Contribution of toothfish depredated on fishing lines to the energy intake of killer whales off the Crozet Islands: a multi-scale bioenergetic approach

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ABSTRACT: Fisheries modify prey availability for marine predators by extracting resources but also by providing them with new feeding opportunities. Among these, depredation, which occurs when predators feed on fish caught on fishing gear, is a behavior developed by many species as a way to acquire food through limited foraging effort. However, the extent to which depredated resources from fisheries contribute to the energetic requirements and affect the demography of depredating individuals is unknown. We investigated the contribution of Patagonian toothfish *Dissostichus eleginoides* depredated on longlines to the energetic requirements of killer whales *Orcinus orca* around the Crozet Islands (southern Indian Ocean) over the period 2007–2018. Our results indicate that during days when depredation occurred, depredating individuals fulfilled on average 94.1% of their daily energetic requirements with depredated toothfish. However, the contribution varied from 1.2 to 13.3% of the monthly energetic requirements and from 2.4 to 8.8% of the yearly energetic requirements of the total population. Together, these findings suggest that intake of depredated toothfish can be substantial at a fine scale (daily and individually), potentially leading to temporary provisioning effects and changes in predation pressures. These effects become minor (<10%), however, when considering the full population over a whole year. The contribution of depredated fish to the annual energetic requirements of the population has increased in recent years, likely due to larger fishing quotas and greater opportunities for whales to depredate, which stresses the importance of accounting for depredation in ecosystem-based management of fishing activity.

KEY WORDS: Marine mammals · Depredation · Bioenergetic model · Fisheries interaction · Ecosystem-based management · Top predator conservation · *Dissostichus eleginoides* · *Orcinus orca*

1. INTRODUCTION

The increase in exploitation of marine resources over the past 60 yr has intensified interactions between fisheries and large marine predators (Northridge 1984, 1991, Pauly et al. 1998, DeMaster et al. 2001, Read 2008). Although fisheries decrease prey availability for predators through resource extraction, they can also provide new feeding opportunities to these species. As a way of acquiring food through reduced foraging effort, many species of sharks and marine mammals have learned to feed on

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fish caught on fishing gear, and fishery discards or baits are often used by seabirds (Grémillet et al. 2008, Votier et al. 2013, Tixier et al. 2021). This behavior, termed 'depredation,' has emerged as a worldwide issue in a broad range of fisheries using various fishing techniques (Reeves et al. 2001, Read 2008, Tixier et al. 2021). Longlining stands as the technique most affected by depredation because catches are fully exposed in the water column (Gilman et al. 2006, Read 2008, Hamer et al. 2012, Mitchell et al. 2018).

While depredation has socio-economic impacts on fishing industries through reduced catch rates and damage to fishing gear, it also has effects on biodiversity and ecosystem functioning (Gilman et al. 2006, 2008, Hamer et al. 2012, Mitchell et al. 2018). Among these effects, bycatch and injuries to the predators from direct interactions with fishing gear have been documented in many fisheries (Werner et al. 2015). However, the ecological consequences of depredation, including potential changes in the diet of predators caused by the facilitated access to fish caught on gear, has received less attention. Quantifying these changes, which may alter both predator population dynamics and the natural predatory role of depredating species in ecosystems, is crucial to assess the full trophic impacts of fishing and inform fishery management.

Determining the extent to which predators feed on fishery catches, and specifically how the intake of this resource contributes to the energy requirements of individuals, are central to assessing the ecological effects of depredation. Such information is especially relevant in situations where large-scale fisheries experience high levels of depredation. This is the case for the Patagonian toothfish *Dissostichus eleginoides* (hereafter 'toothfish') longline fishery operating in the French exclusive economic zone (EEZ) of the Crozet subantarctic islands (southern Indian Ocean: 46° S, 51° E). With approximately 280 t (representing 30% of the total catch) of toothfish removed from longlines every year by both killer whales *Orcinus orca* and sperm whales *Physeter macrocephalus*, this fishery is one of the most affected by depredation across longline fisheries globally (Tixier et al. 2019a, 2020). In the Crozet EEZ, toothfish has been targeted as a commercial species since 1996, and the fishery is highly regulated, with fishery observers monitoring all fishing operations and catches from 7 licensed longliners of the fleet (Duhamel & Williams 2011). This fishery is managed by the French government (Administration of the French Overseas Territories, Terres australes et antarctiques françaises), within the general framework of the Convention for the Conservation of Antarctic Marine Living Resources (Hureau 2011). However, the Crozet EEZ experienced substantial illegal, unregulated, unreported (IUU) fishing from 1996 to 2002, resulting in overfishing of local toothfish stocks and severe impacts on predators interacting with vessels (bycatch of seabirds, intentional killing of depredating whales; Guinet et al. 2015, Pruvost et al. 2015).

At Crozet, reports of killer whale depredation began as soon as the fishery started in 1996. It primarily occurs during the hauling part of the fishing process, i.e. when fishers retrieve the longline set (a main line bearing a series of hooks deployed on the seafloor at depths of 500–2000 m) and as toothfish catches become accessible in the water column. When depredating, killer whales repeatedly dive along the line within close range of the vessel and directly remove individual toothfish from the hooks, regardless of whether hauling occurs during the day or at night. These killer whales remove an average of 179 t of toothfish per year from longlines and primarily belong to a local population called the 'Crozet killer whales.' This population has been monitored from the shore of Possession Island (the main island of the archipelago) since 1964 and from fishing vessels off the Crozet Islands since 2003 (Guinet 1988, Guinet & Tixier 2011, Tixier et al. 2021). These killer whales experienced a sharp decline in the late 1990s primarily caused by IUU vessels using lethal measures to prevent depredation interactions; the population currently includes between 89 and 94 individuals (Poncelet et al. 2010, Tixier et al. 2017, 2021). To a lesser extent, depredation events involve Type-D killer whales, a genetically distinct form from the Crozet killer whales found in offshore waters only (Pitman et al. 2011, Tixier et al. 2016).

The Crozet killer whale population has a generalist feeding ecology based on energy-dense prey, including seals, penguins, baleen whales and fish (Guinet 1992, Tixier et al. 2019b, Guinet et al. 2000). According to stable isotope analyses, toothfish was found to be an important prey item, composing more than 30% of the diet of Crozet killer whales irrespective of fishery interactions (Tixier et al. 2019b). Killer whales can hunt toothfish by performing deep dives as suggested by satellite tags and time-depth recorders showing active foraging behavior at the bottom of a Crozet seamount (Richard et al. 2020). These findings support the hypothesis that toothfish was a likely component of the natural diet of killer whales prior to the beginning of the fishery (Guinet et al.

2015). However, the extent to which depredation modifies the importance of that resource for killer whales remains unclear. As toothfish is a deep-water fish, found between 200 and 2000 m, fishing vessels greatly facilitate access to this highly energetic prey for killer whales, increasing toothfish availability in the first meters of the water column during hauling. From these energetic benefits, it can be assumed that killer whales will favor acquiring food through depredation over foraging naturally on toothfish or other natural prey in their diet. Under this assumption, and if toothfish consumed from longlines largely contributes to the prey intake of killer whales, depredation may strongly alter the ecological role of this top predator and, subsequently, the functioning and structure of the local ecosystem.

In the present study, we used a bioenergetic modeling approach to estimate the contribution of depredated toothfish to the energetic requirements of the Crozet killer whales at different temporal scales. Specifically, our first objective was to quantify this contribution at a daily scale when depredation occurred, for individuals involved in these events and for all killer whales in the population. The second objective was to assess the overall contribution of depredated toothfish over larger temporal scales (months and years) and across all killer whale individuals regardless of whether they interacted with the fishery during these time periods. We discuss the implications of our results on fishery management.

2. MATERIALS AND METHODS

2.1. Killer whale abundance

We used data collected under the French Southern Ocean Fishery Observer Program (Gasco 2011) by fishery observers from 2007 to 2018. Fishery observers are assigned on board 100% of the fishing vessels that are allowed to operate in the Crozet EEZ and collect fishery and scientific data on target and non-target species, as well as data on the occurrence and abundance of killer whales involved in depredation events. These data were extracted from the 'PECHEKER' database hosted and managed by the French National Museum of Natural History (Martin & Pruvost 2007, Pruvost et al. 2011). Trained observers conducted visual surface observations during hauling, which is when killer whales come into the vicinity of vessels to feed on catches being brought up by fishers. This observation effort was systematic when light and weather conditions were suitable and

covered on average 90 ± 1% (SE) of the longline sets per year (n = 12 yr; on average, 1005 ± 81 longlines yr^{-1} are deployed). As killer whales rarely leave fish remains on hooks, the occurrence of depredation on a given longline set was confirmed when whales were present and observed repeatedly diving towards the longline being hauled, being surrounded by seabirds and leaving fish oil slicks in the water when coming back to the surface.

For all longline sets with confirmed killer whale depredation, observers systematically recorded the number of killer whales present from visual surface observations. Observers were trained to provide minimum and maximum abundance estimates for each depredated set. Observers were also trained to collect photo-identification data and took photographs of killer whale individuals present using DSLR cameras fitted with 100–400 mm telelenses following a standardized protocol (Gasco et al. 2016). Unlike for the visual observation effort, the photo-identification effort was not systematic and covered on average 31 ± 2.6% of longline sets depredated by killer whales per year (n = 12 yr).

Visual abundance estimates of killer whales per depredated longline set were used for bioenergetic analyses conducted on a daily scale. When killer whales depredated on multiple longline sets hauled by a given vessel during the same day, we used the mean value calculated from the lowest minimum and the highest maximum recorded that day for that vessel. When multiple vessels experienced killer whale depredation when simultaneously operating in the Crozet EEZ during the same day, we used the sum of the average number of killer whales per vessel as the total number of individuals that depredated that day (hereafter the 'daily depredating individuals'). We considered that double counting a whale depredating on different vessels on the same day was negligible since it has only been seen a few times since 2003 (P. Tixier pers. obs.). Observers did not differentiate between the 2 forms of killer whales when visually estimating abundances per depredated set and therefore, daily estimates may have included individuals from both the Crozet and the Type-D form. However, the frequency of occurrence of Type-D killer whales during depredation events was assumed minor compared to that of the Crozet killer whales based on a previous assessment (11 vs. 89% of depredated longline sets for the 2 forms, respectively; Tixier et al. 2016).

Abundance estimates retrieved from photo-identification data were used for bioenergetic analyses conducted at monthly and yearly scales. At Crozet,

photo-identification (from fishing vessels, but also from the shore of Possession Island) allows for high detection rates of the Crozet killer whales (>0.99, Tixier et al. 2017) but is too sporadic for Type-D killer whales to representatively capture all individuals from this form. Because of low detection rates, Type-D killer whales were excluded from analyses at the monthly and yearly scales. Photographs were used to identify and count depredating individuals based on an existing long-term photo-identification database and catalogue (Tixier et al. 2021). From these data, and for each year, individuals were differentiated into calves (individuals <2 yr old, considered un-weaned), juveniles (≥2 and <10 yr old) and adults (≥10 yr old). For killer whales, sex could only be assigned to adults based on secondary sexual characteristics not being visible from the surface until the whale was ≥10 yr of age (hereafter 'monthly' and 'yearly depredating individuals;' Tables 1 & 2). We used the total number of individuals photo-identified per year from both fishing vessels and Possession Island as the total population abundance of the Crozet killer whales (hereafter 'all individuals').

2.2. Estimation of depredated toothfish biomass

When depredating toothfish from longlines, killer whales generally remove the entire fish from the hooks, leaving no quantifiable evidence; indirect statistical methods are thus necessary to estimate the

quantity (or biomass) of fish caught on the lines. This quantity was estimated by Tixier et al. (2020) using a generalized additive model. The model was fitted to the catch per unit effort at the level of each longline set (1 main line bearing a series of approximately 5000 hooks deployed on the seafloor with 1 buoy at each end). The model incorporated the presence and the number of depredating killer whales around fishing vessels (excluding longline sets for which this information was not available, ~10%) along with the depth, location, soak time, vessel, year and month as covariates. The amount of toothfish depredated by killer whales was estimated as the difference between the amount of toothfish expected to have been landed on vessels if whale depredation had not occurred (predicted catch in the absence of whales) and the amount of toothfish expected to have been landed if whale depredation had occurred (predicted catch in the presence of whales) depending on the number of depredating individuals present.

Estimates of depredated toothfish (in t, with 95% confidence intervals, CIs) were obtained for each longline set for which the occurrence of killer whale depredation was confirmed by fishery observers, and summed by day, month and year for the analyses (Tables 1 & 2). However, when fishery observers could not conduct visual observations, the dataset included longline sets for which the occurrence of killer whale depredation was unknown. This bias is limited for the large-scale analyses (months and years) because the proportion of non-observed sets has remained rela-

Table 1. Summary of the annual data collected at Crozet between 2007 and 2018 and used in our study. $Nb_{kw,i}$: number of weaned killer whale individuals used in the analysis; calves (number in parentheses) were excluded from the analyses. 'All individuals', include depredating individuals, and since 2014, all individuals of the population have been depredating. Toothfish biomass (t), including the catch landed by the fishery and the depredated biomass (Q_i) were retrieved from Tixier et al. (2020). Fishing days included in $Nb_{days,i}$ ($Nb_{days,i}$ represents fishing days in daily analysis and all days for monthly and yearly analyses)

| Year | $Nb_{kw,i}$ | | Toothfish biomass | | Number of fishing days | |
	All individuals	Depredating individuals	Depredated by killer whales (Q_i)	Landed by fishing vessels	Total	With depredation (%)
2007	72 (4)	64 (3)	70.6	392	168	83 (49.4)
2008	79 (4)	71 (4)	135.0	868.6	184	100 (54.3)
2009	89 (6)	82 (6)	192.0	880.6	222	171 (77.0)
2010	85 (4)	80 (4)	109.5	649	139	98 (70.5)
2011	78 (2)	74 (1)	137.0	706.7	95	60 (63.2)
2012	74 (6)	69 (5)	269.0	814.2	143	99 (69.2)
2013	84 (6)	81 (5)	213.0	777.2	173	101 (58.4)
2014	89 (3)	89 (3)	229.8	732.6	139	94 (67.6)
2015	85 (5)	85 (5)	186.4	836.3	196	119 (60.7)
2016	80 (7)	80 (7)	185.1	1059.2	184	116 (63.0)
2017	83 (8)	83 (8)	223.8	1170.9	240	139 (57.9)
2018	81 (6)	81 (6)	277.2	1101.1	235	134 (57.0)

Table 2. Summary of the monthly data collected at Crozet in 2009 and used in our study. $Nb_{kw,i}$: number of killer whales is the number of weaned individuals used in the analysis; calves (number in parentheses) were excluded from the analyses. 'All individuals' include depredating individuals. Toothfish biomass (t), including the catch landed by the fishery and the depredated biomass (Q_i) were retrieved from Tixier et al. (2020). Fishing days included in $Nb_{days,i}$ ($Nb_{days,i}$ represents fishing days only in daily analysis and all days for monthly and yearly analyses)

| Month | $Nb_{kw,i}$ | | Toothfish biomass | | Number of fishing days | |
	All individuals	Depredating individuals	Depredated by killer whales (Q_i)	Landed by fishing vessels	Total	With depredation (%)
January	89 (6)	45 (1)	4.0	13.3	11	3 (27.3)
February	89 (6)	65 (2)	24.8	153.8	28	24 (85.7)
March	89 (6)	12	11.7	45.2	15	13 (86.7)
April	89 (6)	46 (6)	26.3	143	30	26 (86.7)
May	89 (6)	56 (2)	39.8	143.5	31	25 (80.6)
June	89 (6)	26 (3)	13.9	35.6	24	21 (87.5)
July	89 (6)	NA	8.0	34.1	30	12 (40.0)
August	89 (6)	38 (1)	14.8	35.4	13	10 (76.9)
September	89 (6)	22 (2)	16.0	30.8	9	9 (100.0)
October	89 (6)	8 (2)	4.5	8	5	5 (100.0)
November	89 (6)	11	20.8	82.3	18	17 (94.4)
December	89 (6)	11 (1)	3.7	12.6	8	6 (75.0)

tively constant (12.7 ± 3.4% SE across months in 2009 and 9.7 ± 1% across years), and we estimated the overall contribution of depredated fish in monthly or annual requirements (including all days of the time period, regardless of whether there was fishing activity and/or depredation). Indeed, if depredation had occurred during these unrecorded sets, the amount of toothfish removed was undetermined; hence the summed quantities should be considered as minimum estimates. However, on a daily basis, the potential bias of unrecorded sets was considered significant because we were only interested in analysis on days with depredation; it was therefore necessary to remove days with at least 1 unrecorded set from the analysis, and we only considered 100%-observed days.

2.3. Contribution of depredated toothfish to the energetic requirements of killer whales

The contribution of depredated toothfish to the energetic requirements (C_i, Eqs. 1 & 5) of killer whales was assessed at 3 temporal scales. Annual assessments were conducted over the period 2007–2018, and daily and monthly assessments were performed for the year 2009 only. This specific year was representative of the time series in terms of both the extent and the temporal distribution of the fishing effort (Table 1). It was also chosen because 2 fishing trips had observers dedicated to collecting data on killer whales, resulting in extensive photo-

identification effort and increased accuracy of abundance estimates.

C_i was estimated at different temporal scales of i (day, month, year) using several parameters: one was fixed (the energetic content of Patagonian toothfish; ED) and the others varied depending on the time scale i considered: the depredated biomass (Q_i in t), the number of killer whales, excluding calves ($Nb_{kw,i}$), the number of days (fishing days in daily analysis and all days for monthly and yearly analyses; $Nb_{days,i}$) and the daily prey energetic requirements ($DPER_{year}$):

$$\overline{C} = \frac{\text{Energy intake from depredation}}{\text{Killer whale energetic requirements}} \times 100 \quad (1)$$

The energy intake from depredation was calculated from the ED (in kJ g^{-1}) and Q_i.

ED was assumed to be 9 kJ g^{-1} wet weight, which is the value used in the most recent study and close to the mean value of the 3 ED values found in the literature (10.5, 7.8 and 9 kJ g^{-1}, respectively, in Eder & Lewis 2005, Vanella et al. 2005, and Schaafsma et al. 2018).

Q_i was the sum on different time scales i (day, month or year) of the model outputs we used (see Section 2.2; Tables 1 & 2). If $Q_i \sim N(\overline{Q}_i, se_{Q_i})$, then

$$C_i \sim N\left(\frac{\overline{Q}_i \times \text{ED}}{Nb_{kw,i} \times \text{DPER} \times Nb_{days,i}}, \frac{se_{Q_i} \times \text{ED}}{Nb_{kw,i} \times \text{DPER} \times Nb_{days,i}}\right) \quad (2)$$

Energetic requirements of killer whales were calculated with the $Nb_{kw,i}$ (see Section 2.1), $Nb_{days,i}$ and $DPER_{year}$ depending on the time scale i (Tables 1 & 2

and see Table S1 in the Supplement at www.int-res.com/articles/suppl/m668p149_supp.pdf).

$DPER_{year}$ is the mean value of individual energetic requirements per day and was calculated from the basal metabolic rate (BMR in kJ d^{-1}), which was estimated separately for juveniles, adult females and males using a generic model (Kleiber 1975, Barlow et al. 2008, Spitz et al. 2018, Lefort et al. 2020). As BMR is a function of individual body mass (M in kg), and measuring individual body mass is almost impossible from field studies on wild cetacean populations, we used a length–mass regression for killer whales of the South African subregion: $M_g = 8.6791 \times L_g^{3.2769}$, where g is the class of individuals (adult female [f], adult male [m] or juvenile [j]; Best 2007, Reisinger et al. 2011a). BMR_g (Eq. 3) was estimated for each class g of the population, where L_g was 6.75 and 7.75 m for adult females and adult males, respectively (Best et al. 2010), which appears to be consistent with the few data from individuals stranding in Crozet (French Marine Mammal Stranding Database, www.observatoire-pelagis.cnrs.fr/pelagis-2/bases-de-donnees/), and 4 m for juveniles (Esteban et al. 2016, see detailed values in Table S2) as:

$$BMR_g = 293.1 \times M_g^{0.75} \qquad (3)$$

$DPER_{year}$ (Eq. 4) was consequently estimated as a function of the weighted average BMR_g calculated every year depending on the demographic composition of the population, p(g,year), where p(j,year) is the proportion of juveniles in the population in each year, p(f,year) is the proportion of adult females, and p(m,year) is the proportion of adult males per year (see Table S1):

$$DPER_{year} = \beta \times \frac{\sum[BMR_g \times p(g,\text{year})]}{\alpha} \qquad (4)$$

where β is the energetic cost of physiological and physical activities and α is the assimilation efficiency (Williams et al. 2004, Spitz et al. 2012).

Different values of β have been used in previous studies on cetaceans, ranging from 1.2 to 6 (Barlow et al. 2008, Santos et al. 2014, Spitz et al. 2018). Killer whales are among the cetacean species with the highest cost of living, e.g. cost of foraging, reproduction and thermoregulation, so we used a value of β = 5.5 (Noren 2011, Santos et al. 2014, Lefort et al. 2020). α was estimated at 0.85 for killer whales (Williams et al. 2004, Noren 2011, Reisinger et al. 2011a, Lefort et al. 2020).

Once these parameters were estimated, the contribution of depredated toothfish to the energetic requirements of killer whales was calculated as:

$$\overline{C}_i = \frac{Q_i \times ED}{Nb_{kw,i} \times DPER_{year} \times Nb_{days,i}} \times 100 \qquad (5)$$

Q_i, $Nb_{kw,i}$ and $Nb_{days,i}$ are given in Tables 1 & 2, and C_i was estimated for depredating individuals and all individuals at each time scale.

All statistics were performed using R version 4.0.3 (R Core Team 2020).

3. RESULTS

3.1. Contribution of the depredated toothfish to daily prey requirements

Data from a total of 113 fishing days during which depredation occurred in 2009 (51% of all days with fishing and 66% of all fishing days with depredation) were used to assess the contribution of depredated toothfish to killer whale energetic requirements (C_i) at the daily scale. During these 113 days, the mean daily toothfish biomass depredated by killer whales was 1.2 ± 0.08 t (SE), ranging from 0.1 to 4.9 t, and the mean number of daily depredating individuals was 9.3 ± 0.5, ranging from 3 to 30 individuals. Consequently, the median daily intake was estimated to 103 kg (14–418 kg) of depredated toothfish per individual involved in depredation. With killer whale $DPER_{2009}$ estimated at 995 MJ d^{-1} (see Table S1), the daily C_i during days when depredation occurred was estimated to be 94.1% (95% CI: 80.4–107.8%) for depredating individuals (Table 3). The daily C_i was estimated to be higher than 100% during 48% of the days studied (55 of the 113 fishing days; see Fig. S1). When considering the daily energetic requirements of all killer whales of the population in 2009 (n = 89 weaned individuals, comprising 17 weaned juveniles, 19 adult males and 53 adult females; see Table S1), the mean daily C_i was estimated at 8.5% (95% CI: 7.5–9.4%).

Table 3. Estimates of the mean daily contribution (%) of depredated toothfish to the energetic requirements (C_i) of daily depredating killer whales (daily mean ± SE and min–max shown) and of all individuals of the population for the year 2009 (n = 113 fishing days)

	No. of ind.	C_i
Depredating killer whales	9.3 ± 0.5 3–30	94.1 (95% CI: 80.4–107.8)
All killer whales	89	7.3 (95% CI: 0–14.7)

3.2. Intra-annual variation

In 2009, the monthly number of killer whale individuals identified while depredating toothfish varied from 8 in October to 65 in February. The monthly C_i was not estimated for depredating individuals in July because no photo-identification effort could be conducted during hauling in July despite 39 longline sets depredated (6% of all sets depredated in 2009). Also, 1 day was removed from the analysis because visual estimates of depredating killer whales during this day exceeded the total number of depredating individuals determined by photo-identification during this month. For the same reason, for 4 days, the number of depredating killer whales was the minimum estimate from fishery observers.

The depredated biomass of toothfish per month ranged from 3.7 t in December to 40 t in May (Table 2). For those 2 months, a total of 11 and 56 killer whale individuals were identified depredating, respectively, resulting in monthly C_i values of 9.9% (95% CI: 8.5–11.4%) and 21.2% (95% CI: 18.1–24.2%) (Fig. 1). Monthly C_i was at a minimum in January (2.7%, n = 45 individuals) and a maximum in November (60.6%, n = 11 individuals). When considering monthly energetic requirements of all 89 weaned individuals of the population in 2009, the monthly C_i ranged from 1.2% (95% CI: 1.0–1.4%) in December to 13.3% (95% CI: 11.4–15.2%) in May (Fig. 1).
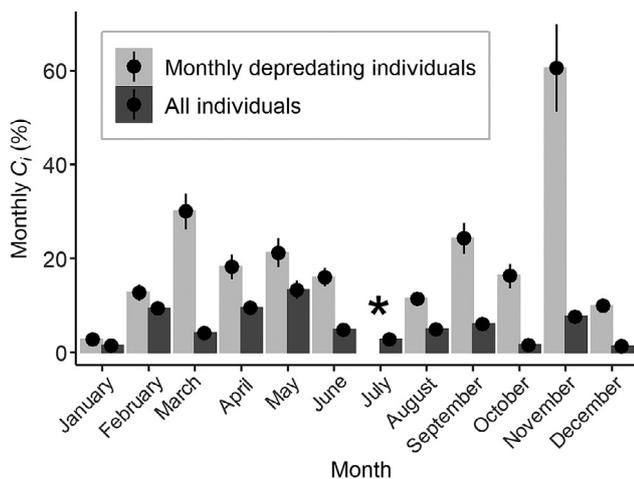
3.3. Inter-annual variation

In 2009, 82 weaned killer whale individuals (92% of all weaned individuals identified that year) were identified at least once while depredating toothfish, and a total of 195 t of toothfish was estimated to have been depredated by killer whales (Table 1). As such, over the whole year, which comprised 171 fishing days with depredation, 51 fishing days without depredation and 143 days without any fishing, the annual C_i in 2009 was 5.9% (95% CI: 5.1–6.7%) for yearly depredating individuals and 5.4% (95% CI: 4.7–6.2%) when considering all individuals (Fig. 2).

The proportion of the Crozet killer whale population interacting with the fishery increased from 89–96% between 2007 and 2013, to 100% between 2014 and 2018 (Table 1). Overall, the mean number of yearly depredating killer whales was 78, ranging from 64 to 89 individuals, and the mean biomass of toothfish depredated by killer whales was 185 t yr^{-1} (range: 71–277 t yr^{-1}; n = 12 yr; Table 1). Over this period, the DPER$_{year}$ of killer whales varied between 951 and 1036 MJ d^{-1} ind.$^{-1}$, depending on yearly group composition (see details in Table S1). For both depredating individuals and all individuals of the population, annual C_i was the lowest in 2007 with 2.7% (95% CI: 2.2–3.2%) (n = 64 depredating individuals) and 2.4% (95% CI: 2.0–2.9%] (n = 72 weaned individuals) and increased to 8.5% (95% CI: 7.4–9.9%) in 2018 (n = 81 weaned individuals, all depredating). C_i was highest in 2012, with 9.4%

Fig. 1. Contribution of depredated toothfish to monthly energetic requirements (C_i) of the Crozet killer whales for depredating individuals only (n = 333 d) and for all individuals in the population (n = 365 d) in 2009. Error bars are 95% CI. ★In July, the contribution was not estimated for depredating individuals due to lack of data
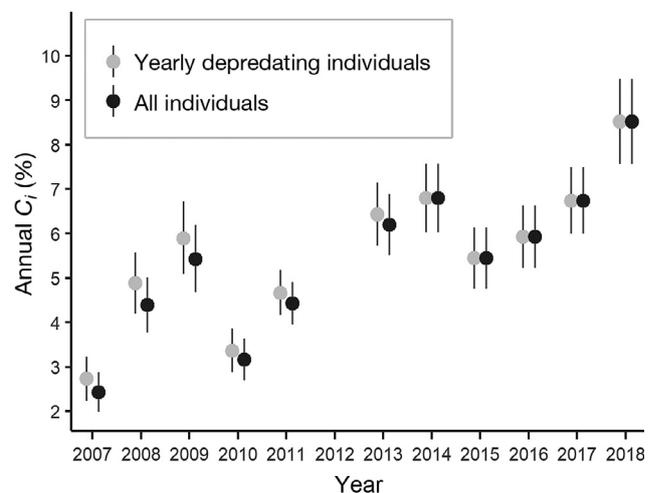

Fig. 2. Contribution of depredated toothfish to the annual energetic requirements (C_i) of the Crozet killer whales, for depredating individuals only and for all individuals in the population between 2007 and 2018 (n = 12 yr). Error bars are 95% CI

(95% CI: 8.4–10.5%) (n = 69 depredating individuals) and 8.8% (95% CI: 7.8–9.8%) (n = 74 weaned individuals; Fig. 2).

4. DISCUSSION

We used a bioenergetic approach to estimate the contribution of a prey, to which access is facilitated by longline fishing operations, to the energetic requirements of killer whales. Our findings suggest that during days when killer whales interacted with fishing vessels, individuals generally fulfilled the entirety of their daily requirements with toothfish acquired from depredation on longlines. This contribution became minor when calculated across the whole population over larger time scales, since only small subsets of individuals interacted with the fishery on a given day and the fishery does not operate all year round. However, as toothfish caught on fishing gear represents an easy-to-capture prey potentially favored by this top predator over natural foraging activities, we discuss the various ecological implications of depredation.

4.1. Contrasting benefits from depredation according to time scale and population scale

Killer whales that interacted with the fishery during a given day generally fulfilled, and even exceeded, their daily energetic requirements with toothfish depredated on longlines. As access to this resource requires low foraging cost, this intake is likely to maximize energetic benefits for these individuals and subsequently their fitness. This is similar to other forms of anthropogenic food subsidy effect found in other predators feeding for instance on fishery discards or on human wastes in terrestrial systems (Beckmann & Lackey 2008, Bino et al. 2010, Oro et al. 2013, Newsome et al. 2015). For the Crozet killer whales, this assumption is supported by the reproductive output of females, which is positively correlated to the fishery interaction rate (Tixier et al. 2015a). This positive effect was also documented in killer whales depredating large Atlantic bluefin tuna *Thunnus thynnus* caught by a dropline fishery in the Strait of Gibraltar (Esteban et al. 2016). However, while the fitness of the Crozet killer whales may be enhanced by the energetic benefits of depredation, this provisioning effect did not positively influence the demographic trajectory of the whole population.

Regardless of its potential energetic benefits, depredation can be risky for individuals engaging in such behavior, as interaction with the fishing gear can lead to injuries, bycatch and/or lethal responses from fishers (Werner et al. 2015). At Crozet, bycatch of killer whales has never been recorded and the risk of being shot by fishers from the legally operating and highly regulated fleet is no longer a threat. However, individuals may still be subject to detrimental interactions with IUU vessels potentially operating in the periphery of the Crozet EEZ and known to use lethal means to repel depredating whales. This has been hypothesized as one of the main reasons preventing recovery of the Crozet killer whale population from the mass mortality experienced during the late 1990s to early 2000s (Poncelet et al. 2010, Guinet et al. 2015, Busson et al. 2019). In addition, the limited contribution of depredated toothfish to the total energetic requirements of the whole population estimated in this study (2.4–8.8% yr^{-1}) may have been overestimated, as it does not consider the number of Type-D killer whales also depredating at Crozet. Together, these observations may partly elucidate why, despite Crozet being the area with the highest depredation levels across toothfish fisheries (Tixier et al. 2019a, 2020), intake of depredated toothfish has not been sufficient to accelerate the recovery of the Crozet killer whale population from the decline it underwent in the 1990s (Poncelet et al. 2010). Indeed, between 2003 and 2011, this killer whale population still exhibited lower survival rates than those expected if the population was healthy (Tixier et al. 2017).

4.2. Potential effects of depredation: predation release or substitution of natural toothfish prey

Assuming that killer whales would have foraged on prey other than toothfish if fishing vessels were not operating in the area, our findings suggest that depredation can induce a displacement of predation pressure from this top predator within the ecosystem. If killer whales fulfill 100% of their energetic requirements with depredated fish during a given day, it can be assumed that these whales will not spend time foraging on other natural prey species during this day. For the Crozet killer whales, these other natural prey species include southern elephant seals *Mirounga leonina*, king penguins *Aptenodytes patagonicus* and whales (Guinet 1992, Tixier et al. 2019b). As such, the greater the number of individuals simultaneously depredating (some days reaching

30 individuals, approximately 1/3 of the whole population), the more predation pressure on other prey items may be relaxed. This ecological effect may intensify during months of extensive fishing effort for when killer whales had opportunities to interact with many vessels over many days. Overall, months with high fishing effort were associated with large numbers of depredating killer whales and a high contribution of depredated toothfish to the energetic requirements of the whole population (>10%). One exception to this was found in November 2009, when despite high fishing effort (18 fishing days), a limited number of killer whales (n = 11) was observed depredating. This low abundance of killer whales was also observed during the October to December period (n = 8–11), which is also the time of the year when recently weaned elephant seal pups become abundant in inshore waters and may be preferred by the Crozet killer whales over other prey. This potentially explains the fewer individuals observed depredating and the subsequently low contribution of depredated toothfish to the energetic requirements of the whole population during that period. At the scale of a year, predation pressure release effects associated with depredation may be negligible given the minor contribution of depredated toothfish to the annual energetic requirements of the whole population. However, this contribution has increased over the last decade, with estimates becoming twice as high in the late 2010s as they were in the late 2000s, suggesting that if a release of predation pressure occurs, the consequence of depredation on this ecosystem may potentially grow in magnitude in the Crozet EEZ.

Given that toothfish is an important natural prey of the Crozet killer whales, one can also assume that the intake of toothfish through depredation replaces what they would have consumed through natural predation on this species (Tixier et al. 2019b). In that case, short-term changes in trophic interactions incurred by depredation within the ecosystem would be negligible. This assumption is supported by an isotopic study showing that the contribution of toothfish as a prey in diet of Crozet killer whales was similar in previous months whether they depredated or not (Tixier et al. 2019b). However, this finding was obtained from a low sample size and requires further research to be confirmed.

As toothfish size increases with depth (Péron et al. 2016), large toothfish that are present at depths >1500 m are mostly out of reach of killer whales. By setting longlines between 500 and 2000 m deep, the fishery provides access to larger fish than what depredating killer whales would have captured nat-urally. Indeed, while killer whales can dive deeper than 1000 m, they rarely exceed 500 m when naturally foraging in subantarctic waters (Reisinger et al. 2015, Towers et al. 2019, Richard et al. 2020). Determining whether depredation provides these killer whales with larger amounts of toothfish and/or larger individuals than they would have naturally consumed remains crucial information for the toothfish stock assessment because of the potential modification of natural mortality rate, and therefore, for the management of the fishery.

4.3. Uncertainties in the contribution of depredated toothfish to killer whale energetic requirements

In bioenergetic models, uncertainties are one of the greatest limitations, as results depend on assumptions and estimated parameters only (Santos et al. 2014, Spitz et al. 2018). Among the required parameters for the estimation of C_i, we investigated the impact of the depredated biomass (Q_i). However, we did not test for other parameters such as toothfish energetic density, killer whale abundance or daily energetic requirements. Estimation of predator abundance (size of the daily depredating group) is likely to be the largest source of uncertainty, even more when the abundance is low (Smith et al. 2015, Vincent et al. 2016, Spitz et al. 2018). Here, counting error for the number of killer whales could have a significant impact on the results, as it is also a main parameter of the model estimating the depredated quantity (Tixier et al. 2020). Nevertheless, as Crozet killer whales have been monitored since 1964 via photo-identification, with a consistently high effort since 2003, individuals are well known and can easily be identified (Guinet 1991, 1992, Tixier et al. 2017). While the social organization of this population was disrupted by an additive mortality event in the 1990s–2000s (Busson et al. 2019), social units showed an apparent high stability in recent years (Tixier et al. 2021), similar to what was observed before this event in the late 1980s (Guinet 1992). Knowledge on social unit composition could be used in the future to compensate for limited photo-identification during depredation events to improve the accuracy of abundance estimates for depredating individuals, assuming that the presence of an individual during these events implies the presence of other members of its unit. Furthermore, this study used the total number of individuals photo-identified per year as a proxy of the full population size, with

the potential caveat of missing individuals and not accounting for temporary migration effects in and out of the study area. High detection rates of all Crozet killer whales through photo-identification and limited temporary migrations (Tixier et al. 2015a, 2017), paired with a low interannual variation in the values used here, suggest a good representation of the full population size. The accuracy of these estimates could also be improved in the future through capture–mark–recapture methods or annual censuses (Reisinger et al. 2011b, Towers et al. 2020).

The variability of DPER within a year and among individuals could also be investigated. Here, we used a mean annual value of an average individual derived from the length distribution of the South African population. However, their body length and the composition of daily depredating groups could vary. So too could their sex, age-specific energetic requirements and the reproductive/lactating status, which depend on physiological parameters (Renouf & Gales 1994). This variability in the DPER could thus moderate our result of depredated fish fulfilling (even exceeding) the daily energetic requirements of killer whales. Conversely, the fact that half of the time, the contribution of depredated fish exceeded the energetic needs could also suggest that energetic needs are not consistent and that individuals are sometimes over-consuming compared to their average requirements (Renouf & Gales 1994, Williams et al. 2007).

4.4. Perspectives

The contribution of depredated toothfish to the annual energetic requirements of the whole Crozet killer whale population has increased over the last 12 yr, from 2 to 8%. Both the total allowable catch for toothfish and the amount of depredated toothfish have increased since the early 2010s at Crozet, resulting in a relatively stable depredation rate (22% of depredated catch out of the total catch; Tixier et al. 2020). However, over the same period, the total annual number of depredating killer whales and the interaction rate (62% of fishing days with depredation) has remained steady. Therefore, this suggests that a growing contribution of depredated toothfish in the intake of these killer whales is not due to individuals interacting more frequently with the fishery, but instead due to the fishery providing individuals with increasing opportunities to depredate (increasing the number of fishing days).

Under this assumption, an increase in the toothfish total allowable catch at Crozet would be ex-

pected to further increase the contribution of depredated fish to the energetic intake of the Crozet killer whales, leading to potentially greater impacts on the local ecosystem through the provisioning and predation pressure release effects mentioned in Section 4.2. Similarly, an increase in the number of fishing vessels or number of fishing days would be expected to increase the contribution of depredated fish to killer whale energetic intake. Assessing the magnitude of such effects will only be possible through a better understanding of the extent to which depredated toothfish changes the natural diet and energetic ratios of the Crozet killer whales. Such assessment will be crucial to model the full range of impacts associated with fishing in this region and can be used towards a comprehensive ecosystem-based management of the fishing activity (Clavareau et al. 2020).

Among other potential management responses, implementing measures that can effectively mitigate interactions with killer whales would minimize the ecosystem impacts of depredation. At Crozet, the use of acoustic deterrents and pots as an alternative type of fishing gear have both been inconclusive (Guinet et al. 2015, Tixier et al. 2015b). Changes in fishing practices including the use of shorter longline sets, hauling longlines faster and targeting areas and times of the year where/when killer whales are less likely to interact with vessels have shown more promising results (Tixier et al. 2015c). Fishers also use the move-on technique by leaving areas where they are subject to depredation and by traveling large distances so as not to be followed by the whales. These responses have been implemented as recommendations at Crozet, but still require socio-economic implication assessments before they are converted into regulations.

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