



### Comparison of approaches for incorporating depredation on fisheries catches into Ecopath

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4 **1 Comparison of approaches for incorporating depredation on**  
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6 **2 fisheries catches into Ecopath**  
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3 **24 Abstract**  
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6 **25** Ecosystem-based approaches are increasingly used in fisheries management to account for the  
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8 **26** direct trophic impacts of fish population harvesting. However, fisheries can also indirectly alter  
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10 **27** ecosystem structure and functioning, for instance via the provision of new feeding opportunities  
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12 **28** to marine predators. For instance, marine depredation, where predators feed on fishery catches  
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14 **29** on fishing gear, is a behaviour developed by many marine species globally. This behaviour can  
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16 **30** modify both the ecological role of predators and fisheries performance. Yet, these ecosystem-  
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18 **31** wide effects of depredation are rarely considered holistically. In this study, we explored  
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20 **32** different ways of incorporating depredation into an Ecopath trophic model. We assessed,  
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22 **33** through a subantarctic case study, how three alternative model structures can account for  
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24 **34** depredation effects on fishery catches, predator and non-commercial prey populations, as well  
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26 **35** as target fish stocks. While none adequately addresses all facets of depredation, the alternative  
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28 **36** models can to some extent capture how depredation can lead to increased fishing pressure on  
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30 **37** stocks. As structural specificities of Ecopath prevented us from representing other depredation  
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32 **38** effects such as provisioning effects for predator populations, we conclude this study with a set  
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34 **39** of guidance to effectively capture the complex effects of depredation in marine ecosystems and  
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36 **40** fisheries models.  
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43 **41 Keywords:** marine predators, Kerguelen, Crozet, Ecopath, model structure, depredation,  
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45 **42** ecosystem model  
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## 49 Introduction

50 Fisheries can alter the structure and the functioning of marine ecosystems through  
51 multiple direct and indirect pathways ([Hall, 1999](#)). While resource extraction is a primary driver  
52 of change in trophic interactions, fisheries may also provide new feeding opportunities in the  
53 form of resource subsidies for some predators. These food subsidies can lead to new interactions  
54 between species in marine ecosystems and involve discards as well as the target resource itself,  
55 which, when caught on fishing gear, may represent an easy-to-catch prey for a broad range of  
56 large marine predators ([Votier et al., 2010](#)). In fact, and concomitantly with the global  
57 expansion of fisheries over the past 60 years, many large marine predator species, primarily  
58 sharks and marine mammals, have begun feeding on fishery catches as a new way of acquiring  
59 food ([Read, 2008](#); [Mitchell et al., 2018](#)).

60 This behaviour, termed “depredation”, has been reported globally in coastal and  
61 offshore fisheries across all sectors (industrial, artisanal and recreational) and a range of fishing  
62 techniques including traps, nets and hooks-and-lines ([Northridge, 1984](#); [Gilman et al., 2007](#);  
63 [Mitchell et al., 2018](#)). Depredation is a type of human wildlife interaction that impacts many  
64 components of socio-ecosystems including fisheries and human fishing communities,  
65 depredating species, exploited fish stocks and other ecosystem components ([Northridge, 2018](#)).  
66 From the many impacts that have been studied in marine or terrestrial systems, four main  
67 theoretical pathways are likely to simultaneously modify ecosystem structure and dynamics: (i)  
68 *provisioning*: depredation improves fitness of depredating individuals through a facilitated  
69 access to prey, subsequently enhancing predator populations ([Oro et al., 2013](#); [Tixier et al.,](#)  
70 [2015](#)); (ii) *alteration of predation pressures*: depredation modifies the role of predators by  
71 displacing their foraging efforts and prey preferences ([Newsome et al., 2015](#)); (iii) *decrease in*  
72 *fishing performance*: removals of fish from gear by predators reduce catch rates of fishers; (iv)

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3 73 *increased fishing pressure on stocks*: fishers increase their fishing effort to compensate for catch  
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5 74 losses caused by predators ([Peterson et al., 2013](#)).

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8 75 Because depredation can induce complex changes in marine socio-ecosystem dynamics,  
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10 76 it is essential for ecosystem-based fisheries management to account for this behaviour. While  
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12 77 ecosystem-based fisheries management is increasingly supported by a suite of modelling  
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14 78 approaches, especially trophic modelling ([Hollowed, 2000](#)) using Ecopath ([Plagányi and](#)  
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16 79 [Butterworth, 2004](#)), Atlantis ([Fulton et al., 2011](#)), or diverse size- ([Blanchard et al., 2014](#)) or  
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18 80 traits-based models ([Jacobsen et al., 2017](#); [Trenkel, 2018](#)), to date, none have incorporated  
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20 81 depredation on fishery catches. In fact, very few studies have examined the effects of  
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22 82 depredation through holistic approaches. The primary reason for not incorporating depredation  
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24 83 in ecosystem models lies in the absence of consensus on how to conceptually or mathematically  
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26 84 capture this form of interaction at the interface between ecological and human components. For  
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28 85 example, in Ecopath models ecological groups and human activities are independently  
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30 86 represented, as like other ecosystem models, Ecopath originally focused on food webs and  
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32 87 trophic flows ([Fulton et al., 2003](#)). By essence, this constitutes a structural hurdle to capture  
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34 88 depredation as a behaviour-mediated interaction emerging at the interface between marine  
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36 89 populations and fisheries. Indeed, the Ecopath model architecture lacks flexibility to easily  
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38 90 capture depredation given that, on the one hand, ecological interactions (i.e. predation) between  
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40 91 species or functional groups are captured via a diet matrix while, on the other hand, fishing  
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42 92 extracts target species biomass from of the system. Nevertheless, inclusion of depredation in  
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44 93 ecosystem models appears as an essential challenge to tackle, given that this behaviour likely  
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46 94 changes food-web structure with subsequent consequences on ecosystem dynamics.

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49 95 Here, we explore ways of incorporating depredation into the user-friendly and  
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51 96 widespread Ecopath modelling framework ([Christensen et al., 2008](#)). Using a subantarctic case  
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53 97 study of marine mammal depredation on commercial fisheries ([Roche et al., 2007](#)), we assessed  
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3 98 how three alternative model formulation can capture the ecosystem-level effects of depredation.  
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5 99 Relative to a baseline model that did not include depredation, we specifically compared how  
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8 100 effectively each model captured consequences of depredation in terms of: (1) changes in fishing  
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10 101 and predation mortalities on target species, (2) mutual impacts of depredation-related groups  
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12 102 (i.e. depredating, target species and fishery), and (3) broader ecosystem-level consequences.  
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## 17 104 **Material and Methods**

### 19 105 *Ecopath modelling framework*

21 106 The Ecopath framework models biomasses and trophic flows within an ecosystem  
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23 107 assuming a mass-balanced equilibrium for a given time period (Ecopath.org, [Christensen and](#)  
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25 108 [Walters, 2004](#)). Ecopath models capture interactions between species or functional groups, i.e.  
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28 109 groups of species that share similar ecological roles ([Piroddi et al., 2015](#)). In Ecopath, functional  
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30 110 groups are modelled as producers, consumers or detritus with no dynamics. Groups may be  
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33 111 further sub-divided according to life stages (multi-stanza) ([Christensen and Walters, 2004](#)).  
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35 112 Fisheries are represented using a dedicated formalism that allows for catches to be distributed  
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37 113 between landings and discards.

40 114 Two master Ecopath equations describe biomass flows between functional groups.  
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42 115 Equation 1 defines the total biological production (P)<sub>i</sub> of functional group *i* as:

$$45 116 \quad (P | B)_i \times B_i = \frac{Y_i + \sum_j B_j \times (Q | B)_j \times DC_{ji} + E_i + BA_i}{EE_i} \quad (1)$$

48 117 Where: (P/B)<sub>i</sub> is the production (P) to biomass (B) ratio for functional group *i*; EE<sub>i</sub> the  
49  
50 118 ecotrophic efficiency, i.e. losses other than through predation and fishing; Y<sub>i</sub> fishery yield,  
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52  
53 119 (Q/B)<sub>j</sub> the consumption (Q) to biomass (B) ratio for predator *j*, DC<sub>ij</sub> the proportion of group *i*  
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55 120 in the diet of predator *j*, E<sub>i</sub> the net migration rate for group *i* (immigration – emigration; here  
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58 121 set to zero for all groups), BA<sub>i</sub> the biomass accumulation rate, ([Christensen et al., 2008](#); [Piroddi](#)  
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60 122 [et al., 2015](#)).

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3 123 The second equation calculates biomass consumption of consumer group  $i$  as the sum  
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5 124 of group biomass production, loss via respiration processes (R) modulated by the amount of  
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8 125 unassimilated food (GS) (Equation 2).

$$10 \quad 126 \quad Q_i = \frac{P_i + R_i}{1 - GS_i} \quad (2)$$

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14 127 Assuming the modelled ecosystem is at equilibrium over the study period, the Ecopath  
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16 128 software estimates unknown parameters to achieve mass balance ([Christensen et Walters, 2004](#);  
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18 129 [Piroddi et al., 2015](#)). While fisheries landings and discards as well as diet composition of each  
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21 130 functional group are specified from available data, P/B, Q/B and P/C ratios, equilibrium  
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23 131 biomasses and ecotrophic efficiency (EE) of model groups are often estimated by Ecopath.

### 24 25 132 26 27 133 *Modelling depredation*

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30 134 As a complex behaviour-mediated interaction between fishers and depredating species,  
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32 135 depredation can induce a range of direct and indirect effects, including:

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34 136 i) Enhancing *physiological performance of the depredating species via a*  
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37 137 *facilitated access to food resources*. The depredated resource has a high-energy content for the  
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39 138 depredating species as prey catching and handling only requires limited effort ([Tixier et al.,](#)  
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41 139 [2015](#));

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44 140 ii) *kleptoparasitism* ([Northridge, 2018](#)): Removal of fish caught on fishing gear  
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46 141 induces extra costs to fishers while benefiting to depredating species as described in (i);

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48 142 iii) *Additional fishing pressure* on the exploited and depredated fish population: this  
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51 143 only occurs when fishers deploy extra fishing effort to maintain their total catch despite the  
52  
53 144 reduced yields ([Gilman et al., 2007](#); [Tixier et al., 2015](#); [Werner et al., 2015](#));

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55 145 iv) *Released predation pressure* on other prey groups. By accessing a new food  
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57 146 source, the depredating species decreases the extent to which they feed on other food sources  
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60 147 ([Gilman et al., 2007](#)).

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3 148 The above list of potential short-term depredation effects is not comprehensive as indirect long-  
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5 149 term effects encompass, among others, a range of potential socio-economics consequences to  
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8 150 fisheries.

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10 151 This study aimed at capturing complex depredation-related effects within the Ecopath  
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12 152 modelling framework. Note, that to-date, Ecopath models can only represent three types of  
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14 153 variables, namely: detritus groups, functional groups and fisheries. Because depredating species  
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17 154 cannot directly feed on fisheries catches in Ecopath, and to avoid nonsensical assumptions in  
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19 155 terms of population dynamics, we decided to explicitly capture depredated fish biomass as a  
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21 156 detritus group consumed by the depredating species. We proposed three alternative model  
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23 157 formulations to incorporate this ‘depredated target species’ detritus group into a baseline  
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26 158 Ecopath model that does not capture depredation (Figure 1).

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28 159 1) *Baseline* model: in this baseline model, depredation is ignored and only the natural  
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31 160 predatory behaviour of depredating species is incorporated. Fishing of the target species  
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33 161 produces landings and discards, and natural predation interactions are based on the diet  
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35 162 matrix (Figure 1a).

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37 163 2) *Food subsidy* model: this model explicitly captures that depredation can act as a food  
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40 164 subsidy for the depredating species. The “depredated target species” detritus group  
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42 165 represents the depredated biomass of the target species, which is entirely consumed by  
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44 166 the depredating species. Here, we distribute the total diet contribution of the target  
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47 167 species to the depredating species (as defined in the *baseline* case) between the  
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49 168 proportion of depredation from the “depredated target species” and the proportion of  
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51 169 natural predation on the “target species”. Thus, we assume that the overall contribution  
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54 170 of the target species to the depredating species diet (both via predation and depredation)  
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56 171 is unchanged relative to the *baseline* model. Followingly, proportional contributions of  
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58 172 other preys to depredating species diet, as well as the diet matrix for all other groups,  
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3 173 remain unchanged. We assumed that the distribution of target species across the three  
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5 174 target species life stages (see below) was similar in the depredated fraction and in the  
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8 175 landings.

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10 176 3) *Increased fishing effort* model: by including depredated biomass into commercial  
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12 177 fishery discards, this model captures an overall increase in the caught biomass of target  
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14 178 species, which now accounts for the sum of landings, discards as well as biomass of  
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17 179 catch removed from the fishing gear by the depredating species. Both commercial  
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19 180 fishery discards and depredated biomass then feed into two distinct detritus groups, the  
20  
21 181 “organic matter” and the “depredated target species”, respectively. The “depredated  
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23 182 target species” contributes to depredating species diet as described above for the *food*  
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25 183 *subsidy* model (Figure 1c). Conversely to the *food subsidy* model, this formulation  
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27 184 explicitly captures that depredating species feed on fisheries catches.

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30 185 4) *Competing fishery* model: by representing depredation as an additional fishery (distinct  
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32 186 from the commercial fishery), this model does not only account for additional fishing  
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34 187 pressure on target species due to depredation but also explicitly captures competition  
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36 188 between fishers and depredating species. As in the *increased fishing effort* model, the  
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38 189 “depredation” fishery discards all its catches into the “depredated target species” that is  
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40 190 consumed by the depredating species group (as described above for other models). The  
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42 191 commercial fishery produces landings and discards (Figure 1d). In this model, the target  
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44 192 species group is thus exposed to two competing fisheries (i.e. the commercial and the  
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46 193 depredation fishery).

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#### 52 53 195 *Comparison of alternative model formulations*

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56 196 We compared how the alternative model formulations, which respectively account for  
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58 197 depredation as (1) *food subsidy*, (2) *increased fishing effort* or (3) *competing fishery*, capture  
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3 198 depredation effects relative to the *baseline* model with no depredation. To facilitate model  
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5 199 comparison, all P/B and Q/B ratios estimated for the *baseline* model, as well as other input  
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7 200 parameters (i.e. biomass, diet matrix etc.) were kept constant across all models, except for  
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9 201 model-specific adaptations as presented above (section “Modelling depredation”). Therefore,  
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11 202 for each model, only the biomass of toothfish groups (represented as a multi-stanza population)  
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13 203 were re-estimated by Ecopath, keeping the biomass of the small adult stanza fixed.

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15 204 Quantitative comparison of the three alternative depredation model formulations  
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17 205 relative to the *baseline model* relied on three complementary metrics, predation mortality,  
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19 206 fishing mortality, and mixed trophic impact, to assess changes in: (1) fishing and predation  
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21 207 mortality on target species, (2) mutual impacts of the groups directly involved in depredation  
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23 208 (i.e. depredating, target species and fishery), and (3) ecosystem impacts of depredating species.  
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25 209 Rationales for using these three metrics are:

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27 210 Changes in predation mortality are expected to reflect release in natural predation due  
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29 211 to depredating species switching diet to feed on fisheries catches of the same species. Predation  
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31 212 mortality (M2) corresponds to the sum of all mortalities due to all  $n$  predator groups feeding on  
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33 213 prey group  $i$  (Equation 3), as follows:

$$214 \quad M2_i = \sum_{j=1}^n Q_j \times DC_{ji} \quad (3)$$

34  
35 215 where  $Q_j$  is the total consumption rate of predating group  $j$  (Equation 2), and  $DC_{ij}$  is the fraction  
36  
37 216 of group  $i$  in the diet of predator  $j$ .  $Q_j$  is calculated as the product of  $B_j$ , the biomass of group  $j$   
38  
39 217 and  $Q_j/B_j$ , the consumption/biomass ratio for group  $j$  ([Christensen et al., 2008](#), [Piroddi et al.,](#)  
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41 218 [2015](#)).

42  
43 219 The mortality due to fishing is calculated either as (i) the sum of landings and discards  
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45 220 divided by the biomass of the target group in the *baseline* and *food subsidy* models; or, (ii) the

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3 221 sum of landings, discards and depredated biomass divided by target group biomass in the  
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5 222 *increased fishing effort and competing fishery* models.

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7 223 Finally, changes in mixed trophic impacts (referred to as ‘impacts’ hereafter) summarise  
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9 224 how alternative formulations modify the cascading effects of depredation-related groups on  
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11 225 other model groups. The mixed trophic impact indicates how a long-term increase in a given  
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13 226 group biomass can affect the equilibrium biomass of other groups via all direct and indirect  
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15 227 feedback loops ([Ulanowicz and Puccia, 1990](#)). The impact indicator is a matrix whose  $ij$ th  
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17 228 element represents the interaction between the impacting group  $i$  and the impacted group  $j$ . This  
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19 229 indicator considers fisheries as predators, which means landings and discards correspond to  
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21 230 their prey intake in the model ([Christensen et al., 2008](#); [Piroddi et al., 2015](#)).

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28 232 *Case study*

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30 233 The commercial longline fishery operating in the Exclusive Economic Zones of  
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32 234 Kerguelen and Crozet Islands (French subantarctic islands located between 45°S and 50°S,  
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34 235 50°E and 70°E) is conducted by seven licensed vessels and targets Patagonian toothfish  
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36 236 (*Dissostichus eleginoides*) (hereafter “toothfish” - [Guinet et al., 2015](#)). As the fishery holds the  
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38 237 largest quota for that fish species across subantarctic waters, it is also the fishery most affected  
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40 238 by depredation. Killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) are  
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42 239 the two primary depredating species, together removing an estimated 279 t of toothfish per year  
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44 240 at Crozet and 250 t per year at Kerguelen, equivalent to 30% and 6% of the total catches, in the  
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46 241 two areas respectively ([Gasco et al., 2015](#); [Tixier et al., 2020](#)).

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49 242 Our Ecopath models represented the marine ecosystem of Crozet and Kerguelen in  
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51 243 2017. The two areas were considered as a single area for highly mobile species, such as sharks,  
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53 244 birds, and some marine mammals. For less mobile groups, such as benthic groups, which are  
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55 245 similar at the community level but do show differences at the species level, especially among  
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3 246 benthic fish, between Crozet and Kerguelen ([Duhamel et al., 2005](#)) the food-web was duplicated  
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5 247 for each of the two areas (i.e. area-specific groups as used in [Piroddi et al., 2017](#)). Similarly,  
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7 248 two longline fisheries - Kerguelen fishery and Crozet fishery - were incorporated to account for  
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9 249 the large differences in catches between the two areas (80% of the total quota was caught at  
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11 250 Kerguelen). A total of 59 functional groups were considered in the model: 38 area-specific  
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13 251 groups and 21 groups shared between Crozet and Kerguelen (Figure 2; Table S1).

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17 252 Toothfish was modelled as three weight-based stanza for each area to represent different  
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19 253 life stages of the species: juveniles (< 2 kg), small (2 - 5 kg) and large adults (> 5 kg). Sperm  
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21 254 whales extensively depredate on toothfish catches both at Crozet and Kerguelen, but individuals  
22  
23 255 are strongly segregated between the two areas ([Labadie et al., 2018](#)). Therefore, this species  
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25 256 was divided into two area-specific groups in the model. Unlike sperm whales, killer whales  
26  
27 257 depredate almost exclusively at Crozet ([Labadie et al., 2018](#)). Although two killer whale  
28  
29 258 morphotypes occur at Crozet and are both observed depredating on toothfish catches ([Tixier et](#)  
30  
31 259 [al., 2016](#)), only the so-called “Crozet killer whales” were presented in the study due to the lack  
32  
33 260 of information on the other morphotype (type-D). Abundance estimates for killer whales were  
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35 261 taken from [Tixier et al. \(2017\)](#) and those for sperm whales from [Labadie et al. \(2018\)](#). The  
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37 262 natural diet of sperm whales was assumed to be mostly composed of cephalopods and, to a  
38  
39 263 lesser extent, of adult toothfish ([Clarke, 1980](#); [Cherel and Duhamel, 2004](#)). For the Crozet killer  
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41 264 whales, natural prey included pinnipeds, whales, penguins and toothfish ([Tixier et al., 2019](#)).  
42  
43 265 Population size estimates and diet compositions for all pinnipeds and bird populations were  
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45 266 derived from [Guinet et al. \(1996\)](#) and [Cherel et al. \(2004\)](#), as well as from expert consultation.  
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47 267 Data for the remaining functional groups were taken from the literature and from previously  
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49 268 developed Ecopath models for Kerguelen, the Falkland Islands and the Antarctic Peninsula  
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51 269 ([Pruvost et al., 2005](#)). Species were generally aggregated into functional groups when sharing  
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53 270 similar trophic and ecological niches. However, species caught by the fishery, including both  
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3 271 target and by-catch species, were modelled separately. The main by-catch species of the  
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5 272 toothfish fishery at Crozet and Kerguelen represent approximately 6% of the total catches and  
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7  
8 273 are grenadiers (*Macrourus spp.*), blue antimora (*Antimora rostrata*), and whiteleg skate  
9  
10 274 (*Amblyraja taaf*) at Crozet and kerguelen sandpaper skate (*Bathyraja irrasa*) and eaton's skate  
11  
12 275 (*Bathyraja eatonii*) at Kerguelen). Blue antimora is fully discarded, while the other species are  
13  
14  
15 276 partly or fully retained ([CCAMLR, 2018a](#); [CCAMLR, 2018b](#)). As this work primarily focused  
16  
17 277 on inclusion of depredation, the Ecopath models neglected fisheries by-catch given their  
18  
19 278 marginal volumes in the French Patagonian toothfish fishery. Full details on model  
20  
21 279 parameterisation are provided in Supplementary material.

22  
23  
24 280 Data on fishery catches, including both landings and discards, were collected by the  
25  
26 281 French Southern Ocean Fishery Observer Program ([Gasco, 2011](#)) and extracted from the  
27  
28 282 "PECHEKER" database ([Martin and Pruvost, 2007](#); [Pruvost et al., 2011](#)). Toothfish population  
29  
30 283 estimates were obtained from spawning stock biomass estimates ([Massiot-Granier et al., 2019a](#);  
31  
32 284 [Massio-Granier et al., 2019b](#)). Depredation rates were set at 30% of the total catches for Crozet  
33  
34 285 and 2% of the total catches at Kerguelen as estimated for 2017 following the methodology used  
35  
36 286 by [Gasco et al., \(2015\)](#). Further details on the data used are available in Supplementary material  
37  
38 287 (Table S2). For clarity, we primarily present the results from the Crozet region hereafter.  
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## 43 44 289 **Results**

### 45 46 290 *Fishing and predation mortality*

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49 291 Relative to the *baseline* model, fishing mortality was unchanged in the *food subsidy*  
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51 292 model but increased by ~15% in the *increased fishing effort* and the *competing fishery* models  
52  
53 293 (Figure 3a). The increase relative to the *baseline* model was equal across all toothfish stages in  
54  
55 294 the *competing fishery* model, and varied from 14.9% (juvenile toothfish) to 15.2% (large  
56  
57 295 toothfish) in the *increased fishing effort* model.  
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3 296 Natural predation mortality on toothfish decreased similarly by less than 3% in all *food*  
4  
5 297 *subsidy*, *increased fishing effort* and *competing fishery* models relative to the *baseline* model.  
6  
7 298 The maximum relative decline was 2.3% for small adult toothfish (Figure 3b). For other killer  
8  
9 299 whale prey groups, natural predation mortality increased by 0.4 to 0.6% in the *food subsidy*  
10  
11 300 model, on filtering marine mammal, and fur seals and king penguin, respectively. Natural  
12  
13 301 predation on other prey groups did not change in the *increased fishing effort* and the *competing*  
14  
15 302 *fishery* models relative to the *baseline* model (Figure 4). Note that this difference in the *food*  
16  
17 303 *subsidy* model partially comes from a ~1.8% increase in the equilibrium biomass of killer  
18  
19 304 whales relative to all other models. Except for this killer whale biomass in the *food subsidy*  
20  
21 305 model, equilibrium biomasses for all groups were similar across all models. Despite similar  
22  
23 306 input parameters set evenly across all models, this slight change unexpectedly emerged from  
24  
25 307 mass-balancing the *food subsidy* model, possibly because it did not include any feedback  
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27 308 between ‘depredated target species’ and the commercial fishery.  
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### 35 310 *Mutual effects of depredation-related groups*

37 311 Mixed trophic impacts of predators and fisheries were overall consistent across all  
38  
39 312 depredation models, except for slight model specific differences: fisheries activity, sperm whale  
40  
41 313 natural predation and sperm whale depredation all positively impacted juvenile toothfish but  
42  
43 314 were detrimental to larger life stages (Figure 5). Natural predation by killer whales positively  
44  
45 315 impacted all toothfish stages (Figure 5). The small toothfish stage was negatively impacted by  
46  
47 316 fishing and depredation, but only marginally positively affected by killer whales natural  
48  
49 317 predation (Figure 5). In the *competing fishery* model, killer whales depredation positively  
50  
51 318 impacted small toothfish life stages but negatively the two larger all toothfish life stages (Figure  
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53 319 5).

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3 320 Except for the positive impact of killer whales (+ ~0.03), depredating species (i.e. sperm  
4  
5 321 whales and in the *competing fishery* model the "depredation fishery", which includes  
6  
7 322 depredation from killer whales and sperm whales) were detrimental to the toothfish longline  
8  
9 323 fishery (Figure 6). Sperm whales had the largest negative impact on the commercial fishery (-  
10  
11 324 0.07 to -0.08). These negative impacts of depredating groups on the fishery suggest that the  
12  
13 325 depredation models were able to capture losses in fishery performance due to depredation.  
14  
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16  
17 326 Impacts of the commercial fishery were negative on all depredating groups, with a  
18  
19 327 stronger impact on sperm whales than killer whales (i.e. respectively -0.04 and -0.022; Figure  
20  
21 328 7). Note however that the "depredated toothfish" component was estimated to be beneficial to  
22  
23 329 both sperm (+ ~0.004) and killer (+ ~0.02) whales (Figure 7).  
24  
25

26 330 As a side result, we also observed marginal decreases in trophic levels of the depredating  
27  
28 331 species in the *food subsidy*, *increased fishing effort* and *competing fishery* models relative to  
29  
30 332 the *baseline* model, by ~0.3% for sperm whales down to ~1.8% for killer whales (Figure S2).  
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33 333

### 34 334 *Ecosystem effects of depredating species*

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37 335 Overall, impacts of killer whales (i.e. "killer whale" in the *food subsidy* model and  
38  
39 336 *increased fishing effort* model, and both depredating and naturally-predating components in the  
40  
41 337 *competing fishery* model), were negative on most of their prey groups including diving seabirds  
42  
43 338 fur seals and elephant seals (females and pups) across all models (Figure 8). Most prey groups,  
44  
45 339 including marine mammals and penguins, were marginally (> 0.1%) less negatively impacted  
46  
47 340 by killer whales in the three alternative *depredation* models relative to the *baseline* model. Due  
48  
49 341 to a direct release in natural predation pressure, killer whales were estimated to positively  
50  
51 342 impact all toothfish groups (Figure 8).  
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56 343 Larger impacts of sperm whales (absolute estimate of mixed trophic impact > 0.03;  
57  
58 344 Figure 9) only concerned groups that are directly related to the commercial fishery, either  
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3 345 because they are involved in depredation (i.e. small and large toothfish), or accidentally caught  
4  
5 346 as bycatch such as blue antimora and whiteleg skate (Figure 9). Sperm whale impacts varied  
6  
7 347 slightly across the alternative models and appeared to be marginally buffered in the *increased*  
8  
9 348 *fishing effort* model.

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12 349 The ecosystem effects of depredation captured by the different Ecopath models are  
13  
14 350 summarised in table 1.

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## 18 19 352 **Discussion**

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21 353 Ecosystem models are pivotal tools to account for multiple drivers of ecological  
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23 354 systems, such as interactions between species (i.e. predation, competition) and environmental  
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25 355 conditions ([Hollowed, 2000](#); [Plagányi and Butterworth, 2004](#)). They can also include the effects  
26  
27 356 of anthropogenic activities (e.g. harvesting), which often leads to competition between natural  
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29 357 populations and humans. Because depredation generates a number of effects beyond direct  
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31 358 competition between humans and wildlife which have to date not received much attention in  
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33 359 ecosystem modelling frameworks ([Peterson et al., 2013](#); [Werner et al., 2015](#)), their complex  
34  
35 360 consequences on socio-ecosystem dynamics are not well understood and remain challenging to  
36  
37 361 anticipate. In the following sections, we discuss how the alternative Ecopath model  
38  
39 362 formulations developed to explicitly represent depredation in a case study can to some extent  
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41 363 capture consequences of depredation on marine ecosystem structure and dynamics. Given the  
42  
43 364 structural constraints of the Ecopath framework to represent complex consequences of  
44  
45 365 depredation at the interface between fisheries and marine predators, we also identify a number  
46  
47 366 of limitations in the proposed model formulations and provide guidance for future research in  
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49 367 ecosystem modelling to better capture the range of socio-ecological effects associated with  
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51 368 depredation.

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3 370 *A first step towards model-based assessment of the ecosystem effects of depredation in marine*  
4  
5 371 *systems*  
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8 372 Our study provides the first model-based assessment of the system-level impacts of  
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10 373 depredation in marine systems. By comparing three alternative depredation-explicit Ecopath  
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12 374 model formulations with a *baseline* model that neglects depredation processes, we assess how  
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14 375 including depredation can affect estimates of fishing mortality and predation pressure. In our  
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16 376 models of the Kerguelen/Crozet system, fishing mortality increased with the inclusion of  
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18 377 depredation, but changes in other indicators, including predation mortality, were marginal.

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21 378 By incorporating depredation as part of fishery catches, the *increased fishing effort*  
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23 379 model and the *competing fishery* model explicitly captured the increase in fishing mortality  
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25 380 induced by depredation. Both models estimated a ~15% increase in fishing mortality due to  
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27 381 toothfish depredation by killer and sperm whales. Since depredation has only been qualitatively  
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29 382 reported to increase fishing mortality in other longline fisheries ([Werner et al., 2015](#); [Peterson](#)  
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31 383 [and Hanselman, 2017](#)), this result is noteworthy. Because depredation can be a cryptic source  
32  
33 384 of fishing mortality, it is not systematically detected (e.g., species depredating on fishing gear  
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35 385 at depth, when fishers are away or leaving limited evidence when removing fish) and is only  
36  
37 386 rarely quantified ([Tixier et al., 2020](#)), such estimates are necessary to improve accuracy of fish  
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39 387 stock assessments and hence to support sustainable fishery management ([Gilman et al., 2013](#)).  
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41 388 However, our estimate of increased fishing mortality due to depredation is case-specific and  
42  
43 389 method-dependent. First, the French toothfish fishery operates in a remote region, where only  
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45 390 a small fleet (7 vessels) targets a commercially valuable stock that was unexploited until the  
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47 391 1970s ([Duhamel and Williams, 2011](#)). While depredation increased fishing mortality by 15%,  
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49 392 the estimated depredated biomass (~279 t per year; [Tixier et al., 2020](#)) only represents a minor  
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51 393 fraction (possibly 1%) of the estimated population biomass used for the model. Although this  
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53 394 suggests a limited impact of depredation on toothfish in this region, a similar increase in fishing  
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3 395 mortality in response to depredation may have a greater impact in other regions where stocks  
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5 396 have been heavily exploited. Indeed, fishery catches represent a higher proportion of the  
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7 397 depleted stock biomass in intensively exploited stocks so any further increase in fishing effort  
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9 398 (for instance due to depredation) could have severe impacts for fully or over-exploited  
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11 399 stocks. Here the subantarctic longline fishery, which operates in a remote hard-to-access area  
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13 400 and is well-regulated, exploits a rather abundant stock so we can assume that the estimated 15%  
14  
15 401 increase in fishing mortality due to depredation is not too critical for toothfish stock  
16  
17 402 sustainability. Moreover, changes in fishing mortality in a depredation-impacted system may  
18  
19 403 depend on whether fishers can increase their fishing effort to recoup catch losses. Fisheries with  
20  
21 404 different management systems and more restrictive fishing seasons may offer fewer  
22  
23 405 opportunities to compensate for depredation losses. For instance, in South Georgia where the  
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25 406 toothfish fishery is also subject to killer and sperm whale depredation, fishing is restricted to  
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27 407 winter months only ([Towers et al. 2019](#)).

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33 408 In the proposed depredation-explicit models, depredation only induced a marginal  
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35 409 release in predation pressure on natural prey species of depredating sperm whales and killer  
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37 410 whales. All alternative models predicted a slight decrease of around 2% in direct predation of  
38  
39 411 both killer and sperm whales on toothfish. Note that this directly results from the assumption  
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41 412 that the total consumption of toothfish by whales at Crozet remained unchanged, in relation to  
42  
43 413 study of [Tixier et al. \(2019b\)](#) which found no difference between the contribution of toothfish  
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45 414 to the diet of depredating and non-depredating killer whales, i.e. that natural predation on  
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47 415 toothfish was partially replaced by depredation on toothfish catches. Toothfish is a natural prey  
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49 416 of sperm whales but is likely to only marginally contribute to their diet that is largely dominated  
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51 417 by cephalopods, as evidenced in Antarctic waters ([Yukhov, 1972](#)). As such, access to toothfish  
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53 418 on fishing gear likely increases the contribution of this prey in the diet of individuals engaging  
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55 419 in depredation, subsequently releasing predatory pressures of these individuals on other of their  
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3 420 primary cephalopod prey species. However, the extent to which this release, which may be  
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5 421 spatially restricted to areas where fishing occurs and depend on the proportion of depredating  
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7 422 individuals in the sperm whale population, alters the full ecosystem, is still unknown. Cascading  
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9 423 impacts are likely greater when depredated species are naturally mostly absent from their diet,  
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11 424 as is the case for harbour seals (*Phoca vitulina*) depredating eels from fyke-nets in Sweden  
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14 425 ([Lundström et al., 2010](#)).

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17 426 The magnitude of predation release on wild prey may not only depend on the importance  
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19 427 of the depredated species for a predator's natural diet but also on the predator's trophic position,  
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21 428 population abundance and the extent to which it gains energy from depredation. Most species  
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23 429 depredating on fishery catches are higher trophic level species such as large sharks and marine  
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25 430 mammals, and changes in predation pressures from these top-predators are likely to generate  
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27 431 greater top-down cascading ecosystem effects than changes from meso-predators ([Newsome et](#)  
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29 432 [al., 2015](#)). Population size and energetic requirements of the depredating species, paired with  
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31 433 the energetic value of the depredated fish, will dictate its overall consumption.  
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### 37 435 *Inclusion of depredation in Ecopath: limitations and recommendations*

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39 436 While the depredation-explicit models to some extent capture increase in fishing  
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41 437 pressure and release in predation pressures as consequences of depredation, a range of other  
42  
43 438 processes (for instance, facilitated access to food resources for predators, or decrease in fishing  
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45 439 gear capturability) were not accurately captured (if at all) in these models. These limitations in  
46  
47 440 the proposed model formulations are largely due to structural constraints of the Ecopath  
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49 441 modelling framework.  
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53 442 Facilitated access to prey, which can potentially enhance depredating species' individual  
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55 443 and population performance, was partially incorporated via two modelling tricks: (1) by adding  
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57 444 a specific 'depredated target species' detritus group; and, consequently, by (2) separating out  
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3 445 depredation from natural predation on target species. However, depredation was only linked to  
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5 446 the commercial fishery as a “discard” component in the *increased fishing effort* and in the  
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7 447 *competing fishery* models because catches cannot appear in the diet matrix in Ecopath. These  
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10 448 alternative model structures theoretically allow for a positive impact of depredated fish biomass  
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12 449 on depredating species. However, this positive impact does not capture how reduced foraging  
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14 450 effort due to facilitated access to food resource can enhance certain life history parameters of  
15  
16 451 the depredating species (i.e. life expectancy, fecundity, or growth; [Tixier et al., 2015](#)). To  
17  
18 452 achieve this, it would be necessary to increase the assimilation rate of depredated resources  
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20 453 relative to predation, and adapt information about population growth rate (i.e. P/B).

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24 454 Adding ‘depredated target species’ as an additional detritus group in Ecopath allows the  
25  
26 455 partial incorporation of two separate depredation effects (i.e. release of predation pressure and  
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28 456 facilitated access to food resources) but it skews estimates of trophic levels in the model. For  
29  
30 457 instance, representing the depredated biomass as a detritus group directly leads to an  
31  
32 458 underestimation of the depredating species’ trophic level in Ecopath, given that detritus groups  
33  
34 459 are assigned a basal trophic level (= 1) in Ecopath ([Christensen et al., 2008](#)). Thus, caution  
35  
36 460 should be exercised when using a depredation-explicit model to study trophic levels in Ecopath.  
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38  
39 461 In the Crozet/Kerguelen case study, a reduction in the depredating species’ trophic levels is  
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41 462 unrealistic since the depredated fish, toothfish, is among the highest trophic levels well above  
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43 463 most other natural prey items of killer and sperm whales ([Tixier et al., 2019](#)). Similarly, a  
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45 464 decrease in trophic level would seem misleading in many other depredation cases, such as in  
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47 465 the wide-ranging tropical longline fisheries where sharks and odontocetes heavily depredate on  
48  
49 466 high trophic level groups (i.e. tuna and swordfish; [Rabearisoa et al., 2018](#)). Moreover,  
50  
51 467 depredation-related changes in trophic level are likely to depend on predator switching their  
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53 468 diet preferences towards the easily-accessible resource (rather than foraging for their natural  
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55 469 preys; [Jacoby et al., 1999](#)). While trophic levels of depredating species at Crozet/Kerguelen  
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3 470 should remain unchanged under the assumption that their overall toothfish consumption is not  
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5 471 changed by depredation, trophic levels of depredating species are most likely to increase as the  
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7 472 proportional contribution of depredation in their diet increases ([Jacoby et al., 1999](#)).  
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9 473 Conversely, species increasing their consumption of low trophic level prey when depredating,  
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11 474 as evidenced in cases where predators remove bait from fishing gears (e.g. [Thode et al., 2016](#)),  
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13 475 are likely to decrease their trophic level.  
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17 476 Decline in fishery performance could not be fully captured in any of the models. Indeed,  
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19 477 none of the three depredation-explicit models explicitly captured depredation as a loss in gear  
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21 478 capturability and/or as an extra cost to the fishery, but rather represent depredated biomass as  
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23 479 discards recycled by the depredating species. While the *competing fishery* model incorporated  
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25 480 depredation as a virtual fishery to capture the supplementary negative effect of killer and sperm  
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27 481 whales on the fishery via removal of catches from fishing gears, it did not explicitly quantify  
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29 482 energy gains for the depredating species and efficiency loss for the fishery. Moreover, model  
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31 483 realism also depends on data availability, which represent a major limitation of any ecosystem  
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33 484 model. For instance, in our case, a single virtual fishery represented toothfish biomass  
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35 485 depredated by both sperm whales and killer whales as data were insufficient to discriminate  
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37 486 impacts of their respective depredation. To include depredation, some data are added to those  
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39 487 traditionally used in ecosystem models, such as the quantity of resource depredated or the  
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41 488 depredation rate. In addition to this, it is necessary to know in what proportion depredation  
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43 489 modifies the depredating species' diet.  
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49 490 In addition to analysing how to account for the greatest number of expected impacts  
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51 491 associated with depredation, evaluating alternative model structures also helped delineate the  
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53 492 limitations of each model formulation. While all alternative models were derived from the same  
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55 493 *baseline* model, each of the three depredation-explicit models posed different modelling choices  
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3 494 in terms of model group aggregation and feedback structure, which can significantly impact  
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5 495 ecosystem model predictions ([Pinnegar et al., 2005](#); [Marzloff et al., 2011](#)).

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8 496 Note for instance, that we endeavoured to keep equilibrium biomasses for all groups  
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10 497 similar across all models by setting similar input parameters across all models. All equilibrium  
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12 498 biomasses were identical across models except for an unexpected ~1.8% increase in the  
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14 499 equilibrium biomass of killer whale in the *food subsidy* model (which possibly explains the  
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16  
17 500 observed difference in natural predation mortality due to depredating killer whales relative to  
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19 501 other models). We suspect that this slight change in the *food subsidy* model emerged from the  
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21 502 Ecopath mass-balancing algorithm, as this model does not include any feedback between  
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23 503 ‘depredated target species’ and the commercial fishery. In the *increased fishing effort* model,  
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25 504 depredation was included into the commercial fishery but depredating species and fishing gear  
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27 505 were aggregated into a single ‘caught toothfish’ functional group. This aggregated  
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29 506 representation is ecologically questionable given that ecosystem models shall ideally  
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31 507 discriminate between prey and predator populations ([Fulton et al., 2003](#)), while one could argue  
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33 508 that the amount of fishing gear can be comparable to a predator population abundance for the  
34  
35 509 target species. Indeed, fishers and depredating species do not compete for hooked fish, since  
36  
37 510 only one model group removes the total fish caught. Moreover, the *increased fishing effort*  
38  
39 511 model did not discriminate between the predation and depredation effects of depredating  
40  
41 512 species on the commercial fishery. This distinction appears relevant in our case study for killer  
42  
43 513 whales, as natural predation on competitors of toothfish for food may be indirectly beneficial  
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45 514 for the fishery while depredation negatively affects that same fishery. However, disaggregating  
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47 515 the fishery into a ‘depredating species’ fishery and a commercial fishery, as done in the  
48  
49 516 *competing fishery* model, does not seem completely realistic as separating out a single fishery  
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51 517 into two independent components in the Ecopath model. Indeed, in the case of an increase in  
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53 518 commercial fishing effort, the virtual depredation fishery should be affected similarly, assuming  
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3 519 a direct relationship between fishing effort and depredation rate. However, this is not the case  
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5 520 in this model as the two fisheries remain fully separated.  
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10 522 *Recommendations for depredation-resolving ecosystem models*  
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12 523 Due to structural constraints and lack of flexibility of the Ecopath framework to capture  
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14 524 behaviour-mediated processes, this study could not fully capture the complexity of interactions  
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17 525 between fisheries and depredating species. For these reasons, we decided not to pursue with  
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19 526 dynamic simulations with Ecopath with Ecosim. Depredation is the consequence of behavioural  
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21 527 innovations and adaptations of marine predator species to new feeding opportunities offered by  
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23 528 fisheries, including actively searching and/or following fishing vessels or purposely using  
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26 529 human equipment to feed on aggregated, easy-to-catch resources despite the associated risk  
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28 530 ([Bearzi et al., 2019](#)). These adaptations are time-dependent, occurring at the inter-annual level  
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30  
31 531 when individuals progressively learn depredation (e.g. [Tixier et al., 2016](#)) or extend their spatial  
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33 532 range of interaction with vessels (e.g., [Schakner et al., 2014](#)), or at the intra-annual level when  
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35 533 individuals only switch to depredation when natural prey are scarce.  
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37 534 Medium- and long-term consequences of depredation for depredating populations not  
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39 535 only result from positive provisioning effects but also from injuries or lethal risks related to  
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41 536 interactions with fisheries. If depredation supplies more energy than the natural diet,  
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44 537 depredation may enhance fitness and, therefore, the reproductive performances of individuals.  
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46 538 This was found for killer whales depredating on toothfish catches at Crozet and depredating on  
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48 539 tuna catches in the Strait of Gibraltar ([Guinet et al., 2015](#); [Tixier et al., 2015](#); [Esteban et al.,](#)  
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50 540 [2016](#)). If the energy gain due to depredation relative to natural feeding is large, depredating  
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53 541 populations could expand (in particular if also benefiting from dedicated conservation effort),  
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56 542 which could further enhance the magnitude of depredation long-term impacts on the ecosystem.  
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58 543 However, this scenario may be only realistic in a situation where the risks of fatal interactions  
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3 544 with fishing gears and vessels are limited. Unlike depredating species in the Crozet/Kerguelen  
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5 545 fishery and to a greater extent for in the Southern Ocean (where high level of regulations reduce  
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7 546 potential fisheries negative impacts on marine predators), depredating species can be exposed  
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9 547 to the accidental risk of getting caught in fishing gear and/or intentional shooting from fishers  
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11  
12 548 ([Dans et al., 2003](#); [Azevedo et al., 2017](#)). Depredating species bycatch such as marine mammals  
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14 549 often reported in many static net and trawl fisheries ([Read, 2008](#)). These bycatches should be  
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16 550 considered in future studies aiming to address the full range of ecosystem effects resulting from  
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19 551 depredation.

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21 552 While considering depredation related processes in ecosystem models is important, this  
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23 553 study only partially addresses this challenge, which will require further development in future  
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25 554 studies. Future ecosystem modelling studies should consider temporal variations in the size of  
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27 555 depredating species populations and in the composition of their diet associated with changes in  
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29 556 prey availability. However, to provide accurate input information, further understanding of the  
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31 557 socio-ecosystem interactions generated locally by depredation is needed. Firstly, and as raised  
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33 558 by the findings of the present study, understanding the extent to which depredated resources  
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35 559 replace natural prey in depredating species' diets appears as a critical element to investigate.  
36  
37 560 Secondly, assessing whether the balance between benefits and costs is positive or negative for  
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39 561 depredating species is pivotal to determining long-term depredating species' population growth  
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41 562 rates. In summary, we present a pilot study exploring, within the constrained Ecopath  
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43 563 framework, alternative ways of incorporating depredation on fisheries catches. By assessing  
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45 564 how different model formulations affected estimates of natural predation and fishing mortality  
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47 565 on different model groups, the study provides a number of insights concerning the ecosystem  
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49 566 effects of a depredation-impacted subantarctic fishery. The results also highlight the limitations  
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51 567 of Ecopath-based modelling to address complex behaviour-mediated processes. Thus, the  
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53 568 development of dedicated models that can accurately capture complex multi-faceted socio-  
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3 569 economic and ecological impacts inherent to depredation conflicts is essential to identify the  
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5 570 conditions needed for long-term coexistence of fisheries and marine predators, and to contribute  
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8 571 to ecosystem-based management of marine ecosystem.  
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### 11 12 573 **Supplementary material**

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14 574 The following supplementary material is available at *ICESJMS* online. Supplementary  
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16 575 materials contain a more exhaustive description of model construction, as well as an assessment  
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18 576 of data availability. It also presents additional figures on depredating species trophic level.  
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### 47 48 588 **Data Availability Statement**

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50 589 The data underlying this article cannot be shared publicly for reasons of confidentiality.  
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769 **Tables**

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771 **Table 1.** Summary of results across the alternative Ecopath models applied to the longline fisheries around Crozet island. Blank fields means that  
 772 the effect was not detected for a given model, a ✓ means the effect was found, while; ✗ denotes that a model produced the opposite effect.

Effect in model	Fig	Model			
		<i>baseline</i>	<i>food subsidy</i>	<i>Increased fishing effort</i>	<i>Competing fishery</i>
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		✗		
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			✗	✓
prey access facilitation by fishery for depredating by killer whales and sperm whales	7			✓	✓

## Figures legend

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, d) *competing fishery* model, depredation is an independent fishery. L landings biomass, D discards biomass, De depredated biomass and P<sub>D</sub> depredating species population biomass P<sub>T</sub> Target species population biomass.

Figure 2. Simplified flow diagram of the *baseline* Ecopath model. Functional groups specific to Crozet are framed in orange, 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).

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 and 3 *competing fishery* model. Toothfish are modelled as three weight-based stages: juveniles (< 2.07 kg), small adults (2.07-5 kg) and large adults (> 5kg).

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 and 3 *competing fishery* model.

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 *food subsidy* model, 2 *increased fishing effort* model and 3 *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 (> 5kg; right panel). In the *competing fishery* model, "Depredation 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

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3 whale” and “sperm whale” groups include both effects of depredation and natural predation by  
4 these groups.  
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6  
7 Figure 6. Impact indicator of depredating marine mammal species on the Crozet longline  
8 fishery. The "depredation fishery" group corresponds to toothfish removed by sperm whale and  
9 killer whale. Models are numbered from 0 to 3: 0 *baseline* model with no depredation, 1 *food*  
10 *subsidy* model, 2 *increased fishing effort* model and *competing fishery* model. "Depredation  
11 fishery" represents depredation by both sperm and killer whales in *competing fishery* model,  
12 while "killer whale" and "sperm whale" only represent natural predation by these groups. In the  
13 two other depredation model, “killer whale” and “sperm whale” groups include both effects of  
14 depredation and natural predation by these groups.  
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22 Figure 7. Mixed Trophic Impacts of the Crozet longline fishery on the subgroups of depredating  
23 killer whales (left) and sperm whales (right). Models are numbered from 0 to 3: 0 *baseline*  
24 model with no depredation, 1 *food subsidy* model, 2 *increased fishing effort* model and 3  
25 *competing fishery* model. "Depredation fishery" represents depredation by both sperm and  
26 killer whales in *competing fishery* model (but excludes the naturally-predating components of  
27 these groups).  
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33 Figure 8. Killer whale mixed trophic impact on all functional groups in the Crozet ecosystem.  
34 Only large effects (absolute value > 0.03) are shown. Estimates are provided for each models,  
35 which are numbered from 0 to 3: 0 *baseline* model with no depredation, 1 *food subsidy* model,  
36 2 *increased fishing effort* model and 3 *competing fishery* model (where ‘3DS’ and ‘3DF’  
37 distinguish between the impact of the ‘depredating species’ group and the ‘depredating fishery’,  
38 respectively). "Depredation fishery" represents depredation by both sperm and killer whales in  
39 *competing fishery* model, while "killer whale" and "sperm whale" only represents the natural  
40 predation by these groups. In the two other depredation model, “killer whale” and “sperm  
41 whale” groups include both depredation and natural predation effects of these groups.  
42 Functional group preceded by \* are part of killer whales diet.  
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3 Figure 9. Sperm whale mixed trophic impacts on all functional groups in Crozet ecosystem  
4 Only large effects (absolute value > 0.03) are shown. Estimates are provided for each models,  
5 which are numbered from 0 to: 0 *baseline* model with no depredation, 1 *food subsidy* model, 2  
6 *increased fishing effort* model and 3 *competing fishery* model (where ‘3DS’ and ‘3DF’  
7 distinguish between the impact of the ‘depredating species’ group and the ‘depredating fishery’,  
8 respectively). "Depredation fishery" represents depredation by both sperm and killer whales in  
9 *competing fishery* model, while "killer whale" and "sperm whale" only represents the natural  
10 predation by these groups. In the two other depredation model, “killer whale” and “sperm  
11 whale” groups include both depredation and natural predation effects of these groups.  
12 Functional group preceded by \* are part of sperm whales diet.  
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For Review Only

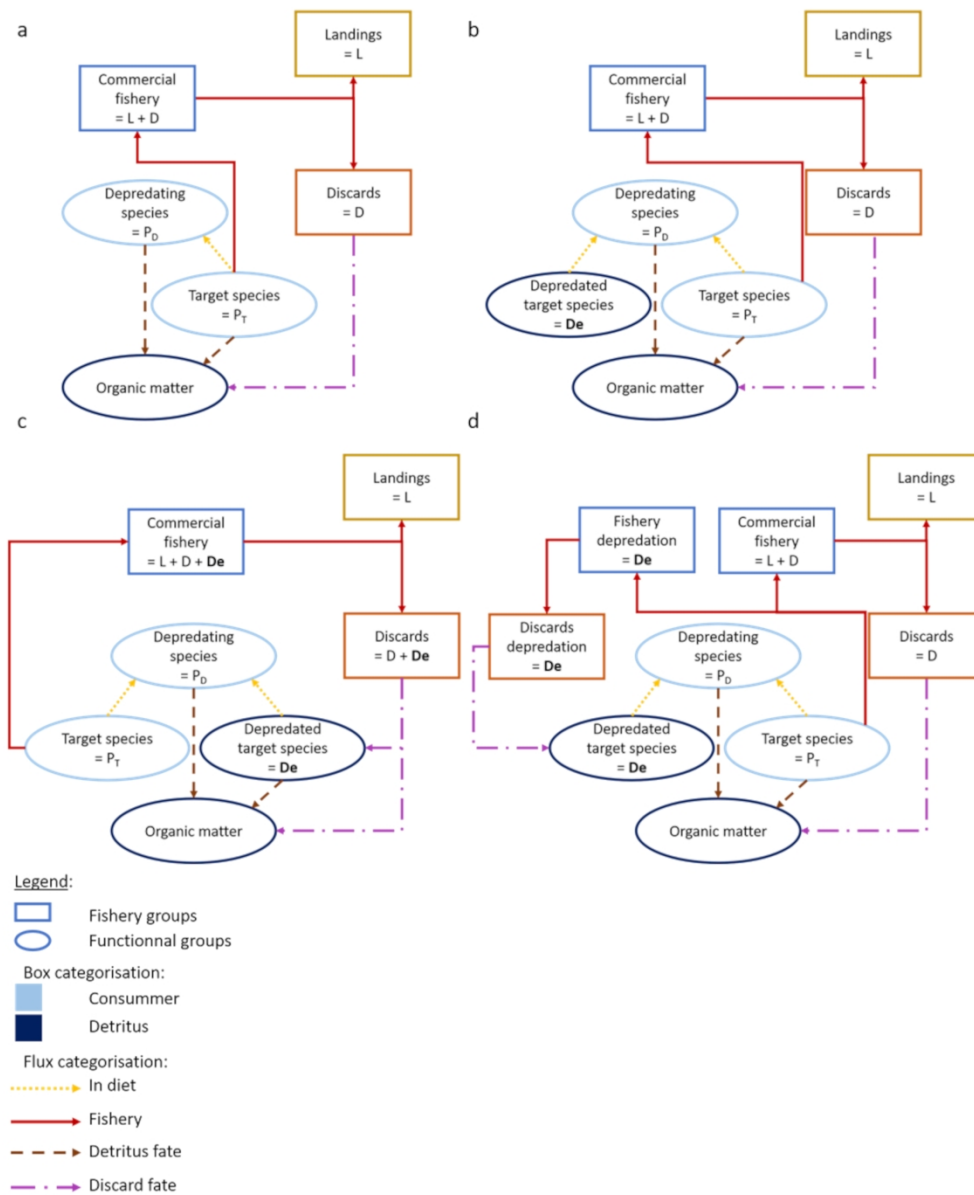


Figure 1. Schematic representations of alternative Ecopath model structures for including depredation on a target species. a) baseline model: no depredation; b) food subsidy model, depredated biomass is represented as a detritus group, c) increased fishing effort model, depredation incorporated into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

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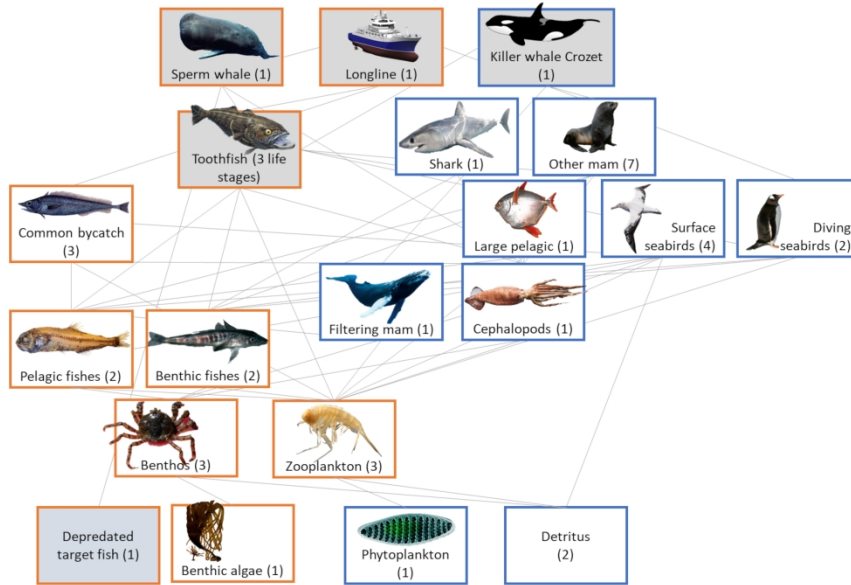


Figure 2. Simplified flow diagram of the baseline Ecopath model. Functional groups specific to Crozet are framed in orange, those occurring both around Crozet and Kerguelen Islands in blue. Figures in brackets correspond to the number of functional groups explicitly defined in the model. Focal groups 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).

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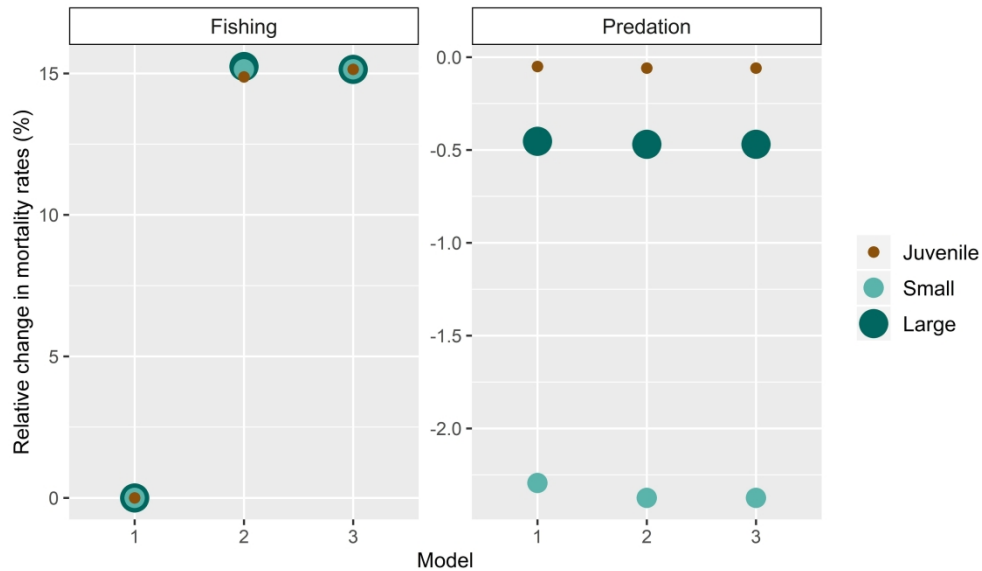


Figure 3. Effects of alternative Ecopath model formulation on Patagonian toothfish fishing (a) and natural predation (b) mortality. Estimates from the three alternative depredation models are expressed relatively to the baseline model (no depredation). Models are numbered from 1 to 3: 1 food subsidy model, 2 increased fishing effort model and 3 competing fishery model. Toothfish are modelled as three weight-based stages: juveniles (< 2.07 kg), small adults (2.07-5 kg) and large adults (> 5kg).

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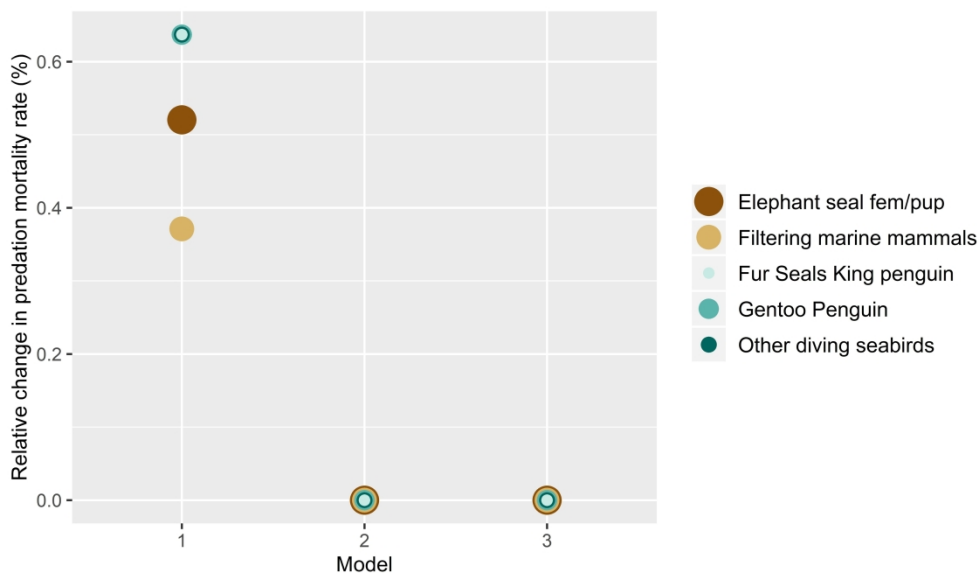


Figure 4. Relative change in killer whale predation mortality rates on non-commercial prey groups across alternative depredation models (relative to the baseline model with no depredation). Models are numbered from 1 to 3: 1 food subsidy model, 2 increased fishing effort model and 3 competing fishery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

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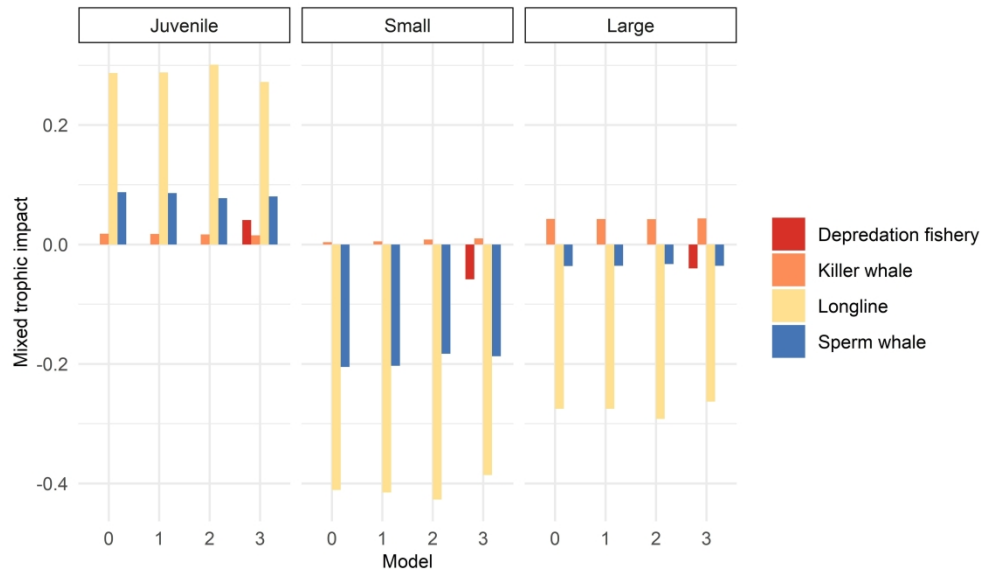


Figure 5. Impact indicator of longline fishery and depredating marine mammals on the three different toothfish life stages in the four Ecopath models, without depredation (0 for baseline model) and with depredation (1 food subsidy model, 2 increased fishing effort model and 3 competing fishery model). 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 (> 5kg; right panel). In the competing fishery model, "Depredation 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.

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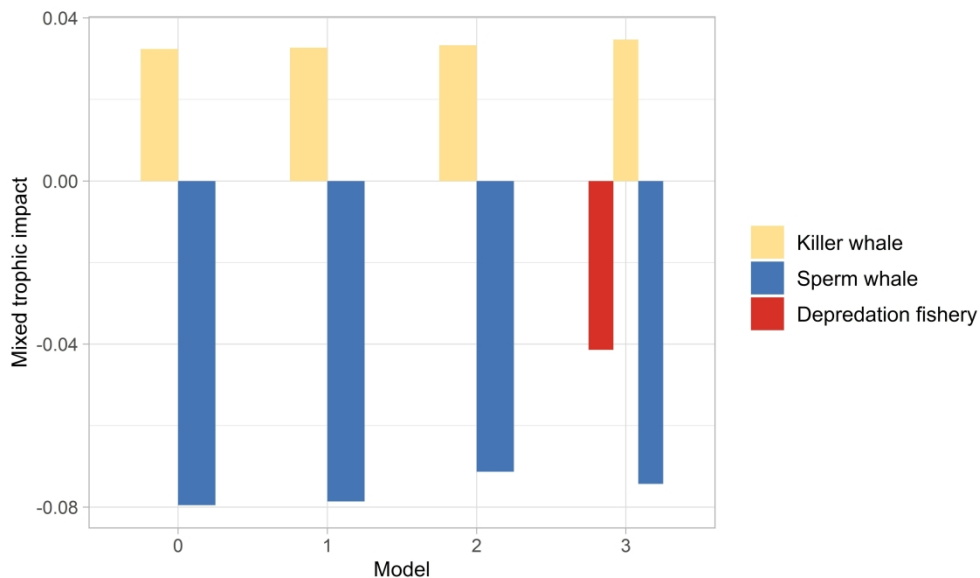


Figure 6. Impact indicator of depredating marine mammal species on the Crozet longline fishery. The "depredation fishery" group corresponds to toothfish removed by sperm whale and killer whale. Models are numbered from 0 to 3: 0 baseline model with no depredation, 1 food subsidy model, 2 increased fishing effort model and 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 model, "killer whale" and "sperm whale" groups include both effects of depredation and natural predation by these groups.

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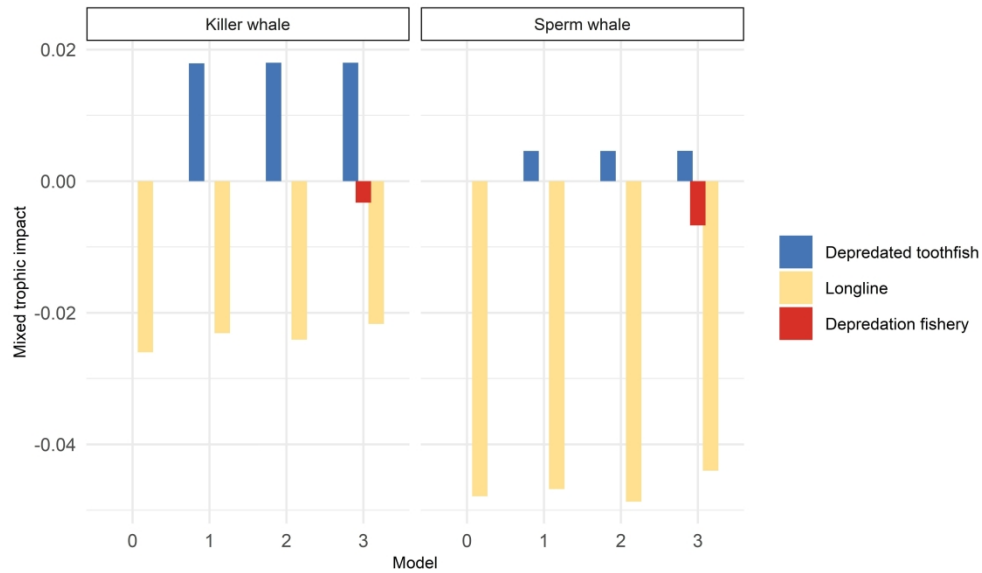


Figure 7. Mixed Trophic Impacts of the Crozet longline fishery on the subgroups of depredating killer whales (left) and sperm whales (right). Models are numbered from 0 to 3: 0 baseline model with no depredation, 1 food subsidy model, 2 increased fishing effort model and 3 competing fishery model. "Depredation fishery" represents depredation by both sperm and killer whales in competing fishery model (but excludes the naturally-predating components of these groups).

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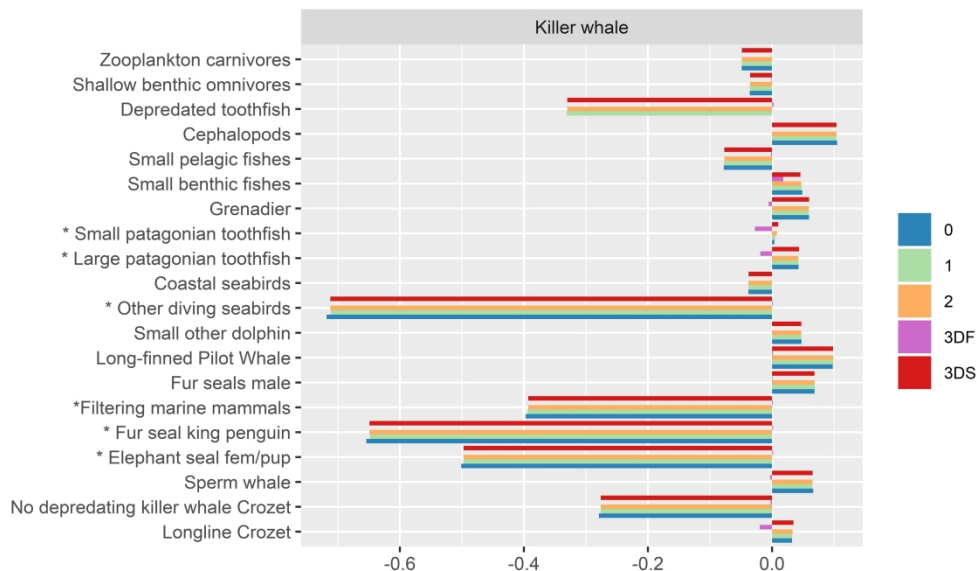


Figure 8. Killer whale mixed trophic impact on all functional groups in the Crozet ecosystem. Only large effects (absolute value > 0.03) are shown. Estimates are provided for each models, which are numbered from 0 to 3: 0 baseline model with no depredation, 1 food subsidy model, 2 increased fishing effort model and 3 competing fishery model (where '3DS' and '3DF' distinguish between 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 represents the natural predation by these groups. In the two other depredation model, "killer whale" and "sperm whale" groups include both depredation and natural predation effects of these groups. Functional group preceded by \* are part of killer whales diet.

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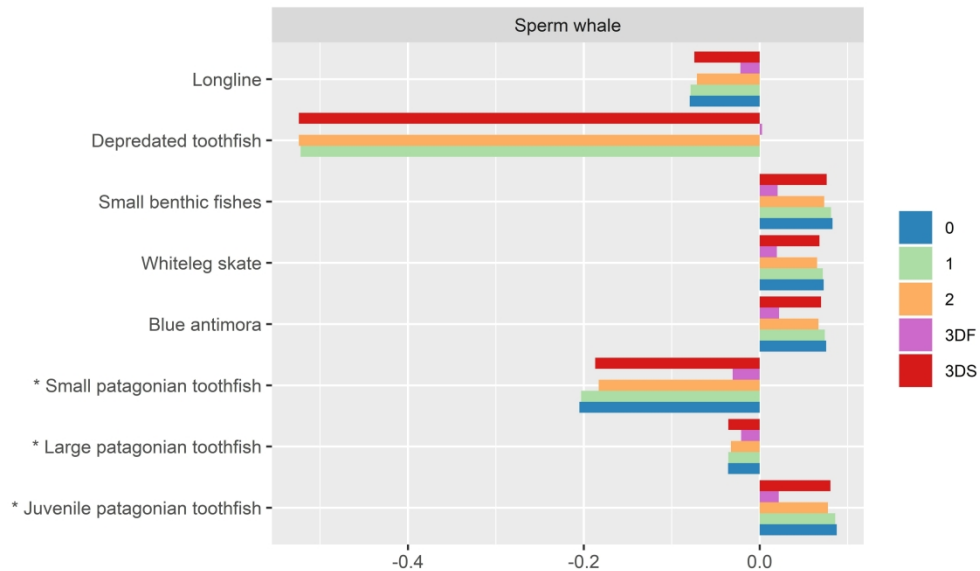


Figure 9. Sperm whale mixed trophic impacts on all functional groups in Crozet ecosystem Only large effects (absolute value > 0.03) are shown. Estimates are provided for each models, which are numbered from 0 to: 0 baseline model with no depredation, 1 food subsidy model, 2 increased fishing effort model and 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 represents the natural predation by these groups. In the two other depredation model, "killer whale" and "sperm whale" groups include both depredation and natural predation effects of these groups. Functional group preceded by \* are part of sperm whales diet.

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