

¹ On the vulnerability of food webs to multiple
² stressors

³ *David Beauchesne^{1,2,*}, Kevin Cazelles³, Philippe Archambault², Dominique
⁴ Gravel⁴*

⁵ ¹Institut des sciences de la mer, Université du Québec à Rimouski, Rimouski, QC, Canada

⁶ ²Québec Océan, Département de biologie, Université Laval, Québec, QC, Canada

⁷ ³Department of Integrative Biology, University Of Guelph, Guelph, Ontario, Canada N1G
⁸ 2W1

⁹ ⁴Département de biologie, Université de Sherbrooke, Sherbrooke, QC, Canada

¹⁰

¹¹ **Running title:** Of food webs and multiple stressors

¹²

¹³ **Keywords:** antagonism, synergism, non-additive effects, multiple stressors, cumulative
¹⁴ impacts, holistic, indirect effect,

¹⁵

¹⁶ **Type of article:** Ideas and Perspectives

¹⁷

¹⁸ **Abstract word count:**

¹⁹ **Main text word count:**

²⁰ **Number of references:**

²¹ **Number of figures:**

²² **Number of tables:**

²³ **Number of text boxes:**

²⁴

²⁵ **Correspondence:**

²⁶ David Beauchesne

²⁷ david.beauchesne@uqar.ca

²⁸ 1-514-553-4975

²⁹

³⁰ **Statement of authorship:**

³¹

³² **Data accessibility statement:**

³³ **Proposal letter**

³⁴ **Instructions**

³⁵ *Unsolicited proposals, which will be evaluated by the Ideas and Perspectives or*
³⁶ *Reviews and Syntheses Editors, in consultation with the Editorial Board and*
³⁷ *Editor-in-Chief, prior to a full submission. Proposals should be no more than*
³⁸ *300 words long, describe the nature and novelty of the work, the contribution*
³⁹ *of the proposed article to the discipline, and the qualifications of the author(s)*
⁴⁰ *who will write the manuscript. Proposals should be sent to the Editorial Office*
⁴¹ *(ecolets@cefe.cnrs.fr).*

⁴² **Notes**

- ⁴³ • In it's current form, I believe that the contribution portion is not good enough
⁴⁴ • I wonder whether the qualifications should be more in depth.
⁴⁵ • Right now, the letter is 43 words over the word limit.
⁴⁶ • Also, this text might be better than the current abstract

⁴⁷ **Letter**

⁴⁸ Evaluating the effects of multiple sources of stress in natural environments has become an
⁴⁹ increasingly important issue as the effects of intensifying global change and expanding hu-
⁵⁰ man activities result in complex stress exposure regimes. Even though the non-additive
⁵¹ effects of multiple stressors have been investigated empirically for a few decades now, there
⁵² remains a general lack of theoretical understanding of their impacts on natural systems.
⁵³ In particular, the role of species and their interactions in mediating the effects of multiple
⁵⁴ disturbances through ecological ecommunities networks, although widely acknowledged, has
⁵⁵ yet to be formally explored. We propose the first such formal exploration by exhaustively
⁵⁶ simulating the impacts of all possible pathways of effects on the dynamics of 3-species mo-
⁵⁷ tifs using Lotka-Volterra models. We uncover that interaction types and species position
⁵⁸ greatly influence sensitivity to and amplification of multiple disturbances and that indirect
⁵⁹ pathways of effects are the main cause of non-additive effects. In particular, predators in
⁶⁰ food chain and omnivory interactions act as both weak entry points (*i.e.* highly sensitive to
⁶¹ disturbances) and biotic amplifiers (*i.e.* affected synergistically by disturbances). We then
⁶² use the simulated sensitivity and amplification scores as heuristics to infer trophic vulnera-
⁶³ bility of species based on topology and realized pathways of effects in the food web of the
⁶⁴ Northern Gulf of St. Lawrence, Canada, prior to a groundfish stock collapse in the 1990s.
⁶⁵ We find that heavily exploited species appear to be the most vulnerable trophically, while
⁶⁶ fisheries transitioned to insensitive or beneficiary species post-collapse. This contribution is
⁶⁷ significant and timely for two main reasons. First, from a theory stand point, this is the first
⁶⁸ exhaustive exploration of mitigation and amplification of multiple disturbances via trophic
⁶⁹ motifs. Second, we provide a clear link between theory and management by illustrating how

70 our framework can be applied to detect most sensitive species in a real food web exposed
71 to various stressors. Our group of co-authors is singularly positioned to write this paper.
72 D. Beauchesne and P. Archambault both have strong backgrounds in environmental assess-
73 ments in general and cumulative impacts in particular. K. Cazelles and D. Gravel are both
74 experts in theoretical ecology with strong backgrounds and recognition in the field.

⁷⁵ **1 Abstract**

⁷⁶ Evaluating the effects of multiple sources of stress in natural environments has become an in-
⁷⁷ creasingly important issue as the effects of intensifying global change and expanding human
⁷⁸ activities result in complex stress exposure regimes. Even though the non-additive effects of
⁷⁹ multiple stressors have been investigated empirically for a few decades now, there remains a
⁸⁰ general lack of theoretical understanding of their impacts on natural systems. In particular,
⁸¹ the role of species and their interactions in mediating the effects of multiple disturbances
⁸² through ecological communities, although widely acknowledged, has yet to be formally ex-
⁸³ plored. We propose the first such formal exploration by exhaustively simulating trophic
⁸⁴ impacts through all possible pathways of effects on the dynamics of 3-species motifs using
⁸⁵ Lotka-Volterra models. We uncover that interaction types and species position greatly influ-
⁸⁶ ence sensitivity to and amplification of multiple disturbances and that indirect pathways of
⁸⁷ effects are the main source of non-additive effects. In particular, predators in food chain and
⁸⁸ omnivory interactions act as both weak entry points (*i.e.* highly sensitive to disturbances)
⁸⁹ and biotic amplifiers (*i.e.* affected synergistically by disturbances). We then use the simu-
⁹⁰ lations results as heuristics to infer trophic vulnerability of species based on topology and
⁹¹ realized pathways of effects in the food web of the Northern Gulf of St. Lawrence, Canada,
⁹² prior to a groundfish stock collapse in the 1990s. We find that heavily exploited species
⁹³ appear to be the most vulnerable trophically, while fisheries transitioned to insensitive or
⁹⁴ beneficiary species post-collapse.

95 **2 Introduction**

96 Ecosystems worldwide are increasingly affected by a vast array of environmental pressures,
97 commonly referred to as stressors (Boonstra *et al.* 2015; Halpern *et al.* 2019). Pressures may
98 be driven by natural or human-induced biophysical processes such as ocean acidification and
99 warming, or directly from anthropogenic activities such as fisheries. These drivers can be
100 defined as any externality that affects environmental processes and disturbs natural systems.
101 Individually, drivers have been found to impact all levels of biological organization and cause
102 dramatic changes to whole ecosystems. Ocean acidification can reduce coral and mollusk
103 calcification, metabolic, growth and mortality rates, and has been linked to altered carbon
104 fluxes in ecological networks (Fabry *et al.* 2008; Kroeker *et al.* 2013; Bove *et al.* 2019).
105 Fisheries have caused the collapse of commercial species, decreased the mean trophic level
106 in coastal and oceanic environments by targetting large predators and impaired a variety of
107 essential ecosystem services (Pauly *et al.* 1998; Myers & Worm 2003; Worm *et al.* 2006).
108 Rarely do drivers occur individually, and the list of potentially interacting drivers affecting an
109 ecosystem at any given point in time or space can be extensive (Halpern *et al.* 2019). Global
110 changes and local human activities thus result in increasingly intricate environmental stress
111 exposure regimes, compounding the pathways of effects through which natural systems can be
112 impacted (Halpern *et al.* 2019). For example, coral reefs contend with a suite of pressures
113 including fishing, warming temperatures, ocean acidification and water quality that may
114 impact species in contrasting ways (McClanahan *et al.* 2014; Harborne *et al.* 2017). Drivers
115 can then combine to induce complex and sometimes unpredictable effects (Côté *et al.* 2016).
116 Dramatic examples include up to 100-fold increases of the sensitivity of certain organisms
117 to toxicants (*e.g.* pesticides) when exposed to other environmental stressors (*e.g.* parasites;
118 Liess *et al.* 2016) and the reversal of the positive effects of acidification on primary producer
119 biomass by warmer waters in boreal lakes (Christensen *et al.* 2006).
120 The potential for complex interactions between drivers remains the largest uncertainty when

¹²¹ studying or predicting environmental impacts (Darling & Côté 2008; Côté *et al.* 2016).
¹²² Interactive drivers effects have thus been extensively investigated to uncover instances of
¹²³ non-additive effects, *i.e.* when the effect of multiple interacting drivers is greater (synergism)
¹²⁴ or lower (antagonism) than the sum of their individual parts. These studies have found non-
¹²⁵ additive effects of multiple drivers to be the norm rather than the exception across ecosystems
¹²⁶ globally (*e.g.* Darling & Côté 2008; Crain *et al.* 2008; Piggott *et al.* 2015; Jackson *et al.*
¹²⁷ 2016).

¹²⁸ Species sensitivity to environmental pressures can be highly variable, which further com-
¹²⁹ pounds the complexity of mutliple drivers studies. For example, hypoxia decreases overall
¹³⁰ habitat quality but has species-dependent effects, ranging from well-adapted (*e.g.* north-
¹³¹ ern shrimp *Pandalus borealis* and Greenland halibut *Reinhardtius hippoglossoides*; Pillet *et*
¹³² *al.* 2016) to avoidance behaviour (*e.g.* Atlantic cod *Gadus morhua*; Chabot & Claireaux
¹³³ 2008), and mortality (*e.g.* sessile benthic invertebrates; Eby *et al.* 2005; Belley *et al.*
¹³⁴ 2010). Moreovers, species are also embedded in a complex web of interactions that provides
¹³⁵ indirect pathways of effects through which pressures may permeate entire ecological com-
¹³⁶ munities (Wootton 2002; Bascompte 2009; Montoya *et al.* 2009; O’Gorman & Emmerson
¹³⁷ 2009; O’Gorman *et al.* 2012). Indirect effects, *i.e.* when two or more direct effects are
¹³⁸ linked by a single species involved in both effects, may be as important of, and propagate
¹³⁹ faster than, direct effects (Wootton 1993, 2002; Menge 1995; Yodzis 2000). Empirical ex-
¹⁴⁰ amples of trophic cascades are abundant throughout all types of ecosystems globally (Estes
¹⁴¹ *et al.* 2011). In multi-species systems, where both direct and indirect effects are operating
¹⁴² simultaneously, it is expected that the effects of environmental pressures will be amplified
¹⁴³ or dampened through biotic interactions (Ives 1995; Wootton 2002; Thompson *et al.* 2018).
¹⁴⁴ Community dynamics and how species are embedded in complex networks is therefore likely
¹⁴⁵ to affect their sensitivity to environmental pressures.

¹⁴⁶ Confronted with the challenge of managing and preserving complex systems, there is an
¹⁴⁷ urgent need for the development of theoretical frameworks that properly consider the com-

plexities of multiple drivers and ecological networks in ways that are informative to management. From a practical standpoint, single-driver and single-species assessments remain overwhelmingly applied (O'Brien *et al.* 2019), while most multiple drivers studies have typically focused on habitats (*e.g.* Ban *et al.* 2010; Halpern *et al.* 2019). This conveniently circumscribes assessments to a set of tractable units, but it also ignores systems complexity and aggregates biological processes operating at lower levels organization (Halpern & Fujita 2013; Giakoumi *et al.* 2015). Studies have also relied on the use of null models that provide little insights into the mechanisms underlying ecological responses to the effects of multiple drivers (Griffen *et al.* 2016; Jackson *et al.* 2016; De Laender 2018; Schäfer & Piggott 2018). Theoretically, species interactions have long been identified as key components to the sensitivity of whole networks to disturbances (*e.g.* Ives 1995; Wootton 2002; O'Gorman & Emmerson 2009; O'Gorman *et al.* 2012), but the effects of multiple disturbances on networks have yet to be formally explored.

In this paper, we address this issue by exhaustively investigating how multiple environmental pressures permeate complex ecological networks and the role of species and their interactions (*i.e.* food web topology) in buffering against or amplifying the effects of disturbances. In doing so, we seek to answer questions of particular significance to management: 1) should species interactions be considered in impact assessments, 2) should the effects of stressors be evaluated separately or in combination, 3) which species are most vulnerable to disturbances based on their trophic position, and

3 Of food web and multiple disturbances

3.1 Conceptualizing disturbances

Drivers can disturb the dynamics of ecological communities by disrupting a variety of biological processes (Figure 1A) such as behaviour (*e.g.* Chabot & Claireaux 2008; Hale *et*

¹⁷² *al.* 2017), reproduction [*e.g.* ref], physiology (*e.g.* Dupont-Prinet *et al.* 2013), mortality
¹⁷³ (*e.g.* Belley *et al.* 2010), and species interactions (*e.g.* Wootton 2002; Guiden *et al.* 2019).

¹⁷⁴ Multiple processes may be affected by a single driver, while multiple drivers may target a
¹⁷⁵ single process. For instance, fishing could affect the behaviour and the mortality of cod,
¹⁷⁶ while ocean warming and ocean acidification may affect physiological processes of benthic
¹⁷⁷ invertebrates such as calcification rates. The potential number of univariate and multivari-
¹⁷⁸ ate pathways of effects through which community dynamics may be affected is extensive and
¹⁷⁹ increases exponentially with the number of species and the number on links in a network.

¹⁸⁰ A thorough understanding of the impacts of disturbance regimes and community dynamics
¹⁸¹ would be necessary to fully capture the effects of multiple drivers, but the complexity of
¹⁸² empirical food webs in itself is prohibitive to investigations of community dynamics. Studying
¹⁸³ smaller subgraphs - community motifs or modules - has thus emerged as an alternative to
¹⁸⁴ gather insights into the dynamics and stability of complex ecological communities (Holt
¹⁸⁵ 1997; Holt & Hochberg 2001). Motifs are collections of n -species that, when put together,
¹⁸⁶ construct whole food webs (Milo *et al.* 2002; Stouffer *et al.* 2007). They form the backbone
¹⁸⁷ of food webs and provide a mesoscale characterization of community structure (Bascompte
¹⁸⁸ & Melián 2005; Stouffer *et al.* 2007). A species can be described as a function of all n -species
¹⁸⁹ motifs it is involved in in an empirical food web (Figure 1B; Stouffer *et al.* 2012).

¹⁹⁰ There are 13 distinct 3-species motifs composed of 30 unique positions (Milo *et al.* 2002;
¹⁹¹ Stouffer *et al.* 2007, 2012). Four 3-species motifs have received particular attention in
¹⁹² theoretical and empirical studies due to their roles [ref] and prevalence (Camacho *et al.* 2007;
¹⁹³ Stouffer & Bascompte 2010) in food webs: tri-trophic food chain, omnivory or intraguild
¹⁹⁴ predation, exploitative competition and apparent competition.

¹⁹⁵ Motif dynamics has been studied extensively to uncover how structural properties of food
¹⁹⁶ webs can benefit community persistence and stability (Allesina & Pascual 2008; Kondoh
¹⁹⁷ 2008; Stouffer & Bascompte 2010, 2011; Monteiro & Faria 2016) and to assess the structural

198 roles of species within food webs (Stouffer *et al.* 2012; Cirtwill & Stouffer 2015). These
199 provide meaningful insights for conservation efforts. For example, results from Stouffer *et*
200 *al.* (2012) suggest that certain species may benefit whole community persistence based on
201 their trophic position, and that the diversity of trophic roles found in empirical food webs
202 does not correlate to species richness. This means that strictly using species richness as
203 a conservation measure may ignore the benefits to community persistence provided by the
204 trophic roles of individual species. Using trophic roles as targets may thus be valuable for
205 community conservation (Stouffer *et al.* 2012).

206 Managers are not only tasked with species conservation, however. For example, the dynamics
207 of coexisting species is particularly important to practitioners whose mandate is to moni-
208 tor and manage exploited populations using holistic approaches such as ecosystem based
209 fisheries management. In this context, population fluctuations are at least as important as
210 species persistence. As such, studying the dynamics of persistent communities is of partic-
211 ular relevance to management in the context of multiple environmental pressures (Figure
212 1C).

213 Here, we study the equilibrium dynamics, i.e. when species are constrained to coexistence,
214 of the most prevalent 3-species motifs in food webs (i.e. food chain, omnivory, exploitative
215 competition, and apparent competition) to exhaustively investigate how trophic position and
216 interaction type influences the sensitivity to and the amplification of the effects of multiple
217 disturbances. We then use the simulations to infer species trophic vulnerability in complex
218 food webs as a function of species position in food web and realized pathways of effects.

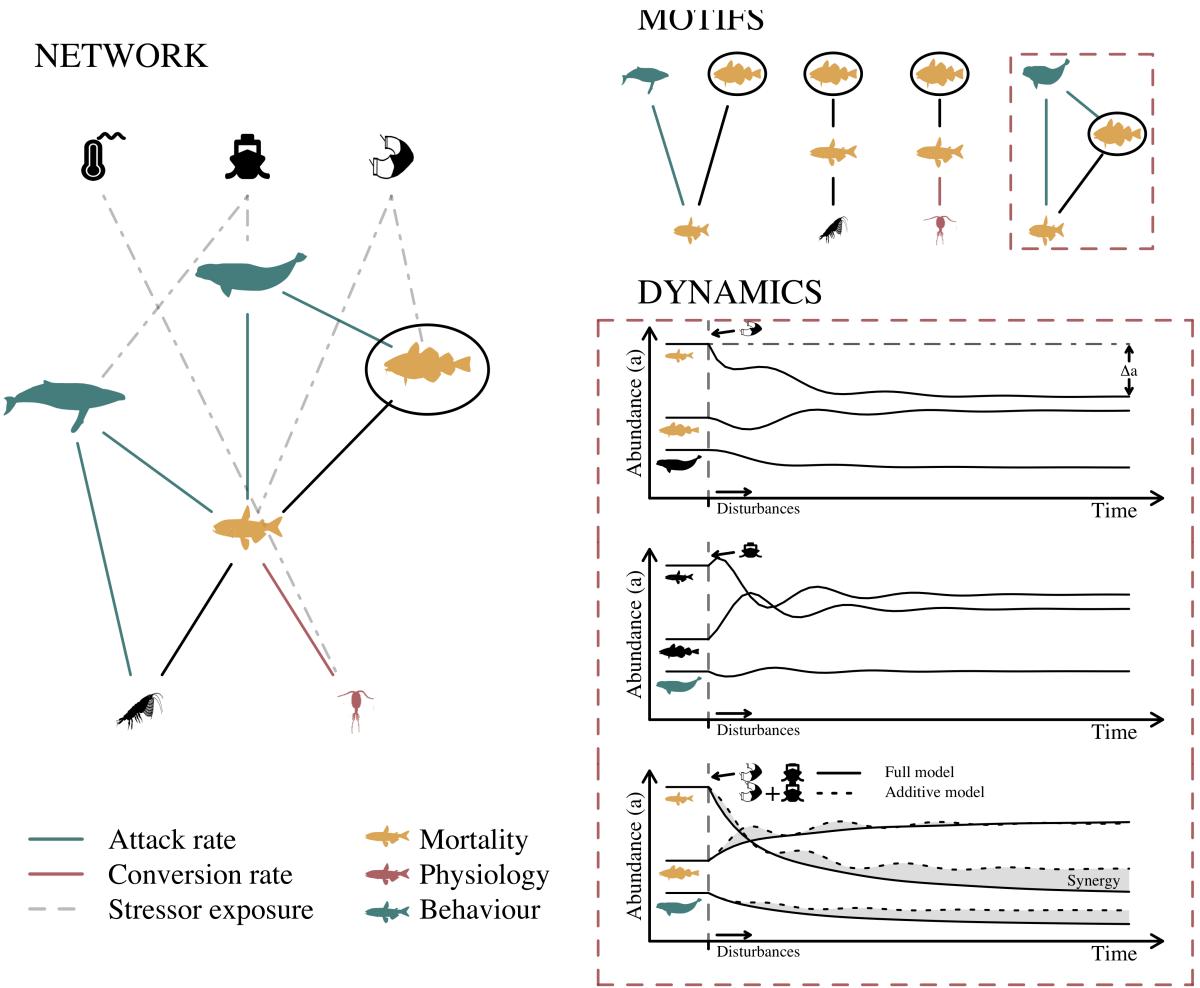


Figure 1: Conceptualization of the effects of multiple sources of environmental stress on the dynamics of a theoretical food web. A) Drivers such as sea surface temperature, marine traffic and fisheries penetrate food webs through various pathways of effects by disturbing ecological processes governing populations and communities. For instance, marine traffic disturbs whale feeding behaviour, which may lead to decreased attack rates on prey species. B) A species position in a food web can be decomposed in a suite of n -species submodules called motifs that are informative of the role played by a species in the entire food web. Different types of interaction types will lead to different types of community dynamics and a species can be described as a function of the number and types of interactions it is involved in. For instance, the interactions of the meso-predator can be decomposed into 1 exploitative competition, 2 food chains and 1 omnivory motifs. C) The dynamics of motifs can uncover if and how disturbances arising from individual and multiple drivers are propagated and amplified through different types of species interactions. Variations in species abundance due to driver induced disturbances provide an evaluation of motif species sensitivity (C1-3). The difference between the summed effects of individual drivers (*i.e.* additive model; C1-2) and the joint effects of multiple drivers (*i.e.* full model; C3) provides an evaluation of disturbance amplification.

219 **3.2 Sumulating disturbances**

220 **3.2.1 Models formulation**

221 The dynamics of tri-trophic food chain, omnivory, exploitative and apparent competition
222 motifs were modeled using Lotka-Volterra equation systems (Table S1). Two additional
223 motifs were included as controls to test the importance of species interactions in mediating
224 the effecs of disturbances, *i.e.* a partially connected motifs with a disconnected species and
225 a predator-prey interaction, and a fully disconnected motif with three fully independent
226 species.

227 Resources were modeled using logistic growth equations of the form

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

228 where X_i denotes species i , r_i is the intrinsic resource growth rate, α_{ii} is the density-
229 dependent effect of the resource on itself and α_{ij} is the rate at which consumer j affects
230 resource i , *i.e.* the attack rate.

231 Consumers were modeled using a Type I functional response of the form

$$\frac{dX_j}{dt} = X_j(-m_j + \sum_i e_{ij}\alpha_{ij}X_i - \alpha_{jk}X_k),$$

232 where m_j is the mortality rate of species j and e_{ij} is the rate at which resource i biomass is
233 transformed into consumer j biomass, *i.e.* the conversion rate, and is a scaling parameter of
234 the attack rate which cannot exceed 1.

235 Models were solved at equilibrium to study the effects of disturbances on persistent motif dy-
236 namics. As no equilibrium exists for the exploitative competition motif with Lotka-Volterra
237 models of the selected forms, competitive parameters of the form

$$\alpha_{jj}\alpha_{jk}X_jX_k - \alpha_{jj}X_j^2,$$

238 were included to the consumer models to constrain growth and limit competitive exclusion.

239 Refer to table S1 for the detailed equation systems of all motifs considered.

240 **3.2.2 Models parameterization**

241 Model dynamics was to be constrained by species coexistence, meaning that abundances
242 for all species was to be positive before and after disturbances were simulated. To achieve
243 this, we first arbitrarily set the values of a number of initial model parameters. Intrinsic
244 growth (r) and resource density-dependence (α_{ii}) were fixed to 1 and 0.001, respectively, to
245 bound all resource solutions. Competitive parameters for the exploitative competition motif
246 were also fixed at 0.001, and conversion rates (e) were fixed to 0.5. We then set an interval
247 of possible values for mortality ($m \in [0.01, 0.5]$) and attack ($\alpha_{ij} \in [0.0001, 0.01]$) in which
248 we extracted 100 sets of initial values. Values were identified using a simulated annealing
249 algorithm optimizing for consumer abundance. Sets of parameters were only retained if initial
250 abundances and abundances resulting from all possible pathways of effect were positive (see
251 next section).

252 **3.2.3 Disturbances**

253 For each motif, a 1% change in initial equilibria equation parameter values was applied
254 to simulate negative disturbances (*e.g.* an increase in mortality). Parameters selected to
255 simulate disturbances were those related to population growth (r and m) and conversion and
256 attack rates (e and α_{ij}). Those parameters were used as they can be linked to disturbance
257 effects on common biological processes affected by disturbances, *i.e.* mortality, physiology
258 and behaviour.

259 For each motif, all possible mortality, resource growth, conversion and attack rates parameter
 260 combinations were simulated. This resulted in a total of 930 unique pathways of effects
 261 for all motifs combined (food chain, competitive exploitation and apparent competition:
 262 7 parameters, 127 pathways of effects; omnivory: 9 parameters, 511 pathways of effects;
 263 partially connected 5 parameters, 31 pathways of effects; disconnected: 3 parameters, 7
 264 pathways of effects).

265 3.3 Motifs vulnerability

266 3.3.1 Trophic sensitivity

267 For all 13 unique motif positions considered and all unique pathways of effects, we define $s_{i,j}$
 268 as:

$$s_{i,j} = \frac{a_{i,j} - a_i}{a_i},$$

269 where a_i is the initial abundance at position i without disturbance, and $a_{i,j}$ is the abundance
 270 at position i with disturbance due to pathway of effect j . Note that, by definition, $s_{i,j}$ is
 271 bounded negatively to -1, as abundances cannot fall below 0. We define the sensitivity score
 272 of position i for single pathway of effect j $S_{i,j}$ as the mean of $s_{i,j}$ over the 100 sets of initial
 273 conditions.

274 The overall position sensitivity S_i was evaluated using the mean of $S_{i,j}$ over the set of all
 275 possible pathways of effect ($K^{(i)}$) for a given position i :

$$S_i = \frac{1}{|K^{(i)}|} \sum_{j \in K^{(i)}} S_{i,j}$$

276 We define *weak entry points* as particularly sensitive pathways of effect ($|S_{i,j}| > 1$) or motif
 277 positions ($|S_i| > 1$), while *biotic sinks* are insensitive pathways of effects ($|S_{i,j}| = 0$) or motif

278 positions ($|S_i| = 0$).

279 3.3.2 Trophic amplification

280 A score of trophic amplification ($A_{i,j}$) was measured to evaluate non-additive arising through
281 trophic pathways of effects:

$$A_{i,j} = S_{i,K_j} - \sum_{k_j \in K_j} S_{i,j},$$

282 where K_j is a multivariate pathway of effect j and k_j are unitary pathways of effect compo-
283 sition j . The amplification score evaluates the deviance of a multivariate pathway of effect
284 and the sum of the univariate effects composing the pathway of effect, *i.e.* the additive
285 model. Thus, a value of 0 identifies a null of additive effect, a value below 0 identifies an
286 antagonistic effect, and a value over 0 identifies synergistic effects.

287 A score of position amplification (A_i) was evaluated using the mean of the set of all possible
288 pathways of effect (K^i) for a give position i :

$$A_i = \frac{1}{|K^{(i)}|} \sum_{j \in K^{(i)}} A_{i,j}$$

289 We define biotic amplifiers as multivariate pathways of effect or motif positions that are more
290 affected than expected from an additive model ($A_{i,j} > 0.0002$, $A_i > 0.0002$). Biotic buffers
291 are multivariate pathways of effect or motif positions that are less afefcted than expected
292 from an additive model ($A_{i,j} < 0.0002$, $A_i < 0.0002$).

293 **3.4 Species vulnerability**

294 **3.4.1 Scores**

295 IMPORTANT COMMENT: For now, I present the topological score, but I am not
296 sure whether it should be presented at all since I ultimately do not really use it in
297 my discussion. Except if we end up presenting it in the paper to make the point
298 that although it would provide a proxy of trophic vulnerability (which we will be
299 using for my last thesis chapter), it does not really capture realized vulnerability
300 when actual drivers are considered. This is not so true for sensitivity, but it
301 certainly is for amplification. See Figure 9 for a biplot of topological vs realized
302 scores.

303 We broadly refer to species vulnerability as the combination of trophic sensitivity and trophic
304 amplification, as defined in this study. Two sets of scores are presented at the species level,
305 using the simulated disturbances for all possible pathways of effects as heuristics to infer
306 species trophic vulnerability.

307 The first set are topological scores of trophic sensitivity and amplification based on the
308 frequency at which species occupy one of the 4 main motif positions we considered, *i.e.* food
309 chain, omnivory, exploitative and apparent competition, in an empirical food web:

$$S_m = \sum_i f_{m,i} S_i,$$

$$A_m = \sum_i f_{m,i} A_i,$$

310 where S_m and A_m are the sensitivity and amplification scores of species m , respectively, $f_{m,i}$
311 is the frequency at which species m occupies position i in a food web, and S_i and A_i are the

312 mean trophic sensitivity and amplification scores at position i , respectively. Note that for
313 species vulnerability, we do not consider the control motifs any further.

314 The second set are realized scores of trophic sensitivity and amplification based on realized
315 pathways of effects, *i.e.* known or suspected effects of drivers affecting mortality, behaviour
316 or physiology of species in empirical food webs:

$$S_m^* = \sum_{j \in K^{i*}}^{position} S_{i,j},$$

$$A_m^* = \sum_{j \in K^{i*}}^{position} A_{i,j},$$

317 where S_m^* and A_m^* are the sensitivity and amplification scores of species m , respectively, j
318 are pathways of effect, K^{i*} is the set of realised pathways of effects for position i , and $S_{i,j}$
319 and $A_{i,j}$ are the sensitivity and amplification scores for pathway of effect j on position i

320 Realized pathways of effect are identified using the following rules:

321 1. impacts of drivers on the mortality of resources and consumers are considered as dis-
322 turbances to resource growth rates and to consumer mortality rates (r, m).

323 2. impacts on the behaviour of resources and consumers are considered as disturbances
324 to consumer attack rates (α_{ij}).

325 3. impacts on the physiology of resources and consumers are considered as disturbances
326 to consumer conversation rates (e).

327 By using these scores, we essentially assume that the realized vulnerability of a species will
328 be the sum of all individual 3-species pathways of effect through which a species may be
329 impacted.

³³⁰ **3.4.2 Empirical food webs**

³³¹ We evaluated the vulnerability of species in 3 empirical webs from the Southern (SSL) and
³³² Northern (NSL) Gulf, and Estuary (ESL) of St. Lawrence in eastern Canada (Morissette
³³³ *et al.* 2003; Savenkoff *et al.* 2004; Savenkoff 2012). The Southern and Northern Gulf of
³³⁴ St. Lawrence food webs correspond to the mid-1980s, prior to a groundfish stock collapse in
³³⁵ the early 1990s, while the St. Lawrence Estuary food web corresponds to the early 2010s.
³³⁶ The total number of species and functional groups differs between food webs ($n_{SSL} = 30$;
³³⁷ $n_{NSL} = 32$; $n_{ESL} = 41$), yet there is significant overlap ($n_{all} = 21$). Food webs resolution is
³³⁸ biased towards commercial fish for all food webs. In the food webs, interactions are identified
³³⁹ as a percent of species or functional group in the diet of another species or functional group.
³⁴⁰ Only diet percent > 0.1 were considered as interactions in our analysis. Note that detailed
³⁴¹ vulnerability results are only presented and discussed for the Northern Gulf food web. Results
³⁴² for the Estuary and Southern Gulf are available as supplementary material (Figures S1, S2).

³⁴³ \rightarrow

³⁴⁴ **3.4.3 Drivers**

³⁴⁵ Climate change related drivers (*i.e.* acidification, hypoxia, and bottom and surface temper-
³⁴⁶ ature anomalies) are prevalent in the St. Lawrence System, with the exception of hypoxia
³⁴⁷ in the Southern Gulf (Beauchesne 2019). Marine traffic is widespread, especially in the
³⁴⁸ Northern Gulf and the Estuary, which serve as the main seaway to inland North-America
³⁴⁹ (Beauchesne 2019). Fisheries have changed through time after the collapse of groundfish
³⁵⁰ stocks in the early 1990s. Species affected by fisheries were identified using the catch data
³⁵¹ provided in the description of the food web models (Morissette *et al.* 2003; Savenkoff *et al.*
³⁵² 2004; Savenkoff 2012). Geartype used was identified using landing data from logbooks from
³⁵³ the Department of Fisheries and Ocean's Canada [dfo2016b].

³⁵⁴ The impacts of specific drivers on species and functional groups was done following broad

rules to simplify the number of assumptions required. Our approach does not seek to establish the vulnerability of a particular species to all types of drivers, but rather to make general inference on species trophic vulnerability based of its trophic position and the supposed effects of drivers on biological processes driving community dynamics. Detailed literature search or expert knowledge could be used to get a better sense of the proximate effects of drivers on species, but this is beyond the scope of our objectives.

The first criteria used to evaluate the effect of drivers on species and functional groups was a broad evaluation of direct exposure to individual drivers. Acidification, hypoxia and bottom temperature anomalies are widespread in the deep habitats of the St. Lawrence, while surface temperature anomalies and marine traffic are operating on the surface layer (Beauchesne 2019). As such, species of functional groups in deep or surface habitats were considered as exposed to deep or surface drivers, respectively. Hypoxia was considered as impacting the physiology or behaviour of species or functional groups with low or high mobility, respectively (???). Temperature anomalies were considered as impacting the physiology of species with low mobility only. Ocean acidification was assumed to affect the physiology of exposed carbonate-secreting organisms (*e.g.* mollusks and crustaceans; Kroeker *et al.* 2013). Marine traffic was considered as primarily impacting whale behaviour (Christiansen *et al.* 2013; Lesage *et al.* 2017). The impact of fisheries was assumed to target the mortality rates of species with positive catch rates. Catches of certain species or functional groups of seals and seabird through hunting, and whales through bycatch, is reported for the empirical food webs of the St. Lawrence (Morissette *et al.* 2003; Savenkoff *et al.* 2004; Savenkoff 2012). We thus considered that the mortality rates of seabirds and marine mammals with reported catches was disturbed.

378 **4 Food web vulnerability to multiple disturbances**

379 **4.1 Motifs vulnerability**

380 The simulations uncover, as anticipated, that interaction motifs (*i.e.* food chain, omnivory,
381 exploitative and apparent competition) are more sensitive and more likely to amplify the
382 effects of multiples disturbances than control motifs (Figures 2, 3). Species in omnivory and
383 food chain motifs are generally more sensitive and likely to amplify the effects of disturbances
384 than species in competitive interaction motifs (Figure 2, 3).

385 Biotic sinks are composed almost exclusively of pathways targeting control motif positions
386 and simulations on control motifs largely result in additive affects (Figure 2). Weak entry
387 points, biotic buffers and biotic amplifiers, meanwhile, are prevalent for all interaction motifs
388 (Figure 2). This is particularly true for species in the omnivory motif and for the top predator
389 in the food chain motif, whose trophic sensitivity and amplification scores are highly variable
390 (Figure 2).

391 Species position also greatly influences trophic sensitivity to and amplification of distur-
392 bances. In general, top predators are weak entry points for all interaction types (Figure 3).
393 In contrast, non-additive effects on top predators depends on interaction type. Pathways of
394 effect on top predators in omnivory and food chain interactions largely result in synergistic
395 or antagonistic effects, and predators are, on average, biotic amplifiers (Figure ref{position}).
396 Predators in competitive interactions, meanwhile, are less affected by non-additive effects
397 and are fringe biotic buffers (Figure ref{position}).

398 Resources are largely weak entry points for all motifs, yet the effect are typically negative
399 in food chain and omnivory interactions, and positive in competitive interactions (Figures
400 2, 3). Altough resources are, on average, neither biotic buffers or amplifiers, the effects of
401 individual pathways of effects are mostly non-additive (Figure 2). The effects of disturbances
402 on other interactions are mostly additive. (Figure 2).

⁴⁰³ Meso-predators, which are found only in omnivory and food chain interactions, are weak
⁴⁰⁴ entry points and generally benefit from disturbances (Figure 2). Meso-predators in omnivory
⁴⁰⁵ interactions are, on average, fringe biotic buffers, but like all other positions in the omnivory
⁴⁰⁶ motif, most individual pathways of effect result in either antagonistic or synergistic effects
⁴⁰⁷ (Figure 3).

⁴⁰⁸ The nature of the pathways of effects also influences trophic sensitivity and amplification.
⁴⁰⁹ Unsurprisingly, multivariate pathways of effects are generally more impactful to species sen-
⁴¹⁰ sitivity and hold a higher proportion of weak entry points than univariate pathways (Figure
⁴¹¹ 2). Similarly, targeting multiple biological processes results in greater sensitivity and ampli-
⁴¹² fication (Figure 2). There are however a few generalities worth noting. Mortality and growth
⁴¹³ rates are driving heightened trophic sensitivities, yet do not individually contribute to non-
⁴¹⁴ additive effects (Figure 4). Instead, trophic amplification is largely driven by disturbances
⁴¹⁵ on species species interactions (*i.e.* attack (α_{ij}) and conversion (e) rates; Figure 4).

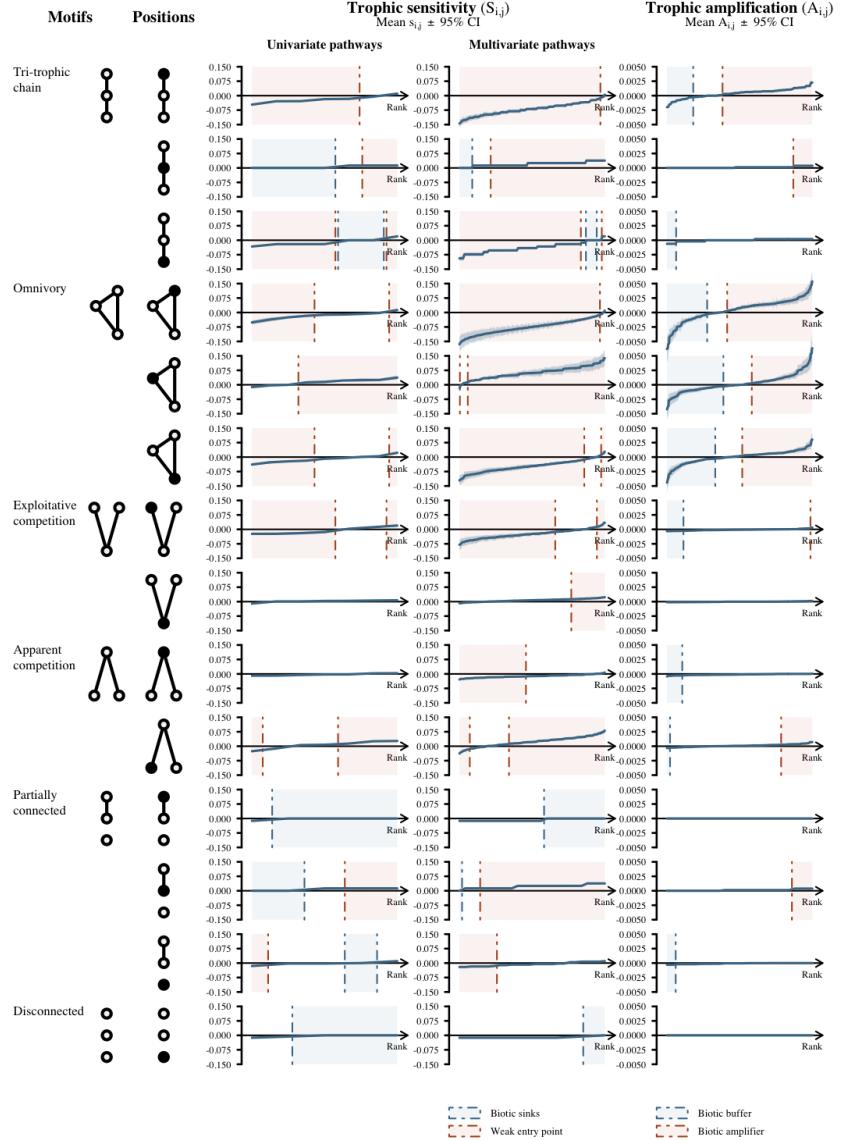


Figure 2: Ranking of trophic sensitivity ($S_{i,j}$) and amplification ($A_{i,j}$) scores for all univariate and multivariate pathways of effects on all 13 unique motif positions in the three-species motifs explored, *i.e.* tri-trophic food chain, omnivory, exploitative competition, apparent competition, partially connected and disconnected. Trophic sensitivity is the variation in species initial abundance at equilibrium and the abundance after disturbances are simulated through univariate or multivariate pathways of effect. Pathways of effects identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified by red and blue regions, respectively. Trophic amplification is the deviance of a multivariate pathway of effect and the sum of the univariate effects composing the pathway of effect, *i.e.* the additive model. Pathways of effect identified as biotic buffers (*i.e.* synergistic effect of disturbances) and biotic buffers (*i.e.* antagonistic effect of disturbances) are identified by the red and blue regions, respectively.

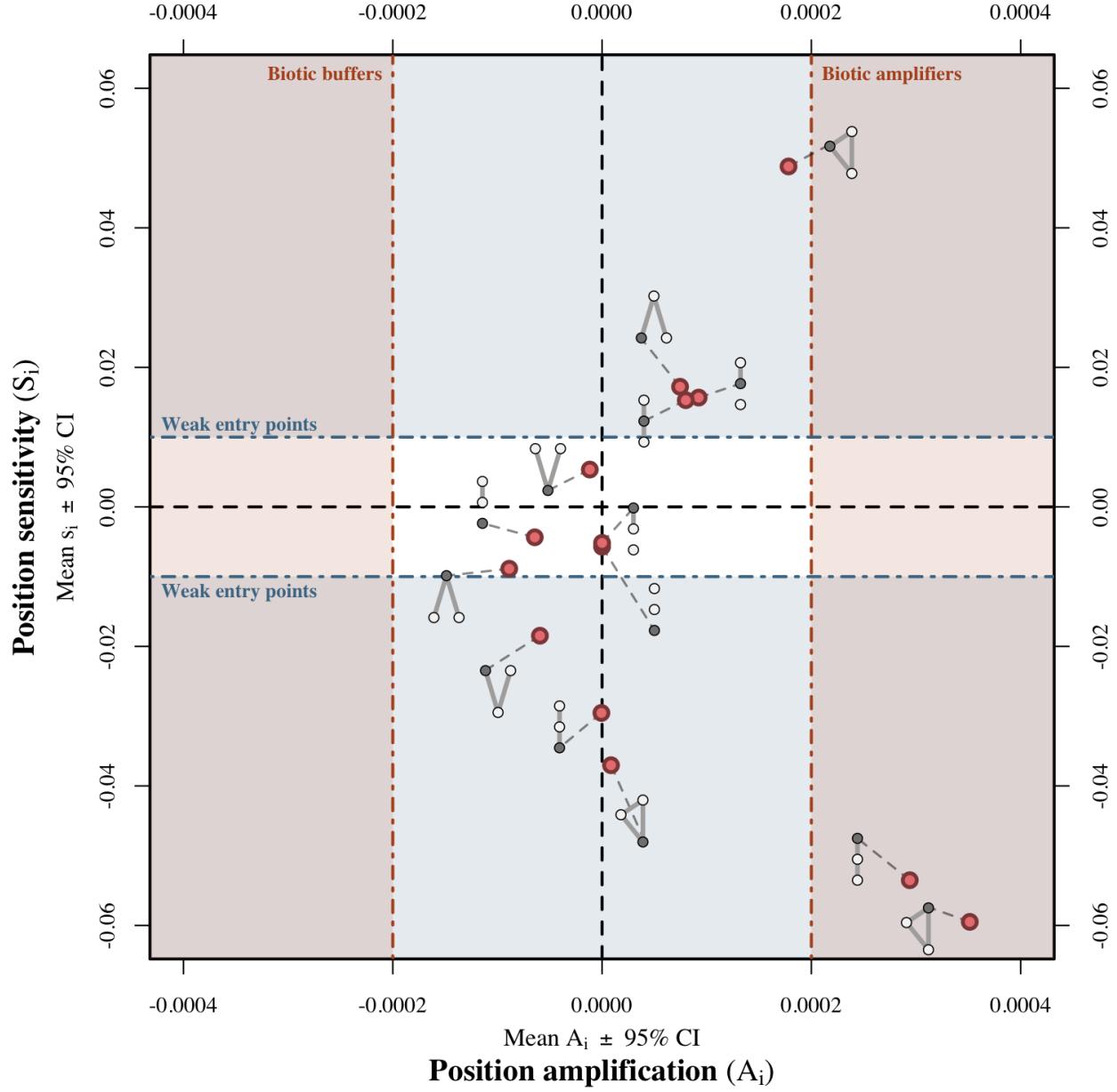


Figure 3: Ranking of 13 motif positions as a function of position sensitivity (S_i) and amplification (A_i) scores in the three-species motifs explored, *i.e.* tri-trophic food chain, omnivory, exploitative competition, apparent competition, partially connected and disconnected. Position sensitivity is mean value of the variation in species initial abundance at equilibrium and the abundance after disturbances are simulated for all univariate and multivariate pathways of effect on a motif position. Motif positions identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified by the blue regions. Position amplification is the mean deviance of a multivariate pathway of effect and the sum of the univariate effects composing the pathway of effect, *i.e.* the additive model, for all multivariate pathways of effect on a motif position. Motif positions identified as biotic buffers (*i.e.* synergistic effect of disturbances) and biotic buffers (*i.e.* antagonistic effect of disturbances) are identified by the red regions.

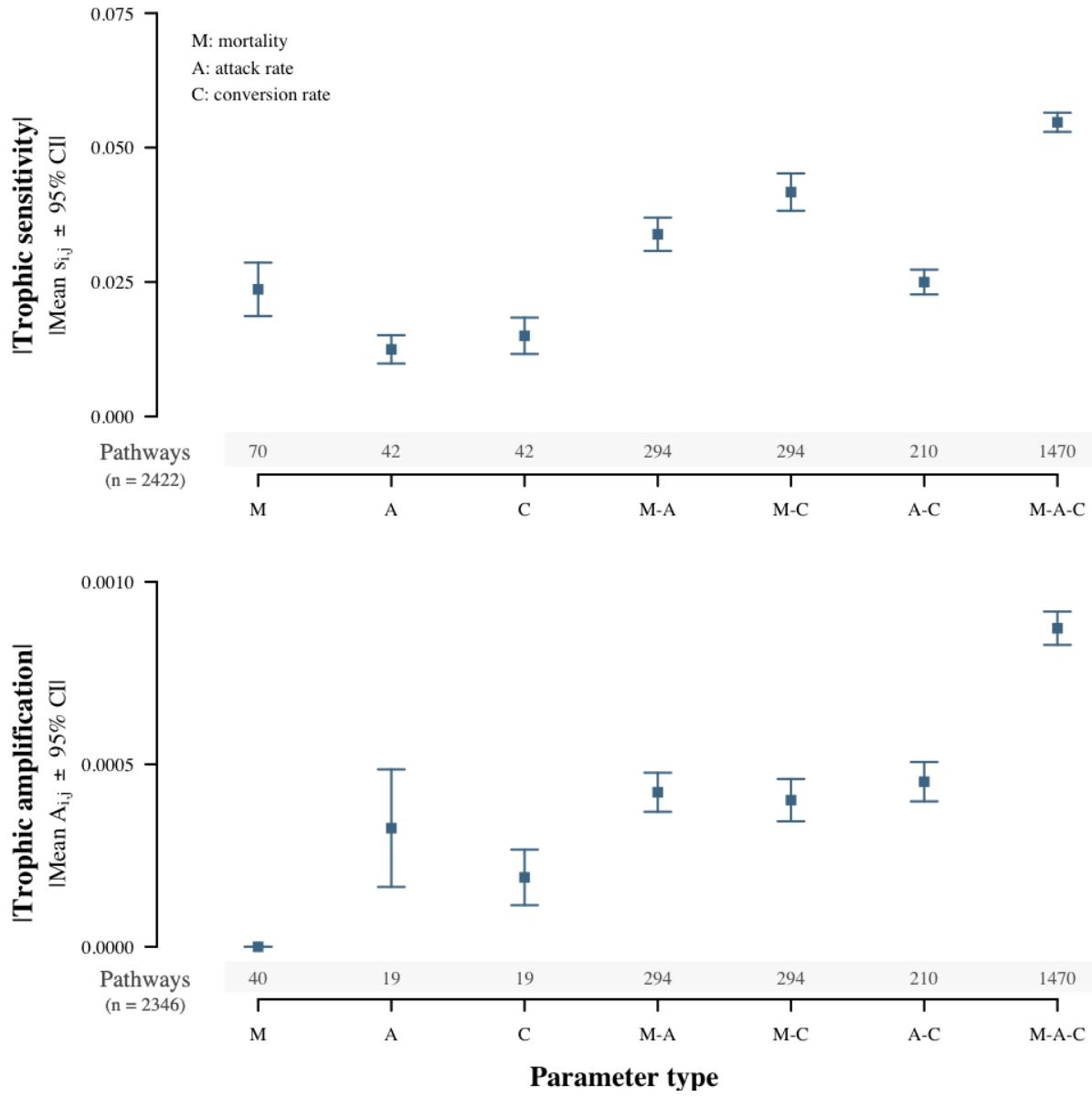


Figure 4: Absolute values of the mean trophic sensitivity ($S_{i,j}$; A) and amplification ($A_{i,j}$; B) as a function of the types of parameter composing a pathway of effect. All pathways of effect targeting a specific parameter type (*i.e.* mortality, attack and conversion rates) were grouped to evaluate their respective and combined effect on trophic sensitivity and amplification.

⁴¹⁶ **Other figures:**

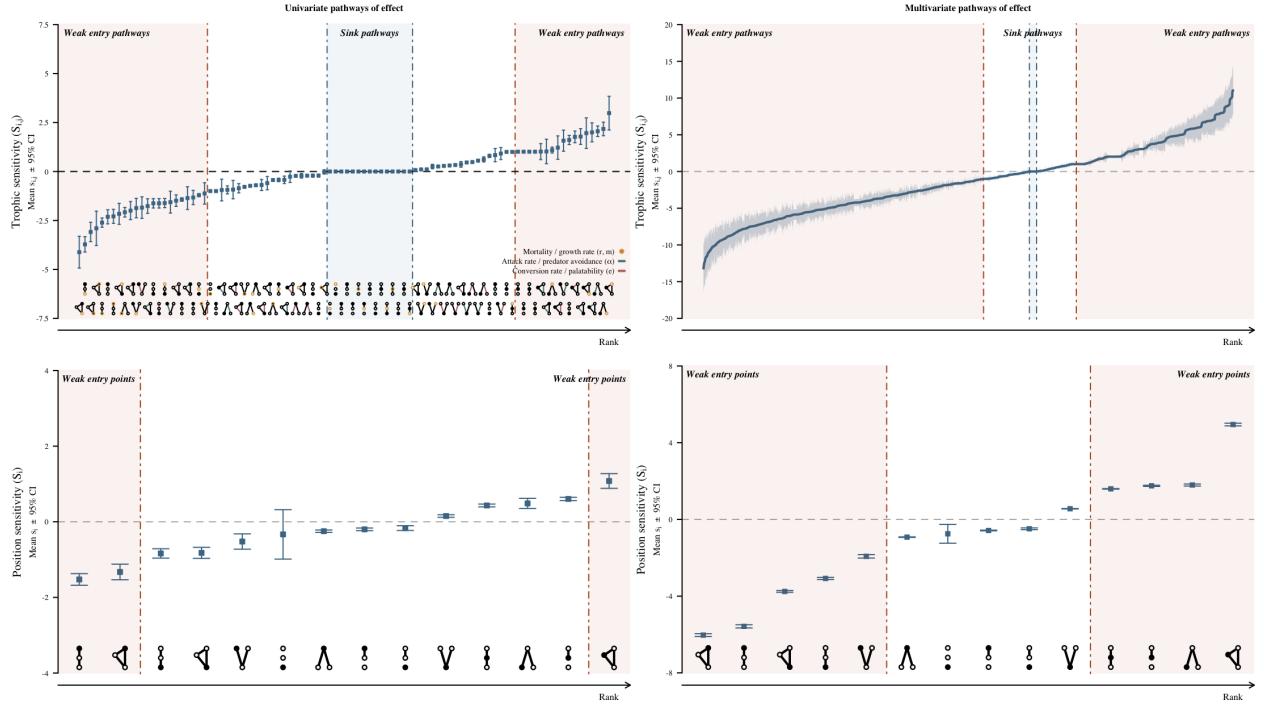


Figure 5: Ranking of all univariate and multivariate pathways of effect as a function of trophic (A,B) and position (C,D) sensitivity. Pathways and motif positions identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified by the red and blue regions, respectively.

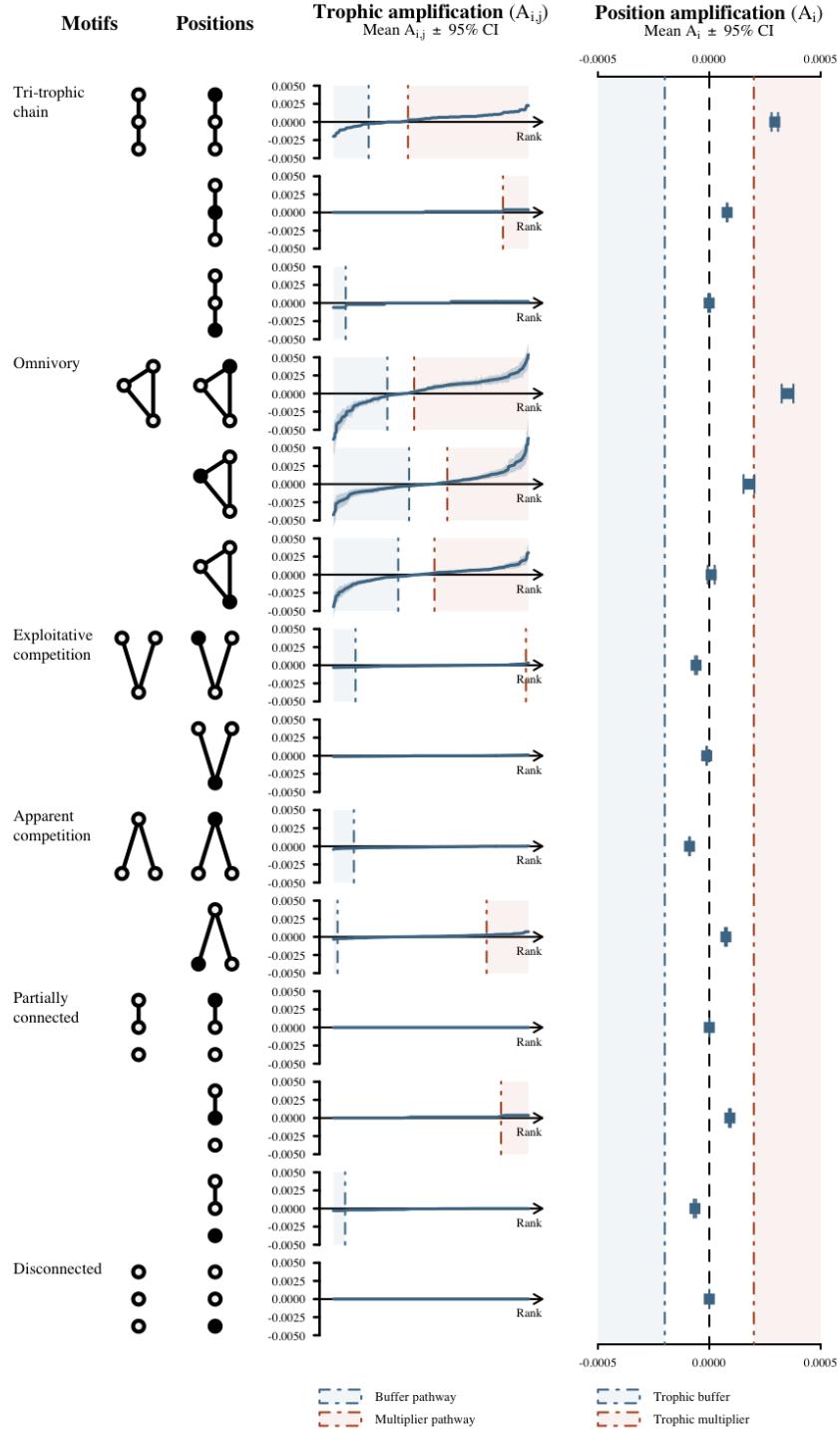


Figure 6: Ranking of all multivariate pathways of effect as a function of trophic and position amplification, for each motif position. Pathways and motif positions identified as biotic buffers (*i.e.* affected synergistically by disturbances) and biotic buffers (*i.e.* affected antagonistically by disturbances) are identified by the red and blue regions, respectively.

417 4.2 Species vulnerability

418 Based on their trophic position, the most vulnerable species in the Northern St. Lawrence
419 are large predators that are never or rarely resources themselves such large demersal fish
420 (*i.e.* demersals, atlantic cod and greenland halibut; Figure 7). These species largely appear
421 to be both weak entry points and biotic amplifiers (Figure 7). Resources are generally less
422 sensitive, depending on their position in food webs. Large crustaceans, for example, are
423 positive weak entry points and biotic amplifiers, which is likely due to their position as both
424 predator and resource in the food web (*e.g.* resource in apparent competition; Figure 7).
425 Other species like redfish and shrimp are in motif positions leading both to positive (*e.g.*
426 meso-predator in omnivory interaction) and negative (*e.g.* resources in omnivory interations)
427 effects in motif-scale simulations (Figure 7). This likely leads to counteracting effects that
428 dampen their overal sensitivity to disturbances. Species sensitivity and amplification scores
429 do not co-vary. In fact, few species are biotic buffers, with most acting as biotic amplifiers
430 to some degree (Figure 7).

431 Species targeted by multiple drivers are not necessarily the most vulnerable based on their
432 trophic position. For example, even though the mortality, physiology and behaviour of
433 shrimp were expected to be impacted by drivers, it is nonetheless insensitive based on its
434 trophic position (Figure 7). In contrast, species impacted by few drivers like cetaceans, or
435 no drivers at all like harbour seals, may nonetheless be highly vulnerable due to their trophic
436 position (Figure 7).

437 Focusing on cod, shrimp and large crustaceans, 3 species with contrasting vulnerabilities in
438 the St. Lawrence, we see that different driver combinations and food web topologies lead to
439 differet species vulnerability (Figure 8). Combinations of drivers may increase or dampen
440 over effects on species sensitivity. For instance, fisheries and climate combine to increase and
441 decrease sensitivity of cod and shrimp, respectively (Figure 8). Driver combinations may
442 also lead to effect amplification even though a driver group has no effect. The combined

⁴⁴³ effect of fisheries and climate drivers on shrimp leads to drastically increased amplification
⁴⁴⁴ scores even if fisheries in isolation does not lead to non-additive effects (Figure 8).

⁴⁴⁵ Food web topology also impacts a species vulnerability. Based on topology, cod seem more
⁴⁴⁶ vulnerable in the Northern Gulf of St. Lawrence than in the Estuary and Southern Gulf
⁴⁴⁷ (Figure 8). Shrimp and crustaceans, meanwhile, are more sensitive in the Estuary, although
⁴⁴⁸ amplification is more important in the Gulf (Figure 8). Contrasts between food webs may
⁴⁴⁹ even lead to flipped species vulnerabilities. Large crustaceans seem to be negative entry
⁴⁵⁰ points and biotic buffers in the Estuary, yet they positive weak entry points and biotic
⁴⁵¹ amplifiers in the Gulf (Figure 8).

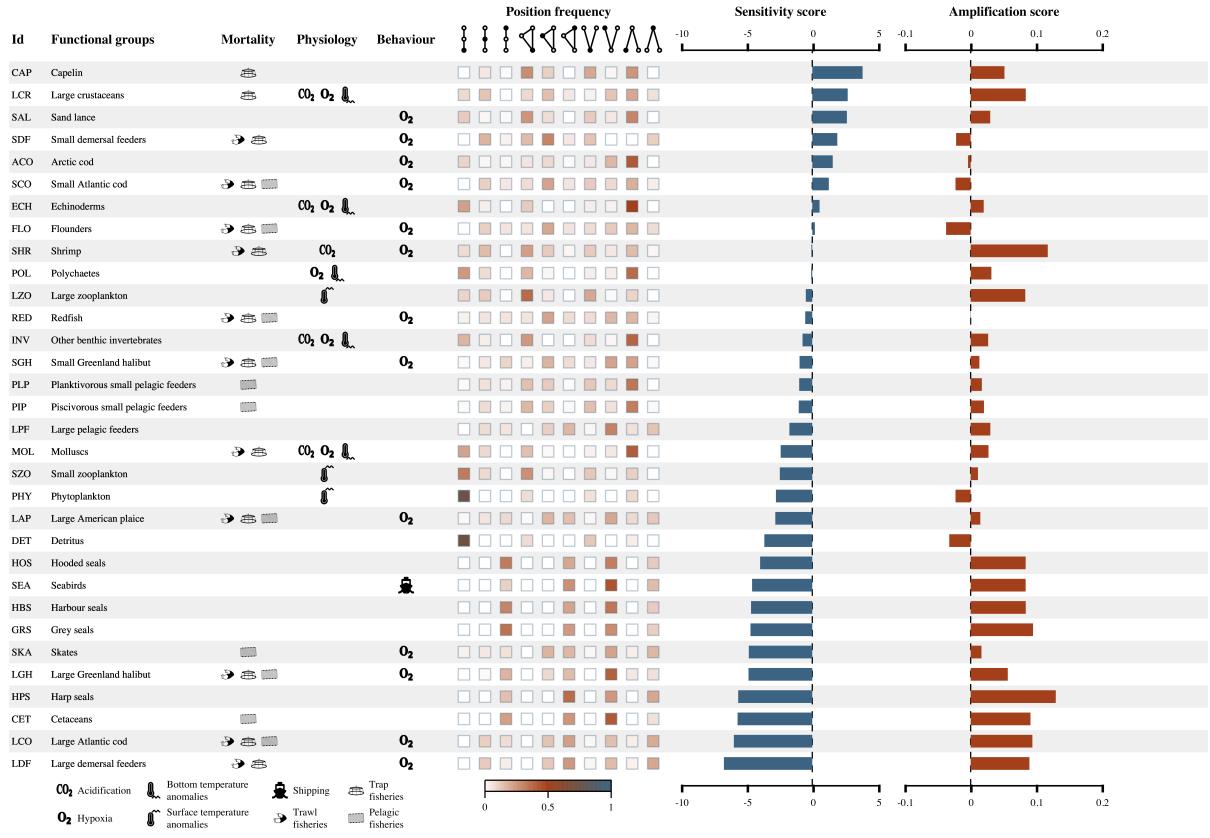


Figure 7: Change in species and functional groups sensitivity and amplification scores as a function of realized pathways of effects for an empirical food web of the Northern Gulf of St. Lawrence in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers supposed to be affecting population level mortality, physiology and behaviour, and the frequency at which they are found in each unique position of the food chain, omnivory, exploitative and apparent competition motifs. Important drivers in the Northern 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 [?]. Species position and driver effects on biological processes were used to identify realized pathways of effects between all 3-species combinations in the food web. The right-hand side of the table presents the species sensitivity and amplification scores, which corresponds to the sum of the simulated effects of all realized pathways of effects for each species and functional group (Figure 2). Negative and positive sensitivity scores mean that overall pathways affecting a species have negative or positive effects, respectively. The species with the most negative and positive scores are weak entry points (*i.e.* highly sensitive to disturbances), while species with null scores are biotic sinks (*i.e.* insensitive to disturbances). Similarly, negative and positive amplification scores mean that overall pathways affecting a species result in antagonistic or synergistic effects, respectively. Species with negative or positive scores are thus biotic buffers and biotic amplifiers, respectively.

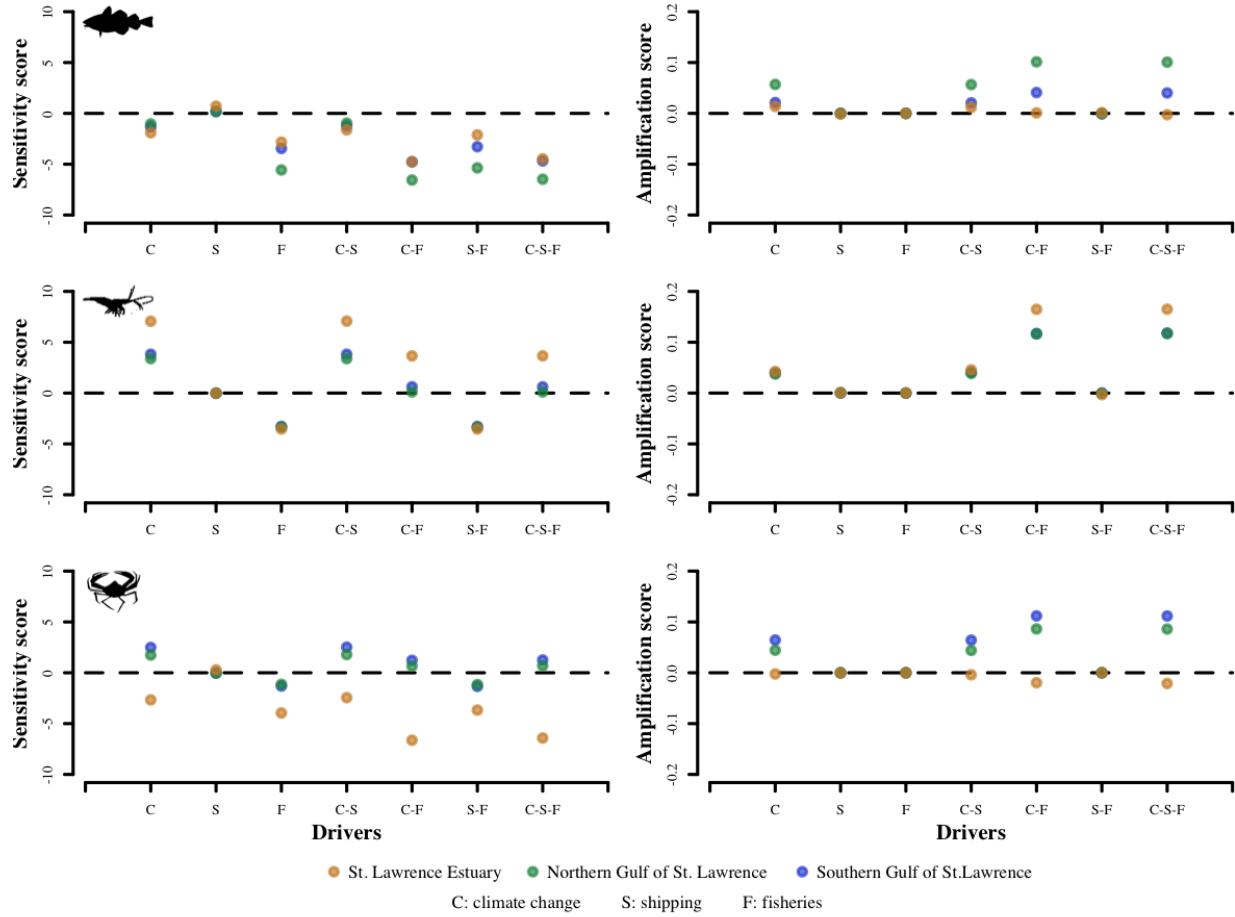


Figure 8: Realized sensitivity (S_m^*) and amplification (A_m^*) scores for Atlantic cod (*Gadus morhua*), shrimp (*Pandalus borealis*) and large crustaceans (*Crustacea*), 3 species or functional groups part of the food webs of the Southern and Northern Gulf of St. Lawrence in the mid-1980s [?] and the St. Lawrence Estuary [?]. Scores are presented when groups of drivers are considered individually and in combination.

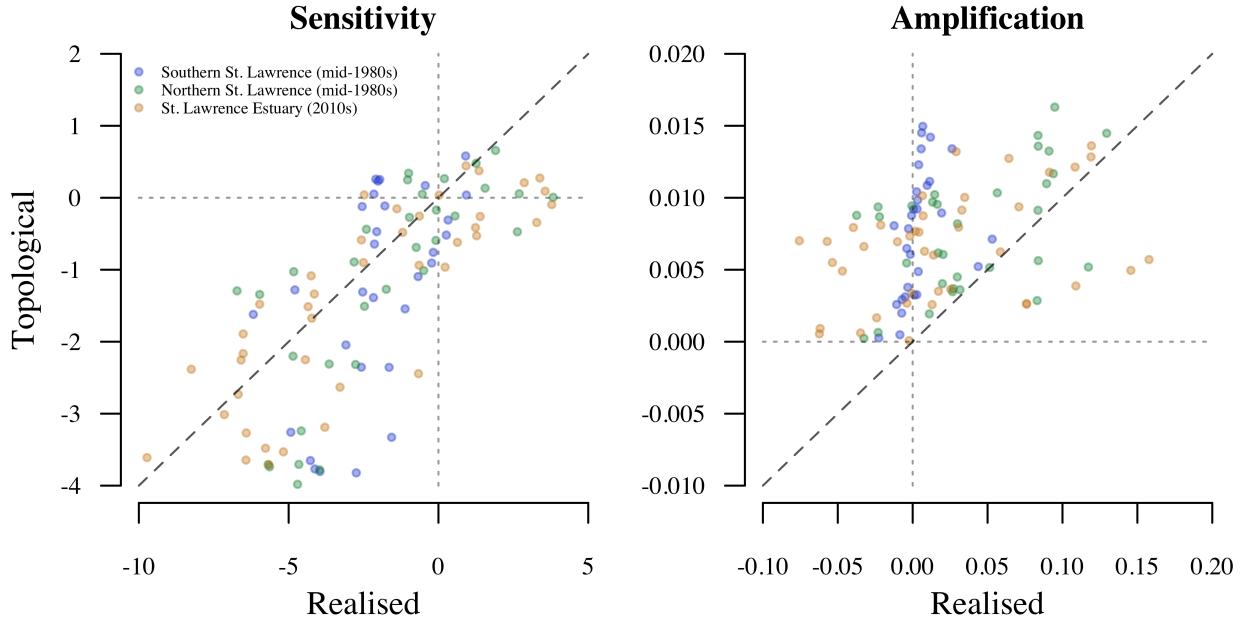


Figure 9: Biplot of the realized and topological species sensitivity (S_m^* , S_m) and amplification (A_m^* , A_m) scores in the food webs of the Southern and Northern Gulf of St. Lawrence in the mid-1980s [?] and the St. Lawrence Estuary [?].

452 5 What it all means

453 In conceptualizing the effects of multiple environmental pressures on food webs and the role
 454 of species and their interactions in spreading disturbances, we sought to use well-established
 455 ecological theory to answer questions of particular relevance to management.

456 *Should species interactions be considered in impact assessments?*

457 We first find, as expected, that species interactions should be explicitly considered in impact
 458 assessments, as they greatly influence trophic vulnerability to the effects of disturbances.
 459 This supports longstanding evidence that interactions play a crucial role in spreading the
 460 effects of individual disturbances through food webs (e.g. Menge 1995; Wootton 1993, 2002;
 461 Yodzis 2000), and unsurprisingly extends this conclusion to multiple disturbances.

462 We further uncover the that type of interactions a species is involved in influences its vul-
 463 nerability to disturbances. Omnivory and food chain in particular are highly responsive to

⁴⁶⁴ disturbances, while exploitative and apparent competition are less vulnerable. [...]

⁴⁶⁵ **Notes:**

- ⁴⁶⁶ • Read up on individual modules and the work done by Stouffer
- ⁴⁶⁷ • “Additionally, note that the exploitative competition module is unstable in isolation
- ⁴⁶⁸ due to competitive exclusion.” (In Stouffer2012, but I doubt I should cite him for this.
- ⁴⁶⁹ This is just a placeholder)

⁴⁷⁰ We also provide evidence that species interactions rather than population growth or mortality
⁴⁷¹ are driving non-additive effects at the community scale. [...] This means that the effects
⁴⁷² of drivers should not be studied outside of the context of species interactions when studying
⁴⁷³ population dynamics.

⁴⁷⁴ **Notes:**

- ⁴⁷⁵ • KEV: Importance of interaction paramters (McCann, from Kev, about reactivity(?) of
- ⁴⁷⁶ interaction paramters in Lotka-Voltera models)

⁴⁷⁷ ***Should the effects of stressors be evaluated separately or in combination?***

⁴⁷⁸ Secondly, we find that the effects of multiple disturbances should be considered in combina-
⁴⁷⁹ tion, as non-additive effects often arise from disturbances to two or more biological processes.

⁴⁸⁰ **Notes:**

- ⁴⁸¹ • Species in omnivory interactions and top predator in food chain are particularly sus-
⁴⁸² ceptible to non-additive effects, with most pathways resulting in either synergistic or
⁴⁸³ antagonistic effects.
- ⁴⁸⁴ • There is a lot of variability among individual pathways of effect, so that predicting
⁴⁸⁵ whether a species will be a biotic buffer or a biotic amplifier is particularly challenging.
⁴⁸⁶ Indeed, differentiating between biotic buffers and amplifiers seems to require a thorough
⁴⁸⁷ understanding of the pathways of effects at play, as there is so much variability.

- 488 • Lot of variability in the nature of the non-additive effect, with no precise indication
489 of what drives a species to be a biotic buffer or a biotic amplifier, suggesting that
490 considering effects of pressures in combination is the only valid way to truly capture
491 the effects of multiple disturbances.

492 ***Which species are most vulnerable to disturbances based on their trophic posi-***
493 ***tion?***

494 Lastly, we identify species that are particularly vulnerable to disturbances at the motif-
495 scale, and use these generalities as heuristics to infer species trophic vulnerability in complex
496 networks.

497 At the motif scale, predators in food chain and omnivory interactions are the most vulnerable
498 by acting as both weak entry points and biotic amplifiers.

499 **Notes:** - Species themselves are more or less sensitivite, with predators in omnivory and
500 food chain both weak entry points and biotic amplifiers. - Trophic cascades, compensatory
501 effects - Estes *et al.* (2011); - Compensatory effect suppression Thompson *et al.* (2018) -
502 The fact that resources and predators are most affected, look at O'Gorman *et al.* (2012) -
503 Predators and resources

504 At the species scale:

505 **Notes:** - Groundfish stock collapse: a trophic hint? - Exploited species before the groundfish
506 stock collapse of the 1990s (\textit{e.g.} demersal feeders, Atlantic cod, Greenland halibut)
507 are all negative weak entry points and biotic amplifiers. - Exploited species after the collapse
508 are either positive weak entry points and biotic amplifiers (\textit{e.g.} large crustaceans)
509 or biotic sinks (\textit{e.g.} shrimp). - We find that heavily exploited species appear to
510 be the most vulnerable trophically, while fisheries transitioned to insensitive or beneficiary
511 species post-collapse. - Using the most common offshore environmental pressure in the
512 St. Lawrence System, food webs and simulations as heuristics, we find that [...] - Using
513 the most common environmental pressures in the Northern Gulf of St. Lawrence with the

514 topology of a food web from the mid-1980s to identify realized pathways of effect between
515 all 3-species combinations, and their simulated scores as heuristics, we ranked species and
516 functional groups as a function of their overall trophic sensitivity and amplification.

517 6 The way forward

- 518 • Limits:
 - 519 – No interaction strength
 - 520 – No driver intensity
 - 521 – Simple model formulations
- 522 • In the absence of appropriate knowledge, it is reasonable to first explore the simplest
523 possibilities, which will provide novel hypotheses to test theoretically and empirically
524 in follow-up studies (Wootton 2002).
- 525 • Even if our simulations are simplifications of realworld system, they still provide com-
526 pelling evidence that reinforce the need to explicitly consider the complexity of eco-
527 logical systems.
- 528 • Name new hypotheses to test theoretically and empirically.
 - 529 – a) IDEAS?
 - 530 – b)
 - 531 – ...
- 532 • This framework is also so flexible that we could easily include other drivers typically
533 found in systems, such as pollution or seal hunting.
- 534 • Spatial and temporal vulnerability of species.

535 • Other models could be used to explicitly incorporate things like competition,

536 • Positive effects of drivers (*e.g.* nutrients on growth, at least initially)

537 • Management and conservation:

538 – Our results reinforce that holistic approaches are necessary to properly consider
539 the effects of environmental pressures on complex communities. Although this
540 has been hinted at, no other study [...]

541 – Single species may be vulnerable (or not) in different contexts, so that the struc-
542 ture of a network should be considered and conservation targets may change as
543 the vulnerability of species changes in time and space as a function of network
544 structure and driver combinations.

545 **7 Supplementary Material**

546 **7.1 Models**

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	$\frac{dX_i}{dt} = X_i(r_i - \alpha_{ii}X_i)$ $\frac{dX_j}{dt} = X_j(r_j - \alpha_{jj}X_j)$ $\frac{dX_k}{dt} = X_k(r_k - \alpha_{kk}X_k)$	$r_i, r_j, r_k = 1$ $\alpha_{ii}, \alpha_{jj}, \alpha_{kk} = 0.001$

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

7.2 Supplementary figures

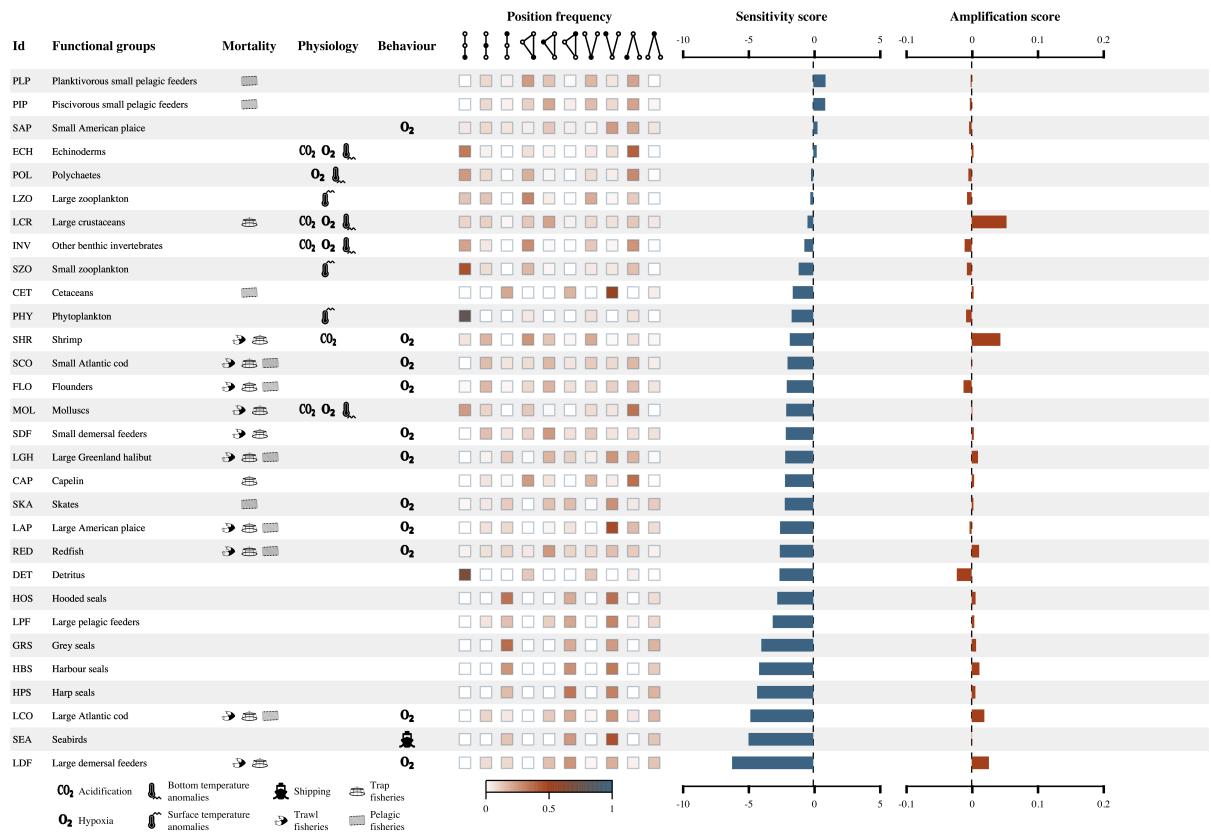


Figure 10: Change in species and functional groups sensitivity and amplification scores as a function of realized pathways of effects for an empirical food web of the Southern Gulf of St. Lawrence in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers supposed to be affecting population level mortality, physiology and behaviour, and the frequency at which they are found in each unique position of the food chain, omnivory, exploitative and apparent competition motifs. Important drivers 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 [?]. Species position and driver effects on biological processes were used to identify realized pathways of effects between all 3-species combinations in the food web. The right-hand side of the table presents the species sensitivity and amplification scores, which corresponds to the sum of the simulated effects of all realized pathways of effects for each species and functional group (Figure 2). Negative and positive sensitivity scores mean that overall pathways affecting a species have negative or positive effects, respectively. The species with the most negative and positive scores are weak entry points (*i.e.* highly sensitive to disturbances), while species with null scores are biotic sinks (*i.e.* insensitive to disturbances). Similarly, negative and positive amplification scores mean that overall pathways affecting a species result in antagonistic or synergistic effects, respectively. Species with negative or positive scores are thus biotic buffers and biotic amplifiers, respectively.

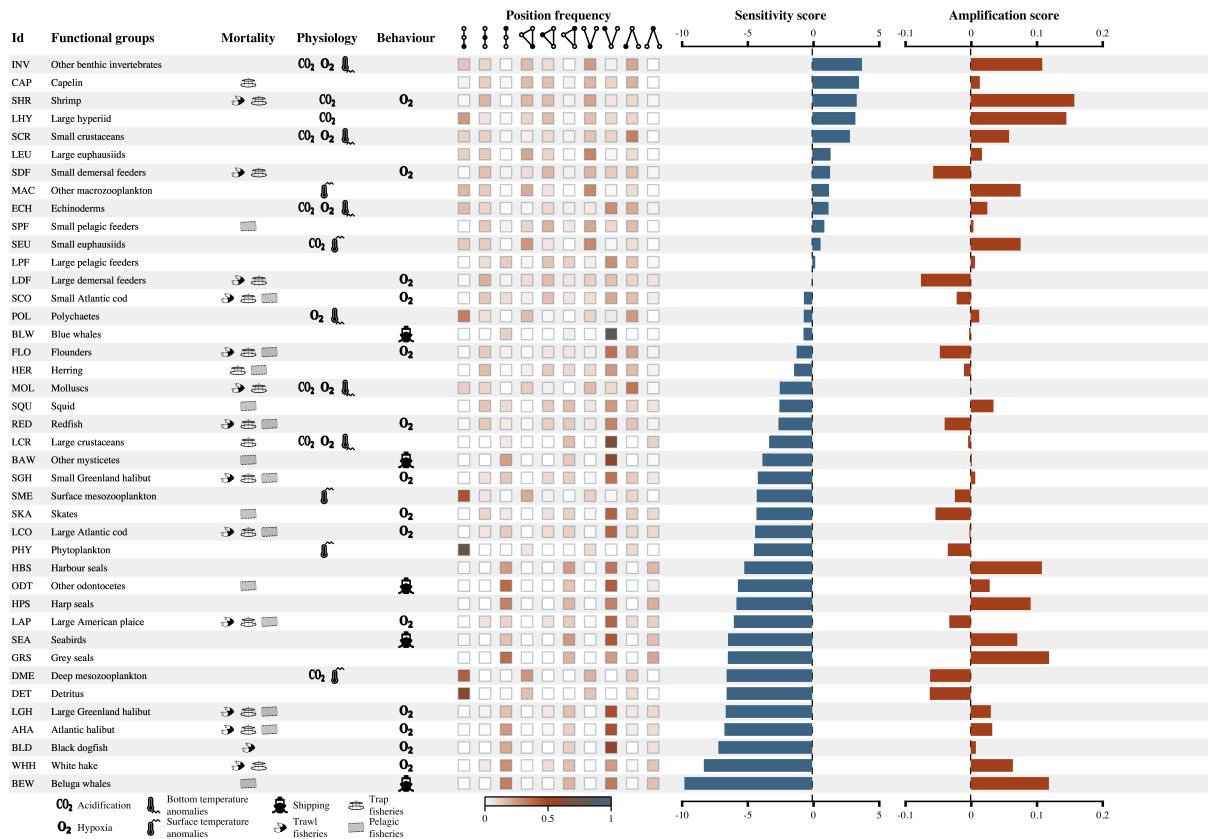


Figure 11: Change in species and functional groups sensitivity and amplification scores as a function of realized pathways of effects for an empirical food web of the St. Lawrence Estuary in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers supposed to be affecting population level mortality, physiology and behaviour, and the frequency at which they are found in each unique position of the food chain, omnivory, exploitative and apparent competition motifs. Important drivers 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 [?]. Species position and driver effects on biological processes were used to identify realized pathways of effects between all 3-species combinations in the food web. The right-hand side of the table presents the species sensitivity and amplification scores, which corresponds to the sum of the simulated effects of all realized pathways of effects for each species and functional group (Figure 2). Negative and positive sensitivity scores mean that overall pathways affecting a species have negative or positive effects, respectively. The species with the most negative and positive scores are weak entry points (*i.e.* highly sensitive to disturbances), while species with null scores are biotic sinks (*i.e.* insensitive to disturbances). Similarly, negative and positive amplification scores mean that overall pathways affecting a species result in antagonistic or synergistic effects, respectively. Species with negative or positive scores are thus biotic buffers and biotic amplifiers, respectively.

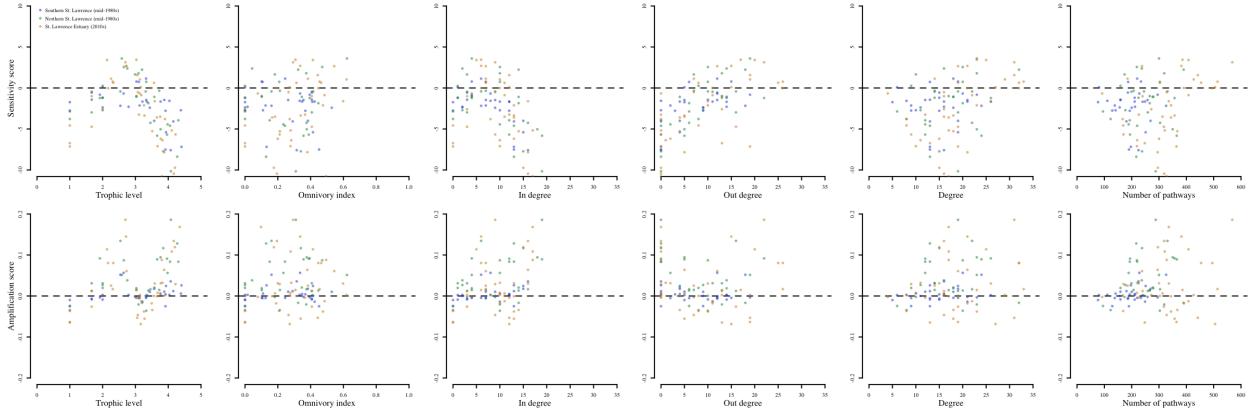


Figure 12: Species sensitivity and amplification scores as a function of network metrics: 1) trophic level, 2) omnivory index, 3) in-degree, 4) out-degree, 5) degree and 6) number of pathways of effect for the food webs of the Southern and Northern Gulf of St. Lawrence in the mid-1980s [?] and the St. Lawrence Estuary in the 2010s [?].

548 8 References

- 549 Allesina, S. & Pascual, M. (2008). Network structure, predatorPrey modules, and stability
550 in large food webs. *Theoretical Ecology*, 1, 55–64.
- 551 Ban, N.C., Alidina, H.M. & Ardrion, J.A. (2010). Cumulative impact mapping: Advances,
552 relevance and limitations to marine management and conservation, using Canada’s Pacific
553 waters as a case study. *Marine Policy*, 34, 876–886.
- 554 Bascompte, J. (2009). Disentangling the Web of Life. *Science*, 325, 416–419.
- 555 Bascompte, J. & Melián, C.J. (2005). Simple Trophic Modules for Complex Food Webs.
556 *Ecology*, 86, 2868–2873.
- 557 Beauchesne, D. (2019). Next Generation Planning - Structuring and Sharing Environmental
558 Drivers Data for the St. Lawrence. *Frontiers in Marine Science*, 1, 1.
- 559 Belley, R., Archambault, P., Sundby, B., Gilbert, F. & Gagnon, J.-M. (2010). Effects of
560 hypoxia on benthic macrofauna and bioturbation in the Estuary and Gulf of St. Lawrence,
561 Canada. *Continental Shelf Research*, 30, 1302–1313.

- 562 Boonstra, W.J., Ottosen, K.M., Ferreira, A.S.A., Richter, A., Rogers, L.A. & Pedersen,
563 M.W. *et al.* (2015). What are the major global threats and impacts in marine environments?
564 Investigating the contours of a shared perception among marine scientists from the bottom-
565 up. *Marine Policy*, 60, 197–201.
- 566 Bove, C.B., Ries, J.B., Davies, S.W., Westfield, I.T., Umpanhowar, J. & Castillo, K.D.
567 (2019). Common Caribbean corals exhibit highly variable responses to future acidification
568 and warming. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20182840.
- 569 Camacho, J., Stouffer, D.B. & Amaral, L.A.N. (2007). Quantitative analysis of the local
570 structure of food webs. *Journal of Theoretical Biology*, 246, 260–268.
- 571 Chabot, D. & Claireaux, G. (2008). Environmental hypoxia as a metabolic constraint on
572 fish: The case of Atlantic cod, *Gadus morhua*. *Marine Pollution Bulletin*, 5th International
573 Conference on Marine Pollution and Ecotoxicology, 57, 287–294.
- 574 Christensen, M.R., Graham, M.D., Vinebrooke, R.D., Findlay, D.L., Paterson, M.J. &
575 Turner, M.A. (2006). Multiple anthropogenic stressors cause ecological surprises in boreal
576 lakes. *Global Change Biology*, 12, 2316–2322.
- 577 Christiansen, F., Rasmussen, M. & Lusseau, D. (2013). Whale watching disrupts feeding
578 activities of minke whales on a feeding ground. *Marine Ecology Progress Series*, 478, 239–
579 251.
- 580 Cirtwill, A.R. & Stouffer, D.B. (2015). Concomitant predation on parasites is highly variable
581 but constrains the ways in which parasites contribute to food web structure. *The Journal
582 of Animal Ecology*, 84, 734–744.
- 583 Côté, I.M., Darling, E.S. & Brown, C.J. (2016). Interactions among ecosystem stressors and
584 their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*,
585 283, 20152592.
- 586 Crain, C.M., Kroeker, K. & Halpern, B.S. (2008). Interactive and cumulative effects of

- 587 multiple human stressors in marine systems. *Ecology Letters*, 11, 1304–1315.
- 588 Darling, E.S. & Côté, I.M. (2008). Quantifying the evidence for ecological synergies. *Ecology*
589 *Letters*, 11, 1278–1286.
- 590 De Laender, F. (2018). Community-and ecosystem-level effects of multiple environmental
591 change drivers: Beyond null model testing. *Global change biology*, 24, 5021–5030.
- 592 Dupont-Prinet, A., Vagner, M., Chabot, D. & Audet, C. (2013). Impact of hypoxia on
593 the metabolism of Greenland halibut (*Reinhardtius hippoglossoides*). *Canadian Journal of*
594 *Fisheries and Aquatic Sciences*, 70, 461–469.
- 595 Eby, L.A., Crowder, L.B., McClellan, C.M., Peterson, C.H. & Powers, M.J. (2005). Habitat
596 degradation from intermittent hypoxia: Impacts on demersal fishes. *Marine Ecology Progress Series*
597 *Series*, 291, 249–262.
- 598 Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J. & Bond, W.J. *et al.*
599 (2011). Trophic Downgrading of Planet Earth. *Science*, New Series, 333, 301–306.
- 600 Fabry, V.J., Seibel, B.A., Feely, R.A. & Orr, J.C. (2008). Impacts of ocean acidification on
601 marine fauna and ecosystem processes. *ICES Journal of Marine Science*, 65, 414–432.
- 602 Giakoumi, S., Halpern, B.S., Michel, L.N., Gobert, S., Sini, M. & Boudouresque, C.-F. *et al.*
603 (2015). Towards a framework for assessment and management of cumulative human impacts
604 on marine food webs. *Conservation Biology*, 29, 1228–1234.
- 605 Griffen, B.D., Belgrad, B.A., Cannizzo, Z.J., Knotts, E.R. & Hancock, E.R. (2016). Re-
606 thinking our approach to multiple stressor studies in marine environments. *Marine Ecology*
607 *Progress Series*, 543, 273–281.
- 608 Guiden, P.W., Bartel, S.L., Byer, N.W., Shipley, A.A. & Orrock, J.L. (2019). Predator-
609 Prey Interactions in the Anthropocene: Reconciling Multiple Aspects of Novelty. *Trends in*
610 *Ecology & Evolution*, 34, 616–627.
- 611 Hale, R., Piggott, J.J. & Swearer, S.E. (2017). Describing and understanding behavioral

- 612 responses to multiple stressors and multiple stimuli. *Ecology and Evolution*, 7, 38–47.
- 613 Halpern, B.S., Frazier, M., Afflerbach, J., Lowndes, J.S., Micheli, F. & O'Hara, C. *et al.*
- 614 (2019). Recent pace of change in human impact on the world's ocean. *Scientific Reports*, 9,
- 615 11609.
- 616 Halpern, B.S. & Fujita, R. (2013). Assumptions, challenges, and future directions in cumu-
- 617 lative impact analysis. *Ecosphere*, 4, art131.
- 618 Harborne, A.R., Rogers, A., Bozec, Y.-M. & Mumby, P.J. (2017). Multiple Stressors and
- 619 the Functioning of Coral Reefs. *Annual Review of Marine Science*, 9, 445–468.
- 620 Holt, R.D. (1997). Community modules. In: *Multitrophic Interactions in Terrestrial Ecosys-*
- 621 *tems, 36th Symposium of the British Ecological Society* (eds. Grange, A.C. & Brown, V.K.).
- 622 Blackwell Science, Oxford, pp. 333–349.
- 623 Holt, R.D. & Hochberg, M.E. (2001). Indirect interactions, community modules and bio-
- 624 logical control: A theoretical perspective. *Evaluating indirect ecological effects of biological*
- 625 *control*, 13–37.
- 626 Ives, A.R. (1995). Measuring Resilience in Stochastic Systems. *Ecological Monographs*, 65,
- 627 217–233.
- 628 Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D. & Chimimba, C.T. (2016). Net effects
- 629 of multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology*, 22,
- 630 180–189.
- 631 Kondoh, M. (2008). Building trophic modules into a persistent food web. *Proceedings of the*
- 632 *National Academy of Sciences*, 105, 16631–16635.
- 633 Kroeker, K.J., Kordas, R.L., Crim, R., Hendriks, I.E., Ramajo, L. & Singh, G.S. *et al.*
- 634 (2013). Impacts of ocean acidification on marine organisms: Quantifying sensitivities and
- 635 interaction with warming. *Global Change Biology*, 19, 1884–1896.
- 636 Lesage, V., Omrane, A., Doniol-Valcroze, T. & Mosnier, A. (2017). Increased proximity of

- 637 vessels reduces feeding opportunities of blue whales in the St. Lawrence Estuary, Canada.
- 638 *Endangered Species Research*, 32, 351–361.
- 639 Liess, M., Foit, K., Knillmann, S., Schäfer, R.B. & Liess, H.-D. (2016). Predicting the
640 synergy of multiple stress effects. *Scientific Reports*, 6, 32965.
- 641 McClanahan, T.R., Graham, N.A. & Darling, E.S. (2014). Coral reefs in a crystal ball:
642 Predicting the future from the vulnerability of corals and reef fishes to multiple stressors.
643 *Current Opinion in Environmental Sustainability*, Environmental change issues, 7, 59–64.
- 644 Menge, B.A. (1995). Indirect Effects in Marine Rocky Intertidal Interaction Webs: Patterns
645 and Importance. *Ecological Monographs*, 65, 21–74.
- 646 Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D. & Alon, U. (2002). Network
647 Motifs: Simple Building Blocks of Complex Networks. *Science*, 298, 824–827.
- 648 Monteiro, A.B. & Faria, L.D.B. (2016). The interplay between population stability and food-
649 web topology predicts the occurrence of motifs in complex food-webs. *Journal of theoretical
650 biology*, 409, 165–171.
- 651 Montoya, J., Woodward, G., Emmerson, M.C. & Solé, R.V. (2009). Press perturbations and
652 indirect effects in real food webs. *Ecology*, 90, 2426–2433.
- 653 Morissette, L., Despatie, S.-P., Savenkoff, C., Hammill, M.O., Bourdages, H. & Chabot, D.
654 (2003). Data gathering and input parameters to construct ecosystem models for the northern
655 Gulf of St. Lawrence(Mid-1980 s). *Can. Tech. Rep. Fish. Aquat. Sci./Rapp. Tech. Can.
656 Sci. Halieut. Aquat.*, 100.
- 657 Myers, R.A. & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities.
658 *Nature*, 423, 280.
- 659 O'Brien, A.L., Dafforn, K.A., Chariton, A.A., Johnston, E.L. & Mayer-Pinto, M. (2019).
660 After decades of stressor research in urban estuarine ecosystems the focus is still on single
661 stressors: A systematic literature review and meta-analysis. *Science of The Total Environ-*

- 662 *ment.*
- 663 O’Gorman, E.J. & Emmerson, M.C. (2009). Perturbations to trophic interactions and the
664 stability of complex food webs. *Proceedings of the National Academy of Sciences*, 106,
665 13393–13398.
- 666 O’Gorman, E.J., Fitch, J.E. & Crowe, T.P. (2012). Multiple anthropogenic stressors and
667 the structural properties of food webs. *Ecology*, 93, 441–448.
- 668 Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998). Fishing Down
669 Marine Food Webs. *Science*, 279, 860–863.
- 670 Piggott, J.J., Townsend, C.R. & Mattheai, C.D. (2015). Reconceptualizing synergism and
671 antagonism among multiple stressors. *Ecology and Evolution*, 5, 1538–1547.
- 672 Pillet, M., Dupont-Prinet, A., Chabot, D., Tremblay, R. & Audet, C. (2016). Effects of
673 exposure to hypoxia on metabolic pathways in northern shrimp (*Pandalus borealis*) and
674 Greenland halibut (*Reinhardtius hippoglossoides*). *Journal of Experimental Marine Biology
675 and Ecology*, 483, 88–96.
- 676 Savenkoff, C. (2012). *Input data and parameter estimates for ecosystem models of the lower
677 St. Lawrence Estuary (20082010)*. Canadian Technical Report of Fisheries and Aquatic
678 Sciences 2999, Department of Fisheries and Oceans, Mont-Joli, Québec, Canada.
- 679 Savenkoff, C., Bourdages, H., Swain, D.P., Despatie, S.-P., Hanson, J.M. & Méthot, R. *et
680 al.* (2004). *Input data and parameter estimates for ecosystem models of the southern Gulf
681 of St. Lawrence (mid-1980s and mid-1990s)*. Canadian Technical Report of Fisheries and
682 Aquatic Sciences 2529, Department of Fisheries and Oceans, Mont-Joli, Québec, Canada.
- 683 Schäfer, R.B. & Piggott, J.J. (2018). Advancing understanding and prediction in multiple
684 stressor research through a mechanistic basis for null models. *Global Change Biology*, 24,
685 1817–1826.
- 686 Stouffer, D.B. & Bascompte, J. (2010). Understanding food-web persistence from local to

- 687 global scales. *Ecology Letters*, 13, 154–161.
- 688 Stouffer, D.B. & Bascompte, J. (2011). Compartmentalization increases food-web persis-
689 tence. *Proceedings of the National Academy of Sciences*, 108, 3648–3652.
- 690 Stouffer, D.B., Camacho, J., Jiang, W. & Nunes Amaral, L.A. (2007). Evidence for the
691 existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society
692 B: Biological Sciences*, 274, 1931–1940.
- 693 Stouffer, D.B., Sales-Pardo, M., Sirer, M.I. & Bascompte, J. (2012). Evolutionary Conser-
694 vation of Species' Roles in Food Webs. *Science*, 335, 1489–1492.
- 695 Thompson, P.L., MacLennan, M.M. & Vinebrooke, R.D. (2018). Species interactions cause
696 non-additive effects of multiple environmental stressors on communities. *Ecosphere*, 9,
697 e02518.
- 698 Wootton, J.T. (1993). Indirect Effects and Habitat Use in an Intertidal Community: Inter-
699 action Chains and Interaction Modifications. *The American Naturalist*, 141, 71–89.
- 700 Wootton, J.T. (2002). Indirect effects in complex ecosystems: Recent progress and future
701 challenges. *Journal of Sea Research*, Structuring Factors of Shallow Marine Coastal Com-
702 munities, Part I, 48, 157–172.
- 703 Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C. & Halpern, B.S. *et al.* (2006).
704 Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science*, 314, 787–790.
- 705 Yodzis, P. (2000). Diffuse Effects in Food Webs. *Ecology*, 81, 261–266.