

PERSPECTIVE

On the sensitivity of food webs to multiple stressors

David Beauchesne^{1,2}  | Kevin Cazelles³ | Philippe Archambault¹ | Laura E. Dee⁴ | Dominique Gravel⁵¹Département de biologie, ArcticNet, Québec Océan, Université Laval, Québec, QC, Canada²Institut des sciences de la mer, Université du Québec à Rimouski, Rimouski, QC, Canada³Department of Integrative Biology, University Of Guelph, Guelph, ON, Canada⁴Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA⁵Département de biologie, Université de Sherbrooke, Sherbrooke, QC, Canada**Correspondence**David Beauchesne, ArcticNet, Québec Océan, Département de biologie, Université Laval, Av. de la Médecine, bureau 3058, Québec, QC G1V 0A6, Canada.
Email: david.beauchesne@hotmail.com**Funding information**

Fonds de Recherche du Québec - Nature et Technologies; Natural Sciences and Engineering Research Council of Canada

Editor: Tim Wootton**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 conceptualise how stressors propagate through food webs and explore how they affect simulated three-species motifs and food webs of the Canadian St. Lawrence System. We find that overlooking species interactions invariably underestimate 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 and prone to synergistic and antagonistic 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 conceptualising 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.

KEY WORDS

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

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 organisation and disturb whole ecosystems. For example, ocean acidification reduces coral and mollusk calcification, metabolic, growth and mortality rates, and has been linked to altered carbon fluxes in ecological networks (Bove et al., 2019; Fabry et al., 2008; Kroeker et al., 2013).

Fisheries decrease the mean trophic level in coastal and oceanic environments by targeting large predators, impair essential ecosystem services and have induced the collapse of numerous commercial species (Myers & Worm, 2003; Pauly et al., 1998; Worm et al., 2006). Furthermore, stressors rarely occur individually (Halpern et al., 2019). For example, coral reefs face a suite of pressures including fishing, warming temperatures, ocean acidification and water pollution (Harborne et al., 2017; McClanahan et al., 2014). Interactions between stressors are pervasive (e.g. Crain et al., 2008; Piggott et al., 2015; Jackson et al., 2016) and unpredictable (Côté et al., 2016; Darling & Côté, 2008). For instance, the susceptibility of corals to temperature-induced bleaching increases with nutrient enrichment (Lapointe et al., 2019; Wiedenmann et al., 2013), and the sensitivity of certain organisms to toxicants

can be multiplied by a factor of up to 100 when exposed to other stressors (Liess et al., 2016). Multiple stressors can thus interact in complex ways, amplifying or dampening the direct effects of stressors on species.

Beyond their direct effects, stressors ripple through ecological communities by way of the interactions structuring the complex networks in which species are embedded (Bascompte, 2009; Montoya et al., 2009; O’Gorman & Emmerson, 2009; O’Gorman et al., 2012; Wootton, 2002). Because species depend on one another, surprising indirect effects arise from species interactions in complex systems, such as a predator positively affecting its own prey (Abrams, 1992). Ample empirical evidence exists of such trophically mediated indirect effects across ecosystems (Estes et al., 2011; Paine, 1980). Classic examples include sea otters (*Enhydra lutris*) indirectly shielding kelp forests from browsing by sea urchins [*Strongylocentrotus* spp.; Estes and Palmisano (1974)] and fish indirectly favouring the pollination of terrestrial plants by controlling predatory dragonfly populations (Knight et al., 2005). A species’ susceptibility to trophically mediated indirect effects is influenced by its trophic role and position. For example, species with diversified diets are more resilient than species with specialised diets (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 ecological interactions), also influence the propagation of stressors and the stability of whole systems (Bartley et al., 2019; Montoya et al., 2009; O’Gorman et al., 2019; Wootton, 2002). Stressors can modify these structural properties and rewire entire food webs (Bartley et al., 2019; Blanchard, 2015; Kortsch et al., 2015). 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.

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 (De Laender, 2018; Griffen et al., 2016; Jackson et al., 2016;

Schäfer & Piggott, 2018). While these approaches have provided 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 on species embedded in ecological communities 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 multiple stressors and species interactions in ways that are informative to management are urgently needed. Our objective is, thus, to conceptualise and investigate the role of species and their interactions in mediating the effects of multiple stressors through ecological communities. In doing so, we seek to answer questions of particular significance to management: **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 conceptualise 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’ 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 using the motif concepts explored in Stouffer et al., (2007), Stouffer and Bascompte (2010) and Stouffer et al., (2012). 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.

OF FOOD WEBS AND MULTIPLE STRESSORS

Community dynamics

We begin by conceptualising community dynamics with a simplified six-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; Box 1).

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 (Abrams et al., 1996; Wootton, 1993, 2002). 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 (Menge, 1995; Wootton, 1993, 2002; Yodzis, 2000). Trophic cascades, that is, the propagation of effects by consumers downward through whole food webs (e.g. cod–capelin–krill; Figure 1a) and apparent competition, that is, 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).

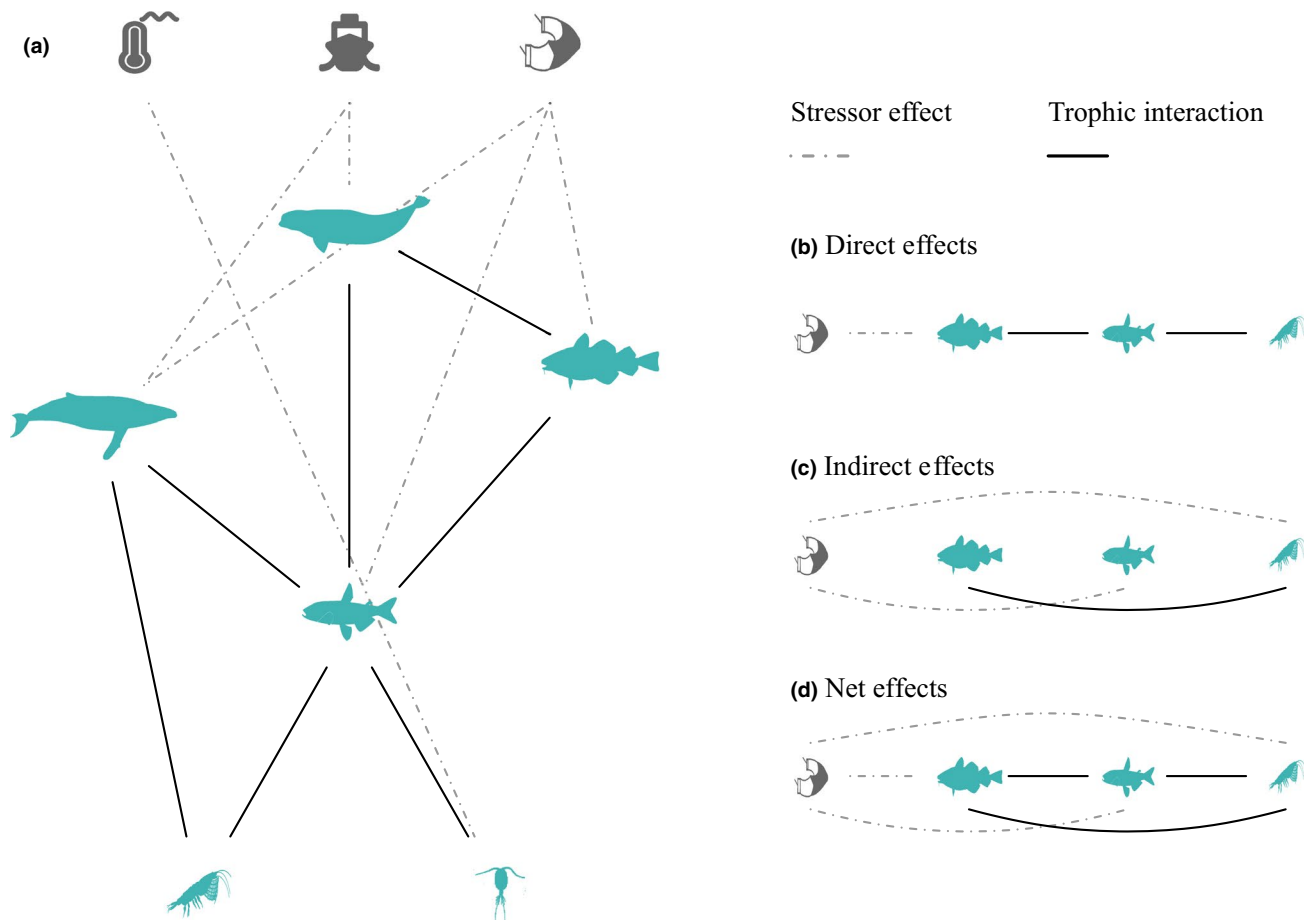


FIGURE 1 (a) Conceptualisation of the effects of multiple stressors on a simplified six-species food web composed of populations of krill (Euphausiacea), copepods (Copepoda), capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*), beluga (*Delphinapterus leucas*) and humpback (*Megaptera novaeangliae*) whales, and affected by climate change-induced temperature anomalies, commercial shipping and trawl fishing. **Direct** (e.g. cod and capelin; (b)) and **indirect** (e.g. cod and krill; (c)) effects arise from species interactions and the integration of both types of effects provides the overall **net effect** (d). 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 (d). Terms in bold are defined in the glossary

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, for example, 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. 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;
10. Trophic variance: difference between the effective and expected effects of unitary pathways of effect, that is, the average effect of an integrative pathway of effect;
11. Species motif census: in a food web of n -species, the collection of p -species motifs ($p \leq n$) in which a species is involved.

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 three 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., 2014). For example, hypoxia can induce a variety of species-specific responses, ranging from adaptation to avoidance to mortality (Belley et al., 2010; Chabot & Claireaux, 2008; Eby et al., 2005; Pillet et al., 2016).

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 form 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, 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). In recognising the importance of net effects in assessing the effect of one species on another, one must also recognise 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 recognised that if density dependence—that is, 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

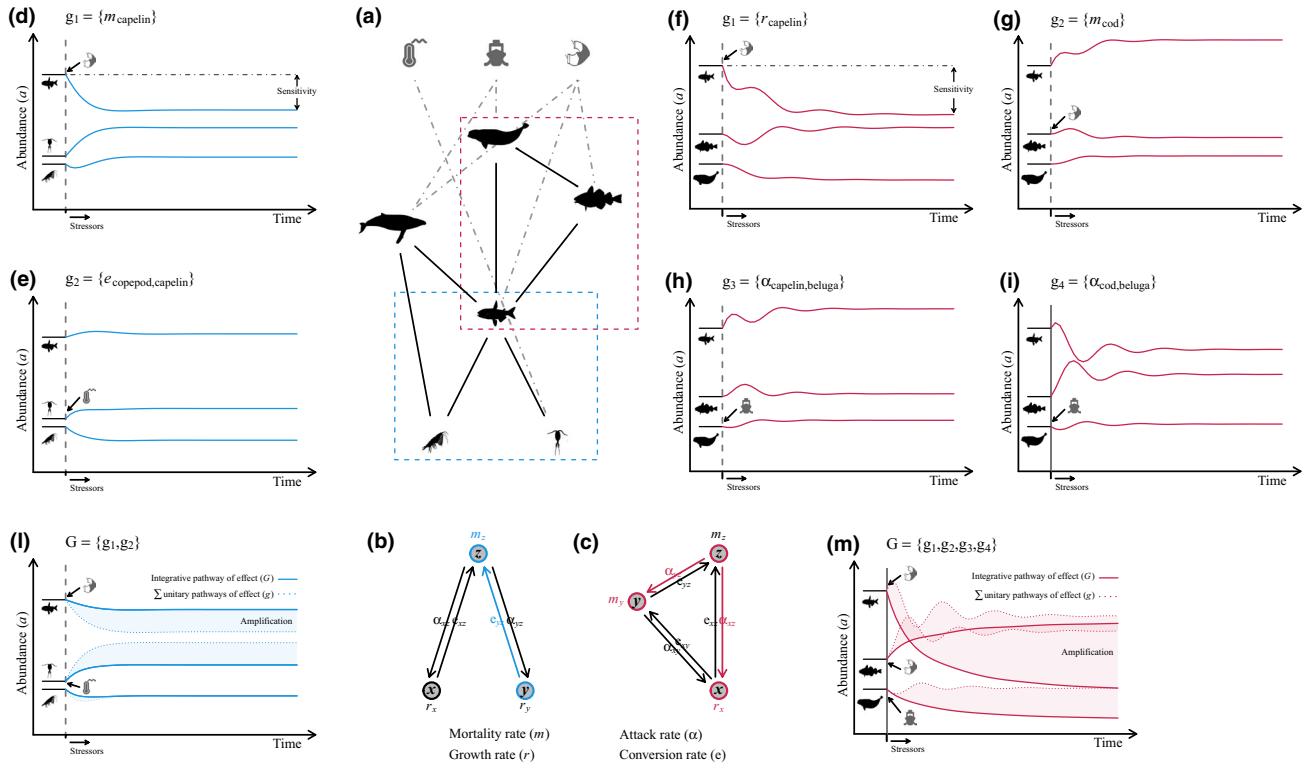


FIGURE 2 (a) Conceptualisation of the effects of multiple stressors on a simplified six-species food web composed of populations of krill (Euphausiacea), copepods (Copepoda), capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*), beluga (*Delphinapterus leucas*) and humpback (*Megaptera novaeangliae*) 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 form 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–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

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, that is, 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.

Evaluating species responses to multiple stressors

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 (Berlow et al., 2004; Montoya et al., 2009; Wootton, 2002). Likewise, we propose to evaluate how pre-stressor species abundances at equilibrium shift after the permanent appearance of stressors in a system—that is, press perturbations—as a measure of their net effect.

Trophic sensitivity

We define a species (m) **trophic sensitivity** ($S_{m,G}$) as the net effect—that is, the variation in equilibrium abundance after the appearance of stressors—resulting from an integrative pathway of effect G (Figure 2d,f):

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

where a_m and $a_{m,G}$ are the pre- and post-stressors abundances of species m respectively. Note that by definition $S_{m,G}$ is bounded negatively to -1 , as species abundances cannot be negative.

Trophic amplification

In multispecies systems, where many direct and indirect trophic effects are operating simultaneously, effects of stressors can be amplified or dampened through biotic interactions (Ives, 1995; Thompson et al., 2018; Wootton, 2002). 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):

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

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.

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 (Montoya et al., 2009; Wootton, 2002). Comparing the effective and expected effects of a unitary pathway of effect—that is, the average effect of an integrative pathway of effect—provides a measure of variance associated with trophic sensitivity to an integrative pathway of effect (G) that we define as **trophic variance** ($V_{m,G}$):

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

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.

HANDLING FOOD WEB COMPLEXITY

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, 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 (Montoya et al., 2009; Wootton, 2002).

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 characterisation of the structural properties of communities (Bascompte & Melián, 2005; Bramon Mora et al., 2018; Stouffer & Bascompte, 2010, 2011; Stouffer et al., 2007). Investigations into three-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 three-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 proposed concepts and metrics, 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 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 the pathway of effect $G = \{r_{capelin}, m_{cod}, \alpha_{capelin,beluga}, \alpha_{cod,beluga}\}$ (Figure 2c). 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 capelin's ability to assimilate them (i.e. conversion rate ($e_{copepods,capelin}$), and fishing affects capelin mortality ($m_{capelin}$); this results in the pathway of effect $G = \{m_{capelin}, e_{copepods,capelin}\}$ (Figure 2b). This pathway of effects reduces the capelin and krill populations and increases the abundance of copepods (Figure 2l).

We see that the effects of unitary pathways of effect may induce contrasting population trajectories. An increase in capelin mortality due to fishing ($g_1 = \{r_{capelin}\}$) favours cod and reduces capelin and beluga abundances (Figure 2f), as cod are likely released from beluga predation [i.e. mesopredator release; Ritchie and Johnson (2009)]; this indirect effect could exacerbate the effect of fishing on capelin by favouring one of its predators. Meanwhile, increasing cod mortality due to fishing ($g_2 = \{m_{cod}\}$) favours 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 and Loreau (2009)]. A similar scenario appears when the attack rates of beluga on capelin ($g_3 = \{\alpha_{capelin,beluga}\}$) are 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, yet shipping likely disrupts the top-down control of beluga on cod to the detriment of capelin (Figure 2i). For the apparent competition, increasing capelin mortality ($g_1 = \{m_{capelin}\}$) decreases capelin abundance and benefits prey species (Figure 2d). Decreasing conversion rates of copepods by capelin ($g_2 = \{e_{copepods,capelin}\}$), meanwhile, transfer some of the predation pressure from copepods to krill to decrease its abundance (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, the net effect of shipping and fishing affects on capelin and beluga synergistically (i.e. positive trophic amplification) and cod antagonistically (i.e. negative trophic amplification; Figure 2m). Through the

apparent competition interaction, effects of fishing and temperature anomalies appear antagonistic for capelin and copepods, and 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 ($V_{krill,G} = 0.10$).

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 (Cirtwill & Stouffer, 2015; Stouffer et al., 2012). 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 three-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 summarise trophic sensitivities (S_m) and amplifications (A_m) across a species motif census (M) by summing motif scale trophic sensitivities and amplifications (Figure 3):

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

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

where G^i is a pathway of effect through motif i . Summarising 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 three-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

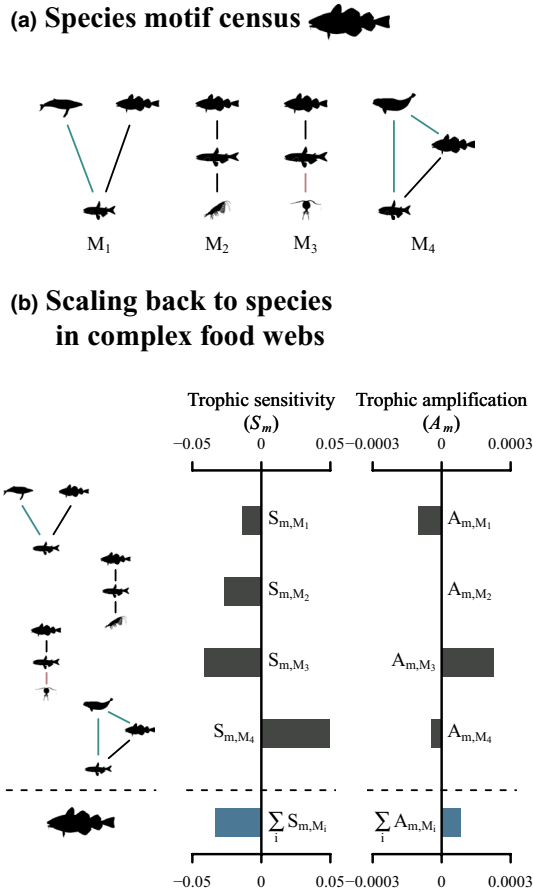


FIGURE 3 (a) A species motif census (M) is composed of all the positions it holds in a food web. (b) A pathway of effect and resulting trophic sensitivities and amplification can be evaluated across a species motif census, the sum of which summarises that species overall trophic sensitivity and amplification. Terms in bold are defined in the glossary

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).

SIMULATING THE EFFECTS OF MULTIPLE STRESSORS ON MOTIFS

In the previous sections, we conceptualised how multiple stressors affect species in the context of food webs, defined metrics to evaluate the net effects of stressors and illustrated how to use motifs to evaluate the expected trophic sensitivity, amplification and variance of species in 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 seven ecological processes and 127 distinct pathways of effect for the tri-trophic food chain, competitive exploitation and apparent competition motifs, and nine 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.

Models and simulations

We used generalised 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 seven pathways of effect. Species dynamics were modelled using equations of the form:

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

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 , that is, the attack rate and e_{ij} is the rate at which the biomass of species i is transformed into biomass of species j biomass, that is, the conversion rate, and is a scaling parameter of the attack rate which cannot exceed 1. We studied the equilibrium dynamics of coexisting species, that is, 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, 2 and 3. 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 trophic sensitivities to all pathways of effect, which would not be possible if species went extinct. 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 approaches 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 constant and negative species-specific responses, and constant density dependence, to control for their effect and focus on the role of species interactions in mediating the effects of stressors. 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 be incorporated and explored in our work.

Effects of stressors on motifs

We observe 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 (Figure 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 (Figure 5, S1). In omnivory and tri-trophic food chain interactions, predators and resources are negatively affected through most pathways of effect; mesopredators in those interactions, meanwhile, largely benefit from the effects of stressors (Figure 5, S1). In exploitative and apparent competition interactions, consumers are either negatively affected or unaffected by stressors, whereas resources are either positively affected 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 cancelling each other out (Figure 6).

Based on knowledge of community stability, our results may appear counterintuitive. 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 parameterisation 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). Therefore, 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 research avenue would be to explore the geometry of the feasibility domain for the different motifs considered (see Song et al., 2018), which is beyond the scope of our study.

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 that predicting whether a species will be affected synergistically or antagonistically by stressors requires precise knowledge of the pathways of effect.

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 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

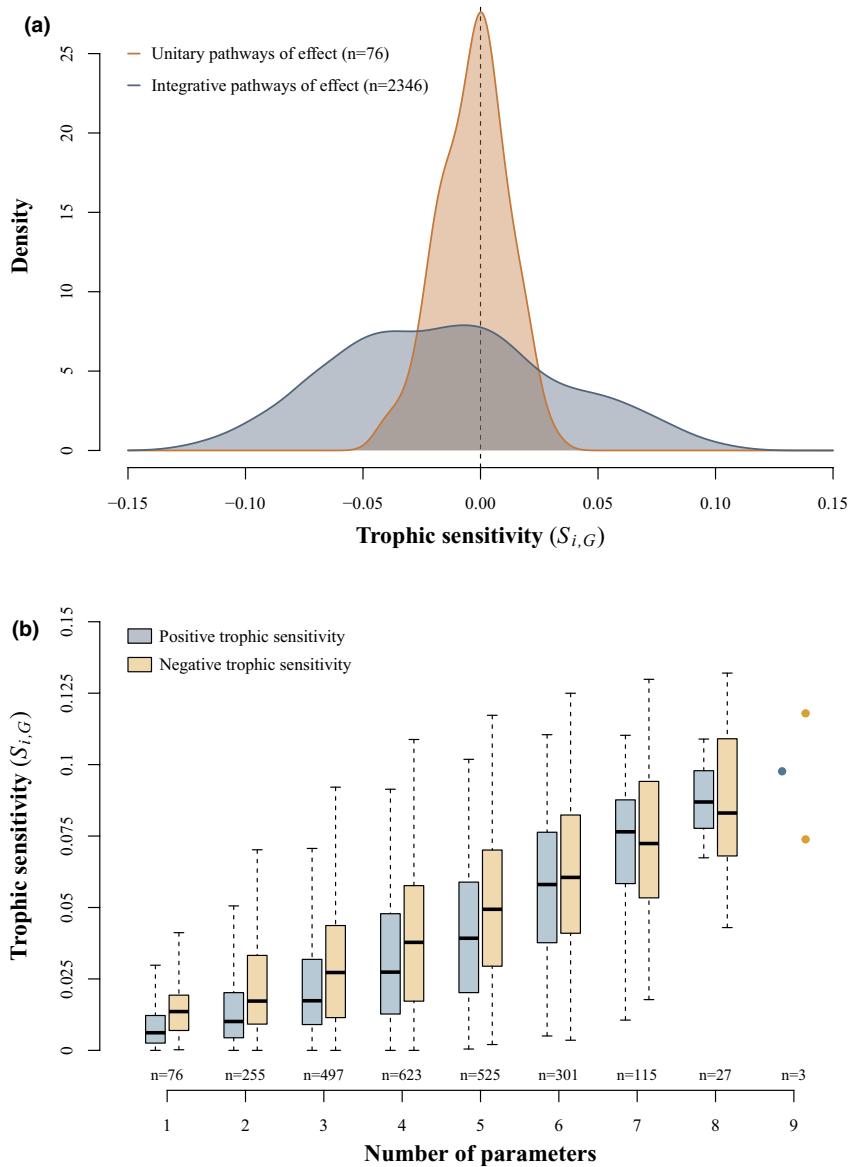


FIGURE 4 (a) Density plot of the trophic sensitivity ($S_{i,G}$) of 14 unique motif positions (i) resulting from all unitary (g ; orange) and integrative (G ; blue) pathways of effect simulated on the dynamics of three-species motifs (i.e. tri-trophic food chain, omnivory, exploitative competition, apparent 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

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 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 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).

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

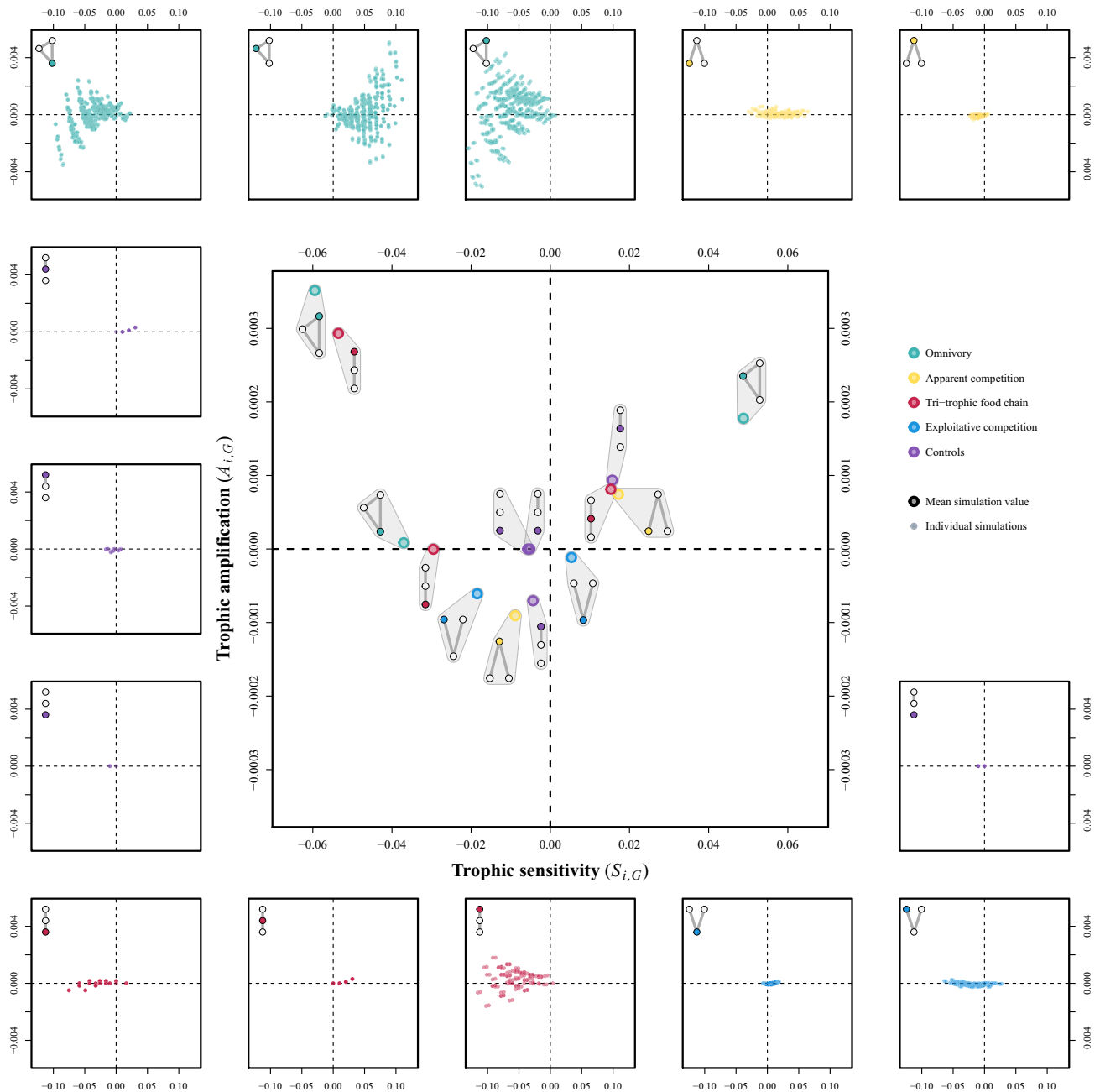


FIGURE 5 The main scatterplot in the centre presents the mean trophic amplification (A_i) as a function of the mean trophic sensitivity (S_i) to all possible pathways of effect (G) for the 14 unique three-species motif positions explored, that is, tri-trophic food chain ($n = 3$; red), omnivory ($n = 3$; 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. Motif positions with positive trophic sensitivities (x -axis) are, on average, positively affected (i.e. increases in abundance) across pathways of effect; conversely, motif positions with negative trophic sensitivities are, on average, negatively affected across pathways of effect. Motif positions with positive trophic amplifications (y -axis) are, on average, synergistically affected across pathways of effect; motif positions with negative trophic amplifications are, on average, antagonistically affected across pathways of effect. The surrounding plots are the results of individual simulations for each motif position, identified in the upper left portion of each scatterplot. The scatterplots have the same axes as the main scatterplot and can be interpreted in the same way

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).

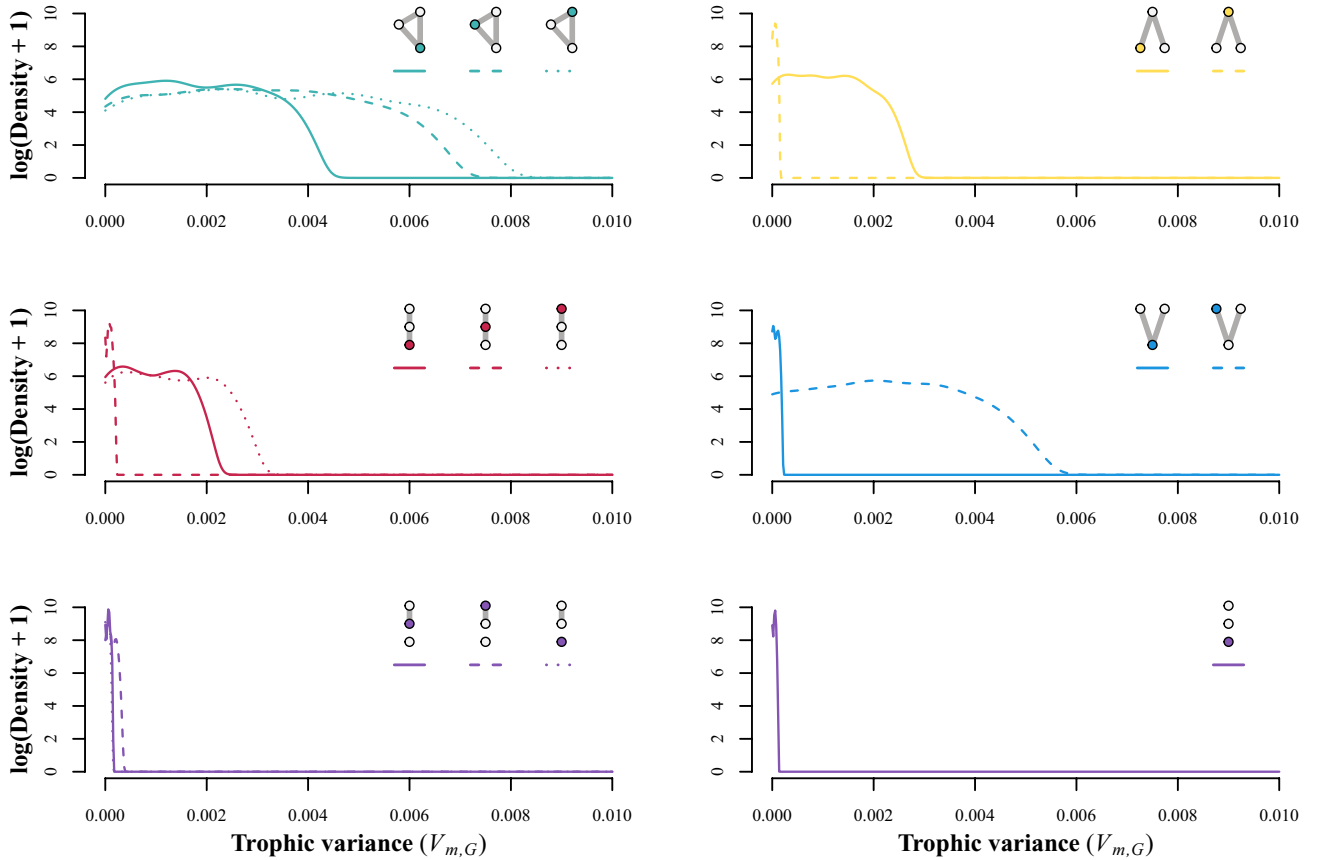
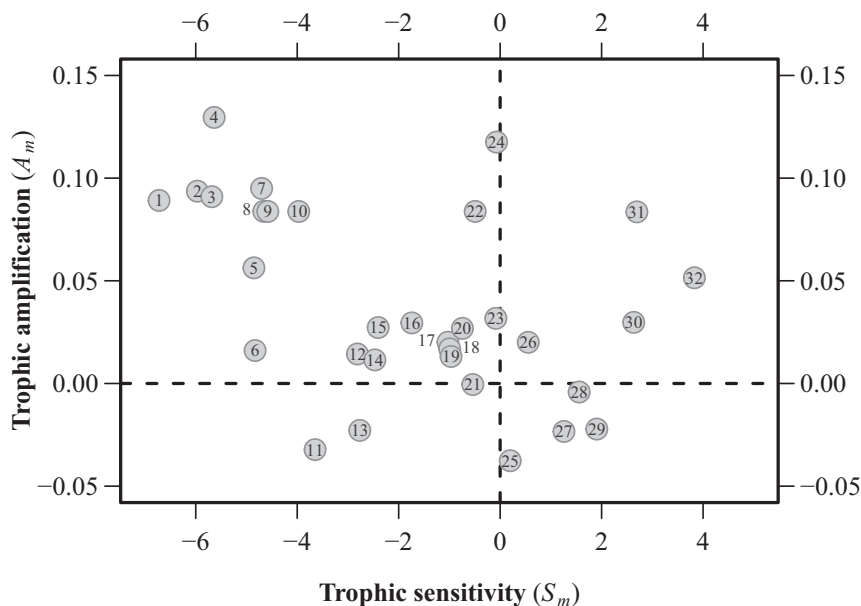


FIGURE 6 Density plots of the trophic variance ($V_{i,G}$) of 14 unique motif positions (i) for all integrative (G ; blue) pathways of effect (G) formed of more than one ecological parameters and simulated on the dynamics of three-species motifs (i.e. tri-trophic food chain, omnivory, exploitative competition,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

We used empirical data on the topology of food webs in three regions of the St. Lawrence: the Northern Gulf [mid-1980s; Morissette et al. (2003)], the Southern Gulf [mid-1980s; Savenkoff et al., (2004)] and the Estuary [early 2000s; Savenkoff (2012)]. We used the topology of the empirical food webs to evaluate the motif census for each species. 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 three-species interactions is not realistic, we used the results from the simulations on theoretical motifs to infer—rather than a modelling approach—a species sensitivity to stressors as a function of its position in a food web. 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.

We summarise 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 (Figure 7, S3). Third, a species sensitivity to the effects of stressors can be driven exclusively by indirect exposure, as 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 affected by stressors; marine mammals and seabirds



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

that were not directly affected by stressors were highly susceptible to the indirect effects of stressors and to non-additive effects (Figure 7, S3).

These observations are expected as apex predators are both preferentially targeted for hunting and fishing, and more vulnerable to trophically mediated effects (Estes *et al.*, 2011; Pauly *et al.*, 1998; 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 (Morissette *et al.*, 2009; Savenkoff *et al.*, 2007) and elsewhere in the Northern Atlantic Ocean (Frank *et al.*, 2005; Worm & Myers, 2003). 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 (Morissette *et al.*, 2009; Savenkoff *et al.*, 2007) 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 (Gavrillchuk *et al.*, 2014; Morissette *et al.*, 2009). 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. Species like cod, shrimp and large crustaceans had variable trophic sensitivities and amplifications between food webs: 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 altered trophic sensitivity and amplification. Fisheries and climate combined 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 Q3 by suggesting that a species sensitivity to stressors is network specific, that is, it will vary with the structure of local food webs and exposure to specific stressors.

THE WAY FORWARD

Here, our objective was to conceptualise 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 evaluate the effects of multiple stressors on food webs.

Scaling from motifs to food webs

One priority is to investigate whether the dynamics of three-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 cancelled or reinforced through food webs (Montoya et al., 2009; Wootton, 2002) and is currently the most parsimonious approach. Still, it remains unclear whether motif dynamics scale up linearly to dynamics of whole food webs, although some evidence suggests it might be the case (Rip et al., 2010; e.g. Stouffer & Bascompte, 2010). Further investigations are warranted to explore whether a species' trophic sensitivity and amplification scales linearly with trophic sensitivities across its motif census. It is nonetheless worth stressing that, at the motif scale, the metrics we developed consider nonlinear dynamics and non-additive effects resulting from the effects of multiple stressors.

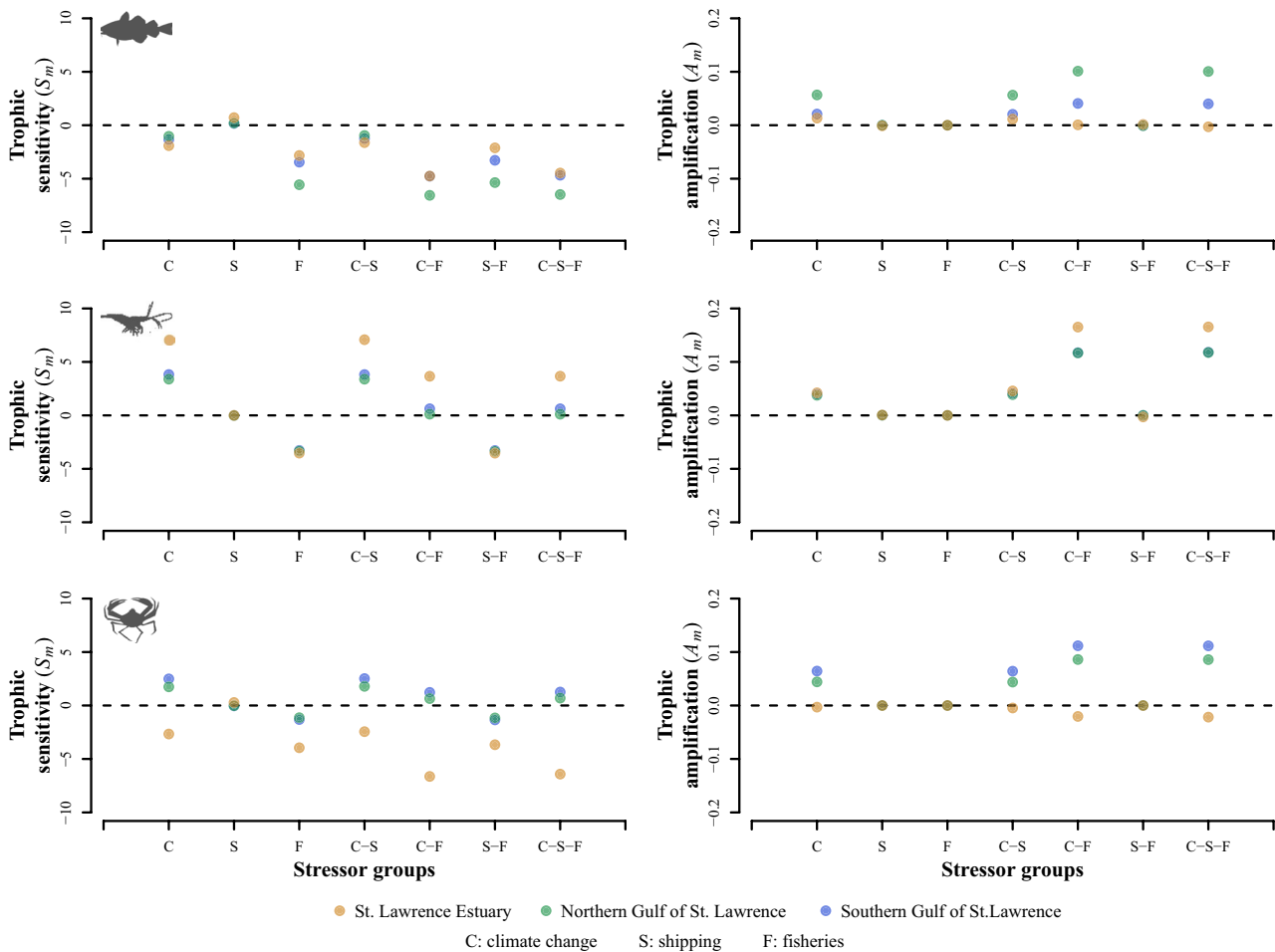


FIGURE 8 Comparison of the trophic sensitivities (S_m) and amplifications (A_m) to the effects of different groups of stressors (Figure 7) for Atlantic cod (*Gadus morhua*), shrimp (*Pandalus borealis*) and large crustaceans (*Crustacea*) between the food webs of the Southern and Northern Gulf of St.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

Density dependence and interaction strength

To focus on trophically mediated indirect effects, we 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). Targeting density dependence parameters to explore their influence on the magnitude of indirect effects would provide valuable insights for species whose dynamics is driven by density dependence. Similarly, although we simulated the effects of stressors on conversion and attack rates, we did not explicitly explore the role of interaction strength in mediating the effects of stressors. The importance of interaction strengths is well documented in the literature, and 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). 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 strengths (e.g. weak, medium, strong) influence the net effects of stressors.

Considering species-specific sensitivity to stressors

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 a species life span, and stressors may travel through different pathways of effect throughout a species life stages. 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 allow us to assess the relative contribution of the direct and indirect effects of multiple stressors to their overall net effects.

CONCLUSIONS

In conceptualising the effects of stressors on food webs, we sought to tackle the challenge of incorporating the

complexities of real-world systems to cumulative effects assessments and answer questions of particular significance for environmental management. We found that species interactions should be considered to avoid underestimating the net effect of stressors (Q1), that the effects of multiple stressors on populations should be assessed jointly at the scale of ecological communities to properly consider non-additive effects (Q2) and that species most sensitive to stressors are apex predators, who tend to be negatively affected by stressors, and mesopredators, who tend to benefit from the effects of stressors (Q3). However, a species’ 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, but also on indirect effects and the structure of communities. Our results suggest that environmental impact assessments, even if focused on single species or single stressors, should consider the complexities of ecological communities and the specific pathways of effect through which stressors penetrate communities. 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 and providing evidence for the conservation of ecological communities and the application of holistic environmental approaches [e.g. McCann (2007); Tylanakis et al., (2008); tylianakis2010; O’Gorman et al., (2012); Kaiser-Bunbury and Blüthgen (2015); Harvey et al., (2017); Dee et al., (2017); Thompson et al., (2018)].

Adopting holistic environmental approaches and scaling management to complex ecological communities will necessitate a paradigm shift towards whole systems rather than piecemeal management. 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—that is, increasing the number of populations monitored—and resolution—that is, from species to populations to individuals—of the biological data used for management. While monitoring whole systems may be deemed unrealistic, environmental monitoring initiatives and emerging technologies already in place could assist this paradigm shift. Knowledge on the distribution and intensity of stressors (e.g. Halpern et al., 2015; Beauchesne et al., 2020), species occurrences (e.g. GBIF, 2020; OBIS 2020), interactions (e.g. Poelen et al., 2014; Poisot et al., 2016) and abiotic data (e.g. Assis et al., 2018) are openly available, and their quality and robustness is improving owing to relentless methodological and technological advancements (e.g. functional traits, environmental DNA, artificial intelligence). We believe that combining sound theory with exhaustive ecological data-based knowledge through robust inference will

lead to management that considers the complexities of ecosystems and decision-making that provides solutions tailored to management areas characterised by unique ecological dynamics and socioeconomic realities.

ACKNOWLEDGEMENTS

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

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.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13841>.

DATA AVAILABILITY STATEMENT

The code to replicate this study is available from Zenodo, <https://doi.org/10.5281/zenodo.5014237>. 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).

ORCID

David Beauchesne  <https://orcid.org/0000-0002-3590-8161>

REFERENCES

- Abrams, P.A. (1992) Predators that benefit prey and prey that harm predators: Unusual effects of interacting foraging adaptation. *The American Naturalist*, 140, 573–600.
- Abrams, P.A., Menge, B.A., Mittelbach, G.G., Spiller, D.A. & Yodzis, P. (1996) The role of indirect effects in food webs. In: Polis, G.A. & Winemiller, K.O. (Eds.) *Food webs: Integration of patterns & dynamics*. Boston, MA: Springer US, pp. 371–395.
- Allesina, S., Bodini, A. & Bondavalli, C. (2006) Secondary extinctions in ecological networks: Bottlenecks unveiled. *Ecological Modelling, Special issue on the Fourth European Conference on Ecological Modelling*, 194, 150–161.
- Archambault, P., Schloss, I.R., Grant, C. & Plante, S. (Eds) (2017) Les hydrocarbures dans le golfe du Saint-Laurent - Enjeux sociaux, économiques et environnementaux. Notre Golfe, Rimouski, Qc, Canada.
- Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O. et al. (2018) Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, 27, 277–284.
- Ban, N.C., Alidina, H.M. & Ardron, J.A. (2010) Cumulative impact mapping: Advances, relevance and limitations to marine management and conservation, using Canada's Pacific waters as a case study. *Marine Policy*, 34, 876–886.
- Bartley, T.J., McCann, K.S., Bieg, C., Cazelles, K., Granados, M., Guzzo, M.M. et al. (2019) Food web rewiring in a changing world. *Nature Ecology & Evolution*, 3, 345–354.
- Bascompte, J. (2009) Disentangling the web of life. *Science*, 325, 416–419.
- Bascompte, J. & Melián, C.J. (2005) Simple trophic modules for complex food webs. *Ecology*, 86, 2868–2873.
- Beauchesne, D., Daigle, R.M., Vissault, S., Gravel, D., Bastien, A., Bélanger, S. et al. (2020) Characterizing exposure to and sharing knowledge of drivers of environmental change in the St. Lawrence system in Canada. *Frontiers in Marine Science*, 7, 383.
- 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.O., 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., 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, 59.
- 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.

- 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*, 9, 222–228.
- Côté, I.M., Darling, E.S. & Brown, C.J. (2016) Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20152592.
- Crain, C.M., Kroeker, K. & Halpern, B.S. (2008) Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, 11, 1304–1315.
- Darling, E.S. & Côté, I.M. (2008) Quantifying the evidence for ecological synergies. *Ecology Letters*, 11, 1278–1286.
- David, P., Thébault, E., Anneville, O., Duyck, P.-F., Chapuis, E. & Loeuille, N. (2017) Chapter one - impacts of invasive species on food webs: A review of empirical data. In: Bohan, D.A., Dumbrell, A.J. & Massol, F. (Eds.), *Advances in Ecological Research, Networks of Invasion: A Synthesis of Concepts*. Oxford; London; Cambridge, MA; San Diego, CA: Academic Press, Elsevier, pp. 1–60.
- De Laender, F. (2018) Community- and ecosystem-level effects of multiple environmental change drivers: beyond null model testing. *Global change biology*, 24, 5021–5030.
- Dee, L.E., Allesina, S., Bonn, A., Eklöf, A., Gaines, S.D., Hines, J. et al. (2017) Operationalizing network theory for ecosystem service assessments. *Trends in Ecology & Evolution*, 32, 118–130.
- Dee, L.E., Okamoto, D., Gårdmark, A., Montoya, J.M. & Miller, S.J. (2020) Temperature variability alters the stability and thresholds for collapse of interacting species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1814), 20190457–<https://doi.org/10.1098/rstb.2019.0457>.
- Dempsey, D.P., Gentleman, W.C., Pepin, P. & Koen-Alonso, M. (2018) Explanatory power of human and environmental pressures on the fish community of the grand bank before and after the biomass collapse. *Frontiers in Marine Science*, 5, 37.
- 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*. New York, NY: Springer.
- 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.
- Gavrillchuk, 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.
- GBIF (2020) GBIF: The Global Biodiversity Information Facility (2020) What is GBIF?. Available from <https://www.gbif.org/what-is-gbif> Accessed 2020-07-20.
- Gellner, G. & McCann, K.S. (2016) Consistent role of weak and strong interactions in high- and low-diversity trophic food webs. *Nature Communications*, 7, 11180.
- Gonzalez, A. & Loreau, M. (2009) The causes and consequences of compensatory dynamics in ecological communities. *Annual Review of Ecology, Evolution, and Systematics*, 40, 393–414.
- Griffen, B.D., Belgrad, B.A., Cannizzo, Z.J., Knotts, E.R. & Hancock, E.R. (2016) Rethinking our approach to multiple stressor studies in marine environments. *Marine Ecology Progress Series*, 543, 273–281.
- Guiden, P.W., Bartel, S.L., Byer, N.W., Shipley, A.A. & Orrock, J.L. (2019) Predator in the Anthropocene: Reconciling multiple aspects of novelty. *Trends in Ecology & Evolution*, 34, 616–627.
- Halpern, B.S., Frazier, M., Afflerbach, J., Lowndes, J.S., Micheli, F., O'Hara, C. et al. (2019) Recent pace of change in human impact on the world's ocean. *Scientific Reports*, 9, 11609.
- Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C. et al. (2015) Cumulative human impacts: Raw stressor data (2008 and 2013). Knowledge Network for Biocomplexity.
- Harborne, A.R., Rogers, A., Bozec, Y.-M. & Mumby, P.J. (2017) Multiple stressors and the functioning of coral reefs. *Annual Review of Marine Science*, 9, 445–468.
- Harvey, E., Gounand, I., Ward, C.L. & Altermatt, F. (2017) Bridging ecology and conservation: From ecological networks to ecosystem function. *Journal of Applied Ecology*, 54, 371–379.
- Hodgson, E.E., Essington, T.E. & Halpern, B.S. (2017) Density dependence governs when population responses to multiple stressors are magnified or mitigated. *Ecology*, 98, 2673–2683.
- Hodgson, E.E. & Halpern, B.S. (2019) Investigating cumulative effects across ecological scales. *Conservation Biology*, 33, 22–32.
- Hodgson, E.E., Halpern, B.S. & Essington, T.E. (2019) Moving beyond silos in cumulative effects assessment. *Frontiers in Ecology and Evolution*, 7, 211.
- Holt, R.D. (1977) Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, 12, 197–229.
- Holt, R.D. (1997) Community modules. In: Grange, A.C. & Brown, V.K. (Eds.) *Multitrophic interactions in terrestrial ecosystems, 36th symposium of the british ecological society*. Oxford: Blackwell Science, pp. 333–349.
- Holt, R.D. & Hochberg, M.E. (2001) Indirect interactions, community modules and biological control: a theoretical perspective. In: Wajnberg, E., Scott, J.K., Quimby, P.C. (Eds.), *Evaluating indirect ecological effects of biological control. Key papers from the symposium "Indirect ecological effects in biological control", Montpellier, France, 17-20 October 1999*. Wallingford: CAB International, pp. 13–37. <https://doi.org/10.1079/9780851994536.0000>
- Ives, A.R. (1995) Measuring resilience in stochastic systems. *Ecological Monographs*, 65, 217–233.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J. et al. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629–637.
- Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D. & Chimimba, C.T. (2016) Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology*, 22, 180–189.
- Kaiser-Bunbury, C.N. & Blüthgen, N. (2015) Integrating network ecology with applied conservation: a synthesis and guide to implementation. *AoB PLANTS*, 7, plv076.
- Klaise, J. & Johnson, S. (2017) The origin of motif families in food webs. *Scientific Reports*, 7, 16197.
- Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A. & Holt, R.D. (2005) Trophic cascades across ecosystems. *Nature*, 437, 880–883.
- Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A.V. & Aschan, M. (2015) Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151546.

- Kroeker, K.J., Kordas, R.L., Crim, R., Hendriks, I.E., Ramajo, L., Singh, G.S. et al. (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology*, 19, 1884–1896.
- Lange, R. & Marshall, D. (2017) Ecologically relevant levels of multiple, common marine stressors suggest antagonistic effects. *Scientific Reports*, 7, 6281.
- Lapointe, B.E., Brewton, R.A., Herren, L.W., Porter, J.W. & Hu, C. (2019) Nitrogen enrichment, altered stoichiometry, and coral reef decline at Looe Key, Florida Keys, USA: A 3-decade study. *Marine Biology*, 166, 108.
- Liess, M., Foit, K., Knillmann, S., Schäfer, R.B. & Liess, H.-D. (2016) Predicting the synergy of multiple stress effects. *Scientific Reports*, 6, 32965.
- Lindmark, M., Ohlberger, J., Huss, M. & Gårdmark, A. (2019) Size-based ecological interactions drive food web responses to climate warming. *Ecology Letters*, 22, 778–786.
- McCann, K. (2007) Protecting biostructure. *Nature*, 446, 29.
- McCann, K., Hastings, A. & Huxel, G.R. (1998) Weak trophic interactions and the balance of nature. *Nature*, 395, 794.
- McClanahan, T.R., Graham, N.A. & Darling, E.S. (2014) Coral reefs in a crystal ball: predicting the future from the vulnerability of corals and reef fishes to multiple stressors. *Current Opinion in Environmental Sustainability, Environmental Change Issues*, 7, 59–64.
- Menge, B.A. (1995) Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. *Ecological Monographs*, 65, 21–74.
- Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D. & Alon, U. (2002) Network motifs: Simple building blocks of complex networks. *Science*, 298, 824–827.
- Monteiro, A.B. & Faria, L.D.B. (2016) The interplay between population stability and food-web topology predicts the occurrence of motifs in complex food-webs. *Journal of Theoretical Biology*, 409, 165–171.
- Montoya, J., Woodward, G., Emmerson, M.C. & Solé, R.V. (2009) Press perturbations and indirect effects in real food webs. *Ecology*, 90, 2426–2433.
- Morissette, L., Castonguay, M., Savenkoff, C., Swain, D.P., Chabot, D., Bourdages, H. et al. (2009) Contrasting changes between the northern and southern Gulf of St. Lawrence ecosystems associated with the collapse of groundfish stocks. *Deep Sea Research Part II: Topical Studies in Oceanography*, 56, 2117–2131.
- Morissette, L., Despatie, S.-P., Savenkoff, C., Hammill, M.O., Bourdages, H. & Chabot, D. (2003). Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980 s). *Can. Tech. Rep. Fish. Aquat. Sci./Rapp. Tech. Can. Sci. Halieut. Aquat.*, 100.
- Myers, R.A. & Worm, B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature*, 423, 280.
- O'Brien, A.L., Dafforn, K.A., Chariton, A.A., Johnston, E.L. & Mayer-Pinto, M. (2019) After decades of stressor research in urban estuarine ecosystems the focus is still on single stressors: A systematic literature review and meta-analysis. *Science of The Total Environment*, 684, 753–764. <https://doi.org/10.1016/j.scitotenv.2019.02.131>.
- O'Gorman, E.J. & Emmerson, M.C. (2009) Perturbations to trophic interactions and the stability of complex food webs. *Proceedings of the National Academy of Sciences*, 106, 13393–13398.
- O'Gorman, E.J., Fitch, J.E. & Crowe, T.P. (2012) Multiple anthropogenic stressors and the structural properties of food webs. *Ecology*, 93, 441–448.
- O'Gorman, E.J., Petchey, O.L., Faulkner, K.J., Gallo, B., Gordon, T.A.C., Neto-Cerejeira, J. et al. (2019) A simple model predicts how warming simplifies wild food webs. *Nature Climate Change*, 9, 611–616.
- OBIS (2020). Ocean Biogeographic Information System. Intergovernmental Oceanographic Commission of UNESCO. www.iobis.org. Accessed 2020-07-27.
- Oppenheimer, M., Campos, M., Warren, R., Birkmann, J., Luber, G., O'Neill, B. et al. (2015) Emergent risks and key vulnerabilities. In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R. & White, L.L. (Eds.), *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge; New York, NY: Cambridge University Press, pp. 1039–1099.
- Orr, J.A., Vinebrooke, R.D., Jackson, M.C., Kroeker, K.J., Kordas, R.L., Mantyka-Pringle, C. et al. (2020) Towards a unified study of multiple stressors: Divisions and common goals across research disciplines. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20200421.
- Otto, S.A., Niiranen, S., Blenckner, T., Tomczak, M.T., Müller-Karulis, B., Rubene, G. et al. (2020) Life cycle dynamics of a key marine species under multiple stressors. *Frontiers in Marine Science*, 7, 296.
- Paine, R.T. (1980) Food webs: Linkage, interaction strength and community infrastructure. *Journal of Animal Ecology*, 49, 667–685.
- Paine, R.T. (1992) Food-web analysis through field measurement of per capita interaction strength. *Nature*, 355, 73.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998) Fishing down marine food webs. *Science*, 279, 860–863.
- Piggott, J.J., Townsend, C.R. & Matthaei, C.D. (2015) Reconceptualizing synergism and antagonism among multiple stressors. *Ecology and Evolution*, 5, 1538–1547.
- Pillet, M., Dupont-Prinet, A., Chabot, D., Tremblay, R. & Audet, C. (2016) Effects of exposure to hypoxia on metabolic pathways in northern shrimp (*Pandalus borealis*) and Greenland halibut (*Reinhardtius hippoglossoides*). *Journal of Experimental Marine Biology and Ecology*, 483, 88–96.
- Poelen, J.H., Simons, J.D. & Mungall, C.J. (2014) Global biotic interactions: An open infrastructure to share and analyze species-interaction datasets. *Ecological Informatics*, 24, 148–159.
- Poisot, T., Baiser, B., Dunne, J.A., Kéfi, S., Massol, F., Mouquet, N. et al. (2016) Mangal making ecological network analysis simple. *Ecography*, 39, 384–390.
- RCoreTeam (2019) R: A Language and Environment for Statistical Computing.
- Rip, J.M.K., McCann, K.S., Lynn, D.H. & Fawcett, S. (2010) An experimental test of a fundamental food web motif. *Proceedings of the Royal Society B: Biological Sciences*, 277, 1743–1749.
- Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M. et al. (2015) Collapse of the world's largest herbivores. *Science Advances*, 1, e1400103.
- Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12, 982–998.
- Savenkoff, C. (2012). Input data and parameter estimates for ecosystem models of the lower St. Lawrence Estuary (2008). Canadian Technical Report of Fisheries and Aquatic Sciences 2999, Department of Fisheries and Oceans, Mont-Joli, Québec, Canada.
- Savenkoff, C., Bourdages, H., Swain, D.P., Despatie, S.-P., Hanson, J.M., Méthot, R. et al. (2004) Input data and parameter estimates for ecosystem models of the southern Gulf of St. Lawrence (mid-1980s and mid-1990s). Canadian Technical Report of Fisheries and Aquatic Sciences 2529, Department of Fisheries and Oceans, Mont-Joli, Québec, Canada.
- Savenkoff, C., Swain, D.P., Hanson, J.M., Castonguay, M., Hammill, M.O., Bourdages, H. et al. (2007) Effects of fishing and predation in a heavily exploited ecosystem: Comparing periods before and after the collapse of groundfish in the southern Gulf of St. Lawrence (Canada). *Ecological Modelling*, 204, 115–128.

- Savenkoff, C., Vézina, A.f., Roy, S., Klein, B., Lovejoy, C., Therriault, J.-C. et al. (2000) Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part I. Seasonal variations. *Deep Sea Research Part II: Topical Studies in Oceanography*, 47, 585–607.
- Schäfer, R.B. & Piggott, J.J. (2018) Advancing understanding and prediction in multiple stressor research through a mechanistic basis for null models. *Global Change Biology*, 24, 1817–1826.
- Schloss, I.R., Archambault, P., Beauchesne, D., Cusson, M., Ferreyra, G., Levasseur, M. et al. (2017). Cumulative potential impacts of the stress factors associated with human activities on the St. Lawrence marine ecosystem. In: *Hydrocarbon in the Gulf of St. Lawrence - Social, economic and environmental issues*. Archambault, P., Schloss, I.R., Grant, C. & Plante, S. (eds). Notre Golfe, Rimouski, Qc, Canada, pp. 133–165.
- Song, C., Rohr, R.P. & Saavedra, S. (2018) A guideline to study the feasibility domain of multi-trophic and changing ecological communities. *Journal of Theoretical Biology*, 450, 30–36.
- Stier, A.C., Samhoury, J.F., Novak, M., Marshall, K.N., Ward, E.J., Holt, R.D. et al. (2016) Ecosystem context and historical contingency in apex predator recoveries. *Science Advances*, 2, e1501769.
- Stouffer, D.B. & Bascompte, J. (2010) Understanding food-web persistence from local to global scales. *Ecology Letters*, 13, 154–161.
- Stouffer, D.B. & Bascompte, J. (2011) Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences*, 108, 3648–3652.
- Stouffer, D.B., Camacho, J., Jiang, W. & Nunes Amaral, L.A. (2007) Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1931–1940.
- Stouffer, D.B., Sales-Pardo, M., Sirer, M.I. & Bascompte, J. (2012) Evolutionary conservation of species' roles in food webs. *Science*, 335, 1489–1492.
- TheSageDevelopers, (2019). SageMath, the Sage Mathematics Software System Version 8.8.
- Thompson, P.L., MacLennan, M.M. & Vinebrooke, R.D. (2018) Species interactions cause non-additive effects of multiple environmental stressors on communities. *Ecosphere*, 9, e02518.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11, 1351–1363.
- Vander Zanden, M.J., Casselman, J.M. & Rasmussen, J.B. (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, 401, 464–467.
- Wiedenmann, J., D'Angelo, C., Smith, E.G., Hunt, A.N., Legiret, F.-E., Postle, A.D. et al. (2013) Nutrient enrichment can increase the susceptibility of reef corals to bleaching. *Nature Climate Change*, 3, 160–164.
- Wittmer, H.U., Elbroch, L.M. & Marshall, A.J. (2013) Good intentions gone wrong: Did conservation management threaten Endangered huemul deer *Hippocamelus bisulcus* in the future Patagonia National Park? *Oryx*, 47, 393–402.
- Wootton, J.T. (1993) Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. *The American Naturalist*, 141, 71–89.
- Wootton, J.T. (2002) Indirect effects in complex ecosystems: Recent progress and future challenges. *Journal of Sea Research, Structuring Factors of Shallow Marine Coastal Communities, part I*, 48, 157–172.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S. et al. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314, 787–790.
- Worm, B. & Myers, R.A. (2003) Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology*, 84, 162–173.
- Yodzis, P. (2000) Diffuse effects in food webs. *Ecology*, 81, 261–266.

How to cite this article: Beauchesne, D., Cazelles, K., Archambault, P., Dee, L.E. & Gravel, D. (2021) On the sensitivity of food webs to multiple stressors. *Ecology Letters*, 00, 1 – 19. <https://doi.org/10.1111/ele.13841>