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Original Article

Comparison of approaches for incorporating depredation on fisheries catches into Ecopath

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Ecosystem-based approaches are increasingly used in fisheries management to account for the direct trophic impacts of fish population harvesting. However, fisheries can also indirectly alter ecosystem structure and functioning, for instance via the provision of new feeding opportunities to marine predators. For instance, marine depredation, where predators feed on fishery catches on fishing gear, is a behaviour developed by many marine species globally. This behaviour can modify both the ecological role of predators and fisheries performance. Yet, these ecosystem-wide effects of depredation are rarely considered holistically. In this study, we explored different ways of incorporating depredation into an Ecopath trophic model. We assessed, through a subantarctic case study, how three alternative model structures can account for depredation effects on fishery catches, predator and non-commercial prey populations, as well as target fish stocks. While none adequately addresses all facets of depredation, the alternative models can to some extent capture how depredation can lead to increased fishing pressure on stocks. As structural specificities of Ecopath prevented us from representing other depredation effects such as provisioning effects for predator populations, we conclude this study with a set of guidance to effectively capture the complex effects of depredation in marine ecosystems and fisheries models.

Keywords: Crozet, depredation, Ecopath, ecosystem model, Kerguelen, marine predators, model structure

Introduction

Fisheries can alter the structure and the functioning of marine ecosystems through multiple direct and indirect pathways (Hall, 1999). While resource extraction is a primary driver of change in trophic interactions, fisheries may also provide new feeding opportunities in the form of resource subsidies for some

predators. These food subsidies can lead to new interactions between species in marine ecosystems and involve discards as well as the target resource itself, which, when caught on fishing gear, may represent an easy-to-catch prey for a broad range of large marine predators (Votier *et al.*, 2010). In fact, and concomitantly with the global expansion of fisheries over the past 60 years, many large marine predator species, primarily sharks, and marine mammals have begun feeding on fishery catches as a new way of acquiring food (Read, 2008; Mitchell *et al.*, 2018).

This behaviour, termed "depredation", has been reported globally in coastal and offshore fisheries across all sectors (industrial, artisanal, and recreational) and a range of fishing techniques including traps, nets, and hooks-and-lines (Northridge, 1984; Gilman *et al.*, 2007; Mitchell *et al.*, 2018). Depredation is a type of human wildlife interaction that impacts many components of socio-ecosystems including fisheries and human fishing communities, depredating species, exploited fish stocks, and other ecosystem components (Northridge, 2018). From the many impacts that have been studied in marine or terrestrial systems, four main theoretical pathways are likely to simultaneously modify ecosystem structure and dynamics: (i) *provisioning*: depredation improves fitness of depredating individuals through a facilitated access to prey, subsequently enhancing predator populations (Oro *et al.*, 2013; Tixier *et al.*, 2015); (ii) *alteration of predation pressures*: depredation modifies the role of predators by displacing their foraging efforts and prey preferences (Newsome *et al.*, 2015); (iii) *decrease in fishing performance*: removals of fish from gear by predators reduce catch rates of fishers; and (iv) *increased fishing pressure on stocks*: fishers increase their fishing effort to compensate for catch losses caused by predators (Peterson *et al.*, 2013).

Because depredation can induce complex changes in marine socio-ecosystem dynamics, it is essential for ecosystem-based fisheries management to account for this behaviour. While ecosystem-based fisheries management is increasingly supported by a suite of modelling approaches, especially trophic modelling (Hollowed, 2000) using Ecopath (Plagányi and Butterworth, 2004), Atlantis (Fulton *et al.*, 2011), or diverse size- (Blanchard *et al.*, 2014) or traits-based models (Jacobsen *et al.*, 2017; Trenkel, 2018), to date, none have incorporated depredation on fishery catches. In fact, very few studies have examined the effects of depredation through holistic approaches. The primary reason for not incorporating depredation in ecosystem models lies in the absence of consensus on how to conceptually or mathematically capture this form of interaction at the interface between ecological and human components. For example, in Ecopath models, ecological groups and human activities are independently represented, as like other ecosystem models, Ecopath originally focused on food webs and trophic flows (Fulton *et al.*, 2003). By essence, this constitutes a structural hurdle to capture depredation as a behaviour-mediated interaction emerging at the interface between marine populations and fisheries. Indeed, the Ecopath model architecture lacks flexibility to easily capture depredation given that, on the one hand, ecological interactions (i.e. predation) between species or functional groups are captured via a diet matrix while, on the other hand, fishing extracts target species biomass from the system. Nevertheless, inclusion of depredation in ecosystem models appears as an essential challenge to tackle,

given that this behaviour likely changes food-web structure with subsequent consequences on ecosystem dynamics.

Here, we explore ways of incorporating depredation into the user-friendly and widespread Ecopath modelling framework (Christensen *et al.*, 2008). Using a subantarctic case study of marine mammal depredation on commercial fisheries (Roche *et al.*, 2007), we assessed how three alternative model formulations can capture the ecosystem-level effects of depredation. Relative to a baseline model that did not include depredation, we specifically compared how effectively each model captured consequences of depredation in terms of: (i) changes in fishing and predation mortalities on target species, (ii) mutual impacts of depredation-related groups (i.e. depredating, target species, and fishery), and (iii) broader ecosystem-level consequences.

Material and methods
Ecopath modelling framework
The Ecopath framework models biomasses and trophic flows within an ecosystem assuming a mass-balanced equilibrium for a given time period (Ecopath.org, Christensen and Walters, 2004). Ecopath models capture interactions between species or functional groups, i.e. groups of species that share similar ecological roles (Piroddi *et al.*, 2015). In Ecopath, functional groups are modelled as producers, consumers, or detritus with no dynamics. Groups may be further sub-divided according to life stages (multi-stanza) (Christensen and Walters, 2004). Fisheries are represented using a dedicated formalism that allows for catches to be distributed between landings and discards.

Two master Ecopath equations describe biomass flows between functional groups. Equation (1) defines the total biological production $(P)_i$ of functional group i as:

$$(P/B)_i \times B_i = \frac{Y_i + \sum_j B_j \times (Q/B)_j \times DC_{ji} + E_i + BA_i}{EE_i},$$
(1)

where $(P/B)_i$ is the production (P) to biomass (B) ratio for functional group i; EE_i is the ecotrophic efficiency, i.e. losses other than through predation and fishing; Y_i is the fishery yield, $(Q/B)_j$ is the consumption (Q) to biomass (B) ratio for predator j, DC_{ij} is the proportion of group i in the diet of predator j, E_i is the net migration rate for group i (immigration–emigration; here set to zero for all groups), and BA_i is the biomass accumulation rate (Christensen *et al.*, 2008; Piroddi *et al.*, 2015).

The second equation calculates biomass consumption of consumer group i as the sum of group biomass production, loss via respiration processes (R) modulated by the amount of unassimilated food (GS):

$$Q_i = \frac{P_i + R_i}{1 - GS_i} .$$
(2)

Assuming the modelled ecosystem is at equilibrium over the study period, the Ecopath software estimates unknown parameters to achieve mass balance (Christensen and Walters, 2004; Piroddi *et al.*, 2015). While fisheries landings and discards as well as diet composition of each functional group are specified from available data, P/B, Q/B, and P/C ratios, equilibrium biomasses,

and ecotrophic efficiency (*EE*) of model groups are often estimated by Ecopath.

Modelling depredation

As a complex behaviour-mediated interaction between fishers and depredating species, depredation can induce a range of direct and indirect effects, including:

(i) Enhancing *physiological performance of the depredating species via a facilitated access to food resources*. The depredated resource has a high-energy content for the depredating species as prey catching and handling only require limited effort (Tixier *et al.*, 2015);

(ii) *Kleptoparasitism* (Northridge, 2018): Removal of fish caught on fishing gear induces extra costs to fishers while benefiting to depredating species as described in (i);

(iii) *Additional fishing pressure* on the exploited and depredated fish population: This only occurs when fishers deploy extra fishing effort to maintain their total catch despite the reduced yields (Gilman *et al.*, 2007; Tixier *et al.*, 2015; Werner *et al.*, 2015);

(iv) *Released predation pressure* on other prey groups: By accessing a new food source, the depredating species decreases the extent to which they feed on other food sources (Gilman *et al.*, 2007).

The above list of potential short-term depredation effects is not comprehensive as indirect long-term effects encompass, among others, a range of potential socio-economic consequences to fisheries.

This study aimed at capturing complex depredation-related effects within the Ecopath modelling framework. Note that, to date, Ecopath models can only represent three types of variables, namely: detritus groups, functional groups, and fisheries. Because depredating species cannot directly feed on fisheries catches in Ecopath, and to avoid nonsensical assumptions in terms of population dynamics, we decided to explicitly capture depredated fish biomass as a detritus group consumed by the depredating species. We proposed three alternative model formulations to incorporate this "depredated target species" detritus group into a baseline Ecopath model that does not capture depredation (Figure 1).

(1) *Baseline* model: In this baseline model, depredation is ignored and only the natural predatory behaviour of depredating species is incorporated. Fishing of the target species produces landings and discards, and natural predation interactions are based on the diet matrix (Figure 1a).

(2) *Food subsidy* model: This model explicitly captures that depredation can act as a food subsidy for the depredating species. The "depredated target species" detritus group represents the depredated biomass of the target species, which is entirely consumed by the depredating species. Here, we distribute the total diet contribution of the target species to the depredating species (as defined in the *baseline* case) between the proportion of depredation from the "depredated target species" and the proportion of natural predation on the "target species". Thus, we assume that the overall contribution of the target species to the depredating species diet

(both via predation and depredation) is unchanged relative to the *baseline* model. Followingly, proportional contributions of other preys to depredating species diet, as well as the diet matrix for all other groups, remain unchanged. We assumed that the distribution of target species across the three target species life stages (see below) was similar in the depredated fraction and in the landings.

(3) *Increased fishing effort* model: By including depredated biomass into commercial fishery discards, this model captures an overall increase in the caught biomass of target species, which now accounts for the sum of landings, discards as well as biomass of catch removed from the fishing gear by the depredating species. Both commercial fishery discards and depredated biomass then feed into two distinct detritus groups, the "organic matter" and the "depredated target species", respectively. The "depredated target species" contributes to depredating species diet as described above for the *food subsidy* model (Figure 1c). Conversely to the *food subsidy* model, this formulation explicitly captures that depredating species feed on fisheries catches.

(4) *Competing fishery* model: By representing depredation as an additional fishery (distinct from the commercial fishery), this model does not only account for additional fishing pressure on target species due to depredation but also explicitly capture competition between fishers and depredating species. As in the *increased fishing effort* model, the "depredation" fishery discards all its catches into the "depredated target species" that is consumed by the depredating species group (as described above for other models). The commercial fishery produces landings and discards (Figure 1d). In this model, the target species group is thus exposed to two competing fisheries (i.e. the commercial and the depredation fishery).

Comparison of alternative model formulations

We compared how the alternative model formulations, which respectively account for depredation as (i) *food subsidy*, (ii) *increased fishing effort*, or (iii) *competing fishery*, capture depredation effects relative to the b*aseline* model with no depredation. To facilitate model comparison, all *P/B* and *Q/B* ratios estimated for the *baseline* model, as well as other input parameters (i.e. biomass, diet matrix) were kept constant across all models, except for model-specific adaptations as presented above (section "Modelling depredation"). Therefore, for each model, only the biomass of toothfish groups (represented as a multi-stanza population) was re-estimated by Ecopath, keeping the biomass of the small adult stanza fixed.

Quantitative comparison of the three alternative depredation model formulations relative to the baseline model relied on three complementary metrics: predation mortality, fishing mortality, and mixed trophic impact. These metrics were chosen to assess changes in: (1) fishing and predation mortality on target species, (2) mutual impacts of the groups directly involved in depredation (i.e. depredating, target species and fishery), and (3) ecosystem impacts of depredating species.

Changes in predation mortality are expected to reflect release in natural predation due to depredating species switching diet to feed on fisheries catches of the same species. Predation mortality (M2) corresponds to the sum of all mortalities due to all *n* predator groups feeding on prey group *i*, as follows:

(a)

Landings = L

Commercial fishery = L + D

Discards = D

Depredating species = P_D

Target species = P_T

Organic matter

(b)

Landings = L

Commercial fishery = L + D

Discards = D

Depredating species = P_D

Depredated target species = **De**

Target species = P_T

Organic matter

(c)

Landings = L

Commercial fishery = L + D + **De**

Discards = D + **De**

Depredating species = P_D

Target species = P_T

Depredated target species = **De**

Organic matter

(d)

Landings = L

Fishery depredation = **De**

Commercial fishery = L + D

Discards depredation = **De**

Depredating species = P_D

Discards = D

Depredated target species = **De**

Target species = P_T

Organic matter

Legend:

☐ Fishery groups

◯ Functionnal groups

Box categorisation:

■ (light) Consumer

■ (dark) Detritus

Flux categorisation:

·········▶ In diet

──────▶ Fishery

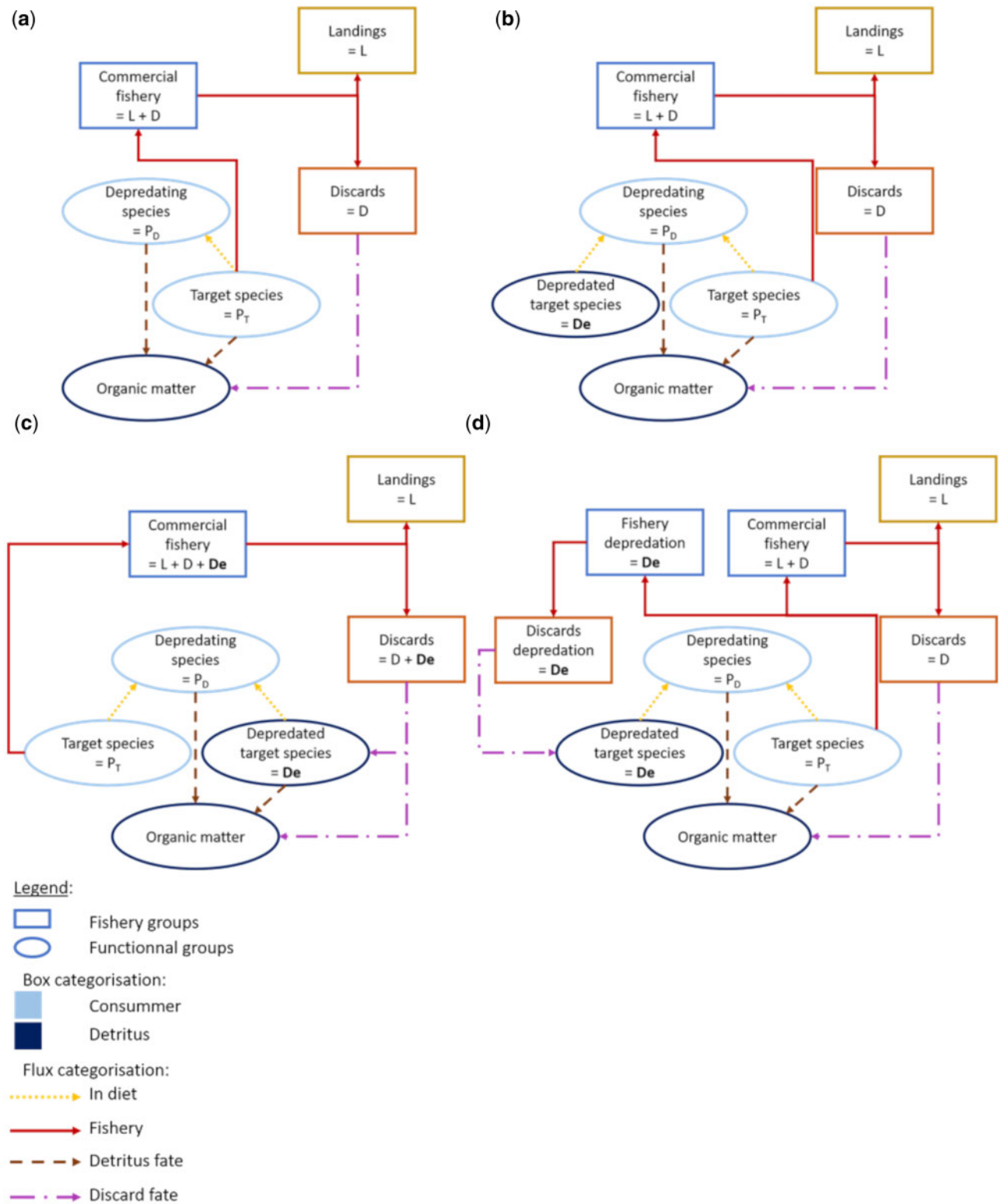── ── ──▶ Detritus fate

── · ── ·▶ Discard fate

Figure 1. Schematic representations of alternative Ecopath model structures for including depredation on a target species. (a) *Baseline* model: no depredation; (b) *food subsidy* model: depredated biomass is represented as a detritus group, (c) *increased fishing effort* model: depredation incorporated into the commercial fishery, and (d) *competing fishery* model: depredation is an independent fishery. L, landings biomass; D, discards biomass; De, depredated biomass; P_D, depredating species population biomass; P_T, target species population biomass.

$$M2_i = \sum_{j=1}^{n} Q_j \times DC_{ji}, \qquad (3)$$

where Q_j is the total consumption rate of predating group j (2), and DC_{ij} is the fraction of group i in the diet of predator j. Q_j is calculated as the product of B_j, the biomass of group j, and Q_j/B_j is the consumption/biomass ratio for group j (Christensen *et al.*, 2008, Piroddi *et al.*, 2015).

The mortality due to fishing is calculated either as (i) the sum of landings and discards divided by the biomass of the target group in the *baseline* and *food subsidy* models or (ii) the sum of landings, discards, and depredated biomass divided by target group biomass in the *increased fishing effort* and *competing fishery* models.

Finally, changes in mixed trophic impacts (referred to as "impacts" hereafter) summarize how alternative formulations modify the cascading effects of depredation-related groups on other model groups. The mixed trophic impact indicates how a long-term increase in a given group biomass can affect the equilibrium biomass of other groups via all direct and indirect feedback loops (Ulanowicz and Puccia, 1990). The impact indicator is a matrix whose ijth element represents the interaction between the impacting group i and the impacted group j. This indicator considers fisheries as predators, which means landings and discards correspond to their prey intake in the model (Christensen *et al.*, 2008; Piroddi *et al.*, 2015).

Case study

The commercial longline fishery operating in the Exclusive Economic Zones of Kerguelen and Crozet Islands (French subantarctic islands located between 45 and 50°S and 49 and 71°E) is conducted by seven licenced vessels and targets Patagonian toothfish (*Dissostichus eleginoides*) (hereafter "toothfish"—Guinet *et al.*, 2015). As the fishery holds the largest quota for that fish species across subantarctic waters, it is also the fishery most affected by depredation. Killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) are the two primary depredating species, together removing an estimated 279 t of toothfish per year at Crozet and 250 t per year at Kerguelen, equivalent to 30 and 6% of the total catches, in the two areas, respectively (Gasco *et al.*, 2015; Tixier *et al.*, 2020).

Our Ecopath models represented the marine ecosystem of Crozet and Kerguelen in 2017. The two areas were considered as a single area for highly mobile species, such as sharks, birds, and some marine mammals. For less mobile groups, such as benthic groups, which are similar at the community level but do show differences at the species level, especially among benthic fish, between Crozet and Kerguelen (Duhamel *et al.*, 2005), the food web was duplicated for each of the two areas (i.e. area-specific groups as used in Piroddi *et al.*, 2017). Similarly, two longline fisheries—Kerguelen fishery and Crozet fishery—were incorporated to account for the large differences in catches between the two areas (80% of the total quota was caught at Kerguelen). A total of 59 functional groups were considered in the model: 38 area-specific groups and 21 groups shared between Crozet and Kerguelen (Figure 2; Supplementary Table S1).

Toothfish was modelled as three weight-based stanza for each area to represent different life stages of the species: juveniles (<2 kg), small (2–5 kg), and large adults (>5 kg). Sperm whales extensively depredate on toothfish catches both at Crozet and

Kerguelen, but individuals are strongly segregated between the two areas (Tixier *et al.*, 2019a). Therefore, this species was divided into two area-specific groups in the model. Unlike sperm whales, killer whales depredate almost exclusively at Crozet (Labadie *et al.*, 2018). Although two killer whale morphotypes occur at Crozet and are both observed depredating on toothfish catches (Tixier *et al.*, 2016), only the so-called "Crozet killer whales" were presented in the study due to the lack of information on the other morphotype (type D). Abundance estimates for killer whales were taken from Tixier *et al.* (2017) and those for sperm whales from Labadie *et al.* (2018). The natural diet of sperm whales was assumed to be mostly composed of cephalopods and, to a lesser extent, of adult toothfish (Clarke, 1980; Cherel and Duhamel, 2004). For the Crozet killer whales, natural prey included pinnipeds, whales, penguins, and toothfish (Tixier *et al.*, 2019b). Population size estimates and diet compositions for all pinnipeds and bird populations were derived from Guinet *et al.* (1996) and Cherel *et al.* (2004), as well as from expert consultation. Data for the remaining functional groups were taken from the literature and from previously developed Ecopath models for Kerguelen, the Falkland Islands, and the Antarctic Peninsula (Pruvost *et al.*, 2005). Species were generally aggregated into functional groups when sharing similar trophic and ecological niches. However, species caught by the fishery, including both target and bycatch species, were modelled separately. The main bycatch species of the toothfish fishery at Crozet and Kerguelen represent ∼6% of the total catches and are grenadiers (*Macrourus* spp.), blue antimora (*Antimora rostrata*), and whiteleg skate (*Amblyraja taaf*) at Crozet and kerguelen sandpaper skate (*Bathyraja irrasa*) and eaton's skate (*Bathyraja eatonii*) at Kerguelen. Blue antimora is fully discarded, while the other species are partly or fully retained (CCAMLR, 2018a, b). As this work primarily focused on inclusion of depredation, the Ecopath models neglected fisheries bycatch given their marginal volumes in the French Patagonian toothfish fishery. Full details on model parameterization are provided in the Supplementary material.

Data on fishery catches, including both landings and discards, were collected by the French Southern Ocean Fishery Observer Program (Gasco, 2011) and extracted from the "PECHEKER" database (Martin and Pruvost, 2007; Pruvost *et al.*, 2011). Toothfish population estimates were obtained from spawning stock biomass estimates (Massiot-Granier *et al.*, 2019a, b). Depredation rates were set at 30% of the total catches for Crozet and 2% of the total catches at Kerguelen as estimated for 2017 following the methodology used by Gasco *et al.* (2015). Further details on the data used are available in Supplementary Table S2. For clarity, we primarily present the results from the Crozet region hereafter.

Results

Fishing and predation mortality

Relative to the *baseline* model, fishing mortality was unchanged in the *food subsidy* model but increased by ∼15% in the *increased fishing effort* and the *competing fishery* models (Figure 3a). The increase relative to the *baseline* model was equal across all toothfish stages in the *competing fishery* model and varied from 14.9% (juvenile toothfish) to 15.2% (large toothfish) in the *increased fishing effort* model.

Natural predation mortality on toothfish decreased similarly by <3% in all *food subsidy*, *increased fishing effort*, and *competing*
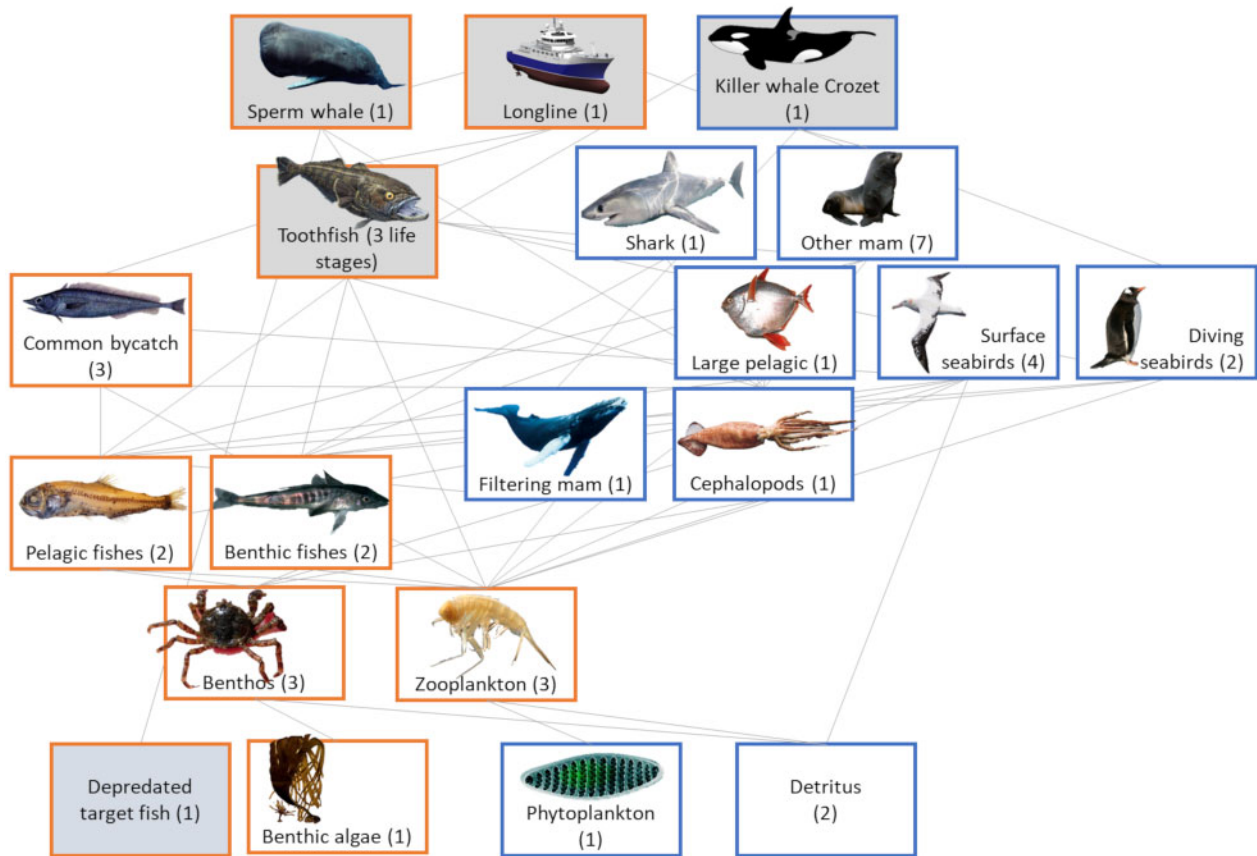
Figure 2. Simplified flow diagram of the *baseline* Ecopath model. Functional groups specific to Crozet are framed in orange, and those occurring both around Crozet and Kerguelen Islands in blue. Figures in brackets correspond to the number of functional groups explicitly defined in the model. Focal groups of this study are highlighted in grey. Connections between longline and sperm and killer whales represent depredation processes (which are included according to different formulations in the three depredation-specific models but excluded in the *baseline* model).

fishery models relative to the *baseline* model. The maximum relative decline was 2.3% for small adult toothfish (Figure 3b). For other killer whale prey groups, natural predation mortality increased by 0.4 to 0.6% in the *food subsidy* model, on filtering marine mammal, and fur seals (*Arctocephalus spp.*) and king penguins (*Aptenodytes patagonicus*), respectively. Natural predation on other prey groups did not change in the *increased fishing effort* and the *competing fishery* models relative to the *baseline* model (Figure 4). Note that this difference in the *food subsidy* model partially comes from a ~1.8% increase in the equilibrium biomass of killer whales relative to all other models. Except for this killer whale biomass in the *food subsidy* model, equilibrium biomasses for all groups were similar across all models. Despite similar input parameters set evenly across all models, this slight change unexpectedly emerged from mass-balancing the *food subsidy* model, possibly because it did not include any feedback between "depredated target species" and the commercial fishery.

Mutual effects of depredation-related groups
Mixed trophic impacts of predators and fisheries were overall consistent across all depredation models, except for slight model-specific differences: fisheries activity, sperm whale natural predation and sperm whale depredation all positively impacted juvenile

toothfish but were detrimental to larger life stages (Figure 5). Natural predation by killer whales positively impacted all toothfish stages (Figure 5). The small toothfish stage was negatively impacted by fishing and depredation, but only marginally positively affected by killer whales natural predation (Figure 5). In the *competing fishery* model, killer whales depredation positively impacted small toothfish life stages but negatively the two larger all toothfish life stages (Figure 5).

Except for the positive impact of killer whales (+~0.03), depredating species (i.e. sperm whales and in the *competing fishery* model the "depredation fishery", which includes depredation from killer whales and sperm whales) were detrimental to the toothfish longline fishery (Figure 6). Sperm whales had the largest negative impact on the commercial fishery (−0.07 to −0.08). These negative impacts of depredating groups on the fishery suggest that the depredation models were able to capture losses in fishery performance due to depredation.

Impacts of the commercial fishery were negative on all depredating groups, with a stronger impact on sperm whales than killer whales (i.e. −0.04 and −0.022, respectively; Figure 7). Note however that the "depredated toothfish" component was estimated to be beneficial to both sperm (+~0.004) and killer (+~0.02) whales (Figure 7).
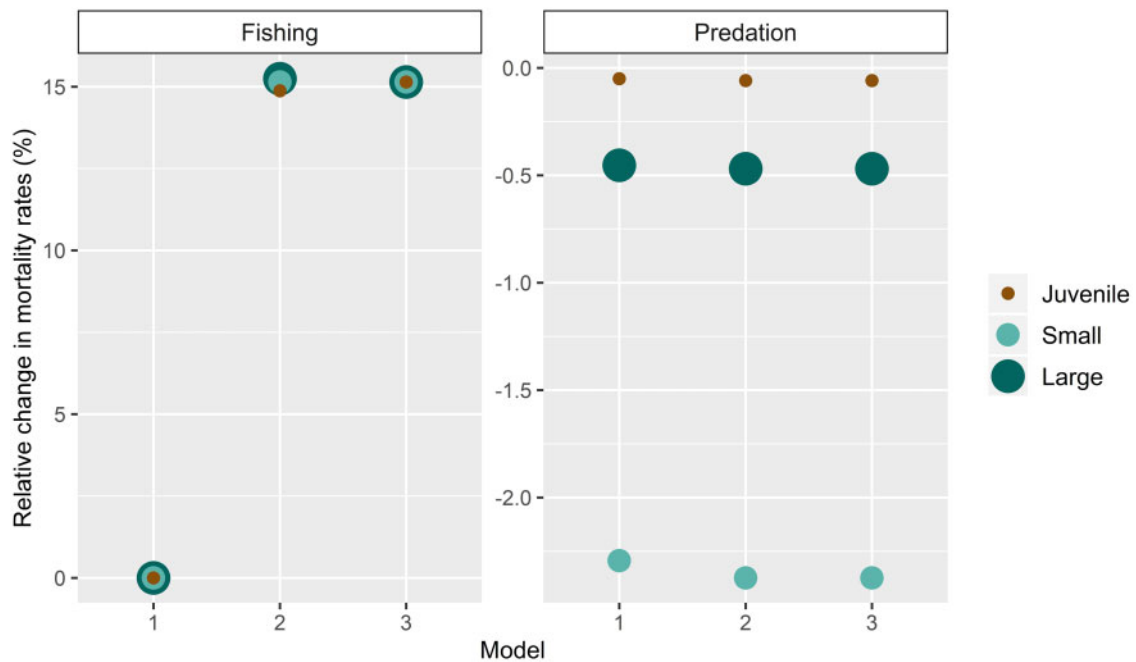
Figure 3. Effects of alternative Ecopath model formulation on Patagonian toothfish fishing (a) and natural predation (b) mortality. Estimates from the three alternative depredation models are expressed relatively to the *baseline* model (no depredation). Models are numbered from 1 to 3: 1, *food subsidy* model; 2, *increased fishing effort* model; 3, *competing fishery* model. Toot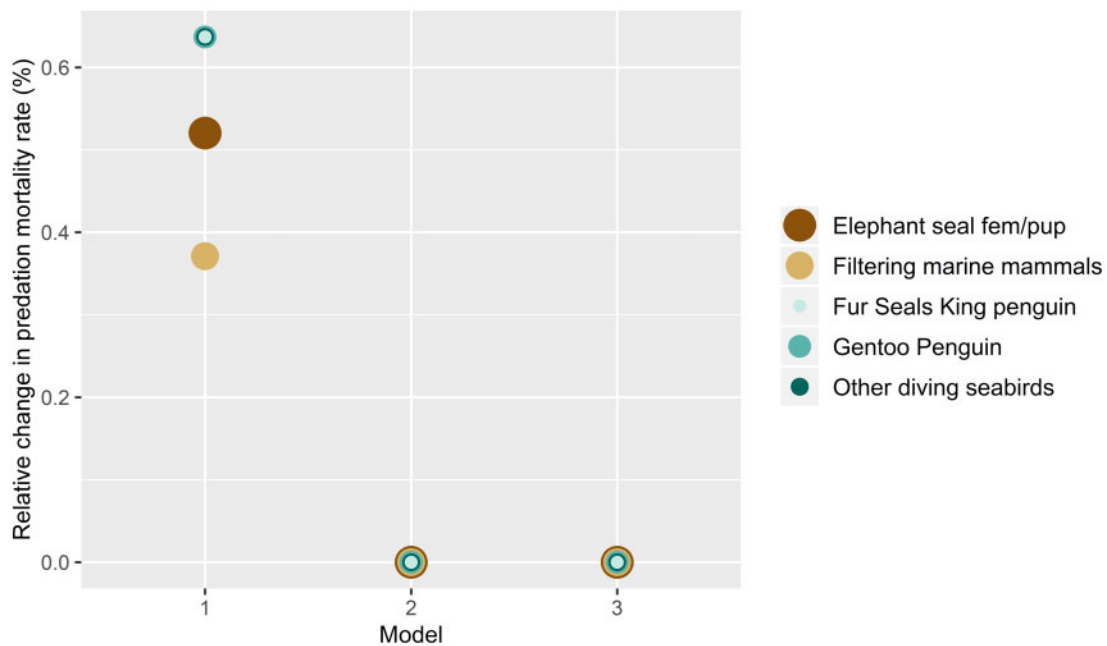hfish are modelled as three weight-based stages: juveniles (<2.07 kg), small adults (2.07–5 kg), and large adults (>5 kg).

Figure 4. Relative change in killer whale predation mortality rates on non-commercial prey groups across alternative depredation models (relative to the *baseline* model with no depredation). Models are numbered from 1 to 3: 1, *food subsidy* model; 2, *increased fishing effort* model; 3, *competing fishery* model.

As a side result, we also observed marginal decreases in trophic levels of the depredating species in the *food subsidy*, *increased fishing effort*, and *competing fishery* models relative to the *baseline* model, by ∼0.3% for sperm whales down to ∼1.8% for killer whales (Supplementary Figure S2).

Ecosystem effects of depredating species

Overall, impacts of killer whales (i.e. "killer whale" in the *food subsidy* model and *increased fishing effort* model, and both depredating and naturally predating components in the *competing fishery* model) were negative on most of their prey groups including
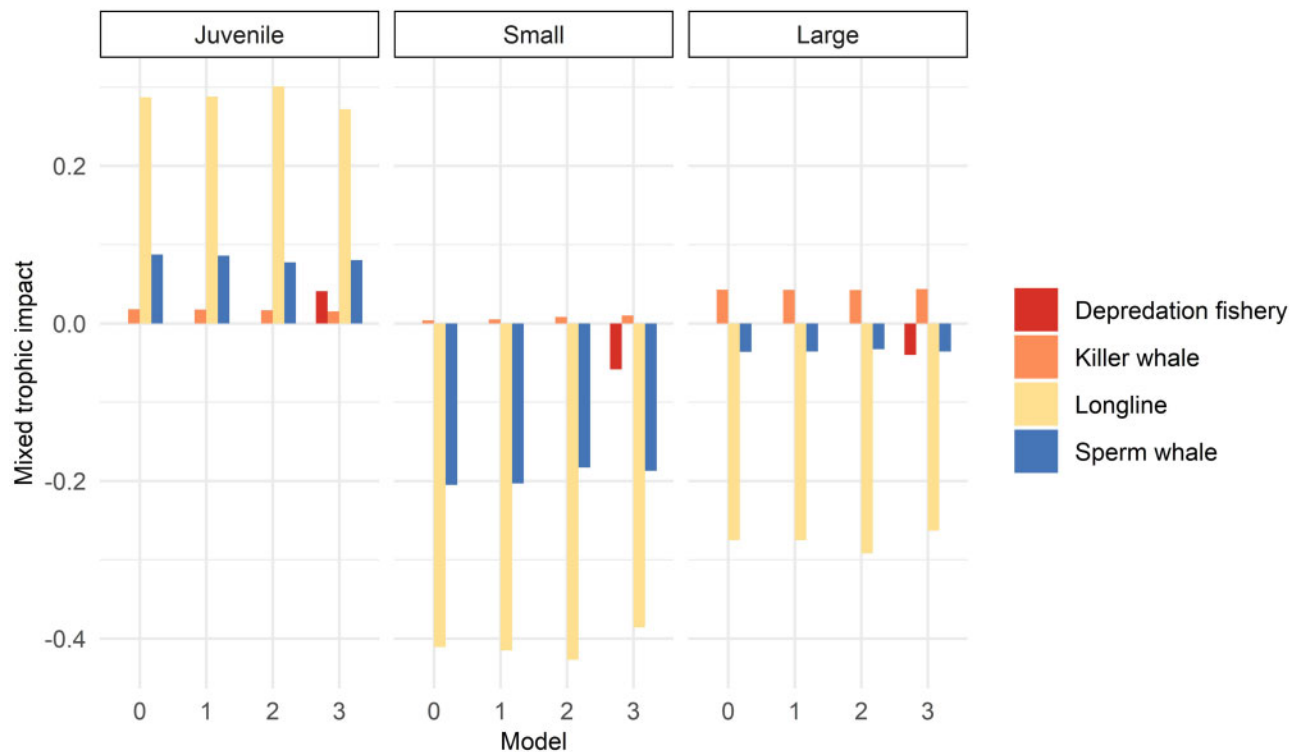
Figure 5. Impact indicator of longline fishery and depredating marine mammals on the three different toothfish life stages in the four Ecopath models, without depredation (0 for *baseline* model) and with depredation (1 for *food subsidy* model, 2 for *increased fishing effort* model, and 3 for *competing fishery* model). Toothfish were modelled as three weight-based life stages: juveniles (<2.07 kg; left panel), small adults (2.07–5 kg; central panel), and large adults (>5 kg; right panel). In the *competing fishery* model, "**d**epredation fishery" corresponds to depredation behaviour of sperm whale and killer whale, while "killer whale" and "sperm whale" refer to the naturally predating component of these groups. In the two other depredation models, "killer whale" and "sperm whale" groups include both effects of depredation and natural predation by these groups.

diving seabirds fur seals and elephant seals (females and pups, *Mirounga leonina*) across all models (Figure 8). Most prey groups, including marine mammals and penguins, were marginally (>0.1%) less negatively impacted by killer whales in the three alternative *depredation* models relative to the *baseline* model. Due to a direct release in natural predation pressure, killer whales were estimated to positively impact all toothfish groups (Figure 8).

Larger impacts of sperm whales (absolute estimate of mixed trophic impact >0.03; Figure 9) only concerned groups that are directly related to the commercial fishery, either because they are involved in depredation (i.e. small and large toothfish) or accidently caught as bycatch such as blue antimora and whiteleg skate (Figure 9). Sperm whale impacts varied slighlty across the alternative models and appeared to be marginally buffered in the *increased fishing effort* model.

The ecosystem effects of depredation captured by the different Ecopath models are summarized in Table 1.

Discussion

Ecosystem models are pivotal tools to account for multiple drivers of ecological systems, such as interactions between species (i.e. predation, competition) and environmental conditions (Hollowed, 2000; Plagányi and Butterworth, 2004). They can also include the effects of anthropogenic activities (e.g. harvesting), which often leads to competition between natural populations

and humans. Because depredation generates a number of effects beyond direct competition between humans and wildlife, which have to date not received much attention in ecosystem modelling frameworks (Peterson *et al.*, 2013; Werner *et al.*, 2015), their complex consequences on socio-ecosystem dynamics are not well understood and remain challenging to anticipate. In the following sections, we discuss how the alternative Ecopath model formulations developed to explicitly represent depredation in a case study can to some extent capture consequences of depredation on marine ecosystem structure and dynamics. Given the structural constraints of the Ecopath framework to represent complex consequences of depredation at the interface between fisheries and marine predators, we also identify a number of limitations in the proposed model formulations and provide guidance for future research in ecosystem modelling to better capture the range of socio-ecological effects associated with depredation.

A first step towards model-based assessment of the ecosystem effects of depredation in marine systems

Our study provides the first model-based assessment of the system-level impacts of depredation in marine systems. By comparing three alternative depredation-explicit Ecopath model formulations with a *baseline* model that neglects depredation processes, we assess how including depredation can affect estimates of fishing mortality and predation pressure. In our models of the Kerguelen/Crozet system, fishing mortality increased with
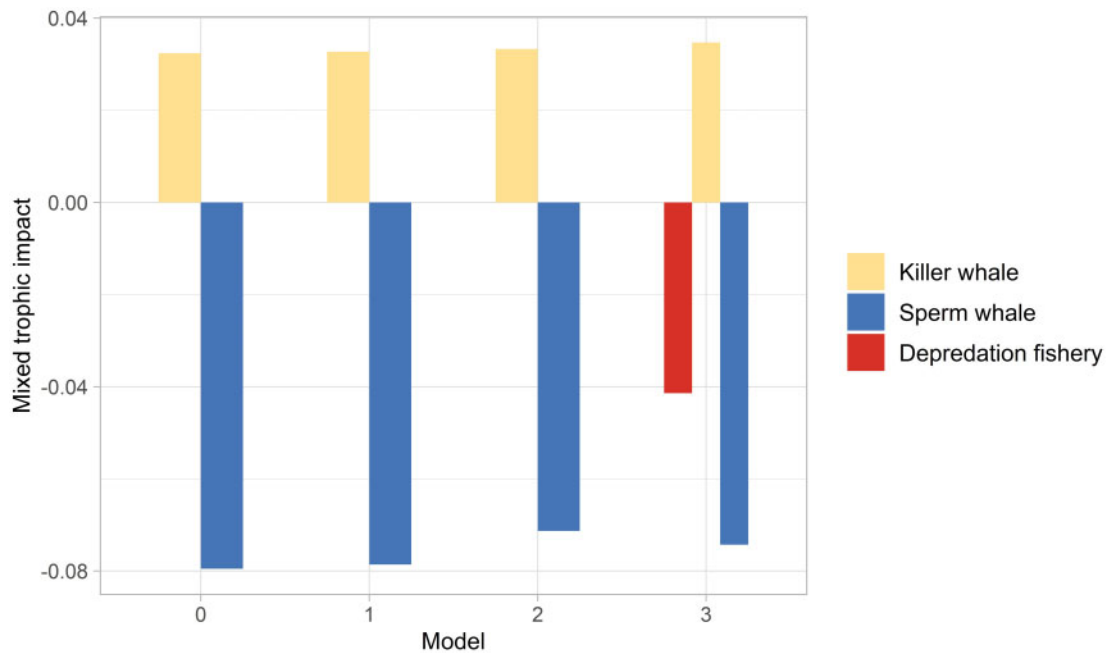
Figure 6. Impact indicator of depredating marine mammal species on the Crozet longline fishery. The "depredation fishery" group corresponds to toothfish removed by sperm whale and killer whale. Models are numbered from 0 to 3: 0, *baseline* model with no depredation; 1, *food subsidy* model; 2, i*ncreased fishing effort* model; 3, *competing fishery* model. "Depredation fishery" represents depredation by both sperm and killer whales in *competing fishery* model, while "killer whale" and "sperm whale" only represent natural predation by these groups. In the two other depredation models, "killer whale" and "sperm whale" groups include both effects of depredation and natural predation by these groups.
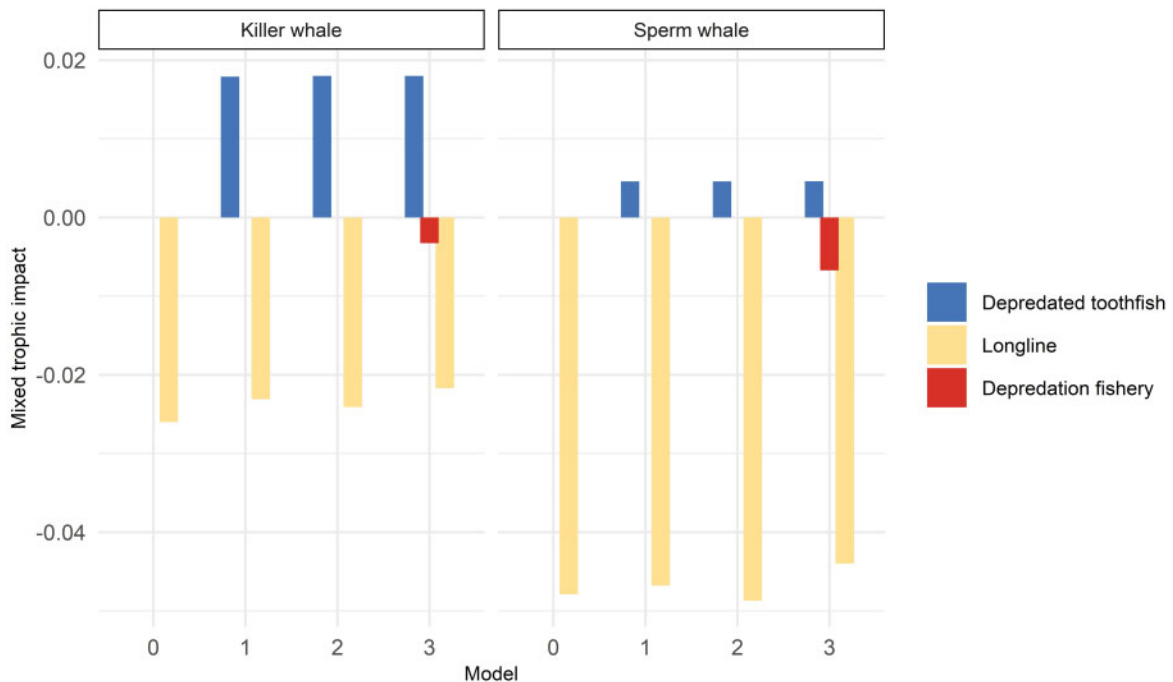

Figure 7. Mixed trophic impacts of the Crozet longline fishery on the subgroups of depredating killer whales (left) and sperm whales (right). Models are numbered from 0 to 3: 0, *baseline* model with no depredation; 1, *food subsidy* model; 2, i*ncreased fishing effort* model; 3, *competing fishery* model. "Depredation fishery" represents depredation by both sperm and killer whales in *competing fishery* model (but excludes the naturally predating components of these groups).
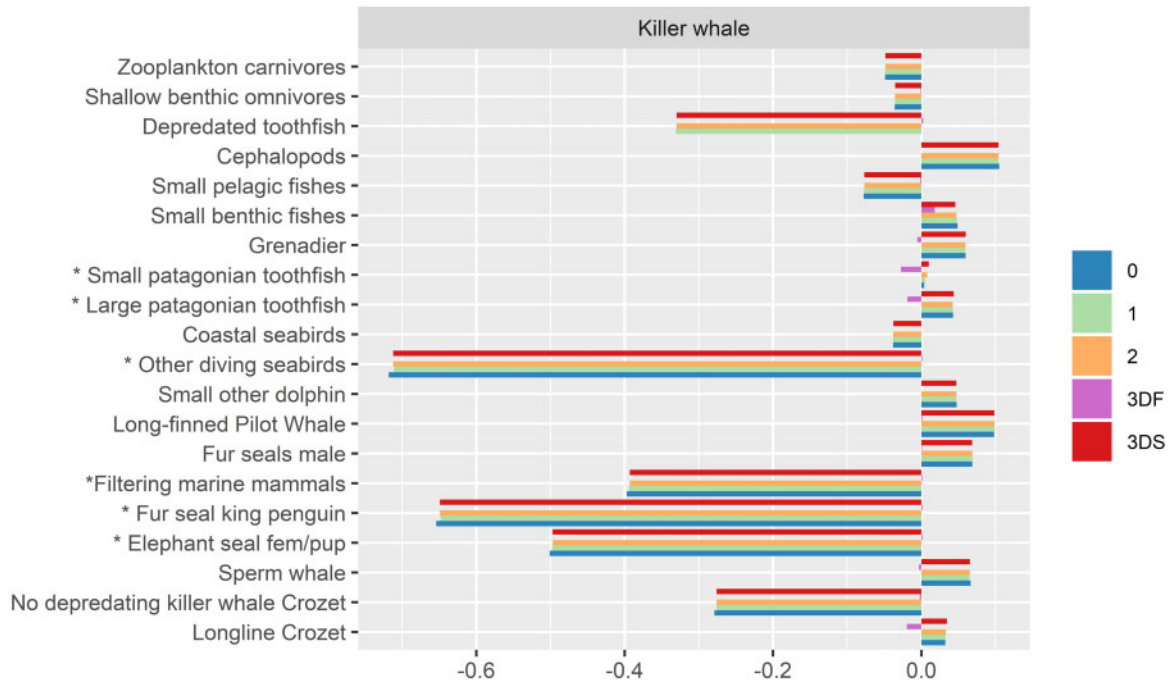
Figure 8. Killer whale mixed trophic impact on all functional groups in the Crozet ecosystem. Only large effects (absolute value >0.03) are shown. Estimates are provided for each models, which are numbered from 0 to 3: 0, *baseline* model with no depredation; 1, *food subsidy* model; 2, i*ncreased fishing effort* model; 3, *competing fishery* model (where "3DS" and "3DF" distinguish between the impact of the "depredating species" group and the "depredating fishery", respectively). "**Depredation fishery**" represents depredation by both sperm and killer whales in *competing fishery* model, while "killer whale" and "sperm whale" only represent the natural predation by these groups. In the two other depredation models, "killer whale" and "sperm whale" groups include both depredation and natural predation effects of these groups. Functional group preceded by * is part of killer whales diet.
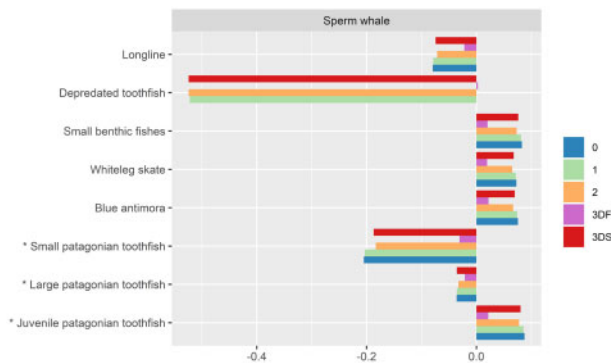

Figure 9. Sperm whale mixed trophic impacts on all functional groups in Crozet ecosystem. Only large effects (absolute value >0.03) are shown. Estimates are provided for each models, which are numbered from 0 to: 0, *baseline* model with no depredation; 1, *food subsidy* model; 2, *increased fishing effort* model; 3, *competing fishery* model (where "3DS" and "3DF" distinguish between the impact of the "depredating species" group and the "depredating fishery", respectively). "**Depredation fishery**" represents depredation by both sperm and killer whales in *competing fishery* model, while "killer whale" and "sperm whale" only represent the natural predation by these groups. In the two other depredation models, "killer whale" and "sperm whale" groups include both depredation and natural predation effects of these groups. Functional group preceded by * is part of sperm whales diet.

the inclusion of depredation, but changes in other indicators, including predation mortality, were marginal.

By incorporating depredation as a part of fishery catches, the *increased fishing effort* model and the *competing fishery* model explicitly captured the increase in fishing mortality induced by depredation. Both models estimated a ~15% increase in fishing mortality due to toothfish depredation by killer and sperm whales. Since depredation has only been qualitatively reported to increase fishing mortality in other longline fisheries (Werner *et al.*, 2015; Peterson and Hanselman, 2017), this result is noteworthy. Because depredation can be a cryptic source of fishing mortality, it is not systematically detected (e.g. species depredating on fishing gear at depth, when fishers are away or leaving limited evidence when removing fish) and is only rarely quantified (Tixier *et al.*, 2020), such estimates are necessary to improve the accuracy of fish stock assessments and hence to support sustainable fishery management (Gilman *et al.*, 2013). However, our estimate of increased fishing mortality due to depredation is case specific and method dependent. First, the French toothfish fishery operates in a remote region, where only a small fleet (seven vessels) targets a commercially valuable stock that was unexploited until the 1970s (Duhamel and Williams, 2011). While depredation increased fishing mortality by 15%, the estimated depredated biomass (~279 t per year; Tixier *et al.*, 2020) only represents a minor fraction (possibly 1%) of the estimated population biomass used for the model. Although this suggests a limited impact

Table 1. Summary of results across the alternative Ecopath models applied to the longline fisheries around Crozet Island.

		Model			
Effect in model	Fig	Baseline	Food subsidy	Increased fishing effort	Competing fishery
Longline fishing pressure (landings + discards) on toothfish	3	✓	✓	✓	✓
Decrease in predation pressure on toothfish (free swimming individuals) by depredating species due to depredation	3		✓	✓	✓
Increase in fishing effort due to depredation by killer whales and sperm whales on toothfish	3–5			✓	✓
Decrease in predation pressure on other natural preys of depredating killer whales and sperm whales	4		X		
Competition for toothfish (free swimming) between depredating killer whales, sperm whales, and fishers	6–7	✓	✓	✓	✓
Competition for hooked toothfish between depredating killer whales and sperm whales and fishers	6–7			X	✓
Prey access facilitation by fishery for depredating by killer whales and sperm whales	7			✓	✓

Blank fields mean that the effect was not detected for a given model, a ✓ means that the effect was found, and X denotes that a model produced the opposite effect.

of depredation on toothfish in this region, a similar increase in fishing mortality in response to depredation may have a greater impact in other regions where stocks have been heavily exploited. Indeed, fishery catches represent a higher proportion of the depleted stock biomass in intensively exploited stocks so any further increase in fishing effort (for instance due to depredation) could have severe impacts for fully or over-exploited stocks. Here, the subantarctic longline fishery, which operates in a remote hard-to-access area and is well-regulated, exploits a rather abundant stock so we can assume that the estimated 15% increase in fishing mortality due to depredation is not too critical for toothfish stock sustainability. Moreover, changes in fishing mortality in a depredation-impacted system may depend on whether fishers can increase their fishing effort to recoup catch losses. Fisheries with different management systems and more restrictive fishing seasons may offer fewer opportunities to compensate for depredation losses. For instance, in South Georgia where the toothfish fishery is also subject to killer and sperm whale depredation, fishing is restricted to winter months only (Towers *et al.*, 2019).

In the proposed depredation-explicit models, depredation only induced a marginal release in predation pressure on natural prey species of depredating sperm whales and killer whales. All alternative models predicted a slight decrease of ∼2% in direct predation of both killer and sperm whales on toothfish. Note that this directly results from the assumption that the total consumption of toothfish by whales at Crozet remained unchanged, in relation to the study of Tixier *et al.* (2019b), which found no difference between the contribution of toothfish to the diet of depredating and non-depredating killer whales, i.e. that natural predation on toothfish was partially replaced by depredation on toothfish catches. Toothfish is a natural prey of sperm whales but is likely to only marginally contribute to their diet that is largely dominated by cephalopods, as evidenced in Antarctic waters (Yukhov, 1972). As such, access to toothfish on fishing gear likely increases the contribution of this prey in the diet of individuals engaging in depredation, subsequently releasing predatory pressures of these individuals on other of their primary cephalopod prey species. However, the extent to which this release, which may be spatially restricted to areas where fishing occurs and depend on the proportion of depredating individuals in the sperm whale

population, alters the full ecosystem is still unknown. Cascading impacts are likely greater when depredated species are naturally mostly absent from their diet, as is the case for harbour seals (*Phoca vitulina*) depredating eels from fyke-nets in Sweden (Lundström *et al.*, 2010).

The magnitude of predation release on wild prey may not only depend on the importance of the depredated species for a predator's natural diet but also on the predator's trophic position, population abundance, and the extent to which it gains energy from depredation. Most species depredating on fishery catches are higher trophic level species such as large sharks and marine mammals, and changes in predation pressures from these top-predators are likely to generate greater top-down cascading ecosystem effects than changes from meso-predators (Newsome *et al.*, 2015). Population size and energetic requirements of the depredating species, paired with the energetic value of the depredated fish, will dictate its overall consumption.

Inclusion of depredation in Ecopath: limitations and recommendations

While the depredation-explicit models to some extent capture increase in fishing pressure and release in predation pressures as consequences of depredation, a range of other processes (for instance facilitated access to food resources for predators, or decrease in fishing gear capturability) were not accurately captured (if at all) in these models. These limitations in the proposed model formulations are largely due to structural constraints of the Ecopath modelling framework.

Facilitated access to prey, which can potentially enhance depredating species' individual and population performance, was partially incorporated via two modelling tricks: (1) by adding a specific "depredated target species" detritus group and (ii), consequently, by separating out depredation from natural predation on target species. However, depredation was only linked to the commercial fishery as a "discard" component in the *increased fishing effort* and in the *competing fishery* models because catches cannot appear in the diet matrix in Ecopath. These alternative model structures theoretically allow for a positive impact of depredated fish biomass on depredating species. However, this positive impact does not capture how reduced foraging effort due to

facilitated access to food resource can enhance certain life history parameters of the depredating species (i.e. life expectancy, fecundity, or growth; Tixier *et al.,* 2015). To achieve this, it would be necessary to increase the assimilation rate of depredated resources relative to predation and adapt information about population growth rate (i.e. *P/B*).

Adding "depredated target species" as an additional detritus group in Ecopath allows the partial incorporation of two separate depredation effects (i.e. release of predation pressure and facilitated access to food resources), but it skews estimates of trophic levels in the model. For instance, representing the depredated biomass as a detritus group directly leads to an underestimation of the depredating species' trophic level in Ecopath, given that detritus groups are assigned a basal trophic level (= 1) in Ecopath (Christensen *et al.,* 2008). Thus, caution should be exercised when using a depredation-explicit model to study trophic levels in Ecopath. In the Crozet/Kerguelen case study, a reduction in the depredating species' trophic levels is unrealistic since the depredated fish, toothfish, is among the highest trophic levels well above most other natural prey items of killer and sperm whales (Tixier *et al.,* 2019a). Similarly, a decrease in trophic level would seem misleading in many other depredation cases, such as in the wide-ranging tropical longline fisheries where sharks and odontocetes heavily depredate on high trophic level groups (i.e. tuna and swordfish; Rabearisoa *et al.,* 2018). Moreover, depredation-related changes in trophic level are likely to depend on predator switching their diet preferences towards the easily accessible resource (rather than foraging for their natural preys; Jacoby *et al.,* 1999). While trophic levels of depredating species at Crozet/Kerguelen should remain unchanged under the assumption that their overall toothfish consumption is not changed by depredation, trophic levels of depredating species are most likely to increase as the proportional contribution of depredation in their diet increases (Jacoby *et al.,* 1999). Conversely, species increasing their consumption of low trophic level prey when depredating, as evidenced in cases where predators remove bait from fishing gears (e.g. Thode *et al.,* 2016) are likely to decrease their trophic level.

Decline in fishery performance could not be fully captured in any of the models. Indeed, none of the three depredation-explicit models explicitly captured depredation as a loss in gear capturability and/or as an extra cost to the fishery but rather represent depredated biomass as discards recycled by the depredating species. While the *competing fishery* model incorporated depredation as a virtual fishery to capture the supplementary negative effect of killer and sperm whales on the fishery via the removal of catches from fishing gear, it did not explicitly quantify energy gains for the depredating species and efficiency loss for the fishery. Moreover, model realism also depends on data availability, which represents a major limitation of any ecosystem model. For instance, in our case, a single virtual fishery represented toothfish biomass depredated by both sperm whales and killer whales as data were insufficient to discriminate impacts of their respective depredation. To include depredation, some data are added to those traditionally used in ecosystem models, such as the quantity of resource depredated or the depredation rate. In addition to this, it is necessary to know in what proportion depredation modifies the depredating species' diet.

In addition to analysing how to account for the greatest number of expected impacts associated with depredation, evaluating alternative model structures helped delineate the limitations of each model formulation. While all alternative models were derived from the same *baseline* model, each of the three depredation-explicit models posed different modelling choices in terms of model group aggregation and feedback structure, which can significantly impact ecosystem model predictions (Pinnegar *et al.,* 2005; Marzloff *et al.,* 2011).

Note for instance, that we endeavoured to keep equilibrium biomasses for all groups similar across all models by setting similar input parameters across all models. All equilibrium biomasses were identical across models except for an unexpected ∼1.8% increase in the equilibrium biomass of killer whale in the *food subsidy* model (which possibly explains the observed difference in natural predation mortality due to depredating killer whales relative to other models). We suspect that this slight change in the *food subsidy* model emerged from the Ecopath mass-balancing algorithm, as this model does not include any feedback between "depredated target species" and the commercial fishery. In the *increased fishing effort* model, depredation was included into the commercial fishery but depredating species and fishing gear were aggregated into a single "caught toothfish" functional group. This aggregated representation is ecologically questionable given that ecosystem models shall ideally discriminate between prey and predator populations (Fulton *et al.,* 2003), while one could argue that the amount of fishing gear can be comparable to a predator population abundance for the target species. Indeed, fishers and depredating species do not compete for hooked fish, since only one model group removes the total fish caught. Moreover, the *increased fishing effort* model did not discriminate between the predation and depredation effects of depredating species on the commercial fishery. This distinction appears relevant in our case study for killer whales, as natural predation on competitors of toothfish for food may be indirectly beneficial for the fishery while depredation negatively affects that same fishery. However, disaggregating the fishery into a "depredating species" fishery and a commercial fishery, as done in the *competing fishery* model, does not seem completely realistic as separating out a single fishery into two independent components in the Ecopath model. Indeed, in the case of an increase in commercial fishing effort, the virtual depredation fishery should be affected similarly, assuming a direct relationship between fishing effort and depredation rate. However, this is not the case in this model as the two fisheries remain fully separated.

Recommendations for depredation-resolving ecosystem models

Due to structural constraints and lack of flexibility of the Ecopath framework to capture behaviour-mediated processes, this study could not fully capture the complexity of interactions between fisheries and depredating species. For these reasons, we decided not to pursue with dynamic simulations with Ecopath with Ecosim. Depredation is the consequence of behavioural innovations and adaptations of marine predator species to new feeding opportunities offered by fisheries, including actively searching and/or following fishing vessels or purposely using human equipment to feed on aggregated, easy-to-catch resources despite the associated risk (Bearzi *et al.,* 2019). These adaptations are time dependent, occurring at the inter-annual level when individuals progressively learn depredation (e.g. Tixier *et al.,* 2016) or extend their spatial range of interaction with vessels (e.g. Schakner *et al.,* 2014), or at the intra-annual level when individuals only switch to depredation when natural prey are scarce.

Medium- and long-term consequences of depredation for depredating populations not only result from positive provisioning effects but also from injuries or lethal risks related to interactions with fisheries. If depredation supplies more energy than the natural diet, depredation may enhance fitness and, therefore, the reproductive performances of individuals. This was found for killer whales depredating on toothfish catches at Crozet and depredating on tuna catches in the Strait of Gibraltar (Guinet *et al.*, 2015; Tixier *et al.*, 2015; Esteban *et al.*, 2016). If the energy gain due to depredation relative to natural feeding is large, depredating populations could expand (in particular if also benefiting from dedicated conservation effort), which could further enhance the magnitude of depredation long-term impacts on the ecosystem. However, this scenario may be only realistic in a situation where the risks of fatal interactions with fishing gear and vessels are limited. Depredating species can be exposed to the accidental risk of getting caught in fishing gear and/or intentional shooting from fishers (Dans *et al.*, 2003; Azevedo *et al.*, 2017). The bycatch of depredating species such as marine mammals is often reported in many static net and trawl fisheries (Read, 2008). Bycatches of depredating species should be considered in future studies aiming to address the full range of ecosystem effects resulting from depredation.

While considering depredation-related processes in ecosystem models is important, this study only partially addresses this challenge, which will require further development in future studies. Future ecosystem modelling studies should consider temporal variations in the size of depredating species populations and in the composition of their diet associated with changes in prey availability. However, to provide accurate input information, further understanding of the socio-ecosystem interactions generated locally by depredation is needed. First, and as raised by the findings of the present study, understanding the extent to which depredated resources replace natural prey in depredating species' diets appears as a critical element to investigate. Second, assessing whether the balance between benefits and costs is positive or negative for depredating species is pivotal to determining long-term depredating species' population growth rates. In summary, we present a pilot study exploring, within the constrained Ecopath framework, alternative ways of incorporating depredation on fisheries catches. By assessing how different model formulations affected estimates of natural predation and fishing mortality on different model groups, the study provides a number of insights on the ecosystem effects of a depredation-impacted subantarctic fishery. The results also highlight the limitations of Ecopath-based modelling to address complex behaviour-mediated processes. Thus, the development of dedicated models that can accurately capture complex multi-faceted socio-economic and ecological impacts inherent to depredation conflicts is essential to identify the conditions needed for the long-term coexistence of fisheries and marine predators and to contribute to ecosystem-based management of marine ecosystem.

Supplementary data
Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability statement
The data underlying this article cannot be shared publicly due to confidentiality agreements in place.

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