



Depredation of Patagonian toothfish (*Dissostichus eleginoides*) by two sympatrically occurring killer whale (*Orcinus orca*) ecotypes: Insights on the behavior of the rarely observed type D killer whales

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ABSTRACT

Sympatric forms of ecologically distinctive killer whales (*Orcinus orca*) have been documented worldwide. This study focused on a new case of such sympatric occurrence of the “Crozet” type and the recently described “type D” killer whales off the Crozet Islands. The two ecotypes are morphologically and genetically distinct, but they both depredate the same local longline fishery. We used observational, photo-identification, and fishing data, collected between 2003 and 2015, to examine differences in their patterns of depredation. Of the 828 sets where ecotype could be confirmed, type D killer whales interacted with 82 (11%) of the sets, including 9 (1%) sets that were simultaneously depredated by both ecotypes. Associations between the two types were never observed. Type D killer whales typically occurred in larger groups and both ecotypes preferentially depredated Patagonian toothfish (*Dissostichus eleginoides*). GLMM modeling revealed that the probability of type D depredation significantly increased throughout the study period, especially in deep waters, and photo-identification data suggested that a subset of all individuals were habituating to depredation. This study documents the partitioning of resources between two distinct ecotypes of killer whales and provides preliminary insight into the feeding ecology of the rare type D killer whale.

Key words: killer whale, *Orcinus orca*, ecotype, type D, subantarctic, depredation, fisheries.

Killer whales (*Orcinus orca*) have one of the broadest worldwide distributions of all top predators (Jefferson *et al.* 1991, Forney and Wade 2006), and feed on a wide array of prey items, ranging from small fish to large whales (Ford *et al.* 2009). A number of different ecotypes of killer whales have been described, based on differences in morphology, genetics, feeding ecology, and acoustical behavior (Baird and Stacey 1988; Bigg *et al.* 1990; Baird *et al.* 1992; Baird and Dill 1995; Ford *et al.* 1998; Saulitis

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et al. 2000; Pitman and Ensor 2003; Pitman *et al.* 2007, 2011; Dahlheim *et al.* 2008; Foote *et al.* 2009, 2011; Morin *et al.* 2010, 2015). Many of these ecotypes occur sympatrically and it is likely that distinct feeding specializations, within a highly structured matrilineal social system, have led to such high levels of genetic differentiation (Hoelzel *et al.* 1998; Morin *et al.* 2010, 2015; De Bruyn *et al.* 2013). In fact, it has been suggested that such a high level of differentiation warrants a separation of many of these ecotypes into distinct species (see Morin *et al.* 2010, 2015). In Antarctic and subantarctic waters, five distinct ecotypes of killer whales have been described (types A, large B, small B, C, and most recently, D (Pitman and Ensor 2003, Pitman *et al.* 2011), all with distinct differences in morphology (Pitman and Ensor 2003, Pitman *et al.* 2011) and genetics (LeDuc *et al.* 2008; Morin *et al.* 2010, 2015; Foote *et al.* 2013), with differences in feeding ecology documented in all but type D (Andrews *et al.* 2008, Durban and Pitman 2011).

Among these five ecotypes, type D killer whales are the least known (Jefferson *et al.* 2007, Pitman *et al.* 2011). They are thought to be pelagically distributed within the Southern Ocean (between 40°S and 60°S), but have rarely been observed (Pitman *et al.* 2011). As a result, knowledge about their ecology, including foraging behavior, remains poor. Type D killer whales are considered to be the most distinct morphotype, with unique characteristics such as an extremely small postocular eye patch, bulbous head, relatively small teeth, and narrow dorsal fin with a sharply pointed tip (Pitman *et al.* 2011).

Among the few available records, type D killer whales have been encountered off New Zealand, South Georgia, Crozet Islands, in the southeast Atlantic, and in the Drake Passage (Pitman *et al.* 2011). However, in recent years, the highest reported encounter rate was found off the Crozet Islands (Guinet and Tixier 2011), Indian sector of the Southern Ocean, with substantial photographic data collected from longline fishing vessels operating within the Crozet Exclusive Economic Zone (EEZ) on the edge of the oceanic shelf (Tixier 2012). In 2003, the year of the first confirmed type D sighting off the Crozet Islands, they were observed depredating fish from longline hooks, *i.e.*, they removed and then consumed the captured fish directly from fishing gear (Guinet and Tixier 2011, Tixier 2012). However, depredation is a behavior they have in common with the Crozet type killer whales, a different ecotype found in Crozet waters (Guinet 1991, 1992; Roche *et al.* 2007; Tixier *et al.* 2010, 2014a).

Although they both interact with the same fishery on the same fishing grounds, the two ecotypes are morphologically and genetically distinct (Guinet and Tixier 2011, Tixier 2012, Foote *et al.* 2013). It has been suggested that Crozet type killer whales are most genetically similar to Antarctic type A killer whales.² Acoustic data are lacking for type D and have remained limited for Crozet type killer whales. However, preliminary observational data suggest differences in both distribution and foraging behavior between the two ecotypes as Crozet type killer whales are seen in both pelagic and inshore waters near the islands (Guinet 1991, Guinet *et al.* 2015), and type D killer whales are only observed in pelagic waters (Pitman *et al.* 2011, Guinet *et al.* 2015). The nearshore distribution of Crozet whales has allowed for 40 yr of intensive monitoring, resulting in a broad understanding of their social behavior, foraging ecology and demographics (Guinet and Tixier 2011, Guinet *et al.* 2015). There are currently 86 individuals in the Crozet population (2014 population estimate),

²Personal communication from Andy Foote, Evolutionary Biology Center, Uppsala University, PO Box 256, 751 05 Uppsala, Sweden, October 2014.

comprising 19 stable and long-lasting matrilineal units each composed on average of 3–4 individuals (Tixier *et al.* 2014a). Crozet type killer whales are extremely opportunistic in their feeding behavior. They have been observed naturally feeding on fish, seabirds, seals, and whales (Guinet 1992) and started to interact heavily with the local Patagonian toothfish (*Dissostichus eleginoides*) fishery as longliners began operating in the area in 1996 (Tixier *et al.* 2010; NG, personal observation).

We used 13 yr (2003–2015) of longline fishery and photo-identification data to compare the spatio-temporal distribution, pattern, frequency, and level of depredation of type D and Crozet type killer whales around the Crozet Islands. Here we provide the first insights into the previously unknown feeding ecology of Type D killer whales around the Crozet Islands and demonstrate that it is possible for two morphologically and genetically distinct ecotypes of killer whales to occur sympatrically, exploit the same natural resource, and still exhibit differences in feeding ecology.

METHODS

Data Collection

Data were collected between 1 September 2003 and 23 February 2015, from the seven French longline fishing vessels licensed to fish Patagonian toothfish in the Crozet and Kerguelen EEZ. Killer whale depredation on longline sets remains negligible in the Kerguelen area (Roche *et al.* 2007), therefore this study focused on the Crozet area (Fig. 1a), in which vessels can operate all year-round. All fishing vessels are 60–70 m in length and can remain at sea fishing for several months as the fish is processed, frozen, and stored onboard. All fishing vessels have a fishery observer aboard to monitor each fishing operation. Longlines consist of series of hooks attached every 1.2 m from each other on the main line. The number of hooks per longline ranges from 1,000 to 20,000, on average between 5,000 and 6,000. Hooks are baited automatically and longlines are set during the night as part of the measures to reduce seabird bycatch. Observers collected detailed fishery data during each haul, including whether odontocetes (killer whales or sperm whales *Physeter macrocephalus*) were present. If killer whales were present, observers provided detailed description of their interactions and photographed each whale. As longlines are set at the bottom, at depths ranging from 500 m to 2,000 m, it is assumed that the killer whales can only access the hooked fish during hauling due to their limited diving abilities. Each hauling event was categorized into one of three states: (1) whales present—killer whales showed typical depredation behavior (*e.g.*, whales were observed making repeated dives within an approximate 500 m range from the vessel, they were usually surrounded by birds when they came to the surface, a slick from the oil of the fish was visible, and/or chunks of fish were observed in the mouth of killer whales or birds, indicating they were depredating); (2) whales absent—weather and light conditions suitable for observation; or (3) whales not observed—conditions unsuitable and/or no observation undertaken. For each longline set that was hauled in the presence of killer whales, observers also provided minimum and maximum estimates of the number of whales present.

Fishing data were collected systematically by fishery observers for each longline set and were accessed using the PECHEKER database (Muséum d'Histoire Naturelle de Paris; Martin and Pruvost 2007). We used information on the date, position, and depth of longline sets during hauling phases. Distinction was made between a civil

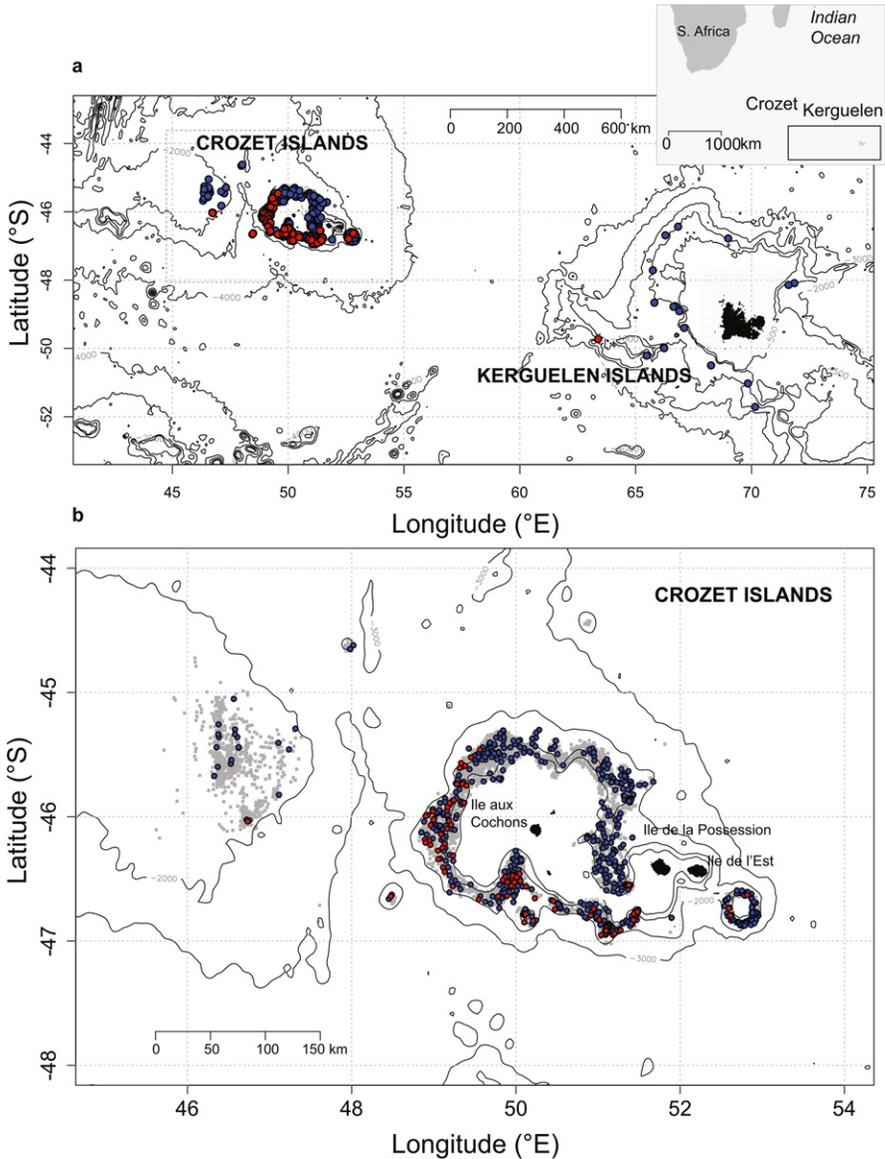


Figure 1. Distribution of longline sets that were depredated by type D killer whales (red circles) and by Crozet type killer whales (blue circles) with (a) depredated sets that were hauled in both the Kerguelen and Crozet EEZs and (b) depredated sets that were hauled in the Crozet EEZ only (gray circles represent the locations of all longline sets that were hauled during the study period).

(calendar) year and a “fishing year.” The latter was adjusted to the 12 mo spanning from 1 September to 31 August, which is the definition used in the regulation of that fishery. Position and depth were recorded for both ends of a longline set, and as most

longlines are set in a straight line, we used the middle position and the median value of depth of longline sets for the analyses. Observers also recorded the number of hooks hauled on each longline as well as the number of undepredated fish (*i.e.*, if the entire fish was landed) for both Patagonian toothfish (target species) and bycatch species. Catch per unit effort (CPUE) was calculated as number of fish per 1,000 hauled hooks.

Photo-identification

Individual killer whales can be identified by naturally occurring nicks and notches on their dorsal fins, dorsal fin shape, and saddle patch pigmentation (Bigg *et al.* 1990). Following protocols described by Bigg *et al.* (1990), observers used a digital SLR camera, equipped with a 400 mm lens, to photograph all whales present, with no emphasis on a particular ecotype if both were present. All individuals were identified and integrated into a catalog that was updated on a regular basis (Tixier *et al.* 2014a, b). As acoustic data were not available during the study period, the initial analysis of the photo-identification data focused on distinguishing which ecotype of killer whale was involved in the depredation event.

We used individual sighting histories to construct social networks of both type D and Crozet type killer whales to determine if there was any social connectivity between the two types. To provide a balance between the representativeness of the data (*i.e.*, include the maximum number of individuals) and its reliability (*e.g.*, include individuals with maximum sighting frequencies), we only included associated individuals that were photographed during the hauling of at least 10 longline sets (individuals were considered as associated if present simultaneously in the same photograph when surfacing). To ensure independence of these association events, a single photograph was used as a single association occurrence when a series of photographs were taken during the same surfacing event and/or during successive surfacing events (*i.e.*, when a series of photographs of the same individuals was taken within a 20 min time interval, which was an approximate value encompassing the maximum recorded dive time of killer whales; Reisinger *et al.* 2015). An unweighted association matrix was constructed from these data (1 if two individuals were photographed simultaneously at least once; 0 if two individuals were never photographed simultaneously). The resulting social network was visualized using the spring-embedding method (Kamada and Kawai 1989).

Loss Due to Depredation

When depredating longline sets, killer whales generally remove the entire fish from the hook and leave no remains. Therefore, we could not estimate the number of depredated fish based on remains and had to use indirect methods. As acoustic data were not available and thus could not be used to assess depredation (Thode *et al.* 2014, 2015), we used instead comparisons of CPUE between nondepredated and depredated longline sets (Gasco *et al.* 2015). Longline sets were identified as nondepredated when neither sperm nor killer whales were confirmed to be present by the fishery observer during hauling. CPUE was assessed for Patagonian toothfish and three bycatch species (or group of species of same genus): grenadier (*Macrourus sp.*), blue antimora (*Antimora rostrata*), and thorny skate (*Raja taaf*). As CPUE is known to greatly vary spatially regardless of depredation, we first created a spatial grid with $0.1^{\circ} \times 0.1^{\circ}$ cells. Then, using fishery catch data, we calculated the CPUE of each cell

as the number of fish per 1,000 hooks using all hooks of nondepredated longline sets that were hauled in that cell over the study period. We performed the same CPUE calculation using depredated longline sets that were hauled when killer whales were the only species to depredate (sperm whales were absent). The ecotype of killer whales was determined from photographs and all longline sets that were simultaneously depredated by Type D and Crozet type whales were omitted. For each ecotype, CPUE was then compared between nondepredated and depredated sets in each cell where both data were available. The resulting difference of CPUE was referred to as “loss due to depredate.”

Statistical Analyses

We used software packages R 3.1.2 (R Development Core Team 2013) for all statistical analyses. We used generalized linear models (GLM, *glm* in R package *stats*) and generalized linear mixed models (GLMM, *lmer* in R package *lme*; Zuur *et al.* 2009) to investigate the differences in the species that were depredated on longlines and differences in the levels of such depredate between type D and Crozet type killer whales. The response variable was the loss due to depredate and the models were fitted with a Gaussian distribution (Shapiro test of normality: $W = 0.865$, $P < 0.001$). The unit of the analysis was the cell and because repeated measures of losses due to depredate were performed within the same cell according to both the species that was caught and to the killer whale ecotype that would depredate, the cell ID was included as a random factor in our models to account for between-measures dependency. The killer whale ecotype was entered as a categorical variable with two levels: type D or Crozet type killer whales. The type of catch was also treated as a categorical variable with four levels: toothfish, grenadier, antimora, and skate. These two experimental variables were tested as both additive and in interaction to examine differences in the species depredated between the type D and Crozet type killer whales. The amount of fish depredated from a longline set has been shown to be significantly impacted by both the fishing practice (Tixier *et al.* 2015a) and the number of depredating killer whales (Tixier 2012). To account for such variability, we also included three numeric variables: mean haul speed, mean length of line, and mean number of killer whales (as estimated by observers) of depredated longline sets that were selected in CPUE calculations in cells.

Temporal and spatial variations of depredate patterns between type D and Crozet type killer whales were also examined using GLM and GLMM. The same procedure of variable selection was used to model the presence (1) or absence (0) data of each killer whale ecotype during depredate events on longline sets where killer whale ecotype could be determined. The response variable was thus binary and models were fitted with a binomial distribution and a log link function. The unit of the analysis was the longline set, *i.e.*, each time a set was hauled and recovered completely. Previous work has demonstrated that the probability of killer whale depredate on longline sets may vary greatly between vessels (Guinet *et al.* 2015). We included vessel ID as a random factor to account for such variability and validate our inference on vessels. However, preliminary visualization of the spatial distribution of depredate events has shown great spatial heterogeneity, especially for type D killer whales. This heterogeneity was also tested as a random factor using a grid over the study area. The size of the cells from this grid was extended to $0.5^\circ \times 0.5^\circ$ to limit the number of levels of the random factor to 47 cell IDs. Time variables were entered in models with two explanatory variables: year (numeric) and month (factor), to evaluate whether a

trend existed over the entire study period, and/or at a seasonal level, irrespective of the probabilities of depredation by either ecotype. The year effect was tested using the fishing year definition to limit heterogeneity in the amount of data between years, especially for civil years 2003 and 2015, which were partially covered. The depths (numeric) at which longlines were set was the third explanatory variable tested in models.

Models were fitted and compared using the Akaike information criterion (AIC, Burnham and Anderson 2002). The significance of explanatory variables was tested by comparing nested models using a likelihood ratio test (LRT).

RESULTS

Data Summary

Between 1 September 2003 and 23 March 2015, a total of 9,432 longline sets were hauled in the Crozet EEZ. Data on presence/absence of killer whales were not available for 867 of these sets and thus were not included in analyses, resulting in 8,565 sets (*i.e.*, 90.8% of the total number). Killer whales from at least one of the two ecotypes were confirmed to be present on 3,724 (43.5%) of these sets over the study period ($0 = 41.3\% \pm 11.0\%$ of longline sets per year).

Photographs were taken on 828 of the 3,724 longline sets that were hauled in the presence of killer whales (22.2%; $\bar{x} = 36.7\% \pm 16.8\%$ per year of depredated longline sets). Type D and Crozet type killer whales were, respectively, present for 11% and 90.1% of the total number of killer whale interactions with the fishery (Table 1), with both ecotypes simultaneously observed depredating only on nine occasions (1.1%). The number of depredating individuals per set was significantly higher for type D ($\bar{x} = 11 \pm 4$, $n = 82$) compared to the Crozet type killer whales ($\bar{x} = 9 \pm 4$, $n = 737$; unpaired *t*-test: $t = 4.49$, $P < 0.001$). Crozet type killer whales were photographed while depredating longline sets during every year of the study, while type D killer whales were photographed in all years except 2005. The maximum number of longline sets depredated by Crozet killer whales was 128 (2008), compared to 23 (2014) for type D killer whales (Fig. 2a).

A total of 73,451 usable photographs of killer whales were taken during the study period, 6% and 94% of type D and Crozet type killer whales, respectively. From these photographs, we were able to identify 39 Type D and 129 Crozet type individuals of both sexes and all age classes (*i.e.*, including newborns, juveniles and adult individuals) that depredated longline sets at least once during the study period (Table 1). The number of newly identified type D individuals plateaued just following fishing year 2009, despite additional depredated sets during that period ($\bar{x} = 3 \pm 5$ new individuals per year between 2004 and 2009; $\bar{x} = 1 \pm 1$ new individuals per year between 2010 and 2014) (Fig. 2a, b). A total of 31 adult type D killer whales were identified in 2014, with 16 of these whales being photographed in every year since 2009 (Tixier *et al.* 2014b). The rate of discovery was higher for the Crozet type killer whales in early years of the study ($\bar{x} = 8 \pm 6$ individuals per year between 2004 and 2010), but leveled off just following fishing year 2010 ($\bar{x} = 2 \pm 3$ individuals per year between 2011 and 2014), with a recent jump in 2013 when seven new individuals were identified (Fig. 2a, b). In 2014, the number of adult Crozet type killer whales totaled 103 identified adult individuals (Tixier *et al.* 2014a).

Table 1. Summary table of available observations, fishing, and photo-identification data recorded during hauling phases of longline sets that were depredated by type D and Crozet type killer whales in the Crozet EEZ. The distinction was made between the number of longline sets that were depredated by the two ecotypes of killer whales separately and simultaneously.

	Type D killer whales	Crozet type killer whales	
Number of photographs	4,437 ^a (6%) 369.7 ± 364.9 ^b	69,014 (94%) 5,751.2 ± 5 072.0	
Number of individual identifications	39 (23.2%) 9.8 ± 9.1	129 (76.8%) 55.3 ± 17.0	
	Type D alone	Both ecotypes together	Crozet type alone
Number of depredated sets	82 (9.9%) 8.2 ± 7.5	9 (1.1%) 0.8 ± 1.0	737 (89.0%) 61.4 ± 35.6

^aTotal.

^bMean ± standard deviation (fishing/year).

Sixty-four adult Crozet type killer whales and 19 adult type D killer whales were photographed associating with other individuals while depredating during at least 10 longline sets and were included in social network analyses. For these individuals, 2,250 photographs showing at least two of these individuals were used as independent association events to construct social networks. Associations between two individuals from the type D and Crozet ecotypes were not documented, resulting in two distinct networks with all individuals (64 adult Crozet type and 19 adult type D whales) linked within their respective networks (Fig. 3).

Losses Due to Killer Whale Depredation

CPUE comparisons between nondepredated and depredated sets were performed in 20 and 104 0.1° × 0.1° cells for type D and Crozet type killer whales, respectively, including 11 cells for which comparisons were made for both ecotypes as they depredated separate sets in the same cell. We found that including the cell as a random factor significantly improved model fit of losses due to depredation over models with only the killer whale ecotype and the type of catch as predictors (LRT: $\chi^2_1 = 31.098$, $P < 0.001$). The haul speed and the length of longline sets as covariates did not improve model fit as expected when compared to models with only the killer whale ecotype and the type of catch as predictors (LRT: $\chi^2_1 = 0.116$, $P = 0.734$ and $\chi^2_1 = 0.333$, $P = 0.564$ for haul speed and length, respectively). The only covariate that significantly improved model fit was the number of killer whales depredating longline sets (LRT: $\chi^2_1 = 14.864$, $P < 0.001$). Therefore, the final model reported here was a generalized linear mixed model with number of depredating individuals, catch type, killer whale ecotype, the interaction between catch type and killer whale ecotype as explanatory variables, and the cell as a random factor.

This model showed no overall differences between type D and Crozet type killer whales on the loss due to depredation for all types of catch (Fig. 4, Table 2). Both

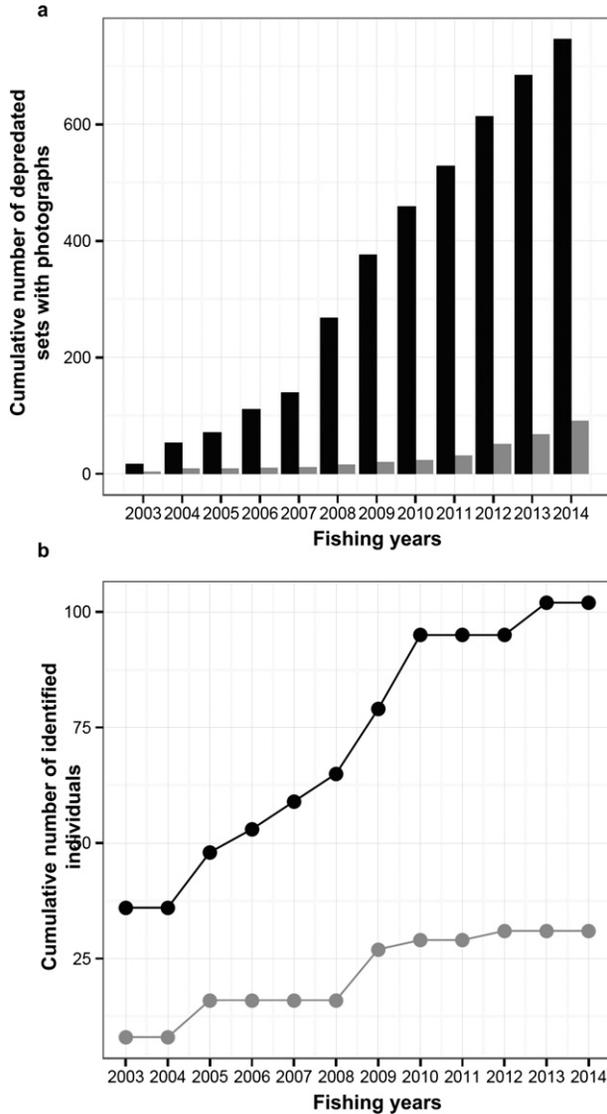


Figure 2. Annual photo-identification effort and number of identified depredating individuals from type D (gray) and Crozet (black) killer whales between fishing years 2003–2014, with (a) the cumulative number of photographically covered and depredated longline sets and (b) the cumulative number of photo-identified adult killer whales (“discovery curves”).

ecotypes of killer whales were found to preferentially depredate Patagonian toothfish on longline sets (*loss_toothfish*: $t = 12.940$, $P < 0.001$). On average, CPUE in number of Patagonian toothfish per 1,000 hooks decreased by $\bar{x} = 26.4\% \pm 74.2\%$ per cell and $\bar{x} = 23.3\% \pm 76.8\%$ per cell when Type D and Crozet type killer whales depredated longline sets respectively. The final model also showed a significant and positive overall linear effect of the number of depredating killer whales on the loss

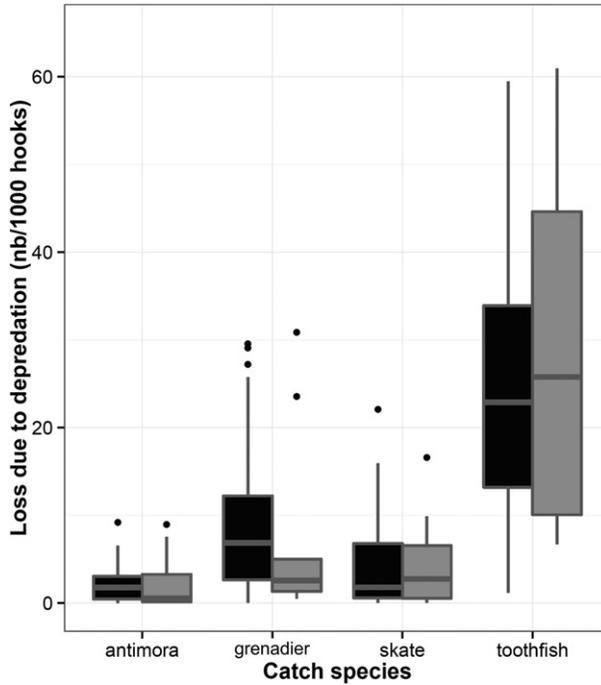


Figure 4. Loss due to depredation by type D (gray) and Crozet type killer whales (black) as estimated from comparisons of observed CPUE between nondepredated and depredated sets within $0.1^\circ \times 0.1^\circ$ spatial cells. CPUE comparisons (in number of fish per 1,000 hauled hooks) were performed for four different catch and bycatch species: Patagonian toothfish, grenadier (“grenadier”), blue antimora (“antimora”), and thorny skate (“skate”).

Table 2. Parameter estimates of the complete GLMM of the CPUE loss due to killer whale depredation. Fixed effects were the number of depredating individuals (nb_ind), the type of catch ($loss_antimora$, $loss_grenadier$, $loss_skate$, and $loss_toothfish$), and the killer whale ecotype (kw_type : Crozet and D). Fixed effects were tested as additive and/or in interaction (*). The random intercept term was the $0.1^\circ \times 0.1^\circ$ cell in which CPUE loss was calculated.

Parameter	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	-7.300	2.277	-3.206	0.001
nb_ind	0.675	0.210	3.210	0.001
$loss_grenadier$	2.934	2.020	1.452	0.147
$loss_skate$	1.913	2.078	0.921	0.357
$loss_toothfish$	26.147	2.020	12.940	<0.001
$kw_type(D)$	-5.403	6.539	-0.826	0.409
$loss_grenadier*kw_type(D)$	-5.185	5.007	-1.036	0.300
$loss_skate*kw_type(D)$	-1.913	5.030	-0.380	0.704
$loss_toothfish*kw_type(D)$	-0.001	5.007	-0.001	0.999

The final models indicated significant between-month variations of the probability of depredation on longline sets for both ecotypes (Table 3). December was the month with highest probability of type D killer whale depredation (0.26, 95% CI: 0.16–

0.30) and lowest probability of Crozet type killer whale depredation (0.77, 95% CI: 0.71–0.83; Fig. 5a). High probability of depredation was also found for type D killer whales in June (0.23, 95% CI: 0.20–0.33), but they were never documented depredating in August, the month of lowest fishing effort ($n = 355$ hauled sets during the study period).

The models suggested a significant year effect on the probability of type D and Crozet type killer whale depredation (Table 3). This effect was positive for type D killer whales (estimate = 1.276 ± 0.211 SE; $z = 6.035$, $P < 0.001$) and negative for Crozet type killer whales (estimate = -1.249 ± 0.220 SE; $z = -5.667$, $P < 0.001$). The probability of depredation by type D killer whales, as estimated by the full model, showed an 84% increase between 2011 and 2014, reaching 0.23 (95% CI: 0.11–0.34) in 2014 (Fig. 5b). Conversely, the probability of depredation by Crozet type killer whales decreased over the study period reaching 0.79 (95% CI: 0.66–0.91) in fishing year 2014.

The depth at which longline sets were hauled had a positive and significant influence on the probability of type D killer whale depredation (estimate = 0.342 ± 0.166 SE; $z = 2.062$, $P = 0.04$; Fig. 6, Table 3). This effect tended to be negative on the probability of Crozet type killer whale depredation (estimate = -0.306 ± 0.169 SE; $z = -1.809$, $P = 0.07$).

DISCUSSION

This study successfully documented the sympatric occurrence of type D and Crozet type killer whales off the Crozet Islands. Both ecotypes were documented depredating local longline fisheries, and on nine occasions, both types simultaneously depredated the same longline set. Social network analysis demonstrated that despite a sympatric occurrence and shared natural resource, there was complete social segregation between the two ecotypes. We were able to show distinct differences in depredation behavior between the two types, providing insight into the feeding ecology of the rarely observed type D killer whale.

Table 3. Summary output of the GLMM models fitted with a binomial distribution on the presence/absence data of type D or Crozet type killer whales during hauling of depredated sets. AIC and LRT outputs of the tested models are provided. Numeric explanatory variables were fishing year (*year*) and depth of longline sets (*depth*). Month (*month*) was tested as a factor with 12 levels.

	Parameters	df	AIC	LRT	P
Type D	(NULL)		(531.40)		
	<i>Year</i>	1	524.81	46.16	<0.001
	<i>Month</i>	11	494.75	36.10	<0.001
	<i>Depth</i>	1	482.78	4.13	0.042
Crozet	(NULL)		(496.40)		
	<i>Year</i>	1	496.75	42.02	<0.001
	<i>Month</i>	11	462.42	27.69	0.004
	<i>Depth</i>	1	457.87	3.14	0.076

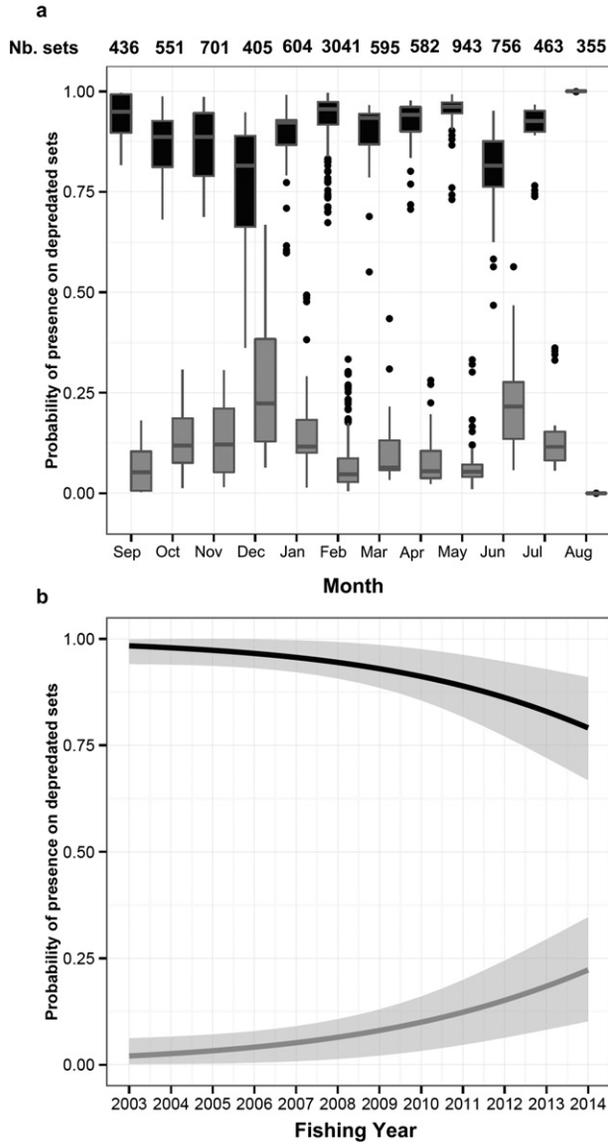


Figure 5. Time variations of binomial probabilities of presence of type D (gray) and Crozet type killer whales (black) on depredated longline sets as predicted by final model maximum likelihood outputs with (a) between-month predictions depicted as boxplots (the total number of sets that were hauled during the study period is given for each month), and (b) linear trend of predictions over the study period (solid curves) and 95% confidence intervals of fitted estimates (light gray shade).

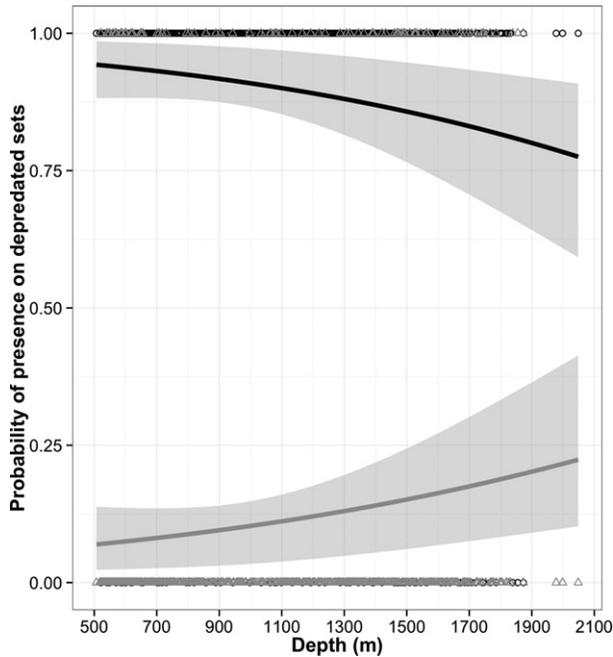


Figure 6. Influence of depth on the binomial probabilities of presence of type D (gray) or Crozet type killer whales (black) on depredated longline sets as predicted by final model maximum likelihood outputs. The linear trends of predictions (solid curves) and 95% confidence intervals of fitted estimates (light gray shade) are depicted, as well as the observed presence/absence data of type D (circles) and Crozet type killer whales (triangles).

Behavioral Patterns of Depredation

This study demonstrates that both killer whale ecotypes do preferentially depredate Patagonian toothfish during hauling operations of longline sets, and shows a significant reduction in toothfish CPUE when either of the two ecotypes is present. The use of CPUE may imply bias due a large number of influencing temporal, spatial, environmental, and biological factors (Maunder and Punt 2004), as well as factors related to the natural distribution of whales (Roche *et al.* 2007). However, a similar decrease in CPUE was reported as the main indicator of depredation for the Crozet type killer whales (Tixier *et al.* 2010), as well as for other odontocete species that have been documented to depredate worldwide (Clark and Agnew 2010, Hamer *et al.* 2012, Peterson *et al.* 2014).

Our results suggest seasonal variability in the probability of both type D and Crozet type killer whale depredation. The natural ecology of type D killer whales is so poorly known that it makes it difficult to speculate about the underlying processes explaining such variability. In December, the probability of depredation was highest for the type D killer whales and lowest for the Crozet type killer whales. Based on our existing knowledge on the Crozet type killer whales, it is likely that the observed decrease during this period was related to the elephant seal (*Mirounga leonina*) breeding period (October–December), during which, some social groups that are known to interact with the fishery, concentrate along shorelines and prey upon newly weaned

elephant seal pups (Guinet 1992, Guinet and Bouvier 1995, Tixier *et al.* 2010). It is likely that the lower occurrence of Crozet type killer whales during this period has resulted in the increased occurrence of type D killer whales through exclusive competition. However, there is no such correlation between the foraging ecology of Crozet type killer whales and the remaining seasonal variability for Type D depredation, including an increase in June and total absence of depredation in August. It is likely that existing seasonal patterns in natural ecology of type Ds are responsible for the variability, but continued and expanded research efforts are necessary to make such inference. Other studies on the depredation of longline fisheries by killer whales have suggested that observed seasonal variability in depredation frequency may be linked to the natural ecology of depredating individuals. For instance, Clark and Agnew (2010) reported a seasonal trend in the incidence of depredation by type B killer whales (likely small Bs) off South Georgia and suggested that such variability could be correlated with long-distance seasonal movements documented for this ecotype (Durban and Pitman 2011). Similarly, studies on the depredation of large terrestrial predators on livestock have revealed that seasonal patterns are often negatively correlated with intraannual variations of natural prey availability (*e.g.*, Patterson *et al.* 2004).

Preliminary Insights on Type D Killer Whale Ecology

The probability of type D killer whale depredation was higher on longline sets that were hauled in deeper waters than in shallower waters. We suggest that type Ds likely spend most of their time in pelagic waters off the Crozet Islands and are therefore more likely to detect and interact with fishing vessels when they operate in deeper waters, farther from the insular shelf. This is consistent with the fact that most encounters of type D killer whales, excluding encounters from fishing vessels, occurred in deep oceanic waters, which is likely to be the favored habitat of this form (Pitman *et al.* 2011). In addition, the depredation events of type D whales are primarily distributed in the southwest part of the Crozet fishing area. The opposite trend is observed for the Crozet type killer whales, which exhibit an increasing probability of depredation on sets in shallower waters, consistent with previous findings (Tixier *et al.* 2015a), and their depredation events are uniformly distributed across the fishing area. This suggests that, unlike the type D killer whales, the Crozet type killer whales are likely to be naturally distributed on the insular shelf closer to the islands, a pattern that is supported by existing knowledge on their prey preferences and foraging strategies observed in inshore waters (Guinet 1991, 1992).

Given the described differences in habitat preference for type D and Crozet type killer whales, one would expect that the feeding ecology would also be quite different. However, both ecotypes readily depredate Patagonian toothfish from longline fisheries, bringing to question whether either type would naturally feed on toothfish or if it is simply a high quality prey item that is made available to both types during fisheries operations. Other studies have shown that most odontocete species that have been observed depredating are naturally fish-eaters (Read 2008, Hamer *et al.* 2012). For instance, sperm whales depredating in the Southern Ocean are known to feed naturally on toothfish (Yukhov 1982). Also, the longline fisheries operating in Alaskan waters are only depredated by the fish-eating killer whale ecotype (*i.e.*, “resident” killer whales) (Matkin *et al.* 2007, Peterson *et al.* 2013, Fearnbach *et al.* 2014). The marine mammal eating ecotype (*i.e.*, Bigg’s killer whales) has never been observed interacting with fishing vessels, although they inhabit the same waters as the

“resident” killer whales (Peterson *et al.* 2013). This suggests that natural prey preferences are likely key determinants of adopting a depredation behavior, especially in killer whales for which a large part of foraging behavior is culturally driven (Ford *et al.* 1998, Rendell and Whitehead 2001). The type D killer whales, based on both our results and on their previously described oceanic habitat, may also feed naturally on fish in deep waters. In this habitat, the limited diving abilities of killer whales (maximum recorded dives were between 500 and 800 m; Reisinger *et al.* 2015), may restrict their foraging activity to the epipelagic and mesopelagic zones of the water column. In this case, benthopelagic species such as the Patagonian toothfish would likely be inaccessible to type D killer whales in oceanic waters. However, we cannot exclude the possibility that type D killer whales have greater diving abilities than other forms of killer whales, which may allow them to access toothfish naturally on the deeper slopes where the species is reported (Collins *et al.* 2010). Other than fish, type D killer whales may also forage on large cephalopods, which are abundant in oceanic waters. Epipelagic cephalopods are known to be a primary prey item for a number of marine predators of the Southern Ocean, including seabirds and deep-diving marine mammals such as long-finned pilot whales (*Globicephala melas*) (Cherel *et al.* 2004, Fontaine *et al.* 2015). Killer whales have occasionally been observed foraging on cephalopods, for example in western Alaska (Hanson and Walker 2014, J. Durban,³ P. Wade⁴). Future analyses of stable isotopes and fatty acids from skin and blubber biopsy samples (Herman *et al.* 2005) will provide insight into the natural diet of type D killer whales.

The Switch to a Depredation Behavior and Competition for a Shared Resource

Our results suggest a significant increase in the proportion of type D killer whale depredation events in recent years. However, the photo-identification data suggest that this increase is not caused by an increasing number of depredating type D killer whales, but rather by the same individuals increasing their frequency of depredation. While some type D killer whales have been observed interacting with the fishery during one year only of the study period, a subset of 51% of all identified adults has been observed every year since 2009 (Tixier *et al.* 2014b). This suggests that a set of type D individuals have recently added depredation to their foraging behaviors and may be habituating to this new behavior. The direct energetic benefit provided by the highly calorific and easy-to-catch depredated Patagonian toothfish is assumed to be the main factor explaining such prey-switching and habituation patterns. In addition, recent studies have emphasized a positive influence of artificial food provisioning from depredation on fisheries on the reproductive output of the Crozet type killer whales (Tixier *et al.* 2015b). Such benefits may also apply to the type D killer whales and further demographic analyses of photo-identification data will help answer these questions.

Increasing depredation of type D killer whales may increase competition for toothfish with the sympatric Crozet type killer whales in future years. Our results demonstrate that type D and Crozet type killer whales are socially segregated, despite the fact that they simultaneously depredated the same longline sets. During these events,

³Personal communication from John Durban, Southwest Fisheries Science Center, NOAA, 8901 La Jolla Shores Drive, La Jolla, CA 92037-1508, January 2015.

⁴Personal communication from Paul Wade, National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Seattle, WA 98115-6349, January 2015.

there was no observed association between the ecotypes and each type remained in close association with one another, maintaining a distance of at least 300 m from each other (PT, personal observation). In contrast, individuals spread out around the vessel when only one ecotype is present. No aggression has been observed between the two ecotypes to date, but it is likely that there is and will continue to be competition for these natural resources.

Finally, such increase of type D killer whale depredation may also strengthen the impacts on the local Patagonian toothfish fishery. This fishery is among the most affected by odontocete depredation worldwide, with the highest interaction rates with killer and sperm whales of all other Patagonian toothfish longline fisheries (Guinet *et al.* 2015). Depredation was estimated to cause a loss of nearly 270 tonnes of toothfish per year (Gasco *et al.* 2015), with dire consequences on socioeconomics for the fishing industry (*i.e.*, additional expenditures for vessels spending more time at sea to finish their quota) and on fish stock management. In addition, in recent years, type D individuals that were primarily encountered in the Crozet EEZ have also been observed depredating longline sets in the Kerguelen EEZ. This documents the presence of type D killer whales in Kerguelen waters for the first time and suggests that these whales move long distances for natural foraging and/or to follow fishing vessels as observed by killer whales in waters of the northern North Pacific (see Fearnbach *et al.* 2014).

In conclusion, this study provides the first evidence of depredation by type D killer whales and although this is an artificial foraging behavior, our results provide preliminary insights into the unknown natural ecology of type D killer whales. We described the sympatric occurrence and shared depredation behavior of two distinct ecotypes of killer whales and explored the spatio-temporal patterns of their depredation behavior. The Crozet island study area provides a unique opportunity to study the type D killer whale, and future efforts will be dedicated to exploring the demography, movements, and natural feeding ecology of this rarely seen ecotype.

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