

Influence of artificial food provisioning from fisheries on killer whale reproductive output

P. Tixier¹, M. Authier², N. Gasco³ & C. Guinet¹

¹ Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372, CNRS-Université de la Rochelle, Villiers en Bois, France

² Observatoire PELAGIS, UMS 3462 du CNRS, Université de La Rochelle, La Rochelle, France

³ Département des Milieux et Peuplements Aquatiques, Muséum National d'Histoire Naturelle, Paris, France

Keywords

demography; depredation; fisheries; food provisioning; killer whale; longlines; reproduction; top predator.

Correspondence

Paul Tixier, Centre d'Etudes Biologiques de Chizé (CEBC), UMR7372, CNRS-Université de la Rochelle, Villiers en Bois 79360, France.

Email: tixier@cebc.cnrs.fr

Editor: Trevor Branch

Associate Editor: Rob Williams

Received 31 July 2013; accepted 03 July 2014

doi:10.1111/acv.12161

Abstract

Prey availability is a critical factor influencing demographic trajectories of long-lived, top predators, which may therefore be strongly affected by artificial food provisioning. In the Crozet archipelago, killer whales feed on a wide range of species including birds, marine mammals and fish. Following the development of the Patagonian toothfish fisheries in 1996, killer whales began to also depredate longlines. Social groups, hereafter referred to as matriline, exhibited different levels of interaction; some were involved in most of the depredation events, while others were never observed interacting with fisheries. These differences in interaction levels influenced reproduction. An extensive photo-identification effort from 2003 to 2012 allowed us to estimate the probability of calving for 21 reproductive females. Using multi-model inference, we found a positive effect of depredation on female calving rate. These results suggest an effect of artificial food provisioning on female reproductive output with potentially far-reaching consequences on the demography of the Crozet killer whale population. Our findings evidence the need to account for both intra-population heterogeneity and level of interaction with fisheries when assessing conservation strategies of long-lived marine predators involved in similar depredation worldwide.

Introduction

The relationship between resource availability and demography has long been studied (e.g. Fox, 1975; Skogland, 1985; Saunders, Hobbs & Margules, 1991). Prey availability is a critical factor in a predator's survival and reproduction, particularly for specialist species (Leibold, 1996; Preisser, Bolnick & Grabowski, 2009); the more specialized a predator, the more sensitive it is to natural or anthropogenic changes in its prey's availability (e.g. Fuller & Sievert, 2001).

Over the past 50 years, overfishing in the marine environment has tremendously impacted marine predator populations (Pauly, Watson & Alder, 2005). In addition to negative consequences on demography, prey depletion has also increased interactions between fisheries and marine predators competing for the same resource (Trites, Christensen & Pauly, 1997; Read, 2005). Such interactions are currently a major issue worldwide, involving a broad range of fisheries and numerous species including seabirds and marine mammals (Northridge & Hofman, 1999). These species are the most at risk because they feed extensively on fish discards and/or directly remove captures from fishing gear (i.e. depredation behavior). Some studies have shown that there is an increased risk of mortality in local populations that interact with fisheries (e.g. Lewison *et al.*, 2004). This is not

only because of death or serious injuries to animals caught in fishing gear, but fishers can retaliate (e.g. use of explosives or guns to repel predators) against animals whose depredation of longlines, trawlers or gillnets often causes heavy economic losses to fishing companies (Lewison *et al.*, 2004). However, additional food sources provided by fisheries may complement an individual's energy intake and can consequently enhance fitness (Botsford, Castilla & Peterson, 1997).

Killer whales *Orcinus orca* are top marine predators that feed on a wide range of prey items and can interact with fisheries worldwide (Dahlheim, 1988; Hucke-Gaete, Moreno & Arata, 2004; Purves *et al.*, 2004). Killer whales around the Crozet archipelago (Southern Indian Ocean S 46°25'; E 51°59') have been the focus of field studies since the 1970s. Two distinct morphotypes exist in the area: type-D killer whales (Pitman *et al.*, 2010) and the 'Crozet killer whales'. They both interact with fisheries, but are genetically segregated (Foote *et al.*, 2013). This study focused on the Crozet killer whales, which are genetically closer to type-A Antarctic killer whales. They are the most commonly encountered type in the waters surrounding the Crozet archipelago. Individuals from the Crozet killer whales belong to stable and long-lasting matriline. In 1996, both legal and illegal Patagonian toothfish *Dissotichus*

eleginoides longline fisheries started in Crozet waters. Within the first year, matriline were observed depredating longlines with an estimated intake of 116 ± 27 tons of toothfish annually (Tixier *et al.*, 2010). These matriline have undergone a period of increased mortality between 1996 and 2002 attributed to negative interactions with illegal fishers using fire guns and explosives to repel the whales (Poncelet, Barbraud & Guinet, 2010). The presence of French navy vessels in the Crozet EEZ since 2003 ended the poaching of toothfish as well as the incidental mortality of killer whales. Nevertheless, killer whales continue to interact with seven licensed longliners, without direct risk to the animals, however, as they do not get caught on hooks or entangled in longlines within that fishery.

Killer whales are extremely long-lived, with some females thought to be 90 years old (Olesiuk, Bigg & Ellis, 1990). Reproductive maturity occurs by age 10 for most females, and females produce calves approximately every 5–6 years over their reproductive life span (Olesiuk, Ellis & Ford, 2005). Recent studies have emphasized the positive effect of resource abundance and availability on killer whale reproductive output (Ford *et al.*, 2009; Ward, Holmes & Balcomb, 2009). However, these studies were conducted on the highly specialized fish-eating killer whale populations of the north-east Pacific. Unlike these populations, the Crozet killer whales appear to be generalists, feeding on fish, seabirds, seals and whales (Guinet, 1992), and depredating the Patagonian toothfish. However, depredation varies across matriline: some were involved in most depredation events while others were never observed depredating longlines (Tixier *et al.*, 2010). The income of a highly energetic and easy-to-catch resource such as depredated toothfish may therefore substantially differ between killer whale matriline, with expected consequences on female calving rate.

Paired with an extensive photo-identification effort, this intra-population variation of specialization level to depredation occurring between matriline provides an opportunity to study the impacts of a human activity on an apex predator's reproduction. The aim of this study was therefore to assess whether artificial food provisioning from fisheries has any measurable effect on calving rate of females among matriline based on their level of interaction with longlines.

Methods

Photo-identification data and fecundity table

Between 2003 and 2012, independent and trained photographers (equipped with DSLR cameras, minimum 300-mm zoom lens) were stationed on land (Possession Island, Crozet archipelago) and longliners to produce an extensive photo-identification catalog (Bigg *et al.*, 1990).

A total of 43 217 individual photographs were entered into the 1964–2012 database available for the Crozet killer whales. We assessed females that were of reproductive age

(10–46 years old, based on Olesiuk *et al.*, 2005) between 2003 and 2012 and selected only those females that were encountered and photographed at least once per year during the study period.

A fecundity table was constructed with 21 females that met both criteria (Table 1). They belonged to 18 different matriline (Tixier, Gasco & Guinet, 2011). Calving rate was calculated as the number of calves born during a given year out of the total number of reproductive females available that year. A calf was assigned to one female when repeatedly seen surfacing by her side. Calf birth year was estimated using last date that a female was encountered without calf and the date she was reseen with a calf by her side. In cases where the range between these two dates was greater than a year, morphological information on the calf was used to determine if its birth occurred during current year, or the year prior.

Indices measuring female-level interaction with fisheries

Annual female killer whale interactions with fisheries can be assessed in three different ways using raw fishing data paired with photo-identification data: (1) the number of exposed hooks, which is calculated as the cumulated number of hooks on all longlines with photographic coverage that were hauled out in presence of a given female (noted 'Hooks'); (2) a between individuals relative interaction rate, which is calculated as the total number of longlines with photographic coverage and hauled out in the presence of a given female over the total number of longlines with photographic coverage and hauled out in presence of any identified female; (3) the number of days of interaction which is calculated as the cumulated number of days during which a given female was photographed interacting with at least one longline hauled out during that day.

The most relevant index for this study was the number of depredated hooks per female per year. It is a measure of the amount of fish potentially available to whales interacting with longlines and is the most relevant variable to test hypotheses on the effect of artificial food provisioning on killer whale reproduction. Because the number of hooks greatly varies among longlines (from 2000 up to 20 000), the interaction rate, calculated as a percentage of longlines exposed to depredation, appears to be a less informative index. Likewise, the number of interaction days provides little information on the quantity of consumed fish as it does not account for the number of exposed hooks per whale, which can greatly vary within a day.

The absence of dispersion, either short or long term, of individuals from matriline (Guinet, 1991; Poncelet *et al.*, 2010; Tixier *et al.*, 2010) allowed us to extend our dataset to all depredated longlines for which at least one other member of a given matriline was photographed, meaning that the female was present, but was missed by the photographer, if the female was again photographed consecutively to that encounter.

Table 1 Histories of annual interaction level with fisheries (number of depredated longline hooks) and calving events of the 21 reproductive females used in the analysis over the 2003–2012 period

Female ID	Matriline	2003–2012		2003		2004		2005		2006		2007		2008		2009		2010		2011		2012	
		Mean nb Hooks ± SD × 1000	Hooks × 1000	Hooks × 1000	Calf	Hooks × 1000	Calf	Hooks × 1000	Calf	Hooks × 1000	Calf	Hooks × 1000	Calf	Hooks × 1000	Calf	Hooks × 1000	Calf	Hooks × 1000	Calf	Hooks × 1000	Calf	Hooks × 1000	Calf
C069	C128	0 ± 0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C116	C037	0 ± 0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C201	C195	1.65 ± 3.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4.50	1	12.00	0	0
C101	C101	8.78 ± 20.5	62.58	0	0	0	0	0	0	0	0	0	1	25.20	0	0	0	0	0	0	0	0	0
C190	C190	22.68 ± 38.89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	36.74	0	7.50	1	109.77	0	72.8
C021	C021	26.69 ± 38.47	0	0	0	0	0	91.8	0	91.80	0	49.50	1	33.75	0	0	0	0	0	0	0	0	0
C121	C121	35.82 ± 52.18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34.65	0	83.25	1	107.28	0	133.02
C143	C121	35.82 ± 52.18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34.65	0	83.25	0	107.28	1	133.02
C010	C010	44.56 ± 55.86	7.79	0	0	90.90	0	6.15	1	7.50	0	78.75	0	105.75	0	148.80	0	0	0	0	0	0	0
C024	C024	46.69 ± 71.69	7.79	1	0	0	0	0	0	0	0	182.25	0	47.25	0	170.40	0	59.25	0	0	0	0	0
C172	C138	47.59 ± 71.44	0	0	0	0	0	0	0	0	0	0	0	0	0	125.10	0	91.86	0	55.44	0	203.52	
C138	C138	51.52 ± 72.98	0	0	0	0	0	0	0	0	0	0	0	0	0	125.10	0	91.86	0	94.70	0	203.52	
C006	C002	62.57 ± 41.6	30.85	0	0	123.70	0	81.26	0	0	0	15.00	0	63.90	0	47.10	0	106.5	1	107.13	0	50.25	
C132	C012	66.87 ± 85.89	0	1	45.00	0	1	45.00	0	0	0	184.65	0	0	0	193.45	0	-	-	-	-	-	-
C111	C111	72.34 ± 63.17	33.32	0	0	0	0	0	0	82.35	0	158.85	1	12.00	0	98.10	0	129.75	0	46.8	0	162.27	
C013	C013	82.38 ± 72.11	72.33	1	0	0	0	6.15	0	33.00	0	209.25	0	22.25	1	129.60	0	133.50	0	55.44	0	162.27	
C119	C119	85.95 ± 90.23	0	0	0	0	0	19.12	0	100.80	0	113.25	0	29.40	0	259.20	1	141.00	0	7.50	0	189.27	
C106	C139	98.01 ± 123.3	0	0	0	0	0	9.13	0	100.80	0	137.25	1	52.50	0	170.40	0	59.25	0	42.48	0	408.27	
C137	C012	111.12 ± 114.37	0	0	45.00	0	0	45.00	0	0	0	184.65	0	0	0	193.45	1	140.25	0	152.64	0	350.25	
C017	C016	115.96 ± 80.03	48.95	0	0	0	0	158.40	0	36.00	1	228.75	0	135.00	0	189.30	0	131.25	0	-	-	-	-
C019	C018	193.92 ± 105.08	56.87	0	142.20	0	0	167.40	1	231.9	0	245.25	0	84.00	0	245.10	0	184.50	0	150.48	1	431.52	

-, indicates years during which a female was not observed.

Table 2 Summary of the number of calves (Calf) produced annually by reproductive female killer whales (Fem) whether they interacted with fisheries (D) or not (ND) during the birth year (t ; lag 0)

Year (t)	Lag 0		Lag 1				Lag 2					
	Calf (D)	Calf (ND)	Fem (D)	Fem (ND)	Calf (D)	Calf (ND)	Fem (D)	Fem (ND)	Calf (D)	Calf (ND)	Fem (D)	Fem (ND)
2003	2	1	8	13	–	–	–	–	–	–	–	–
2004	0	0	4	14	0	0	6	11	–	–	–	–
2005	2	0	10	11	2	0	5	16	2	0	8	13
2006	1	2	6	13	1	2	8	11	0	3	3	15
2007	3	1	12	7	3	1	8	11	2	2	9	9
2008	1	0	7	10	1	0	9	8	1	0	5	12
2009	2	0	15	6	1	1	10	10	2	0	11	9
2010	4	0	13	5	3	1	12	5	1	3	10	9
2011	2	0	9	6	2	0	12	5	2	0	12	5
2012	2	0	10	7	2	0	8	9	2	0	12	6

The year before ($t - 1$; lag 1) or 2 years before calving ($t - 2$; lag 2).
–, indicates years during which a female was not observed.

Previous breeding status of females and time lags in interaction with fisheries

Availability of females to reproduction was determined using the average 12-month lactation period for this species and the 2-year minimum calving intervals reported in other killer whale populations (Olesiuk *et al.*, 2005; Kuningas, Similä & Hammond, 2013). Females that calved during a given year were either omitted or assigned lower calving probabilities during the following year. It was indeed impossible for females to calf year after year because of the 12-month lactation period in killer whales. This state-dependency was further referred to as ‘previous breeding status’ when modeling calving probabilities of females.

The influence of resource availability as a covariate on killer whale reproduction was tested using a 1-year time lag in previous studies because of the 18-month gestation period of killer whales (Ford, Ellis & Olesiuk, 2005). We used the same lag to test the effect of the interaction level with fisheries on female calving rate. However, two alternative time lags of 0 and 2 were also considered in analyses to evaluate support for the following hypotheses: a time lag of 0 (‘lag 0’), that is the level of interaction with fisheries during the year of calving (t), which may be appropriate too as some killer whale calves are not seen until they are several months old; and a time lag of 2 years ($t - 2$: ‘lag 2’), which, in addition to the 1-year time lag ($t - 1$: ‘lag 1’), may also be appropriate to rigorously assess the influence of the amount of depredated toothfish on calving rate because the gestation period is longer than 1 year.

Exploratory analyses on observed data

Calving events (Table 1) were used to preliminarily assess annual calving rates of females (number of calves per female per year) from observed data. Annual calving rates were calculated as the total number of calves born during a given year out of the total number of reproductive females available that year (females calving the year before were omitted in calculations for that year). Paired (by year) t -tests were

performed to compare annual calving rates (calculated for year t) between depredating (D) and non-depredating females (ND). Females were assigned this binary state based on photographic data and for the three distinct time lags whether they interacted or not with fisheries during the birth year (lag 0), the year before (lag 1) or 2 years before calving (lag 2) (Table 2). Comparisons were made for the three time lags distinctively. Mean calving rates are reported with their standard error (SE).

Pregnancy and lactation costs may respectively translate in increased levels of interaction during the year of birth or during years preceding the year of birth. To evaluate support for these hypotheses and to limit bias when interpreting results, paired t -tests were also performed on observed data to examine between-year variations of interaction levels with fisheries according to calving events. For each female we compared the mean number of hooks exposed to depredation by this female during years t or $t - 1$ or $t - 2$, with the mean number of hooks exposed to depredation by this female during all years of the study period excluding years t , $t - 1$ and $t - 2$, respectively. Mean number of hooks per female per year is reported with its standard deviation (SD).

Modeling calving probabilities: a latent variable formulation

Let y_{it} be a latent variable reflecting the energetic stores of a female in matriline i in year t . y_{it} is not directly observable with our data. However, a manifestation of y_{it} is whether female i gave birth to a calf in year t , or not. Thus our response variable $Calf_{it}$ may be viewed as coarsened data:

$$Calf_{it} = \begin{cases} 1 & \text{if } y_{it} \geq 0 \\ 0 & \text{if } y_{it} < 0 \end{cases}$$

Only the sign of y_{it} is known, but not its magnitude. We are interested in testing the hypothesis that the magnitude of y_{it} depends on the interaction rate of a female with longliners, that is $\beta_2 > 0$ in the following model:

$$y_{it} = \beta_0 + \beta_1 \times pbs_{it} + \beta_2 \times \text{interaction}_{it} + \text{matriline}_i + \text{year}_t + \varepsilon_{it}$$

β_1 measures state-dependence; it takes in account the previous breeding status of females ('pbs') as described earlier. The indicator variable pbs_{it} was thus constructed so that if $\text{Calf}_{it} = 1$:

- $pbs_{it} = 0$,
- $pbs_{i(t+1)} = 1$,
- $pbs_{i(t+2)} = \frac{1}{2}$, and
- $pbs_{i(t+3)} = 0$.

This model specifies that there is a higher probability of calving 2 years after first birth than 1 year after. matriline_i is a random effect, accounting for the fact that the same matriline is observed over several years. Likewise, year_t is a year-level random effect and ε_{it} is the residual term. This formulation is equivalent to a generalized linear model with Bernoulli data (Albert & Chib, 1993). The distributional assumption of the residuals ε_{it} determines the link function. If for example, a standard normal distribution is assumed, the probit link is recovered. The latent variable y_{it} is related to a female's probability of calving: $\text{Pr}(\text{Calf}_{it}) = \Phi(y_{it})$, where $\Phi()$ is the cumulative distribution function (CDF) of the standard normal distribution.

However, the normal distribution has a drawback: it is relatively light-tailed, therefore, it is not robust to outliers. Robustness relates to the fatness of the tails of a distribution. The logistic distribution has heavier tails than the normal, and is often preferred for the analysis of binary data (logit link). Here, we are concerned about outliers in our data: one female for example has interacted with as many as 431 520 fishing hooks in 2012, but 95% of the values are below 200 000 hooks. Such outliers may have a disproportionate influence on our inferences. We therefore assumed the residuals ε_{it} to follow a Student- t distribution 7 degrees of freedom (d.f.) and scale chosen to approximate the standard logistic distribution (Liu, 2004). The induced link function is called the robit, and the interested reader is referred to Liu (2004) for theoretical justifications, and to Gelman & Hill (2007) for practical implementation. Thus, the robit link is the CDF of a Student- t distribution of mean 0, scale 1.5484 and 7 d.f. (Liu, 2004 – see also Supporting Information Appendix S1 for model implementation in WinBUGS, Spiegelhalter *et al.*, 2003 – and Supporting Information Appendix S4).

Multi-model inference and model selection

To test whether females benefited from the depredation of longliners, we compared four different models in a multi-model inference framework (Link & Barker, 2009). We tested the null model against the three distinct time lags previously described.

1 a null model: $y_{it} = \beta_0 + \beta_1 \times pbs_{it} + \text{matriline}_i + \text{year}_t + \varepsilon_{it}$;

2 a model with a proxy for interaction rate with no time lag (lag 0):

$$y_{it} = \beta_0 + \beta_1 \times pbs_{it} + \beta_2 \times \text{interaction}_{it} + \text{matriline}_i + \text{year}_t + \varepsilon_{it};$$

3 a model with a proxy for interaction rate with a one-year lag (lag 1):

$$y_{it} = \beta_0 + \beta_1 \times pbs_{it} + \beta_3 \times \text{interaction}_{i(t-1)} + \text{matriline}_i + \text{year}_t + \varepsilon_{it};$$

4 a model with a proxy for interaction rate with a two-year lag (lag 2):

$$y_{it} = \beta_0 + \beta_1 \times pbs_{it} + \beta_4 \times \text{interaction}_{i(t-2)} + \text{matriline}_i + \text{year}_t + \varepsilon_{it}.$$

Because interaction is hard to measure precisely in the field, we assessed the sensitivity of our results to alternative proxies of interactions between killer whales and longliners (Supporting Information Appendix S2).

Each model was equally weighted *a priori*. However, we did not estimate Bayes factors (Link & Barker, 2009), but reported both model posterior probabilities and the recently proposed widely applicable information criterion (WAIC, Gelman, Hwang & Vehtari, 2013).

Effect sizes

Gelman & Pardoe (2007) proposed computing average predictive comparisons (APC), that is the expected change (on a probability scale) to a specified change in an input (here interaction rate with fisheries). We used APC as measure of effect size to assess how calving probability changed with interaction with longliners. The APC for interacting with fisheries was computed for each model (see equations 5 and 8 in Gelman & Pardoe, 2007), then averaged using model posterior weights.

Model fitting

Our models were fit with WinBUGS (Lunn, Best & Spiegelhalter, 2000) in R (R development Core Team, 2010). We used Student- t priors (mean = 0, scale = 10, d.f. = 7) from Gelman (2008) for fixed effects and half Student- t priors (mean = 0, scale = 1, d.f. = 3) for variance components. These priors are informative, but weakly so. If the data are informative, these priors have a negligible influence (Gelman, 2006; Gelman *et al.*, 2008). Four Markov chains were run with different initial values for a total of 260 000 iterations per chain with the first 10 000 discarded as 'burn in'. We used the Bayesian model averaging framework of Link & Barker (2009, chapter 7) to obtain model-averaged coefficients. A master model with an indicator variable for model identity (m_{ID}) was run (see WinBUGS code)

$$y_{it} = \beta_0 + \beta_1 \times pbs_{it} + \text{matriline}_{it} + \text{year}_t + \varepsilon_{it} + \begin{cases} 0 & \text{if } m_{ID} = 1 \\ \beta_2 \times \text{interaction}_{it} & \text{if } m_{ID} = 2 \\ \beta_3 \times \text{interaction}_{i(t-1)} & \text{if } m_{ID} = 3 \\ \beta_4 \times \text{interaction}_{i(t-2)} & \text{if } m_{ID} = 4 \end{cases}$$

m_{ID} was given a categorical distribution with equal prior probabilities. Model posterior probabilities were computed from the indicator variable m_{ID} . Model convergence was assessed using the Gelman–Rubin diagnostic (Cowles & Carlin, 1996) and was achieved if all parameters had a potential scale reduction factor < 1.1. Finally variance components were graphically compared (Gelman, 2005).

Results

Exploratory analysis: calving rates

The 21 females in reproductive age were encountered 324 times over the 10-year study period (1.7 ± 1.4 sd encounters per female per month). Two females disappeared from their matriline during the study period and presumably died: C132 (matriline C012) missing since 2010 and C017 (matriline C016) since 2011. A total of 23 births were recorded from the 21 females (Table 1). Mean annual calving rate calculated from observed data and using all non-lactating females (depredated and non-depredated) was 0.123 (SE = 0.021; $n = 10$ years).

Two females never interacted with fisheries (C069 and C116) and were exclusively encountered from the land. These two females produced a total of 1 calf in 10 years. Nineteen females interacted at least once with fisheries. These 19 females produced 22 calves in 10 years.

Calving rates estimated from observed data were higher for depredated females than for non-depredated females when interaction with fisheries occurred either during the birth year (lag 0) or the year before (lag 1) (paired t -test, $t = 5.25$; d.f. = 9; $P < 0.001$ and $t = 2.44$; d.f. = 8; $P = 0.04$ respectively – Fig. 1a,b). Mean calving rate was 0.195 (SE = 0.044; $n = 9$ years) for depredated females the year before (lag 1) and 0.064 (SE = 0.028; $n = 9$ years) calves per female per year for non-depredated females the year before (lag 1). No difference was detected between depredated and non-depredated females 2 years before (lag 2) ($t = 0.914$; d.f. = 7; $P = 0.391$ – Fig. 1c).

Exploratory analysis: interaction level with fisheries

Among the 19 depredated females, C201 (matriline C195) exhibited the lowest level of interaction with fisheries (mean_(hooks) = 1.65 ± 3.90 (sd) $\times 10^3$ hooks per year, averaged over the 2003–2012 period; Fig. 1) and C019 (matriline C018) interacted the most with fisheries (mean_(hooks) = $193.92 \times 10^3 \pm 105.08 \times 10^3$ (sd) hooks per year, averaged over the 2003–2012 period). Overall maximum interaction

rate occurred in 2012 with C019 observed depredated a total of 431.52×10^3 hooks. The mean number of hooks with which female killer whales interacted during years of calving t or previous years $t - 1$ and $t - 2$ was not different from the mean number of hooks with which they interacted over all the other years. (paired t -tests, $t = 1.33$, d.f. = 20, $P = 0.2$ for year t ; $t = -0.16$, d.f. = 20, $P = 0.88$ for year $t - 1$ and $t = -1.41$, d.f. = 17, $P = 0.18$ for year $t - 2$).

Modeling of calving probabilities

To quantify the effect of the number of depredated hooks on female calving probability with the three different time lags (0, 1 and 2), the dataset was restricted to $N = 163$ observations, 21 females and 8 years of data (the first 2 years were discarded because of missing values for lagged covariates). The estimated mean calving probability was 0.145 [95% highest posterior density (HPD) interval: 0.074–0.220]. However, if a female had bred the previous year, this probability was down to 0.008 (95% HPD interval: 0.000–0.032).

The calving probability was best described by the number of depredated hooks and a 1-year time lag [WAIC(hooks)_{lag1} = 115.81 vs. WAIC(\emptyset) = 117.70; Table 3 and Fig. 2]. However, the model posterior probability for a model without interaction with fisheries was similar to that of the model with 1-year lagged interaction rates, suggesting that our data are not overwhelmingly supporting the hypothesis of an effect of interaction rate on calving probability. The model-averaged APC for interaction rate with longliners was an increase of 3.9% (SE: 0.6%) of calving probability. Model-averaged regression coefficients are presented in Table 4 where both 99 and 95% HPD intervals are reported. Matriline and year-level variances were very small (Fig. 2). Models with alternative proxies of interaction rates were also run with similar quantitative results detailed in Supporting Information Appendix S2.

Discussion

Despite the difficulty of precisely measuring females' interactions with fisheries, and a small sample size, our data suggest a positive influence of interacting with fisheries on killer whale reproductive output. In particular, we estimated a small positive effect for interacting with fisheries on the probability of calving the following year (*c.* +4%). Effect sizes are model-averaged, and thus unlikely to be overestimations. However, this effect is unambiguously positive. Depredated longliners may greatly influence the demography of extremely long-lived species such as killer whales. Here the model-based estimate for calving rate of the Crozet female killer whales (0.145 calves per female per year) translates in a female calving interval averaging 8–9 years. As female reproductive age ranges from 10 to 46 years, the female Crozet killer whales may only produce on average three to four calves during their reproductive lifespan. In this context, even an increase of as small as 4% in calving probability may have long-term demographic consequences: reproduction is one of the most sensitive

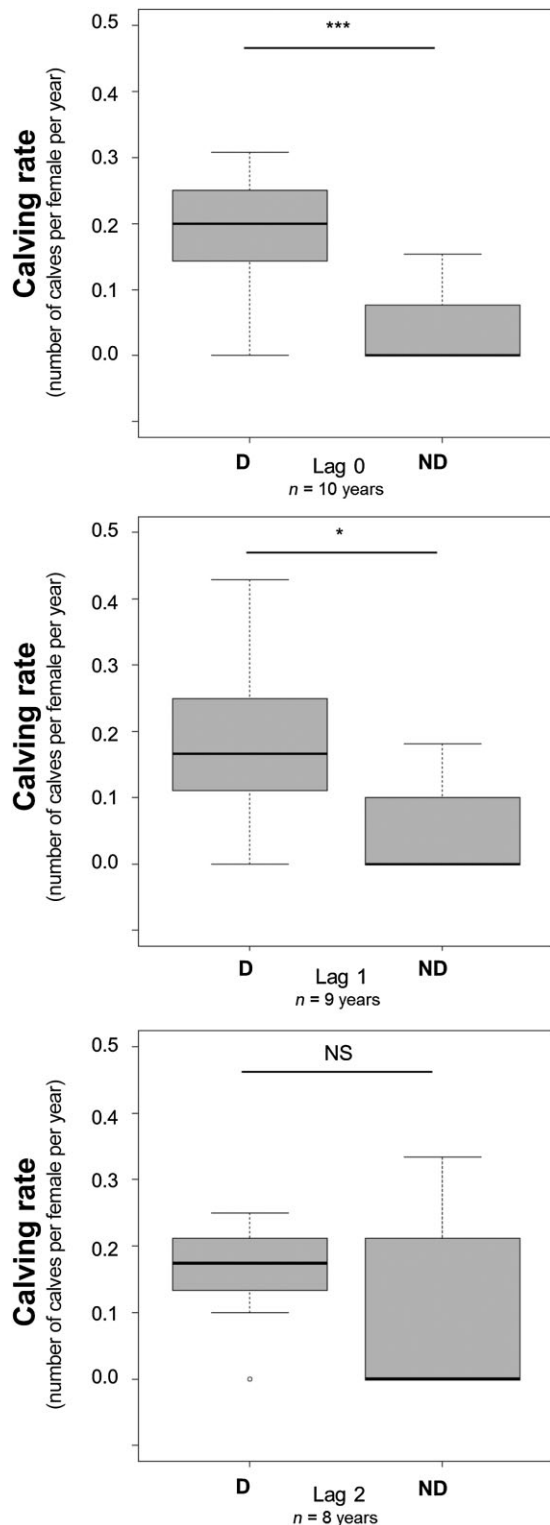


Figure 1 Boxplots of annual calving rates of reproductive female killer whales whether they interacted with fisheries (*D*) or not (*ND*): (a) during the birth year (t ; lag 0). (b) During the year before ($t - 1$; lag 1) and (c) 2 years before calving ($t - 2$; lag 2). Paired t -tests significance codes: (***) if $P < 0.001$; (*) if $0.1 < P < 0.05$; (NS, not significant) if $P > 0.05$.

demographic parameters to environmental changes for an apex and long-lived predator such as killer whales (Ward *et al.*, 2009).

Influence of artificial food provisioning versus reproduction energy costs

This study provides support that artificial provisioning contributes to the observed variations of female calving probability. First, overall comparisons of calving rates between females interacting with fisheries and females not interacting showed that mean calving rates are higher for females depredating longlines, a finding that is apparent in an exploratory and a more complex modeling analysis. The model-based estimate for calving rate (0.145 calves per female per year) is very close to the naïve estimate (0.123 calves per female per year), because matriline- and year-level variances were very small, a finding consistent with that of Ward *et al.* (2009) for north-east Pacific ‘resident’ killer whales. Second, although a number of other factors such as composition of matriline (e.g. age structure) or between-matriline variations of foraging specialization on natural prey, may influence their calving probability (Olesiuk *et al.*, 1990; Brault & Caswell, 1993; Ward *et al.*, 2009), both calving rate and calving interval were higher within matriline interacting with fisheries. Third, one may ask whether matriline are more likely to interact with the fishery in years during which there is a pregnant or a lactating female within that matriline because of additional energy needs (Williams *et al.*, 2011). While we cannot completely rule out that females modulate their interaction rate according to their breeding status, the very small matriline and year-level variances comparisons on observed data suggested that this was not the case. The level of interaction within a group did not vary significantly either during the years prior or just following the occurrence of a birth compared with all other years for that female matriline (see Results from the exploratory analysis). Fourth, three of the 21 females started to interact with fisheries for the first time during the study period, but none of these switches of foraging behavior were correlated to calving events. Finally, recent capture–mark–recapture analyses also showed higher survival rates for all adult killer whales interacting with fisheries than survival rates of killer whales not depredating longlines (Tixier *et al.*, unpublished). This suggests that depredation benefits all members of matriline and not only reproductive females. Females belonging to matriline interacting heavily with fisheries may be more likely to breed compared with those not interacting, most likely because they are in better body condition.

Positive relationships between fecundity and resource abundance and availability and accessibility are widely documented in prey–predator dynamics studies (e.g. Brand & Keith, 1979; Ford & Pitelka, 1984; Pons & Migot, 1995). Ford *et al.* (2009) and Ward *et al.* (2009) showed linear and positive correlations between salmon abundance and reproductive female killer whale fecundity within the ‘resident’ populations of British Columbia. To our knowledge, such

Table 3 Model selection with WAIC (Gelman *et al.*, 2013)

Variable(hooks)	<i>lppd</i>	<i>p</i> WAIC2	WAIC	Prior probability	Posterior probability	APC (%)
∅	-55.00	3.85	117.70	0.25	0.315	0.0 ± 0.0
Lag 0	-53.34	4.86	116.39	0.25	0.265	6.4 ± 1.3
Lag 1	-53.11	4.80	115.81	0.25	0.331	5.8 ± 1.3
Lag 2	-54.49	4.94	118.85	0.25	0.089	1.1 ± 1.2
						3.7 ± 0.6

lppd is the log pointwise predictive density $\sum \log\{E[\rho(y_{\text{obs}}|\theta)]\}$ and *p*WAIC is an approximation to the effective number of parameters in the model computed as $\sum V\{\log[\rho(y_{\text{obs}}|\theta)]\}$. See Gelman *et al.* (2013) for details. The best model with respect to WAIC is in bold. Model posterior probabilities are also reported and suggest mixed support for an effect of depredation on calving rate. However, if present, this effect is estimated to be positive.

APC, average predictive comparison; WAIC, widely applicable information criterion.

Table 4 Regression coefficients of the intercept

	HPD lower bound		Mean	HPD upper bound	
	99%	95%		99%	95%
Intercept	-2.71	-2.43	-1.81	-1.21	-1.03
Calf lag	-12.04	-8.81	-4.37	-0.70	-0.13
(Hooks) lag 0	-0.17	0.00	0.22	1.33	1.84
(Hooks) lag 1	-0.18	0.00	0.30	1.48	1.98
(Hooks) lag 2	-0.38	0.00	0.04	0.59	1.19

State-dependent variable (Calf lag) and the three tested 'number of hooks' variables with lag 0. Lag 1 and lag 2 (years). Both 99 and 95% highest posterior density (HPD) intervals are reported.

correlations between artificial food resource provided by fisheries and marine mammal species have not been documented previously, although fisheries depredation is common worldwide. A positive effect was shown in seabirds and marine mammals feeding on fisheries waste or interacting with fish farms (e.g. Naylor *et al.*, 2000; Furness, 2002). Tixier *et al.* (2010) estimated that Crozet killer whales depredated about 17.7% of the total amount of toothfish caught on longlines between 2003 and 2008, which represented about 116 tons of biomass per year. In 2012, the C018 matriline interacted with 53% of all depredated longlines by killer whales, which gave them access to a minimum of 431 520 hooks and approximately up to 10 tons of toothfish for each of the five individuals of that matriline.

Intra-population specializations and divergent demographic trajectories

In the light of the divergent demographic trajectories between matrilineal lines that interact with the fishery and those that do not, why do only a select few matrilineal lines of the population interact with fisheries? A hypothesis is that interaction rates may be driven by cultural differences in foraging habits. In time, this may change (Rendell & Whitehead, 2001), but some matrilineal lines may never adapt to feeding off of longlines. For instance, sympatric killer whale populations can be highly specialized in their prey choice (Ford *et al.*, 1998) such as the fish-eating population of the north-east Pacific, which are highly dependent on Chinook salmon (Ford & Ellis, 2006). A large part of killer whale behavior, including foraging traditions, relies on cultural transmission

(Ford *et al.*, 1998). We cannot rule out that natural inter-matriline variations of foraging strategies existed prior to fisheries, as already documented in other populations (e.g. Baird & Dill, 1995). Unfortunately, the foraging ecology prior to fisheries of matrilineal lines interacting the most with fisheries is unknown for the Crozet population. While the latter is generalist, it is possibly composed of inter-matriline variation in the various prey items of their diet (including depredated fish), which may have greatly contributed to the divergent demographic trajectories reported here and during the 1990s (see Supporting Information Appendix S3 for details).

Consequences on natural resource conservation and fishery management

Fishery depredation, while influencing the demographic trajectory of the Crozet killer whales, is by no means the main provider of food for the Crozet killer whales. Indeed, on average, killer whales interact 14.7 ± 11.5 days per year with the fishery. Nevertheless, our study showed interacting for a fortnight with fisheries can trigger a 4% increase in calving probability. Can artificial provisioning thus be provided by fisheries sustain an artificially high killer whale population? The calving rate of the Crozet killer whales as a whole (0.145 calves per female per year from the model) remains low when compared with other populations. Olesiuk *et al.* (1990) calculated a calving rate of 0.17 for once exploited killer whales and 0.2 for unexploited 'resident' killer whales of the north-east Pacific. This suggests that the 1990s decline may be still impacting the reproduction of Crozet killer whales, and density-dependent effects are currently unlikely in this population. In addition, the non-interacting component of the population is now rapidly declining because of combined effects unsuccessful reproduction over nearly three decades and increased mortality in recent years because of aging individuals (Poncelet *et al.*, 2010). However, the Crozet southern elephant seal *Mirounga leonina* population has been growing over the last decade. We might expect a reversal of the demographic trajectory and a recovering of the Crozet killer whales in the decades to come because of the combined effect of supplementary food provided by the fishery and the progressive recovery of major natural prey items such as elephant seals.

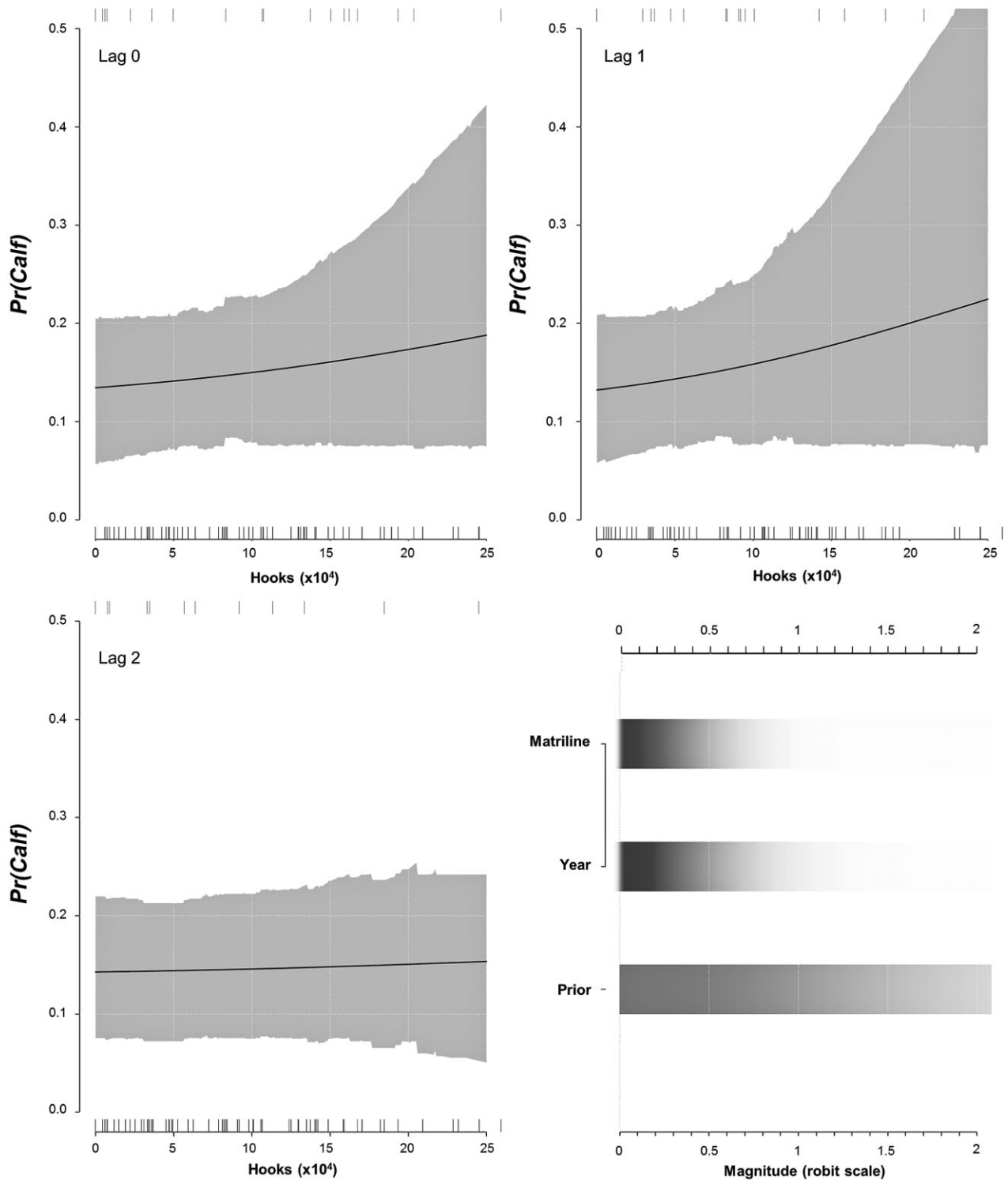


Figure 2 Influence of the level of interaction with fisheries of reproductive females on their probability of calving $Pr(Calf)$. Graphical summary of results obtained when interaction level with fisheries is approximated by the number of depredated hooks ($Hooks$). Upper left corner: model with lag 0 (t); upper right corner: model with lag 1 ($t - 1$); lower left corner: model with lag 2 ($t - 2$); and lower right corner: estimated magnitude of matriline- and year-level standard deviations.

A demographic recovery of the Crozet killer whales could also have consequences on fisheries. The depredation levels reported in the Crozet EEZ are among the largest ever recorded for a similar type of depredation in the world, and cause substantial financial losses to fishing companies (Tixier *et al.*, 2010). Depredation is also expected to impact fish stocks as the amount of captured fish that is depredated by killer whales remains difficult to estimate and therefore to account when defining quotas for vessels.

To conclude, this study, which used long-term monitoring data, provides an example of the consequences of artificial provisioning from fisheries on the demography and ecology of an apex predator. The findings have real-world implications beyond just depredation and raise a number of broad questions about ecosystem-based management of natural resources. More specifically, what are the ecological mechanisms triggering a switch in foraging behavior? How important are culturally transmitted foraging habits on the demography of an apex predator under different environmental pressures? As conservation policies are often designed at the population level, this study is illustrative of the critical need to account for intra-population heterogeneity and cultural foraging habits in conservation plans of such species.

Acknowledgments

This work was conducted as part of the 109 programs with the Institut Polaire Français. Funding and logistic support was provided by the Terres Australes et Antarctiques Françaises, the Réserve Naturelle des Terres Australes and the Reunion Island Fisheries Companies. We are grateful to the Muséum National d'Histoire Naturelle of Paris, and particularly to Guy Duhamel. Special thanks to all the photographers who helped collect photo-identification material. We are grateful to Dr Andy Foote and Jennifer Linton-Harding for proofreading the paper. We are thankful to Robert Pitman and especially to the reviewers for their insightful comments and suggestions to clarify and improve the paper.

References

- Albert, J.H. & Chib, S. (1993). Bayesian analysis of binary polychotomous response data. *J. Am. Stat. Assoc.* **88**, 669–679.
- Baird, R.W. & Dill, L.M. (1995). Occurrence and behavior of transient killer whales: seasonal and pod-specific variability, foraging behavior and prey handling. *Can. J. Zool.* **73**, 1300–1311.
- Bigg, M.A., Olesiuk, P.F., Ellis, G.M., Ford, J.K.B. & Balcomb, K.C. (1990). *Social organization and genealogy of resident killer whales in the coastal waters of British Columbia and Washington State*. Report of the International Whaling Commission, Special Issue. 12, 383–405.
- Botsford, L.W., Castilla, J.C. & Peterson, C.H. (1997). The management of fisheries and marine ecosystems. *Science* **277**, 509–515.
- Brand, C.J. & Keith, L.B. (1979). Lynx demography during a snowshoe hare decline in Alberta. *J. Wildl. Manage.* **43**, 827–849.
- Brault, S. & Caswell, H. (1993). Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* **74**, 1444–1454.
- Cowles, M.K. & Carlin, B.P. (1996). Markov chain Monte Carlo convergence diagnostics: a comparative review. *J. Am. Stat. Assoc.* **91**, 883–904.
- Dahlheim, M.E. (1988). *Killer whale (Orcinus orca) depredation on longline catches of sablefish (Anoplopoma fimbria) in Alaskan waters*. NAWFC Processed Report, Northwest and Alaska Fisheries Center, Seattle, Washington. pp. 88–14.
- Foote, A.D., Morin, P.A., Pitman, R.L., Ávila-Arcos, M.C., Durban, J.W., van Helden, A., Sinding, M.H.S. & Gilbert, M.T.P. (2013). Mitogenomic insights into a recently described and rarely observed killer whale morphotype. *Polar Biol.* **36**, 1519–1523.
- Ford, J.K.B. & Ellis, G.M. (2006). Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Mar. Ecol. Prog. Ser.* **316**, 185–199.
- Ford, J.K.B., Ellis, G.M., Barrett-Lennard, L.G., Morton, A.B., Palm, R.S. & Balcomb, K.C. (1998). Dietary specialization in two sympatric populations of killer whales in coastal British Columbia and adjacent waters. *Can. J. Zool.* **76**, 1456–1471.
- Ford, J.K.B., Ellis, G.M. & Olesiuk, P.F. (2005). *Linking prey and population dynamics: did food limitation cause recent declines of 'resident' killer whales (Orcinus orca) in British Columbia?* Canadian Science Advisory Secretariat Research Document 2005/42.
- Ford, J.K.B., Ellis, G.M., Olesiuk, P.F. & Balcomb, K.C. (2009). Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? *Biol. Lett.* **6**, 139–142.
- Ford, R.G. & Pitelka, F.A. (1984). Resource limitation in populations of the California vole. *Ecology* **15**, 122–136.
- Fox, L.R. (1975). Some demographic consequences of food shortage for the predator, *Notonecta hoffmanni*. *Ecology* **56**, 868–880.
- Fuller, T.K. & Sievert, P.R. (2001). Carnivore demography and the consequences of changes in prey availability. In *Carnivore conservation*: 163–178. Gittleman, T.L., Funk, S.M., Macdonald, D.W. & Wayne, R.K. (Eds). Cambridge, UK: Cambridge University Press.
- Furness, R.W. (2002). Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. *ICES J. Mar. Sci.* **59**, 261–269.
- Gelman, A. (2005). ANOVA – why is it more important than ever (with discussion). *Ann. Stat.* **33**, 1–53.
- Gelman, A. (2006). Prior distributions for variance parameters in hierarchical models. *Bayesian Anal.* **1**, 515–534.

- Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* **27**, 2865–2873.
- Gelman, A. & Hill, J.K. (2007). *Data analysis using regression and multilevel hierarchical models*. Cambridge, UK: Cambridge University Press.
- Gelman, A. & Pardoe, I. (2007). Average predictive comparisons for models with nonlinearity, interactions, and variance components. *Sociol. Methodol.* **37**, 23–51.
- Gelman, A., Jakulin, A., Grazia Pittau, M. & Su, Y.-S. (2008). A weakly informative default prior distribution for logistic and other regression models. *Ann. Appl. Stat.* **2**, 1360–1383.
- Gelman, A., Hwang, J. & Vehtari, A. (2013). Understanding predictive information criteria for Bayesian models. *Stat. Comput.* **24**, 997–1016.
- Guinet, C. (1991). The killer whales *Orcinus orca* of the Crozet archipelago – some comparisons with other populations. *Rev. Ecol. Terre Vie* **46**, 321–337.
- Guinet, C. (1992). Predation behavior of killer whales around Crozet Islands. *Can. J. Zool.* **70**, 1656–1667.
- 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.
- Kuningas, S., Similä, T. & Hammond, P.S. (2013). Population size, survival and reproductive rates of northern Norwegian killer whales (*Orcinus orca*) in 1986–2003. *J. Mar. Biol. Assoc. U.K.* **94**, 1277–1291. (doi: 10.1017/S0025315413000933).
- Leibold, M.A. (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.
- Lewison, R.L., Crowder, L.B., Read, A.J. & Freeman, S.A. (2004). Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol. Evol.* **19**, 598–604.
- Link, W.A. & Barker, R.J. (2009). *Bayesian inference with ecological applications*. 1st edn. London: Academic Press.
- Liu, C. (2004). Robit regression: a simple robust alternative to logistic and probit regression. In *Applied Bayesian modeling and causal inference from incomplete data perspectives: 227–238*. Gelman, A. & Meng, X.L. (Eds). New York: Wiley.
- Lunn, W.T.A., Best, N. & Spiegelhalter, D. (2000). WinBUGS – a Bayesian modelling framework: concept, structure, and extensibility. *Stat. Comput.* **10**, 325–337.
- Naylor, R.L., Goldberg, R.J., Primavera, J.H., Kautsky, N., Beveridge, M.C.M., Clay, J., Folke, C., Lubchenco, J., Mooney, H. & Troell, M. (2000). Effect of aquaculture on world fish supplies. *Nature* **405**, 1017–1024.
- Northridge, S.P. & Hofman, R.J. (1999). Marine mammal interactions with fisheries. In *Conservation and management of marine mammals: 99–119*. Twiss, J.R. & Reeves, R.R. (Eds). Washington, DC: Smithsonian Institution Press.
- 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*. Report of the International Whaling Commission, Special, 209–243.
- Olesiuk, P.F., Ellis, G.M. & Ford, J.K.B. (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.
- Pauly, D., Watson, R. & Alder, J. (2005). Global trends in world fisheries: impacts on marine ecosystems and food security. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **360**, 5–12.
- Pitman, R.L., Durban, J.W., Greenfelder, M., Guinet, C., Jorgensen, M., Olson, P.A., Plana, J., Tixier, P. & Towers, J.R. (2010). Observations of a distinctive morphotype of killer whale (*Orcinus orca*), type D, from subantarctic waters. *Polar Biol.* **34**, 303–306.
- 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. Cet. Res. Manag.* **11**, 41–48.
- Pons, J.M. & Migot, P. (1995). Life-history strategy of the herring gull: changes in survival and fecundity in a population subjected to various feeding conditions. *J. Anim. Ecol.* **64**, 592–599.
- Preisser, E.L., Bolnick, D.I. & Grabowski, J.H. (2009). Resource dynamics influence the strength of non-consumptive predator effects on prey. *Ecol. Lett.* **12**, 315–323.
- Purves, M.G., Agnew, D.J., Balguerias, E., Moreno, C.A. & 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 (2010). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL: <http://www.R-project.org> (accessed 27 August 2014).
- Read, A.J. (2005). By-catch and depredation. In *Marine mammal research: conservation beyond crisis: 5–17*. Reynolds, J.E., Perrin, W.F., Reeves, R.R., Montgomery, S. & Ragen, T.J. (Eds). Baltimore, Maryland: Johns Hopkins University Press.
- Rendell, L. & Whitehead, H. (2001). Culture in whales and dolphins. *Behav. Brain Sci.* **24**, 309–324.
- Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991). Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* **5**, 18–32.
- Skogland, T. (1985). The effects of density-dependent resource limitations on the demography of wild reindeer. *J. Anim. Ecol.* **54**, 359–374.

- Spiegelhalter, D., Best, T., Best, N. & Lunn, D., (2003). *WinBUGS user manual version 1.4*. URL: http://www.politicalbubbles.org/bayes_beach/manual14.pdf (accessed 7 September 2014).
- 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. (2011). Killer whales of the Crozet islands, photo-identification catalogue 2003–2011. (doi: 10.6084/m9.figshare.1085960).
- Tixier, P., Pardo, D., Barbraud, C., Gasco, N., Duhamel, G. & Guinet, C. (unpublished). Demographic consequences of behavioral heterogeneity and interaction with fisheries within a generalist killer whale population. *Oecologia* (unpublished).
- Trites, A.W., Christensen, V. & Pauly, D. (1997). Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *J. North West Atl. Fish. Soc.* **22**, 173–187.
- Ward, E.J., Holmes, E.E. & Balcomb, K.C. (2009). Quantifying the effects of prey abundance on killer whale reproduction. *J. Appl. Ecol.* **46**, 632–640.
- Williams, R., Krkošek, M., Ashe, E., Branch, T.A., Clark, S., Hammond, P.S., Hoyt, E., Noren, D.P., Rosen, D. & Winship, A. (2011). Competing conservation objectives for predators and prey: estimating killer whale prey requirements for Chinook salmon. *PLoS ONE* **6**, e26738.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

- Appendix S1.** Scale mixture of normals and the robit link.
- Appendix S2.** Alternative proxies for female killer whales' interaction level with longline fisheries operating around Crozet archipelago.
- Appendix S3.** Retrospective of the Crozet killer whales demographic trajectories.
- Appendix S4.** Data and WinBUGS codes of analyses.