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Quantifying the effects of sensory stress on trophic cascades

Gabriel Ng[1,2] · Marissa L. Baskett[3] · Brian Gaylord[1,4]

Abstract

Predators mediate the strength of trophic cascades indirectly by decreasing the number of prey consuming a basal resource and by altering prey responses that dictate prey foraging. The strength of these indirect effects further depends on abiotic factors. For example, attributes of the environment, such as turbulent flows in aquatic habitats that disrupt spatial information available from chemical cues, can impose "sensory stresses" that impair the ability of predators or prey to detect each other. The multi-faceted impacts of sensory stress on both the predators and prey create challenges in predicting the overall effect on the trophic cascade. Here, we explore how sensory stress affects the strength of trophic cascades using a tri-trophic dynamical model that incorporates the sensory environment and anti-predatory responses. We explore two crucial parameters that govern outcomes of the model. First, we allow predation rates to either strengthen or weaken depending on whether prey or predators are more sensitive to sensory stress, respectively. Second, we explore scenarios where anti-predatory responses can either drive a strong or weak reduction in prey foraging. We find that sensory stress usually weakens trophic cascades except in scenarios where predators are relatively unaffected by sensory stress and the loss of anti-predatory responses does not affect prey foraging. The model finally suggests that "hydra effects" can manifest, whereby an increase in prey population occurs despite an increase in per capita predation. This last feature emerges due to the interaction between logistic growth of the basal resource and anti-predatory responses reducing the over-consumption of the basal resource.

Keywords Trophic cascade · Density-mediated indirect interactions · Trait-mediated indirect interactions · Sensory stress · Population model

Introduction

Trophic cascades, a foundational aspect of predator–prey interactions, play a key role in the abundance and distribution of basal resources (Hairston et al. 1960, Carpenter et al. 1985, Estes and Duggin 1995, Bonaviri et al. 2017). Trophic cascades are the indirect consequences on a basal resource resulting from higher-order consumers, which include both predators and parasites, consuming prey and from consumers altering prey foraging rates. The former is termed a density-mediated indirect interaction (DMII) because it arises from a reduction in prey density. In contrast, the latter is a trait-mediated indirect interaction (TMII), as the reduction in prey foraging arises from higher-order consumers inducing a change in one or more prey attributes (Peacor and Werner 1997). Usually, the prey traits that respond to predators are ones with anti-predatory utility. For example, the presence of predators can activate behavioral fear responses, such as fleeing or hiding (Schmitz et al. 1997; Trussell et al. 2003; Ripple and Beschta 2012), inducible morphological changes that provide increased protection for prey (Harvell 1990; Trussell and Nicklin 2002; Matassa and Trussell 2011; Lord et al. 2019), or physiological changes that decrease the vulnerability of prey to predators (Relyea 2007; Hay 2009; Donelan and Trussell 2018). Actuation of such anti-predatory responses can alter the ability of prey to acquire their own food, the basal resource. While arising from different mechanisms, both DMIIs and TMIIs play a substantial role in trophic cascades (Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005).

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The presence and strength of trophic cascades vary substantially between studies (Strong 1992; Shurin et al. 2002; Borer et al. 2005) and are highly dependent on environmental conditions intrinsic to tri-trophic systems. For example, strong abiotic stressors like wave action and thermal stress can operate with disproportionate effect on top consumers to alter the magnitude and relevance of predation (Menge 1978; Menge and Sutherland 1987; Menge et al. 1994; Bonaviri et al. 2017). The strength of TMIIs can also depend on the hunger state of prey and thus their propensity to forage even in the presence of predators (Lima and Bednekoff 1999; Matassa and Trussell 2014; Gravem and Morgan 2016).

One relatively understudied category of environmental factors that if understood more clearly can better predict the behavior of trophic cascades is sensory stressors. Sensory stressors are habitat attributes that hinder the ability of predator and prey to acquire information and make it harder for either, or both, species to detect the other (Ferner et al. 2009; Pruett and Weissburg 2018). Not only can such factors reduce predation outright and therefore DMIIs, but they can also influence the fear response in prey, which affects both a prey's vulnerability to predation and consequent TMIIs (Weissburg et al. 2014). Fluid turbulence, for instance, can disrupt a waterborne chemical plume, degrading the ability of prey to respond to cue molecules emitted by a predator (Weissburg and Zimmer-Faust 1994; Smee and Weissburg 2006). Such decreases in sensory ability under stressful conditions can also apply to predators, in particular those that must search for prey using chemical gradients, in both aquatic (Weissburg and Zimmer-Faust 1994; Robinson et al. 2011, Fagan et al. 2022) and terrestrial environments (Wyatt et al. 1993). For example, low or varying intensities of light can degrade predation success in organisms that rely on visual information (Clarke et al. 1996; Meager et al. 2005, 2006; Strod et al. 2008). More broadly, anthropogenic disturbances impair a range of sensory pathways (Nagelkerken and Munday 2016; Rivest et al. 2019) and might interfere not only with cue detection per se, but also with other aspects of the sensory pathway (e.g., reduced production of cues in stressful environments, disruption of cue transmission, impaired response to cue processing) (Connaughton et al. 2002, Munday et al. 2010, Turner and Chislock 2010, Jellison et al. 2016, Draper and Weissburg 2019, Rivest et al. 2019). Sensory stressors also have the potential to directly impede predation independent of disrupting the sensory pathway, such as at high levels of turbulence or dense habitat structure hindering predator movement or prey capture (Menge and Sutherland 1987). Here, we confine our attention to sensory stressors that only affect predator and prey detection.

Although effects of sensory stress on individual taxa (e.g., a predator or prey in isolation) are often readily intuited, the multi-faceted dimensions of sensory stress can make overall implications for the trophic cascade difficult to predict (Pruett and Weissburg 2018). Take first just the predator and prey: if both utilize the same sensory modality, sensory stress both weakens the predator's ability to capture prey and the prey's ability to mount an effective anti-predatory response. In a conceptual model of sensory stress, Weissburg et al. (2014) propose that the "winner" in such an interaction would likely be the organism least sensitive to sensory stress. One situation where this could occur is if either the predator or prey uses a secondary sensory modality to detect cues. For example, while *Tegula funebralis*, the black turban snail, can detect water-borne chemical cues released by its predator, the intertidal sea star *Pisaster ochraceus* (Jellison et al. 2016; Morgan et al. 2016), *P. ochraceus* also uses chemical contact cues to locate prey (Ferrier et al. 2016; Zimmer et al. 2016). As a result, under turbulent fluid conditions, *P. ochraceus* might be expected to be more resilient to sensory stress. If prey are more affected by sensory stress than predators, predation should dominate the predator–prey interaction, causing stronger top-down control on the prey population (McQueen et al. 1989; Worm and Myers 2003). In this regard, the model of Weissburg et al. (2014) provides a strong framework for predicting whether DMIIs or TMIIs will dominate in the presence of sensory stress. Yet left unclear, however, is how an overall trophic cascade might change as a function of sensory stress. Consider an anti-predatory response tied to prey fleeing or hiding. If the response is impaired under sensory stress, prey mortality could increase. At the same time, a reduced ability of prey to detect predators could encourage them to forage rather than flee or hide (Jellison and Gaylord 2019) although the opposite outcome of increased vigilance could also occur (Lima 1987). In the case of increased foraging by prey, sensory stress could conceivably create a "zero sum" situation for the basal resource. Fewer prey might remain to consume a basal resource, but those that remain could eat more of it. This scenario assumes that sensory stress does not directly impair prey foraging and, while not explored here, if prey foraging were affected, it would add further complex dynamics to the system. As a result, knowing which species is more sensitive to sensory stress provides only an incomplete prediction regarding how a trophic cascade might change with sensory stress.

Ascertaining how sensory stress might impact a trophic cascade therefore requires an evaluation of how predation and anti-predatory responses indirectly affect the basal resource. Here we create a simple tri-trophic model and incorporate sensory stress into the system to explore its potential effects on trophic cascades. Predation benefits the basal resource through consumption of prey that would otherwise eat the basal resource. In contrast, anti-predatory responses of prey benefit the basal resource only
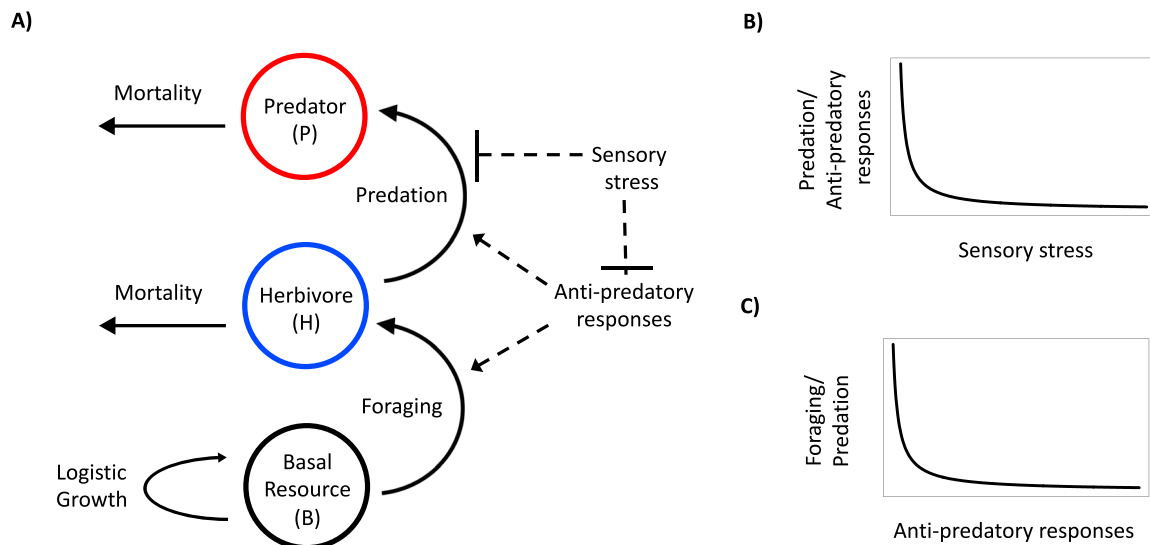
A)

Fig. 1 **A** Conceptual diagram of the sensory stress model. Circles denote the three populations within this tri-trophic model, and solid arrows denote the flow of energy through the food chain. Dashed arrows denote the processes affected by sensory stress or anti-predatory responses. How (**B**) sensory stress and (**C**) anti-predatory responses affect these processes assuming all other variables are held constant

if the responses reduce prey foraging instead of forming inducible morphological structures or chemical compounds (Harvell 1990; Iyengar and Harvell 2002; Lass and Spaak 2003). The range of possible outcomes from such factors has been explored in the theory of tri-trophic predator-prey dynamics (Rosenzweig and MacArthur1963; Abrams and Fung 2010), with studies documenting how prey and predator movement (Zhang et al. 2015; Sadowski and Grosholz 2019), handling time (Hastings and Powell 1991; McCann and Yodzis 1994), and inducible defenses (Ramos-Jiliberto et al. 2008; Khater et al. 2016) can affect their outcome. To this end, we extend the theory of tri-trophic interactions to include the effects of sensory stress on species interactions and the overall effects on trophic cascades.

Methods

Our model (Fig. 1) examines how sensory stress affects the strength of a trophic cascade by quantifying the basal resource abundance within a tri-trophic system as a proxy for trophic cascade strength. Note that this proxy differs from the typical empirical approach to estimating trophic cascade strength, based on proportional differences in basal resource abundance with and without predators (Okuyama and Bolker 2007). We chose abundance relative to the carrying capacity as our metric because basal resource in the absence of predators converge to the same abundance in all the scenarios, and this metric provides further insights to predator–prey dynamics in our results. Additionally, we

quantify that impacts' sensory stressors have on the predator and prey populations to reveal the dynamics that drive changes in the trophic cascade. We build upon the simplest possible model that encapsulates the relevant dynamics in a phenomenological manner for generalizability to other related predator–prey models (White and Marshall 2019). We also focus on parameter values appropriate for marine intertidal invertebrates (Yodzis and Innes 1992), to facilitate conceptual translation to a real-world system, although applicability to specific taxa should not be inferred.

The model follows the interaction between a basal resource (*B*), an herbivorous prey heterotroph (*H*), and its predator (*P*) over time based on the classic Lotka-Volterra predator–prey construct. The basal resource experiences logistic growth with growth rate *r* and carrying capacity *K* in the absence of prey consumption. Both the prey and predators have growth rates dependent on the amount of resources consumed with per capita feeding rates of $g(P)$ and $j(P)$, respectively, that depend on predator abundance in order to model the effects of TMIIs. The prey and predators convert resources consumed into population growth with efficiencies c_H and c_P, respectively, where we assume that both predators and prey are specialists such that their production relies only on the resources modeled. Prey and predators also experience constant per capita natural mortalities at rates d_H and d_P, respectively. The basic structure of the model is thus:

$$\frac{dB}{dt} = rB\left(1 - \frac{B}{K}\right) - g(P)BH \qquad (1)$$

$$\frac{dH}{dt} = g(P)c_H BH - j(P)HP - d_H H \qquad (2)$$

$$\frac{dP}{dt} = j(P)c_P HP - d_P P \qquad (3)$$

We model feeding rates $g(P)$ and $j(P)$ as asymptotically declining functions of predator density P, starting with maximum feeding rates a and b for prey and predators respectively in the absence of predators. This structure represents a type I functional response in the absence of predators (see Holling 1965, 1966). Though a type II functional response might often be more representative of foraging behavior (Holling 1966), it adds further complexity and potentially limit cycles to the dynamics (Hastings and Powell 1991; McCann and Yodzis 1994). The presence of predators, however, causes prey to enact their anti-predatory responses resulting in a reduction in foraging on the basal resource and concurrently making it harder for predators to capture them. Asymptotic declines in prey feeding rate as a function of predator abundance are consistent with other models that incorporate fear (Krivan and Schmitz 2004; Sadowski and Grosholz 2019) and have been demonstrated empirically in dose–response experiments, such as the decreasing proportion of tadpole prey activity as a function of the number of predatory dragonfly nymphs (Buskirk and Arioli 2002; McCoy et al. 2012). This relationship between predator abundance and feeding rates is modulated by the intensity of the anti-predatory responses in prey f and by the extent to which anti-predatory responses affect prey foraging m. Large values of m capture scenarios where a given benefit against predators is accompanied by a substantial decline in prey foraging as in many anti-predatory behavioral responses that include hiding or fleeing from predators (Preisser et al. 2005). In contrast, when m is negligible, prey receive safety benefits (as governed by f), but their foraging rates remain nearly unchanged, such as in morphological inducible defenses (Harvell 1990).

We model the effect of sensory stress on feeding rates as an asymptotically declining function of both the anti-predatory response and predation rate. The anti-predatory response and predation rate have an inverse relationship with the amount of sensory stress s in the model such that as the sensory stress parameter s increases, both the anti-predatory response and predation rate approach zero. Therefore, s appears twice in the predation rate $j(P)$, once in its effect on the prey anti-predatory response and a second occurrence on its direct effect on predators catching prey. Predation rate is further modulated by the relative sensitivity to sensory stress the predators experience compared to prey n. Although few studies examine feeding behavior under a range of sensory environments, Meager et al. (2010) demonstrated a negative asymptotic relationship with foraging

distances of cod over a range of light levels, consistent with the functional form of sensory stress used here. The functional forms for $g(P)$ and $j(P)$ with the inclusion of anti-predatory responses and sensory stress thus are:

$$g(P) = \frac{a}{1 + \frac{fmP}{1+s}} \qquad (4)$$

$$j(P) = \frac{b}{\left(1 + \frac{fP}{1+s}\right)(1+ns)} \qquad (5)$$

Our formulations assume that strong sensory stress attenuates anti-predatory responses in prey but does not interfere with prey food acquisition. This feature applies in numerous systems where basal resources, such as phytoplankton or benthic macroalgae, remain abundant even with prey consuming them, and require little search effort to find (Lubchenco 1978; Officer et al. 1982; Cubit 1984). While it is possible that sensory stress by itself can cause a response of increased vigilance in prey (Lima 1987), we focus on conditions where the presence of sensory stress does not directly influence prey foraging efforts (Baskerville-Bridges et al. 2004, Utne-Palm 2002). These simplified representations of underlying biological processes do not address all possible attributes of predatory-prey interactions in nature, but they allow for an initial evaluation of how the parameters of interest influence the fundamental operation of a common type of tri-trophic food web.

Model analysis

To simplify the model, we non-dimensionalize the equations following the approach of Hastings and Powell (1991). Using the substitutions of Table 1, which rescales time in terms of basal resource generations and rescales population

Table 1 Substitutions made to non-dimensionalize Eqs. 6, 7, and 8

Non-dimensional parameters/variables	Substitutions used	Values used in model
B^*(basal resource)	$\frac{B}{K}$	-
H^*(prey)	$\frac{H}{c_H K}$	-
P^*(predator)	$\frac{P}{c_H c_P K}$	-
t^*(time)	rt	-
a^*(foraging rate per capita)	$\frac{ac_H K}{r}$	2.17
b^*(predation rate per capita)	$\frac{bc_H c_P K}{r}$	0.1
d_H^*(prey mortality per capita)	$\frac{d_H}{r}$	0.056
d_P^*(predator mortality per capita)	$\frac{d_P}{r}$	0.01
f^*(anti-predatory response)	$fc_H c_P K$	1

sizes in terms of the basal resource carrying capacity, the nondimensional equations become:

$$\frac{dB^*}{dt^*} = B^*(1 - B^*) - \frac{a^*B^*H^*}{\left(1 + \frac{f^*mP^*}{1+s}\right)} \tag{6}$$

$$\frac{dH^*}{dt^*} = \frac{a^*B^*H^*}{\left(1 + \frac{f^*mP^*}{1+s}\right)} - \frac{b^*H^*P^*}{\left(1 + \frac{f^*P^*}{1+s}\right)(1+ns)} - d_H^*H^* \tag{7}$$

$$\frac{dP^*}{dt^*} = \frac{b^*H^*P^*}{\left(1 + \frac{f^*P^*}{1+s}\right)(1+ns)} - d_P^*P^* \tag{8}$$

We numerically integrate Eqs. 6–8 through time using the *desolve* package in the statistical software, R, running the simulations until the populations reach equilibrium (Soetaert et al. 2010). For all model runs, we assume nondimensionalized anti-predatory responses (f^*) of modest strength, such that they play a meaningful role in dynamics but do not overwhelm or prevent predators or prey feeding activities. Parameter values used for the model are in Table 1; consumption rates are derived from Yodzis and Innes (1992) for invertebrate consumers and calculated to fit our model formulation and to ensure stable solutions. A sensitivity analysis shows that changes in these values do not alter the qualitative outcomes of the model (see Supplemental 1). We conduct these integrations across 4 scenarios in which we specify given values of both the relative sensitivity of predators to sensory stress, n, and the extent to which anti-predatory responses influence prey foraging, m (Fig. 2). To explore different levels of relative predators and prey

susceptibility to sensory stress, we constructed scenarios where prey are more sensitive to sensory stress ($n = 0.002$; scenarios I and II) and where predators are more sensitive ($n = 25$; scenarios III and IV). To explore different levels of reduction in foraging from anti-predatory responses, scenarios I and III have strong reductions in foraging coupled with anti-predatory responses ($m = 2$), and scenarios II and IV have weak reductions in foraging associated with anti-predatory responses ($m = 0.2$). For each case, we explore the equilibrium population numbers of the three trophic levels at increasing levels of sensory stress. In all scenarios, the predators eventually approach extinction—defined as $\overline{P} < 0.0001$—and further increases in stress do not alter the outcome of the prey and basal resource, marking the endpoint of our simulation. While we use one set of initial conditions ($B^* = 0.8$, $H^* = 0.5$, and $P^* = 0.2$), we also verify that the solutions found are the only stable equilibria for our given parameter combinations (see Supplemental 2).

To parse out the biological mechanisms driving changes in the tri-trophic populations as a result of sensory stress, we calculate the proportion of the basal resource the prey population consumes at equilibrium, denoted as v:

$$v = \frac{a^*H^*}{\left(1 + \frac{f^*P^*}{1+s}\right)} \tag{9}$$

and also the proportion of the prey population the predators consume, denoted as w:

$$w = \frac{b^*P^*}{\left(1 + \frac{f^*mP^*}{1+s}\right)(1+ns)} \tag{10}$$

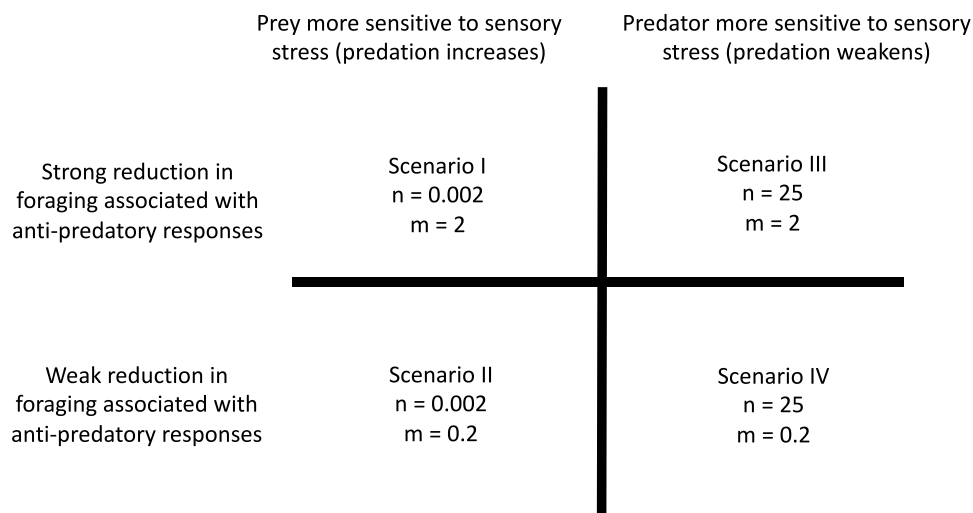|	Prey more sensitive to sensory stress (predation increases)	Predator more sensitive to sensory stress (predation weakens)
Strong reduction in foraging associated with anti-predatory responses	Scenario I n = 0.002 m = 2	Scenario III n = 25 m = 2
Weak reduction in foraging associated with anti-predatory responses	Scenario II n = 0.002 m = 0.2	Scenario IV n = 25 m = 0.2

Fig. 2 The four qualitatively different scenarios explored in the sensory stress model, characterized by representative values of the parameters n (the relative sensitivity to sensory stress between predators and prey) and m (the extent to which anti-predatory responses impact prey foraging). Scenarios I and II correspond to instances where prey are more sensitive to sensory stress, while predators are more sensitive in scenarios III and IV. Prey display fear responses that cause strong reductions in their foraging on the basal resource in scenarios I and III, while the fear responses in scenarios II and IV do not impair prey foraging substantially

As noted above, our proxy for the strength of the trophic cascade is the population size of the basal resource. Although the strength of a trophic cascade is typically defined as the proportional change in basal resource abundance in the presence versus absence of predators (Okuyama and Bolker 2007), in our four scenarios, the basal resource approaches the same equilibrium value in the absence of predators. This convergence arises because the parameters that distinguish the scenarios (the extent to which anti-predatory responses impact prey foraging, *m*, and the relative sensitivity of predators to sensory stress compared to prey, *n*) do not influence the population models in the absence of predators. Therefore, the basal resource population has a direct correlation with the strength of the trophic cascade in our study and is proportional to other measures of the strength of trophic cascades (Okuyama and Bolker 2007). We also note that the non-dimensionalized values of the basal resource represent the proportion of the carrying capacity the basal resource reaches, a metric that influences its growth rate and plays a key role in explaining the patterns in the food chain.

For purposes of visualizing population outcomes for the predators and prey, we normalize their population levels to the population levels in the absence of sensory stress, such that in the absence of sensory stress, the population levels sit at 1. This scaling facilitates comparison of patterns over a range of sensory stress. Similarly, we scale the sensory stress levels such that the maximum stress level (when predators approach extinction) is set to 1.

Results

When prey are more sensitive than predators to sensory stress (scenarios I and II)

In both scenarios I and II, top-down control of prey increases with sensory stress with differing outcomes on the basal resource. Because prey are more sensitive to sensory stress, anti-predatory responses rapidly diminish as sensory stress is introduced to the system. As a result, predation rates increase initially (Fig. 3A, B), and prey populations decrease (Fig. 4A, B). However, at higher levels of sensory stress, the anti-predatory response in prey is effectively absent, such that further levels of stress only hinder the capacity of predators to capture prey. This outcome causes the predator populations to display unimodal curves that ultimately decline towards extinction in both scenarios I and II at higher levels of stress. Consequently, prey populations rebound across these intensities of sensory stress as they are released from predation (Fig. 4A, B).

Even though both scenarios I and II exhibit stronger top-down control at low levels of sensory stress, the basal resource (reflective of the strength of the tropic cascade)
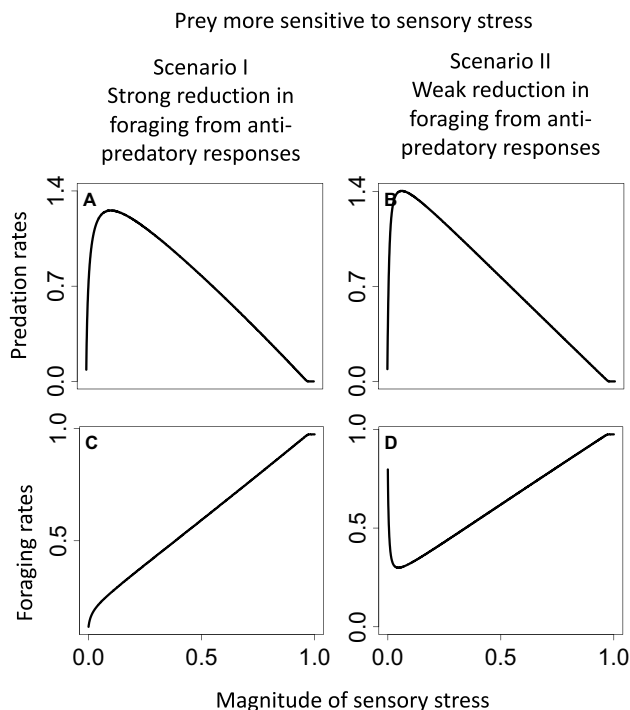

Fig. 3 The predation (*w*) and foraging rates (*v*) of the predator and prey, respectively, for scenarios I (*n*=0.002, *m*=2) and II (*n*=0.002, *m*=0.2) where prey are more sensitive to sensory stress across a range of increasing values for sensory stress *s*. Total predation rates (panels **A**, **B**) display a unimodal pattern with sensory stress since prey rapidly lose their anti-predatory responses in both scenarios. Total foraging rates (panels **C**, **D**) display different patterns with sensory stress depending on the type of anti-predatory responses prey have between the two scenarios

responds differently depending on the type of anti-predatory responses prey exhibit. In scenario I where anti-predatory responses are accompanied by decreases in prey foraging, the loss of anti-predatory responses with sensory stress drives a corresponding increase in prey foraging (Fig. 3C). Such elevated foraging arises because prey no longer detect or recognize the dangers of a predator and act as "foolhardy" consumers (see also Jellison and Gaylord 2019). In turn, the enhanced foraging weakens the trophic cascade despite the increase in top-down control at low levels of sensory stress (Fig. 4C). By contrast, if prey foraging does not decline as anti-predatory responses become degraded under rising sensory stress, a strengthening of the trophic cascade can occur (Fig. 4D; see low levels of sensory stress) due to reductions in the prey population and corresponding declines in prey consumption of the basal resource (Fig. 3D).

When predators are more sensitive than prey to sensory stress (scenarios III and IV)

In scenarios III and IV, sensory stress diminishes predators' influence on prey, resulting in increased numbers of prey
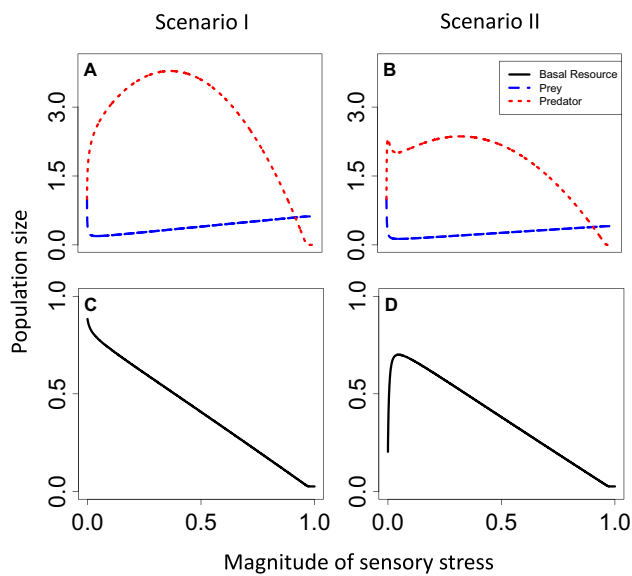
Fig. 4 The response of the three trophic levels across a range of increasing sensory stress s values for scenarios I ($m=2$) and II ($m=0.2$) when prey are more sensitive to sensory stress ($n=0.002$). Panels **A** and **B** depict the predator and prey populations for their respective scenarios and panels **C** and **D** represent the basal resource population. The strength of the trophic cascade (i.e., basal resource population size) responds differently to sensory stress depending on the type of antipredatory response the prey has. Predator and prey populations are scaled to their population size when sensory stress is absent and basal resource abundance represents the proportion of the carrying capacity

Fig. 5 The predation (w) and foraging (v) rates of the predator and prey, respectively, for scenario III I ($n=25$, $m=2$) and IV ($n=25$, $m=0.2$) across a range of values for sensory stress s. Total predation rates decline with sensory stress in both scenarios (panels **A**, **B**) since predators are more sensitive to sensory stress with a corresponding increase in foraging rates by prey (panels **C**, **D**)

capable of foraging on the basal resource (Fig. 5C, D). This trend, in turn, drives a weakening of the trophic cascade (Fig. 6C, D). However, the predator and prey populations between the two scenarios respond differently despite similar changes in predation and foraging rates: predators and prey exhibit unimodal responses to sensory stress in scenario III and monotonic declines in scenario IV (Fig. 6A, B). The difference between the two scenarios arises from food limitation for the prey when sensory stress is absent. In scenario III, the basal resource sits at 88% of its carrying capacity in the absence of sensory stress (Fig. 6C). Consequently, when prey are released from predation in the presence of sensory stress, they can take advantage of the abundant basal resource, causing their population to initially grow (Fig. 6A). In fact, it is this increase in the prey population in scenario III that drives the increase in the predator population, despite the decrease in proportion of the prey population consumed. In contrast, in scenario IV, the basal resource is only at 20% of its carrying capacity in the absent of sensory stress (Fig. 6D). Because the basal resource follows a logistic growth curve, the maximum basal resource growth rates occur around half the carrying capacity (Larkin 1977). Therefore, the increase in basal resource consumption exacerbates food limitation, which causes a decline in prey numbers and drives a corresponding decrease in predator numbers (Fig. 6B).
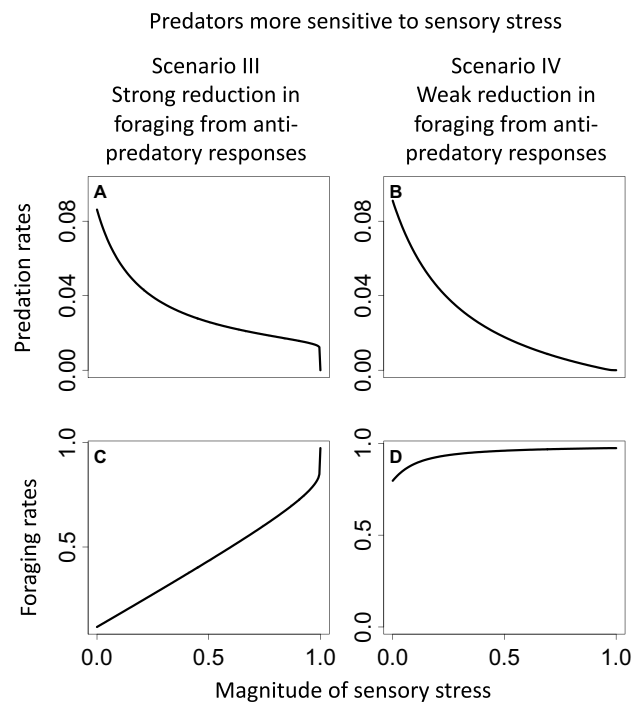
The difference in basal resource population size when sensory stress is absent hinges upon how anti-predatory responses impact prey foraging. In scenario III where the anti-predatory response is tied strongly to reduced prey foraging, both TMII and DMII work in tandem to enhance the trophic cascade, resulting in a relatively high basal resource population when sensory stress is absent. In contrast, when anti-predatory responses do not result in significant reductions in prey foraging in scenario IV, TMII is mostly absent from the predators' indirect effect on the basal resource. This situation results in a reduced basal resource population in the absence of sensory stress. Thus, when prey increase their foraging in scenario IV, they drive the basal resource further away from half its carrying capacity, reducing the birth rates of the prey and the predators.

Discussion

Overall, our model shows that sensory stress typically weakens trophic cascades. However, such diminishing indirect effects arise through different processes depending on the scenario (summarized in Table 2). When predators are more sensitive to sensory stress (i.e., scenarios III and IV),
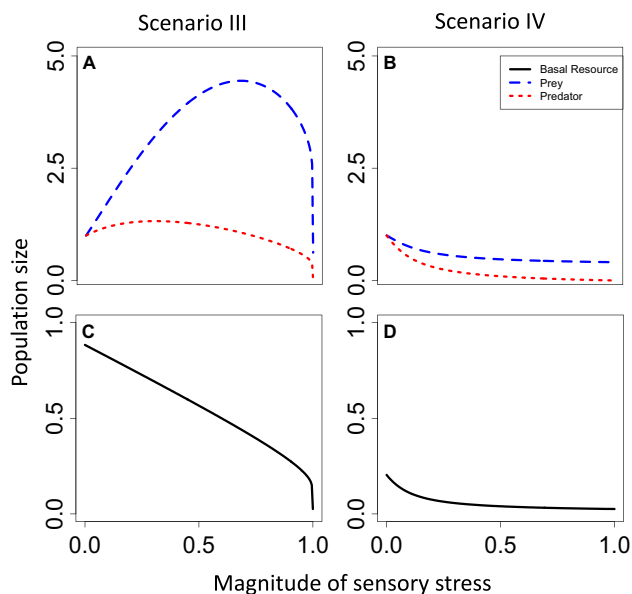
Fig. 6 The response of the three trophic levels across a range of increasing sensory stress s values for scenarios III ($m=2$) and IV ($m=0.2$) when predators are more sensitive to sensory stress ($n=25$). Panels **A** and **B** depict the predator and prey populations for their respective scenarios and panels **C** and **D** represent the basal resource population. The trophic cascade weakens in both scenarios (i.e., the basal resource declines) with sensory stress. Predator and prey populations are scaled to their population size when sensory stress is absent and basal resource abundance represents the proportion of the carrying capacity

the prey experience a release from predation, resulting in increased foraging on the basal resource. By contrast, sensory stress can weaken a trophic cascade by causing prey to become less fearful and responsive to the presence of predators. This scenario occurs when the prey's anti-predatory response is strongly tied to their foraging effort and when prey are more susceptible to sensory stress than predators (scenario I). This weakening of the trophic cascade occurs despite greater total predation on the prey population. Only when the anti-predatory responses in prey do not strongly affect prey foraging, and prey are more sensitive to sensory stress (scenario II) do we observe a strengthening of the trophic cascade at low levels of sensory stress.

The four scenarios described in our model represent several types of predator–prey interactions commonly found within coastal marine habitats. There are clear situations where one species in a predator–prey pair is more sensitive to sensory stress than the other. *T. funebralis*, the black turban snail, is affected by low-pH seawater, causing *T. funebralis* to cease its escape behavior in the presence of a predatory intertidal sea star, *Leptasterias hexactis* (Gravem and Morgan 2016; Jellison and Gaylord 2019). Because *L. hexactis* is relatively unaffected by low-pH seawater in its ability to capture *T. funebralis*, this example represents a

predator–prey pair where the prey is more vulnerable to a particular sensory stress. In fact, the *L. hexactis* and *T. funebralis* pair operates in analogy to scenario I and, indeed, shows a similar outcome to that predicted by the present model (Jellison and Gaylord 2019). However, when predators and prey share the same sensory modality to detect each other, it is difficult to project which species might be more sensitive to sensory stress. In this case, empirical data comparing the performance of both species simultaneously under sensory stress is required (Smee et al. 2010).

Prey also exhibit a wide range of anti-predatory responses, only some of which influence foraging activities of the prey. Gastropods and bryozoans can produce inducible defenses (Harvell 1990; Grünbaum 1995; Bourdeau 2010; Barclay et al. 2019) that do not impact foraging, suggesting that at least some members of these taxa might adhere to scenarios II and IV. Numerous other prey species have anti-predatory responses that result in strong TMIIs, consistent with scenarios I and III (Trussell et al. 2003; Wirsing et al. 2008; Jellison et al. 2016). Moreover, although the dichotomy between morphological inducible defenses and fear behavior is often distinct, there are also cases where the link between anti-predatory response and prey foraging is ambiguous. Energetic costs associated with inducible defenses might cause prey to forage more (Chivers et al. 2007), or conversely, morphological inducible defenses might hinder prey foraging by making locomotion more costly or feeding activities more awkward (Grünbaum 1995). Studies have additionally indicated that some morphological inducible defenses arise as a byproduct of changes in prey foraging behavior; for example, higher feeding rates in some marine snails result in faster growing (but also thinner) shells (Bourdeau 2010; Bourdeau and Johansson 2012). Such connections between these two types of plastic responses can cause them to blur together conceptually.

Our model can also help explain differences in findings among studies that have attempted to quantify the strength of trophic cascades (Shurin et al. 2002; Borer et al. 2005). In three of our scenarios, unimodal curves occur for the predator and prey populations as sensory stress increases (scenarios I, II, and III). However, the basal resource displays a monotonic decline in only two of these scenarios (scenarios I and III). The latter case suggests the possibility that if attributes of the sensory environment are ignored, one could draw different conclusions as to whether indirect effects are substantial or not in a system, depending on the level of sensory stress active during an experiment.

The results from our model are based on equilibrium analysis and therefore represent an expected long-term outcome that might not align with results from empirical studies that reflect shorter timescales and could exhibit extended transient dynamics (Hastings 2004). While we do not directly examine transient dynamics, the consumption

Table 2 The summary results from our sensory stress model. We summarize what limits the prey population in each of the four different scenarios and whether this results in a strengthening or weakening of the trophic cascade at low sensory stress levels

Scenarios	I	II	III	IV
Trophic level more sensitive to sensory stress	Prey	Prey	Predators	Predators
Amount of reduction in foraging from anti-predatory responses	Strong	Weak	Strong	Weak
Prey population limited by:	Predators	Predators	Basal resource	Basal resource
Effect on trophic cascade at low sensory stress levels	Weakens	Strengthens	Weakens	Weakens

rates we calculate in Eqs. 9 and 10 can provide insights to experimental systems that are too brief to incorporate the effects of reproduction and predation-independent mortality. For example, the results in scenarios I and II could be observed within an empirical study because the mechanism behind the differences in basal resource consumption between the two scenarios is partly due to a difference in prey foraging rates (Fig. 3C, D). In contrast, the result in scenario IV where there is a decrease in all three trophic populations due to resource limitation might not manifest within an experimental setting, because this outcome arises through reproduction and mortality patterns manifesting over multiple generations. The extent of transient dynamics are also contingent upon other factors such as initial conditions and stochasticity (Hastings 2004), and future model extensions that incorporate these factors in the context of transient analyses can better enable the comparison between model predictions and empirical findings.

The role of fear in trophic cascades

Our sensory stress model also reveals that the presence of fear responses in prey do not necessarily strengthen trophic cascades. This finding can be non-intuitive because numerous studies have shown that TMIIs constitute a significant portion to the overall strength of a trophic cascade (Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005). Although fear responses can indeed decrease foraging activities of prey (Ng and Gaylord 2020), those same responses also have as a byproduct the counteracting tendency to weaken trophic cascades via their reduction in predation rates. Tethering studies, which remove a majority of prey's anti-predatory responses, suggest that the presence of escape responses in prey can lead to a significant decrease in predation (Barbeau and Scheibling 1994; Aronson and Heck 1995; Bullard and Hay 2002). Many fear responses counteract the weakening of DMIIs through the addition of TMIIs. Yet, as our model shows, the presence of sensory stress can influence the relative strength of DMIIs and TMIIs depending on how strongly coupled anti-predatory responses are to prey foraging. Identifying the overall effect of fear in trophic cascades is therefore crucial (Peers et al. 2018; Prugh et al. 2019)

because many different factors, such as sensory stress (Ferner et al. 2009), state of the prey (Gravem and Morgan 2016), and anthropogenic disturbances (Kwan et al. 2015; Jellison et al. 2016; Rivest et al. 2019) can influence the intensity of the fear response.

Assumptions of the model

Our conceptual examination includes several model simplifications that could affect scenario outcomes. We assume that immigration and emigration are negligible and that non-consumptive mortality rates in prey and predators are density independent. We also assume that that neither predators nor prey have an appreciable handling time when consuming their respective food sources. These simplifying assumptions allow us to create a relatively strong baseline trophic cascade in the absence of sensory stress that, while potentially absent in more complex communities (Polis et al. 2000), allows us to identify the key processes driving the effects of sensory stress on the tri-trophic systems.

The model also makes several assumptions about how sensory stress can influence predators and prey. For example, it anticipates that the pertinent environmental stressors are mild enough to avoid physically hindering predation or foraging efforts such that prey can forage normally at high levels of sensory stress. Given that we simulate scenarios where the sensory stress is significant enough to effectively remove all of the detection ability of predators and prey, it is possible that those environmental stresses would physically impair the predators and prey. As such, the high levels of sensory stress simulated in our sensory stress model likely would introduce processes that directly limit predation and foraging rates (Menge and Sutherland 1987). The model is also most easily conceived as accounting for predators and prey that only use one sensory modality to detect each other. If they utilize a secondary modality (Rivest et al. 2019), the effects of sensory stress might be more akin to low and intermediate intensities as it then will be unable to completely remove the ability of one or both species to detect the other.

The model only focuses on scenarios where sensory stress does not directly affect prey foraging on the basal resource. Although such an assumption likely holds when the basal resource is distributed in sizeable sessile patches,

like mussel or algae beds, it might apply less well to cases where the basal resource is patchy. Including this additional effect of sensory stress in our model would likely add further dynamical complexity while also causing prey populations to approach extinction at high levels of sensory stress. A further simplification is that we have structured anti-predatory responses to operate independent of prey density (Krivan and Schmitz 2004). This assumption is appropriate for prey species where group vigilance is not a common behavior. However, there are species that exhibit group vigilance where the strength of anti-predatory responses is partitioned among the group members (Elgar 1989; Lima and Bednekoff 1999) or allocated to certain individuals (Rauber and Manser 2017); in such cases, only a threshold of anti-predatory response might be required to safely protect the entire prey population. The existence of such a threshold would suggest that a population as a whole would not need to decrease foraging efforts substantially to generate effective anti-predatory responses. This situation could be represented by an *m* that is density dependent on prey population size.

The presence of environmental stress in our system should prompt an adaptative response in both predators and prey to the sensory stressors. Numerous studies have shown that populations can rapidly adapt to environmental stressors (Sih et al. 2011; Sanford and Kelly 2011). Both predators and prey species might alter their foraging behavior to minimize the effects of sensory stress, certain behavioral syndromes might be selected for (Jeffries et al. 2021), or they can potentially rely on secondary sensory modalities to forage (Rivest et al. 2019). However, our model does not assume that sensory stress is acting in a predictable or sustained manner. Rather, the model provides results that highlight population dynamics in the absence of selection, which can provide predictions on how predators and prey might adapt (Harvey et al. 1983).

As noted previously, our analysis examines the tri-trophic populations and their dynamics at equilibrium. Therefore, the model does not make explicit predictions on the transient dynamics of the system, such as results from empirical experiments that span fewer than one generation. However, the mechanisms we propose for the observed patterns from the model still yield testable predictions that can be useful for future empirical studies.

Hydra effect

The presence of sensory stress and its action in the current model additionally reveals the potential for so-called hydra effects (Abrams 2009) to manifest when anti-predatory responses are present. Hydra effects occur when a population stabilizes at larger numbers despite experiencing higher levels of per capita mortality, suggesting that increased mortality can respond with a disproportionate increase in birth rates (Zipkin et al. 2009; Sieber and Hilker 2012). This phenomenon can have ecological implications when managing for invasive species (Grosholz et al. 2021). In a certain subset of our scenarios, prey exist in larger numbers at absent to low sensory stress levels than at extremely high levels when predators are absent (Fig. 6A, B). This outcome is unexpected because in the absence of predators, predation and the costs of anti-predatory responses should not negatively impact the prey population.

The mechanism behind the hydra effect in our model derives from anti-predatory responses limiting the foraging effort by prey (Abrams 2009, Schröder et al. 2014, McIntire and Juliano 2018). In the absence of predators, prey and basal resource reach their equilibrium levels as a two-trophic system. The introduction of predators limits the foraging efforts by prey through fear, causing the basal resource to stabilize at higher numbers (Fig. 6C, D). This is a classic incarnation of a trophic cascade mediated by a TMII. However, due to the logistic growth of the basal resource where growth rate is maximal at half the carrying capacity, there is a disproportionate increase in basal resource abundance with the decrease in per capita prey foraging effort. Consequently, prey consume more basal resource despite the lower feeding effort because of this increased abundance (Abrams 2009, Schröder et al. 2014). The possibility for TMIIs to positively affect prey populations might be an understudied mechanism for generating a hydra effect (McIntire and Juliano 2018) and would only be observed across multiple generations. Our model adds to a growing body of literature showing theoretical support for its existence but has few empirical studies (Schröder et al. 2014, but see Peacor 2002; McIntire and Juliano 2018; Grosholz et al. 2021). In particular, our model suggests that this type of hydra effect can arise in any predator–prey interactions with TMIIs, and can be revealed when a process, such as sensory stress, removes the anti-predatory behavior.

Declarations

Competing interests The authors declare no competing interests.

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