet and Kerguelen Islands (Southern Ocean)

GUILLEMETTE LABADIE,[1] PAUL TIXIER[2], CHRISTOPHE BARBRAUD, RÉMI FAY, Centre d'Etudes Biologiques de Chizé (CEBC), CNRS and Université de La Rochelle, UMR7372, France; NICOLAS GASCO, GUY DUHAMEL, Museum national d'histoire naturelle, Département des Milieux et Peuplements Aquatiques, CP 26, 43 rue Cuvier, Paris, 75005, France; CHRISTOPHE GUINET, Centre d'Etudes Biologiques de Chizé (CEBC), CNRS and Université de La Rochelle, UMR7372, France.

ABSTRACT

Age and sex dependent spatial segregation has resulted in limited knowledge of the ecology and demography of sperm whale adult males feeding seasonally in high latitudes. This study focused on adult males interacting with the Patagonian toothfish (*Dissostichus eleginoides*) fishery operating off the Kerguelen and Crozet Archipelagos. Demographic parameters were estimated using a 10-yr-long photoidentification data set paired with multistate closed robust design capture-markrecapture models. The examination of a set of 29,078 photographs taken from fishing vessels during sperm whale depredation events resulted in identification of 295 individuals with nine visiting both study areas. Dispersal between both study regions was estimated to be 1% per year. The mean annual number of interacting sperm whales was estimated to $n = 82$ (95% CI 58–141) in Crozet and $n = 106$ (95% CI 76–174) in Kerguelen. Transient proportions were 13% in Crozet and 26% in Kerguelen. Corrected for transience, apparent survival estimates were 0.953 (95% CI 0.890–0.993) in Crozet, and 0.911 (95% CI 0.804–0.986) in Kerguelen. These survival and population size estimates are the first for depredating adult males in high latitudes, and can be used in evaluating the current conservation status of this historically harvested stock and to investigate depredation trends in 35 both Crozet and Kerguelen Islands.

Key words: abundance, Antarctic, mark-recapture, multistate, robust design, sperm whale, *Physeter macrocephalus*.

Sperm whales (*Physeter macrocephalus*) are widely distributed across oceans of both hemispheres. Yet, sperm whales are amongst the cetacean species that were impacted the most historically by the whaling industry, especially in subpolar regions, where extensive whaling lasted until the early 1980s (Reeves and IUCN/SSC Cetacean Specialist Group 2003). In the Southern Ocean, 395,000 sperm whales were caught from 1904 to 1983, which likely contributed to the global decline of populations (Rice

[1]Corresponding author (e-mail: guillemette.labadie@gmail.com).
[2]Current address: School of Life and Environmental Sciences, Deakin University, 221 Burwood Highway, Burwood, Victoria, 3125, Australia

1989). The species is now classified as vulnerable on the IUCN's Red List (Taylor *et al.* 2008), but a number of populations remains as data deficient.

The distribution patterns of sperm whales vary with age and sex of individuals. While adult females and immatures are primarily found in tropical and subtropical regions all year round, adult males have larger latitudinal ranges encompassing sub-polar regions (Rice 1989). When maturing, males disperse from their natal group and may travel long distances to reach cold waters of high latitudes, which are used as primary feeding grounds. They seasonally return to warm waters for reproduction (Caldwell *et al.* 1966, Rice 1989). The movement patterns, between or within breeding and feeding grounds, as well as demographic characteristics of adult males after dispersing, remain poorly known. The spatial segregation between adult males and females has resulted in limited knowledge of the ecology of adult male sperm whales visiting the high latitudes due to the difficulty to implement long term monitoring in these regions. Given current knowledge, it is generally assumed that sperm whales in high latitudes areas are all males (Caldwell *et al.* 1966, Best 1979).

Adult male sperm whales have a different feeding ecology than females but also differ in social organization and geographical distribution. While females are known to form units that are highly stable over periods of years (Whitehead *et al.* 1991), adult males are solitary or in loose aggregations with other males when present on feeding grounds of high latitudes (Best 1979). In these regions, male sperm whales have a higher fish intake than females and immatures in waters of low latitudes, which feed primarily on squid (Kawakami 1980, Rice 1989). Also, males are involved in interactions with demersal longline fisheries operating in high latitude regions of both hemispheres (Yano and Dahlheim 1995, Secchi and Vaske 1998, Hill *et al.* 1999, Donoghue *et al.* 2002, Straley *et al.* 2015). First interactions with sperm whales were described by observers during the 1993/94 fishing season (SC-CAMLR 1994). An increase of sperm whale depredation (*i.e.*, whales feeding on fish that are hooked and captured by fishermen) was reported on various fisheries in different sub-polar regions, although it was very difficult to observe and quantify (Hucke-Gaete *et al.* 2004, Kock *et al.* 2006, Roche *et al.* 2007). Usually, direct depredation was not observed or in some cases, fish remains indicated that fish had been taken off the line (Purves *et al.* 2004). The main clue that observers relied on to identify depredation consisted of sperm whales observed diving next to the vessel during the time when the lines were being hauled. Depredation on sablefish (*Anoploma fimbria)* in the Northeastern Pacific (Sigler *et al.* 2008, Straley *et al.* 2015) and on Patagonian toothfish (*Dissostichus elegenoides)* in the Southern Ocean (Kock *et al.* 2006) were the most documented situations. Sperm whale depredation is often paired with killer whale (*Orcinus orca*) depredation in the same regions (Peterson *et al.* 2013). Previous studies have emphasized major socio-economic consequences caused by large amounts of fish taken by both species (Roche *et al.* 2007, Read 2008, Peterson and Carothers 2013). However, the impact of these interactions with fishing vessels on depredating adult male sperm whales remain poorly investigated due to the lack of long-term data sets. Impacts were only reported occasionally (*i.e.*, when there was lethal sperm whale entanglement in fishing gear) (Hamer *et al.* 2012, SC-CAMLR 2012).

In the Southern Ocean, adult male sperm whale depredation level on the Patagonian toothfish fishery, operating off Crozet and Kerguelen Archipelagos, are the highest of all other similar depredation situations of subantarctic waters (Guinet *et al.* 2014, SC-CAMLR 2014). Between 2005 and 2007, sperm whales were reported to depredate 57.6% and 33.6% of the longline sets that were hauled into the Crozet and Kerguelen Exclusive Economic Zones (EEZ), respectively (Roche *et al.* 2007). When

depredating, the mean number of sperm whales observed was 4.1 ± 3.4 (range 1–30) individuals in Crozet and 2.5 ± 1.8 (range 1–15) in Kerguelen. Sometimes, and especially when killer whales were present, sperm whales were observed associating with each other (Roche *et al.* 2007). The fishery started in the early 1990s and has undergone major illegal, unreported and unregulated fishing activity (IUU) until the early 2000s, leading to a significant decline of fish stocks (SC-CAMLR 1997). While IUU is known to have greatly impacted the local depredating killer whale population (Poncelet *et al.* 2010), impacts on depredating sperm whales are still unknown. These impacts may be even more significant since the Crozet and Kerguelen Archipelagos are among the last regions of the world where sperm whales were commercially exploited (1981, Headland 1989) and adult male sperm whales feeding in these waters are thought to be recovering from decades of whaling.

Patagonian toothfish fishing in Crozet and Kerguelen EEZ are subject to strict regulations under the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) jurisdiction. Currently, there are seven licensed fishing vessels operating within the French subantarctic EEZ. Each vessel has a fishery observer aboard who records all fishing operations and collects data for fish stock assessment. In addition, since 2005, fishery observers collect photo-identification data on sperm whales interacting with fishing vessels. In the two study areas, all sperm whales are thought to be male.

Using this 10-yr-long photo-identification data set, spanning 2005–2014, the aim of this study was to provide the first insight on demography and movement patterns of depredating adult male sperm whales in Crozet and Kerguelen waters. By applying capture-mark-recapture (CMR) methods to photo-identification data, the first objective was to estimate abundance and survival rates, two key parameters to assess the viability and the recovery of populations of long-lived species. These parameters are of primary importance to determine the conservation status of depredating populations and to evaluate the stock of depredating male sperm whales and their food consumption. The second objective was to investigate the movement patterns and long-term site fidelity of depredating individuals when foraging in high-latitude regions.

MATERIAL AND METHODS

Data Collection and Photo-identification

Observation and photo-identification data on sperm whales were collected by fishery observers from seven licensed Patagonian toothfish longliners. The data were collected between 1 January 2005 and 6 June 2014 in the Crozet and the Kerguelen EEZs during hauling of depredated longline sets. Depredated sets were identified when sperm whales were observed within a 500 m range of the vessel exhibiting typical depredation foraging behavior, *i.e.*, individuals remaining in the vicinity of the vessel during the entire hauling time and alternating between resting phases at the surface and long dives. Fishing vessels usually move several kilometers to reach the entire longline. Several long lines are generally set successively within a restricted area and are referred to as a fishing set. Therefore, a depredated fishing set represents our observation unit. Information on date, time, and position of longline sets were obtained from the PECHEKER database (Martin and Pruvost 2007) for each sperm whale observation. The fishing year, as defined by the government regulations and quotas for this fishery, spans from 1 September to 31 August. To ensure homogeneity

in the amount of data between years, we used fishing years instead of calendar years throughout the study. However, the amount of data can greatly vary within fishing years due to changes in fishing effort, which was measured by using the numbers of hooks set (Table 1) and the presence of vessels on fishing grounds, which depended on quota and catch rate. As a result, vessels may fish year round but will spend larger proportions of their fishing time in the Kerguelen EEZ due to larger quotas. In addition, an increase in the number of hooks set will have as a consequence an increase in the fishing time and an increase in the time spent for sperm whales observations. The fishery is closed in Kerguelen between 1 February and 15 March, and vessels usually move to the Crozet EEZ during this period.

Fishery observers were all equipped with DSLR cameras with minimum 300 mm lenses to capture pictures for photo-identification during hauls when sperm whales were present. Observers were all trained to focus their photographic effort on the tail flukes, which are visible when whales initiate a long dive.

Individual sperm whales can be reliably identified using marks on both ventral and dorsal surfaces of their tail flukes (Arnbom 1987). Previous studies have shown that these marks are conserved over years, allowing for correct re-identification of

Table 1. (a) Number of all sperm whale pictures taken, of usable pictures, of photographic identifications of individual sperm whales and identified animals, and the number of hook during the studies in Crozet (2005–2014) and Kerguelen (2007–2014). (b) Number of hook and the number of days of photographic effort for the restricted time and/or restricted area data set during the studies in Crozet (2005–2014) and Kerguelen (2007–2014).

	Full		Restricted time and/or restricted area	
	Crozet	Kerguelen	Crozet	Kerguelen
(a)				
Total of sperm whale representations	5,888	12,235	4,213	8,815
Usable sperm whales representations	3,117	5,187	2,448	4,325
Sightings	592	821	436	612
Number of different identified individuals	114	181	103	145
Hook	48,849,544	132,868,438	16,628,021	47,597,577

	Restricted time and/or restricted area			
	Crozet		Kerguelen	
Primary period	Hook	Photograph effort (d)	Hook	Photograph effort (d)
(b)				
1	2,182,267	7	7,994,589	40
2	1,544,764	14	8,042,016	40
3	1,919,616	9	8,058,353	48
4	3,174,259	26	8,534,048	38
5	2,663,443	23	7,349,404	32
6	2,295,698	21	7,619,167	22
7	1,542,199	14		
8	1,305,775	4		

individuals (Childerhouse *et al.* 1996). Other features like dorsal fin or knuckles along peduncle were not used for individual identification. Individual representation on photographs was assigned a quality index (Q) varying from 0 (unusable) to 3 (very good) depending on focus of pictures, and the distance and the angle between the photographer and the whale. If there were several individuals on a photograph, a quality index was assigned for each individual. Photographs in the group Q > 0 were often taken using burst mode, *i.e.*, series of pictures of one individual's tail taken successively during one dive sequence. In this case, only the best photograph of the series was recorded in the database. The best photographs were selected to identify individuals and then a unique alpha-numeric code was attributed to each newly identified sperm whale, which was then compiled in a reference photo-identification catalogue (Labadie *et al.* 2015). Each identified sperm whale was assigned a level of marking or M ranging from 0 (poorly marked) to 2 (well marked) based on size, shape, and number of notches on the tail flukes, as well as presence of other distinctive features such as holes. Following existing photo-identification methodology (Poncelet *et al.* 2010), we only used Q2 and Q3 representations to identify individuals whatever the level of marking. Changes and new marks overtime were monitored through exhaustive descriptions of tail flukes of each individual in a database. In the same database, all observations of identified sperm whales around Crozet and Kerguelen were recorded with details of sighting location and date, vessel identity, photographic equipment, and quality index (Q) of the individual representation on photographs. The two study areas (Kerguelen and Crozet) were divided into 4 zones equally sized within each area (A, B, C, D; Fig. 1). Sighting location allowed to link the observation with one of the four zones. An individual sighting was defined as when one given individual was identified for a given fishing set. If one individual was seen several times during the hauling time, only one photograph among sequence of photographs taken (*i.e.*, burst mode) was retained. Individual capture histories, *i.e.*, lists of first sighting and resightings, were constructed for each individual from photo-identification data. For each occasion, we represented an encounter with an individual by a "1, 2, 3, or 4" if the individual was encountered in zone A-B-C-D, respectively, and by "0" if the individual was not seen (because it died or was not encountered).

Modeling Abundance, Survival, and Site Fidelity at the Local Scale

Capture-mark-recapture analyses were used to estimate annual survival, annual abundance, and site fidelity at the local scale (*i.e.*, within the Kerguelen and Crozet regions) of sperm whales interacting with the fishery in Crozet and Kerguelen EEZs. As only nine individuals were sighted in both Crozet and Kerguelen during the study period, we ran demographic analyses separately for the two sites and modelled site fidelity and dispersal at the regional scale using a multistate model (*i.e.*, between Kerguelen and Crozet, see below). We referred to them as "populations."

Previous studies have shown that occurrence of adult male sperm whales in high latitudes regions may be seasonal (Best 1979, Rice 1989). To account for such variations, as well as within-year changes in fishing effort, and thus observation effort (Table 1), CMR analyses were performed using multistate closed robust design models (Pollock 1982; Kendall *et al.* 1995, 1997). Multistate closed robust design uses an open multistate CMR model combined with closed population models allowing for the estimation of survival, transitions between states and temporary emigration of individuals within the study population between primary sessions (Pollock 1982). Primary sessions were defined *a posteriori* so as to include the months with the highest
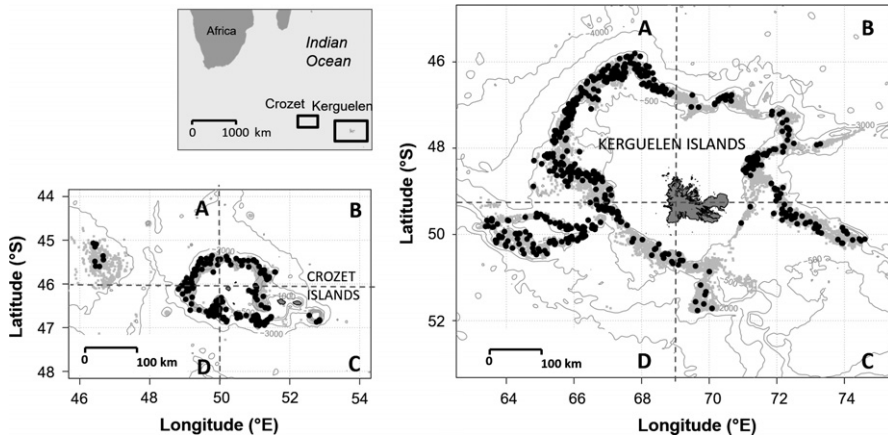
Figure 1. Distribution of adult male sperm whale sightings from fishing vessels in the Crozet (top) and Kerguelen EEZs. Black dots are the distribution of all longline sets that were depredated by sperm whales and for which photo-identification was performed. Gray dots represent the locations of all longline sets (fishing effort) that were hauled in the two areas between 2005 and 2014.

fishing and observation effort during each year (Appendix I, Fig. 1). For each fishing season, the primary period for Kerguelen was defined as spanning from 12 October to 31 January and from 31 December to 24 March in Crozet, corresponding to the period where most unique sightings were made. Each primary period was divided into approximately four secondary periods consisting, on average, of 1 mo, with the aim of having approximately the same number of observations in each. The number of secondary periods within primary period varied from two to five depending on the number of observations (Appendix I, Table 1). The two populations were assumed to be closed (Kendall *et al.* 1995, 1997) during these secondary periods. The closure assumption was tested using program CLOSETEST (Stanley and Burnham 1999).

To allow for between-year comparison of abundance estimates, bias due to variation in spatial sampling was minimized by restricting our data set only to fishing grounds on which fishing vessels operated every year during the study period. The Kerguelen EEZ was divided into $0.5° \times 0.5°$ spatial cells, and we only used cells in which at least one longline was set annually and in which photographic effort occurred every year from 2007 to 2014 (*i.e.*, 37 cells covering approximately 50% of the total fishing area; Fig. 1). In Crozet, data from 32 cells covering 100% of the study area were used in the analyses.

To model site fidelity at the local scale each study area (Kerguelen and Crozet) was divided into four equal zones (A, B, C, D; Fig. 1) and each sighting of an individual sperm whale during a primary period was assigned to the zone (*i.e.*, state) where it was observed. A supplementary zone (E) corresponding to the area located outside the study area was considered as a fifth zone to model temporary emigration from the study area. Individuals were allowed to transit between these five states between primary periods, but were only recorded if they are encountered in the study area (zones A, B, C, and D; Fig. 1). Individual encounter histories were coded according to the secondary and primary sampling periods and the zone where the individual was encountered. For example, the following capture history 110 300 indicated that the

individual was seen in zone A during the first two secondary sessions of the first primary session, was not seen during the third secondary session of the first primary session, and that the individual was seen in zone C during the first secondary session of the second primary session and was not seen during the second and third secondary sessions of the second primary session.

After space and time restrictions on the data, abundance analyses were performed using a subset of 1,048 animal sightings of 145 individuals in Kerguelen and 103 individuals in Crozet (Appendix I, Table 1). Using this restricted data set, we used the Huggins formulation of multistate closed robust design models (Huggins 1989, 1991). Parameters directly estimated by the model were:

S_i^r = probability that an individual in state r survives between primary session i–1 and i.

ψ_i^{rs} = probability that an individual is in state s at primary session i, given that the individual was in state r at primary session i–1 and that it survived until i. The sum of the transition probabilities equals 1. Therefore, the probability of remaining in a state between primary session i–1 and i is $\psi_i^{rr} = 1 - \sum_{r \neq s} \psi_i^{rs}$.

P_i^r = probability that an individual was sighted at the primary session i in state r, conditional on survival and presence within the study area.

C_i^r = probability that an individual was resighted at the primary session i in state r, conditional on survival and presence within the study area.

N_i^r = population abundance during primary session i in state r.

Population abundance (n) was conditioned out of the likelihood of Huggins models and was a derived parameter (Huggins 1989, 1991).

Many cetacean studies based on photo-identification data show that there are transients within monitored populations (Richter *et al.* 2003, Forestell *et al.* 2011). Transient individuals can be operationally defined as individuals having a zero probability of survival after their initial capture (Pradel *et al.* 1997). Therefore, the presence of transient animals invalidates the estimates of survival in capture-recapture models designed for the study of "residents" only. The term "resident" was used for individuals sighted during more than one year of the study period. Transience could reflect a real biological process with individuals passing through the study area or could reflect a statistical artifact when, for example, the study area is small compared to the area used by a population. We considered the latter situation to apply in our study case. To test for transient effects we rebuilt capture histories by pooling all secondary sessions within each primary session and used the program U-CARE (Choquet *et al.* 2005). When the presence of transients was detected, we took transience effects into account in the robust design models by modeling survival as a function of two age classes (Pradel *et al.* 1997). The first age class is the year of first marking and the second age class is all subsequent years.

Due to the limited size of the data sets, parameters S and ψ were constrained to be constant between years (*i.e.*, primary sessions), parameter S was constrained to be identical between states, parameters P and C were constrained to be constant within primary sessions but were year and state dependent. We then tested for variations of P and C between years and between states. Since individuals could not be observed in state 5 (*i.e.*, zone E outside the study area) parameters P and C were fixed to 0 for state 5. We also tested for variations of Ψ between states and for equality of the capture and recapture probabilities to identify potential trap-dependence.

Heterogeneity in the sighting and resighting probabilities may be expected in CMR studies due to inter individual differences in behavior. Due to the lack of data, the presence of heterogeneity was tested only once the best model structure on S, Ψ, P, and C was determined. Heterogeneity (π) in sighting and resighting probabilities was modeled using a finite mixture model to the best fitting model (Pledger 2000).

We then tested whether time variation in sighting and resighting probabilities could be explained by variations in observation effort from 2005 to 2014 for Crozet and from 2008 to 2014 for Kerguelen. Observation effort was estimated for each secondary period and each zone using the number of hooks set as an indication of fishing effort.

There is no goodness-of-fit test available for our initial multi-state closed robust design model. We thus assessed the fit of the fully time dependent closed robust design model using program RDSURVIV (Hines 1996) by modifying the predefined models in the program so as to expand the number of parameters. We assumed that if the fit of this model was good then a more complex multistate closed robust design model would also fit to the data. Program RDSURVIV computes a G test statistic and permits testing the fit of robust design models including time and behavioral effects, but not heterogeneity (Kendall *et al.* 1995). Goodness-of-fit tests were performed for Crozet and Kerguelen separately.

The following assumptions were made for the multi-state closed robust design model:

1 We considered that during the study period and within the study area we had a random sampling without concentrating effort in any particular area.
2 The population was assumed closed to immigration, emigration, births, and deaths for all years within primary periods.
3 All marks were correctly read and recorded on each sighting occasion.
4 Marks were not lost or neglected.
5 All individuals used the study area within the study period, but not necessarily every year (allowing for random temporary emigration).
6 Survival rate was assumed to be the same for all nontransient sperm whales in the population, regardless of availability for capture.
7 We considered no heterogeneity in capture probabilities over secondary periods.

By selecting only photographs where the identification was certain and by restricting photographs of higher and medium quality to minimize error related bias, assumptions (3) and (4) were considered to be fulfilled (Stevick *et al.* 2001).

Modeling Site Fidelity at the Regional Scale

Site fidelity was assessed at a large scale between the Crozet and Kerguelen areas which are 800 km apart. We used multisite capture-recapture analysis (Schwarz *et al.* 1993) to estimate individual site fidelity at an annual time step, controlling for both capture and survival probability. We considered two states corresponding to individuals observed at Kerguelen or at Crozet and individual capture histories were coded accordingly. Parameters directly estimated by the model were:

π_i^t = Probability to be in site i when first encountered at time t.
φ_i^t = Apparent survival probability between time t and $t+1$ for individuals in site i at time t.

ψ_{ij}^{t} = Conditional movement probability between site i at time t to j at time $t+1$ given that the individual survived to $t + 1$.
C_i^t = Resighting probability at time t for individual at site i.

To avoid over parameterization of the model, we constrained apparent survival to be constant over time. As observation effort differed between sites and years, we modeled site specific capture probabilities as a function of fishing effort, *i.e.*, the annual number of hooks within the 37 and 32 spatial cells in Kerguelen and Crozet respectively, as described above.

Assumptions 1, 3, 4, 5, and 6 previously described for the multistate closed robust design model were also made for the multistate model. Additionally, this model assumes that all individuals have the same transition probability between states and that all individual make the transition simultaneously. Goodness-of-fit (GOF) tests for multisite models were performed using program U-CARE 2.3.2 (Choquet *et al.* 2009*a*).

Model Selection and Parameter Estimation

Multistate closed robust design analyses were carried out with the program MARK (Kendall 2001) and multisite capture-recapture analysis with E-SURGE (Choquet *et al.* 2009*b*). Model selection was done using Akaike Information Criteria (Hurvich and Tsai 1989). When models had an ΔAICc < 2, they were considered to have equivalent support from the data (Burnham and Anderson 2002). The effect of fishing efforts (FE) on sighting and resighting probabilities was tested using ANODEV (Grosbois *et al.* 2008).

RESULTS

Data Summary

Between 1 January 2005 and 6 June 2014, a total of 33,596 longline sets were hauled, 8,070 sets in the Crozet EEZ and 25,526 sets in the Kerguelen EEZ. Sperm whales interacted with 4,284 sets in the Crozet EEZ and 9,597 sets in the Kerguelen EEZ, which represented 61.3% of the 6,990 sets and 42.3% of the 22,711 sets for which presence/absence data were available, respectively.

The examination of a set of 29,078 photographs taken when sperm whales interacted with vessels during hauling resulted in 18,123 sperm whale representations which were visually analyzed. Of these 9,819 were unusable for photo-identification using the flukes (quality <Q1) and 8,304 for which the flukes were visible with a quality >Q1 (Table 1). After selecting the best photographs from each picture sequence of the same individual, a total of 1,413 individual representations were recorded, 907 Q2 and 506 Q3. These representations, which were further referred to as sightings of identified individuals, were recorded for 874 longline sets that were depredated by sperm whales off the Crozet and Kerguelen EEZs (Fig. 1, Table 1). The number of sightings, and the number of sightings per unit of fishing effort (*i.e.*, 100 longline sets hauled) greatly varied between months (Appendix S1, Fig. 1a, b). The number of sightings per unit of fishing effort was the highest between October and March in the Kerguelen EEZ (maximum in January with = 30 ± 7 SE sightings/100 sets), and between December and February in the Crozet EEZ (maximum in February with = 19 ± 9 SE sightings/100 sets).

Table 2. Site-specific tests for population closure. Analyses were performed using program CloseTest (Stanley and Burnham 1999) separately for the secondary sampling periods within each primary period. *P*-values >0.05 indicate population closure.

Primary period	Closure test χ^2	df	P
Crozet			
1	—	—	—
2	0.45	1	0.50
3	—	—	—
4	0.98	3	0.80
5	0.98	1	0.32
6	6.7	2	0.04
7	2.16	2	0.34
8	—	—	—
Kerguelen			
1	2.66	4	0.62
2	18.31	4	<0.01
3	11.84	2	<0.01
4	10.53	6	0.10
5	0.82	3	0.84
6	0.58	2	0.75

A total of 295 depredating individual adult male sperm whales were identified during the study period, including 21 poorly marked (M0), 227 medium marked (M1) and 47 highly marked (M2) individuals. A total of 181 individuals were identified in the Kerguelen EEZ and 114 were identified in the Crozet EEZ. After restricting our data set only to fishing grounds on which fishing vessels operated every year during the study period, a total of 145 individuals were identified in the Kerguelen EEZ and 103 were identified in the Crozet EEZ (Table 1). The quality index of the sightings and the level of marking of each individual in the restricting data set are given in Table 2 in Appendix S2. The number of newly identified individuals per year (*i.e.*, discovery rate) suggested that a plateau was reached in recent years for the two locations (Fig. 2).

Individual capture histories showed that 5%, 9%, 60%, and 26% of depredating individuals (*n* = 297) were encountered in zone A, B, C and D, respectively, in Crozet, and 52%, 14%, 11%, and 23% of depredating individuals (*n* = 365) were encountered in zone A, B, C, and D, respectively, in Kerguelen. This cumulated number of depredating individuals was larger than the total number of individual for each study area because an individual could be seen, for example, in zone A for the first primary period, and then in zone C for the third primary period. This individual would be, thus, counted twice: once because the whale was encountered in zone A, and once in zone C. On 145 different individuals observed in Kerguelen, and 103 in Crozet, 45% were sighted in different zones in both areas.

Closure Tests

Closure tests suggested that during most primary sessions the populations in Crozet and Kerguelen could be considered as closed (Table 2). Results highlighted some additions to the population due to the presence of transients. For fishing seasons with
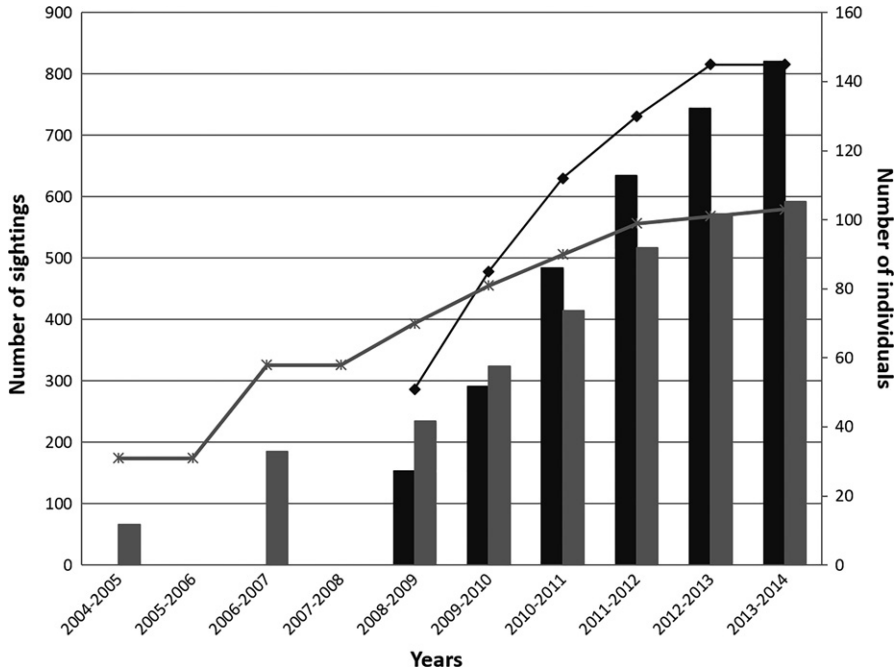
Figure 2. Cumulative number of sightings (bar) and cumulative number of identified individuals (line) per year in Kerguelen (black) and Crozet (gray) EEZs.

little data (2013 for Kerguelen; 2005 and 2009 for Crozet) preventing us from testing the population closure assumption, the latter was assumed.

Goodness-of-fit

The trap-dependence test did not show evidence for a behavioral response to capture for any of the primary period. The χ^2 statistics (Test 2.CT), indicated that the assumption of homogeneous capture was not violated (Crozet: $\chi^2 = 1.911$, df = 5, $P = 0.861$; Kerguelen: $\chi^2 = 2.582$, df = 3, $P = 0.461$).

Goodness-of-fit analyses indicated no lack of fit of the fully time dependent models including behavioral effects (Crozet: $G = 207.1$, df = 258, $P = 0.990$; Kerguelen: $G = 255.4$, df = 314, $P = 0.993$). The test for transience (TEST3.SR) was significant, indicating the presence of transients in Crozet (*P*-level of the χ^2 statistic = 0.001) and Kerguelen (*P*-level of the χ^2 statistic = 0.001).

Model Selection

At Crozet, capture and recapture probabilities varied between primary sessions, *i.e.*, were year dependent. However, there was no difference between capture and recapture probabilities (Table 3, model C1 *vs.* models C2, C8, C9, C10). Transition probabilities were entirely state dependent, and thus varied between pair of zones (Table 3, model C1 *vs.* models C7, C11). Presence of heterogeneity of capture was

not supported (model C1 *vs* models C2, C4, C6, C12). We found a significant positive effect of the fishing effort on capture probabilities (model C5; $\beta_{\text{fishery}} = 0.59$, 95% CI 0.23–0.941), which explained 30% of the time variation in capture probabilities.

At Kerguelen, capture and recapture probabilities varied between primary sessions and between each zone. Moreover, there was no difference between capture and recapture probabilities (Table 3, model K6 *vs.* models K7, K11, K12). Transition probabilities were partly state dependent and did not vary according to the arrival zone (Table 3, model K2 *vs.* models K6, K10). Presence of heterogeneity of capture was not supported (model K2 *vs.* models K3, K4, K5, K8). We found a significant positive effect ($\beta_{\text{photos}} = 0.30$, 95% CI 0.07–0.53) of the fishing effort on capture

Table 3. Selection of candidate multistate closed robust design models for estimating demographic parameters (apparent survival [S] of "resident" [a2] and transient [a1] individuals) of mature male sperm whales which were interacting with fishing vessels around Crozet and Kerguelen EEZs. Results of model selection include: number of mathematical parameters (k), the deviance (Dev), and Akaike Information Criterion value corrected for small sample size (AICc). The selected model is in bold. ψ_i^{rs} is the probability of an individual in state s (zone) in year i was in state r (zone) in year i-1. $\psi_i^{r.}$ indicates that transition probabilities were similar for all zones at time I, $\psi_i^{.s}$ indicates that transition probabilities were similar for all zones at time i-1, $\psi_i^{..}$ indicates that transition probabilities were similar for all zones. P is the probability of capture, C is the probability of recapture, π is the heterogeneity, and FE is the fishery effort.

Model	Robust design models	k	Dev	AICc	ΔAICc	AICc weight	ANODEV (F)	P
Crozet Archipelago								
C1	$S_{a1,a2}\psi_i^{rs}P_.^r=C_.^r$	31	1,623	1,692.8	0.0	0.92		
C2	$S_{a1,a2}\pi_.\psi_i^{rs}P_.^r=C_.^r$	33	1,623	1,697.8	5.0	0.08		
C3	$S_{a1,a2}\psi_i^{rs}P_.^r=C_i^r$	55	1,567	1,702.7	10.0	0.01		
C4	$S_{a1,a2}\pi_i\psi_i^{rs}P_.^r=C_.^r$	36	1,624	1,706.4	13.5	0.0		
C5	$\mathbf{S_{a1,a2}\psi_i^{rs}P_{FE}=C_{FE}}$	25	1,661	1,715.9	23.0	0.0	12.94	0.001
C6	$S_{a1,a2}\pi_.^r\psi_i^{rs}P_.^r=C_.^r$	40	1,623	1,716.1	23.2	0.0		
C7	$S_{a1,a2}\psi_i^{r.}P_.^r=C_.^r$	13	1,697	1,725.0	32.2	0.0		
C8	$S_{a1,a2}\psi_i^{rs}P_.^rC_i^r$	88	1,501	1,752.7	59.9	0.0		
C9	$S_{a1,a2}\psi_i^{rs}P_{..}=C_{..}$	24	1,701	1,754.0	61.1	0.0		
C10	$S_{a1,a2}\psi_i^{rs}P_{T,.}=C_{T,.}$	27	1,697	1,757.3	64.5	0.0		
C11	$S_{a1,a2}\psi_i^{..}P_.^r=C_.^.$	12	1,743	1,768.7	75.9	0.0		
C12	$S_{a1,a2}\pi_i^r\psi_i^{rs}P_.^r=C_.^r$	64	4,401	4,565.4	2,872.5			
Kerguelen Archipelago								
K1	$\mathbf{S_{a1,a2}\psi_i^{r.}P_{FE}=C_{FE}}$	14	2,093	2,121.8	0.0	0.88	9.42	0.005
K2	$S_{a1,a2}\psi_i^{r.}P_i^r=C_i^r$	32	2,056	2,126.1	4.2	0.11		
K3	$S_{a1,a2}\pi_.\psi_i^{r.}P_i^r=C_i^r$	34	2,056	2,130.9	9.1	0.0		
K4	$S_{a1,a2}\pi_i\psi_i^{r.}P_i^r=C_i^r$	37	2,056	2,138.3	16.4	0.0		
K5	$S_{a1,a2}\pi_i^r\psi_i^{r.}P_i^r=C_i^r$	39	2,056	2,143.2	21.4	0.0		
K6	$S_{a1,a2}\psi_i^{rs}P_i^r=C_i^r$	47	2,036	2,143.9	22.0	0.0		
K7	$S_{a1,a2}\psi_i^{rs}P_i^rC_i^r$	72	1,995	2,174.7	52.8	0.0		
K8	$S_{a1,a2}\pi_i^r\psi_i^{r.}P_i^r=C_i^r$	57	2,056	2,191.2	69.4	0.0		
K9	$S_{a1,a2}\psi_i^{rs}P_i^rC_i^r$	29	25,582	25,645.0	23,523.1	0.0		
K10	$S_{a1,a2}\psi_i^{..}P_i^r=C_i^r$	28	39,471	39,531.6	37,409.8	0.0		
K11	$S_{a1,a2}\psi_i^{rs}P_i^.=C_i^.$	24	39,483	39,534.3	37,412.4	0.0		
K12	$S_{a1,a2}\psi_i^{rs}P_i=C_i^.$	27	39,479	39,537.2	37,415.4	0.0		

probabilities (model K1), which explained 38% of the time variation in capture probabilities.

Estimates of Abundance, Survival, and Site Fidelity at the Local Scale

The estimated annual average number of interacting sperm whales was $n = 82$ (95% CI 58–141 in Crozet and $n = 106$ (95% CI 76–174) in Kerguelen. The robust design multistate model gave also the abundance for each stratum: $n = 35$ (95% CI 20–92) for zone A, $n = 44$ (95% CI 25–129) for zone B, $n = 379$ (95% CI 270–604) for zone C and $n = 162$ (95% CI 107–304) for zone D in Crozet. For Kerguelen, the abundance for each stratum was $n = 247$ (95% CI 190–3,630 for zone A, $n = 113$ (95% CI 75–206) for zone B, $n = 67$ (95% CI 44–142) for zone C, and $n = 157$ (95% CI 108–272) for zone D.

Model estimates of apparent survival for depredating nontransient male adult sperm whales were 0.953 (95% CI 0.890–0.993) in Crozet and 0.924 (95% CI 0.802–0.992) in Kerguelen (Table 4). For depredating transient sperm whales the survival rate was lower than for residents: 0.833 (95% CI 0.746–0.914) in Crozet and 0.660 (95% CI 0.534–0.769) in Kerguelen. Average monthly sighting and resighting probabilities were 0.145 (SE = 0.019) in Crozet for each stratum and 0.156 (SE = 0.006) in Kerguelen. For the later, capture probabilities varied between states: 0.210 (SE = 0.05) for zone A, 0.095 (SE = 0.05) for zone B, 0.182 (SE = 0.09) for zone C, and 0.138 (SE = 0.05) for zone D. Thus, average sighting probabilities during each primary session varied between 0.060 and 0.251 at Crozet and between 0.023 and 0.245 at Kerguelen.

For Crozet, transition probabilities between each zone varied from 0.02 (from zone C to zone A) to 0.61 (from zone D to zone C). The transition probability from outside the study area (zone E) to the study area (zones A, B, C, D) was $\Psi = 0.32$ (SE = 0.23), suggesting that sperm whales that temporarily emigrated from the study area during year i were more likely to remain outside in the following year. The site fidelity probability varied from 0.10 (SE = 0.08) in zone A to 0.63 (SE = 0.06) in zone C.

For Kerguelen, transition probabilities between each zone varied from 0.09 (from zone A to the other zones) to 0.20 (from zone C to the other zones). The transition probability from the area outside the study area to the study area was $\Psi = 0.29$ (SE = 0.17), suggesting that sperm whales that temporarily emigrated from the study area

Table 4. Parameter estimates from the selected multistate robust design capture-mark-recapture model to evaluate demographic parameters (apparent survival (S) of resident (a2) and transient (a1) individuals), transient proportion, and site fidelity of mature male sperm whales which were interacting with fishing vessels around Crozet and Kerguelen EEZs.

	Crozet	Kerguelen
S_{a2} (95% CI)	0.953 (0.890–0.993)	0.924 (0.802–0.992)
S_{a1} (95% CI)	0.833 (0.746–0.915)	0.660 (0.534–0.796)
Transient proportion	0.126	0.258
Site fidelity A-A	0.096 (0.008–0.288)	0.613 (0.452–0.753)
Site fidelity B-B	0.383 (0.119–0.673)	0.231 (0.059–0.488)
Site fidelity C-C	0.630 (0.511–0.739)	0.139 (0.018–0.368)
Site fidelity D-D	0.141 (0.044–0.278)	0.406 (0.192–0.634)
n (95% CI)	82 (58–141)	106 (76–174)

Note: n indicates the mean annual abundance.

during year i were more likely to remain outside in the following year. The site fidelity probability varied from 0.14 (SE = 0.09) in zone C to 0.61 (SE = 0.08) in zone A.

Site Fidelity at the Regional Scale

Goodness-of-fit tests indicated that the general multisite models fitted the data correctly (χ^2_{284}, $P = 0.12$). Results suggested that sperm whales showed high site fidelity at large scale (Table 5, M1 *vs.* M2, ΔAICc = 532) without difference between sites (Table 5, M2 *vs.* M3, ΔAICc = –2). Annual movement probability between the two archipelagos was estimated at only 0.01 (95% CI 0.007, 0.02) and archipelago fidelity was estimated at 0.99 (95% CI 0.976, 0.993).

<div align="center">DISCUSSION</div>

Demographic assessments on sperm whales have been primarily performed on populations inhabiting waters of low latitudes (Whitehead and Gordon 1986, Watkins *et al.* 1993). This study is among the first to provide survival and abundance estimates, as well as preliminary insights of movements of depredating adult male sperm whales on two major feeding grounds in the Southern Ocean based on long-term monitoring data sets. As sperm whale populations in the Southern Ocean have been historically intensively harvested, our findings have implications for conservation of this vulnerable species 35 yr after whaling ceased.

It should be noted that our results concern only a part of the whole male sperm whale population that had a specific behavior of depredating longlines. This study population represented an unknown proportion of the entire population of male sperm whales in high latitude.

Model Assumptions

Although some major assumptions of the models used were considered fulfilled, others were probably not (Appendix S2). The study was based on the assumption of random sampling but since the geographic coverage was not systematic; the sampling was probably not nonrandom. Indeed, sighting and resighting data were recorded from fishing vessels, which concentrated their effort in particular areas, and only

Table 5. Testing for site fidelity at large scale for Crozet and Kerguelen populations between 2005 and 2014. Results of model selection include: number of mathematical parameters (k), the deviance (Dev) and Akaike Information Criterion value corrected for small sample size (AICc). The selected model is in bold.

Model	Hypothesis tested	k	Dev	AICc
1	Individuals moved uniformly between site *i.e.*, $\psi^t_{ij} = \psi^t_{ii}$	7	3,128.6	3,142.4
2	**Individuals showed site fidelity *i.e.*,** $\psi^t_{ij} \neq \psi^t_{ii}$?	**8**	**2,594.3**	**2,610.5**
3	Individuals showed different degree of fidelity according to site *i.e.*, $\psi^t_{ij} \neq \psi^t_{ji} \neq \psi^t_{ii}$	9	2,594.3	2,612.5

sperm whales interacting with fishing vessels were detected. Therefore, our estimates only apply to these depredating individuals, which may be a subset of the whole population. As previous studies have shown that depredating individuals may be only a part of all individuals composing a population of odontocetes (Matkin *et al.* 2007, Tixier *et al.* 2010), such behavioral heterogeneity may also occur among sperm whales of the Crozet and Kerguelen waters. This is suggested by recent photographs of sperm whales taken from a nonfishing vessel around Kerguelen, which showed previously unknown individuals (GL, unpublished data). While we cannot rule out that the survival and transition probabilities from the nondepredating part of the population may differ from our estimates, such sampling bias may primarily result in abundance estimates of the population as a whole being underestimated. The proportion of nondepredating individuals, which could only be assessed through dedicated surveys, remains unknown and therefore could not be used to correct our estimates.

Importance of the Crozet and Kerguelen Areas

This study indicated a strong spatial segregation of adult male sperm whales between Crozet and Kerguelen. As the reproduction areas of the male sperm whales studied here are unknown and genetic data are lacking, whether these are two distinct populations remains unclear, although they were considered as such from a demographic point of view in our analyses. However, previous studies conducted in the North Pacific Ocean have suggested that adult male sperm whales may exhibit philopatry (*i.e.*, they return to the tropical/temperate region of their birth to mate) but share high latitude feeding grounds with males from other populations (Mesnick *et al.* 2011). While male sperm whales observed around Crozet and Kerguelen may include individuals from different populations, the spatial segregation of individuals between the two sites may only be a consequence of fidelity to preferred feeding grounds. This assumption is further supported by the observed long-term site fidelity of adult male sperm whales within Crozet and within Kerguelen, with multiple sightings of depredating individuals remaining in size-limited spatial ranges over periods of years. With nearly 70% of depredating individuals sighted during more than one year of the study period and identified as "residents" in demographic models, it is likely that some individuals return to these feeding areas over many years. Such fidelity may be primarily explained by high and predictable abundance of local resources, which was suggested as the main driver of adult male sperm whale movements and residency time in other high latitude areas (Jaquet *et al.* 2000, Mizroch and Rice 2013).

Both Crozet and Kerguelen clusters showed similar seasonality patterns with decreased sighting frequencies during winter months, which was assumed to be due to whales migrating at lower latitudes for reproduction purposes (Rice 1989, Sagnol *et al.* 2015). This finding has direct implications in the management of the sperm whale depredation issue. The number of interactions per month reached minimum values in fall and winter. Therefore, fishers should concentrate their fishing activity in winter months to minimize interaction rates and therefore decrease fish losses by depredating sperm whales.

Estimates of Abundance and Survival at the Local Scale

The total cumulated number of identified depredating individuals was larger than mean annual abundance estimates. This is expected since the total cumulated

numbers do not take into account mortality and permanent emigration, and the numbers estimated using the multistate closed robust design models are annual estimates. In addition, the abundance estimates produced in this study (106 depredating individuals for Kerguelen between 2008 and 2014 and 82 for Crozet between 2005 and 2014) may be influenced by temporary emigration/immigration effects. Our findings suggest that whales are not present every year in the study areas and that their return to the study areas may occur after more than 1 yr of absence. Given such a temporary emigration/immigration behavior, the duration of the study, and the unknown return time interval, the model may have underestimated the total number of depredating sperm whales.

Trends in depredating sperm whale abundance estimates could not be tested for between 2005 and 2014 for the Crozet area, nor between 2007 and 2014 for the Kerguelen area. Historical records for these two areas are lacking and the study periods may be too short to emphasize demographic trends using photo-identification data. It is likely that sperm whale populations of Crozet and Kerguelen underwent a period of recovery following the end of whaling in the early 1980s similar to the recovery reported for most of the cetacean populations historically harvested in the Southern Ocean (Gambell 1999, Christensen 2006, Lotze *et al.* 2011). Additional years of monitoring are needed to provide evidence with lower uncertainty around estimates of whether the studied populations are significantly increasing or decreasing.

Survival estimates were 0.924 for Kerguelen and 0.953 for Crozet for individuals qualified as residents in the analysis, thus lower than apparent survival estimates reported from female sperm whale populations in the Eastern Caribbean Sea (0.96, Whitehead and Gero 2014), but similar to those from the Scientific Committee of the International Whaling Commission (1982), which estimated an apparent survival for male sperm whales equal to 0.94. While sex and age variations of apparent survival of sperm whales may bring uncertainty to such comparison (Evans and Hindell 2004), our estimates for depredating adult male sperm whales are consistent with the expected survival rates of such a long-lived and slowly maturing species (Whitehead 2003). The apparent survival of adult male sperm whales may also be influenced by depredation levels of individuals. We assumed depredation had no effect on estimates. However, previous studies have shown that interactions with fisheries may substantially impact survival, both negatively and positively (Tixier 2012, Tixier *et al.* 2017). Negative impacts include incidental bycatch of sperm whales that became entangled in the fishing gear and subsequently drowned, which was reported on three occasions since 2003.[3] Also, sperm whales depredating on longlines in the late 1990s off the Crozet and Kerguelen may have suffered from lethal responses by IUU vessels using explosive firearms to repel the whales; this was found to be the case for the Crozet killer whales (Poncelet *et al.* 2010). Since the early 2000s IUU fishing has been negligible in the French EEZs, but we are unable to assess if depredation had a positive or negative effect on the demographic performances of sperm whales. The three mortality events associated with this demersal longline fishery over a 12 yr period are unlikely to have affected significantly the demographic parameters of that population. We expect depredation to have a positive (or no) influence on the demographic performances of sperm whales depredating the most with fisheries as an artificial food resource. Interacting sperm whales, which was

---

[3]Personal communication from Nicolas Gasco, Museum national d'histoire naturelle, Département des Milieux et Peuplements Aquatiques, CP 26, 43 rue Cuvier, Paris, 75005, France, February 2016.

also found in killer whales (Tixier *et al.* 2017), may benefit from interacting with the fishery as they are artificially fed. For instance, after IUU fishing stopped in the Crozet EEZ, both reproduction and survival rates were higher in killer whale groups interacting the most with Patagonian toothfish fisheries (Tixier *et al.* 2015, 2017). Recent depredation estimates indicated that sperm whales took at least 65 tons of Patagonian toothfish per year from fishing gear between 2003 and 2013 (Gasco *et al.* 2015). Such an income of highly calorific and easy-to-catch resources could be demographically beneficial for the whales. This assumption may be further tested in years to come using the results of this study and the photo-identification monitoring from fishing vessels to assess the influence of between-individual variation of interaction rates with fisheries on their survival probability.

Literature Cited

Arnbom, T. 1987. Individual identification of sperm whales. Report of the International Whaling Commission 37(20):1–204.

Best, P. B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. Pages 227–289 *in* H. E. Winn and B. L. Olla, eds. Behavior of marine animals. Springer US, New York, NY.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel inference: A Practical information-theoretic approach. Springer Science & Business Media, Berlin, Germany.

Caldwell, D. K., M. C. Caldwell and D. W. Rice. 1966. Behavior of the sperm whale, *Physeter catodon* L. Pages 677–717 *in* K. S. Norris, ed. Whales, dolphins, and porpoises. University of California Press, Berkeley, CA.

Childerhouse, S. J., S. M. Dawson and E. Slooten. 1996. Stability of fluke marks used in individual photoidentification of male sperm whales at Kaikoura, New Zealand. Marine Mammal Science 12:447–451.

Choquet, R., A. M. Reboulet, J. D. Lebreton, O. Gimenez and R. Pradel. 2005. U-CARE 2.2 user's manual (Utilities–CApture-REcapture). CEFE, Montpellier, France.

Choquet, R., J. D. Lebreton, O. Gimenez, A. M. Reboulet and R. Pradel. 2009*a*. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture–REcapture data. Ecography 32:1071–1074.

Choquet, R., L. Rouan and R. Pradel. 2009*b*. Program E-SURGE: A software application for fitting multievent models. Pages 845–865 *in* D. L. Thomson, E. G. Cooch and M. J. Conroy, eds. Modeling demographic processes in marked populations. Springer Science + Business Media, New York, NY.

Christensen, L. B. 2006. Marine mammal populations: Reconstructing historical abundances at the global scale. Fisheries Centre Research Reports 14(9), University of British Columbia, Vancouver, Canada.

Donoghue, M., R. Reeves and G. S. Stone, eds. 2002. Report of the Workshop on Interactions between Cetaceans and Longline Fisheries, Apia, Samoa. New England Aquarium Aquatic Forum Series Report 03-1.

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

Forestell, P. H., G. D. Kaufma and M. Caloupka. 2011. Long term trends in abundance of humpback whales in Hervey Bay, Australia. Journal of Cetacean Research and Management (Special Issue) 3:237–241.

Gambell, R. 1999. The International Whaling Commission and the contemporary whaling debate. Pages 179–198 *in* J. R. Twiss and R. R. Reeves, eds. Conservation and management of marine mammals. Smithsonian Institution Press, Washington, DC.

Gasco, N., P. Tixier, G. Duhamel and C. Guinet. 2015. Comparison of two methods to assess fish losses due to depredation by killer whales and sperm whales on demersal longlines. CCAMLR Science 22:1–14.

Grosbois, V., O. Gimenez, J. M. Gaillard, *et al*. 2008. Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews 83:357–399.

Guinet, C., P. Tixier, N. Gasco and G. Duhamel. 2014. Long-term studies of Crozet Island killer whales are fundamental to understanding the economic and demographic consequences of their depredation behaviour on the Patagonian toothfish fishery. ICES Journal of Marine Science 72:1587–1597.

Hamer, D. J., S. J. Childerhouse and N. J. Gales. 2012. Odontocete bycatch and depredation in longline fisheries: A review of available literature and of potential solutions. Marine Mammal Science 28:E345–E374.

Headland, R. K. 1989. Chronological list of Antarctic expeditions and related historical events. Cambridge University Press, Cambridge, U.K.

Hill, P. S., J. L. Laake and E. Mitchell. 1999. Results of a pilot program to document interactions between sperm whales and longline vessels in Alaska waters. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-108. 42 pp.

Hines, J. E. 1996. RDSURVIV user's manual. Biological Resources Division, USGS, Patuxent Wildlife Research Center, Laurel, MD.

Hucke-Gaete, R., C. A. Moreno and C. J. Arata. 2004. Operational interactions between cetaceans and the Patagonian toothfish (*Dissostichus eleginoides*) industrial fishery off southern Chile. CCAMLR Science 11:127–140.

Huggins, R. M. 1989. On the statistical analysis of capture experiments. Biometrika 76:133–140.

Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics 47:725–732.

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

International Whaling Commission. 1982. Report of the sub-committee on sperm whales. Report of the International Whaling Commission 32.

Jaquet, N., S. Dawson and E. Slooten. 2000. Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. Canadian Journal of Zoology 78:407–419.

Kawakami, T. 1980. A review of sperm whale food. Scientific Reports of the Whales Research Institute, Tokyo 32:199–218.

Kendall, W. L. 2001. The robust design for capture-recapture studies: Analysis using program MARK. Pages 357–360 *in* R. Field, R. J. Warren, H. Okanna and P. R. Sievert, eds. Wildlife, land, and people: Priorities for the 21st century. Proceedings of the Second International Wildlife Management Congress. The Wildlife Society, Bethesda, MD.

Kendall, W. L., K. H. Pollock and C. Brownie. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. Biometrics 51:293–308.

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

Kock, K. H., M. G. Purves and G. Duhamel. 2006. Interactions between cetacean and fisheries in the Southern Ocean. Polar Biology 29:379–388.

Labadie, G., P. Tixier, L. Trudelle, J. Vacquie Garcia, N. Gasco and C. Guinet. 2015. Sperm whales of the Crozet and Kerguelen islands - Photo-identification catalogue 2014.

Lotze, H. K., M. Coll, A. M. Magera, C. Ward-Paige and L. Airoldi. 2011. Recovery of marine animal populations and ecosystems. Trends in Ecology & Evolution 26:595–605.

Martin, A., and P. Pruvost. 2007. Pecheker, relational database for analysis and management of fisheries and related biological data from the French Southern Ocean fisheries monitoring scientific programs. Muséum National d'Histoire Naturelle, Paris, France.

Matkin, C. O., L. G. Barrett-Lennard, H. Yurk, D. Ellifrit and A. W. Trites. 2007. Ecotypic variation and predatory behavior among killer whales (*Orcinus orca*) off the eastern Aleutian Islands, Alaska. Fishery Bulletin 105:74–87.

Mesnick, S. L., B. L. Taylor, F. I. Archer, *et al.* 2011. Sperm whale population structure in the eastern and central North Pacific inferred by the use of single-nucleotide polymorphisms, microsatellites and mitochondrial DNA. Molecular Ecology Resources 11(s1):278–298.

Mizroch, S. A., and D. W. Rice. 2013. Ocean nomads: Distribution and movements of sperm whales in the North Pacific shown by whaling data and Discovery marks. Marine Mammal Science 29:E136–E165.

Peterson, M. J., and C. Carothers. 2013. Whale interactions with Alaskan sablefish and Pacific halibut fisheries: Surveying fishermen perception, changing fishing practices and mitigation. Marine Policy 42:315–324.

Peterson, M. J., F. Mueter, D. Hanselman, C. Lunsford, C. Matkin and H. Fearnbach. 2013. Killer whale (*Orcinus orca*) depredation effects on catch rates of six groundfish species: Implications for commercial longline fisheries in Alaska. ICES Journal of Marine Science 70:1220–1232.

Pledger, S. 2000. Unified maximum likelihood estimates for closed capture-recapture models using mixtures. Biometrics 56:434–442.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. The Journal of Wildlife Management 46:752–757.

Poncelet, E., C. Barbraud and C. Guinet. 2010. Population dynamics of killer whales in Crozet Archipelago, southern Indian Ocean: A mark recapture study from 1977 to 2002. Journal of Cetacean Research and Management 11:41–48.

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

Purves, M. G., D. J. Agnew, E. Balguerias, C. A. Moreno and B. Watkins. 2004. Killer whale (*Orcinus orca*) and sperm whale (*Physeter macrocephalus*) interactions with longline vessels in the Patagonian toothfish fishery at South Georgia, South Atlantic. CCAMLR Science 11:111–126.

Read, A. J. 2008. The looming crisis: Interactions between marine mammals and fisheries. Journal of Mammalogy 89:541–548.

Reeves, R. R., and IUCN/SSC Cetacean Specialist Group, eds. 2003. Dolphins, whales, and porpoises: 2002–2010 conservation action plan for the world's cetaceans. IUCN, Gland, Switzerland.

Rice, D. W. 1989. Sperm whales *Physeter macrocephalus* Linnaeus, 1758. Pages 177–233 *in* S. H. Ridgeway and R. Harrison, eds. Handbook of marine mammals. Volume 4. Academic Press, London, U.K.

Richter, C. F., S. Dawson and E. Slooten. 2003. Sperm whale watching off Kaikoura, New Zealand: Effects of current activities on surfacing and vocalisation patterns. Department of Conservation, Wellington, N.Z.

Roche, C., C. Guinet, N. Gasco and G. Duhamel. 2007. Marine mammals and demersal longline fishery interactions in Crozet and Kerguelen Exclusive Economic Zones: An assessment of depredation levels. CCAMLR Science 14:67–82.

Sagnol, O., C. Richter, F. Reitsma and L. Field. 2015. Estimating sperm whale (*Physeter macrocephalus*) daily abundance from a shore-based survey within the Kaikoura submarine canyon, New Zealand. New Zealand Journal of Marine and Freshwater Research 49:41–50.

SC-CAMLR. 1994. Report of the Working Group on Fish Stock Assessment. No. SC-CAMLR-XIII, Annex 4. CCAMLR, Hobart, Australia.

SC-CAMLR. 1997. Report of the Sixteenth Meeting of the Scientific Committee. No. SC-CAMLR XVI. CCAMLR, Hobart, Australia.

SC-CAMLR. 2012. Report of the thirty-first Meeting of the Scientific Committee. No. SC-CAMLR-XXXI. CCAMLR, Hobart, Australia.

SC-CAMLR. 2014. Report of the thirty-third Meeting of the Scientific Committee. No. SC-CAMLR-XXXIII.: CCAMLR, Hobart, Australia.

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

Secchi, E. R., and T. Vaske. 1998. Killer whale (Orcinus orca) sightings and depredation on tuna and swordfish longline catches in southern Brazil. Aquatic Mammals 24:117–122.

Sigler, M. F., C. R. Lunsford, J. M. Straley and J. B. Liddle. 2008. Sperm whale depredation of sablefish longline gear in the northeast Pacific Ocean. Marine Mammal Science 24:16–27.

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

Stevick, P. T., P. J. Palsboll, T. D. Smith, M. V. Bravington and P. S. Hammond. 2001. Errors in identification using natural markings: Rates, sources, and effects on capture recapture estimates of abundance. Canadian Journal of Fisheries and Aquatic Sciences 58:1861–1870.

Straley, J., V. O'Connell, J. Liddle, *et al.* 2015. Southeast Alaska Sperm Whale Avoidance Project (SEASWAP): A successful collaboration among scientists and industry to study depredation in Alaskan waters. ICES Journal of Marine Science 72:1598–1609.

Taylor, B. L., R. Baird, J. Barlow, *et al.* 2008. Physeter macrocephalus. The IUCN Red List of Threatened Species. IUCN, Gland, Switzerland.

Tixier, P. 2012. Depredation par les orques (*Orcinus orca*) et les cachalots (*Physeter macrocephalus*) sur les palangriers a la legine australe dans la zee de l'archipel de crozet [Killer whale (*Orcinus orca*) and sperm whale (*Physeter macrocephalus*) depredation on Patagonian toothfish longline fisheries operating in the Crozet Exclusive Economic Zone]. Ph.D. dissertation, Université d'Aix Marseille II, Marseille, France. 367 pp.

Tixier, P., N. Gasco, G. Duhamel, M. Viviant, M. Authier and C. Guinet. 2010. Interactions of Patagonian toothfish fisheries with killer and sperm whales in the Crozet Islands Exclusive Economic Zone: An assessment of depredation levels and insights on possible mitigation strategies. CCAMLR Science 17:179–195.

Tixier, P., M. Authier, N. Gasco and C. Guinet. 2015. Influence of artificial food provisioning from fisheries on killer whale reproductive output: Artificial food provisioning and killer whale reproduction. Animal Conservation 18(2):207–218.

Tixier, P., C. Barbraud, D. Pardo, N. Gasco, G. Duhamel and C. Guinet. 2017. Demographic consequences of fisheries interaction within a killer whale (*Orcinus orca*) population. Marine Biology 164:170.

Watkins, W. A., M. A. Daher, K. M. Fristrup, T. J. Howald, D. Sciara and G. Notarbartolo. 1993. Sperm whales tagged with transponders and tracked underwater by sonar. Marine Mammal Science 9:55–67.

Whitehead, H. 2003. Sperm whales: Social evolution in the ocean. University of Chicago Press, Chicago, IL.

Whitehead, H., and S. Gero. 2014. Using social structure to improve mortality estimates: An example with sperm whales. Methods in Ecology and Evolution 5:27–36.

Whitehead, H., and J. Gordon. 1986. Methods of obtaining data for assessing and modelling sperm whale populations which do not depend on catches. Reports of the International Whaling Commission (Special Issue 8):149–166.

Whitehead, H., S. Waters and T. Lyrholm. 1991. Social organization of female sperm whales and their offspring: Constant companions and casual acquaintances. Behavioral Ecology and Sociobiology 29:385–389.

Yano, K., and M. E. Dahlheim. 1995. Killer whale, *Orcinus orca*, depredation on longline catches of bottomfish in the southeastern Bering Sea and adjacent waters. Fishery Bulletin 93:355–372.

Supporting Information

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12469/suppinfo.

Appendix S1. Method.

Figure S1. (a) Mean number of sperm whale sightings per month. (b) Mean number of sperm whale sightings per 100 longline sets hauled per month in the Crozet EEZ (gray: averages over the 2005–2014 period) and in the Kerguelen EEZ (black: averaged over the 2007–2014 period). Error bars are the SE of the mean.

Figure S2. Map of Crozet (top) and Kerguelen (down) divided into four equally sized areas.

Figure S3. Large scale site fidelity with (a) number of identified individual sperm whales and sighted in the Crozet EEZ only, the Kerguelen EEZ only and sighted at least once in both sites; (b) details on the number of sightings per site for individuals sighted at least once in both sites during the study period.

Table S1. Total number of identified sperm whales during sample j (Cj), number of newly identified (Nj) and resighted (Rj) and cumulative number identified (M) interacting male sperm whales per fishing season for Crozet (Cro) and Kerguelen (Ker), 2004–2014.

Table S2. Number of individual selected in each distinctiveness level and number of sightings in each quality index and in Crozet (2005–2014) and Kerguelen (2007–2014) for the restricted time and/or restricted area data set.

Appendix S2. Model assumptions.