Université du Québec
à Rimouski

ÉVALUATION DES EFFETS CUMULATIFS DES CHANGEMENTS GLOBAUX SUR LES ÉCOSYSTÈMES

Le cas de l'estuaire et du golfe du Saint-Laurent

Thèse présentée

dans le cadre du Programme de doctorat en océanographie

en vue de l'obtention du grade de Philosophiae Doctor

PAR

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Décembre 2020

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Dépôt initial le 25 septembre 2020 Dépôt final le 21 décembre 2020

à Catherine, Liam et Alyssa,

à la mémoire de Charles, Yvette et Thérèse

REMERCIEMENTS

Beaucoup de temps s'écoule entre le début et la fin d'une thèse. Notre vie continue et plusieurs personnes nous marquent par leur arrivée, leur passage, ou leur départ. Je commence ainsi mes remerciements en accueillant la génération qui s'est ajoutée à ma vie et en saluant celle qui m'a quittée. Liam et Alyssa, je vous aime de tout mon cœur et je suis heureux d'avoir la chance d'être votre père. Je vous souhaite d'être heureux et passionnés, et je vous promets d'être présent pour rire ou pleurer avec vous des obstacles qui se présenteront sur votre chemin. Grand-papa Charles, grand-maman Yvette, et grand-maman Thérèse : votre présence a enrichi ma vie et je vous remercie pour tous les beaux moments que nous avons partagés et qui ont contribué à façonner la personne que je suis devenue. Je nourris l'espoir d'inspirer mes enfants comme vous avez su m'inspirer.

Phil, ton enthousiasme infini et ton humour n'ont d'égal que ton fin esprit stratégique et ta volonté de voir les gens qui t'entourent réussir. Tu as su m'encourager à poursuivre mes idées les plus farfelues en y contribuant systématiquement un soupçon de folie supplémentaire. Je te remercie d'avoir cru en moi et de m'avoir encouragé à entreprendre cette grande aventure ; elle n'aurait pas été la même sans toi et je serai toujours reconnaissant pour ces années passées en ta compagnie. Au plaisir de poursuivre notre collaboration dans les prochaines années !

Dom, merci d'avoir accepté de travailler avec quelqu'un qui avait le désir d'ajouter un soupçon de théorie dans sa vie sans réellement comprendre ce que ça impliquait. À notre première rencontre, tu as dessiné, sur ton tableau, comment tu envisagerais étudier la propagation de perturbations à travers les communautés écologiques. Je n'ai rien compris ! Tu m'as permis d'ouvrir une porte sur un monde qui m'était auparavant inconnu et au sein duquel j'ai appris à me plaire, si ce n'est d'y être à mon aise ! J'ai appris à réfléchir différemment et dans ce processus j'ai aussi ajouté plusieurs cordes à mon arc qui auront, j'en suis convaincu, une influence plus que significative pour le reste de ma carrière. Merci !

Jean-Claude, tu étais mon patron, puis tu es devenu membre de mon comité de thèse. À toutes ces étapes, je te remercie pour ton humour et ta franchise absolue. Après la lecture de mon séminaire 1, tu m'as dit : "Ouf ! C'était lourd !". Eh bien, je peux maintenant te dire, après relecture en fin de projet, que tu avais raison ! Merci pour cette franchise et pour m'avoir fait confiance après ma maîtrise. J'apporterai une bonne bouteille de scotch à mon prochain passage à Rimouski !

Je tiens également à remercier Isabelle et Fanny pour avoir accepté de réviser ma thèse et pour les commentaires et discussions constructives lors de la soutenance. J'espère avoir la chance de continuer ces échanges dans le futur.

Le type de projet que j'ai entrepris est impossible sans l'apport d'un nombre incalculable de collaborateurs qui agissent souvent dans l'ombre. Plusieurs d'entre vous aviez un sourire en coin lorsque je vous exposais mes idées de grandeur, mais vous vous êtes tout de même empressés de me prêter main forte. Peter, Chris, Hugo, Simon, Pascal, Philippe, Clément, Florian, Ben, Michel, Alfonso, Anne-Sophie, Andréanne, Simon, Guillaume, Claudette, Deryck, Jean-François, Matthew, Geneviève, Hugues, Benoît, Denis, Guy, Claude, Christian, et tout ceux que j'oublie ou dont j'ignore l'existence, je vous remercie infiniment. Ce sont des scientifiques comme vous qui nous permettront d'appliquer des approches de gestion environnementale écosystémiques !

Kev, un merci particulier ! Tu as incarné ce que j'envisage lorsque je pense au mot "*collaboration*". Tu as éclairé – et agrémenté – mon chemin théorique et informatique, et en cours de route tu es devenu un ami inestimable. Peu importe ce que le futur me réserve, je suis persuadé que tu y occuperas une place. En attendant, on pourra vider Bowmore lorsque j'aurai terminé d'écrire !

Rémi, merci pour ta collaboration tout au long de ma thèse, mais surtout merci pour toutes les conversations scientifiques et philosophiques que nous avons eu, ensemble ou avec Peter et Ryan !

Charlotte, Marie, Elliot, Valérie et Laurie : merci pour le sel !

Jésica, je me sens choyé d'avoir débuté ma thèse à temps pour que nos chemins se croisent. Ton écoute, ta présence et ta personnalité ont ensoleillé mon parcours. Au plaisir de continuer de partager de beaux moments dans le futur, et surtout de célébrer le mariage de nos enfants !

À tous les membres des laboratoires d'écologie benthiques, d'écologie intégrative, de Québec Océan et de CHONe, je suis heureux d'avoir pu partager ces années de science avec vous ! J'ai déjà hâte au prochain 5 à 7, ou au prochain congrès !

Steve, Nico et Kev (encore), mes amis geek, ce n'est peut-être pas vous qui m'avez amené à travailler sur les effets cumulatifs et les communautés, mais c'est très certainement vous qui m'avez aidé à m'outiller pour parvenir à mes fins. Lorsque l'envie de coder me reprendra -- sans doute dans quelques heures -- vous recevrez un message de ma part pour m'aider à trouver où j'ai bien pu faire une erreur!

Maman, papa, Gilles, vous êtes des parents extraordinaires ! Merci pour vos encouragements et pour votre support. Vous me dites souvent que vous êtes fiers de moi. Je peux vous dire en retour que je suis fier d'être votre fils. Vous pouvez maintenant vous réjouir : à 34 ans, je quitte enfin les bancs d'école ; vous pourrez arrêter de me demander si je dois étudier le soir ou la fin de semaine !

Cath. Nous nous sommes rencontrés tout juste après que j'aie décidé de me lancer dans un projet de thèse. Tu n'avais aucune idée dans quoi tu t'embarquais ! Tu croyais commencer une relation avec un homme, mais c'est un homme-étudiant que tu as eu.

Pour ceux qui ont des doutes, ce n'est pas la même chose ! En commençant ma thèse, je me suis rapproché de toi qui était à Québec... en déménageant de Montréal vers Rimouski ! Tu es venue m'y rejoindre parce que tu croyais en nous, et j'ai fait la même chose un an plus tard... parce que Phil est déménagé à l'Université Laval ! Les joies d'être en couple avec un étudiant gradué ! Maintenant que cette aventure s'achève, ça sera à mon tour de te payer un voyage en Asie ! Je te remercie de m'avoir enduré et aimé pendant toutes ces années ! Je n'aurais pu imaginer une meilleure partenaire pour me suivre, me supporter et m'encourager. Je ne pourrais surtout imaginer une meilleure partenaire pour partager les joies – et la folie – d'être parents. Merci pour ta présence, pour être la mère de mes enfants, et pour la personne que tu es. Mon rayon de soleil, je t'aime.

AVANT-PROPOS

Mon projet de doctorat s'insère dans le Canadian Healthy Oceans Network (CHONe) du CRSNG. CHONe avait deux thèmes principaux de recherche, soit les stratégies de conservation des écosystèmes marins ainsi que l'identification des principaux stresseurs, incluant les effets cumulatifs, qui altèrent la biodiversité marine et les fonctions et services écosystémiques. Mon projet était à l'origine un projet de maîtrise sur l'identification d'indicateurs de conditions benthiques à l'échelle du Golfe du Saint-Laurent et devait mener à la caractérisation des principales sources de stress au sein du Saint-Laurent. En fonction de mes intérêts de recherche, nous avons développé ce projet de maîtrise en un projet de doctorat qui vise également l'intégration des interactions écologiques pour l'évaluation des effets cumulatifs directs et indirects des stresseurs environnementaux sur les communautés écologiques.

Mes travaux de thèse ont mené à la préparation de 5 articles scientifiques, dont 3 sont publiés, 1 est en révision et le dernier est en préparation. J'ai également contribué à la rédaction d'un chapitre de livre sur l'évaluation des effets cumulatifs au sein du Système du Saint-Laurent et un article de vulgarisation scientifique. J'ai également présenté mes travaux de recherche à de multiples conférences à travers 11 présentations orales et 9 affiches scientifiques. Une liste complète des publications et conférences est disponible à la fin de l'avant-propos.

Je veux reconnaître les nombreuses sources de support financier et scientifique dont j'ai bénéficié tout au long de ma thèse. Je débute en remerciant les organismes subventionnaires qui ont rendu mon projet possible. Je remercie le Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG), qui m'a octroyé une bourse d'études supérieures de doctorat (ES D), et le Fonds de recherche du Québec – Nature et Technologies (FRQNT), qui m'a octroyé une bourse de doctorat en recherche.

Je tiens également à remercier les multiples regroupements de recherche dont j'ai été membre pendant ma thèse et qui m'ont fourni du support scientifique et financier, ainsi que des expériences inoubliables et enrichissantes autant d'un point de vue personnel que professionnel. Merci à Québec Océan, le Centre de la science de la biodiversité (CSBQ), le programme Computational Biodiversity Science and Services (BIOS^2), Notre Golfe et Takuvik. Je remercie également le regroupement CHONe et ses partenaires, soit le Département Pêches et Océans Canada et l'INREST en tant que représentant du Port de Sept-Îles et de la Ville de Sept-Îles. Je remercie également l'Observatoire Global du Saint-Laurent (OGSL) pour son support technique dans l'établissement de la plateforme *eDrivers* et pour la collaboration prévue qui ira au-delà de ma thèse.

Je remercie également divers ministères provinciaux et fédéraux qui ont contribué au projet, que ce soit par du support financier, du temps d'experts ou des données. Un merci particulier à Pêches et Océans Canada, sans qui ce projet n'aurait été possible. Merci également au Ministère de l'Environnement et de la Lutte contre les changements climatiques (MELCC) et au Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec (MAPAQ) du Gouvernement du Québec, au Département Agriculture, Aquaculture et Pêches du Gouvernement du Nouveau-Brunswick, au Département de Pêcheries et de l'Aquaculture du Gouvernement de la Nouvelle-Écosse, et au Département de Pêcheries, de Foresterie et d'Agriculture du Gouvernement de Terre-Neuve-et-Labrador.

Finalement, je tiens à remercier l'Université du Québec à Rimouski, l'Université Laval et l'Université de Sherbrooke pour m'avoir accueilli, fournit des locaux de travail et du support administratif.

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RÉSUMÉ

Les écosystèmes sont de plus en plus soumis aux effets cumulatifs d'une variété de stresseurs environnementaux en réponse à la demande croissante en ressources naturelles et à l'intensification des changements climatiques. Ces observations stimulent une demande croissante pour les approches de gestion écosystémique et les évaluations régionales des effets cumulatifs. Pourtant, une gestion environnementale par silos centrée sur les évaluations par espèces et stresseurs individuels demeure la norme. Cette absence d'approches holistiques est particulièrement inquiétante pour la gestion d'espèces exploitées ou en péril puisque leur dynamique, comme celle de toutes espèces, est régie par le réseau d'interactions liant les espèces entre elles au sein d'une communauté écologique et à travers lequel les effets des stresseurs peuvent se propager indirectement. Cette disparité entre les besoin d'approches holistiques et la pratique est partiellement expliquée par un manque généralisé de connaissances théoriques des effets de multiples stresseurs sur les communautés écologiques et par des contraintes logistiques et méthodologiques. Dans ce contexte, l'objectif général de ma thèse est d'évaluer les effets cumulatifs des changements climatiques et des activités humaines sur les communautés écologiques du Système du Saint-Laurent au Canada. Les hypothèses générales de la thèse sont que les interactions influencent la propagation indirecte et non-additive des effets de multiples stressors à travers les communautés et que, en tant que tel, les interactions et les stresseurs devraient être considérés conjointement au sein d'analyse d'effets cumulatifs communauté-centrée.

La thèse est divisée en trois parties. Dans la première partie (chapitre 1), je conceptualise la propagation des stresseurs environnementaux à travers les réseaux trophiques et j'explore théoriquement comment des stresseurs simulés affectent des motifs à trois espèces et des communautés du Système du Saint-Laurent. Nous trouvons que négliger les interactions écologiques sous-estime systématiquement les effets des stresseurs et que les effets synergiques et antagonistes sont fréquents à travers les interactions. À l'échelle des réseaux, nous trouvons que les prédateurs apicaux sont négativement affectés, alors que les méso-prédateurs bénéficient des effets des stresseurs dans le Système du Saint-Laurent. Par contre, la sensibilité des espèces dépend de la structure des réseaux trophiques. Le travail théorique proposé au chapitre 1 permet de valider les hypothèses générale de la thèse et offre un cadre accessible et appuyé par la théorie écologique pour inclure les interactions écologiques à l'évaluation des effets cumulatifs.

La deuxième partie de ma thèse aborde des défis logistiques et méthodologiques pour l'évaluation des effets cumulatifs des changements climatiques et des activités humaines sur les communautés du Système du Saint-Laurent. Au chapitre 2, j'aborde le défi de caractériser les interactions écologiques au sein de systèmes où peu de données sont disponibles. Je présente une nouvelle méthode d'apprentissage non supervisée pour prédire les interactions binaires à partir de la proximité taxonomique entre espèces et d'une collection d'interactions empiriques connues entre espèces marines. Les résultats suggèrent que les interactions écologiques peuvent être prédites avec précision, ce qui pourrait promouvoir leur utilisation pour la gestion environnementale. Au chapitre 3, j'identifie des enjeux environnementaux et suggère des priorités de recherche et de gestion pour promouvoir les évaluations d'effets cumulatifs et la gestion écosystémique dans le Système du Saint-Laurent. Au chapitre 4, je caractérise la distribution et l'intensité de stresseurs environnementaux issus des activités humaines et des changements climatiques dans le Système du Saint-Laurent. À partir de collaborations, d'initiatives environnementales existantes et de portails de données ouvertes, 22 stresseurs d'origine côtière, du climat, de la pêche et du trafic maritime ont été caractérisés. Les résultats du chapitre 4 démontrent que les stresseurs sont répandus partout dans le Système du Saint-Laurent et que l'estuaire, la gyre d'Anticosti, et les milieux côtiers sont particulièrement exposés aux stresseurs.

Dans la troisième partie de la thèse (chapitre 5), je présente une évaluation des effets cumulatifs sur 193 espèces du Système du Saint-Laurent à partir d'une nouvelle approche communauté-centrée qui considère les interactions écologiques et les effets indirects. L'approche proposée s'appuie sur le cadre théorique présenté au chapitre 1 et utilise les résultats et méthodes des chapitres 2, 3 et 4. Je compare cette approche à une approche conventionnelle espèce-centrée pour exposer des propriétés émergentes provenant des interactions écologiques et des effets sur des espèces qui seraient normalement ignorés. Pour certaines espèces, considérer les interactions écologiques pourraient être l'unique moyen d'évaluer les effets des stresseurs environnementaux. Les poissons et les mammifères marins sont particulièrement susceptibles aux effets indirects de tous les types de stresseurs considérés ; ceci est un contraste marqué avec le nombre limité de stresseurs qui les affectent directement.

En alliant théorie, gestion environnementale et bio-informatique, ma thèse montre que les interactions écologiques sont un élément clé à considérer pour l'évaluation des effets de multiple stresseurs et propose une approche accessible pour les intégrer aux évaluations d'effets cumulatifs. Mes résultats sont particulièrement pertinents pour la gestion d'espèces exploitées et en péril, pour qui nous ignorons potentiellement des risques importants en négligeant les effets indirects provenant des interactions entre espèces. Développer ces capacités holistiques est essentiel en vue d'opérationnaliser un mode de gestion environnementale écosystémique.

Mots clés : effets cumulatifs, stresseurs environnementaux, effets indirects, interactions biotiques, effets non-additifs, communautés écologiques, réseaux trophiques, Système du Saint-Laurent, activités humaines, changements

climatiques.

ABSTRACT

With demands for natural resources increasing alongside populations, and the effects of climate change intensifying, ecosystems worldwide are increasingly burdened with the cumulative effects of a vast array of environmental stressors. These observations stimulate a growing demand for ecosystem-based approaches and regional cumulative effects assessments. Yet environmental management still overwhelmingly operates in silos, focusing instead on single-stressor and single-species assessments. This is particularly concerning for exploited and endangered species whose dynamics, like that of all species, is driven by the network of interactions structuring ecological communities and through which the effects of stressors can propagate indirectly. A general lack of theoretical understanding of the effects of multiple stressors on ecological communities, and methodological and logistical constraints explain part of this discrepancy. In this context, the general objective of this thesis is to evaluate the cumulative effects of climate change and human activities on the ecological communities of the St. Lawrence System in eastern Canada. The general hypotheses guiding the thesis are that species interactions influence the indirect and non-additive spread of the effects of multiple stressors through communities and that, as such, species interactions and stressors should be considered together in network-scale cumulative effects assessments.

The thesis is divided in three parts. In the first part (chapter 1), I conceptualize how stressors propagate through food webs and explore theoretically how they affect simulated 3-species motifs and food webs of the Canadian St. Lawrence System. We find that overlooking species interactions invariably underestimates the effects of stressors, and that synergistic and antagonistic effects through species interactions are prevalent. At the scale of food webs, we find that apex predators are generally negatively affected and mesopredators benefit from the effects of stressors in the St. Lawrence System, but that species sensitivity is dependent on food web structure. The theoretical simulations proposed in chapter 1 validate the general hypotheses of the thesis and provide an accessible and theory-grounded framework for the inclusion of species interactions in cumulative effects assessments.

The second part of the thesis addresses logistical and methodological challenges for the cumulative effects assessment of climate change and human activities on communities of the St. Lawrence System. In chapter 2, I address the challenge of characterizing ecological interactions in data-deficient ecosystems. I present a new unsupervised machine learning method to predict interactions between any given set of species, given pairwise taxonomic proximity and a collection of known empirical interactions between marine species. Results from chapter 2 suggest that ecological interactions can be predicted with high accuracy, which could promote their use for environmental management. In chapter 3, I identify environmental issues and suggest research and management priorities to promote cumulative effects assessment and ecosystem-based management in the St. Lawrence System. In chapter 4, I characterize the distribution and intensity of environmental stressors arising from human activities and climate change in the St. Lawrence System. Through collaborations, existing environmental initiatives and open data portals, data-based indicators for 22 coastal, climate, fisheries, and marine traffic stressors were developed. Results from chapter 4 show that stressors are widespread and that coastal areas and the Estuary, Anticosti Gyre, and coastal areas are particularly exposed to cumulative exposure and cumulative hotspots.

In the third part of the thesis (chapter 5), I present a cumulative effects assessment on 193 species of the St. Lawrence System using a novel network-scale approach that explicitly considers ecological interactions and indirect effects. The approach is built on the framework presented in chapter 1 and uses results and methods from chapters 2, 3 and 4. I compare our approach to a conventional species-scale assessment to expose transgressive properties arising from species interactions and uncover cumulative effects to species that would otherwise be overlooked. Fishes and marine mammals appear particularly prone to indirect effects from all types of stressors ; this contrasts considerably with the limited number of stressors affecting them directly. For certain species, considering interactions may even be the only means of assessing the effects of stressors.

In pairing theory, environmental management and computational capabilities, my thesis shows that ecological interactions are key to assess the effects of multiple stressors on species and proposes an accessible approach to integrate interactions to cumulative effects assessments. This is particularly relevant to the management of exploited and endangered species for which we may currently ignore significant threats by overlooking the less obvious yet no less significant effects arising from species interactions. Developing these holistic capabilities is essential to operationalize ecosystem-based management.

Keywords : cumulative effects, environmental stressors, indirect effects, biotic interactions, non-additive effects, ecological network, food web, St. Lawrence System, human activities, climate change.

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INTRODUCTION GÉNÉRALE

Contexte général de la thèse

L'intensification continue des activités humaines et des changements globaux sur les écosystèmes met en évidence le besoin d'adopter des approches de gestion qui sont en mesure de considérer la complexité des problématiques environnementales auxquelles nous sommes confrontés. Cette nécessité n'a rien de nouveau, puisque la notion de gestion écosystémique est apparue dans la littérature scientifique au courant des années 1970. Malgré les efforts déployés et une littérature riche sur la gestion écosystémique, la mise en œuvre de programmes de gestion environnementale demeure majoritairement fragmentée en de multiples programmes isolés. L'évaluation des effets cumulatifs des multiples pressions environnementales découlant des changements climatiques et des activités humaines – un élément crucial à l'application de programmes de gestion écosystémique – est affligée d'un constat similaire : une approche par silos considérant les espèces et les pressions environnementales individuellement demeure la norme. Ces observations sont particulièrement inquiétantes pour la gestion d'espèces exploitées ou en péril puisque leur dynamique, comme celle de toutes espèces, est régie par le réseau d'interactions liant les espèces entre elles au sein d'une communauté écologique. Les interactions écologiques brillent pourtant par leur absence généralisée au sein de la littérature scientifique en gestion et conservation environnementale malgré plusieurs décennies de connaissances accumulées démontrant leur importance. Ce sont ces observations qui ont motivé mes travaux de thèse, à travers lesquels j'ai particulièrement réfléchi à l'intégration des effets indirects issus des interactions écologiques à l'évaluation des effets cumulatifs – *i.e.* combiné ou simultané – des changements climatiques et des activités humaines dans un contexte de gestion écosystémique.

Cette introduction vise à cerner les enjeux et thématiques explorés au sein de ma thèse. Je débute en présentant différents enjeux environnementaux reliés aux changements climatiques et aux activités humaines. Je présente l'importance de considérer les pressions environnementales et les interactions écologiques conjointement pour l'évaluation des effets cumulatifs. Je discute ensuite de gestion écosystémique et de processus d'évaluation des effets cumulatifs, des défis associés à leur implémentation, et de leurs applications actuelles. Finalement, je contextualise les défis de recherche abordés dans le cadre de mes travaux de recherche en vue d'atteindre l'objectif général de ma thèse : évaluer les effets cumulatifs des changements climatiques et des activités humaines sur les communautés écologiques de l'estuaire et du golfe du Saint-Laurent.

Changements climatiques et activités humaines

Un constat global

Au moment de déposer ma proposition de projet de thèse à l'automne 2015, un constat global inquiétant était disponible quant à la diversité des pressions environnementales observées dans les milieux naturels, en particulier dans les milieux marins (Duarte, 2014; Boonstra et al., 2015). Les changements climatiques et les émissions anthropiques de gaz à effet de serre s'intensifiaient sans signe de ralentissement (IPCC, 2014). L'accroissement de la population mondiale, disproportionnellement dirigée vers les milieux côtiers, accentuait les besoins en ressources naturelles (Smith, 2011). L'empreinte des activités humaines était omniprésente et en croissance pour la majorité des milieux marins et côtiers (Halpern et al., 2015a). Prioriser la recherche sur les effets de multiples pressions environnementales sur les milieux naturels était ainsi largement réclamé (Rudd, 2014; Parsons et al., 2014). Au moment d'écrire ces lignes à l'été 2020, la situation a évolué, mais le constat demeure le même : les changements climatiques s'intensifient (IPCC, 2019), la population mondiale et les besoins en ressources naturelles continuent de croître (FAO, 2020), l'empreinte des activités humaines s'amplifie (Halpern et al., 2019), et améliorer les connaissances relatives aux effets de multiples pressions environnementales sur les milieux naturels demeure un enjeu prioritaire de recherche (Jarvis et Young, 2019; Williams et al., 2020).

Stresseurs environnementaux

Une diversité importante de pressions environnementales, communément appelées stresseurs environnementaux, sont issues des changements climatiques et des activités humaines (Duarte, 2014; Boonstra et al., 2015). L'utilisation du terme stresseur est contentieux dans la littérature (Dreujou et al., 2020). Je débute ainsi en définissant un stresseur environnemental comme une externalité qui affecte des processus environnementaux, comme une augmentation du taux de mortalité d'une population animale. Un stresseur peut être engendré par des processus biophysiques d'origine naturelle ou humaine, comme l'acidification, ou par des activités humaines, comme la pêche ou la navigation. Individuellement, les stresseurs environnementaux peuvent affecter tous les niveaux d'organisation biologique. La pêche a ainsi entraîné la chute de plusieurs stocks d'espèces commerciales, une diminution des niveaux trophiques océaniques moyens en ciblant préférentiellement les grands prédateurs, et la dégradation d'une variété de services écosystémiques essentiels, comme l'approvisionnement alimentaire et la qualité de l'eau (Pauly et al., 1998; Jackson et al., 2001; Myers et Worm, 2003; Worm et al., 2006). Similairement, l'acidification des océans affecte les taux métaboliques, la croissance et la mortalité des mollusques et des coraux, et peut altérer les flux de carbone au sein de communautés écologiques (Fabry et al., 2008; Kroeker et al., 2013; Bove et al., 2019).

L'intensification de l'empreinte des changements climatiques et des activités humaines entraîne un chevauchement spatio-temporel croissant entre un grand nombre de stresseurs environnementaux (Halpern et al., 2015b, 2019). Par exemple, les récifs coralliens sont confrontés à plusieurs stresseurs environnementaux tels que la pêche, une hausse des températures, une acidification et une augmentation de la pollution (McClanahan et al., 2014; Harborne et al., 2017). En considérant 19 stresseurs environnementaux, Halpern et al. (2015b) montrent que la quasi-totalité des océans sont soumis à plusieurs stresseurs, et que certaines régions sont exposées à l'ensemble des stresseurs considérés. Il en résulte un potentiel d'interactions complexes entre les effets combinés des stresseurs qui augmente exponentiellement avec le nombre de stresseurs (Côté et al., 2016). Les effets des stresseurs peuvent alors se combiner de façon non-linéaire et non-additive, et résulter en des effets supérieurs – *i.e.* des effets synergiques – ou inférieurs – *i.e.* des effets antagonistes – à leurs effets individuels (Crain et al., 2008; Darling et Côté, 2008; Piggott et al., 2015; Côté et al., 2016; Jackson et al., 2016). Par exemple, la sensibilité des récifs coralliens au blanchiment causé par les hausses de température peut être supérieure lors d'enrichissement en nutriments, comme des fertilisants et des rejets d'égouts (Wiedenmann et al., 2013; Lapointe et al., 2019). Similairement, Liess et al. (2016) ont établi, grâce à une méta-analyse, que les effets de substances toxiques – *e.g.* pesticides – peuvent être jusqu'à cent fois plus néfastes lorsque d'autres stresseurs environnementaux agissent simultanément sur certains organismes. Christensen et al. (2006) ont pu établir, en diminuant expérimentalement le pH d'un lac en Ontario dans les années 1980 et 1990, que les effets positifs d'une acidification sur la production primaire peuvent être annulés par une hausse de température.

Effets sur les populations et les communautés

Les stresseurs environnementaux affectent les populations et les communautés en perturbant directement les processus écologiques – *e.g.* la mortalité, le comportement ou les interactions écologiques – qui gouvernent leur dynamique (*e.g.* Galic et al., 2018;

Guiden et al., 2019; Hodgson et al., 2019; Hodgson et Halpern, 2019). À l'échelle des populations, les effets des stresseurs dépendent de la sensibilité spécifique à chaque espèce, qui correspond à la prédisposition d'une espèce à être affectée par un stresseur (Oppenheimer et al., 2015). Par exemple, l'hypoxie (< ~30 % saturation d'oxygène) , bien qu'elle dégrade la qualité des habitats, peut engendrer des réponses très variables selon les espèces. La crevette nordique (*Pandalus borealis*) et le flétan du Groenland (*Reinhardtius hippoglossoides*) sont généralement bien adaptés aux milieux hypoxiques (Pillet et al., 2016). La morue atlantique (*Gadus morhua*), quant à elle, modifie son comportement et évite généralement les milieux hypoxiques (Chabot et Claireaux, 2008). Pour d'autres espèces comme les invertébrés benthiques sessiles, l'hypoxie peut résulter en une augmentation des taux de mortalité (Eby et al., 2005; Belley et al., 2010). Ces effets correspondent aux effets directs des stresseurs sur les populations et sont généralement évalués par de l'échantillonnage *in situ* ou des expériences factorielles.

Les espèces sont également dépendantes les unes des autres et sont liées par les interactions écologiques qui structurent les communautés. Plusieurs types d'interactions existent au sein d'une communauté : la compétition, l'antagonisme (p.ex. prédation et parasitisme) et les relations facilitantes (p.ex. mutualisme et commensalisme). Dans le cadre de ma thèse, je m'intéresse aux interactions prédatrices, ou trophiques, qui structurent les réseaux trophiques et qui assurent un transfert d'énergie et de matières au sein des communautés. Les espèces influencent la dynamique d'autres espèces directement et indirectement. Les effets directs surviennent lorsqu'une espèce en affecte une autre sans la participation d'une troisième espèce, tel un prédateur qui consomme une proie (Abrams et al., 1996; Wootton, 2002). Un effet indirect survient lorsqu'une espèce en affecte une autre en passant par une espèce intermédiaire, comme l'effet du même prédateur sur les ressources de sa proie (Abrams et al., 1996; Wootton, 1993, 2002). Il est estimé que la majorité des espèces d'un réseau sont séparées d'au plus trois liens trophiques et que cette distance diminue au sein de réseaux ayant une diversité plus importante (Williams et al., 2002). Dans les réseaux trophiques, où plusieurs effets directs et indirects agissent simultanément, les effets de perturbations peuvent être amplifiés ou réduits par les interactions trophiques (Ives, 1995; Wootton, 2002; Thompson et al., 2018). Un prédateur peut ainsi exercer un effet net positif sur une proie malgré une interaction directe négative (Montoya et al., 2009). L'intégration des effets directs et indirects qui se propagent à travers le réseau d'interactions pour affecter une espèce donnée résulte en un effet net (Abrams et al., 1996).

Les observations empiriques d'effets indirects sont abondants dans la littérature (*e.g.* Paine, 1980; Estes et al., 2011). Un cas maintenant classique d'effet indirect est la chaîne d'interaction qui lie la loutre de mer (*Enhydra lutris*) aux forêts de laminaires en milieu marin. Estes et Palmisano (1974) a démontré que la structure des communautés littorales et sublittorales des îles Aléoutiennes, en Alaska, était contrôlée par la présence ou l'absence de populations de loutre de mer. Lorsque présente, la loutre de mer contrôle l'herbivorie imposée par les oursins de mer (*Strongylocentrotus spp.*) sur les forêts de laminaires. Lorsque les loutres de mer sont absentes, l'herbivorie des oursins de mer diminuent significativement l'abondance des forêts de laminaires.

C'est par ce réseau d'interactions qui structure les communautés écologiques que les effets des stresseurs environnementaux peuvent se propager indirectement d'une espèce à l'autre (Wootton, 2002; Bascompte, 2009; Montoya et al., 2009; O'Gorman et Emmerson, 2009; O'Gorman et al., 2012). Les effets indirects peuvent d'ailleurs avoir une magnitude supérieure et affecter des populations plus rapidement que les effets directs (Wootton, 1993, 2002; Menge, 1995; Yodzis, 2000). La structure d'un réseau, qui se caractérise par le nombre d'interactions, leur configuration et leur intensité, peut influencer la propagation des stresseurs et la stabilité de réseaux (Wootton, 2002; Montoya et al., 2009; Bartley et al., 2019; O'Gorman et al., 2019). Les stresseurs environnementaux peuvent influencer l'ensemble de ces propriétés et restructurer les réseaux entiers (Blanchard, 2015; Kortsch et al., 2015; Bartley et al., 2019). La sensibilité d'une espèce aux effets indirects dépend quant à elle de son rôle et de sa position dans un réseau trophique. Par exemple, les espèces ayant une diète diversifiée sont généralement plus résilientes face aux perturbations que les espèces ayant une diète spécialisée (Clavel et al., 2011) ; les prédateurs apicaux sont généralement plus sensibles aux effets indirects (Ripple et al., 2015; Stier et al., 2016).

Une simple caractérisation des effets directs des stresseurs environnementaux sur des espèces est insuffisante afin de convenablement évaluer les effets des stresseurs. Une évaluation explicite des effets indirects permettant une évaluation des effets nets apparaît comme une nécessité dans le cadre d'évaluation des effets de multiples stresseurs. Il s'agit toutefois d'un défi de taille, considérant la complexité des communautés écologiques et le nombre de stresseurs environnementaux auxquels certains écosystèmes sont exposés.

Vers une gestion de la structure des communautés

Les sections précédentes mettent en évidence le besoin d'adopter des approches environnementales holistiques considérant les interactions écologiques pour l'évaluation et la gestion des pressions exercées par les changements climatiques et les activités humaines sur les communautés écologiques (Halpern et al., 2008a; Halpern et Fujita, 2013; Hodgson et al., 2019). Les approches environnementales holistiques sont des stratégies de planification, d'évaluation, de gestion ou de suivi environnemental qui utilisent une pensée systémique qui considère et priorise la complexité des écosystèmes (Dreujou et al., 2020). Des approches de gestion et d'évaluation des effets environnementaux cumulatifs existent déjà dans la littérature. Dans le cadre de ma thèse, j'ai voulu déterminer si les approches existantes fournissent déjà une solution à l'évaluation des effets de multiples stresseurs sur les communautés écologiques. Plus particulièrement, je me suis intéressé à la gestion écosystémique et à l'évaluation des effets cumulatifs dans le cadre d'évaluation d'impacts environnementaux.

Gestion écosystémique et effets cumulatifs

Une approche de gestion écosystémique semble idéale pour la gestion des effets de multiples stresseurs sur les communautés. Née dans les années 1970, la gestion écosystémique est décrite ainsi par Christensen et al. (1996) :

> *"Ecosystem management is management driven by explicit goals, executed by policies, protocols, and practices, and made adaptable by monitoring and research based on our best understanding of the ecological interactions and processes necessary to sustain ecosystem composition, structure, and function."*

La gestion écosystémique prône une gestion des écosystèmes et des interactions qui les structurent dans leur ensemble, incluant les aspects humains, plutôt que par composantes individuelles (Christensen et al., 1996; Rosenberg et McLeod, 2005; Leslie et McLeod, 2007). La gestion écosystémique et les outils d'aide à la décision connexes, comme la planification spatiale marine et la planification systématique de la conservation, citent généralement l'évaluation des effets cumulatifs comme principe fondamental visant la gestion proactive des activités humaines et des milieux naturels (Halpern et al., 2008a). Tout comme la gestion écosystémique, l'évaluation des effets cumulatifs n'est toutefois pas récente. Elle a pour racines la gestion des ressources naturelles et les processus d'évaluation d'impacts environnementaux (Halpern et Fujita, 2013) et fait partie de la législation de certains pays depuis déjà plusieurs décennies, dont les États-Unis (National Environmental Policy Act 40 CFR §1508.7, 1969), le Canada (Loi canadienne sur l'évaluation environnementale L.C. 1992, ch. 37), l'Australie, et divers pays européens (Halpern et Fujita, 2013). La littérature scientifique et la littérature grise regorgent de publications fournissant des définitions diversifiées, des cadres d'application, des guides de bonnes pratiques et des principes directeurs pour l'évaluation des effets cumulatifs dans le cadre d'évaluations d'impacts environnementaux (*e.g.* Peterson et al., 1987; Hegmann et al., 1999; Krausman et Harris, 2011). Il en résulte une myriade de définitions et d'approches, comme le témoignent les revues de littérature de Therivel et Ross (2007) et de Duinker et al. (2013).

En son sens large, les effets cumulatifs sont définis par le Conseil canadien des ministres de l'environnement (Conseil canadien des ministres de l'environnement, 2014) comme un *"changement dans l'environnement causé par les multiples interactions des activités humaines et des processus naturels qui s'accumulent dans le temps et l'espace"* et l'évaluation des effets cumulatifs comme une *"procédure systématique qui vise à identifier, à analyser et à évaluer les effets cumulatifs"*. Ces définitions établissent clairement la nature systématique des effets cumulatifs et de leur évaluation, et un lien clair avec la gestion écosystémique. Les effets cumulatifs sont toutefois communément définis en termes plus restrictifs dans les textes de politiques, de lois et de régulations (Jones, 2016). La loi canadienne sur l'évaluation environnementale de 1992 définit ainsi les effets cumulatifs comme suit :

> *"[. . .] les effets cumulatifs que [la] réalisation [d'un projet], combinée à l'existence d'autres ouvrages ou à la réalisation d'autres projets ou activités, est susceptible de causer à l'environnement".*

Aux États-Unis, la loi sur la politique environnementale nationale (National Environmental Policy Act) de 1969 (CEQ regulation 40 CFR §1508.7) définit les effets cumulatifs de façon similaire :

> *"The impact on the environment which results from the incremental impact of the action when added to other past, present, and reasonably foreseeable future actions regardless of what agency (Federal or non-federal) or person undertakes such other actions. Cumulative impacts can result from*

> *individually minor but collectively significant actions taking place over a period of time".*

Ces définitions, qui régissent l'application des évaluations d'effets cumulatifs au Canada et aux États-Unis, témoignent d'une vision beaucoup plus restreinte des effets cumulatifs et de leur inclusion aux processus d'évaluations d'impacts environnementaux. L'évaluation pratique des effets cumulatifs se concentre ainsi davantage à l'approbation de projets individuels (*stressor-based*) en concentrant les évaluations sur les stresseurs imposés par ce projet plutôt qu'à l'effet total observé sur l'environnement (Duinker et Greig, 2006; Therivel et Ross, 2007; Gunn et Noble, 2011). Les évaluations d'effets cumulatifs, en tant que composante d'une évaluation d'impacts environnementaux par projet, se résument typiquement par une brève conclusion suggérant que les actions du projet proposé n'ont aucun effet cumulatif significatif pressenti (Duinker et Greig, 2006; Duinker et al., 2013; Sinclair et al., 2017). Jones (2016) résume bien ces propos :

> *"[Cumulative effects assessment] is, at least partially, a token bureaucratic requirement for development consent, which serves as a symbolic gesture to pacify environmentalists or reinforce conservation values".*

Il n'est donc pas surprenant de constater un écart important entre les considérations relatives à l'évaluation holistique des effets cumulatifs suggérées par la définition du Conseil canadien des ministres de l'environnement et au sein de multiples ouvrages scientifiques (voir Duinker et al., 2013), et les évaluations pratiques des effets cumulatifs (*e.g.* Dubé, 2003; Gunn et Noble, 2011; Sinclair et al., 2017).

Plusieurs scientifiques dénoncent ainsi les performances d'un système d'évaluations d'effets cumulatifs jugé imparfait et parfois même dommageable, réclamant plutôt l'utilisation d'approches régionales pour l'évaluation des effets cumulatifs (*e.g.* Dubé, 2003; Duinker et Greig, 2006; Jones, 2016; Sinclair et al., 2017).

Selon Sinclair et al. (2017), une évaluation régionale des effets cumulatifs peut être définie comme suit :

> *“[A Regional Effects Assessment (REA)] is an [environmental assessment] whose primary or sole defining feature is its regional scope and its focus on understanding the interactions between human activities and the natural world. This means that in just about all aspects other than its spatial limitations, an REA should be comprehensive and integrated.”*

À l’instar d’une approche par projet, l’approche régionale s’intéresse plutôt aux effets (*effect-based*) totaux et à la viabilité de récepteurs environnementaux d’intérêt, communément appelés composantes valorisées (valued ecosystem components ; Beanlands et Duinker, 1983; Sinclair et al., 2017). Bien que cette approche soit généralement considérée plus efficace, plusieurs contraintes limitent son application en pratique. Par exemple, des mesures environnementales sont nécessaires afin d’établir les effets d’un ou de plusieurs stresseurs sur une composante valorisée ; ceci rend forcément les évaluations réactives puisque les effets doivent être observés pour établir qu’un stresseur a un effet significatif sur une composante valorisée (Dubé, 2003). Une approche idéale permettrait plutôt de combiner les approches d’évaluations des effets cumulatifs basées sur les effets et sur les stresseurs – *i.e. effect-based* et *stressor-based* (Dubé, 2003; Sinclair et al., 2017). De plus, la complexité inhérente à l’évaluation des effets cumulatifs, que ce soit au niveau des besoins en données ou de la complexité des méthodes d’application, inhibe généralement les capacités – et la volonté – d’évaluations des effets cumulatifs (voir Sinclair et al., 2017). L’absence d’une approche par système est ainsi citée comme une limitation des évaluations régionales des effets cumulatifs (Gunn et Noble, 2011), ce qui met en doute l’applicabilité des approches développées dans le cadre d’évaluations d’impacts environnementaux pour la gestion écosystémique.

Les évaluations d'impacts environnementaux sur les milieux naturels demeurent ainsi majoritairement centrés sur des stresseurs individuels (O'Brien et al., 2019; Hodgson et al., 2019). Il en est de même pour les évaluations d'effets sur les communautés écologiques : malgré leur importance reconnue (*e.g.* De Laender, 2018; Bruder et al., 2019; Hodgson et al., 2019; Orr et al., 2020) et l'émergence d'approches d'évaluations des effets de multiples stresseurs (*e.g.* Hodgson et al., 2017; Galic et al., 2018; Thompson et al., 2018; Otto et al., 2020), la structure des réseaux et les interactions écologiques demeurent largement absentes de la littérature en gestion environnementale (Kollmann et al., 2016; Heinen et al., 2020). Une approche par silos demeure ainsi la norme malgré les besoins de gestion et d'évaluations des effets holistiques.

Une approche holistique prometteuse

L'étude de Halpern et al. (2008b) a enclenché un pas majeur vers une évaluation holistique et spatialement explicite des effets cumulatifs des activités humaines sur les océans mondiaux en évaluant les effets cumulatifs de 17 stresseurs environnementaux sur 20 types d'écosystèmes marins. Cette étude a démontré que peu de milieux demeurent libres de l'empreinte des activités humaines et que la majorité des écosystèmes sont affectés par de multiples stresseurs environnementaux. Les mises à jour publiées par le même groupe en 2015 (Halpern et al., 2015b) et en 2019 (Halpern et al., 2019) indiquent également un accroissement généralisé des effets cumulatifs sur les océans.

La méthode développée par Halpern et al. (2008b) permet de combiner la diversité des composantes valorisées (*i.e.* les espèces dans le cadre de ma thèse), des stresseurs et des sensibilités de chaque composante valorisée à chaque stresseur. La méthode requiert ainsi trois types de données : 1) la présence ou l'absence cartographiée des composantes valorisées (C_i), 2) la distribution spatiale et l'intensité relative (*i.e.* normalisée entre 0 et

1) des stresseurs environnementaux considérés (S_j) et 3) la sensibilité relative de chaque composante valorisée à chaque stresseur ($\mu_{i,j}$). Ces données sont ensuite incorporées au sein d'une grille constituée de cellules de tailles homogènes et caractérisant l'aire d'étude visée. Enfin, les prédictions d'effets cumulatifs (E_C) sont calculées pour chaque cellule (x) de la grille par la sommation de l'ensemble des effets individuels des stresseurs sur l'ensemble des composantes valorisées :

$$E_{C_x} = \sum_{i=1}^{n} \sum_{j=1}^{m} C_{i,x} * S_{j,x} * \mu_{i,j} \tag{0.1}$$

Cette méthode propose le calcul d'un indicateur relatif des effets cumulatifs afin de prédire les risques associés aux effets de plusieurs stresseurs environnementaux sur des composantes valorisées. Les prédictions d'effets cumulatifs calculés peuvent être décomposées afin d'évaluer la part relative des effets d'un seul ou de plusieurs stresseurs sur une ou plusieurs composantes valorisées (Figure 1). Par exemple, les prédictions d'effets cumulatifs pourraient être décomposées afin d'explorer les effets cumulatifs sur une seule composante valorisée, ou d'identifier les régions les plus à risque dans une zone d'étude. Une exploration exhaustive de l'ensemble des combinaisons stresseurs-composantes valorisées est possible, offrant la capacité d'analyser différents scénarios de gestion et de répondre à différentes questions d'intérêt. Cette méthode d'évaluation peut alors mener à des recommandations claires et ciblées dans un contexte de gestion écosystémique et permet d'optimiser et de prioriser des actions de gestion prises dans une région d'intérêt (Halpern et al., 2015b). Elle offre également une approche flexible et quantitative pouvant intégrer différents types de données parfois difficilement comparables, comme des données biophysiques avec des connaissances qualitatives (Halpern et al., 2008b; Halpern et Fujita, 2013; Halpern et al., 2015b).

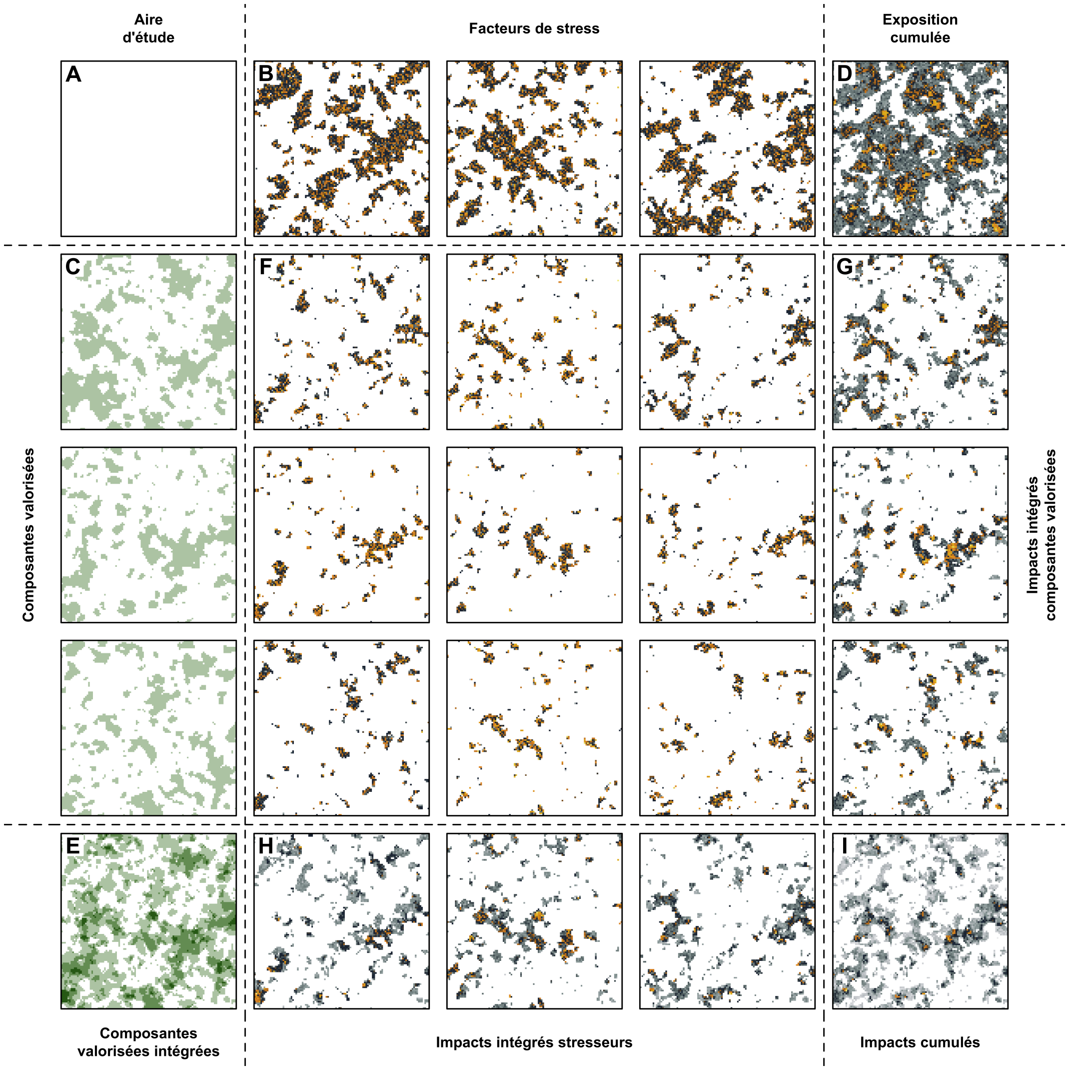

Figure 1: Exemple fictif d'évaluation spatiale des effets cumulatifs selon la méthodologie proposée par Halpern et al. 2008b. L'évaluation débute par la délimitation d'une zone d'étude d'intérêt (**A**). Un portrait de la zone d'étude est ensuite effectué en caractérisant la répartition des facteurs de stress (**B**) et les composantes valorisées (**C**) permettant d'atteindre les objectifs de l'évaluation. La sommation de l'ensemble des facteurs de stress permet d'identifier les milieux qui sont les plus exposés au cumul de stress, *i.e.* l'exposition cumulée (**D**). La somme des composantes valorisées, quant à elle, permet d'identifier les milieux de la zone d'étude où un plus grand nombre de composantes valorisées se chevauchent (**E**). En combinant la répartition des facteurs de stress et composantes valorisées ainsi que la vulnérabilité des composantes valorisées aux facteurs de stress, une évaluation relative d'effets individuels est obtenue (**F**). Il est possible d'évaluer l'impact de l'ensemble des facteurs de stress sur une seule composante valorisée (**G**) ; similairement, il est possible d'évaluer l'impact d'un seul facteur de stress sur l'ensemble des composantes valorisées (**H**). La sommation de l'ensemble des impacts individuels fournit l'évaluation relative des effets cumulatifs intégrant l'ensemble des combinaisons entre facteurs de stress et composantes valorisées (**I**).

Considérer la structure des communautés

La méthode proposée par Halpern et al. (2008b) permet de prédire les effets pressentis de stresseurs environnementaux sur des composantes valorisées et d'attribuer ces effets à des stresseurs spécifiques ; elle répond ainsi à l'appel de Dubé (2003), Jones (2016) et plusieurs autres en combinant les approches d'évaluations des effets cumulatifs basés sur les stresseurs (*i.e. stressor-based*) et celles basées sur les effets (*i.e. effect-based*). Elle est toutefois caractérisée par certaines limitations qui ne lui permettent pas de considérer la structure des communautés écologiques. (voir Halpern et Fujita, 2013; Hodgson et al., 2019). L'approche de Halpern et al. (2008b) tient pour acquis que les effets cumulatifs des stresseurs environnementaux sont linéaires et additifs, *i.e.* que les effets des stresseurs et les composantes valorisées sont indépendants entre eux. Les effets non-additifs et non-linéaires ne peuvent ainsi être capturés et la méthode n'évalue que les effets directs des stresseurs environnementaux (Hodgson et al., 2019), ignorant conséquemment les effets indirects qui transitent par les interactions écologiques. La plupart des évaluations qui utilisent l'approche développée par Halpern et al. (2008b) utilisent ainsi des habitats ou des écosystèmes comme composantes valorisées. Ces dernières ont permis de circonscrire les évaluations à un nombre limité d'éléments à considérer et à appuyer la gestion de milieux dont l'importance écologique est bien démontrée, comme les récifs coralliens et les milieux humides. Ces évaluations peuvent toutefois difficilement guider la gestion d'espèces exploitées commercialement et d'espèces en péril qui font partie de réseaux écologiques complexes (Halpern et Fujita, 2013; Giakoumi et al., 2015). Quelques évaluations d'effets cumulatifs ont été menées sur des groupes d'espèces de mégafaune marine (Maxwell et al., 2013; Trew et al., 2019). Les effets indirects sur les espèces y sont considérés qualitativement par l'évaluation de sensibilités aux stresseurs spécifiques à chaque espèce et leurs effets sont assumés inférieurs aux effets directs (Maxwell et al., 2013). Une évaluation permettant de quantifier et de discriminer les effets directs et indirects demeure toutefois absente de la littérature malgré le besoin reconnu d’approches considérant la structure des communautés pour l’évaluation des effets cumulatifs (Giakoumi et al., 2015). Plusieurs auteurs considèrent d’ailleurs qu’il est irréaliste d’aspirer à une connaissance exhaustive des effets indirects dans un contexte de gestion environnementale (*e.g.* Schindler et Hilborn, 2015; Hodgson et al., 2019). Dans le cadre de ma thèse, je présente le raisonnement inverse : j’insiste sur l’importance de considérer les interactions écologiques afin de capturer les effets indirects des stresseurs environnementaux lors d’évaluations d’effets cumulatifs.

Structure et objectifs de la thèse

L’objectif central de ma thèse est d’évaluer les effets cumulatifs des changements climatiques et des activités humaines sur les communautés écologiques de l’estuaire et du golfe du Saint-Laurent au Canada. Deux hypothèses de base structurent ma thèse :

1. Les interactions écologiques influencent la propagation indirecte des effets de multiples stresseurs et, en tant que tel, devraient être considérées lors d’évaluations des effets cumulatifs sur des espèces individuelles ou sur des communautés écologiques ;
2. Les interactions écologiques peuvent favoriser la propagation d’effets non-additifs de multiples stresseurs à travers les communautés écologiques ; les effets de multiples stresseurs devraient ainsi être évalués conjointement lors d’évaluations d’effets cumulatifs.

Comme présenté plus tôt, la méthode d’évaluation des effets cumulatifs proposée par Halpern et al. (2008a) se base sur trois pilliers : 1) la caractérisation des stresseurs environnementaux, 2) la distribution des espèces et 3) la sensibilité spécifique des espèces à chaque stresseur (Figure 2). Dans le cadre de ma thèse, j’ajoute deux pilliers supplémentaires en vue de considérer les interactions écologiques : 4) la description de la structure des communautés écologiques, *i.e.* le métaréseau d'interactions, et 5) l'évaluation de la sensibilité des espèces aux effets indirects issus de la propagation des effets des stresseurs environnementaux à travers les interactions écologiques (Figure 2).

L'atteinte de l'objectif général de ma thèse est ainsi divisée en trois parties (Figure 2). Dans la première partie, j'explore les suppositions de base de ma thèse et j'articule un cadre théorique sur la propagation indirecte des stresseurs environnementaux à travers les interactions écologiques (Chapitre 1). Ce cadre théorique sert de modèle conceptuel pour l'entièreté de la thèse. La deuxième partie de ma thèse (Chapitres 2, 3 et 4) adresse des défis logistiques et méthodologiques en vue de décrire les pilliers de l'évaluation des effets cumulatifs et d'appliquer le cadre théorique développé en première partie. Les chapitres 1 et 5 de la thèse abordent également certaines considérations méthodologiques et logistiques pour l'évaluation des effets cumulatifs. Finalement, la troisième partie de ma thèse applique le modèle conceptuel développé en première partie et combine l'ensemble des chapitres pour proposer une évaluation des effets cumulatifs des changements climatiques et des activités humaines sur les communautés écologiques de l'estuaire et du golfe du Saint-Laurent qui considère la propagation indirecte des effets des stresseurs environnementaux par les interactions écologiques (Chapitre 5).

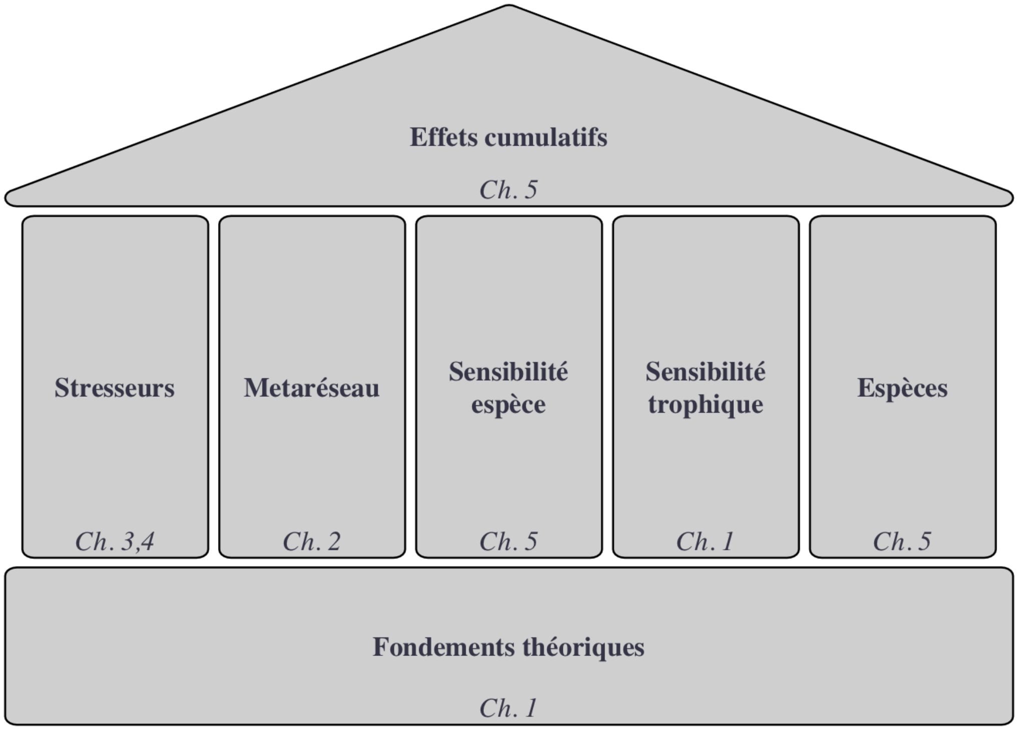

Figure 2: Schéma conceptuel pour l'évaluation des effets cumulatifs sur les communautés écologiques qui guide la structure de la thèse.

Système du Saint-Laurent

Les évaluations d'effets cumulatifs devraient être effectuées à une échelle permettant d'appuyer l'adoption de mesures de gestion efficaces et ciblées (Halpern et Fujita, 2013). L'analyse globale proposée par Halpern et al. (2008b), bien qu'elle soit informative, ne permet pas d'appuyer la gestion d'enjeux environnementaux locaux ou régionaux. Plusieurs évaluations ont ainsi raffiné l'analyse planétaire en limitant l'étendue spatiale à une zone de gestion et en ciblant des enjeux locaux ou régionaux (*e.g.* Halpern et al., 2009; Ban et al., 2010; Micheli et al., 2013). Par exemple, des données d'hypoxie ($<$ 30 % saturation d'oxygène) globales étant indisponibles, ce facteur de stress a été laissé de côté pour les évaluations d'effets cumulatifs planétaires

(Halpern et al., 2008b, 2015b, 2019). Il s'agit néanmoins d'un stresseur environnemental important dans les chenaux profonds de l'estuaire et du golfe du Saint-Laurent (Benoît et al., 2012) et pour lequel des données spatiales sont disponibles régionalement (Blais et al., 2019). Sélectionner une zone d'étude restreinte apparaît ainsi comme une nécessité en vue d'appliquer l'évaluation des effets cumulatifs dans un contexte de gestion écosystémique. Dans le cadre de ma thèse, je concentre ainsi mes travaux sur l'estuaire et le golfe du Saint-Laurent auxquels je fais référence en tant que Système du Saint-Laurent.

L'estuaire, d'une longueur approximative de 400 km, est l'un des plus grands estuaires au monde. Le golfe, quant à lui, est une mer intérieure qui atteint une largeur de plus de 300 km et qui s'ouvre à l'océan Atlantique par les détroits de Cabot et de Belle-Isle au sud et au nord de Terre-Neuve, respectivement. Ensemble, ils forment un vaste système socio-écologique caractérisé par des conditions environnementales hétérogènes et des processus océanographiques complexes (El-Sabh et Silverberg, 1990; White et Johns, 1997; Dufour et Ouellet, 2007; Saucier et al., 2003; Galbraith et al., 2018). On y trouve ainsi une diversité importante d'habitats qui accueillent des communautés écologiques diversifiées et productives (Savenkoff et al., 2000). Le Système du Saint-Laurent draine près de 25 % des réserves mondiales d'eau douce en formant un continuum écologique avec le bassin des Grands Lacs, où habitent plus de 45 millions de Nord Américains (Statistics-Canada, 2017). Les côtes du Système du Saint-Laurent hébergent 80 % de la population du Québec et la majorité des populations des maritimes – *i.e.* Terre-Neuve, la Nouvelle-Écosse, le Nouveau-Brunswick et l'Île-du-Prince-Édouard – ,et ce, principalement dans l'estuaire et le sud du Golfe (Schloss et al., 2017; Statistics-Canada, 2017).

Le Système du Saint-Laurent est d'une importance primordiale pour l'économie canadienne. Les principales activités économiques qui s'y déroulent sont la pêche commerciale, le transport maritime, le tourisme et l'aquaculture. La pêche commerciale cible plus de 50 espèces incluant les poissons de fond et pélagiques, les mollusques et les crustacés. On y trouve également plus de 2000 sites aquacoles, localisés principalement dans le sud du Golfe. Le Système du Saint-Laurent est également une porte d'entrée vers l'est du Canada et des États-Unis. De nombreux navires y transitent ainsi chaque année en direction des quelques 40 ports en mesure d'accueillir des navires commerciaux ou vers le bassin des Grands Lacs.

La disponibilité et l'accessibilité des ressources, combinées à un positionnement stratégique pour le transport et le tourisme maritime, augmentent rapidement l'intérêt porté au Système du Saint-Laurent, comme en témoigne la stratégie maritime québécoise dévoilée au début de mon projet de thèse (Government of Québec, 2015). Cette stratégie vise un accroissement de l'utilisation du Système du Saint-Laurent à des fins d'exploitations des ressources maritimes. Cet accroissement se traduirait principalement par une amélioration et une augmentation des capacités des infrastructures portuaires, une augmentation du trafic maritime à caractère industriel et de l'industrie touristique ainsi qu'une valorisation des produits issus des activités de pêche et d'aquaculture (Government of Québec, 2015). Déjà, plusieurs projets de développement ou d'agrandissements portuaires ont vu le jour, ce qui augmentera le volume du trafic maritime qui transitera par la voie navigable. La présence d'hydrocarbures suscite également de l'intérêt pour le Système du Saint-Laurent, avec le site Old Harry chevauchant la limite entre Québec et Terre-Neuve, et plus de 60 000 km de relevés sismiques effectués depuis les années 1970. Une augmentation de l'empreinte des activités humaines est donc prévisible pour le Système du Saint-Laurent dans les prochaines années.

Structure des chapitres

Partie 1 : cadre théorique

Chapitre 1 : À propos de la sensibilité des réseaux trophiques aux effets de multiples stresseurs

Les fondements pratiques et théoriques sur les effets de multiples stresseurs demeurent imparfaits (Côté et al., 2016; De Laender, 2018) et l'incapacité de l'approche de Halpern et al. (2008b) à considérer les interactions écologiques n'est pas unique à leur méthode. D'un point de vue empirique, les contraintes pratiques et méthodologiques à l'évaluation des effets de multiples stresseurs et de leurs interactions sur les communautés écologiques sont apparentes. Les designs expérimentaux factoriels et répliqués et les méthodes statistiques requises imposent des défis logistiques et méthodologiques importants (Jones, 2016). Les approches expérimentales et *in situ* sont ainsi limitées à un faible nombre de stresseurs et d'espèces. De plus, les études qui s'intéressent aux effets de multiples stresseurs utilisent typiquement des modèles nuls permettant d'identifier des effets non-additifs, sans toutefois décrire les mécanismes écologiques qui régissent les effets de multiples stresseurs (Griffen et al., 2016; Jackson et al., 2016; De Laender, 2018; Schäfer et Piggott, 2018).

D'un point de vue théorique, l'importance des interactions écologiques pour la propagation de multiples stresseurs ne peut actuellement pas guider concrètement leur inclusion au sein d'évaluations pratiques d'effets cumulatifs. Montoya et al. (2009) fournissent l'exploration des effets de perturbations sur les réseaux trophiques la plus informative à notre connaissance. Les auteurs démontrent que l'importance des effets indirects est majeure pour la propagation de perturbations à travers des réseaux trophiques. Leurs résultats ne peuvent toutefois être étendus aux effets de multiples stresseurs. Le rôle joué par les interactions écologiques dans le contexte des effets de multiples stresseurs nécessite toujours une exploration théorique formelle, et cette dernière devrait être structurée afin de fournir des recommandations claires pour la gestion. L'objectif du chapitre 1 est ainsi de tester les suppositions de base de ma thèse – *i.e.* les interactions écologiques et les stresseurs environnementaux doivent être considérés conjointement lors d'évaluations d'effets cumulatifs – et d'articuler un cadre théorique sur la propagation des effets des stresseurs à travers les communautés écologiques.

Partie 2 : considérations méthodologiques et logistiques

Chapitre 2 : Prédire les interactions biotiques au sein de milieux pauvres en données

Un défi à l'inclusion des interactions aux évaluations d'effets cumulatifs est la caractérisation de la structure des réseaux trophiques (Polis, 1991; Martinez, 1992; Pascual et Dunne, 2006). La quantité d'interactions potentielles entre les espèces d'un réseau est imposante. À titre d'exemple, un réseau trophique simple composé de sept espèces compte potentiellement 42 interactions directes et jusqu'à 13 650 interactions indirectes (Dodds et Nelson, 2006). Observer l'ensemble des interactions, et surtout l'absence d'interactions, devient un défi logistique majeur qui rend la description empirique de la structure des communautés particulièrement complexe (Dunne, 2006; Morales-Castilla et al., 2015). Des méthodes permettent de prédire les interactions en utilisant des proxy comme des traits fonctionnels, la phylogénie et la distribution des espèces (*e.g.* Gravel et al., 2013; Morales-Castilla et al., 2015; Bartomeus et al., 2016; Albouy et al., 2019). Les données requises pour l'application de ces méthodes demeurent toutefois importantes. L'objectif du chapitre 2 est de développer une méthode permettant de prédire les interactions trophiques dans un contexte où peu de données sont disponibles afin d'accroître leur disponibilité pour les évaluations d'effets cumulatifs et la gestion environnementale.

Chapitre 3 : L'évaluation des impacts cumulés dans l'estuaire et le golfe du Saint-Laurent : vers une planification systémique de l'exploitation des ressources

Chapitre 4 : Caractériser et partager les connaissances sur l'exposition aux stresseurs environnementaux dans le Système du Saint-Laurent au Canada

Tel que décrit précédemment, le Système du Saint-Laurent occupe une place primordiale pour l'économie du Canada. Il est également caractérisé par un mode de gestion complexe qui implique cinq juridictions provinciales – *i.e.* Terre-Neuve, la Nouvelle-Écosse, le Nouveau-Brunswick, l'Île-du-Prince-Édouard et le Québec – et une juridiction fédérale. Les données, les expertises et les pouvoirs décisionnels sont donc partagés entre plusieurs acteurs. Une diversité d'enjeux caractérisent ainsi le Système du Saint-Laurent, qui bénéficierait d'une approche de gestion écosystémique. Au moment de débuter ma thèse, les rapports de Dufour et Ouellet (2007) et de Benoît et al. (2012) étaient les seuls ouvrages récents offrant une vue d'ensemble des enjeux environnementaux au sein du Système du Saint-Laurent. L'objectif du chapitre 3 est ainsi de contextualiser ces enjeux environnementaux et d'identifier les défis associés à l'évaluation des effets cumulatifs dans un contexte de gestion écosystémique au sein du Système du Saint-Laurent. L'objectif du chapitre 4, quant à lui, est de caractériser la distribution et l'intensité des stresseurs environnementaux d'importances, qui constitue un élément essentiel à une évaluation des effets cumulatifs au sein du Système du Saint-Laurent.

Partie 3 : évaluation des effets cumulatifs

Chapitre 5 : Les interactions écologiques amplifient les effets cumulatifs dans les écosystèmes marins

Le chapitre 5 rassemble l’ensemble des chapitres précédents afin d’atteindre l’objectif général de la thèse, soit d’évaluer les effets cumulatifs des changements climatiques et des activités humaines sur les communautés écologiques du Système du Saint-Laurent. En s’appuyant sur les quatre chapitres précédents, ce chapitre cherche à assouplir le postulat d’indépendance entre les espèces imposés par l’approche originale de Halpern et al. (2008a) afin de considérer la structure des communautés écologiques pour l’évaluation des effets cumulatifs.

ARTICLE 1

À PROPOS DE LA SENSIBILITÉ DES RÉSEAUX TROPHIQUES AUX EFFETS DE MULTIPLES STRESSEURS

1.1 Résumé

Évaluer les effets de multiples stresseurs sur les écosystèmes est de plus en plus important en raison des changements globaux. Le rôle des interactions écologiques pour la propagation des effets des stresseurs, bien que largement reconnue, n'a toujours pas été formellement explorée. Nous avons conceptualisé comment les stresseurs se propagent à travers les réseaux trophiques et nous avons exploré comment les stresseurs affectent des motifs à 3 espèces simulés et des réseaux trophiques du Système du Saint-Laurent canadien. Nous trouvons que négliger les interactions écologiques sous-estime systématiquement les effets des stresseurs et que les effets synergiques et antagonistes sont fréquents à l'échelle des réseaux trophiques. Nous trouvons également que différents types d'interactions influencent la sensibilité des espèces aux effets des stresseurs : les espèces impliquées dans des interactions omnivores et des chaînes tri-trophiques sont particulièrement sensible (points d'entrée faibles) et susceptibles aux effets synergiques (amplificateurs biotiques) et antagonistes (tampons biotiques). Finalement, nous trouvons que les prédateurs apicaux sont négativement affectés, alors que les méso-prédateurs bénéficient des effets des stresseurs dû à leur position trophique respective dans le Système du Saint-Laurent. Toutefois, la sensibilité des espèces dépend de la structure des réseaux trophiques. Par notre conceptualisation des effets de multiples stresseurs sur les réseaux trophiques, nous rapprochons la théorie de la pratique et démontrons que la complexité de la structure des communautés écologiques est essentielle à une évaluation des effets nets des stresseurs sur les espèces.

Ce premier article, intitulé *"On the sensitivity of food webs to multiple stressors"* a été corédigé par moi-même, Kevin Cazelles, Laura Dee, Philippe Archambault et Dominique Gravel. Il est actuellement en révision pour resoumission dans la revue *Ecology Letters* en tant qu'article de type *Ideas and Perspectives.* L'article est actuellement disponible en version *preprint* (https://doi.org/10.22541/au.159621485.58777803). Tous les auteurs ont contribué à l'élaboration des objectifs de l'article. En tant que premier auteur, j'ai été en charge de la conceptualisation, des simulations, des analyses, des figures et j'ai dirigé la rédaction de l'article. Kevin Cazelles a contribué à ces étapes. Tous les auteurs ont contribué aux bases de données, aux analyses et à l'écriture de l'article selon leur expertise respective et ont contribué à la révision de l'article. Les résultats issus de cet article ont été présentés en version abrégée lors du *Forum québécois en sciences de la mer* à Rimouski (Canada) à l'automne 2019.

Beauchesne, D., Cazelles, K., Archambault, P., Dee, L., Gravel, D., 2020. On the sensitivity of food webs to multiple stressors (preprint). Preprints. https://doi.org/10.22541/au.159621485.58777803

Les sections suivantes sont celles de l'article en révision.

1.2 Title

On the sensitivity of food webs to multiple stressors

1.3 Authors

David Beauchesne, Kevin Cazelles, Philippe Archambault, Laura E. Dee, Dominique Gravel

1.4 Abstract

Evaluating the effects of multiple stressors on ecosystems is becoming increasingly vital with global changes. The role of species interactions in propagating the effects of stressors, although widely acknowledged, has yet to be formally explored. Here, we conceptualize how stressors propagate through food webs and explore how they affect simulated 3-species motifs and food webs of the Canadian St. Lawrence System. We find that overlooking species interactions invariably underestimates the effects of stressors, and that synergistic and antagonistic effects through food webs are prevalent. We also find that interaction type influences a species' sensitivity to stressors; species in omnivory and tri-trophic food chain interactions in particular are sensitive (weak entry points) and prone to synergistic (biotic amplifiers) and antagonistic (biotic buffers) effects. Finally, we find that apex predators were negatively affected and mesopredators benefited from the effects of stressors due to their trophic position in the St. Lawrence System, but that species sensitivity is dependent on food web structure. In conceptualizing the effects of multiple stressors on food webs, we bring theory closer to practice and show that considering the intricacies of ecological communities is key to assess the net effects of stressors on species.

Keywords: Antagonism, synergism, non-additive effects, multiple stressors, cumulative effects, holistic, indirect effects, food webs, ecological networks, motifs

1.5 Introduction

Ecosystems worldwide are increasingly affected by multiple environmental pressures, commonly referred to as stressors (Boonstra et al., 2015; Halpern et al., 2019). Stressors can be defined as external drivers that affect ecological processes and disturb natural systems; they are driven by natural or human-induced biophysical processes, such as ocean acidification and warming, or from anthropogenic activities, such as fisheries and harvesting. Individually, stressors affect all levels of biological organization and cause dramatic changes to whole ecosystems. For example, ocean acidification reduces coral and mollusk calcification, metabolic, growth and mortality rates, and has been linked to altered carbon fluxes in ecological networks (Fabry et al., 2008; Kroeker et al., 2013; Bove et al., 2019). Fisheries decrease the mean trophic level in coastal and oceanic environments by targeting large predators, impair a variety of essential ecosystem services and have induced the collapse of numerous commercial species (Pauly et al., 1998; Myers and Worm, 2003; Worm et al., 2006). However, stressors rarely occur individually (Halpern et al., 2019). For example, coral reefs face a suite of pressures including fishing, warming temperatures, ocean acidification and water pollution (McClanahan et al., 2014; Harborne et al., 2017). Interactions between stressors are pervasive (*e.g.* Crain et al., 2008; Piggott et al., 2015; Jackson et al., 2016), and unpredictable (Darling and Côté, 2008; Côté et al., 2016). For instance, the sensitivity of corals to temperature-induced bleaching increases with nutrient enrichment (Wiedenmann et al., 2013; Lapointe et al., 2019), and the sensitivity of certain organisms to toxicants can be multiplied by a factor of up to 100 when they are exposed to other stressors (Liess et al., 2016). In contrast, the positive effects of acidification on primary producer biomass can be reversed by warming waters (Christensen et al., 2006). Thus, multiple stressors can interact in complex ways, amplifying or dampening the direct effects of stressors on species.

Beyond their direct effects, stressors ripple through ecological communities by way of the interactions structuring the complex networks in which species are embedded (Wootton, 2002; Bascompte, 2009; Montoya et al., 2009; O'Gorman and Emmerson, 2009; O'Gorman et al., 2012). Because species depend on one another, surprising indirect effects arise from species interactions in complex systems, such as a predator positively affecting its own prey (Abrams, 1992). Ample empirical evidence exists of such trophically-mediated effects across ecosystems globally (Paine, 1980; Estes et al., 2011).

Classic examples include sea otters (*Enhydra lutris*) indirectly shielding kelp forests from browsing by sea urchins (*Strongylocentrotus* spp.; Estes and Palmisano, 1974) and fish indirectly favouring the pollination of terrestrial plants by controlling predatory dragonfly populations (Knight et al., 2005). A species's sensitivity to trophically-mediated effects is influenced by its trophic role and position. For example, species with diversified diets (*i.e.* generalists) are more resilient than species with specialized diets (*i.e.* specialists; Clavel et al., 2011), and apex predators are generally more vulnerable to trophically-mediated effects (Ripple et al., 2015; Stier et al., 2016). How ecological networks are structured, *i.e.* the number, configuration and strength of interactions between species, also influence the propagation of stressors and the stability of whole systems (Wootton, 2002; Montoya et al., 2009; Bartley et al., 2019; O'Gorman et al., 2019). Stressors can modify these structural properties and rewire entire food webs (Blanchard, 2015; Kortsch et al., 2015; Bartley et al., 2019). Links can be added or removed (*i.e.* topological rewiring; Bartley et al., 2019) through primary and secondary species extinctions (*e.g.* Allesina et al., 2006; Eklöf and Ebenman, 2006), climate-related distributional shifts (*e.g.* Kortsch et al., 2015; Bartley et al., 2019) or invasive species introductions (*e.g.* Vander Zanden et al., 1999; David et al., 2017). Alteration to the flow of energy also arises when consumers modify their space and resource use (*i.e.* interaction strength rewiring; Bartley et al., 2019). Indirect effects that arise from species interactions thus have important, yet underexplored, implications for the effects of multiple stressors on populations of interacting species – and are likely to depend on network structure.

Despite the potential for stressors to interact and indirectly affect species through interactions, single-stressor and single-species assessments remain the norm (O'Brien et al., 2019), and most large-scale multiple stressors studies remain focused on direct effects to habitats rather than to species and communities (*e.g.* Ban et al., 2010; Halpern et al., 2019). Furthermore, methodologies tend to assume that the effects of multiple stressors are additive (*e.g.* Halpern et al., 2019) and rely on null models providing little insights into the ecological mechanisms governing how multiple stressors combine to affect ecosystems (Griffen et al., 2016; Jackson et al., 2016; De Laender, 2018; Schäfer and Piggott, 2018). While these approaches have revealed important insights into the effects of stressors, they may under or overestimate the effects that arise from interactions between species and among stressors. This gap constrains our ability to predict the consequences of multiple stressors for interacting species in complex ecosystems – in which both direct and indirect effects of stressors are likely common, yet widely omitted. Recent publications discuss the importance of ecological networks for multiple stressors research (*e.g.* De Laender, 2018; Bruder et al., 2019; Hodgson et al., 2019; Orr et al., 2020) and theory-driven modelling approaches have emerged to evaluate the effects of multiple stressors on ecosystems (*e.g.* Hodgson et al., 2017; Galic et al., 2018; Thompson et al., 2018; Otto et al., 2020), yet the importance of species interactions for multiple stressors research has yet to be formally explored.

Confronted with the challenge of managing and preserving complex systems, holistic approaches that consider the complexities of multiple stressors in ways that are informative to management are urgently needed. In response, our objective is to conceptualize and investigate the role of species and their interactions in mediating the effects of multiple stressors on ecological communities. In doing so, we seek to answer questions of particular significance to management and the application of holistic environmental approaches: **Q1**) should species interactions be considered in environmental effects assessments, **Q2**) should the effects of stressors be evaluated separately or in combination, and **Q3**) if interactions do matter, which species are most sensitive to the effects of multiple stressors based on their trophic position? First, we conceptualize how multiple stressors permeate ecological communities using a new and broadly applicable quantitative framework, simulating the effects of stressors on the equilibrium dynamics of the most frequent 3-species motifs in diverse food webs (*i.e.* tri-trophic food chain, omnivory, exploitative competition, and apparent competition) to explore the many pathways through which species can be affected by one or more stressors. Second, we apply this framework to a real-world system to explore the sensitivity of species to stressors in the St. Lawrence System, in Eastern Canada using three empirical food webs from different regions, exposed to up to eight different sources of stress.

1.6 Of food webs and multiple stressors

In the following sections, we conceptualize how multiple stressors permeate ecological communities by directly and indirectly disrupting the dynamics of interacting species. We then use a new and broadly applicable quantitative framework to investigate how species responses to the effects of single and multiple stressors depend on the structure of ecological communities and a species's trophic position. Our work builds on concepts from Wootton (2002) and Montoya et al. (2009) on indirect effects and the spread of disturbances through food webs and extends their work to consider multiple stressors by using the motif concepts explored in Stouffer et al. (2007), Stouffer and Bascompte (2010) and Stouffer et al. (2012).

1.6.1 Species interactions: a gateway through ecological communities

1.6.1.1 Community dynamics

We begin by conceptualizing community dynamics with a simplified 6-species food web composed of populations of krill (Euphausiacea) and copepods (Copepoda) capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*), and beluga (*Delphinapterus leucas*) and humpback (*Megaptera novaeangliae*) whales (Figure 3A). The dynamics of this community are driven by ecological processes operating at the scale of individual populations (*e.g.* reproduction and mortality) and of the whole community (*e.g.* consumer-resource interactions). Species influence the dynamics of other species both directly and indirectly, even in the absence of stressors. **Direct effects** arise when a species affects another without the involvement of a third species (Abrams et al., 1996; Wootton, 2002). For example, cod consumes capelin in our system, directly affecting its prey and weaving the dynamics of both populations together (Figure 3A).

Indirect effects arise when a species affects another through at least one intermediary species, which results in an interaction chain also known as a density-mediated indirect effect (Wootton, 1993, 2002; Abrams et al., 1996). In our system, krill is indirectly affected by cod through their respective interaction with capelin (Figure 3A). Indirect effects can be as important as, and propagate faster than, direct effects (Wootton, 1993, 2002; Menge, 1995; Yodzis, 2000). Trophic cascades, *i.e.* the propagation of effects by consumers downward through whole food webs (*e.g.* cod-capelin-krill; Figure 3A) and apparent competition, *i.e.* alternate prey species of a generalist predator (*e.g.* krill-capelin-copepod; Figure 3A) are well-documented and common types of indirect effects in empirical food webs (*e.g.* Holt, 1977; Paine, 1980; Menge, 1995; Estes et al., 2011).

In food webs, the **net effect** of a single or of multiple species on another is the integration of all individual direct and indirect effects propagating to a focal species (Abrams et al., 1996). For example, the net effect of cod on beluga depends on the direct effect linking both species and the indirect effect of cod on beluga through capelin (Figure 3A).

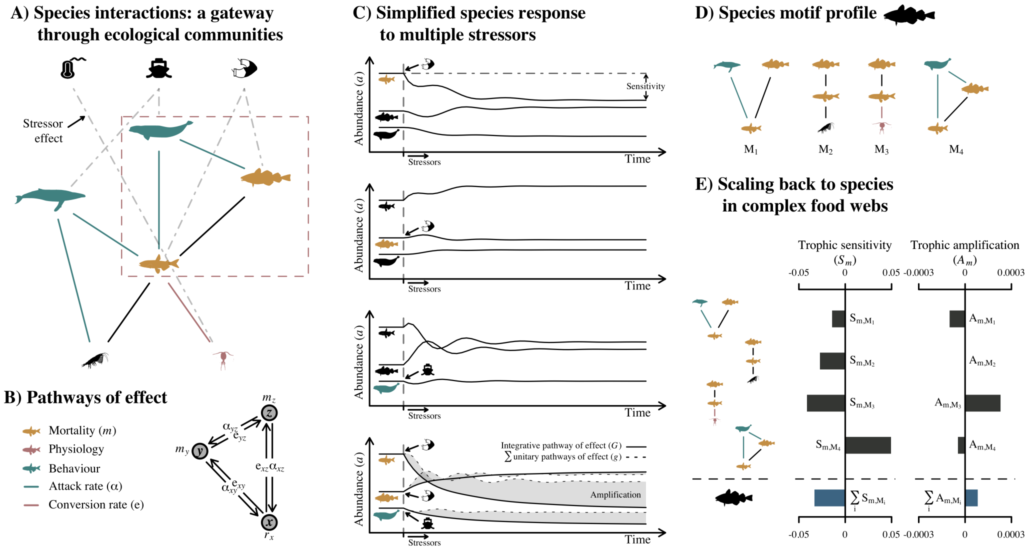

Figure 3: Conceptualization of the effects of multiple stressors on a simplified 6-species food web composed of populations of krill (Euphausiacea), copepods (Copepoda), capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*), beluga (*Delphinapterus leucas*) and humpback (*Megaptera novaeangliae*) whales, and affected by climate change-induced temperature anomalies, commercial shipping and trawl fishing. A) **Direct** (*e.g.* cod and capelin) and **indirect** (*e.g.* cod and krill) **effects** arise from species interactions and the integration of both types of effects provides the overall **net effect**. Through species interactions, the species-specific effects of stressors propagate indirectly through the food web. B) **Stressors** affect food webs by disrupting ecological processes such as mortality rates (m; *e.g.* effect of fisheries on cod), attack rates (α; *e.g.* effect of shipping on beluga) and conversion rates (e; effect of temperature anomalies on copepods). **Species-specific sensitivities** drive species responses to stressors, while the net effect of stressors is dependent on food web structure. The collection of ecological processes through which stressors directly and indirectly affect ecological communities for what we define as a **pathway of effect**. C) Here, the food web is simplified by focusing on subsets of species interactions – such as the omnivory interaction linking beluga, cod and capelin – called motifs. Disrupting ecological processes affects community dynamics and results in variations in species abundances (**trophic sensitivity**; S_m). Effects to individual ecological processes arise through **unitary pathways of effects** (g) and result in contrasting population trajectories (1-3). Unitary pathways of effect combine to form an **integrative pathway of effect** (G) and collectively affect species in a community (4). The difference between the sum of trophic sensitivities to unitary pathways of effect ($g \in G$) and trophic sensitivity to the integrative pathway of effect identifies synergistic and antagonistic effects (**trophic amplification**; A_m). D) A **species motif census** (M) is composed of all the positions it holds in a food web. E) A pathway of effect and resulting trophic sensitivities and amplification can be evaluated across a species motif census, the sum of which summarizes that species overall trophic sensitivity and amplification. Terms in bold are defined in the glossary.

1.6.1.2 Moving beyond direct effects of stressors

Stressors affect populations and whole communities by disrupting the ecological processes that govern their dynamics (*e.g.* Galic et al., 2018; Guiden et al., 2019; Hodgson et al., 2019; Hodgson and Halpern, 2019). To illustrate, consider that 3 distinct sources of stress appear in the system described above: climate change-induced temperature anomalies, commercial shipping and trawl fishing (Figure 3A). The magnitude and nature of the direct effects of stressors on populations depend on **species-specific sensitivity**, which can be broadly defined as the predisposition of a species to be adversely affected by stressors (Oppenheimer et al., 2015). For example, hypoxia can induce a variety of species-specific responses, ranging from adaptation to avoidance to mortality (Eby et al., 2005; Chabot and Claireaux, 2008; Belley et al., 2010; Pillet et al., 2016). Stressors can also have one or more non-mutually exclusive pathways to directly affect a species, such as effects to mortality, growth, feeding rates, and metabolism. Identifying and quantifying species-specific sensitivities is best addressed through *in situ* sampling and targeted experimental investigations. These have limited applicability for communities influenced by many stressors, and are thus beyond the capabilities of most empirical research. Considering species-specific sensitivities is also beyond the scope of our objectives. We thus intentionally consider that species-specific responses are constant and negative across species to investigate the role of species interactions in mediating the effects of stressors in ecological communities (see next sections). Still, species-species sensitivities could readily be incorporated and explored in our work to consider species-scale and network-scale responses simultaneously.

Through species interactions, these direct effects of stressors on ecological processes can indirectly propagate to other species in the system. For example, in our system, temperature anomalies could affect the reproductive capabilities of copepods (*i.e.* population growth rate) and the effectiveness of their predators to assimilate them (*i.e.* conversion rate), shipping could alter the feeding behaviour of whales (*i.e.* attack rate), and fisheries could affect the mortality of cod and capelin (Figure 3A, B).

The direct effect of shipping on beluga and humpback whales behaviour would then indirectly propagate to their prey by altering their attack rates and decreasing predation pressure (Figure 3A). By extension to trophically-mediated net effects in food webs described above, the net effect of a single or of multiple stressors on a species must integrate all direct and trophically-mediated indirect effects propagating to a focal species. In this context, the collection of ecological processes through which stressors directly and indirectly affect ecological communities form what we define as a **pathway of effect** (see next sections and glossary for more details).

1.6.2 Handling food web complexity using motifs

The number and complexity of pathways of effect through which a species may affect or be affected by other species – and through which stressors may permeate communities – increases exponentially with the number of species and interactions in a network (Menge, 1995). To illustrate this, let us imagine that community dynamics are governed by the resource population growth ($n = 2$) and consumer mortality ($n = 4$) rates, and interactions attack ($n = 7$), and conversion ($n = 7$) rates (Figure 3B). Our six-species system would then be driven by 20 distinct ecological processes, offering over 1 000 000 unique pathways (2^{20}) of effect through which the system could be disrupted; this complexity has hindered studies investigations on the effects of disturbances on community dynamics (Wootton, 2002; Montoya et al., 2009).

Studying smaller subgraphs – community motifs or modules – emerged as an alternative to gather insights into the dynamics and stability of ecological communities (Holt, 1997; Holt and Hochberg, 2001). Motifs are collections of n-species that, when put together, construct whole food webs (Milo et al., 2002; Stouffer et al., 2007). They form the backbone of food webs and provide a mesoscale characterization of the structural properties of communities (Bascompte and Melián, 2005; Stouffer et al., 2007; Stouffer and Bascompte, 2010, 2011; Bramon Mora et al., 2018). Investigations into 3-species motifs are particularly common in the literature (*e.g.* Menge, 1995; Milo et al., 2002; Stouffer et al., 2007, 2012). On average, 95% of 3-species motifs in empirical food webs are composed of tri-trophic food chain (*e.g.* cod-capelin-krill; Figure 3A), omnivory or intraguild predation (*e.g.* beluga-cod-capelin; Figure 3A), exploitative competition (*e.g.* humpback whale-capelin-beluga; Figure 3A) and apparent competition (*e.g.* krill-capelin-copepod; Figure 3A) motifs (Camacho et al., 2007; Stouffer and Bascompte, 2010). Focusing on motifs rather than whole food webs restricts the complexity we must contend with to better understand the role of species and their interactions in mediating the effects of multiple stressors. For example, affecting omnivory interactions is possible through 9 ecological processes and 511 unique pathways of effect (Figure 3B). We now shift our focus to the dynamics of those four motifs particularly relevant to the structural properties of empirical food webs.

1.6.3 Simplified species responses to multiple stressors

We begin by illustrating the effects of stressors on the dynamics of a single motif affected by a specific pathway of effect, the omnivory interaction connecting cod, beluga and capelin in our system (Figure 3C), to formalize the concepts we are using to explore the effects of stressors through food webs. We then move to a holistic assessment of all motifs and pathways of effect (next section). While concepts are presented in the context of motifs for simplicity, it is worthwhile noting that the concepts apply to complex networks.

Net effects are typically measured as variations in equilibrium species abundances or densities in food webs following removals or a press perturbation, which integrate all trophically-mediated effects operating on the system collectively (Wootton, 2002;

Berlow et al., 2004; Montoya et al., 2009). Likewise, we evaluate how pre-stressor species abundances at equilibrium shift after the permanent appearance of stressors in a system as a measure of their net effect. The effects of stressors travel through communities using **unitary pathways of effect** (g); this occurs when an ecological process is affected, such as an increase in cod mortality ($g = \{m_y\}$; Figure 3B). Unitary pathways of effect can induce contrasting population trajectories. Fishing increases capelin mortality ($g = \{r_x\}$) favours cod and reduces capelin and beluga abundances (Figure 3C-1). In this scenario, cod are likely released from beluga predation due to their drop in numbers (*i.e.* mesopredator release; Ritchie and Johnson, 2009). This trophically-mediated effect could ultimately exacerbate the effect of fishing on capelin by favouring one of its predators. Meanwhile, increasing cod mortality ($g = \{m_y\}$) results in the growth of the capelin and beluga populations (Figure 3C-2). Surprisingly, the cod population remains relatively unchanged (Figure 3C-2), likely because the increase in prey availability offsets the effect of fishing (*i.e.* compensatory dynamics; Gonzalez and Loreau, 2009). Finally, the beluga population appears insensitive to the effect of shipping ($g = \{\alpha_{xz}\}$ and $g = \{\alpha_{yz}\}$); yet shipping likely disrupts the top-down control of beluga on cod to the benefit of cod and to the detriment of capelin (Figure 3C-3).

Unless a single ecological process is affected, unitary pathways of effect combine to form an **integrative pathway of effect** (G), which is the set of all unitary pathways of effect that combine across species to collectively affect a community. Shipping and fishing collectively affect our system through an integrative pathway of effect ($G = \{r_x, m_y, \alpha_{xz}, \alpha_{yz}\}$) that benefits cod and reduces capelin and beluga (Figure 3B-4). We define a species (m) **trophic sensitivity** ($S_{m,G}$) as the net effect – *i.e.* the variation in equilibrium abundance after the appearance of stressors – resulting from an integrative pathway of effect G (Figure 3B):

$$S_{m,G} = \frac{a_{m,G} - a_m}{a_m}, \tag{1.1}$$

where a_m and $a_{m,G}$ are the pre- and post-stressors abundances of species m, respectively. In the remainder of the text, the term pathway of effect without a qualifier (*i.e.* integrative or unitary) refers to integrative pathways of effect. Note that by definition $S_{m,G}$ is bounded negatively to -1, as species abundances cannot be negative. We refer to species that are highly susceptible to the effects of stressors – whether positively or negatively – as **weak entry points** and distinguish between negative and positive weak entry points.

In multi-species systems, where many direct and indirect trophic effects are operating simultaneously, effects of stressors can be amplified or dampened through biotic interactions (Ives, 1995; Wootton, 2002; Thompson et al., 2018). Uncovering synergies and antagonisms has been a hallmark of investigations into the effects of multiple stressors (*e.g.* Crain et al., 2008; Darling and Côté, 2008; Côté et al., 2016; Galic et al., 2018; Thompson et al., 2018). These so-called **non-additive effects** arise when the net effect of disruptions to multiple ecological processes (*i.e.* an integrative pathway of effect) is greater (*i.e.* a synergistic effect) or lower (*i.e.* an antagonistic effect) than combined net effects of disruptions to individual ecological processes (*i.e.* unitary pathways of effect). We define a species (m) **trophic amplification** ($A_{m,G}$) as the difference between its trophic sensitivity to an integrative pathway of effect (G) and the sum of its trophic sensitivities to the unitary pathways of effect forming G ($g \in G$; Figure 3C-4):

$$A_{m,G} = \sum_{g \in G} \frac{1}{|G|} S_{m,G} - S_{m,g}, \tag{1.2}$$

where $|G|$ is the number of unitary pathways of effect g forming the integrative pathway of effect G. Synergisms and antagonisms are identified by positive and negative trophic amplifications, respectively. From this definition of non-additive effects, a single stressor can elicit non-additive effects by disrupting multiple ecological processes. In contrast, non-additive effects are usually defined as arising from more than one stressor.

However, we argue that, at the scale of communities, a stressor could indeed elicit non-additive effects on its own. In our system, shipping and fishing elicit synergistic effects on capelin and beluga, and a slightly antagonistic effect on cod. We refer to species as **biotic amplifiers** if they are affected synergistically by an integrative pathway of effect (*i.e.* positive trophic amplification) or as **biotic buffers** if they are affected antagonistically by an integrative pathway of effect (*i.e.* negative trophic amplification). Hence, capelin and beluga are biotic amplifiers, whereas cod is a biotic buffer (Figure 3C-4).

A species' trophic sensitivity – or lack thereof – can also arise from different mechanisms. Some unitary pathways of effect may reinforce each other, whereas others may cancel each other out (Wootton, 2002; Montoya et al., 2009). For example, the positive effect of cod mortality on capelin (Figure 3C-2) is offset by the negative effects on capelin mortality and beluga behaviour (Figure 3C-1, C-3, C-4). Comparing the effective and expected effects of a unitary pathway of effect – *i.e.* the average effect of an integrative pathways of effect – provides a measure of variance associated to trophic sensitivity to an integrative pathway of effect (G) that we define as **trophic variance** ($V_{m,G}$):

$$V_{m,G} = \sum_{g \in G} \left(\frac{1}{|G|} S_{m,G} - S_{m,g} \right)^2 . \tag{1.3}$$

Low variance arises from sets of unitary pathways of effect whose individual effects are relatively similar, whereas high variance identifies sets of contrasting unitary pathways of effect. Ecologically, this means that even if a species sensitivity to stressors is low, it may still be subjected to competing individual effects that disturb their population dynamics; the likelihood of observing ecological surprises would thus be heightened for species with high trophic variance. In our system, beluga ($V_{beluga,G} = 0.22$) and capelin ($V_{capelin,G} = 0.18$) are exposed to unitary pathways of effect that tend cancel each other out, whereas cod ($V_{cod,G} = 0.09$) is mostly exposed to unitary pathways of effect that reinforce each other.

1.6.4 Holistic assessment of the effects of multiple stressors

1.6.4.1 Models and simulations

We have thus far defined the trophic sensitivity, amplification and variance of species involved in an omnivory interaction and exposed to a specific pathway of effect (Figure 3C-4); there are far more potential pathways of effect. Restricting effects to resource growth, mortality, conversion and attack rates, there are 7 ecological processes and 127 distinct pathways of effect for the tri-trophic food chain, competitive exploitation and apparent competition motifs, and 9 ecological processes and 511 distinct pathways of effect for the omnivory motif. We now explore all these pathways of effect using generalized Lotka-Volterra equation systems with Type 1 functional response (see Table 1 in Supporting Information). Two additional motifs were included as controls to test the importance of species interactions in mediating the effects of stressors: a partially connected motif with a disconnected species and a predator-prey interaction resulting in 31 distinct pathways of effects, and a disconnected motif with three fully independent species resulting in 7 pathways of effect. Species dynamics were modeled using equations of the form:

$$\frac{dX_i}{dt} = X_i(r_i - \alpha_{ii}X_i + \sum_j e_{ij}\alpha_{ij}X_j), \tag{1.4}$$

where X_i denotes species i, r_i is the intrinsic growth rate and is positive for resources (*i.e.* autotrophs) and negative for consumers (*i.e.* heterotrophs), α_{ii} is the density-dependent effect of species i on itself, α_{ij} is the rate at which species j affects species i, *i.e.* the attack rate, and e_{ij} is the rate at which the biomass of species i is transformed into biomass of species j biomass, *i.e.* the conversion rate, and is a scaling parameter of the attack rate which cannot exceed 1. We studied the equilibrium dynamics of coexisting species, *i.e.* species abundances remained positive after the appearance of stressors. Consequently, we included competitive interaction parameters between consumers $(\alpha_{jk}, \alpha_{jj})$ for the exploitative competition motif, as no coexistence may occur for this motif in the absence of other interactions. Refer to Table 1 for the equation systems of all motifs.

We simulated the dynamics of the effects of stressors on motifs with 100 different sets of initial parameter values. Parameter values were fixed for intrinsic growth rate $(r = 1)$, density-dependence $(\alpha_{ii} = 0.001)$, competitive parameters $(\alpha_{jk} = \alpha_{jj} = 0.001)$, and conversion rates $(e = 0.5)$. Parameter values were randomly selected within a fixed range for mortality rates $(m \in [0.01, 0.5])$ and attack rates $(\alpha_{ij} \in [0.0001, 0.01])$. All possible pathways of effect were simulated by modifying the equilibria equation parameter values by 1%. Parameters were modified to simulate negative effects. For example, mortality rates were increased by 1%. Negative effects were simulated on resource growth rates (r) mortality rates (m), conversion rates (e) and attack rates (α_{ij}). Sets of parameter values were randomly selected so that species abundances resulting from all possible pathways of effect were positive. Parameter combinations were thus rejected if any solutions resulting in negative abundances and parameters were redrawn until 100 feasible and coexisting communities were found. Equilibria were solved using SageMath (TheSageDevelopers, 2019) and simulations were performed using R (RCoreTeam, 2019).

The trophic sensitivity $(S_{i,G})$, trophic amplification $(A_{i,G})$ and trophic variance $(V_{i,G})$ of motif positions (i) were evaluated using equations 1 and 2. The expected trophic sensitivity (S_i) and trophic amplification (A_i) of motif positions were evaluated as the average trophic sensitivity and amplification over all pathways of effect. Arbitrary thresholds were used to identify negative ($S_{i,G} < 1$) and positive ($S_{i,G} > 1$) weak entry points, biotic buffers ($A_{i,G} < 0.02$) and biotic amplifiers ($A_{i,G} > 0.02$). These thresholds are used for discussion purposes to identify species that are more or less sensitive and prone to non-additive effects.

1.6.4.2 Effects of multiple stressors on simulated communities

We observe, as anticipated, that species interactions play a crucial role in mediating the effects of stressors through food webs and that considering species in isolation underestimates the effects of stressors. Pathways of effect targeting multiple ecological processes lead to greater trophic sensitivities (Figure 4); similarly, the effects of stressors to interactions consistently result in greater trophic sensitivities than effects of stressors to controls (Figures 4,5).

The type of interaction a species is involved in also influences its sensitivity to the effects of stressors. Omnivory and tri-trophic food chain interactions are generally more sensitive than exploitative and apparent competition interactions (Figure 4,5). In omnivory and tri-trophic food chain interactions, predators and resources are negatively affected through most pathways of effect, *i.e.* they are negative entry points; mesopredators in those interactions, meanwhile, largely benefit from the effects of stressors and are positive weak entry points (Figures 4,5). In exploitative and apparent competition interactions, consumers are either negative weak entry points or unaffected by stressors, whereas resources are either positive weak entry points or unaffected by stressors (Figure 4,5). The insensitivity of consumers in apparent competition and resources in exploitative competition arises from negligible effects of stressors rather than unitary pathways of effect cancelling each other out (see trophic variance in Figure 4).

Non-additive effects also arise from species interactions; in fact, non-additive effects are largely exclusive to species in omnivory interactions and to predators in tri-trophic food chains, with most pathways of effect resulting in antagonistic or synergistic effects (Figure 4). This high variability in non-additive effects suggests that typecasting species as biotic buffers – *i.e.* antagonistically affected by stressors – or biotic amplifiers – *i.e.* synergistically affected by stressors – requires precise knowledge on the pathways of effect operating on a system. We can, nevertheless, typecast species in omnivory interactions and the predator in tri-trophic food chains as acutely susceptible to non-additive effects.

Our results show that the effects of stressors are invariably greater when species interactions are taken into account. These results provide an answer to the first management question (**Q1**) we submitted in the introduction by suggesting that environmental effects assessments should explicitly consider species interactions and the structure of food webs to avoid under-estimating the net effects of stressors. This observation is also supported by long standing evidence for the importance of interactions in spreading the effects of disturbances through food webs (*e.g.* Menge, 1995; Wootton, 1993, 2002; Yodzis, 2000; Montoya et al., 2009; O'Gorman and Emmerson, 2009; Burns et al., 2014), and we extend this conclusion to the effects of multiple stressors (see also Thompson et al., 2018).

The prevalence of non-additive effects arising from species interactions, particularly through omnivory and tri-trophic food chain interactions, also answers our second management question (**Q2**) by highlighting the importance of holistic effect assessments, rather than conventional individual assessments (O'Brien et al., 2019), to avoid overestimating or underestimating the net effects of multiple stressors. This is especially true considering that omnivory and tri-trophic food chain interactions are both particularly susceptible to the effects of stressors and important building blocks for the structure of empirical food web (*e.g.* Bascompte and Melián, 2005; Stouffer et al., 2007; Monteiro and Faria, 2016; Klaise and Johnson, 2017).

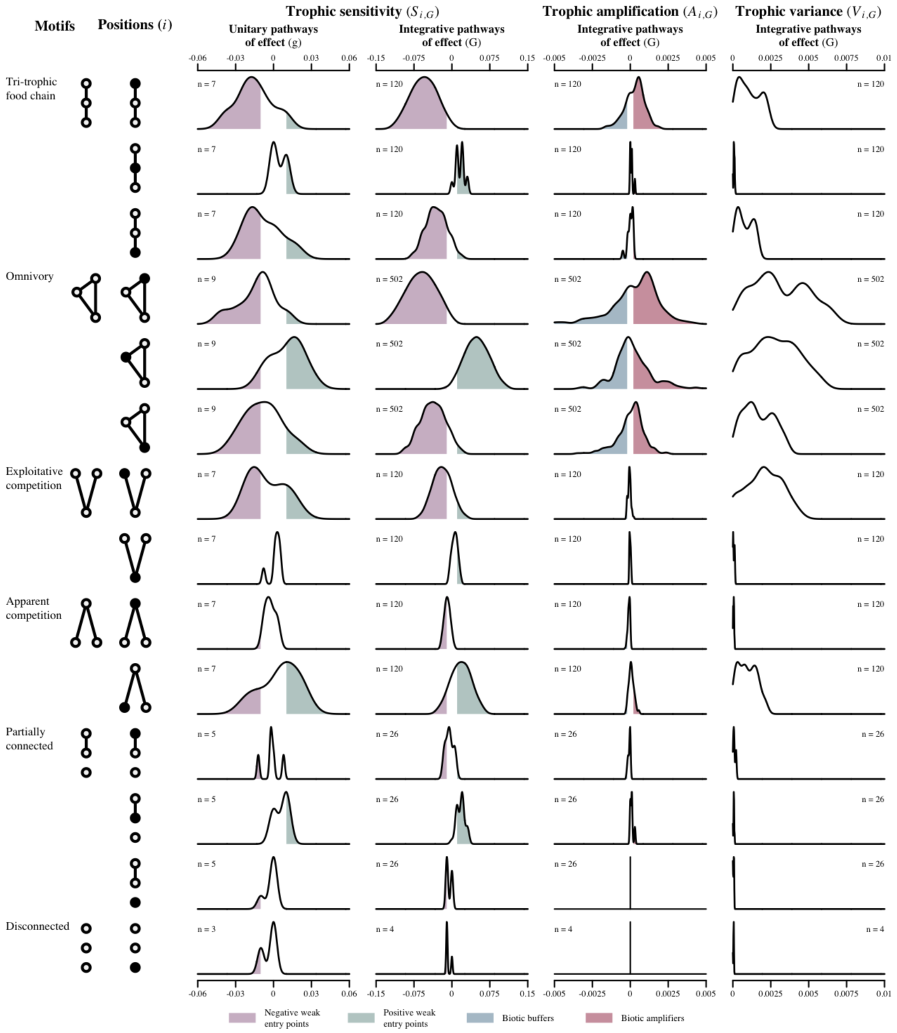

Figure 4: Density plots of the trophic sensitivity ($S_{i,G}$), amplification ($A_{i,G}$) and trophic variance ($V_{i,G}$) of 13 unique motif positions (i) resulting from all unitary (g) and integrative (G) pathways of effect simulated on the dynamics of 3-species motifs (*i.e.* tri-trophic food chain, omnivory, exploitative competition, apparent competition, partially connected and disconnected). Effects of stressors on individual ecological processes form unitary pathways of effect that collectively affect food webs through integrative pathways of effect. The density distributions result from 1% modifications to equilibria equation parameter values - *i.e.* mortality (m), attack (α) and conversion (e) rates - simulating all possible pathways of effect (n). A species trophic sensitivity is the difference in equilibrium abundance before and after the permanent appearance of stressors; a species trophic amplification is the difference between its trophic sensitivity to an integrative pathway of effect and the sum of its trophic sensitivity to unitary pathways of effect. Pathways of effect that lead to a position being a weak entry point (*i.e.* highly sensitive to disturbances), a biotic buffer (*i.e.* synergistically affected by stressors) or a biotic amplifier (*i.e.* antagonistically affected by stressors) are identified as colored areas under the density curves.

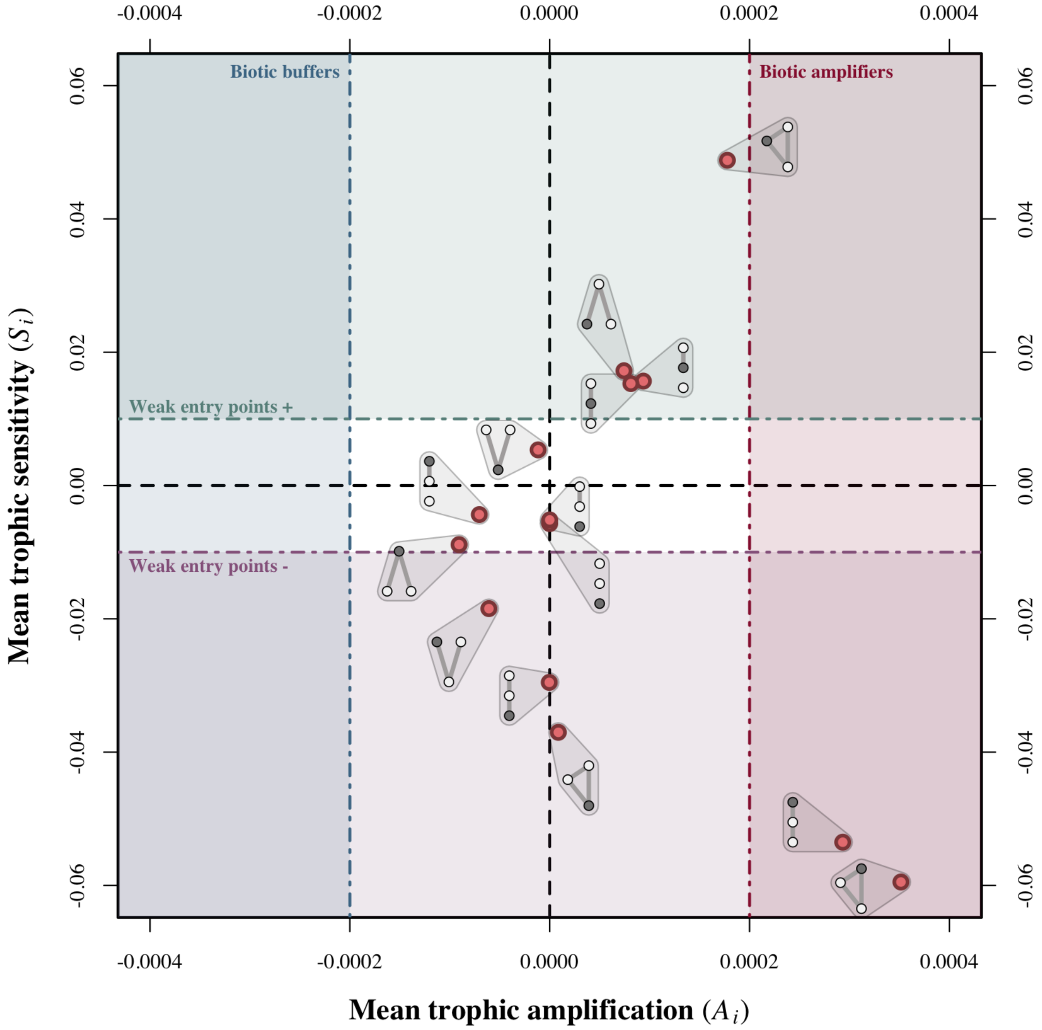

Figure 5: Mean trophic sensitivity (S_i) as a function of mean trophic amplification (A_i) to all possible pathways of effect (G) for the 13 unique 3-species motif positions explored, *i.e.* tri-trophic food chain, omnivory, exploitative competition, apparent competition, partially connected and disconnected. The red points identify trophic sensitivities and amplifications for motif positions, which are identified as solid points in the motifs grouped with each red point. Motif positions with positive trophic sensitivities (y-axis) are, on average, positively affected (*i.e.* increases in abundance) across pathways of effect; conversely, motif positions with negative trophic sensitivities are, on average, negatively affected across pathways of effect. Motif positions with positive trophic amplifications (x-axis) are, on average, synergistically affected across pathways of effect; motif positions with negative trophic amplifications are, on average, antagonistically affected across pathways of effect. Motif positions identified as weak entry points (*i.e.* highly sensitive to disturbances), biotic buffers (*i.e.* synergistically affected by stressors) and biotic amplifiers (*i.e.* antagonistically affected by stressors) are identified as colored areas on the graph.

1.7 Scaling back to food webs

Thus far, we conceptualized the role of species and their interactions in mediating the effects of multiple stressors in ecological communities, we simplified food web complexity using motifs, and we evaluated how different configurations of species interactions influence trophic sensitivity and amplification. We now scale back to species in food webs. As a food web can be deconstructed into n-species motifs, it can be pieced back together to assess the structural roles of species and their interactions in food webs (Stouffer et al., 2012; Cirtwill and Stouffer, 2015). In a food web of n-species, the collection of p-species motifs ($p \leq n$) a species is involved in forms a **species motif census**. Here we solely consider 3-species motifs. In our example, cod is twice a predator in food chains, once a consumer in an omnivory interaction and once a consumer in exploitative competition (Figure 3D). A species motif census can be informative of expected trophic sensitivities and amplifications. Each 3-species interaction is affected through a specific pathway of effect from which we can evaluate trophic sensitivity and amplification (Figure 3D, E). For example, cod is negatively affected through the food chains and competitive exploitation interactions, whereas it benefits from effects through the omnivory interaction (Figure 3E). Effects to cod are also amplified through the food chain with capelin and copepod, yet buffered through the omnivory and exploitative competition interactions (Figure 3E).

We summarize trophic sensitivities (S_m) and amplifications (A_m) across a species motif census (M) by summing individual trophic sensitivities and amplifications (Figure 3E):

$$S_m = \sum_{i \in M} S_{i,G^i}; \tag{1.5}$$

$$A_m = \sum_{i \in M} A_{i,G^i}, \tag{1.6}$$

where G^i is a pathway of effect through motif i. Summarizing by adding individual trophic sensitivities and amplifications allows for individual pathways of effect to reinforce and cancel each other out. For instance, we expect pathways of effect to negatively and synergistically affect cod in our system, even though cod benefits or is antagonistically affected through certain pathways of effect across its motif census (Figure 3E).

1.7.1 An empirical illustration: the St. Lawrence System

We scale back to food webs by evaluating a species' trophic sensitivity and amplification in empirical food webs from the St. Lawrence System in eastern Canada. The St. Lawrence System is formed by one of the largest estuaries in the world and a vast interior sea. Variable environmental and oceanographic processes make it suitable for the establishment of diverse and productive ecological communities (El-Sabh and Silverberg, 1990; Savenkoff et al., 2000). The St. Lawrence System also provides a wealth of ecosystem services; it sustains rich commercial fisheries, grants access to one of the most densely populated regions in North-America through more than 40 ports, is home to an expanding aquaculture production, and has an expanding tourism industry (Beauchesne et al., 2016; Archambault et al., 2017; Schloss et al., 2017). These human-induced stressors blend with climate related stressors that result in intricate cumulative exposure regimes across the St. Lawrence System (Beauchesne et al., 2020b).

1.7.1.1 Food webs

We use empirical data on food webs in the three main regions of the St. Lawrence for different periods: the Northern Gulf of St. Lawrence (mid-1980s; Morissette et al., 2003), the Southern Gulf of St. Lawrence (mid-1980s; Savenkoff et al., 2004), and the St. Lawrence Estuary (early 2000s; Savenkoff, 2012). The total number of species and functional groups differs between food webs ($n_{SSL} = 30$; $n_{NSL} = 32$; $n_{ESL} = 41$;), yet there is significant overlap ($n_{all} = 21$). Food web resolution is biased towards commercial fish for all food webs. Interactions were identified as a species or functional group's diet composition in percent. Only diet percent > 0.1 were considered as interactions. Note that detailed results are only presented and discussed for the Northern Gulf of St. Lawrence food web; see Supporting Figures 8 and 9 for the results for the Estuary and Southern Gulf.

1.7.1.2 Effects of stressors

The most prevalent sources of offshore human- and climate-induced stress in the St. Lawrence System are shipping, trawl, trap and pelagic fisheries, ocean acidification, hypoxia, and bottom- and surface-water temperature anomalies (Beauchesne et al., 2020b). We inferred the effects of individual sources of stress on the ecological processes governing these food webs (Figure 6) based on expert knowledge and the scientific literature:

1. Position in the water column – *i.e.* deep or surface-dwelling species – determines exposure to stressors. Acidification, hypoxia and bottom temperature anomalies are widespread in the deep layers of the St. Lawrence, whereas surface temperature anomalies and shipping are prevalent in the surface layer (Beauchesne et al., 2020b);

2. Mobility determines vulnerability to hypoxia and temperature anomalies. Hypoxia and temperature anomalies were considered as affecting the physiology of species with low mobility, whereas the behaviour of mobile species was considered affected by hypoxia only;
3. Ocean acidification affects the physiology of carbonate-secreting organisms (*e.g.* mollusks and crustaceans; Kroeker et al., 2013);
4. Shipping affects the behaviour of large surface-dwelling species such as whales (Christiansen et al., 2013; Lesage et al., 2017);
5. Fisheries cause mortality. The catch data provided in the food web descriptions provided a list of targeted species (Morissette et al., 2003; Savenkoff et al., 2004; Savenkoff, 2012). The gear types used to capture targeted species were identified with landing data from the Department of Fisheries and Ocean's Canada (DFO, 2016b). Reported whale bycatch and seals and seabird hunting were considered as effects to mortality (Morissette et al., 2003; Savenkoff et al., 2004; Savenkoff, 2012).

1.7.1.3 Pathways of effect

The motif census of each species was evaluated from the structure of each food web (Figure 6). For each 3-species interaction in which a species was identified, the realized pathway of effect was identified as a function of affected ecological processes (Figure 6). The following rules were applied to identify realized pathways of effect: 1) effects to mortality disrupt resource growth rates (r) and consumer mortality rates (m), 2) effects to behaviour disrupt consumer attack rates (α_{ij}), and 3) effects to physiology disrupt consumer conversion rates (e). Simulation results from the holistic exploration of the effects of stressors on motifs were then used as heuristics to infer the trophic sensitivity and amplification of species to specific pathways of effect in the food webs.

1.7.1.4 Trophic sensitivity and amplification in the St. Lawrence System

The most trophically sensitive species in the mid-1980s Northern St. Lawrence were most frequently positioned as predators in food chain, omnivory and exploitative competition interactions (Figure 6); these positions are generally negatively affected by stressors (Figure 5). The least sensitive species, meanwhile, generally occupied positions that benefit from the effects of stressors, such as mesopredators in omnivory interactions (Figure 5), or positions that are less sensitive to stressors, such as resources in exploitative competition (Figure 5). Trophic sensitivities and amplifications were not correlated in the Northern St. Lawrence; in fact, most species were prone to synergistic effects, regardless of their trophic sensitivity to stressors (Figure 6). Furthermore, the number of stressors affecting a species does not necessarily translate to greater trophic sensitivities or amplifications. For example, the trophic sensitivity of shrimp was low even though its mortality, physiology and behaviour were all potentially affected by stressors; marine mammals and seabirds, on the other hand, were highly susceptible to the effects of stressors and to non-additive effects, even in the absence of direct effects from stressors (Figure 6).

We can summarize the results for the mid-1980s Northern St. Lawrence food web with three ecological observations that answer our third management question (**Q3**). First, the trophic position of large apex predators (*e.g.* Atlantic cod, Greenland halibut and large demersals) and marine mammals rendered them highly susceptible to the effects of stressors and prone to synergistic effects, *i.e.* they were negative weak entry points and biotic amplifiers (Figure 6). Second, forage species, meanwhile, were trophically positioned so that they either benefited synergistically from the effects of stressors, making them positive weak entry points and biotic amplifiers (*e.g.* capelin and crustaceans; Figure 6), or were insensitive to stressors (*e.g.* shrimp; Figure 6). Third, a species sensitivity to the effects of stressors can be driven exclusively by indirect exposure; focusing on a single species and direct effects may be incapable of identifying underlying causes of population dynamics.

These observations are expected, as apex predators are both preferentially targeted for hunting and fishing, and more vulnerable to trophically-mediated effects (Pauly et al., 1998; Estes et al., 2011; Ripple et al., 2015; Stier et al., 2016); they also complement our understanding of the slow recovery of groundfish stocks following collapses of the early to mid-1990s in the St. Lawrence (Savenkoff et al., 2007; Morissette et al., 2009) and elsewhere in the Northern Atlantic Ocean (Worm and Myers, 2003; Frank et al., 2005). Triggered by overfishing and poor environmental conditions (Dempsey et al., 2018), the groundfish stock collapse resulted in dramatic shifts in trophic structure that saw the fall of piscivorous groundfish and the rise of small pelagics and benthic crustaceans (Savenkoff et al., 2007; Morissette et al., 2009) that mostly endure 30 years later (Bourdages et al., 2018). Marine mammals, meanwhile, shifted their resource use and their biomass increased in the St. Lawrence (Morissette et al., 2009; Gavrilchuk et al., 2014). Trophic interpretations explaining the shifts in trophic structure and the difficulties in fish stock recovery are plentiful (*e.g.* Jackson et al., 2001; Worm and Myers, 2003; Frank et al., 2005); perhaps the recovery of fish stocks is also hampered by the combination of stressors affecting the system and the structure of the food web.

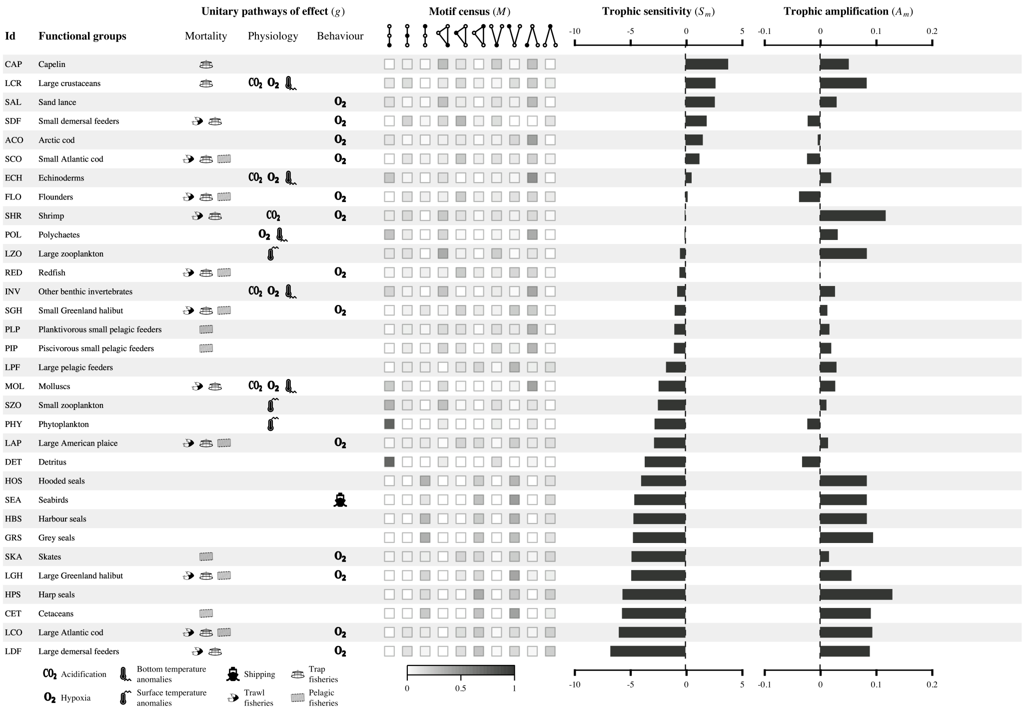

Figure 6: Trophic sensitivities (S_m) and amplifications (A_m) of species and function groups of the Northern Gulf of St. Lawrence in the mid-1980s (Morissette *et al.* 2003). A species trophic sensitivity and amplification is summarized using the sum of simulated trophic sensitivities ($S_{i,G}$) and amplifications ($A_{i,G}$) to pathways of effect (G; Figure 4) across a species motif census (M). The left-hand side of the figure presents species and functional groups, unitary pathways of effects (g) arising from individual stressors and their potential effects on population level mortality, physiology and behaviour, and the motif census (M) of species and functional groups measured as the frequency of times they hold unique positions in tri-trophic food chain, omnivory, exploitative and apparent competition interactions structuring of the food web. Main stressors in the Northern Gulf of St. Lawrence were fisheries (*i.e.* demersal destructive, demersal non-destructive high-bycatch and pelagic high-bycatch), climate change (*i.e.* ocean acidification, hypoxia and bottom and surface temperature anomalies), and shipping (Beauchesne *et al.* 2020). effects of stressors on individual ecological processes form unitary pathways of effect (g) that collectively affect food webs through integrative pathways of effect (G). The right-hand side of the figure presents trophic sensitivities and amplifications of species and functional groups. Negative or positive trophic sensitivities denote expected decreases or increases in species abundance as a response to pathways of effect. Species or functional groups with lowest or highest trophic sensitivities are positive or negative weak entry points (*i.e.* highly sensitive to disturbances), respectively. Negative or positive trophic amplifications identify species or functional groups expected to be affected synergistically (*i.e.* biotic amplifiers) or antagonistically (*i.e.* biotic buffers) by stressors.

Still, trophic sensitivities and amplifications depend on the structure of the local communities. Indeed, species like cod, shrimp and large crustaceans have variable trophic sensitivities and amplifications in the 3 food webs analysed: cod was more susceptible to the effects of stressors in the North than in other regions of the St. Lawrence, shrimp benefited more from the effects of stressors in the Estuary, and large crustaceans benefited in the Gulf, yet were negatively affected in the Estuary (Figure 7). Similarly, stressor type alters a species' trophic sensitivity and amplification. For instance, fisheries and climate combine to increase and decrease sensitivity of cod and shrimp, respectively (Figure 7). Stressors can also strengthen or weaken their respective effects. For instance, fisheries weaken the effect of climate stressors on shrimp, although it greatly increases trophic amplification (Figure 7). These observations nuance the answer to our third management question (**Q3**) by showing that a species sensitivity to stressors is not only species-specific, as known from past work, but also network-specific, *i.e.* it will vary with the structure of local food webs and with exposure to specific stressors. Modifications to food web structure, or assessment of the effects of stressors in different systems, are thus likely to result in different species responses.

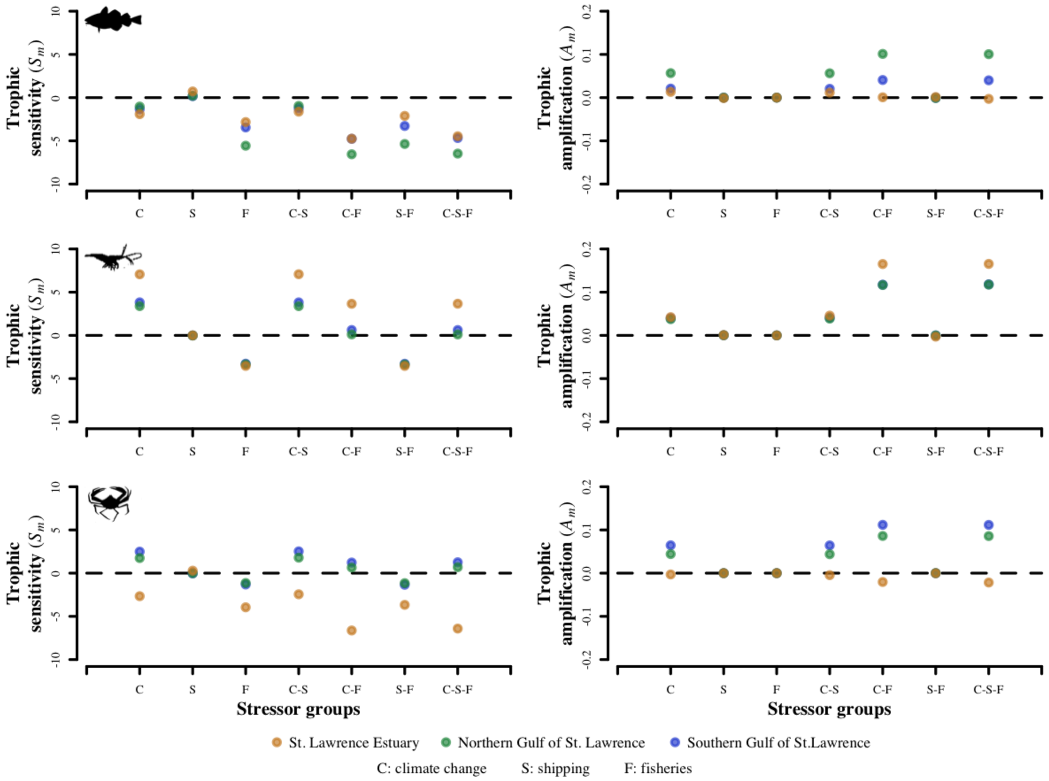

Figure 7: Comparison of the trophic sensitivities (S_m) and amplifications (A_m) to the effects of different groups of stressors (Figure 6) for Atlantic cod (*Gadus morhua*), shrimp (*Pandalus borealis*) and large crustaceans (*Crustacea*) between the food webs of the Southern and Northern Gulf of St. Lawrence in the mid-1980s (Morissette *et al.* 2003; Savenkoff *et al.* 2004) and the St. Lawrence Estuary in the early 2010s (Savenkoff 2012).

1.8 The way forward

Here, our objective was to conceptualize and investigate the role of species and their interactions in propagating the effects of multiple stressors through food webs. We proposed a theory-grounded approach to evaluate the effects of stressors that can be used to assess a species sensitivity to the effects of stressors based on its trophic position in a food web. This approach provides a novel way to assess both indirect and non-additive effects of multiple stressors through species interactions, a feat that remains largely elusive to managers and existing cumulative effects assessments. Still, many unresolved questions remain to efficiently evaluate the effects of multiple stressors on food webs, which we highlight next.

1.8.0.1 Scaling from motifs to food webs

One priority is to investigate whether the dynamics of 3-species motifs scale linearly with the dynamics of whole food webs. Scaling up motifs to whole food webs through an additive approach is a plausible assumption considering that direct and indirect effects can be canceled or reinforced through food webs (Wootton, 2002; Montoya et al., 2009). More importantly, this is the most parsimonious approach given the current gaps in theoretical knowledge; indeed, it remains unclear whether motif dynamics scale up linearly to dynamics of whole food webs, although some evidence suggest it might be the case (*e.g.* Stouffer and Bascompte, 2010; Rip et al., 2010). Further investigations should be conducted to explore whether a species' trophic sensitivity and amplification scales linearly with trophic sensitivities across its motif census. That being said, it is worth stressing that, at the motif scale, the metrics we developed consider nonlinear dynamics of the effects of multiple stressors and that the current formulation of the framework allows for the assessment of non-additive effects.

1.8.0.2 Interaction strength

While we considered the strength of species interactions by simulating effects of stressors on conversion and attack rates, we did not explicitly explore the role played by interaction strength in mediating the effects of stressors. The importance of interaction strengths is well documented in the literature, and the variations in network structure and interaction strengths are expected to increase uncertainty in food webs; this is, however, not specific to the propagation of the effects of multiple stressors through food webs, but a longstanding challenge in theoretical ecology (*e.g.* Paine, 1992; McCann et al., 1998; Montoya et al., 2009; O'Gorman and Emmerson, 2009; Gellner and McCann, 2016). Still, exploring how modifications to interaction strengths modulate the spread of multiple stressors through communities would provide valuable insights and could be achieved through our frameworks by testing how categories of strength intensities (*e.g.* weak, medium, strong) influence the net effects of stressors through species interactions.

1.8.0.3 Considering species-specific sensitivity to stressors

Here, to focus on the contribution of species interactions in mediating the effects of stressors, we controlled for species-specific sensitivities by considering that species have uniform responses to stressors. However, future work could relax this assumption, particularly as more information on species-specific sensitivities to different stressors becomes available through theoretical modelling (*e.g.* Lindmark et al., 2019; Otto et al., 2020; Dee et al., 2020) and experimental manipulations (*e.g.* Pillet et al., 2016; Lange and Marshall, 2017). Species-specific sensitivities also vary throughout its life span and stressors may affect an organism using different pathways of effect throughout its life history. Considering life history strategies would therefore help in capturing species responses to stressors (Otto et al., 2020). Combining species-specific responses through a network approach, as done here, could ultimately allow us to assess the relative contribution of the direct and indirect effects of multiple stressors to their overall net effects.

1.9 Conclusions

In conceptualizing the effects of stressors on food webs, we also sought to tackle the challenge of incorporating the complexities of real-world systems to cumulative effects assessments and answer questions of particular significance for environmental management. We found that species interactions should be considered to avoid underestimating the net effect of stressors (**Q1**), that the effects of multiple stressors on populations should be assessed jointly at the scale of ecological communities to properly consider non-additive effects (**Q2**), and that species most sensitive to stressors are apex predators, who tend to be negatively affected by stressors, and mesopredators, who tend to benefit from the effects of stressors (**Q3**). However, a species's sensitivity to the effects of stressors depends on the local structure of the community in which it is embedded. This finding is particularly relevant for management, as it shows that the effects of stressors do not solely depend on their frequency, intensity and species-specific vulnerabilities. Indeed, effects of stressors on a species may be fully driven by indirect effects and the structure of the community. Our results suggest that environmental impact assessments, even if focused on a single species or a single stressor, should consider the complexities of ecological communities and the specific pathways of effect through which stressors penetrate communities to properly evaluate their effects. Failure to do so could lead to inaccurate predictions of species responses, both quantitatively and qualitatively, and in turn lead to ineffective, or even detrimental, management actions (*e.g.* Wittmer et al., 2013; Stier et al., 2016). We thus join others in advocating for and providing evidence in support of the conservation of ecological communities and the application of holistic environmental approaches (*e.g.* McCann, 2007; Tylianakis et al., 2008, 2010; O'Gorman et al., 2012; Kaiser-Bunbury and Blüthgen, 2015; Harvey et al., 2017; Dee et al., 2017; Thompson et al., 2018).

Adopting holistic environmental approaches and scaling management to complex ecological communities will necessitate a paradigm shift towards whole systems management rather than the piecemeal management of components of interest only. As we strive to improve the spatiotemporal extent and resolution of environmental data used for management, it seems equally fitting that we should also strive to improve the extent – *i.e.* increasing the number of populations monitored – and resolution – *i.e.* from species to populations to individuals – of the biological data used for management. While monitoring whole systems may be deemed logistically unrealistic, environmental monitoring initiatives and emerging technologies already in place could assist in such a paradigm shift. Knowledge on the distribution and intensity of stressors (*e.g.* Halpern et al., 2015a; Beauchesne et al., 2020b), on species occurrences (*e.g.* GBIF, 2020; OBIS, 2020), on species interactions (*e.g.* Poelen et al., 2014; Poisot et al., 2016) and on abiotic data (*e.g.* Assis et al., 2018) are now openly available and their quality and robustness is progressively improving owing to relentless methodological and technological advancements (*e.g.* functional traits, environmental DNA, artificial intelligence). Ultimately, we believe that combining sound theory with exhaustive ecological data-based knowledge through robust inference will lead to management that explicitly consider the complexities of ecosystems and decision-making that provides solutions tailored to the context in which management is undertaken, *i.e.* for a specific area characterized by unique ecological dynamics and socioeconomic realities.

1.10 Text boxes

Box 1. Glossary of key terms defined and used throughout the manuscript.

1. **Direct effect**: effect of a species on another without the involvement of a third species;
2. **Indirect effect**: effect of a species on another involving an intermediary species;
3. **Net effect**: in food webs, the net effect of a single or of multiple species on another

is the integration of all individual direct and indirect effects propagating to a focal species;

4. **Stressor**: externality that arises from natural or human-induced biophysical processes or from anthropogenic activities and that directly affects ecological processes;
5. **Species-specific sensitivity**: the predisposition of a species to be affected by stressors, *e.g.* through changes in its mortality, growth, or metabolic rates;
6. **Pathway of effect**: the collection of ecological processes through which stressors directly and indirectly affect ecological communities. A unitary pathway of effect occurs when an ecological process is affected, whereas an integrative pathway of effect is the set of all unitary pathways of effect that combine across species to collectively affect a community;
7. **Trophic sensitivity**: difference in species equilibrium abundance before and after the permanent appearance of stressors;
8. **Weak entry point**: highly susceptible species to a pathway of effect, whether to its benefit (*i.e.* positive weak entry point) or to its detriment (*i.e.* negative weak entry point);
9. **Non-additive effect**: net effect of disruptions to multiple ecological processes (*i.e.* an integrative pathway of effect) that is greater (*i.e.* a synergistic effect) or lower (*i.e.* an antagonistic effect) than combined net effects of disruptions to individual ecological processes (*i.e.* unitary pathways of effect);
10. **Trophic amplification**: the difference between a species trophic sensitivity to an integrative pathway of effect and the sum of its trophic sensitivities to unitary pathways of effect;
11. **Trophic variance**: difference between the effective and expected effects of unitary pathways of effect, *i.e.* the average effect of an integrative pathways of effect;
12. **Biotic buffer**: species affected antagonistically by an integrative pathway of effect;

13. **Biotic amplifier**: species affected synergistically by an integrative pathway of effect;
14. **Species motif census**: in a food web of n-species, the collection of p-species motifs ($p \leq n$) in which a species is involved.

1.11 Acknowledgements

We thank the Fond de Recherche Québécois Nature et Technologie (FRQNT) and the Natural Science and Engineering Council of Canada (CRSNG) for financial support. This project is supported by Québec Océan, the Quebec Centre for Biodiversity Science (QCBS) and Takuvik networks. This research is also sponsored by the NSERC Canadian Healthy Oceans Network and its Partners: Department of Fisheries and Oceans Canada and INREST (representing the Port of Sept-Îles and City of Sept-Îles). We also thank C. Carrier-Belleau, E. Dreujou and R.M. Daigle for helpful comments on earlier versions of the manuscript.

1.12 Supporting information

Table 1: Systems of Lotka-Volterra equations used to model the effects of multiple disturbances on the six 3-species motifs explored.

Motifs	**Equation systems**	**Initial parameters values**
Tri-trophic food chain	$\frac{dX_i}{dt} = X_i(r_i - \alpha_{ii}X_i - \alpha_{ij}X_j)$ $\frac{dX_j}{dt} = X_j(e_{ij}\alpha_{ij}X_i - \alpha_{jk}X_k - m_j)$ $\frac{dX_k}{dt} = X_k(e_{jk}\alpha_{jk}X_j - m_k)$	$r_i = 1$ $\alpha_{ii} = 0.001$ $\alpha_{ij}, \alpha_{jk} \in [0.0001, 0.01]$ $e_{ij}, e_{jk} = 0.5$ $m_j, m_k \in [0.01, 0.5]$
Omnivory	$\frac{dX_i}{dt} = X_i(r_i - \alpha_{ii} - \alpha_{ij}X_j - \alpha_{ik}X_k)$ $\frac{dX_j}{dt} = X_j(e_{ij}\alpha_{ij}X_i - \alpha_{jk}X_k - m_j)$ $\frac{dX_k}{dt} = X_k(e_{ik}\alpha_{ik}X_i + e_{jk}\alpha_{jk}X_j - m_k)$	$r_i = 1$ $\alpha_{ii} = 0.001$ $\alpha_{ij}, \alpha_{ik}, \alpha_{jk} \in [0.0001, 0.01]$ $e_{ij}, e_{ik}, e_{jk} = 0.5$ $m_j, m_k \in [0.01, 0.5]$
Exploitative competition	$\frac{dX_i}{dt} = X_i(r_i - \alpha_{ii} - \alpha_{ij}X_j - \alpha_{ik}X_k)$ $\frac{dX_j}{dt} = X_j(e_{ij}\alpha_{ij}X_i - \alpha_{jj}\alpha_{jk}X_k - \alpha_{jj}X_j - m_j)$ $\frac{dX_k}{dt} = X_k(e_{ik}\alpha_{ik}X_i - \alpha_{kk}\alpha_{kj}X_j - \alpha_{kk}X_k - m_k)$	$r_i = 1$ $\alpha_{ii}, \alpha_{jj}, \alpha_{kk}, \alpha_{jk}, \alpha_{kj} = 0.001$ $\alpha_{ij}, \alpha_{ik}, \in [0.0001, 0.01]$ $e_{ij}, e_{ik} = 0.5$ $m_j, m_k \in [0.01, 0.5]$
Apparent competition	$\frac{dX_i}{dt} = X_i(r_i - \alpha_{ii}X_i - \alpha_{ik}X_k)$ $\frac{dX_j}{dt} = X_j(r_j - \alpha_{jj}X_j - \alpha_{jk}X_k)$ $\frac{dX_k}{dt} = X_k(e_{ik}\alpha_{ik}X_i + e_{jk}\alpha_{jk}X_j - m_k)$	$r_i, r_j = 1$ $\alpha_{ii}, \alpha_{jj} = 0.001$ $\alpha_{ik}, \alpha_{jk} \in [0.0001, 0.01]$ $e_{ik}, e_{jk} = 0.5$ $m_k \in [0.01, 0.5]$
Partially disconnected	$\frac{dX_i}{dt} = X_i(r_i - \alpha_{ii}X_i - \alpha_{ik}X_k)$ $\frac{dX_j}{dt} = X_j(r_j - \alpha_{jj}X_j)$ $\frac{dX_k}{dt} = X_k(e_{ik}\alpha_{ik}X_i - m_k)$	$r_i, r_j = 1$ $\alpha_{ii}, \alpha_{jj} = 0.001$ $\alpha_{ik} \in [0.0001, 0.01]$ $e_{ik} = 0.5$ $m_k \in [0.01, 0.5]$
Disconnected	$\frac{dX_i}{dt} = X_i(r_i - \alpha_{ii}X_i)$ $\frac{dX_j}{dt} = X_j(r_j - \alpha_{jj}X_j)$ $\frac{dX_k}{dt} = X_k(r_k - \alpha_{kk}X_k)$	$r_i, r_j, r_k = 1$ $\alpha_{ii}, \alpha_{jj}, \alpha_{kk} = 0.001$

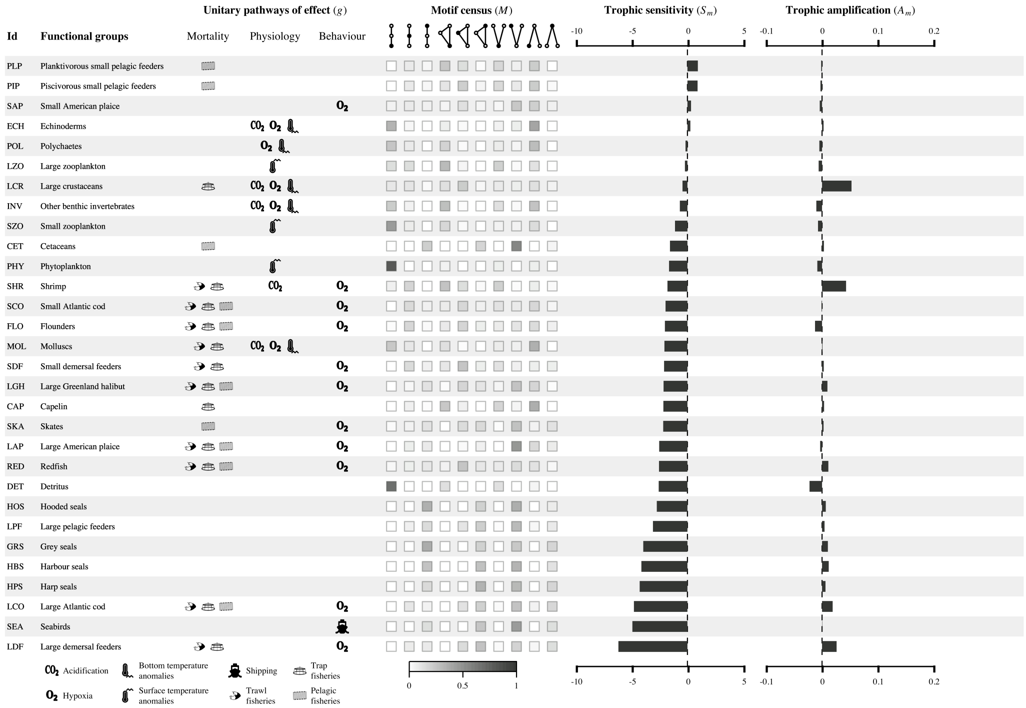

Figure 8: Change in species and functional groups sensitivity and amplification scores as a function of realized pathways of effects for an empirical food web of the Southern Gulf of St. Lawrence in the mid-1980s (Savenkoff et al., 2004). A species trophic sensitivity and amplification is summarized using the sum of simulated trophic sensitivities ($S_{i,G}$) and amplifications ($A_{i,G}$) to pathways of effect (G) across a species motif census (M). The left-hand side of the figure presents species and functional groups, unitary pathways of effects (g) arising from individual stressors and their potential effects on population level mortality, physiology and behaviour, and the motif census (M) of species and functional groups measured as the frequency of times they hold unique positions in tri-trophic food chain, omnivory, exploitative and apparent competition interactions structuring of the food web. Main stressors in the Southern Gulf of St. Lawrence are fisheries (*i.e.* demersal destructive, demersal non-destructive high-bycatch and pelagic high-bycatch), climate change (*i.e.* ocean acidification, hypoxia and bottom and surface temperature anomalies), and shipping (Beauchesne et al., 2020b). effects of stressors on individual ecological processes form unitary pathways of effect (g) that collectively affect food webs through integrative pathways of effect (G). The right-hand side of the figure presents trophic sensitivities and amplifications of species and functional groups. Negative or positive trophic sensitivities denote expected decreases or increases in species abundance as a response to pathways of effect. Species or functional groups with lowest or highest trophic sensitivities are positive or negative weak entry points (*i.e.* highly sensitive to disturbances), respectively. Negative or positive trophic amplifications identify species or functional groups expected to be affected synergistically (*i.e.* biotic amplifiers) or antagonistically (*i.e.* biotic buffers) by stressors.

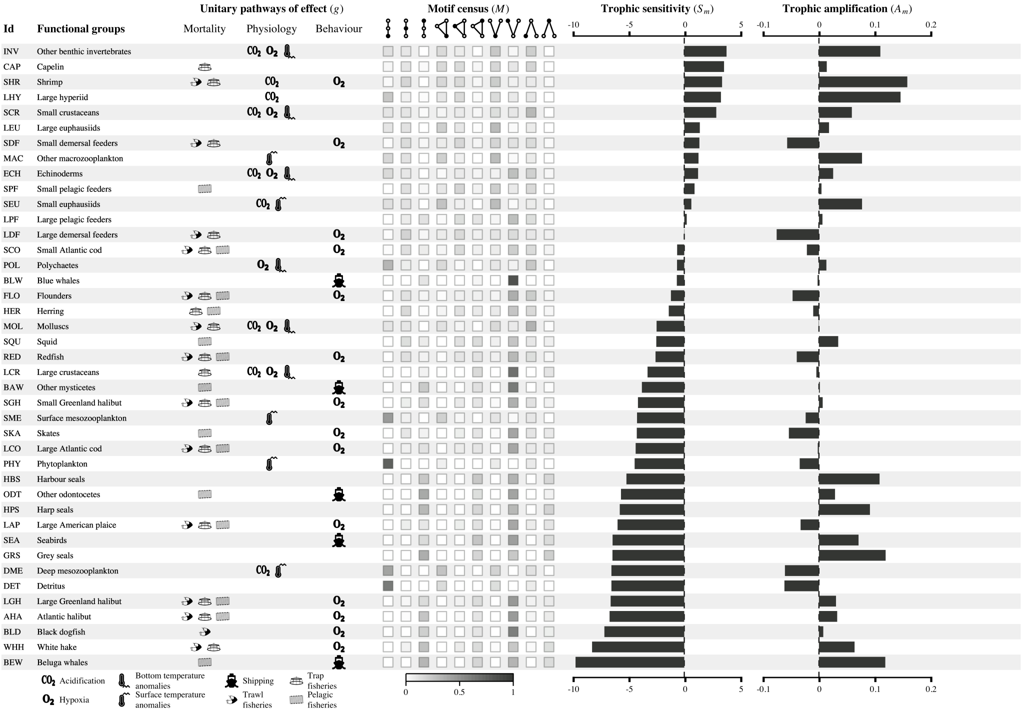

Figure 9: Change in species and functional groups sensitivity and amplification scores as a function of realized pathways of effects for an empirical food web of the St. Lawrence Estuary in the mid-1980s (Savenkoff, 2012). A species trophic sensitivity and amplification is summarized using the sum of simulated trophic sensitivities ($S_{i,G}$) and amplifications ($A_{i,G}$) to pathways of effect (G) across a species motif census (M). The left-hand side of the figure presents species and functional groups, unitary pathways of effects (g) arising from individual stressors and their potential effects on population level mortality, physiology and behaviour, and the motif census (M) of species and functional groups measured as the frequency of times they hold unique positions in tri-trophic food chain, omnivory, exploitative and apparent competition interactions structuring of the food web. Main stressors in the St. Lawrence Estuary are fisheries (*i.e.* demersal destructive, demersal non-destructive high-bycatch and pelagic high-bycatch), climate change (*i.e.* ocean acidification, hypoxia and bottom and surface temperature anomalies), and shipping (Beauchesne et al., 2020b). effects of stressors on individual ecological processes form unitary pathways of effect (g) that collectively affect food webs through integrative pathways of effect (G). The right-hand side of the figure presents trophic sensitivities and amplifications of species and functional groups. Negative or positive trophic sensitivities denote expected decreases or increases in species abundance as a response to pathways of effect. Species or functional groups with lowest or highest trophic sensitivities are positive or negative weak entry points (*i.e.* highly sensitive to disturbances), respectively. Negative or positive trophic amplifications identify species or functional groups expected to be affected synergistically (*i.e.* biotic amplifiers) or antagonistically (*i.e.* biotic buffers) by stressors.

ARTICLE 2

PRÉDIRE LES INTERACTIONS BIOTIQUES AU SEIN DE MILIEUX PAUVRES EN DONNÉES

2.1 Résumé

Les réseaux d'interactions écologiques, comme les réseaux trophiques, sont complexes à caractériser. Une caractérisation empirique requiert des observations exhaustives, alors qu'une caractérisation théorique requiert une quantité importante de données pour valider les modèles. Nous nous sommes ainsi demandé si des données aisément disponibles, telles que des observations empiriques d'interactions écologiques au sein d'une variété d'écosystèmes, pourraient être mises à profit afin de prédire les interactions écologiques au sein de milieux où peu de données sont disponibles. Nous avons assemblé un catalogue d'interactions biotiques à partir d'une collection de 94 réseaux trophiques empiriques, des bases de données détaillant des interactions prédateurs-proies, et des interactions disponibles sur la base de données Global Biotic Interactions (GloBI). Nous avons utilisé une méthode d'apprentissage non supervisée pour prédire les interactions binaires sachant la proximité taxonomique entre taxa et les ensembles de consommateurs et de ressources extraites du catalogue d'interactions biotiques. Nos résultats suggèrent que les interactions binaires peuvent être prédites avec une forte précision. Bien que les résultats semblent dépendants de la quantité d'informations disponibles dans le catalogue d'interactions, la proximité taxonomique complémente efficacement le catalogue pour améliorer les prédictions, surtout lorsque peu d'informations empiriques sont disponibles. Considérant son pouvoir prédictif, cette méthode pourrait promouvoir l'utilisation des réseaux trophiques et des descripteurs à l'échelle des réseaux pour certains domaines scientifiques nécessitant des connaissances sur les inter-

actions écologiques, et pour la recherche en milieux éloignés où la récolte de données empiriques pose un défi logistique. Les caractéristiques des réseaux pourraient ainsi être évaluées efficacement et utilisées pour établir des corrélations avec les niveaux de stress environnementaux. Ceci pourrait améliorer les évaluations de vulnérabilité des écosystèmes aux changements globaux, offrant également de nouvelles avenues de recherche prometteuses pour la recherche scientifique et la gestion environnementale.

Ce deuxième article, intitulé *"Thinking outside the box – predicting interactions in data-poor environments."* a été corédigé par moi-même, Philippe Desjardins-Proulx, Philippe Archambault et Dominique Gravel. Il a été publié dans un numéro spécial de la revue *Vie et Milieu-Life and Environment* sur les réseaux trophiques à l'automne 2016. Tous les auteurs ont contribué à l'élaboration des objectifs de l'article. J'ai conceptualisé l'approche développée conjointement avec Philippe Desjardins-Proulx. L'approche développée est inspirée en partie des travaux menés par ce dernier. J'ai été en charge de structurer et formater les bases de données utilisées, des analyses, des figures et j'ai dirigé la rédaction de l'article. Tous les auteurs ont contribué à l'écriture de l'article selon leur expertise respective et ont contribué à la révision de l'article. Les résultats issus de cet article ont été présentés en version abrégée lors de la *Réunion annuelle du Centre de la science de la biodiversité Québécois (CSBQ)* à Montréal (Canada), à la 15^{e} *Assemblée Générale Annuelle de Québec Océan* à l'automne 2016, en tant que conférencier invité à l'Université Sherbrooke à l'hiver 2017 et à la conférence *Canadian Society for Ecology and Evolution Meeting* à Victoria au printemps 2017.

Beauchesne, D., Desjardins-Proulx, P., Archambault, P., Gravel, D., 2016. Thinking outside the box - Predicting biotic interactions in data-poor environments. Vie et Milieu-Life and Environment 66, 333–342.

Les sections suivantes sont celles de l'article publié.

2.2 Title

Thinking outside the box – predicting biotic interactions in data-poor environments

2.3 Authors

David Beauchesne, Philippe Desjardins-Proulx, Philippe Archambault, Dominique Gravel

2.4 Abstract

Large networks of ecological interactions, such as food webs, are complex to characterize, be it empirically or theoretically. The former requires exhaustive observations, while the latter generally requires ample data to be validated. We therefore wondered whether readily available data, namely empirically described interactions in a variety of ecosystems, could be combined to predict species interactions in data deficient ecosystems. To test this, we built a biotic interactions catalogue from a collection of 94 empirical food webs, detailed predator-prey interaction databases and interactions from the Global Biotic Interactions (GloBI) database. We used an unsupervised machine learning method to predict interactions between any given set of taxa, given pairwise taxonomic proximity and known consumer and resource sets found in the interaction catalogue. Results suggest that pairwise interactions can be predicted with high accuracy. Although conclusions are seemingly dependent on the comprehensiveness of the catalogue knowledge of taxonomy was found to complement well the catalogue and improve predictions, especially when empirical information available is scarce. Given its high accuracy, this methodology could promote the use of food webs and network

level descriptors in certain fields of ecological science in which data is typically hard to gather and in remote and frontier location where empirical data is hard to gather. Network characteristics could then be efficiently evaluated and correlated to levels of environmental stressors in order to improve vulnerability assessments of ecosystems to global changes, opening promising avenues for further research and for management initiatives.

Keywords: Interactions, machine learning, food webs, K-nearest neighbour, taxonomy, St. Lawrence

2.5 Introduction

Large networks of ecological interactions, such as food webs, are complex to characterize (Polis, 1991; Martinez, 1992; Pascual and Dunne, 2006). Empirical descriptions require exhaustive observations, while theoretical inference generally requires ample data to be validated. For this reason, studies focusing on communities of interacting species remain understudied, even though we acknowledge the importance of considering the reticulated nature of complex networks (Ings et al., 2009; Tylianakis et al., 2008). When time is of the essence, the long term studies required quickly become impractical and the use of network level approaches relegated to the sideline.

Alternatively, an approach currently gaining in popularity is to predict interactions using proxies such as functional traits, phylogenies and spatial distributions (e.g. Morales-Castilla et al., 2015; Bartomeus et al., 2016). For example, multiple traits can play a significant role in community dynamics and influence the presence and intensity of biotic interactions, like the influence of body size on predator-prey interactions, a literal take on *big fish eats small fish* (Cohen et al., 2003; Brose et al., 2006; Gravel et al., 2013; Séguin et al., 2014). However, the time required to gather the necessary data to apply those methods may still be restrictive, or the data be unavailable altogether, so much so that other methods such as imputation techniques have been developed to fill the gaps in knowledge (e.g. Penone et al., 2014; Schrodt et al., 2015).

We therefore wondered whether more readily available data could be used to infer interactions in data deficient ecosystems. There is an increasing amount of data describing worldwide species interactions, some freely available through the Global Biotic Interactions (GloBI) database (Poelen et al., 2014). Similarly, while phylogenies can be challenging to construct and require ample data, a taxonomical description of species is easily accessible through initiatives like the World Register of Marine Species (WoRMS; Bailly et al., 2016). More than simple nomenclature, evolutionary processes are thought to influence and shape consumer-resource relationships (Mouquet et al., 2012; Rohr and Bascompte, 2014) so that taxonomically related species would be more likely to share similar types of both consumers and resources (Eklöf et al., 2012; Morales-Castilla et al., 2015; Gray et al., 2015). Based on that assumption, taxonomy might be a useful surrogate in predicting interactions for species lacking detailed information on their biology, but which have a taxonomically related species for which such information is available.

The objective of this work is thus to combine empirical biotic interactions originating from a variety of ecosystems with taxonomic relatedness to predict interactions in data deficient ecosystems. The concept underlying our methodology is that instead of constraining ourselves to a specific environment, we would look to other environments – outside the box – to glean insights as to the inner workings of an area of interest. As an example, we compare the observed interactions in the southern Gulf of St. Lawrence in Canada (SGSL; Savenkoff et al., 2004) with predictions made using our approach.

2.6 Methods

The objective of our methodology is to predict the interactions between all pairs of taxa within an arbitrary set N_1, using a set of taxa N_0 with empirically described interactions from which we can extract pairs of consumers and resources and their taxonomy. We couple the use of empirical data with an unsupervised machine learning method to achieve this.

2.6.1 Biotic interaction catalogue

We built a biotic interaction catalogue to serve as a set of taxa N_0 for with empirically described interactions. The empirical data used to construct the interaction catalogue was gathered in two successive steps. The first consisted of gathering data from a collection of 94 empirical food webs from which we extracted pairwise taxa interactions (see Brose et al., 2005; Kortsch et al., 2015; University of Canberra, 2016). We also used a detailed predator-prey interaction database describing trophic relationships between marine fishes and their prey (Barnes et al., 2008). From these datasets, only interactions between taxa at the taxonomic scale of the family or higher were selected for inclusion in the catalogue. Data used came exclusively from marine and coastal ecosystems and encompassed a wide variety of organisms: fungi, algae, parasites, phytoplankton, zooplankton, benthic and pelagic invertebrates, demersal and pelagic fishes, marine birds and marine mammals.

As empirical food webs are vastly dominated (96%) by unobserved or absent interactions ("0", hereafter referred to non-interactions), these datasets yielded a highly skewed distribution of interactions vs non-interactions. To counterbalance this, the second step of data compilation consisted of extracting observed interactions from the Global Biotic Interaction (GloBI) database (Poelen et al., 2014), which describes binary interactions for a wide range of taxa worldwide. We extracted all trophic interactions available on GloBI for species belonging to the families of taxa identified through step 1. Interactions were extracted using the ‘rGloBI‘ package in R (Poelen et al., 2015). As per step 1, only interactions between taxa at the taxonomic scale of the family or higher were retained.

The nomenclature used between datasets and food webs varied substantially. Taxa names thus had to be verified, modified according to the scientific nomenclature and validated. This process was performed using the Taxize package in R (Chamberlain and Szöcs, 2013; Chamberlain et al., 2014) and manually verified for errors. The same package was used to extract the taxonomy of all taxa for which interactions were obtained in previous steps. The complete R code and data used to build the catalogue is available at https://github.com/david-beauchesne/Interaction_catalog.

2.6.2 Unsupervised machine learning

We use the K-nearest neighbor (KNN) algorithm (Murphy, 2012) to predict pairwise interactions for a set of taxa S. The KNN algorithm predicts missing entries or proposes additional entries by a majority vote based on the K nearest (i.e. most similar) entries (see Box 1 for an example). In this case, taxa are described by a set of resources when considered as a consumer, a set of consumers when considered as a resource and their taxonomy (i.e. kingdom, phylum, class, order, family, genus, species). Similarity between taxa was evaluated using the Tanimoto similarity measure, which compares two vectors x and y with $n = |\mathbf{x}| = |\mathbf{y}|$ elements, and is defined as the size of the intersection of two sets divided by their union:

$$\text{tanimoto}(\mathbf{x}, \mathbf{y}) = \frac{|\mathbf{x} \cap \mathbf{y}|}{|\mathbf{x} \cup \mathbf{y}|}, \tag{2.1}$$

where $\cap$ is the intersect and $\cup$ the union of the vectors. Adding a weighting scheme, we can measure the similarity using two different sets of vectors $\{\mathbf{x}, \mathbf{y}\}$ and $\{\mathbf{u}, \mathbf{v}\}$:

$$\text{tanimoto}_t(x, y, u, v, w_t) = w_t\text{tanimoto}(\mathbf{x}, \mathbf{y}) + (1 - w_t)\text{tanimoto}(\mathbf{u}, \mathbf{v}), \tag{2.2}$$

where w_t the weight (in $[0; 1]$). For our analyses, the first element on the right-hand side of (5.2) is the Tanimoto similarity measured using the taxonomy of two taxa. The second is the Tanimoto similarity between the sets of resources (or consumers) of the same taxa. When $w_t = 0$ only resource or consumer sets are used to compute similarity, while $w_t = 1$ solely uses taxonomy. This approach to consider the relative contribution of two sets of vectors to the Tanimoto similarity was developed by Desjardins-Proulx et al. (2016).

2.6.3 Predicting interactions

The algorithm was built on a series of logical steps that ultimately predicts a candidate resources list C_R for each taxon in N_1 based on empirical data available and the similarity among consumers and among resources (Figure 10). For all consumer taxa T_C in N_1, the algorithm first verifies, for all resources in resource set T_R, if they are found the N_0 (Step S1, Figure 10). When it does, all T_R taxa that are also in N_1 are added as predicted resources for T_C (Steps S2 and S3). This corresponds to what we refer to as the catalogue contribution to resource predictions. In essence, two taxa in N_1 that are known to interact through empirical data in the catalogue are automatically assumed to interact in N_1.

Otherwise, the algorithm passes to what we refer to as the predictive contribution to resource predictions (Steps S4 to S16), with candidate resources for T_{Ci} (focal taxa for explanation) identified with the KNN algorithm. For each resource in T_R that were not in N_1 (Step S2), K most similar resources $T_{R'}$ are identified from N_1 (Step S4). If similar resources $T_{R'}$ have a similarity value above a minimal similarity threshold set to 0.3 in our analysis, they are added to C_R as candidate resources. If not, they are automatically discarded (Steps S5 to S7). This minimal threshold is an arbitrary parameter used to avoid predicting resources that have very small and insignificant similarity and hence is very unlikely to share consumers and resources with the taxa it is being compared to.

Then for all consumer taxa T_C in N_1, K most similar consumers $T_{C'}$ are identified from N_0. This step aims at extracting sets of potential resources T_R from similar types of consumers found in the catalogue (Step S8). Resources T_R are added to candidate resources C_R for T_{Ci} if they are also found in N_1 (Steps S10 to S12). Otherwise, Steps S4 to S7 are duplicated to identify potential similar resources for T_{Ci} in N_1 from the set of resources T_R of similar consumers $T_{C'}$ (Steps S13 to S16). A simple working example is presented at Box 1. A comprehensive mathematical description of the algorithm and the parameters used is however available through Figure 10 and the complete R code and data used for the algorithm is available at https://github.com/david-beauchesne/Predict_interactions.

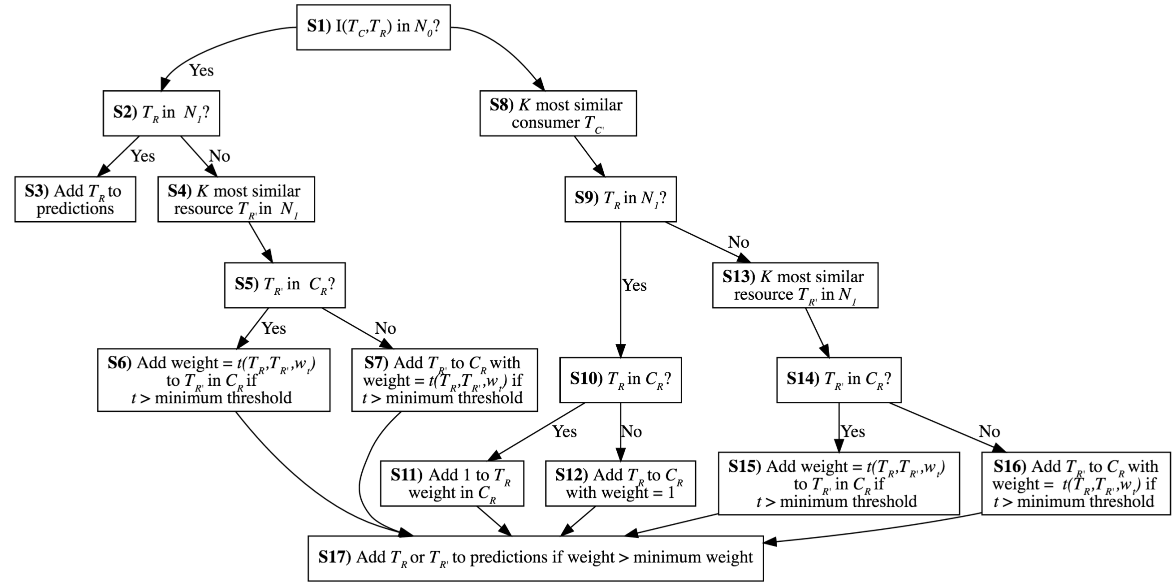

Figure 10: Description of 17 logical steps (S1-S17) used by the algorithm to suggest a list of candidate resources (C_R) for each consumer taxa (T_C) in a set of N_1 for which interactions are predicted, using a set of taxa N_0 with empirically described interactions. Interactions between consumer and resource taxa are denoted as I(T_C,T_R). K is the number of most similar neighbours selected for the KNN algorithm; t stands for tanimoto in equation 1; w_t is the weight given to sets of resources and consumers in equation 2; the minimum threshold is a value setting the minimal similarity value accepted for taxa to be considered as close neighbours in the KNN algorithm; the weight is the value added to a candidate resource each time it is added to C_R; the minimum weight is the minimal weight value accepted for candidate resources to be selected as predicted sources in the algorithm.

2.6.4 Algorithm prediction accuracy

We used datasets including more than 50 taxa (Christian and Luczkovich, 1999; Link, 2002; Thompson et al., 2004; Brose et al., 2005; Barnes et al., 2008; Kortsch et al., 2015) to assess the prediction accuracy of the algorithm. Testing accuracy of a particular dataset was done by first removing from the catalogue all pairwise interacting taxa originating from that dataset. Accuracy was evaluated using three different statistics:

1. $Score_y$ is the fraction of interactions correctly predicted:

$$Score_y = \frac{a}{a+c} \tag{2.3}$$

2. $Score_{\neg y}$ is the fraction of non-interactions correctly predicted:

$$Score_{\neg y} = \frac{d}{b+d} \tag{2.4}$$

3. TSS, The True Skilled Statistics (TSS) evaluated prediction success by considering both true and false predictions, returning a value ranging from 1 (prefect predictions) to -1 (inverted predictions; Allouche et al., 2006):

$$TSS = \frac{(ad-bc)}{(a+c)(b+d)} \tag{2.5}$$

where a is the number of interactions correctly predicted (*i.e.* true positives), b is the number of non-interactions predicted as interactions (*i.e.* false positives), c is the number of observed interactions predicted as non-interactions (*i.e.* false negatives) and d is the number of non-interactions correctly predicted (*i.e.* true negatives). These three statistics give a different perspective on prediction accuracy, focusing in turn on true interactions and non-interactions, and on both true and false predictions. It is however important to note that false positives and true negatives are solely representative of the datasets used rather than the environment itself. However extensive the datasets may be, unobserved interactions may not necessarily mean a true absence of interaction.

For each statistic, we evaluated prediction accuracy 1) for the complete algorithm, 2) for predictions made through the predictive portion of the algorithm (Steps S4-S16; Figure 10) and 3) for the catalogue contribution of the algorithm (Steps S1-S3; Figure 10). We evaluated these steps separately in order to partition the relative contribution of the catalogue and of the predictions made using the KNN algorithm to the overall predictive accuracy of the algorithm. Multiple w_t values were also tested to evaluate whether taxa similarity measured as a function of resource/consumer sets or taxonomy contributed more significantly towards increased predictive accuracy. The same was done with multiple K values.

Finally, we evaluated the influence of the comprehensiveness of the catalogue on prediction accuracy. We selected the arctic marine food web from Kortsch et al. (2015) as a test. This food web was selected as it is highly detailed taxonomically. Furthermore, once removed from the catalogue, almost 100% of its taxa still had information available on sets of consumers and resources, which necessary for testing the impact of catalogue comprehensiveness on prediction accuracy. We iteratively and randomly (n = 50 randomizations) removed a percentage of empirical data describing the food web taxa from the catalogue before generating new predictions with the algorithm. We also tested w_t values of 0.5 and 1 to evaluate whether taxonomic similarity could support predictive accuracy in cases when empirical data for species in N_1 in the catalogue is unavailable.

2.7 Results

2.7.1 Biotic interaction catalogue

The data compilation process allowed us to build an interaction catalogue composed of 276708 pairwise interactions (interactions = 72110; non-interactions = 204598). A total of 9712 taxa (Superfamily = 15; Family = 591; Subfamily = 29; Tribe = 8; Genus = 1972; Species = 7097) are included in the catalogue, 4159 of which have data as consumers and 4375 as resources.

2.7.2 Algorithm predictive accuracy

The overall predictive accuracy of the algorithm ranges between 80% to almost 100% in certain cases (Figure 11). Both interactions and non-interactions are well predicted by the algorithm. TSS scores are lower than $Score_y$ and $Score_{\neg y}$ due to misclassified interactions and non-interactions. This can also be observed through the effect of varying K values, which increases the number of potential candidate resources for each taxa in the predictive portion of the algorithm. Prediction accuracy increases for interactions, while it decreases for non-interactions, as K values increase.

Similarity being predominantly measured with resource/consumer sets (w_t closer to 0) yielded better predictions than when measured with taxonomy (w_t closer to 1; Figure 11). Resource/consumer sets therefore appears to serve as a better measure of similarity between taxa for interactions predictions. It is nonetheless interesting to note that although the predictive contribution of the algorithm decreases as w_t increases, an increased mean and decreased variability values for the TSS and $Score_y$ statistics is also observed (Figure 11). This suggests that while resource/consumer similarity yields higher predictive accuracy, taxonomy better complement the catalogue contribution by predicting interactions not captured through empirical data, effectively increasing the predictive accuracy of the complete algorithm.

The partitioning of the catalogue and predictive portions of the algorithm reveals the importance of the comprehensiveness of the catalogue in prediction accuracy (Figures 11, 12). As the amount of empirical data available in the catalogue increases so does the overall accuracy of the algorithm (Figures 12). While prediction accuracy of the predictive portion of the algorithm is somewhat lower, it nonetheless supports high prediction efficiency when the catalogue comprehensiveness is lower (Figures 12). Prediction accuracy still remains around 75% with only 40% of N_1 taxa found in the catalogue (Figures 12). Furthermore, the use of taxonomy for similarity measurements is more efficient when empirical data is scarcer and no different than resource/consumer sets for the complete algorithm when ample data is available (Figures 12).

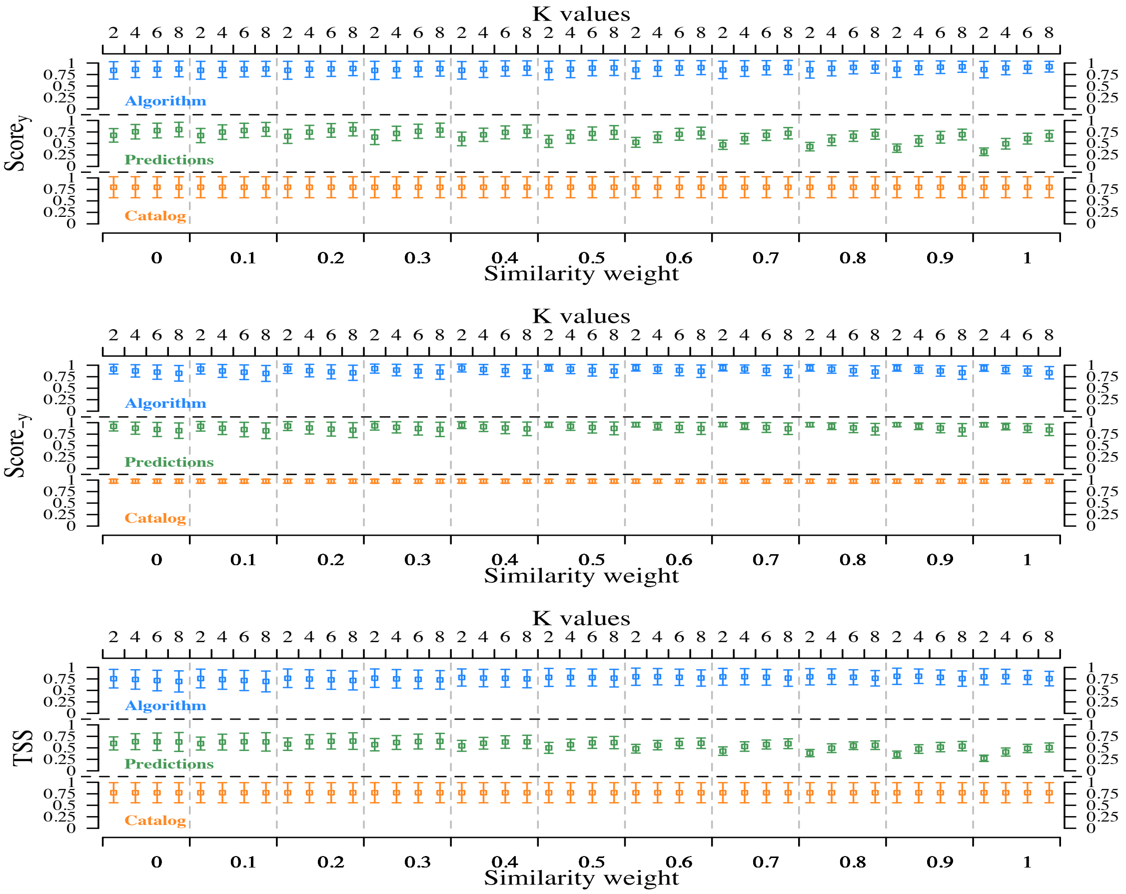

Figure 11: Representation of the three statistics (*i.e.* $Score_y$, $Score_{\neg y}$ and TSS) used to evaluate the accuracy of the algorithm as a function of K values tested (*i.e.* 2, 4, 6 and 8 most similar seighbours, top x-axis) and weight for taxonomy (bottom x-axis), which varies between 0 and 1. A weight of 0 means that similarity is measured only using set of resources/consumers for each taxa, while a weight of 1 means that similarity is based solely on taxonomy. For each statistic, the topmost panel presents prediction accuracy for the complete algorithm, the middle panel corresponds to predictions made through the predictive portion of the algorithm (Steps S4-S16; Figure 10) and the bottom panal presents the catalogue contribution for the algorithm (Steps S1-S3; Figure 10). Note that the sum of the predictive and catalogue contributions can be over 100% as there is overlap between predictions made through both. The 7 datasets used for this analysis contained over 50 taxa (Christian and Luczkovich, 1999; Link, 2002; Brose et al., 2005; Thompson et al., 2004; Barnes et al., 2008; Kortsch et al., 2015)

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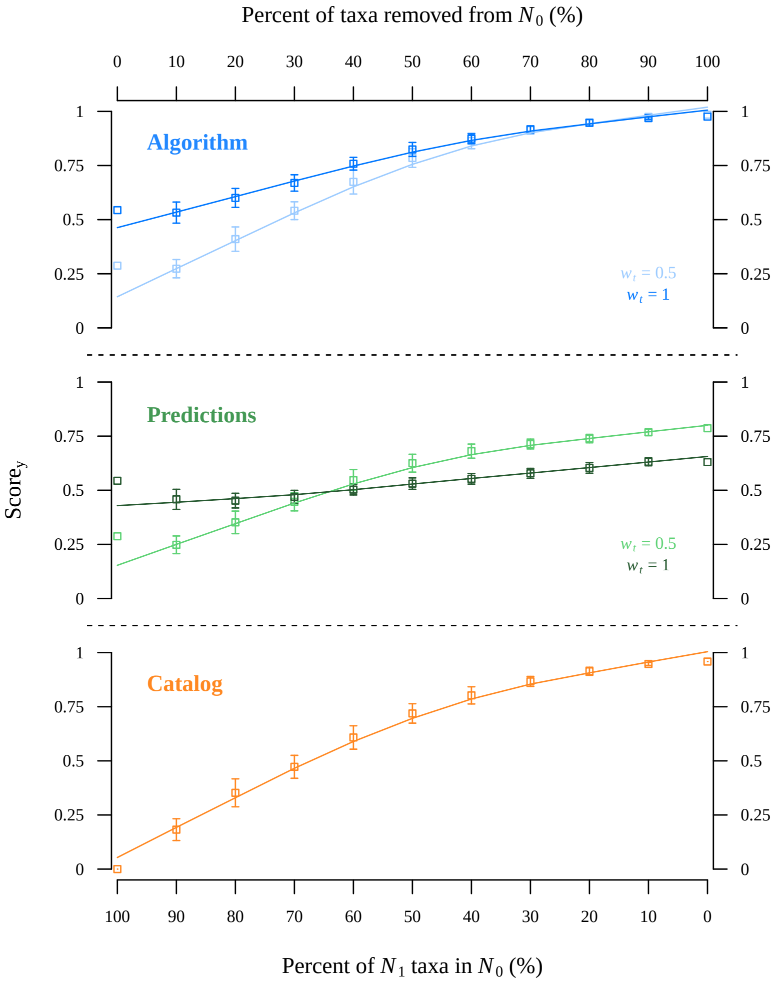


Figure 12: Representation of $Score_y$ as a function of catalogue comprehensiveness, *i.e.* the amount of information on sets of consumer and resources available in the catalogue. The sensitivity of the algorithm to data accuracy was evaluation with the arctic food web from Kortsch et al. (2015). This food web was highly detailed taxonomically. Once removed from the catalogue, almost 100% of its taxa still had information available on sets of consumers and resources, which necessary for testing the impact of catalogue comprehensiveness on prediction accuracy. A random percentage of data available in the catalogue for taxa in the food web (*i.e.* 0 to 100%) was iteratively removed (n = 50 randomizations) before generating new predictions with the algorithm. w_t values of 0.5 and 1 were evaluated to verify the usefulness of taxonomy in supporting predictive accuracy. The topmost panel presents prediction accuracy for the complete algorithm, the middle panel corresponds to predictions made through the predictive portion of the algorithm (Steps S4-S16; Figure 10) and the bottom panel presents the catalogue contribution for the algorithm (Steps S1-S3; Figure 10). Note that the sum of the predictive and catalogue contributions can be over 100% as there is overlap between predictions made through both.

2.7.3 Southern Gulf of St. Lawrence

As an example, we predict interactions in the southern Gulf of St. Lawrence (SGSL) in eastern Canada. The empirical data and taxa list come from Savenkoff et al. (2004). They present a list of 29 functional groups for a total of 80 taxa presented at least at taxonomical scale of the family. Other coarser functional groups were not used for this example (see Table 2 in Supplementary information (SI) and Savenkoff et al. (2004) for a complete description of documented groups). We used the algorithm to predict interactions between all 80 taxa selected. As their interaction data are reported for functional groups rather than taxa, we then aggregated them back to their original functional groups to compare with interactions presented in Savenkoff et al. (2004). In total, there were empirical data available in the catalogue for 78% of SGSL taxa (62/80). The algorithm correctly predicted close to 80% of interactions ($a = 135/170$) and non-interactions ($d = 354/455$) extracted from Savenkoff et al. (2004). It also predicted an additional 101 interactions that were not noted in Savenkoff et al. (2004) and failed to predict 36 observed interactions that were, resulting in a TSS score of 0.57. A visual comparison of results obtained from the algorithm with interactions noted in Savenkoff et al. (2004) is available at Figure 13. The network presented is centered on the observed and predicted interactions of the capelin (*Mallotus villosus*) and piscivorous small pelagic feeders (e.g. *Scomber scombrus* and *Illex illecebrosus*).

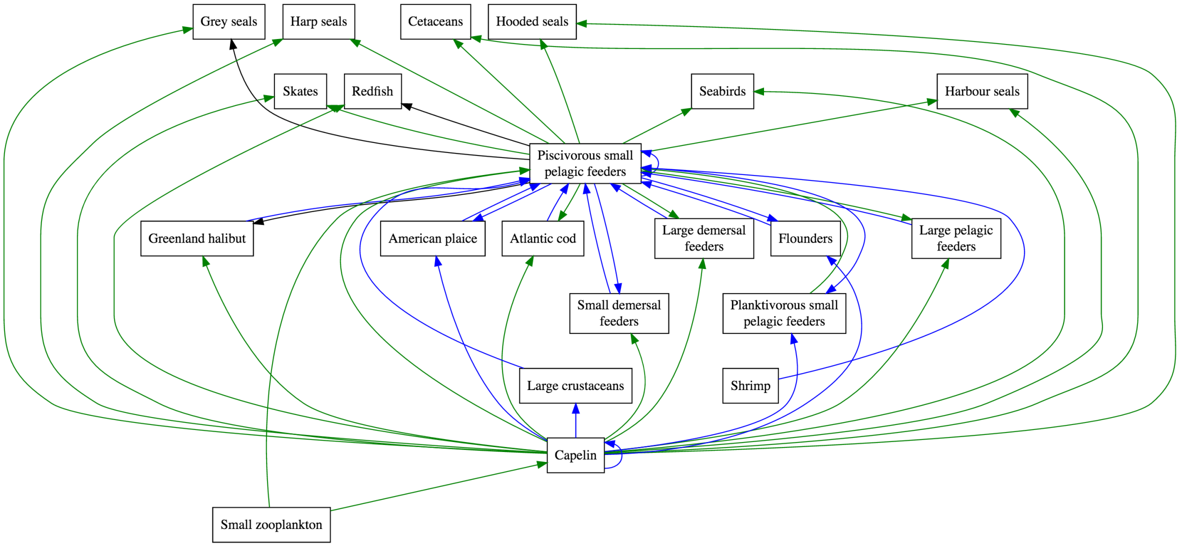


Figure 13: Example of predicted interactions with the network of the southern Gulf of St. Lawrence (Savenkoff et al., 2004), centered around the interactions of the capelin (*Mallotus villosus*) and piscivorous small pelagic feeders (*e.g. Scomber scombrus and Illex illecebrosus*). Edge with colors green were both predicted and observed (26), black were observed only (3) and blue were predicted only (19). Arrows are pointed towards consumers.

2.8 Discussion

2.8.1 Algorithm accuracy

We show that out of the box interaction inference for a set of taxa with incomplete or unavailable preexisting information can be achieved with high accuracy using a combination of empirical data describing biotic interactions and taxonomic relatedness. Although the efficiency of the algorithm is dependent on the comprehensiveness of the interactions catalogue, taxonomic proximity acts as a complement to increase the number of observed interactions correctly predicted. Taxonomic proximity also supports the efficiency of the algorithm when information gleaned through the catalogue is scarce.

2.8.2 Usefulness of taxonomic relatedness

We found that taxonomy can be highly useful in complementing predictions made using empirical data. Much like the findings from Eklöf and Stouffer (2016), evolutionary history provides a significant background from which inferences on network structure can be made. Nonetheless, while evolutionary history plays a significant role in influencing consumer-resource trait matching and food web structure (Mouquet et al., 2012; Rohr and Bascompte, 2014), phylogenetic constraints do not necessarily account efficiently for certain traits such as body size (Eklöf and Stouffer, 2016). Complementing our methodology with additional, higher-order information such as functional traits (*e.g.* metabolism and body size) could thus yield even more efficient results, especially in cases where the catalogue lacks data on taxa for which interactions have to be predicted. Similarly, using phylogenies rather than taxonomy could enhance the resolution at which evolutionary history is considered. This could be achieved through recent efforts to extensively describe all-encompassing phylogenies (e.g. Hedges et al., 2015). Complementing our approach by making it more data dependent could undermine the premise under which this method was built and which constitutes its main strength, *i.e.* predicting interactions in data deficient environments using readily available data. The flexibility of our methodology would however easily allow for the inclusion of alternate sources of data. Therefore, high-order data such as phylogenies could and should be used in instances where ample data is available, making the use of this methodology broader than simply in instances when data is unavailable.

2.8.3 Interactions classification

That $Score_y$ and $Score_{\neg y}$ are inversely proportional means that non-interactions are misclassified as interactions in the process of increasing $Score_y$, consequently decreasing $Score_{\neg y}$. This could either stem from the algorithm poorly predicting non-interactions or from the empirical data itself. Accuracy evaluation assumes that non-interactions from empirical food web are observed data, yet it is usually not the case. Most empirical webs have a strong focus attributed to higher order consumer species and often uneven effort made to thoroughly detail species interactions (Dunne, 2006). Furthermore, the methodologies used to obtain consumer-resource data, often relying on gut content analyses, which is efficient at observing interactions, may be inefficient to detect absence of interactions in natural systems (Dunne, 2006). This is especially true with our methodology, where we predict interactions between species whose co-occurrence may have been observed in the other ecosystems we are using to predict interactions. Misclassified interactions could thus be real, albeit unobserved through empirical data available.

2.8.4 Southern Gulf of St. Lawrence

The St Lawrence example (Figure 13 and SI) provides adequate material to discuss predictions in greater detail. The algorithm fails to predict 20% of interactions presented in Savenkoff et al. (2004). Interactions that failed to be predicted were mainly centered on invertebrate species (e.g. polychaetes and mollusks) and taxonomically diverse functional groups described by coarse taxonomic categories (e.g. diatoms) alongside few species in Savenkoff et al. (2004) (e.g. piscivorous small pelagic feeders; Table 3). As we focused on the taxa at least at the scale of family, it is likely that their functional groups had a broader range of possible interactions included than what the algorithm could predict using only a few taxa. Furthermore, the efficiency of the algorithm greatly depends on the underlying empirical data that defines the catalogue. If the empirical data used to build the catalogue focuses on higher order consumers, it should come as no surprise that the algorithm would be afflicted by the same limitations.

On the other hand, the algorithm also predicts substantially more interactions than those presented in Savenkoff et al. (2004) (Figure 13; Table 4). For instance, an important number of additional interactions were predicted for small piscivorous pelagic feeders as consumers (Figure 13). When considering that these species are typically considered as resources, it should be unsurprising that the broad range of interactions composing the catalogue and from which predictions are made results in new consumer interactions being predicted for those species. An ecological interpretation can therefore be easily provided to explain these additional interactions, such as small piscivorous pelagic feeders consuming cod, likely representing a consumption of cod eggs and/or juveniles. This greatly exemplifies the point we made in the previous section with regards to misclassified interactions being real rather than false positives. The resulting TSS score is therefore greatly diminished by classifying additional interactions as false positives. We therefore believe that the TSS score for the St. Lawrence analysis represents an underestimation of the efficiency of our methodology to predict interactions.

2.8.5 Perspectives

We show that out of the box interaction inference can be achieved with high accuracy using readily available data, suggesting that ecological networks are characterized by a degree of predictability and that this predictive value can be recovered through learning (see Tamaddoni-Nezhad et al., 2013; Gray et al., 2015). This adds weight to claims that regularities can be observed and predicted in network structure (Eklöf and Stouffer, 2016).

We believe that our methodology offers promising avenues for further applied research and management initiatives. The flexibility of our methodology allows it to take advantage of multiple types of data. Complementing and testing our methodology with additional ecological information such as functional traits and phylogenies would therefore be highly valuable. Interaction strength and species co-occurrence are additional major attributes affecting the probability of observing interactions and the resulting network structure. Interaction strength is instrumental to understanding community dynamics, stability and robustness (Laska and Wootton, 1998; Morales-Castilla et al., 2015), while the co-occurrence of species encloses valuable information on interactions and is obviously a pre-requisite for interactions to exist (Cazelles et al., 2016). Considering them in our methodology would be highly valuable to correctly assess interactions in a given ecosystem and predict the spatial distribution of interaction networks.

The significance of this approach also extends to other areas of ecological research where gathering data can be highly difficult, such as the reconstruction of interaction networks forming palaeocommunities (e.g. Yeakel et al., 2013, 2014). Predicted networks of taxa known to co-occur could be used in hindsight to evaluate the influence of major events such as biodiversity collapse or significant climatic regime shifts on the structure of past ecological communities.

Ultimately, given its high efficiency and simplicity, our methodology could help in promoting the use and the accessibility of food webs and network level descriptors for integrative management initiatives such as cumulative impacts assessments and systematic planning (Giakoumi et al., 2015; Beauchesne et al., 2016), especially for remote locations and frontier areas where empirical data is hard to gather. Network characteristics could be efficiently evaluated and correlated to levels of multiple environmental stressors to assess the vulnerability of ecosystems to global changes (Albouy et al., 2014). We believe that the development of such predictive approaches could represent the first much needed steps towards the use of ecological networks in systematic impacts assessments.

2.9 Acknowledgements

We thank the Fond de Recherche Québécois Nature et Technologie (FRQNT) and the Natural Science and Engineering Council of Canada (CRSNG) for financial support. This project is also supported by Québec Océan, the Quebec Centre for Biodiversity Science (QCBS), and the Notre Golfe and CHONeII networks. We also wish to thank K. Cazelles for the help, constructive comments and suggestions. We also thank David Bohan and an anonymous reviewer for their constructive comments and suggestions.

2.10 Box 1

The algorithm follows a series of logical steps to predict resources for all taxa in an arbitrary set of taxa N_1 using a set of taxa N_0 with empirically described interactions from which we can extract sets of consumers and resources and their taxonomy. In this example, we are predicting interactions for a fictitious $N_1 = \{T_1, T_9, T_{10}, T_{11}, T_{12}\}$ using N_0 with information on 12 taxa. This catalogue holds information on consumer or resource for 10 taxa and the taxonomy for all 12 taxa in the list.

N_0 taxa ID	taxonomy	resource	consumer
T_1	$\{a, b, c\}$	$\{T_2, T_3, T_{12}\}$	$\{T_4\}$
T_2	$\{e, f, g\}$		$\{T_1, T_5\}$
T_3	$\{i, j, k\}$		$\{T_5\}$
T_4	$\{m, n, o\}$	$\{T_1, T_5\}$	
T_5	$\{a, b, d\}$	$\{T_8, T_9\}$	$\{T_4\}$
T_6	$\{i, q, r\}$	$\{T_2, T_8\}$	$\{T_4\}$
T_7	$\{e, f, h\}$		$\{T_1, T_6\}$
T_8	$\{s, t, u\}$		$\{T_5, T_6\}$
T_9	$\{s, t, v\}$		$\{T_5\}$
T_{10}	$\{i, j, l\}$		
T_{11}	$\{m, n, p\}$		
T_{12}	$\{q, r, s\}$		$\{T_1\}$

Similarity between all pairs of taxa in N_0 is measured for consumer, resource and taxonomic proximity using equation 1. The upper triangular matrix represents similarity measured with taxa sets of resources/consumers, while the lower triangular represents taxonomic similarities. For consumer/resource set similarities, values of 0 mean that similarity equals 0 for both similarity measurements.

$\text{tanimoto}(T_Cx, T_Cy)$ / $\text{tanimoto}(T_Rx, T_Ry)$

	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9	T_{10}	T_{11}	T_{12}
T_1	-	0	0	0	0/1	0.3/1	0	0	0	0	0	0
T_2	0	-	0/0.5	0	0	0	0/0.3	0/0.3	0/0.5	0	0	0/0.5
T_3	0	0	-	0	0	0	0	0/0.5	0/1	0	0	0
T_4	0	0	0	-	0	0	0	0	0	0	0	0
T_5	0.5	0	0	0	-	0.3/1	0	0	0	0	0	0
T_6	0	0	0.2	0	0	-	0	0	0	0	0	0
T_7	0	0.5	0	0	0	0	-	0/0.3	0	0	0	0/0.5
T_8	0	0	0	0	0	0	0	-	0	0	0	0
T_9	0	0	0	0	0	0	0	0.5	-	0	0	0
T_{10}	0	0	0.5	0	0	0.2	0	0	0	-	0	0
T_{11}	0	0	0	0.5	0	0	0	0	0	0	-	0
T_{12}	0	0	0	0	0	0.5	0	0.2	0.2	0	0	-

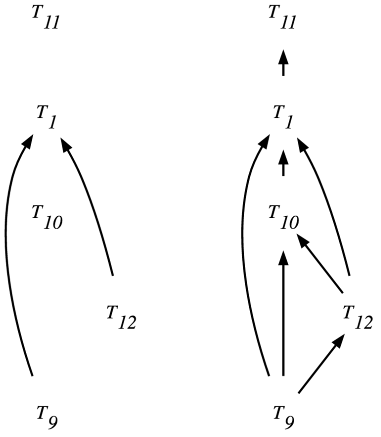
$\text{tanimoto}(T_Tx, T_Ty)$

From these, the algorithm goes through logical steps (Figure 10) to identify a candidate resource list C_R for each taxon in N_1 using either empirical data directly or K most similar taxa with equation 2. Going through the process for T_1, using $K = 1$ and $w_t = 1$:

The logical steps allow us to predict a set of resources for $T_1 = \{T_9, T_{10}, T_{12}\}$. Doing it for all taxa in N_1 with $w_t = 0$ and 1 predicts the following networks:

$\boldsymbol{w_t = 0}$ $\boldsymbol{w_t = 1}$

Steps		Catalogue	Prediction
1	$I(T_1, T_R)$ in N_0?		
2	T_R in N_1?		
4-7	$T_2 = \text{no} \rightarrow t(T_2, T_{R'}, w_t) = \text{NA}$	$\{\}$	$\{\}$
4-7	$T_3 = \text{no} \rightarrow t(T_2, T_{R'}, w_t) = T_{10} = 0.5$	$\{\}$	$\{T_{10}\}$
3	$T_{12} = \text{yes}$	$\{T_{12}\}$	$\{T_{10}\}$
8	$t(T_1, T_{C'}, w_t) = T_5 = 0.5$		
9	I(T_5,T_R) in N_1?		
13-16	$T_8 = \text{no} \rightarrow t(T_8, T_{R'}, w_t) = T_9 = 0.5$	$\{T_{12}\}$	$\{T_9, T_{10}\}$
10-12	$T_9 = \text{yes}$	$\{T_9, T_{12}\}$	$\{T_9, T_{10}\}$



2.11 Supporting information

Table 2: List of functional groups included in the dataset presented in Savenkoff et al. (2004) with their taxa composition. Only taxa that were at least at the scale of the family were used to predict interactions. List adapted from Savenkoff et al. (2004).

Functional group name	Functional group main taxa composition
Cetaceans	*Balaenoptera physalus*, *B. acutorostrata*, *Megaptera novaeangliae*, *Phocoena phocoena*, *Lagenorhynchus acutus*, *L. albirostris*
Harp seals	*Pagophilus groenlandicus*

Functional group name	Functional group main taxa composition
Hooded seals	*Cystophora cristata*
Grey seals	*Halichoerus grypus*
Harbour seals	*Phoca vitulina*
Seabirds	*Phalacrocorax carbo*, *P. auritus*, *Larus delawarensis*, *L. argentatus*, *L. marinus*, *Sterna hirundo*, *S. paradisaea*, *Cepphus grylle*, *Oceanodroma leucorhoa*, *Morus bassanus*, *Rissa tridactyla*, *Uria aalge*, *Alca torda*, *Fratercula arctica*
Atlantic cod	*Gadus morhua*
Greenland halibut	*Reinhardtius hippoglossoides*
American plaice	*Hippoglossoides platessoides*
Flounders	*Limanda ferruginea*, *Glyptocephalus cynoglossus*, *Pseudopleuronectes americanus*
Skates	*Amblyraja radiata*, *Malacoraja senta*, *Leucoraja ocellata*
Redfish	*Sebastes mentella*, *S. fasciatus*
Large demersal feeders	*Urophycis tenuis*, *Melanogrammus aeglefinus*, *Centroscyllium fabricii*, *Anarhichassp.*, *Cyclopterus lumpus*, *Lycodessp.*, Macrouridae, Zoarcidae, *Lophius americanus*, *Hippoglossus hippoglossus*
Small demersal feeders	*Myoxocephalussp.*, *Tautogolabrus adspersus*, *Zoarcesamericanus*, large demersal juveniles
Capelin	*Mallotus villosus*
Large pelagic feeders	*Squalus acanthias*, *Pollachius virens*, *Merluccius bilinearis*, *Cetorhinus maximus*
Piscivorous small pelagic feeders	*Scomber scombrus*, *Illex illecebrosus*, piscivorous myctophids and other mesopelagics, piscivorous large pelagic juveniles
Planktivorous small pelagic feeders	*Clupea harengus harengus*, *Scomberesox saurus*, *Gonatussp.*, planktivorous myctiphids and other mesopelagics, planktivorous large pelagic juveniles
Shrimp	*Argis dentata*, *Eualus macilentus*, *E. gaimardi*, *Pandalus montagui*
Large crustaceans	*Chionoecetes opilio*, *Hyassp.*
Echinoderms	*Echinarachnius parma*, *Stronglyocentrotus pallidus*, *Ophiura robusta*
Molluscs	*Mesodesma deauratum*, *Cyrtodaria siliqua*
Polychaetes	*Parexogone hebes*

Functional group name	Functional group main taxa composition
Small zooplankton	*Oithona similis*, *Temora longicornis*, *Pseudocalanussp.*, *Calanus finmarchicus*, tunicates, meroplankton, heterotrophic protozoa
Phytoplankton	*Chaetoceros affinis*, *Chaetocerossp.*, *Leptocylindrus minimus*, *Thalassiiosira nordenskioldii*, *Thalassiiosirasp.*, *Fragilariopsissp.*, other diatoms, mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes and Prymnesiophytes

Table 3: List of functional groups for which observed interactions in Savenkoff et al. (2004) were not predicted by the algorithm (c).

Consumer	Resource
Grey seals	Skates
Seabirds	Skates
Harbour seals	Skates
Cetaceans	Shrimp
Shrimp	Phytoplankton
Mollusks	Phytoplankton
Polychaetes	Phytoplankton
Grey seals	Large crustaceans
Flounders	Planktivorous small pelagic feeders
Flounders	Echinoderms
Small demersal feeders	Echinoderms
Grey seals	American plaice
Hooded seals	Flounders
Harp seals	Flounders
Skates	Mollusks
Large crustaceans	Mollusks
Atlantic cod	Mollusks
American plaice	Mollusks
Flounders	Mollusks
Small demersal feeders	Mollusks
Harbour seals	Mollusks
Seabirds	Small zooplankton
Skates	Polychaetes
Shrimp	Polychaetes

Consumer	Resource
Large crustaceans	Polychaetes
Atlantic cod	Polychaetes
American plaice	Polychaetes
Flounders	Polychaetes
Small demersal feeders	Polychaetes
Polychaetes	Polychaetes
Large pelagic feeders	Polychaetes
Large demersal feeders	Polychaetes
Grey seals	Piscivorous small pelagic feeders
Greenland halibut	Piscivorous small pelagic feeders
Redfish	Piscivorous small pelagic feeders

Table 4: List of functional groups for which interactions were predicted by the algorithm, but not observed in Savenkoff et al. (2004) (*b*).

Consumer	Resource
Skates	Skates
Atlantic cod	Skates
Hooded seals	Shrimp
Piscivorous small pelagic feeders	Shrimp
Planktivorous small pelagic feeders	Phytoplankton
Planktivorous small pelagic feeders	Large crustaceans
Hooded seals	Large crustaceans
Echinoderms	Large crustaceans
Flounders	Large crustaceans
Seabirds	Large crustaceans
Greenland halibut	Large crustaceans
Piscivorous small pelagic feeders	Large crustaceans
Redfish	Large crustaceans
Planktivorous small pelagic feeders	Planktivorous small pelagic feeders
American plaice	Planktivorous small pelagic feeders
Echinoderms	Echinoderms
Large demersal feeders	Echinoderms
Planktivorous small pelagic feeders	Atlantic cod
American plaice	Atlantic cod
Flounders	Atlantic cod
Greenland halibut	Atlantic cod
Piscivorous small pelagic feeders	Atlantic cod
Cetaceans	American plaice

Consumer	Resource
Planktivorous small pelagic feeders	American plaice
Hooded seals	American plaice
American plaice	American plaice
Flounders	American plaice
Harbour seals	American plaice
Piscivorous small pelagic feeders	American plaice
Redfish	American plaice
Large pelagic feeders	American plaice
Cetaceans	Flounders
Planktivorous small pelagic feeders	Flounders
American plaice	Flounders
Flounders	Flounders
Piscivorous small pelagic feeders	Flounders
Redfish	Flounders
Large crustaceans	Capelin
Planktivorous small pelagic feeders	Capelin
Piscivorous small pelagic feeders	Small demersal feeders
Cetaceans	Small zooplankton
Large crustaceans	Small zooplankton
Large pelagic feeders	Small zooplankton
Large demersal feeders	Small zooplankton
Atlantic cod	Seabirds
Seabirds	Seabirds
Large demersal feeders	Seabirds
Harbour seals	Harbour seals
Skates	Greenland halibut
Cetaceans	Greenland halibut
Planktivorous small pelagic feeders	Greenland halibut
Atlantic cod	Greenland halibut
American plaice	Greenland halibut
Flounders	Greenland halibut
Small demersal feeders	Greenland halibut
Harbour seals	Greenland halibut
Piscivorous small pelagic feeders	Greenland halibut
Redfish	Greenland halibut
Large pelagic feeders	Greenland halibut
Planktivorous small pelagic feeders	Piscivorous small pelagic feeders
American plaice	Piscivorous small pelagic feeders
Flounders	Piscivorous small pelagic feeders
Small demersal feeders	Piscivorous small pelagic feeders
Piscivorous small pelagic feeders	Piscivorous small pelagic feeders

Consumer	Resource
Atlantic cod	Redfish
Harp seals	Redfish
Seabirds	Redfish
Redfish	Redfish
Large pelagic feeders	Redfish
Skates	Large pelagic feeders
Planktivorous small pelagic feeders	Large pelagic feeders
Hooded seals	Large pelagic feeders
Atlantic cod	Large pelagic feeders
American plaice	Large pelagic feeders
Flounders	Large pelagic feeders
Small demersal feeders	Large pelagic feeders
Harp seals	Large pelagic feeders
Seabirds	Large pelagic feeders
Greenland halibut	Large pelagic feeders
Piscivorous small pelagic feeders	Large pelagic feeders
Redfish	Large pelagic feeders
Large pelagic feeders	Large pelagic feeders
Large demersal feeders	Large pelagic feeders
Skates	Large demersal feeders
Cetaceans	Large demersal feeders
Planktivorous small pelagic feeders	Large demersal feeders
Atlantic cod	Large demersal feeders
American plaice	Large demersal feeders
Flounders	Large demersal feeders
Small demersal feeders	Large demersal feeders
Seabirds	Large demersal feeders
Greenland halibut	Large demersal feeders
Piscivorous small pelagic feeders	Large demersal feeders
Redfish	Large demersal feeders
Large pelagic feeders	Large demersal feeders
Large demersal feeders	Large demersal feeders

ARTICLE 3

L'ÉVALUATION DES IMPACTS CUMULÉS DANS L'ESTUAIRE ET LE GOLFE DU SAINT-LAURENT : VERS UNE PLANIFICATION SYSTÉMIQUE DE L'EXPLOITATION DES RESSOURCES

3.1 Résumé

L'intensification de l'empreinte humaine dans l'estuaire et le golfe du Saint-Laurent impose une planification systémique de l'exploitation des ressources marines. Une évaluation régionale des impacts cumulés dans le Saint-Laurent demeure pourtant encore attendue. Un nombre important d'activités (p. ex. transport maritime, pêche, aquaculture) caractérise l'exploitation humaine du Saint-Laurent. Ces activités imposent plusieurs stresseurs environnementaux (p. ex. destruction de l'habitat) affichant un chevauchement spatial croissant. Individuellement, ils peuvent affecter la structure et le fonctionnement des écosystèmes. Imposés simultanément, les stresseurs peuvent agir en synergie et entraîner des effets non linéaires imprévisibles. Ces effets demeurent largement incompris et conséquemment ignorés lors d'évaluations d'impacts environnementaux, qui demeurent orientées sur des espèces ou secteurs uniques et l'approbation de projets. Plusieurs défis relatifs aux impacts cumulés dans le Saint-Laurent doivent être relevés : 1) améliorer l'état des connaissances des impacts de multiples stresseurs sur les écosystèmes, 2) améliorer l'applicabilité des méthodes d'évaluation d'impacts cumulés, 3) identifier des indicateurs d'impacts cumulés, 4) créer un protocole de suivi environnemental et d'impacts humains, et de partage de données et 5) développer une capacité de gestion adaptative pour le Saint-Laurent. La planification systémique de l'utilisation des ressources naturelles au sein du Saint-Laurent nécessitera une vision intégrative de la structure et du fonctionnement

des écosystèmes ainsi que des vecteurs de stress qui leur sont imposés. Une telle approche ne sera réalisable que lorsque nous aurons développé les infrastructures et les outils nécessaires à une gestion écosystémique du Saint-Laurent.

Ce troisième article a été corédigé par moi-même, Cindy Grant, Dominique Gravel et Philippe Archambault. Il a été publié dans un numéro spécial de la revue *Le Naturaliste Canadien* sur le Saint-Laurent à l'été 2016. Tous les auteurs ont contribué à l'élaboration des objectifs de l'article et à sa rédaction. J'ai été en charge des figures et j'ai dirigé la rédaction de l'article. Tous les auteurs ont contribué à l'écriture et à la révision de l'article.

Beauchesne, D., Grant, C., Gravel, D., Archambault, P., 2016. L'évaluation des impacts cumulés dans l'estuaire et le golfe du Saint-Laurent : vers une planification systémique de l'exploitation des ressources. Le Naturaliste Canadien 140, 45-55. https ://doi.org/10.7202/1036503ar.

Les sections suivantes sont celles de l'article publié.

3.2 Titre

L'évaluation des impacts cumulés dans l'estuaire et le golfe du Saint-Laurent : vers une planification systémique de l'exploitation des ressources

3.3 Auteurs

David Beauchesne, Cindy Grant, Dominique Gravel, Philippe Archambault

3.4 Résumé

L'intensification de l'empreinte humaine dans l'estuaire et le golfe du Saint-Laurent impose une planification systémique de l'exploitation des ressources marines. Une évaluation régionale des impacts cumulés dans le Saint-Laurent demeure pourtant encore attendue. Un nombre important d'activités (p. ex. transport maritime, pêche, aquaculture) caractérise l'exploitation humaine du Saint-Laurent. Ces activités imposent plusieurs stresseurs environnementaux (p. ex. destruction de l'habitat) affichant un chevauchement spatial croissant. Individuellement, ils peuvent affecter la structure et le fonctionnement des écosystèmes. Imposés simultanément, les stresseurs peuvent agir en synergie et entraîner des effets non linéaires imprévisibles. Ces effets demeurent largement incompris et conséquemment ignorés lors d'évaluations d'impacts environnementaux, qui demeurent orientées sur des espèces ou secteurs uniques et l'approbation de projets. Plusieurs défis relatifs aux impacts cumulés dans le Saint-Laurent doivent être relevés : 1) améliorer l'état des connaissances des impacts de multiples stresseurs sur les écosystèmes, 2) améliorer l'applicabilité des méthodes d'évaluation d'impacts cumulés, 3) identifier des indicateurs d'impacts cumulés, 4) créer un protocole de suivi environnemental et d'impacts humains, et de partage de données et 5) développer une capacité de gestion adaptative pour le Saint-Laurent. La planification systémique de l'utilisation des ressources naturelles au sein du Saint-Laurent nécessitera une vision intégrative de la structure et du fonctionnement des écosystèmes ainsi que des vecteurs de stress qui leur sont imposés. Une telle approche ne sera réalisable que lorsque nous aurons développé les infrastructures et les outils nécessaires à une gestion écosystémique du Saint-Laurent.

Mots clés : activités humaines, effets non linéaires, gestion adaptative, stresseurs environnementaux, synergie

3.5 Abstract

The intensification of human activity in the Estuary and Gulf of St. Lawrence (Canada) imposes the need for a systematic planning approach for the use of marine resources. There is, however, currently no regional cumulative impact assessment for the St. Lawrence. Many of the human activities in this area (e.g., shipping, fisheries and aquaculture) impose environmental threats (e.g., habitat destruction) that may jeopardize ecosystem structure and function. Increasingly, these threats are overlapping spatially, which induces synergies causing unpredictable non-linear effects on ecosystems. These effects are still poorly understood and consequently neglected in environmental impact assessments, which remain focused on single species or sectors, and on the approval of specific projects. To efficiently evaluate cumulative impacts in the St. Lawrence, it will be important to : 1) improve our knowledge concerning the impacts of multiple threats to ecosystems ; 2) improve the accessibility to, and the applicability of, cumulative impact tools ; 3) identify relevant human and environmental indicators of cumulative impacts ; 4) create a data sharing, and human impact and environmental monitoring protocol ; and 5) develop an adaptive management approach for the St. Lawrence. Systematic planning of the use of natural resources in the St. Lawrence will require an integrated overview of the structure and function of its ecosystems, and of the sources of stresses affecting them. Such an approach will only be feasible once the necessary infrastructures and tools for ecosystem-based management of the area have been developed.

Keywords : adaptive management, environmental stressors, human activities, non-linear effects, synergy

3.6 Introduction

Que ce soit à travers des activités comme la pêche ou le transport maritime, l'homme impose de profonds changements sur la structure et le fonctionnement des écosystèmes marins et compromet leur intégrité (Myers et Worm, 2003; Worm et al., 2006; Estes et al., 2011). L'intensification des activités humaines entraîne un chevauchement spatial croissant des différents stresseurs, de telle sorte que peu de milieux demeurent libres de l'empreinte humaine (Halpern et al., 2008b, 2015b). L'intégrité des écosystèmes est ainsi attaquée sur plusieurs fronts, avec des conséquences parfois imprévisibles.

Les activités humaines en milieu marin ont ainsi été collectivement qualifiées de syndromes d'ordre supérieur de changements globaux océaniques (Duarte, 2014; Boonstra et al., 2015). Les impacts cumulés ont alors été identifiés comme principale priorité de recherche en sciences marines par plus de 2 000 scientifiques venant des sciences physiques, écologiques et sociales (Rudd, 2014) et sont mentionnés répétitivement parmi les questions de recherche marine prioritaires au Canada (Fissel et al., 2012).

La disponibilité et l'accessibilité aux ressources marines augmentent rapidement l'intérêt porté à l'estuaire et au golfe du Saint-Laurent (EGSL). Ce vaste écosystème est d'ailleurs actuellement identifié en tant que vecteur clé pour la croissance économique du Québec (Government of Québec, 2015). Cette stratégie maritime laisse présager un accroissement imminent des activités humaines au sein d'un écosystème où les impacts des pressions anthropiques actuelles demeurent largement incompris (Dufour et Ouellet, 2007; Benoît et al., 2012).

L'intensification de l'empreinte humaine dans le Saint-Laurent imposerait une planification systémique de l'exploitation (c'est-à-dire toute activité extractive ou non extractive) de ses ressources marines. À l'instar de la planification systémique de la conservation (Margules et Pressey, 2000), la planification systémique de l'exploitation des ressources viserait à suivre une démarche objective et proactive de gestion, basée sur des objectifs clairs et qui intègre l'ensemble des activités susceptibles d'affecter les ressources naturelles. L'accumulation des impacts imposés à la structure et au fonctionnement des écosystèmes du Saint-Laurent demeure toutefois encore largement incomprise, comme ailleurs sur le monde (Halpern et al., 2008b; Halpern et Fujita, 2013). Les évaluations d'impacts environnementaux canadiennes sont ainsi encore aujourd'hui orientées sur des espèces ou des secteurs uniques et se concentrent davantage sur l'approbation de projets (Dubé et al., 2006; Duinker et Greig, 2006; Crowder et Norse, 2008).

Il se dégage ainsi une incohérence entre la volonté d'assurer une gestion durable des ressources, nécessitant une vision holistique, et une gestion isolée des stress sur les écosystèmes. Une évaluation des impacts cumulés dans le Saint- Laurent demeure ainsi inexistante. L'objectif de cet article est d'établir un état des connaissances sur les impacts cumulés dans le Saint-Laurent. Nous identifions également les principaux défis de recherche et de gestion à relever afin de permettre une évaluation des impacts cumulés efficace pour le Saint-Laurent.

3.7 Les impacts cumulés au Canada

Pour définir convenablement les impacts cumulés, il importe de définir certaines notions. Une activité humaine est un processus par lequel l'homme exploite ou altère un milieu naturel (p. ex. la pêche ; Halpern et al., 2007). Un stresseur environnemental est un processus d'origine naturelle ou anthropique pouvant perturber un milieu au-delà de ses limites de tolérance (Kappel et al., 2012). L'extraction de biomasse occasionnée par la pêche peut ainsi être considérée comme un stresseur environnemental.

Similairement, une variable d'état, comme la température, peut également entraîner un stress environnemental lorsqu'elle varie au-delà de ses limites naturelles de variabilité. Ces anomalies peuvent alors être caractérisées et considérées comme des stresseurs environnementaux. Une perturbation est l'effet mesurable d'un ou plusieurs stresseurs sur des variables biotiques ou abiotiques (Dunne et al., 2002; Montoya et al., 2009). Finalement, un impact est un changement mesuré en comparant un point initial à un point final pour un indicateur et une intensité de référence (Dubé et al., 2006).

Les impacts cumulés correspondent à l'accumulation ou à l'accroissement progressif d'un ou de plusieurs impacts sur le milieu naturel (Peterson et al., 1987). La législation canadienne définit les impacts cumulés comme : l'impact sur l'environnement résultant des effets d'un projet combinés à ceux d'autres projets et activités antérieurs, actuels et imminents (Government of Canada, 1992). Cette définition considère, entre autres, des échelles spatiales et temporelles variables, les interactions avec d'autres activités passées, présentes et futures, l'importance relative des impacts et leur intensité (Hegmann et al., 1999). De façon plus imagée, les impacts cumulés s'apparentent à la mort par un millier de coupures (Therivel et Ross, 2007).

L'évaluation des impacts cumulés permet de considérer l'ensemble des stresseurs imposés sur un milieu naturel (Hegmann et al., 1999; Dubé et al., 2006; Krausman et Harris, 2011). Le processus d'évaluation des impacts cumulés ne cherche pas à remplacer les évaluations d'impacts ciblées sur des secteurs ou des espèces particulières, qui demeurent essentielles. Ces évaluations négligent toutefois de considérer les interactions et le chevauchement spatiotemporel entre les activités et les processus par lesquels elles affectent l'intégrité des milieux perturbés (Halpern et al., 2008a). L'évaluation des impacts cumulés agit ainsi en tant qu'extension à ces évaluations pour favoriser une gestion systémique de l'exploitation du milieu naturel (Krausman et Harris, 2011).

L'incohérence entre la législation relative à l'évaluation des impacts cumulés et l'application réelle de ces évaluations est manifeste ; le processus se concentre davantage sur l'approbation de projets individuels plutôt que sur la protection environnementale (Duinker et Greig, 2006). En effet, une approche par secteur ou par espèce est habituellement adoptée lors de l'évaluation des impacts de projets (Dubé et al., 2006; Crowder et Norse, 2008), ignorant de fait les interactions potentielles de multiples pressions environnementales exercées simultanément. Une image partielle et une approche réactive se dégagent alors des pratiques usuelles d'évaluation des impacts environnementaux, menant plusieurs scientifiques à dénoncer les performances d'un système jugé imparfait et nécessitant une restructuration majeure (Kennett, 1999; Duinker et Greig, 2006).

3.8 Évaluation des impacts cumulés

Plusieurs méthodologies ont été développées afin d'évaluer les impacts cumulés (voir Krausman et Harris, 2011). Dans le cadre de cet article, nous nous concentrerons toutefois sur les exercices récents qui étudient les impacts cumulés en milieu marin. Plusieurs exemples peuvent être trouvés dans la littérature (p. ex. Halpern et al., 2008b, 2015b; Vörösmarty et al., 2010; Korpinen et al., 2013). L'étude de Halpern et al. (2008b) a enclenché une transition vers une étude systémique des impacts cumulés sur les océans. Cette étude a démontré que peu d'écosystèmes demeurent aujourd'hui libres de l'empreinte humaine à l'échelle planétaire et que la majorité des écosystèmes sont affectés par de multiples stresseurs environnementaux. Ce constat est d'ailleurs supporté par la majorité des études similaires (p. ex. Ban et Alder, 2008; Ban et al., 2010; Micheli et al., 2013). Une mise à jour de l'évaluation initiale (Halpern et al., 2015b) a également démontré un accroissement des impacts cumulés entre 2008 et 2013 sur près de 60 % du globe.

Les résultats obtenus par ces 2 études (Halpern et al., 2008b, 2015b) nous fournissent l'unique évaluation d'impacts cumulés sur les écosystèmes du Saint-Laurent. On y observe des impacts cumulés d'intensité faible ou intermédiaire, ainsi qu'une augmentation des impacts cumulés entre 2008 et 2013. Il s'agit toutefois d'une comparaison planétaire qui permet uniquement une comparaison des impacts relatifs imposés sur les différentes régions du globe. Cette analyse néglige conséquemment les particularités locales et les données à fine résolution disponibles à l'échelle du Saint-Laurent. Par exemple, des données d'hypoxie (< 30 % saturation d'oxygène) globale étant indisponibles, ce facteur de stress n'a pu être considéré. Il s'agit toutefois d'un enjeu d'importance identifié pour le Saint-Laurent (Benoît et al., 2012) et pour lequel des données spatiales y sont actuellement disponibles (p. ex. Gilbert et al., 2007). De la même manière, des données d'anomalies de températures de surface à fine résolution associées aux changements climatiques sont disponibles à l'échelle régionale (Galbraith et al., 2012). Ce constat étant partagé pour d'autres régions, plusieurs analyses ont été effectuées à des échelles locales et régionales afin de raffiner les résultats obtenus à l'échelle planétaire, permettant ainsi de capturer plus fidèlement les particularités d'une région d'intérêt (Halpern et al., 2009; Selkoe et al., 2009). Ces analyses permettent alors de guider convenablement les gestionnaires en leur fournissant des évaluations adaptées à leurs besoins, à l'échelle où sont prises les décisions.

3.9 Évaluation régionale des impacts cumulés dans le Saint-Laurent

L'approche préconisée par Halpern et al. (2008b) nécessite la caractérisation de 3 types de variables en vue de calculer un score d'impacts cumulés, soit : 1) une cartographie des stresseurs environnementaux dans le lieu d'étude, 2) une cartographie des éléments naturels d'intérêt (p. ex. écosystèmes ou espèces) et 3) une évaluation de la vulnérabilité des éléments naturels aux stresseurs environnementaux. Ces éléments sont ensuite croisés spatialement afin d'évaluer la co-occurrence, ou l'exposition, des éléments naturels d'intérêt aux stresseurs environnementaux. Une approche intégrative pour l'étude de l'écologie du Saint-Laurent est déjà bien documentée et permet d'identifier des milieux d'intérêt écologiques. Citons par exemple l'identification des habitats benthiques, épipélagiques et côtiers (Dutil et al., 2011, 2012), l'identification des zones d'intérêt écologique et biologique (ZIEB ; Pêches et Océans Canada, 2007) et la cartographie des types de communautés benthiques dans le nord du golfe du Saint-Laurent (Moritz et al., 2013).

L'évaluation des impacts cumulés nécessite une étape additionnelle, c'est-à-dire l'évaluation du chevauchement spatial entre les milieux naturels et l'ensemble des stresseurs environnementaux historiques, actuels et émergents (figure 14). Cette vision intégrative demeure toutefois absente pour l'évaluation des sources de stress dans le Saint-Laurent. À notre connaissance, les rapports de Dufour et Ouellet (2007) et Benoît et al. (2012) sont les seuls ouvrages récents offrant une vue d'ensemble des différentes activités humaines et des sources de stress environnementaux dans le Saint-Laurent. Ces derniers ont identifié divers enjeux environnementaux en fonction de leur importance et leur probabilité d'agir cumulativement dans l'EGSL. La description des stresseurs du Saint-Laurent provient essentiellement de ces 2 rapports, à moins d'indication contraire.

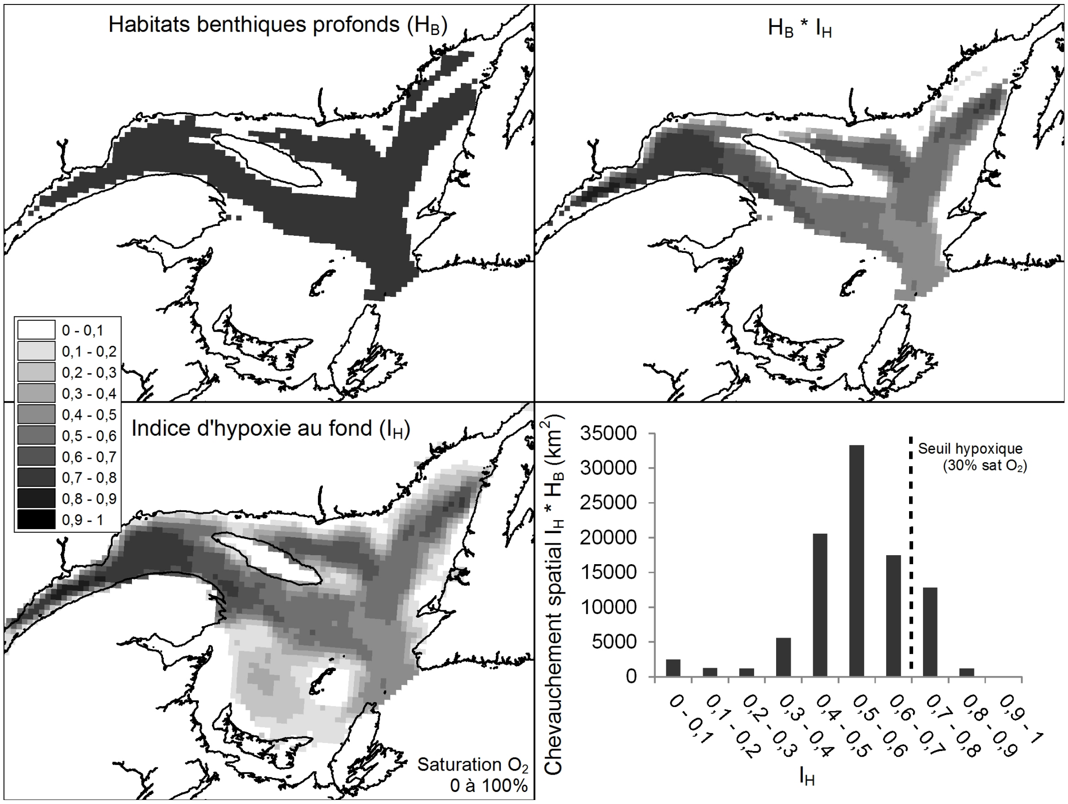


Figure 14: Cartographie des habitats benthiques profonds HB et d'un indice d'hypoxie IH pour l'estuaire et le golfe du Saint-Laurent. L'indice d'hypoxie a été calculé en normalisant les valeurs de saturation en oxygène au fond entre 0 et 1, de telle sorte que la saturation en oxygène diminue plus la valeur de l'indice tend vers 1. La combinaison des habitats benthi (HB * IH) permet de visualiser le chevauchement spatial entre les deux variables. L'histogramme présente la superficie des habitats benthiques en fonction de classes IH. Cette cartographie met en évidence la nécessité de considérer l'exposition des éléments écologiques d'intérêt aux différents stresseurs qui leur sont imposés. Les données d'habitats benthiques profonds et de saturation en oxygène proviennent de Dutil *et al.* (2011).

Le potentiel d'exploitation des ressources fait du Saint-Laurent un vecteur économique d'une importance capitale pour le Québec et le Canada. Les principales activités économiques sont la pêche commerciale, le transport maritime, le tourisme et l'aquaculture (Tableau 5). Les pêches commerciales et récréatives touchent, dans le Saint-Laurent, une cinquantaine d'espèces incluant les poissons de fond, les poissons pélagiques, les mollusques et les crustacés, de même que les algues et les phoques. La pression exercée par les activités de pêche sur les stocks a entraîné, au cours des dernières décennies, l'essor de l'aquaculture. Près de 2 000 sites aquacoles sont recensés dans l'EGSL, mais presque tous sont concentrés dans le sud du golfe. Les côtes de l'Île-du-PrinceÉdouard, de la Nouvelle-Écosse et du Nouveau-Brunswick produisent ainsi la quasi-totalité des moules et des huîtres d'élevage issues de l'EGSL.

Mis à part le potentiel commercial de ses espèces, le Saint-Laurent soutient le commerce de marchandises diverses et de nombreux navires y transitent chaque année. Avec plus de 40 ports en mesure d'accueillir des navires commerciaux, l'EGSL est en tête de liste lorsqu'il est question de transport maritime dans l'est du pays. De plus, avec la navigation de plaisance et l'augmentation du nombre de croisières et d'excursions en mer, le Saint-Laurent est non seulement un atout économique dans les secteurs de l'exploitation des ressources naturelles et du transport maritime, mais également un lieu d'intérêt pour l'industrie touristique.

Le Saint-Laurent accueillera également diverses activités émergentes, tandis que d'autres actuellement pratiquées s'intensifieront dans un futur proche. La stratégie maritime québécoise prévoit, entre autres, une amélioration et une augmentation des capacités des infrastructures portuaires, une augmentation du trafic maritime à caractère industriel et touristique, et une valorisation des produits issus des activités de pêche et d'aquaculture (Government of Québec, 2015). La présence d'hydrocarbures suscite également un intérêt grandissant pour l'EGSL, avec le prospect Old Harry chevauchant la limite entre le Québec et Terre-Neuve, et plus de 60 000 km de relevés sismiques effectués depuis les années 1960 (Pêches et Océans Canada, 2013b). Malgré un moratoire en place depuis 1997 pour la portion québécoise du golfe, un intérêt clair est attribué à l'exploration des hydrocarbures dans le Saint-Laurent (p. ex. Pêches et Océans Canada, 2013a), suggérant qu'une exploitation des hydrocarbures peut être pressentie dans le Saint- Laurent. Des activités de pêche émergente, comme l'exploitation du concombre de mer (*Cucumaria frondosa*), sont également en essor dans le Saint-Laurent (p. ex. Campagna et al., 2005).

Finalement, les changements climatiques vont vraisemblablement imposer des changements importants sur la structure et le fonctionnement des écosystèmes du Saint-Laurent et pourraient exacerber l'impact de stresseurs déjà observés dans le Saint-Laurent comme les anomalies de températures de surface (Dufour et Ouellet, 2007).

Tableau 5: Principales activités humaines au sein de l'EGSL décrites en fonction des stresseurs environnementaux qui leur sont associés (inspiré de Dufour et Ouellet, 2007; Benoît et al., 2012). Ne sont pas présentes dans ce tableau les boucles de rétroaction à travers lesquelles un stresseur peut affecter une autre activité humaine, telle que l'hypoxie qui influence la distribution des ressources halieutiques et ainsi les activités de pêche commerciale.

		Stress environnementaux															
Activité	Sous-activité	Acidification	Apports d'eau douce	Collisions	Contaminants	Courants/masses d'eau	Déchets/eaux usées	Destruction de l'habitat	Déversements accidentels hydrocarbures	Éléments nutritifs/déchets organiques	Élimination en mer	Espèces envahissantes	Hypoxie	Obstruction du courant	Parasites/maladies	Perturbation/dérangement	Prélèvement de la biomasse
Pêche	Pêche commerciale et récréative						X	X	X						X	X	
	Usines de transformation						X					X			X		
Aquaculture*										X		X		X	X		
Transport maritime	Entretiens des voies navigables*		X		X			X			X					X	
	Transport de marchandises et de personnes*			X	X		X		X			X				X	
	Transport relié aux activités de pêche			X	X		X		X							X	
	Infrastructures portuaires*							X						X			

		Stress environnementaux															
Activité	Sous-activité	Acidification	Apports d'eau douce	Collisions	Contaminants	Courants/masses d'eau	Déchets/eaux usées	Destruction de l'habitat	Déversements accidentels hydrocarbures	Éléments nutritifs/déchets organiques	Élimination en mer	Espèces envahissantes	Hypoxie	Obstruction du courant	Parasites/maladies	Perturbation/dérangement	Prélèvement de la biomasse
Production hydroélectrique	Modification du bassin versant	X	X		X					X			X				
Activités en milieu terrestre	Établissements humains	X				X	X	X	X	X			X	X	X	X	
	Activités industrielles	X			X		X			X			X				
	Agriculture	X	X		X		X			X			X				
Industrie pétrolière et gazière en mer	Prospection sismique															X	
	Forage exploratoire							X								X	
	Exploitation[**]	X			X		X	X	X	X			X			X	
Tourisme	Aménagement côtier				X		X	X	X							X	
	Navigation de plaisance[*]			X	X		X		X			X				X	

[*]Activités ou sous-activités pour lesquelles une intensification est prévisible dans un futur proche
[*]∗Activités ou sous-activités émergentes

3.10 Impacts combinés de multiples stresseurs environnementaux

L'étendue spatiotemporelle et le chevauchement important des activités humaines peuvent multiplier les stresseurs environnementaux imposés sur une quantité considérable de ressources et de processus écologiques (MacDonald, 2000). D'abord, l'ensemble des activités humaines pratiquées dans le Saint-Laurent peut perturber directement et de plusieurs façons la biodiversité, par exemple la destruction de l'habitat et l'extraction de biomasse par la pêche (Tableau 5). De plus, plusieurs activités humaines peuvent être à la source de stress indirect, comme le dérangement engendré par le trafic maritime et l'exploitation des hydrocarbures (Tableau 5). Même individuellement, chaque stresseur peut affecter la structure et le fonctionnement des écosystèmes (Jackson et al., 2001; Steffen et al., 2007). Ainsi, la surpêche a entraîné une chute du stock de poissons démersaux du Saint-Laurent (Frank et al., 2005). En contrepartie, certaines activités de pêche semblent avoir atteint un seuil de perturbation au-delà duquel l'application de stress supplémentaire n'affecte plus les communautés (Moritz et al., 2015). Le trafic maritime affecte également le comportement de mammifères marins dans le Saint-Laurent (p. ex. Lesage et al., 1999). À l'inverse, des impacts positifs peuvent parfois être observés, par exemple lors d'accroissement de la biomasse d'espèces commerciales sous certains sites d'aquaculture de moules aux Îles-de-la-Madeleine et à l'Île-du-Prince-Édouard (Clynick et al., 2008; D'Amours et al., 2008; Drouin et al., 2015).

Imposés simultanément ou lors d'ajouts successifs, les stresseurs environnementaux possèdent toutefois un fort potentiel d'interactions (Worm et al., 2002) qui peut entraîner des effets écologiques synergiques ou antagonistes difficiles à prédire (figure 15 ; Crain et al., 2008; Darling et Côté, 2008; Halpern et al., 2008a; Krausman et Harris, 2011). Les impacts cumulés de multiples stresseurs peuvent ainsi être supérieurs ou inférieurs à la somme de leur impact respectif (figure 15). Malgré cela, les analyses d'impacts cumulés continuent généralement de supposer des effets additifs entre stresseurs. Les effets non linéaires peuvent s'exprimer selon divers mécanismes. Par exemple, l'acidification peut causer des problèmes respiratoires par hypercapnie chez certaines espèces, qui nécessitent alors un apport accru en oxygène (Pörtner et al., 2005; Mucci et al., 2011). Ainsi, chaque effet peut être bénin lorsque pris individuellement, mais les conséquences de stress faibles qui sont néanmoins synchronisées peuvent être dramatiques. L'effet de l'acidification peut ainsi être exacerbé lorsqu'on l'observe en milieu pauvre en oxygène (Pörtner et al., 2005; Mucci et al., 2011). Bien que les effets individuels puissent être aisément prévisibles au-delà d'un seuil individuel, comme le cas de l'hypoxie, la gestion de ces stresseurs devient incertaine sous ces seuils lorsque plusieurs stresseurs en interactions sont présents (figure 16).

Des effets non linéaires peuvent également survenir en raison de la complexité des interactions biotiques formant la structure des communautés, qui peut être à la base d'une propagation indirecte des perturbations au sein des écosystèmes (Yodzis, 2000; Montoya et al., 2009; O'Gorman et Emmerson, 2009). Puisque les impacts des stresseurs peuvent être très contrastés entre espèces, la réponse des communautés aux stresseurs multiples dépend de la co-tolérance des espèces à chaque stresseur (Vinebrooke et al., 2004). La communauté intègre ainsi l'ensemble des stress pouvant affecter l'abondance, la diversité et l'état des individus, des populations et des communautés au sein d'un écosystème (Adams, 2005; Montoya et al., 2009; Burns et al., 2014). La chute des poissons démersaux du Saint-Laurent a ainsi entraîné des cascades trophiques dans le golfe (Frank et al., 2005). Les effets non linéaires pressentis demeurent toutefois inconnus (deYoung et al., 2008; Halpern et Fujita, 2013; Côté et al., 2016). Ces derniers sont ainsi largement ignorés dans le cadre d'évaluations d'impacts cumulés, qui assument généralement une relation linéaire additive entre le nombre de stresseurs et les impacts totaux observés (Halpern et al., 2008b).

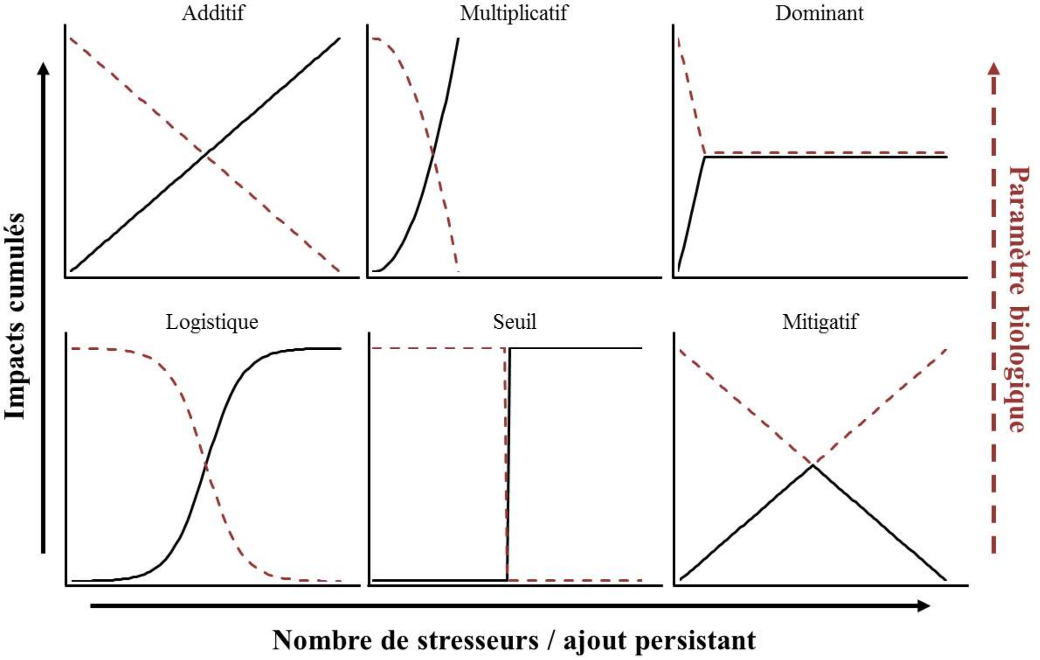


Figure 15: Représentation théorique de l'évolution des impacts cumulés en fonction de l'ajout persistant d'un stresseur unique ou d'autres stresseurs. Les impacts cumulés sont également représentés par un marqueur biologique de changement au niveau d'une variable d'intérêt (p. ex. abondance ou connectance d'un réseau). Les stresseurs peuvent interagir de plusieurs façons : les impacts totaux peuvent correspondre à la somme des impacts individuels, les impacts de plusieurs activités peuvent causer une multiplication des effets individuels, un stresseur unique peut dominer l'effet des autres stresseurs, les impacts peuvent croître logistiquement ou abruptement lors de l'atteinte d'un seuil de tolérance, et l'effet d'un stresseur peut être antagoniste à celui d'un autre stresseur et ainsi mitiger son effet. Finalement, les impacts totaux observés peuvent correspondre à une combinaison de plusieurs de ces cas théoriques (Inspirée de Peterson *et al.* (1987) et Halpern *et al.* (2008a)).

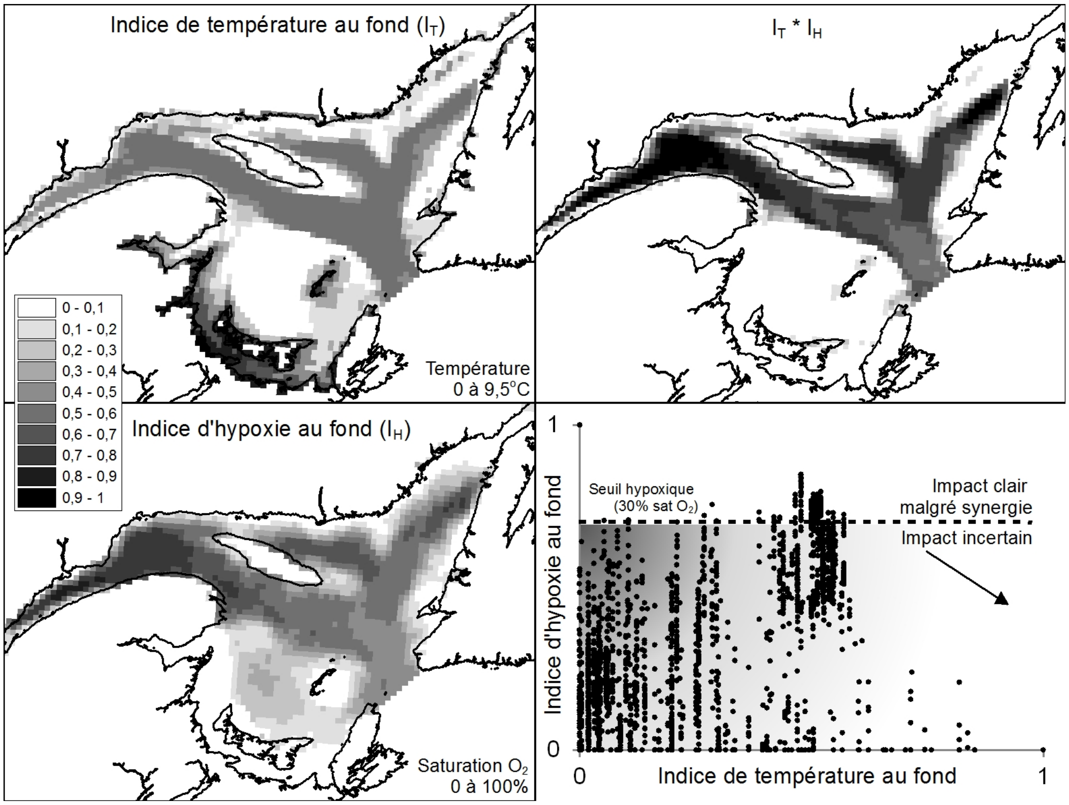


Figure 16: Cartographie d'indices de température IT et d'hypoxie IH pour l'estuaire et le golfe du Saint-Laurent révèle l'importance d'étudier les impacts cumulés. Les indices ont été calculés en normalisant les valeurs de température moyenne et de saturation en oxygène au fond entre 0 et 1, de telle sorte que les températures augmentent et la saturation en oxygène diminue plus la valeur de leur indice tend vers 1. La combinaison des deux indices (IT * IH) permet de visualiser l'interaction spatiale entre les deux variables. Le graphique de IH en fonction de IT fournit une représentation graphique de l'interaction entre les deux variables. Le seuil hypoxique nous sert de limite conceptuelle au-delà de laquelle un impact du stresseur est aisément prévisible malgré une interaction avec la température qui exacerbe son effet. Tel que représenté par la zone ombragée du graphique, les effets sont incertains sous ce seuil, les zones foncées étant plus à risque. Les données de température et de saturation en oxygène proviennent de Dutil *et al.* (2011).

3.11 Le cas de la morue du golfe du Saint-Laurent

La morue (*Gadus morhua*) fournit un exemple intéressant des impacts de multiples stresseurs environnementaux et de la nécessité d'adopter une approche intégrative lors d'évaluations d'impacts. La morue a connu un déclin draconien dans les années 1990 ayant mené à l'imposition de moratoires sur l'exploitation des poissons de fond et éventuellement à sa désignation en voie de disparition (stock de morue du nord du golfe) par le Comité pour la situation des espèces en péril au Canada (COSEPAC). À la suite de ce déclin causé par une surpêche importante, la température de l'eau, la pression de prédation sur les juvéniles, la compétition pour les ressources et les pêcheries semblent maintenant agir en synergie pour limiter le rétablissement de ce stock de morue (Bundy et Fanning, 2005; Bousquet et al., 2014). L'échec du rétablissement semble donc causé par une combinaison de facteurs environnementaux, d'interactions biotiques avec des prédateurs et des compétiteurs et par les activités humaines. Il est donc clair que seule l'adoption d'une approche intégrative, autant pour les variables environnementales que pour les vecteurs de stress, permet une compréhension adéquate de la situation de la morue dans le golfe du Saint-Laurent.

3.12 Défis de recherche et de gestion

L'étude des impacts cumulés constitue un enjeu essentiel pour le Saint-Laurent. Cet enjeu demeure particulièrement complexe à plusieurs égards, et de nombreux défis d'ordre législatif, économique, social et scientifique doivent être relevés. Nous présentons ainsi 5 défis de recherche et de gestion prioritaires en vue de permettre une évaluation des impacts cumulés dans le Saint-Laurent.

Défi 1. Améliorer l'état des connaissances des impacts de stresseurs multiples sur la structure et le fonctionnement des écosystèmes

Les interactions pressenties entre de multiples stresseurs et leur propagation non linéaire au sein des communautés demeurent largement incomprises (Côté et al., 2016). La diversité des stresseurs imposés cause une multiplication des chemins d'impacts potentiels (MacDonald, 2000; Montoya et al., 2009). L'utilisation d'approches expérimentales pour l'étude des impacts cumulés est ainsi limitée à cause du nombre de stresseurs et de leurs interactions potentielles. Les études expérimentales s'intéressent alors typiquement à un nombre limité de stresseurs sur des espèces ou communautés restreintes (p. ex. McElroy, 2014), limitant les généralisations possibles de ces études. L'approfondissement des fondements théoriques sur les effets de multiples stresseurs est ainsi indispensable à une compréhension des impacts cumulés sur les écosystèmes (Côté et al., 2016).

Pour répondre à ces lacunes, nous suggérons l'établissement d'un programme scientifique visant l'acquisition de connaissances théoriques sur les effets de multiples stresseurs sur les composantes des écosystèmes. À l'instar de plusieurs expériences qui ont révélé le rôle bénéfique d'une biodiversité croissante sur le fonctionnement des écosystèmes (Duffy, 2009), nous suggérons de mettre en place des expérimentations stresseurs-fonctionnement des écosystèmes (SFE). En variant le nombre de stresseurs, nous évaluerons la fréquence et les conditions menant à des effets non linéaires. De plus, puisque des effets non linéaires peuvent être causés par les interactions indirectes au sein des communautés, nous recommandons de porter une attention toute particulière à l'étude des impacts de multiples stresseurs sur la structure des communautés.

Défi 2. Améliorer et faciliter l'applicabilité des méthodes d'évaluation des impacts cumulés

Diverses suppositions de base sont adoptées par les méthodes d'évaluation des impacts cumulés (Halpern et Fujita, 2013), comme l'additivité de l'impact des stresseurs (voir défi 1) et l'utilisation typique des écosystèmes comme échelle d'organisation écologique d'intérêt pour les analyses (Halpern et al., 2008b; Ban et al., 2010; Allan et al., 2013). Les analyses à l'échelle des écosystèmes assument toutefois une réponse identique des composantes des écosystèmes à l'ensemble des stresseurs. Des méthodes considérant ces limitations devraient ainsi être élaborées. Par contre, l'accroissement de la complexité des méthodologies nécessite habituellement une expertise approfondie et une quantité considérable de données, limitant leur applicabilité dans le cadre d'évaluations des impacts cumulés (Krausman et Harris, 2011). Nous suggérons donc le développement d'outils accessibles, nécessitant une quantité de données minimale, et considérant la complexité des composantes structurant les écosystèmes. Par exemple, diverses approches prédictives, comme les modèles de répartition d'espèces (p. ex. Phillips et al., 2006) et les modèles de structure des communautés (p. ex. Gravel et al., 2013; Albouy et al., 2014), permettent de caractériser la structure complexe des écosystèmes aisément à partir d'une quantité restreinte de données. Utilisés en combinaison avec une cartographie des stresseurs du Saint-Laurent, ces derniers pourraient améliorer et faciliter les processus d'évaluation d'impacts environnementaux.

Défi 3. Identifier des indicateurs d'impacts cumulés pour le Saint-Laurent

L'utilisation d'indicateurs permet de prioriser et d'optimiser les efforts déployés en identifiant des éléments qui capturent une part importante des changements observés ou anticipés dans un milieu d'intérêt (Pereira et al., 2013). De plus, les indicateurs appuient le développement de protocoles standardisés permettant des comparaisons à l'échelle régionale à partir de données récoltées localement (Pereira et al., 2013). Nous suggérons donc d'identifier des indicateurs permettant de capturer convenablement les impacts cumulés dans le Saint-Laurent. Des indicateurs environnementaux standardisés provenant d'une initiative internationale récente qui identifie des variables essentielles de biodiversité (VEB) pourraient guider cette initiative (p. ex. répartition et abondance des espèces, diversité taxonomique et structure des habitats ; Pereira et al., 2013). Nous suggérons également de démarrer une initiative similaire visant l'identification de variables essentielles de stresseurs (VES) afin d'identifier et de standardiser des variables caractérisant les stresseurs environnementaux d'origine anthropique et naturelle dans le Saint-Laurent. Finalement, nous suggérons de poursuivre les travaux dans le domaine de l'identification de signaux précurseurs de changements qui permettent de définir et de détecter des signaux révélateurs de transitions écologiques (p. ex. augmentation de la variabilité et de l'autocorrélation dans un système ; Boettiger et al., 2013). L'identification et le suivi de ce type d'indicateurs permettraient d'anticiper des changements environnementaux majeurs au sein du Saint-Laurent en vue d'opérer dans un mode de gestion de risques environnementaux proactif.

Défi 4. Créer un protocole de suivi environnemental et humain et une plateforme de partage d'informations

Un défi de gestion devrait viser à accroître l'accessibilité et la disponibilité de données caractérisant la structure des écosystèmes et les activités humaines, ce qui représente un enjeu majeur pour permettre une évaluation intégrative de l'état du Saint-Laurent. Nous suggérons ainsi l'établissement d'un protocole de suivi environnemental et humain dédié à l'évaluation systémique de l'état des écosystèmes et de l'intensité des activités humaines dans l'EGSL. Ce protocole devrait impérativement valoriser des suivis existants (p. ex. pêches plurispécifiques de Pêches et Océans Canada ; Pêches et Océans Canada, 2015), qui pourraient permettre une évaluation de base des impacts cumulés dans le Saint-Laurent. Certaines de ces données ne sont toutefois pas standardisées à l'échelle du Saint- Laurent et n'ont pas pour objectif la planification systémique de l'exploitation des ressources. Un protocole de suivi ayant cet objectif spécifique devrait ainsi être élaboré et devrait viser le suivi périodique des indicateurs éventuellement identifiés par l'atteinte du défi 3 et l'application de méthodes d'évaluation d'impacts cumulés (p. ex. Halpern et al., 2008b). Des protocoles et programmes internationaux déjà élaborés, comme ceux issus du Group on Earth Observations Biodiversity Observation Network (GEO BON ; Scholes et al., 2012) et du Census of Marine Life (CoML, 2010) pourraient également guider une telle initiative afin de favoriser sa cohérence avec d'autres projets ailleurs dans le monde.

De plus, ce protocole devrait impérativement viser un partage efficace et une standardisation régionale des données récoltées entre les régions administratives du Saint- Laurent (Québec, Terre-Neuve-et-Labrador, Nouvelle-Écosse, Nouveau-Brunswick et Île-du-Prince-Édouard). Ce protocole devrait valoriser des plateformes actuellement en place, comme l'Observatoire global du Saint-Laurent (Observatoire Global du Saint-Laurent, 2016) et des réseaux comme Notre Golfe (Archambault et al., 2016). Un accent tout particulier devrait être donné par tous les acteurs académiques, gouvernementaux et privés à l'accès libre aux données, un élément qui encouragerait l'application d'une démarche scientifique rigoureuse et transparente telle qu'appliquée dans un système de révision par les pairs.

Défi 5. Développer une capacité de gestion adaptative pour le Saint-Laurent

Les défis identifiés visent essentiellement l'élaboration d'approches diagnostiques permettant l'évaluation des impacts cumulés. Ces dernières sont nécessaires afin d'assurer une gestion efficace d'un milieu d'intérêt. Par contre, tous les stresseurs ne peuvent être gérés similairement ou avec autant de succès, et certains imposent des changements qui sont inévitables, comme les changements climatiques. Les outils de gestion adoptés doivent ainsi avoir la capacité d'intégrer les particularités inhérentes à l'ensemble des stresseurs considérés conjointement. De plus, les outils diagnostiques proposés ne seront vraisemblablement pas développés à court terme. Dans l'intérim, il importe alors d'employer des mesures de gestion robustes face à l'incertitude associée aux effets de multiples stresseurs sur les milieux naturels (Côté et al., 2016). Nous suggérons ainsi de développer une capacité de gestion adaptative conséquente à une approche de gestion écosystémique (p. ex. Rice et Rochet, 2005) permettant de considérer les bouleversements inévitables et l'incertitude associée à ces derniers en vue d'assurer le maintien de la structure et du fonctionnement des écosystèmes du Saint-Laurent.

3.13 Conclusion

L'intensification imminente des activités humaines dans le Saint-Laurent met en évidence la nécessité d'adopter une approche de planification systémique de l'exploitation de ses ressources naturelles. Toutefois, l'état des connaissances sur les pressions exercées sur le Saint-Laurent nous permet d'obtenir qu'une compréhension imparfaite des impacts cumulés. À long terme, il nous apparaît ainsi impératif de viser l'amélioration de nos connaissances sur les effets de multiples stresseurs sur la structure et le fonctionnement des écosystèmes, le développement de méthodologies robustes et accessibles d'évaluation d'impacts cumulés, l'identification d'indicateurs régionaux standardisés capturant convenablement les impacts cumulés et de consolider le tout au sein d'un protocole d'acquisition, de suivi et de partage des données visant la planification systémique de l'exploitation des ressources naturelles. Finalement, une approche de gestion adaptative permettrait de tester et d'employer, à court terme, des mesures de gestion robustes face à l'incertitude associée aux effets de multiples stresseurs sur les écosystèmes du Saint-Laurent. La planification systémique de l'utilisation des ressources naturelles au sein du Saint-Laurent requiert une vision intégrative des écosystèmes et des vecteurs de stress qui leur sont imposés. Une telle approche ne sera réalisable que lorsque nous aurons développé ces infrastructures et ces outils, nécessaires à une gestion écosystémique du Saint-Laurent.

3.14 Remerciements

Nous remercions le Fonds de recherche québécois nature et technologie (FRQNT) et le Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG) pour l'aide financière. Ce projet est soutenu par Québec-Océan, le réseau Notre Golfe, le Centre de la Science de la Biodiversité du Québec (CSBQ) et le réseau CHONeII.

ARTICLE 4

CARACTÉRISER ET PARTAGER LES CONNAISSANCES SUR L'EXPOSITION AUX STRESSEURS ENVIRONNEMENTAUX DANS LE SYSTÈME DU SAINT-LAURENT AU CANADA

4.1 Résumé

Le Système du Saint-Laurent est un système socio-écologique vaste et complexe qui soutient une myriade de secteurs économiques. Cet écosystème est affecté par plusieurs pressions humaines qui se chevauchent et qui peuvent interagir avec les effets des changements climatiques. L'objectif de cet article était de caractériser la distribution et l'intensité des stresseurs environnementaux dans le Système du Saint-Laurent. Nous avons rassembler des données sur 22 stresseurs d'origine côtière, du climat, de la pêche et du trafic maritime à partir de collaborations, d'initiatives environnementales existantes et de portails de données ouvertes. Nous montrons que peux de milieux du Saint-Laurent sont libres d'exposition cumulée. L'estuaire, la gyre d'Anticosti, et les milieux côtiers sont particulièrement exposés, surtout près des centres urbains. Nous avons identifié 6 groupes distincts identifiant des régions exposées à des stresseurs similaires. Nous montrons que différentes combinaisons de stresseurs sont typiques de certaines régions du Saint-Laurent et que les milieux côtiers sont exposés à tous les types de stresseurs. Deux groupes particulièrement préoccupants capturent la majorité des points chauds d'exposition cumulée et montrent une convergence de groupes de stresseurs différents à la tête du Chenal Laurentien. Le partage des connaissances acquises sur les stresseurs environnementaux dans le Saint-Laurent est devenu une priorité dans le cadre de ce projet. C'est pourquoi nous initions *eDrivers*, une plateforme de connaissances ouvertes qui réunit des experts commis à structurer, standardiser et

partager les connaissances sur les stresseurs environnementaux en support à la science et la gestion holistique. *eDrivers* a été construit selon des principes directeurs visant à soutenir les standards de gestion des données et de science ouverte existants. Nous anticipons ainsi que l'initiative améliorera graduellement les connaissances qui y sont partagées. Nous croyons que *eDrivers* est une solution indispensable qui pourra influencer radicalement la recherche et la gestion à large échelle en accroissant l'accessibilité et l'interopérabilité des connaissances sur les stresseurs environnementaux.

Ce quatrième article, intitulé *"Characterizing exposure to and sharing knowledge of drivers of environmental change in the St. Lawrence System in Canada"* a été corédigé par moi-même, Rémi M. Daigle, Steve Vissault, Dominique Gravel, Andréane Bastien, Simon Bélanger, Pascal Bernatchez, Marjolaine Blais, Hugo Bourdages, Clément Chion, Peter S. Galbraith, Benjamin S. Halpern, Camille Lavoie, Christopher W. McKindsey, Alfonso Mucci, Simon Pineault, Michel Starr, Anne-Sophie Ste-Marie et Philippe Archambault. Il a été publié dans la revue *Frontiers in Marine Science* au sein de la section spéciale *Global Change and the Future Ocean* à l'été 2020. J'ai établi les objectifs et la structure de l'article avec Rémi M. Daigle, Dominique Gravel et Philippe Archambault. J'ai structuré et formaté les données, effectué les analyses, été en charge des développements techniques et dirigé la rédaction de l'article. Tous les co-auteurs ont contributé aux données, aux analyses et à la rédaction selon leur expertise respective et contribué à la révision de l'article. Les résultats issus de cet article ont été présentés en version abrégée lors de la *Réunion scientifique annuelle de Québec Océan* à Rivière-du-Loup (Canada) à l'automne 2017 et à la *Réunion annuelle du regroupement de recherche Canadian Healthy Oceans Network (CHONe)* à Ottawa (Canada) à l'hiver 2018.

Beauchesne, D., Daigle, R.M., Vissault, S., Gravel, D., Bastien, A., Bélanger, S., Bernatchez, P., Blais, M., Bourdages, H., Chion, C., Galbraith, P.S., Halpern, B.S., Lavoie, C., McKindsey, C.W., Mucci, A., Pineault, S., Starr, M., Ste-Marie, A.-S.,

Archambault, P., 2020. Characterizing Exposure to and Sharing Knowledge of Drivers of Environmental Change in the St. Lawrence System in Canada. Front. Mar. Sci. 7. https://doi.org/10.3389/fmars.2020.00383

Les sections suivantes sont celles de l'article publié.

4.2 Title

Next Generation Planning - Structuring and Sharing Environmental Drivers Data for the St. Lawrence System

4.3 Authors

David Beauchesne, Rémi M. Daigle, Steve Vissault, Dominique Gravel, Andréane Bastien, Simon Bélanger, Pascal Bernatchez, Marjolaine Blais, Hugo Bourdages, Clément Chion, Peter S. Galbraith, Benjamin S. Halpern, Camille Lavoie, Christopher W. McKindsey, Alfonso Mucci, Simon Pineault, Michel Starr, Anne-Sophie Ste-Marie, Philippe Archambault

4.4 Abstract

The St. Lawrence is a vast and complex socio-ecological system providing a wealth of services that sustain numerous economic sectors. This ecosystem is subject to significant human pressures that overlap and potentially interact with climate-driven environmental changes. Our objective in this paper was to systematically characterize the distribution and intensity of drivers of environmental change (hereafter, drivers) in the St. Lawrence System. We gathered data-based indicators for 22 coastal, climate, fisheries, andmarine traffic drivers through collaborations, existing environmental initiatives and open data portals. We show that few areas of the St. Lawrence are free of cumulative exposure. The Estuary, Anticosti Gyre, and coastal areas are particularly exposed, especially in the vicinity of urban centers. We identified six distinct clusters with similar suites of co-occurring drivers and show that certain driver combinations are inherent to different regions of the St. Lawrence and that coastal areas are exposed to all driver types. Of particular concern are two clusters capturing most exposure hotspots and that show the convergence of contrasting cumulative exposure profiles at the head of the Laurentian Channel. Sharing knowledge of drivers emerged as a priority to facilitate future environmental assessment efforts. We thus launch *eDrivers*, an open knowledge platform gathering experts committed to structuring, standardizing and sharing knowledge on drivers of environmental change in support of holistic science and management. *eDrivers* was built on a series of guiding principles upholding existing data management and open science standards. We therefore expect it to evolve through time to address knowledge gaps and refine current driver layers. Ultimately, we believe that *eDrivers* represents a much needed solution that could radically influence broad scale research and management practices by increasing knowledge accessibility and interoperability.

Keywords: ocean observing systems, St. Lawrence, environmental drivers, cumulative exposure, threat complex, multiple stressors, global change

4.5 Introduction

The St. Lawrence System, formed by one of the largest estuaries in the world and a vast interior sea, is a complex socialecological system characterized by highly variable environmental conditions and oceanographic processes (El-Sabh and Murty, 1990; White and Johns, 1997; Dufour and Ouellet, 2007). It constitutes a unique and heterogeneous array of habitats suited for the establishment of diverse and productive ecological communities (Savenkoff et al., 2000). As a result, the St. Lawrence System has benefited the Canadian economy. It sustains a rich fisheries industry targeting more than 50 species, serves as the gateway to eastern North-America by granting access to more than 40 ports and is the most densely populated Canadian region, hosts a booming tourism industry and an expanding aquaculture production, fosters emerging activities, and boasts a yet untapped hydrocarbon potential (Beauchesne et al., 2016; Archambault et al., 2017; Schloss et al., 2017). With major investments recently made and more forthcoming in economic and infrastructure development and research (*e.g.*, Government of Québec, 2015; RQM, 2018), an intensification of the human footprint is likely in the St. Lawrence System. Consequently, the St. Lawrence System is exposed to an increasing number of drivers of environmental change, as is observed across ecosystems globally (see Halpern et al., 2015b, 2019). We broadly define drivers of environmental change (hereafter, drivers) as any externality that affects environmental processes and disturbs natural systems. Drivers may originate from natural or human-induced biophysical processes (*e.g.*, sea surface-water temperature anomalies and hypoxia) or directly from anthropogenic activities (*e.g.*, fisheries and marine pollution). The potential for complex interactions between co-occurring drivers is the largest uncertainty when studying or predicting environmental impacts (Darling and Côté, 2008; Côté et al., 2016). Multiple drivers can combine non-additively and result in effects that are greater (synergistic effect) or lower (antagonistic effect) than the sum of individual effects (Crain et al., 2008; Darling and Côté, 2008; Côté et al., 2016).

Increasing exposure and the experiences of past ecological tragedies in the St. Lawrence System such as the collapse of cod fisheries (Frank et al., 2005; Dempsey et al., 2018) and the decline of the beluga and right whale populations (Plourde et al., 2014) together urge the need to characterize the distribution, intensity and co-occurrence of drivers in the system. Research on the effects of drivers in marine environments, nonetheless, remains overwhelmingly focused on single driver assessments (O'Brien et al., 2019). Whereas, co-occurring drivers may not interact, driver co-occurrence is a requirement for interactions to exist. Knowledge of their co-distribution can therefore identify areas where driver interactions are most likely observed.

Characterizing drivers is also a necessary step for the application of holistic management approaches. Holistic approaches typically involve, but are not limited to, selecting and describing valued ecosystem components (*e.g.* habitats and species) and drivers (*e.g.*, marine traffic and ocean acidification), assessing the exposure and vulnerability of valued components to drivers, selecting a proper spatio-temporal scale, monitoring, and public and stakeholder participation (Dubé and Munkittrick, 2001). Gathering environmental knowledge for holistic initiatives can, however, be a very challenging and time consuming—not to say painful—process. On one hand, there is an overwhelming and expanding wealth of data available. Such information overload may inhibit our ability to make decisions based on scientific information, promote massive duplication of effort, disproportionately appropriate research funds to certain sectors, and obscure knowledge gaps amid a sea of information (Eppler and Mengis, 2004). On the other hand, crucial data are lacking and remain largely unavailable or inaccessible for a variety of reasons, including proprietary rights, lack of organizational time, capacity and training, and, in some cases, an unwillingness to share; this curtails our ability for appropriate decision-making.

Current initiatives facilitate the data gathering process by assembling, organizing and sharing environmental knowledge, such as the Ocean Biogeographic Information System (OBIS; OBIS, 2020) for biotic data and Bio-ORACLE (Assis et al., 2018) for abiotic data. However, equivalent platforms for drivers have largely focused on single drivers (*e.g.*, Global Fishing Watch) and platforms collating data-based indicators and knowledge on multiple drivers in a comparable and interoperable way remain conspicuously missing (but see Halpern et al., 2015a). This is in spite of integrated management and assessment approaches requiring efficient data reporting, standardized data management practices, and tools tailored to the study of the effects of multiple drivers (Dafforn et al., 2016; Stock et al., 2018).

The main goal of this study is to characterize the distribution and intensity of drivers in the St. Lawrence System. More specifically, our objectives are to: (1) identify areas of high cumulative exposure to drivers and (2) characterize areas with similar cumulative exposure profiles, *i.e.*, areas exposed to similar suites of co-occurring drivers. An additional objective emerged while addressing the main goal of this manuscript: sharing information about the distribution and intensity of drivers of environmental change in the St. Lawrence. We achieve this through the development of an open knowledge platform, *eDrivers*, that was designed to facilitate the widespread availability of driver characterization for holistic assessments and management approaches. Here, we present its guiding principles and accompanying tools.

4.6 Materials and Methods

4.6.1 Estuary and Gulf of St. Lawrence

The St. Lawrence System is composed of the St. Lawrence Estuary and the Gulf of St. Lawrence (Figure 17). The Estuary is defined by the limit of seawater intrusion, close to Île d'Orléans, to the west and by its connection to the Gulf near Pointe-des-Monts. The surface layer is composed of freshwater flowing seaward, primarily from the Great Lakes Basin through the St. Lawrence River. Atlantic waters intrude landwards at depth into the Gulf and Estuary from Cabot Strait, but as well as from the Strait of Belle Isle (see below).

The topology of the Northern Gulf is characterized by three deep channels (250–

500 m). The Laurentian Channel is the main channel connecting the Estuary to the Atlantic through Cabot Strait. The Esquiman and Anticosti channels are two secondary channels that branch off from the Laurentian Channel to the north toward the Strait of Belle Isle and the Labrador and north of Anticosti Island, respectively. The Southern Gulf hosts the Magdalen Shallows, a vast area with an average depth of ~50 m. The water column in the Gulf and St. Lawrence Estuary includes a seasonal cold intermediate layer that separates the surface and deep layers. Seasonal sea ice affects circulation in the St. Lawrence. Finally, three islands impact the physical dynamics of the St. Lawrence: the Anticosti Island to the north, the Îles de la Madeleine in the middle of the Magdalen Shallows and Prince Edward Island to the south. See (Saucier et al., 2003) and (Galbraith et al., 2018) for more information on the physical oceanography of the St. Lawrence.

The St. Lawrence drains over 25 % of global freshwater reserves through its connection to the Great Lakes Basin, which is home to over 45 million North Americans, *i.e.*, 15 and 30 million in Canada and the United States, respectively. The coasts of St. Lawrence System, as delimited by our study area (Figure 17), boast a much lower population of approximately 1 million Canadians living within 10 km of the coast, with populations mainly located in a few coastal cities in the Estuary and the Southern Gulf (Statistics-Canada, 2017).

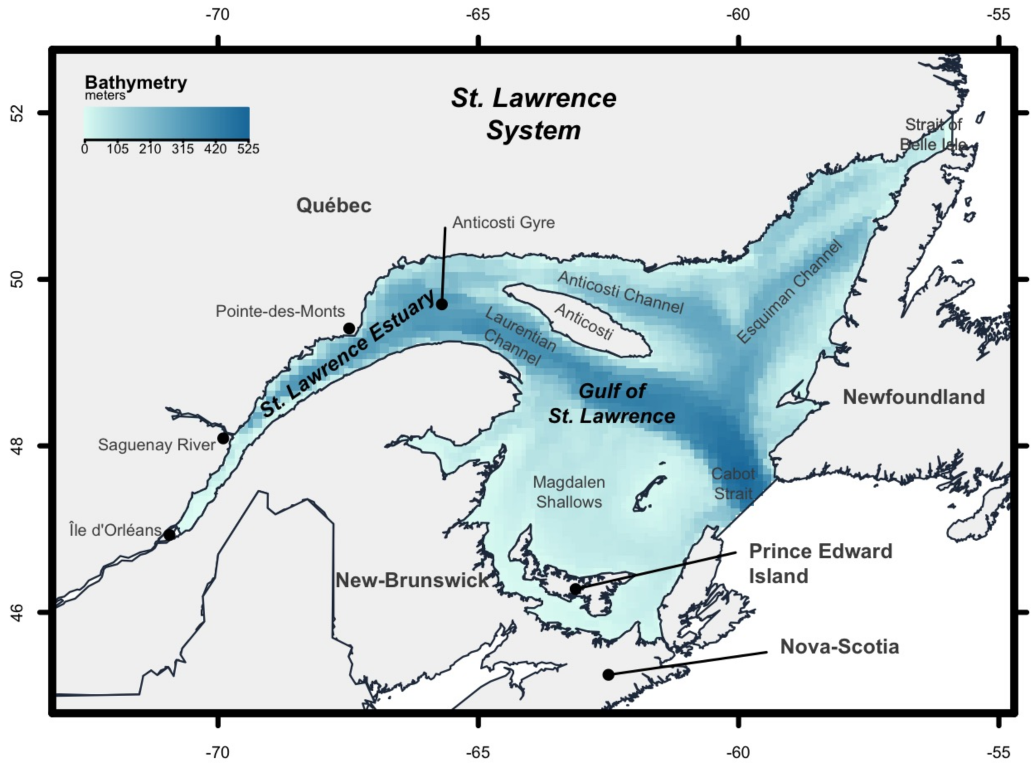


Figure 17: Description of the St. Lawrence System in Eastern Canada, composed of the St. Lawrence Estuary and the Gulf of St. Lawrence. The Estuary is defined by the limit of seawater intrusion, close to Île d'Orléans, to the west and by its connection to the Gulf near Pointe-des-Monts. The Gulf is an interior sea connected to the Atlantic by Cabot Strait and the Strait of Belle Isle to the south and north of Newfoundland, respectively.

4.6.2 Drivers

Drivers, as broadly defined in this study, are data-based indicators of environmental conditions and human activities that are often referred to as driving forces, stressors, pressures, or states in the scientific and environmental assessment literature (*e.g.*, Kristensen, 2004; Halpern et al., 2019). Defining such categories, however, can be difficult and is often context- and ecosystem-specific (Gari et al., 2015; Dempsey et al., 2018). As such, we refrain from articulating our work around a specific framework or imposing categories on data-based products that may change with a user's objective. Instead, we focus on available data-based indicators that contribute to evaluate the ecosystem's cumulative exposure to multiple threats.

Drivers selection was informed by a global cumulative impact assessment initiative (Halpern et al., 2008b, 2015b, 2019) and available from the National Center for Ecological Analysis and Synthesis (NCEAS) online data repository (Halpern et al., 2015a), regional holistic evaluations of the state of the St. Lawrence (Dufour and Ouellet, 2007; Benoît et al., 2012), and communications with regional experts (Table 6). Where regional data on drivers were unavailable, available global data at a resolution adequate for the scale of the St. Lawrence System were used instead (*e.g.*, marine pollution).

We characterized the intensity and distribution of 22 drivers (Table 6). Drivers incorporated in the analyses are varied in origin, *i.e.*, from terrestrial (*e.g.*, nutrient input) to marine (*e.g.*, shipping), and from large scale biophysical processes (*e.g.*, temperature anomalies) to localized anthropogenic activities (*e.g.*, fisheries). Drivers were divided into four groups: coastal, climate, fisheries, and marine traffic (Table 6). All data layers and methodologies are described in the Supplementary Materials. As in Halpern et al. (2019), drivers with non-normal frequency distributions were log-transformed to avoid underestimating intermediate driver values. All drivers were scaled between 0 and 1 to allow comparisons. The 99th quantile of individual driver distribution was used as the upper limit for scaling to control for extreme values that may or may not represent real observations. The St. Lawrence System was divided into a regular grid of 1 km^2 cells into which all drivers were integrated (Figure 24).

Table 6: List of drivers currently available on *eDrivers* and used for the analyses presented in this paper.

Groups	Drivers	Acronym	Spatial resolution	Temporal resolution	Years	Units	Source
Climate	Acidification	ACID	Lat/long	August-September	2018	Ω $Aragonite$	Starr and Chassé (2019)
Climate	Hypoxia	HYP	Lat/long	August-September	2018	$ml\ L^{-1}$	Blais et al. (2019)
Climate	Bottom-water temperature	SBT-	2 km^2	Monthly	1981-2010 vs. 2013-2017	negative anomalies	Galbraith et al. (2018)
Climate	Bottom-water temperature	SBT+	2 km^2	Monthly	1981-2010 vs. 2013-2017	positie anomalies	Galbraith et al. (2018)
Climate	Sea level rise	SLR	Modeled 0.25 degree	10 days	1992-2012	mm	Halpern et al. (2015a)
Climate	Surface-water temperature	SST-	2 km^2	Monthly	1981-2010 vs. 2013-2017	negative anomalies	Galbraith et al. (2018)
Climate	Surface-water temperature	SST+	2 km^2	Monthly	1981-2010 vs. 2013-2017	positive anomalies	Galbraith et al. (2018)
Coastal	Aquaculture	AQUA	Lat/long	-	Variable, between 1990-2016	$presence-absence$	MAPAQ (2016); DFO (2016a); AAF (2016); FA (2016); FFA (2016)
Coastal	Coastal development	CD	15 arc-second	Annual	2015-2016	$nanoWatts\ cm^{-2}\ sr^{-1}$	Earth observation group (2019)
Coastal	Direct human impact	DHI	Dissemination areas	Annual	2016	population	Statistics-Canada (2017)
Coastal	Inorganic pollution	IP	Modeled 1 km^2	Annual	2000-2001	-	Halpern et al. (2015a)
Coastal	Nutrient import	NI	Modeled 1 km^2	Annual	2007-2010	t fertilizer	Halpern et al. (2015a)
Coastal	Organic pollution	OP	Modeled 1 km^2	Annual	2007-2010	t pesticide	Halpern et al. (2015a)
Coastal	Toxic algae	TA	-	-	-	Expert based	Bates et al. (2019)
Fisheries	Demersal, destructive	DD	Lat/long	Event based	2010-2015	kg	DFO (2016b)
Fisheries	Demersal, non-destructive, high-bycatch	DNH	Lat/long	Event based	2010-2015	kg	DFO (2016b)
Fisheries	Demersal, non-destructive, low-bycatch	DNL	Lat/long	Event based	2010-2015	kg	DFO (2016b)

Groups	Drivers	Acronym	Spatial resolution	Temporal resolution	Years	Units	Source
Fisheries	Pelagic, high-bycatch	PHB	Lat/long	Event based	2010-2015	kg	DFO (2016b)
Fisheries	Pelagic, low-bycatch	PLB	Lat/long	Event based	2010-2015	kg	DFO (2016b)
Marine traffic	Invasive species	INV	Modeled 1 km^2	Annual	2011	t port volume	Halpern et al. (2015a)
Marine traffic	Marine pollution	MP	Modeled 1 km^2	Event based and annual	2003-2011 and 2011	n lanes t port volume	Halpern et al. (2015a)
Marine traffic	Shipping	SHP	0.1 degree	Event based	2003-2011	n lanes	Halpern et al. (2015a)

4.6.3 Cumulative exposure

We begin by providing a simplified two-driver example that focuses on the co-occurrence of hypoxia and demersal destructive fisheries, two drivers that mostly occur in deeper St. Lawrence waters. Driver co-occurrence was evaluated spatially by summing the scaled intensity of drivers in each grid cell. The intensity at which pairs of drivers co-occur was evaluated using a two-dimensional kernel density. This example demonstrates how driver co-occurrence was evaluated and serves as a stepping stone to the integrative indicators used hereafter, *i.e.*, cumulative exposure and cumulative hotspots (objective 1).

We evaluated cumulative exposure (E_C) for each grid cell as the sum of scaled driver intensities:

$$E_{C_x} = \sum_{i=1}^{n} D_{i,x} \tag{4.1}$$

where x is a grid cell, i is a driver and D is the scaled intensity of driver i. A grid cell with a high E_C value is either characterized by multiple drivers at low relative intensity, a few drivers at high relative intensity, or both.

We also identified cumulative hotspots (H_C) – *i.e.*, areas where drivers co-occur at high relative intensities – as the number of drivers in each grid cell with scaled intensity contained over their respective 80th percentile:

$$H_{C_x} = \sum_{i=1}^{n} \mathbb{1}(D_{i,x} \, \epsilon \, P_{80,D_i}) \tag{4.2}$$

where, x is a grid cell, i is a driver and D is the scaled intensity of driver i and P_{80,D_i} is the 80th percentile of driver i.

4.6.4 Cumulative Exposure Profiles

4.6.4.1 Clustering

We identified areas with similar cumulative exposure profiles (objective 2) using a clustering approach (Bowler et al., 2019). We used a partional $k - medoids$ clustering algorithm, CLARA (CLustering for Large Applications; Kaufman and Rousseeuw, 1990), which was designed for large datasets. The CLARA algorithm uses the PAM (Partition Around Medoids) algorithm on a sample from the original dataset to identify a set of k objects that are representative of all other objects, *i.e.*, *medoids* and that are central to the cluster they represent. The goal of the algorithm is to iteratively minimize intra-cluster dissimilarity. Iterations are compared on the basis of the average dissimilarity between cluster objects and representative *medoid* to select the optimal set of k *medoids* that minimizes average dissimilarity. We used the clustering algorithm with the Manhattan distance since this measure is less affected by extreme values (Legendre and Legendre, 2012), as is the *k-medoids* clustering algorithm (Kaufman and Rousseeuw, 1990). We used 100 iterations using samples of 10,000 observations (*i.e.*, ~5% of observations) to identify clusters. Analyses were performed using the `cluster` R package (Maechler et al., 2018). Partitional clustering algorithms require a user-defined number of clusters. Values of k ranging from 2 to 10 were tested and validated by selecting the number of clusters that maximized the average silhouette width (Kaufman and Rousseeuw, 1990) and minimized the total within-cluster sum of squares (Figure 26).

4.6.4.2 Inter-cluster dissimilarity

Differences between clusters were explored by measuring the total inter-cluster dissimilarity and the contribution of each driver to the total inter-cluster dissimilarity using a similarity percentage analysis (SIMPER) with Manhattan distance (Figure 27; Clarke, 1993). The Manhattan distance was again preferred for continuity with the clustering analysis and to ensure that outliers did not have a strong influence on the analysis. As the drivers dataset is large ($\sim$ 250,000 observations), we used a bootstrap procedure for the SIMPER analysis, randomly selecting 5% of each cluster to run the analysis and repeating the process over 300 iterations. We also compared the mean intensity of each driver within each cluster to better capture the inter-cluster dissimilarity.

4.6.4.3 Intra-cluster similarity

Intra-cluster similarity was evaluated calculating the intracluster Manhattan distance and by transforming the mean contribution to distance (M_c) of each driver by $0.1/(0.1 + M_c)$ to obtain a similarity measure for each driver (S_d). The total similarity is the sum of all S_d (Figure 28). As with the intercluster dissimilarity, we used a bootstrap procedure for the intra-cluster similarity, randomly selecting 25 % of each cluster observation to run the analysis and repeating the process over 50 iterations. We did not use the bootstrap procedure for clusters with less than 40,000 observations since computation time was manageable.

4.7 Results and Discussion

4.7.1 Cumulative exposure

We first present the simplified hypoxia-fisheries example to demonstrate how driver co-occurrence was evaluated. Hypoxic bottom waters area mainly found at the head of the Laurentian, Anticosti, and Esquiman channels (Figure 18A). Demersal destructive fisheries are concentrated along the Laurentian Channel, the heads of the Anticosti and Esquiman channels and around the Îles de la Madeleine (Figure 18B). By combining both drivers, we observe that hypoxia and demersal destructive fisheries co-occur mostly at high relative intensity (Figure 18D) in the vicinity of the Anticosti Gyre and the heads of the Esquiman and Anticosti channels (Figure 18C); these are the areas where we might expect interactions between these drivers to be more likely.

We now focus on the integrative exposure indicators. Apart from the northeastern Gulf, cumulative exposure is ubiquitous in the St. Lawrence (Figure 19). Cumulative exposure is generally highest along coasts (Figure 19), with hotspots located in the vicinity of coastal cities (Figure 20). In general, offshore areas are less exposed to cumulative drivers, with the Estuary and the Anticosti Gyre being notable exceptions (Figures 19, 20). This is not to say that offshore areas are free from exposure, as most of the St. Lawrence is exposed to multiple overlapping drivers (Figures 19, 20). For example, the heads of the Anticosti and Esquiman channels are highly exposed to cumulative drivers (Figure 19).

These results are consistent with observations elsewhere in the world, where cumulative exposure conspicuously arises from and markedly intensifies close to coastal cities and at the mouth of rivers draining highly populated areas (*e.g.*, Halpern et al., 2015b; Feist and Levin, 2016; Mach et al., 2017; Stock et al., 2018). These are areas where human activities (*e.g.*, coastal development and shipping) and footprints (*e.g.*, pollution runoff) are most intense (Feist and Levin, 2016), and on which is overlaid a background of natural disturbances (Micheli et al., 2016). They are also the areas in which the most dramatic increases in exposure are expected, with populations increasing more rapidly along coasts than inland (Feist and Levin, 2016). In the St. Lawrence, large coastal cities are mostly located along the Estuary and the southwestern Gulf, whereas the northeastern Gulf is largely uninhabited or home to small coastal communities. Certain smaller coastal communities with high cumulative exposure are characterized by large industries (*e.g.*, Sept-Îles and Charlottetown).

As for offshore exposure, the Estuary, along with the St. Lawrence River, provide access to and serves as the primary drainage outflow of the Great Lakes Basin, which is home to over 45 million North Americans and is the most densely populated region in Canada (Statistics-Canada, 2017). Most marine traffic thus converges into the Estuary.

Whereas, we cannot ascertain that high exposure areas are the most impacted, we can safely predict that these are the areas where studying ecosystem state will be the most complex due to the uncertainty associated with driver co-occurrence, an uncertainty bound to increase rapidly with the number of co-occurring drivers (Côté et al., 2016).

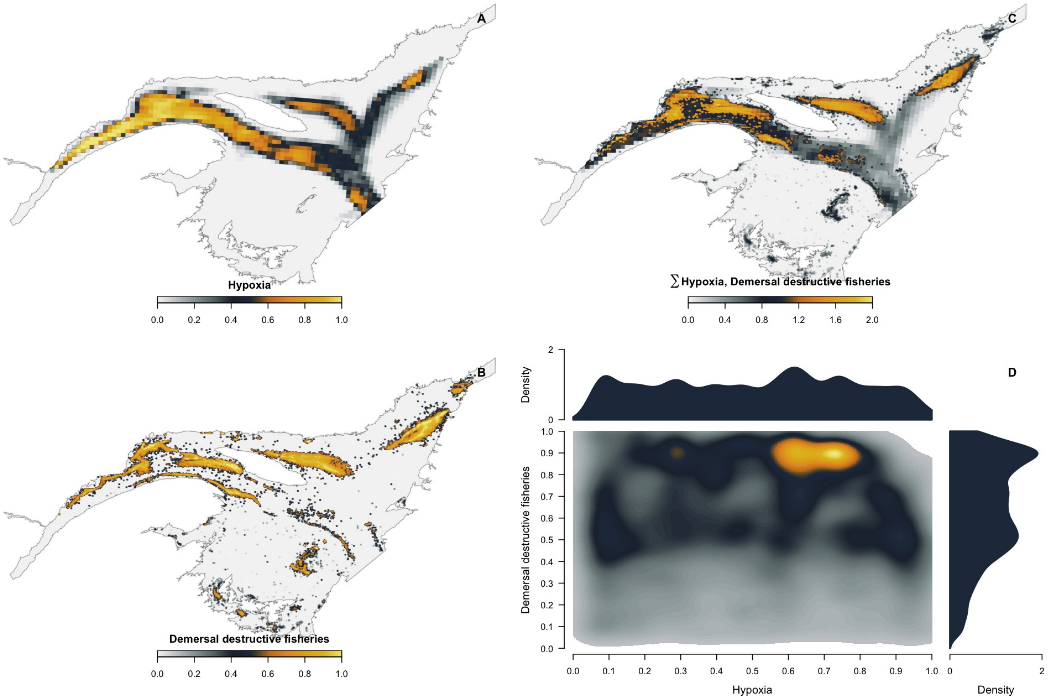


Figure 18: Simplified 2-driver example of driver co-occurrence between hypoxia and demersal destructive fisheries in the St. Lawrence. An index of hypoxia (**A**) was created using bottom-water dissolved oxygen between 2013 and 2017 Blais et al. (2019). Demersal destructive fisheries (*i.e.*, trawl and dredges) (**B**) intensity was evaluated from fisheries catch data collected between 2010 and 2015 used to measure annual area weighted total biomass (kg) in 1 km^2 grid cells DFO (2016b). See Supplementary Materials for more information on specific methodologies. Relative hypoxic stress and demersal destructive fisheries intensity was summed (**C**) to visualize their combined spatial distribution and intensity. Finally, individual density and the co-intensity of hypoxia and demersal destructive fisheries was investigated with a two-dimensional kernel analysis (**D**).

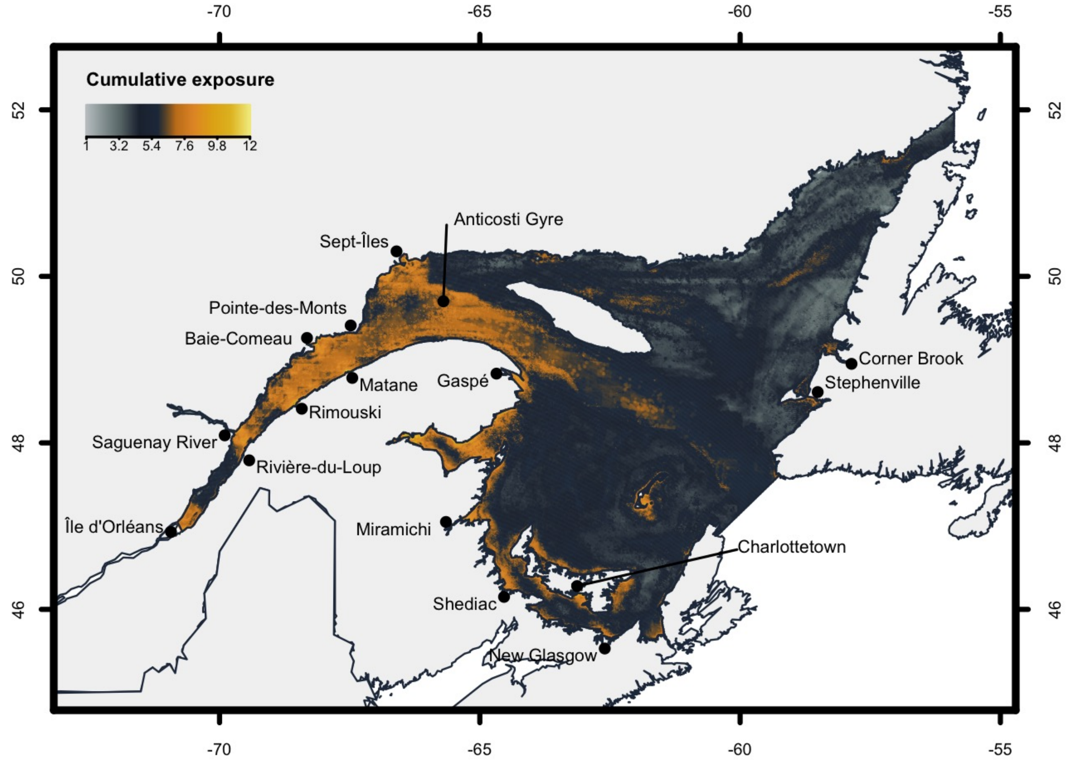


Figure 19: Distribution of cumulative exposure in the St. Lawrence System.

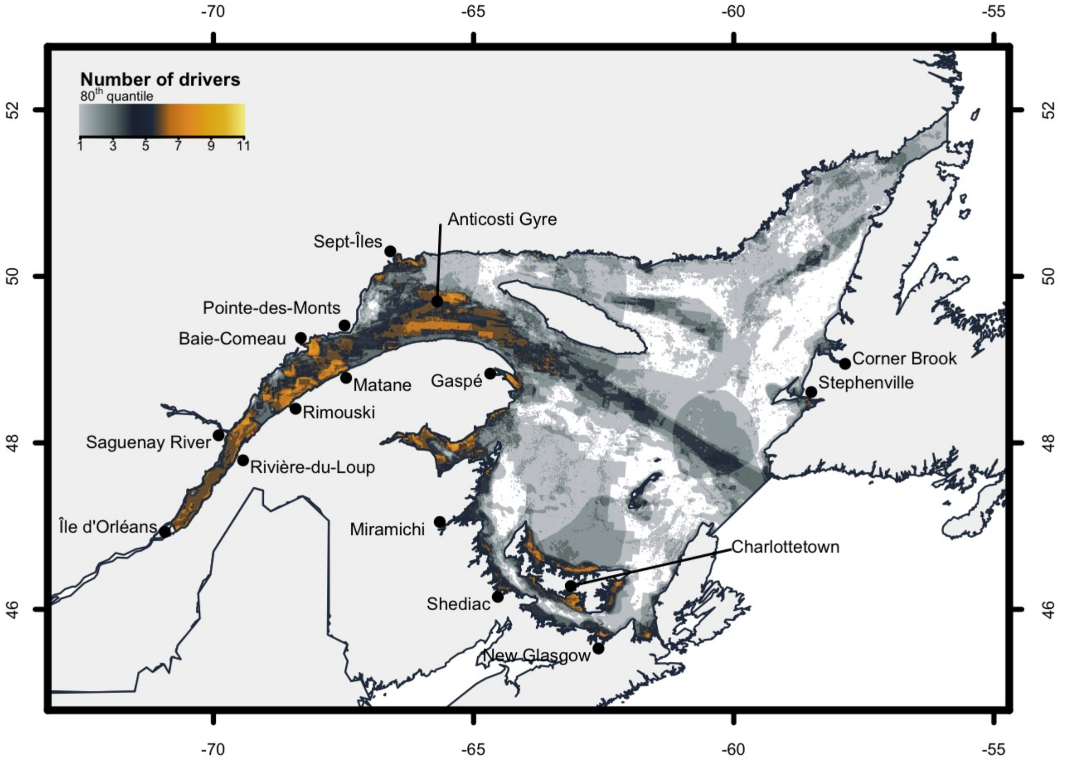


Figure 20: Distribution of cumulative hotspots in the St. Lawrence System.

4.7.2 Cumulative Exposure Profiles

While informative, the hypoxia-fisheries example focuses on a single pair of drivers and falls short of the number of drivers typically overlapping at high intensities throughout the St. Lawrence (Figure 20). The number of drivers overlapping in the St. Lawrence increases with cumulative exposure (Figure 25). Areas with high exposure such as the Estuary, the Anticosti Gyre, and the southwestern Gulf coastline (Figures 19, 20) are thus areas where driver interactions are most likely and where they can arise between a host of different drivers. Identifying areas with similar cumulative exposure profiles provides a crucial tool to simplify the multi-dimensional complexity of overlapping drivers (Bowler et al., 2019). This could facilitate assessments of the state of species, habitats, and ecosystems located within or moving through areas exposed to similar suites of drivers.

Six distinct clusters were identified in the St. Lawrence (Figure 21, 25, 26). Based on their distribution and representative drivers, clusters can be divided into three offshore and three coastal clusters (Figure 21, 27, 28). Coastal clusters (1–3; Figure 21) include all types of drivers other than hypoxia; they are also the most exposed clusters, both in terms of driver overlap and intensity. Cluster 1 encompasses the coastline and is characterized by higher direct human impact (*i.e.*, population density). Cluster 2 is differentiated from other clusters by the presence of aquaculture sites. Cluster 3 is the most exposed and has a distribution similar to the most exposed coastal hotspots (Figure 20). This cluster is characterized by high intensities of land-based drivers (*e.g.*, nutrient input), demersal non-destructive high bycatch fisheries (*e.g.*, trap fishing), climate drivers and marine traffic drivers in the vicinity of ports.

Offshore clusters (4–6; Figure 21) are generally characterized by high intensity climate and marine traffic drivers. Cluster 4 is differentiated by demersal non-destructive high bycatch fisheries, higher marine traffic drivers compared to cluster 5, and generally corresponds to the whole Southern Gulf. Cluster 5 is characterized by more fisheries types (*i.e.*, demersal destructive and pelagic high bycatch), generally lower intensity marine traffic drivers, and is located almost exclusively in the Northern Gulf. Finally, cluster 6 is the most exposed offshore cluster and includes all offshore hotspots (Figure 20). It is characterized by high intensity hypoxia, marine traffic and pollution, as well as demersal destructive and pelagic high bycatch fisheries. This cluster corresponds primarily to the Laurentian Channel and incorporates parts of the Esquiman and Anticosti channels.

Clusters 3 and 6 capture most coastal and offshore hotspots and are the two most exposed clusters in the St. Lawrence. They offer some insight into the potential importance of considering spatial dynamics in areas intersecting multiple clusters. For example, clusters 3 and 6 meet at the mouth of the Saguenay River. This area is particularly dynamic, with deep Atlantic waters advected through estuarine circulation mixing with surface waters from the St. Lawrence and Saguenay rivers (Dufour and Ouellet, 2007). This results in the convergence of climate drivers from the bottom of the Laurentian Channel and marine traffic drivers (cluster 6) with terrestrial run-off from river outflows and direct human impacts (*i.e.*, population density; cluster 3).

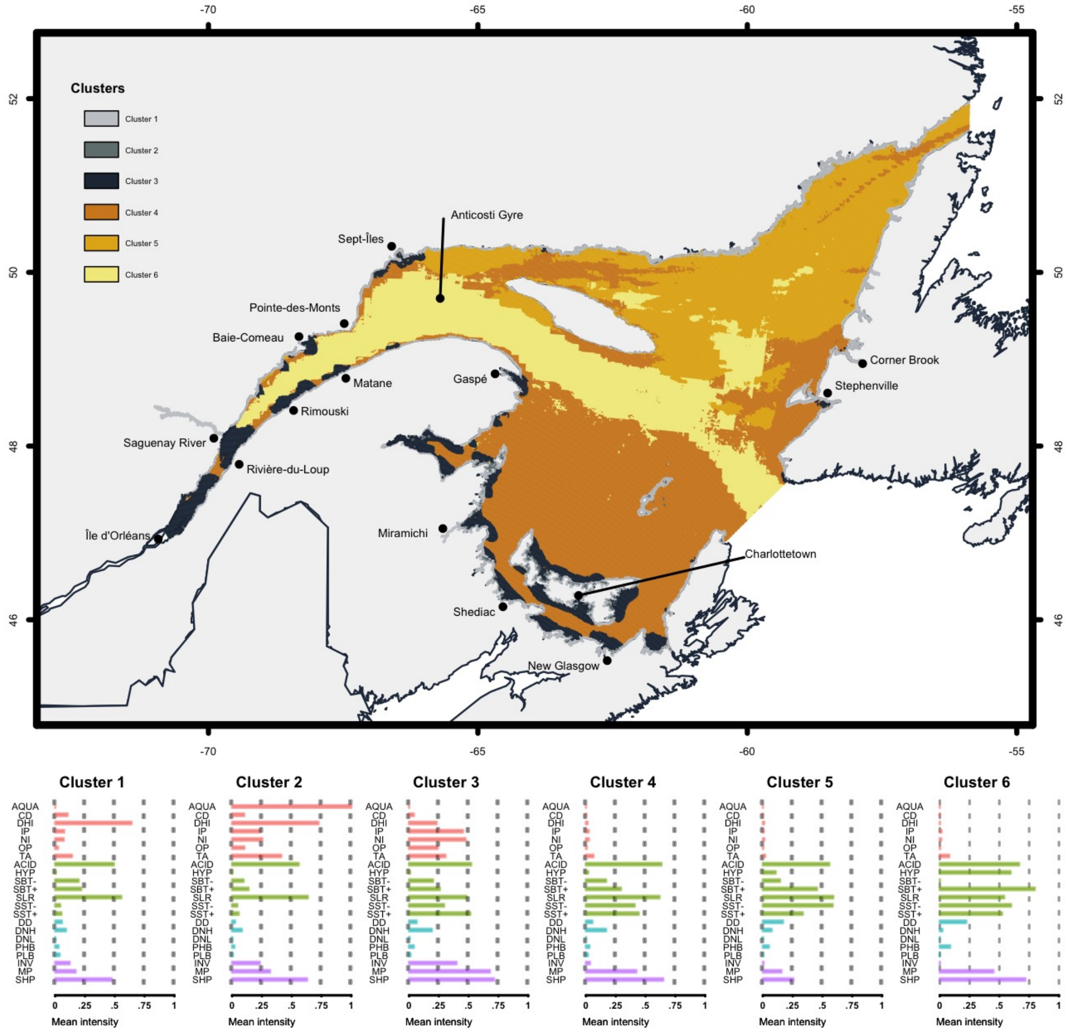


Figure 21: Distribution of areas with similar cumulative exposure profiles in the Estuary and Gulf of St. Lawrence, identified through a clustering approach (Top). Mean intensity of all coastal (red), climate (green), fisheries (blue), and marine traffic (purple) drivers within each cluster (Bottom). Refer to Table 6 for acronym meaning and to the Supplementary Materials for more details.

4.8 Open Knowledge Platform: *eDrivers*

Sharing the knowledge acquired through the description of drivers in the St. Lawrence emerged as a priority to curtail the need to contact dozens of experts across multiple organizations and over extensive periods of time to assemble the data needed for integrated research and management. It is also a requirement to ensure that this manuscript will not quickly become an outdated snapshot of drivers distribution and intensity in the St. Lawrence System, but rather serve as a stepping stone toward an adaptive and ever-improving collection of knowledge.

As such, we are launching *eDrivers*, an open knowledge platform focused on sharing knowledge on the distribution and intensity of drivers and on gathering a community of experts committed to structuring, standardizing and sharing knowledge on drivers in support of science and management. In launching this initiative, our objective is to uphold the highest existing standards of data management and open science. We identified four guiding principles (section 5.1) to meet this objective and structure of the initiative (Figure 22).

4.8.1 Guiding Principles

4.8.1.1 Unity and inclusiveness

Why:

Operating over such large scales in time, space, and subject matter requires a vast and diverse expertise that cannot possibly be possessed by any one individual or organization. Consequently, we envision an initiative that seeks to mobilize all individuals and entities with relevant expertise.

How:

By promoting, consolidating, and working with experts involved in existing and highly valuable environmental initiatives already in place in the St. Lawrence. Notable examples of environmental initiatives are the annual review of physical (Galbraith et al., 2018), chemical, and biological (Blais et al., 2019) oceanographic conditions in the St. Lawrence, the fisheries monitoring program (DFO, 2016b), the annual groundfish and shrimp multidisciplinary survey (Bourdages et al., 2018), the characterization of benthic (Dutil et al., 2011), epipelagic and coastal (Dutil et al., 2012) habitats of the St. Lawrence, and Canada's shoreline classification (ECCC, 2018). There are also nascent efforts to share information on several human activities in the St. Lawrence such as the Marine Spatial Data Infrastructure portal, which provides data on zoning, shipping, port activities, and other human activities in Canadian waters, including the St. Lawrence system (Government of Canada, 2018).

By working with existing data portals whose objective is to share environmental data. We are thus collaborating actively with the St. Lawrence Global Observatory (SLGO) to develop the initiative and to host the platform on their web portal. The mission of SLGO is to promote and facilitate the accessibility, dissemination, and exchange of official and quality data and information on the St. Lawrence ecosystem through the networking of organizations and data holders to meet their needs and those of users, to improve knowledge, and to assist decision-making in areas such as public safety, climate change, transportation, resources, and biodiversity conservation. SLGO is also one of three regional associations spearheading the Canadian Integrated Ocean Observing System (CIOOS[1]), which will focus on integrating oceanographic data from multiple sources to make them accessible to end-users and to enable the national coordination of ocean observing efforts by integrating isolated or inaccessible data, and

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[1] https://cioos.ca

by identifying gaps or duplications in observations and research efforts. We are also developing collaborations with the Portal on water knowledge [2], an initiative from the Québec provincial government. The aim of this portal is to collect and share accurate, complete, and up-to-date resources on water and aquatic ecosystems to support the mandate of relevant actors and stakeholders working in water and aquatic ecosystems management.

By actively inviting, seeking, and developing collaborations as well as encouraging constructive criticism from the inception and throughout the lifetime of the platform.

By inviting external community contributions (Figure 22). External researchers or entities wishing to submit marine data will be able to do so through SLGO web portal. Submissions through other data portals will also be accepted either through the development of data sharing agreements or with the caveat that shared data are under an open source license and that they adhere to the platform data standards.

4.8.1.2 Findability, accessibility, interoperability and reusability

Why:

Open knowledge has been propelled to the forefront of scientific research in an era of open, collaborative, and reproducible science. By moving toward large scale, cross-disciplinary research and management projects, there is a growing need to increase the efficiency of data discovery, access, interoperability, and analysis (Reichman et al., 2011; Wilkinson et al., 2016). Our goal is to foster efficient and functional open science by creating a fully open, transparent and replicable open knowledge platform.

How:

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[2] http://www.environnement.gouv.qc.ca/eau/portail/

By building an infrastructure adhering to the FAIR Data Principles, which states that data and metadata must be Findable, Accessible, Interoperable, and Reusable. These (sub)principles focus on the ability of humans and machines to automatically find and (re)use data and knowledge (Wilkinson et al., 2016). As the FAIR Data Principles already exist as a unified set of principles, we adopt them as a set of guiding subprinciples to our initiative.

By making data and associated tools accessible through a variety of ways: the SLGO web portal, two R packages called `eDrivers`[3] and `eDriversEx`[4] to access the data through SLGO's API and to provide analytical tools to explore data, respectively, and a Shiny application[5] to explore drivers data interactively (Figure 22). Note that the data are currently contained within and accessible through the `eDrivers` R package only, as we are actively working to allow users to download selected layers from SLGO's web portal and geoserver. The functions available in *eDrivers* to access the data have however been developed to ensure forward compatibility once the data are migrated to SLGO's geoserver.

By defining clear data and metadata standards and specifications to support the regional standardization of current and future protocols and practices and to favor interoperability with national and international initiatives like the Essential Ocean Variables (EOV) identified by the Global Ocean Observing System (GOOS). As such, we will adopt the metadata standard currently targeted for CIOOS, *i.e.*, the North American Profile of ISO 19115:2014—Geographic information— Metadata, a schema favored for geospatial data in Canada and the United States.

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[3] https://github.com/orgs/eDrivers/eDrivers

[4] https://github.com/orgs/eDrivers/eDriversEx

[5] https://david-beauchesne.shinyapps.io/eDriversApp/

By providing version control and code access to the workflows set up to generate driver layers from raw data, the R packages and the Shiny application through a GitHub organization called *eDrivers*[6].

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[6] https://github.com/orgs/eDrivers/

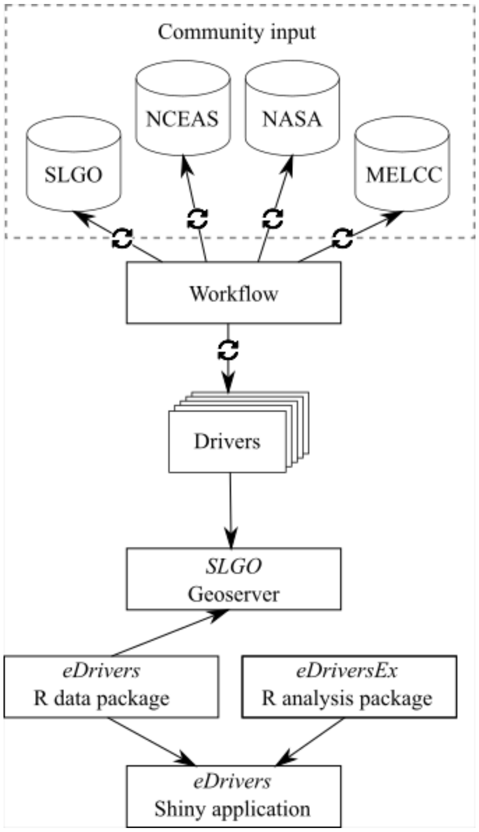

Figure 22: Diagram of the platform structure. Community input in the form of raw data is accessed through the St. Lawrence Global Observatory (SLGO; https://ogsl.ca/en) repository—the platform host—or through open access repositories (*e.g.*, NASA data). The raw data are then processed through a workflow hosted on the *eDrivers* GitHub organization (https://github.com/eDrivers). Data processing may be as simple as data rescaling or make use of more complex methodologies. All data is then hosted on SLGO's geoserver and accessible through their API. We developed a R package called *eDrivers* to access the driver layers through R and we are actively developing a second R package called *eDriversEx* that will include analytical tools to explore drivers data. Finally, we have developed a Shiny application, *eDrivers* app, that allows users to explore drivers data interactively (https://david-beauchesne. shinyapps.io/eDriversApp/). All R components of the project are hosted and available on the *eDrivers* GitHub organization. Iterative and adaptive processes are identified by circular arrows.

4.8.1.3 Adaptiveness

Why:

In the face of uncertainty and in an effort to address impending environmental changes, adaptive management has been identified as the chief strategy to guide efficient decision making (*e.g.*, Margules and Pressey, 2000; Keith et al., 2011; Jones, 2016; Chion et al., 2018) and has already been discussed in the context of multi-drivers and cumulative impact assessments (Halpern et al., 2015b; Beauchesne et al., 2016; Côté et al., 2016; Schloss et al., 2017). Adaptive management can only be truly achieved through a commitment to adaptive monitoring and data reporting (Margules and Pressey, 2000; Halpern et al., 2012; Lubchenco and Grorud-Colvert, 2015). We further contend that adaptive management requires the development of adaptive monitoring tools and infrastructures, which we seek to address through a continuously-evolving platform.

How:

By setting up mechanisms structuring cyclic reviews of platform content, for the integration of new material (*e.g.*, data and methods) as it becomes available or accessible, and by striving to provide time-series data that are crucial to assess temporal trends and potentially early-warning signals of ecosystem change (Figure 22).

4.8.1.4 Recognition

Why:

Like peer-reviewed publications, data must also be given its due importance in scientific endeavors and thus be considered as legitimate citable products contributing to the overall scientific output of data providers (Task Group on Data Citation Standards and PractOut of Cite, Out of Mind: The Current Sices and PractOut of Mind:

The Current Sices, 2013; FORCE11, 2014). Appropriate citations should therefore be provided for all data layers used and shared by the platform.

How:

By adhering to the Data Citation Principles (FORCE11, 2014), which focus on citation practices that provide appropriate credit to data products.

4.8.2 Using *eDrivers*

Using *eDrivers* is simplified through the tools already in place and will be increasingly accessible as the initiative evolves and other tools are developed to ease user experience. We provide an example of the ease with which the data can be accessed and used with the `eDrivers` R package to reproduce Figure 18 (Box 1). The code to reproduce all the analyses and figures in this manuscript is also available on GitHub[7].

4.9 Perspectives

Understanding how ecosystem state will be affected by global change requires a comprehensive understanding of how threats are distributed and interact in space and time, which in turn hinges on appropriate data tailored to multi-driver studies (Dafforn et al., 2016; Stock et al., 2018; Bowler et al., 2019). In the St. Lawrence, we found that few areas are free from cumulative exposure and that the whole Estuary, the Anticosti Gyre, and coastal southwestern Gulf are particularly exposed to cumulative drivers, especially close to urban areas. We also identified six geographically distinct areas that display similar cumulative exposure profiles; these reveal that coastal areas are particu-

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[7] https://github.com/orgs/eDrivers/eDriversMS

larly exposed to all types of drivers and that certain driver combinations are inherent to certain regions of the St. Lawrence. These results allow us to efficiently identify areas in need of heightened scrutiny from a science and management perspective.

Through *eDrivers*, these observations will be iteratively improved toward an increasingly robust assessment of cumulative exposure and areas with similar cumulative exposure profiles as gaps in knowledge are addressed or approaches to describe drivers are refined. Arguably, the most meaningful benefit anticipated from *eDrivers* will be the gain in efficient access to comparable data-based knowledge on the exposure of ecosystems to multiple threats. This could pay quick scientific and management dividends by efficiently drawing on the knowledge and efforts of a wide range of contributors, by expanding avenues of scientific inquiry, by decreasing overall effort duplication and research costs, and by increasing research efficiency (Franzoni and Sauermann, 2014).

Critically, *eDrivers* will allow the scientific and governmental communities to identify key knowledge gaps that will assist in prioritizing and optimizing research efforts. Ultimately, we believe that *eDrivers* will operationalize evidence-based decision making by streamlining data management and research, allowing science output to be available and interpretable on a time scale relevant to management (see Sutherland et al., 2004; Reichman et al., 2011). The platform will thus greatly facilitate the application of broad scale, holistic research and management approaches such as marine spatial planning, ecosystem-based management, and strategic environmental assessments (*e.g.*, Rice, 2011; Halpern et al., 2015b; Jones, 2016).

The next step will be the inclusion of other types of knowledge to our initiative. Our focus has been on a single element required for fully operational impact assessments. Data that provide knowledge on the exposure of ecosystems to drivers are called stressor-based indicators (Dubé and Munkittrick, 2001; Dubé, 2003). These indicators efficiently identify potential local impacts and can be proactively linked to decision-making, yet assume complete knowledge of drivers and fail to diagnose impacts on valued components or non-additive effects. In contrast, effect-based indicators are direct measurements of valued components (*e.g.*, species abundance and biodiversity) and inherently capture the effects of multiple drivers (Dubé and Munkittrick, 2001; Dubé, 2003). Whereas, effect-based indicators are considered superior to stressor-based indicators, they fail to ascribe observed effects to specific drivers. Stressor-based and effect-based indicators are, therefore, both required to diagnose causes of ecosystem change (Jones, 2016). As a collection of knowledge on stressor-based indicators, *eDrivers* should be weaved with other, comparable, collections of knowledge describing valued ecosystem components that can be linked to drivers and allow for a better understanding of cumulative impacts. Ultimately, interdisciplinary collections of knowledge could be weaved together through social-ecological meta-networks analyses (Dee et al., 2017). In turn, these could be used in conceptual frameworks to help to establish causal relationships between drivers and valued ecosystem components such as the DPSIR (Driving forces–Pressure– State–Impact–Response) framework (Kristensen, 2004; Gari et al., 2015). Within such frameworks, data-based indicators provided through *eDrivers* could be categorized as driving forces, pressures or states, depending on the objective and context of a study.

Significant effort is still needed to bring our vision to fruition. Foremost is to maintain our efforts to foster collaborations, develop platform content and identify key knowledge gaps. A fair and efficient organizational structure will be developed in order to manage *eDrivers* as a community and appropriate funding must be secured to continue building this community and ensure the longterm viability of the initiative, although the partnership with SLGO partly addresses this issue. We also wish to provide users with enhanced capabilities and flexibility in using the interactive tool and R package. This could include creating automatic reports and more flexibility for user-defined driver-based indicators.

Finally, terrestrial and coastal environments must be incorporated, as sources of stress within those habitats extend to the marine environments. Moreover, despite coastal areas being recognized as the most exposed to environmental threats, we continue to delineate terrestrial and marine realms, considering coastlines as an impermeable barrier. Whereas, there is a sensible rationale for this division, we must strive to eliminate it if we are to appropriately study and predict the impacts of global change (*e.g.*, see Bowler et al., 2019).

Despite the challenges and work ahead, we are hopeful that this initiative will be very successful. Ultimately, *eDrivers* represents a much needed solution to address important issues in data management that could radically shift broad scale research and management practices toward efficient, adaptive and holistic ecosystem-based management in the St. Lawrence and elsewhere in the world. All it requires to be successful is for the scientific and political communities to fully commit to open knowledge, adaptive monitoring and, most of all, an integrated vision of ecosystem management.

4.10 Data availability statement

The datasets generated for this study are openly available. Requests to corresponding author should be made for access to raw data.

4.11 Author contributions statement

DB, RD, DG and PA conceived the manuscript and the underlying objectives. DB prepared/formatted the data, performed the analyses, was in charge of technical developments and lead the drafting of the manuscript. All co-authors contributed to data, analyses and writing based on their respective expertise and contributed to the revision of the manuscript.

4.12 Acknowledgements

We thank the Fond de Recherche Québécois Nature et Technologie (FRQNT) and the Natural Science and Engineering Council of Canada (CRSNG) for financial support. This project is also supported by Québec Océan, the Quebec Centre for Biodiversity Science (QCBS), Takuvik, and the Notre Golfe networks. This research is also sponsored by the NSERC Canadian Healthy Oceans Network and its Partners: Department of Fisheries and Oceans Canada and INREST (representing the Port of Sept-Îles and City of Sept-Îles).

4.13 Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars. 2020.00383/full#supplementary-material

4.14 Listings

Box 1. Code snippet demonstrating how to use the `eDrivers` R package to reproduce figure 18.

```r
# Install and load eDrivers package
devtools::install_github('eDrivers/eDrivers')
library(eDrivers)

# Load data
drivers <- fetchDrivers(drivers = c('Hypoxia','FisheriesDD'),
                        brick = T)[[1]]

# Transform data
drivers <- log(drivers + 1)
```

```
drivers <- drivers / cellStats(drivers, 'max')

# Visualize data and combination
plot(drivers)
plot(sum(drivers, na.rm = T))
# Identify values > 0 and not NAs
drivers$FisheriesDD[drivers$FisheriesDD < 0] <- NA
drivers$Hypoxia[drivers$Hypoxia < 0] <- NA
id0 <- !is.na(values(drivers$FisheriesDD)) &
       !is.na(values(drivers$Hypoxia))

# 2D kernel for driver co-intensity
library(MASS)
coInt <- kde2d(x = values(drivers[[1]])[id0],
               y = values(drivers[[2]])[id0],
               n = 500, lims = c(0, 1, 0, 1))
image(coInt, zlim = c(0,max(coInt$z)))

# Driver density distribution
plot(density(drivers$FisheriesDD[id0]))
plot(density(drivers$Hypoxia[id0]))
```

4.15 Supplementary material

4.15.1 Drivers description

Table 7: List of drivers currently available on *eDrivers* along with their respective acronym used in the figures in the supplementary material.

Groups	Drivers	Acronym	Source
Climate	Acidification	ACID	Starr and Chassé (2019)
Climate	Hypoxia	HYP	Blais et al. (2019)
Climate	Bottom-water temperature	SBT-	Galbraith et al. (2018)
Climate	Bottom-water temperature	SBT+	Galbraith et al. (2018)
Climate	Sea level rise	SLR	Halpern et al. (2015a)
Climate	Surface-water temperature	SST-	Galbraith et al. (2018)
Climate	Surface-water temperature	SST+	Galbraith et al. (2018)
Coastal	Aquaculture	AQUA	MAPAQ (2016); DFO (2016a); AAF (2016); FA (2016); FFA (2016)
Coastal	Coastal development	CD	Earth observation group (2019)

Groups	Drivers	Acronym	Source
Coastal	Direct human impact	DHI	Statistics-Canada (2017)
Coastal	Inorganic pollution	IP	Halpern et al. (2015a)
Coastal	Nutrient import	NI	Halpern et al. (2015a)
Coastal	Organic pollution	OP	Halpern et al. (2015a)
Coastal	Toxic algae	TA	Bates et al. (2019)
Fisheries	Demersal, destructive	DD	DFO (2016b)
Fisheries	Demersal, non-destructive, high-bycatch	DNH	DFO (2016b)
Fisheries	Demersal, non-destructive, low-bycatch	DNL	DFO (2016b)
Fisheries	Pelagic, high-bycatch	PHB	DFO (2016b)
Fisheries	Pelagic, low-bycatch	PLB	DFO (2016b)
Marine traffic	Invasive species	INV	Halpern et al. (2015a)
Marine traffic	Marine pollution	MP	Halpern et al. (2015a)
Marine traffic	Shipping	SHP	Halpern et al. (2015a)

4.15.1.1 Climate

Acidification

Oceans are the largest reservoirs and sinks of atmospheric carbon dioxide (CO_2). Its uptake increases seawater acidity and lowers the saturation state of waters with respect to calcite (Ω_C) and aragonite (Ω_A), the two most common $CaCO_3$ polymorphs that constitute the shells and skeletons of many marine organisms (Mucci et al., 2017). Ocean acidification can have deleterious effects on carbonate-secreting organisms (*e.g.* mollusks and crustaceans) and certain physiological processes in non-calcifying organisms (Fabry et al., 2008; Kroeker et al., 2013).

When Ω_C or Ω_A decrease below 1, water becomes undersaturated and corrosive to the skeletal minerals of carbonate-secreting organisms. Note that if $\Omega_A < 1$, the waters may still be supersaturated with respect to calcite since it is 50% more soluble than aragonite. However, organisms have wide ranging responses to changes in Ω_C and Ω_A. For example, most corals stop calcifying at $\Omega_A < 2$ (Kleypas et al., 2006; Bove et al., 2019), while other organisms may have adapted to precipitate $CaCO_3$ even when seawater is undersaturated with respect to calcite ($\Omega_C < 1$ or $\Omega_A < 0.65$; *e.g.* Uthicke et al., 2016).

We used Ω_A to characterize ocean acidification in the bottom waters of the St. Lawrence. The data come from the Department of Fisheries and Oceans' (DFO) Atlantic Zone Monitoring Program (AZMP; Galbraith et al., 2018) surveys and DFO's multispecies surveys (Bourdages et al., 2018) collected in August-September of 2017 (Starr and Chassé, 2019). Ω_A, pH, and dissolved oxygen (O_2) were measured at 117 stations in the Estuary and Gulf of St. Lawrence in the summer of 2018. The majority of sampling stations were located in the Southern Gulf ($n = 84$), the Estuary and Northern Gulf ($n = 33$).

The carbonate speciation was determined through pH and total alkalinity (TA) measurements. Samples for pH and TA were collected with no head space in 500 mL borosilicate glass flasks, and 250 μL of saturated $HgCl_2$ solution was added to each sample and processed following the "Guide to best practices for Ocean CO2 Measurements" (Dickson et al., 2007).

pH_T was determined spectrophotometrically using the indicator dye m-cresol purple (Sigma-Aldrich). Absorbance was measured at 730, 578 and 434 nm before and after dye addition in 10 cm quartz cells thermostated at 25 ± 0.05^oC (Dickson et al., 2007). A similar procedure was carried out before each set of sample measurement using a TRIS (Tris (hydroxymethyl) -aminomethane) buffer prepared at a practical salinity (S) of approximately 30 (Millero, 1986). Certified Reference Material (CRM) (supplied by Professor Andrew Dickson, Scripps Institution of Oceanography, San Diego, USA) was used for quality control of our pH TRIS buffer.

TA was determined by potentiometric titration in an open cell using an automated Radiometer potentiometric titrator (Titrilab 865) and a pH combination electrode (pHC2001) in a continuous titrant addition mode, an algorithm specifically designed for shallow end-point detection (Dickson et al., 2007). The 0.1M HCl titrant in a solution of 0.6M NaCl was calibrated using CRM provided by Professor Andrew G. Dickson.

The carbonate system parameters (including Ω_A) were corrected for *in situ* pressure and temperature using the algorithm CO2SYS (Lewis et al., 1998) with measured pH, TA, soluble reactive phosphate and silicate concentrations as input parameters.

To account for the low sample size in the Northern Gulf, we used the correlation between O_2 and CO_2, which are linked through the stoichiometry of the respiration reaction in waters that are isolated from the atmosphere (Mucci et al., 2011). Metabolic CO_2 increases in water through biotic processes such microbial respiration of organic matter (Mucci et al., 2011). In deep waters, found in the Laurentian, Anticosti and Esquiman Channels, variations of Ω_A are largely governed by the addition of metabolic CO_2, whereas, near the air-sea interface, O_2 is replenished faster than CO_2 can escape (Zeebe and Wolf-Gladrow, 2001). The impact of respiration on carbonate chemistry is highest in hypoxic regions, where metabolic CO_2 accumulates to high concentrations (Mucci et al., 2011).

We explored the correlation between Ω_A and O_2 in the data and found no significant correlation at the scale of the whole St. Lawrence (*p-value*: 0.08; R^2: 0.03). Nevertheless, a correlation between Ω_A and O_2 exists in the Northern St. Lawrence (*p-value*: < 0.01; R^2: 0.49), but not in the Southern St. Lawrence (*p-value*: 0.85; R^2: < 0.01). Furthermore, the correlation observed in the north between Ω_A and O_2 is especially strong when deep Channel waters (*Deep* model: *p-value*: < 0.01; O_2: 0.20; R^2: 0.97) are separated from shallower regions (*Shallow* model: *p-value*: < 0.01; O_2: 0.07; R^2: 0.96), with Ω_A increasing more steeply with increasing O_2 in the deep Channels. This stronger correlation is likely caused by the lack of gas exchange with the atmosphere or the surface mixed layer and the importance of metabolic CO_2 in deep waters, some of which may have mean ages of up to 20 years (Mucci et al., 2011). In the Northern Gulf, the acidification trends with depth and distance from the Cabot Strait along the Laurentian, Anticosti and Esquiman Channels due to the progressive oxygen depletion and metabolic carbon dioxide accumulation (Mucci et al., 2011).

There are likely different dynamics at play in the Southern Gulf, such as waters with lowered alkalinity and salinity caused by the surface, seaward-flowing Gaspé Current. These waters have lower buffering capacities to decreasing pH and Ω_A. Furthermore, the accumulation of metabolic carbon dioxide produced by rapid oxic degradation of organic matter in the sandy and permeable sediments of the Magdalen Shelf or in the Gaspé current could decrease Ω_A in the Southern Gulf (Starr and Chassé, *personal communication*).

We thus divided their analysis between the Southern and Northern St. Lawrence. The St. Lawrence was divided along the 350m isobath on the southern slope of the Laurentian Channel, from the Cabot Strait to the tip of the Gaspé Peninsula. The Ω_A distribution in the Southern St. Lawrence was modeled using the exponential kriging model.

We predicted Ω_A using O_2 for the Northern St. Lawrence. Whereas there are few published datasets on Ω_A in the St. Lawrence, there is a robust time-series on oxygen concentrations in the water column available through the Department of Fisheries and Oceans' (DFO) Atlantic Zone Monitoring Program (AZMP; Galbraith et al., 2018). We used oxygen concentration data collected between 2013 and 2017 (Blais et al., 2019) and interpolated oxygen % saturation using cokriging with depth as a covariable, as done in Dutil et al. (2011). Bathymetric data come from Dutil et al. (2011) and have a 100 km^2 resolution. For more details, refer to the hypoxia data layer description. The *Deep* model was used to transform O_2 values to Ω_A in grid cells with depth $>$ 350m, while the *Shallow* model was applied to cells with depth $<$ 350m.

Based on the wide range of Ω_A levels at which organisms are negatively affected (see above), we built an index of acidification stress (A_s) ranging between 0 and 1 that slowly increases as Ω_A decreases to ≈ 2, increases more rapidly close to $\Omega_A = 1$ and reaches its peak at $\Omega_A \approx 0.5$:

$$A_s = \frac{-3}{.99 + e^{-2*\Omega_A}} + 3 \tag{4.3}$$

Hence, the higher the acidification stress, the higher the index of acidification becomes.

Hypoxia

The data used to characterize hypoxia come from the Department of Fisheries and Oceans' (DFO) Atlantic Zone Monitoring Program (AZMP; Galbraith et al., 2018) survey in late spring and fall of 2013 to 2017, as well as from DFO's annual multispecies surveys for the northern Gulf in August and for the Magdalen Shallows in September. We provide a brief summary of data and methods to describe hypoxia in this document. For more details, refer to Blais et al. (2019).

Oxygen concentration were measured at every station using an oxygen probe (Sea-Bird SBE43) mounted on a CTD. The probe is calibrated against seawater samples taken directly from the Niskin bottles at every cast and analyzed by Winkler titration (see Blais et al., 2019, for calibration procedure). The data used is the last depth sampled on the CTD profile, which is typically ~10m above the bottom. Note that this depth does not necessarily correspond to the depth of the oxygen minimum. The oxygen minimum is typically found along the 27.25 isopycnal, often situated as much as 100 m above bottom in the Lower Estuary. Oxygen concentration ($\mu M\ L^{-1}$) is converted to oxygen saturation, taking into account the salinity and temperature at the selected depth.

We interpolated oxygen saturation using cokriging with depth as a covariable, as done in Dutil et al. (2011). Bathymetric data come from Dutil et al. (2011) and have a 100 km^2 resolution. According to Diaz and Rosenberg (1995), severe hypoxia occurs when dissolved oxygen falls below 2 $ml\ L^{-1}$, to 62.5 $\mu mol\ L^{-1}$ or ~20% saturation. This is considered as the level necessary to maintain most animal life. Accordingly, Chabot and Claireaux (2008) studied the effects of hypoxia on the energy budget of cod in the St. Lawrence and found that behavioural effects began manifesting themselves below 70% oxygen saturation and that survival becomes jeopardized below ~20% saturation. We used these observations to create an index of hypoxia using an inverted logistic curve that slowly increases below 70% oxygen saturation and increases acutely as it reaches its peak intensity between 20 and 30% oxygen saturation:

$$H_s = \frac{-1}{.99 + 200 * e^{-0.15 * O_2}} + 1 \tag{4.4}$$

Hence, the higher the hypoxic stress, the higher the index of hypoxia becomes.

Bottom-water temperature anomalies

The data used to characterize bottom-water temperature anomalies come from the Department of Fisheries and Oceans' (DFO) Atlantic Zone Monitoring Program (AZMP; Galbraith et al., 2018). We provide a brief summary of data and methods to characterize the bottom-water temperature climatology and anomalies in this document. For more details, refer to Galbraith et al. (2018).

Bottom-water temperatures are interpolated in the Gulf using conductivity-temperature-depth (CTD) sampling performed annually through DFO's multispecies surveys for the northern Gulf in August and for the Magdalen Shallows in September. Using this sampling survey, temperatures are horizontally interpolated at each 1 m depth layer on a 2 km resolution grid. Bottom-water temperatures are then extracted by using a bathymetry layer from the Canadian Hydrographic Survey (Dutil et al., 2012) and selecting the interpolated temperature from the layer corresponding to the bottom depth at each grid point.

We used temperature anomalies, *i.e.* deviations from long-term normal conditions between 1981 and 2010, to measure an annual index of stress associated with extreme temperatures between 2013 and 2017. Temperature anomalies were calculated using the difference between grid cell values with 1981-2010 climatological averages. Anomaly time series were normalized by their standard deviation (SD) to allow comparisons between areas of the St. Lawrence with different temperature ranges. For example, temperatures observed in deep channels are less variable than in shallower regions of the St. Lawrence. Hence, if anomalies were expressed in degrees Celsius, it would underestimate the relative importance of anomalies in deep channels when compared to shallower regions. Grid cells whose monthly value exceeded ± 0.5 standard deviation (SD) from the long-term average were considered as anomalous (Galbraith et al., 2018). Outliers in the data were defined as those that fell beyond the interquartile range * 3, identified as extreme outliers by Tukey (1977). Outlier values were capped to correspond to the 5th and 95th percentile values. Anomalies were divided into positive and negative anomalies and the absolute value of anomalies were used as an indicator of the intensity of bottom-water temperature anomalies. The mean anomaly intensity between 2013 and 2017 for each grid cell was used to generate the final index of bottom-water temperature anomalies.

Surface-water temperature anomalies

The data used to characterize surface-water temperature anomalies come from the Department of Fisheries and Oceans' (DFO) Atlantic Zone Monitoring Program (AZMP; Galbraith et al., 2018). We provide a brief summary of data and methods to characterize the surface-water temperature climatology and anomalies in this document. For more details, refer to Galbraith et al. (2018).

The surface-water layer is characterized using sea surface-water temperature (SST) monthly composites from Advanced Very High Resolution Radiometer (AVHRR) satellite images obtained from the National Oceanic and Atmospheric Administration (NOAA) and European Organization for the Exploitation of Meteorological Satellites (EUMETSAT). Images used are from DFO's Maurice Lamontagne Institute at a 1 km resolution from 1985-2013 and from DFO's Bedford Institute of Oceanography (BIO) Operational Remote Sensing group at a 1.5 km resolution since 2014. Monthly anomalies were constructed as the difference between monthly averages and the 1985-2010 climatological mean for each month.

Surface-water temperature anomalies were characterized following the same method used for bottom-water temperature anomalies. Only the months of May to November were included to avoid biases associated with the presence of ice cover. Monthly anomalies from May to November values were summed to obtain an indicator of annual surface-water temperature anomaly intensity in each grid cell. The mean anomaly intensity between 2013 and 2017 for each grid cell was used to generate the final index of surface-water temperature anomalies.

Sea-level rise

The data used to characterize sea-level rise risk come from the global cumulative impacts assessment on habitats (Halpern et al., 2008b, 2015b) and available on the NCEAS online data repository (Halpern et al., 2015a). We provide a brief summary of data and methods in this document. For more details, refer to Halpern et al. (2015a).

Sea-level rise was characterized by Nicholls and Cazenave (2010) using NASA's satellite altimetry data (Topex/Poseidon, Jason-1&2, GFO, ERS-1&2, and Envisat missions) and available at http://www.aviso.altimetry.fr/en/data/products/ocean-indicatorsproducts/mean-sea-level/products-images.html

The rate of sea-level rise ($mm/year$) was measured between 1992 and 2012 and transformed as a net change value (mm) by multiplying by the number of years considered. Only positive values were selected under the assumption that only positive sea-level rise is likely to cause environmental stress.

For the St. Lawrence, we overlaid the raw data layers (Halpern et al., 2015a) with our 1 km^2 grid cell using weighted area average.

4.15.1.2 Coastal

Aquaculture

As aquaculture sites are managed at the provincial level in the St. Lawrence, data on aquaculture sites come from various sources (MAPAQ, 2016; DFO, 2016a; AAF, 2016; FA, 2016; FFA, 2016). Invertebrates aquaculture is especially important in the southern and western Gulf. Fish and algae aquaculture, on the other hand, remains marginal. Considering this, we only included invertebrates aquaculture for the aquaculture driver layer. However, if fish or algae farming were to become more important, these drivers should be incorporated in future analyses as individual layers, as impacts vary between types of aquaculture.

Aquaculture activities are highly localized and potential effects do not or rarely extend beyond the location of the farms. We therefore only considered the location of sites to characterize the distribution of this driver. We were unable to characterize site production in terms of biomass farmed, which could provide an indication of the intensity of aquaculture activities. As such, we considered aquaculture as binary presence-absence data.

Coastal development

Terrestrial stable lights at night mostly represent light from human settlements and industrial sites with electricity. We thus used lights at night as a proxy of coastal infrastructure development.

The data come from the Nighttime Lights Time Series. Nighttime light products are compiled by the Earth Observation Group at the National Oceanic and Atmospheric Administration's (NOAA) National Centers for Environmental Information (NCEI). They use globally available nighttime data obtained from the Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band (DNB) of the Defense Meteorological Satellite Program (DMSP) to characterize global average radiance ($nanoWatts$ cm^{-2} sr^{-1}) composite images at a 15 arc-second (~200 m) resolution.

We used the annual Version 1 Nighttime VIIRS DNB composites between 2015 and 2016 (Earth observation group, 2019) to characterize coastal development in coastal areas of the St. Lawrence. As the effects of coastal development are likely acute in its direct vicinity, we extracted average radiance values using a 2 km buffer around grid cells within 2 km of the coast. We used a weighted area average to extract the radiance values.

Direct human impact

As in Halpern et al. (2008b) and Halpern et al. (2015a), we used the sum of coastal populations as a proxy of direct human impact. We used Statistics Canada dissemination area population count from the 2016 census to obtain coastal population size around the St. Lawrence (Statistics-Canada, 2017). Dissemination areas are the smallest standard geographic area in which census data are disseminated. They combine to cover all of Canada and are highly variable in shapes and sizes. For example, their sizes range from 0.0003 to over 44000 km^2 in our study area. The census provides population count within the boundary of each dissemination area, which we used to evaluate total coastal population.

As the effects of direct human impacts are likely acute mostly in coastal areas we calculated total population in grid cells within 2 km of the coast. Total population was measured in a 10 km buffer around each coastal cell. The total population in each buffer was the sum of intersecting dissemination areas divided by the intersection area between buffers and dissemination areas:

$$DHI_j = \sum_{k=1}^{n_j} P_k * \frac{A_{j,k}}{Atot, k} \tag{4.5}$$

where j is a buffered grid cell, k is a dissemination area intersecting j, P is the population in k, A is the area of the k overlapping with j and A_{tot} is the total area of k. This approach was favoured to reduce the effects of very large dissemination areas overlapping with buffers on a very small percentage of their total area.

Inorganic pollution

The data used to characterize inorganic pollution come from the global cumulative impacts assessment on habitats (Halpern et al., 2008b, 2015b) and available on the NCEAS online data repository (Halpern et al., 2015a). We provide a brief summary of data and methods in this document. For more details, refer to Halpern et al. (2015a).

Inorganic pollution was modeled using impervious surface area (*i.e.* artificial surfaces such as paved roads) under the assumption that most of this pollution source comes from urban runoff. Inorganic pollution originating from point-sources or in areas lacking paved roads is therefore not captured by this layer. The data obtained was aggregated at the watershed scale. Spread into coastal and marine environments was modeled using a diffusive plume model from each watershed pourpoints (*e.g.* river mouths).

For the St. Lawrence, we overlaid the raw data layers (Halpern et al., 2015a) with our 1 km^2 grid cell using weighted area average.

Nutrient pollution

The data used to characterize nutrient pollution come from the global cumulative impacts assessment on habitats (Halpern et al., 2008b, 2015b) and available on the NCEAS online data repository (Halpern et al., 2015a). We provide a brief summary of data and methods in this document. For more details, refer to Halpern et al. (2015a).

Annual fertilizer use in tonnes (t) was used as a proxy of nutrient pollution. The data used came from the Food and Agriculture Organization of the United Nations (FAO). Gaps in data were modeled using a linear regression between fertilizer and pesticides or agricultural gross domestic product (GDP). Dasymetric maps were then used to distribute fertilizer data over the landscape using 2009 data from the Moderate Resolution Imaging Spectroradiometer (MODIS) at ~500 m resolution and aggregated to watersheds. Diffusive plume models from each watershed pourpoint (*e.g.* river mouths) were then used to model the distribution and intensity of nutrient pollution in coastal and marine environments.

For the St. Lawrence, we overlaid the raw data layers (Halpern et al., 2015a) with our 1 km^2 grid cell using weighted area average.

Organic pollution

The data used to characterize organic pollution come from the global cumulative impacts assessment on habitats (Halpern et al., 2008b, 2015b) and available on the NCEAS online data repository (Halpern et al., 2015a). We provide a brief summary of data and methods in this document. For more details, refer to Halpern et al. (2015a).

Annual pesticide use in tonnes (t) was used as a proxy of organic pollution. The data used came from the FAO and gaps in data were modeled using a linear regression between pesticides and fertilizers or agricultural GDP. The same methodology as that used to characterized nutrient pollution was then applied to organic pollution.

For the St. Lawrence, we overlaid the raw data layers (Halpern et al., 2015a) with our 1 km^2 grid cell using weighted area average.

Toxic algae

The data we use to describe the risk of toxic algae come from an expert based map delineating the areas where coastal areas are at risk from five different toxins (Bates et al., 2019). The map presents coastal areas at risk from 5 different toxins: 1) paralytic shellfish poisoning (PSP) toxins from the regular presence of the dinoflagellate *Alexandrium catenella* (previously *Alexandrium tamarense*) at high concentrations, 2) amnesic shellfish poisoning (ASP) toxins from domoic acid 3) diarrhetic shellfish poisoning (DSP) toxins, 4) spirolides and 5) pectenotoxins, two toxins produced by dinoflagellates occurring in the St. Lawrence.

The information provided on this expert map on the 5 toxins (Bates et al., 2019). was georeferenced and transformed as vectorized objects. We calculated a toxic algae risk (T) index for each cell (x) in the 1 km^2 study grid. For each toxin (t), a value of 1 was attributed to all grid cells overlapping with areas identified at risk on the expert map and a value of 0.5 for grid cells overlapping with areas where ASP and DSP toxins were observed without exceeding legal thresholds. The value for all 5 toxins was them summed for all grid cells:

$$TA_{i,x} = \sum_{i=1}^{5} i_x \tag{4.6}$$

4.15.1.3 Fisheries

The impacts of fisheries activities in the St. Lawrence are evaluated using DFO's fisheries logbooks program (DFO, 2016b). While logbooks are not mandatory for all fisheries in the St. Lawrence, they still provide a very thorough overview of the spatial distribution and intensity of fishing activities. The data we used span 6 years from 2010 to 2015 and detail 218323 fishing events (36387 ± 3147 fishing events per year). There were 31 targeted species and a total of 53 species caught in the dataset.

Fishing activities are performed using a variety of gear types: trap, trawl, dredge, driftnet, hand line, longline, scuba diving, purse seine, seine, beach seine and jig fishing. Intensity of fishing activities was divided among gear types and based on their respective types of environmental impacts (Table 8). For example, traps and trawls have very different effects on a system. Gear classification was done using the classification presented in Halpern et al. (2008b) and Halpern et al. (2015a) and is broken down into 5 distinct classes: demersal destructive (DD), demersal, non-destructive, low-bycatch (DNL), demersal, non-destructive, high-bycatch (DNH), pelagic, low-bycatch (PLB) and pelagic, high-bycatch (PHB). This categorization divides the fisheries data into 5 distinct driver layers characterizing fishing activities.

Gear types can be further classified into fixed or mobile engines based on their mobility. We used these two mobility classes to generate a buffer of impact around each fishing activity coordinates to consider potential spatial uncertainty associated with locations, the fact that mobile engines can be tracted over several kilometers during fishing activities, and because we do not have the beginning and end points of mobile fishing events. Buffer sizes for fixed and mobile engine was of 200 and 2000 meters, respectively.

Table 8: Classification of gear types in the fisheries dataset based on their environmental impact and mobility.

Gear type	Classification	Mobility
Trap	DNH	Fixed
Trawl	DD	Mobile
Dredge	DD	Mobile
Driftnet	PHB	Fixed
Hand lines	PLB	Fixed
Longline	PHB	Fixed
Scuba diving	DNL	Fixed
Purse seine	PLB	Fixed
Seine	DNH	Fixed
Beach seine	DNH	Fixed
Trap	DNH	Fixed
Jig fishing	PLB	Fixed

To characterize the intensity of fishing activities (FI), we used a biomass yield density index. We multiplied the total annual biomass captured in each grid cell j, regardless of species, by the proportion of fishing area in each grid cell:

$$FI_j = \sum_{k=1}^{n_j} B_{tot,k} * \frac{A_{j,k}}{A_{tot,k}} \tag{4.7}$$

where j is a grid cell, k is a fishing event, B_{tot} is the total biomass of a fishing event k, A is the area of a fishing event k overlapping a cell j and A_{tot} is the total area of the fishing event k. This formula gives an intensity measurement in biomass units, which is kg in our case. Since we measure the intensity within a 1 km^2 grid cell, the intensity evaluation is in $kg * km^{-2}$. This metric distributes the biomass captured within each grid cell as a function of overlapping fishing area and provides an overview of how impacted each grid cell is in terms of extracted biomass.

4.15.1.4 Marine traffic

Shipping

The data used to characterize shipping come from the global cumulative impacts assessment on habitats (Halpern et al., 2008b, 2015b) and available on the NCEAS online data repository (Halpern et al., 2015a). We provide a brief summary of data and methods in this document. For more details, refer to Halpern et al. (2015a).

Two data sources were used to characterize shipping. The first set of data is gathered as part of the World Meteorological Organization Voluntary Observing Ships' (VOS) scheme. Ships participating in the program gather meteorological data along with observation location as part of an open-ocean climate dataset. The data spans 20 years and annually covers 10-20% of ships worldwide. Data used spanned 2003 to 2011.

The second set of data comes from the Automatic Identification System (AIS), an initiative launched in 2002 that sought to improve marine safety by providing mariners with real-time vessel traffic. Through the International Maritime Organization SOLAS agreement, all vessels of over 300 gross tonnage on international voyages and those carrying passengers are now required to be equipped with AIS transceivers. These transceivers use Global Positioning System technology to locate vessels every 10 minutes. The data used were from November 2010 to December 2011. Data used come mostly from vessels that move globally (*i.e.* cargo, tanker and passenger), as they are required to carry AIS transceivers, but also include data from fishing, high-speed, pleasure and support classes. Shipping intensity was evaluated as the number of fishing tracks at a 0.1 decimal degrees resolution. For more details on data and methods used, consult (Walbridge, 2013).

For the St. Lawrence, we overlaid the raw data layers (Halpern et al., 2015a) with our 1 km^2 grid cell using weighted area average.

Invasive species

The data used to characterize invasive species risk come from the global cumulative impacts assessment on habitats (Halpern et al., 2008b, 2015b) and available on the NCEAS online data repository (Halpern et al., 2015a). We provide a brief summary of data and methods in this document. For more details, refer to supplementary materials provided in Halpern et al. (2008b) and Halpern et al. (2015a).

Cargo volume was used as a proxy of invasion risk under the assumption that risk of invasion is proportional to tonnes of goods transferred through ports. Cargo throughput in metric tonnes for the year 2011 was accessed through a variety of sources (see supplementary material in Halpern et al., 2015a, for more details) and cross-matched with entries in the World Port Index database (WPI; available from the National Geospatial-Intelligence Agency). A gap-filling procedure using linear regression and sets of predictors related to port volume and available in the WPI dataset was then applied to the WPI dataset to predict missing cargo volume entries. Finally, volume data was distributed in marine environments adjacent to ports using a diffusive plume model with an exponential decay function that set the maximum spread distance to approximately 1000 km. The plume model was then clipped to areas less than 60 m deep, as invasive species are more likely to invade shallow areas.

For the St. Lawrence, we overlaid the raw data layers (Halpern et al., 2015a) with our 1 km^2 grid cell using weighted area average.

Marine pollution

The data used to characterize marine pollution risk come from the global cumulative impacts assessment on habitats (Halpern et al., 2008b, 2015b) and available on the NCEAS online data repository (Halpern et al., 2015a). Marine pollution was considered to be mainly driver by the shipping industry. As such, the driver layer was constructed by combining the shipping (*i.e.* shipping lanes) and invasive species (*i.e.* cargo volume) layers. invasive. For more details, refer to supplementary materials provided in Halpern et al. (2008b) and Halpern et al. (2015a).

For the St. Lawrence, we overlaid the raw data layers (Halpern et al., 2015a) with our 1 km^2 grid cell using weighted area average.

4.15.2 Driver intensity and distribution

We evaluated the frequency distribution of each drivers to verify whether data should be transformed (Figure 23). In light of this, we log-transformed the following driver layers

- Coastal development
- Direct human impact
- All fisheries data
- Hypoxia
- Inorganic pollution
- Invasive species
- Nutrient pollution
- Organic pollution

— Bottom-water temperature anomalies
— Shipping

To allow for relative intensity comparison, all driver layers were subsequently normalized between 0 and 1 using the 99th quantile to further control for extreme values (Figure 24).

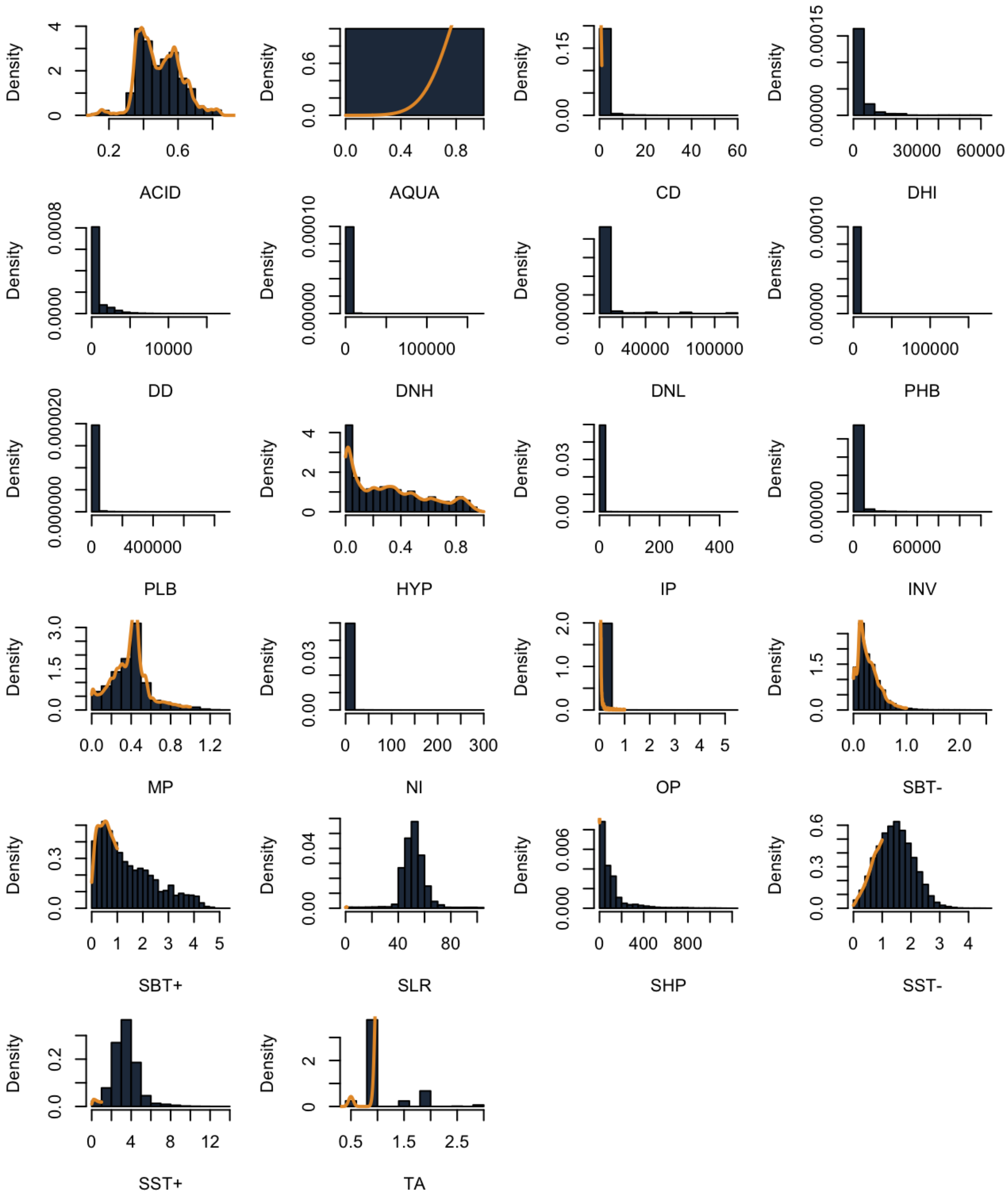

Figure 23: Frequency distribution of the untransformed data for all driver layers.

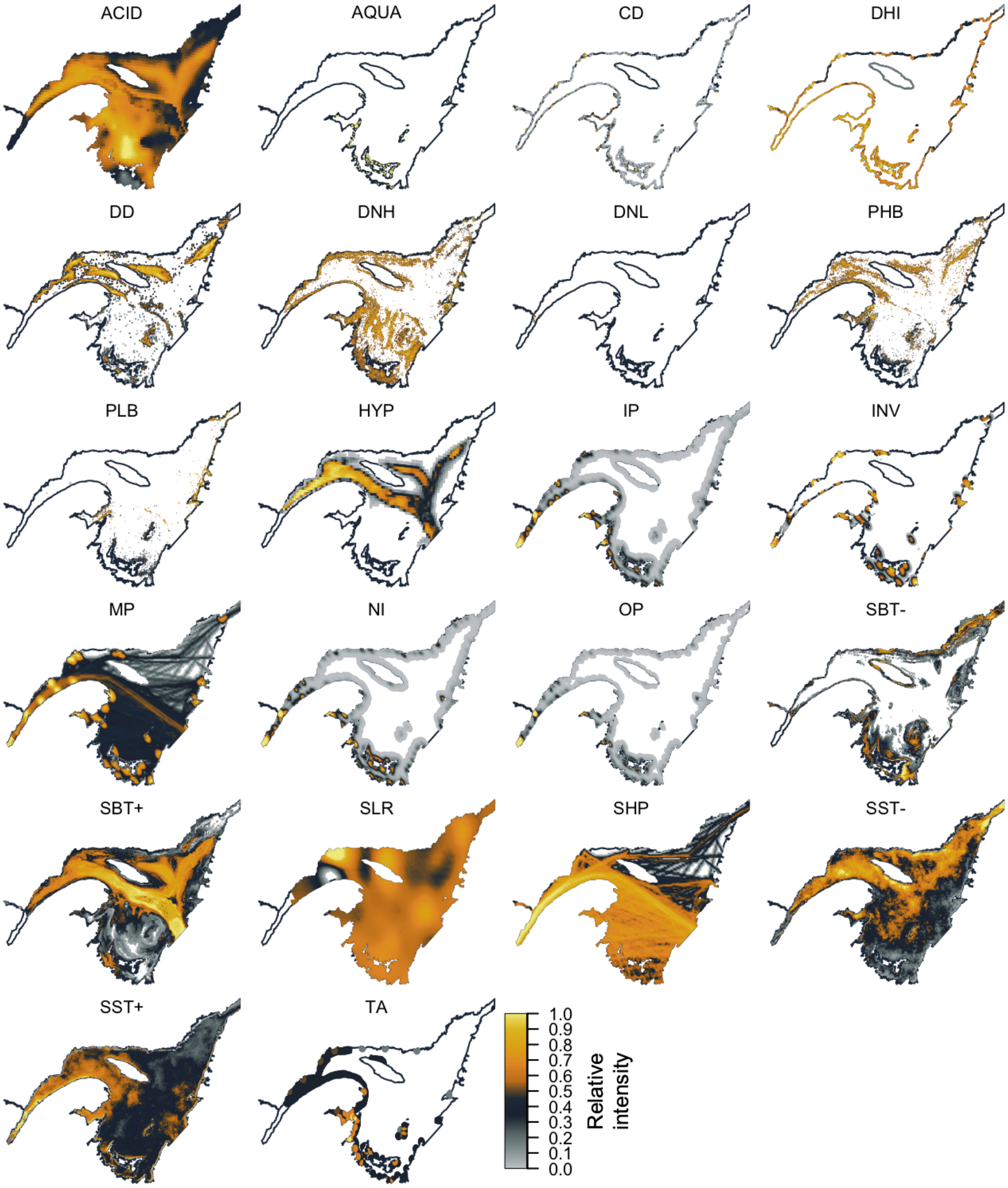

Figure 24: Distribution and intensity of transformed and normalized drivers in the Estuary and Gulf of St. Lawrence available on *eDrivers*.

4.15.3 Cumulative exposure

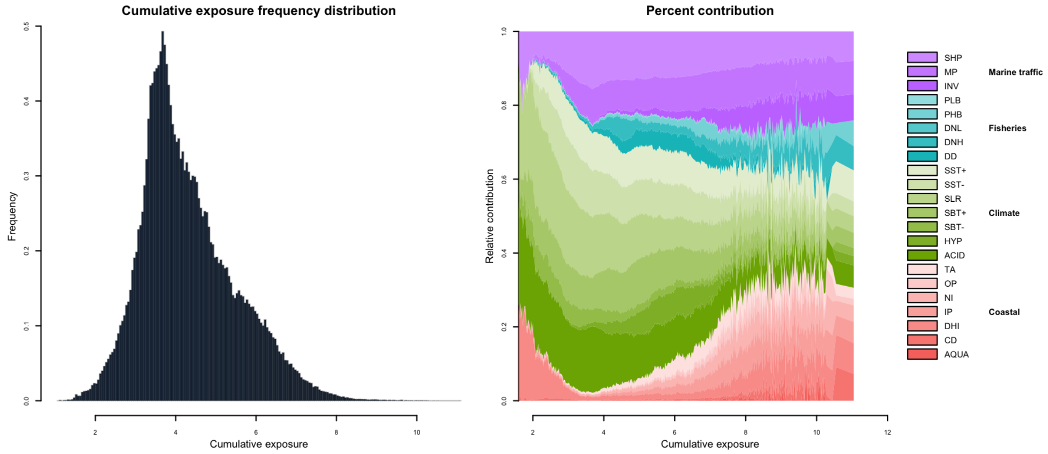

Figure 25: Frequency distribution of cumulative exposure (*i.e.* sum of normalized driver intensity in each grid cell) and percent contribution of each driver to the frequency distribution of cumulative exposure in the Estuary and Gulf of St. Lawrence.

4.15.4 Cumulative exposure profiles

4.15.4.1 Clustering

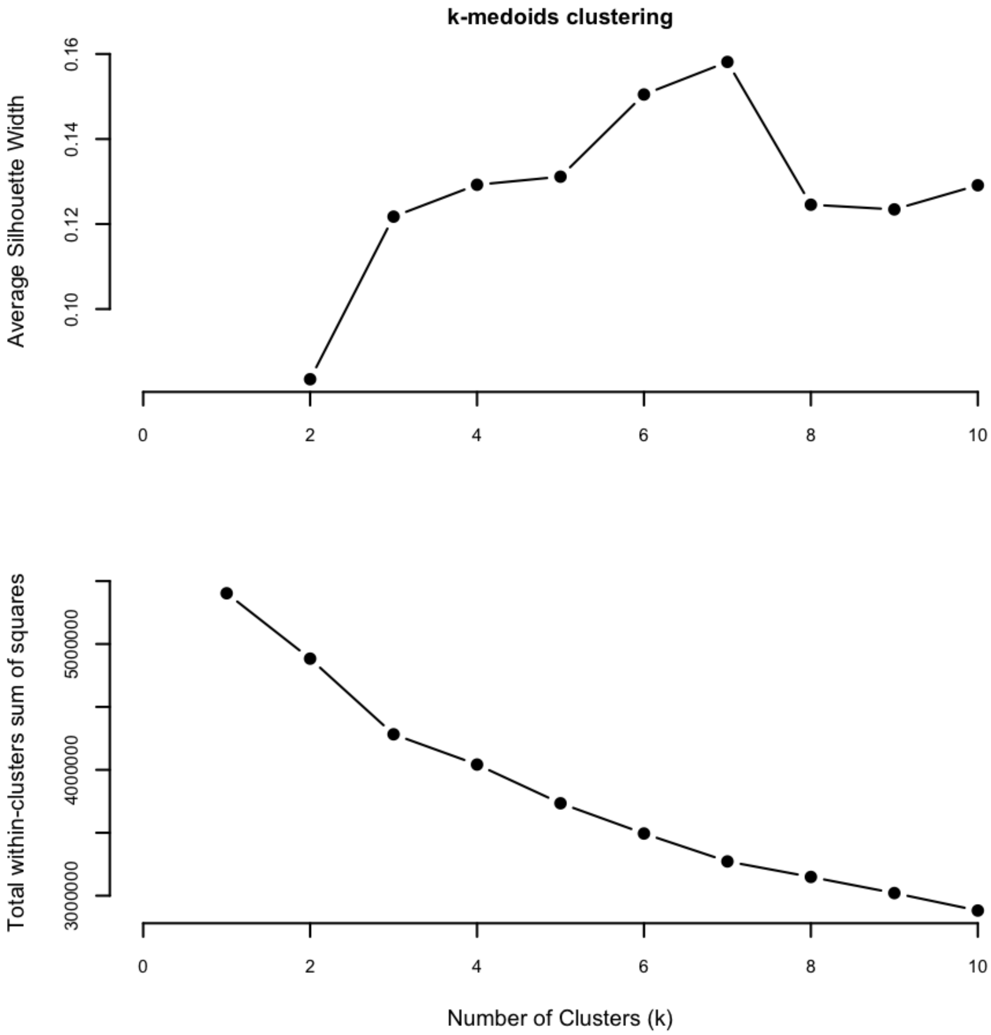

Figure 26: Validation procedure for the *k-medoids* and *k-means* clustering algorithms based on the number of cluster that maximizes average silhouette width (upper panels; Kaufman and Rousseeuw, 1990) and minimizes the total within-cluster sum of squares (WSS; lower panels).

4.15.4.2 Inter-cluster dissimilarity

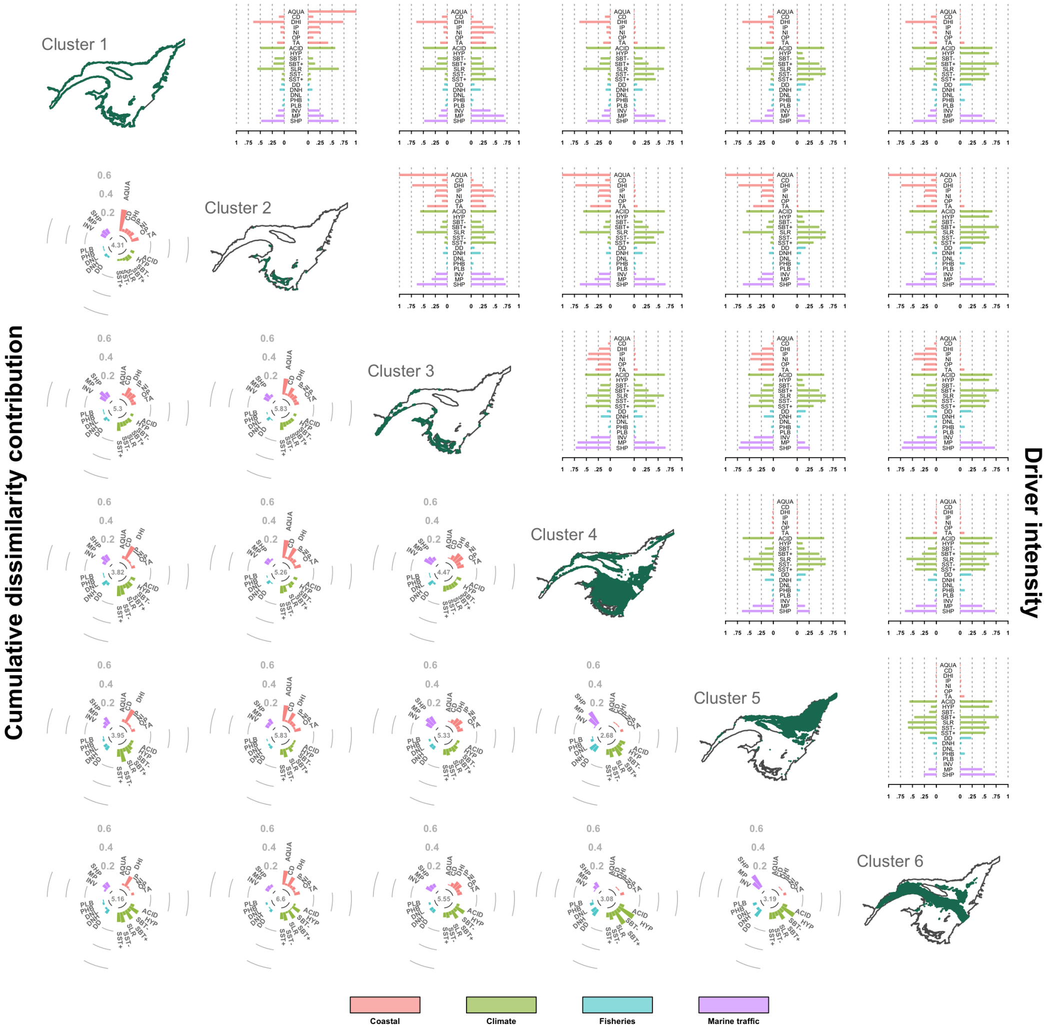

Figure 27: Evaluation of inter-cluster dissimilarity using a similarity percentage analysis (SIMPER) with Manhattan distance (Clarke, 1993). The figure diagonal presents the distribution of the 6 clusters identified using the *k-medoids* clustering algorithm. The lower triangle shows all combinations of inter-cluster dissimilarity with circular barplots showing the percent contribution to total dissimilarity of each driver and with the total inter-cluster dissimilarity in the center of the barplots. The upper triangle shows the average relative intensity of each driver for all driver combinations, with barplots to the left and the right representing the row and columns clusters, respectively.

4.15.4.3 Intra-cluster similarity

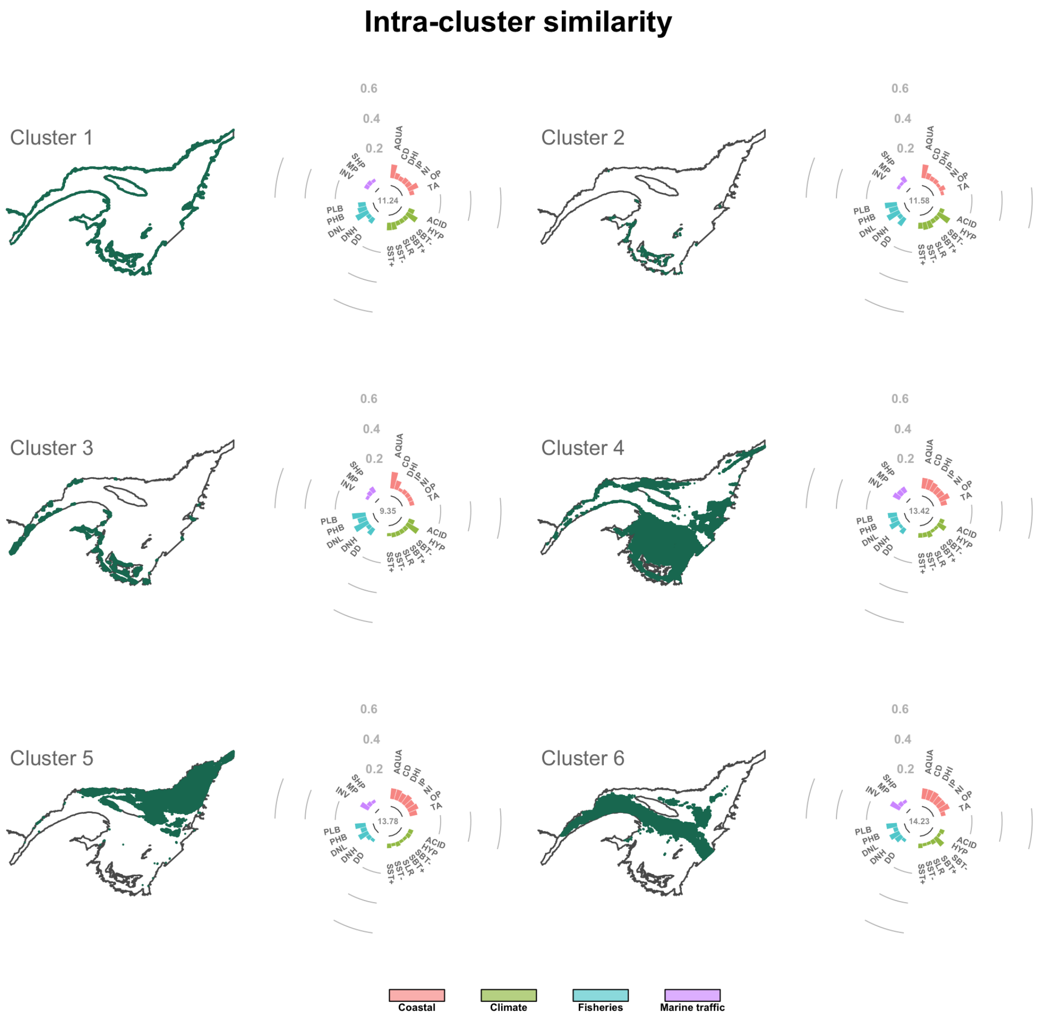

Figure 28: Evaluation of intra-cluster similarity using the Manhattan distance transformed to a similarity index. The distribution of the 6 clusters is presented along with circular barplots showing the percent contribution to total similarity of each driver and with the total intra-cluster similarity in the center of the barplots.

ARTICLE 5

LES INTERACTIONS ÉCOLOGIQUES AMPLIFIENT LES EFFETS CUMULATIFS DANS LES ÉCOSYSTÈMES MARINS

5.1 Résumé

Les interactions écologiques sont un couteau à deux tranchants: les connexions qui sont vitales à l'existence des communautés écologiques complexes qui ont inspiré la métaphore de Darwin sur les rivages emmêlés (*"tangled bank"*) sont également les connexions qui permettent aux effets des changements climatiques et des activités humaines de se propager à travers les communautés. Les interactions écologiques demeurent pourtant absentes de la littérature sur la gestion environnementale. Ici, nous évaluons les effets cumulatifs des changements climatiques et des activités humaines sur les espèces du Système du Saint-Laurent à l'aide d'une nouvelle approche à l'échelle des réseaux qui permet de considérer les interactions qui structurent les communautés. Nous comparons notre approche avec une évaluation conventionnelle espèce-centée pour exposer des propriétés émergentes provenant des interactions écologiques et trouvons des effets sur des espèces qui seraient normalement ignorés. Pour certaines espèces, considérer les interactions écologiques pourraient être l'unique moyen d'évaluer les effets des stresseurs environnementaux. Les poissons et les mammifères marins sont particulièrement susceptibles aux effets indirects de tous les types de stresseurs considérés; ceci est un contraste marqué avec le nombre limité de stresseurs qui les affectent directement. Nos résultats sont particulièrement pertinents pour la gestion d'espèces exploitées et en péril, pour qui nous ignorons potentiellement des risques importants en négligeant les effets indirects provenant des interactions entre espèces.

Ce cinquième article, intitulé *"Ecological interactions amplify cumulative effects in marine systems"* a été corédigé par moi-même, Kevin Cazelles, Rémi M. Daigle, Dominique Gravel et Philippe Archambault. Cet article est le résultat de l'entièreté de la thèse. Il combine les travaux présentés aux chapitres précédents et propose des analyses supplémentaires en vue d'effectuer une évaluation des effets cumulatifs communauté-centrée pour le Système du Saint-Laurent. J'ai structuré et établi les objectifs de cet article conjointement avec Dominique Gravel et Philippe Archambault. J'ai structuré et formaté les données, effectué les analyses et été en charge des développements techniques. Kevin Cazelles et Rémi M. Daigle ont contribué à ces étapes. J'ai dirigé la rédaction de l'article. Tous les co-auteurs ont contributé à la rédaction et aux révisions de l'article. Considérant l'originalité des analyses proposées et de la méthodologie développée, j'ai espoir que cet article sera intéressant pour une revue à haut facteur d'impact. C'est la raison pour laquelle cet article est présenté dans un format court, avec la méthodologie à la fin.

Les sections suivantes sont celles de l'article en préparation.

5.2 Title

Ecological interactions amplify cumulative effects in marine ecosystems

5.3 Authors

David Beauchesne, Kevin Cazelles, Rémi M. Daigle, Dominique Gravel, Philippe Archambault

5.4 Summary

Species interactions are a double-edged sword (Gilarranz et al., 2017): those connections that are so vital to the existence of the complex ecological communities that inspired Darwin's famous "*tangled bank*" metaphor are also those that allow the cumulative effects of climate change and human activities to indirectly spread through communities (Estes and Palmisano, 1974; Paine, 1980; Wootton, 2002; Bascompte, 2009; Estes et al., 2011). Still, species interactions remain conspicuously absent from the environmental management literature (Kollmann et al., 2016; Heinen et al., 2020). Here, we assess the cumulative effects of global change and human activities on the species of the St. Lawrence System in eastern Canada using a novel network-scale approach that explicitly considers the underlying web of interactions structuring communities. We compare our novel approach to a conventional species-scale assessment to expose transgressive properties arising from species interactions and uncover cumulative effects to species that would otherwise be overlooked. Fishes and marine mammals in particular are prone to indirect effects from all types of stressors; this contrasts considerably with the limited number of stressors affecting them directly. Our approach is, to our knowledge, the first ecosystem based approach relevant to the management of exploited and endangered species which can evaluate the less obvious yet no less significant trophically-mediated effects arising from species interactions in a multiple stressors framework.

5.5 Main

With demands for natural resources increasing with populations (FAO, 2017), and the effects of climate change intensifying (IPCC, 2019), ecosystems worldwide are increasingly burdened with the cumulative effects of a vast array of stressors (Halpern et al., 2015b, 2019). For example, coral reefs face a suite of stressors including fishing, warming temperatures, ocean acidification, and water pollution (McClanahan et al., 2014; Harborne et al., 2017). While the magnitude and nature of the direct effects of stressors on species depend on species-specific sensitivities (Oppenheimer et al., 2015), stressors can also indirectly ripple through entire ecological communities because of the organization of life as networks of interacting species (Estes and Palmisano, 1974; Paine, 1980; Wootton, 2002; Bascompte, 2009; Estes et al., 2011). This is particularly significant considering that indirect effects may be as significant as, and propagate faster than, direct effects (Wootton, 2002; Menge, 1995). The propagation of the effects of stressors depends on the number, configuration and strength of the interactions structuring a community (Wootton, 2002; Montoya et al., 2009); stressors can modify these structural properties and rewire – that is, reconfigure – entire communities and alter the flow of energy in the system (Blanchard, 2015; Kortsch et al., 2015; Bartley et al., 2019). Properly evaluating the net effects of stressors on species should therefore consider species-specific sensitivities, trophically-mediated indirect effects and the structure of local communities (Beauchesne et al., 2020a). Management actions considering community structure and species interactions can lead to efficient and cost-effective outcomes, such as the restoration of kelp forests through the recovery of sea otters (*Enhydra lutris*), an important keystone species (*sensu* Power et al., 1996) on the Pacific Coast of North America (Estes and Palmisano, 1974; Estes et al., 2010).

These observations stimulate a growing demand for the management of the structural properties of whole communities to preserve ecosystems (McCann, 2007; Tylianakis et al., 2010; McDonald-Madden et al., 2016; Heinen et al., 2020) and for a broader application of regional cumulative effects assessments (Jones, 2016; Hodgson et al., 2019), which are integral components of an ecosystem-based approach to environmental management (Christensen et al., 1996). Yet environmental management still overwhelmingly operates in silos, focusing on single-stressor and single-species assessments (Hodgson et al., 2019; O'Brien et al., 2019). Quantitative methods to assess and map the cumulative effects of stressors were developed to address this issue (Halpern et al., 2008b; Maxwell et al., 2013) and used extensively in marine ecosystems (Halpern et al., 2015a, 2019; Trew et al., 2019). However, these methods assume that the ecological units on which cumulative effects are assessed, such as habitats (Halpern et al., 2019) or species (Maxwell et al., 2013; Trew et al., 2019), are independent. Applied to species, these approaches capture species-specific responses to the cumulative effects of stressors, *i.e.* their direct effect; yet they ignore the complexities of the processes governing ecosystem dynamics (Halpern and Fujita, 2013; Giakoumi et al., 2015; Hodgson et al., 2019), including trophically-mediated indirect effects and community structure.

Here, we expand conventional cumulative effects assessment approaches (Halpern et al., 2008b; Maxwell et al., 2013) with recent progress in theoretical ecology (Stouffer et al., 2007, 2012; Beauchesne et al., 2020a) to relax the assumption of independence between species and propose a novel network-scale assessment of cumulative effects. We focus on sub-networks of species interactions called motifs (*sensu* Milo et al., 2002) to assess cumulative effects. Motifs are subsets of n-species that, when put together, construct whole food webs and provide a mesoscale characterization of the structural properties of ecological communities (Bascompte and Melián, 2005; Stouffer et al., 2007; Stouffer and Bascompte, 2010, 2011; Bramon Mora et al., 2018). We then compare our approach to conventional species-scale assessments. Given that effects of stressors can only arise where stressors co-occur with species, and that effects should increase with the number of stressors, their intensity and the number of species, we expect both the species-scale and the network-scale assessments to predict similar distribution of overall cumulative effects. However, we expect the differences between the species-scale and network-scale approaches to reveal how indirect effects refine the assessment, which we refer to as transgressive properties arising from species interactions.

Although our approach is general, we focus our assessment on the St. Lawrence System, in eastern Canada. This system is formed by one of the largest estuaries in the world and a vast interior sea. Together, they host diverse and productive ecological communities (El-Sabh and Silverberg, 1990; Savenkoff et al., 2000) and provide a wealth of ecosystem services benefiting the Canadian economy: a rich commercial fisheries industry, a seaway that grants access to one of the most densely populated regions in North-America and more than 40 ports, an expanding aquaculture production, and a thriving tourism industry (Beauchesne et al., 2016; Schloss et al., 2017). We demonstrate our approach by assessing and mapping the cumulative effects of 18 stressors on 193 taxa between 2010 and 2015 at a 1 km^2 scale. We use data-based or theoretically-derived indicators of the distribution and intensity of stressors (Beauchesne et al., 2020b), the distribution of species, the metaweb of species interactions, species-specific sensitivities to stressors, and species sensitivity to stressors as a function of their trophic position and specific pathways of effects (see Methods; Beauchesne et al., 2020a).

5.5.1 Results

5.5.1.1 Network-scale cumulative effects assessment

An overview of the interactions likely to affect a species' dynamics – and the propagation of stressors – can be obtained through the collection of n-species motifs in which a species is involved in a food web (Stouffer et al., 2012); we refer to this as a species' motif census (Beauchesne et al., 2020a). By assessing and summarizing cumulative effects across a species' motif census, we consider direct effects to the species of interest, trophically-mediated indirect effects arising from effects to species with which the focal species is interacting, and the structure of local communities (see Methods). We then sum the cumulative effects of all species in each 1 km^2 grid cell to obtain a community-aggregated assessment of cumulative effects (see Methods). We find that no area of the St. Lawrence System and few taxa are free of cumulative effects (Fig.

29) and that cumulative effects are greater in areas where multiple stressors co-occur at high relative intensities and converge with diverse local communities (Supplementary figs. 32, 33, 34).

As expected, the network-scale and species-scale are strongly correlated (Spearman's rank correlation $p_s = 0.91$, P < 0.001; Supplementary fig. 35). The difference between both assessments uncovers transgressive properties arising from species interactions, which we evaluate as the log ratio of a species network-scale assessment over its species-scale assessment; we then sum species transgressive properties for all species in a grid cell to highlight areas where the assessments differ most. We find that the distribution of transgressive properties is similar to that of cumulative effects assessments (network-scale: $p_s = 0.99$, P < 0.001; species-scale: $p_s = 0.89$, P < 0.001; Supplementary fig. 35); this suggests that interactions dampen or amplify the relative magnitude of the species-scale approach as a function of the structure of local food webs.

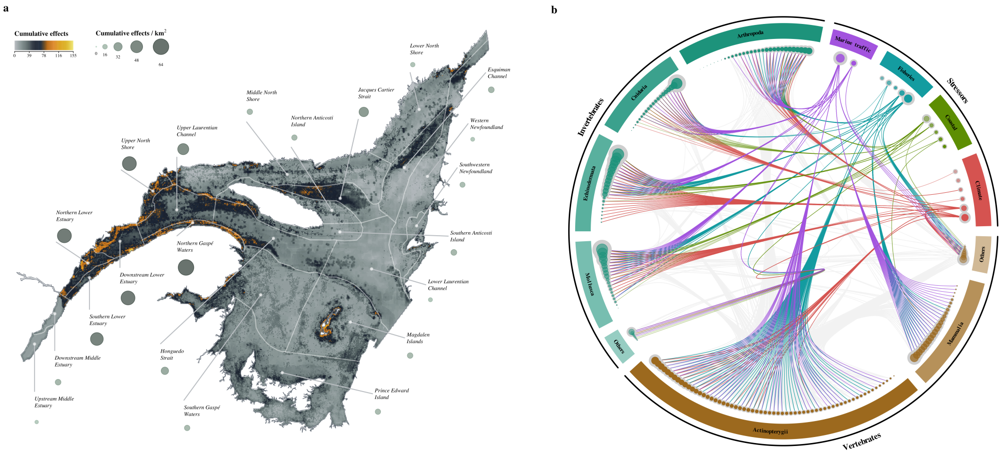

Figure 29: **Network-scale cumulative effects assessment in the St. Lawrence System.** a) Network-scale relative cumulative effects assessment of 18 stressors on 193 taxa in the St. Lawrence System explicitly considering the underlying structure of the ecological community. Grey points represent the cumulative effects scores / km^2 in bioregions of the St. Lawrence. b) Multiplex network presenting the metaweb of interactions between the 193 taxa considered (grey connections), the presence of an effect of individual stressors on each taxa (colored connections), the overall cumulative effect on each taxon (taxa point size) and the mean effect of stressors (stressor point size).

5.5.1.2 Role of interactions for individual species assessments

We explore cumulative effects to individual species (i) by summarizing individual assessments regionally as the average cumulative effects (C_i) over a species' predicted distribution (C_i/km^2). We find that the network-scale assessment amplifies regional cumulative effects for most species (Fig. 30). The difference between the species-scale and network-scale assessments is correlated with a species' mean trophic sensitivity (p_s = 0.85, P < 0.001; Fig. 30) and mean indirect effects (p_s = 0.95, P < 0.001), which captures transgressive properties arising from species interactions.

There are 3 broad mechanisms by which cumulative effects are amplified through indirect effects. First, a species may be directly and indirectly affected by the same set of stressor(s). For example, groundfish populations – Atlantic halibut (*Hippoglossus hippoglossus*), American plaice (*Hippoglossoides platessoides*), witch flounder (*Glyptocephalus cynoglossus*), Atlantic cod (*Gadus morhua*), redfish (*Sebastes spp.*), and Greenland halibut (*Reinhardtius hippoglossoides*) – are generally affected by all stressor types directly and indirectly (Fig 30; Supplementary fig. 36a). The network-scale assessment shows that interactions and local community structure modulate the relative magnitude of the effects across groundfish species distributions. The groundfish populations of the St. Lawrence System collapsed in the early 1990s due to overfishing (Savenkoff et al., 2007; Morissette et al., 2009) and shifts in trophic structure have been cited as the likely cause for their slow recovery (*e.g.* Jackson et al., 2001; Frank et al., 2005). For such species, cumulative effects are likely under- or overestimated when interactions are overlooked.

Second, a species may be indirectly affected by stressors that were not captured by the species-scale assessment. For example, monkfish (*Lophius americanus*), a demersal predator frequently caught as bycatch in St. Lawrence fisheries, is directly affected by fisheries and climate stressors, yet affected by all stressors indirectly; furthermore, the magnitude of indirect effects to monkfish supplants that of direct effects (Fig 30; Supplementary fig. 36b). For such species, a general increase in the magnitude of cumulative effects may be expected and overlooking interactions likely results in underestimating cumulative effects and overlooking stressors whose effects arise solely through indirect pathways.

Third, a species may be indirectly affected by stressors in locations that were not highlighted by species-scale assessments. The beluga whale (*Delphinapterus leucas*), an endangered and emblematic predator population whose high-profile conservation efforts have yielded no apparent recovery, is an eye-catching example in the St. Lawrence System (Plourde et al., 2014; Williams et al., 2017). The population is mostly affected directly by marine traffic and coastal stressors along the coast and across vessel tracks. However, the network-scale assessment shows that the beluga population is indirectly affected by all stressor types and highlights areas along the coast that were not captured by the species-scale assessment (Fig 30; Supplementary fig. 36c). This supports recent reports discussing the importance of trophically-mediated effects in the lack of recovery of the beluga population (Plourde et al., 2014; Williams et al., 2017). For such species, considering interactions may be most important and the only way to capture all sources of stress and identify areas where management measures are missing.

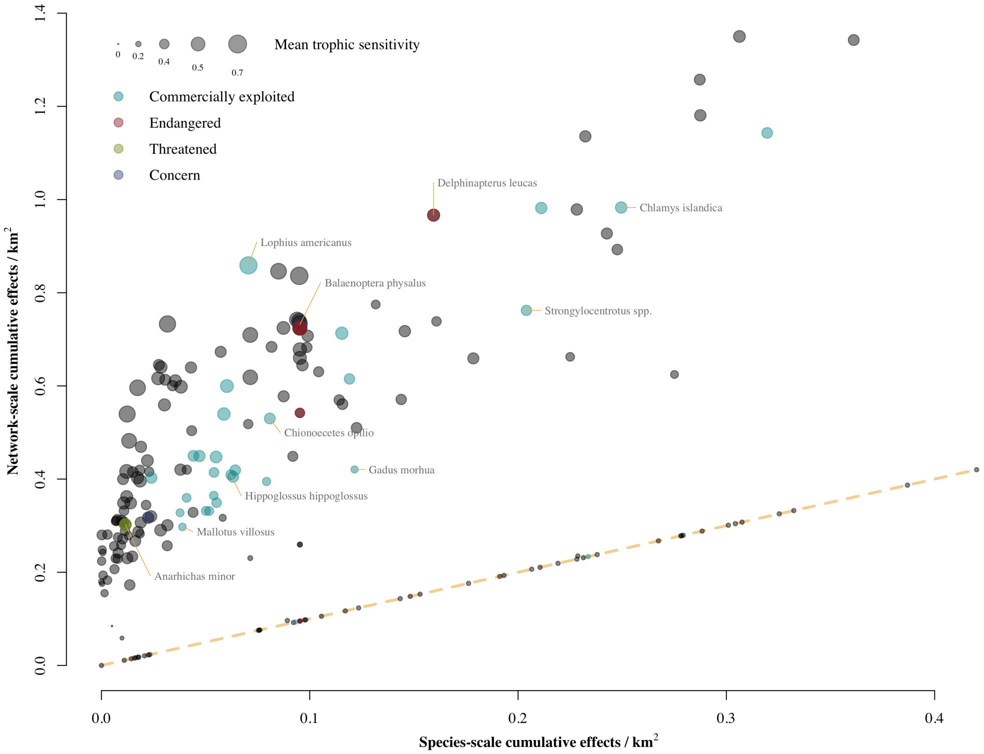

Figure 30: **Comparison of network-scale and species-scale cumulative effects for individual species.** Scatterplot of the mean network-scale cumulative effects as a function of the species-scale cumulative effect over a species predicted distribution (C/km^2) for all 193 taxa considered. The size of the point is the trophic sensitivity of each taxon, corresponding to the scaled trophic sensitivity given a species' position in a food web and stressors entry points Beauchesne et al. (2020a). Taxa along the orange line are those for which the network-scale and species-scale assessments are equal, that is species which have no predicted interaction.

5.5.1.3 Cumulative effects to taxonomic groups

Taxonomic groups have previously been used to showcase broad-scale ecological trends that can be informative for science and management (Tittensor et al., 2010; Kroeker et al., 2013; Sydeman et al., 2015); we thus explored cumulative effects among and between taxonomic groups by classifying taxa into 8 groups divided among invertebrates ($n = 5$) and vertebrates ($n = 3$). We find that the contribution of stressors to direct and indirect effects varies between taxonomic groups and that the spatial distribution of their cumulative effects also differs (Fig. 31; Supplementary fig. 37). Direct effects are greatest on invertebrates, except for arthropods, and dominated by climate and coastal stressors, whereas direct effects to vertebrates are relatively milder and limited to a few stressors – that is, fisheries for fishes and marine traffic for marine mammals (Fig. 31; Supplementary figs. 38, 39). Indirect effects, meanwhile, are prevalent across taxa and from all stressor types, yet the relative importance of direct effects, compared to indirect effects, is lower for vertebrates (Fig. 31; Supplementary figs. 38, 39).

These results reflect broad taxa-specific sensitivities to the effects of stressors. Invertebrates are predominantly benthic species with limited mobility, many of which feed by filtering the water column, have calcified exoskeletons, or both; these traits make them generally more susceptible to the effects of stressors affecting the physico-chemical properties of their environment, and particularly to the effects of climate stressors (Kroeker et al., 2010, 2013). Vertebrates, on the other hand, are generally mobile and active species, and thus capable of minimizing their exposure to stressors. Fishes are ectothermic and more susceptible to the effects of physico-chemical variations in their environment when compared to endothermic mammals. Yet both fishes and marine mammals are much less sensitive than invertebrates to climate stressors (Kroeker et al., 2010; Sydeman et al., 2015); instead, fishes and marine mammals tend to be most affected by changes operating through trophically-mediated effects (Sydeman et al., 2015; Stier et al., 2016).

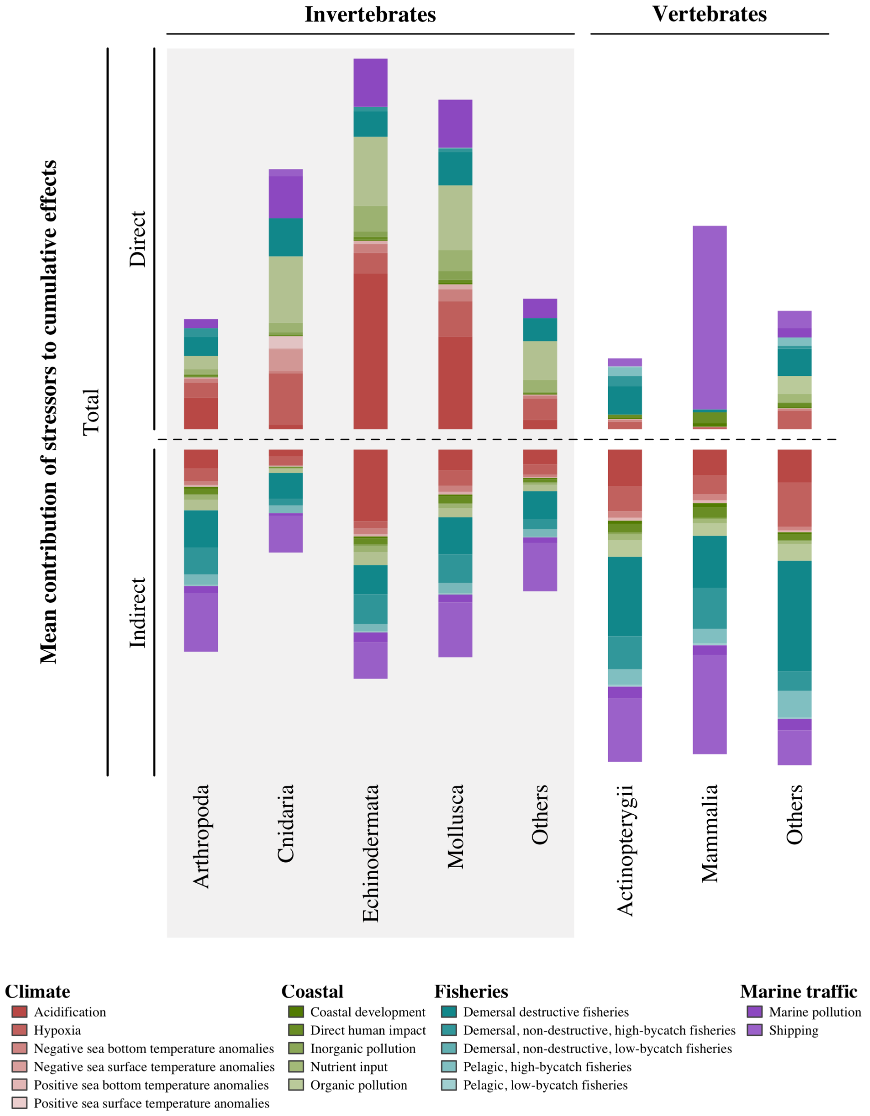

Figure 31: **Contribution of stressors to network-scale cumulative effects of taxa classified by taxonomic groups.** Mean contribution of 18 stressors to the regional cumulative effects assessment (C/km^2) of 193 taxa in the St. Lawrence System classified into 8 taxonomic groups. Taxonomic groups for invertebrates and vertebrates are divided at the phyla and classes level, respectively. For each group, the mean contribution per species was used to evaluate stressor contribution to cumulative effects. The contribution can be divided as the direct and indirect contributions of each stressor to the cumulative effects on each taxon. Direct effects are those attributable to the effect of a stressor on a focal species, while indirect effects are the mean effects of stressors spreading through all 3-species interactions a taxon is involved in. The total contribution to cumulative effect is the sum of the direct and indirect contributions.

5.5.2 Discussion

In this study, we show that considering species interactions to assess the cumulative effects of climate change and human activities uncovers transgressive properties that would otherwise be overlooked by conventional species-scale assessments. For many species of the St. Lawrence System, our approach reveals that indirect effects outweigh direct effects, uncovers novel sources of stress, or both. For species that are particularly susceptible to indirect effects, like fishes and marine mammals, properly assessing cumulative effects seems achievable solely through the lens of species interactions. Most commercially exploited species and species at risk in the St. Lawrence System fall in that category; this is worrisome, as it suggests that current management plans and recovery strategies may ignore significant threats by overlooking indirect effects. In cases where the mitigation of direct effects are currently insufficient, impractical, or even impossible, considering indirect effects provides a complementary outlook for management actions to mitigate alternate pathways of effects. This is particularly critical in the context of climate change, over which we possess little to no management control locally; still, management plans should be devised with an understanding of the effects of climate change on species (Elliott, 2011; Brown et al., 2013; Dempsey et al., 2017).

The approach we propose to evaluate cumulative effects can offer specific guidance for management and conservation by quantitatively predicting the relative magnitude of both direct and indirect effects of all stressors on all species. Our approach can efficiently identify the pathways of effect that pose the greatest risk to a species of interest, or identify early warning signals for species or areas without management plans that are at risk from cumulative effects. Once identified, these pathways of effect could be further investigated empirically through targeted *in situ* sampling, mensurative or manipulative experiments (*sensu* Hulbert 1984), and the empirical findings could help refine the cumulative effects assessment. Fostering such a feedback loop between predictive capabilities and empirical investigations is key to building an adaptive capacity in the context of ecosystem-based management (also see Hodgson et al., 2019).

Our approach retains some limitations and assumptions of conventional species-scale cumulative effects assessments (see Halpern and Fujita, 2013; Halpern et al., 2015b; Hodgson et al., 2019), the most important being that species-specific responses to multiple stressors – that is, how a single species responds to the effects of multiple stressors acting simultaneously – are assumed linear and additive. However, nonlinear responses and non-additive effects are prevalent in natural systems (Crain et al., 2008; Côté et al., 2016). Still, our approach considers the nonlinear dynamics and non-additive effects of multiple stressors arising from a species interactions (see Methods; Beauchesne et al., 2020a). Much of the limitations and assumptions of our approach are representative of a general lack of knowledge and data for the application of holistic environmental approaches. Once available, knowledge and data could be accommodated to improve the individual components that make up the assessment, that is the distribution and intensity of stressors, the distribution of species, the metaweb of species interactions, species-specific sensitivities to stressors, and trophic sensitivities. These individual components are flexible, grounded in theory and data-oriented; the expanding corpus of openly available environmental knowledge and computational capabilities can thus be leveraged to independently and incrementally improve their quality and, in doing so, enhance the quality of cumulative effects assessments.

After decades of accumulated empirical and theoretical knowledge on the significance of trophically-mediated indirect effects (Estes and Palmisano, 1974; Paine, 1980; Wootton, 2002; Estes et al., 2011), the importance of species interactions and community structure in understanding the effects of global changes is increasingly recognised: species cannot be considered in a vacuum (Tylianakis et al., 2008; O'Gorman and Emmerson, 2009; Gilarranz et al., 2016, 2017; O'Gorman et al., 2019; Waller et al., 2020; Beauchesne et al., 2020a). Here, we quantitatively show the gains in ecological understanding we can achieve by considering the less obvious yet no less damaging effects of multiple stressors propagating through species interactions. Our results suggest that we should strive to distance ourselves from species-centric approaches in favour of holistic approaches to monitor and preserve biostructures (*sensu* McCann, 2007). Still, few approaches combine holistic capabilities and broad applicability. In pairing theory, environmental management and computational capabilities, our approach offers an accessible perspective and concrete tools to assess the individual and cumulative effects of climate change and human activities on ecological communities. We believe that building such holistic capabilities is currently one of the most important challenges in fulfilling the unkept promise of ecosystem-based management.

5.6 Methods

5.6.1 General model

Whole food webs can be decomposed into collections of p-species interactions called motifs (Milo et al., 2002) that provide a mesoscale characterization of the structural properties of ecological networks (Bascompte and Melián, 2005; Stouffer et al., 2007; Stouffer and Bascompte, 2010, 2011; Bramon Mora et al., 2018). In a n-species food web ($n \geq p$), the collection of p-species motifs ($p \leq n$) in which species i is involved in ($M_i = \{m_{i,1}, m_{i,2}, ..., m_{i,x}\}$) forms its species motif census (M_i; Stouffer et al., 2012; Beauchesne et al., 2020a). The motif census provides an overview of all the interactions and connected species likely to affect a species' dynamics. Here, we focus exclusively on the most abundant 3-species motifs in empirical food webs (*i.e.* trophic food chain, omnivory, exploitative and apparent composition; Camacho et al., 2007; Stouffer and Bascompte, 2010) to assess a species motif census, although the general model would be applicable to any p-species motifs.

For any 3-species motif $m_{i,x}$ in species i's motif census (M_i), we evaluate the net effect of all stressors on the 3 species as the sum of their direct effects on all species involved – that is, the sum of species-specific responses $S_{m_{i,x}}$ – as in Halpern et al. (2008b):

$$S_{m_{i,x}} = \sum_{k=1}^{3} \sum_{j} D_j * \mu_{k,j}, \tag{5.1}$$

where k are the 3 species involved in motif $m_{i,x}$, D_j is the standardized intensity of stressor j (scaled between 0 and 1; see Stressors data) and $\mu_{k,j}$ is the relative species-specific sensitivity of species k to stressor j (range between 0 and 1; see Specie-specific sensitivity). The relative contribution of stressors to direct effects are those that affect focal species i, whereas the relative contribution to indirect effects are those that affect the species interacting with species i in $m_{i,x}$.

Here, we wish to explicitly consider that a species' response to stressors depends on its own response as well as the response of species it interacts with. However, if we only considered $S_{m_{i,x}}$ to evaluate cumulative effects, we would assume that all species involved in interaction $m_{i,x}$ respond the same way to the effects of all stressors. We know this to be false. Indeed, a species sensitivity to trophically-mediated effects – which we refer to as a species' trophic sensitivity ($T_{i,m_{i,x}}$) – depends on the structure of the community, its trophic position and the specific entry points of stressors in the system (Beauchesne et al., 2020a). We use simulated trophic sensitivities as weighting factors (scaled between 0 and 1) to modulate the effects of stressors to focal species i's given its trophic position and the specific pathways of effects – *i.e.* the entry points – through which stressors affect interacting species (see Trophic sensitivity below and Beauchesne et al., 2020a, for more details):

$$C_{i,m_{i,x}} = T_{i,m_{i,x}} * S_{m_{i,x}}, \tag{5.2}$$

where $C_{i,m_{i,x}}$ is the cumulative effect of all stressors on species i in $m_{i,x}$, and $T_{i,m_{i,x}}$ is the trophic sensitivity of species i to the effects of stressors in $m_{i,x}$. We then summarize cumulative effects on species i by averaging the cumulative effects across a species' motif census to obtain an unbiased measure of the topological configuration of species interactions (Stouffer et al., 2012):

$$C_{N_{i,x}} = \frac{1}{|M_i|} \sum_{m_{i,x} \in M_i} C_{i,m_{i,x}}, \tag{5.3}$$

where C_{N_i} is the network-scale cumulative effects assessment on species i and $|M_i|$ is the number of motifs in the motif census of species i. Finally, we summarize over all n species locally to obtain a community-aggregated assessment of network-scale cumulative effects:

$$C_N = \sum_i C_{N_i}, \tag{5.4}$$

We do not control for local species richness because we consider that effects of stressors should be considered greater in areas where richness is greater. The full model is thus:

$$C_N = \sum_i \frac{1}{|M_i|} \sum_{m_{i,x} \in M_i} T_{i,m_{i,x}} * \sum_{k=1}^{3} \sum_j D_j * \mu_{k,j} \tag{5.5}$$

5.6.2 Stressors data

We used the spatial distribution and intensity of 18 stressors available through an open-knowledge platform called *eDrivers* (Beauchesne et al., 2020b). Stressors are divided in 4 groups: land-based (*i.e.* inorganic pollution, organic pollution, nutrient input, coastal development, and direct human impact), climate (*i.e.* positive and negative bottom-water and surface-water temperature anomalies, ocean acidification, and hypoxia), fisheries (*i.e.* demersal destructive, demersal non-destructive high-bycatch, demersal non-destructive low-bycatch, pelagic high-bycatch, and pelagic low-bycatch) and marine traffic (*i.e.* shipping and marine pollution; Table 9). Methods to characterize each stressor are described in Beauchesne et al. (2020b). Stressors with non-normal frequency distributions were log-transformed to avoid underestimating intermediate stressor intensity values (Halpern et al., 2019). All stressors were scaled between 0 and 1 to obtain relative intensities and allow comparisons between stressors. For each stressor, the 99th quantile of intensity distribution was used as the upper bound for scaling to control for extreme values that may or may not be real observations.

5.6.3 Biotic data

We used data from 4 monitoring programs conducted by Fisheries and Oceans Canada (DFO) to obtain a list of taxa with observed occurrences in the St. Lawrence System (Table 10). We included a list of 30 known whale and seal species in the St. Lawrence System and used distribution ranges available from the IUCN Species Red List of Threatened Species for 24 of the 30 marine mammals species (Table 10; IUCN, 2020). We curated the list of taxa used for the analyses by grouping and removing taxa based on expert knowledge and bibliographic research. For example, species of the same genus and hard to distinguish were grouped; species that were identified as probable misidentifications or outliers were removed from the data. The curation process yielded 424953 taxa occurrences and 434851 taxa absences for 391 taxa between 2010 and 2015 (Tables 10, 13). The curation process was documented and is available on GitHub (https://github.com/eBiotic/Biotic). All species scientific names were resolved using the `taxize` R package (Chamberlain and Szöcs, 2013; Chamberlain et al., 2019).

5.6.4 Abiotic data

We used environmental data characterizing the bottom-water and surface-water salinity, temperature, oxygen, primary productivity, pH (surface) and aragonite (bottom) conditions in the St. Lawrence System. We also considered latitude, longitude and depth, for a total of 13 environmental descriptors. The data was accessed through various regional (Dutil et al., 2011, 2012; Galbraith et al., 2018; Starr and Chassé, 2019; Blais et al., 2019) and global (Assis et al., 2018) environmental monitoring programs and public repositories (Table 11).

5.6.5 Traits data

We documented the body composition, the maximal body size, the type of marine environment in which species are found, the feeding mode, the mobility and the phylum (Table 12) of all 391 taxa. We extracted traits data from the World Register of Marine Species (WoRMS; WoRMS Editorial Board, 2017), FishBase (Froese and Pauly, 2019), SeaLifeBase (Palomares and Pauly, 2019), the Encyclopedia of Life (Encyclopedia of Life, 2020) and the Global Biotic Interaction (GloBI) database (Poelen et al., 2014, 2019). We used the `taxize` (Chamberlain and Szöcs, 2013; Chamberlain et al., 2019), `worrms` (Chamberlain, 2020) and `rfishbase` (Boettiger et al., 2012) R packages to extract traits data. Any taxon for which traits were unavailable programmatically were searched manually on the WoRMS and Encyclopedia of Life web portals. We also documented whether a species was targeted by fisheries or caught as bycatch by local fisheries using data from DFO's Fisheries Logbook Program (DFO, 2016b).

5.6.6 Data representation

All datasets are presented at a 1 km^2 resolution even though some source data had coarser resolutions (Table 9). We resampled and reprojected data when necessary using nearest neighbour estimates, which preserves the values of the source data. By doing so, we assume that the coarser data are evenly distributed across finer-scale cells with which they overlap. We used the NAD83 / Quebec Lambert projection (EPSG: 32198), which is well suited to represent and preserve surface area within our study system.

5.6.7 Metaweb

We predicted the metaweb of the St. Lawrence System, *i.e.* the network of biotic interactions, using a recommender approach (Beauchesne et al., 2016). Here, we provide a brief overview of the approach, but refer to Beauchesne et al. (2016) for more details. The approach consists of a series of logical steps that predict a candidate resource list for each taxon based on empirical data available and the similarity among consumers and resources. It uses the K-nearest neighbour algorithm (KNN; Murphy, 2012) to predict pairwise interactions given taxonomic and dietary similarity between consumers and resources and is informed by a catalogue of empirically known biotic interactions worldwide (Beauchesne et al., 2016). The interactions catalogue was built using food web data (Brose et al., 2005; Kortsch et al., 2015; University of Canberra, 2016), predator-prey interactions (Barnes et al., 2008) and pairwise interactions from the GloBI database (Poelen et al., 2014, 2019). We limited the compendium to taxa found in marine and coastal ecosystems. Taxa similarity was evaluated from taxonomic classification and sets of consumers or resources using the Tanimoto similarity measure. A weight of 0.5 was given to taxonomy and consumers or resources to consider them simultaneously (Desjardins-Proulx et al., 2016). The taxonomy of all taxa considered was accessed and validated from WoRMS (WoRMS Editorial Board, 2017) using the `taxize` package (Chamberlain and Szöcs, 2013; Chamberlain et al., 2019). We included the main phytoplankton and zooplankton taxa found in the St. Lawrence System to predict the metaweb (Morissette et al., 2003; Savenkoff et al., 2004; Savenkoff, 2012); we then grouped predictions under phytoplankton or zooplankton. This yielded a total of 393 taxa (S), considering all 391 taxa identified through the biotic data and the addition of phytoplankton and zooplankton. We predicted a metaweb structured by 4880 links (L), a link density ($L_{moy} = L/S$) of 12.42 and a connectance ($C = L/S^2$) of 0.03, which is within range of most reported food webs (Dunne et al., 2002).

5.6.8 Species-specific sensitivity

We evaluated the relative species-species sensitivity of all 391 taxa to each stressor using a trait-matching approach. For each stressor, we identified traits that were known or suspected to influence a species sensitivity to the effects of the stressor (Table 14). For example, the feeding strategy of an organism affects its sensitivity to nutrient and metal loading (Ellis et al., 2017), whereas its body composition affects its sensitivity to ocean acidification (Kroeker et al., 2013). Traits were categorized to reflect their relative contribution to the sensitivity of a taxa to the effects of a stressor. For example, suspension feeders are generally more affected by nutrients and metals than deposit feeders (Ellis et al., 2017), whereas calcifying organisms are more vulnerable to the effects of ocean acidification than non-calcifying organisms (Kroeker et al., 2013). Traits were categorized by giving a weight between 0 and 1 that reflects their relative contribution to the sensitivity of a taxa to a stressor: a weight of 0 represent a trait rendering taxa insensitive to the effects of a stressor, whereas a weight of 1 represents a trait associated with the highest relative sensitivity of a taxon to the effects of the stressor. If a taxon had multiple traits in a single category (*e.g.* crawler and swimmer), the maximal sensitivity weight was retained. This sensitivity assessment was informed by expert knowledge and bibliographic research. Trait-matching rules and relative sensitivity weights for each stressor are available in Table 14. The relative sensitivity of each taxon to a stressor was then evaluated as the product of the relative sensitivity weight of all traits associated with taxa sensitivity to the effects of the stressor. For example, the relative sensitivity to ocean acidification was evaluated using environment, mobility, body composition and phylum traits (Table 14). This process yielded a relative sensitivity assessment ranging between 0 and 1.

5.6.9 Taxa distribution

We extrapolated and mapped the distribution of taxa in the St. Lawrence System using the Random Forest ensemble learner (Breiman, 2001). We used the default parameters proposed by the `randomForest` R package to classify the presence or absence of taxa: 500 trees and the number of variables in the random subset at each node set to the square root of the number of variables (Liaw and Wiener, 2002). We only considered taxa with at least 50 observations, yielding a total of 169 taxa (Table 13). Each taxon was modeled using all 13 environmental descriptors (Table 11). We generated pseudo-absences for taxa without absences in the dataset ($n = 5$) by randomly sampling the study area at least 5 km away from observed points; for these taxa, we generated the same number of pseudo-absences as observed occurrences (Barbet-Massin et al., 2012). We measured the performance of the models for each taxon using the sensitivity, specificity, accuracy and True Skilled Statistics (TSS; Table 13; Allouche et al., 2006). For each taxon, we predicted spatial distribution within the same 1 km^2 resolution grid used for stressors. Individual taxa distributions were then smoothed using bisquare kernel smoothing (Dos Santos et al., 2018) with a 5 km radius to avoid potentially granular distributions that would affect estimations of species co-occurrence. For marine mammals, we used distribution ranges available from the IUCN Species Red List of Threatened Species for 24 species (IUCN, 2020). Our dataset includes distribution maps for 193 taxa in the St. Lawrence System. We assumed that phytoplankton and zooplankton species were present throughout the St. Lawrence System since these taxa are missing from our dataset and are required to properly consider trophic dynamics.

5.6.10 Trophic sensitivity

We provide a brief overview of the approach used by Beauchesne et al. (2020a) to evaluate a species' sensitivity to multiple stressors given its trophic position, *i.e* its trophic sensitivity. The effects of multiple stressors on the dynamics of the most empirically abundant 3-species motifs – *i.e.* tri-trophic food chain, omnivory, exploitative competition and apparent competition – were simulated using Lotka-Volterra models (Gellner and McCann, 2016). The dynamics of a single species regulated by density-dependent growth was also simulated; this control was included to consider disconnected species in the metaweb, which may arise due to insufficient data or because a species consumes detritus, bacteria or particulate organic matter. It was also used for the species-scale cumulative effects assessment so that disconnected species had the same cumulative effects results in the network-scale and species-scale assessments.

Negative effects of stressors were simulated by modifying combinations of equilibria equation parameters of population resource growth, mortality, attack and conversion rates (*i.e.* up to 9 parameters and 511 distinct pathways of effect; Beauchesne et al., 2020a). Modifications to parameters simulate effects of stressors on ecological processes; these represent the pathways through which stressors directly and indirectly affect ecological communities. The set of all ecological processes affected by stressors across species combine to collectively affect a community and form a pathway of effect. For each 3-species motif, all possible pathways of effects were simulated; this resulted in 127 unique pathways of effect for tri-trophic food chain, exploitative competition and apparent competition motifs through 7 parameters, 511 pathways of effect for the omnivory motif through 9 parameters, and 1 pathway of effect for disconnected species through 1 parameter. For each pathway of effect, a species's trophic sensitivity was defined as the difference in its equilibrium abundance before and after the permanent appearance of stressors in the system; this represents the net effect of stressors on species and integrates all direct and indirect effects propagating to a focal species (Abrams et al., 1996; Beauchesne et al., 2020a).

Here, due to the challenge of empirically distinguishing effects to specific ecological processes, we simplified pathways of effects and broadly considered effects to a species density rather than effects to specific ecological processes as in Beauchesne et al. (2020a). We used trophic sensitivities across possible pathways of effect simulated in Beauchesne et al. (2020a) as heuristics to assess a species' trophic sensitivity to the effects of stressors given its position in 3-species motifs. We used the absolute values of simulated trophic sensitivities and considered that any effect to a species' population dynamics, whether negative or positive, can propagate and disturb the dynamics of an ecological community. We then simplified pathways of effects as a function of their effects to the density of each species. For example, a pathway of effect targeting the mortality of a consumer was considered to affect the density of that consumer, whereas a pathway of effect targeting the attack rate of a consumer was considered to affect the density of both the consumer and the resource. We averaged trophic sensitivities to pathways of effects according to their contribution to the effects on species density, resulting in 8 possible pathways of effect for all 3-species motifs and 2 pathways of effect for the single species, each with a pathway of effect where no effects are observed. Trophic sensitivities were scaled between 0 and 1 for the analyses.

5.7 Code availability

The code to reproduce the analyses is available at https://github.com/david-beauchesne/FoodWeb-CumulativeImpact. The code to produce the stressor layers is available through the eDrivers GitHub organization (https://github.com/eDrivers) and described in Beauchesne et al. (2020b). The code to extract traits is available at https://github.com/eBiotic/Traits. The code to produce taxa distribution is available at https://github.com/eBiotic/Biotic. The code to predict species interactions is available at https://github.com/david-beauchesne/Predict_interactions and https://github.com/davidbeauchesne/Interaction_catalog, and described in Beauchesne et al. (2016). The code to predict the St. Lawrence metaweb is available at https://github.com/david-beauchesne/MetawebEGSL. The code to evaluate species-specific sensitivities is available at https://github.com/david-beauchesne/Species_Vulnerability. The code to evaluate trophic sensitivity is available at https://github.com/david-beauchesne/FoodWeb-MultiStressors and described in Beauchesne et al. (2020a). The open-source software R 3.6.0 was used for analyses (RCoreTeam, 2019). See table 15 in the supplementary materials for a list of all R packages used.

5.8 Acknowledgments

We thank the Fond de Recherche Québécois Nature et Technologie (FRQNT) and the Natural Science and Engineering Council of Canada (CRSNG) for financial support. This project is supported by Québec Océan, the Quebec Centre for Biodiversity Science (QCBS) and Takuvik networks. This research is also sponsored by the NSERC Canadian Healthy Oceans Network and its Partners: Department of Fisheries and Oceans Canada and INREST (representing the Port of Sept-Îles and City of Sept-Îles). This research was enabled in part by support provided by WestGrid (www.westgrid.ca) and

Compute Canada (www.computecanada.ca). We thank L. Tréau de Coeli for support in curating biotic datasets, and P. Calosi and C. Carrier-Belleau for support in ascribing sensitivities to traits.

5.9 Author contribution

DB, DG, and PA conceived the manuscript and the underlying objectives. DB prepared/formatted the data, performed the analyses, was in charge of technical developments and led the drafting of the manuscript. KC and RD contributed to technical developments and analyses for the manuscript. All co-authors contributed to the revision of the manuscript.

5.10 Supplementary material

5.10.1 Supplementary tables

5.10.1.1 Stressors data

Table 9: List of stressors from Beauchesne et al. (2020b)

Groups	Drivers	Spatial resolution	Temporal resolution	Years	Units	Source
Climate	Acidification	Lat/Lon	August-September	2018	Ω *Aragonite*	Starr and Chassé 2019
Climate	Bottom-water temperature	~2 km^2	Monthly	Climatology: 1980-2010; Current: 2013-2017	negative anomalies	Galbraith et al. 2018
Climate	Bottom-water temperature	~2 km^2	Monthly	Climatology: 1980-2010; Current: 2013-2017	positive anomalies	Galbraith et al. 2018
Climate	Hypoxia	Lat/Lon	August-September	2013-2017	$ml\ L^{-1}$	Blais et al. 2019
Climate	Surface-water temperature	~2 km^2	Monthly	Climatology: 1980-2010; Current: 2013-2017	negative anomalies	Galbraith et al. 2018

Groups	Drivers	Spatial resolution	Temporal resolution	Years	Units	Source
Climate	Surface-water temperature	~2 km^2	Monthly	Climatology: 1980-2010; Current: 2013-2017	positive anomalies	Galbraith et al. 2018
Coastal	Coastal development	15 arc-second	Annual	2015-2016	$nanoWatts$ cm^{-2} sr^{-1}	Earth observation group 2019
Coastal	Direct human impact	Variable: $<$ 1 to $>$ 40000 km^2	Annual	2016	population count	Statistics Canada 2017
Coastal	Inorganic pollution	Modeled 1 km^2	Annual	2000-2001	-	Halpern et al. 2015
Coastal	Nutrient import	Modeled 1 km^2	Annual	2007-2010	t fertilizer	Halpern et al. 2015
Coastal	Organic pollution	Modeled 1 km^2	Annual	2007-2010	t pesticide	Halpern et al. 2015
Fisheries	Demersal, destructive	Lat/Lon	Event based	2010-2015	kg	DFO 2016
Fisheries	Demersal, non-destructive, high-bycatch	Lat/Lon	Event based	2010-2015	kg	DFO 2016
Fisheries	Demersal, non-destructive, low-bycatch	Lat/Lon	Event based	2010-2015	kg	DFO 2016
Fisheries	Pelagic, high-bycatch	Lat/Lon	Event based	2010-2015	kg	DFO 2016
Fisheries	Pelagic, low-bycatch	Lat/Lon	Event based	2010-2015	kg	DFO 2016
Marine traffic	Marine pollution	Modeled 1 km^2	Event based & annual	2003-2011 & 2011	n lanes + t port volume	Halpern et al. 2015
Marine traffic	Shipping	0.1 degree	Event based	2003-2011	n lanes	Halpern et al. 2015

5.10.1.2 Biotic data

Table 10: Description of the data used to obtain taxa list and occurrences. Except for IUCN data, monitoring programs are all conducted or managed by the Government of Canada's Department of Fisheries and Oceans (DFO).

Programs	Description	Sampling	Period	Taxa	Occurrences Absences	Years	Source
= Multidisciplinary Research Survey	Scientific survey	Random stratified	August-September	293	44497 434851	2011-2015	Bourdages et al. 2018
Fisheries Logbooks	Fisheries landings	Fisheries-specific	Fishing season	48	271236 0	2010-2015	DFO 2016
At-Sea Observers	Fishing observers	Fisheries-specific	Fishing season	200	93230 0	2010-2015	-
Sentinel Fisheries	Scientific fisheries	Fisheries or random stratified	Fishing season or July	99	15990 0	2011-2015	-
Marine Mammals	IUCN Species Red List of Threatened Species	-	-	30	24	-	IUCN 2020
Total	-	-	-	391	424953 434851		

5.10.1.3 Abiotic data

Table 11: List of abiotic descriptors used to extrapolate and map taxa distribution in the St. Lawrence System.

Environmental descriptors	Units	Spatial resolution	Source
Depth	m	10 x 10 km	Dutil et al. 2011
Latitude	m	-	-
Longitude	m	-	-
Surface			
pH	-	5 arcmin	Assis et al. 2018
Dissolved oxygen	$mol.m^{-3}$	5 arcmin	Assis et al. 2018
Primary productivity	$g.m^{-3}.day^{-1}$	5 arcmin	Assis et al. 2018
Salinity	-	2.5 x 2.5 km	Dutil et al. 2012
Temperature	$°C$	~2 km^2	Galbraith et al. 2018
Bottom			
Aragonite	Ω *Aragonite*	Modeled $1km^2$	Starr and Chassé 2019
Oxygen saturation	%	Modeled $1km^2$	Blais et al. 2019
Primary productivity	$g.m^{-3}.day^{-1}$	5 arcmin	Assis et al. 2018
Salinity	-	10 x 10 km	Dutil et al. 2011
Temperature	$°C$	~2 km^2	Galbraith et al. 2018

5.10.1.4 Traits

Table 12: List of traits used to characterize the relative vulnerability of taxa to stressors and description of each trait category.

Traits	Categories	Description
Body composition	Biogenic silica	Organism with skeleton formed by microscopic particles of silica
	Bone	Organism with solid skeleton made of bones
	Cartilaginous	Organism with solid skeleton made of cartilage
	Chitinous	Organism with solid skeleton made of chitin
	Non-calcifying	Organism devoid of calcifying skeleton
	Soft-bodied, aragonite	Organism with aragonite in soft tissues
	Soft-bodied, calcite	Organism with calcite in soft tissues
	Soft-bodied, calcium phosphate	Organism with calcium phosphate in soft tissues
	Soft-bodied, calcium sulfate	Organism with calcium sulfate in soft tissues
	Skeleton, aragonite	Organism with solid skeleton made of or containing aragonite
	Skeleton, calcite	Organism with solid skeleton made of or containing calcite
	Skeleton, calcium phosphate	Organism with solid skeleton made of or containing calcium phosphate
	Skeleton, high-magnesium calcite	Organism with solid skeleton made of or containing high-magnesium calcite
	Skeleton, phosphatic	Organism with solid skeleton made of or containing phosphates
Environment	Bathydemersal	Living and/or feeding on or near the bottom, below 200 m
	Bathypelagic	Occurring mainly in open water below 200 m, not feeding on benthic organisms
	Benthic	Living and feeding on the bottom
	Benthopelagic	Living and/or feeding on or near the bottom, as well as in midwater, between 0 and 200 m
	Demersal	Living and/or feeding on or near the bottom, between 0 and 200 m
	Pelagic	Occurring mainly in the water column between 0 and 200 m, not feeding on benthic organisms
Feeding type	Deposit feeder	Organism that lives on or in the sediments and consumes organic material on the sea floor
	Selective filter feeder	Organism that actively and selectively filters waters to consume plankton or nutrients suspended in the water
	Grazer	Organism that feeds on plants
	Parasite	Organism that lives in or on another organism, benefiting at the other organism's expense
	Plankton	Organism feeding exclusively on plankton
	Predator	Organism that actively hunts prey
	Scavenger	Organism that feeds on dead plant or animal material, or refuse

Traits	Categories	Description
	Suspension feeder	Organism that captures and consumes particules suspended in the water, such as plankton, bacteria, detritus and particulate organic matter
	Xylophagous	Organism feeding on or boring into wood
Fisheries landings	Targeted species	Applicable to fisheries only. Taxa targeted by fishing activities.
	Bycatch	Applicable to fisheries only. Taxa bycatch by fishing activities.
	Others	Applicable to fisheries only. Taxa not targeted or caught by fishing activities
Mobility	Burrower	Organism that lives in a burrow dug in the sediments
	Crawler	Organism that crawls slowly on the bottom
	Mobile	Free-ranging organism
	Sessile	Immobile or fixed organism
	Swimmer	Organism with limited swimming ability
Phylum	Annelida	-
	Arthropoda	-
	Brachiopoda	-
	Bryozoa	-
	Chordata	-
	Cnidaria	-
	Ctenophora	-
	Echinodermata	-
	Echiura	-
	Mollusca	-
	Porifera	-
	Sipuncula	-
Size	0-100 cm	Body length between 0 and 100 cm
	100-200 cm	Body length between 100 and 200 cm
	200-300 cm	Body length between 200 and 300 cm
	300+ cm	Body length greater than 300 cm

5.10.1.5 Taxa list

Table 13: List of taxa with number of occurrences

Taxa	Occurrences	Absences	Sensitivity	Specificity	Accuracy	TSS
Acipenser oxyrinchus	7					
Actinauge sp.	253	1383	0.63	0.96	0.9	0.58
Actinostola sp.	301	1335	0.56	0.95	0.88	0.52
Aega psora	47					
Alcyonidium sp.	13					
Alepocephalus bairdii	5					
Alosa aestivalis	1					
Alosa pseudoharengus	155	1527	0.6	0.98	0.94	0.58
Alosa sapidissima	19					
Aluterus schoepfii	4					
Amblyraja hyperborea	1					
Amblyraja radiata	6105	766	0.99	0.81	0.97	0.8
Amicula vestita	3					
Ammodytes sp.	521	1280	0.42	0.89	0.76	0.32
Ampelisca sp.	3					
Amphiura sp.	19					
Anarhichas denticulatus	17					
Anarhichas lupus	1149	1427	0.85	0.94	0.91	0.79
Anarhichas minor	413	1588	0.64	0.98	0.93	0.62
Anguilla rostrata	16					
Anisarchus medius	127	1514	0.57	0.98	0.95	0.55
Anomia sp.	7					
Anonyx sp.	88	1548	0.07	0.99	0.94	0.06
Antalis sp.	1					
Anthoptilum grandiflorum	292	1344	0.7	0.95	0.91	0.65
Aphroditella hastata	129	1507	0.19	0.99	0.92	0.17
Arcoscalpellum michelottianum	16					
Arctica islandica	20					
Arctozenus risso	1403	1056	0.95	0.92	0.93	0.86
Argentina silus	42					
Argis dentata	229	1438	0.82	0.98	0.96	0.8
Argyropelecus aculeatus	37					
Argyropelecus gigas	21					
Aristaeopsis edwardsiana	2					
Arrhoges occidentalis	104	1532	0.41	0.99	0.95	0.4
Artediellus sp.	623	1217	0.6	0.9	0.81	0.5
Ascidiacea	1139	777	0.75	0.72	0.74	0.47
Aspidophoroides monopterygius	748	1120	0.7	0.82	0.77	0.52
Aspidophoroides olrikii	110	1527	0.31	0.98	0.94	0.29
Astarte sp.	210	1426	0.23	0.97	0.88	0.2
Asterias sp.	137	1509	0.13	0.98	0.91	0.11

Taxa	Occurrences	Absences	Sensitivity	Specificity	Accuracy	TSS
Astropecten duplicatus	11					
Atlantopandalus propinqvus	55	1583	0.15	1	0.97	0.14
Atolla wyvillei	21					
Aulacofusus brevicauda	1					
Aurelia aurita	143	1493	0.14	0.97	0.9	0.11
Balaena mysticetus	0					
Balaenoptera acutorostrata	1	-	-	-	-	-
Balaenoptera borealis	1	-	-	-	-	-
Balaenoptera musculus	1	-	-	-	-	-
Balaenoptera physalus	1	-	-	-	-	-
Balanidae	24					
Balistes vetula	1					
Bathyarca sp.	1					
Bathylagus euryops	4					
Bathypolypus sp.	421	1392	0.56	0.92	0.83	0.48
Bathyraja spinicauda	574	1613	0.84	0.95	0.92	0.79
Benthodesmus elongatus	1					
Beringius turtoni	2					
Bolocera sp.	392	1244	0.66	0.94	0.87	0.6
Boltenia ovifera	72	1564	0.34	0.99	0.96	0.33
Boreogadus saida	438	1534	0.75	0.94	0.9	0.69
Boreomysis sp.	1					
Boreotrophon sp.	47					
Borostomias antarcticus	1					
Bothus ocellatus	4					
Brisaster fragilis	457	1203	0.87	0.95	0.93	0.82
Brosme brosme	15					
Bryozoa	207	1441	0.16	0.98	0.88	0.14
Buccinum sp.	11288	1108	0.98	0.84	0.97	0.83
Caberea ellisii	18					
Calocaris templemani	19					
Cancer borealis	6					
Cancer irroratus	23823	1473	1	0.94	0.99	0.94
Cardium sp.	1					
Careproctus reinhardti	157	1579	0.65	0.98	0.95	0.64
Centroscyllium fabricii	534	1529	0.82	0.94	0.91	0.76
Ceramaster granularis	83	1553	0.28	0.99	0.96	0.27
Ceratias holboelli	2					
Cetorhinus maximus	3					
Chauliodus sloani	6					
Chionoecetes opilio	68291	493	1	0.46	0.99	0.46
Chiridota laevis	1					
Chirona hameri	15					
Chlamys islandica	10821	1461	0.99	0.92	0.98	0.9
Ciliatocardium ciliatum	99	1538	0.26	0.98	0.94	0.25
Clupea harengus	15658	778	0.99	0.48	0.96	0.47
Colga villosa	34					
Colus sp.	84	1553	0.02	0.99	0.94	0.02

Taxa	Occurrences	Absences	Sensitivity	Specificity	Accuracy	TSS
Coregonus clupeaformis	1					
Coryphaena hippurus	2					
Coryphaenoides rupestris	320	0	0.94	0.91	0.93	0.86
Cottunculus microps	10					
Cottunculus thomsonii	1					
Crangon septemspinosa	4					
Crenella faba	3					
Crossaster papposus	697	952	0.87	0.91	0.89	0.78
Cryptacanthodes maculatus	394	1574	0.79	0.98	0.94	0.77
Cryptopsaras couesii	3					
Ctenodiscus crispatus	716	958	0.79	0.86	0.83	0.65
Cucumaria frondosa	988	1609	0.97	0.99	0.98	0.96
Cuspidaria sp.	174	1462	0.49	0.98	0.93	0.47
Cyanea capillata	250	1387	0.28	0.92	0.82	0.2
Cyclocardia borealis	8					
Cyclopterus lumpus	607	1480	0.71	0.94	0.88	0.65
Cyrtodaria siliqua	30					
Cystophora cristata	1	-	-	-	-	-
Delphinapterus leucas	1	-	-	-	-	-
Delphinus delphis	1	-	-	-	-	-
Dendronotus sp.	33					
Diplopteraster multipes	9					
Dipturus laevis	4					
Dipturus linteus	27					
Doridoxa ingolfiana	10					
Drifa glomerata	65	1571	0.03	0.99	0.95	0.02
Duva florida	89	1547	0.06	0.99	0.94	0.05
Echinarachnius parma	21					
Echiodon dawsoni	1					
Enchelyopus cimbrius	1981	952	0.94	0.89	0.92	0.83
Ensis leei	128	0	0.99	1	1	0.99
Epimeria loricata	32					
Epizoanthus erdmanni	118	1518	0.08	0.99	0.92	0.06
Epizoanthus incrustatus	1					
Erignathus barbatus	0					
Eualus fabricii	73	1563	0.34	0.99	0.96	0.33
Eualus gaimardii	66	1572	0.2	0.99	0.96	0.19
Eualus macilentus	129	1510	0.49	0.98	0.94	0.47
Eubalaena glacialis	1	-	-	-	-	-
Eudistoma vitreum	35					
Eumesogrammus praecisus	355	1379	0.5	0.94	0.85	0.44
Eumicrotremus derjugini	1					
Eumicrotremus spinosus	317	1423	0.48	0.95	0.87	0.43
Eusergestes arcticus	69	1571	0.68	0.99	0.98	0.67
Eusirus cuspidatus	35					
Flabellum sp.	29					
Gadus morhua	22539	500	0.99	0.32	0.98	0.31

Taxa	Occurrences	Absences	Sensitivity	Specificity	Accuracy	TSS
Gadus ogac	618	1544	0.83	0.98	0.93	0.8
Gaidropsarus sp.	103	1606	0.57	0.99	0.97	0.56
Gasterosteus aculeatus aculeatus	115	1548	0.16	0.98	0.93	0.14
Gersemia rubiformis	436	1200	0.54	0.87	0.78	0.4
Globicephala melas	1	-	-	-	-	-
Glyptocephalus cynoglossus	8860	779	0.99	0.84	0.98	0.83
Gonatus fabricii	1					
Gonostomatidae	59	1593	0.08	0.99	0.96	0.08
Gorgonocephalus sp.	622	1091	0.71	0.89	0.82	0.59
Grampus griseus	1	-	-	-	-	-
Gymnelus viridis	67	1569	0.22	0.99	0.97	0.22
Gymnocanthus tricuspis	374	1268	0.48	0.91	0.82	0.4
Halichoerus grypus	1	-	-	-	-	-
Halichondria panicea	78	1558	0.1	0.99	0.95	0.09
Halipteris finmarchica	92	1544	0.39	0.99	0.96	0.38
Hamingia arctica	2					
Helicolenus dactylopterus	7					
Heliometra glacialis	7					
Hemithiris psittacea	30					
Hemitripterus americanus	461	1521	0.63	0.97	0.9	0.6
Henricia sp.	627	1012	0.57	0.79	0.71	0.36
Hiatella arctica	23					
Hippasteria phrygiana	458	1380	0.59	0.91	0.83	0.51
Hippoglossina oblonga	2					
Hippoglossoides platessoides	18677	248	1	0.33	0.99	0.33
Hippoglossus hippoglossus	21086	1267	0.99	0.5	0.96	0.48
Homarus americanus	10671	1499	0.99	0.97	0.99	0.96
Hormathia nodosa	59	1585	0.07	1	0.97	0.07
Howella sherborni	2					
Hyas araneus	1688	1250	0.91	0.91	0.91	0.81
Hyas coarctatus	798	934	0.77	0.82	0.8	0.6
Hymenopenaeus debilis	4					
Hyperia galba	30					
Hyperoodon ampullatus	1	-	-	-	-	-
Icelus sp.	208	1437	0.29	0.96	0.88	0.25
Illex illecebrosus	360	1419	0.39	0.92	0.82	0.31
Isurus oxyrinchus	19					
Kajikia albida	1					
Kogia breviceps	1	-	-	-	-	-
Lagenorhynchus acutus	1	-	-	-	-	-
Lagenorhynchus albirostris	1	-	-	-	-	-
Lamna nasus	34					
Lampanyctus sp.	17					
Larus sp.	3					
Lebbeus groenlandicus	58	1578	0.67	1	0.99	0.66
Lebbeus microceros	11					

Taxa	Occurrences	Absences	Sensitivity	Specificity	Accuracy	TSS
Lebbeus polaris	243	1393	0.54	0.96	0.9	0.49
Leptagonus decagonus	673	1369	0.76	0.93	0.87	0.69
Leptasterias sp.	410	1236	0.6	0.9	0.83	0.51
Leptoclinus maculatus	869	1025	0.79	0.82	0.8	0.6
Leptychaster arcticus	8					
Leucoraja erinacea	37					
Leucoraja ocellata	331	1623	0.78	0.97	0.94	0.75
Limanda ferruginea	7434	1237	0.98	0.94	0.98	0.92
Liparis atlanticus	2					
Liparis fabricii	28					
Liparis gibbus	268	1405	0.41	0.95	0.86	0.36
Liparis liparis liparis	1					
Liponema multicorne	27					
Lithodes maja	2592	1289	0.96	0.83	0.92	0.79
Lophius americanus	1550	1591	0.89	0.86	0.87	0.75
Lumpenus fabricii	6					
Lumpenus lampretaeformis	645	1413	0.83	0.94	0.91	0.78
Lycenchelys paxillus	129	1626	0.7	0.99	0.97	0.69
Lycenchelys verrillii	69	1585	0.17	1	0.96	0.17
Lycodes lavalaei	345	1343	0.54	0.93	0.85	0.48
Lycodes pallidus	495	0	0.99	0.95	0.97	0.93
Lycodes polaris	20					
Lycodes reticulatus	31					
Lycodes terraenovae	129	1594	0.51	0.98	0.94	0.49
Lycodes turneri	2					
Lycodes vahlii	552	1380	0.81	0.95	0.91	0.76
Macoma sp.	18					
Macrourus berglax	39					
Mactromeris polynyma	959	1632	0.98	1	0.99	0.98
Maera loveni	3					
Malacocephalus occidentalis	1					
Malacoraja senta	1765	1000	0.95	0.87	0.92	0.82
Malacosteus niger	1					
Mallotus villosus	7766	602	0.98	0.63	0.95	0.61
Margarites sp.	125	1515	0.12	0.99	0.93	0.11
Maurolicus muelleri	1					
Megaptera novaeangliae	1	-	-	-	-	-
Megayoldia thraciaeformis	92	1544	0.35	0.98	0.95	0.33
Melanogrammus aeglefinus	322	1616	0.78	0.98	0.95	0.76
Melanostigma atlanticum	1014	1289	0.93	0.94	0.93	0.87
Melita dentata	2					
Menidia menidia	2					
Mentodus rostratus	1					
Mercenaria mercenaria	12					
Merluccius bilinearis	1581	1286	0.89	0.83	0.86	0.71
Mesodesma sp.	19					
Metridium senile	2					
Microgadus tomcod	64	0	0.95	0.94	0.94	0.89

Taxa	Occurrences	Absences	Sensitivity	Specificity	Accuracy	TSS
Micromesistius poutassou	18					
Modiolus modiolus	5					
Molpadia sp.	10					
Molva dypterygia	1					
Monodon monoceros	0					
Morone saxatilis	3					
Morus bassanus	5					
Mugil cephalus	1					
Munida valida	1					
Munidopsis curvirostra	122	1515	0.58	0.98	0.95	0.57
Musculus sp.	20					
Mustelus canis	1					
Mya arenaria	2					
Mya truncata	9					
Myctophidae	270	1517	0.66	0.96	0.92	0.62
Myoxocephalus sp.	1681	1239	0.87	0.88	0.88	0.75
Mytilus sp.	79	1560	0.18	0.99	0.95	0.17
Myxine glutinosa	3412	1066	0.98	0.91	0.97	0.89
Naticidae	273	1523	0.58	0.99	0.93	0.57
Naucrates ductor	1					
Nealotus tripes	1					
Nemichthys scolopaceus	21					
Neohela monstrosa	19					
Neolithodes grimaldii	20					
Neoscopelus macrolepidotus	9					
Neptunea sp.	114	1522	0.04	0.99	0.92	0.02
Nezumia bairdii	1838	1153	0.97	0.93	0.95	0.9
Novodinia americana	1					
Nucella lapillus	1					
Nuculana sp.	39					
Nymphon sp.	50	1586	0	1	0.97	0
Oceanites sp.	1					
Odobenus rosmarus	0					
Oediceros saginatus	1					
Ommastrephes sp.	1					
Omosudis lowii	1					
Ophiacantha bidentata	113	1523	0.19	0.98	0.93	0.17
Ophiopholis aculeata	187	1454	0.38	0.96	0.89	0.34
Ophioscolex glacialis	18					
Ophiura sp.	276	1407	0.55	0.95	0.89	0.5
Orcinus orca	1	-	-	-	-	-
Osmerus mordax mordax	148	1536	0.72	0.99	0.97	0.71
Pagophilus groenlandicus	1	-	-	-	-	-
Pagurus sp.	512	1152	0.7	0.9	0.84	0.6
Palio dubia	1					
Pandalus borealis	48179	895	1	0.88	1	0.88
Pandalus montagui	468	1193	0.77	0.95	0.9	0.71

Taxa	Occurrences	Absences	Sensitivity	Specificity	Accuracy	TSS
Panomya norvegica	3					
Paralichthys dentatus	1					
Paraliparis calidus	33					
Paraliparis copei copei	29					
Paramphithoe hystrix	26					
Parvicardium pinnulatum	1					
Pasiphaea multidentata	1282	1136	0.94	0.91	0.92	0.85
Pasiphaea tarda	6					
Pennatula aculeata	412	1224	0.7	0.91	0.86	0.61
Pennatula grandis	504	1437	0.76	0.93	0.89	0.69
Peprilus triacanthus	13					
Periphylla periphylla	187	1449	0.21	0.95	0.87	0.16
Petromyzon marinus	11					
Phascolion strombus strombus	9					
Phoca vitulina	1	-	-	-	-	-
Phocoena phocoena	1	-	-	-	-	-
Pholis gunnellus	1					
Phycis chesteri	399	1439	0.73	0.96	0.91	0.69
Physeter macrocephalus	1	-	-	-	-	-
Plesionika martia	3					
Pleurobrachia pileus	94	1542	0.11	0.98	0.93	0.09
Pollachius virens	250	1627	0.73	0.98	0.95	0.71
Polyipnus clarus	45					
Polynoidae	87	1551	0.02	0.99	0.94	0.02
Pomatomus saltatrix	1					
Pontophilus norvegicus	334	1304	0.7	0.95	0.9	0.65
Poraniomorpha sp.	22					
Porifera	1172	694	0.77	0.6	0.7	0.37
Prionace glauca	12					
Pseudarchaster parelii	60	1576	0	0.99	0.96	-0.01
Pseudopleuronectes americanus	10889	1422	0.99	0.95	0.98	0.94
Psilaster andromeda	79	1557	0.51	0.99	0.97	0.5
Psolus fabricii	135	1501	0.3	0.97	0.92	0.27
Psolus phantapus	54	1582	0.11	1	0.97	0.11
Pteraster militaris	186	1450	0.17	0.97	0.88	0.14
Pteraster obscurus	3					
Pteraster pulvillus	65	1571	0.33	0.99	0.96	0.32
Ptychogena lactea	189	1447	0.17	0.95	0.86	0.13
Pusa hispida	0					
Pycnogonum litorale	8					
Rajella fyllae	21					
Reinhardtius hippoglossoides	27772	765	1	0.8	0.99	0.79
Remora remora	1					
Reteporella grimaldii	1					
Rhachotropis aculeata	93	1543	0.32	0.99	0.95	0.3
Rossia sp.	341	1388	0.4	0.91	0.81	0.32

Taxa	Occurrences	Absences	Sensitivity	Specificity	Accuracy	TSS
Sabinea sarsii	58	1578	0.38	0.99	0.97	0.37
Sabinea septemcarinata	136	1500	0.69	0.98	0.96	0.67
Salmo salar	19					
Scaphander punctostriatus	106	1530	0.22	0.98	0.93	0.19
Sclerocrangon boreas	95	1570	0.6	0.99	0.97	0.59
Scomber scombrus	9523	1436	0.97	0.89	0.96	0.86
Scomberesox saurus saurus	6					
Scophthalmus aquosus	5612	1603	0.99	0.99	0.99	0.99
Sebastes sp.	15084	614	0.99	0.78	0.98	0.77
Securiflustra securifrons	37					
Sepioloidea sp.	2					
Sergia robusta	8					
Serripes groenlandicus	18					
Serrivomer beanii	10					
Similipecten greenlandicus	29					
Solaster endeca	254	1412	0.3	0.96	0.85	0.25
Somniosus microcephalus	2					
Spirontocaris liljeborgii	144	1492	0.19	0.98	0.91	0.17
Spirontocaris phippsii	13					
Spirontocaris spinus	119	1517	0.62	0.99	0.96	0.61
Spisula solidissima	315	1634	0.99	1	1	0.99
Squalus acanthias	149	1634	0.47	0.98	0.94	0.46
Staurostoma mertensii	59	1608	0.15	0.99	0.96	0.15
Stauroteuthis syrtensis	2					
Stegocephalus inflatus	110	1526	0.15	0.98	0.93	0.13
Stenella coeruleoalba	1	-	-	-	-	-
Stenella frontalis	0					
Stephanasterias albula	13					
Stephanauge sp.	75	1561	0.24	0.99	0.96	0.23
Stichaeus punctatus punctatus	14					
Stomias boa ferox	7					
Stomphia coccinea	179	1459	0.41	0.96	0.9	0.37
Strongylocentrotus sp.	2929	841	0.9	0.84	0.87	0.73
Stylocordyla borealis	75	1561	0.05	0.99	0.95	0.04
Symbolophorus veranyi	20					
Synaphobranchus kaupii	3					
Syscenus infelix	264	1377	0.68	0.95	0.9	0.62
Tachyrhynchus erosus	2					
Tautogolabrus adspersus	36					
Tellina sp.	1					
Terebratulina septentrionalis	61	1575	0.11	0.99	0.96	0.11
Teredo navalis	3					
Thuiaria thuja	43					
Thunnus alalunga	1					
Thunnus obesus	1					
Thunnus thynnus	3941	0	0.99	0.99	0.99	0.98
Thysanoessa longicaudata	2					

Taxa	Occurrences	Absences	Sensitivity	Specificity	Accuracy	TSS
Tonicella sp.	6					
Trachyrincus murrayi	7					
Tremaster mirabilis	1					
Triglops sp.	420	1266	0.54	0.93	0.84	0.47
Trigonolampa miriceps	2					
Tritia sp.	2					
Tursiops truncatus	1	-	-	-	-	-
Ulvaria subbifurcata	20					
Urasterias lincki	1					
Urophycis chuss	7					
Urophycis regia	1					
Urophycis tenuis	6242	1120	0.97	0.73	0.93	0.7
Urticina felina	89	1634	0.7	0.99	0.97	0.69
Velutinidae	8					
Wimvadocus torelli	2					
Xenodermichthys copei	14					
Xiphias gladius	1					
Xylophaga atlantica	3					
Yoldia sp.	7					
Ziphius cavirostris	1	-	-	-	-	-
Zoarces americanus	62	1615	0.37	0.99	0.97	0.36

5.10.1.6 Species-specific sensitivity

Table 14: Relative species-specific sensitivity scores for each stressor.

Stressors	Traits	Category	Sensitivity
Ocean acidification	Environment	Bathydemersal	1.00
		Bathypelagic	0.00
		Benthic	1.00
		Benthopelagic	0.50
		Demersal	1.00
		Pelagic	0.00
	Mobility	Burrower	0.75
		Crawler	0.75
		Mobile	0.25
		Sessile	1.00
		Swimmer	0.75
	Body composition	Biogenic silica	0.00
		Bone	0.00
		Cartilaginous	0.00
		Chitinous	0.00
		Non-calcifying	0.00
		Soft-bodied, aragonite	0.00
		Soft-bodied, calcite	0.00
		Soft-bodied, calcium phosphate	0.00
		Soft-bodied, calcium sulfate	0.00
		Skeleton, aragonite	0.90
		Skeleton, calcite	0.80
		Skeleton, calcium phosphate	0.80
		Skeleton, high-magnesium calcite	1.00
		Skeleton, phosphatic	0.00
	Phylum	Annelida	0.00
		Arthropoda	0.50
		Brachiopoda	0.50
		Bryozoa	1.00
		Chordata	0.00
		Cnidaria	1.00
		Ctenophora	0.00
		Echinodermata	1.00
		Echiura	0.00
		Mollusca	1.00
		Porifera	0.00
		Sipuncula	0.00
Bottom-water temperature anomalies	Environment	Bathydemersal	1.00
		Bathypelagic	0.00
		Benthic	1.00
		Benthopelagic	0.50
		Demersal	1.00
		Pelagic	0.00
	Mobility	Burrower	0.75
		Crawler	0.75

Stressors	Traits	Category	Sensitivity
		Mobile	0.25
		Sessile	1.00
		Swimmer	0.75
	Feeding type	Deposit feeder	1.00
		Selective filter feeder	0.00
		Grazer	1.00
		Parasite	0.00
		Plankton	0.50
		Predator	0.50
		Scavenger	0.50
		Suspension feeder	1.00
		Xylophagous	0.50
Surface-water temperature anomalies	Environment	Bathydemersal	0.00
		Bathypelagic	0.00
		Benthic	0.00
		Benthopelagic	0.50
		Demersal	0.00
		Pelagic	1.00
	Mobility	Burrower	0.75
		Crawler	0.75
		Mobile	0.25
		Sessile	1.00
		Swimmer	0.75
	Feeding type	Deposit feeder	1.00
		Selective filter feeder	0.00
		Grazer	1.00
		Parasite	0.00
		Plankton	0.50
		Predator	0.50
		Scavenger	0.50
		Suspension feeder	1.00
		Xylophagous	0.50
Hypoxia	Environment	Bathydemersal	1.00
		Bathypelagic	0.00
		Benthic	1.00
		Benthopelagic	0.50
		Demersal	1.00
		Pelagic	0.00
	Mobility	Burrower	0.75
		Crawler	0.75
		Mobile	0.25
		Sessile	1.00
		Swimmer	0.75
	Feeding type	Deposit feeder	1.00
		Selective filter feeder	0.00
		Grazer	1.00
		Parasite	0.00
		Plankton	0.50
		Predator	0.50
		Scavenger	0.50
		Suspension feeder	1.00
		Xylophagous	0.50

Stressors	Traits	Category	Sensitivity
Coastal development	Mobility	Burrower	0.75
		Crawler	0.75
		Mobile	0.50
		Sessile	1.00
		Swimmer	0.75
	Size	0-100 cm	0.25
		100-200 cm	0.50
		200-300 cm	0.75
		300+ cm	1.00
Direct human impact	Mobility	Burrower	0.75
		Crawler	0.75
		Mobile	0.50
		Sessile	1.00
		Swimmer	0.75
	Size	0-100 cm	0.25
		100-200 cm	0.50
		200-300 cm	0.75
		300+ cm	1.00
Inorganic pollution	Feeding type	Deposit feeder	0.75
		Selective filter feeder	0.00
		Grazer	0.00
		Parasite	0.00
		Plankton	0.00
		Predator	0.00
		Scavenger	0.50
		Suspension feeder	1.00
		Xylophagous	0.00
	Mobility	Burrower	0.75
		Crawler	0.75
		Mobile	0.25
		Sessile	1.00
		Swimmer	0.75
Nutrient input	Feeding type	Deposit feeder	0.75
		Selective filter feeder	0.00
		Grazer	0.00
		Parasite	0.00
		Plankton	0.00
		Predator	0.00
		Scavenger	0.50
		Suspension feeder	1.00
		Xylophagous	0.00
	Mobility	Burrower	0.75
		Crawler	0.75
		Mobile	0.25
		Sessile	1.00
		Swimmer	0.75
Organic pollution	Feeding type	Deposit feeder	0.75
		Selective filter feeder	0.00
		Grazer	0.00
		Parasite	0.00
		Plankton	0.00

Stressors	Traits	Category	Sensitivity
		Predator	0.00
		Scavenger	0.50
		Suspension feeder	1.00
		Xylophagous	0.00
	Mobility	Burrower	0.75
		Crawler	0.75
		Mobile	0.25
		Sessile	1.00
		Swimmer	0.75
Demersal destructive fisheries	Landings	Targeted species	1.00
		Bycatch	0.75
		Others	0.25
For *Others* only	Environment	Bathydemersal	1.00
		Bathypelagic	0.00
		Benthic	1.00
		Benthopelagic	0.50
		Demersal	1.00
		Pelagic	0.00
	Mobility	Burrower	0.75
		Crawler	0.75
		Mobile	0.25
		Sessile	1.00
		Swimmer	0.75
Demersal non-destructive high-bycatch fisheries	Landings	Targeted species	1.00
		Bycatch	0.75
		Others	0.00
Demersal non-destructive low-bycatch fisheries	Landings	Targeted species	1.00
		Bycatch	0.75
		Others	0.00
Pelagic high-bycatch fisheries	Landings	Targeted species	1.00
		Bycatch	0.75
		Others	0.00
Pelagic low-bycatch fisheries	Landings	Targeted species	1.00
		Bycatch	0.75
		Others	0.00
Marine pollution	Feeding type	Deposit feeder	0.75
		Selective filter feeder	0.00
		Grazer	0.00
		Parasite	0.00
		Plankton	0.00
		Predator	0.00
		Scavenger	0.50
		Suspension feeder	1.00
		Xylophagous	0.00
	Mobility	Burrower	0.75
		Crawler	0.75
		Mobile	0.25
		Sessile	1.00
		Swimmer	0.75
Shipping	Environment	Bathydemersal	0.00

Stressors	Traits	Category	Sensitivity
		Bathypelagic	0.00
		Benthic	0.00
		Benthopelagic	0.50
		Demersal	0.00
		Pelagic	1.00
	Size	0-100 cm	0.00
		100-200 cm	0.50
		200-300 cm	0.75
		300+ cm	1.00

Table 15: List of R packages used listed in alphabetical order. All analyses were carried out with the R programming language version. All analyses were carried out with the R programming language version 3.6.0 (R Core Team, 2019).

Name	Version	Repository	Source
btb	0.1.30	CRAN	Dos Santos et al. (2018)
eDrivers	0.0.1	GitHub	Beauchesne (2020)
fasterize	1.0.0	CRAN	Ross (2018)
kableExtra	1.1.0	CRAN	Zhu (2019)
magrittr	1.5	CRAN	Bache and Wickham (2014)
motifcensus	0.0.2.9000	GitHub	Cazelles and Beauchesne (2020)
randomForest	4.6.14	CRAN	Liaw and Wiener (2002)
raster	2.8.19	CRAN	Hijmans (2019)
rfishbase	3.0.3	CRAN	Boettiger et al. (2012)
rglobi	0.2.19	CRAN	Poelen et al. (2019)
rmarkdown	2.1	CRAN	Xie et al. (2018); Allaire et al. (2020)
sf	0.7.4	CRAN	Pebesma (2018)
sp	1.3.1	CRAN	Pebesma and Bivand (2005), Bivand et al. (2013)
taxize	0.9.8	CRAN	Chamberlain and Szöcs (2013), Chamberlain et al. (2019)
tidyverse	1.2.1	CRAN	Wickham (2017)
worrms	0.4.0.98	CRAN	Chamberlain (2020)

5.10.2 Supplementary figures

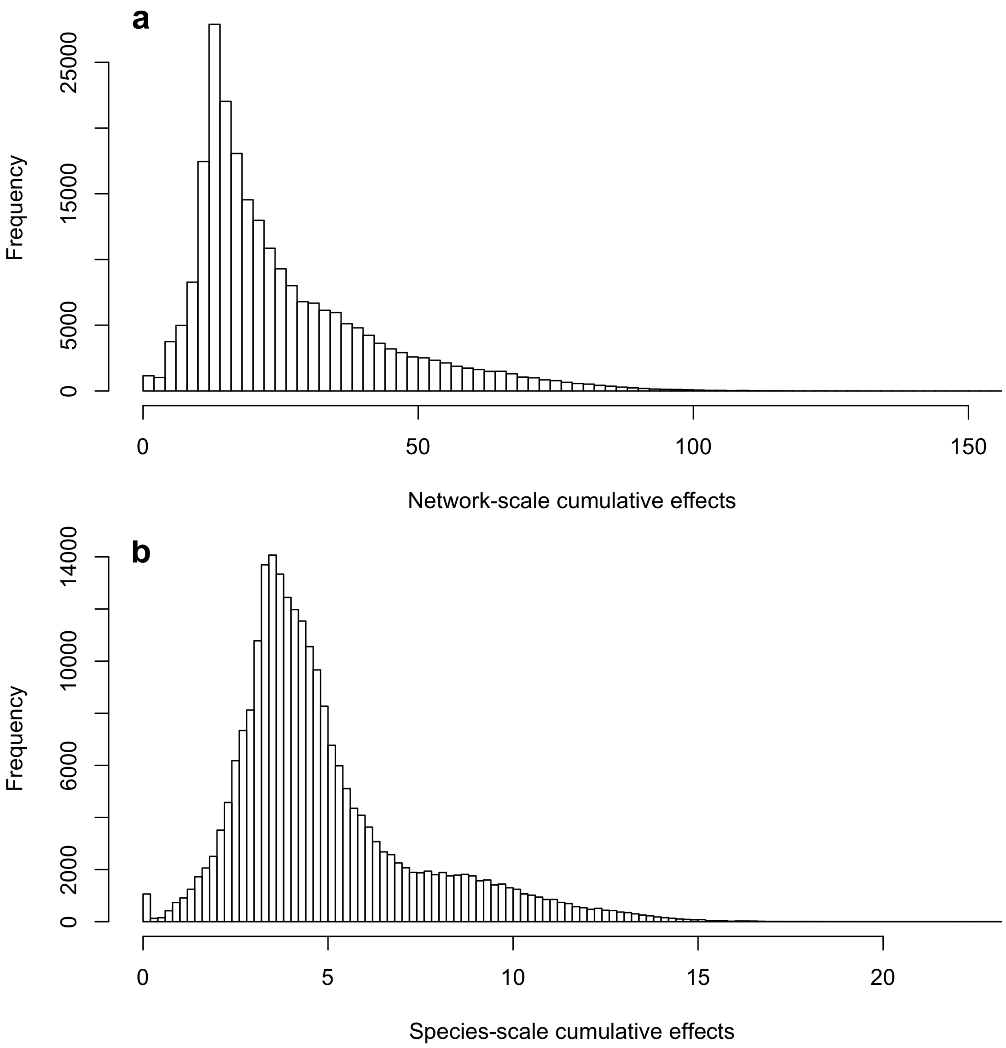

Figure 32: Histogram of cumulative effects scores in each 1 km^2 grid cell for a) the network-scale cumulative effects assessment and b) species-scale cumulative effects assessment approaches.

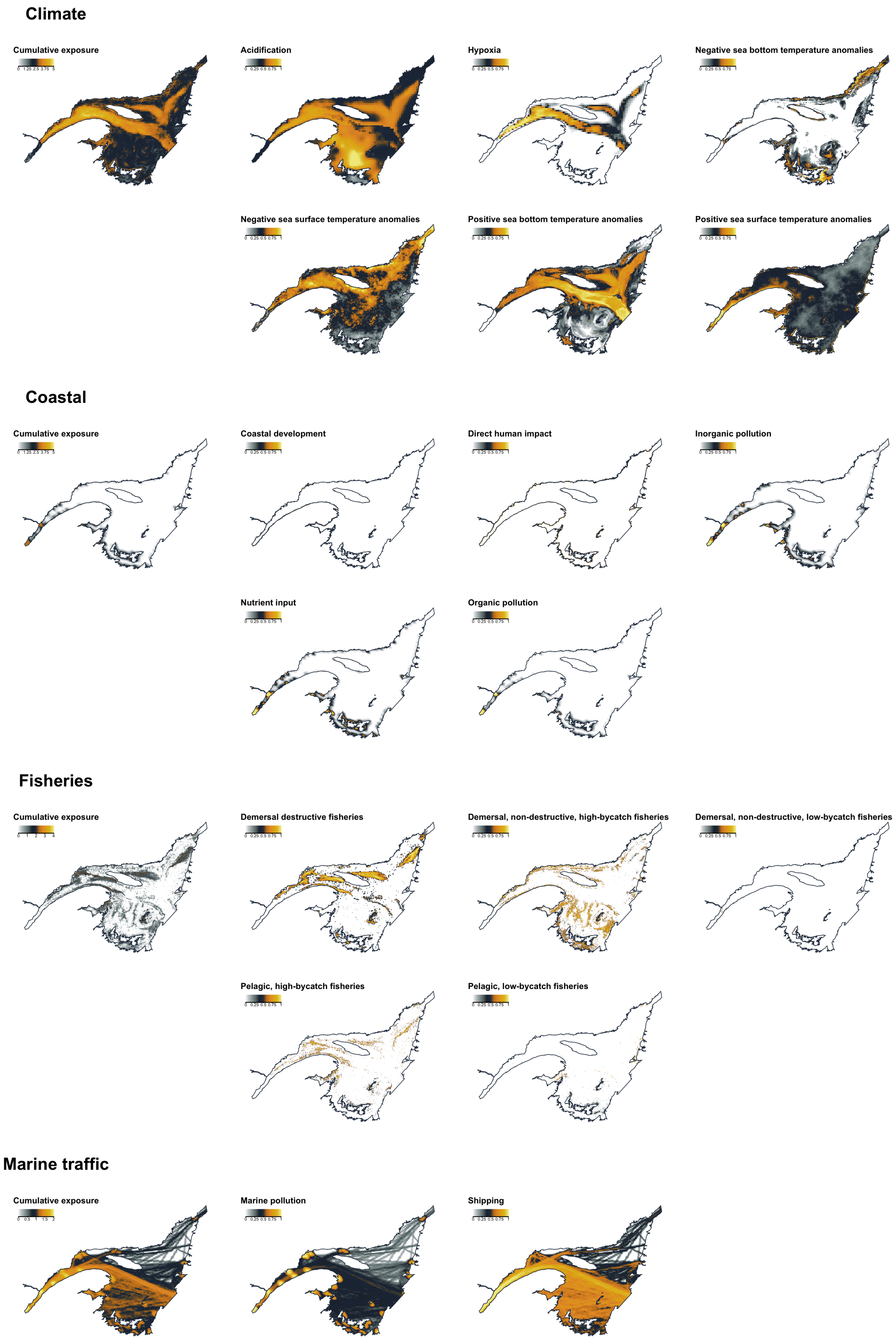

Figure 33: Distribution and intensity of stressors in the St. Lawrence system. The cumulative exposure of groups of stressors are evaluated as the sum of the scaled intensities of individual stressors in that group (Beauchesne et al., 2020b).

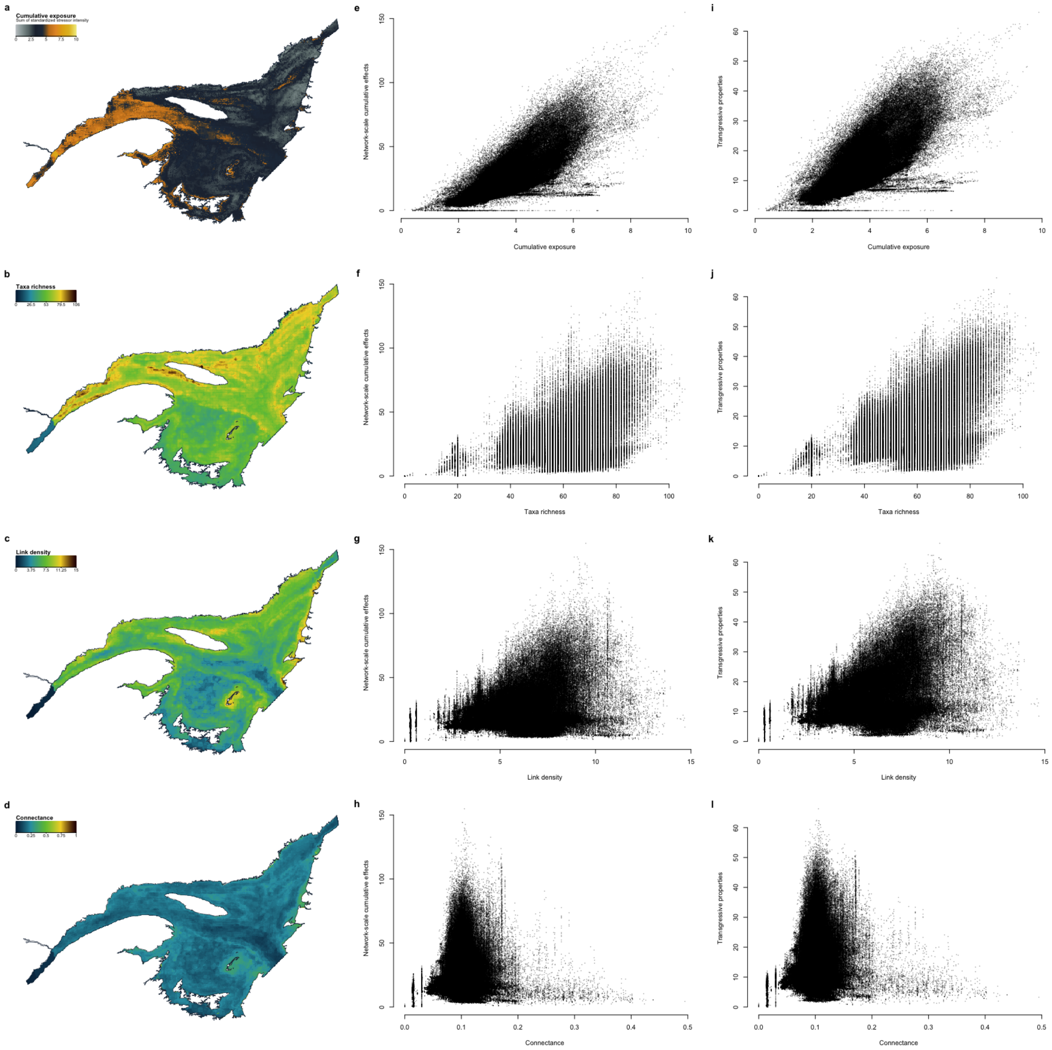

Figure 34: Regional metrics for stressors and ecological communities in the St. Lawrence System. Spatial distribution of the cumulative exposure (*i.e.* sum of normalized driver intensity in each grid cell) arising from the 18 stressors considered (a), taxa richness (b), link density (c) and connectance (d). Network-scale cumulative effects and transgressive properties arising from species interactions (*i.e.* the sum of individual species log ratio between the network-scale and species-scale cumulative effects assessments) as a function of cumulative exposure (e,i), taxa richness (f,j), link density (g,k) and connectance (h,l).

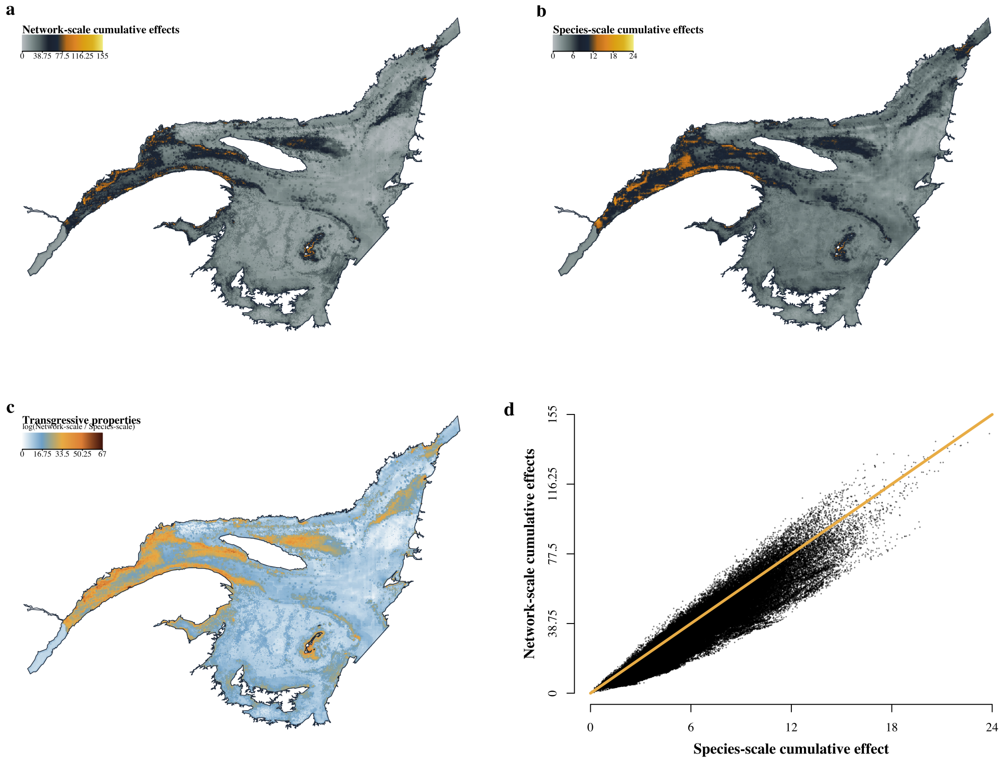

Figure 35: a) Network-scale relative cumulative effects assessment of 18 stressors on 193 taxa in the St. Lawrence System explicitly considering the underlying structure of the ecological community. b) Species-scale relative cumulative effects assessment of 18 stressors on 193 taxa in the St. Lawrence System ignoring the underlying structure of the ecological community, *i.e.* the environmental impact assessment *status quo* or individual approach to cumulative effects assessment. c) Spatial distribution of transgressive properties arising from species interactions, measured as the sum of the log ratio of individual species network-scale assessment over species-scale assessment in each 1 km^2 grid cell. d) Scatterplot of the network cumulative effects score as a function of the individual cumulative effect score for each 1 km^2 grid cell. The orange line is the 1:1 identity line.

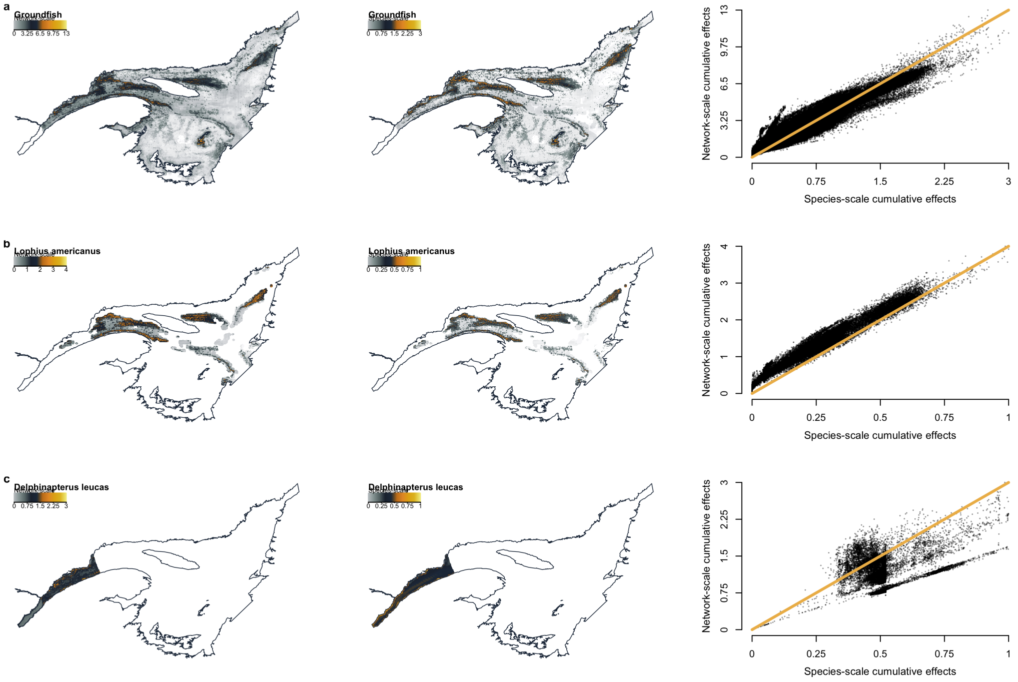

Figure 36: Comparison of the network-scale and species-scale cumulative effects assessments for a) groundfish species (*i.e.* Atlantic halibut *Hippoglossus hippoglossus*; American plaice *Hippoglossoides platessoides*; witch flounder *Glyptocephalus cynoglossus*; Atlantic cod *Gadus morhua*; redfish *Sebastes spp.*; Greenland halibut *Reinhardtius hippoglossoides*), b) monkfish (*Lophius americanus*) and c) beluga whales (*Delphinapterus leucas*).

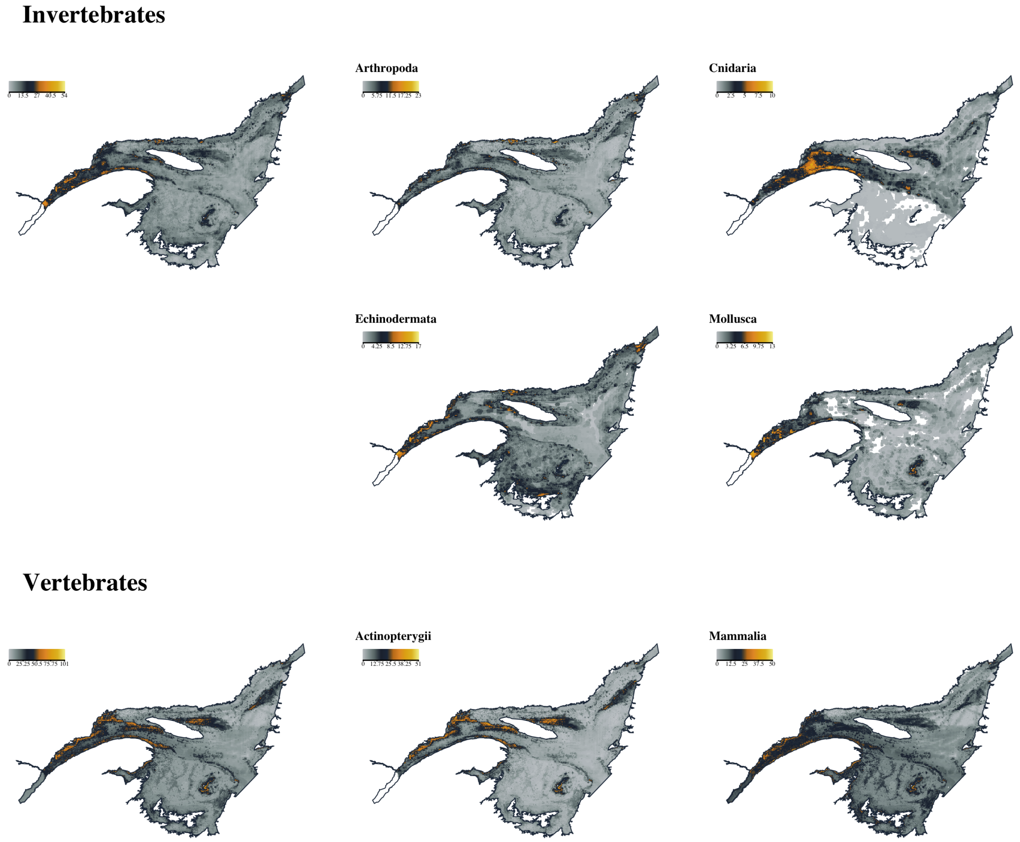

Figure 37: Network-scale cumulative effects assessment for 193 taxa of the St. Lawrence System classified into 8 taxonomic groups divided at the phyla level for invertebrates and classes level for vertebrates.

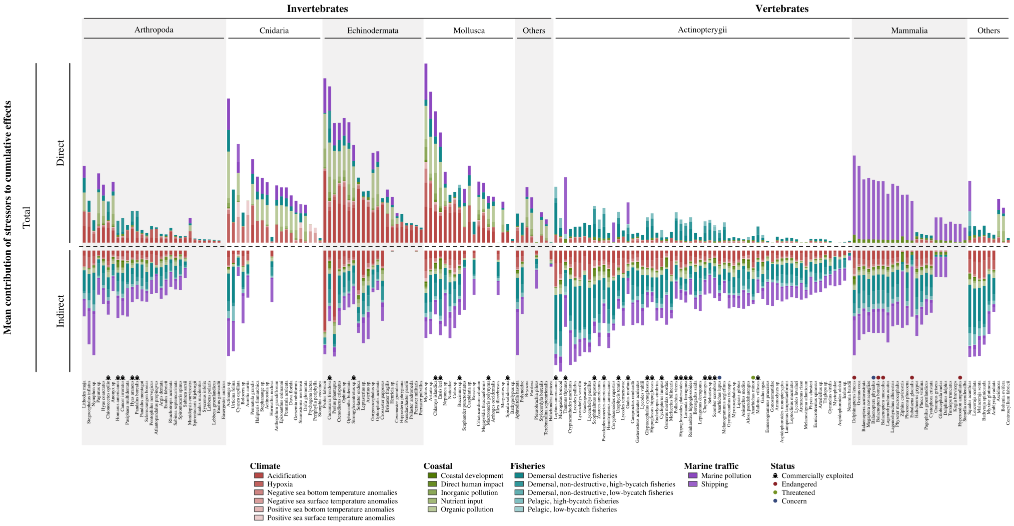

Figure 38: Mean contribution of 18 stressors to the regional cumulative effects assessment (C/km^2) of 193 taxa in the St. Lawrence System classified into 8 taxonomic groups. Taxonomic groups for invertebrates and vertebrates are divided at the phyla and classes level, respectively. The contribution can be divided as the direct and indirect contributions of each stressor to the cumulative effects on each taxa. Direct effects are those attributable to the effect of a stressor on a focal species, while indirect effects are the mean effects of stressors spreading through all 3-species interactions a taxa is involved in. The total contribution to cumulative effect is the sum of the direct and indirect contributions. Commercially exploited taxa and endangered, threatened and species of concern under the Canadian species at risk act are identified on the figure next to taxa names.

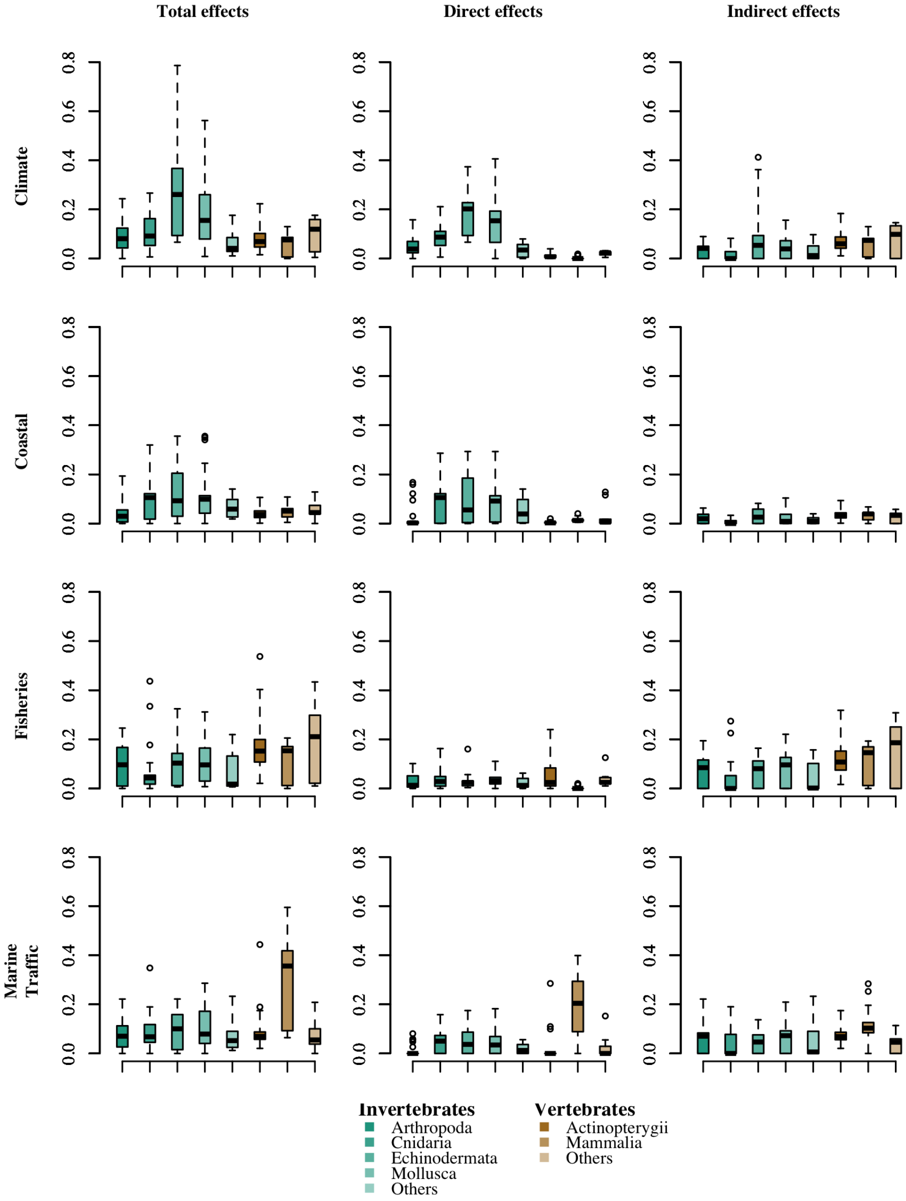

Figure 39: Contribution of 18 stressors to the regional cumulative effects assessment (C/km^2) of 193 taxa in the St. Lawrence System. Stressors are classified into 4 groups and the contribution is the sum of stressors in each group. Taxa are classified into 8 taxonomic groups divided at the phyla level for invertebrates and classes level for vertebrates. The contribution can be divided as the direct and indirect contributions of each stressor to the cumulative effects on each taxa. Direct effects are those attributable to the effect of a stressor on a focal species, while indirect effects are the mean effects of stressors spreading through all 3-species interactions a taxa is involved in. The total contribution to cumulative effects is the sum of the direct and indirect contributions.

CONCLUSION GÉNÉRALE

Utiliser la théorie pour informer la gestion environnementale

Dans un contexte d'intensification des pressions environnementales et de gestion environnementale écosystémique, l'objectif général de ma thèse était d'évaluer les effets cumulatifs des changements climatiques et des activités humaines sur les communautés écologiques du Système du Saint-Laurent. La thèse était motivée par deux suppositions de base qui stipulent que les interactions écologiques et les stresseurs environnementaux devraient être considérés conjointement afin de capturer adéquatement les effets directs et indirects des stresseurs sur les espèces. Ce type de problématique nécessite l'utilisation d'approches holistiques en mesure de considérer la complexité inhérente aux réseaux écologiques et à la variété des stresseurs environnementaux auxquels sont soumis les écosystèmes. Les approches expérimentales et l'échantillonnage *in situ* étant limités dans ce contexte, je me suis plutôt tourné vers la théorie écologique afin d'explorer les suppositions de base de ma thèse et d'informer l'évaluation des effets cumulatifs dans le Système du Saint-Laurent. La figure 40 présente un aperçu graphique des résultats de la thèse à partir du schéma conceptuel de l'évaluation des effets cumulatifs présenté en introduction de la thèse.

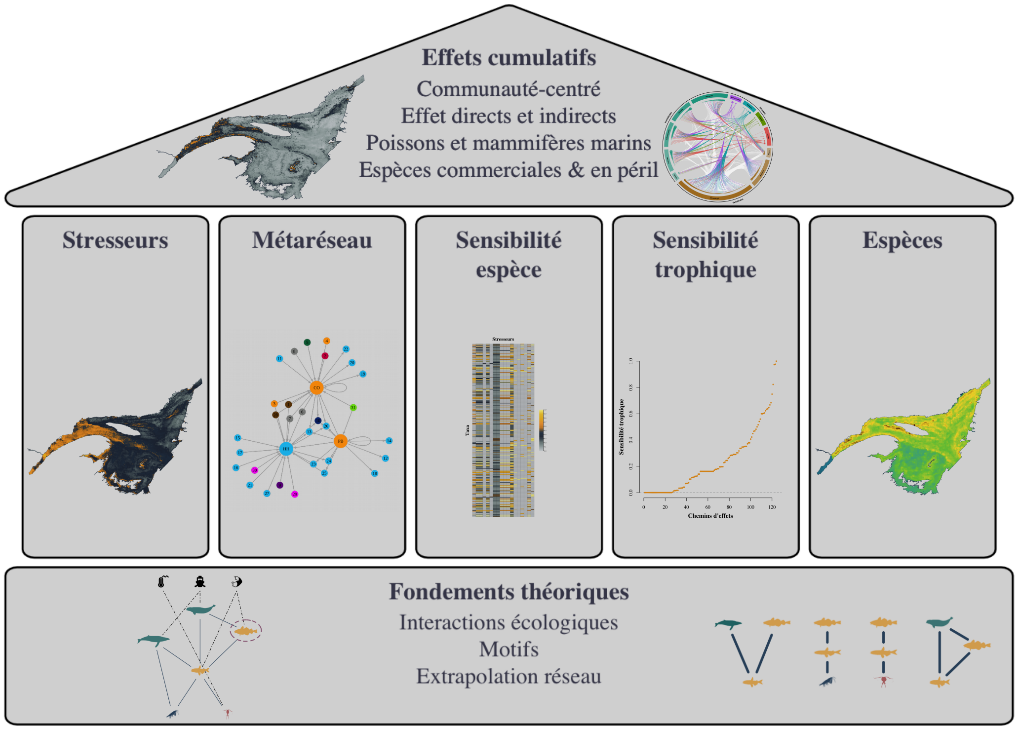

Figure 40: Principaux résultats de la thèse superposés au schéma conceptuel pour l'évaluation des effets cumulatifs sur les communautés écologiques.

Stresseurs environnementaux et interactions écologiques

Au chapitre 1, j'ai articulé un cadre théorique sur les effets de multiples stresseurs environnementaux sur les réseaux d'interactions écologiques et exploré les hypothèses générales de ma thèse sur l'importance des interactions écologiques pour les évaluations des effets de multiples stresseurs. Le cadre théorique proposé souligne l'importance d'une approche communauté-centrée qui repose sur l'évaluation des effets nets – *i.e.* l'intégration des effets directs et indirects des stresseurs sur les espèces – plutôt qu'une approche espèce-centrée qui repose strictement sur l'évaluation des effets directs.

L'exploration des effets de multiples stresseurs proposée au chapitre 1 a permis de valider les hypothèses générales de ma thèse, du moins d'un point de vue théorique : les interactions écologiques et les stresseurs environnementaux devraient être considérés conjointement lors d'évaluations des effets cumulatifs. En effet, les interactions écologiques amplifient systématiquement les effets des stresseurs et l'importance et la nature de l'amplification dépendent du type d'interactions et de la position trophique occupée par une espèce au sein de l'interaction. Par exemple, les méso-prédateurs au sein d'interactions tri-trophiques et omnivores sont des points d'entrée faibles positifs puisqu'ils bénéficient généralement des effets des stresseurs. À l'inverse, les prédateurs apicaux au sein des mêmes interactions sont généralement des points d'entrée faibles négatifs puisque les stresseurs nuisent fortement à leur dynamique. Les effets non-additifs issus des interactions écologiques sont également fréquents. La majorité des chemins d'effets affectant les espèces au sein d'interactions omnivores résultent en effets non-additifs, de telle sorte que ces espèces sont normalement des amplificateurs biotiques (*i.e.* une espèce affectée synergiquement par les stresseurs) ou des tampons biotiques (*i.e.* une espèce affectée de façon antagoniste par les stresseurs).

À l'échelle des réseaux trophiques, la sensibilité – ou l'insensibilité – de certaines espèces aux effets de multiples stresseurs dépend largement de leur position trophique. Les prédateurs apicaux, comme le béluga, la morue et le flétan, sont ainsi généralement des points d'entrée faibles négatifs et des amplificateurs biotiques. À l'inverse, des espèces fourragères comme le capelan et la crevette peuvent bénéficier ou être insensibles aux effets des stresseurs environnementaux. Pour d'autres espèces comme les phoques, les effets des stresseurs environnementaux ne sont perceptibles qu'en considérant les effets indirects. Toutes ces observations dépendent toutefois aussi de la structure du réseau trophique et des chemins d'effets spécifiques affectant les espèces d'une communauté. Un crustacé dans l'estuaire n'est pas soumis aux mêmes pressions environnementales et aux mêmes types d'effets indirects qu'un crustacé dans le golfe. Les résultats du chapitre 1 mettent ainsi en évidence que la sensibilité d'une espèce aux effets de multiples stresseurs, en plus de dépendre de sa sensibilité spécifique à chaque stresseur, dépend également de sa position trophique, de la structure locale de la communauté et des chemins d'effets spécifiques empruntés par les stresseurs environnementaux au sein de la communauté.

En d'autres mots : la population de bélugas de l'estuaire du Saint-Laurent n'est pas sensible parce que les bélugas sont sensibles ; elle l'est puisqu'elle est affectée directement et indirectement par une combinaison de facteurs environnementaux propres à l'estuaire qui agissent de concert pour affecter sa dynamique.

Appliquer la théorie pour l'évaluation des effets cumulatifs

Dans une optique de développement d'une approche prédictive et spatialement explicite pour l'évaluation des effets cumulatifs, appliquer le cadre théorique proposé au chapitre 1 nécessite une quantité considérable de connaissances et de données. Selon la méthode proposée par Halpern et al. (2008b), une évaluation des effets cumulatifs nécessite une caractérisation de la distribution et de l'intensité des stresseurs environnementaux considérés, de la distribution des composantes valorisées – *i.e.* des espèces pour ma thèse – et de la sensibilité aux stresseurs individuels spécifique à chaque espèce. Mes travaux de thèse ajoutent à cette liste la caractérisation spatiale des réseaux d'interactions écologiques.

Les chapitre 2 à 5 de ma thèse ont été dédiés à assembler les données et à développer des méthodes nécessaires à l'évaluation des effets cumulatifs des changements climatiques et des activités humaines sur les communautés du Système du Saint-Laurent. J'ai développé une approche prédictive permettant de reconstruire la structure de réseaux d'interactions écologiques (chapitre 2). J'ai cerné les enjeux environnementaux prioritaires pour l'évaluation des effets cumulatifs (chapitre 3) et assemblé une base de données intégrative fournissant une description de la distribution spatiale et de l'intensité de 22 stresseurs environnementaux dans le Système du

Saint-Laurent (chapitre 4). J'ai également utilisé des données d'occurrence d'espèces et de conditions environnementales – *e.g.* profondeur, salinité et température – afin de prédire la distribution potentielle de 193 taxa, et prédit la sensibilité spécifique de chaque taxon à chaque stresseur à partir de traits fonctionnels (chapitre 5).

L'article présenté au chapitre 5 rassemble ces données et méthodes et applique le cadre théorique articulé au chapitre 1 pour proposer une approche d'évaluations des effets cumulatifs communauté-centrée pour les espèces du Système du Saint-Laurent. Les résultats du chapitre 5 montrent que les interactions écologiques amplifient les effets cumulatifs pour la majorité des espèces du Système du Saint-Laurent et que la part relative des effets indirects supplante fréquemment celle des effets directs. Ce constat est particulièrement frappant pour les poissons et les mammifères marins, pour qui les effets indirects sont intenses et proviennent de l'ensemble des stresseurs environnementaux considérés. Pourtant, ces espèces sont affectées directement presqu'exclusivement par les pêcheries et le trafic maritime. Ces observations sont importantes pour la gestion des espèces commerciales et en péril puisqu'elles suggèrent que nous ignorons potentiellement des menaces significatives qui surviennent exclusivement par les interactions écologiques. Le cas de figure de la population de bélugas est particulièrement marquant puisque l'analyse proposée révèle des stresseurs qui l'affecte strictement à partir de chemins indirects et au sein de milieux non relevés par une approche espèce-centrée.

Implications pour la gestion environnementale

Les résultats de ma thèse démontrent l'importance de considérer la structure des communautés écologiques et la diversité des pressions environnementales pour convenablement évaluer les effets des stresseurs sur les espèces. En d'autres mots, évaluer les effets de stresseurs environnementaux sur une espèce prend son sens lorsqu'elle est articulée dans le contexte de la communauté dans laquelle cette espèce est imbriquée. Mes travaux de thèse ajoutent ainsi une voix supplémentaire à celles d'autres scientifiques qui réclament déjà une gestion holistique des biostructures (*e.g.* McCann, 2007; Tylianakis et al., 2008, 2010; O'Gorman et al., 2012; Harvey et al., 2017; Thompson et al., 2018; Orr et al., 2020).

Le désir d'appliquer des approches holistiques se confronte toutefois rapidement à une vision pragmatique lors de la mise en application. La gestion holistique envisagée nécessite une compréhension des effets de l'ensemble des stresseurs environnementaux sur la dynamique de l'ensemble des populations animales d'un écosystème pour l'évaluation adéquate des effets cumulatifs. À la vue de cette complexité, je comprends à quel point il est décourageant pour des évaluateurs d'aborder les effets cumulatifs à l'aide d'approches holistiques. Sinclair et al. (2017) décrit cette réalité avec éloquence :

> *"Once assessors enter the underworld of cumulative effects, they most often exit as quickly as possible, hoping that others (e.g., [environmental impact statement] reviewers and decision-makers) will sympathize with their unease and agree that cumulative effects are just too difficult to grapple with in a meaningful way."*

Le cadre théorique articulé au chapitre 1, en simplifiant les réseaux grâce à la notion de motifs, offre une perspective accessible et appuyée par la théorie écologique (*e.g.* Milo et al., 2002; Stouffer et al., 2007, 2012) pour explorer les effets de stresseurs sur les communautés. L'approche proposée au chapitre 5, quant à elle, offre une application accessible du cadre théorique pour évaluer les effets cumulatifs et considère explicitement les effets indirects issus des interactions écologiques. La combinaison de l'entièreté des chapitres de la thèse mène ainsi à la toute première évaluation quantitative des effets cumulatifs qui considère à la fois les effets directs et indirects des stresseurs environnementaux sur les espèces. Il s'agit, à mon avis, d'une avancée majeure vers l'application d'approches de gestion écosystémique qui pourrait permettre de guider la gestion des activités humaines, d'optimiser les campagnes d'échantillonnage *in situ* en identifiant des milieux ou espèces particulièrement à risque, et de guider l'élaboration d'expériences ciblées pour tester les effets absolus de combinaisons et d'intensité de stresseurs sur des espèces en interaction.

Limites et opportunités

L'approche d'évaluation des effets cumulatifs proposée au chapitre 5 conserve certaines des limites et suppositions de l'approche développée par Halpern et al. (2008b ; voir Halpern et Fujita, 2013 ; Halpern et al., 2015b ; Hodgson et al., 2019). Premièrement, notre approche fournit une évaluation relative des effets plutôt qu'une évaluation de la réponse, ou de la condition, des espèces face aux stresseurs environnementaux. Décrire les réponses empiriques de l'ensemble des espèces qui composent une communauté à une diversité importante de diversité de pressions environnementales est toutefois peu réaliste logistiquement et sans doute impossible pour la majorité des écosystèmes. Les approches prédictives comme celle proposée au chapitre 5 et par Halpern et al. (2008b) sont ainsi particulièrement utiles puisqu'elles permettent d'intégrer une quantité importante de connaissances écologiques en une évaluation quantitative qui est comparable entre espèces, stresseurs et localisations (Halpern et al., 2015b).

Deuxièmement, l'approche proposée suppose que les réponses spécifiques aux espèces – *i.e.* les effets directs – sont linéaires et additives. Il est pourtant bien connu que les réponses non-linéaires et non-additives sont courantes (*e.g.* Crain et al., 2008; Côté et al., 2016). L'étude de ces réponses individuelles occupe une place prépondérante dans la littérature scientifique sur les effets de multiples stresseurs environnementaux. Ces réponses sont toutefois davantage explorées à travers des approches expérimentales ou de l'échantillonnage terrain, et sont limitées pour des évaluations à l'échelle de communautés complètes. C'est pourquoi j'ai opté pour une évaluation relative de la sensibilité spécifique des espèces aux stresseurs considérés à partir de traits fonctionnels au chapitre 5. Bien que cette approche pourra sans doute être critiquée par des scientifiques ayant une expertise plus pointues, comme des physiologistes, elle a permis d'évaluer efficacement la sensibilité relative de plusieurs centaines d'espèces à près de 20 stresseurs environnementaux. Néanmoins, lorsque disponibles, les réponses des espèces aux stresseurs environnementaux pourraient aisément remplacer les résultats de l'évaluation relative par traits fonctionnels.

Il est toutefois important de noter que l'objectif de ma thèse n'était pas d'explorer les effets de plusieurs stresseurs sur la sensibilité spécifique aux espèces. Je me suis plutôt intéressé à l'inclusion des effets indirects issus des interactions écologiques. À cet égard, les règles heuristiques issus du chapitre 1 et utilisées au chapitre 5 intègrent les effets non-linéaires et non-additifs à l'échelle des interactions à trois espèces. De plus, plusieurs des limites et suppositions sont représentatives de lacunes en connaissances et en données requises pour l'application d'approches environnementales holistiques plutôt que spécifiques aux approches proposées au chapitre 5 et à l'approche de Halpern et al. (2008a). Lorsqu'elles sont disponibles, les connaissances et données peuvent généralement être intégrées pour améliorer les évaluations d'effets cumulatifs.

Troisièmement, la distribution des stresseurs environnementaux et des espèces proposée nous a permis de caractériser leur chevauchement spatial, sans toutefois considérer leur chevauchement temporel. Une supposition implicite aux analyses effectuées dans le cadre de ma thèse est ainsi un chevauchement temporel entre les stresseurs environnementaux et les espèces. Une absence de chevauchement temporel pourrait toutefois influencer l'exposition réelle des espèces aux stresseurs et les interactions potentielles entre stresseurs. Les effets cumulatifs pourraient ainsi être surestimés s'il y a absence de chevauchement temporel. La dynamique temporelle des stresseurs et des espèces pourrait toutefois être considérée à l'aide de séries temporelles robustes. On peut entre autres penser aux données climatiques et de pêcheries issues des programmes de suivis environnementaux de Pêches et Océans Canada.

Finalement, l'approche proposée est construite à partir d'une série de modules qui caractérisent un système d'étude et des attributs biologiques : la distribution et l'intensité des stresseurs, la distribution des espèces, le méta-réseau d'interactions écologiques, les réponses spécifiques aux espèces aux stresseurs, et la sensibilité trophique. Ces modules sont flexibles, basés sur des fondements théoriques et guidés par les données ; la quantité grandissante de connaissances et de données environnementales accessibles ouvertement et le développement des capacités computationnelles pourront être mis à profit pour améliorer la qualité des modules individuels et de l'évaluation des effets cumulatifs. Ces modules sont également largement discutés au sein de la littérature scientifique et de nouvelles approches sont régulièrement publiées. Les modèles de distributions des espèces sont activement développés (Norberg et al., 2019) ; des méthodes quantitatives pour prédire les interactions écologiques et atténuer les difficultés logistiques de leur échantillonnage *in situ* sont de plus en plus disponibles (Morales-Castilla et al., 2015; Beauchesne et al., 2016; Albouy et al., 2019; Poisot et al., 2020) ; les connaissances sur la sensibilité spécifique des espèces aux stresseurs environnementaux sont explorés grâce à des exercices de modélisation (Lindmark et al., 2019; Dee et al., 2020; Otto et al., 2020) et des manipulations expérimentales (Pillet et al., 2016; Lange et Marshall, 2017). De plus, des initiatives de science ouverte fournissent une quantité croissante de données sur lesquelles l'approche proposée au chapitre 5 repose : la distribution et l'intensité des stresseurs (Halpern et al., 2015a; Beauchesne et al., 2020b), l'occurrence d'espèces (GBIF, 2020; OBIS, 2020), les traits fonctionnels (WoRMS Editorial Board, 2017; Froese et Pauly, 2019; Palomares et Pauly, 2019; Encyclopedia of Life, 2020), les interactions écologiques (Poelen et al., 2014; Poisot et al., 2016) et les données abiotiques (Assis et al., 2018). Il semble ainsi raisonnable de croire que les limites présentées s'atténueront et que l'applicabilité de la méthode proposée s'accentuera progressivement.

Perspectives

Dans la sous-section précédente, j'ai énuméré quelques perspectives relatives aux limites de mon projet de thèse. Dans les sous-sections suivantes, je présente quatre grandes perspectives de développement futur visant à poursuivre les travaux initiés au cours de ma thèse et à favoriser l'application d'approches de gestion environnementale holistiques.

Opérationnaliser la gestion environnementale

L'application d'approches environnementales holistiques, comme l'évaluation des effets cumulatifs, repose sur une quantité importante de données et de connaissances. Il s'agit d'une limitation majeure fréquemment citée dans la littérature sur les effets cumulatifs (*e.g.* Jones, 2016; Hodgson et al., 2019) et pour les approches environnementales holistiques en général (Dreujou et al., 2020). Les données ou connaissances nécessaires sont parfois indisponibles, inaccessibles, ou inexistantes. Même lorsque les données sont disponibles, il peut être particulièrement difficile d'assembler une base de données permettant des analyses holistiques à large échelle. C'est une réalité à laquelle j'ai été confronté tout au long de ma thèse et qui est partagée par d'autres projets dans le Système du Saint-Laurent. Par exemple, un projet en cours depuis quelques années vise l'identification de milieux d'intérêt pour la conservation en vue d'établir un réseau d'aires marines protégées dans le Système du Saint-Laurent. Une telle initiative nécessite des connaissances similaires à celles assemblées dans le cadre de ma thèse. Ces besoins croissants en données et connaissances holistiques mettent en évidence une nécessité fondamentale pour la gestion environnementale du futur : le besoin de valoriser les connaissances acquises, de les structurer de façon interopérable – *i.e.* faciliter l'union de bases de données distinctes –, de les rendre disponibles pour tous et de se doter d'infrastructures maximisant nos capacités de gestion adaptative (Reichman et al., 2011; Poisot et al., 2013; Wilkinson et al., 2016; Williams et al., 2020). C'est la raison d'être d'initiatives de données ouvertes comme le *Global Biodiversity Information Facility* (GBIF ; GBIF, 2020), le *Ocean Biodiversity Information System* (OBIS ; OBIS, 2020), le *World Register of Marine Species* (WoRMS ; WoRMS Editorial Board, 2017) et Bio-ORACLE (Assis et al., 2018).

Dans ce contexte, un objectif sous-jacent à ma thèse était de valoriser et de partager les connaissances et données environnementales acquises. Les approches que j'ai développées sont accessibles et permettent de valoriser les connaissances acquises dans le Système du Saint-Laurent et ailleurs dans le monde. Par exemple, j'ai utilisé des connaissances disponibles ouvertement afin de prédire les interactions écologiques (chapitre 2). J'ai également tenté de favoriser le partage des données acquises pendant ma thèse. J'ai ainsi mis en place, avec de nombreux collaborateurs, une plateforme de connaissances ouvertes nommée *eDrivers* qui réunit des experts commis à structurer, à standardiser et à partager les connaissances sur les stresseurs environnementaux dans le Système du Saint-Laurent en support à la science et la gestion holistique (chapitre 4). Cette initiative est accompagnée d'un package R[1] (Beauchesne, 2020) qui fournit un accès ouvert aux données de stresseurs environnementaux et d'un outil interactif qui permet l'exploration des couches spatiales individuelles ou en combinaison[2]. J'ai utilisé des outils de programmation, principalement le langage R, tout au long de ma thèse afin d'assurer la reproductibilité et la transparence de mes travaux, et le code associé à

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[1] R est un logiciel libre destiné aux statistiques, la science des données et les graphiques (https ://www.r-project.org/)

[2] https ://david-beauchesne.shinyapps.io/eDriversApp/

toutes les analyses effectuées pour ma thèse est disponible sur GitHub[3].

Ce travail amorcé pendant ma thèse devrait être poursuivi. Les outils développés pour structurer, partager et explorer les données de stresseurs environnementaux du Système du Saint-Laurent devraient être élargis afin d'inclure tous les éléments nécessaires à l'évaluation des effets cumulatifs présentée au chapitre 5. Pour simplifier le message clé de ce chapitre, j'ai limité la présentation des résultats de l'évaluation des effets cumulatifs à quelques exemples spécifiques. L'approche proposée permet toutefois d'explorer l'ensemble des combinaisons espèces-stresseurs possibles. En plus de partager les données et de fournir une capacité d'exploration interactive, un outil interactif permettrait ainsi d'explorer des questions spécifiques à certaines espèces, stresseurs, ou groupes d'espèces et de stresseurs. Le travail amorcé avec divers experts devrait également être poursuivi afin de valoriser leurs connaissances et leurs données, d'assurer la pérennité du projet et d'améliorer les connaissances partagées à travers le temps. Ce type d'initiative est, je crois, nécessaire au développement de nos capacités de gestion adaptative et de gestion environnementale pour le Système du Saint-Laurent et ailleurs. De plus, amener divers experts disciplinaires à partager un objectif commun pourrait faciliter et encourager des initiatives interdisciplinaires.

Scénarios de gestion dans un contexte de changements climatiques

Dans un futur rapproché, il est attendu que les changements climatiques continueront de s'intensifier et que les activités humaines s'intensifieront. Par exemple, les changements climatiques modifient les niches climatiques des espèces et peuvent entraîner une redistribution et une restructuration des communautés (*e.g.* Thuiller,

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[3] GitHub est un service web d'hébergement et de gestion de développement de logiciels utilisé par plus de 40 millions d'utilisateurs partout à travers le monde (https ://github.com/). Le code associé à mes travaux de thèse est disponible sur mon profil personnel (https ://github.com/david-beauchesne) et à travers l'organisation *eDrivers* (https ://github.com/orgs/eDrivers/).

2004; McKenney et al., 2007; Blois et al., 2013; Bartley et al., 2019). Albouy et al. (2014) a ainsi estimé que les modifications prévues aux niches climatiques des poissons en Mer Méditerranée résulteraient en une perte de 54 espèces endémiques et une diminution du nombre d'interactions écologiques de plus de 73% d'ici 2100. Les modifications aux conditions environnementales combinées à l'accroissement du trafic maritime peuvent également favoriser l'invasion de nouvelles espèces (Goldsmit et al., 2020), avec des conséquences parfois importantes sur les communautés (Vander Zanden et al., 1999; David et al., 2017). On peut ainsi s'attendre à une redistribution des liens qui structurent les communautés à des extinctions locales et à l'invasion de nouvelles espèces face aux changements climatiques (Bartley et al., 2019). Ces changements, pour lesquels nous n'avons peu ou pas d'emprise de gestion locale, s'ajouteront à une empreinte humaine croissante (*e.g.* Elliott, 2011; Brown et al., 2013; Dempsey et al., 2017). Par exemple, Halpern et al. (2019) démontre que, bien que l'intensité des pêcheries diminue dans plusieurs pays, les activités humaines continuent généralement de croître en milieux côtiers globalement. Plus près de nous, plusieurs projets de développements portuaires en cours augmenteront le volume annuel du trafic maritime dans le Système du Saint-Laurent.

Considérés collectivement, ces changements prédits nous suggèrent que nous serons bientôt confrontés à de nouveaux enjeux environnementaux complexes. Par exemple, quelles seraient les conséquences d'une augmentation du trafic maritime dans le Chenal Laurentien, l'arrivée d'une nouvelle espèce invasive dans les ports de l'estuaire et le déplacement vers le nord de la distribution de certaines espèces face aux changements climatiques ? Face à ces questions complexes, des approches prédictives permettant de tester des scénarios de gestion dans un contexte de changements climatiques deviennent un atout majeur (Dubé, 2003; Jones, 2016; Hodgson et al., 2019).

La méthode proposée au chapitre 5, à l'instar de la méthode proposée par Halpern et al. (2008b), fournit ce type de capacité en proposant un cadre prédictif qui permet d'évaluer les risques associés aux effets de plusieurs stresseurs environnementaux sur les espèces. Des prédictions de changements environnementaux pourraient ainsi être incorporées à l'approche proposée au chapitre 5. L'accroissement du trafic maritime pourrait être prédit selon les projets de développements portuaires proposés dans le Système du Saint-Laurent et à partir d'indicateurs socioéconomiques (*e.g.* Sardain et al., 2019). Les effets potentiels des espèces invasives pourraient être prédits en identifiant les espèces dont l'invasion est vraisemblable à partir de leurs attributs biologiques, de leur historique d'invasion et selon les vecteurs d'invasions disponibles (*e.g.* navires internationaux) ; leurs habitats potentiels pourraient être prédits à partir de modèles de distribution d'espèces et de données climatiques projetées (Goldsmit et al., 2018, 2020). Leur position potentielle au sein du réseau trophique du Système du Saint-Laurent pourrait finalement être évaluée grâce à l'approche développée au chapitre 2 pour prédire les interactions écologiques. La distribution future des espèces au sein du Système du Saint-Laurent pourrait être modélisée afin d'explorer les modifications à la co-occurrence des espèces et à la structure locale des communautés (*e.g.* Albouy et al., 2014). Dans le cadre d'évaluations d'impacts environnementaux, il serait également possible d'explorer une gamme de scénarios visant le développement de nouveaux projets économiques pour le Système du Saint-Laurent. Par exemple, quels seraient les effets d'un accroissement de la capacité portuaire à Québec vs le développement d'un nouveau port en Gaspésie ?

L'approche proposée au chapitre 5 permettrait d'explorer ces questions individuellement ou collectivement au sein d'un cadre holistique et régional, et d'offrir des recommandations pour les gestionnaires. La capacité de tester ce type de scénarios de gestion est, à mon avis, essentielle afin d'appuyer la gestion proactive des activités humaines dans un contexte de changements climatiques et de gestion écosystémique.

Assurer un continuum terre-côte-mer

Les résultats du chapitre 4 ont démontré une exposition cumulée importante en milieux côtiers, particulièrement à l'embouchure des rivières et des centres urbains. Les milieux les plus affectés identifiés par l'analyse des effets cumulatifs du chapitre 5, quant à eux, sont près de la côte, mais sont généralement localisés davantage en milieux marins. Cette distinction entre les chapitre 4 et 5 ne doit pas être interprétée comme une absence d'effets cumulatifs en milieux côtiers malgré une exposition cumulée majeure ; elle est plutôt représentative de l'absence de connaissances généralisée en milieux côtiers et de l'utilisation de données biotiques marines.

Les évaluations d'effets cumulatifs planétaires sur les écosystèmes marins démontrent que les écosystèmes côtiers – *e.g* herbiers, récifs coralliens et mangroves – sont les plus touchés et ceux pour lesquels l'accroissement des effets cumulatifs est le plus rapide (Halpern et al., 2008b, 2015b, 2019). L'accroissement des populations mondiales et les effets des changements climatiques sont plus drastiques en milieux côtiers (Smith, 2011; IPCC, 2019). Les côtes sont ainsi soumises à une convergence des effets des changements climatiques, du ruissellement des pressions environnementales terrestres par les bassins hydrographiques, et des pressions humaines directes. Il n'est donc pas étonnant de constater que les effets cumulatifs y sont généralement supérieurs. Bien qu'il existe un continuum évident entre les écosystèmes terrestres, marins et côtiers, nous continuons tout de même de considérer ces domaines indépendamment. Les défis logistiques à l'intégration de ces trois domaines sont significatifs et justifient généralement cette division, tant au niveau de la science que de la gestion (Webb, 2012; Kerr et al., 2014). Pourtant, abandonner cette segmentation écologique apparaît une nécessité afin de capturer les effets de stresseurs environnementaux qui convergent souvent en milieux côtiers. L'approche d'évaluation des effets cumulatifs proposée au chapitre 5 n'est pas spécifique au domaine marin et pourrait être utilisée afin d'effectuer une évaluation des effets cumulatifs cohérente environnementalement en considérant des données terrestres, côtières et marines simultanément.

Adopter une pensée systémique

La situation environnementale planétaire constitue un problème complexe qui nécessite une pensée systémique. Ce besoin est généralement bien compris et largement discuté dans la littérature. C'est d'ailleurs pourquoi des approches comme la gestion écosystémique et l'évaluation des effets cumulatifs existent. Malgré cette compréhension, nous continuons majoritairement d'utiliser des approches réductionnistes. La pensée réductionniste est tellement ancrée dans nos façons de faire que nous l'appliquons même pour des approches systémiques. Un extrait de Rice (2011) dans son article sur la gestion écosystémique des pêcheries intitulé *"Managing fisheries well : delivering the promises of an ecosystem approach"* résume bien ces propos :

> *"Over time, evidence accumulated of the complexity of direct and indirect effects of ocean physics and species relationships, and the diverse interactions of the effects of these forcers with fisheries. The complexity of ecosystem processes are inherently interesting and familiar to ecologists, but carry a risk getting lost in complexity for its own sake. For science to best support management, it is necessary to consider when each term in the population dynamics equation actually matters to sustainable exploitation."*

En quelques phrases, l'auteur présente l'importance reconnue des effets directs et indirects pour la gestion des pêcheries, puis il relègue l'étude de la complexité des écosystèmes à un exercice intellectuel pour les écologistes ; nous devrions plutôt concentrer nos efforts sur les éléments les plus importants assurant l'exploitation durable des populations animales dans un contexte de gestion écosystémique des pêcheries. La volonté d'identifier *la* cause expliquant un phénomène est manifeste en science en général (*e.g.* Fulton et al., 2014; Tsoukas, 2018; Fried et Robinaugh, 2020). Notre penchant pour la science réductionniste est amplement justifiée. C'est elle qui m'a permis d'articuler un cadre théorique pour l'évaluation des effets cumulatifs communauté-centrée présentée au chapitre 1 ; c'est également elle qui a permis l'accumulation incrémentielle de connaissances écologiques qui appuient le développement de programmes de gestion et de suivis environnementaux, et elle qui permettra éventuellement de valider et d'affiner les prédictions du chapitre 5. L'approche réductionniste apporte toutefois son lot de subjectivité, qui décroît avec l'accumulation progressive d'une base d'évidences scientifiques (Harding, 1998). Cette accumulation de connaissances nécessite toutefois du temps, un luxe typiquement indisponible pour la gestion et la prise de décision.

Une pensée systémique permettrait de poser un regard descendant – *top-down* – sur des problématiques complexes et d'identifier les facteurs qui peuvent exercer une influence significative sur un système d'intérêt (Jordan, 2013). Une pensée systémique aurait-elle assurée le rétablissement de la population de bélugas de l'estuaire, ou empêchée la chute des stocks de poissons de fond du Système du Saint-Laurent ? Bien sûr que non. Les connaissances écologiques et les capacités technologiques développées par la gestion de ces problématiques nous fournissent aujourd'hui la capacité de structurer une pensée systémique pour la gestion environnementale. Dans ce contexte, une pensée systémique pourrait valoriser les connaissances accumulées et guider – sans remplacer – la recherche réductionniste pour optimiser l'accumulation de nouvelles données et d'améliorer notre base de connaissances scientifiques (Jordan, 2013), assurant une boucle de rétroactions entre les approches environnementales holistiques et la recherche scientifique.

En alliant théorie, gestion environnementale et bio-informatique, ma thèse offre une perspective accessible et des outils concrets en vue d'appliquer une pensée systémique dans un contexte de gestion écosystémique. La méthode d'évaluations des effets cumulatifs proposée offre la capacité de considérer explicitement la complexité des communautés écologiques et la diversité des pressions environnementales pour prédire les effets directs et indirects sur les espèces. Les connaissances utilisées sont largement disponibles ouvertement ou vouées à la devenir de plus en plus. Bien que plusieurs questions demeurent, la méthode proposée offre un cadre prédictif qui pourra être exploré, validé et amélioré par des expériences et de l'échantillonnage terrain. J'espère ainsi que les concepts, méthodes et outils développés dans le cadre de ma thèse permettront d'appuyer une pensée systémique opérationnelle, transparente et ouverte qui sera au coeur de nos approches de gestion environnementale. Comme noté en préface du livre *General System Theory* de Lugwig von Bertalanffy : *"The crises we face are systemic in nature. To overcome those crises we need to understand how systems work. To arrive at such an understanding we need to think systematically."*

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