

On the sensitivity of food webs to multiple stressors

David Beauchesne^{1,2}, Kevin Cazelles³, Philippe Archambault²,
Laura E. Dee⁴, Dominique Gravel⁵

¹ArcticNet, Québec Océan, Département de biologie, Université Laval, Québec, QC, Canada

²Institut des sciences de la mer, Université du Québec à Rimouski, Rimouski, QC, Canada

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

⁴Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA

⁵Département de biologie, Université de Sherbrooke, Sherbrooke, QC, Canada

Running title: Of food webs and multiple stressors

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

Type of article: Ideas and Perspectives

Abstract word count: 195188

Main text word count: 73037900

Text box 1 word count: 338303

Number of references: 123124

Number of figures: 5 8

Number of tables: 0

Number of text boxes: 1

E-mail addresses:

David Beauchesne: david.beauchesne@hotmail.com

Kevin Cazelles: kevin.cazelles@gmail.com

Philippe Archambault: philippe.archambault@bio.ulaval.ca

Laura E. Dee: Laura.Dee@colorado.edu

Dominique Gravel: dominique.gravel@usherbrooke.ca

Correspondence:

David Beauchesne

1045 Av. de la Médecine, bureau 3058, Québec, QC, G1V 0A6
david.beauchesne@hotmail.com
1-514-553-4975

Statement of authorship: All the authors conceived the manuscript and the underlying objectives. DB performed the simulations, analyses, formatted the figures and led the drafting of the manuscript with significant contributions from KC. All co-authors contributed to data, analyses and writing based on their respective expertise and contributed to the revision of the manuscript.

Data accessibility statement: Empirical food web data for the St. Lawrence System used for this study are openly available from the primary sources in which they were published (Morissette *et al.* 2003; Savenkoff *et al.* 2004; Savenkoff 2012).

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' susceptibility 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.

1 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

73 mollusk calcification, metabolic, growth and mortality rates, and has been linked to altered
74 carbon fluxes in ecological networks (Fabry *et al.* 2008; Kroeker *et al.* 2013; Bove *et al.*
75 2019). Fisheries decrease the mean trophic level in coastal and oceanic environments by
76 targeting large predators, impair a variety of essential ecosystem services and have induced
77 the collapse of numerous commercial species (Pauly *et al.* 1998; Myers & Worm 2003;
78 Worm *et al.* 2006). However, stressors rarely occur individually (Halpern *et al.* 2019).
79 For example, coral reefs face a suite of pressures including fishing, warming temperatures,
80 ocean acidification and water pollution (McClanahan *et al.* 2014; Harborne *et al.* 2017).
81 Interactions between stressors are pervasive (*e.g.* Crain *et al.* 2008; Piggott *et al.* 2015;
82 Jackson *et al.* 2016), and unpredictable (Darling & Côté 2008; Côté *et al.* 2016). For
83 instance, the susceptibility of corals to temperature-induced bleaching increases with
84 nutrient enrichment (Wiedenmann *et al.* 2013; Lapointe *et al.* 2019), and the sensitivity
85 of certain organisms to toxicants can be multiplied by a factor of up to 100 when they are
86 exposed to other stressors (Liess *et al.* 2016). In contrast, the positive effects of acidification
87 on primary producer biomass can be reversed by warming waters (Christensen *et al.* 2006).
88 Thus, multiple stressors can interact in complex ways, amplifying or dampening the direct
89 effects of stressors on species.

90 Beyond their direct effects, stressors ripple through ecological communities by way of the
91 interactions structuring the complex networks in which species are embedded (Wootton
92 2002; Bascompte 2009; Montoya *et al.* 2009; O’Gorman & Emmerson 2009; O’Gorman *et al.*
93 2012). Because species depend on one another, surprising indirect effects arise from species
94 interactions in complex systems, such as a predator positively affecting its own prey (Abrams
95 1992). Ample empirical evidence exists of such trophically-mediated effects across ecosystems
96 globally (Paine 1980; Estes *et al.* 2011). Classic examples include sea otters (*Enhydra*
97 *lutris*) indirectly shielding kelp forests from browsing by sea urchins [*Strongylocentrotus*
98 spp.; Estes & Palmisano (1974)] and fish indirectly favouring the pollination of terrestrial
99 plants by controlling predatory dragonfly populations (Knight *et al.* 2005). A species’s

susceptibility 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 & 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 & 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. We then simulate 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. Finally, 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 the topology of three empirical food webs from different regions exposed to up to eight different sources of stress.

2 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 & Bascompte (2010) and Stouffer *et al.* (2012).

2.1 Community dynamics

We begin by conceptualizing community dynamics with a simplified 6-species food web composed of populations of copepods (Copepoda), krill (Euphausiacea), capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*), and beluga (*Delphinapterus leucas*) and humpback (*Megaptera novaeangliae*) whales (Figure 1A). 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 1B).

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 1C). 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 1A) and apparent competition, *i.e.* alternate prey species of a generalist predator (*e.g.* krill-capelin-copepod; Figure 1A) 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).

Net effects are the integration of all direct and indirect effects propagating to a focal species in a food web (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 1D). Properly assessing community dynamics requires knowledge of direct and indirect effects propagating through a multitude of pathways that result in an observed net effect (Abrams *et al.* 1996).

2.2 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 & 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 1A). The magnitude and nature of the direct effects of stressors on populations depend on **species-specific sensitivity**, which can be defined broadly 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 & 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 susceptibilities 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 susceptibilities 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-specific susceptibilities could readily be incorporated and explored in our work to consider species-scale and network-scale responses simultaneously.

Individual stressors can have one or more non-mutually exclusive pathways to directly affect a species, such as effects to mortality, growth, feeding rates, and metabolism. For instance, humpback whales feeding and mortality rates may both be affected by shipping (Figure 1A). Multiple stressors can also combine to affect a single individual ecological process, such as a decrease in the feeding rate of humpback whales due to shipping and trawl fishing (Figure 1A). In such a case, the feeding rate of humpback whales would be a joint function of the intensity of shipping and trawl fishing in the system. The collection of ecological processes through which stressors directly affect ecological communities forms what we define as a **pathway of 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 2C). 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. 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.

Through species interactions, the direct effects of stressors on ecological processes forming pathways of effect indirectly propagate to other species in the food web. 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 ??A, B). For example, the direct effects of shipping on beluga and humpback whales behaviour would indirectly propagate to their prey by altering their feeding rates and decreasing predation pressure (Figure 1B, C). 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). In recognizing the importance of net effects in assessing the effect of one species on another, one must also recognize the importance of net effects of single or multiple stressors on species. As such, properly assessing the effects of stressors on species should integrate all direct and trophically-mediated indirect effects propagating to a focal species (Figure 1D).

It must be recognized that if density-dependence – *i.e.* the negative effect of a population density on its own per capita growth rate – is an important driving factor for the dynamics of a population, or if trophic interaction strength is weak, then indirect effects may become weaker or even trivial (Abrams *et al.* 1996); one could then simply consider the direct effects of stressors. Still, there is ample empirical evidence for trophically-mediated indirect effects and for the propagation of the effects of stressors through food webs (*e.g.* O’Gorman & Emmerson 2009; Estes *et al.* 2011; O’Gorman *et al.* 2012). Furthermore, we would also expect indirect effects of the same direction and type if density dependence was weaker or stronger. Given the aim of our study, *i.e.* to understand the propagation of stressors through species interactions, we thus intentionally focus on instances where density dependence is not the regulating factor for population and community dynamics.

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 ??B). 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 & 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 & Melián 2005; Stouffer *et al.* 2007; Stouffer & 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 ??A), omnivory or intraguild predation (*e.g.* beluga-cod-capelin; Figure ??A), exploitative competition (*e.g.* humpback whale-capelin-beluga; Figure ??A) and apparent competition (*e.g.* krill-capelin-copepod; Figure ??A) motifs (Camacho *et al.* 2007; Stouffer & 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 ??B). We now shift our focus to the

dynamics of those four motifs particularly relevant to the structural properties of empirical food webs.

2.3 Evaluating 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 ??C), 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 species removals or a press perturbation; these measured variations integrate all direct and trophically-mediated indirect effects operating on the system collectively (Wootton 2002; Berlow *et al.* 2004; Montoya *et al.* 2009). Likewise, we propose to evaluate how pre-stressor species abundances at equilibrium shift after the permanent appearance of stressors in a system – *i.e.* press perturbations – 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 ??B). 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 ??C-1). In this scenario, cod are likely released from beluga predation due to their drop in numbers [*i.e.* mesopredator release; Ritchie & 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 ??C-2). Surprisingly,

the cod population remains relatively unchanged (Figure ??C-2), likely because the increase in prey availability offsets the effect of fishing [*i.e.* compensatory dynamics; Gonzalez & 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 ??C-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 ??B-4).

2.3.1 Trophic sensitivity

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 2D,F):

$$S_{m,G} = \frac{a_{m,G} - a_m}{a_m}, \quad (1)$$

where a_m and $a_{m,G}$ are the pre- and post-stressors abundances of species m , respectively. ~~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.

2.3.2 Trophic amplification

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 & 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 the 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 2L,M):

$$A_{m,G} = \sum_{g \in G} \left(\frac{1}{|G|} S_{m,G} - S_{m,g} \right), \quad (2)$$

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 (*i.e.* negative trophic amplification) by a pathway of effect . Hence, capelin and beluga are biotic amplifiers,~~

whereas cod is a biotic buffer (Figure ??C-4).

2.3.3 Trophic variance

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 ??C-2) is offset by the negative effects on capelin mortality and beluga behaviour (Figure ??C-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 pathway of effect – provides a measure of variance associated to trophic sensitivity to an integrative pathway of effect (G) that we define as **trophic variance** ($V_{m,G}$):

$$V_{m,G} = \sum_{g \in G} \left(\frac{1}{|G|} S_{m,G} - S_{m,g} \right)^2. \quad (3)$$

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.

3 Handling food web complexity

3.1 Using motifs to simplify food webs

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 for the remainder of the manuscript that community dynamics in our system 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 2A). 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 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 & 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 & Melián 2005; Stouffer *et al.* 2007; Stouffer & 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), omnivory or intraguild predation (*e.g.* beluga-cod-capelin), exploitative competition (*e.g.* humpback whale-capelin-beluga) and apparent competition (*e.g.* krill-capelin-copepod) motifs (Figure 2A) (Camacho *et al.* 2007; Stouffer & 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.

To illustrate the concepts and metrics presented in the previous section using motifs, we use two fictitious interactions from our system: the omnivory interaction connecting beluga, cod and capelin, and the apparent competition interaction connecting copepods, krill and capelin (Figure 2A). Shipping and fishing combine to collectively affect the omnivory interaction by altering the feeding behaviour of the beluga whale population, and by increasing the mortality of the cod and capelin populations. The ecological processes affected are thus capelin intrinsic growth rate ($r_{capelin}$), cod mortality rate (m_{cod}), and beluga attack rates on capelin ($\alpha_{capelin,beluga}$) and cod ($\alpha_{cod,beluga}$); this results in an integrative pathway of effect $G = \{r_{capelin}, m_{cod}, \alpha_{capelin,beluga}, \alpha_{cod,beluga}\}$ (Figure 2C). Here, we use growth rate for capelin, since it is now the new basal resource in the simplified system. This pathway of effects reduces the abundance of capelin and beluga (*i.e.* negative trophic sensitivity) and benefits the cod population (*i.e.* positive trophic sensitivity; Figure 2M). In the apparent competition interaction, temperature anomalies affect the physiological conditions of copepods and decrease capelin's ability to assimilate them (*i.e.* conversion rate ($e_{copepods,capelin}$), and fishing once again affects capelin mortality ($m_{capelin}$); this results in the integrative pathway of effect $G = \{m_{capelin}, e_{copepods,capelin}\}$ (Figure Figure 2B). This pathway of effects elicits negative trophic sensitivities for the capelin and krill populations (*i.e.* decreases in abundance), while the copepod population exhibits positive trophic sensitivity (*i.e.* increase in abundance; Figure 2L).

If we investigate unitary pathways of effects, however, we see that the effects of stressors may induce contrasting population trajectories. In the omnivory interaction, an increase in capelin mortality due to fishing ($g_1 = \{r_{capelin}\}$) favours cod and reduces capelin and beluga abundances (Figure 2F). In this scenario, cod are likely released from beluga predation due to their decrease in abundance [*i.e.* mesopredator release; Ritchie & 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 due to fishing ($g_2 = \{m_{cod}\}$) results in the growth of the capelin and beluga populations (Figure 2G).

Surprisingly, the cod population remains relatively unchanged, likely because the increase in prey availability offsets the effect of fishing [*i.e.* compensatory dynamics; Gonzalez & Loreau (2009)]. A similar scenario appears when the attack rates of beluga on capelin ($g_3 = \{\alpha_{capelin,beluga}\}$) is decreased by shipping (Figure 2H). Finally, disrupting the attack rates of beluga on cod due to shipping ($g_4 = \{\alpha_{cod,beluga}\}$) does not appear to adversely affect the beluga population, while shipping likely disrupts the top-down control of beluga on cod to the benefit of cod and to the detriment of capelin (Figure 2I). Similarly, the unitary pathways of effects on the apparent competition result in contrasting dynamics. The increase in capelin mortality ($g_1 = \{m_{capelin}\}$) results in a decrease in capelin abundance that benefits both prey species (Figure 2D). The decrease in the conversion rates of copepods by capelin ($g_2 = \{e_{copepods,capelin}\}$), meanwhile, surprisingly serves to transfer some of the predation pressure from copepods to krill, with krill populations decreasing as a result (Figure 2E).

Comparing population trajectories of the unitary pathways of effects with the integrative pathway of effect provides a measure of non-additive effects. Through the omnivory interaction, we see that the net effect of shipping and fishing elicit synergistic effects on capelin and beluga (**i.e.** positive trophic amplification) and a slightly antagonistic effect on cod (*i.e.* negative trophic amplification; Figure 2M). Through the apparent competition interaction, meanwhile, effects of fishing and temperature anomalies appear antagonistic for capelin and copepods, while they are additive for krill (Figure 2L).

Unitary pathways of effect also have contrasting effects on species. For example, the positive effects of cod mortality and beluga feeding rates on capelin (Figure 2G,H) are offset by the negative effects on capelin mortality and beluga feeding rates on cod (Figure 2F,I). Indeed, the trophic variance suggests that beluga ($V_{beluga,G} = 0.29$) and capelin ($V_{capelin,G} = 0.25$) are exposed to unitary pathways of effect that tend cancel each other out, whereas cod ($V_{cod,G} = 0.07$) is mostly exposed to unitary pathways of effect that reinforce each other. Effects propagating through the apparent competition interaction, meanwhile, tend to reinforce each other for to a greater degree for capelin ($V_{capelin,G} = 0.05$), than copepods

($V_{copepods,G} = 0.14$) and krill ($V_{krill,G} = 0.10$).

3.2 Scaling back to 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 & 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**. In our system, cod is twice a predator in food chains, once a consumer in an omnivory interaction and once a consumer in exploitative competition (Figure 3), which forms its motif census. Each 3-species interaction in which cod is involved is affected through a specific pathway of effect for which we can evaluate an expected trophic sensitivity and amplification (Figure 3). We summarize trophic sensitivities (S_m) and amplifications (A_m) across a species motif census (M) by summing motif scale trophic sensitivities and amplifications (Figure 3):

$$S_m = \sum_{i \in M} S_{i,G^i}; \quad (4)$$

$$A_m = \sum_{i \in M} A_{i,G^i}, \quad (5)$$

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. This approach is akin to that used by Stouffer *et al.* (2012) to evaluate a species role for community persistence as a function of the 3-species motifs it is involved in. For example, the net effect of stressors through the food chains and competitive exploitation motifs negatively affects cod, whereas it benefits from the net effect of stressors through the omnivory motif (Figure 3). Effects to cod are also amplified through the food chain with capelin and copepod, yet buffered through the omnivory and exploitative competition

interactions (Figure 3). Through equations 4 and 5, we would expect cod to be negatively and synergistically affected by stressors in our system, even though cod might benefit or be antagonistically affected through certain pathways of effect across its motif census (Figure 3).

4 Simulating the effects of multiple stressors on motifs

In the previous sections, we conceptualized how multiple stressors affect species in the context of food webs, defined metrics to evaluate the net effects of stressors, and illustrated how motifs can be leveraged to evaluate the expected trophic sensitivity, amplification and variance of species in complex food webs. To investigate how a species position in trophic interactions affects its sensitivity to the net effects of stressors, we now simulate pathways of effect through tri-trophic food chains, omnivory, exploitative competition, and apparent competition motifs. 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 (Table S1 in Supporting Information); we simulate and explore all these pathways of effect.

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 ??C-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 We used generalized Lotka-Volterra equation systems with Type 1 functional response (Table S1) to simulate the effects on stressors on tri-trophic food chain, competitive exploitation and apparent competition motifs. Two additional motifs were included as controls to assess 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:

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

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 (α_{jk}, α_{jj}) for the exploitative competition motif, as no coexistence may occur for this motif in the absence of other interactions. Refer to Table S1 for the equation systems of all motifs.

We simulated the effects of stressors on motif dynamics 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 through resource growth rates (r) mortality rates (m), conversion rates (e) and attack rates

(α_{ij}) were simulated by modifying the equilibria equation parameter values by 1% to simulate negative effects. For example, mortality rates were increased by 1%. Sets of parameter values were randomly selected with the added constraint that species abundances resulting from all possible pathways of effect remained 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. 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. Equilibria were solved using SageMath (TheSageDevelopers 2019) and simulations were performed using R (RCoreTeam 2019).

By constraining models so that all species abundances remain positive throughout all simulations, we are controlling for species extinctions. Still, it should be noted that our results and approach do not suggest that species affected by multiple stressors cannot go extinct. The goal of our simulations is to find whether certain species are more or less sensitive to the effects of multiple stressors based on their trophic position. To achieve this, simulations must capture the full range of possible trophic sensitivities to increasingly complex pathways of effect, which would not be possible if species were allowed to go extinct. Ultimately, what we are proposing are simulations of multiple, simultaneous, weak press perturbations to study the dynamics of a system in the neighbourhood of the equilibrium. In spirit, this is similar to approach used in press perturbation experiments (*e.g.* Bender *et al.* 1984; Montoya *et al.* 2009); in practice our approach is akin to a sensitivity analysis.

We also intentionally considered that species-specific responses are constant and negative across species to control for their effect and focus on the role of species interactions in mediating the effects of stressors in ecological communities. 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. Still, if known, species-specific sensitivities could readily be incorporated and explored in our work to consider species-scale and network-scale responses simultaneously. Similarly, we kept density-dependence constant to control for their effect and focus on trophically-mediated indirect effects.

~~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.~~

4.2 Effects of stressors on motifs

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 5, S1).

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 (Figures 5, S1). 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 entry points~~ (Figures 5, S1). In exploitative and apparent competition interactions, consumers are either **negatively affected** ~~negative entry points~~ or unaffected by stressors, whereas resources

are either ~~positively affected~~ ~~positive entry points~~ or unaffected by stressors (Figure 5,S1).

The insensitivity of consumers in apparent competition and resources in exploitative competition arises from negligible effects of stressors rather than unitary pathways of effect canceling each other out (Figure 6).

Based on knowledge of community stability, our results may appear counterintuitive at first glance. Indeed, omnivory and tri-trophic motifs show the strongest variations in abundances in our simulations, while their persistence has been found to be higher than the other three-species motifs (Stouffer & Bascompte 2010). A complementary analysis of motif stability (based on leading eigenvalue of the Jacobian matrix) revealed two important elements. First, initial parameterization yielded a higher stability for apparent competition and exploitative competition than for omnivory and tri-trophic food chains. Second, the stability of tri-trophic food chain and omnivory interactions increases as pathways of effects become more complex (Figure S2), whereas the stability of apparent and exploitative competition interactions decreases (Figure S2). Thus, interestingly enough, gains in stability for the omnivory and the tri-trophic food chain are associated with important variations in species abundance. While we do not have a definitive explanation for this, we anticipate that a promising avenue to better understand these results would be to explore the geometry of the feasibility domain for the different motifs considered here (see Song *et al.* 2018), which is beyond the scope of our study.

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 5, S1). This high variability in non-additive effects (Figures 5, 6) suggests ~~predicting whether a species will be affected synergistically or antagonistically by stressors~~ ~that typecasting species as biotic buffers – *i.e.* antagonistically affected by stressors – or biotic amplifiers – *i.e.* synergistically affected by stressors – ~requires precise knowledge of the pathways of effect affecting a system. ~~We can, nevertheless, typecast~~ Still, species in omnivory interactions and

the predator in tri-trophic food chains are 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 underestimating 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 (Wootton 1993, 2002; *e.g.* Menge 1995; Yodzis 2000; Montoya *et al.* 2009; O’Gorman & 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 & Melián 2005; Stouffer *et al.* 2007; Monteiro & Faria 2016; Klaise & Johnson 2017).

~~# 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 & 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 ??D). 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 ??D, 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 ??E). Effects to cod are also amplified through the food chain with capelin and copepod, yet buffered through the omnivory and exploitative competition interactions (Figure ??E).

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

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

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

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 ??E).

5 Applications: the St. Lawrence System

We illustrate how our framework can be applied to empirical food webs using data from the St. Lawrence System. 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 & 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.* 2020).

We used empirical data on the topology of 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)]. We used the topology of the empirical food webs to evaluate the motif census for each species and functional group. For each motif in a species motif census, we evaluate which pathway of effect – if any – is affecting the motif. We consider the most prevalent sources of offshore human- and climate-induced stress in the St. Lawrence System to identify pathways of effect; these are shipping, trawl, trap and pelagic fisheries, ocean acidification, hypoxia, and bottom- and surface-water temperature anomalies (Beauchesne *et al.* 2020). As modelling or observing each pathway of effect on empirical 3-species interactions is not realistic, we used the results from the simulations on theoretical motifs to infer – rather than model – a species sensitivity to stressors as a function of its position in a food web (see section *Simulating the effects of multiple stressors on motifs* for more details). We thus use the topology of empirical food webs rather than a modelling framework. For each observed pathway of effect, we used the corresponding simulated trophic sensitivities and amplifications as heuristics of a species expected sensitivity to the effects of stressors. We then evaluate a species expected trophic sensitivity and amplification across its motif census using equations 4 and 5. Refer to Appendix 1 and Figures S3, S4 and S5 in Supplementary information for more details.

~~### 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 Figures S1 and S2 in Supporting Information for the results for the Estuary and Southern Gulf.~~

~~#### 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.* 2020). We inferred the effects of individual sources of stress on the ecological processes governing these food webs (Figure 7) 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.* 2020);~~
- ~~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 2016). Reported whale bycatch and seals and seabird hunting were considered as effects to mortality (Morissette *et al.* 2003; Savenkoff *et al.* 2004; Savenkoff 2012).

Pathways of effect

The motif census of each species was evaluated from the structure of each food web (Figure 7). 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 7). 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.

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 7); 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 7). 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 7).

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 sensitive to the effects of stressors and prone to synergistic effects, *i.e.* they were negative weak entry points and biotic amplifiers (Figure 7). Second, forage species 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 7), or were insensitive to stressors (*e.g.* shrimp; Figure 7). 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 thus miss the underlying causes of population dynamics.

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, large apex predators (*e.g.* Atlantic cod, Greenland halibut and large demersals) and marine mammals were expected to be highly sensitive to the effects of stressors and prone to synergistic effects (Figure 7); this is mainly due to their trophic position, which was predominantly as predators in food chains, omnivory and exploitative competition interactions (Figure S3). Second, forage species were either expected to benefit synergistically from the effects of stressors by mostly occupying trophic positions such as mesopredators in omnivory interactions (*e.g.* capelin and crustaceans) or be insensitive to the effects of stressors by occupying trophic positions such as resources in exploitative competition interactions (Figures 7, S3). Third, a

species sensitivity to the effects of stressors can be driven exclusively by indirect exposure, the number of stressors affecting a species does not necessarily translate to greater trophic sensitivities or amplifications (Figure S3). 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 (Figures 7, S3). Focusing on a single species and direct effects may thus miss the 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 & 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 & 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.

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 8). 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 8). 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 8). 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.

6 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.

6.1 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 (Rip *et al.* 2010; *e.g.* Stouffer & Bascompte 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.

6.2 Density-dependence and interaction strength

In order to focus our investigation on trophically-mediated indirect effects, we intentionally kept density-dependence constant. However, the magnitude of indirect effects may be weakened by strong density-dependence dynamics in a system (Abrams *et al.* 1996). Specifically targeting density-dependence parameters in simulations and exploring how they influence the magnitude of the indirect effects of stressors would provide valuable insights for the effects of stressors on species whose dynamics is driven by density-dependence. Similarly, 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 & Emmerson 2009; Gellner & 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.

6.3 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; Dee *et al.* 2020; Otto *et al.* 2020) and experimental manipulations (*e.g.* Pillet *et al.* 2016; Lange & 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.

7 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 under-estimating 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 sensitivities. 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); tylianakis2010; O’Gorman *et al.* (2012); Kaiser-Bunbury & 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

877 to individuals – of the biological data used for management. While monitoring whole
878 systems may be deemed logistically unrealistic, environmental monitoring initiatives and
879 emerging technologies already in place could assist in such a paradigm shift. Knowledge
880 on the distribution and intensity of stressors (*e.g.* Halpern *et al.* 2015; Beauchesne *et*
881 *al.* 2020), on species occurrences (*e.g.* GBIF 2020; OBIS 2020), on species interactions
882 (*e.g.* Poelen *et al.* 2014; Poisot *et al.* 2016) and on abiotic data (*e.g.* Assis *et al.*
883 2018) are now openly available and their quality and robustness is progressively improving
884 owing to relentless methodological and technological advancements (*e.g.* functional traits,
885 environmental DNA, artificial intelligence). Ultimately, we believe that combining sound
886 theory with exhaustive ecological data-based knowledge through robust inference will lead
887 to management that explicitly consider the complexities of ecosystems and decision-making
888 that provides solutions tailored to the context in which management is undertaken, *i.e.* for
889 a specific area characterized by unique ecological dynamics and socioeconomic realities.

890 **8 Acknowledgements**

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

898 **9 References**

899 Abrams, P.A. (1992). Predators that Benefit Prey and Prey that Harm Predators: Unusual
900 Effects of Interacting Foraging Adaptation. *The American Naturalist*, 140, 573–600.

901 Abrams, P.A., Menge, B.A., Mittelbach, G.G., Spiller, D.A. & Yodzis, P. (1996). The Role
902 of Indirect Effects in Food Webs. In: *Food Webs: Integration of Patterns & Dynamics*
903 (eds. Polis, G.A. & Winemiller, K.O.). Springer US, Boston, MA, pp. 371–395.

904 Allesina, S., Bodini, A. & Bondavalli, C. (2006). Secondary extinctions in ecological
905 networks: Bottlenecks unveiled. *Ecological Modelling*, Special issue on the Fourth
906 European Conference on Ecological Modelling, 194, 150–161.

907 Archambault, P., Schloss, I.R., Grant, C. & Plante, S. (Eds.). (2017). *Les hydrocarbures*
908 *dans le golfe du Saint-Laurent - Enjeux sociaux, économiques et environnementaux*. Notre
909 Golfe, Rimouski, Qc, Canada.

910 Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A. & Clerck, O.D. (2018).
911 Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global*
912 *Ecology and Biogeography*, 27, 277–284.

913 Ban, N.C., Alidina, H.M. & Ardron, J.A. (2010). Cumulative impact mapping: Advances,
914 relevance and limitations to marine management and conservation, using Canada’s Pacific
915 waters as a case study. *Marine Policy*, 34, 876–886.

916 Bartley, T.J., McCann, K.S., Bieg, C., Cazelles, K., Granados, M., Guzzo, M.M., *et al.*
917 (2019). Food web rewiring in a changing world. *Nature Ecology & Evolution*, 3, 345–354.

918 Bascompte, J. (2009). Disentangling the Web of Life. *Science*, 325, 416–419.

919 Bascompte, J. & Melián, C.J. (2005). Simple Trophic Modules for Complex Food Webs.
920 *Ecology*, 86, 2868–2873.

921 Beauchesne, D., Daigle, R.M., Vissault, S., Gravel, D., Bastien, A., Bélanger, S., *et al.*
922 (2020). Characterizing Exposure to and Sharing Knowledge of Drivers of Environmental
923 Change in the St. Lawrence System in Canada. *Frontiers in Marine Science*, 7.

- 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.
- Belley, R., Archambault, P., Sundby, B., Gilbert, F. & Gagnon, J.-M. (2010). Effects of hypoxia on benthic macrofauna and bioturbation in the Estuary and Gulf of St. Lawrence, Canada. *Continental Shelf Research*, 30, 1302–1313.
- Bender, E.A., Case, T.J. & Gilpin, M.E. (1984). Perturbation Experiments in Community Ecology: Theory and Practice. *Ecology*, 65, 1–13.
- Berlow, E.L., Neutel, A.-M., Cohen, J.E., de Ruiter, P.C., Ebenman, B., Emmerson, M., *et al.* (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73, 585–598.
- Blanchard, J.L. (2015). A rewired food web. *Nature*, 527, 173–174.
- Boonstra, W.J., Ottosen, K.M., Ferreira, A.S.A., Richter, A., Rogers, L.A., Pedersen, M.W., *et al.* (2015). What are the major global threats and impacts in marine environments? Investigating the contours of a shared perception among marine scientists from the bottom-up. *Marine Policy*, 60, 197–201.
- Bourdages, H., Marquis, M.-C., Nozères, C. & Ouellette-Plante, J. (2018). *Assessment of northern shrimp stocks in the Estuary and Gulf of St. Lawrence in 2017: Data from the research survey. DFO Can. Sci. Advis. Sec. Res. Doc. 2018/057. Iv + 67 p. (No. 2018/057).*
- Bove, C.B., Ries, J.B., Davies, S.W., Westfield, I.T., Umbanhowar, J. & Castillo, K.D. (2019). Common Caribbean corals exhibit highly variable responses to future acidification and warming. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20182840.

- Bramon Mora, B., Gravel, D., Gilarranz, L.J., Poisot, T. & Stouffer, D.B. (2018). Identifying a common backbone of interactions underlying food webs from different ecosystems. *Nature Communications*, 9, 1–8.
- Bruder, A., Frainer, A., Rota, T. & Primicerio, R. (2019). The Importance of Ecological Networks in Multiple-Stressor Research and Management. *Frontiers in Environmental Science*, 7.
- Burns, T.P., Rose, K.A. & Brenkert, A.L. (2014). Quantifying direct and indirect effects of perturbations using model ecosystems. *Ecological Modelling, Systems Ecology: A Network Perspective and Retrospective*, 293, 69–80.
- Camacho, J., Stouffer, D.B. & Amaral, L.A.N. (2007). Quantitative analysis of the local structure of food webs. *Journal of Theoretical Biology*, 246, 260–268.
- Chabot, D. & Claireaux, G. (2008). Environmental hypoxia as a metabolic constraint on fish: The case of Atlantic cod, *Gadus morhua*. *Marine Pollution Bulletin*, 5th International Conference on Marine Pollution and Ecotoxicology, 57, 287–294.
- Christensen, M.R., Graham, M.D., Vinebrooke, R.D., Findlay, D.L., Paterson, M.J. & Turner, M.A. (2006). Multiple anthropogenic stressors cause ecological surprises in boreal lakes. *Global Change Biology*, 12, 2316–2322.
- Christiansen, F., Rasmussen, M. & Lusseau, D. (2013). Whale watching disrupts feeding activities of minke whales on a feeding ground. *Marine Ecology Progress Series*, 478, 239–251.
- Cirtwill, A.R. & Stouffer, D.B. (2015). Concomitant predation on parasites is highly variable but constrains the ways in which parasites contribute to food web structure. *The Journal of Animal Ecology*, 84, 734–744.
- Clavel, J., Julliard, R. & Devictor, V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment*,

973 9, 222–228.

974 Côté, I.M., Darling, E.S. & Brown, C.J. (2016). Interactions among ecosystem stressors and
975 their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*,
976 283, 20152592.

977 Crain, C.M., Kroeker, K. & Halpern, B.S. (2008). Interactive and cumulative effects of
978 multiple human stressors in marine systems. *Ecology Letters*, 11, 1304–1315.

979 Darling, E.S. & Côté, I.M. (2008). Quantifying the evidence for ecological synergies. *Ecology*
980 *Letters*, 11, 1278–1286.

981 David, P., Thébault, E., Anneville, O., Duyck, P.-F., Chapuis, E. & Loeuille, N. (2017).
982 Chapter One - Impacts of Invasive Species on Food Webs: A Review of Empirical Data.
983 In: *Advances in Ecological Research*, Networks of Invasion: A Synthesis of Concepts (eds.
984 Bohan, D.A., Dumbrell, A.J. & Massol, F.). Academic Press, pp. 1–60.

985 De Laender, F. (2018). Community-and ecosystem-level effects of multiple environmental
986 change drivers: Beyond null model testing. *Global change biology*, 24, 5021–5030.

987 Dee, L.E., Allesina, S., Bonn, A., Eklöf, A., Gaines, S.D., Hines, J., *et al.* (2017).
988 Operationalizing Network Theory for Ecosystem Service Assessments. *Trends in Ecology*
989 *& Evolution*, 32, 118–130.

990 Dee, L.E., Okamtoto, D., Gårdmark, A., Montoya, J.M. & Miller, S.J. (2020). Temperature
991 variability alters the stability and thresholds for collapse of interacting species. *bioRxiv*,
992 2020.05.18.102053.

993 Dempsey, D.P., Gentleman, W.C., Pepin, P. & Koen-Alonso, M. (2018). Explanatory Power
994 of Human and Environmental Pressures on the Fish Community of the Grand Bank
995 before and after the Biomass Collapse. *Frontiers in Marine Science*, 5.

996 DFO. (2016). *Zonal Interchange File Format (ZIFF) data. A compilation of landing*
997 *data from logbook data between 2010 and 2015. Gestion des données, Institut*

Maurice Lamontagne, Department of Fisheries and Oceans (DFO) Mont-Joli, Canada.

Department of Fisheries and Oceans.

Eby, L.A., Crowder, L.B., McClellan, C.M., Peterson, C.H. & Powers, M.J. (2005). Habitat degradation from intermittent hypoxia: Impacts on demersal fishes. *Marine Ecology Progress Series*, 291, 249–262.

Eklöf, A. & Ebenman, B. (2006). Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology*, 75, 239–246.

El-Sabh, M.I. & Silverberg, N. (1990). *Oceanography of a Large-Scale Estuarine System*. Springer New York.

Estes, J.A. & Palmisano, J.F. (1974). Sea Otters: Their Role in Structuring Nearshore Communities. *Science*, 185, 1058–1060.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., *et al.* (2011). Trophic Downgrading of Planet Earth. *Science*, New Series, 333, 301–306.

Fabry, V.J., Seibel, B.A., Feely, R.A. & Orr, J.C. (2008). Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science*, 65, 414–432.

Frank, K.T., Petrie, B., Choi, J.S. & Leggett, W.C. (2005). Trophic Cascades in a Formerly Cod-Dominated Ecosystem. *Science*, 308, 1621–1623.

Galic, N., Sullivan, L.L., Grimm, V. & Forbes, V.E. (2018). When things don't add up: Quantifying impacts of multiple stressors from individual metabolism to ecosystem processing. *Ecology Letters*, 21, 568–577.

Gavrilchuk, K., Lesage, V., Ramp, C., Sears, R., Bérubé, M., Bearhop, S., *et al.* (2014). Trophic niche partitioning among sympatric baleen whale species following the collapse of groundfish stocks in the Northwest Atlantic. *Marine Ecology Progress Series*, 497, 285–301.

1022 GBIF. (2020). GBIF: The Global Biodiversity Information Facility (2020) What is GBIF?
1023 Available from <https://www.gbif.org/what-is-gbif> Accessed 2020-07-20.

1024 Gellner, G. & McCann, K.S. (2016). Consistent role of weak and strong interactions in high-
1025 and low-diversity trophic food webs. *Nature Communications*, 7, 11180.

1026 Gonzalez, A. & Loreau, M. (2009). The Causes and Consequences of Compensatory
1027 Dynamics in Ecological Communities. *Annual Review of Ecology, Evolution, and*
1028 *Systematics*, 40, 393–414.

1029 Griffen, B.D., Belgrad, B.A., Cannizzo, Z.J., Knotts, E.R. & Hancock, E.R. (2016).
1030 Rethinking our approach to multiple stressor studies in marine environments. *Marine*
1031 *Ecology Progress Series*, 543, 273–281.

1032 Guiden, P.W., Bartel, S.L., Byer, N.W., Shipley, A.A. & Orrock, J.L. (2019). Predator–Prey
1033 Interactions in the Anthropocene: Reconciling Multiple Aspects of Novelty. *Trends in*
1034 *Ecology & Evolution*, 34, 616–627.

1035 Halpern, B.S., Frazier, M., Afflerbach, J., Lowndes, J.S., Micheli, F., O’Hara, C., *et al.*
1036 (2019). Recent pace of change in human impact on the world’s ocean. *Scientific Reports*,
1037 9, 11609.

1038 Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C., *et al.* (2015).
1039 Cumulative human impacts: Raw stressor data (2008 and 2013). Knowledge Network
1040 for Biocomplexity.

1041 Harborne, A.R., Rogers, A., Bozec, Y.-M. & Mumby, P.J. (2017). Multiple Stressors and
1042 the Functioning of Coral Reefs. *Annual Review of Marine Science*, 9, 445–468.

1043 Harvey, E., Gounand, I., Ward, C.L. & Altermatt, F. (2017). Bridging ecology and
1044 conservation: From ecological networks to ecosystem function. *Journal of Applied*
1045 *Ecology*, 54, 371–379.

- 1046 Hodgson, E.E., Essington, T.E. & Halpern, B.S. (2017). Density dependence governs when
1047 population responses to multiple stressors are magnified or mitigated. *Ecology*, 98,
1048 2673–2683.
- 1049 Hodgson, E.E. & Halpern, B.S. (2019). Investigating cumulative effects across ecological
1050 scales. *Conservation Biology*, 33, 22–32.
- 1051 Hodgson, E.E., Halpern, B.S. & Essington, T.E. (2019). Moving Beyond Silos in Cumulative
1052 Effects Assessment. *Frontiers in Ecology and Evolution*, 7.
- 1053 Holt, R.D. (1977). Predation, apparent competition, and the structure of prey communities.
1054 *Theoretical population biology*, 12, 197–229.
- 1055 Holt, R.D. (1997). Community modules. In: *Multitrophic Interactions in Terrestrial*
1056 *Ecosystems, 36th Symposium of the British Ecological Society* (eds. Grange, A.C. &
1057 Brown, V.K.). Blackwell Science, Oxford, pp. 333–349.
- 1058 Holt, R.D. & Hochberg, M.E. (2001). Indirect interactions, community modules and
1059 biological control: A theoretical perspective. *Evaluating indirect ecological effects of*
1060 *biological control*, 13–37.
- 1061 Ives, A.R. (1995). Measuring Resilience in Stochastic Systems. *Ecological Monographs*, 65,
1062 217–233.
- 1063 Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J.,
1064 *et al.* (2001). Historical Overfishing and the Recent Collapse of Coastal Ecosystems.
1065 *Science*, 293, 629–637.
- 1066 Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D. & Chimimba, C.T. (2016). Net effects of
1067 multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology*, 22,
1068 180–189.
- 1069 Kaiser-Bunbury, C.N. & Blüthgen, N. (2015). Integrating network ecology with applied
1070 conservation: A synthesis and guide to implementation. *AoB PLANTS*, 7.

1071 Klaise, J. & Johnson, S. (2017). The origin of motif families in food webs. *Scientific Reports*,
1072 7, 16197.

1073 Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A. & Holt, R.D. (2005). Trophic
1074 cascades across ecosystems. *Nature*, 437, 880–883.

1075 Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A.V. & Aschan, M. (2015). Climate
1076 change alters the structure of arctic marine food webs due to poleward shifts of boreal
1077 generalists. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151546.

1078 Kroeker, K.J., Kordas, R.L., Crim, R., Hendriks, I.E., Ramajo, L., Singh, G.S., *et al.*
1079 (2013). Impacts of ocean acidification on marine organisms: Quantifying sensitivities
1080 and interaction with warming. *Global Change Biology*, 19, 1884–1896.

1081 Lange, R. & Marshall, D. (2017). Ecologically relevant levels of multiple, common marine
1082 stressors suggest antagonistic effects. *Scientific Reports*, 7, 6281.

1083 Lapointe, B.E., Brewton, R.A., Herren, L.W., Porter, J.W. & Hu, C. (2019). Nitrogen
1084 enrichment, altered stoichiometry, and coral reef decline at Looe Key, Florida Keys,
1085 USA: A 3-decade study. *Marine Biology*, 166, 108.

1086 Lesage, V., Omrane, A., Doniol-Valcroze, T. & Mosnier, A. (2017). Increased proximity of
1087 vessels reduces feeding opportunities of blue whales in the St. Lawrence Estuary, Canada.
1088 *Endangered Species Research*, 32, 351–361.

1089 Liess, M., Foit, K., Knillmann, S., Schäfer, R.B. & Liess, H.-D. (2016). Predicting the
1090 synergy of multiple stress effects. *Scientific Reports*, 6, 32965.

1091 Lindmark, M., Ohlberger, J., Huss, M. & Gårdmark, A. (2019). Size-based ecological
1092 interactions drive food web responses to climate warming. *Ecology Letters*, 22, 778–786.

1093 McCann, K. (2007). Protecting biostructure. *Nature*, 446, 29–29.

1094 McCann, K., Hastings, A. & Huxel, G.R. (1998). Weak trophic interactions and the balance
1095 of nature. *Nature*, 395, 794.

- 1096 McClanahan, T.R., Graham, N.A. & Darling, E.S. (2014). Coral reefs in a crystal ball:
1097 Predicting the future from the vulnerability of corals and reef fishes to multiple stressors.
1098 *Current Opinion in Environmental Sustainability*, Environmental change issues, 7, 59–64.
- 1099 Menge, B.A. (1995). Indirect Effects in Marine Rocky Intertidal Interaction Webs: Patterns
1100 and Importance. *Ecological Monographs*, 65, 21–74.
- 1101 Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D. & Alon, U. (2002). Network
1102 Motifs: Simple Building Blocks of Complex Networks. *Science*, 298, 824–827.
- 1103 Monteiro, A.B. & Faria, L.D.B. (2016). The interplay between population stability and
1104 food-web topology predicts the occurrence of motifs in complex food-webs. *Journal of*
1105 *theoretical biology*, 409, 165–171.
- 1106 Montoya, J., Woodward, G., Emmerson, M.C. & Solé, R.V. (2009). Press perturbations and
1107 indirect effects in real food webs. *Ecology*, 90, 2426–2433.
- 1108 Morissette, L., Castonguay, M., Savenkoff, C., Swain, D.P., Chabot, D., Bourdages, H., *et*
1109 *al.* (2009). Contrasting changes between the northern and southern Gulf of St. Lawrence
1110 ecosystems associated with the collapse of groundfish stocks. *Deep Sea Research Part II:*
1111 *Topical Studies in Oceanography*, The Proceedings of the ECONORTH Symposium on
1112 Ecosystem Dynamics in the Norwegian Sea and Barents Sea, 56, 2117–2131.
- 1113 Morissette, L., Despatie, S.-P., Savenkoff, C., Hammill, M.O., Bourdages, H. & Chabot,
1114 D. (2003). Data gathering and input parameters to construct ecosystem models for the
1115 northern Gulf of St. Lawrence(mid-1980 s). *Can. Tech. Rep. Fish. Aquat. Sci./Rapp.*
1116 *Tech. Can. Sci. Halieut. Aquat.*, 100.
- 1117 Myers, R.A. & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities.
1118 *Nature*, 423, 280.
- 1119 O’Brien, A.L., Dafforn, K.A., Chariton, A.A., Johnston, E.L. & Mayer-Pinto, M. (2019).
1120 After decades of stressor research in urban estuarine ecosystems the focus is still on

1121 single stressors: A systematic literature review and meta-analysis. *Science of The Total*
1122 *Environment*.

1123 O’Gorman, E.J. & Emmerson, M.C. (2009). Perturbations to trophic interactions and the
1124 stability of complex food webs. *Proceedings of the National Academy of Sciences*, 106,
1125 13393–13398.

1126 O’Gorman, E.J., Fitch, J.E. & Crowe, T.P. (2012). Multiple anthropogenic stressors and
1127 the structural properties of food webs. *Ecology*, 93, 441–448.

1128 O’Gorman, E.J., Petchey, O.L., Faulkner, K.J., Gallo, B., Gordon, T.A.C., Neto-Cerejeira,
1129 J., *et al.* (2019). A simple model predicts how warming simplifies wild food webs. *Nature*
1130 *Climate Change*, 9, 611–616.

1131 OBIS. (2020). Ocean Biogeographic Information System. Intergovernmental Oceanographic
1132 Commission of UNESCO. www.iobis.org. Accessed 2020-07-27.

1133 Oppenheimer, M., Campos, M., Warren, R., Birkmann, J., Luber, G., O’Neill, B., *et al.*
1134 (2015). Emergent risks and key vulnerabilities. In: *Climate Change 2014 Impacts,*
1135 *Adaptation and Vulnerability: Part A: Global and Sectoral Aspects*. Cambridge University
1136 Press, pp. 1039–1100.

1137 Orr, J.A., Vinebrooke, R.D., Jackson, M.C., Kroeker, K.J., Kordas, R.L., Mantyka-Pringle,
1138 C., *et al.* (2020). Towards a unified study of multiple stressors: Divisions and common
1139 goals across research disciplines. *Proceedings of the Royal Society B: Biological Sciences*,
1140 287, 20200421.

1141 Otto, S.A., Niiranen, S., Blenckner, T., Tomczak, M.T., Müller-Karulis, B., Rubene, G.,
1142 *et al.* (2020). Life Cycle Dynamics of a Key Marine Species Under Multiple Stressors.
1143 *Frontiers in Marine Science*, 7.

1144 Paine, R.T. (1980). Food Webs: Linkage, Interaction Strength and Community
1145 Infrastructure. *Journal of Animal Ecology*, 49, 667–685.

1146 Paine, R.T. (1992). Food-web analysis through field measurement of per capita interaction
1147 strength. *Nature*, 355, 73.

1148 Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998). Fishing Down
1149 Marine Food Webs. *Science*, 279, 860–863.

1150 Piggott, J.J., Townsend, C.R. & Matthaei, C.D. (2015). Reconceptualizing synergism and
1151 antagonism among multiple stressors. *Ecology and Evolution*, 5, 1538–1547.

1152 Pillet, M., Dupont-Prinet, A., Chabot, D., Tremblay, R. & Audet, C. (2016). Effects of
1153 exposure to hypoxia on metabolic pathways in northern shrimp (*Pandalus borealis*)
1154 and Greenland halibut (*Reinhardtius hippoglossoides*). *Journal of Experimental Marine*
1155 *Biology and Ecology*, 483, 88–96.

1156 Poelen, J.H., Simons, J.D. & Mungall, C.J. (2014). Global biotic interactions: An open
1157 infrastructure to share and analyze species-interaction datasets. *Ecological Informatics*,
1158 24, 148–159.

1159 Poisot, T., Baiser, B., Dunne, J.A., Kéfi, S., Massol, F., Mouquet, N., *et al.* (2016). Mangal
1160 – making ecological network analysis simple. *Ecography*, 39, 384–390.

1161 RCoreTeam. (2019). R: A Language and Environment for Statistical Computing.

1162 Rip, J.M.K., McCann, K.S., Lynn, D.H. & Fawcett, S. (2010). An experimental test of a
1163 fundamental food web motif. *Proceedings of the Royal Society B: Biological Sciences*,
1164 277, 1743–1749.

1165 Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., *et al.* (2015).
1166 Collapse of the world’s largest herbivores. *Science Advances*, 1, e1400103.

1167 Ritchie, E.G. & Johnson, C.N. (2009). Predator interactions, mesopredator release and
1168 biodiversity conservation. *Ecology Letters*, 12, 982–998.

1169 Savenkoff, C. (2012). *Input data and parameter estimates for ecosystem models of the lower*
1170 *St. Lawrence Estuary (2008–2010)*. Canadian Technical Report of Fisheries and Aquatic

1171 Sciences 1999, Department of Fisheries and Oceans, Mont-Joli, Québec, Canada.

1172 Savenkoff, C., Bourdages, H., Swain, D.P., Despatie, S.-P., Hanson, J.M., Méthot, R., *et al.*
1173 (2004). *Input data and parameter estimates for ecosystem models of the southern Gulf of*
1174 *St. Lawrence (mid-1980s and mid-1990s)*. Canadian Technical Report of Fisheries and
1175 Aquatic Sciences 2529, Department of Fisheries and Oceans, Mont-Joli, Québec, Canada.

1176 Savenkoff, C., Swain, D.P., Hanson, J.M., Castonguay, M., Hammill, M.O., Bourdages, H., *et*
1177 *al.* (2007). Effects of fishing and predation in a heavily exploited ecosystem: Comparing
1178 periods before and after the collapse of groundfish in the southern Gulf of St. Lawrence
1179 (Canada). *Ecological Modelling*, 204, 115–128.

1180 Savenkoff, C., Vézina, A.F., Roy, S., Klein, B., Lovejoy, C., Therriault, J.-C., *et al.* (2000).
1181 Export of biogenic carbon and structure and dynamics of the pelagic food web in the
1182 Gulf of St. Lawrence Part 1. Seasonal variations. *Deep Sea Research Part II: Topical*
1183 *Studies in Oceanography*, 47, 585–607.

1184 Schäfer, R.B. & Piggott, J.J. (2018). Advancing understanding and prediction in multiple
1185 stressor research through a mechanistic basis for null models. *Global Change Biology*, 24,
1186 1817–1826.

1187 Schloss, I.R., Archambault, P., Beauchesne, D., Cusson, M., Ferreyra, G., Levasseur, M.,
1188 *et al.* (2017). Cumulative potential impacts of the stress factors associated with human
1189 activities on the St. Lawrence marine ecosystem. In: *Hydrocarbon in the Gulf of St.*
1190 *Lawrence - Social, economic and environmental issues* (eds. Archambault, P., Schloss,
1191 I.R., Grant, C. & Plante, S.). Notre Golfe, Rimouski, Qc, Canada, pp. 133–165.

1192 Song, C., Rohr, R.P. & Saavedra, S. (2018). A guideline to study the feasibility domain of
1193 multi-trophic and changing ecological communities. *Journal of Theoretical Biology*, 450,
1194 30–36.

1195 Stier, A.C., Samhouri, J.F., Novak, M., Marshall, K.N., Ward, E.J., Holt, R.D., *et al.*
1196 (2016). Ecosystem context and historical contingency in apex predator recoveries.

1197 *Science Advances*, 2, e1501769.

1198 Stouffer, D.B. & Bascompte, J. (2010). Understanding food-web persistence from local to
1199 global scales. *Ecology Letters*, 13, 154–161.

1200 Stouffer, D.B. & Bascompte, J. (2011). Compartmentalization increases food-web
1201 persistence. *Proceedings of the National Academy of Sciences*, 108, 3648–3652.

1202 Stouffer, D.B., Camacho, J., Jiang, W. & Nunes Amaral, L.A. (2007). Evidence for the
1203 existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal
1204 Society B: Biological Sciences*, 274, 1931–1940.

1205 Stouffer, D.B., Sales-Pardo, M., Sirer, M.I. & Bascompte, J. (2012). Evolutionary
1206 Conservation of Species’ Roles in Food Webs. *Science*, 335, 1489–1492.

1207 TheSageDevelopers. (2019). SageMath, the Sage Mathematics Software System Version 8.8.

1208 Thompson, P.L., MacLennan, M.M. & Vinebrooke, R.D. (2018). Species interactions cause
1209 non-additive effects of multiple environmental stressors on communities. *Ecosphere*, 9,
1210 e02518.

1211 Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008). Global change and
1212 species interactions in terrestrial ecosystems. *Ecology letters*, 11, 1351–1363.

1213 Vander Zanden, M.J., Casselman, J.M. & Rasmussen, J.B. (1999). Stable isotope evidence
1214 for the food web consequences of species invasions in lakes. *Nature*, 401, 464–467.

1215 Wiedenmann, J., D’Angelo, C., Smith, E.G., Hunt, A.N., Legiret, F.-E., Postle, A.D., *et al.*
1216 (2013). Nutrient enrichment can increase the susceptibility of reef corals to bleaching.
1217 *Nature Climate Change*, 3, 160–164.

1218 Wittmer, H.U., Elbroch, L.M. & Marshall, A.J. (2013). Good intentions gone wrong: Did
1219 conservation management threaten Endangered huemul deer *Hippocamelus bisulcus* in
1220 the future Patagonia National Park? *Oryx*, 47, 393–402.

- 1221 Wootton, J.T. (1993). Indirect Effects and Habitat Use in an Intertidal Community:
1222 Interaction Chains and Interaction Modifications. *The American Naturalist*, 141, 71–89.
- 1223 Wootton, J.T. (2002). Indirect effects in complex ecosystems: Recent progress and future
1224 challenges. *Journal of Sea Research*, Structuring Factors of Shallow Marine Coastal
1225 Communities, part I, 48, 157–172.
- 1226 Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., *et al.* (2006).
1227 Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science*, 314, 787–790.
- 1228 Worm, B. & Myers, R.A. (2003). Meta-Analysis of Cod-Shrimp Interactions Reveals Top-
1229 Down Control in Oceanic Food Webs. *Ecology*, 84, 162–173.
- 1230 Yodzis, P. (2000). Diffuse Effects in Food Webs. *Ecology*, 81, 261–266.

10 Figure legends

Figure 1. A) 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. **Direct** (*e.g.* cod and capelin; B) and **indirect**; **C** (*e.g.* cod and krill) **effects** arise from species interactions and the integration of both types of effects provides the overall **net effect** (C). Through species interactions, the direct effects of stressors (*e.g.* trawl fishing on cod; B) propagate indirectly through the food web (*e.g.* trawl fishing on krill; C) and the integration of both types of effects provides the overall net effect of a stressors on a species (B). Terms in bold are defined in the glossary.

Figure 2. (A) 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. Here, the food web is simplified by focusing on subsets of species interactions called motifs, such as the omnivory interaction linking beluga, cod and capelin in red and the apparent competition linking capelin, krill and copepods in blue. (B,C) **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 the direct effect of 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**. (D,F) Disrupting ecological processes affects

community dynamics and results in variations in species abundances (**trophic sensitivity**; S_m). (D to I) Effects to individual ecological processes arise through **unitary pathways of effects** (g) and result in contrasting population trajectories. (L,M) Unitary pathways of effect combine to form an **integrative pathway of effect** (G) and collectively affect species in a community. 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). Terms in bold are defined in the glossary.

Figure 3. A) A **species motif census** (M) is composed of all the positions it holds in a food web. B) 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.

Figure 4. A) Density plot of the trophic sensitivity ($S_{i,G}$) of 14 unique motif positions (i) resulting from all unitary (g ; orange) and integrative (G ; blue) 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). In this figure, unitary pathways of effects are those consisting of only a single ecological parameter, while integrative pathways of effect are composed of more than one ecological parameters. B) Magnitude of simulated trophic sensitivities as a function of the number of ecological processes included in a pathway of effect.

Figure 5. The main scatterplot in the center presents the mean trophic amplification (A_i) as a function of the mean trophic sensitivity (S_i) to all possible pathways of effect (G) for the 14 unique 3-species motif positions explored, *i.e.* tri-trophic food chain ($n = 3$; red), omnivory ($n = 3$; green), exploitative competition ($n = 2$; blue), apparent competition ($n = 2$; yellow), partially connected ($n = 3$; purple) and disconnected ($n = 1$; purple). The symbol grouped with each data point identifies the motif position it corresponds to.

1283 Motif positions with positive trophic sensitivities (x -axis) are, on average, positively affected
1284 (*i.e.* increases in abundance) across pathways of effect; conversely, motif positions with
1285 negative trophic sensitivities are, on average, negatively affected across pathways of effect.
1286 Motif positions with positive trophic amplifications (y -axis) are, on average, synergistically
1287 affected across pathways of effect; motif positions with negative trophic amplifications are,
1288 on average, antagonistically affected across pathways of effect. The surrounding plots are the
1289 results of individual simulations for each motif position, identified in the upper left portion
1290 of each scatterplot. The scatterplots have the same axes as the main scatterplot and can be
1291 interpreted in the same way.

1292 **Figure 6.** Density plots of the trophic variance ($V_{i,G}$) of 14 unique motif positions (i) for all
1293 integrative (G ; blue) pathways of effect (G) formed of more than one ecological parameters
1294 and simulated on the dynamics of 3-species motifs (*i.e.* tri-trophic food chain, omnivory,
1295 exploitative competition, apparent competition, partially connected and disconnected).

1296 **Figure 7.** Scatterplot of the trophic amplification (A_m) as a function of trophic sensitivity
1297 (S_m) for species and function groups of the Northern Gulf of St. Lawrence in the mid-1980s
1298 (Morissette *et al.* 2003). A species trophic sensitivity and amplification is summarized using
1299 the sum of simulated trophic sensitivities ($S_{i,G}$) and amplifications ($A_{i,G}$) to pathways of
1300 effect (G ; Figure 2) across a species motif census (M ; Figure 3). Negative or positive trophic
1301 sensitivities denote species that are expected to be negatively affected or benefit from the
1302 effects of stressors, respectively. Negative or positive trophic amplifications identify species
1303 or functional groups expected to be affected synergistically or antagonistically by stressors.

1304 **Figure 8.** Comparison of the trophic sensitivities (S_m) and amplifications (A_m) to the
1305 effects of different groups of stressors (Figure 7) for Atlantic cod (*Gadus morhua*), shrimp
1306 (*Pandalus borealis*) and large crustaceans (*Crustacea*) between the food webs of the Southern
1307 and Northern Gulf of St. Lawrence in the mid-1980s (Morissette *et al.* 2003; Savenkoff *et al.*
1308 2004) and the St. Lawrence Estuary in the early 2010s (Savenkoff 2012).

11 Figures

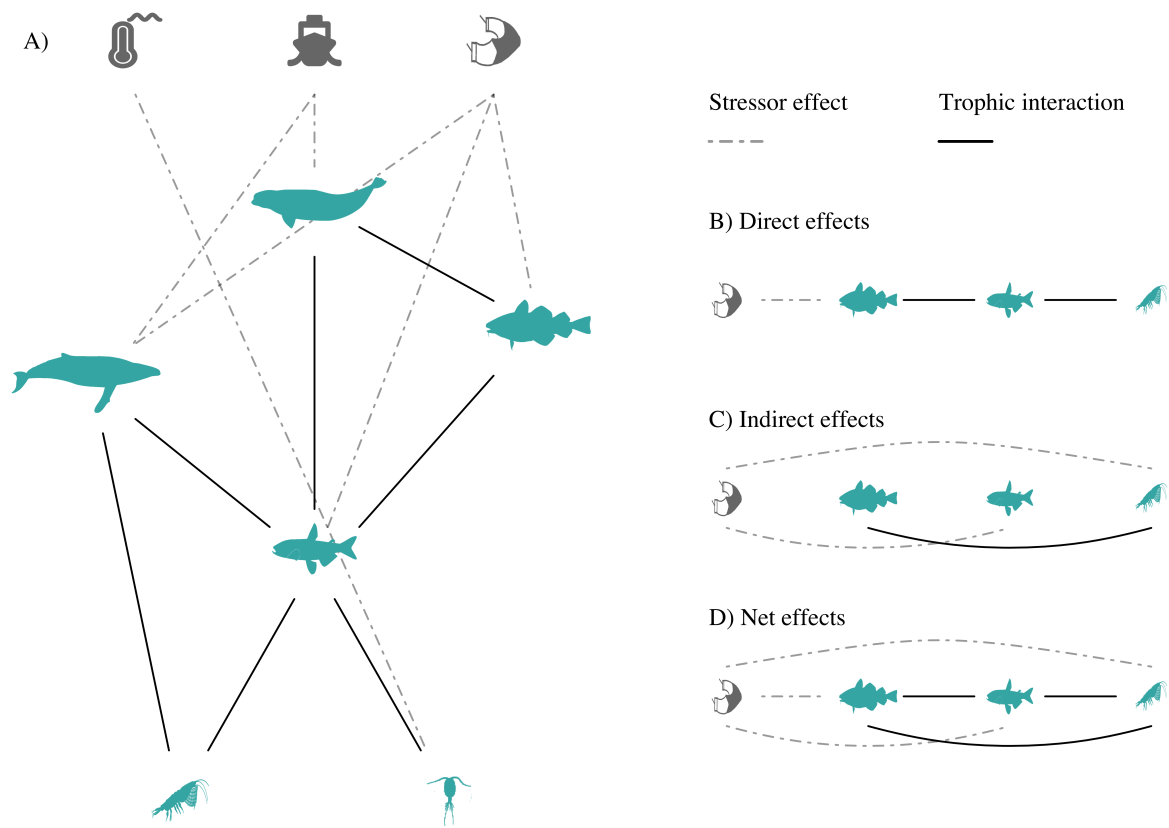


Figure 1

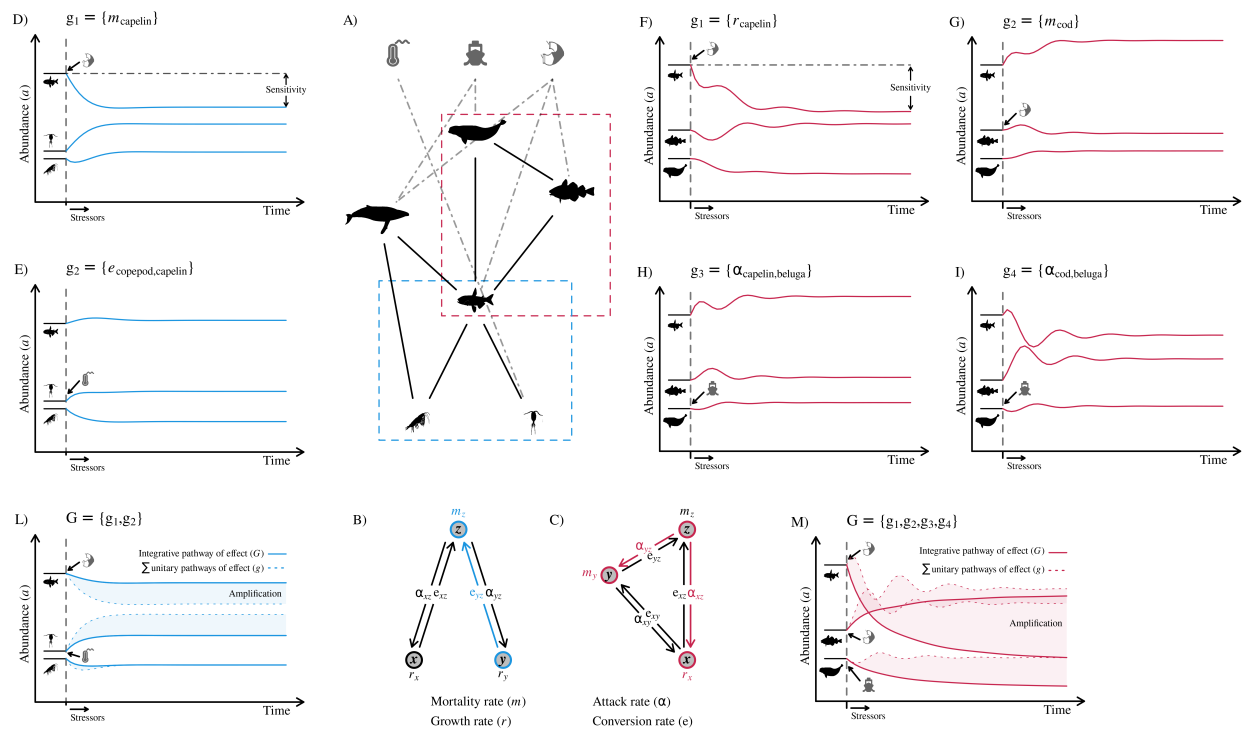
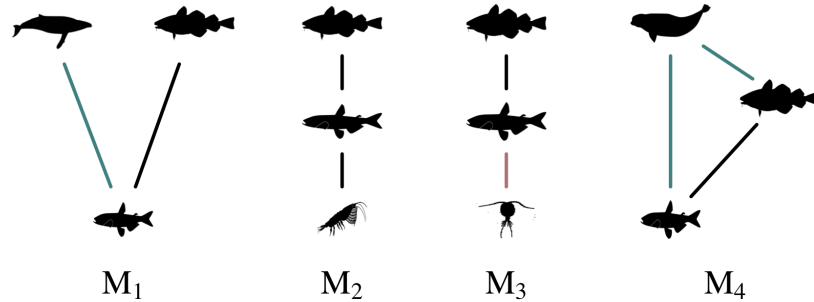


Figure 2

A) Species motif census



B) Scaling back to species in complex food webs

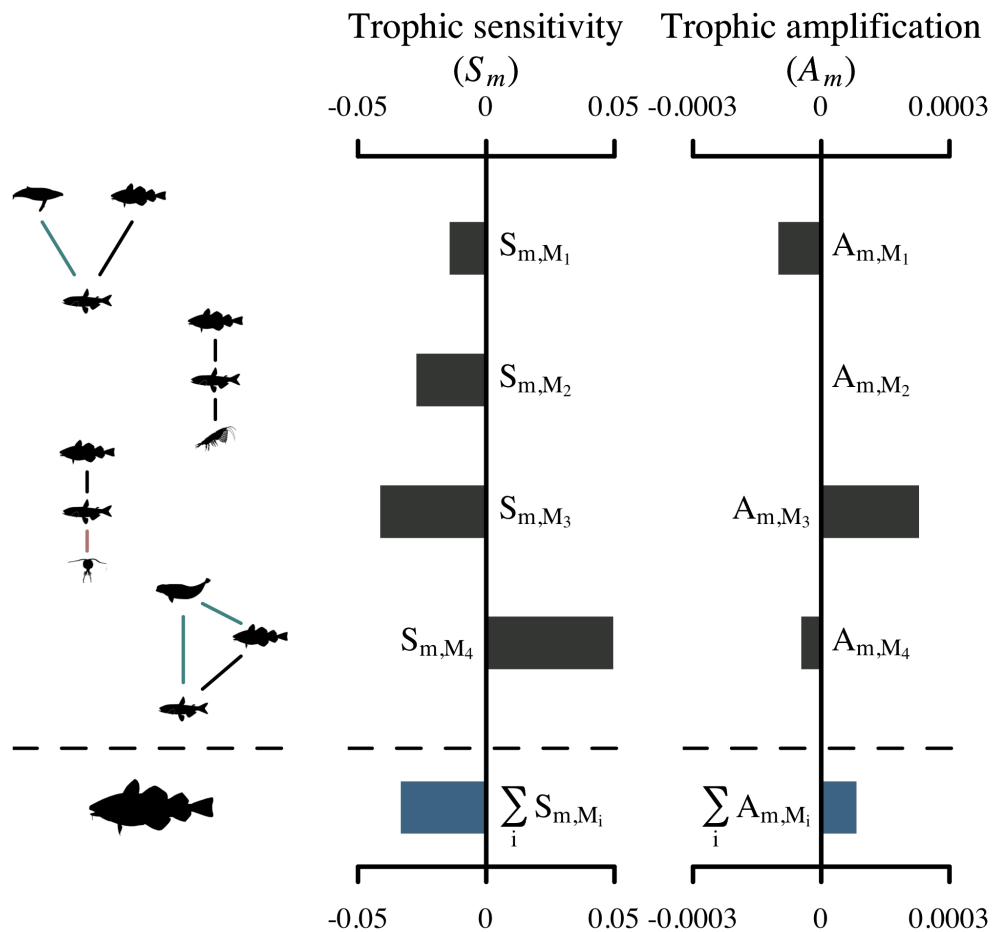


Figure 3
56

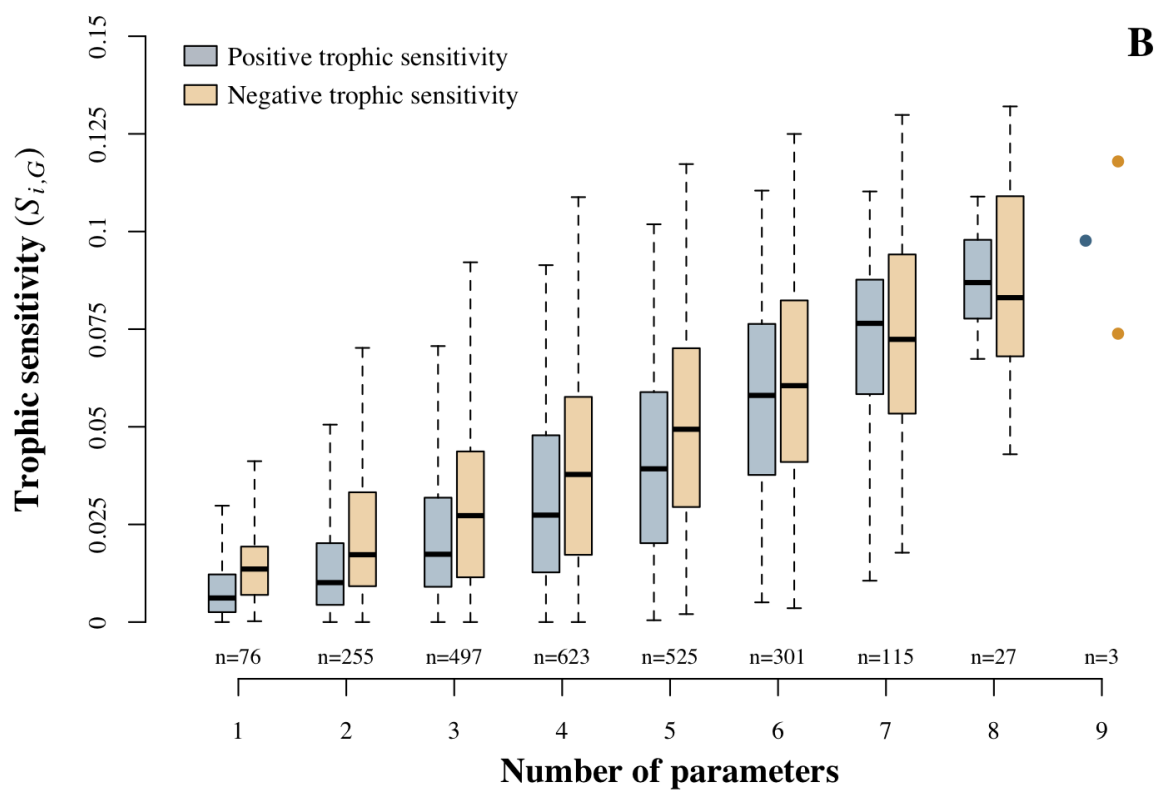
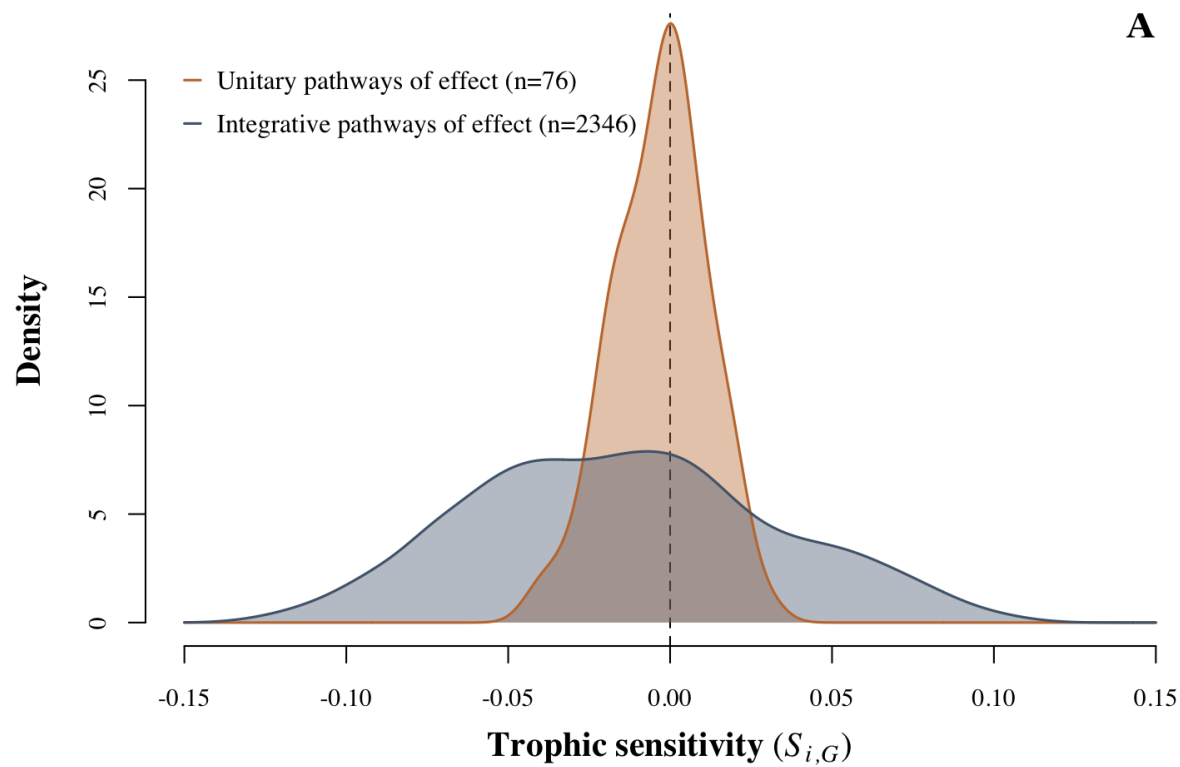


Figure 4

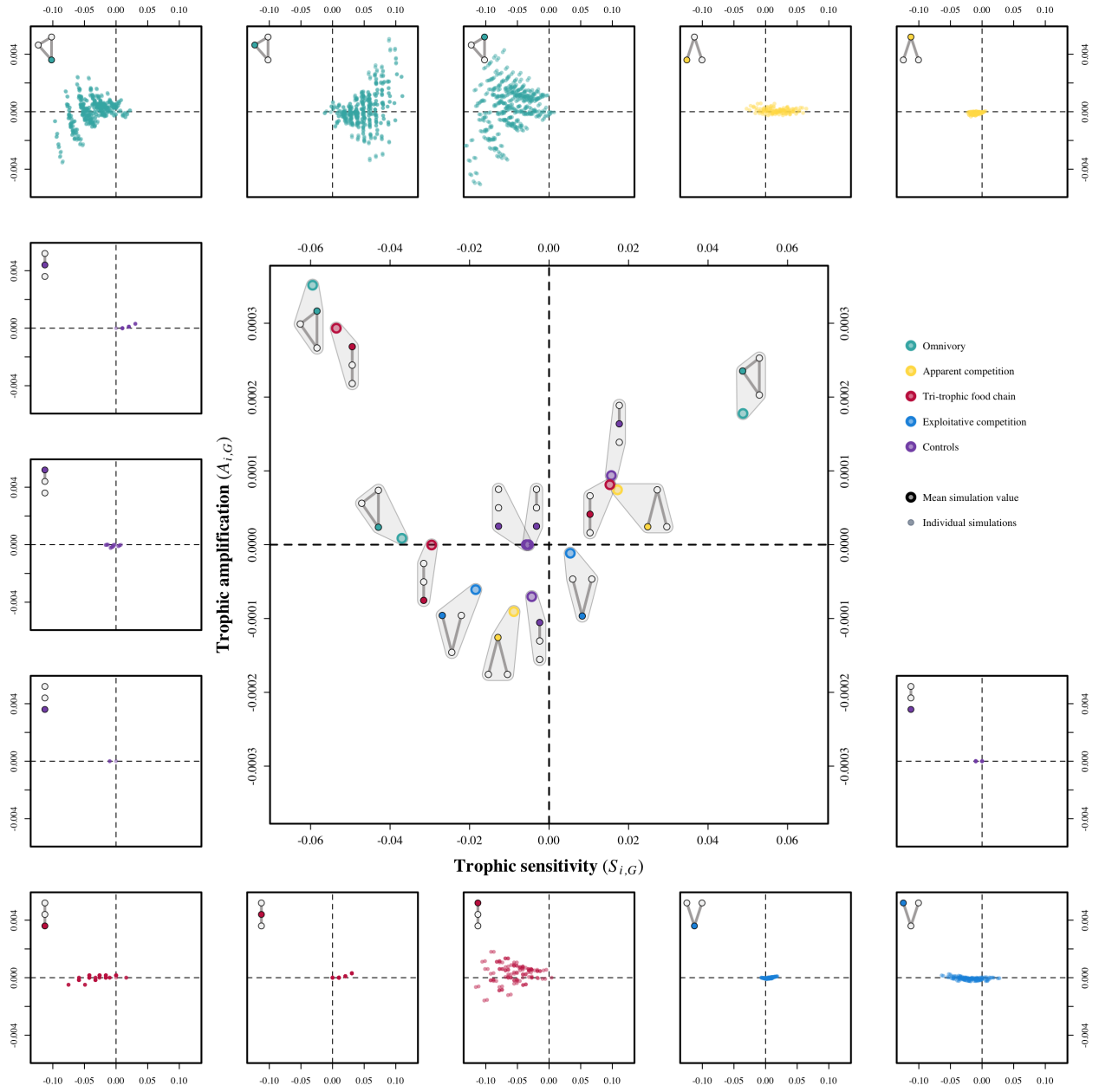


Figure 5

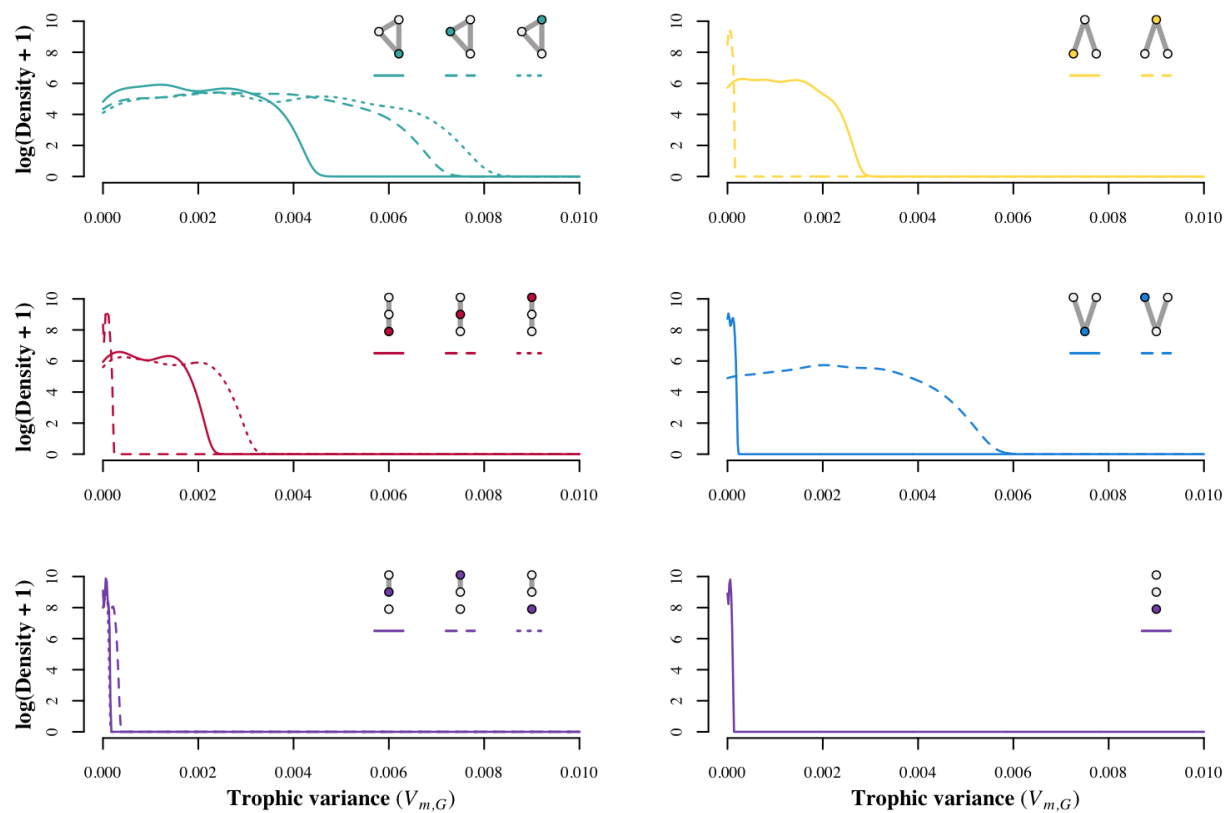
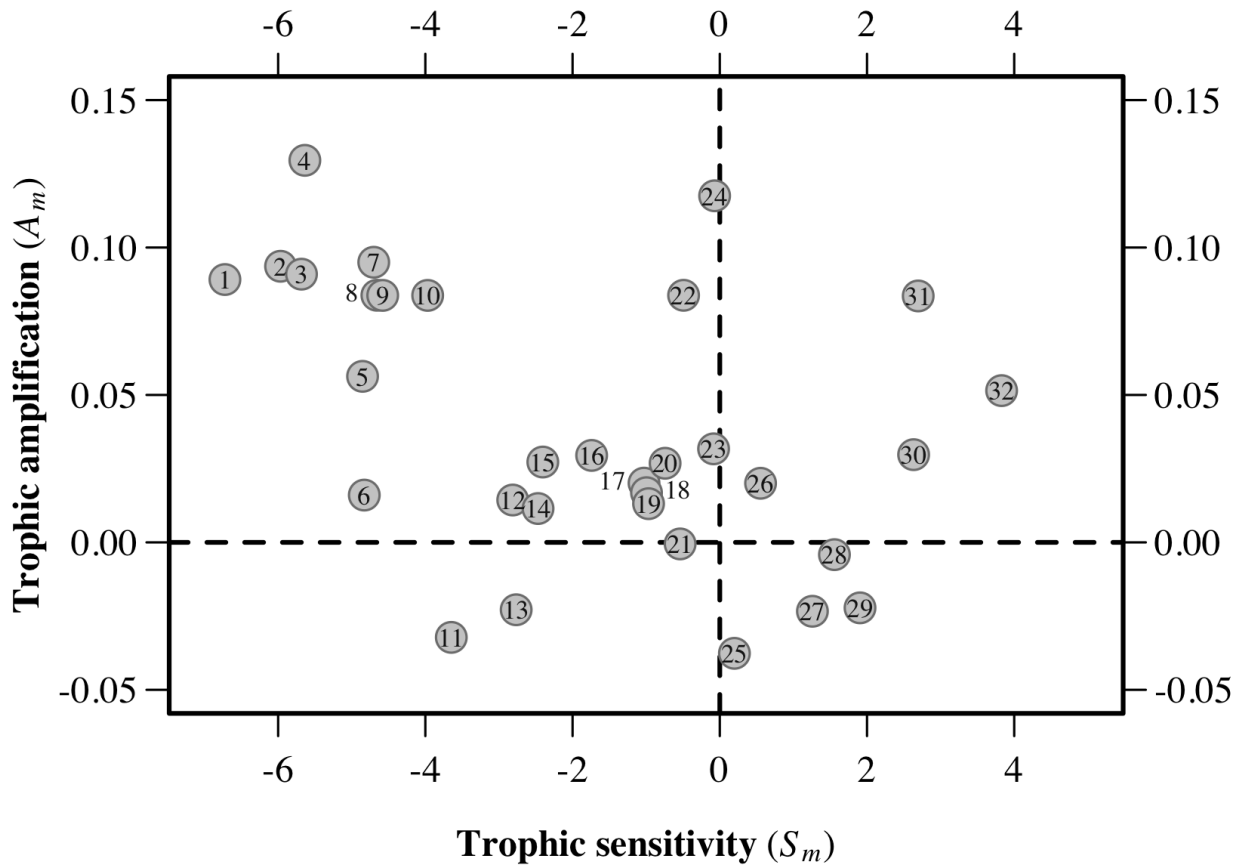


Figure 6



- | | | |
|----------------------------|---|----------------------------|
| 1. Large demersal feeders | 12. Large American plaice | 23. Polychaetes |
| 2. Large Atlantic cod | 13. Phytoplankton | 24. Shrimp |
| 3. Cetaceans | 14. Small zooplankton | 25. Flounders |
| 4. Harp seals | 15. Molluscs | 26. Echinoderms |
| 5. Large Greenland halibut | 16. Large pelagic feeders | 27. Small Atlantic cod |
| 6. Skates | 17. Piscivorous small pelagic feeders | 28. Arctic cod |
| 7. Grey seals | 18. Planktivorous small pelagic feeders | 29. Small demersal feeders |
| 8. Harbour seals | 19. Small Greenland halibut | 30. Sand lance |
| 9. Seabirds | 20. Other benthic invertebrates | 31. Large crustaceans |
| 10. Hooded seals | 21. Redfish | 32. Capelin |
| 11. Detritus | 22. Large zooplankton | |

Figure 7

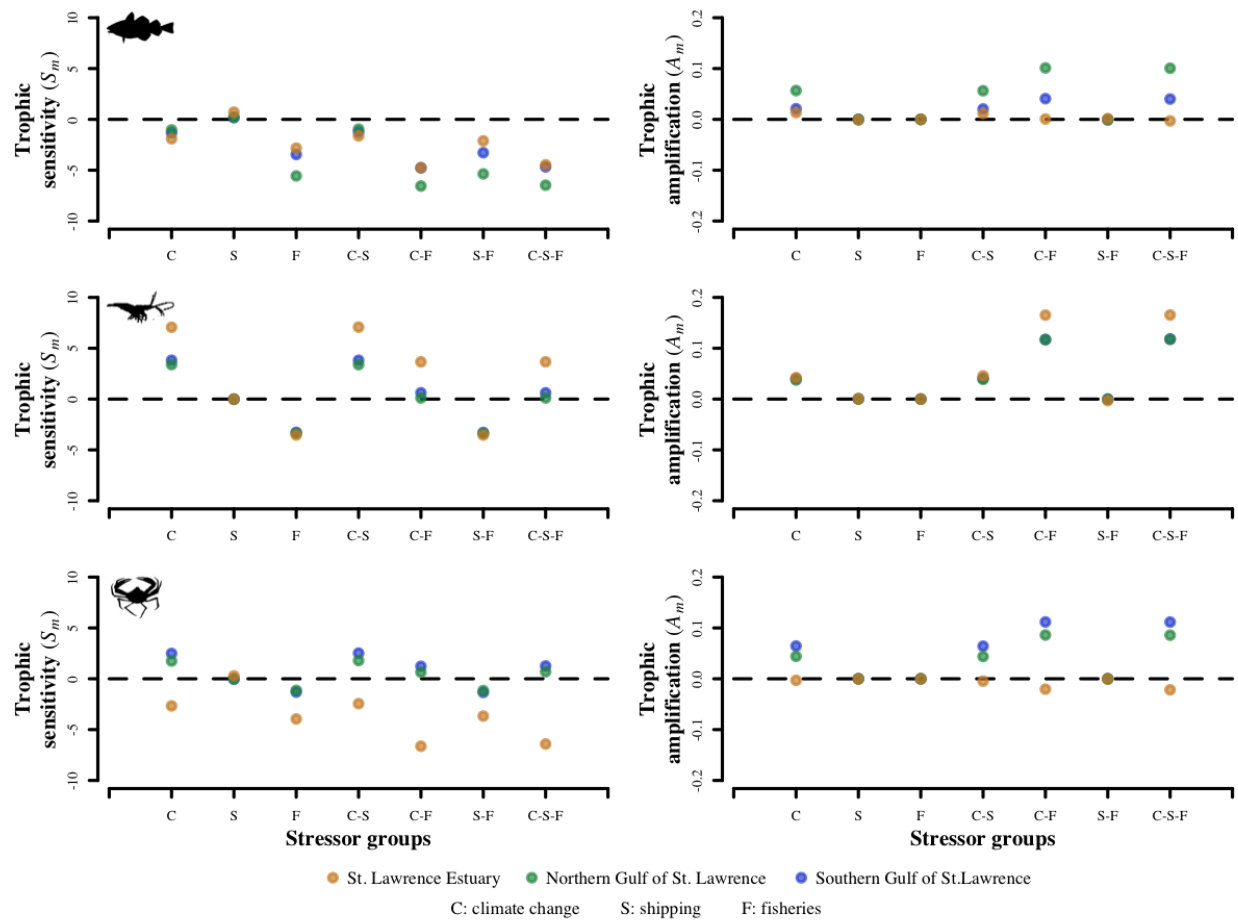


Figure 8

12 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:** the integration of all direct and indirect effects propagating to a focal species in a food web;
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. **(Integrative) 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);~~
8. **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);
9. **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;

- 1336 10. **Trophic variance:** difference between the effective and expected effects of unitary
1337 pathways of effect, *i.e.* the average effect of an integrative pathway of effect; 12-
1338 ~~**Biotic buffer:** species affected antagonistically by an integrative pathway of effect;~~
1339 ~~13. **Biotic amplifier:** species affected synergistically by an integrative pathway of~~
1340 ~~effect;~~
- 1341 11. **Species motif census:** in a food web of n -species, the collection of p -species motifs
1342 ($p \leq n$) in which a species is involved.