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Lyndsay Clavareau

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L'UNIVERSITE
DE BRETAGNE OCCIDENTALE

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Spécialité : « *Ecologie marine* »

Par

Lyndsay CLAVAREAU

Effects Of Depredation On Marine Systems: Insights From A Global Literature Review And Applications Of Alternative Modelling Approaches To Regional Case Studies

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Unité de recherche : Laboratoire d'écologie benthique côtière (IFREMER-DYNECO-LEBCO) – Ecologie et Modèles pour l'Halieutique (IFREMER – EMH)

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« Il y a quelques années de cela, peu importe combien exactement, comme j'avais la bourse vide ou presque, et que rien d'intéressant ne me retenait à terre, l'idée me vint de naviguer un peu et de revoir le monde marin. »

Herman Melville, Moby Dick, 1851

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Chapitre 1 : Introduction générale

1.1. Contexte

La population mondiale compte aujourd'hui 7,8 milliards d'êtres humains, alors qu'elle ne comptait que 3,7 milliards d'individus en 1970. Ce doublement de la population humaine ces 50 dernières années, a engendré un développement accru des activités anthropiques avec des conséquences notables sur l'ensemble des écosystèmes de la planète (Ellis & Ramankutty, 2008; Vitousek et al., 1997). En effet, il a été estimé qu'entre un tiers et la moitié de la surface terrestre a été transformée par l'activité anthropique, et la transformation la plus importante est liée à l'utilisation des terres pour produire des biens et des services (Vitousek et al., 1997). En milieu marin, il n'y a pratiquement plus aucune zone, autre que celles situées à des latitudes extrêmement élevées, qui ne soit pas altérée par l'homme (Tickler et al., 2018; **Figure 1.1**). En l'espace de 50 ans, les ressources marines ont été exploitées de manière accrue et particulièrement prononcée le long de la côte et des eaux archipélagiques (Tickler et al., 2018; **Figure 1.1**). Cette expansion peut être liée à la globalisation de la motorisation qui a permis un développement de la flotte de pêche mondiale passant de 1,7 à 3,7 millions de navires entre 1950 et 2015 (Rousseau et al., 2019). Parallèlement, grâce au développement de nouvelles techniques, l'homme a pu s'éloigner de la côte et exploiter les ressources au large, augmentant ainsi la pression de pêche sur un plus large spectre d'espèces cibles ainsi que sur les écosystèmes qui les soutiennent (Jackson et al., 2001).

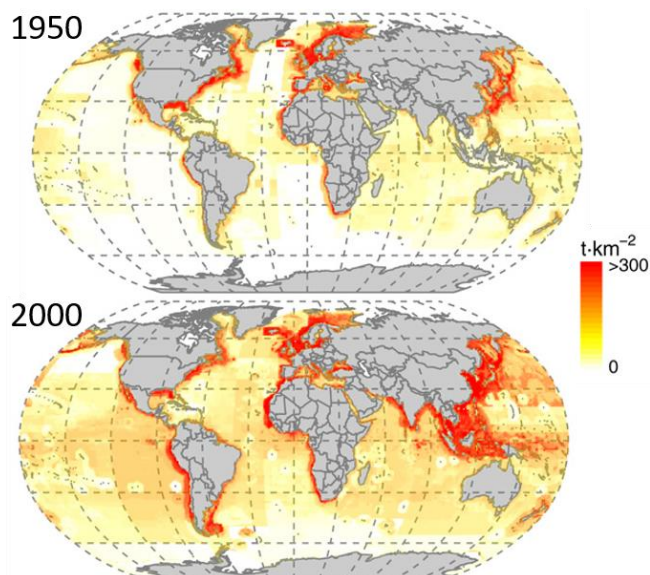


Figure 1.1 : Cartographie de la distribution et de l'intensité des captures de la pêche industrielle en 1950 et 2000. Ces deux cartes illustrent l'intensification à l'échelle globale de la pêche industrielle (en terme de capture annuelle moyenne en tonnes métrique par kilomètre carré par lieu de capture) (Tickler et al., 2018).

Du dysfonctionnement du cycle de l'azote à l'extinction de la biodiversité en passant par la surexploitation des ressources marines, les modifications de l'environnement dues aux activités humaines sont telles qu'elles ont conduit à la définition d'une nouvelle ère géologique : l'anthropocène (Beau & Larrère, 2018; Steffen et al., 2007). Dans ce contexte, les interactions entre l'homme et la faune sauvage sont inévitables, menant à de nombreux conflits. Ces conflits homme-faune sauvage concernent un large spectre de situations dans le monde impliquant des activités humaines variées et de nombreuses espèces animales.

1.2. Les conflits homme-faune sauvage

Les conflits hommes-faune sauvage sont définis comme toute action de l'homme ou de la faune sauvage ayant un effet négatif sur l'autre (Conover, 2002; Kudrenko et al., 2020) et peuvent être classés selon 6 catégories : les attaques sur les humains, la chasse récréative, les prises accessoires, la transmission de maladies, la destruction des cultures et enfin la déprédation (Figure 1.2 ; Woodroffe et al., 2005).

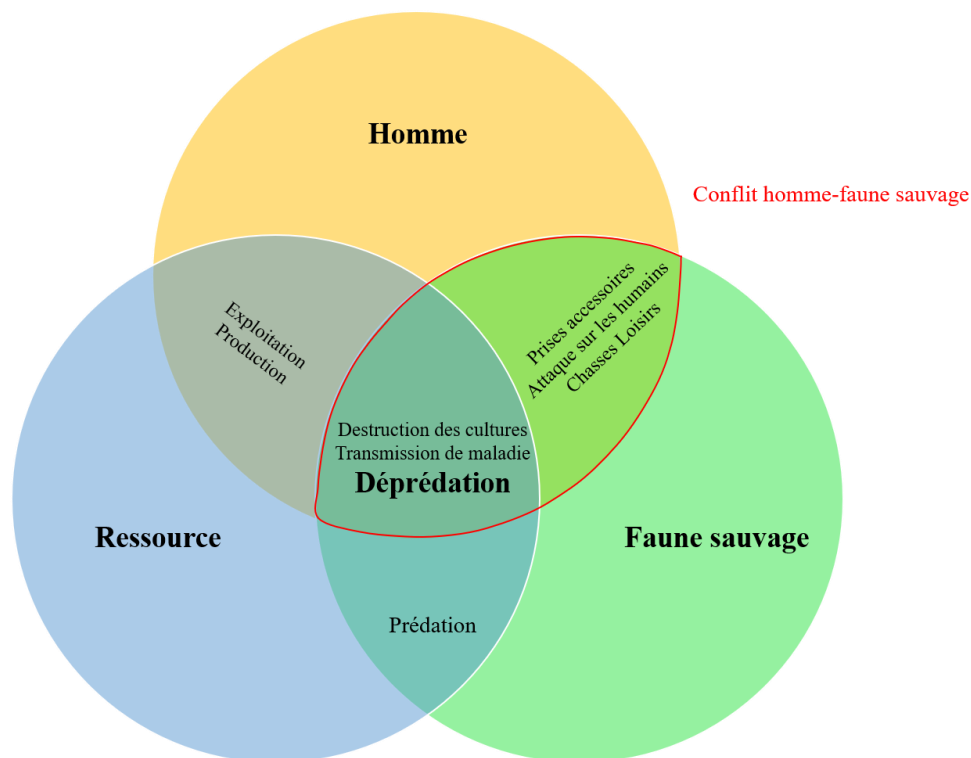


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1.2.1. *Les attaques sur les humains*

Les attaques sur les humains par des grands prédateurs ont été documentées dans plusieurs régions du monde et déclenchent de vifs conflits (Quigley & Herrero, 2005). Un total de 338 attaques d'ours brun a par exemple été dénombré entre 1932 et 2017 en Russie (Kudrenko et al., 2020). Pour ces attaques, les causes ont été renseignées 182 fois, indiquant le plus souvent que les ours ont été provoqués ou dérangés (38%) ou encore surpris (21%), et seulement 18% des incidents semblent refléter un comportement de prédateur (Kudrenko et al., 2020). Dans le milieu marin, bien que demeurant rares, les attaques concernent essentiellement les requins. Ces attaques ont été de plus en plus fréquemment rapportées ces dernières années, notamment aux Etats-Unis, en Afrique du Sud, en Australie, au Brésil, autour de l'île de la Réunion, et aux Bahamas (Chapman & McPhee, 2016).

1.2.2. *La chasse récréative*

La chasse récréative, définie par la poursuite et la mise à mort d'animaux principalement à des fins de loisirs et d'agrément (Loveridge et al., 2006), est une pratique très ancienne. Réservée à la noblesse au moyen âge, la chasse récréative se démocratise vers la révolution Française (Di Minin et al., 2021). Toutefois, à travers les siècles, les carnivores ont toujours été considérés comme des concurrents (Sillero-Zubiri & Laurenson, 2001). Il arrive donc que ceux-ci soient tués lorsqu'ils entrent en compétition avec les amateurs de chasse récréative, comme par exemple les loups, les ours et les lynx afin de protéger le daim (*Dama dama*) et le cerf élaphe (*Cervus elaphus*) dans les réserves de chasse royales de la New Forest (Royaume-Uni) et de Bialowiesza (Pologne) (Sillero-Zubiri & Laurenson, 2001).

1.2.3. *Les prises accessoires*

Les prises accessoires désignent toutes les captures ne correspondant pas aux espèces ou aux tailles des organismes visées par l'homme. Elles sont essentiellement engendrées par les activités de pêche utilisant des engins peu sélectifs comme les chaluts ou les filets dérivants. Par exemple, dans l'océan Atlantique, la quantité annuelle de captures accessoires liée à la pêche au thon à la senne tournante est estimée à 6 400 tonnes, soit 7,5% de la quantité de thon capturée (Amandè et al., 2010). Ces prises accessoires incluent des espèces de requins et des raies classées sur liste rouge de l'IUCN telles que le requin marteau (*Sphyrna zygaena*) et la raie Manta (*Manta birostris*) (Amandè et al., 2010). Simultanément à l'expansion de la pêche, liés à l'accroissement des besoins humains ces 50 dernières années, les prises accessoires ont augmenté et sont devenues une préoccupation majeure en termes de conservation et de gestion de la pêche.

1.2.4. *La transmission de maladies*

Les interactions entre la faune sauvage et les cultures ou les élevages peuvent mener à la transmission de maladies telles que la tuberculose bovine, la maladie du charbon et la brucellose. Par exemple, le coût de la tuberculose bovine sur les élevages en Ethiopie a été estimé à 75,2 millions de dollars en 2005 et à 358 millions de dollars en 2011 (Tschopp et al., 2012). Certaines de ces maladies comme la rage, la listériose et la salmonellose, appelées zoonoses, peuvent être transmises des animaux à l'homme. A titre d'exemple, le raton laveur (*Procyon lotor*), porteur du virus de la rage, entraîne la mort d'environ 50 000 personnes par an (Thirgood et al., 2005).

1.2.5. *La destruction des cultures*

La destruction des cultures est une forme de conflit homme-faune sauvage qui peut être engendrée par des rongeurs, mais aussi et le plus fréquemment par des gastéropodes, des nématodes, des arthropodes, des arachnides (acariens), des mille-pattes ou encore des crustacés (cloportes). Bien que de petite taille, ces espèces sont capables de détruire de grandes surfaces de cultures céréalières en très peu de temps (Naughton-Treves & Treves, 2005). A titre d'exemple, on estime que les arthropodes détruisent 18 à 26 % de la production agricole annuelle mondiale (Culliney, 2014).

1.2.6. *La déprédation*

La déprédation est un comportement développé par de nombreuses espèces sauvages dès lors qu'elles se nourrissent sur une ressource soit produite (e.g. cultures ; Barnes & Douglas-Hamilton, 1982), soit élevée (e.g. animaux domestiques, animaux d'élevages, aquacultures ; Burr et al., 2020a; Dickman & Hazzah, 2016), soit exploitée (e.g. capture de pêche ; Mitchell et al., 2018; Read, 2008) par l'homme. Ce comportement a été documenté partout dans le monde et impacte un large spectre d'activités de subsistance humaines. Par exemple, la déprédation est régulièrement observée aux Etats Unis, avec le cas du coyote (*Canis latrans*) attaquant les moutons (Figure 1.3.a; Mitchell et al., 2004), ou les cormorans à aigrette (*Phalacrocorax auritus*) volant les poissons chats (*Ictalurus punctatus*) dans les fermes aquacoles du Mississippi (Figure 1.3.b; Burr et al., 2020a, 2020b), au Sri Lanka avec le cas de l'éléphant d'Asie (*Elephas maximus*) ravageant les cultures céréalières (Figure 1.3.c; Santiapillai et al., 2010), ou encore en mer Baltique, avec le cas des phoques gris (*Halichoerus grypus*) prélevant les captures de saumon (*Salmo salar*) (Figure 1.3.d; Fjälling, 2005; Königson et al., 2011).

La déprédation est largement documentée dans la littérature scientifique (Sillero-Zubiri & Laurenson, 2001) notamment due à son impact sur l'ensemble du socio-écosystème.

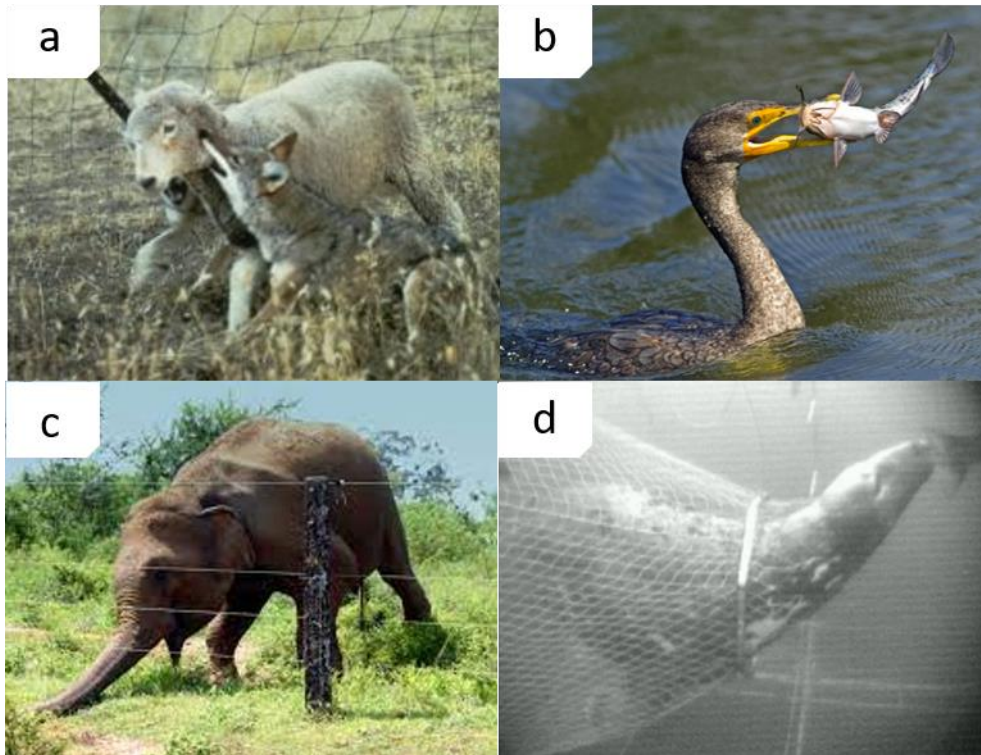


Figure 1.3 : a) Coyote (*Canis latrans*) déprédant un mouton ©USDA National Wildlife Research Center ; b) Cormoran à aigrette (*Phalacrocorax auritus*) subtilisant un poisson chat (*Ictalurus punctatus*) juvénile provenant de l'aquaculture ©J. Avery ; c) Eléphant d'Asie (*Elephas maximus*) à la lisière d'une barrière électrifiée au Sri Lanka ©Prithviraj ; d) Phoque gris (*Halichoerus grypus*) pillant un piège à saumon (*Salmo salar*) (Königson et al., 2011).

1.3. Conséquences diverses liées à la déprédation

1.3.1. Impact sur l'homme

La déprédation impacte socio-économiquement les activités agricoles et halieutiques. Les coûts induits peuvent être directs, causés par la perte des ressources produites ou exploitées. Par exemple, aux Etats Unis, la déprédation sur les cultures a causé un manque à gagner de 619 millions de dollars pour les agriculteurs en 2001 (NAAS, 2002). Toujours aux Etats Unis, les attaques de coyotes sur le bétail induisent une perte de 40 millions de dollars chaque année pour les éleveurs (Mitchell et al., 2004) et la déprédation par les cormorans à aigrette sur le poisson chat des fermes aquacoles a été estimé à 2,1 millions de dollars en 1988 (Stickley & Andrews, 1989). Dans le milieu marin, les pêcheurs observent fréquemment des marques de dents sur la ressource piégée par les engins de pêche (Figure 1.4), voire retrouve uniquement la tête des individus capturés (Figure 1.4a). Au Chili, les pertes en poisson causées par la déprédation par les lions de mer d'Amérique du Sud (*Otaria flavescens*) dans les pêcheries artisanales représentent 19,3 millions de dollars en 2003 (Goetz et al., 2008 ; Oliva et al., 2003).

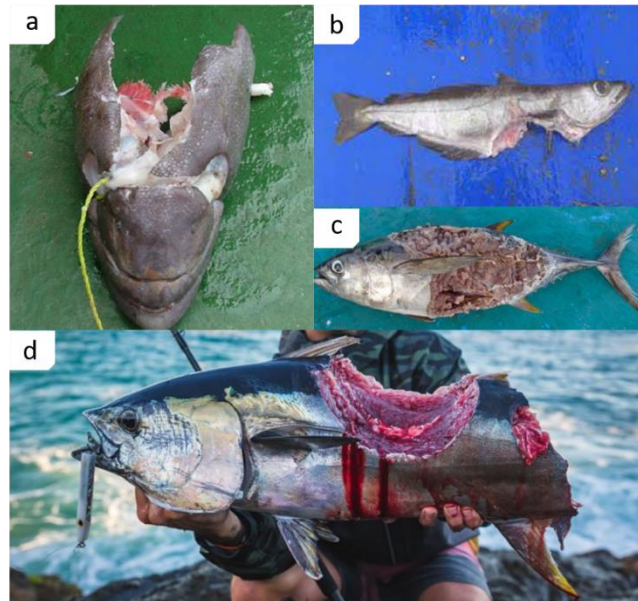


Figure 1.4 : a) Léguine australe (*Dissostichus eleginoides*) déprédée par un cachalot (*Physeter macrocephalus*). ©Michael Unwin ; b) Lieu jaune (*Pollachius pollachius*) déprédée par un phoque (Cosgrove et al., 2013) ; c) Thon albacore (*Thunnus albacares*) adulte déprédée par un calmar volant à dos violet (*Sthenoteuthis oualaniensis*) (Moazzam, 2019) ; d) Albacore déprédée par un requin. ©Patrick Linehan.

Les coûts induits par la déprédation peuvent également être indirects quand ils sont liés à des efforts de prévention de la déprédation et de protection de la ressource, à des efforts de production ou d'exploitation supplémentaires afin de compenser les pertes et de maintenir le rendement de l'activité, ou à des dégâts causés par les espèces déprédatrices sur le matériel. De nombreux moyens techniques et stratégies de mitigation ont vu le jour ces dernières années et ont été proposés et testés afin de réduire la déprédation dans de nombreuses régions du monde (Perera, 2009; Tixier et al., 2021a). Toutefois, l'efficacité de ces moyens de mitigation reste limitée et ils peuvent engendrer des coûts supplémentaires conséquents. De plus, maintenir un rendement élevé accroît les coûts liés à l'activité notamment via une augmentation de la durée de l'activité, des masses salariales et/ou de la consommation de carburant (Maccarrone et al., 2014; Peterson et al., 2014). Enfin, la déprédation peut engendrer des dégâts matériels, tels que la destruction des clôtures autour des cultures par les éléphants (Perera, 2009), ou les dommages portés aux casiers par l'otarie de Californie (*Zalophus californianus californianus*) (Beeson & Hanan, 1996). Bien que difficilement quantifiables, les coûts indirects associés à la déprédation peuvent être significatifs et parfois compromettre la viabilité des activités humaines concernées.

De plus, l'augmentation du temps et de la charge de travail causée par la déprédation peut avoir des conséquences sociales importantes, accroître les risques d'accidents du travail ou encore impacter la qualité de vie des personnes impliquées lorsque l'activité dont elles dépendent est compromise.

1.3.2. *Impact sur la faune sauvage*

La faune sauvage ayant développée le comportement de déprédation peut, quant à elle, être positivement comme négativement impactée. La disponibilité et la facilité d'accès à des ressources produites ou exploitées par l'homme peut en effet améliorer la condition et la survie des individus, et les performances démographiques des populations (Esteban et al., 2016; Newsome et al., 2015; Tixier, et al., 2015a). Le temps de recherche ainsi que l'énergie investie dans l'acquisition de nourriture est réduite en comparaison avec la prédation naturelle, particulièrement dans le cas où la ressource déprédée est hypercalorique (Fertl, 2009; Read, 2008).

Toutefois, l'exploitation des ressources peut également engendrer la raréfaction des ressources naturelles des prédateurs, pouvant directement agir sur leur reproduction et leur survie. A titre d'exemple, dans le milieu marin, plus de 90 millions de tonnes de poissons par an sont capturées tous engins de pêche confondus, dont plus de 30 % sont considérés comme surexploités (FAO 2016), diminuant fortement la disponibilité de la ressource pour de nombreux prédateurs marins. La production et l'exploitation des ressources a également mené à la destruction ou la fragmentation d'habitat impactant la biodiversité, et de ce fait fragilise les écosystèmes et réduit leur résilience (Kideghesho et al., 2006; Laurance, 2010). Bien que certaines espèces animales semblent résister à la fragmentation ou la destruction de leur habitat (Nee & May, 1992; Purvis et al., 2001), d'autres sont particulièrement vulnérables à ces changements (Belovsky, 1987; Gittleman et al., 2001; Woodroffe, 2000). Une grande taille, des comportements sociaux complexes, des populations de faible densité, une spécialisation dans les niches exploitées, un niveau trophique élevé et une large distribution sont notamment des caractéristiques spécifiques susceptibles de rendre ces espèces plus sensibles aux modifications de leurs environnements (Diamond, 1984; McKinney, 1997; Purvis et al., 2001; Terborgh, 1974).

La déprédation peut impacter négativement la faune sauvage au travers d'interactions directes avec l'homme ou avec le matériel. Tout d'abord, afin de protéger leurs ressources, les hommes peuvent engager des contrôles létaux, comprenant le piégeage, l'empoisonnement, l'intoxication, l'utilisation d'explosifs ou encore le tir par arme à feu (Brand & Nel, 1997; Naughton-Treves & Treves, 2005; Tuytens et al., 2000). Par exemple, de telles mesures ont été utilisées pour diminuer la déprédation par les sangliers au Texas où des tirs aériens depuis un hélicoptère ont été effectués (Davis et al., 2018) ou encore la déprédation par les orques sur les captures de hareng en Norvège, où une cinquantaine d'orques en moyenne ont été abattues chaque année entre 1938 et 1980 (Ford et al., 2000). Dans certaines régions du monde, ces contrôles létaux ont eu pour conséquence le déclin important des populations de prédateurs, le rétrécissement extrême de la distribution des survivants ou l'élimination de populations locales (Johnson et al., 2001 ; Mech, 1970 ; Naughton-Treves & Treves, 2005).

Dans le milieu marin, entrer en interaction avec les activités de pêche accroît également les risques de blessures ou de captures accidentelles (**Figure 1.5**). Un grand nombre de pêcheries, côtières et hauturières, et utilisant des engins de pêche différents, est impacté par la déprédation dans le monde (Mitchell et al., 2018; Tixier et al., 2021a). Les captures accidentelles sont fréquentes dans les filets statiques ou les chaluts (Read, 2008). En mer Baltique, la capture accidentelle de phoques gris, venant déprédater les prises de saumons dans les filets, est régulièrement documentée (Westerberg et al., 2008).

A long terme, les impacts positifs ou négatifs de la déprédation sur la faune sauvage ayant développée ce comportement peuvent modifier la densité des populations de ces espèces, engendrant avec elles des effets en cascade. Par exemple, en modifiant des processus tels que la compétition, les interactions prédateur-proie et le transfert de nutriments entre biotopes et écosystèmes, la déprédation et l'accès facilité aux ressources que ce comportement permet affectent les communautés, les réseaux trophiques et les écosystèmes (Oro et al., 2013).

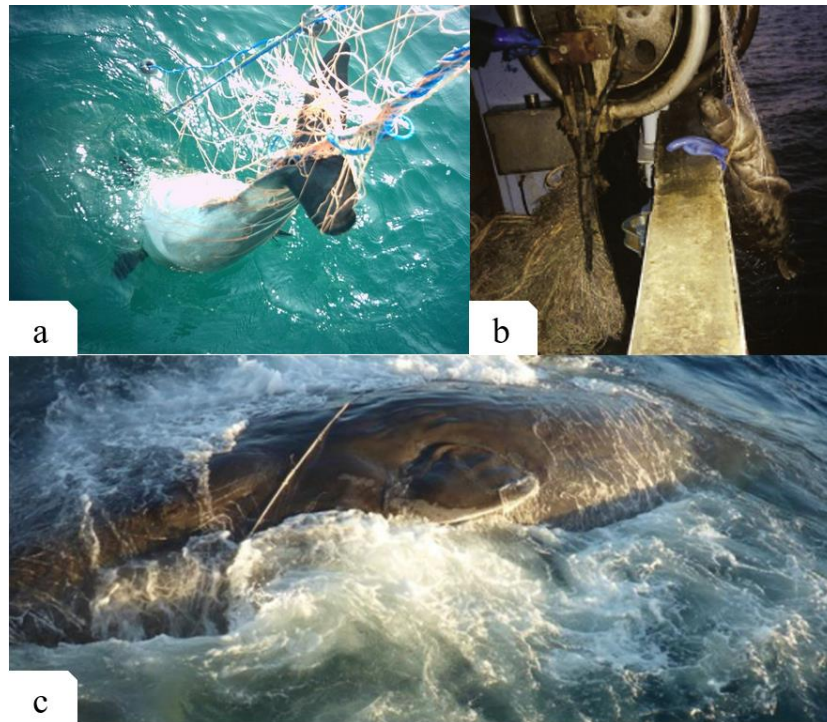


Figure 1.5 : a) Prise accessoire d'un marsouin commun (*Phocoena phocoena*) dans un filet maillant. ©Sedat Gönener ; b) Phoque gris (*Halichoerus grypus*) pris dans les filets. ©Dave Sanderson ; c) Enchevêtrement d'un cachalot (*Physeter macrocephalus*) dans une palangre. ©Gabriel Devique.

Bien qu'un large spectre d'espèces ait développé le comportement de déprédation, une majorité d'entre elles est de niveau trophique supérieur. Ainsi, la déprédation et les changements que ce comportement induit dans les pressions de prédation exercées par ces prédateurs supérieurs sont susceptibles de générer des effets écosystémiques via des rétroactions en cascade (descendante ou

« top down ») (Newsome et al., 2015). Par ailleurs, ces prédateurs supérieurs incluent généralement des espèces plus vulnérables à la perte d'habitat et aux changements environnementaux d'origine anthropique (Gittleman et al., 2001).

1.4. Rôle de la modélisation

Si l'abattage a été le principal moyen de gérer ce conflit pendant des décennies, l'état de conservation critique de la plupart des grands carnivores a obligé les gestionnaires à envisager d'autres mesures non létales pour atténuer la déprédation (Treves & Karanth, 2003). En 50 ans, la disparition de 68% des populations d'animaux sauvages révèle l'urgence de mettre en place des plans de conservation efficaces. Cependant, la conservation de ces espèces peut poser des défis difficiles à concilier avec le maintien de la viabilité économique des activités anthropiques telles que l'exploitation ou la production de ressources (i.e. pêche, chasse, élevage et agriculture). En particulier dans le cas de la déprédation qui peut impacter l'ensemble des compartiments du socio-écosystème, il semble urgent d'identifier les bons compromis entre activités humaines et conservation de la diversité, y compris des populations de prédateurs.

Dans ce contexte, les approches de modélisation peuvent contribuer à l'élaboration et à l'évaluation de solutions durables afin de concilier le maintien des activités humaines et la conservation de la faune sauvage. Suite à la naissance et à la démocratisation de l'ordinateur dans les années 1980 d'une part, et au développement théorique d'autre part, les approches de modélisation se sont multipliées dans les dernières décennies. On assiste par exemple dans les années 1990 à une diversification des langages de programmation et dans les années 2000 à l'essor de la massification des flux de données et de techniques de simulation intégrative (Varenne, 2016). Les approches de modélisation permettent alors l'inclusion une grande variété de données et de connaissances, facilitent l'explication et la compréhension d'un phénomène, en intégrant les processus et mécanismes d'interaction et permettent de tester des théories écologiques ou des scénarios via des outils de simulation (Varenne, 2016). En effet, les approches de modélisations se sont peu à peu complexifiées notamment pour gagner en réalisme. En halieutique par exemple, les évaluations de stock plurispécifiques succèdent aux approches monospécifiques et les modèles de flotte unique ont évolué vers des modèles multi-flottes (Hollowed, 2000; Nielsen et al., 2021). Par ailleurs, le développement de modèles multi-espèces a permis une meilleure estimation de la mortalité naturelle et du recrutement ainsi qu'une meilleure compréhension des relations géniteurs-recrues et de la variabilité des taux de croissance (Hollowed, 2000). Dans le même esprit, de nombreuses approches écosystémiques voient également le jour, au cours des dernières décennies, on assiste même à une prolifération de modèles dit « end-to-end ». Ces approches de modélisation diffèrent des modèles antérieurs de par ce qu'elles tentent de représenter, soit les activités d'exploitation ou de production humaine, l'ensemble du système écologique et l'environnement abiotique associé (Fulton, 2010; Travers et al., 2007). Ces

approches intègrent ainsi les processus physiques et biologiques à différentes échelles et permettent une intégration dynamique des différentes composantes de l'écosystème (Fulton, 2010; Travers et al., 2007). Récemment, la dimension humaine est complétée avec l'inclusion de paramètres sociologiques menant à l'émergence de modèles socio-écosystémiques (Boudouresque et al., 2020). Le concept de socio-écosystème est crucial dans la mesure où il souligne le fait que l'homme fait partie intégrante des écosystèmes.

Grâce aux développements technologiques et théoriques, les approches de modélisation sont désormais à même de décrire explicitement les différents impacts liés aux activités humaines et suffisamment robustes afin d'appuyer les stratégies de gestions.

1.5. Problématiques et objectifs de la thèse :

Toutefois, peu de modèle intègre la déprédation, bien que cela semble crucial afin de prendre en compte les impacts multiples liés à ce comportement sur les diverses composantes du socio-écosystème. Située à l'interface entre les composantes écologique et humaine, des données de natures diverses sont nécessaires (e.g. biologiques, socio-économiques, géochimiques ou encore biophysiques) afin de capturer explicitement ce comportement. Etant donné la complexité et la diversité des effets associés à la déprédation, il peut donc être difficile de mettre en œuvre des approches de modélisation, en partie liées à la nécessité d'une recherche interdisciplinaire, de grands ensembles de données et d'outils intégrés (Tixier et al., 2021a).

L'objectif principal de cette thèse est donc d'identifier les limites, manques et priorités pour le développement d'approches de modélisation intégrant la déprédation. Dans un second temps, cette thèse a évalué la capacité de deux approches de modélisation existantes pour caractériser les conséquences de la déprédation marine et, plus spécifiquement, comprendre les enjeux et conditions requises pour que les activités d'exploitation halieutique et les déprédateurs marins puissent co-exister. Une revue systématique (chapitre 2) et l'utilisation d'approches de modélisation, évaluant les effets de la déprédation sur les systèmes marins (chapitre 3 et 4), permettent de répondre en partie à ces objectifs. Cette thèse a donc été organisée autour de trois méthodologies valorisées via des articles scientifiques :

- **Le chapitre 2** identifie les principales lacunes dans les connaissances et met en évidence les principales orientations futures pour parvenir à une inclusion efficace de la déprédation dans les études de modélisation en réalisant une revue systématique. Une revue systématique consiste en la collecte, l'évaluation critique et la synthèse rigoureuse et reproductible des divers éléments tirés d'études existantes (Crowther et al., 2010; Haddaway et al., 2020).

- **Le chapitre 3** utilise Ecopath, une approche de modélisation statique et équilibrée en masse (Christensen and Walters, 2004), afin d'évaluer les effets de la déprédation sur l'écosystème dans une étude de cas bien documentée impliquant des mammifères marins et une pêche commerciale.
- **Le chapitre 4** s'appuie sur une modélisation qualitative afin d'évaluer les conditions de persistance d'une ressource exploitée, d'une pêche et d'une espèce déprédatrice touchés par la déprédation, et la façon dont la déprédation marine affecte les réponses à long terme d'un système soumis à différents scénarios.

Enfin, dans le chapitre 5 s'appuie sur les résultats obtenus dans les chapitres 2 à 4 afin de produire des recommandations qui visent à mieux comprendre et prévoir les effets de la déprédation au niveau du socio-écosystème. Les limites, manques et priorités sont discutés dans le but d'inclure plus rigoureusement la déprédation dans les futures approches de modélisations.

1.6. Cas d'intérêt : Crozet-Kerguelen

De par la grande disponibilité en données historiques concernant la pêche et ses interactions avec les mammifères marins, les îles Crozet et Kerguelen représentent un cas d'étude privilégié pour aborder la question de la déprédation marine. Crozet-Kerguelen est également l'un des sites d'études pilote du projet ANR ORCADEPRED dans lequel s'inscrit ce travail de thèse. Ainsi, le travail de doctorat s'est largement ancré autour de ce cas pour appréhender concrètement les processus liés à la déprédation.

Découvertes en 1772 dans le sud de l'océan Indien, les îles Crozet et Kerguelen sont à plus de 27 000 km de distance du moindre continent (Hureau, 2011; **Figure 1.6**). Malgré cet isolement, un effort scientifique important et régulier y est mené depuis plus de 60 ans, permettant le développement d'une connaissance approfondie du milieu et des populations animales. Certaines populations d'oiseaux et de mammifères marins, dont les orques de Crozet, font ainsi l'objet de suivis à long terme. Aussi, la création d'une Zone Exclusive Economique, autour des archipels en 1978 (**Figure 1.6**), a facilité la gestion des activités d'exploitation dans cette zone. Ces activités sont limitées à une pêche légale dont l'intégralité des opérations est suivie par des contrôleurs de pêche des Terres Australes et Antarctiques Françaises (TAAF), qui embarquent systématiquement sur l'ensemble des navires de pêche. Ces contrôleurs collectent une grande variété de données et les soumettent au Muséum National d'Histoire Naturelle (MNHN) qui est en charge des analyses afin de fournir des recommandations conciliant activités de pêche et conservation de la biodiversité. Ces derniers sont également en charge de faire respecter l'ensemble des mesures réglementaires à bord.

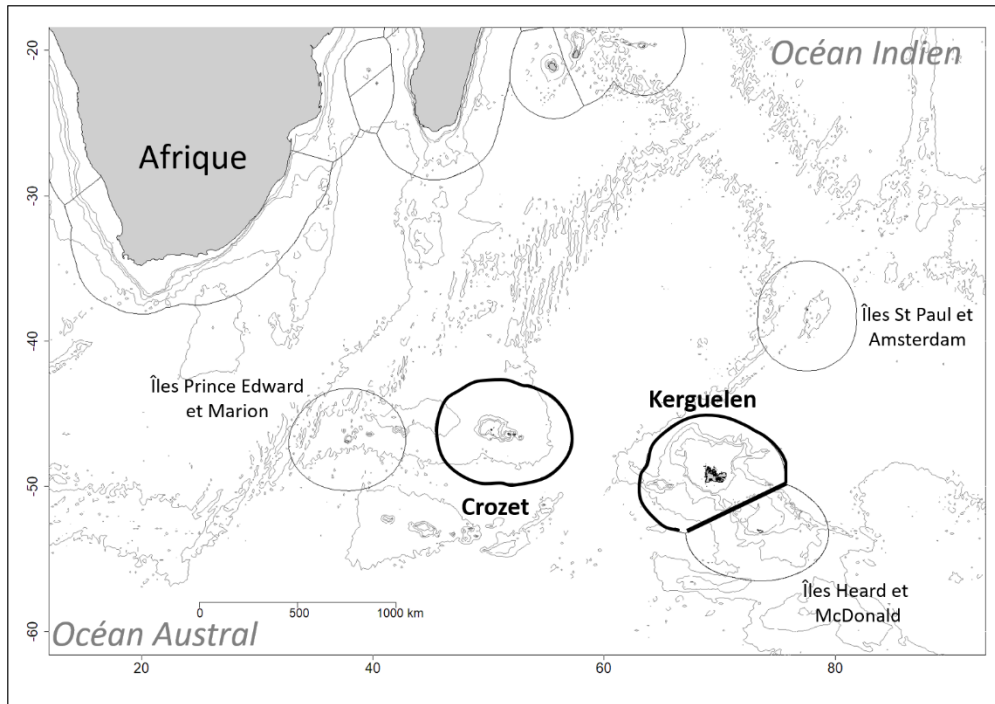


Figure 1.6 : Géolocalisation des Zones Economiques Exclusives (ZEE) de Crozet et Kerguelen (en gras).

Dans les ZEE de Crozet et Kerguelen, l'espèce ciblée par la pêche légale est la légine australe (*Dissostichus eleginoides*), un grand poisson benthopélagique de la famille des Nototheniidae, pouvant atteindre plus de 2 m de long, peser plus de 200 kg et vivre au-delà de 50 ans (**Figure 1.7; Collins et al., 2010**). La légine australe est distribuée le long d'une large gamme de profondeurs en fonction de leur stade de vie, l'une des plus étendue de tous les téléostéens (**Duhamel et al., 2005**), englobant de vastes zones sur les plateaux sud de la Patagonie et du Chili, les plateaux péri-insulaires entourant les îles subantarctiques, et les bancs et monts sous-marins de l'océan Austral (**Arkhipkin et al., 2003**). Les larves pélagiques peuvent être observées dans les 500 premiers mètres de la colonne d'eau, alors que les grands adultes sont trouvés jusqu'à 2 500 m de profondeur (**Evseenko et al., 1995**). La maturité sexuelle est atteinte aux alentours de 70 à 80 cm de long, soit environ 10 ans pour les femelles et 7 ans pour les mâles (**AAD, 2013**). Un dimorphisme sexuel est présent chez cette espèce, les femelles étant de plus grande taille que les mâles (**Collins et al., 2010**). En effet, la plupart des individus de plus de 120 cm sont des femelles (**Gasco, 2013; Welsford et al., 2011**). Le plateau de Kerguelen abrite l'une des plus grandes populations de légine australe au monde, probablement due aux grandes zones propices à cette espèce ainsi qu'au niveau élevé de productivité primaire (**Péron et al., 2016**). Leur chair de grande qualité explique leur haute valeur économique atteignant 30 à 35 US\$/kg (**Grilly et al., 2015**). Il est à noter que le prix moyen des importations de légine a augmenté de 62% entre 2007 et 2012 (**Grilly et al., 2015**) et qu'à l'heure actuelle cette pêche est la première pêche française en termes de chiffre d'affaires annuel.



Figure 1.7 : Léginge australe (*Dissostichus eleginoides*) ©Nicolas Gasco

En raison de sa haute valeur commerciale, le braconnage sévit entre 1990 et 2003 et de manière plus ponctuelle jusqu'en 2008. Cette pression de pêche illégale a été estimée à près de trois fois la quantité autorisée, menaçant potentiellement les stocks locaux de léginge. En effet, cette espèce longévive, à croissance lente et maturation tardive (Collins et al., 2010), est particulièrement vulnérable aux changements de pression. Entre 1997 et 2004, vingt navires illicites, non déclarés et non réglementés ont été arrêtés et confisqués par la marine nationale (Duhamel & Williams, 2011). Dans les ZEE françaises, les principes de gestion écosystémique des pêches recommandés par la commission pour la conservation des ressources marines vivantes de l'antarctique (CCAMLR) sont appliqués. Initialement au chalut, l'exploitation officielle de la léginge australe débute en 1986, mais c'est en 1996 à Crozet et en 1998 à Kerguelen que les premiers palangriers français commencent à opérer dans cette région (Duhamel, 2003; Duhamel & Williams, 2011; CCAMLR, 2020a, 2020b; **Figure 1.8**). En effet, afin de préserver les écosystèmes marins, l'exploitation au chalut de fond a été interdite en 2002, seule la palangre démersale, plus sélective et respectueuse des fonds marins, est alors autorisée (**Figure 1.8**). De plus, la pêche dans les eaux de moins de 500 m de profondeur est interdite afin d'éviter la capture de léginge juvénile (Gasco, 2011). Dans le but d'appliquer les objectifs de développement durable de l'Organisation des Nations Unies et plus spécifiquement l'objectif 14 « Conserver et exploiter de manière durable les océans, les mers et les ressources marines aux fins du développement durable », un premier plan de gestion pour la pêcherie à la léginge australe a été mis en place en 2015 et pour une durée de 4 ans (Arrêté n°2019-59). Celui-ci a été renouvelé et couvre désormais la période 2019-2025. Ce plan de gestion fixe notamment les axes de gestion pour répondre aux enjeux environnementaux, économiques et scientifiques liés à la pêcherie (Arrêté n°2019-59). Il est également à noter que depuis 2016, la majeure partie des eaux de Crozet et Kerguelen sont classées en réserve naturelle marine des Terres australes françaises et que depuis 2019 les Terres et mers australes françaises sont inscrites au patrimoine mondial de l'Unesco.

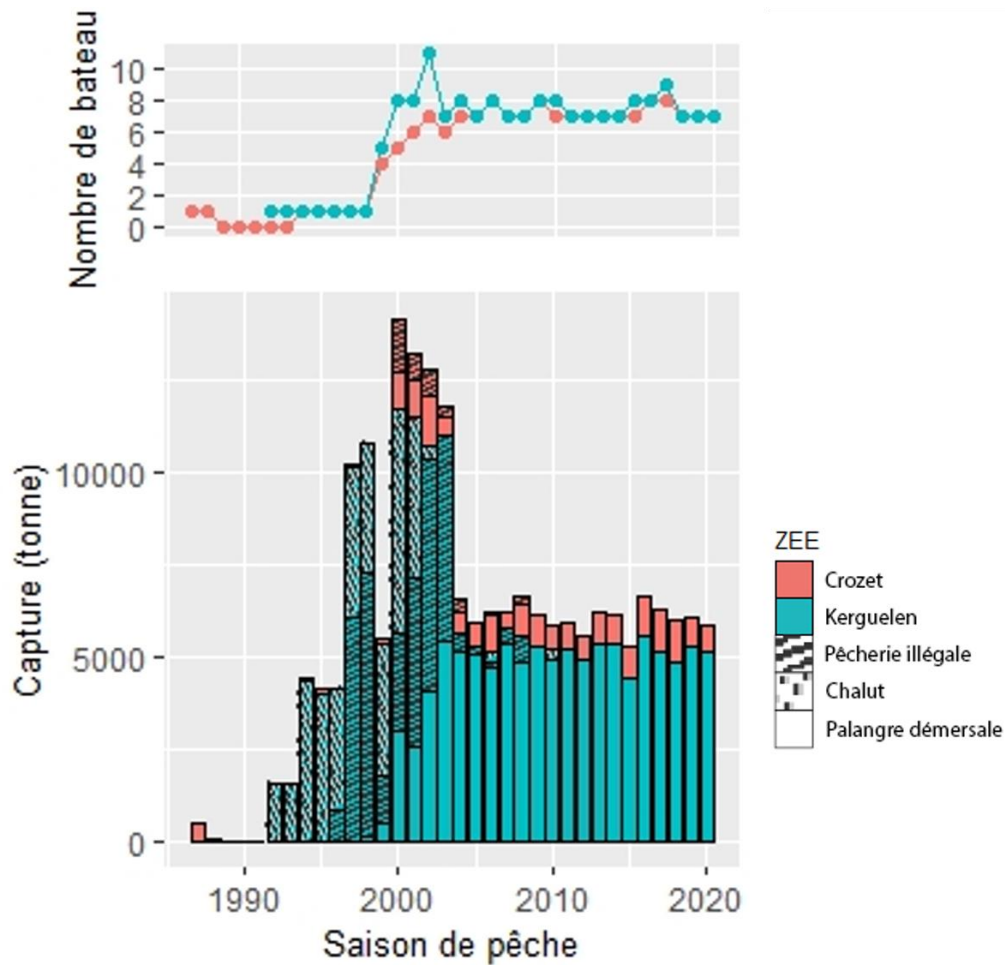


Figure 1.8 : Evolution du nombre de bateaux dans les eaux de Crozet-Kerguelen entre 1987 et 2020. Evolution de la quantité de capture de légine australe en tonne distinguée en fonction de leur provenance (ZEE) et du type de pêche (chalut, palangre démersale, pêche illégale) (CCAMLR, 2020a; 2020b)

Depuis 2004, environ 5 000 tonnes de légine sont capturées légalement par an dans les eaux de Kerguelen et 1 000 tonnes dans les eaux de Crozet, partagées entre 4 armements pour un total de 7 bateaux de 50 à 60 m de long (Figure 1.8 ; Duhamel & Williams, 2011). Les quotas autorisés en 2020 sont précisément de 5 200 tonnes à Kerguelen et 800 tonnes à Crozet (JO TAAF, 2020 ; CCAMLR, 2020a; 2020b). La saison de pêche s'étend de septembre à août. Les pêcheurs effectuent 3 à 4 marées (i.e. temps entre le départ d'un navire de pêche de son port d'attache jusqu'à son retour) par saison avec une interruption à Kerguelen du 1^{er} février à mi-mars, afin de se conformer à la mesure de conservation des oiseaux de mer. Les palangres démersales servant à capturer la légine sont des lignes d'une dizaine de kilomètres de long, couvertes d'hameçons espacés de 1,2 m, reliées à une bouée en surface. Les activités de pêche sont menées sur la pente du plateau océanique entre 500 m et 2 500 m de profondeur et sont découpées en différentes étapes. Tout d'abord les hameçons sont appâtés et les palangres déployées en mer, une opération appelée « filage », réalisée uniquement de nuit, et durant une à plusieurs heures. Une fois mises à l'eau, les palangres sont laissées immergées plusieurs heures

voire quelques jours avant d'être remontées à bord, une opération appelée « virage », où les captures sont récupérées. Si elle est plus sélective que d'autres techniques comme par exemple le chalut de fond, la palangre a la particularité d'exposer ses captures tout au long du processus de pêche, ce qui les rend facilement accessibles pour les prédateurs (Fertl, 2009). Les palangres pélagiques et démersales sont d'ailleurs les engins de pêche les plus impactés par la déprédation (Gilman et al., 2007; Read, 2008; Werner et al., 2015).



Figure 1.9 : Orque déprédant du poisson provenant des palangres à Crozet
©Anthony Pere

Autour des deux archipels, trois espèces de mammifères marins ont été reconnues responsables des événements de déprédation : l'orque (*Orcinus orca*), le cachalot (*Physeter macrocephalus*), et dans une moindre mesure l'otarie à fourrure (*Arctocephalus spp.*) (Figure 1.9) (Roche et al., 2007). Directement ou indirectement impactés par la pêche baleinière, les orques et les cachalots ont vu leurs populations décliner drastiquement dans le courant du XX^{ème} siècle. En effet, près de 400 000 grands cachalots ont été tués dans l'hémisphère sud entre 1900 et 1960 (Boyd, 2002; Clapham & Baker, 2018). Les orques, quant à elles, ont vu leurs ressources naturelles s'amoinrir, avec la disparition de 70% de la population d'éléphants de mer entre 1970 et 1990 (Duhamel & Williams, 2011). Bien qu'aujourd'hui ces deux espèces font l'objet de protections et de mesures de conservation, afin de permettre à leurs populations de se maintenir, un déclin de 5% de la taille de population des orques entre 2005 et 2020 a été observé (Tixier et al., 2021b). Les causes de cette mortalité anormalement élevée restent à déterminer mais pourraient inclure des interactions létales avec les pêcheries illégales (Busson et al., 2019; Tixier et al., 2017, 2021b), d'ores et déjà impliquées

dans la drastique réduction de la population, de près de 60%, dans les années 1990 (Poncelet et al., 2010).

Trois écotypes d'orques (« Crozet », « type D » et « type C ») ont été documentés autour des archipels de Crozet et Kerguelen (Pitman et al., 2011; Pitman & Ensor, 2003). Les écotypes désignent différentes populations d'orques définies sur la base de différences morphologiques, génétiques, écologiques et enfin comportementales (Ford, 1998; Morin et al., 2010; Pitman et al., 2011; Pitman & Ensor, 2003). Les orques de type Crozet sont généralistes dans leurs préférences alimentaires, avec des proies incluant l'éléphant de mer austral (*Mirounga leonina*), des manchots (*Eudyptes sp.*), des poissons et d'autres cétacés. Parmi ces poissons, on retrouve la légine australe récemment confirmée comme proie naturelle de l'orque de Crozet (Richard et al., 2020; Tixier et al., 2019). De plus, cette population d'orque est l'une des rares pratiquant l'échouage volontaire afin de capturer les pinnipèdes (Guinet, 1991). Contrairement aux orques de Crozet, qui sont rencontrées dans les eaux côtières et hauturières, les orques de Type D sont uniquement rencontrées dans les eaux hauturières et leur écologie alimentaire reste méconnue (Jefferson et al., 2007 ; Pitman et al., 2011). Enfin, les orques de type C sont principalement distribuées le long des zones côtières et peuvent être considérées comme spécialistes dans leurs préférences alimentaires principalement composées de poisson (Pitman et al., 2007; Pitman & Ensor, 2003).

Concernant le cachalot, seuls les mâles adultes sont observés au large des archipels Crozet et Kerguelen (Labadie et al., 2018). En effet une ségrégation spatiale, dépendant de l'âge et du sexe chez cette espèce, conduit les mâles à se nourrir de manière saisonnière dans les hautes latitudes (Rice, 1989). La légine australe fait partie du régime alimentaire naturel du cachalot, qui peut atteindre les 2 000 m de profondeur grâce à ses capacités exceptionnelles de plongée.

Les cachalots et deux écotypes d'orque, les orques de Crozet et les orques de Type D, sont impliqués dans les événements de déprédation autour de ces deux archipels (Labadie et al., 2018; Tixier et al., 2016). Toutefois, les orques de Crozet sont observées bien plus fréquemment que les orques de type D, respectivement présent pour 89% et 9,9% du nombre total d'interactions entre les orques et la pêcherie à Crozet entre 2003 et 2015 (Tixier et al., 2016). Il a été estimé que les orques et les cachalots prélèvent environ 30% des captures totales par an à Crozet et 6% à Kerguelen depuis 2003 (Tixier et al., 2010, 2020). Toutefois, alors que les orques causent la majorité des pertes annuelles à Crozet, avec un total de 179 tonnes en comparaison à 100 tonnes attribuées aux cachalots, à Kerguelen, les cachalots sont responsables de la quasi-totalité des pertes annuelles avec un total de 247 tonnes en comparaison à 2,1 tonnes pour les orques (Tixier et al., 2020). Les quantités de légine déprédées autour de ces îles sont d'ailleurs parmi les plus élevées de l'océan Austral. A titre d'exemple, seules 4,8 tonnes sont prélevées à Heard et McDonald, soit 0,2% des captures totales (Tixier et al., 2020).

Outre fluctuer en fonction de l'espèce impliquée ou de la zone concernée, les niveaux de déprédation peuvent également varier entre les navires d'une même flotte, notamment en fonction du comportement des pêcheurs. A Crozet et à Kerguelen, la manière dont les pêcheurs utilisent spatio-temporellement cette zone a été classée en trois types de comportement distinct : l'exploitation, l'exploration et un mixte entre les deux (Janc et al., 2021). De façon surprenante, les pêcheurs expérimentés privilégient l'exploitation de parcelles productives où les fréquences d'interactions avec les déprédateurs sont élevées, ce qui est certes optimale à court terme afin d'accroître leur rendement, mais est également susceptible d'intensifier les pressions sur le stock et d'impacter négativement les populations de déprédateurs (Janc et al., 2021).

Ce cas de déprédation a été étudié depuis 2007 par le projet ANR ORCADEPRED, qui tente de comprendre le comportement de déprédation et l'écologie des espèces concernées afin de proposer aux compagnies de pêche des solutions opérationnelles et technologiques à la déprédation, dans lequel s'inscrit cette thèse.

Bien que les données soient nombreuses et variées, nous avons été dans l'incapacité de représenter toute la complexité de ce cas d'étude. Certains aspects ont donc été simplifiés en adéquation avec les données et connaissances à notre disposition.

Clé de lecture de ce manuscrit

Tout au long de ce manuscrit, les différentes sections, figures et annexes porteront le numéro du chapitre auxquels elles appartiennent suivi du numéro correspondant à leur ordre de citation. A titre d'exemple, la première section du chapitre 1, intitulée : Contexte, est la section 1.1. Les chapitres 2 à 4 sont au formats articles et lorsque des annexes peuvent compléter les informations de ceux-ci, elles succèderont directement au chapitre en question. Le référencement des différentes citations est présent à la fin du manuscrit. Enfin, un sommaire présente l'enchaînement et le contenu de l'ensemble du manuscrit.

Chapter 2: A global review of depredation modelling across terrestrial and marine realms

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Abstract

Depredation, a behaviour developed by wild species feeding on resources derived from human activities, can impact several components of socio-ecological systems. While modelling approaches are essential to inform and support effective ecosystem-based management actions, uptake of novel complex human-wildlife interaction such as depredation has been little studied. We conducted a systematic literature review to identify major knowledge gaps and to prioritise future research directions to better capture depredation in modelling studies. A vast majority of published modelling studies relate to application of statistical models to quantify specific aspects of depredation: factors influencing depredation or depredating species distribution; change in yield; depredation rate; effectiveness of mitigation measures; or, contribution of depredated resource to depredating species diet. Only a few published studies integrated information across humans (farmers, fishers) and depredating and depredated species, which is crucial to understand complex changes in socio-ecosystem dynamics induced by depredation. Overall, 8% of the modelling studies focused mainly on a handful of specific depredation case studies. Terrestrial cases were more documented than marine ones, which are often partially studied. To address major knowledge gaps, we recommend further quantification of depredation-related interactions across whole socio-ecosystems towards holistic approaches.

5.1. Introduction

In the second half of the 20th century, the industrial revolution improved human health conditions and resulted in important population growth (Steffen et al., 2007). Subsequent increase in human activities has led to serious conflicts involving people and wildlife, commonly called human-wildlife conflicts (Nyhus, 2016; Woodroffe et al., 2005). Human wildlife-conflicts include threats posed by wildlife to human life, economic security, or recreation; or the perception that wildlife threatens human safety, health, food, and property (Nyhus, 2016).

Among these human-wildlife conflicts, depredation, when wild species feed on resources raised, grown or caught by humans, is one of the most documented examples (Sillero & Laurenson, 2001). Depredation has been reported worldwide in both terrestrial and marine ecosystems, and includes crop raiding by terrestrial herbivores (Barnes & Douglas-Hamilton, 1982), attacks on livestock by terrestrial predators (Dickman & Hazzah, 2016), and marine predators removing fish from fishing gear or aquaculture farms (Mitchell et al., 2018; Northridge et al., 2013; Read, 2008).

Depredation can induce complex changes in socio-ecosystem dynamics by impacting both the depredating species and the resources exploited or produced by humans (i.e. crop, livestock, farmed fish, fishery). On the one hand, by facilitating access to food, depredation can change the ecological role of predators and, by altering predation pressures, can subsequently lead to cascading effects in ecosystems (Clavareau et al., 2020). On the other hand, depredation can compromise the profitability of human activities by decreasing yield or by damaging equipment (Dickman & Hazzah, 2016; Wickens et al., 1992). For instance, mean annual costs to the toothfish fishery in Kerguelen due to killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) depredation are estimated to sum up to two million euros between 2003 and 2008 (Tixier et al., 2010). In the United States, the estimated cost of wildlife depredation on crop, which are mainly attributed to deer (NASS, 2002), was \$619 million for 2001.

Modelling approaches are pivotal to characterise complex multi-faceted depredation impacts, and to support management of socio-ecological systems. Indeed, modelling allows the inclusion of a wide variety of data, as well as interactions and mechanism of multiple elements (Varenne, 2016), and, can also be used to test hypotheses and project scenarios to assess and predict the resilience and sustainability of socio-ecosystems (Dambacher et al., 2015; Marzloff et al., 2016). Supporting management actions seems crucial, especially as this conflict is likely to intensify in the coming decades. However, given the complexity and diversity of effects associated with depredation, it can be difficult to implement modelling approaches, partly related to the need for interdisciplinarity research, large data sets and integrated tools (Tixier et al., 2021a).

In this study, by conducting a systematic review of published literature, we aimed to identify the major knowledge gaps and to highlight key future directions to better capture depredation in modelling studies. Specifically, in this review, we: i) assessed the current state of depredation

modelling across both terrestrial and marine cases by examining the types of models used, their purpose and the variables they considered, and ii) discussed the priority needs to improve our understanding of the conflict through modelling and, therefore, our capacity to mitigate it.

5.2. Methods

5.2.1. Systematic review process

We conducted a comprehensive and systematic review of the scientific literature that used models to study depredation and that was published between 1995 and 2021 (April 20) on the Web of Science. We used “depredation” as the primary search term (*a*) and extended the search to terms associated with depredation on 4 groups of resources. For depredation on crops, we added ‘crop raiding OR crop damage’ (*b*). For depredation on livestock, we added ‘livestock attack OR livestock damage’ (*c*). For depredation on farmed fish, we added ‘stock attack OR (aquaculture AND interaction)’ (*d*). For depredation on fishery catches, we added ‘catch remov* OR catch damage’ (*e*). All these specific terms were associated with ‘wildlife OR predat*’ (*f*) to focus on damage caused by wild species, as well as ‘mammal* OR shark*’ (*g*) commonly observed in the marine realm. Terms such as ‘law’, ‘chemi*’, ‘nest*’ or ‘bacteri*’ (*h*) were excluded to restrict the search to publications addressing depredation as per the definition given above. To focus the search on studies that used a modelling approach, we added ‘model*’ (*i*) to the set of terms listed above.

The final search equation was a combination of the above elements as follows:

$$((a \text{ OR } b \text{ OR } c \text{ OR } d \text{ OR } e) \text{ AND } (f \text{ OR } g)) \text{ NOT } h \text{ AND } i$$

Terms from the equation were searched in abstracts, keywords and titles.

5.2.2. Preliminary paper screening, data coding and extraction

Out of a total of 4,112 publications that addressed depredation, 758 (18%) of which were associated with modelling (i.e. matched the final search equation). Among these publications, 313 (41%) were considered relevant for this review as relying on models as a methodology, while others were discarded either because modelling was only mentioned, or because they actually focused on natural predation (rather than depredation). The number of publications for which depredation modelling was reported was the primary metric used to explore patterns.

In each selected publication, we systematically collected information on: type of exploited or produced resources by human subject to depredation, depredating species and depredated resource involved, geographical location of the depredation case, study purpose, type of model used as well as the variables that were considered in the model.

The number of publications was, first, summarized by type of exploited or produced resource by human, and in a second time by country for terrestrial cases and major fishing areas of the Food and Agriculture Organization (FAO) for marine cases.

Six categories were used to characterise the aims and purposes of the selected studies: (1) “perception” for studies about the perception of depredation or depredating species by humans; (2) “*socio-economic consequences*” for these publications that focused on depredation impacts on food production or exploitation activities; (3) “*depredating species ecology*” for these publications that assessed either the distribution, diet and population size or dynamics of depredating species; (4) “*factors influencing depredation*” for studies that focused on environmental or anthropogenic factors influencing depredation, distribution or abundance of the depredating species; (5) “quantification of *depredation*” for these publications that either assessed the risk (probability), rate or frequency of depredation events, or the change in yield caused by depredation; (6) “*mitigation*”: publications that aimed to investigate ways to mitigate depredation or to assess the effectiveness of existing mitigation measures.

Modelling approaches were grouped into 3 high-level categories, statistical, mechanistic or conceptual and then assigned to more specific sub-categories as follows: statistical models were further discriminated between regression models and hidden Markov models; and mechanistic models were divided into population dynamics models, individual-based models, trophic models, qualitative models and economic models.

Component and variable involved in depredation systems were grouped, and illustrated through a conceptual diagram (**Figure 2.1**). In a depredation context, humans, depredated and depredating species are in close interaction, and are the three main components of the socio-ecosystem. Depredated and depredating species are part of and interact with the rest of the biocenosis. Within the socio-ecosystem, in addition to human exploitation or production activity, anthropogenic pressure and management have an impact, and were thus considered. All components interact or evolve within the biotope. Each of these components has been included in published models using a variety of variables. For humans, these variables were human occurrence, human perception (i.e. towards depredation or depredating species), economic aspects (i.e. costs and profits), personal information (i.e. age, gender, ethnicity), social data (i.e. wealth, education, religion, occupation) and activity details (gear or agriculture technique, operation characteristics, number of farm or boat owned, yield and effort) (**Figure 2.1**). For the biocenosis, depredating and depredated species, we identified diet, species, distribution, occurrence, population size (i.e. abundance and density), dynamics (i.e. mortality, breeding and growth rate) and population structure (i.e. life stage or age, body mass and sex) (**Figure 2.1**). Depredation, whether expressed as a rate of loss, or frequency of events or probabilities of occurrence, is a variable attached to depredating species because of its definition as behaviour developed by wild species feeding on resources derived from various human activities.

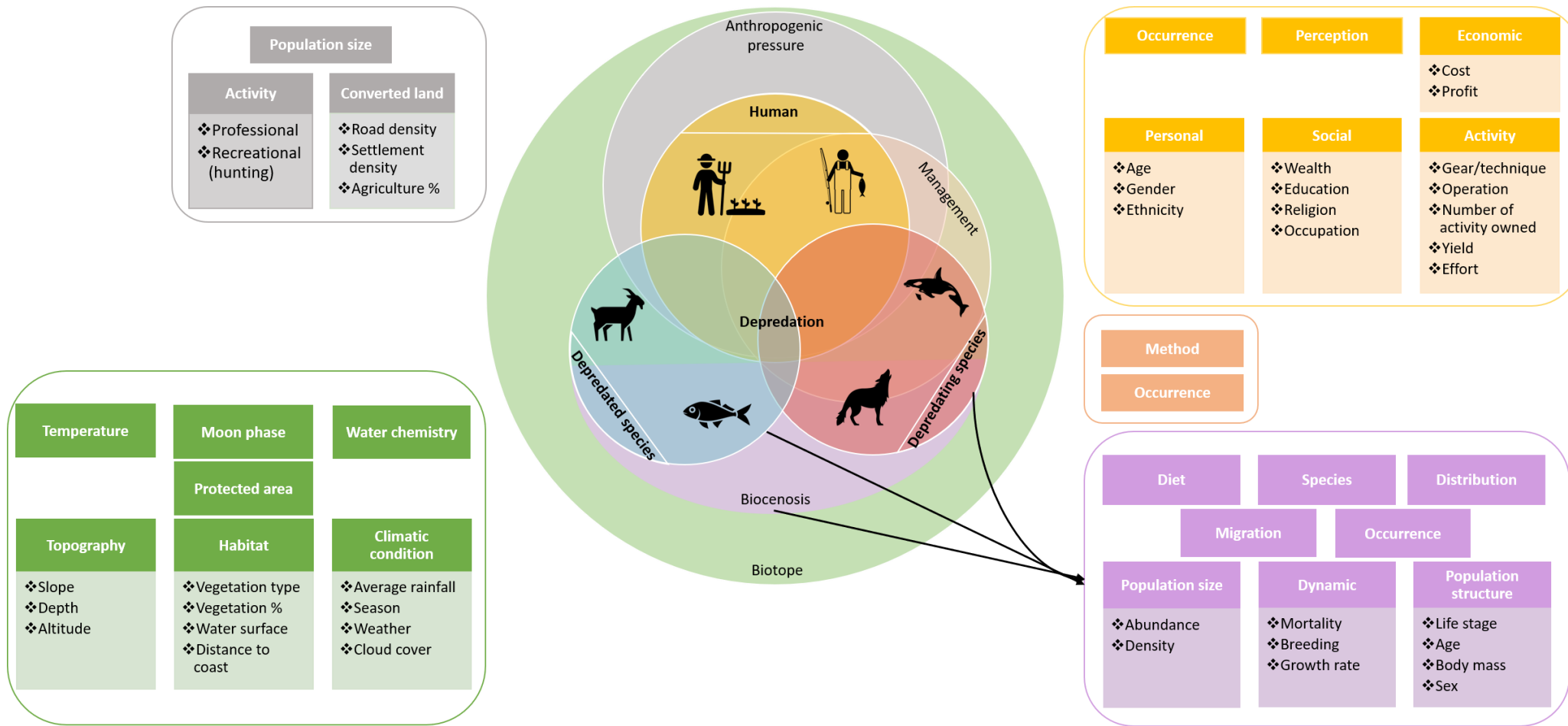


Figure 2.1: Conceptual diagram of system components involved in depredation. The main components correspond to humans, depredating species and depredated species, while additional components are biocenosis, biotope, anthropic pressure and mangement. Variables describing each component which were encountered in the reviewed publications are listed in boxes.

Management was included through its occurrence or the method used (**Figure 2.1**). For biotope, we identified the variables temperature, moon phase, water chemistry, protected area, topography (i.e. slope, depth, altitude), habitat (i.e. vegetation type, vegetation coverage, water surface and distance to coast in marine realm), and climatic condition (i.e. average rainfall, season, weather and cloud cover) (**Figure 2.1**). Finally, the variables describing anthropic pressure were population size, activity (i.e. recreational or professional), and land use (i.e. agriculture coverage, road and settlement density) (**Figure 2.1**).

5.3. Results

The main results were then summarised in three sections. The first section details the regional cases grouped by exploited or produced resources by human (i.e. crop, livestock, farmed fish and fisheries) as well as their spatial distribution. The second section focuses on the most commonly used modelling approaches and their purpose. Finally, the third section quantifies the variables that were most commonly used for each component.

5.3.1. Global scope of regional cases

The number of publications using modelling to study depredation has increased since 1996, with 85% of the 313 reviewed publications published after 2010 (**Figure 2.2**). Out of 264 publications (84%) on terrestrial depredation, 53% concerned livestock, 42% crops and 5% both (**Figure 2.3**). In the marine realm, 49 publications (16%) were identified, among which 76% studied depredation on fishery catches, 22% on farmed fish, and 2% on both (**Figure 2.3**). Depredating species belonged to 13 orders: Anseriformes, Artiodactyla, Carnivora, Cetacea, Gruiformes, Icteridae, Octopoda, Passeriformes, Pelecaniformes, Primates, Proboscidae, Rodentia and Suliformes, corresponding to around hundred species.

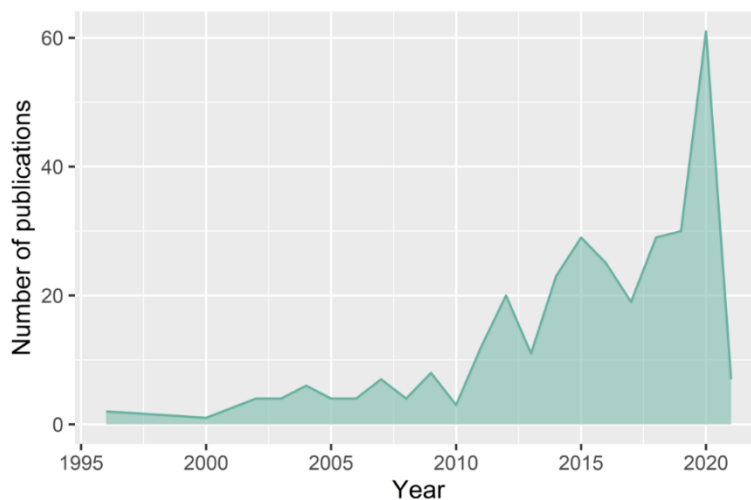


Figure 2.2: Number of publications addressing depredation using modelling approaches between 1996 and April 2021 (source: Web of Science).

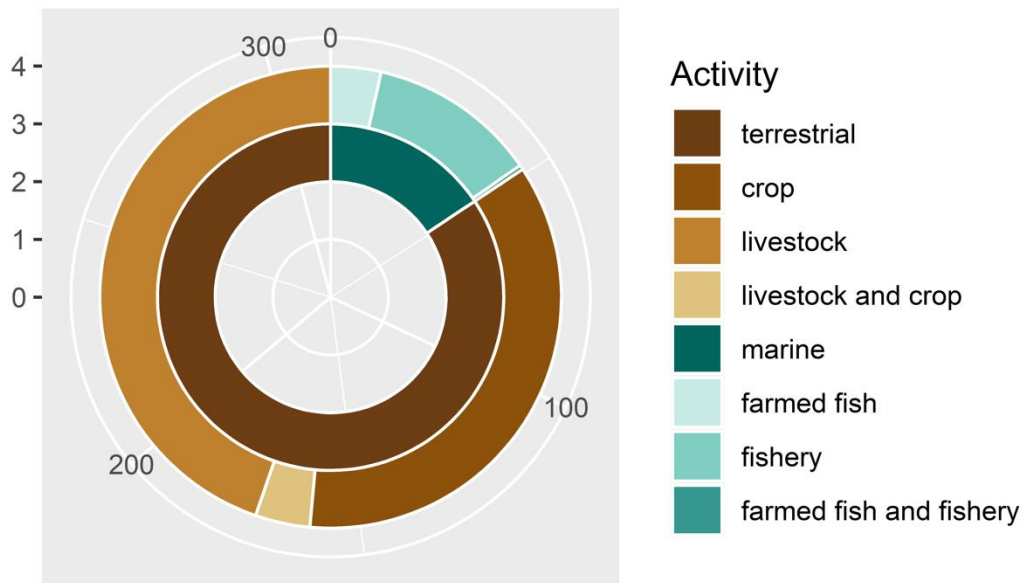


Figure 2.3: Distribution of reviewed depredation modelling publications according to the human activities concerned.

Publications addressing depredation using a modelling approach were distributed over 61 countries (31%) around the world and 12 FAO areas (44%; **Figure 2.4; Figure 2.5**).

In the terrestrial realm, 51 publications were from the United States (**Figure 2.4**), covering 27 states, and primarily studied grey wolf (*Canis lupus*) depredation on livestock. The states with most studies were Idaho, Montana, Wisconsin, Wyoming and Washington (Bradley et al., 2015; Clark et al., 2020; Hanley et al., 2018a, 2018b; Kompaniyets & Evans, 2017; Olson et al., 2019, 2014; Stenglein et al., 2015; Treves et al., 2011; Treves & Rabenhorst, 2017; Wielgus & Peebles, 2014; Young & Kinka, 2019). Next came India and Nepal, with 20 and 14 publications respectively, focusing mostly on big cats depredation on livestock (**Figure 2.4**). The depredating species involved were tiger (*Panthera tigris*), leopard (*Panthera pardus*), snow leopard (*Panthera uncia*) and Indian lion (*Panthera leo persica*) (Athreya et al., 2015; Carter et al., 2012, 2014; Chetri et al., 2017, 2019; Dhungana et al., 2016, 2018; Hanson et al., 2020; Karanth et al., 2013; Karanth & Ranganathan, 2018; Khanal et al., 2020; Kusi et al., 2020; Lamichhane et al., 2019; Loch-Temzelides, 2021; Meena et al., 2014; Miller et al., 2015, 2016a, 2016b; Naha et al., 2020; Sharma et al., 2015; Upadhyaya et al., 2020; Watts et al., 2019; Zabel et al., 2011). Twelve publications studied Italian and Tanzanian cases (**Figure 2.4**). In Italy, six studies concerned wolf depredation on livestock (Ciucci et al., 2018; Dondina et al., 2015; Marucco & McIntire, 2010; Milanesi et al., 2019, 2015; Zingaro and Boitani, 2017), while the other six were on wild pig (*Sus scrofa*) depredation on crop (Amici et al., 2012; Cappa et al., 2019; Cerri et al., 2017; Ficetola et al., 2014; Greco et al., 2021; Lombardini et al., 2016). In Tanzania, the emblematic case of elephant (*Loxodonta africana*) depredation on crops was investigated in three publications (Denninger Snyder et al., 2021; Kiffner et al., 2021; Scheijen et al., 2019), while big cat

depredation on livestock was investigated in four publications (Beattie et al., 2020; Holmern et al., 2007; Koziarski et al., 2016; Kushnir et al., 2014). Ten publications were from Brazil, where another case of big cat depredation on livestock was frequently investigated, especially jaguar (*Panthera onca*) depredation on cattle (Figure 2.4; Carvalho et al., 2015; Gese et al., 2018; Michalski et al., 2006; Tortato et al., 2015; Zanin et al., 2015). Finally, each of the 55 other countries were the focus of less than ten publications (Figure 2.4).

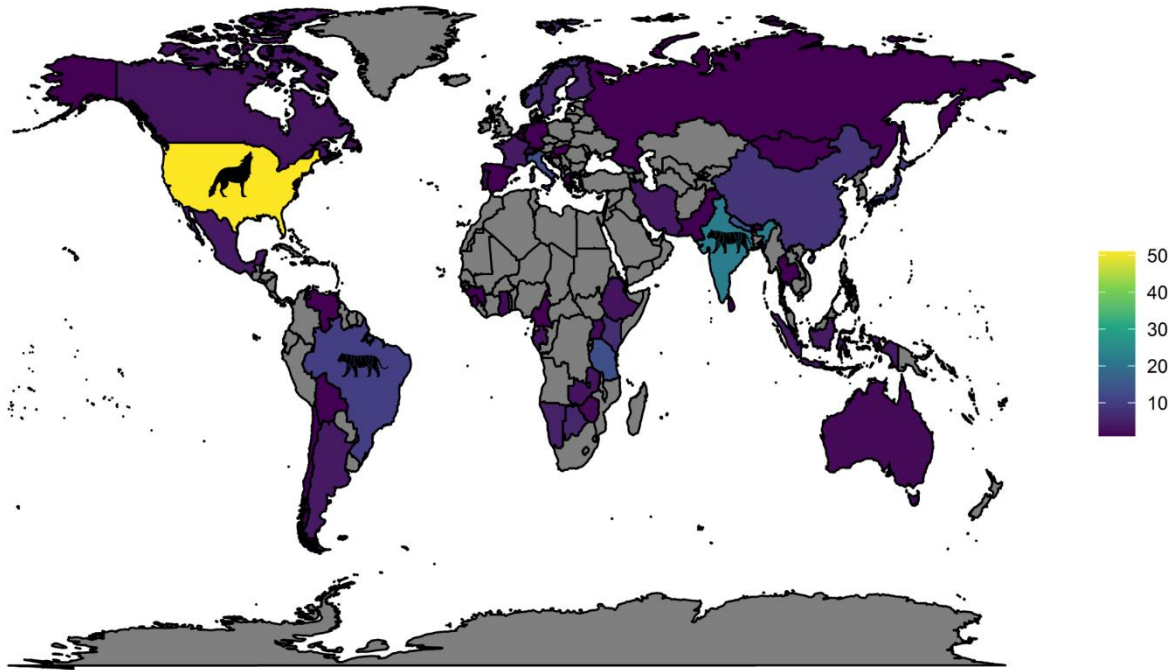


Figure 2.4: Geographic distribution of the reviewed depredation modelling publications in the terrestrial realm summarized by country.

In the marine realm, 9 publications concerned the Northeast Atlantic (FAO area 27). Four among them investigated depredation by harbour seal (*Phoca vitulina*) on salmon fisheries (Figure 2.5; Fjälling, 2005; Götz and Janik, 2016; Holma et al., 2014; Thompson et al., 2007). Seven publications were from the Southern Indian Ocean (FAO area 58), dealing with the depredation by killer whale (*Orcinus orca*) and sperm whale (*Physeter macrocephalus*) on the toothfish fishery in the Crozet and Kerguelen archipelagos (Figure 2.5; Clavareau et al., 2020; Labadie et al., 2018; Tixier et al., 2020, 2019, 2016, 2015a, 2015b). Six publications were found for the Mediterranean and Black Sea (FAO area 37), studying the depredation of bottlenose dolphin (*Tursiops truncatus*) on farmed fish and fishery catches (Figure 2.5; Bonizzoni et al., 2021, 2014; Díaz López, 2019; Methion & Díaz López, 2019; Pardalou & Tsikliras, 2020; Pennino et al., 2015). There were 5 publications from the Northeast Pacific and Western Central Atlantic (FAO area 67 and 31 respectively) (Figure 2.5). Killer whale and sperm whale depredation on sablefish (*Anaploma fimbria*) was investigated in the Gulf of Alaska (Figure 2.5; Peterson et al., 2014; Peterson & Hanselman, 2017; Schakner et al., 2014; Straley et al., 2015; Thode et al., 2014) and that of double-crested cormorant (*Phalacrocorax auritus*) on

farmed catfish (*Ictalurus spp.*) in the Mississippi (**Figure 2.5**; Burr et al., 2020a, 2020b, 2020c; Dorr et al., 2012). Finally, less than 3 publications dealt with 7 other FAO areas (**Figure 2.5**).

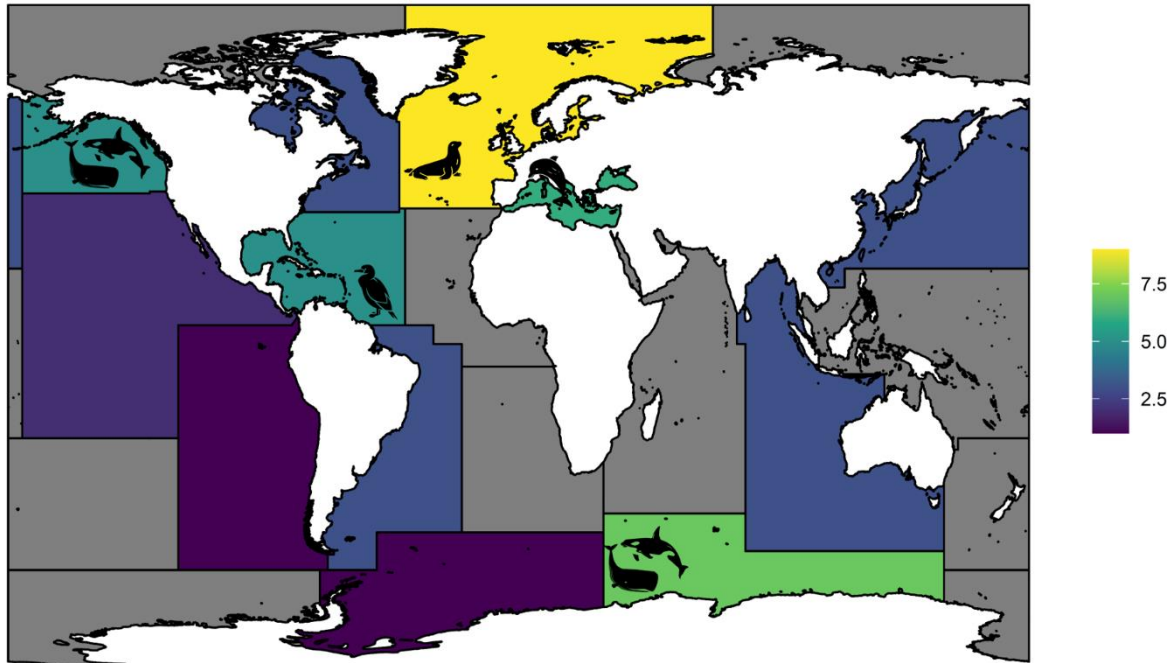


Figure 2.5: Geographic distribution of the number of reviewed depredation modelling publications in the marine realm summarized by FAO area.

5.3.2. Modelling approaches and study purposes

Statistical models dominated in both terrestrial and marine studies with a total of 264 publications (85%), followed by mechanistic models with 36 publications (12%) and conceptual models with only 6 publications (1%) (**Figure 2.6**). The majority of studies applying statistical models used regression models (89%), followed by machine learning (8%) and hidden Markov models (1%) (**Figure 2.6**). Mechanistic models consisted of economic models (31%), population dynamics models (14%) and individual based models (22%) (**Figure 2.6**). Occasionally, trophic and qualitative models were mentioned (7 publications). Conceptual models were only used in six terrestrial regional cases (**Figure 2.6**).

These modelling approaches were used for diverse purposes. One of the main goals was to determine factors influencing depredation, which was mentioned in 127 publications (41%; **Figure 2.6**). Seasonal and spatial factors were found to influence occurrence and severity of depredation (Beattie et al., 2020; Passadore et al., 2015). For instance, African lion (*Panthera leo*) depredation on livestock was related to vegetative productivity and proximity to surface water in Tanzania (Beattie et al., 2020), while distance to coast explained killer whale depredation on catch of the Uruguayan pelagic longline fishery (Passadore et al., 2015). The second purpose was the quantification of depredation, which was addressed in 87 publications (28%; **Figure 2.6**). Depredation rates greatly

varied between cases. For instance, whale depredation was estimated to be 30% of the total toothfish catches in Crozet (Tixier et al., 2020), while deer and elk damages were estimated affecting 7.2% of safflower plants in Utah (Haney & Conover, 2013). Mitigation was the third main purpose and was reported in 55 publications (18%; **Figure 2.6**). Most modelling approaches compared the rate of loss as well as frequency of events or probability of occurrence of depredation with and without mitigation or among various mitigation measures. Fences or protective enclosures were often reported in terrestrial regional cases, notably to reduce elephant depredation on crops in Tanzania (Scheijen et al., 2019). In the marine realm, deterrent devices were commonly mentioned. A deterrent device was notably tested to reduce bottlenose dolphin depredation on coastal gillnet fishery catches (Waples et al., 2013). The ecology of the depredating species was studied in 24 publications (8%), and most of these publications attempted to assess the size and spatial distribution of depredating populations (**Figure 2.6**; Burr et al., 2020b; Giefer & An, 2020). The socio-economic consequences and perception of humans were addressed in 14 and 13 publications, respectively (4%; **Figure 2.6**). Fifty percent of publications classified as related to socio-economic consequences investigated economic impacts. Human perception towards depredation or depredating species was mostly mentioned in the context of implementation of new mitigation measures or re-introduction of emblematic species, e.g. snow leopard in Nepal (Hanson et al., 2020; Loch-Temzelides, 2021).

Some study purpose categories were addressed with specific modelling approaches. In particular, depredation quantification was mainly achieved using statistical models, specifically regression (86%) and machine learning models (14%; **Figure 2.6**). In contrast, socio-economic consequences were mainly studied with mechanistic models (77%), of which 60% were economic models, 20% individual based models, and 10% each population dynamics models and trophic models (**Figure 2.6**).

5.3.3. *System components and variables*

Among the three main system components, i.e. humans, depredated and depredating species, depredating species were reported in most reviewed publications (268 publications; 86%), followed by depredated species (159; 51%) and lastly humans (87; 28%) (**Figure 2.7**). Concerning other components, biotope was mentioned in most reviewed publications (176; 56%), followed by management (67; 21%), anthropic pressure (61; 19%), and biocenosis (32; 11%) (**Figure 2.8**).

5.3.4. *Terrestrial versus marine realm*

Similarities were observed between the terrestrial and marine realm in terms of the most commonly studied variables for each component. For depredating species, depredation behaviour was most common, and was mentioned in 122 publications (39%; **Figure 2.7**), either in the form of depredation rate, occurrence or frequency of events. For depredated species and biocenosis, the size of populations, documented as abundance or density, was the most common variable, reported respectively in 65

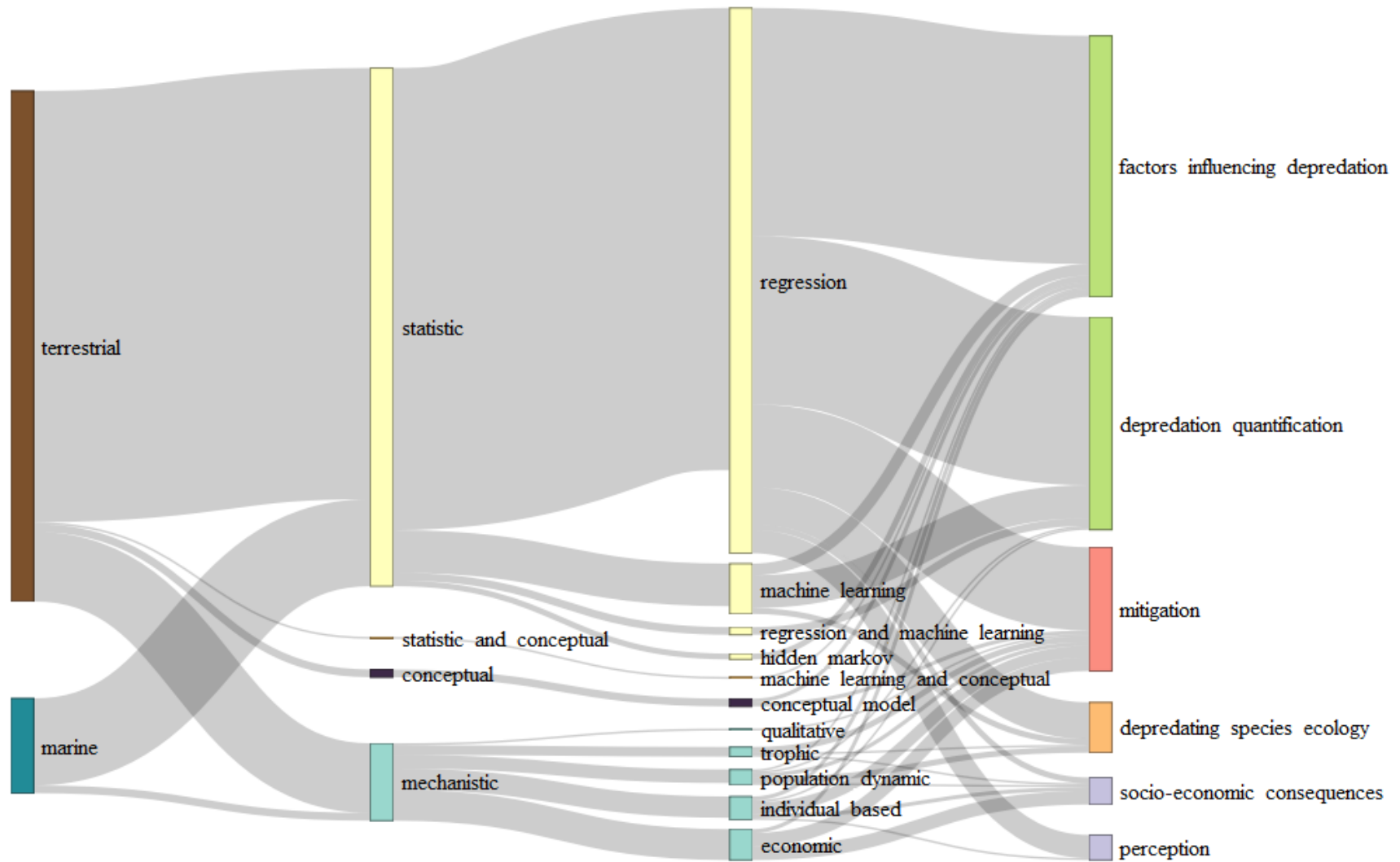


Figure 2.6: Categorisation of reviewed depredation modelling publications according to modelling approach and study purpose.

(20%) and 26 publications (8%). Population size of the depredating species was also frequently used, just behind depredation behaviour and occurrence (56, 18%) (**Figure 2.7**). Population size of biocenosis, depredated and depredating species were mainly used as explanatory factors for the occurrence or intensity of depredation. For instance, prey abundance explained common dolphin depredation in the Azores (Cruz et al., 2016) and wolf depredation on livestock in Portugal (Pimenta et al., 2018). For biotope, habitat was the most common variable, mentioned in 142 publications (45%), followed by topography (41; 13%) (**Figure 2.8**). Like population size, habitat and topography were primarily used to explain occurrence and intensity of depredation, such as forest coverage and slope in the case of elephant depredation on crops (Ngama et al., 2019).



Figure 2.7: Percentage of reviewed depredation modelling publications that include specific variables related to each of the three main system components (i.e. depredating species, depredated species and humans). In the first and second column, percentage are expressed relatively to the total number of reviewed papers per realms, i.e., 264 terrestrial studies (brown) and 49 marine studies (blue). While, the third column expressed the overall inclusion of variables in all the 313 publications.

In the marine realm, the occurrence and the dynamics (i.e. mortality, breeding and growth rate) of depredating species were the variables most commonly reported (30% and 10% of 49 publications, respectively). These two variables were reported in 14% and 5% of the terrestrial studies (i.e. 264

publications), respectively (**Figure 2.7**). For instance, a study aimed at identifying the causes of seal depredation also considered bycatch mortality of seals and hence their population dynamics (Cosgrove et al., 2015). Conversely, in the terrestrial realm, population structure (6%) of depredating species and human related information such as social (6%), personal (6%) and perception (3%) were more frequently reported than in the marine realm (2%, 2%, 0% and 0%) (**Figure 2.7**). Social and personal information were mainly found in publications studying perceptions of the conflict, for example in the case of translocation of blue sheep to reduce livestock depredation by snow leopards (Hanson et al., 2020). Protected area was frequently included in modelling approaches, mentioned in 22 publications, but in terrestrial studies only. Anthropogenic pressure information, was most commonly documented through human population size or converted land, mentioned each in 33 publications (**Figure 2.8**). Both were mainly used to identify factors influencing depredation or for creating depredation risk maps, as previously mentioned for habitat and topography.

5.3.5. *Depredating versus depredated species*

In marine realm, the occurrence, population size and dynamics were more frequently reported for the depredating species (30, 20 and 10% of the 49 marine studies, respectively for each variable) than for the depredated species (respectively 8%, 8% and 4%) (**Figure 2.7**). The occurrence of the depredating species was mainly used to identify factors influencing its distribution (e.g., Bonizzoni et al., 2021; Mul et al., 2020). In particular, the generalized additive model of Bonizzoni et al., (2021) indicated that trawling influenced the dolphin distribution in the Adriatic Sea and increased the chances of encountering them 4.5 fold. Conversely, population structure (10%) and species identity (10%) of the depredated species were more commonly reported than for the depredating species (each 2%) (**Figure 2.7**). Briceño et al., (2015) found that in South Australian fishery the risk of pot predation by the Maori octopus (*Pinnoctopus cordiformis*) increased with rock lobster (*Jasus edwardsii*) size and was higher for males.

5.3.6. *Integration of system components*

We assessed the integration level of the components of socio-ecosystems associated with depredation cases (human activity, depredating species and depredated resource) into models used in the reviewed studies. Among the 313 studies, 33% used models that incorporated both the depredating species and depredated resource, and 32% that incorporated the depredating species only (**Figure 2.9**). Models considering both the human activity and the depredating species were found in 13% of the publications and were equally in terrestrial and marine studies (20 and 21 publications, respectively) (**Figure 2.9**).

Models incorporating all three major components were found in only 8% of the reviewed publications, including 18 terrestrial studies and 6 marine studies (**Figure 2.9**). These terrestrial studies primarily focused on conservation or aimed to create depredation risk maps.

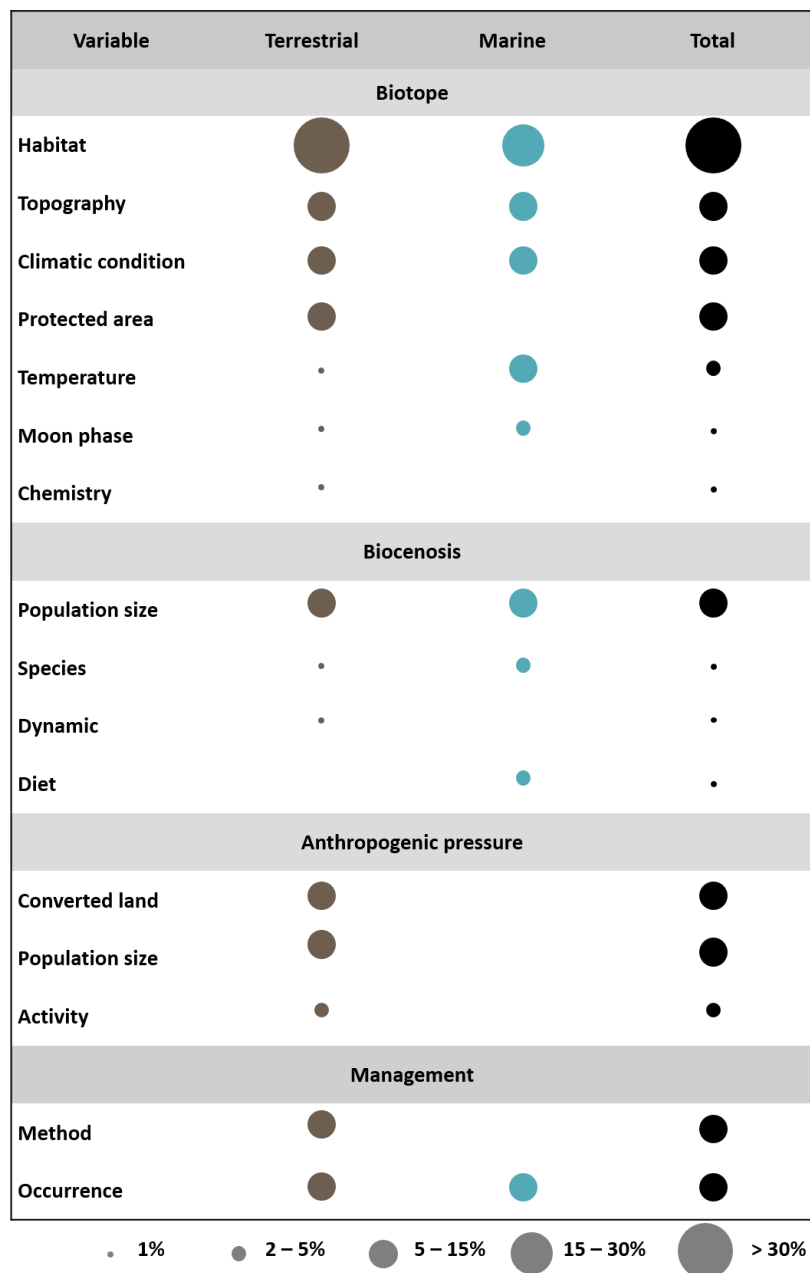


Figure 2.8: Percentage of reviewed depredation modelling publications including variables describing additional system components biotope, biocenosis, anthropogenic pressure and management in terrestrial (brown) and marine (blue) realms.

Conservation orientated terrestrial studies focused on two carnivore species, snow leopard and lion. By quantifying depredation probabilities or identifying factors influencing depredation or socio-economic consequences, 3 of the 18 publications supported the implementation of mitigation measures subsequent to the re-introduction of snow leopard (Chetri et al., 2019; Din et al., 2019; Loch-Temzelides, 2021). For instance, Chetri et al., (2019), found that the probability of livestock losses increased with herd size, affecting more owners (humans) of large herds. Furthermore, 3 other publications were embedded in a conservation and human-lion coexistence context (Beck et al., 2019;

Dunnink et al., 2020; Hazzah et al., 2013). These studies identified factors influencing depredation and assessed human perception towards depredating species through conceptual or regression models (Beck et al., 2019; Dunnink et al., 2020; Hazzah et al., 2013). Hazzah et al., (2013) demonstrated that higher education was associated with positive perceptions toward lions and lower reported propensity to kill them. Three publications used regression models to identify areas with high risk of depredation as support to the implementation of mitigation actions and, for that purpose, combined characteristics of the human activity with information on the occurrence of depredation, the depredating species and the density of the depredated resource (Karanth et al., 2012; Pimenta et al., 2018; Treves et al., 2004). For instance, in Wisconsin, wolf depredation on livestock was associated with farm size, crop farming and road density (Treves et al., 2004). In the marine realm, 3 publications investigated the influence of environmental factors, species composition, yield and gear type on depredation and assessed the probability of depredation through regression models (Cruz et al., 2016; Pardalou & Tsikliras, 2020). In the Aegean Sea, the gears most commonly depredated by dolphin were gill nets and trammel nets with small mesh sizes, mainly targeting surmullet (*Mullus surmuletus*), red mullet (*Mullus barbatus*), common sole (*Solea solea*), European hake (*Merluccius merluccius*), and caramote prawn (*Melicertus kerathurus*) (Pardalou & Tsikliras, 2020).

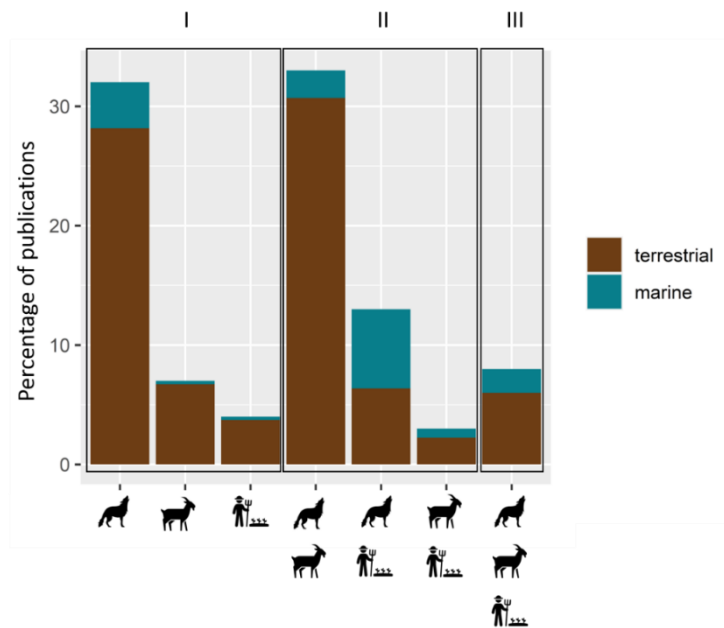


Figure 2.9: Percentage of reviewed depredation modelling publications including one (I), two (II) or three (III) system components among humans illustrated by the farmer icon, depredating species illustrated by the wolf icon or depredated species illustrated by the goat icon for terrestrial (brown) and marine (blue) realms.

5.4. Discussion

Depredation is a worldwide issue and is likely to escalate in the coming decades. In the following sections, we build upon this systematic literature review to discuss key drivers for modelling

approaches, as well as the major knowledge gaps and thus identify future research priorities to better capture depredation in modelling approaches.

5.4.1. Key drivers for modelling approaches

Terrestrial and marine depredation cases have been reported worldwide, but implementation of dedicated modelling approaches greatly vary across regions. For instance, a large number of published modelling studies on marine depredation focus on the north-eastern Atlantic Ocean. While the intensive research focus on certain regional cases can somehow be related to the severity of depredation (Tixier et al., 2021a), we identified a number of additional factors that can determine the amount of modelling research efforts towards specific depredation case studies, in particular: the viability of the human production or exploitation activity and the ecological status of the species involved (both exploited resource and depredating species).

Firstly, the viability of the human exploitation or production activity depends to some extent on the economic value of the depredated resource, which may be associated with variation in the use of models in studies. Economic models were predominant among mechanistic models used in studies aiming at assessing the impact of depredation on the profitability of the activity when the depredated resource had a high economic value. This is for instance, on the case for Baltic salmon and toothfish in subantarctic waters (Grilly et al., 2015; Oglend, 2013), and these two regions yielded numerous studies estimating the loss of fish caused by depredation (Fjälling, 2005; Tixier et al., 2020, 2019, 2016). Profitability also depends on the importance of this activity in the global economy. The United States are the world's largest beef and buffalo meat producer, producing 12 million tons in 2014, followed by Brazil with 10 million tons (Ritchie & Roser, 2017). This probably explains the numerous publications on wolf depredation on livestock in the United States, more specifically on cattle (Bradley et al., 2015; Clark et al., 2020; Hanley et al., 2018a, 2018b; Kompaniyets & Evans, 2017; Olson et al., 2019, 2014; Stenglein et al., 2015; Treves et al., 2011; Treves & Rabenhorst, 2017; Wielgus & Peebles, 2014; Young & Kinka, 2019) and by big cat in Brazil (Carvalho et al., 2015; Gese et al., 2018; Michalski et al., 2006; Tortato et al., 2015; Zanin et al., 2015).

Secondly, the issue poses to the long-term viability of the human exploitation or production activity depends also on the level of depredation risk which are frequently assessed through modelling approaches. Typically, there may be greater concern about depredation increasing in the future for species for which this behaviour may become prevalent at the individual level, but also across individuals in populations, through learning pathways. Typically, wolf, snow leopard, lion, seal, killer whale and sperm whale are all capable of social learning, which has a major influence on the acquisition of depredation behaviour (Nyhus, 2016), and therefore a high potential for spreading among individuals. The high transmission potential of depredation behaviour can thus explain the number of publications dealing with these specific case studies. In this context, a model of social transmission was used to examine the spread of longline depredation behaviour among sperm whales

in the Gulf of Alaska (Schakner et al., 2014). This model provided circumstantial evidence for social transmission of depredation behaviour, probably influenced by human activities, which have created a situation in which there is spatial-temporal overlap with foraging sperm whales (Schakner et al., 2014).

Thirdly, most studies using models to investigate depredation cases focus on species of high conservation concern. A large number of publications indeed involved protected species such as wolf, snow leopard, lion, seal, killer whale and sperm whale (Dunnink et al., 2020; Hanselman et al., 2018; Loch-Temzelides, 2021; Skonhofs, 2017; Thompson et al., 2007; Tixier et al., 2019). Depredating species such as lion, snow leopard and sperm whale are classified as vulnerable by the IUCN, which is not the case of other depredating species like elk, wild pig, cephalopods or grey seal for example (iucnredlist.org). To avoid further extinctions, it seems crucial to reconcile conservation of vulnerable species with the continuation of human exploitation or production activities. This probably explains the dominance of these emblematic species in the reviewed studies. However, conservation objectives may be jeopardized because depredation can compromise human well-being and motivate a negative sentiment and retaliation towards wildlife (Salerno et al., 2020), which might explain the large number of publications aimed at assessing human perception towards depredating species or depredation in general. In the same vein, numerous publications used models to examine the effectiveness of mitigation measures (Kiffner et al., 2021) or to support their implementation by identifying high risk areas where efforts should be focused (Chetri et al., 2019; Din et al., 2019; Loch-Temzelides, 2021). However, to date, few mitigations measure seem to be effective in the long term.

Fourthly, variation in the extent to which models have been used to study depredation may also be explained by the state of the depredated resource. In marine cases, more publications have addressed depredation on fishery catches than depredation on farmed fish, and this is likely because depredation on fishery catches adds uncertainty to the assessment of fish stocks which sustainability is already jeopardized by past or current overexploitation. Most of the time, fishers compensate for catch losses by increasing fishing effort, which results in increased stock mortality. Assessing the impacts of depredation on exploited stocks is thus essential to improve the accuracy of fish stock assessments and hence to support sustainable fishery management (Gilman et al., 2013). However, this has rarely been investigated.

5.4.2. *Depredation species reduced to a notion of loss*

In this review, we found that in most modelling studies the depredating species was reduced to its depredation behaviour, representing a cause for loss for human activities. This finding is probably due to an anthropocentric view of the conflict. Indeed, framing of human-wildlife conflict, in general, commonly focuses on the detrimental impact that wildlife has on humans such as loss of income, destruction of building, physical injury or human mortality (Locke, 2013; Shoreman-Ouimet & Kopnina, 2015). This may explain in part the dominance of depredation estimates among the variables

documented for depredating species and the rare studies on the ecology of depredating species, as well as that occurrence and population size of depredating species were used to explain the severity of the conflict or to quantify losses. Other variables were scarce and this can be explained by the low availability of data for wild species compared to farmed or wild exploited species that may be monitored or managed. However, better knowledge of the ecology of depredating species seems essential, especially to evaluate and project wider long-term ecosystem consequences of depredation. A topic deserving more research is the enhancement of certain life history parameters due to facilitated food access (Tixier et al., 2015a) and its potential cascading effects.

5.4.3. *Contrasting situation in terrestrial and marine realm*

Despite the growing number of publications addressing depredation through modelling approaches, the study of marine cases remains rare, although depredation affects coastal and offshore fisheries as well as a broad range of fishing techniques worldwide (Gilman et al., 2007; Mitchell et al., 2018). Terrestrial depredation has been known since the beginning of agriculture several millennia ago, with for instance, the case of elephant depredation in Africa (Barnes & Douglas, 1982). This early knowledge may explain the greater number of publications applying modelling to terrestrial depredation. Marine depredation has emerged as problematic around 1970s, concomitantly with the global expansion of fisheries and the emergence of non-lethal mitigation in a conservation context (Hamer et al., 2012; Mitchell et al., 2018; Read, 2008; Tixier et al., 2021a). The study of depredation in the marine realm is therefore relatively recent, which implies limited availability of data. Moreover, in the marine realm data are more difficult to acquire than in the terrestrial realm. Notably, depredation is not systematically detected and recorded, and rarely quantified. Predators may depredate on fishing gear at depth, when fishers are away or leave limited evidence when removing fish (Tixier et al., 2020). Thus, in cases where depredation has been observed or left clear evidence, data are mainly qualitative (Peterson & Hanselman, 2017; Werner et al., 2015).

5.4.4. *Source of data*

Testimonials or questionnaires provide essential information allowing, among other thing, to estimate the severity of the conflict. However, this type of information has various biases and can lead to disparities between reality and perception (Hill, 2018). For instance, farmers in Sulawesi have reported depredation on crops by macaques (*Macaca maura*) on most days, while camera traps estimated depredation on crops to occur only 23% of days (Zak & Riley, 2017). This disparity may be related to synergies between people's individual experience, wider societal practices, cultural norms, outlooks and beliefs (Dickman, 2012; Hill, 2018). The perception of a human, whose activity is impacted by depredation, varies notably in relation to the value of the depredated resource. For instance, people are much less tolerant of chimpanzees when depredation affects cash crops such as sugar cane (Hill, 2018). Moreover, animals thought to be a threat to human safety and large animals that are more

visible are often blamed disproportionately for depredation (Hill, 2018). However, based on religious beliefs and these cultural norms, together with the sharing of conservation benefits, some large carnivore may be more tolerated such as tiger in Nepal (Upadhyaya et al., 2020). Finally, respondents who are highly educated and self-sufficient are more likely to support conservation (Hazzah et al., 2013; Upadhyaya et al., 2020).

5.4.5. *Dominance of statistical models*

Statistical models largely dominated in the reviewed studies, which can to some extent be explained by purpose of the study. Indeed, the dominance of statistical models such as regression and machine learning in depredation studies can be explained by the fact that these models are well suited to predict the risk of depredation, via the identification of influencing factors or the quantification of depredation, through probabilities (Tredennick et al., 2021). Moreover, availability of data being reduced in numerous cases, statistical models seem adequate because they are often less greedy in terms of quantitative data. However, specific tool used for model is less important than the approach used to validate predictions (Tredennick et al., 2021), which is little undertaken.

5.4.6. *Lack of holistic modelling approaches*

Depredation is a behaviour-mediated interaction emerging at the interface between wildlife populations and human activities. However, few publications integrated information across humans (farmers, fishers), depredating and depredated species. This is crucial for understanding the complex changes in system dynamics induced by depredation. Specifically, provisioning effects on life history parameters of depredating populations or negative effects due to bycatch or lethal practices, as well as changes in natural predation pressure due to facilitated access to food resources are likely to change the role of predators in ecosystems (Newsome et al., 2015). In addition, depredation can compromise the profitability of human activities via a decrease in yield or destruction of equipment (Dickman & Hazzah, 2016; Wickens et al., 1992). Therefore, holistic modelling approaches are needed to assess and predict the resilience and sustainability of depredation-impacted socio-ecosystems, and thus to inform effective ecosystem-based management actions (Dambacher et al., 2015; Marzloff et al., 2016). Accounting for both socio-economic and ecological aspects of the conflict in multi-agent-based models (e.g. Marley et al., 2017), bio-economic models (Béné et al., 2001; Gourguet et al., 2013; Trijoulet et al., 2018), qualitative models (Dambacher et al., 2015; Marzloff et al., 2016; Szymkowiak & Rhodes-Reese, 2020), or ecosystem models (Christensen & Walters, 2004; Fulton et al., 2011) can help to identify, understand and balance the trade-offs occurring in socio-ecosystems subject to depredation (Tixier et al., 2021a).

Conceptual models, being focused on the main aspects of a system through a formal description of it, from the object perspective, and showing the relevant concepts and relationships that make up this system (Nieva & Wegmann, 2002), could assist in the development of these statistical

and mechanistic models. However, conceptual models that can help to understand the system as a whole were rare. Indeed, only few conceptual models were found and concerned only terrestrial depredation cases, such as wolf, by big cat, elephant and elk (Amit & Jacobson, 2017; Beck et al., 2019; Brewster et al., 2019; Rowland et al., 2018; Santos et al., 2007; Shaffer et al., 2019).

Moreover, the low number of publications using models that incorporated all three major components (humans, depredating and depredated species) can be explained by a lack of data. Cases with sufficient historical monitoring data for applying a holistic modelling approach include killer whale depredation on the toothfish fishery in Crozet (Clavareau et al., 2020; Labadie et al., 2018; Tixier et al., 2020, 2019, 2016, 2015a, 2015b) and grey wolf depredation on cattle in Wisconsin (Olson et al., 2014, 2019; Stenglein et al., 2015; Treves et al., 2011; Treves & Rabenhorst, 2017). Importantly, interdisciplinary studies can help to solve problems related to human-wildlife conflicts such as depredation (Beck et al., 2019; Nyhus, 2016; Shaffer et al., 2019). Indeed, the diverse data needed to build models require interdisciplinary cooperation to synthesize multiple historic, contemporary, and projected datasets from the biophysical, social and economic sciences (Shaffer et al., 2019). However, as Tixier et al., (2021a) demonstrated, such integrative modelling studies are currently lacking for marine depredation, while interdisciplinary research has led to major advances on both the understanding and the mitigation of the depredation conflict.

Acknowledgement

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Chapter 3: Comparison of approaches for incorporating depredation on fisheries catches into Ecopath

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Abstract

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.

3.1. 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 (Mitchell et al., 2018; Read, 2008).

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 (Gilman et al., 2007; Mitchell et al., 2018; Northridge, 1984). 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., 2015a); (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; (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 & 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 of 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 & Walters, 2004; Heymans et al., 2016). Using a subantarctic case study of marine mammal depredation on commercial fisheries (Roche et al., 2007), we assessed how three alternative model formulation 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: (1) changes in fishing and predation mortalities on target species, (2) mutual impacts of depredation-related groups (i.e. depredating, target species and fishery), and (3) broader ecosystem-level consequences.

3.2. Material and Methods

3.2.1. 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 & Walters, 2004). Ecopath models capture interactions between species or functional groups, i.e. groups of species that share similar ecological roles (Christensen & Walters, 2004). 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 & 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 (Eq.1) defines the total biological production (P)_i of functional group i as:

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

Where: (P/B)_i is the production (P) to biomass (B) ratio for functional group i; EE_i the ecotrophic efficiency, i.e. losses other than through predation and fishing; Y_i fishery yield, (Q/B)_j the consumption (Q) to biomass (B) ratio for predator j, DC_{ij} the proportion of group i in the diet of predator j, E_i the net migration rate for group i (immigration – emigration; here set to zero for all groups), BA_i the biomass accumulation rate, (Christensen & Walters, 2004; 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) (Eq. 2).

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

Assuming the modelled ecosystem is at equilibrium over the study period, the Ecopath software estimates unknown parameters to achieve mass balance (Christensen & 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.

3.2.2. 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 requires limited effort (Tixier et al., 2015a);
- (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., 2015a; 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-economics 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 3.1**).

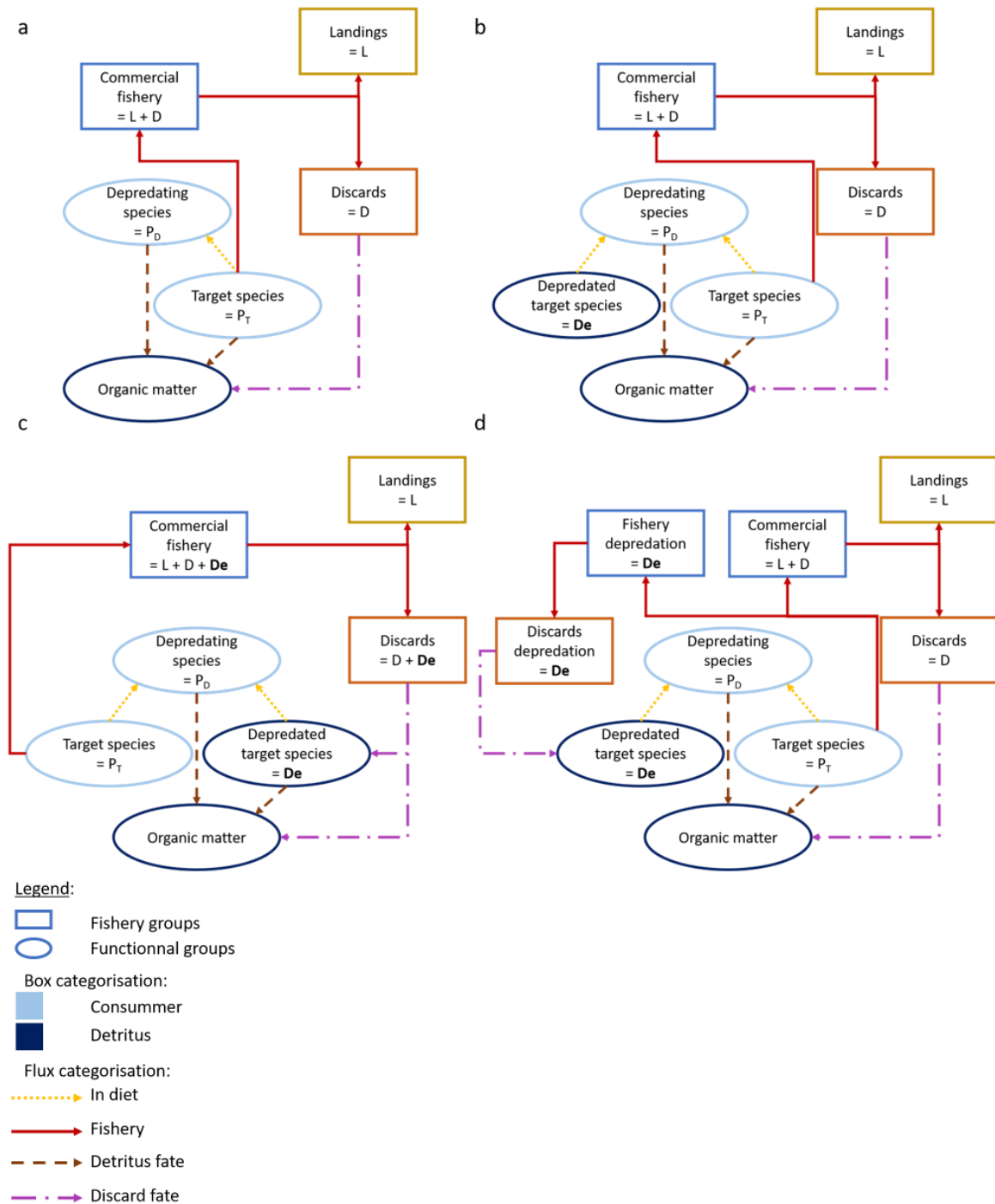


Figure 3.1: Schematic representations of alternative Ecopath model structures for including depredation on a target species. a) *baseline* model: no depredation; b) *food subsidy* model, depredated biomass is represented as a detritus group, c) *increased fishing effort* model, depredation incorporated into the commercial fishery, d) *competing fishery* model, depredation is an independent fishery. L landings biomass, D discards biomass, De depredated biomass and P_D depredating species population biomass P_T Target species population biomass.

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 3.1a**).

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 (**Figure 3.1b**). 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 3.1c**). 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 captures 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 3.1d**). In this model, the target species group is thus exposed to two competing fisheries (i.e. the commercial and the depredation fishery).

3.2.3. Comparison of alternative model formulations

We compared how the alternative model formulations, which respectively account for depredation as (1) *food subsidy*, (2) *increased fishing effort* or (3) *competing fishery*, capture depredation effects relative to the *baseline* 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 etc.) 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) were 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, 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. Rationales for using these three metrics are:

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 (Eq. 3), as follows:

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

where Q_j is the total consumption rate of predating group j (Eq. 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 , the consumption/biomass ratio for group j (Piroddi et al., 2015; Christensen et al., 2008).

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) summarise 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 & Puccia, 1990). The impact indicator is a matrix whose ij th 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 (Piroddi et al., 2015; Christensen et al., 2008).

3.2.4. Case study

The commercial longline fishery operating in the Exclusive Economic Zones of Kerguelen and Crozet Islands (French subantarctic islands located between 45°S and 50°S, 50°E and 70°E) is conducted by seven licensed 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 3.2; Table S3.1).

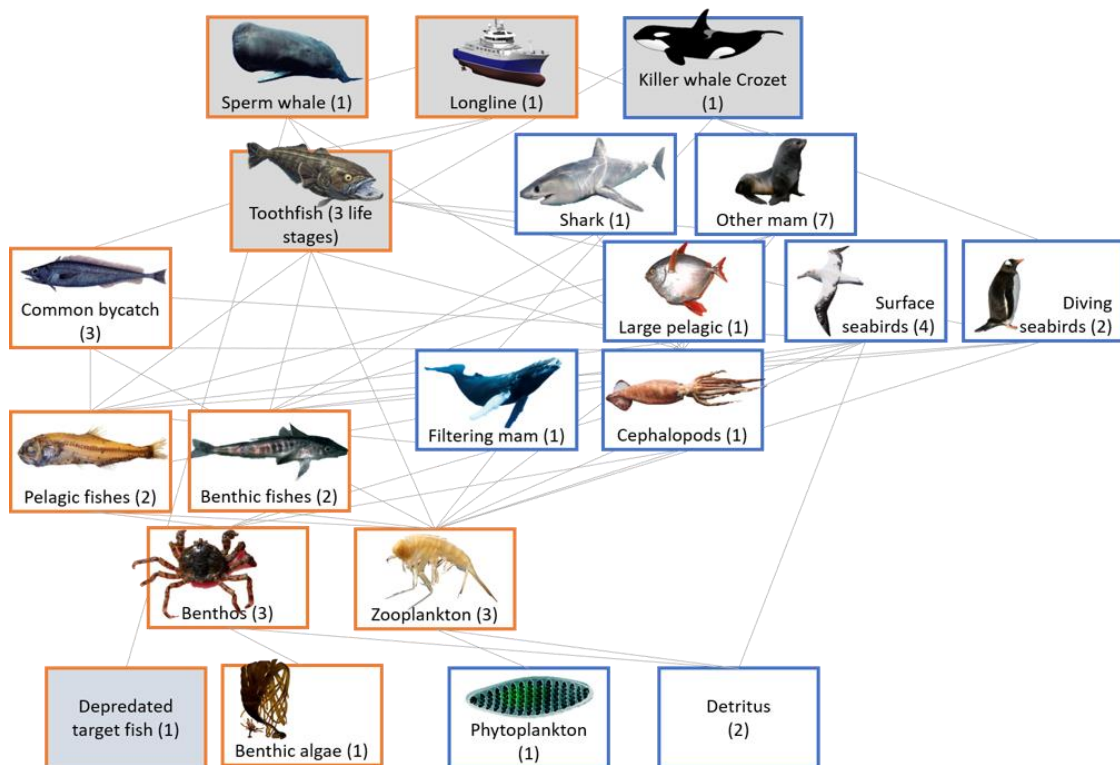


Figure 3.2: Simplified flow diagram of the *baseline* Ecopath model. Functional groups specific to Crozet are framed in orange, those occurring both around Crozet and Kerguelen Islands in blue. Figures in brackets correspond to the number of functional groups explicitly defined in the model. Focal groups 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).

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 (Labadie et al., 2018). 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 & 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 by-catch species, were modelled separately. The main by-catch species of the toothfish fishery at Crozet and Kerguelen represent approximately 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; CCAMLR, 2018b). As this work primarily focused on inclusion of depredation, the Ecopath models neglected fisheries by-catch given their marginal volumes in the French Patagonian toothfish fishery. Full details on model parameterisation are provided in 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 & Pruvost, 2007; Pruvost et al., 2011). Toothfish population estimates were obtained from spawning stock biomass estimates (Massiot-Granier et al., 2019a; Massio-Granier et al., 2019b). 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 material (Table S3.2). For clarity, we primarily present the results from the Crozet region hereafter.

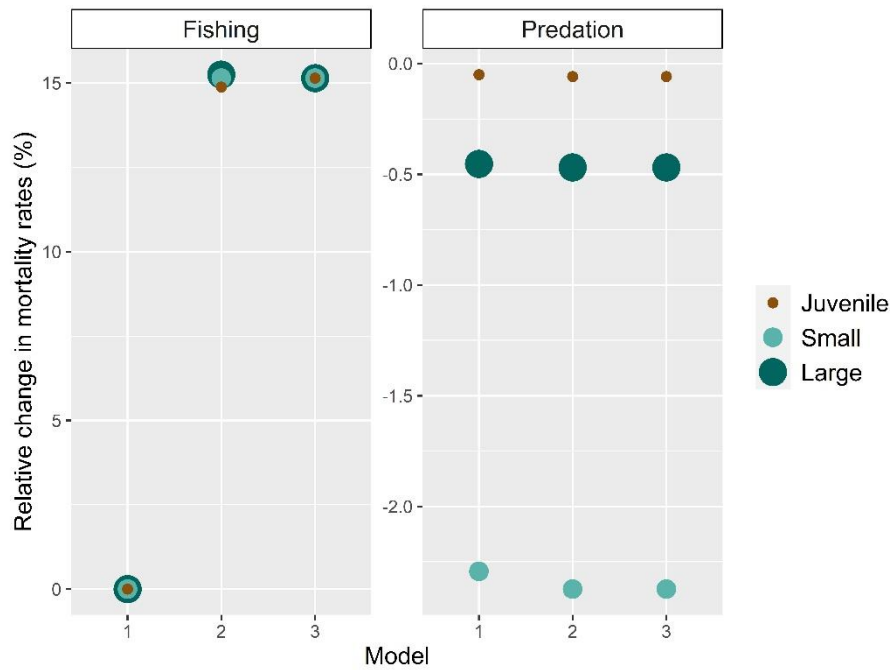


Figure 3.3: Effects of alternative Ecopath model formulation on Patagonian toothfish fishing (a) and natural predation (b) mortality. Estimates from the three alternative depredation models are expressed relatively to the *baseline* model (no depredation). Models are numbered from 1 to 3: 1 *food subsidy* 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).

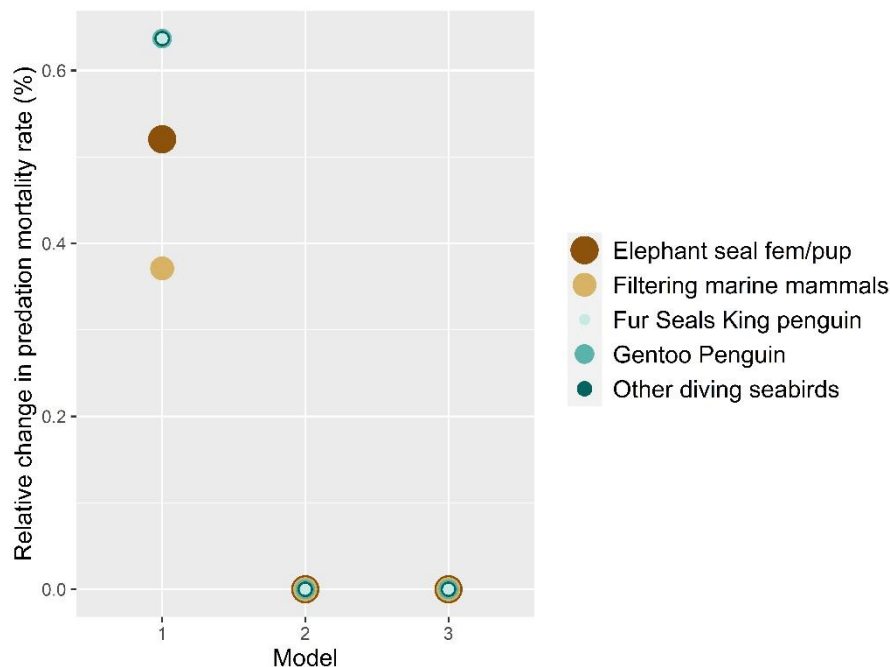


Figure 3.4: Relative change in killer whale predation mortality rates on non-commercial prey groups across alternative depredation models (relative to the *baseline* model with no depredation). Models are numbered from 1 to 3: 1 *food subsidy* model, 2 *increased fishing effort* model and 3 *competing fishery* model.

3.3. Results

3.3.1. 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 3.3a**). 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 less than 3% in all *food subsidy*, *increased fishing effort* and *competing fishery* models relative to the *baseline* model. The maximum relative decline was 2.3% for small adult toothfish (**Figure 3.3b**). 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 and king penguin, 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 3.4**). 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.

3.3.2. 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 3.5**). Natural predation by killer whales positively impacted all toothfish stages (**Figure 3.5**). The small toothfish stage was negatively impacted by fishing and depredation, but only marginally positively affected by killer whales natural predation (**Figure 3.5**). In the *competing fishery* model, killer whales depredation positively impacted small toothfish life stages but negatively the two larger all toothfish life stages (**Figure 3.5**).

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 3.6**). 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.

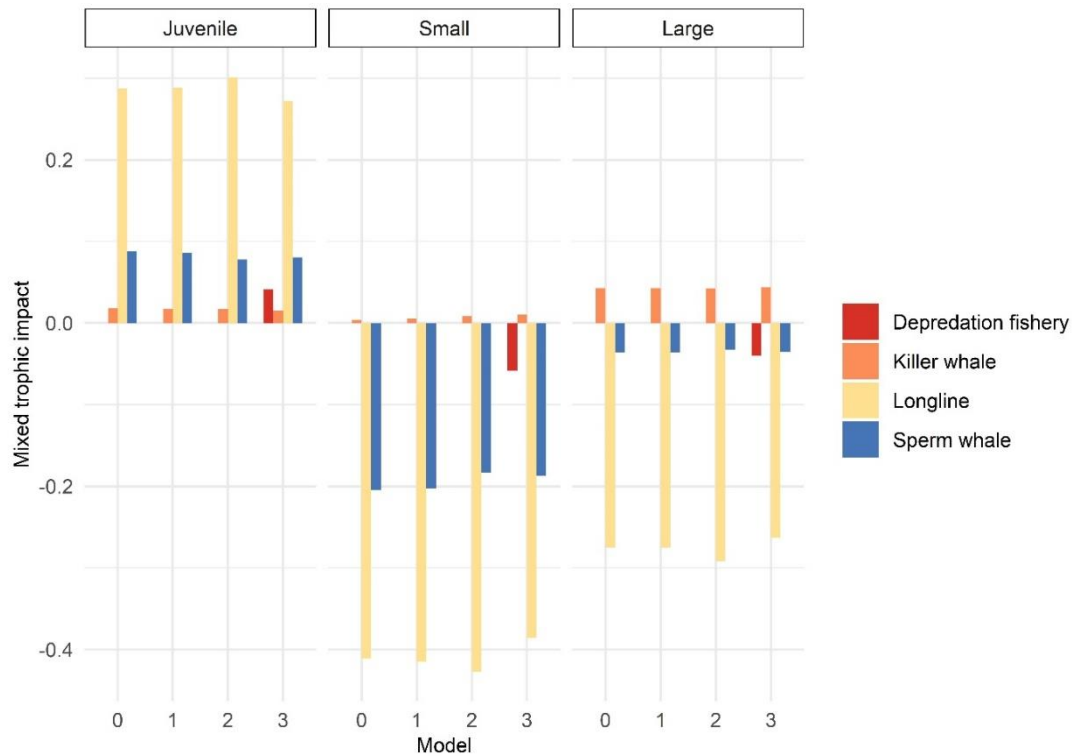


Figure 3.5: Impact indicator of longline fishery and depredated marine mammals on the three different toothfish life stages in the four Ecopath models, without depredation (0 for *baseline* model) and with depredation (1 *food subsidy* model, 2 *increased fishing effort* model and 3 *competing fishery* 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.

Impacts of the commercial fishery were negative on all depredated groups, with a stronger impact on sperm whales than killer whales (i.e. respectively -0.04 and -0.022; Figure 3.7). Note however that the "depredated toothfish" component was estimated to be beneficial to both sperm (+ ~0.004) and killer (+ ~0.02) whales (Figure 3.7).

As a side result, we also observed marginal decreases in trophic levels of the depredated 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 (Figure S3.2).

3.3.3. Ecosystem effects of depredated species

Overall, impacts of killer whales (i.e. "killer whale" in the *food subsidy* model and *increased fishing effort* model, and both depredated and naturally-predating components in the *competing fishery* model), were negative on most of their prey groups including diving seabirds fur seals and elephant seals (females and pups) across all models (Figure 3.8). Most prey groups, including marine mammals

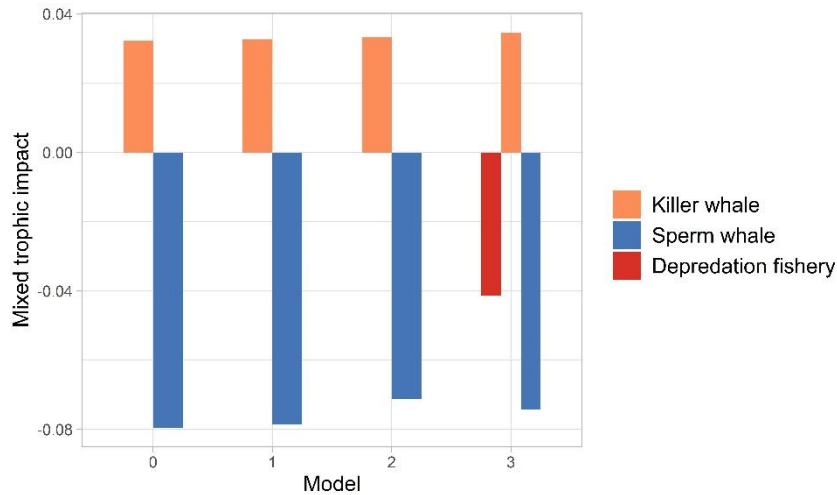


Figure 3.6: Impact indicator of depredating marine mammal species on the Crozet longline fishery. The "depredation fishery" group corresponds to toothfish removed by sperm whale and killer whale. Models are numbered from 0 to 3: 0 *baseline* model with no depredation, 1 *food subsidy* model, 2 *increased 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.

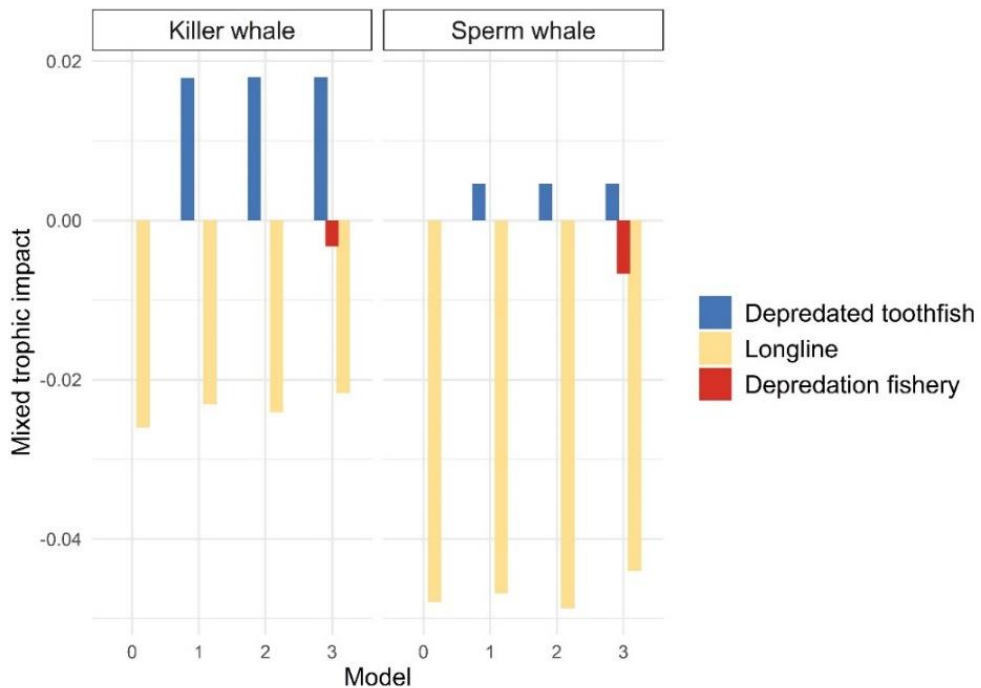


Figure 3.7: Mixed Trophic Impacts of the Crozet longline fishery on the subgroups of depredating killer whales (left) and sperm whales (right). Models are numbered from 0 to 3: 0 *baseline* model with no depredation, 1 *food subsidy* model, 2 *increased fishing effort* model and 3 *competing fishery* model. "Depredation fishery" represents depredation by both sperm and killer whales in *competing fishery* model (but excludes the naturally-predating components of these groups).

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 3.8**).

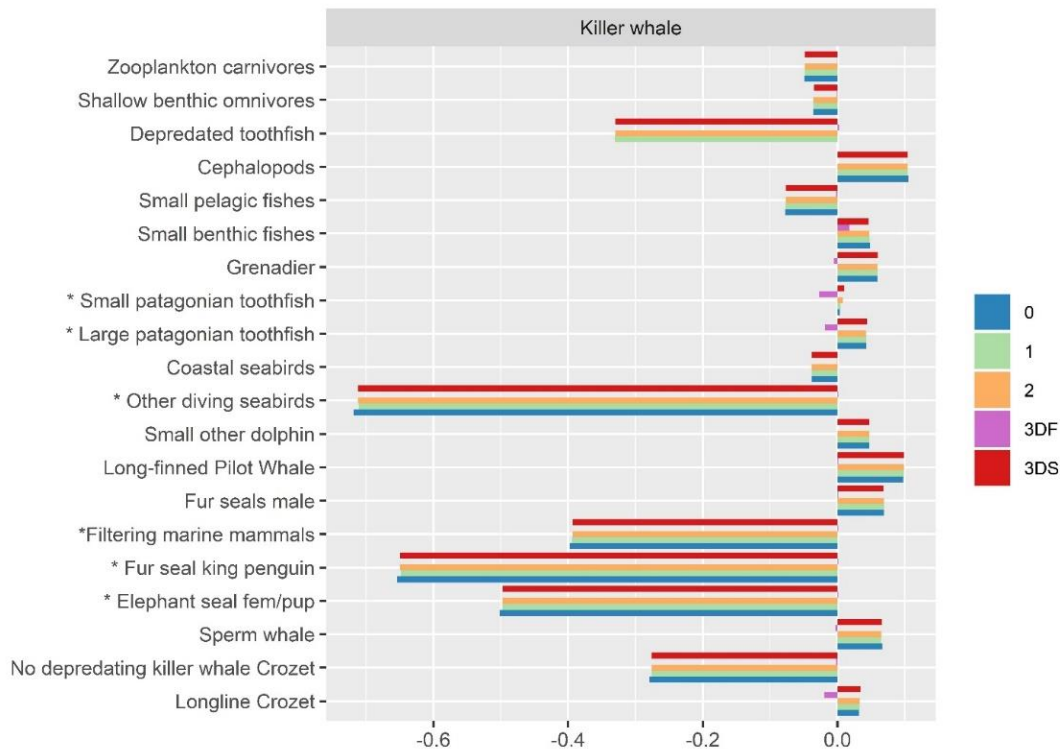


Figure 3.8: Killer whale mixed trophic impact on all functional groups in the Crozet ecosystem. Only large effects (absolute value > 0.03) are shown. Estimates are provided for each model, which are numbered from 0 to 3: 0 *baseline* model with n depredation, 1 *food subsidy* model, 2 *increased fishing 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 killer whales diet.

Larger impacts of sperm whales (absolute estimate of mixed trophic impact > 0.03 ; **Figure 3.9**) 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 accidentally caught as bycatch such as blue antimora and whiteleg skate (**Figure 3.9**). Sperm whale impacts varied slightly 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 summarised in **Table 3.1**.

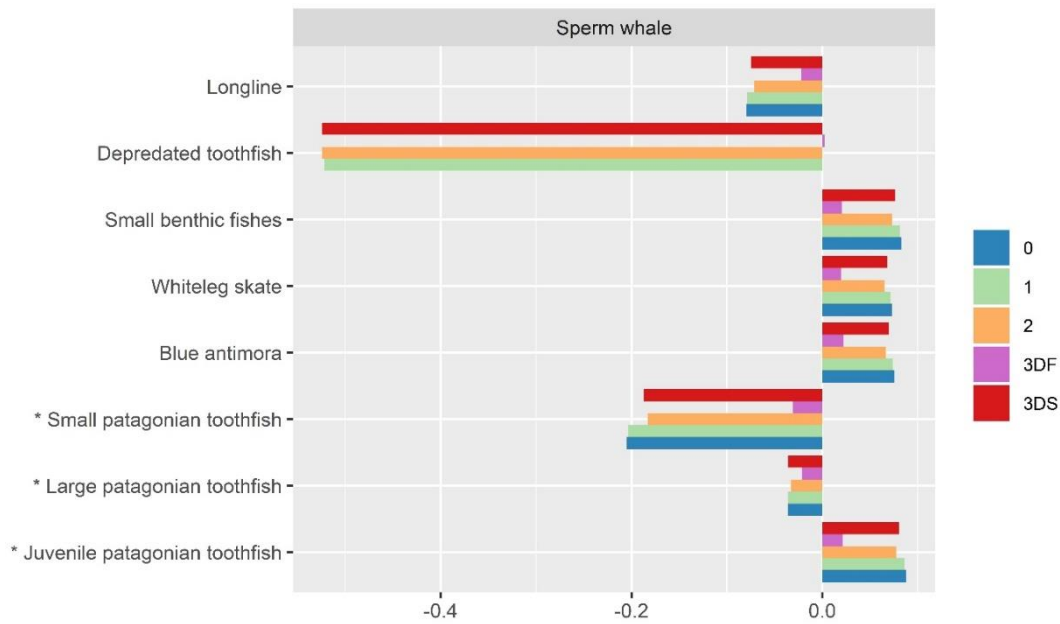


Figure 3.9: Sperm whale mixed trophic impacts on all functional groups in Crozet ecosystem. Only large effects (absolute value > 0.03) are shown. Estimates are provided for each model, which are numbered from 0 to: 0 *baseline* model with no depredation, 1 *food subsidy* model, 2 *increased fishing effort* 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.

Table 3.1: Summary of results across the alternative Ecopath models applied to the longline fisheries around Crozet island. Blank fields means that 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			
		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		×		
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			√	√

3.4. 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 & 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.

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

By incorporating depredation as 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 (Peterson & Hanselman, 2017; Werner et al., 2015), 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 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 (7 vessels) targets a commercially valuable stock that was unexploited until the 1970s (Duhamel & 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 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 around 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 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.

3.4.2. 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, consequently, by (2) 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., (2015a). 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., 2019b). 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 removal of catches from fishing gears, 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 represent 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 also 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 (Marzloff et al., 2011; Pinnegar et al., 2005).

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.

3.4.3. 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 modelling approach. 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 (Esteban et al., 2016; Guinet et al., 2015; Tixier et al., 2015a). 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 gears and vessels are limited. Unlike depredating species in the Crozet/Kerguelen fishery and to a greater extent for in the Southern Ocean (where high level of regulations reduce potential fisheries negative impacts on marine predators), depredating species can be exposed to the accidental risk of getting caught in fishing gear and/or intentional shooting from fishers (Azevedo et al., 2017; Dans et al., 2003). Depredating species

bycatch such as marine mammals often reported in many static net and trawl fisheries (Read, 2008). These bycatches 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. Firstly, 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. Secondly, 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 concerning the ecosystem effects of a depredation-impacted subantarctic fishery. The results also highlight the limitations of Ecopath model 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 long-term coexistence of fisheries and marine predators, and to contribute to ecosystem-based management of marine ecosystem.

Supplementary material

Supplementary material is available in the following section. Supplementary materials contain a more exhaustive description of model construction, as well as an assessment of data availability. It also presents additional figures on depredating species trophic level.

Acknowledgements

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Supplementary material: Comparison of approaches for incorporating depredation on fisheries catches into Ecopath

Appendix 3.1: Ecopath model

3.1.1. Functional groups

The functional group structure of the Ecopath model was based on the model by Pruvost et al. (2005) for Kerguelen Island (575,000 km²) for the period 1987-1988 using data from oceanographic surveys (Pruvost et al., 2005). When no data were available, results of similar Ecopath models were used (Erfan & Pitcher, 2005; Palomares et al., 2005). The model by Pruvost et al (2005) included 23 groups (2 primary production groups, 3 zooplankton groups, 3 benthic epifauna groups, 2 cephalopod groups, 7 fish groups, 2 bird groups and 3 marine mammal groups). For this study model structure was revised to better resolve functional groups and to include Crozet Island (**Figure S3.1**). The final model included 59 groups (3 primary production groups, 6 zooplankton groups, 6 benthic epifauna groups, 1 cephalopod group, 22 fish groups, 6 bird groups, 11 marine mammal groups and 3 detritus groups; **Table S3.1**). The model covers 3,075,704 km²; Crozet Island 574,558 km² and Kerguelen Island 567,732 km² respectively (**Figure S3.1**).

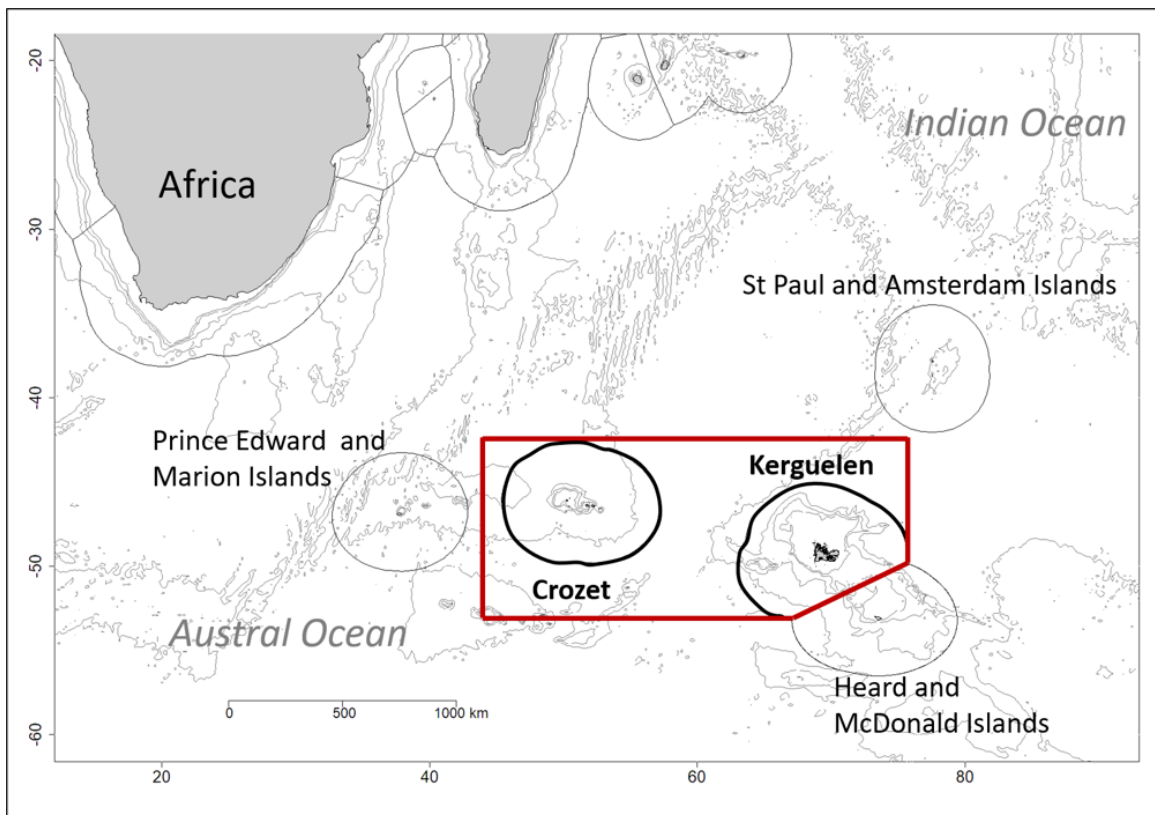


Figure S3.1: Model area (red square) including Crozet and Kerguelen Islands EEZ (thick black lines).

Table S3.1: Functional group definition. Groups highlighted in grey were assumed to cover the entire surface of the model (i.e. including Crozet and Kerguelen black lines in **Figure S3.1**).

Functional group (Pruvost et al., 2005)	Functional group (this study)
Phytoplankton	
Benthic algae	
Zooplankton herbivores	
Zooplankton omnivores	
Zooplankton carnivores / Euphasiacea	
Benthic shallow herbivores	
Benthic shallow omnivores	
Deep benthic omnivores	
Small cephalopods	Cephalopods
Large cephalopods	
Other benthic species	Small benthic fishes
Large benthic fishes	Large benthic fishes
	Blue antimora
	Macrourus sp.
Small pelagic fishes	Small pelagic fishes
	Myctophidae
Large pelagic fishes	
Adult toothfish	Small adult toothfish
	Large adult toothfish
Juvenile toothfish	
Shark	Bathyraja sp.
	Whiteleg skate
	Shark
Diving seabirds	King penguin + Fur seal female and pup
	Coastal seabirds
	Other diving seabirds
	Gentoo penguin
Surface seabirds	Albatrosses
	Large petrel
	Small petrel
Filtering marine mammals	
Hunting mammals	Elephant seal female and pup
	Elephant seal adult male
	Fur seal male
	Commerson's dolphin
	Southern long-finned pilot whale
	Small other dolphin
Top predators	Killer whale Crozet morphotype
	Sperm whale

3.1.2. Data and parameter values

A large amount of data was collected from published scientific literature related to species diets and population estimates (**Table S3.2**). Distribution depths for pelagic species as well as distance to the coast for birds were also collected to determine their distribution within the study area (Kerguelen/Crozet). Their distribution within the area is then entered into the model as a percentage by

dividing their distribution area by the surface covered by the model (3,075,704 km²). For instance, habitat area of species attached to Crozet plateau correspond to 0,187 (i.e. 574,558 / 3,075,704; **Table S3.3**). Since the biomass is given in t/km² in the model, this information allows us to calculate the biomass in tonnes, by multiplying area covered by the model, species habitat area and their biomass, all three components being necessary for the model. **Table S3.2** lists data sources and assumptions.

3.1.3. Diet composition for depredating species

Depredation behaviour seems not to have resulted in a diet shift of Crozet killer whales (Tixier et al., 2019). Therefore, the depredated toothfish was subtracted from the total part of Patagonian toothfish in the diet of killer whales. The amount of depredated toothfish was taken from [Tixier et al. \(2019a\)](#). Based on population abundance estimates (i.e. 96 for killer whales and 114 for sperm whales in Crozet), the total estimated biomass of depredated fish (i.e. ~279 t per year [Tixier et al. \(2020\)](#)) was proportionally distributed between the two depredating species thanks the depredation rate of each depredating species (i.e. 30% total depredation rate in Crozet, including 16% from sperm whale and 14% from killer whale; Roche et al., 2007). Assuming the daily food requirements per depredating individual (i.e. 90 kg.day⁻¹ for killer whales, C. Guinet, comm. Pers; 1,200 kg.day⁻¹ for sperm whales, [\(Drouot et al., 2004; Evans & Hindell, 2004; Faure, 2019\)](#) and population informations above, we calculated the percentage of depredated fish in their diet. Since information on the separate depredation rate for each depredating species is rare, we assumed that the involvement of each functional group in depredation was constant over time, and we applied information from a study covering the period 2003-2005 ([Roche et al., 2007](#)) to our period.

Table S3.2: Data sources: ■ estimated for this study, ■ literature, ■ no data, ■ MNHN, ■ Copernicus, ■ IPEV, ■ CEBC, ■ no data needed. Data quality (0: poor, 1: approximate, 2: good). × data not available for this study, ~ data available

Functional group	Habitat area (1)		Biomass (2)		P/B (3)		Q/B (4)		Diet (5)		Quality	References
	K	C	K	C	K	C	K	C	K	C		
Kerguelen (K)/Crozet (C)	K	C	K	C	K	C	K	C	K	C		
Organic matter											0	Pruvost et al., 2005
Carrion carcasses											0	
Depredated toothfish biomass											2	
Phytoplankton											2	Pruvost et al., 2005
Benthic algae			×		×						0	Pruvost et al., 2005
Zooplankton herbivores											0	Pruvost et al., 2005 ; Hunt et al., 2008
Zooplankton omnivores											0	Pruvost et al., 2005 ; Atkinson & Snýder, 1997 ; Cherel et al., 2008 ; Hunt et al., 2008
Zooplankton carnivores											0	Pruvost et al., 2005 ; Cherel et al., 2008 ; Hunt et al., 2008
Benthic shallow herbivores			×		×		×				0	Pruvost et al., 2005
Benthic shallow omnivores			×		×		×				0	Pruvost et al., 2005 ; Ferrari & Dearborn, 1989
Deep benthic omnivore			×		×		×				0	Pruvost et al., 2005 ; Boschen et al., 2013 ; Ferrari & Dearborn, 1989
Cephalopods											0	Pruvost et al., 2005 ; Cherel et al., 2008 ; Cherel & Duhamel, 2004 ; Rodhouse, 2013
Small benthic fishes											1	Pakhomov et al., 1996 ; Erfan & Pitcher, 2005 ; Duhamel et al., 2005
Large benthic fishes											1	Erfan & Pitcher, 2005 ; Duhamel et al., 2005 ; Hunt et al., 2008
Blue antimora											1	Duhamel et al., 2005
Macrourus sp.											1	Laptikhovsky, 2005 ; Pakhomov et al., 1996
Small pelagic fishes											1	Duhamel et al., 2005 ; Duhamel et al., 2019 ; Hunt et al., 2008
Myctophidae			×								0	Duhamel et al., 2005 ; Arkhipkin et al., 2003 ; Cherel et al., 2008 ; Pakhomov et al., 1996
Large pelagic fishes											1	Erfan & Pitcher, 2005
Juvenile toothfish											1	Cheung & Pitcher, 2005 ; Duhamel et al., 2005 ; Arkhipkin et al., 2003 ; Cherel et al., 2008 ; Pakhomov et al., 1996
Small adult toothfish											2	Cheung & Pitcher, 2005 ; Duhamel et al., 2005 ; Arkhipkin et al., 2003 ; Cherel et al., 2008 ; Pakhomov et al., 1996
Large adult toothfish											2	Cheung & Pitcher, 2005 ; Duhamel et al., 2005 ; Arkhipkin et al., 2003 ; Cherel et al., 2008 ; Pakhomov et al., 1996

Supplementary material: Comparison of approaches for incorporating depredation on fisheries catches into Ecopath

Bathyraja sp.																					2	Duhamel et al., 2005	
Whiteleg skate																						1	Duhamel et al., 2005
Shark																						1	Pruvost et al., 2005 ; Cherel & Duhamel, 2004
King penguin + fur seal female and pup																						2	Ridoux et al., 1988 ; Ridoux, 1994 ; Cherel & Ridoux, 1992; Cherel et al., 1997 ; Cherel et al., 2008; Guinet et al., 1996, 2001; Loots et al., 2007
Coastal seabirds																						1	Ridoux 1994 ; Fonteneau & Cook, 2013; Guinet et al., 1996
Others diving seabirds																						1	Ridoux et al., 1988 ; Cherel et al., 2008 Bost et al., 1994; Cherel et al., 2008; Lescroël et al., 2004
Gentoo penguin																						1	Ridoux, 1994 ; Ridoux et al., 1988 ; Cherel et al., 2008 ; Bost et al., 1994; Cherel et al., 2008; Lescroël et al., 2004
Albatrosses																						1	Rodhouse, 2013
Small petrel																						1	Ridoux, 1994 ; Bocher, 2002; Bocher et al., 2000; Cherel et al., 2002a, 2002b; Connan et al., 2007; Rodhouse, 2013;
Large petrel																						1	Ridoux, 1994 ; Bocher, 2002; Bocher et al., 2000; Cherel et al., 2002a, 2002b; Connan et al., 2007; Rodhouse, 2013;
Filtering marine mammal																						0	Jefferson et al., 1991
Elephant seal female and pup																						2	Cherel et al., 2008; Guinet et al., 1996
Elephant seal male																						2	Cherel et al., 2008; Guinet et al., 1996
Fur seal male																						2	Cherel et al., 1997 Cherel et al., 2008; Guinet et al., 1996, 2001; Loots et al., 2007
Commerson's dolphin																						0	Pauly, 1998
Southern long-finned pilot whale																						0	Beasley et al., 2019; Mansilla et al., 2012
Small others dolphin																						0	Pauly, 1998
Killer whale Crozet morphotype																						2	Amelot, 2019 ; Tixier et al., 2019, 2020
Sperm whale																						1	Yuhkov et al., 1972, Clarke et al., 1980 ; Cherel & Duhamel, 2004; Labadie et al., 2018

Table S3.3: Habitat area, production (P/B) and consumption (Q/B) values used in study.
K: Kerguelen Island; C Crozet island (see **Figure S.3.1**).

Functional group	Habitat area	P/B	Q/B
Organic matter	1.0		
Carrion carcasses	1.0		
Depredated toothfish biomass (K)	0.183		
Depredated toothfish biomass (C)	0.187		
Phytoplankton	1.0	150	
Benthic algae (K)	0.0826	4.0	
Benthic algae (C)	0.0635	4.0	
Zooplankton herbivores (K & C)	0.5	11.3	24
Zooplankton omnivores (K & C)	0.5	10.8	43
Zooplankton carnivores (K & C)	0.5	0.950	3.8
Benthic shallow herbivores (K)	0.826	2.0	10.0
Benthic shallow herbivores (C)	0.0635	2.0	10.0
Benthic shallow omnivores (K)	0.0826	2.1	10.0
Benthic shallow omnivores (C)	0.0635	2.1	10.0
Deep benthic omnivores (K)	0.171	3.0	10.0
Deep benthic omnivores (C)	0.0232	3.0	10.0
Cephalopods	0.0232	0.9	3.0
Small benthic fishes (K)	0.776	0.65	6.5
Small benthic fishes (C)	0.171	0.65	6.5
Large benthic fishes (K)	0.084	0.552	2.3
Large benthic fishes (C)	0.0324	0.552	2.3
Blue antimora (K)	0.171	0.325	1.082
Blue antimora (C)	0.186	0.953	3.175
<i>Macrourus</i> sp. (K)	0.170	0.880	2.933
<i>Macrourus</i> sp. (C)	0.0239	1.967	6.556
Small pelagic fishes (K)	0.173	0.569	3.048
Small pelagic fishes (C)	0.179	0.569	3.048
Myctophidae (K)	0.136	1.086	6.389
Myctophidae (C)	0.0834	1.086	6.389
Large pelagic fishes	0.94	02.62	1.0
Juvenile toothfish (K)	0.0259	0.358	
Small adult toothfish (K)	0.183	0.256	1.1
Large adult toothfish (K)	0.183	0.187	
Juvenile toothfish (C)	0.0184	0.361	
Small adult toothfish (C)	0.187	0.254	1.1
Large adult toothfish (C)	0.187	0.188	
<i>Bathyraja</i> sp.	0.177	0.127	0.825
Whiteleg skate	0.186	1.390	8.176
Sharks	0.940	0.170	0.851
King penguin + fur seal female and pup	0.812	0.180	39.85
Coastal seabirds	0.00193	0.156	58.1
Others diving seabirds	0.629	0.180	55.02
Albatrosses	1.0	0.425	53.15
Small petrel	1.0	0.192	87.19
Large petrel	1.0	0.591	73.90
Filtering marine mammal	0.965	0.540	4.612
Elephant seal female and pup	0.261	0.2	12.44
Elephant seal male	1.0	0.2	7.982
Fur seal male	1.0	0.240	16.66
Commerson's dolphin	0.042	0.130	16.38
Southern long-finned pilot whale	1.0	0.190	7.982
Small others dolphin	1.0	0.1240	14.84

Killer whale Crozet morphotype	0.704	0.180	7.581
Sperm whales (K)	0.184	0.33	4.745
Sperm whales (C)	0.187	0.33	4.745

Appendix 3.2: Relative change in trophic level

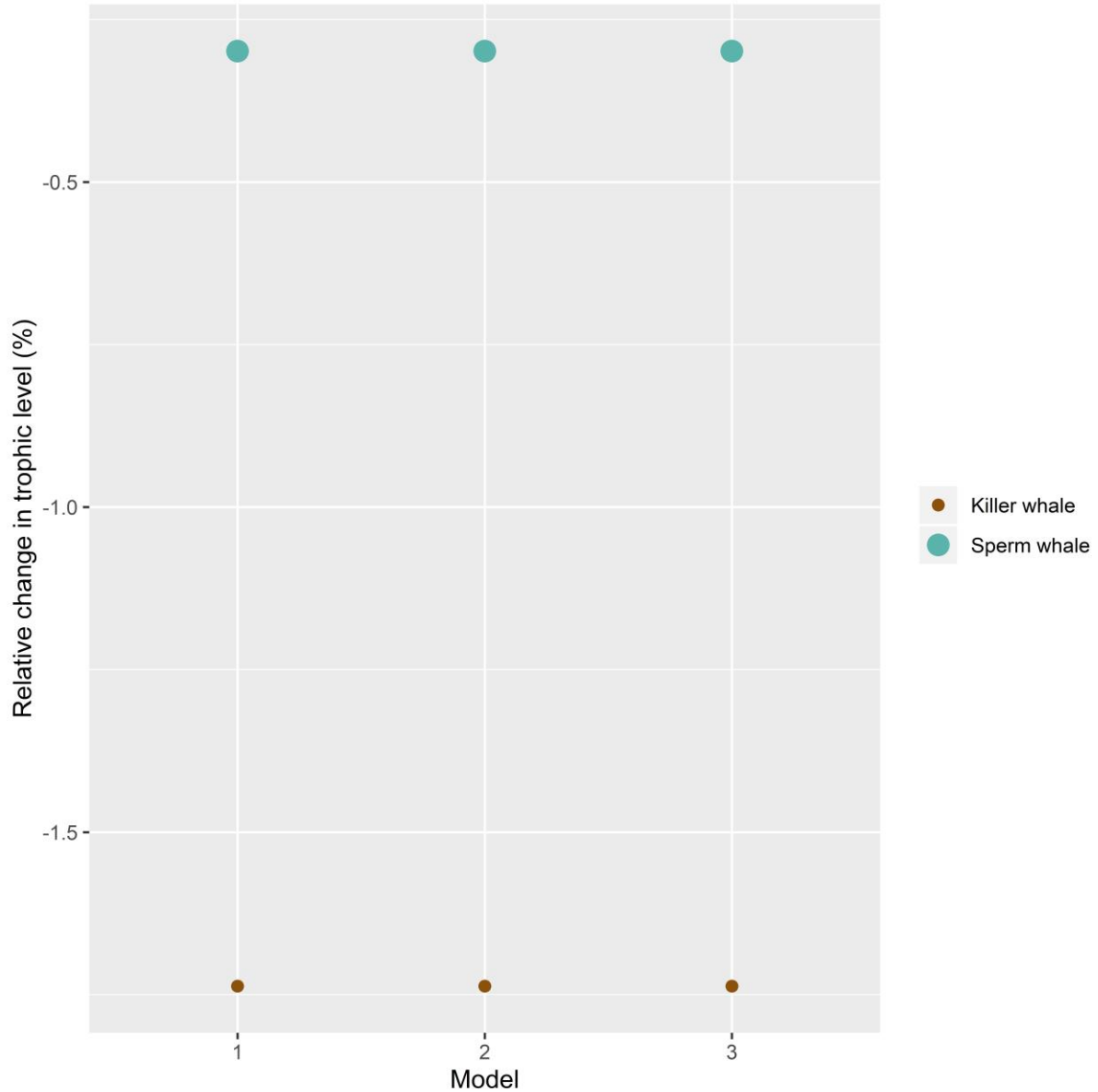


Figure S3.2: Relative change in trophic level of killer whales and sperm whales around Crozet Island as estimated by alternative Ecopath models including depredation compared to the *baseline* model ignoring depredation.

Chapter 4: Exploitation and depredation rates determine viability of depredation-impacted fisheries

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Abstract

While depredation can broadly affect several components of marine socio-ecological systems, it has been little studied via modelling approaches. Here we used qualitative modelling of system feedback (Puccia and Levins' loop analysis) and a system of ordinary differential equations that capture a simplified representation of the effects of depredation on fisheries catches, to develop a holistic understanding of long-term dynamics. We then assess response of the depredation-impacted fishery to three sustained perturbation (permanent change) scenarios: i) increased fishing effort, ii) increased abundance of the depredating species or iii) increased exploited stock size. The results indicated that the persistence of depredation-impacted fisheries depends on (1) fishers' success in retrieving fish onboard being relatively greater than the ability of depredating species to remove the catch from the gear and (2) sustainable management of the exploited and depredated stock. Moreover, the results highlighted that the expected response of depredation-impacted systems falls into broad categories, which partially depend on (1) the population dynamics of the target stock and its exploitation status, and (2) the ecology of the depredating species and the magnitude of its competition with fishers. In all categories, an increase in the abundance of the depredating species leads to a decrease in fishery yield, which is likely to lead to an intensification of fishing effort to compensate for losses. However, this is only sustainable for well-managed stocks, harvested by a fishery that is sufficiently profitable to support extra costs induced by an increase in fishing effort. Qualitative modelling further showed that a number of processes that are critical for the co-existence of fishers, exploited stock and depredating species, are rarely quantified. We therefore propose a suite of recommendations for future work to better capture depredation in marine ecosystem and fisheries models.

4.1. Introduction

Species feeding on plants or animals that are cultivated or raised, or have been caught by humans is a behaviour known as “depredation”, which can lead to severe human-wildlife conflicts (Gilman et al., 2007; Mitchell et al., 2018). Depredation is a worldwide concern that includes crop raiding by terrestrial herbivores (Barnes & Douglas-Hamilton, 1982), attacks on livestock by terrestrial predators (Dickman & Hazzah, 2016), and marine predators removing fish from fishing gear or aquaculture farms (Mitchell et al., 2018; Read, 2008). In the marine realm, depredation has been reported globally in coastal and offshore fisheries from all sectors (industrial, artisanal, and recreational) and a range of fishing techniques including traps, nets, and hooks-and-lines (Gilman et al., 2007; Mitchell et al., 2018; Northridge, 1984). Depredation has been reported on both catches and baits. However, this study only focuses on catch depredation as this corresponds to most documented marine cases.

Depredation on fisheries catches, primarily by sharks and marine mammals, can substantially impact regional socio-ecosystems and compromise the profitability or the viability of commercial and subsistence fisheries (Read, 2008; Tixier et al., 2021a). Indeed, a decrease in catch rates due to depredation directly induces a decrease in profitability for fishers (Lauriano et al., 2009; Purves et al., 2004; Roche et al., 2007). Furthermore, when the ratio between depredated and landed catch becomes large enough, depredation can jeopardize the socio-economic viability of the fishing activity (Tixier et al., 2018; Matkin et al., 1986). Reported depredation rates vary from 1% to 67% of landings across case studies (Hernandez-Milian et al., 2008; Köningson, 2011), but can, at the scale of individual fishing events, reach up to 100% of catches. This is observed, for instance, when killer whales (*Orcinus orca*) depredate on catches of longline fisheries on the North Pacific Ocean (Peterson et al., 2013), leading a large number of vessels to change their fishing gear to pots (Hanselman et al., 2011). Change in gear is one of the main mitigation methods that can be classified as follows: lethal action, deterrence, behavioural avoidance measures, physical device, adjustment in gear use, and change in gear or target species (Tixier et al., 2021a). Most of the time, fishers compensate for catch losses by increasing fishing effort, which results in increased stock mortality. If exploited fish stocks are subject to many cryptic sources of fishing mortality, including depredation, stock assessments become inaccurate and can bias fishery management (Gasco et al., 2015)

For the depredating species, depredation is a way to get facilitated access to natural food resources if the species feeds also naturally on the resource it depredates (Tixier et al., 2019) or to a new food resource if the depredated resource is not part of the predator’s natural diet (Lundström et al., 2010). Compared to natural predation, depredation requires reduced effort to catch prey, resulting in higher energy gain per unit effort spent. Facilitated access to food resources can, therefore, potentially enhance the physiological performance and population growth rate of the depredating species. For instance, killer whales depredating on toothfish catches at Crozet island, or those depredating on tuna catches in the Strait of Gibraltar, have shown population-level benefits associated

with an increase in reproductive performance of individuals (Esteban et al., 2016; Guinet et al., 2015; Tixier, et al., 2015a). However, mortality rates of depredating species may also increase due to a higher risk of getting accidentally caught in fishing gear and/or intentional shooting from fishers (Azevedo et al., 2017; Dans et al., 2003).

While depredation can broadly affect several components of marine socio-ecological systems, it has been little studied via modelling approaches. Yet modelling can be helpful to assess and predict the resilience and sustainability of depredation-impacted socio-ecosystems, and thus inform effective ecosystem-based management actions (Dambacher et al., 2015; Marzloff et al., 2016). Among the studies that have addressed depredation through modelling, only a few have examined its overall effects across exploited stocks, fisheries and depredating species (see Clavareau et al., 2020; Szymkowiak & Rhodes-Reese, 2020). For instance, existing studies oppose species conservation (Reijnders, 1981) to fisheries socio-economic viability (Holma et al., 2014), which tends to emphasise the Human-Wildlife conflict but often fails at characterising possible trade-offs and providing integrated scientific decision-support.

In this chapter, we use two complementary approaches to explicitly capture major interactions between a fishery, an exploited stock and a depredating species and, to generically represent the effects of depredation on fisheries catches. Using both qualitative modelling of system feedback (a.k.a. Puccia and Levins' (1985) loop analysis) and a system of ordinary differential equations, we investigate how interactions between marine depredation and fishery harvesting determine overall system dynamics. In particular, we model biomass flow through catches (i.e. fish caught in fishing gear) and landings to track how fishing success depends both on gear catchability and on fishers' ability to retrieve caught individuals on board with minimal loss to depredation. We then assess response of the depredation-impacted fishery to three sustained perturbation (permanent change) scenarios: i) increase in fishing effort, ii) increase in abundance of the depredating species and iii) increase in stock size.

4.2. Material and methods

First, we introduce qualitative modelling of system feedback (Puccia & Levins, 1985; Dambacher et al., 2003) using a generic three-variable (V1, V2, V3) ecosystem model based on Marzloff et al. (2011). Then, we detail the application of a system of ordinary differential equations and a suite of qualitative models to capture depredation on fisheries catches.

4.2.1. Qualitative modelling of system feedback

4.2.1.1 Model representation

Qualitative modelling of system feedbacks (i.e. Puccia & Levins' (1985) loop analysis) provides a well-suited framework to study the dynamics of complex socio-ecosystems based only on a qualitative understanding of key processes between important system components (Dambacher et al., 2003).

Model structure can be represented as a sign directed graph, where variables are shown as nodes that can affect each other positively (as represented by an arrow \rightarrow), or negatively (as represented by a line terminated by a filled circle $-\bullet$) (Figure 4.1a). To account for density-dependent processes or regulating factors that are not explicitly captured, each model variable is self-regulated, as shown by negative self-effects on the graph (Figure 4.1a).

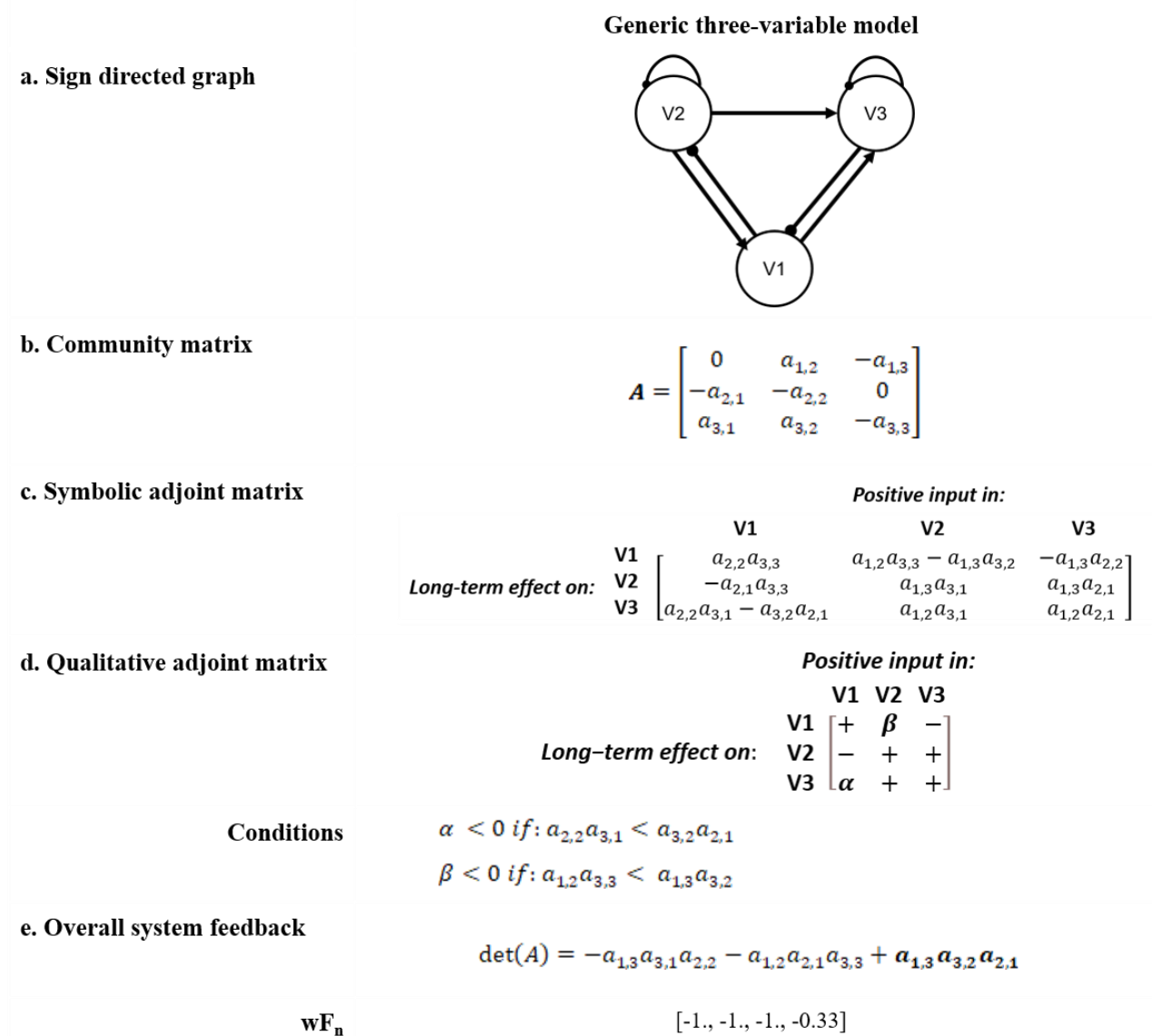


Figure 4.1: Generic three-variable model given as (a) sign-directed graph, (b) community matrix (A), (c) symbolic adjoint matrix (adj(-A)) (d) qualitative adjoint matrix (sign[adj(-A)]). The numbers given in the nodes of the graph define the positions of each variable in the matrices. In the qualitative adjoint matrix, ambiguous press perturbation sign predictions are resolved considering algebraic conditions. (e) Determinant of the community matrix, called overall system feedback (det(A)) is given symbolically with the positive feedback cycles highlighted in bold. wF_n weighted feedback.

Interacting variables can also be described by a set of ordinary differential equations. Predator-prey interactions are typically described using Lotka-Volterra equations, for which the linearized form at an equilibrium point is:

$$\frac{dN}{Ndt} = AN + k \text{ (Eq. 1)}$$

with N a vector, where element N_i represents the abundance of population i ; A the community matrix, where each element $a_{i,j}$ represents the direct effect of population j on population i ; and k is a vector that summarises density-independent processes (e.g. migration). Thus, the sign structure of the community matrix A is equivalent to the network topology captured in a sign directed graph. For instance, in **Figure 4.1**, a positive effect of V2 on V3 is represented in the sign directed graph as an arrow (**Figure 4.1a**) and in the community matrix A as the positive term $a_{3,2}$ (**Figure 4.1b**).

4.2.1.2. Qualitative predictions of responses to permanent change

The adjoint of the community matrix A , denoted $\text{adj}(A)$, can be used to predict qualitative system responses to sustained perturbations in system variables, so called press perturbations (Dambacher et al., 2005). Indeed, the sign of each element in $\text{adj}(A)$ returns the direction of change in the equilibrium abundance of variable i due to an increase (positive input) in the abundance of variable j ; for a decrease (negative input), opposite signs to those in the adjoint matrix are taken. For more details, see Dambacher et al. (2005) or Marzloff et al. (2011). In this study, adjoint matrices are given both in symbolic (**Figure 4.1c**) and qualitative (direction of change) form (**Figure 4.1d**), using the same formalism as Marzloff et al. (2011). When all direct and indirect effects from variable i on j have the same sign, within the symbolic adjoint matrix, then the response of j to a positive (negative) change in i is fully determined, independent of the strength of the links between variables. Fully-determined qualitative predictions are thus given as positive (+), negative (-) or unaffected (0) (Marzloff et al., 2011). For instance, in the symbolic adjoint matrix in **Figure 4.1c**, the second element in the first column is $-a_{2,1}a_{3,3}$ and thus has a negative sign in the qualitative adjoint matrix (**Figure 4.1d**), which means that a positive input in the abundance of V1 has a fully-determined negative effect on V2. However, when both negative and positive, direct and indirect effects contribute to a variable's response, sign prediction is ambiguous. For instance, the response of V3 to a positive input in V1 is ambiguous, as seen from the expression $a_{2,2}a_{3,1} - a_{3,2}a_{2,1}$ in the third element of the first column of the symbolic adjoint matrix in **Figure 4.1c**. Such ambiguous responses are summarised as a greek letter in the qualitative adjoint matrix (e.g. α in **Figure 4.1d**) as their sign depends on the relative strength of positive and negative terms. In certain cases, sign indeterminacy can be elucidated based on expert knowledge or assumptions (for instance about system stability) (Marzloff et al., 2011). However, ambiguous predictions involving a large number of terms are often challenging if not impossible to interpret (Dambacher et al., 2009). In this study, to interpret ambiguous predictions and

determine their signs, we replaced $a_{i,j}$ terms in the community matrix by their equivalent partial derivatives $\frac{\partial N_i}{N_i \partial N_j}$ from the system of equations (Eq. 1) that specifies the dynamics of interacting populations (e.g. exploited stocks, depredating species, fishers) in the context of depredation-impacted fisheries in the following section. Thus, the matrix of partial derivatives, called Jacobian matrix, evaluated at equilibrium corresponds to the community matrix.

4.2.1.3. Stability and potential for alternative states in qualitative predictions

Overall feedback loop analysis allows to define system stability (Dambacher et al., 2003). In response to a temporary perturbation, negative feedback is a process that brings a variable back towards its original value, while positive feedback results in a chain of events that keeps displacing a variable away from its original value in the same direction as the initial change (Levins, 1998; Marzloff et al., 2011). Therefore, system stability depends on negative feedbacks being stronger than positive feedbacks (Dambacher et al., 2003). In addition, we use weighted feedback (wF) as an indicator of overall system stability as detailed in Dambacher et al. (2003). The higher the value of wF, the greater the stability.

In **Figure 4.1d**, when assuming both α and β to be negative due to strong positive feedback cycles, regular patterns in predicted signs suggest the potential for alternative states in system dynamics as discussed in Marzloff et al. (2011). Indeed, the qualitative adjoint matrix suggests that any sustained perturbation will either facilitate the emergence of a state where abundance of V1 increases while these of V2 and V3 decrease; or the opposite state.

Symbolic analyses were performed from graphs drawn with the PowerPlay software, which were then converted into matrix inputs to run the Maple script provided as supplementary information in Dambacher et al. (2002).

4.2.2. Application to depredation-impacted fisheries

In the following section, we present a generic depredation model, both as a system of ordinary differential equations and a qualitative model capturing the dynamics of three variables: exploited stock (S), depredating species (D) and exploiting fishery, which is here quantified as the amount of fishing effort deployed over a given time (E). To explicitly capture how stock exploitation contributes to both landed catches and to food subsidies to the depredating species, we also detail biomass flows via two catch-related variables. Catches (C) quantify the rate (i.e. a biomass per unit of time) at which fish are retained in fishing gear, while landings or landed catches represent the rate at which catches (C) are successfully retrieved by fishers (L). Thus, the qualitative model and the system of equations describe the fate of caught resources that contribute either to depredating species population growth, or to landings. Finally, adjustment in fishing effort (E) to reach a defined target despite for instance loss in landing rate due to depredation, can describe fisheries dynamics over different time scales: during a

fishing trip, fishers will deploy extra effort (until reaching storage capacity or individual quota) to compensate for low catch rates; or over the course of an entire fishing season or year, a fishery will similarly adjust the overall amount of effort deployed to reach the target quota. In addition, the spatial scale of modelled processes relates to a region where an exploited stock is targeted both by a fishery and by a depredating species population. Moreover, a suite of extended alternative models were implemented to explicitly represent different cases, which could include predation and/or mitigation.

4.2.2.1. Generic depredation model

The generic depredation model considers the negative effect of fishing effort on the exploited stock ($E \rightarrow S$) and fishing gear success relative to stock availability ($S \rightarrow C$) and the fishing effort deployed ($E \rightarrow C$). Then catch rate (i.e. fish retained in fishing gear) positively contribute to landing rate if successfully retrieved by fishers ($C \rightarrow L$), and to the abundance of the depredating ($C \rightarrow D$) when removed by the depredating species ($D \rightarrow L$). Finally, fishing effort is regulated by the amount of landings ($L \rightarrow E$) relatively to the allowed quota. The sign directed graph of this model is shown in **Figure 4.2a** and the corresponding community matrix in **Figure 4.2b**.

The model system is composed of five ordinary differential equations corresponding to the dynamics of the exploited stock (S), of the depredating species (D), of the amount of fishing effort deployed (E), of catches (C) and of landings (L).

Dynamics of the exploited stock (S) are modelled using a logistic model:

$$\frac{dS}{dt} = \underbrace{S \times r_S \times \left(1 - \frac{S}{k_S}\right)}_{\text{Population dynamics}} - \underbrace{q \times S \times E}_{\text{Fishery removals}} \quad (\text{Eq. 2})$$

where r_S is the intrinsic stock growth rate (time^{-1}) and k_S the regional carrying capacity (mass) define logistic population growth; and fisheries removals are defined as the product of fishing gear catchability q (number of fishing gears $^{-1}$), the amount of effort deployed E (number of fishing gears. time^{-1}), and stock density S (mass).

Changes in catches rate (C), i.e. the amount of fish caught in fishing gear per unit of time (as opposed to landings that correspond to catches successfully retrieved by fishers), can be described as:

$$\frac{dC}{dt} = \underbrace{q \times S \times E}_{\text{Fishery removals}} \quad (\text{Eq. 3})$$

The dynamics of the depredating species (D), i.e. a marine predator that feeds on fisheries catches on the fishing gear are again modelled assuming logistic population growth and an additional term that captures the increase in physiological performance due to depredation (i.e. facilitated access to food resource):

$$\frac{dD}{dt} = \underbrace{D \times r_D \times \left(1 - \frac{D}{k_D}\right)}_{\text{Population dynamics}} + \underbrace{\varepsilon \times C \times h_c \times D}_{\text{Benefits from depredation}} \quad (\text{Eq. 4})$$

where r_D is the intrinsic predator growth rate (time^{-1}) and k_D its regional carrying capacity (mass) define logistic population growth. Benefits from catch depredation are calculated as the product of the rate of increase ε in population abundance (metabolic and reproductive efficiency) through consumed catch C ($\text{mass} \cdot \text{time}^{-1}$) multiplied by the per depredating species biomass unit removed catch proportion h_c (mass^{-1}), defined as $\alpha_c \times \tau_r$, where α_c corresponds to the seizure rate of catches by the depredating species ($\text{mass}^{-1} \cdot \text{time}^{-1}$) and τ_r corresponds to the required retrieval time (time); D is the depredating species population abundance (mass).

Landing rates (L), i.e. the amount of fish landed per unit of time, depends on catches rate (C) and the fraction of catches removed by the depredating species:

$$\frac{dL}{dt} = C \times \underbrace{\left(1 - \frac{\overbrace{h_c \times D}^{\text{Proportion of catch removed by } D}}{\text{Retrieval success}}\right)}_{\text{Retrieval success}} \quad (\text{Eq. 5})$$

where C corresponds to the rate at which fish get trapped in fishing gear ($\text{mass} \cdot \text{time}^{-1}$). The fraction of catch removed by depredation depends on h_c (mass^{-1}) and D (mass).

Lastly, the dynamics of deployed fishing effort (E), i.e. quantity of fishing gear per unit of time, are modelled assuming quota regulation (Q) as follows:

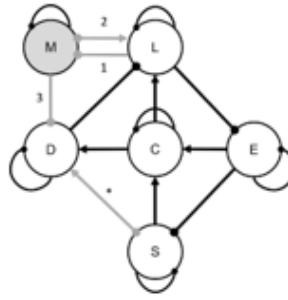
$$\frac{dE}{dt} = \alpha_r \times \left(1 - \frac{L}{Q}\right) \quad (\text{Eq. 6})$$

where α_r is the adjustment rate in fishing effort (number of fishing gears. time^{-1}) needed to achieve the quota; landings and quota have the same unit ($\text{mass} \cdot \text{time}^{-1}$).

4.2.2.2. Alternative models

To capture the diversity of depredation cases, as well as to include additional processes such as natural predation and mitigation measures, a suite of alternative models that extend the generic depredation model were developed. First, to capture natural predation of the depredating species on the stock, two links are added to represent the predator-prey interactions between stock S and depredating species D ($D \rightarrow S$, $S \rightarrow D$) (**Figure 4.2a**; **Figure S4.1**). Second, five alternative model structures aimed to capture various depredation mitigation measures. For this, existing depredation mitigation measures were synthesized in two model structures. The first model structure represented methods that aim at reducing encounter with depredating species, including lethal action and deterrence (**Figure S4.2**). Shooting (i.e. lethal action) or repelling depredating species through deterrence devices, can be represented as direct negative effects of mitigation on the depredating species ($M \rightarrow D$; **Figure S.4.2**). The second model structure describes methods that aim at reducing the capacity of the depredating species to remove catches from the fishing gear, including physical devices, behavioural avoidance

a. Sign directed graph



α_{ij} Definition

Generic model (5 variables)

- $\alpha_{C,E}$ Fishing gear success relative to effort deployed
- $\alpha_{C,S}$ Fishing gear success relative to stock availability
- $\alpha_{S,E}$ Stock fishing mortality relative to effort deployed
- $\alpha_{D,C}$ Increase in population of depredating species through depredation of catches
- $\alpha_{L,C}$ Fishery landing success relative to catches
- $\alpha_{L,D}$ **Modified interaction:** Catch depredation by depredating species
- $\alpha_{E,L}$ Quota limitation of fishing effort
- $\alpha_{D,S}$ Increase in population of depredating species through predation on stock
- $\alpha_{S,D}$ Predation mortality of stock by depredating species

Alternative models (6 variables)

- $\alpha_{D,M}$ **Modified interaction (3):** Encounter reduction with depredating species (1) or benefits from depredation reduction (2) due to mitigation measure
- $\alpha_{M,L}$ Mitigation regulation by landings
- $\alpha_{L,M}$ **Modified interaction:** Depredation success reduction due to landings increase by mitigation measure

b. Community matrix of generic model

$$A = \begin{bmatrix} -\alpha_{E,E} & 0 & 0 & 0 & -\alpha_{L,E} \\ \alpha_{C,E} & -\alpha_{C,C} & 0 & \alpha_{C,S} & 0 \\ 0 & \alpha_{D,C} & -\alpha_{D,D} & 0 & 0 \\ -\alpha_{S,E} & 0 & 0 & -\alpha_{S,S} & 0 \\ 0 & \alpha_{L,C} & -\alpha_{L,D} & 0 & -\alpha_{L,L} \end{bmatrix}$$

c. Jacobian matrix of generic model

$$J = \begin{bmatrix} -\alpha_{E,E} = -\frac{\alpha_r \times (L - Q)}{Q \times E^2} & 0 & 0 & 0 & -\alpha_{E,L} = -\frac{\alpha_r}{Q \times l} \\ \alpha_{C,E} = \frac{q \times S}{C} & -\alpha_{C,C} = -\frac{q \times S \times E}{C^2} & 0 & \alpha_{C,S} = \frac{q \times E}{C} & 0 \\ 0 & \alpha_{D,C} = \epsilon \times h_C & \alpha_{D,D} = -\frac{r_D}{k_D} & 0 & 0 \\ -\alpha_{S,E} = -q & 0 & 0 & -\alpha_{S,S} = -\frac{r_S}{k_S} & 0 \\ 0 & \alpha_{L,C} = \frac{1 - D \times h_C}{L} & -\alpha_{L,D} = -\frac{C \times h_C}{L} & 0 & -\alpha_{L,L} = -\frac{C \times (1 - L)}{L^2} \end{bmatrix}$$

Figure 4.2: Summary of six depredation models, including the generic (eqs. 2 to 6) and extended depredation models given as signed digraph with definitions of interactions (a). Variables included are E: amount of fishing effort, C: catches (i.e. fish retained in fishing gear), D: biomass of depredating species, S: biomass of stock, L landings (i.e. proportion of catches successfully removed by fishers) and M: amount of mitigation effort. The generic depredation model includes only interactions represented by black lines. The five alternative models include additional links represented by grey lines. Models that capture mitigation measures include variable M: models that represent encounter reduction measures include additional links numbered #1 and #3; while depredation success reduction models include additional links #1, #2 and #3. To capture natural predation by depredating species on the exploited stock, additional interactions $S \bullet \rightarrow D$ are included (associated with the * symbol), which can be combined with the generic depredation,

encounter reduction and depredation success reduction models, leading to 3 additional models. Modified interactions are represented as direct interactions as specified in **Appendix 4.3; Figure S4.1; Figure S4.2**. For the generic model the community matrix A (b), as well as the Jacobian matrix J (c) are provided.

measures, adjustment in the deployment of fishing gear and change in gear or target species (**Figure S4.2**). These measures reduce depredation success ($D \rightarrow L$) and thus the benefits from consumed catches ($C \rightarrow D$), which modifies the interaction between two other variables and thus corresponds to modified interactions (i.e. red dashed lines in **Figure S4.2**; Dambacher & Ramos-Jiliberto, 2007). Depredation success reduction results in mitigation measures directly affecting landings positively ($M \rightarrow L$), while decrease in benefits for the depredating species due to reduction in consumed catches results in mitigation measures directly affecting the depredating species negatively ($M \rightarrow D$; **Figure S4.2**). Note that in each case, mitigation is regulated by landing success ($L \rightarrow M$). Finally, mitigation measures can be studied with or without natural predation, by adding predator-prey links ($D \rightarrow S$, $S \rightarrow D$) to the appropriate model (**Figure 4.2**).

4.2.2.3. Press perturbation scenarios

We considered five press perturbations scenarios: i) increase in fishing effort ii) increase in catches; iii) increase in depredating species population size; iv) increase in exploited stock size and v) increase in landings. An increase in fishing effort (positive input in E) mimics scenarios related to catch loss compensation by fishers, which also leads to an increase in catches (i.e. fish retained in fishing gear; positive input in C). An increase in the abundance of the depredating species (positive input in D) could be caused by the enhancement in physiological performance due to facilitated access to food resource (Esteban et al., 2016; Tixier, et al., 2015a) or population recovery following cessation of hunting and/or management of accidental catches (Duhamel & Williams, 2011) An increase in exploited stock population size (positive input in S) is based on the rationale that while many target species have been overexploited by improved fishing technics (Köster et al., 2003; Pauly, 2008), reliable stock assessments support better fishing pressure regulation and hence stock recovery. Finally, an increase in landings (positive input in L) could be caused by improved retrieval success or reduced depredation.

4.3. Results

The main results are summarised below in two sections. The first section details predicted qualitative responses of model systems to press perturbation scenarios. The second section focuses on stability conditions for alternative models that include mitigation measures and natural predation.

4.3.1. Scenarios

Overall, the predicted qualitative responses display similar patterns across the six alternative depredation models considered (**Appendix 4.3; Figure S4.2**). Hence, this section only presents predicted responses for the generic depredation model (**Figure 4.3**). First, we describe results as a whole in the next two sub-sections and then focus on the responses to three common observed scenarios in depredation-impacted fisheries, such as i) an increase in fishing effort, iii) an increase in depredating species and iv) an increase in stock size.

4.3.1.1 Response of depredation-impacted fisheries to press perturbation scenarios

The adjoint matrix for the generic depredation model summarises all press perturbation scenario results (**Figure 4.3**). Each row of this adjoint matrix corresponds to the predicted response of a given variable to press perturbation of the variable noted in the column heading. For instance, the third column represents results for a positive input in the abundance of depredating species (D, scenario ii). The positive sign in the first row indicates a fully-determined positive effect of depredating species on effort (E). Conversely, the expected effect of depredating species on stock (S) is negative (3rd column, 4th row). However, the predicted responses for catches (C) and the depredating species itself (D) are ambiguous and hence denoted by a capital letter. The corresponding symbolic expressions, e.g. $A = a_{C,E}a_{S,S} - a_{C,S}a_{S,E}$, are also provided in **Figure 4.3**. The potential signs of these expressions can be determined considering the relative strength of the positive and negative terms involved.

Ambiguous predicted qualitative (sign) responses, which represented 48% of model predictions and occurred across all press perturbation scenarios and system variable responses (**Figure 4.3**), can partly be elucidated based on qualitative reasoning. Among the ambiguous predicted responses, two repeatedly occurred in the qualitative adjoint matrix of the generic depredation model (“A” and “C” in **Figure 4.3**). They made up 76% of predicted ambiguities and turned out to be interpretable. The “A” ambiguity corresponds to $a_{C,E}a_{S,S} - a_{C,S}a_{S,E}$ and thus involves fishing gear success relative to effort deployed (i.e. $a_{C,E}$) as well as to stock availability (i.e. $a_{C,S}$), stock self-regulation (i.e. $a_{S,S}$) and fishing mortality (i.e. $a_{S,E}$). Once replaced by the corresponding partial derivatives of the generic model (Eqs. 2 to 6), the “A” ambiguity is related to the relative strength of stock production rate (i.e. $S \times \frac{rS}{kS}$) versus exploitation rate (i.e. $q \times E$) (**Figure 4.3**). The “C” ambiguity corresponds to $a_{L,D}a_{D,C} - a_{L,C}a_{D,D}$ and thus implies catches depredation (i.e. $a_{L,D}$), increase in population growth of depredating species through artificial feeding (i.e. $a_{D,C}$), retrieval success (i.e. $a_{L,C}$) and depredating species self-regulation (i.e. $a_{D,D}$) (**Figure 4.3**). Once replaced by the corresponding partial derivatives, the “C” ambiguity is found to depend on $\varepsilon \times C \times h_C^2$ versus $(1 - D \times h_C) \times \left(\frac{rD}{kD}\right)$ which to some extent can be related respectively to the benefits from

Press perturbation scenarios

Qualitative adjoint matrix

Positive input in:

$$\begin{array}{c}
 \text{E} \\
 \text{C} \\
 \text{D} \\
 \text{S} \\
 \text{L}
 \end{array}
 \begin{array}{c}
 \text{E} \\
 \text{C} \\
 \text{D} \\
 \text{S} \\
 \text{L}
 \end{array}
 \begin{array}{c}
 + \\
 A \\
 A \\
 - \\
 B
 \end{array}
 \begin{array}{c}
 C \\
 + \\
 + \\
 -C \\
 -C
 \end{array}
 \begin{array}{c}
 D \\
 A \\
 D \\
 - \\
 -
 \end{array}
 \begin{array}{c}
 S \\
 C \\
 + \\
 E \\
 -C
 \end{array}
 \begin{array}{c}
 L \\
 - \\
 -A \\
 + \\
 +
 \end{array}$$

Long-term effect on:

Ambiguous terms

Interpretability

$$A = a_{C,E}a_{S,S} - a_{C,S}a_{S,E} = \frac{q}{C} \left(S \times \frac{r_S}{k_S} - q \times E \right)$$

Stock production rate ($S \times \frac{r_S}{k_S}$) vs Exploitation rate ($q \times E$)

$$B = (a_{L,C}a_{C,E}a_{D,D}a_{S,S} + a_{L,D}a_{D,C}a_{C,S}a_{S,E}) - (a_{L,D}a_{D,C}a_{C,E}a_{S,S} + a_{L,C}a_{C,S}a_{S,E}a_{D,D})$$

?

$$C = a_{L,D}a_{D,C} - a_{L,C}a_{D,D} = \frac{1}{L} \times \left(\varepsilon \times C \times h_C^2 - \left((1 - D \times h_C) \times \frac{r_D}{k_D} \right) \right)$$

Benefits from depredation success ($\varepsilon \times C \times h_C^2$) vs Depredating species population dynamics $(1 - D \times h_C) \times \frac{r_D}{k_D}$

$$D = a_{C,C}a_{S,S}a_{L,L} + a_{E,L}a_{L,C}(a_{C,E}a_{S,S} - a_{C,S}a_{S,E})$$

If A is positive, so related to a high stock production rate ($S \times \frac{r_S}{k_S}$) compared to their exploitation rate ($q \times E$), then D is positive too. If A is negative, D remains ambiguous.

$$E = a_{E,E}a_{C,C}a_{D,D}a_{L,L} + a_{C,E}a_{E,L}(a_{L,C}a_{D,D} - a_{L,D}a_{D,C})$$

If C is negative, so related to natural population dynamics $(1 - D \times h_C) \times \left(\frac{r_D}{k_D}\right)$ compared to the benefits from depredation success ($\varepsilon \times C \times h_C^2$)

Figure 4.3: Press perturbation scenario results for generic depredation model. Qualitative adjoint matrix with conditions needed to remove sign ambiguity. The steps to move from ambiguities contained in the symbolic adjoint matrix to the corresponding partial derivatives and finally to the algebraic condition in the qualitative adjoint matrix are given in **Appendix 4.2**.

depredation success and to the natural population dynamics of the depredating species associated to the retrieval success of fishers (**Figure 4.3**). Other prediction sign ambiguities involve a larger number of terms, such as B, related to the effect of increase in fishing effort on landings, and are difficult to resolve. The sign of the B condition will depend on the relative strength of feedback related to, on one hand the regulation of fishing effort through landings success and through depredation reduction due to stock depletion (i.e. $(a_{L,C}a_{C,E}a_{D,D}a_{S,S} + a_{L,D}a_{D,C}a_{C,S}a_{S,E})$), and on the other hand the increase in fishing effort through depredation and stock depletion (i.e. $-(a_{L,D}a_{D,C}a_{C,E}a_{S,S} + a_{L,C}a_{C,S}a_{S,E}a_{D,D})$); **Figure 4.3**).

4.3.1.2. Four theoretical categories of depredation-impacted fisheries

Four categories of depredation-impacted fisheries systems can be defined based on overall responses to press perturbation scenarios (**Figure 4.4**). These four categories are determined by two sets of conditions, each with two possible modalities. A first condition depends on the exploited stock production rate (i.e. $S \times \frac{r_S}{k_S}$) relative to its exploitation rate (i.e. $q \times E$); and the second condition somehow relates to the population benefits that the depredating species obtains from depredation success (i.e. $\varepsilon \times C \times h_C^2$) relative to intrinsic population growth rate associated to the retrieval success of fishers $(1 - D \times h_C) \times \left(\frac{r_D}{k_D}\right)$.

We now interpret processes contributing to prediction sign ambiguity becoming resolved. In the case of high stock production rate relative to its exploitation rate (i.e. $S \times \frac{r_S}{k_S} > q \times E$), the sign of “A” is positive as well as that of “D”, which includes term “A” and an additional positive term (**Figure 4.3; Figure 4.4**). Conversely, in the case of high stock exploitation rate relative to its production rate (i.e. $S \times \frac{r_S}{k_S} < q \times E$), the sign of “A” is negative, while the sign of “D” remains ambiguous (**Figure 4.4**). In the case of a depredating species with high natural growth rate relative to benefits from depredation success and the retrieval success of fishers being high (i.e. $(1 - D \times h_C) \times \left(\frac{r_D}{k_D}\right) > \varepsilon \times C \times h_C^2$), the sign of “C” is negative, and sign of “E” is positive (**Figure 4.4**), since “E” corresponds to the inverse of “C” with an additional positive term (**Figure 4.3; Figure 4.4**). Conversely, in case of the depredating species benefiting relatively more from depredation success than its own growth rate and the retrieval success of fishers being low (i.e. $(1 - D \times h_C) \times \left(\frac{r_D}{k_D}\right) < \varepsilon \times C \times h_C^2$), the sign of “C” is positive, and the sign of “E” remains ambiguous (**Figure 4.4**). Thus, sign prediction ambiguities can be resolved in case studies considering the relative strength of different processes.

Among the four categories of depredation-impacted fisheries systems, categories 2 and 3 exhibit predicted responses that suggest a potential for alternative states (**Figure 4.4**). In the second category, increase in effort (E), catch (C), depredation species (D) or stock (S) is beneficial for E, C

Positive input in the abundance of: E C D S L Long-term effects on: E $\begin{bmatrix} + & C & + & C & - \end{bmatrix}$ C $\begin{bmatrix} A & + & A & + & -A \end{bmatrix}$ D $\begin{bmatrix} A & + & D & + & -A \end{bmatrix}$ S $\begin{bmatrix} - & -C & - & E & + \end{bmatrix}$ L $\begin{bmatrix} B & -C & - & -C & + \end{bmatrix}$	$S \times \frac{r_S}{k_S} > q \times E$ $A, D > 0$	$S \times \frac{r_S}{k_S} < q \times E$ $A < 0$
$(1 - D \times h_C) \times \left(\frac{r_D}{k_D}\right) > \varepsilon \times C \times h_C^2$ $C < 0 \text{ \& } E > 0$	Category 1 Positive input in the abundance of: E C D S L Long-term effects on: E $\begin{bmatrix} + & - & + & - & - \end{bmatrix}$ C $\begin{bmatrix} + & + & + & + & - \end{bmatrix}$ D $\begin{bmatrix} + & + & + & + & - \end{bmatrix}$ S $\begin{bmatrix} - & + & - & + & + \end{bmatrix}$ L $\begin{bmatrix} B & + & - & + & + \end{bmatrix}$	Category 2 Positive input in the abundance of: E C D S L Long-term effects on: E $\begin{bmatrix} + & - & + & - & - \end{bmatrix}$ C $\begin{bmatrix} - & + & - & + & + \end{bmatrix}$ D $\begin{bmatrix} - & + & D & + & + \end{bmatrix}$ S $\begin{bmatrix} - & + & - & + & + \end{bmatrix}$ L $\begin{bmatrix} B & + & - & + & + \end{bmatrix}$
$(1 - D \times h_C) \times \left(\frac{r_D}{k_D}\right) < \varepsilon \times C \times h_C^2$ $C > 0$	Category 3 Positive input in the abundance of: E C D S L Long-term effects on: E $\begin{bmatrix} + & + & + & + & - \end{bmatrix}$ C $\begin{bmatrix} + & + & + & + & - \end{bmatrix}$ D $\begin{bmatrix} + & + & + & + & - \end{bmatrix}$ S $\begin{bmatrix} - & - & - & E & + \end{bmatrix}$ L $\begin{bmatrix} B & - & - & - & + \end{bmatrix}$	Category 4 Positive input in the abundance of: E C D S L Long-term effects on: E $\begin{bmatrix} + & + & + & + & - \end{bmatrix}$ C $\begin{bmatrix} - & + & - & + & + \end{bmatrix}$ D $\begin{bmatrix} - & + & D & + & + \end{bmatrix}$ S $\begin{bmatrix} - & - & - & E & + \end{bmatrix}$ L $\begin{bmatrix} B & - & - & - & + \end{bmatrix}$

Figure 4.4: Press perturbation scenario result categories for the generic depredation model for four set of conditions (lines and columns) resolving sign ambiguities in the qualitative adjoint matrix shown in top left-hand corner (same as in **Figure 4.3**).

and D, while being detrimental for landings (L). Conversely, an increase in L benefits to S and L and is detrimental to E, C and D. In systems belonging to category 3, increase in C, S or L will facilitate the emergence of a state where effort decreases, while C, D, S and L will increase (**Figure 4.4**).

4.3.1.3. Focus on three specific scenarios

The three target scenarios related to (i) increase in fishing effort, (ii) an increase in depredating species population and (iii) an increase in stock size (i.e. increase in E, D and S) correspond to columns 1, 3 and 4, respectively (**Figure 4.4**). Predicted responses, to (i) increase in fishing effort and (ii) increase in depredating species population (that respectively correspond to the 1st and 3rd column; **Figure 4.4**), are overall similar in the four broad categories; effort responds positively while stock respond negatively (**Figure 4.4**). Moreover, increase in the abundance of depredating species decreases fishers yield, with its positive impact on effort and negative impact on landings (**Figure 4.4**). The sign of catches and depredating species is positive in these both scenarios, when stock production rate is high relative to its exploitation rate (i.e. $S \times \frac{r_S}{k_S} > q \times E$; **Figure 4.4**). Otherwise, when stock exploitation

rate is high relative to its production rate (i.e. $S \times \frac{r_S}{k_S} < q \times E$), catches and depredating species respond negatively or remains ambiguous in case of depredating species due to its own increase in size (**Figure 4.4**).

In all categories, catches and depredating species respond positively to the increase in stock size (i.e. 4th column; **Figure 4.4**). When depredating species has a high natural growth rate relative to the benefits of depredation success and the retrieval success of fishers is high (i.e. $(1 - D \times h_C) \times \left(\frac{r_D}{k_D}\right) > \varepsilon \times C \times h_C^2$; **Figure 4.4**) predicted sign of stock to its own increase in size is positive and fishers yield increases, since fishing effort is negatively affected and landings positively (**Figure 4.4**). Otherwise, when depredating species benefits relatively more from depredation success than its own growth rate and the retrieval success of fishers is low (i.e. $(1 - D \times h_C) \times \left(\frac{r_D}{k_D}\right) < \varepsilon \times C \times h_C^2$; **Figure 4.4**), stock response remains ambiguous and fishers yield decreases, since fishing effort is positively affected and landings negatively, as observed previously due to the increase in the abundance of depredating species (**Figure 4.4**).

4.3.2. Stability of systems affected by depredation

Processes of terms, included in the overall feedback are identified in **Table 4.1**, and allow to define stability of systems affected by depredation, by comparing their relative strength. All six models are stable if negative feedback cycles are greater than positive ones, and the higher the value of wF, the greater the stability (cf. Dambacher et al. (2003) on stability and Hurwitz criteria I and II). In addition, the two sets of conditions determining the ambiguity sign are part of these processes, implying that stability of the four broad response categories differ according to resolution of the ambiguity sign.

We identified three negative and two positive feedback loops that are common to the generic and the alternative models (**Table 4.1**; **Table S4.1**). Four of these loops impact the level of fishing effort. Two negative feedbacks regulate fishing effort, through landing success ($a_{E,L}a_{L,C}a_{C,E}a_{D,D}a_{S,S}$) or depredation reduction through stock depletion ($a_{E,L}a_{L,D}a_{D,C}a_{C,S}a_{S,E}$; **Table 4.1**). While positive feedbacks drive fishing effort, through depredation ($a_{E,L}a_{L,D}a_{D,C}a_{C,E}a_{S,S}$) or stock depletion ($a_{L,C}a_{C,S}a_{S,E}a_{D,D}$; **Table 4.1**). In addition, there is a negative feedback loop involving self-regulation of each variable ($a_{E,E}a_{C,C}a_{D,D}a_{S,S}a_{L,L}$; **Table 4.1**). Therefore, the stability of depredation-impacted fisheries depends on both fishers' success in retrieving fish onboard being relatively greater than the ability of depredating species to remove catch from gear, and sustainable management of the exploited stock.

Natural predation adds three additional negative feedback loops that stabilise a system compared to the generic depredation model (i.e. with predation wF₅= -0.56 and, without wF₅= -0.2; **Table 4.1**). These feedback loops are related to stock availability, one regulates predation (i.e.

Table 4.1: Loop identification of the overall feedback is listed according to models, as well as weighted feedback (wF_n), which corresponds to stability indicator. For each feedback cycle, its sign (positive (+) or negative (-)) and the level at which it is observed is specified (e.g. >4 corresponds to observed from level 4, as well as in levels above 4). Note, conditional ambiguous stability is in complete form in **Appendix 4.1; Table S4.1.1.**

Feedback cycle	sign	Feedback level	Model					
			1 Generic depredation	2 Depredation and natural predation	3 Encounter reduction	4 Depredation success reduction	5 Encounter reduction and predation	6 Depredation success reduction and predation
Stock depletion drives fishing effort ($\alpha_{E,L}\alpha_{L,C}\alpha_{C,S}\alpha_{S,E}$)	+	>4	×	×	×	×	×	×
Depredation drives fishing effort ($\alpha_{E,L}\alpha_{L,D}\alpha_{D,C}\alpha_{C,E}$)	+	>4	×	×	×	×	×	×
Depredation reduction through stock depletion regulates fishing effort ($\alpha_{E,L}\alpha_{L,D}\alpha_{D,C}\alpha_{C,S}\alpha_{S,E}$)	-	>5	×	×	×	×	×	×
Stock depletion regulates depredating species population through predation ($\alpha_{E,L}\alpha_{L,D}\alpha_{D,S}\alpha_{S,E}$)	-	>4		×			×	×
Landings success regulates fishing effort ($\alpha_{E,L}\alpha_{L,C}\alpha_{C,E}$)	-	>3	×	×	×	×	×	×
Stock availability regulates depredating species population ($\alpha_{S,D}\alpha_{D,C}\alpha_{C,S}$)	-	>3		×			×	×
Mitigation regulates depredating species population ($\alpha_{M,L}\alpha_{L,D}\alpha_{D,M}$)	-	>3			×	×	×	×
Stock availability regulates predation ($\alpha_{D,S}\alpha_{S,D}$)	-	>2		×			×	×
Landings success regulates mitigation ($\alpha_{M,L}\alpha_{L,M}$)	-	>2				×		×
	Hurwitz criteria	wF_n	-0.2	-0.56	-0.33	-0.43	-0.64	-0.71

$a_{D,S}a_{S,D}$) while the other regulates depredating species population size through predation (i.e. $a_{E,L}a_{L,D}a_{D,S}a_{S,E}$) or through facilitated access to food resources (i.e. $a_{S,D}a_{D,C}a_{C,S}$). Stability of alternative models including mitigation measures can also be compared. “Depredation success reduction” adds a negative feedback loop that stabilises the system relative to “Encounter reduction” models, whether or not there is natural predation (i.e. with predation $wF_6 = -0.71$ and, without $wF_6 = -0.43$; with predation $wF_6 = -0.64$ and without $wF_6 = -0.33$; **Table 4.1**). This feedback loop regulates mitigation through landings success.

4.4. Discussion

As depredation is of worldwide concern and is likely to escalate in coming decades, predicting responses to commonly applied perturbation scenarios is an imperative. Here, we identified different depredation impacted system typologies and we assessed processes that influence co-existence between fishers, exploited stock and depredating species.

4.4.1. Main factors determining stability and response to perturbation of depredation-impacted system

We identified four broad categories of depredation-impacted fisheries, whose respective responses to press perturbation scenarios and whose stability partially depend on (1) stock population dynamics and exploitation status, and (2) depredating species’ ecology and its competition for caught fish with fishers. Stock related processes are relatively well known and quantified compared to depredating species-related processes. The former ambiguity is therefore easier to interpret and to relate to concrete cases compared to the later ambiguity.

A number of depredation cases documented in the literature agree with the findings of this study and can be used to illustrate how (ambiguous qualitative prediction) processes related to exploited stock dynamics, i.e. population growth rate and its exploitation status (“A” elements in adjoint matrix, **Figure 4.3**), condition overall long-term dynamics in depredation-impacted fishery. For instance, in the Baltic Sea, cod (*Gadus morhua*) exploitation rate seems higher than its production rate as the stock has been declining for decades (Bagge & Thurow, 1994; Köster et al., 2003). Recruitment failure and high fishing intensity likely explain this decline (Bagge & Thurow, 1994; Köster et al., 2003). Moreover, concurrently to the increase in seal population, which depredates cod in gillnet fishery catches (Tschernij & Larsson, 2003), fishers yield (Köningson, 2011) and the stock have further decreased (Köster et al., 2003). This is consistent with the qualitative predictions of the third and fourth theoretical categories, implying high stock exploitation rate relative to its production rate. With stock and fishers yield declining, this depredation-impacted fishery system seems unsustainable. Conversely, in the Crozet archipelago, the production rate of Patagonian toothfish (*Dissostichus eleginoides*) seems higher than its exploitation rate as the stock is stable or increasing

(CCAMLR, 2018a). Indeed, only a small fleet of longliners exploits toothfish in this region and has been well-managed since 2003 (Duhamel & Williams, 2011). Moreover, concurrently to the increase in numbers of depredating killer whales (Amelot et al., 2021), landings decreased by 12% due to depredation (CCAMLR, 2018a) while catches (i.e. fish trapped in fishing gear) increased as fishers compensated for lost catch with extra effort. These changes are consistent with the qualitative predictions of the first and second theoretical categories, implying high stock production rate relative to exploitation rate. However, the decrease in stock size suggested by qualitative predictions is probably marginal in Crozet, because of the low exploitation rate. With its stock persistence, this depredation-impacted fishery system seems viable if the decrease in fisheries landings does not lead to jeopardize profitability.

Ecological processes related to the depredating species and its competition for caught individuals with fishers (“C” elements in adjoint matrix, **Figure 4.3**) influence overall long-term dynamics in depredation-impacted fisheries. These elements combine a variety of information (i.e. retrieval success, species dynamic) associated with both the depredating species and the fishers, and are therefore rarely informed simultaneously. Documented cases can be associated with these processes but given the limited data, interpretation remains partial. First, the ecology of the depredating species plays a role via the ratio between intrinsic growth rate (r) and carrying capacity (k), which is determined by the reproductive strategy. When the depredating species is short-lived, fast growing, such as Octopus maori (*Octopus maorum*) or pufferfish (*Arothron spp.*) (Anderson, 1999), and the population growth benefits weakly from depredation success, growth is probably driven by other factors. In contrast, if the depredating species is long-lived, slow growing, such as killer whale or grey seal (*Halichoerus grypus*) (Evans & Stirling, 2002; Olesiuk et al., 2005), and the population growth significantly benefits from depredation success, the population is likely to be more strongly impacted by the benefits from depredation success. In particular, it has been found for killer whales depredating on toothfish catches at Crozet or depredating on tuna catches in the strait of Gibraltar, that depredation may enhance fitness, and therefore the reproductive performance of individuals (Esteban et al., 2016; Guinet et al., 2015; Tixier, et al., 2015a). In addition, a k -reproductive strategy is often related to social learning, which has a major influence on the acquisition of a depredation behaviour (Nyhus, 2016), and therefore a high potential for its spread within the population. Second, the strength of the competition for caught individuals between the depredating species and fishers is directly related to the depredation rate, which varies among case studies, from 1% to 67% of landings (Hernandez-Milian et al., 2008; Köningson, 2011). The depredation rate is related to the ability of the depredating species to remove fish from gear and to retrieval success of fishers, which depends on the way skippers adapt their spatial foraging strategies on fishing grounds impacted by depredation, and their experience, as demonstrated in Crozet (Janc et al., 2021).

The ecology of the depredating species determines also the extent of the impact on depredation-impacted fisheries systems, especially the presence or absence of the depredated resource in its natural diet. Little cascading effects or change in ecological role are expected if the overall amount of stock consumed naturally is equivalent to that amount consumed through depredation, as observed for killer whale in Crozet (Clavareau et al., 2020; Tixier et al., 2019). Moreover, depredation has limited impact on stock dynamics because in this case the release in natural predation pressure is offset by an increase in fishing mortality due to effort intensification to maintain total yield (Clavareau et al., 2020). Cascading effects and change in ecological role due to change in predation pressure are likely to be greater when the depredated species is naturally absent from the diet, as is the case for harbour seals (*Phoca vitulina*) depredating eels from fyke-nets in Sweden (Lundström et al., 2010). Moreover, most depredating species are higher trophic level species such as large sharks and marine mammals, and changes in predation pressure from these top-predators are likely to generate greater top-down cascading ecosystem effects than changes from meso-predators (Newsome et al., 2015).

4.4.2. Predicting long-term consequences of depredation can help inform management

We now analyse the long-term predicted consequences of depredation, such as increase in fishing effort to compensate for a decrease in catch rates as well as increase in stock size due to stock recovery, and discuss their sustainability according to the four system categories, illustrated previously through case studies.

From a fisher's perspective, a decline in catch rates (for instance caused by depredation) can be compensated by an increase in fishing effort (Peterson et al., 2013), which is only sustainable for well-managed stocks, harvested by a fishery that is sufficiently profitable to support extra costs related to increased fishing effort. In heavily exploited stocks, fishery intensification to compensate for a decrease in catch rates leads to stock depletion or to fishery collapse. Moreover, when the ratio between depredated and landed resource becomes large enough, depredation can jeopardize the socio-economic viability of the fishing activity (Matkin et al., 1986; Tixier et al., 2018). In addition, over time, generations of depredating individuals that feed largely or exclusively in association with fisheries may become dependent on this for food. A fishery collapse may then have a negative impact on these depredating individuals accustomed to easy access to the resource (Fertl & Leatherwood, 1997).

From a manager's perspective, a decline in catch rates can be mitigated by stock restoration. Indeed, depredation 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), and specifically to enable restoration of depleted stocks. However, increases in fishing yield or in stock size are not guaranteed.

In systems involving long-lived and slow growing depredating species, hence with population growth significantly benefiting from depredation, stock restoration efforts might be negated. As the majority of marine depredating species are marine mammals or sharks (Tixier et al., 2021a), one might expect increasing depredation impacts on fisheries and human fishing communities, as well as on exploited fish stocks and other ecosystem components (Northridge, 2018).

As increases in fishing effort or stock restoration are not appropriate in all cases and do not guarantee a decrease in depredation impacts, increasing retrieval success through mitigation measures seems essential for the co-existence of exploited stock, fishery and depredating species. Numerous technological and behavioural approaches have been used to reduce depredation over the last 40 years (Tixier et al., 2021a). However, their effectiveness remains limited. This lack of success may be partially related to behavioural adaptability and habituation of depredating species (Nitta & Henderson, 1993; Tixier et al., 2015b). According to our model results, methods that try to impede the depredating species' capacity to remove catches from gear seem to be more effective in reducing depredation than methods that try to avoid encounters with depredating species, which is partly consistent with the literature. However, these mitigation methods, such as alternative fishing techniques and strategies, are probably the costliest measures. Thus, to increase profitability, these additional costs should not exceed the benefits gained by minimizing depredation (Trijoulet, 2016; Trijoulet et al., 2018).

4.4.3. Limits and perspectives

With a dedicated focus on interactions between fishery, fish stock and depredating species, this study details key processes and proposes a generic model of marine depredation. However, this generic model only captures depredation on fishery catches whereas marine depredation has also been reported on bait (Gedamke, 2007), as well as on aquaculture farms (Burr et al., 2020a). To represent these cases, model structure would need to be adapted, as it is related to human input, while catch depredation is related to exploited stock dynamics. Moreover, we assumed that the population dynamics of the depredating species will be enhanced via depredation benefits for physiological performance (Esteban et al., 2016; Guinet et al., 2015; Tixier, et al., 2015a). However, 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. Indeed, depredating species can be exposed to intentional shooting from fishers and/or accidental risk of getting caught in fishing gear (Azevedo et al., 2017; Dans et al., 2003). For instance, bycatch of depredating species such as marine mammals is often reported in fixed net and trawl fisheries (Read, 2008). Although depredation supplies may enhance fitness and therefore the reproductive performances of individuals, global benefits from depredation are only realistic in a situation where risks of fatal interactions with fishing gear and vessels are limited. Thus, assessing whether the

balance between benefits and costs is positive or negative for depredating species is pivotal to capture this interaction and for determining long-term population growth rates of depredating species.

This study highlighted how discrepancies in terms of stock status and ecology, depredating species ecology and competition with fishers across depredation-impacted fisheries determine long-term co-existence of fisheries, exploited stocks and marine predators. However, additional factors can be determining, although not taken into account, such as profitability of stock exploitation, which influences sustainability of fisheries. Indeed, fisheries targeting species with high commercial value, such as toothfish in Subantarctic waters experiencing depredation by killer whales (Roche et al., 2007), are generally more sustainable than fisheries targeting species with low commercial value, such as pollock in Irish waters subject to grey seal depredation (Cosgrove et al., 2015), which is almost 24 times less valuable (Pinnegar et al., 2002; Tixier et al., 2021a). Fishery characteristics, such as fleet size, activity history, the selectivity of fishing gear used, as well as the management method can also be decisive, since they influence exploitation status. In addition, other biological and ecological factors of depredating species can influence this conflict and thus co-existence, such as life stage, sex and distribution of food (Nyhus, 2016). However, unlike information on exploited stock status and its exploitation, information related to the ecology of depredating species and quantification of this conflict is rare. Therefore, recommendations to better understand and predict ecosystem-level effects of depredation include the need for further quantification of depredation-related interactions across the whole socio-ecosystem. Depredation rate, which partly influences fisheries viability over time, is notably critical to assess how the system of fishers, exploited stocks and depredating species will evolve. Indeed, its quantification is also essential to better assess the mortality of exploited stocks and thus determine its sustainability and identify effective ecosystem-based management actions.

Supplementary materials

Supplementary material is available in the next section. The supplementary materials contain details on conditional ambiguous stability of each model (**Appendix 4.1**) and methods to identify ambiguity condition (**Appendix 4.2**) as well as a more exhaustive description of model construction (**Appendix 4.3**).

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Supplementary materials: Exploitation and depredation rates determine viability of depredation-impacted fisheries

Appendix 4.1: Conditional ambiguous stability

Table S4.1: Conditional ambiguous stability of each depredation model. E fishing effort, C catches (i.e. fish retained in fishing gear), D biomass of depredating species, S biomass of stock, and L landings (i.e. proportion of catches successfully removed by fishers).

Model	Level	Conditional stability at different feedback levels
Generic depredation	F5	$= a_{E,L}[(a_{L,D}a_{D,C}a_{C,E}a_{S,S} + a_{L,C}a_{C,S}a_{S,E}a_{D,D}) - (a_{L,C}a_{C,E}a_{D,D}a_{S,S} + a_{L,D}a_{D,C}a_{C,S}a_{S,E})] - a_{E,E}a_{C,C}a_{D,D}a_{S,S}a_{L,L}$
	F4	$= a_{E,L}(a_{L,C}a_{C,S}a_{S,E} + a_{L,D}a_{D,C}a_{C,E}) - a_{S,S}a_{L,L}(a_{C,C}a_{D,D} + a_{E,E}a_{C,C} + a_{E,E}a_{D,D}) - a_{E,L}a_{L,C}a_{C,E}(a_{S,S} + a_{D,D}) - a_{E,E}a_{C,C}a_{D,D}(a_{L,L} + a_{S,S})$
Depredation and predation	F5	$= a_{E,L}(a_{L,D}a_{D,C}a_{C,E}a_{S,S} + a_{L,C}a_{C,S}a_{S,E}a_{D,D}) - a_{E,L}a_{L,C}a_{C,E}(a_{D,D}a_{S,S} + a_{D,S}a_{S,D}) - a_{E,E}a_{C,C}a_{L,L}(a_{D,D}a_{S,S} + a_{D,S}a_{S,D}) - a_{E,L}a_{L,D}a_{S,E}(a_{D,C}a_{C,S} - a_{D,S}a_{C,C}) - a_{E,E}a_{D,C}a_{C,S}a_{S,D}a_{L,L}$
	F4	$= a_{E,L}(a_{L,D}a_{D,C}a_{C,E} + a_{L,C}a_{C,S}a_{S,E}) - a_{E,E}a_{S,S}a_{L,L}(a_{D,D} + a_{C,C}) - a_{S,D}a_{D,S}a_{L,L}(a_{C,C} + a_{E,E}) - a_{E,L}a_{L,C}a_{C,E}(a_{D,D} + a_{S,S}) - a_{E,E}a_{C,C}a_{D,D}(a_{L,L} + a_{S,S}) - a_{S,D}a_{D,C}a_{C,S}(a_{L,L} + a_{E,E}) - a_{C,C}(a_{D,D}a_{S,S}a_{L,L} + a_{D,S}a_{S,D}a_{E,E}) - a_{E,L}a_{L,D}a_{D,S}a_{S,E}$
Encounter reduction	F6	$= a_{M,M}a_{E,L}(a_{L,D}a_{D,C}a_{C,E}a_{S,S} + a_{L,C}a_{C,S}a_{S,E}a_{D,D}) - a_{M,M}a_{E,L}(a_{L,C}a_{C,E}a_{D,D}a_{S,S} + a_{L,D}a_{D,C}a_{C,S}a_{S,E}) - a_{C,C}a_{S,S}(a_{M,M}a_{D,D}a_{E,E}a_{L,L} + a_{M,L}a_{L,D}a_{D,M}a_{E,E})$
	F5	$= a_{E,L}(a_{L,D}a_{D,C}a_{C,E}(a_{S,S} + a_{M,M}) + a_{L,C}a_{C,S}a_{S,E}(a_{M,M} + a_{D,D})) - a_{E,L}a_{L,C}a_{C,E}a_{M,M}(a_{S,S} + a_{D,D}) - a_{M,M}a_{D,D}a_{L,L}(a_{E,E}a_{S,S} + a_{E,E}a_{C,C} + a_{C,C}a_{S,S}) - a_{E,E}a_{C,C}a_{S,S}(a_{L,L}a_{M,M} + a_{D,D}a_{M,M} + a_{D,D}a_{L,L}) - a_{M,L}a_{L,D}a_{D,M}(a_{E,E}a_{C,C} + a_{C,C}a_{S,S} + a_{E,E}a_{S,S}) - a_{E,L}(a_{L,C}a_{C,E}a_{D,D}a_{S,S} + a_{L,D}a_{D,C}a_{C,S}a_{S,E})$
	F4	$= a_{E,L}(a_{L,C}a_{C,S}a_{S,E} + a_{L,D}a_{D,C}a_{C,E}) - a_{E,L}a_{L,C}a_{C,E}(a_{D,D} + a_{S,S}) - a_{L,L}a_{S,S}(a_{D,D}a_{E,E} + a_{D,D}a_{C,C} + a_{C,C}a_{E,E} + a_{D,D}a_{M,M} + a_{E,E}a_{M,M} + a_{C,C}a_{M,M}) - a_{M,M}a_{L,L}(a_{C,C}a_{E,E} + a_{D,D}a_{E,E} + a_{D,D}a_{C,C}) - a_{M,L}a_{L,D}a_{D,M}(a_{E,E} + a_{C,C} + a_{S,S}) - a_{M,M}a_{S,S}(a_{D,D}a_{C,C} + a_{D,D}a_{E,E} + a_{C,C}a_{E,E}) - a_{D,D}a_{C,C}a_{E,E}(a_{M,M} + a_{L,L} + a_{S,S}) - a_{E,L}a_{L,C}a_{C,E}a_{M,M}$
Depredation success reduction	F6	$= a_{E,L}a_{M,M}[(a_{L,C}a_{C,S}a_{S,E}a_{D,D} + a_{L,D}a_{D,C}a_{C,E}a_{S,S}) - (a_{L,C}a_{C,E}a_{D,D}a_{S,S} + a_{L,D}a_{D,C}a_{C,S}a_{S,E})] - a_{M,L}a_{E,E}a_{C,C}a_{S,S}(a_{L,M}a_{D,D} + a_{L,D}a_{D,M}) - a_{E,E}a_{C,C}a_{D,D}a_{S,S}a_{L,L}a_{M,M}$
	F5	$= a_{E,L}(a_{L,C}a_{C,S}a_{S,E}(a_{D,D} + a_{M,M}) + a_{L,D}a_{D,C}a_{C,E}(a_{S,S} + a_{M,M})) - a_{M,L}a_{L,M}(a_{C,C}a_{D,D}a_{S,S} + a_{E,E}a_{D,D}a_{S,S} + a_{E,E}a_{C,C}a_{S,S} + a_{E,E}a_{C,C}a_{D,D}) - a_{M,L}a_{L,D}a_{D,M}(a_{C,C}a_{S,S} + a_{E,E}a_{S,S} + a_{E,E}a_{C,C}) - a_{L,L}a_{M,M}(a_{C,C}a_{D,D}a_{S,S} + a_{E,E}a_{D,D}a_{S,S} + a_{E,E}a_{C,C}a_{S,S} + a_{E,E}a_{C,C}a_{D,D}) - a_{D,D}a_{S,S}(a_{E,E}a_{C,C}a_{L,L} + a_{E,E}a_{C,C}a_{M,M} + a_{L,C}a_{C,E}a_{E,L}) - a_{L,D}a_{D,C}a_{C,S}a_{S,E}a_{E,L} - a_{L,C}a_{M,M}(a_{C,E}a_{E,L}a_{S,S} + a_{C,E}a_{E,L}a_{D,D})$
	F4	$= a_{E,L}(a_{L,C}a_{C,S}a_{S,E} + a_{L,D}a_{D,C}a_{C,E}) - a_{L,C}a_{C,E}a_{E,L}(a_{D,D} + a_{S,S}) - a_{D,D}a_{S,S}a_{L,L}(a_{E,E} + a_{C,C} + a_{M,M}) - a_{E,E}a_{C,C}(a_{D,D}a_{L,L} + a_{S,S}a_{L,L} + a_{M,L}a_{L,M} + a_{M,M}a_{L,L} + a_{D,D}a_{M,M} + a_{S,S}a_{M,M} + a_{D,D}a_{S,S}) - a_{D,D}a_{M,M}(a_{C,C}a_{S,S} + a_{E,E}a_{L,L} + a_{C,C}a_{L,L} + a_{E,E}a_{S,S}) - a_{S,S}a_{L,L}a_{M,M}(a_{E,E} + a_{C,C}) - a_{M,L}a_{L,D}a_{D,M}(a_{E,E} + a_{C,C} + a_{S,S}) - a_{M,L}a_{L,M}(a_{E,E}a_{D,D} + a_{E,E}a_{S,S} + a_{C,C}a_{S,S} + a_{D,D}a_{S,S} + a_{D,D}a_{C,C}) - a_{L,C}a_{C,E}a_{E,L}a_{M,M}$
Encounter	F6	$= a_{E,L}a_{M,M}(a_{L,C}a_{C,S}a_{S,E}a_{D,D} + a_{L,D}a_{D,C}a_{C,E}a_{S,S}) - a_{E,E}a_{L,L}a_{M,M}(a_{S,D}a_{D,S}a_{C,C} + a_{C,C}a_{D,D}a_{S,S} + a_{S,D}a_{D,C}a_{C,S}) - a_{D,M}a_{M,L}a_{E,E}(a_{L,C}a_{C,S}a_{S,D} + a_{L,D}a_{D,C}a_{C,S}) - a_{E,L}(a_{L,D}a_{M,M}(a_{D,S}a_{S,E}a_{C,C} + a_{D,C}a_{C,S}a_{S,E}) + a_{L,C}a_{C,E}a_{M,M}(a_{S,D}a_{D,S} + a_{S,S}a_{D,D}))$

reduction and predation	F5	$ \begin{aligned} &= a_{L,C}a_{C,S}a_{S,E}a_{E,L}(a_{M,M} + a_{D,D}) + a_{L,D}a_{D,C}a_{C,E}a_{E,L}(a_{S,S} + a_{M,M}) - a_{L,C}a_{C,E}a_{E,L}(a_{S,D}a_{D,S} + a_{S,S}a_{D,D} + a_{D,D}a_{M,M}) - a_{S,D}a_{E,E}a_{L,L}(a_{D,C}a_{C,S} + a_{D,S}a_{C,C} + a_{E,E}a_{M,M}) \\ &\quad - a_{S,E}a_{E,L}a_{L,D}(a_{D,S}a_{C,C} + a_{D,C}a_{C,S} + a_{D,S}a_{M,M}) - a_{M,L}a_{L,D}a_{D,M}(a_{S,S}a_{C,C} + a_{S,S}a_{E,E} + a_{E,E}a_{C,C}) \\ &\quad - a_{L,L}a_{M,M}(a_{S,D}(a_{D,C}a_{C,S} + a_{D,S}a_{C,C}) + a_{S,S}(a_{C,C}a_{D,D} + a_{E,E}a_{D,D} + a_{E,E}a_{C,C})) + a_{E,E}a_{C,C}a_{D,D} - a_{S,D}a_{E,E}a_{M,M}(a_{D,C}a_{C,S} + a_{D,S}a_{C,C}) \\ &\quad - a_{E,E}a_{C,C}a_{D,D}a_{S,S}(a_{M,M} + a_{L,L}) - a_{L,C}(a_{C,S}a_{S,D}a_{D,M}a_{M,L} + a_{C,E}a_{E,L}a_{S,S}a_{M,M}) \end{aligned} $
	F4	$ \begin{aligned} &= a_{E,L}(a_{L,D}a_{D,C}a_{C,E} + a_{L,C}a_{C,S}a_{S,E}) - a_{E,E}a_{L,L}(a_{C,C}a_{D,D} + a_{C,C}a_{S,S} + a_{D,D}a_{S,S} + a_{D,S}a_{S,D} + a_{C,C}a_{M,M} + a_{D,D}a_{M,M} + a_{S,S}a_{M,M}) \\ &\quad - a_{S,D}a_{M,M}(a_{D,S}a_{C,C} + a_{D,C}a_{C,S} + a_{D,S}a_{E,E} + a_{D,S}a_{L,L}) - a_{M,L}a_{L,D}a_{D,M}(a_{E,E} + a_{C,C}) - a_{E,E}a_{C,C}(a_{D,D}a_{M,M} + a_{D,S}a_{S,D} + a_{D,D}a_{S,S}) \\ &\quad - a_{C,C}a_{D,D}a_{L,L}(a_{S,S} + a_{M,M}) - a_{L,D}(a_{D,S}a_{S,E}a_{E,L} + a_{D,M}a_{M,L}a_{S,S}) - a_{S,D}a_{D,C}a_{C,S}a_{E,E} \end{aligned} $
Depredation success reduction and predation	F6	$ \begin{aligned} &= a_{E,L}a_{M,M}(a_{L,C}a_{C,S}a_{S,E}a_{D,D} + a_{L,D}a_{D,C}a_{C,E}a_{S,S}) - a_{M,L}a_{L,M}a_{E,E}(a_{S,D}a_{D,C}a_{C,S} + a_{S,D}a_{D,S}a_{C,C} + a_{C,C}a_{D,D}a_{S,S}) - a_{E,L}a_{L,D}a_{M,M}(a_{D,C}a_{C,S}a_{S,E} + a_{D,S}a_{S,E}a_{C,C}) \\ &\quad - a_{E,L}a_{L,C}a_{M,M}(a_{C,E}a_{S,D}a_{D,S} + a_{C,E}a_{D,D}a_{S,S}) - a_{E,E}a_{L,L}a_{M,M}(a_{S,D}a_{D,C}a_{C,S} + a_{S,D}a_{D,S}a_{C,C} + a_{C,C}a_{D,D}a_{S,S}) - a_{D,M}a_{M,L}a_{E,E}(a_{L,D}a_{C,C}a_{S,S} + a_{L,C}a_{C,S}a_{S,D}) \end{aligned} $
	F5	$ \begin{aligned} &= a_{L,C}a_{C,S}a_{S,E}a_{E,L}(a_{D,D} + a_{M,M}) + a_{L,D}a_{D,C}a_{C,E}a_{E,L}(a_{S,S} + a_{M,M}) - a_{S,D}a_{L,L}a_{M,M}(a_{D,C}a_{C,S} + a_{D,S}a_{C,C} + a_{D,S}a_{E,E}) - a_{S,S}a_{L,L}a_{M,M}(a_{C,C}a_{D,D} + a_{E,E}a_{D,D} + a_{E,E}a_{C,C}) \\ &\quad - a_{E,E}a_{M,M}(a_{C,C}a_{D,D}a_{L,L} + a_{S,D}a_{D,C}a_{C,S} + a_{C,C}a_{D,D}a_{S,S} + a_{D,S}a_{S,D}a_{S,S}) - a_{M,L}a_{L,D}a_{D,M}(a_{C,C}a_{S,S} + a_{E,E}a_{S,S} + a_{E,E}a_{C,C}) \\ &\quad - a_{M,L}a_{L,M}a_{S,D}(a_{D,C}a_{C,S} + a_{D,S}a_{C,C} + a_{D,S}a_{E,E}) - a_{M,L}a_{L,M}a_{S,S}(a_{D,D}a_{C,C} + a_{E,E}a_{D,D} + a_{E,E}a_{C,C}) - a_{M,L}(a_{L,C}a_{C,S}a_{S,D}a_{D,M} + a_{L,M}a_{D,D}a_{C,C}a_{E,E}) \\ &\quad - a_{L,D}a_{S,E}a_{E,L}(a_{D,C}a_{C,S} + a_{D,S}a_{C,C} + a_{M,M}a_{D,S}) - a_{L,C}a_{C,E}a_{E,L}(a_{S,D}a_{D,S} + a_{S,S}a_{D,D} + a_{S,S}a_{M,M} + a_{M,M}a_{D,D}) - a_{S,D}a_{L,L}a_{E,E}(a_{D,C}a_{C,S} + a_{D,S}a_{C,C}) \\ &\quad - a_{E,E}a_{C,C}a_{D,D}a_{S,S}a_{L,L} \end{aligned} $
	F4	$ \begin{aligned} &= a_{E,L}(a_{L,D}a_{D,C}a_{C,E} + a_{L,C}a_{C,S}a_{S,E}) - a_{S,D}a_{E,E}(a_{D,S}a_{L,L} + a_{D,C}a_{C,S} + a_{D,S}a_{C,C} + a_{D,S}a_{M,M}) - a_{S,D}a_{L,L}(a_{D,S}a_{C,C} + a_{D,C}a_{C,S} + a_{D,S}a_{M,M}) \\ &\quad - a_{S,S}a_{L,L}(a_{C,C}a_{D,D} + a_{E,E}a_{C,C} + a_{E,E}a_{D,D} + a_{E,E}a_{M,M} + a_{M,M}a_{C,C} + a_{M,M}a_{D,D}) - a_{L,C}a_{C,E}a_{E,L}(a_{D,D} + a_{S,S}) \\ &\quad - a_{M,L}a_{L,M}(a_{E,E}a_{S,S} + a_{C,C}a_{S,S} + a_{D,D}a_{S,S} + a_{D,S}a_{S,D} + a_{D,D}a_{E,E} + a_{E,E}a_{C,C} + a_{D,D}a_{C,C}) - a_{M,L}a_{L,D}a_{D,M}(a_{E,E} + a_{C,C} + a_{S,S}) - a_{D,D}a_{S,S}a_{M,M}(a_{E,E} + a_{C,C}) \\ &\quad - a_{S,D}a_{M,M}(a_{D,S}a_{C,C} + a_{D,C}a_{C,S}) - a_{L,L}a_{M,M}(a_{E,E}a_{C,C} + a_{E,E}a_{D,D} + a_{D,D}a_{C,C}) - a_{M,M}(a_{L,C}a_{C,E}a_{E,L} + a_{E,E}a_{C,C}a_{D,D} + a_{E,E}a_{C,C}a_{S,S}) \\ &\quad - a_{E,E}a_{D,D}a_{C,C}(a_{L,L} + a_{S,S}) - a_{L,D}a_{D,S}a_{S,E}a_{E,L} \end{aligned} $

Appendix 4.2: Identification of ambiguity conditions

Steps to move from the ambiguities contained in the adjoint matrix to the corresponding partial derivatives and the identification of ambiguity conditions. i) Identify the ambiguous terms in the adjoint matrix, ii) factor redundant a_{ij} terms, iii) replace each term a_{ij} by the corresponding partial derivative, and finally iv) factor redundant terms. Thirteen predicted ambiguities were observed in the qualitative adjoint matrix of the generic depredation model, corresponding to five different conditions (i.e. A-E).

$$\text{Adjoint matrix} = \begin{bmatrix} + & C & + & C & - \\ A & + & A & + & -A \\ A & + & D & + & -A \\ - & -C & - & E & + \\ B & -C & - & -C & + \end{bmatrix}$$

$$\begin{aligned} A &= a_{C,E} a_{S,S} - a_{C,S} a_{S,E} \\ &= \left(\frac{q \times S}{C}\right) \times \left(\frac{r_s}{k_s}\right) - \left(\frac{q \times E}{C}\right) \times (q) \\ &= \frac{q}{C} \times \left[\left(S \times \frac{r_s}{k_s}\right) - (q \times E) \right] \end{aligned}$$

$$B = (a_{L,C} a_{C,E} a_{D,D} a_{S,S} + a_{L,D} a_{D,C} a_{C,S} a_{S,E}) - (a_{L,D} a_{D,C} a_{C,E} a_{S,S} + a_{L,C} a_{C,S} a_{S,E} a_{D,D}) \quad =?$$

$$\begin{aligned} C &= a_{L,D} a_{D,C} - a_{L,C} a_{D,D} \\ &= \left(\frac{C \times h_c}{L}\right) \times (\varepsilon \times h_c) - \frac{(1 - D \times h_c)}{L} \times \left(\frac{r_D}{k_D}\right) \\ &= \frac{1}{L} \times \left[(C \times h_c^2 \times \varepsilon) - (1 - D \times h_c) \times \left(\frac{r_D}{k_D}\right) \right] \end{aligned}$$

$$\begin{aligned} D &= a_{E,E} a_{C,C} a_{S,S} a_{L,L} + a_{E,L} a_{L,C} (a_{C,E} a_{S,S} - a_{C,S} a_{S,E}) \\ &= \frac{\alpha_r \times (L - Q)}{Q \times E^2} \times \left(\frac{q \times S \times E}{C^2}\right) \times \left(\frac{r_s}{k_s}\right) \times \left(\frac{C \times (1 - D \times h_c)}{L^2}\right) \\ &\quad + \frac{\alpha_r}{Q \times E} \times \frac{(1 - D \times h_c)}{L} \times \left[\left(\frac{q \times S}{C}\right) \times \left(\frac{r_s}{k_s}\right) - \left(\frac{q \times E}{C}\right) \times (q) \right] \\ &= \frac{1}{C \times L} \times \frac{\alpha_r}{Q \times E} \times \left[\frac{(L - Q)}{E} \times \frac{q \times S \times E}{C} \times \frac{r_s}{k_s} \times \frac{C \times (1 - D \times h_c)}{L} + (1 - D \times h_c) \times q \times \left[\left(S \times \frac{r_s}{k_s}\right) - (q \times E) \right] \right] \end{aligned}$$

$$\begin{aligned} E &= a_{E,E} a_{C,C} a_{D,D} a_{L,L} + a_{C,E} a_{E,L} (a_{L,C} a_{D,D} - a_{L,D} a_{D,C}) \\ &= \frac{\alpha_r \times (L - Q)}{Q \times E^2} \times \left(\frac{q \times S \times E}{C^2}\right) \times \left(\frac{r_D}{k_D}\right) \times \left(\frac{C \times (1 - D \times h_c)}{L^2}\right) \\ &\quad + \left(\frac{q \times S}{C}\right) \times \left(\frac{\alpha_r}{Q \times E}\right) \times \left[\frac{(1 - D \times h_c)}{L} \times \left(\frac{r_D}{k_D}\right) - \left(\frac{C \times h_c}{L}\right) \times (\varepsilon \times h_c) \right] \\ &= \frac{1}{C \times L} \times \frac{\alpha_r}{Q \times E} \times \left[\frac{(L - Q)}{E} \times \left(\frac{q \times S \times E}{C}\right) \times \left(\frac{r_D}{k_D}\right) \times \left(\frac{C \times (1 - D \times h_c)}{L}\right) + (q \times S) \times \left[(1 - D \times h_c) \times \left(\frac{r_D}{k_D}\right) - C \times h_c^2 \times \varepsilon \right] \right] \end{aligned}$$

Appendix 4.3: From modified to direct interaction

Details of transition from the modified interaction to the corresponding direct interaction are given in this appendix. Modified interaction results from variable influencing the interaction between two other variables, for more details, see (Dambacher & Ramos-Jiliberto, 2007), and is represented by a dashed red line. As the qualitative modelling approach considers only direct interactions, each modified interaction is translated into a direct interaction.

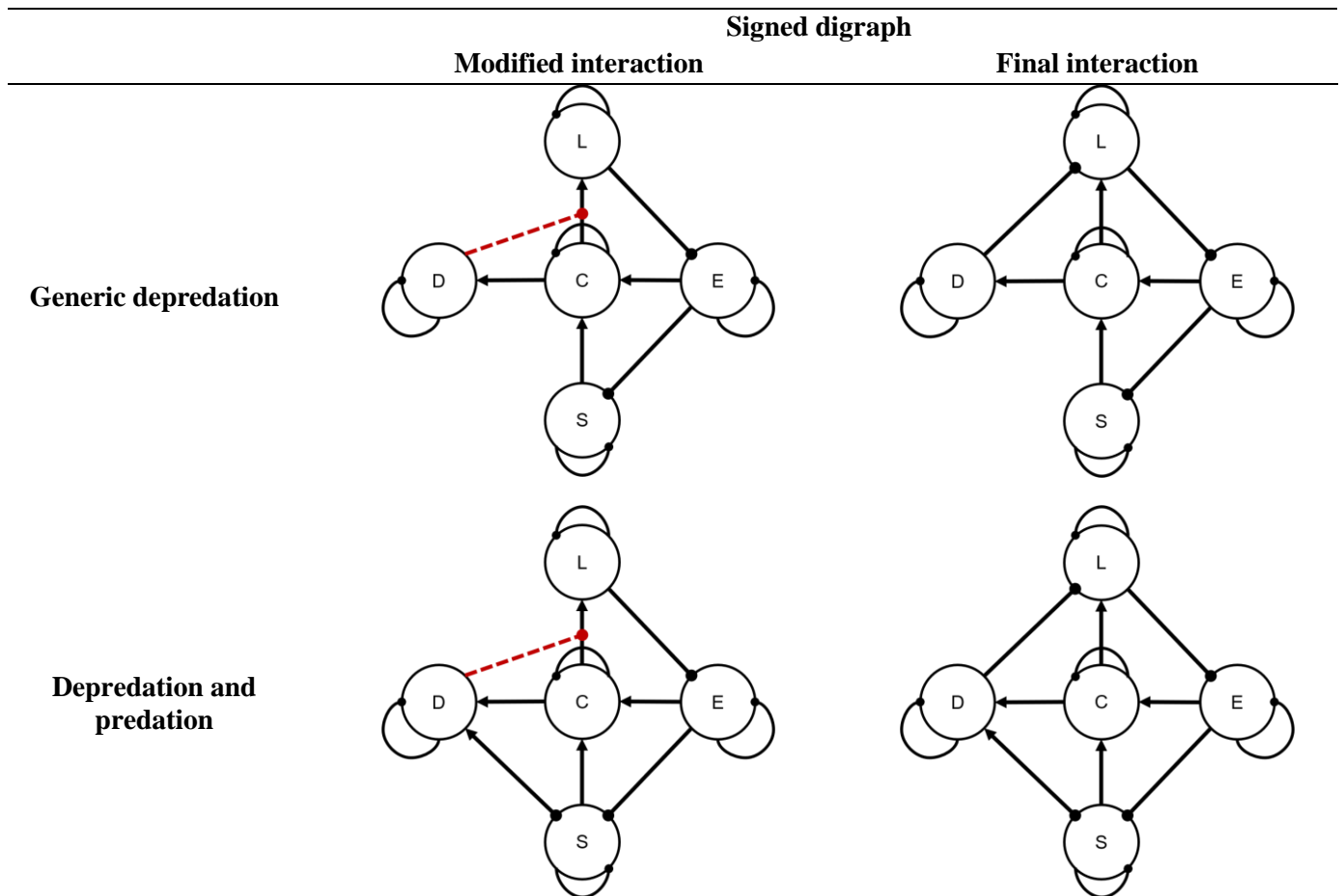


Figure S4.1: Sign directed graph of generic depredation model with and without natural predation. Transition from the modified interaction in red to the corresponding direct interaction in black is given for each model. Variables included are; E: fishing effort, C: catches, D: biomass of depredating species, S: biomass of stock, L: landings.

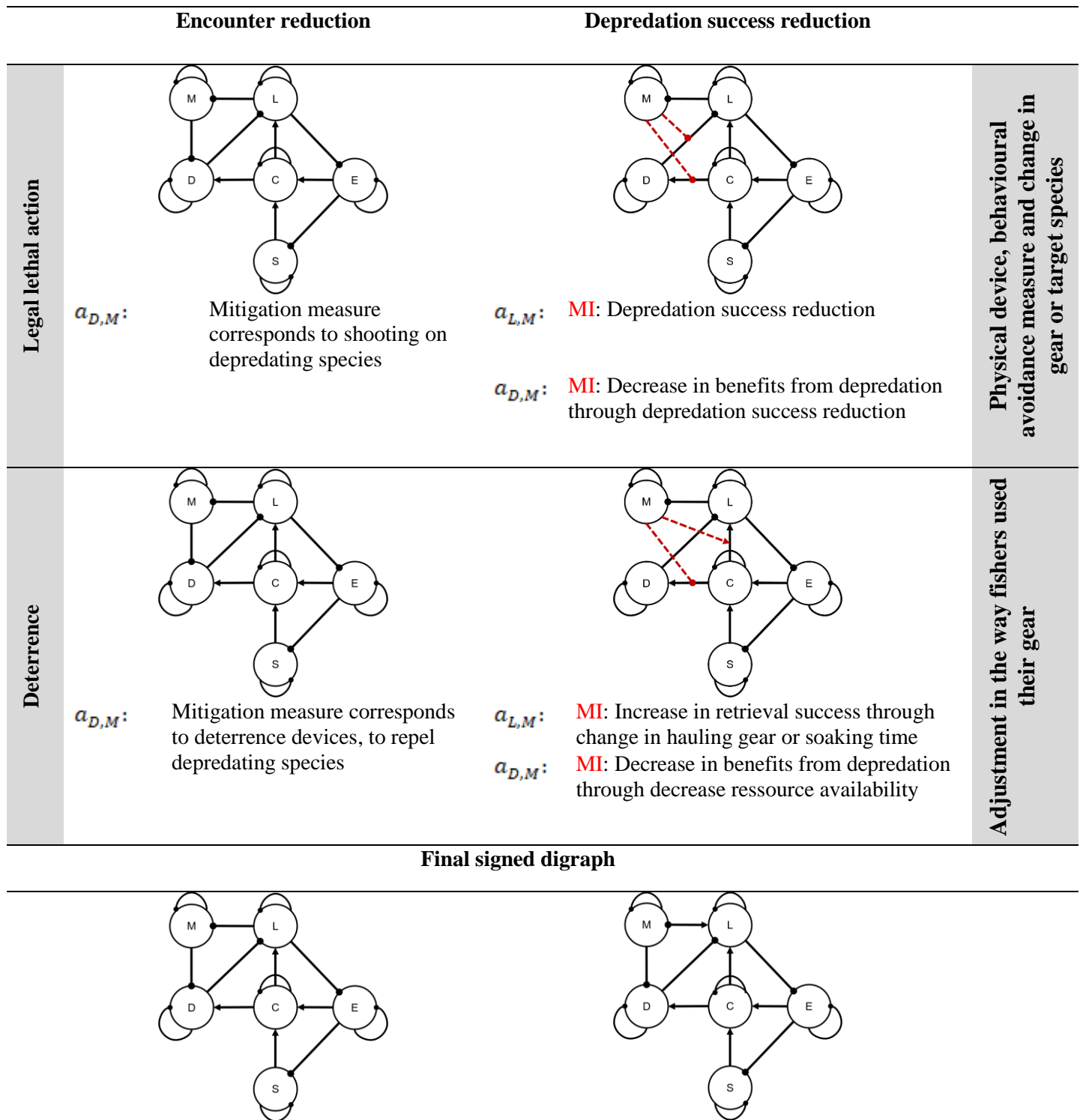


Figure S4.2: Existing mitigation techniques classification in two sign directed graphs. Modified interactions (**MI**) are represented as red dashed line. Variables included are; E: fishing effort, C: catches, D: biomass of depredating species, S: biomass of stock, L: landings and M: mitigation effort.

Chapitre 5 : Discussion générale

Cette thèse visait à explorer le potentiel des approches de modélisation pour prendre en compte les impacts multiples de la déprédation sur les diverses composantes des socio-écosystèmes marins. A défaut de proposer une stratégie de modélisation opérationnelle pour traiter de ce problème complexe qui affecte de nombreuses pêcheries dans l'océan mondial, cette thèse a permis d'amorcer, voire d'approfondir des réflexions notamment conceptuelles autour de conflit Homme-Faune sauvage en milieu marin. (1) Premièrement ce travail a permis d'identifier les limites, manques et priorités pour le développement d'approches de modélisation intégrant la déprédation. Ensuite, cette thèse a évalué (2) le potentiel de deux approches de modélisation en termes de caractérisation des impacts de la déprédation marine, de compréhension des enjeux qui y sont associés et d'identification des conditions requises pour que les activités halieutiques et les prédateurs marins puissent coexister. Enfin, (3) puisque cette thèse s'est principalement ancrée autour d'un cas concret, la dernière section de cette discussion proposera un bilan et des perspectives propres au cas de la déprédation des orques et des cachalots affectant la pêche française ciblant la légine australe autour de Crozet et Kerguelen.

5.1. Quelles sont les limites, manques et priorités actuelles au développement d'approche de modélisation intégrant la déprédation ?

Les résultats découlant de la revue systématique et des deux approches de modélisation (i.e. Ecopath (chapitre 3; [Christensen, 2005](#)) et la modélisation qualitative des boucles de rétroactions (chapitre 4; [Dambacher et al., 2015](#)) ont permis de mettre en évidence des limites, manques et priorités au développement d'approche de modélisation intégrant la déprédation. Ainsi, cette section décrit comment (1) le manque de quantification des processus liés à la déprédation, ainsi que (2) des limites structurelles propres aux outils de modélisation existants, constituent les principaux freins pour le développement d'approches opérationnelles prenant en compte la déprédation marine.

5.1.1 Manque de données

La première limite majeure au développement d'approche de modélisation est la disponibilité réduite de données, sur les niveaux de déprédation ou sur l'écologie du prédateur. Pourtant, une donnée essentielle à l'intégration de la déprédation dans les approches de modélisation est le taux de déprédation. Celui-ci permet, en effet, d'introduire d'une part la notion de perte pour l'homme et d'autre part la notion de gain pour le prédateur, ainsi que toutes les conséquences indirectes que cela implique. Toutefois, il peut être difficile d'obtenir ce type de données, en particulier dans le milieu marin. En effet, la déprédation n'est pas systématiquement détectée ou enregistrée, et rarement quantifiée. Les prédateurs peuvent déprédater les prises sur les engins de pêche en profondeur ou lorsque les pêcheurs sont absents voire laisser peu de traces lorsqu'ils retirent la ressource exploitée

(Tixier et al., 2021a). En outre les preuves de déprédation ne sont pas évidentes. Si les prises sur les engins de pêche peuvent n'être que partiellement consommées par les prédateurs, laissant des signes visibles de déprédation (têtes ou marques de dents), les prises peuvent également être totalement retirées et il est alors difficile de déterminer si la ressource a bien été piégée puis déprédée ou si la ressource n'a même jamais été capturée. Dans le cas où la déprédation a été observée ou a laissé des preuves évidentes, les données sont principalement qualitatives (Peterson & Hanselman, 2017; Werner et al., 2015). Si une approximation du taux de déprédation basée sur des renseignements qualitatifs peut aider à l'évaluation des conséquences de ces événements, l'impact réel de la déprédation peut être sous ou surestimé. Notamment, une quantification de la déprédation basée sur des témoignages ou l'expérience des personnes impliquées dans ce conflit peut conduire à des disparités entre la réalité objective et la perception subjective du risque (Hill, 2018). L'utilisation de caméras combinée à des données acoustiques ou d'accéléromètres peut venir en aide aux approches tentant de quantifier la fréquence des événements de déprédation et/ou la perte engendrée. Par exemple, des caméras sous-marines déployées sur les engins de pêche ont été utilisées afin d'étudier la déprédation des cachalots sur les palangres en Alaska (Mathias et al., 2012; Thode et al., 2015), et ont également révélé la déprédation de légine australe par des éléphants de mer (*Mirounga leonina*) autour des îles Heard et McDonald (van den Hoff et al., 2017). Quant aux accéléromètres ils ont permis de détecter des événements de déprédation par des fausses orques (*Pseudorca crassidens*) sur les palangres pélagiques à Hawaii (Thode et al., 2016) et par des cachalots sur les palangres démersales aux îles Crozet et Kerguelen (Richard et al., 2020).

Au-delà de la quantification du taux de déprédation, il est également clé d'évaluer en quelle proportion la part déprédée couvre les apports énergétiques des prédateurs. Cette information peut déterminer en quelle mesure ce dernier dépend des activités de pêche pour se nourrir. Au fil des générations, les individus prédateurs au sein d'une population peuvent se nourrir en grande partie ou exclusivement des captures de pêche, et ainsi devenir dépendants des pêcheries pour leur alimentation. Le déclin ou la baisse d'activité d'une pêcherie peut alors avoir un impact négatif sur ces individus habitués à une ressource plus facile d'accès (Fertl & Leatherwood, 1997). Une bonne quantification du taux de déprédation permet une évaluation plus précise des sources de mortalité sur les ressources exploitées, ce qui est crucial afin de déterminer des taux d'exploitation adéquats.

Le taux de déprédation n'est néanmoins pas la seule donnée rarement quantifiée. Les connaissances sur l'écologie des espèces prédatrices sont souvent limitées. En effet, ces espèces sont couramment réduites dans les études scientifiques à la perte engendrée par leur comportement (chapitre 2). Pourtant une meilleure connaissance de l'écologie des espèces prédatrices semble essentielle notamment pour évaluer et prédire les conséquences à long terme de la déprédation sur les populations de ces espèces et sur l'écosystème dont elles font partie (chapitre 4). En effet, un élément qui mérite d'être approfondi concerne l'influence de la déprédation sur certains paramètres démographiques de populations de

déprédateurs (Tixier et al., 2015a). Parmi les rares études sur le sujet, une corrélation positive entre la fréquence à laquelle les individus se nourrissent sur les palangres et leur taux de reproduction a par exemple été montrée chez les orques de Crozet (Tixier et al., 2015a). Dans le détroit de Gibraltar, le taux de mise bas des orques ainsi que le taux de croissance de leur population a été estimé plus élevé pour les individus déprédant le thon rouge en comparaison avec les individus sans interaction avec les pêcheries (Esteban et al., 2016). Toutefois, les espèces déprédatrices sont parfois victimes de blessures graves suite à ces interactions pouvant entraîner la mort. A titre d'exemple, les captures accidentelles sont fréquentes dans les filets statiques ou les chaluts (Read, 2008). La quantification des bénéfices et risques liés à la déprédation apportent des informations qui permettent de mieux évaluer le statut des espèces impliquées dans la déprédation ainsi que le devenir de ces populations à long terme. Des effets en cascade peuvent découler de cet accroissement de population ou encore des modifications importantes de son régime alimentaire. L'ampleur du changement de pression de prédation sur les proies naturelles peut non seulement dépendre de l'importance de la ressource déprédée dans le régime alimentaire naturel du prédateur, mais aussi de la position trophique de ce dernier, ainsi que de l'abondance de sa population et du bénéfice qu'il tire de cette interaction avec les pêcheries. La plupart des espèces déprédatrices sont de niveau trophique supérieur, comme les requins et les mammifères marins, ce qui est susceptible d'engendrer des effets en cascade descendants importants sur l'écosystème (Newsome et al., 2015). De plus, une autre particularité des mammifères est leur grande capacité d'apprentissage, ce qui favorise la dispersion du comportement de déprédation et qui mène à se questionner davantage sur l'augmentation de ce conflit à l'avenir (Nyhus, 2016). Des preuves circonstancielles de la transmission sociale du comportement de déprédation ont notamment été mises en évidence chez les cachalots dans le golfe d'Alaska (Schakner et al., 2014). De plus, malgré de nombreuses études focalisées sur des mesures de mitigation permettant d'atténuer la déprédation ainsi que les prises accessoires (Hamer et al., 2012, 2015; Mandelman et al., 2008; Werner et al., 2015), cette capacité d'apprentissage s'est avérée le principal obstacle à l'élaboration de stratégie de mitigation efficace. En effet, bien que des modifications technologiques ou stratégiques permettent à court ou moyen terme de réduire la quantité de ressources déprédée, les déprédateurs s'adaptent souvent sur le long terme en apprenant de nouvelles façon d'utiliser les engins de pêche (Varjopuro, 2011).

Ce manque de quantification et de connaissance engendre une faible intégration de l'ensemble des acteurs du conflit (i.e. homme, ressource exploitée ou produite, déprédateur) (chapitre 2). Les cas bien documentés, bénéficiant de données historiques, permettant une modélisation holistique sont rares. La déprédation étant située à l'interface entre les populations sauvages et les activités humaines, il est crucial d'intégrer l'ensemble de ces compartiments afin de comprendre les changements complexes dans la dynamique du socio-écosystème.

5.1.2. Limite structurelle des approches de modélisation

La seconde limite majeure aux développements d'approches de modélisation est liée aux structures des modèles eux-mêmes, qui rendent l'inclusion de la déprédation complexe. Par exemple, dans le modèle Ecopath, les groupes écologiques et les activités humaines sont représentés de manière indépendante. Comme d'autres modèles écosystémiques, Ecopath est initialement axé sur les réseaux alimentaires et les flux trophiques (Fulton et al., 2003). Par essence, c'est un obstacle structurel à l'intégration de la déprédation en tant qu'interaction à l'interface entre la population marine et les pêcheries. En effet, l'architecture du modèle Ecopath manque de flexibilité pour capturer facilement la déprédation étant donné que, d'une part, les interactions écologiques entre les espèces ou les groupes fonctionnels sont capturés via une matrice de régime alimentaire alors que, d'autre part, la pêche extrait la biomasse des espèces cibles du système (chapitre 3). L'architecture du modèle ne permet donc pas d'inclure les captures directement dans le régime alimentaire des prédateurs.

Les modèles à l'équilibre, comme Ecopath ou la modélisation qualitative, limitent par définition l'évaluation de la déprédation et de ses conséquences sur la dynamique des socio-écosystèmes. En effet, les écosystèmes ne sont pas en équilibre statique mais sont caractérisés par le changement. Ce changement peut être, par exemple, lié à des modifications de structures génétiques, de la biodiversité, de l'environnement ou encore des pressions anthropiques dues à des réponses comportementales humaines variables (Fulton, 2010). Certains de ces changements peuvent être induits par la déprédation, notamment une modification de la biodiversité liée à des effets en cascade (Newsome et al., 2015), et des réponses variables des pêcheurs qui adaptent leurs stratégies afin de réduire les pertes (Janc et al., 2021). Les modèles statiques et/ou à l'équilibre ne capturent donc que partiellement ces événements et leurs conséquences sur l'écosystème (chapitre 3). De plus, les interactions multi-espèces les plus intéressantes afin de déterminer les impacts de la pêche sur les écosystèmes marins sont celles qui provoquent des écarts marqués par rapport à l'état actuel. Les modèles contraints par des processus d'équilibre ont donc peu de chances de saisir ces écarts (Hollowed, 2000). La déprédation fait partie de ces interactions qui impliquent directement et indirectement un grand nombre d'espèces. L'hypothèse d'équilibre pose problème car les interactions entre espèces et les réponses individuelles des espèces à la pression de pêche sont non-linéaires, ce qui peut biaiser les interprétations basées sur ce type de modèle (Plagányi & Butterworth, 2004). Ceci peut être problématique dans la modélisation de socio-écosystèmes hautement dynamiques, incluant notamment des changements de proies par les prédateurs (Walters et al., 1997) ou des innovations comportementales et des adaptations variant au cours de l'année, ou d'une année à l'autre (Bearzi et al., 2019). Les activités de pêche pouvant être saisonnières, le régime alimentaire des espèces déprédatrices varie fort probablement au cours de l'année. Il a été notamment démontré, que les jours de déprédation, les orques déprédatrices ont satisfaits en moyenne 94% de leurs besoins énergétiques quotidiens avec les légines déprédées autour de Crozet (Faure et al., 2021). Cependant cette

contribution n'équivaut qu'à 1 à 13% des besoins énergétiques mensuels et 2 à 9% des besoins énergétiques annuels de la population totale (Faure et al., 2021).

5.2. Apport de la modélisation en soutien à la conservation des espèces sauvages et au maintien des activités

Malgré leurs limites, les approches de modélisation utilisées au cours de cette thèse, à savoir Ecopath (Christensen, 2005; chapitre 3) et la modélisation qualitative des boucles de rétroaction (Dambacher et al., 2015; chapitre 4), ont permis une première inclusion de la déprédation dans ces types d'approches, et se sont montrées complémentaires afin d'étudier ces effets à court et long terme sur les acteurs impliqués dans ce conflit mais aussi sur l'ensemble de l'écosystème. Tout d'abord, ces approches ont, toutes deux, permis de caractériser la compétition entre les déprédateurs et les pêcheurs, ainsi que ses conséquences indirectes comme l'accroissement de la mortalité par pêche pour compenser les pertes liées à la déprédation (chapitre 3, 4).

En complément de l'inclusion de cette conséquence, la modélisation qualitative a permis d'évaluer la viabilité d'un système composé d'une activité de pêche, d'un déprédateur et d'une ressource exploitée, et répondant à la perte de capture due à la déprédation par une intensification de l'effort. Cette viabilité semble dépendre de l'état de la ressource exploitée ainsi que la capacité de la pêcherie à supporter les coûts supplémentaires engendrés par la déprédation (chapitre 4). Cette stratégie est donc envisageable lorsque la ressource exploitée est bien gérée et que l'activité de pêche est suffisamment rentable pour supporter des coûts supplémentaires tels qu'un accroissement de la masse salariale ou une consommation accrue de carburant afin de compléter les quotas de pêche (Maccarrone et al., 2014; Peterson et al., 2014). D'autres scénarios ont pu être explorés, via cette approche, tel que l'augmentation des populations de déprédateurs ou des ressources exploitées (chapitre 4) et semblent particulièrement pertinents dans le cas des socio-écosystèmes impactés par la déprédation. En effet, l'augmentation de l'abondance des déprédateurs peut être causée par l'amélioration des performances physiologiques due à un accès facilité à la ressource alimentaire (Esteban et al., 2016; Tixier et al., 2015a) mais aussi au rétablissement des populations suite à l'arrêt de la chasse, des méthodes de mitigations létales ou encore la gestion des captures accessoires (Duhamel & Williams, 2011; Tixier et al., 2021a). L'analyse des réponses à long terme de ces systèmes face à l'augmentation de l'abondance des déprédateurs a démontré une baisse du rendement des pêcheurs dans tout type de socio-écosystème, ainsi qu'un effet négatif sur la ressource exploitée (chapitre 4). Ensuite, l'augmentation de la taille de la population des ressources exploitées a été étudiée. Bien que de nombreuses espèces cibles aient été surexploitées (Köster et al., 2003; Pauly, 2008), une augmentation ou un recouvrement de ces populations est envisagé notamment grâce à une meilleure régulation des pressions de pêche basée sur leur évaluation. Toutefois, l'analyse des réponses à long terme démontre qu'une augmentation de la disponibilité de la ressource dans ces systèmes affectés par la déprédation ne

garantit pas systématiquement une augmentation du rendement de pêche (chapitre 4). En effet, dans le cas des systèmes affectés par la déprédation, la capturabilité et donc indirectement le rendement de pêche, dépend certes de l'état de la ressource, pouvant être améliorée via des mesures de restauration, mais celle-ci dépend également de la capacité des déprédateurs à prélever la ressource sur les engins. Face à ces deux scénarios, les mesures de mitigation efficaces semblent essentielles afin de permettre à la ressource exploitée, la pêche et les espèces déprédatrices de coexister (chapitre 4).

De par sa résolution écosystémique les modèles Ecopath ont permis d'inclure le changement de pression de prédation sur les proies naturelles du déprédateur et de la ressource exploitée, ce qui n'a pu être le cas des modèles qualitatifs centrés sur les acteurs directs de la déprédation (i.e. pêcheur, déprédateur, ressource exploitée). Par conséquent, les effets en cascade liés aux changements de pression de prédation ont pu être identifiés et quantifiés (chapitre 3). Certes faible dans le cas de Crozet-Kerguelen, les impacts en cascade peuvent être plus importants lorsque la ressource déprédée est absente du régime alimentaire, comme c'est le cas pour les phoques communs (*Phoca vitulina*) déprédant l'anguille des filets en Suède (Lundström et al., 2010).

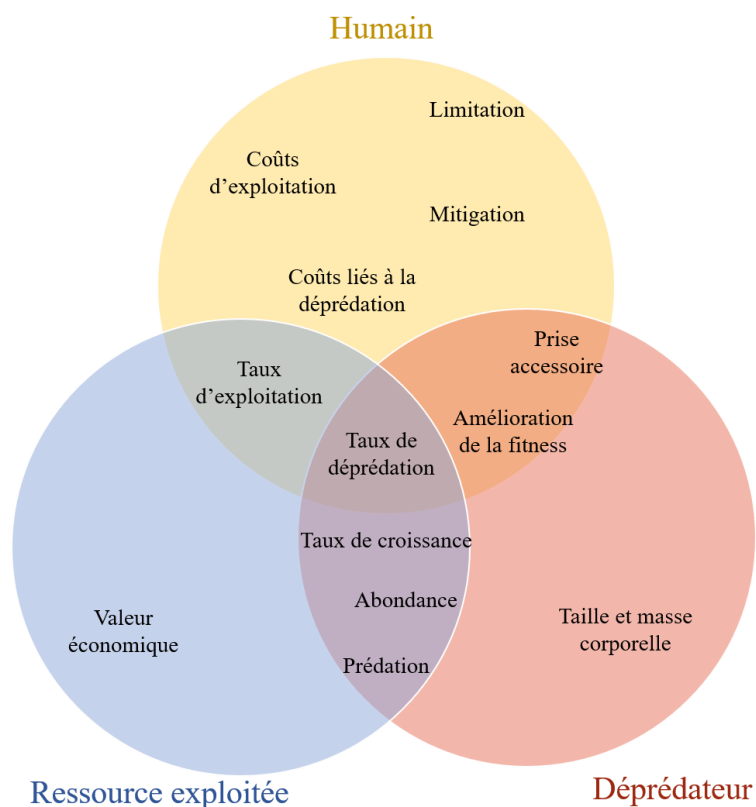


Figure 5.1 : Schéma conceptuel des facteurs majeurs identifiés grâce aux approches de modélisation utilisées au cours de cette thèse, impliquant trois compartiments principaux : l'humain, le déprédateur et la ressource exploitée.

Néanmoins le bénéfice que tire le prédateur de cette interaction n'a pu être inclus dans sa globalité au sein du modèle Ecopath. Cependant, il a été explicitement pris en compte dans les modèles qualitatifs. Il a d'ailleurs été démontré que ce bénéfice joue un rôle important dans la viabilité des socio-écosystèmes affectés par la déprédation. Par exemple, dans les systèmes impliquant des déprédateurs à longue durée de vie et à croissance lente, et donc dont la croissance de la population bénéficie de manière significative de la déprédation, les efforts de restauration des ressources exploitées peuvent être réduits à néant (chapitre 4). La modélisation qualitative a en effet permis d'identifier des processus majeurs impliqués dans les réponses à long terme et la viabilité des socio-écosystèmes notamment : (1) la dynamique de population de la ressource exploitée et son statut d'exploitation ; ainsi que (2) l'écologie du déprédateur et de sa compétition avec les pêcheurs pour la ressource piégée (**Figure 5.1** ; chapitre 4).

En identifiant et quantifiant les impacts la déprédation en générale et selon des scénarios alternatifs, ces deux approches de modélisation permettent d'éclairer les futures actions de gestion (**Figure 5.1**).

5.3. Perspectives pour le développement d'approches de modélisation intégrant la déprédation

Les trois chapitres principaux de cette thèse permettent de prioriser des recommandations afin de mieux comprendre et prévoir les effets de la déprédation sur les socio-écosystèmes marins. Ces recommandations sont illustrées à l'aide d'un modèle conceptuel générique contenant les concepts et relations pertinents et prioritaires qui composent un système affecté par la déprédation dans le milieu marin (**Figure 5.2**). Ce modèle conceptuel contient six compartiments en étroite interaction les uns avec les autres et implique une liste non exhaustive de facteurs majeurs à prendre en compte dans les futures approches de modélisation (**Figure 5.2**).

Tout d'abord, certains facteurs influencent l'occurrence et la sévérité des événements de déprédation. Certains de ces paramètres impactent directement les captures et donc indirectement la déprédation. Dans l'océan Atlantique, les captures d'espadon et de thon sont notamment liées à la phase lunaire, à la couverture nuageuse, à la température de surface de la mer ainsi qu'à la profondeur d'eau, tandis que l'occurrence des événements observés de déprédation par les cétacés est principalement liée à l'abondance des captures ([Hernandez-Milian et al., 2008](#)). La distance par rapport à la côte joue également un rôle important et explique en partie la déprédation des orques sur les captures de la pêche palangrière pélagique Uruguayenne ([Passadore et al., 2015](#)). Le stade de vie ainsi que le sexe de la ressource exploitée peuvent influencer la déprédation. Par exemple, dans le sud-est de l'Australie, le risque de déprédation des casiers par la pieuvre Maori (*Pinnoctopus cordiformis*) augmente notamment avec la taille des langoustes (*Jasus edwardsii*) et est plus élevé pour les mâles ([Briceño et al., 2015](#)). L'abondance de la ressource exploitée ou des proies naturelles peut également affecter la distribution du déprédateur et par conséquent l'occurrence des événements de déprédation,

tel que démontré avec le dauphin commun (*Delphinus delphis*) dans les Açores (Cruz et al., 2016). Certaines techniques et engins de pêche semblent plus impactés que d'autres par la déprédation. Dans la mer Égée, les engins les plus fréquemment déprédés par les dauphins étaient les filets maillants et les trémails à petites mailles, ciblant principalement le rouget-barbet de roche (*Mullus surmuletus*), le rouget de vase (*Mullus barbatus*), la sole commune (*Solea solea*), le merlu commun (*Merluccius merluccius*) et la crevette caramote (*Melicertus kerathurus*) (Pardalou & Tsikliras, 2020). Les déprédateurs peuvent également se montrer sélectifs sur la ressource qu'ils prélèvent (Dalla Rosa & Secchi, 2007; Kock et al., 2006; Nolan et al., 2000; Visser, 2000). En effet, les orques ne retirent que la légine australe et laissent les espèces accessoires, comme le grenadier (*Macrourus sp.*) et la moridée (*Antimora rostrata*) en Géorgie du sud (Kock et al., 2006). En Nouvelle Zélande, les orques ne prélèvent que les requins à grand ailerons (*Galeorhinus galeus*) ainsi que le rouffe antarctique (*Hyperoglyphe antarctica*), et délaissent les autres espèces (Visser, 2000).

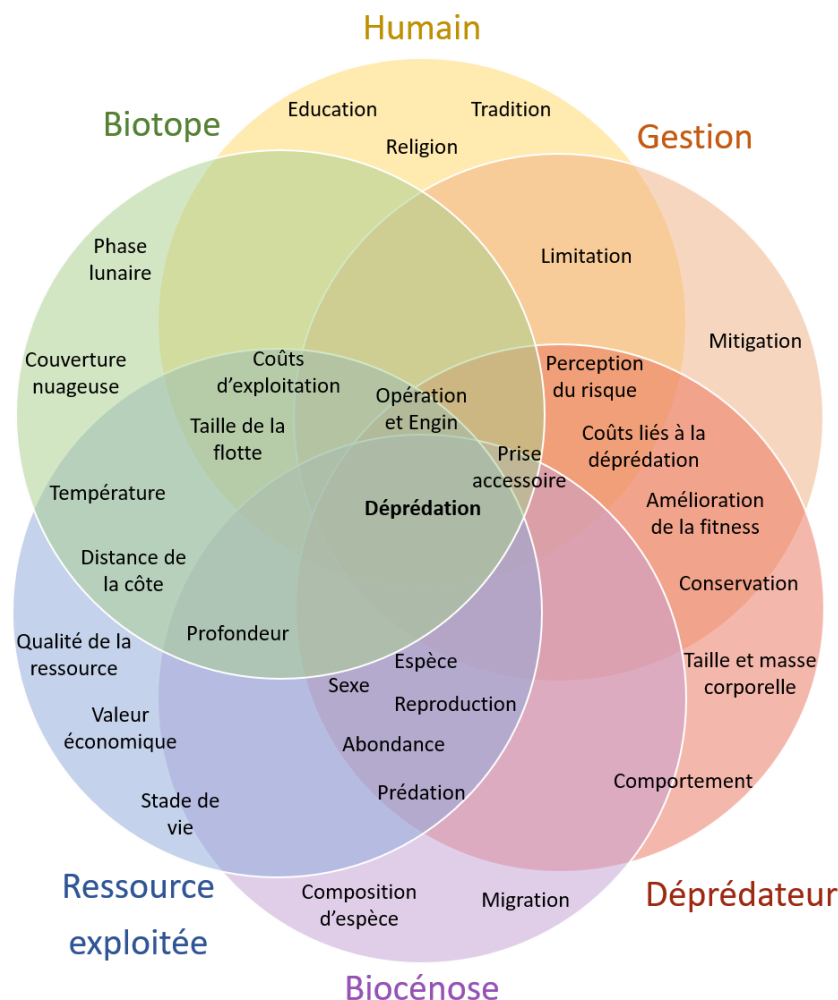


Figure 5.2 : Un modèle conceptuel générique de la déprédation des ressources piégées dans les engins de pêche composé de six compartiments en étroite interaction. La liste de facteurs majeurs est non exhaustive.

Ensuite, afin d'évaluer la viabilité de l'activité humaine, il est important de considérer les divers coûts engendrés par la déprédation mais aussi les bénéfices tirés de la ressource exploitée. Les coûts divergent en fonction de la sévérité des événements de déprédation variant de 1 à 67% des débarquements (Hernandez-Milian et al., 2008 ; Köningson, 2011) mais aussi en fonction des stratégies et mesures de mitigation. Bien que les méthodes qui tentent d'entraver la capacité des prédateurs à retirer les prises des engins de pêche semblent être le plus efficace afin de réduire la déprédation, ces méthodes sont probablement les plus coûteuses. Il est donc primordial que les coûts supplémentaires restent inférieurs aux bénéfices obtenus en minimisant la déprédation (Trijoulet, 2016; Trijoulet et al., 2018). La viabilité de l'activité dépend également de la valeur économique, de la qualité et de l'abondance de la ressource exploitée. Afin de déterminer un niveau d'exploitation adéquat, il est donc primordial de bien évaluer l'ensemble des pressions subies par la ressource exploitée. Cependant, plusieurs composantes de la mortalité par pêche, en particulier les sources cryptiques, ne sont pas systématiquement prises en compte dans la gestion des pêches en raison du manque de données adéquates ou du manque de méthodes d'estimation précises (Chopin et al., 1996; Gilman et al., 2013, 2014; Hall et al., 2000). Les mesures de conservation et de gestion des pêches peuvent alors être compromises lorsque les évaluations de stocks et les modèles de population ne tiennent pas compte des mortalités cryptiques (Coggins et al., 2007; Crowder & Murawski, 1998; Pollock & Pine, 2007). Il est à noter que la déprédation est jusqu'à présent rarement prise en compte.

Toutefois, les mesures de gestion et de conservation, qu'elles concernent les espèces sauvages ou exploitées, peuvent être influencées par l'éducation, les traditions ou encore la religion (Hill, 2018). De plus, la taille et/ou la dangerosité du prédateur ainsi que la valeur économique de la ressource exploitée influencent la perception du risque lié à la déprédation, qui elle-même impacte la propension à tuer ou à conserver les espèces impliquées (Hazzah et al., 2013). Cependant si l'abattage a été le principal moyen de gérer la déprédation pendant des décennies, l'état de conservation critique de la plupart des grands carnivores a obligé les gestionnaires à trouver d'autres réponses non létales afin de réduire ce conflit (Treves & Karanth, 2003). Dans ce contexte, l'ensemble des informations pouvant impacter les mesures de gestion doivent être prises en considération afin d'intégrer toute la complexité du socio-écosystème.

Ce modèle conceptuel générique de la déprédation pourrait aider au développement de modèles statistiques ou mécanistiques lorsque les données nécessaires le permettent, ou encore à cibler l'effort de recherche et de quantification sur certains paramètres précis. De par leurs structures ou leurs approches certains modèles semblent adéquats afin d'intégrer la déprédation de manière holistique. Des modèles écosystémiques, comme Atlantis (Fulton et al., 2011) peuvent en effet quantifier les impacts économiques et écologiques, ainsi que les impacts en cascade engendrés par la déprédation. La modélisation multi-agent (Marley et al., 2017; Piédallu, 2016) et la modélisation qualitative (Dambacher et al., 2015; Marzloff et al., 2016; Szymkowiak & Rhodes-Reese, 2020) peuvent, évaluer

et prévoir l'évolution du socio-écosystème en réponse à divers scénarios. Enfin la modélisation bioéconomique (Béné et al., 2001; Gourguet et al., 2013; Loch-Temzelides, 2021; Skonhofs, 2017; Trijoulet et al., 2018) permet de déterminer une solution optimale conciliant viabilité de l'activité et maintien des populations impliquées. L'ensemble de ces modélisations semble nécessaire pour comprendre et évaluer la résilience ainsi que la durabilité des socio-écosystèmes touchés par la déprédation, afin d'informer des actions de gestion écosystémique efficaces.

Toutefois les différents facteurs nécessaires à la construction de ces modèles intégrant explicitement la déprédation, exigent une coopération interdisciplinaire afin de synthétiser de multiples ensembles de données historiques et contemporaines, provenant des sciences biophysiques, sociales et économiques (Nyhus, 2016; Piédallu, 2016; Shaffer et al., 2019). Jusqu'à présent, une grande partie des études existantes se concentre soit sur les aspects socio-économiques soit sur les dimensions écologiques ou de conservation (Tixier et al., 2021a).

Ces perspectives d'applications focalisées sur les cas marins peuvent s'étendre au cas de déprédation terrestre et plus globalement à l'ensemble des conflits d'usages : attaques sur les humains, chasse récréative, prises accessoires, transmission de maladies, destruction des cultures (Woodroffe et al., 2005). En effet, ces conflits d'usages partagent des caractéristiques communes et peuvent se produire en même temps que les événements de déprédation. Comme précisé précédemment, les événements de déprédation peuvent notamment mener à des prises accessoires de prédateurs (Hamer et al., 2012). Un grand nombre de prises accessoires de phoque a été documenté dans les eaux Irlandaises, où les phoques sont également connus pour déprédater les captures de merlu commun (*Merluccius merluccius*), de la lotte (*Lophius sp.*) et du lieu jaune (*Pollachius pollachius*) (Cosgrove et al., 2013). Des attaques sur les humains peuvent également survenir lorsque les humains tentent de protéger la ressource exploitée ou produite face à des événements de déprédation. La modification de l'aire de distribution provoquée par la déprédation (Blasi et al., 2015 ; Chilvers et al., 2003), peut augmenter les chances de rencontre entre l'homme et les prédateurs, accroissant indirectement la probabilité d'attaque. De plus, les interactions entre la faune sauvage et les ressources produites, dont la déprédation fait partie, peuvent également mener à la transmission de maladies. Il est important de noter que la transmission de ces maladies peut être bidirectionnelle, ce qui constitue une grave menace pour les espèces sauvages vulnérables et les espèces produites indigènes. Enfin des destructions de cultures peuvent s'ajouter aux événements de déprédation provoquant des coûts additionnels qui sont essentiels afin de calculer les pertes dues à la faune sauvage dans leur globalité. Outre, l'intérêt d'inclure l'ensemble des acteurs au sein des futures approches de modélisation, ces conflits pourraient être étudiés au sein d'un même modèle afin de mieux comprendre ces événements et soutenir les actions de gestion efficace à l'échelle du socio-écosystème.

5.4. Bilan et recommandations sur le cas spécifique Crozet-Kerguelen

Grâce à la grande disponibilité en données historiques concernant la pêche et ses interactions avec les mammifères marins, les îles Crozet et Kerguelen représentent un cas d'étude idéal sur lequel une large partie du travail de recherche s'est articulé afin de mettre au point les approches de modélisation. Ainsi, cette section propose un bilan et des perspectives autour de ce cas d'étude, notamment autour de la viabilité de la pêcherie palangrière ciblant la légine australe affectée par la déprédation et les conséquences écosystémiques associées. Afin d'apporter un point de vue dynamique sur le devenir de ce socio-écosystème, cette section décrit également des éléments de contexte régional, où d'important changements tant écologiques qu'environnementaux sont à prévoir dans les prochaines décennies.

5.4.1. Évaluation de l'impact de la déprédation au travers d'approche de modélisation

De par la haute valeur commerciale de la ressource ciblée, sa rentabilité, le faible niveau d'exploitation du stock, la gestion précoce de cette pêcherie restreinte à un petit nombre de bateaux, et de par l'écologie du déprédateur, l'impact de la déprédation des orques et des cachalots sur les palangriers démersaux exploitant la légine australe semble limité. La compensation des pertes de captures causées par la déprédation ne semble ni compromettre la viabilité de l'activité de pêche, ni mettre en péril le stock. En effet, la légine australe est une ressource à forte valeur économique, vendue jusqu'à 35 US\$/kg brut (Grilly et al., 2015). En métropole, son prix de vente de gros est supérieur à 45 € ; en comparaison la lotte, le bar ou le turbot se vendent à moins de 25 € (INSEE, 2017). D'après une étude de l'INSEE basée sur les données de l'année 2014, le chiffre d'affaires de la pêche australe s'élève à 81 millions d'euros avec un taux de marge de 67%, ce qui est beaucoup plus élevé en comparaison avec les pêcheries métropolitaines qui ont un taux de marge plutôt aux alentours de 30% (INSEE, 2017). Toutefois, l'éloignement des îles australes, leur isolement et les conditions climatiques extrêmes impliquent des coûts plus élevés pour les pêcheries à la légine que pour d'autres pêcheries. Notamment les armateurs doivent se munir de navires spécialisés, capables d'opérer de manière autonome dans les eaux subantarctiques pendant plusieurs mois, et donc très onéreux (CGefi, 2019). Les coûts liés à la déprédation s'ajoutent donc à une activité de pêche relativement coûteuse, et bien que globalement ces coûts semblent mineurs par rapport aux bénéfices de l'activité à l'échelle de la pêcherie, ils varient entre les armements. Ces variations sont liées à des différences dans les coûts salariaux, les charges d'exploitation, les stratégies de développement et d'investissement ou encore l'âge des bateaux (CGefi, 2019). Malgré la rentabilité de cette pêcherie, certains armateurs pourraient être mis en difficulté par une hausse des coûts. En ce qui concerne la population de légine australe, elle est stable, voire croissante, malgré son exploitation de 6000 tonnes/an, partagées entre 7 bateaux (Duhamel & Williams, 2011). Grâce à une gestion avancée, le stock semble, en effet, pouvoir supporter le niveau d'exploitation actuel équivalant à 2,5% de la population estimée en 2019 à Kerguelen et à 1,5% à Crozet (CCAMLR, 2020a, 2020b). La population féconde est d'ailleurs estimée

à 60,5% à Kerguelen et à 63% à Crozet (CCAMLR, 2020a, 2020b). Toutefois, la légine, comme de nombreux poissons d'eaux profondes vivant dans des environnements constants, présente des caractéristiques de sélection K en matière d'histoire de vie, telle qu'une croissance lente, une maturité sexuelle tardive, une grande taille corporelle et une longue durée de vie (Collins et al., 2010), ce qui la rend vulnérable à l'augmentation du taux d'exploitation, même très faible. Il faut donc rester vigilant sur la pression supplémentaire de pêche qu'exige la compensation des pertes causées par la déprédation, et surveiller son évolution dans le temps. Par ailleurs, les premiers résultats suggèrent que la déprédation n'induit pas ou peu de modifications du régime alimentaire des orques ayant développées ce comportement à Crozet, impactant donc faiblement la dynamique de la ressource exploitée ou encore la dynamique des autres proies (chapitre 3). En effet, malgré une consommation substantielle à fine échelle (quotidienne ou individuelle), conduisant à des effets temporaires d'approvisionnement et à des changements dans les pressions de prédation, ces effets sont mineurs à l'échelle annuelle (<10% des besoins énergétiques annuels de la population sont comblés par de la légine consommée sur les palangres; Faure et al., 2021). De plus, la quantité globale de légine consommée est similaire entre les orques déprédatrices et non déprédatrices, ce qui suggère que la prédation naturelle des orques sur cette proie serait partiellement remplacée par la déprédation sur les captures (Tixier et al., 2019).

En termes d'impacts écosystémiques de la pêche et de la déprédation, la compréhension des possibles effets en cascade reste difficile à réaliser, particulièrement autour de l'île de Crozet. En effet, les campagnes de pêche scientifique au chalut, utilisées pour évaluer la taille de population des diverses espèces de poissons sont uniquement effectuées autour de Kerguelen (e.g. POKER Martin & Pruvost, 2007) et les informations sont rares autour de l'archipel de Crozet. Cela est notamment due à sa topographie non accessible au chalut de fond. Pourtant, le taux de déprédation équivaut 30% des captures totales, alors qu'il n'atteint que 6% à Kerguelen (Gasco et al., 2015; Tixier et al., 2020). Toutefois, les captures étant plus importantes autour de Kerguelen, la quantité de ressource déprédée chaque année est similaire entre les deux archipels et est estimée à 279 tonnes à Crozet et 250 tonnes à Kerguelen (Gasco et al., 2015; Tixier et al., 2020).

Malgré ce manque de données le modèle écosystémique ECOPATH développé dans le cadre de cette thèse, a tenté de couvrir les 3 075 704 km² englobant ces deux archipels ainsi que les eaux internationales qui les séparent (Annexe 3.S1). Cette thèse a donc permis l'inclusion de Crozet, alors que les précédents modèles écosystémiques se focalisaient sur Kerguelen uniquement (Pruvost et al., 2005; Subramaniam et al., 2019, 2020). Cependant, même si une grande partie des espèces, impliquées directement ou indirectement dans le processus de déprédation, sont inféodées aux plateaux, les déprédateurs ainsi qu'une partie de leurs proies naturelles ont une aire de répartition plus large. En effet, les cachalots utilisent la zone de Crozet et Kerguelen pour se nourrir de manière saisonnière, et rejoignent les basses latitudes afin de se reproduire (Rice, 1989). A l'inverse, les éléphants de mers

mâles se rendent sur ces îles afin de former leur harem et de se reproduire, mais s'éloignent afin de s'alimenter. Enfin, l'écologie tout comme l'aire de répartition des orques de type D (écotypes D – subantarctique) est peu connue, et il est possible que ces orques se déplacent au-delà des limites spatiales de l'étude (Jefferson et al., 2007; Pitman et al., 2011). Une emprise spatiale adéquate du modèle est essentielle afin d'inclure le cycle de vie de ces espèces et leur interaction avec l'ensemble du socio-écosystème (i.e. proie-prédateur, compétition, déprédation). Il pourrait donc être envisagé d'étendre la zone géographique étudiée. Par ailleurs, une extension de la zone accroît la quantité de données nécessaires ainsi que les connaissances requises afin de mieux représenter l'écosystème et ces interactions, et comme précédemment soulevé celles-ci sont souvent limitées.

Dans ce contexte, seul le bénéfice de la déprédation a été considéré pour les prédateurs (Tixier et al., 2015a). En réalité, les données démographiques issues d'un suivi à long-terme indiquent que l'effet positif de la déprédation détecté sur les taux de reproduction des orques (Tixier et al., 2015a) est contre balancé par une surmortalité (taux de survie des individus anormalement bas comparé à celui d'orques d'autres populations) qui persiste au sein de la population de Crozet (Tixier et al., 2017, 2021b). L'observation d'un individu portant la marque d'un impact de balle en 2019 suggère que cette surmortalité pourrait être causée par le fait que ces orques sont encore exposées à des pratiques létales utilisées par des pêcheries opérant illégalement en bordure ou dans les ZEE de Crozet et Kerguelen.

5.4.2. Réflexions prospectives concernant le futur de cet écosystème et de cette pêcherie subantarctique

Afin de comprendre la dynamique complexe du socio-écosystème de Crozet et Kerguelen, la dimension temporelle autant que son hétérogénéité spatiale semble cruciale à considérer. Dans ce contexte, une approche dynamique de modélisation écosystémique serait cruciale afin d'examiner les conséquences de scénarios alternatifs.

Tout d'abord, il est possible que les populations de cachalots soient dans une phase de rétablissement progressif suite à l'arrêt de la chasse commerciale (arrêt au début des années 1980 à Kerguelen). Ce rétablissement probable interroge sur l'évolution des niveaux de déprédation de la part de cette espèce dans les années à venir. Entre 2008 et 2015, la déprédation par les cachalots s'est produite sur 41% des opérations de pêche à Kerguelen, entraînant une perte estimée à un minimum de 2 649 tonnes de légine, soit 5% des captures totales par an (Janc et al., 2018) Si aucune tendance dans la fréquence des événements de déprédation par les cachalots n'a encore été détectée à Kerguelen, où leur déprédation est déjà parmi les plus élevées de la zone subantarctique (Tixier et al., 2019), une augmentation du nombre de cachalots dans la région pourrait mener à une intensification du conflit avec la pêcherie.

Ensuite, bien que les activités illégales de pêche aient été fortement réduites, voire supprimées au sein des ZEE depuis 2004 par la mise en place de mesures de surveillance (Duhamel & Williams, 2011), il

est possible que ces activités persistent à des niveaux non-négligeables en bordure de ZEE. En effet, de par leur isolement, la surveillance et le contrôle de l'exploitation dans les eaux australes sont complexes, et en raison de leur haute valeur économique la légine australe attire de nombreuses flottes. Récemment, des albatros équipés de loggers, détectant et localisant la présence de navires et transmettant immédiatement l'information aux autorités, ont permis d'estimer la proportion de navires de pêche non déclarés opérant dans les eaux nationales et internationales de l'océan Austral (Weimerskirch et al., 2020). Dans les eaux internationales plus d'un tiers des navires ne possédaient aucun système d'identification automatique en fonctionnement (Weimerskirch et al., 2020). Etant donnée l'impact passé des activités de pêche illégales sur la légine, mais aussi les répercussions sur les prises accessoires d'espèces menacées, cette pression de pêche supplémentaire semble essentielle afin d'évaluer la dynamique à long terme des différentes populations impliquées.

Enfin, dans un contexte de changement climatique global, les changements environnementaux à venir dans cette zone subantarctique pourraient avoir des impacts assez critiques sur de nombreuses espèces marines. Notamment, le déplacement vers le sud du courant circumpolaire antarctique et des fronts océaniques associés, la fonte des glaciers, l'augmentation de la température de l'air et la diminution de la vitesse des vents pourraient profondément bouleverser les communautés des régions subantarctiques, du plancton jusqu'aux mammifères ou oiseaux marins (le Roux & McGeoch, 2008; Mélice et al., 2003; Rouault, 2005; Smith, 2002; Subramaniam et al., 2020). En effet, un grand nombre d'espèces locales sont adaptées aux eaux froides et possèdent des capacités de régulation limitées ou très coûteuses d'un point de vue énergétique (Cárdenas et al., 2018; Gutt et al., 2018; Stenni et al., 2017). Par exemple, la répartition spatiale des espèces benthiques autour du plateau de Crozet-Kerguelen devrait subir d'importants changements dans les prochaines décennies (Guillaumot et al., 2018). Ces changements sont également susceptibles de modifier la structure et la fonction des communautés phytoplanctoniques qui peuvent à leur tour affecter la biogéochimie de l'océan Austral, l'exportation de carbone mais aussi la nutrition des niveaux trophiques supérieurs (Deppeler & Davidson, 2017). A Kerguelen, des différences marquées, dépendantes de la stratégie de recherche de nourriture, sont d'ores et déjà visibles chez les éléphants de mer et semblent liées aux changements des communautés phytoplanctoniques (Mestre et al., 2020). Les petits nés de mères s'adonnant à la recherche de nourriture dans l'habitat subantarctique sont en moyenne de 5,8 kg plus lourds que leurs congénères nés de mères favorisant la recherche de nourriture dans l'habitat antarctique au moment du sevrage (Mestre et al., 2020). Bien que cela leur confère un avantage certain, eux seuls ont montré une diminution de la masse au sevrage ces dix dernières années (Mestre et al., 2020), ce qui peut avoir un impact sur le recrutement de la population en raison d'une réduction de la survie (McMahon et al., 2000, 2005, 2003; Postma et al., 2013). Les espèces possédant de vastes niches écologiques et n'étant pas limitées par des barrières biogéographiques semblent pouvoir supporter plus aisément ces

changements environnementaux en comparaison des espèces endémiques, limitées aux zones côtières (Guillaumot et al., 2018).

Si l'ensemble de ces scénarios concernant le changement des conditions océaniques régionales sont susceptibles d'impacter lourdement les communautés écologiques de ces archipels, les réponses individuelles et populationnelles de la légine australe restent difficiles à appréhender. En particulier, les effets complexes de ces changements sur les différents stades de son cycle de vie restent largement méconnus. Or, de par sa grande longévité et sa croissance lente, et puisqu'il constitue une ressource majeure à la fois pour de nombreux grands prédateurs mais aussi pour les activités halieutiques dans la zone, le stock de légine sera particulièrement sensible à l'augmentation des taux de mortalité. Cependant, les connaissances sur l'écologie de la légine australe, telles que les mouvements, la connectivité, le comportement reproductif et l'utilisation de l'habitat sont encore mal compris (Péron et al., 2016). Si des études récentes ont permis de mieux caractériser la structure spatiale du stock de légine et sa niche environnementale (notamment en terme de température de fond, les courants et la concentration en oxygène) (Péron et al., 2016), des études complémentaires sont nécessaires afin de prédire le devenir de leur population face à ces différents scénarios.

En conclusion, les impacts de la déprédation sont multiples, complexes et concernent l'ensemble du socio-écosystème. Ces impacts peuvent en effet mettre en péril la viabilité économique des activités halieutiques. Les coûts induits sont, à la fois, directs, avec une baisse des rendements de pêche due au prélèvement par les déprédateurs des captures dans l'engin de pêche et indirects dus aux efforts et stratégies de prévention et de protection de la ressource, au déploiement de l'effort d'exploitation supplémentaire afin de maintenir le rendement, voire même dus aux dégâts matériels (Beeson & Hanan, 1996; Maccarrone et al., 2014; Perera, 2009; Peterson et al., 2014). Par ailleurs, le prélèvement de la ressource peut bénéficier au déprédateur, en améliorant leur forme physique au niveau individuel, ainsi que leurs performances démographiques (Esteban et al., 2016; Newsome et al., 2015; Tixier et al., 2015a). Ce bénéfice pour le déprédateur peut être particulièrement fort dans le cas où la ressource déprédée est hypercalorique (Read, 2008). Toutefois, prélever la ressource des engins de pêche présente des risques, car cela peut engendrer des blessures, voire la mort des individus au travers de prises accessoires ou de mesure létale de mitigation (Azevedo et al., 2017; Brand & Nel, 1997; Dans et al., 2003; Naughton-Treves & Treves, 2005; Read, 2008; Tuytens et al., 2000). A long terme, la densité de population des déprédateurs peut en être impactée pouvant induire une modification de la pression de prédation sur l'ensemble de leurs proies. La déprédation semble donc être en mesure de provoquer des changements complexes dans la dynamique des socio-écosystèmes marins. Le développement d'approches de modélisation, tenant compte des priorités mis en évidence au travers de cette thèse, et donc capable de saisir avec précision ces impacts socio-économiques et écologique complexes inhérents au conflit de déprédation, semble essentiel afin d'identifier les conditions nécessaires à la coexistence de la faune sauvage et des activités d'exploitation, mais aussi

de production humaine plus largement. Ce qui pourrait également venir en aide aux actions de gestion des écosystèmes.

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Liste des encadrements

Co-encadrement M1 : « Quels sont les facteurs majeurs influençant la déprédation de la pêche à la légine australe, au sein des archipels de Crozet et Kerguelen entre 1996 et 2017 ? » par Andéol Bourgouin 2018-2019

Co-encadrement M2 : « Evaluation préliminaire des impacts trophiques de la déprédation de la pêcherie de légine australe (*Dissostichus eleginoides*) par les cétacés autour des îles Kerguelen et Crozet » par Johanna Faure 2018-2019

Listes des enseignements

Moniteur en Biologie de la diversité, licence 1, Université Bretagne Occidentale

Moniteur en Biologie animale, licence 1, Université Bretagne Occidentale

Titre: Effets de la déprédation sur les systèmes marins : Aperçu d'une analyse documentaire mondiale et application d'autres méthodes de modélisation à des études de cas régionaux

Mots clés : déprédation, conflit homme-faune sauvage, modélisation, socio-écosystèmes, viabilité, coexistence

Résumé : Les espèces qui se nourrissent de plantes ou d'animaux élevés ou capturés par l'homme, un comportement appelé « déprédation », entraînent souvent de graves Conflits Homme-Faune sauvage (CHF). La déprédation a été signalée dans le monde entier et, dans les écosystèmes marins, elle a été développée par de nombreux grands prédateurs se nourrissant des prises de pêche, ce qui a un impact à la fois sur les activités de pêche et les interactions écologiques. Cependant, bien que les approches écosystémiques soient de plus en plus utilisées dans la gestion des pêches, les effets de la déprédation sur l'ensemble de l'écosystème sont encore rarement considérés de manière holistique. Par conséquent, cette thèse a (i) d'identifié les limites, manques et priorités pour le développement d'approches de modélisation intégrant la déprédation et (ii) évalué la capacité de deux approches de modélisation existantes pour caractériser les conséquences de la déprédation marine et, plus spécifiquement, comprendre les enjeux et conditions requises pour que les activités d'exploitation halieutique et les déprédateurs marins puissent co-exister.

Cette thèse est composée de cinq chapitres. Le chapitre 1 présente le contexte dans lequel s'inscrit ces travaux. Le chapitre 2 identifie les principales lacunes dans les connaissances et met en évidence les principales orientations futures pour parvenir à une inclusion efficace de la déprédation dans les études de modélisation en réalisant une revue systématique. Le chapitre 3 utilise le cadre Ecopath pour évaluer les effets de la déprédation sur l'écosystème dans une étude de cas bien documentée impliquant des mammifères marins et une pêcherie commerciale. Le chapitre 4 s'appuie sur une modélisation qualitative pour évaluer les conditions de persistance d'une ressource exploitée, d'une pêcherie et d'une espèce déprédatrice dans les systèmes marins touchés par la déprédation, et la façon dont la déprédation marine affecte les réponses à long terme à des scénarios alternatifs. Enfin, la discussion générale présentée dans le chapitre 5, fournit des recommandations qui vise à mieux comprendre et prévoir les effets de la déprédation au niveau du socio-écosystème.

Title: Effects Of Depredation On Marine Systems: Insights From A Global Literature Review And Applications Of Alternative Modelling Approaches To Regional Case Studies

Keywords: depredation, human-wildlife conflict, modelling, socio-ecosystems, viability, coexistence

Abstract: Species feeding on plants or animals raised or caught by humans, a behaviour termed "depredation", often leads to severe Human-Wildlife Conflicts (HWC). Depredation has been reported worldwide, and in marine ecosystems, has been developed by many large predators feeding on fisheries catches, impacting both fishing activities and ecological interactions. However, although ecosystem-based approaches are increasingly used in fisheries management, the ecosystem-wide effects of depredation are still rarely considered holistically. Therefore, this thesis (i) identified limitations, gaps, and priorities for the development of modelling approaches that incorporate depredation and (ii) evaluated the ability of two existing modelling approaches to characterize the consequences of marine depredation and, more specifically, to understand the issues and conditions required for fishing activities and marine depredating species to co-exist. This thesis is composed of five chapters. Chapter 1 introduces the context this work.

Chapter 2 identifies key knowledge gaps and highlights key future directions for providing effective inclusion of depredation in modelling studies through a systematic review. Chapter 3 uses the Ecopath framework to assess the ecosystem effects of depredation in a well-documented case study involving marine mammals and a commercial fishery. Chapter 4 relies on qualitative modelling of system feedback to assess the conditions for an exploited resource, a fishery and a depredating species to persist in depredation-impacted marine systems, and how marine depredation affects long-term responses to alternative scenarios. Finally, the general discussion presented in Chapter 5, provides recommendations to better understand and predict the effects of depredation at the socio-ecosystem level.