


# Demographic consequences of fisheries interaction within a killer whale (*Orcinus orca*) population

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**Abstract** Individual heterogeneity in foraging behavior has been widely documented within predator populations. In highly social apex predators such as killer whales (*Orcinus orca*), specialization may occur at the matriline level. A small population of killer whales has been documented to occur around the Crozet Islands. These whales feed on a wide range of prey items including seals, penguins and large whales, as well as depredate the local Patagonian toothfish (*Dissostichus eleginoides*) longline fishery. The level of interactions with fisheries varies greatly between matriline. Here, we present the results on the effects of such behavioral heterogeneity on the demographic trends of this killer whale population. We used photo-identification

data from 1977 to 2011 in a mark–recapture framework to test the effect of varying levels of fisheries interactions on adult survival. We documented significant differences in survival between depredating and non-depredating whales, resulting in divergent intra-population demographic trends. These differences showed low survival, and thus a negative effect, for depredating whales when illegal fishing occurred (poachers used lethal methods to deter killer whales from depredating longlines). After illegal fishing stopped (2003–2011), the survival rates of depredating individuals exceeded the survival rates of non-depredating individuals, suggesting a positive influence of “artificial food provisioning”. This effect was further supported by a higher population growth rate for depredating whales. This study highlights the potential demographic costs and benefits that cetaceans face from depredating fisheries and addresses the demographic consequences of both intra-population feeding specialization and the influence of anthropogenic changes in resource availability.

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## Introduction

The method in which individuals acquire food has a fundamental influence on their life-histories. Foraging efficiency, which is primarily influenced by resource availability, has been found to have major consequences on demographic parameters such as survival and reproduction (Hofbauer and Sigmund 1998; Turchin 2003). For instance, growth rates of predator populations have been shown to be positively correlated with prey availability in a number of taxa including birds and mammals (Leibold 1996). The significance of such a correlation may depend upon the level of specialization of the predator (e.g., O'Donoghue et al. 1997). Populations may be composed of individuals with

varying levels of specialization that are likely to respond differently to time–space heterogeneity of resource availability (Bolnick et al. 2003). Intra-population heterogeneity in feeding ecology has primarily been documented in species at the individual level (e.g., Rausher 1984; Wauters et al. 1992; Clark and Yoshimura 1993), but it may also occur at a social unit level in social species, often as a result of individuals within the same social unit having the same specialized feeding behavior (Whiten 2000; Ganas et al. 2004; Marcoux et al. 2007).

The relationship between prey availability and the demographic trends of predators has also been studied in anthropogenically impacted environments, especially those where resource availability has been modified (Fuller and Sievert 2001). In the marine environment, most studies emphasize the negative impact of fisheries on the marine environment, namely the resultant decrease in fish stocks and subsequent effects on the abundance, survival and reproduction of predator populations (Myers and Worm 2003; Branch et al. 2010; Tremblay-Boyer et al. 2011), but fisheries can also increase resource availability through artificial food provisioning. A large number of marine bird and mammal species have been shown to supplement their diet with discard and through depredation (i.e., removal of caught fish from fishing gear by non-targeted predator species) (Botsford et al. 1997). However, these interactions with fisheries also involve risks, such as entanglement in gear resulting in severe injury or death (Tuck et al. 2001; Lewison et al. 2004), or the use of lethal methods by fishers to eliminate animals that are competing for the same resource (Northridge 1991; Trites et al. 1997), that may exceed the benefits of the food provisioning (Northridge and Hoffman 1999).

Killer whales (*Orcinus orca*) are commonly involved in interactions with a number of fisheries, including pelagic longline fisheries harvesting tuna (tribe Thunnini) and swordfish (*Xiphias gladius*) in sub-tropical waters (Dalla Rosa and Secchi 2007), drop lines targeting blue fin tuna (*Thunnus thynnus*) in the Strait of Gibraltar (Guinet et al. 2007) and demersal longline fisheries targeting sablefish (*Anoplopoma fimbria*) or Patagonian toothfish (*Dissostichus eleginoides*) in the high latitudes of both hemispheres (Yano and Dahlheim 1995a; Purves et al. 2004; Matkin et al. 2007; Roche et al. 2007). In Alaska, the mortality observed in killer whale groups interacting with sablefish fisheries, as well as bullet wounds/scars found on individuals, have both provided evidence of the negative consequences of fisheries interactions (Matkin 1986; Dahlheim and Waite 1993; Yano and Dahlheim 1995b). Similarly, heavy poaching activity on Patagonian toothfish was reported within the French Exclusive Economic Zone (EEZ) of the Crozet islands between 1996 and 2002, and the severe injuring and/or killing of depredating killer whales likely led to an observed 60% decline of the

population (Poncellet et al. 2010). After 2002, illegal fishing was reduced to negligible levels by extensive deployment of French navy vessels within the EEZ to monitor fishery activity. Since then, only seven longline vessels are authorized to operate in the EEZ and the fishery is strictly regulated with observers onboard each vessel during every trip at sea. The end of illegal fishing operations halted the exposure of depredating killer whales to lethal interactions with fisherman and no killer whale entanglements have been observed by fisheries observers within the Crozet Island EEZ.

Data collected from longliners since 2003 showed that the Crozet killer whales exhibit a very high level of interaction with fisheries ( $42 \pm 14\%$  of longline sets on average, Tixier et al. 2010), nearly ten times higher than rates of depredation on Patagonian toothfish recorded in Chile and South Georgia (Hucke-Gaete et al. 2004). The overall biomass of depredated toothfish in Crozet was estimated to be  $116 \text{ t}\cdot\text{year}^{-1}$  between 2003 and 2008 (Tixier et al. 2010), providing a significant artificial food intake for whales in this small population (estimated at 85 individuals in 2011). From long-term observation and photo-identification data, individuals from the Crozet killer whales were described as socially organized into highly stable and long-lasting matriline (Guinet 1991, 1992). This social organization was later confirmed by substantial monitoring effort and repeated observations from 2003 to 2011, which indicated that matriline were composed of individuals that were constantly associated over time without any observed dispersion from their natal group (Tixier 2012). However, while all individuals from a same matriline show the same depredation behavior during fishery interaction events, there was a great deal of variability in the level of interaction with fisheries between the 25 recorded matriline in the population (Tixier et al. 2014), with some matriline depredating longlines at high levels, and others never observed depredating (Tixier et al. 2010). Individuals could be, therefore, categorized as either “depredating” or “non-depredating”. In addition to depredating Patagonian toothfish from fisheries, individuals from the Crozet killer whale population have been observed feeding on a number of prey items, ranging from southern elephant seals (*Mirounga leonina*) to large whales (e.g., minke, *Balaenoptera bonaerensis*), as well as king and gentoo penguins (*Aptenodytes patagonicus* and *Pygoscelis papua*) (Guinet 1992; Roche et al. 2007; Tixier et al. 2010). Analyses of between-individuals and between-matriline association patterns show that all killer whales in the Crozet population belong to a single social network (Supplementary Material 1). In addition, only 6% of the Crozet individuals have been photographically identified around adjacent archipelagos (i.e., Marion Island, ~800 km due west of the Crozet islands) despite extensive long-term monitoring effort (Reisinger et al.

2016), and recent genetic analyses indicated reproductive isolation between individuals of the two sites (R. Hoelzel, pers. comm.). Together, these results suggest that all 25 matriline belong to the same and isolated Crozet population, and rule out the possibility that depredating and non-depredating killer whales belong to two separated and non-interbreeding sympatric ecotypes as documented elsewhere (e.g., Ford et al. 1998). Thus, the heterogeneity in the level of depredation between members of a single population provides a unique opportunity to assess what effects these interactions may have on the demography of this small vulnerable killer whale population.

The main objective of this study was to investigate the effects of three contrasted periods of fishing activity (“pre-illegal fishing”: 1977–1995; “illegal fishing”: 1996–2002; “post-illegal fishing”: 2003–2011) on the survival rate of this killer whale population (1977–2011) and as a function of their level of interaction with fisheries. We hypothesized that the level of fisheries interactions should lead to divergent intra-population survival trends for individuals of the population. To address this question, we evaluated whether adult survival rates varied between individuals whether they belonged to depredating or non-depredating matriline. We also developed matrix population models to identify the respective demographic growth rates of the depredating and the non-depredating parts of the population to assess the viability of the Crozet killer whale population as a whole.

## Methods

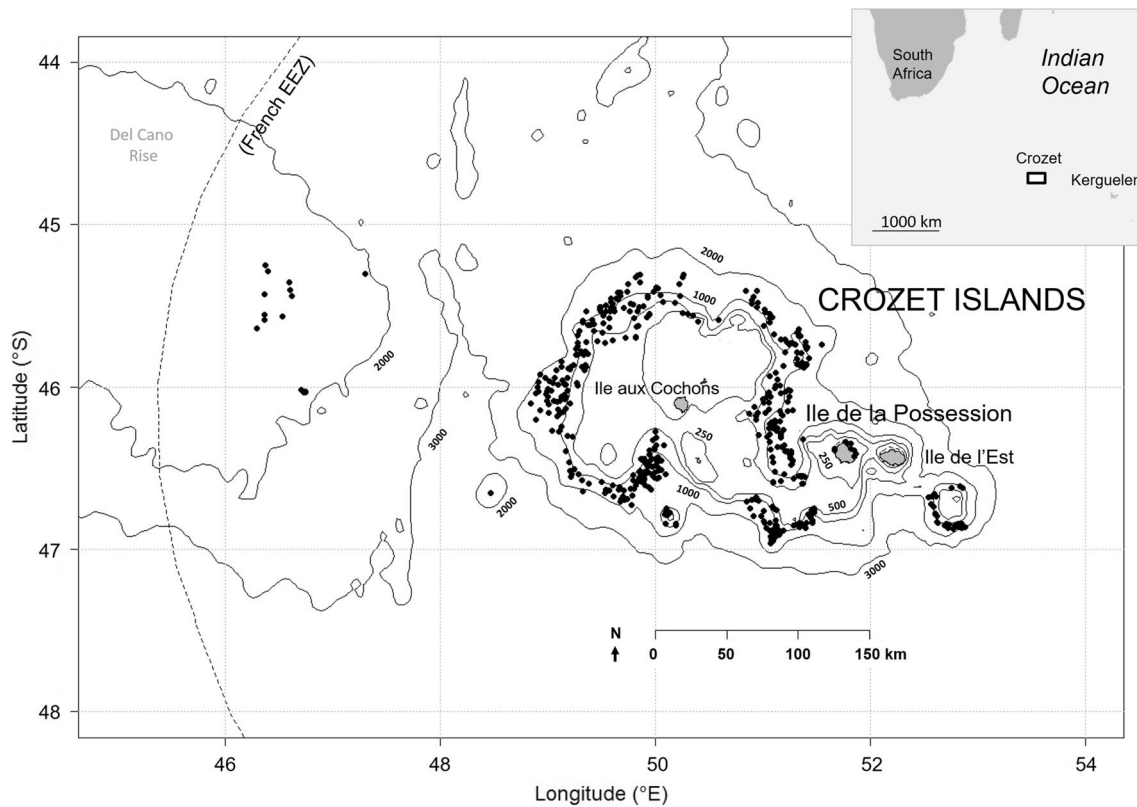
### Photo-identification and histories of capture

Killer whales can be individually identified by distinctive and long-lasting natural markings, and photographs of individuals can be used to construct sighting histories over several decades (e.g., Bigg et al. 1990; Parsons et al. 2009). Using this photo-identification approach, accessible populations of killer whales have been regularly monitored through direct photographic censuses to provide robust estimates of demographic parameters (Olesiuk et al. 2005). Between 1977 and 2011, photo-identification data of killer whales were collected by trained observers on longline vessels (from 1998 only) and by land-based field researchers on Possession Island (Crozet Archipelago—Fig. 1) using film and digital Single Lens Reflex cameras, with a minimum of 300 mm focal length. Effort from land was mostly opportunistic as dedicated surveys only occurred from 1988 to 1990, and 1998, 2000, 2009 and 2011. The highest annual total effort occurred in 2009, with 16,190 individual photo-identifications collected. There were a number of years with low effort, resulting in less than 20 individual

photo-identifications in 1978, 1979, 1981, 1983, 1984, 1991, 1992, 1994 and 1995.

The long-term capture histories of individuals obtained from photo-identification, paired with observation data and biological features of killer whales allowed us to assign sex and age class to all individuals used in the analyses. Age classes were assigned to individuals following Olesiuk et al. (2005), where individuals were considered to be adult if they were >10 years old for females and >18 years old for males. The sex of adult killer whales is primarily differentiated according to the presence of secondary sexual characteristics such as the development of the dorsal fin (Olesiuk et al. 2005; Kuningas et al. 2013). Other individuals were determined to be adult females when no morphological change occurred past the age of 10. Individuals with capture histories <10 years were determined to be females either because they were fully grown when first sighted and no morphological changes occurred throughout the following years, or because they gave birth to a calf during the study period. The calving event of a given female was recorded when the consistent close association of a calf with this female was repeatedly observed. The term “yearling” was used for age class including calves in the first year of life and “juvenile” included individuals estimated to be >1 year old but not mature yet. The date of birth of individuals, estimated from photo-identification data and from specific morphological features of yearlings and juveniles (i.e., body size, skin pigmentation) was primarily used to make such aging assignments. Adult females were also divided into two classes when possible: reproductive (between 10 and 45 years old) and post-reproductive (>45 years old) (Olesiuk et al. 2005). As the birth year was lacking for the latter, we classified as post-reproductive those females that were already adult when first sighted and with no recorded calving events for more than 12 years past the last calving event. Adult females that were first sighted after 1999 and for which no calving event was recorded until 2011 could not be assigned to one of these two classes and were, thus, excluded from analyses using the reproductive status of females.

Each photograph was assigned a grade on: (1) the level of marking (“M”) of the sighted individual, ranging from low (M0) to high (M2), based on the number and size of visible scars and notches on dorsal fin and saddle patch, and (2) the quality (“Q”) of the photographs, ranging from Q0 to Q2, based on image sharpness, and the distance and angle of the photographed. To limit bias due to possible errors of individual identification, the dataset was restricted to include only high quality photographs (Q2) of poorly marked individuals (M0), high (Q2) and medium (Q1) quality photographs of medium-marked individuals (M1) and all qualities (Q2–Q0) of well-marked (M2) individuals. The dataset was further restricted to only include



**Fig. 1** Map of the Crozet study area (with the Crozet EEZ western limit represented by a *dashed line*) showing all killer whale encounters where photo-identification data were collected (*black dots*) from

authorized longline vessels and Possession Island between 1977 and 2011. Encounters from longline vessels occurred on the fishing grounds at the edge of the oceanic shelf, at depths >500 m

individuals that were sighted during more than 1 year of the study as in our database; we considered that multiple sightings over periods of years were needed to formally identify new individuals with no error.

### Modelling adult apparent survival rate

A Capture–Mark–Recapture (CMR) model (Nichols 1992) was developed to estimate variations in survival probability while accounting for imperfect detection from the 35-year sighting histories of adult individuals only, which includes adult males, reproductive and post-reproductive females. We divided our dataset into two groups so that we could assess the effect of depredation: a group of individuals that belonged to matriline that have never been photographed from fishing vessels while depredating, therefore, qualified as non-depredating (ND), and a group of individuals that belonged to matriline that were photographed from fishing vessels and confirmed as depredating on longline sets on at least one occasion, therefore qualified as depredating (*D*). Depredation events were confirmed by the use of observation data from fishery observers, who are trained to distinguish between a true depredation behavior and whales

just travelling in the vicinity of vessels. Depredation is made clear by typical clues visible from the surface: whales are spread out within a 500 m range from the vessel during hauling fishing operations, they repeat long dives in the direction of the line being hauled by fishers and come back to the surface usually surrounded by birds, leaving visible fish oil slicks at the surface—Tixier et al. 2010). In our analyses, we also accounted for the sex of adult individuals. Sex may influence apparent survival estimates given the difference of life expectancy between males and females, which is a specific demographic feature of killer whales. Females have an extended post-reproductive lifespan and have a mean life expectancy that is significantly longer than males (estimated to 30–50 years for females and 20–30 years for males in the NE Pacific “resident” killer whale populations—Olesiuk et al. 2005). This may result in higher apparent survival for females and in a skewed sex ratio among the adult individuals of a killer whale population. We used a multistate CMR model, where survival probability ( $\Phi$ ) and detection probability ( $p$ ) were time ( $t$ ), sex ( $s$ ) and group ( $g$ ) dependent [ $\Phi_{s*t*g}$ ,  $p_{s*t*g}$ ] (Lebreton and Pradel 2002). Since re-sightings of individuals were made using two different sampling methods (observations

**Table 1** Validation of the assumptions involved in the capture–recapture framework used for the estimation of survival of killer whales at Crozet

Assumption	Bias in estimates	Validation	References
Mark recognition and no mark loss	Downwards	<ol style="list-style-type: none"> <li>(1) High, medium and low quality photographs used to identify well-marked individuals, high and medium quality photographs used to identify medium-marked individuals, high quality photographs used to identify poorly marked individuals</li> <li>(2) Several marks (scars and notches on dorsal fin, saddle patch) considered for individual identification</li> <li>(3) Regular sampling over multiple years permitted comprehensive monitoring of marked individuals</li> <li>(4) Only one experienced person was responsible for cataloging photographs ensuring consistency in the recognition of individuals and grading of photographs</li> </ol>	Nelson et al. (1980) Williams et al. (2002)
Instantaneous sampling	Upwards	<ol style="list-style-type: none"> <li>(1) Sampling occasions selected for analyses were relatively short (3–4 months) in comparison with the killer whales lifespan</li> <li>(2) Capture probabilities were relatively high (mean <math>\approx 0.50</math>)</li> </ol>	Carothers (1973) Williams et al. (2002)
Independence of the fate of individuals	None, precision overestimated	<ol style="list-style-type: none"> <li>(1) Fates of individuals are not independent. CMR models for taking into account non-independence are under development</li> </ol>	Lebreton et al. (1992) Williams et al. (2002)
Homogeneous capture and survival probabilities	Upwards or downwards	<ol style="list-style-type: none"> <li>(1) Goodness-of-fit tests indicated that the homogeneous assumption of capture probabilities was violated (<math>\chi^2 = 92.0</math>, <math>df = 57</math>, <math>P = 0.002</math>)</li> <li>(2) Goodness-of-fit tests indicated that the homogeneous assumption of survival probabilities was not violated (<math>\chi^2 = 14.6</math>, <math>df = 27</math>, <math>P = 0.974</math>)</li> <li>(3) Some heterogeneity in capture probabilities was explicitly taken into account into the model structure (sex, group, ...)</li> <li>(4) Survival probabilities remain unbiased even if the sampled population is heterogeneous with respect to recapture</li> <li>(5) Survival estimates are fairly robust to moderate heterogeneity in survival rates of the sampled population</li> </ol>	Pollock and Raveling (1982) Nichols et al. (1982) Williams et al. (2002)
No behavioral response to capture	Trapshy = downwards Traphappy = upwards	<ol style="list-style-type: none"> <li>(1) With photo-identification techniques animals are not physically captured or marked</li> <li>(2) Goodness-of-fit tests for trap dependence indicated trap happiness in behavior (<math>z = -3.71</math>, <math>P &lt; 0.001</math> for non-interacting individuals, <math>z = -2.26</math>, <math>P = 0.024</math> for interacting individuals)</li> <li>(3) Trap dependence was explicitly taken into account into the model structure</li> </ol>	Pradel (1993) Williams et al. (2002)
No permanent emigration	Downwards	<ol style="list-style-type: none"> <li>(1) Only 1 marked individual from Crozet was detected in another population monitored by photo-identification and was never re-observed at Crozet over the 116 marked individuals used in the analysis (0.9%)</li> <li>(2) Matriline membership was highly stable during the study period</li> </ol>	Lebreton et al. (1992) Williams et al. (2002)

**Table 1** (continued)

Assumption	Bias in estimates	Validation	References
No temporary emigration	Random = no bias Markovian = downwards or upwards	(1) Temporary emigration was assessed with a robust design and was random and small (0.012, see Supplementary Material 2) (2) Six marked individuals from Crozet were detected in other populations monitored by photo-identification and were re-observed at Crozet over the 116 marked individuals used in the analysis (5%) (3) Heterogeneity in capture probabilities was explicitly taken into account into the model structure	Lebreton et al. (1992) Kendall et al. (1997) Williams et al. (2002)

from land and observations from vessels), we used three states in the CMR model to account for heterogeneity in re-sighting methods: state 1 corresponded to individuals only observed from land during year  $t$ , state 2 corresponded to individuals only observed from longline vessels during year  $t$ , and state 3 corresponded to individuals observed from land and from longline vessels during year  $t$ . In CMR studies where individual captures and recaptures are made by photo-identification, it is often appropriate to model detection probability as a function of photographic effort (Gowans and Whitehead 2001; Poncelet et al. 2010). To account for variability in photographic effort between locations during the study period, we tested whether detection probability depended on the yearly photographic effort (effort) by building a model where capture probability was a function of the covariate effort depending on where observations were made and using an ANODEV (Grosbois et al. 2008).

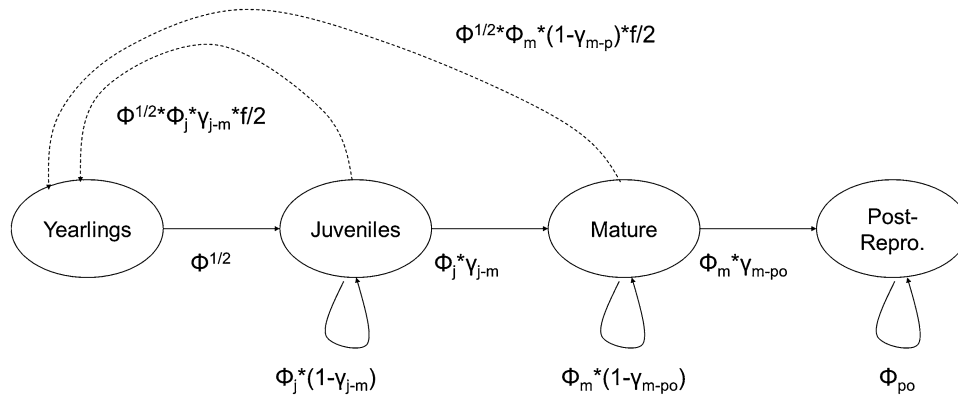
Once we identified the best model to assess detection probability (i.e., whether it was constant, time-, sex-, group- and effort-dependent), we modeled adult survival. First, we tested whether survival probability was constant ( $\cdot$ ), or whether it depended on time, sex, group or a combination of these. Our main goal was to evaluate the effect of depredation for three periods of varying fishery activity: “pre-illegal fishing” (1977–1995), “during illegal fishing” (1996–2002) and “post-illegal fishing” (2003–2011). For depredating whales, we developed a model where survival of a particular group was modeled as a function of these periods. For non-depredating whales, for which no direct interaction with the fishery has ever been observed, we only tested for a linear trend on a logit scale in survival using an ANODEV test.

Several assumptions are involved when using CMR models to estimate demographic parameters. The violation of these assumptions was evaluated using (1) information on the biology of killer whales, (2) detailed specificities of sampling and photo-identification data analysis, (3) goodness-of-fit tests, and (4) additional modeling using a robust

design CMR model (see Table 1 and Supplementary Material 2). Goodness of fit was tested with program U-CARE 2.3.2 (Choquet et al. 2009a) considering only two states (not re-sighted, re-sighted) since individuals did not change between observed states throughout their re-sighting histories. Although the model fitted the data ( $\chi^2 = 83.97$ ,  $df = 95$ ,  $P = 0.784$ ), we detected a positive trap-dependent effect using the specific component of the goodness-of-fit test in U-CARE ( $z = -2.336$ ,  $P = 0.019$  for depredating males and  $z = -2.659$ ,  $P = 0.008$  non depredating females), indicating that individuals were more likely to be re-sighted if they had been sighted on a previous occasion. We thus added a fourth state (not re-sighted), fixing the probabilities of re-sighting to 0 and 1 for the three other states (Gimenez et al. 2003), to run the multistate CMR model with trap dependence [ $\Phi_{s^*t^*g} p^*_{s^*t^*g} p_{s^*t^*g}$ ], where  $p^*$  represents the probability of re-sighting an individual in year  $t + 1$  given it was re-sighted in year  $t$ , and  $p$  represents the probability of re-sighting an individual in year  $t + 1$ , given it was not re-sighted in year  $t$ . A goodness-of-fit test of this model was provided by the three components Test3.SR, Test2.C1 and Test3.Sm. Program E-SURGE 1.9 was used to test the different candidate models and to test for covariate effects (Choquet et al. 2009b). Model selection was based on Akaike Information Criterion (AIC; Burnham and Anderson 2002).

### Modelling population dynamics

To describe the dynamics of females from depredating or non-depredating matriline, we used the life cycle and matrix model developed by Braut and Caswell (1993). We only used females in the analysis because data were too sparse for males (Poncelet et al. 2010). We focused this analysis on the 2003–2011 periods due to sparse data prior to 2003. All individuals that were sighted in at least 2 years of the study period and all previously described age classes were included. Each group was divided into the four biologically defined stages: (1) yearlings, (2) juveniles, (3) mature



**Fig. 2** Life-cycle graph for Crozet Killer whales representing transitions between life stages, where  $\Phi_j$ ,  $\Phi_y$ ,  $\Phi_m$ ,  $\Phi_{po}$ , are the annual survival probabilities for yearling (*y*), juveniles (*j*), reproductive females (*m*) and post-reproductive females (*po*), respectively,  $\gamma_{j-m}$  and  $\gamma_{m-po}$

are the transition probabilities between the juvenile and the mature female stages and between the reproductive female and the post-reproductive stages, respectively, and *f* is the mean calving rate of reproductive females

females (reproductive), and (4) post-reproductive females. A one stage-classified population projection matrix was parameterized following Brault and Caswell (1993) (Fig. 2).

A one stage-classified population projection matrix was parameterized for each group of killer whales (depredating, non-depredating). We used mean calving rates (*f*) of 0.195 (SE = 0.044) for depredating whales and 0.064 (SE = 0.028) calf.reproductive female<sup>-1</sup> year<sup>-1</sup> for non-depredating whales as estimated by Tixier et al. (2015) for the 2003–2012 period. The authors calculated the mean calving rate as the annual ratio of the number of recorded births to the number of reproductive females in each group that was encountered every year between 2003 and 2012 (*n* = 9 depredating females and *n* = 9 non-depredating females). The survival of mature females was estimated for each group from the CMR models described above and we assumed that the survival of mature and post-reproductive females was similar (data were too sparse to allow estimating survival for post-reproductive females). The sex ratio at birth is difficult to assess in the wild, so like Brault and Caswell (1993), we assumed it was even and divided *f* by two to obtain the theoretical number of female calves produced. To estimate yearling and juvenile survival, we developed Cormack-Jolly-Seber (CJS) models (Cormack 1964; Jolly 1965; Seber 1965) using the capture histories of individuals first observed as yearlings between 2003 and 2011 (again data were too sparse before 2003 to allow estimating yearling and juvenile survival). We modeled survival as a function of two age classes (1 and >2 years) (i.e., model [ $\Phi_{a2}$  *p<sub>i</sub>*] and tested for an effect of time on detection probability). From the selected model, we used the survival estimate for age 1 as the yearling survival ( $\Phi_j$ ) and the survival estimate from age 2 as the juvenile survival ( $\Phi_y$ ). Yearling and juvenile survival were not group specific, since the data were too sparse to estimate these

parameters for each group. Transition probabilities were chosen following Brault and Caswell (1993).

We developed stochastic matrix models to estimate the stochastic growth rate of each group. Environmental stochasticity was included for survival of yearling, juvenile, mature and post-reproductive females by sampling yearly values from a beta distribution with mean and process variance equal to those estimated from CMR models (Morris and Doak 2002). For calving rate, environmental stochasticity was included by sampling annual estimates from a log normal distribution with mean and standard deviation equal to those estimated from our reproductive data. The matrix population models were analyzed by Monte Carlo simulations (100,000 iterations) using the package “popbio” (Stubben and Milligan 2007) implemented in the program R 3.1.2 (R Development Core Team 2013). Demographic stochasticity was not implemented here for the sake of simplicity.

## Results

### Photo-identification effort and capture probabilities

A total of 51,318 individual photo-identifications were collected between 1977 and 2011 and resulted in 116 adult individuals that were included in analyses on survival as encountered during at least 2 years of the study period (Table 2). Three individuals (2.5% of all individuals) were removed because they were encountered only once during the study period.

Of these 116 adult killer whales, 34 (29.3%) were males and 82 (70.7%) were females. Ninety-seven individuals (83.6%) could be assigned to 21 matriline that were known to depredate at least once during the study period and 19 individuals (16.4%) could be assigned to 4

matrilines that had never been observed depredating and were only encountered from Possession Island (Tixier et al. 2014). Of the 97 whales known to depredate, 58 individuals (59.8%) were encountered from both land and longline vessels and 39 (40.2%) individuals were only encountered from longline vessels. The mean encounter rate during the study period (1977–2011) was  $7.0 \pm 4.4$  encounters individual<sup>-1</sup> year<sup>-1</sup>, but this encounter rate varied greatly between years due to variability in effort (Table 2).

Goodness-of-fit test of the model with trap dependence indicated no lack of fit ( $\chi^2 = 51.62$ ,  $df = 56$ ,  $P = 0.641$ ). Detection probabilities were best modeled as dependent on group, but not sex or time dependent (Table 3). For example, the detection probability of individuals previously observed from the coast (state 1) was  $0.460 \pm 0.040$  for the depredating group whereas it was  $0.647 \pm 0.036$  for the non-depredating group. However, we found a significant (ANODEV:  $F = 13.2$ ,  $df = 15,256$ ,  $P < 0.001$ ) positive effect of the photo-identification effort on detection probabilities (Table 3, Fig. 3a). Detection probabilities of killer whales when estimated as a function of the photographic effort were generally lower than 0.40 before 2003 and increased between 2003 and 2011 (Fig. 3b). This was likely the result of a switch from film to digital cameras and increased photo-identification effort from fishery observers aboard longline vessels. Dedicated surveys on Possession Island (1987–1989, 1998 and 2000) increased detection probabilities for the period before 2003 (Fig. 3b).

### Modelling apparent adult survival

We documented a declining trend of survival for non-depredating whales (Table 3). Their predicted survival probability from the best model decreased during the study period (slope =  $-2.128 \pm 0.575$ ) from a maximum of 0.999 (95% CI 0.994–0.999) in 1978 to a minimum of 0.747 (95% CI 0.547–0.878) in 2011 (Fig. 4). The survival of depredating killer whales was best modeled using two or three periods (respectively, models 13 and 11 in Table 3). Modeled averaged estimates indicated that survival was lowest during the illegal fishing period ( $0.920 \pm 0.011$ ), highest in the pre-fishing period ( $0.999 \pm 0.001$ ) and intermediate during the post-illegal fishing period ( $0.940 \pm 0.008$ ). Although female survival tended to be higher than male survival (difference in survival 0.009, 95% CI  $-0.019$  to 0.045), there was no significant sex effect on survival, which is likely due to the lack of statistical power of the relatively small sample size.

### Modelling population dynamics

Survival estimates for mature and post-reproductive females were estimated from the CMR models for the

period 2003–2011 and were  $0.946 \pm 0.012$  for depredating whales and  $0.863 \pm 0.0340$  for non-depredating whales (Table 4). There was no evidence for a time effect on detection probability for yearling and juvenile survival estimates. Yearling survival was  $0.8754 \pm 0.0738$  and juvenile survival was  $0.9601 \pm 0.0289$ .

The stochastic population growth rate was 1.0062 (95% confidence interval 1.0058–1.0067) for depredating whales and 0.9273 (95% CI 0.9269–0.9276) for non-depredating whales. The stable stage-specific proportions differed between groups, with more yearlings and post-reproductive females and fewer juveniles in the depredating group compared to the non-depredating group (Table 4).

## Discussion

This study demonstrates how behavioral heterogeneity in feeding behaviors within a population can influence the demographic trends of the population as a whole. We documented significant differences in apparent survival between depredating and non-depredating killer whales, with the most notable changes occurring after illegal fishing vessels started operating in the area. We also documented divergent growth rates of these two behaviorally distinct components of the population in recent years, emphasizing the importance of long-term individual-based monitoring of populations.

### Model assumptions

Most model assumptions were tested and fulfilled. When model assumptions were not fulfilled, we were generally able to modify the model structure to explicitly take into account lack of fit. For example, this was done to take into account trap dependence in detection probabilities. Residual heterogeneity in capture probabilities was not considered problematic since survival estimates remain unbiased even if the sampled population is heterogeneous with respect to recapture, and capture probabilities were reasonably high (Williams et al. 2002). We considered the assumption that no emigration (permanent and temporary) occurred during the study period to be valid given the negligible proportions of marked individuals from Crozet that were detected in other monitored adjacent populations, the highly stable matrilineal social structure of the Crozet killer whales (Guinet 1992; Tixier et al. 2014), and results from a robust design model (Supplementary Material 2). Only one assumption was clearly violated but could not be accounted for in CMR models: the independence of fate of the individuals does not hold for such a highly social animal occurring in groups. Currently, CMR models allowing



**Table 2** Capture-recapture summary statistics for the study period (1977–2011), where  $j$  is the sighting occasion number,  $C_j$  is the number of individuals sighted at occasion  $j$ ,  $R_j$  is the number of individuals re-sighted among  $C_j$ ,  $N_j$  is the number of newly sighted individuals during occasion  $j$ , and  $M_j$  is the cumulative number of marked individuals in the population at the end of occasion  $j$

$j$	Year	Effort (Nb individual photo-identifications)	$C_j$	$R_j$	$N_j$	$M_j$
1	1977	44	3	0	3	3
2	1978	2	1	1	0	3
3	1979	3	1	0	1	4
4	1980	60	5	1	4	8
5	1981	8	1	1	0	8
6	1982	87	1	1	0	8
7	1983	2	3	1	2	10
8	1984	3	1	0	1	11
9	1985	40	4	4	0	11
10	1986	38	2	2	0	11
11	1987	443	37	8	29	40
12	1988	399	50	40	10	50
13	1989	321	52	48	4	54
14	1990	126	36	36	0	54
15	1991	0	0	0	0	54
16	1992	0	0	0	0	54
17	1993	133	37	37	0	54
18	1994	0	0	0	0	54
19	1995	0	0	0	0	54
20	1996	108	23	23	0	54
21	1997	57	8	5	3	57
22	1998	483	39	35	4	61
23	1999	126	17	7	10	71
24	2000	818	24	24	0	71
25	2001	72	9	8	1	72
26	2002	61	11	11	0	72
27	2003	1696	39	25	14	86
28	2004	430	29	28	1	87
29	2005	3876	44	38	6	93
30	2006	1388	40	38	2	95
31	2007	4922	57	50	7	102
32	2008	3720	50	50	0	102
33	2009	16,190	65	55	10	112
34	2010	9220	57	53	4	116
35	2011	6294	55	55	0	116

Photo-identification effort (i.e., number of individual photo-identifications) is also provided

taking into account non-independence of fates are still under development. Simulation studies suggest that this was unlikely to cause bias in survival estimates, but that precision was likely overestimated (Lebreton et al. 1992, Williams et al. 2002). A bootstrap approach in MARK (White and Burnham 1999) allowed assessing a  $\hat{c}$  of 1.213 (computed by dividing the deviance of the original dataset by the mean of 100 deviances from the simulated datasets), indicating that standard errors of parameters estimates should be at least multiplied by 1.101 (i.e.  $\sqrt{\hat{c}}$ , Lebreton et al. 1992).

### Demographic impacts of depredation

Prior to the start of illegal fishing in the Crozet study area in 1996, survival estimates for all adult killer whales were high ( $\Phi > 0.98$ ) and comparable to those of stable fish-eating killer whale populations in northern British Columbia and Norway ( $\Phi > 0.98$  and 0.97, respectively; Olesiuk et al. 1990; Kuningas et al. 2013). However, when the illegal Patagonian toothfish longline fisheries started in 1996, killer whales that were known depredating experienced increased mortality, with survival dropping to a minimum

**Table 3** Modelling detection ( $p$ ) and survival ( $\Phi$ ) probabilities of adult Crozet killer whales from 1977 to 2011

Model #	Model on $\Phi$	Model on $p$	Dev	$np$	AIC	$\Delta$ AIC	$F$ test	$P$	$R^2$
1	$s^*g^*t$	$s^*g^*t$	1430.3	1771	4972.3	2625.3			
2	$s^*g^*t$	$g^*t$	1508.1	955	3418.1	1071.1			
3	$s^*g^*t$	$g$	2648.9	163	2974.9	627.9			
4	$s^*g^*t$	.	2727.6	151	3029.6	682.6			
5	$s^*g^*t$	$g^*$ effort	2151.4	187	2525.4	178.4	13.2	<0.001	43.6
6	$g^*t$	$g^*$ effort	2174.9	119	2412.9	65.9			
7	$g$	$g^*$ effort	2292.6	53	2398.6	51.6			
8	.	$g^*$ effort	2292.6	52	2396.6	49.6			
9	ND <sub>(lin)</sub> $D_{(t)}$	$g^*$ effort	2195.7	87	2369.7	22.7	17.9	<0.001	49.5
10	ND $D_{(t)}$	$g^*$ effort	2216.1	86	2388.1	41.1			
11	<b>ND<sub>(lin)</sub> <math>D_{(T1,2,3)}</math></b>	<b><math>g^*</math>effort</b>	<b>2235</b>	<b>56</b>	<b>2347</b>	<b>0</b>			
12	ND <sub>(lin)</sub> $D_{(T1 = T2,3)}$	$g^*$ effort	2267.8	55	2377.8	30.8			
13	<b>ND<sub>(lin)</sub> <math>D_{(T1, T2 = T3)}</math></b>	<b><math>g^*</math>effort</b>	<b>2237.3</b>	<b>55</b>	<b>2347.3</b>	<b>0.3</b>			

Detection probability was first estimated using models 1–5 (Model on  $p$ ). The models presented here include constant (.), time dependent ( $t$ ), sex dependent ( $s$ ), group dependent ( $g$ ) effect (\* denotes interactions). The photographic effort (effort) was also tested as a co-variate on  $p$ . Survival probability was estimated using models 6–13 (Model on  $\Phi$ ). For each model the deviance (Dev), rank, AIC and  $\Delta$ AIC are given. For models with covariates ANODEV tests ( $F$  test and  $P$  value) and the proportion of variance ( $\times 100$ ) explained by the covariate ( $R^2$ ) are indicated

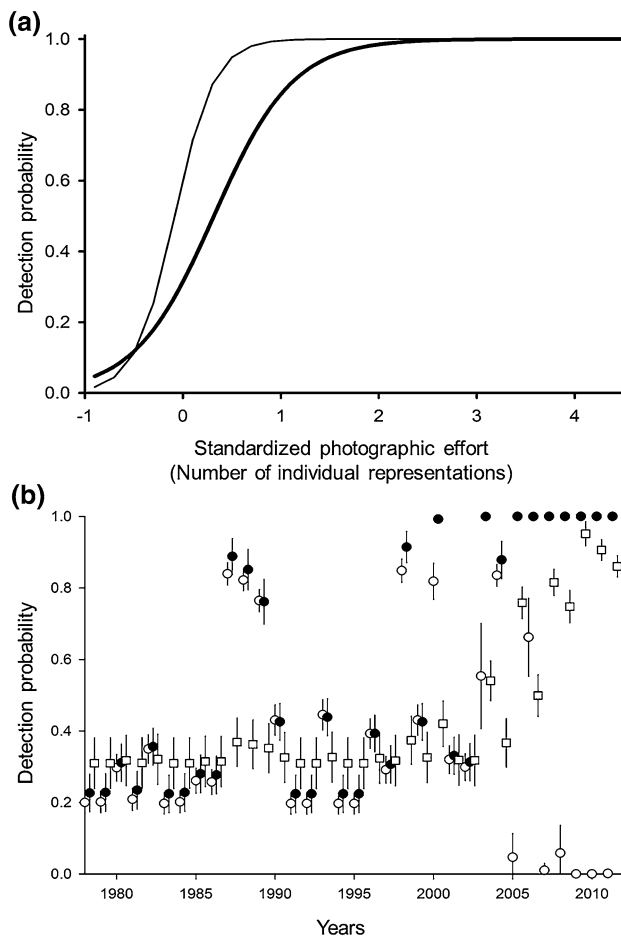
ND non-depredating group,  $D$  depredating group, *lin* linear trend,  $T$  time period (1 = 1977–1995, 2 = 1996–2002, 3 = 2003–2011)

Among models testing for the level of depredation of individuals ( $D$  and ND) and for the three time periods ( $T$ ), the best model with lowest AIC is highlighted (bold)

when illegal fishing was likely operating at its maximum. Such a marked drop in survival estimates for a long-lived species like killer whales provides support for the hypothesis of lethal interactions with illegal Patagonian toothfish fisheries, as postulated by Poncelet et al. (2010). Between 1996 and 2002, illegal fishing vessels caught an estimated toothfish biomass of 26,073  $t$ , with 11,760  $t$  for year 1997 alone (Pruvost et al. 2015), which is 16 times greater than the annual quota set for the seven licensed longliners in 2011. These estimates indicate a substantial magnitude of illegal fishing during the 1996–2002 period, during which illegal vessels operated without a fishery observer onboard, were not subject to regulation, and likely used a number of lethal tactics to repel the depredating whales. Testimonies (albeit few) from fishermen that worked on these vessels, acknowledge the use of both firearms and explosives on killer whales. Similar tactics were documented in Alaska in the 1980s and in the 1990s (Matkin 1986; Dahlheim and Waite 1993), and it is likely that a large number of depredating whales were severely injured or killed during that period. Poncelet et al. (2010) documented a 60% decline in the abundance of killer whales in the Crozet study between 1990 and 2000. No permanent emigration of individuals has been detected (Table 1), and matriline membership was highly stable during the study period, so it is unlikely that dispersal contributed to the documented decline. Therefore, we suggest that the

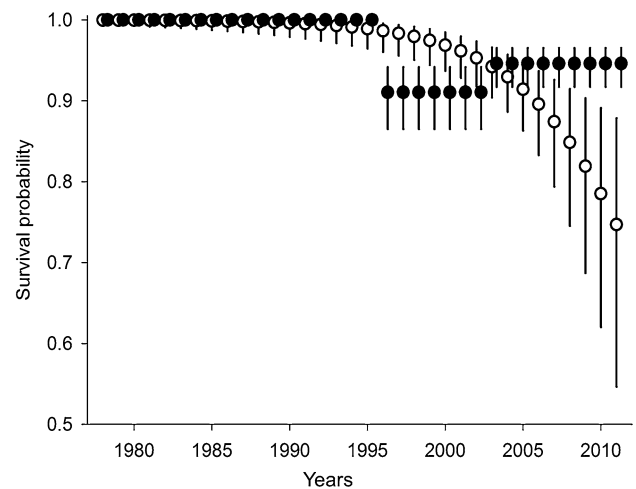
survival trends detected here are the consequence of the death of individuals within matriline.

There have been no reports of killer whales being accidentally caught on hooks or entangled in longlines, indicating that direct negative consequences of depredation on controlled vessels have been limited since 2003. During the post-illegal fishing period, we documented a higher rate of survival for depredating killer whales compared to non-depredating whales, likely a result of individuals benefiting from the food provisioned by longline fisheries and supporting the “artificial food provisioning” hypothesis (Esteban et al. 2016a). This is further supported by results showing that Crozet killer whale fecundity was higher in depredating whales compared to non-depredating whales (Tixier et al. 2015). Tixier et al. (2010) estimated that killer whales would remove about 116  $t$  of toothfish from longlines every year. Such increased availability of a highly energetic resource, although occurring for a small part of the year (e.g., the highest incidence of depredation by a matriline was 37 days in 2012), is likely to have a great impact on demography, as expected through the underlying processes of dependence between prey availability and predator population dynamics. For example, reproduction of the NE Pacific fish-eating killer whales was highly sensitive to between-year variations of prey availability, with significant increase of fecundity the year following high salmon abundance (Ford et al. 2009; Ward et al. 2009).



**Fig. 3** Detection probability: **a** as a function of photographic effort (*thick line*: depredated individuals, *thin line*: non-depredated individuals), and **b** as a function of year (*open circles*: individuals from the depredated group observed from the coast, *filled circles*: individuals from the non-depredated group observed from the coast, *open squares*: individuals from the depredated group observed from vessels). *Error bars* represent  $\pm$ SE of model parameters estimates

For non-depredated whales, we documented a long-term declining trend in survival (0.985 in 1978 to 0.918 in 2011) and a growth rate  $<1$ , with an estimated loss of nearly 7% of individuals from matriline in each year since 2003 (likely under-estimated due to identical survival estimates used for reproductive and post-reproductive females in the analysis). This decline in survival is likely the result of low recruitment for these whales, as previously shown by an extremely low fecundity rate, with 0.02 calves per adult female per year surviving to the age of 1 year during the 1990s (i.e., one calf that survives beyond 1 year produced every 50 years; Guinet 1991; Poncelet et al. 2010). This low fecundity rate was apparent throughout the study and had previously been suggested to be the result of food shortage (Guinet 1991; Poncelet et al. 2010). As a result of continued mortality and an absence of recruitment, it is



**Fig. 4** Survival probability of non-depredated (*empty circles*) and depredated killer whales (*black circles*) estimated from model averaging (models 11 and 13 in Table 3). *Error bars* represent 95% CI of model parameters estimates

likely that these matriline may experience an even higher rate of mortality in future years due to a decrease in foraging success and aging individuals. We anticipate that these matriline will not persist in the long term if the situation remains the same.

In contrast, for depredated whales, adult survival increased after illegal fishing operations ceased in the study area, and Tixier et al. (2015) found an increase in the calving rate, similar to those reported for NE Pacific “resident” populations when growing (Olesiuk et al. 2005). However, although survival of depredated killer whales increased again after 2003, uncertainty (i.e., 95% CI estimates) overlapped with uncertainty of the “poaching” period estimates and survival did not reach the values estimated for the period preceding the beginning of fisheries (1977–1995) and reported for stable or growing killer whale populations (Olesiuk et al. 1990; Kuningas et al. 2013). The current fecundity values observed for killer whales interacting with the fishery ( $0.18 \pm 0.02$  calf.reproductive female<sup>-1</sup> year<sup>-1</sup>) falls within the range of values reported from NE Pacific “resident” killer whales (0.18–0.21; Olesiuk et al. 1990; 2005) and the growing Norwegian killer whale population (0.20, Kuningas et al. 2013). Such high fecundity for depredated whales in the Crozet study area is surprising, given their low survival rate and insignificant growth rate of the population, as survival should be favoured over reproduction in long-lived predators (Cairns 1987; Gaillard et al. 1989, 1998). We suggest four possible explanations for such a decline: (1) similar to the non-depredated group, depredated whales had an unbalanced age class distribution, with a larger than expected proportion of older individuals with increased mortality compared to younger females with high

**Table 4** Estimates of the stochastic population growth rate ( $\lambda_{\text{stoc}}$ ) for depredating ( $D$ ) and non-depredating (ND) killer whales

Parameter	Term	Group	
		ND	$D$
Calving rate $\pm$ SD	$F$	0.0640 $\pm$ 0.0280	0.195 $\pm$ 0.0440
Survival $\pm$ SD	$\Phi_j$	0.9601 $\pm$ 0.0289	0.9601 $\pm$ 0.0289
	$\Phi_y$	0.8754 $\pm$ 0.0738	0.8754 $\pm$ 0.0738
	$\Phi_m$	0.863 $\pm$ 0.0340	0.946 $\pm$ 0.012
	$\Phi_{po}$	0.863 $\pm$ 0.0340	0.946 $\pm$ 0.012
	Age structure (%)	$j$	48.87
	$Y$	2.42	5.04
	$M$	31.56	30.21
	$po$	17.14	23.17
Population growth 95% CI (lower–upper)	$\lambda_{\text{stoc}}$	0.9273 (0.9269–0.9276)	1.0062 (1.0058–1.0066)

$\Phi_j$ ,  $\Phi_y$ ,  $\Phi_m$ ,  $\Phi_{po}$ , are the annual survival probabilities for yearling ( $y$ ), juveniles ( $j$ ), reproductive females ( $m$ ) and post-reproductive females ( $po$ ), respectively,  $f$  is the mean calving rate of reproductive females

SD is provided for calving rate and survival estimates and corresponds to temporal variation. 95% confidence intervals are provided for population growth estimates. The stable stage-specific proportions (%) of all age classes  $y$ ,  $j$ ,  $m$  and  $po$  are also presented

fecundity. However, the depredating whales in this population had a much lower proportion of post-reproductive females compared to the growing NE Pacific “resident” killer whales of British Columbia (0.241 vs. 0.324, respectively) (Brault and Caswell 1993) with a high survival rate (Olesiuk et al. 1990); (2) surviving individuals in matriline that lost most of their members during the illegal fishing period, were more socially vagrant and as a consequence may have experienced a higher mortality rate. Williams and Lusseau (2006) showed that killer whale social networks are vulnerable to targeted removals, especially the socially important individuals of such networks; (3) incidental mortality due to interactions with vessels still fishing illegally in the Crozet EEZ (although the magnitude of illegal fishing has been substantially reduced past 2003, there are still reports of the occasional presence of these vessels in the area—Pruvost et al. 2015), or with fishing vessels operating in international waters without observers onboard. Although previously undocumented, recent observations have confirmed long distance movements by some matriline performing sporadic round trips between the adjacent islands of Marion and Kerguelen Islands, almost 3000 km apart (Reisinger pers. comm.; Roche et al. 2007). This suggests that killer whales could readily travel out of the Crozet EEZ into areas where surveillance level is lower and expose themselves to lethal interactions with fishing boats operating in international waters; and (4) permanent emigration.

### Ecological implications of intra-population foraging specializations

This study is an interesting example of the ecological implications of within-population foraging specialization

at the level of individuals or social units. It is likely that other predator populations with varying levels of specialization are also composed of individuals or social units with preferred foraging habits that have led to food partitioning (Bolnick et al. 2003). Such partitioning may reduce competition, and increase both feeding efficiency and carrying capacity within the population (Begon et al. 2006). However, differences in prey preferences may have consequences on the behavioral ecology and population dynamics in cases where the environment is quickly changing (Kokko and Sutherland 2001). The “least specialized” component of the population should have a larger ecological niche and would, therefore, have greater plasticity to environmental changes, including a greater inclination to switch foraging behavior in the case of decreased prey availability (e.g., Smout et al. 2013). In this study, provisioning from fisheries increased food availability for depredating whales, but two of the primary prey items of the Crozet killer whale population have undergone significant declines over the past five decades: large baleen whales were depleted during the 1960s and 1970s by the whaling industry and the elephant seal population has experienced a decline of nearly 90% (Guinet et al. 1999). It is possible that part of the Crozet killer whales was already naturally feeding on Patagonian toothfish prior to the start of the fishery (Guinet et al. 2015), which is suggested by the fact that some individuals immediately started depredating when fishery operations began. In addition, the depth distribution of Patagonian toothfish (from 200 to >2000 m—Collins et al. 2010) does overlap with the dive range of killer whales, which were recently reported to be able to repeatedly dive to depths exceeding 600 m (Reisinger et al. 2016), making toothfish naturally accessible for the Crozet killer whales.

However, preliminary stable isotopes analyses performed on both depredating and non-depredating individuals, and including individuals that have only been observed from fishing vessels, indicated limited between-matrilines variations in natural prey preferences (Tixier, unpublished). This suggests that other factors, such as the cultural transmission of foraging behavior, as reported in highly social cetacean species (Rendell and Whitehead 2001), may have contributed to the development of intra-population variations among the Crozet killer whales in regards to depredation. While some matrilines may have started depredating independently, others may have adopted the behavior by copying depredating matrilines (i.e., horizontal cultural transmission). Such transmission mechanisms were illustrated by the spread of depredation across the fish-eating killer whales of Southeast Alaska (Matkin et al. 1997) and more recently across sperm whales in South East Alaska (Schakner et al. 2014) and killer whales of the Strait of Gibraltar (Esteban et al. 2016b). Association events of groups known to depredate with other groups were assumed to explain the progressive spread of depredation in areas where this behavior had not been yet (Whitehead et al. 2004). In Crozet, a beneficial behavior such as depredation may have quickly spread horizontally across closely related matrilines that spent a large proportion of time together after it had been initially discovered by only one individual.

### Ecological consequences of divergent demographic trajectories

The rapid loss of a significant part of a top-predator population is likely to alter the habitat use, resource exploitation and niche availability for surviving individuals within the population (Werner and Gilliam 1984; Benton et al. 2006). Lower predator abundance may reduce intra-population competition, as well as decrease density dependence, on resources through decreased predation pressure. Resource partitioning is one of the primary evolutionary responses to competition, and therefore, we may expect the “least specialized” predators to maximize their niche at a lower abundance (Krebs and Davies 1993). The current decline of the non-depredating component of the Crozet killer whale population may increase niche availability for the remaining individuals through an increase of both habitat and resource availability. However, while depredating, whales within the Crozet killer whale population appear to benefit from provisioning from fisheries, as previously mentioned, they only have access to this food source for a small part of the year. Therefore, it is likely that depredating killer whales still rely heavily on naturally occurring prey items such as large whales and seals for a large part of the year. Local prey populations such as the Crozet elephant seal

population, a major prey item the Crozet killer whales (Guinet 1992), are currently recovering (Guinet et al. 1999 and unpublished data), likely in response to decreased predation pressure by killer whales in recent years. Thus, surviving killer whales may benefit from both an increase in abundance of prey populations and a decrease in intra-population competition for resources due to a declining killer whale population. Historically, the same matrilines of killer whales were observed to forage on elephant seal pups, a highly aggregated and localized resource during the breeding season (October–December). These matrilines have shown a high degree of site fidelity to the inshore waters near the breeding colonies, resulting in a high level of competition between matrilines (Guinet 1992). A number of these non-depredating matrilines have perished over the last two decades, and as a result, new matrilines, some with few previous sightings in the area, are starting to use these newly available foraging areas with increasing frequency (Tixier, unpublished data). Although the growth of the Crozet killer whale population as a whole is stable, and there has been a rapid decline of the non-depredating component of whales within the population, depredating whales are showing a positive growth rate. It is likely that these whales will continue to increase in abundance in response to an increase in natural resource availability, continued benefits from food provisioning from fisheries, and possibly a niche extension due to a decline in the overall abundance of the population. The continued growth of this part of the population, paired with urgent conservation measures resulting from this study, may eventually lead to the recovery of the Crozet killer whale population. However, we need to continue monitoring this population to ensure that all sources of mortality are identified and do not increase in future years.

This study provides a unique example of the effects of intra-population heterogeneity in foraging behavior on the demography of an apex predator population that occurs in an environment that has experienced a high level of anthropogenic impact through fisheries interactions. It emphasizes the need for—and the importance of—long-term ecological studies with dedicated monitoring to detect and fully understand the effects of such impacts on vulnerable populations.

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### Compliance with ethical standards

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**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** This article does not contain any studies with animals performed by any of the authors.

**Informed consent** Informed consent was obtained from all individual participants included in the study.

### References

- Begon M, Townsend CR, Harper JL (2006) Ecology: from individuals to ecosystems. Wiley-Blackwell, Oxford
- Benton TG, Plaistow SJ, Coulson TN (2006) Complex population dynamics and complex causation: devils, details and demography. *Proc R Soc Lond Ser B* 273:1173–1181. doi:10.1098/rspb.2006.3495
- Bigg MA, Olesiuk PF, Ellis GM, Ford JKB, Balcomb KC (1990) Social organization and genealogy of resident killer whales in the coastal waters of British Columbia and Washington State. *Rep Int Whal Comm Spec Issue* 12:383–405
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. *Am Nat* 161:1–28. doi:10.1086/343878
- Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. *Science* 277:509–515. doi:10.1126/science.277.5325.509
- Branch TA, Watson R, Fulton EA, Jennings S, McGilliard CR, Pablico GT, Ricard D, Tracey SR (2010) The trophic fingerprint of marine fisheries. *Nature* 468:431–435. doi:10.1038/nature09528
- Brault S, Caswell H (1993) Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* 74:1444–1454. doi:10.2307/1940073
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York
- Cairns DK (1987) Seabirds as indicators of marine food supplies. *Biol Oceanogr* 5:261–271
- Carothers AD (1973) Capture-recapture methods applied to a population with known parameters. *J Anim Ecol* 42(1):125–146. doi:10.2307/3408
- Choquet R, Lebreton JD, Gimenez O, Reboulet AM, Pradel R (2009a) U-CARE: utilities for performing goodness of fit tests and manipulating CApture-REcapture data. *Ecography* 32:1071–1074
- Choquet R, Rouan L, Pradel R (2009b) Program E-SURGE: a software application for fitting multievent models. In: Thomson DL, Cooch EG, Conroy MJ (eds) Modeling demographic processes in marked populations. Environmental and ecological statistics. Springer, New York, pp 847–868
- Clark CW, Yoshimura J (1993) Behavioral responses to variations in population size: a stochastic evolutionary game. *Behav Ecol* 4:282–288. doi:10.1093/beheco/4.3.282
- Collins MA, Brickle P, Brown J, Belchier M (2010) The Patagonian toothfish: biology, ecology and fishery. *Adv Mar Biol* 58:227–300
- Cormack RM (1964) Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438
- Dahlheim ME, Waite JM (1993) Abundance and distribution of killer whales (*Orcinus orca*) in Alaska. Annual Report MMPA Assessment Program, Office of Protected Resources, NMFS, NOAA, Silver Spring
- Dalla Rosa L, Secchi ER (2007) Killer whale (*Orcinus orca*) interactions with the tuna and swordfish longline fishery off southern and south-eastern Brazil: a comparison with shark interactions. *J Mar Biol Assoc UK* 87:135–140. doi:10.1017/S0025315407054306
- Esteban R, Verborgh P, Gauffier P, Giménez J, Guinet C, De Stephanis R (2016a) Dynamics of killer whale, bluefin tuna and human fisheries in the Strait of Gibraltar. *Biol Conserv* 194:31–38
- Esteban R, Verborgh P, Gauffier P, Giménez J, Foote AD, de Stephanis R (2016b) Maternal kinship and fisheries interaction influence killer whale social structure. *Behav Ecol Sociobiol* 70(1):111–122
- Ford JKB, Ellis GM, Barrett-Lennard LG, Morton AB, Palm RS, Balcomb KC (1998) Dietary specialization in two sympatric populations of killer whales in coastal British Columbia and adjacent waters. *Can J Zool* 76(8):1456–1471. doi:10.1139/cjz-76-8-1456
- Ford JKB, Ellis GM, Olesiuk PF, Balcomb KC (2009) Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? *Biol Lett* 6:139–142. doi:10.1098/rsbl.2009.0468
- Fuller TK, Sievert PR (2001) Carnivore demography and the consequences of changes in prey availability. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) Carnivore conservation. Cambridge University Press, Cambridge, pp 163–178
- Gaillard J-M, Pontier D, Allainé D, Lebreton J-D, Trouvilliez J, Clobert J (1989) An analysis of demographic tactics in birds and mammals. *Oikos* 56:59–76. doi:10.2307/3566088
- Gaillard J-M, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol Evol* 13:58–63. doi:10.1016/S0169-5347(97)01237-8
- Ganas J, Robbins MM, Nkurunungi JB, Kaplin BA, McNeilage A (2004) Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *Int J Primatol* 25:1043–1072. doi:10.1023/B:IJOP.0000043351.20129.44
- Gimenez O, Lebreton J-D, Choquet R (2003) Parameter redundancy in multistate capture-recapture model. *Biometrical J* 45:704–722. doi:10.1002/bimj.200390043
- Gowans S, Whitehead H (2001) Photographic identification of northern bottlenose whales (*Hyperoodon ampullatus*): sources of heterogeneity from natural marks. *Mar Mamm Sci* 17:76–93. doi:10.1111/j.1748-7692.2001.tb00981.x
- Grosbois V, Gimenez O, Gaillard JM, Pradel R, Barbraud C, Clobert J, Møller AP, Weimerskirch H (2008) Assessing the impact of climate variation on survival in vertebrate populations. *Biol Rev* 83:357–399. doi:10.1111/j.1469-185X.2008.00047.x
- Guinet C (1991) Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). *Can J Zool* 69:2712–2716. doi:10.1139/z91-383
- Guinet C (1992) Predation behavior of killer whales around Crozet Islands. *Can J Zool* 70:1656–1667

- Guinet C, Jouventin P, Weimerskirch H (1999) Recent population change of the southern elephant seal at Iles Crozet and Iles Kerguelen: the end of the decrease? *Antarct Sci* 11:193–197. doi:[10.1017/S0954102099000255](https://doi.org/10.1017/S0954102099000255)
- Guinet C, Domenici P, de Stephanis R, Barrett-Lennard L, Ford JKB, Verborgh P (2007) Killer whale predation on bluefin tuna: exploring the hypothesis of the endurance-exhaustion technique. *Mar Ecol Prog Ser* 347:111–119. doi:[10.3354/meps07035](https://doi.org/10.3354/meps07035)
- Guinet C, Tixier P, Gasco N, Duhamel G (2015) 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 J Mar Sci* 72(5):1587–1597
- Hofbauer J, Sigmund K (1998) *Evolutionary games and population dynamics*. Cambridge University Press, Cambridge
- Hucke-Gaete R, Moreno C, Arata J (2004) Operational interactions of sperm whales and killer whales with the Patagonian toothfish industrial fishery off southern Chile. *Ccamlr Sci* 11:127–140
- Jolly GM (1965) Explicit estimates from capture-recapture data with both death and immigration-stochastic models. *Biometrika* 52:225–247
- Kendall WL, Nichols JD, Hines JE (1997) Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78(2):563–578. doi:[10.2307/2265960](https://doi.org/10.2307/2265960)
- Kokko H, Sutherland WJ (2001) Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evol Ecol Res* 3:537–551
- Krebs JR, Davies NB (1993) *An introduction to behavioural ecology*. Blackwell, Cambridge
- Kuningas S, Similä T, Hammond PS (2013) Population size, survival and reproductive rates of northern Norwegian killer whales (*Orcinus orca*) in 1986–2003. *J Mar Biol Assoc UK* 94(06):1277–1291. doi:[10.1017/S0025315413000933](https://doi.org/10.1017/S0025315413000933)
- Lebreton JD, Pradel R (2002) Multistate recapture models: modelling incomplete individual histories. *J Appl Stat* 29(1–4):353–369. doi:[10.1080/02664760120108638](https://doi.org/10.1080/02664760120108638)
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118. doi:[10.2307/2937171](https://doi.org/10.2307/2937171)
- Leibold MA (1996) A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence and diversity patterns in communities. *Am Nat* 147:784–812. doi:[10.1086/285879](https://doi.org/10.1086/285879)
- Lewison RL, Crowder LB, Read AJ, Freeman SA (2004) Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol Evol* 19:598–604. doi:[10.1016/j.tree.2004.09.004](https://doi.org/10.1016/j.tree.2004.09.004)
- Marcoux M, Whitehead H, Rendell L (2007) Sperm whale feeding variation by location, year, social group and clan: evidence from stable isotopes. *Mar Ecol Prog Ser* 333:309–314. doi:[10.3354/meps333309](https://doi.org/10.3354/meps333309)
- Matkin CO (1986) Killer whale interactions with the sablefish longline fishery in Prince William Sound, Alaska, 1985, with comments on the Bering Sea. Contract No. 010686. NMFS, NMML, Juneau, Alaska. 10
- Matkin CO, Matkin DR, Ellis GM, Saulitis E, McSweeney D (1997) Movements of resident killer whales in southeastern Alaska and Prince William Sound, Alaska. *Mar Mamm Sci* 13:469–475. doi:[10.1111/j.1748-7692.1997.tb00653.x](https://doi.org/10.1111/j.1748-7692.1997.tb00653.x)
- Matkin CO, Barrett-Lennard LG, Yurk H, Ellifrit D, Trites AW (2007) Ecotypic variation and predatory behavior among killer whales (*Orcinus orca*) off the eastern Aleutian Islands, Alaska. *Fish Bull* 105:74–87
- Morris WF, Doak DF (2002) *Quantitative conservation biology: theory and practice of population viability analysis*. Sinauer Associates, Sunderland
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283. doi:[10.1038/nature01610](https://doi.org/10.1038/nature01610)
- Nelson LJ, Anderson DR, Burnham KP (1980) The effect of band loss on estimates of annual survival. *J Field Ornithol* 51(1):30–38
- Nichols JD (1992) Capture-recapture models. *Bioscience* 42(2):94–102
- Nichols JD, Stokes SL, Hines JE, Conroy MJ (1982) Additional comments on the assumption of homogeneous survival rates in modern bird banding estimation models. *J Wildl Manag* 46(4):953–962. doi:[10.2307/3808228](https://doi.org/10.2307/3808228)
- Northridge SP (1991) An updated world review of interactions between marine mammals and fisheries. FAO Fisheries Technical Paper 251, Supplement 1. <http://www.fao.org/docrep/003/T0452E/T0452E00.HTM>. Accessed January 30 2017
- Northridge SP, Hoffman RJ (1999) Marine mammal interactions with fisheries. In: Twiss JR, Reeves RR (eds) *Conservation and management of marine mammals*. Smithsonian Institution Press, Washington, pp 99–119
- O'Donoghue M, Boutin S, Krebs CJ, Hofer EJ (1997) Numerical responses of coyotes and lynx to the snowshoe hare cycle. *Oikos* 80:150–162. doi:[10.2307/3546526](https://doi.org/10.2307/3546526)
- Olesiuk P, Bigg M, Ellis G (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 Comm* 12:209–242
- Olesiuk PF, Ellis GM, Ford JKB (2005) Life history and population dynamics of northern resident killer whales in British Columbia. Research document 2005/45, Ottawa, Canada: Canadian Science Advisory Secretariat, Fisheries and Oceans Canada. [http://www.dfo-po.gc.ca/csas/Csas/Publications/ResDocs-DocRech/2005/2005\\_045\\_e.htm](http://www.dfo-po.gc.ca/csas/Csas/Publications/ResDocs-DocRech/2005/2005_045_e.htm). Accessed January 30 2017
- Parsons KM, Balcomb KC, Ford JKB, Durban JW (2009) The social dynamics of southern resident killer whales and conservation implications for this endangered population. *Anim Behav* 77(4):963–971. doi:[10.1016/j.anbehav.2009.01.018](https://doi.org/10.1016/j.anbehav.2009.01.018)
- Pollock KH, Raveling DG (1982) Assumptions of modern band-recovery models, with emphasis on heterogeneous survival rates. *J Wildl Manag* 46(1):88–98. doi:[10.2307/3808411](https://doi.org/10.2307/3808411)
- Poncelet E, Barbraud C, Guinet C (2010) Population dynamics of killer whales in Crozet Archipelago, southern Indian Ocean: a mark recapture study from 1977 to 2002. *J Cetacean Res Manag* 11(1):41–48
- Pradel R (1993) Flexibility in survival analysis from recapture data: handling trap dependence. In: Lebreton J-D, North PM (eds) *Marked individuals in the study of bird population*. Birkhäuser Verlag, Basel, pp 29–37
- Pruvost P, Duhamel G, Gasco N, Palomares MD (2015) A short history of the fisheries of Crozet islands. *FCRR* 23(1):31–37
- Purves MG, Agnew DJ, Balguerias E, Moreno CA, Watkins B (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 Sci* 11:111–126
- R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rauscher MD (1984) Tradeoffs in performance on different hosts-evidence from within site and between site variation in the beetle *Deloyala guttata*. *Evolution* 38:582–595. doi:[10.2307/2408708](https://doi.org/10.2307/2408708)
- Reisinger RR, Gröcke DR, Lübcker N, McClymont EL, Hoelzel AR, de Bruyn PN (2016) Variation in the diet of killer whales *Orcinus orca* at Marion Island, Southern Ocean. *Mar Ecol Prog Ser* 549:263–274
- Rendell L, Whitehead H (2001) Culture in whales and dolphins. *Behav Brain Sci* 24:309. doi:[10.1017/S0140525X0100396X](https://doi.org/10.1017/S0140525X0100396X)

- Roche C, Guinet C, Gasco N, Duhamel G (2007) Marine mammals and demersal longlines fishery interactions in Crozet and Kerguelen exclusive economic zones: an assessment of the depredation level. *CCAMLR Sci* 14:67–82
- Schakner ZA, Lunsford C, Straley J, Eguchi T, Mesnick SL (2014) Using models of social transmission to examine the spread of longline depredation behavior among sperm whales in the Gulf of Alaska. *PLoS One* 9:109079. doi:[10.1371/journal.pone.0109079](https://doi.org/10.1371/journal.pone.0109079)
- Seber GAF (1965) A note on the multiple recapture census. *Biometrika* 52:249–259
- Smout S, Rindorf A, Hammond PS, Harwood J, Matthiopoulos J (2013) Modelling prey consumption and switching by UK grey seals. *ICES J Mar Sci* 71:81–89. doi:[10.1093/icesjms/fst109](https://doi.org/10.1093/icesjms/fst109)
- Stubben CJ, Milligan BG (2007) Estimating and analyzing demographic models using popbio package in R. *J Stat Softw* 22:11
- Tixier P (2012) Déprédation par les orques (*Orcinus Orca*) et les cachalots (*Physeter Macrocephalus*) sur les palangriers à la legine australe dans la ZEE de l'archipel de Crozet. Dissertation, University of Aix-Marseille II
- Tixier P, Gasco N, Duhamel G, Guinet C (2010) Interactions of Patagonian toothfish fisheries with killer and sperm whales: an assessment of depredation levels and insights on possible mitigation solutions. *CCAMLR Sci* 17:179–195
- Tixier P, Gasco N, Guinet C (2014) Killer whales of the Crozet islands, photo-identification catalogue 2003–2011. *Vil-liers en Bois: Centre d'Etudes Biologiques de Chizé-CNRS*. doi:[10.6084/m9.figshare.1085960](https://doi.org/10.6084/m9.figshare.1085960) (accessed January 30 2017)
- Tixier P, Authier M, Gasco N, Guinet C (2015) Influence of artificial food provisioning from fisheries on killer whales reproductive output. *Anim Conserv* 18(2):207–208. doi:[10.1111/acv.12161](https://doi.org/10.1111/acv.12161)
- Tremblay-Boyer L, Gascuel D, Watson R (2011) Modelling the effects of fishing on the biomass of the world's oceans from 1950 to 2006. *Mar Ecol Prog Ser* 442:169–185
- Trites AW, Christensen V, Pauly D (1997) Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *J Northwest Atl Fish Soc* 22:173–187
- Tuck GN, Polacheck T, Croxall JP, Weimerskirch H (2001) Modelling the impact of fishery by-catches on albatross populations. *J Appl Ecol* 38:1182–1196. doi:[10.1046/j.0021-8901.2001.00661.x](https://doi.org/10.1046/j.0021-8901.2001.00661.x)
- Turchin P (2003) *Complex population dynamics: a theoretical/empirical synthesis*. Princeton University Press, Princeton
- Ward EJ, Holmes EE, Balcomb KC (2009) Quantifying the effects of prey abundance on killer whale reproduction. *J Appl Ecol* 46:632–640. doi:[10.1111/j.1365-2664.2009.01647.x](https://doi.org/10.1111/j.1365-2664.2009.01647.x)
- Wauters L, Swinnen C, Dhondt AA (1992) Activity budget and foraging behavior of red squirrels in coniferous and deciduous habitats. *J Zool* 227:71–86
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Annu Rev Ecol Syst* 15:393–425. doi:[10.1146/annurev.ecolsys.15.1.393](https://doi.org/10.1146/annurev.ecolsys.15.1.393)
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–138
- Whitehead H, Rendell L, Osborne RW, Würsig B (2004) Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. *Biol Conserv* 120(3):427–437. doi:[10.1016/j.biocon.2004.03.017](https://doi.org/10.1016/j.biocon.2004.03.017)
- Whiten A (2000) Primate culture and social learning. *Cognit Sci* 24:477–508. doi:[10.1016/S0364-0213\(00\)00027-6](https://doi.org/10.1016/S0364-0213(00)00027-6)
- Williams R, Lusseau D (2006) A killer whale social network is vulnerable to targeted removals. *Biol Lett* 2:497–500. doi:[10.1098/rsbl.2006.0510](https://doi.org/10.1098/rsbl.2006.0510)
- Williams BK, Nichols JD, Conroy MJ (2002) *Analysis and management of animal populations*. Academic Press, San Diego
- Yano K, Dahlheim ME (1995a) Killer whale, *Orcinus orca*, depredation on longline catches of bottom fish in the southeastern Bering Sea and adjacent waters. *Fish Bull* 93:355–372
- Yano K, Dahlheim ME (1995b) Behavior of killer whales *Orcinus orca* during longline fishery interactions in the southeastern Bering Sea and adjacent waters. *Fish Sci* 61:584–589