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Increasing numbers of killer whale individuals use fisheries as feeding opportunities within subantarctic populations

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Fisheries can generate feeding opportunities for large marine predators in the form of discards or accessible catch. How the use of this anthropogenic food may spread as a new behaviour, across individuals within populations over time, is poorly understood. This study used a 16-year (2003–2018) monitoring of two killer whale *Orcinus orca* subantarctic populations (*regular* and *Type-D* at Crozet), and Bayesian multistate capture–mark–recapture models, to assess temporal changes in the number of individuals feeding on fish caught on hooks ('depredation' behaviour) of a fishery started in 1996. For both populations, the number of depredating individuals increased during the study period (34 to 94 for *regular*; 17 to 43 for *Type-D*). Increasing abundance is unlikely to account for this and, rather, the results suggest depredation was acquired by increasing numbers of existing individuals. For *regular* killer whales, a plateau reached from 2014 suggests that it took 18 years for the behaviour to spread across the whole population. A more recent plateau was apparent for *Type-D*s but additional years are needed to confirm this. These findings show how changes in prey availability caused by human activities lead to rapid, yet progressive, innovations in killer whales, likely altering the ecological role of this top-predator.

1. Introduction

Over the past century, anthropogenic activities have profoundly altered resource availability for wild species in ecosystems. While decreasing resources through exploitation, humans also generate new feeding opportunities for various opportunistic species, and these food subsidies can greatly affect population dynamics and ecological interactions [1]. For instance, access to human waste and livestock was found to enhance the demographic performances of terrestrial predators and to subsequently change their role in ecosystem functioning [2]. These positive effects are expected to promote individuals switching behaviour towards feeding

on anthropogenic food subsidies [3] and might offer advantages to these opportunistic individuals, leading to the spread of these behaviours. However, evidence of these new feeding strategies spreading over time within and between populations has remained scarce owing to the lack of long-term data.

In the marine environment, fishing is the activity generating most anthropogenic food subsidies [4]. While species such as seabirds foraging on fisheries waste and discards have received much attention [5], studies on species feeding on fish caught on fishing gear have remained challenging. This feeding behaviour, termed 'depredation', has recently emerged as a major human–wildlife conflict globally involving a broad range of fisheries and top-predator species, primarily sharks and marine mammals, and generating substantial socio-economic and ecological impacts [6].

The killer whale, *Orcinus orca*, (hereafter 'KW') is one of the marine top-predator species most frequently reported depredating on fisheries catches [7]. This behaviour has been developed by different forms and populations of KW worldwide and primarily occurs in longline fisheries [8–15]. While depredation can put KW at risk (e.g. death or injury caused by interactions with fishing gear or fishers [16]), access to catches on longlines, as prey requiring low foraging effort, may also enhance the fitness of depredating individuals [11,16,17]. Therefore, it was hypothesized that depredation may develop as an energetically beneficial behaviour in an increasing number of individuals following the commencement of a fishery that provides KW with new feeding opportunities.

In subantarctic waters, the expansion of commercial longlining targeting Patagonian toothfish, *Dissostichus eleginoides*, in the 1990s was concomitant with KW depredation occurring in most fisheries, from southern Chile to the southern Indian Ocean [18]. The incidence of this behaviour is highest around the Crozet Islands (45° S, 50° E), where KW were reported depredating in the first year of the fishery in 1996 and currently take approximately 180 tonnes of toothfish from longlines every year [19]. In this region, two genetically and ecologically distinct forms of KW depredate on toothfish catches: a form frequently observed in both inshore and offshore waters (hereafter the 'regular' KW), generalist in its feeding preferences, with seals, whales, penguins and fish as natural prey [20]; and the 'Type-D' form, only observed in offshore waters, and for which the diet is unknown [21]. Individuals from both forms have been monitored by an extensive photo-identification programme conducted annually (inshore from the coast since the 1960s, offshore from toothfish longliners since the early 2000s). These data indicate a sharp decline of the *regular* population in the 1990s, mainly caused by whales being shot by illegal fishers when depredating, without any sign of recovery since illegal fisheries were made negligible after the early 2000s [16].

Therefore, using *regular* and *Type-D* KW at Crozet as a unique case-study combining long-term monitoring datasets and the recent emergence of opportunities to depredate on fisheries catches, this study investigated how individuals within top-predator populations may switch to feeding on anthropogenic subsidies over time. Individual data collected during depredation events from fishing vessels over a 16-year period (2003–2018) were used to (i) estimate the annual probability of individuals starting to depredate, and (ii) assess the temporal trends in the annual number of depredating individuals.

2. Material and methods

To investigate the probability of KW starting to depredate and the annual numbers of depredating individuals, a Bayesian Jolly–Seber multistate model was developed including data augmentation based on Kéry & Schaub [22]. A simulation approach was performed to test the robustness of the model to violations of three assumptions: (1) recapture probabilities were independent, (2) sex did not influence survival probabilities, and (3) the distinctiveness of individuals did not affect their recapture probability (electronic supplementary material, S1). This model was applied to mark–recapture data (sighting histories) of KW at Crozet for the 2003–2018 period for *regular* KW, and for the 2009–2018 period for *Type-D* KW (this form was first confirmed depredating in 2003 but observations have remained rare and the data are too sparse prior to 2009).

Mark–recapture data were retrieved from photo-identification data: a technique used to individually recognize KW from photographs of their natural markings (electronic supplementary material, S2). Photographs of both *regular* and *Type-D* KW were taken by fishery observers during depredation events from the seven toothfish longliners allowed to operate off the Crozet Islands (at the edge of the shelf). Photographs of individuals taken from the coast of the main island (i.e. Possession Island, outside depredation events) were available for *regular* KW only, making it impossible to estimate the number of non-depredating *Type-D* KW, if existing in the region, from our data. A total of 119 133 photographs usable for KW photo-identification taken during 1913 encounters between 2003 and 2018 were available for the study. These photographs allowed a total of 182 *regular* and 54 *Type-D* KW individuals to be identified. Individuals were assigned a two-level age class (adult or juvenile) based on secondary sexual features, size and number of years sighted with no morphological change (electronic supplementary material, S2).

The multistate model included four states: (1) not yet in the population, (2) present in the population but not depredating, (3) present in the population and depredating, and (4) dead. Each individual could move only forwards from (1) to (2), (2) to (3) and (3) to (4). The population was simulated as an open population including immigration. Emigration was not explicitly estimated, resulting in a possible decrease in apparent survival probability if some KW emigrated. KW were considered to have acquired depredating behaviour after they were observed depredating once based on field observations. Once a KW had acquired the depredating state, it could not go back to the non-depredating state. Every year each individual could be observed in three different ways: C, observed from the coast but not from the fishing vessels (longliners); B, observed from the longliners, and NE, not observed.

The model allowed four groups of parameters to be estimated for *regular* KW ((1),(2),(3),(4)) and three for *Type-D* KW ((1),(2),(3)): (1) annual recapture probability, depending on the photo-identification platform (coast or longliners) for *regular* KW only. This probability was assumed constant over time from the coast, and to have a linear relationship with the effort, without any random effect of time, from longliners. (2) Survival probability, depending on the age class for both *regular* and *Type-D*, and the behaviour (depredating versus non-depredating) for *regular* only. (3) Annual probability of starting to depredate, being the probability of non-depredating individuals to become depredating for *regular* KW, equivalent to the probability to enter the depredating *Type-D* KW population. This probability included a linear effect of time, but no random effect of year. (4) An entry probability, estimated for *regular* KW only, and being the probability of individuals to enter the non-depredating *regular* KW population. This entry probability was set constant over time but including a temporally heterogeneous rate did not change the results (electronic supplementary material, S1).

Table 1. Parameter estimates (mean, lower and upper bounds of 95% credible intervals) for *regular* and *Type-D* KW, including the entry probability (for *regular* KW only), adult and juveniles survival probabilities (depending on the behaviour depredating versus non-depredating for *regular* KW), and recapture probabilities: q, from the coast; and p, from longliners.

KW type	behaviour	*regular*			*Type-D*		
		2.5%	mean	97.5%	2.5%	mean	97.5%
parameters							
entry probability		0.038	0.044	0.051	—	—	—
juvenile survival	non-depredating	0.745	0.876	0.972	—	—	—
	depredating	0.767	0.888	0.970	0.917	0.976	1.000
adult survival	non-depredating	0.889	0.924	0.952	—	—	—
	depredating	0.908	0.926	0.943	0.903	0.942	0.972
q		0.410	0.478	0.546	—	—	—
p		0.929	0.948	0.962	0.601	0.718	0.814

Linear and nonlinear increasing temporal trends in the annual estimated number of depredating KW over the study period were tested to assess if the number of depredating KW kept increasing or stabilized over this period. Variance-weighted models with an order 1 autocorrelation error with year as the continuous predictor were used to determine the trends. The best fit was tested by comparing Akaike information criteria (AIC) using functions gnls and gls from package nlme in R.

3. Results

The mean entry probability for *regular* KW was 0.044 [0.038;0.051] (here and below, 95% credible intervals are presented in square brackets), indicating a low number of new individuals in the population between 2003 and 2018. Juvenile and adult mean survival probabilities were not statistically different and ranged between 0.87 and 0.92 for both KW forms (table 1). Survival probabilities of depredating *regular* KW were slightly higher but not statistically different from that of non-depredating *regular* KW (effect: 0.34 [−0.98;1.38], table 1).

The probability of individuals starting to depredate increased throughout the time period for *regular* KW, from an estimated 60% [0.48;0.72] in 2003 to 83% [0.66;0.94] in 2018 (slope on the logit scale: 0.08 [−0.01;0.18], figure 1). For *Type-D* KW, this probability (confounded with the entry probability) showed a marginal increase, from an estimated 3% [0.02;0.03] in 2009 to 4% [0.02;0.06] in 2018 (slope on the logit scale: 0.05 [−0.01;0.11], figure 1). As the simulation study showed that the probability of depredation slope might be underestimated, these marginally significant results seem to support the hypothesis of an increasing trend in the probability of starting depredation over time.

From the models, estimates of the number of depredating individuals varied from 34 [32;37] in 2003 to 94 [94;96] in 2014 for *regular* KW (figure 2*a*), and from 17 [16;18] in 2010 to 43 [41;46] in 2017 for *Type-D* KW (figure 2*b*). For both forms, the number of depredating individuals significantly increased from 2003 to 2018, as did the proportion of depredating KW within the *regular* population (electronic supplementary material, S3). Trends in the number of depredating KW were best fitted with a nonlinear logistic relationship for *regular* KW (AIC = 126.8, 119.8 and 106.4 for

the null, linear and logistic regression models). A linear relationship was selected for *Type-D* KW (AIC = 65.8, 57.4 and 61.1 for the null, linear and logistic regression models). However, the patterns indicate some plateauing, and the sample size may not allow more complex pattern detection.

In 2018, the number of KW depredating was 86 [86–88] for *regular* and 40 [35–46] for *Type-D*.

4. Discussion

The present study documents increases in the number of individual KW feeding on fisheries catches within populations of two sympatric subantarctic forms of the species between 2003 and 2018. These increases are unlikely to reflect increases in population size given the poor demographic performances of both *regular* and *Type-D* KW over that period. Indeed, the mean annual population growth rate of *regular* KW has remained negative since the early 2000s, and their adult survival (less than 0.93) has been substantially lower than that expected for growing populations (e.g. greater than 0.98 for the 'northern residents' fish-eating KW of the eastern North Pacific, [23]) (this study, [16,24]). For *Type-D* KW, population trends are unknown, but the adult survival estimates (less than 0.95) produced in this study were also low. Therefore, increases in the number of depredating KW at Crozet are likely the result of existing individuals in populations developing depredation as a new behaviour during the study period. This is further supported by an increase in the probability of individuals starting to depredate over time, and by new adults being observed depredating for the first time late during the study period despite substantial photographic effort over preceding years (electronic supplementary material, S2). For *regular* KW, some of these new adults included whole groups previously only observed foraging on seals and penguins [25].

With a fishery that started in 1996, the nonlinear increase in the number of depredating *regular* KW, which plateaued in 2014, suggests that it took approximately 18 years for all 80–100 individuals of the *regular* KW population to start feeding on fishery catches. *Type-D* KW only became consistently observed depredating from 2009 and, although a nonlinear trend in depredating numbers was not detected
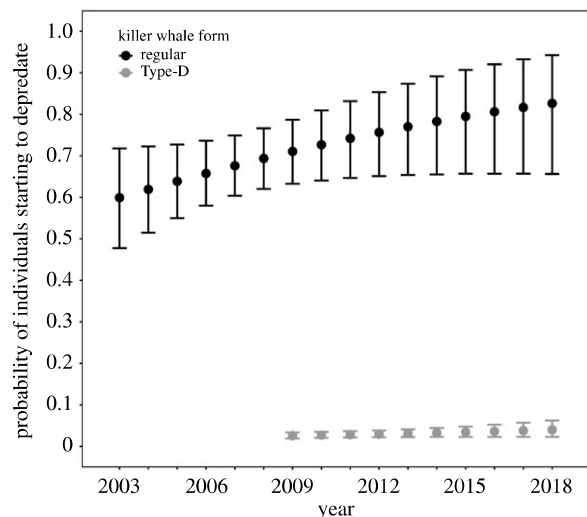
Figure 1. Annual probabilities of individuals starting to depredate, for *regular* KW (black) and *Type-D* KW (grey) for 2003–2018. For *Type-D* KW, estimates were equivalent to the entry probability in the depredating population. Error bars show the 95% credible intervals of the parameters.

(likely because of the limited number of years used in the analysis), a plateau in these numbers was apparent in recent years for this form too. Together, these findings indicate that the behavioural switch to depredation occurred progressively across individuals within populations. Whereas one may expect predators to quickly respond to newly available, high-energy and easy-to-capture prey such as toothfish caught on hooks, the progressive development of depredation by KW may be explained by multiple factors, acting alone or together.

First, the capacity of predators to acquire new feeding strategies and/or to switch diet to new prey may depend on their level of specialization [26]. *Regular* KW, which, as a population, are considered generalist in their feeding preferences [20,27], may include individuals with varying levels of specialization and, therefore, some individuals being more opportunistic and innovative than others in their feeding strategies. Second, as a large part of KW behaviours are socially learnt, one may expect depredation to be progressively horizontally transmitted from groups that have already invented/developed it to other groups [28,29]. While *regular* and *Type-D* KW have been observed simultaneously depredating on the same longline on a few occasions, the social segregation between individuals suggests that depredation has been independently learnt by the two forms (electronic supplementary material, S4). The acceleration in the spread of depredation, as supported by the increasing probability of starting depredation over the years reported here, is typical of horizontal transmission, likely occurring across individuals within each form. For *regular* KW, individuals of which form a single social network whether depredating or not, this transmission may have been further promoted by groups associating more frequently with each other following the 1990s additive mortality event [30]. Third, as documented for terrestrial predators, the propensity of individuals to use anthropogenic subsidies may increase as their natural prey become scarcer and/or if resources provided by humans are predictable in space and in time [31]. At Crozet, toothfish, a natural prey for *regular* KW [20], experienced a period of over-exploitation by illegal fishing until the early 2000s. This period was followed by the
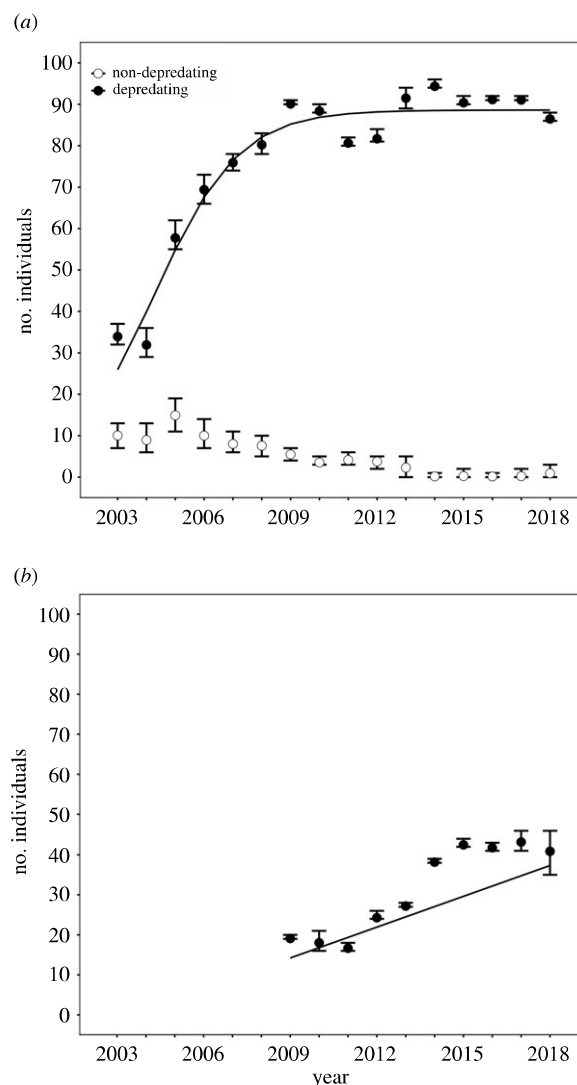

Figure 2. Annual estimates and 95% credible intervals (error bars) of the numbers of depredating individuals (solid circles) and trends (from model predictions—black lines) for (*a*) *regular* and (*b*) *Type-D* KW for 2003–2018. For *regular* KW, estimates of the number of non-depredating individuals (individuals only photographed from the coast) are also provided (empty circles). The decrease in the annual estimates could be due to the death of individuals during the study period.

development of a legal seven-vessel fishery consistently operating every year in the area. Together, a decrease in the natural availability of toothfish paired with increased and predictable opportunities to interact with fisheries may have further engaged individuals to switch to depredation. Lastly, the late development of depredation by some groups may be explained by the fact that it is a risky behaviour and was especially so in the early years of the fishery, when illegal fishers used lethal practices to repel depredating individuals [25].

Increasing numbers of individuals using fisheries as feeding opportunities, reaching a total of greater than 120 (*regular* and *Type-D* combined) at Crozet in recent years, may lead to changes in the role of KW as predators in local ecosystems. This could occur by decreasing predation pressure on natural prey functional groups, in the short term, and by numerically enhancing predator populations, in the long-term [2]. Although the contribution of depredated toothfish to the annual food requirements of KW is limited [32], a facilitated access to this prey through depredation was shown to influence

positively the reproductive output of females of the *regular* form [17]. However, this positive effect was minor, and unlikely to exceed the costs of depredation (e.g. whales being shot by illegal fishers), and, therefore, to help the population to recover, despite increasing numbers of individuals depredating.

In summary, the findings highlight the relatively short time it takes for KW within populations to respond to new feeding opportunities and show how anthropogenic subsidies can rapidly, yet progressively, become prevalent food sources for such top-predators. This study is illustrative of how human activities, by altering the availability of resources in ecosystems, may lead to new behaviours spreading across individuals of species capable of innovating in response to changes in their environment.

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