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The consistency of a species' response to press perturbations with high food web uncertainty

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Abstract. Predicting species responses to perturbations is a fundamental challenge in ecology. Decision makers must often identify management perturbations that are the most likely to deliver a desirable management outcome despite incomplete information on the pattern and strength of food web links. Motivated by a current fishery decline in inland lakes of the Midwestern United States, we evaluate consistency of the responses of a target species (walleye [*Sander vitreus*]) to press perturbations. We represented food web uncertainty with 193 plausible topological models and applied four perturbations to each one. Frequently the direction of the focal predator response to the same perturbation is not consistent across food web topologies. Simultaneous application of management perturbations led to less consistent outcomes compared to the best single perturbation. However, direct manipulation of the adult focal predator produced a desirable outcome in 77% of 193 plausible topologies. Identifying perturbations that produce consistent outcomes in the face of food web uncertainty can have important implications for natural resource conservation and management efforts.

Key words: conservation; ecosystems; indeterminacy; resource management; species dynamics; model uncertainty.

Introduction

How can we increase the abundance of a declining valuable species? How can we decrease the impact of a harmful species? Answering these questions involves food webs, which are among the most complex systems studied by humans (Strogatz 2001, Schmitz 2010). These elaborate networks of ecological interactions govern community dynamics, as shown in marine (Paine 1966, Estes and Palmisano 1974, Estes et al. 1998), freshwater (Carpenter et al. 1985, Power et al. 1985), island (Spiller and Schoener 1990), forest (Terborgh et al. 2001), grassland (Schmitz 2010), rangeland (Sinclair et al. 2010), and other ecosystems. Because of the multiple linkages in food webs, there may be several possible actions that could achieve a particular management goal. For example, to rebuild a declining species one could remove its predators or competitors, or increase production of its prey.

However, ecosystem responses to management perturbations are complex and hard to predict (Pine III et al. 2009). Background data and the research capacity to determine the outcome of management perturbations are often insufficient as new environmental issues manifest (Tallis et al. 2010, Schindler and Hilborn 2015). This can be further complicated when management occurs at large spatial scales such that the food web to be managed varies among locations. Therefore, the success of a management perturbation is likely not dependent on a single "real" food web for any particular species, but rather a set of food webs that may often be poorly resolved. In these situations, scientists face a significant challenge to make recommendations among alternative management perturbations.

Conventional wisdom suggests that the effect of a change of abundance of one species on another cannot be predicted without knowing topology (i.e., network pattern of sign specified pairwise links) and the strength of particular food web links (Yodzis 1988, McCann 2000, Berlow et al. 2004, Novak et al. 2011). If link topology and strengths are unknown, predictions about species dynamics are highly uncertain. However, the direction of a species' response to a particular management perturbation may sometimes be robust to these food web uncertainties. In this sense, it may be possible to quantify the directional consistency (i.e., desirable outcome is achieved with repeated application) of alternative management perturbations with respect to a target species. In the absence of detailed information on the food web, it may be beneficial to know which perturbations have more (or less) consistent outcomes. For instance, decision makers may prefer perturbations that are more consistent (Epstein 1999) as opposed to those that produce large effects but also tend to produce undesirable outcomes. Here we focus on assessing the consistency of focal species responses to press perturbations with a high level of food web link uncertainty. Do certain press perturbations have more consistent outcomes?

We tackle this question by assessing the consistency of species' responses to press perturbations across a range of food web topologies. This topological uncertainty is

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represented by a set of model food webs each with a unique pattern of sign-specified pairwise links. The consistency of the response of a target species to different press perturbation is assessed in the following way. If a press perturbation produces the desirable outcome regardless of food web topology, then it is consistent. A press perturbation that predicts focal species responses with opposing directions for different topologies is less consistent. Consistency also depends on the number of indeterminate outcomes, for which the direction of the focal species response cannot be determined by topology alone. The determinacy of each outcome is assessed using a weighted prediction matrix (i.e., the ratio of net feedback to total feedback calculated from manipulation of the community matrix; Dambacher et al. 2002, 2003*a*).

In this study, we assess the consistency of predicted outcomes of a species of interest to proposed management perturbations. These perturbations are comprised of individual press perturbations and their combinations. We present a simplified example of the problem of perturbation consistency and the approach we used to assess it. Analysis then focuses on a real management issue, the recent decline of inland lake walleye stocks in the Midwestern United States (Hansen et al. 2015*a*).

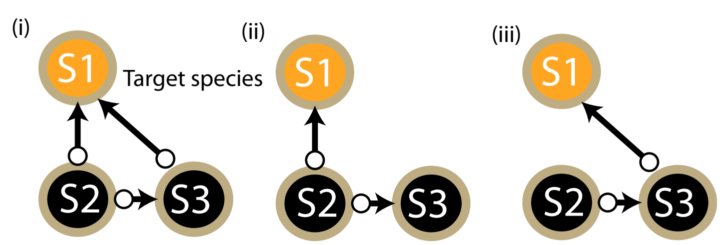
Materials and Methods

Consistency in a simplified three-species food web

Consider managing a set of food webs that are composed of an assemblage of three species S1, S2, and S3 (Fig. 1). Imagine that S1 (target species) has declined and the management goal is to intervene and increase S1 by manipulating the food web. S1 is suspected to eat S2 and S3 but these links are uncertain in any particular food web in the set. This uncertainty can be represented by three topological link patterns (Fig. 1Ai–iii). In this example, food web data are scarce and therefore link strengths are unknown.

Which management action should be applied to increase the target species (S1)? Should S3 be decreased to increase S1 or should S2 be increased? Assessing the consistency of model outcomes includes identifying whether the direction of the response can be determined. As previously mentioned, this determinacy can be assessed using a weighted prediction matrix (Dambacher et al. 2003). With this information, the number of times the desirable outcome is repeated for different food webs (i.e., consistency) can be assessed.

A) Representing food web link uncertainty



B) Consistency of alternative press perturbations

Press perturbation	Predicted outcome direction (S1) (i)	(ii)	(iii)	Interpretation
S2 (+)	S1 (+)	S1 (+)	S1 (+)	Consistent
S3 (+)	S1 (?)	S1 (-)	S1 (+)	Inconsistent

Indeterminate due to link strength uncertainty

Inconsistent due to topological uncertainty

Fig. 1. A simplified example of the consistency of a focal species response to alternate press perturbations. (A) Two sustained perturbations are applied to hypothetical three species food webs. The occurrence of two of the food web linkages is uncertain and data are limited to link topology. Large circles represent species, arrows point in the direction of positive effects, and small circles on the end of a line that links two species indicate negative effects. (B) A summary of perturbation outcomes and interpretation of their consistency. [Color figure can be viewed at wileyonlinelibrary.com]

A press perturbation that adds or removes S2 has a positive effect on S1 (Fig. 1Bi–iii). On the other hand, adding or removing S3 can produce three outcomes. In (i) where S1 eats S2 and S3, the outcome is indeterminate because the direction of S1 cannot be determined by topology alone. The second (ii) and third (iii) web topologies have outcomes that can be determined by topology. However, these predictions are of opposite direction, where the outcome of (ii) is negative and (iii) is positive. In this scenario, the press perturbation of S2 produces the desired outcome most consistently.

Walleye decline in upper Midwest United States

Monitoring of inland lakes of the Midwestern United States suggest a decline in walleye (*Sander vitreus*), a popular game fish that inhabits ~1,000 lakes in Wisconsin alone, and a concurrent rise in Centrarchid species, in particular, black bass (*Micropterus* sp.; Hansen et al. 2015*b*). Black bass harvest by the angling community has declined since the mid-1980s (Hansen et al. 2015*b*). Increased predation on juvenile walleye by adult bass, or a shift in resource exploitation to the advantage of bass are often evoked to explain the walleye decline. Based on these assertions we might predict that walleye populations could be restored through reductions of bass populations. At present, however, the dynamic relationships among walleye, bass, and other organisms in these lakes are uncertain.

Evaluating consistency in response to management perturbations is important for the walleye fishery because of a general lack of information on food web linkages, but also because there is evidence that particular links vary among lakes. Diet observations from a small number of studies across their overlapping range suggest that not only that adult bass eat juvenile walleye (Santucci and Wahl 1993, Frey et al. 2003, Fayram et al. 2005, Freedman et al. 2012), but conversely that adult walleye sometimes eat juvenile bass (Frey et al. 2003, Kelling et al. 2016). Both species may also prey on each other within the same lake (Frey et al. 2003). These studies suggest that bass likely impose a direct negative consumptive effect by eating walleye in some lakes. In other lakes, however, the interaction may be negligible (Freedman et al. 2012, Kelling et al. 2016) or bass may potentially have a positive influence on walleye. Similarly, the degree to which bass and walleye share resources is uncertain but in some lakes considerable overlap in dietary items occurs (Frey et al. 2003, Fayram et al. 2005). In addition, walleye diets may include prey from deeper water habitats like cisco (*Coregonus artedi*) when these prey are available (Chipps and Graeb 2011). Whereas, bass regularly eat a broader range of near-shore invertebrate prey and terrestrial organisms than walleye (Frey et al. 2003). Hence, while we know the kinds of feeding links that may occur in a lake, we are uncertain about the food web link topology and strength.

Uncertainty in food web topology

The food web supporting walleye and bass contains a general structure that is common to many ecosystem types (Polis et al. 1989). Two single-predator sub-webs may be linked if adults of one species feed on the young of the other species (i.e., life history intraguild predation) and/or similar trophic levels share prey (Polis et al. 1989, 1996). Yet, in the bass–walleye food web there is uncertainty in these key structural features.

We illustrate a generalized food web with a diagram that shows all possible sign-specified links between eight species components (Fig. 2A). These eight food web components include two predators each with adult (A1 target species adult and stage we want to manage; A2 non-target species) and juvenile life stages (J1, J2). A resource at the base of the food web (R3) is prey to the juveniles of both predators (J1, J2). This same basal resource is prey to an intermediate level consumer (C1) that is also a potential prey source for both predator adult stages (A1, A2). Two final components of the food web reflect resource pools exclusive to each predator (A1, A2) but are common to both adult (A1) and juvenile (J1) stages within a species.

We include food web link uncertainty by generating a set of food webs each with a different topology. To do this, we add and delete links according to three broad categories (Fig. 2B). First, we consider four possible combinations of predation among adults and juveniles of predator species (Fig. 2Bi–iv; four alternatives). Second, we consider nine alternatives of prey sharing between life stages of the two predator species (Fig. 2Bv–x; nine alternatives). Third, links to each predator exclusive prey sources (R1 or R2) can be connected in three ways for each predator, considering adult and juvenile links (Fig. 2Bxi–xiii; nine alternatives).

A total of 324 ($4 \times 9 \times 9$); Fig. 2B) possible food web topologies were generated. We assumed that all species components must be linked to at least one other food web component. For example, consumers require at least one prey source. We excluded 131 topologies because of these biological constraints. This left 193 plausible food web topologies for analysis. All of the remaining food webs contain eight species components but differ in the number of links (range = 15–21; median = mode = 18 links). These food webs are similar in connectance (range = 0.234–0.328) to well described empirical food webs (Williams and Martinez 2000, Dunne et al. 2002). All 193 webs used in the analysis are stable in that all community matrices have negative diagonal elements and thus positive Routh-Hurwitz determinants (Dambacher et al. 2003*b*).

Indeterminacy assessed with the weighted prediction matrix

We used a qualitative modelling approach that uses the community matrix to represent linkages among

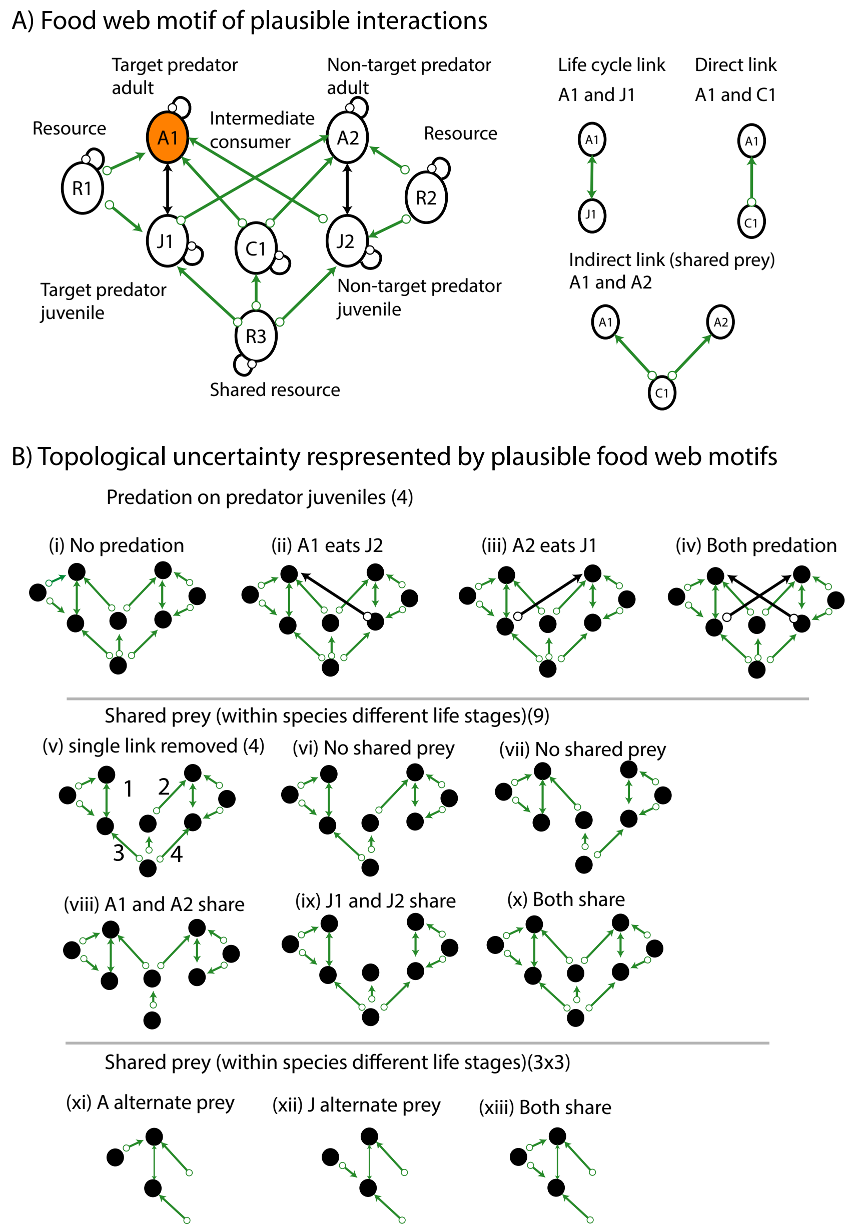


FIG. 2. Conceptual diagrams that show (A) the potential links in a two predator (walleye–bass) food web and (B) uncertainty represented by different topological arrangements. In panel A, a food web is depicted as a sign specified network of linkages with eight species components and three types of interactions. The large circles with inset lettering indicate species components where A1 (orange shading) is the target predator, J1 is the juvenile of the target predator, A2 is the adult non-target predator, J2 is the juvenile non-target predator, C1 is the intermediate consumer, R3 is the shared resource, and R1 and R2 are resources unique to each predator but shared between life stages within predators. Green arrows show instances of direct interaction between species pairs in the food web. Arrowheads indicate a positive and small circles a negative impact of each paired interaction. Double arrow black links show the life cycle. In panel B, species components are solid black and thicker black arrows in highlight the interactions that change. Green arrows are the same as in panel A.

species in a food web. We applied four press perturbations to each community matrix to determine the sign of a target species response. The outcome of the target species response was used to assess the consistency of each press perturbation. The sign of each outcome (positive, negative, indeterminate) was determined by a weighted prediction matrix (**W**) (Dambacher et al. 2002, 2003*a*). Detailed explanation of the loop analysis techniques applied here can be found in several excellent methodological papers (e.g., Dambacher et al. 2002, 2003*a*, Puccia and Levins 2013). Below we outline three general steps used to make our assessment.

First, the growth of a species (or food web component) can be represented as a set of ordinary differential equations

$$\frac{dNi}{dt} = fi(N_1, N_2, \ldots, N_S),\ i = 1, \ldots, S. \quad (1)$$

Here the function f_i represents the relationship between the abundance of (N) of species i and all other species S (Yodzis 1988, Puccia and Levins 2013). The elements a_{ij} of the community matrix (**A**) are then derived from the growth equation, Eq. 1, according to the following general equation (Puccia and Levins 2013):

$$a_{ij} = \frac{\partial\left(\frac{dN_i}{dt}\right)}{\partial N_j}\bigg|_{N=N^*} \quad (2)$$

where N_{ij} represents the abundance of species i and species j, and N* denotes a species abundance at equilibrium. Each a_{ij} represents a change in the population growth rate of a species N_i, to a change in another species N_j, near equilibrium.

In our study, the model is constrained such that the specific parameter values and functional forms for direct interactions of species are not known. In this case, the a_{ij} elements of A were represented by the presence or absence of interactions (1, 0) and their sign (e.g., +1, −1, 0). Each matrix element was assigned according to food web diagrams (e.g., Fig. 2A, C). Each plausible topology of the food web was represented as an individual sign specified matrix.

Second, the complementary feedback matrix was calculated as the adjoint of the community matrix (i.e., adj (**A**); Dambacher et al. 2003*a*). A negative matrix (−**A**) is used in calculations to maintain sign conventions (Dambacher et al. 2003*a*). Given −**A**, the adjoint of −**A** (adj-**A**) provides the net number of complementary feedback loops. This net feedback indicates the outcome of the sum of positive and negative interactions and thus the direction of the response of each component (species) of the food web (N_i). The adj (−**A**) is related to the inverse of the community matrix ($-\mathbf{A}^{-1}$) and its determinant (det(−**A**)) according to the equation

$$-A^{-1} = \frac{\text{adj}(-A)}{\det(-A)}. \quad (3)$$

Therefore, adj(−**A**) can be obtained by rearranging Eq. (3) and dividing $-\mathbf{A}^{-1}$ by det(−**A**)).

Third, the determinacy of a predicted direction of (N_i) response to perturbation was assessed by weighted prediction matrix (**W**). To determine **W** the absolute value of each element of the adjoint matrix was divided by the absolute feedback matrix **T**

$$\mathbf{W} = \frac{|\text{adj}\ \mathbf{A}|}{\mathbf{T}}. \quad (4)$$

In **W,** each element is a ratio of the net number of complementary feedback loops, and the total number of complementary feedback loops (**T**), where **T** is determined by

$$\mathbf{T}_{ij} = \text{permanent}\left(\text{minor} - A^{\#}{}_{ij}\right)^{\boldsymbol{T}} \quad (5)$$

where $A^{\#}{}_{i,j}$ contains the absolute values of the elements of −**A** and $\boldsymbol{T}$ is the transpose of a matrix. The minor is the first minor of $A^{\#}$ with respect to row i and column j. The matrix permanent was calculated using the Mathematica (Wolfram Research, Inc., Version 10.2, Champagne, Illinois, USA). function *permanent* according to previous research (Dambacher et al. 2003*a*, Eves 2012).

Indeterminacy is evaluated for each element of the prediction matrix **W** according to a numerical criterion. An element $\mathbf{W}_{i,j}$ was considered determinate when $\mathbf{W}_{i,j} \geq 0.5$ (Dambacher et al. 2003*a*). Simulation studies of 5 and 10 node (species) models with randomized parameters found that $\mathbf{W}_{\text{i,j}} \geq 0.5$ maintained a predictable sign for >90% of cases examined (Dambacher et al. 2003*a*).

Press perturbations

Four press perturbations were investigated (Fig. 3): (1) an increase of the target predator adult directly (PA1), (2) an increase of the target predator juvenile (PJ1), (3) a decrease of the non-target predator adult (PA2), and (4) a decrease of the non-target predator juvenile (PJ2). The proportion of each of the three possible outcomes (negative, positive, ambiguous) was plotted for the adult predator (A1) response as a proportion of all plausible food web topologies.

To assess the effect of applying multiple press perturbations simultaneously we also grouped single species perturbations by combinations of two, three, and a single perturbation with all four options. The net feedback for each perturbation was summed and divided by the total feedback to calculate indeterminacy for combined press perturbations (Dambacher et al. 2002). We then plotted the proportion of target species predicted to be indeterminate for each perturbation combination group.

Results

We evaluated the response of the target adult predator A1 to a total of 2715 model experiments. These include each of the four perturbations shown in Fig. 4 (and combinations, Fig. 5) applied to each of the 193 food web topologies.

Considering all four single perturbations applied independently, few responses (39%) were sign determined (Fig. 4). That is, it cannot be determined whether the target species we are trying to increase will increase or decrease with the information at hand (Fig. 4). Model outcomes where the direction of the target species response could be determined also differed in direction. Of all 193 responses 34% resulted in the desirable

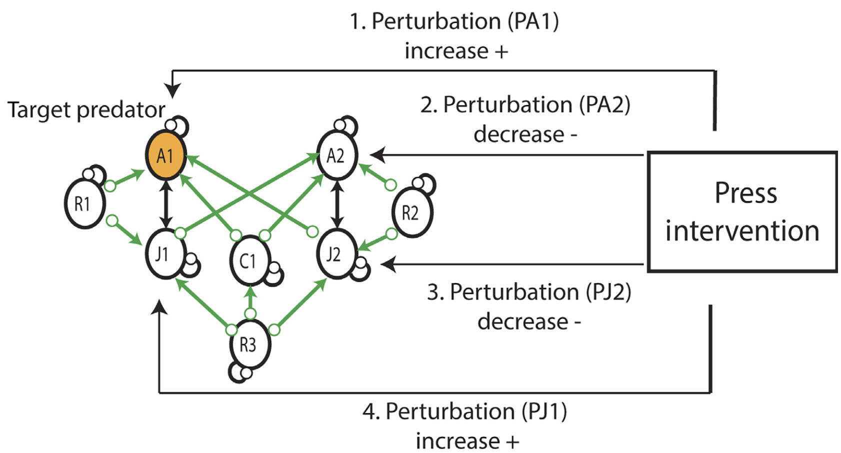


FIG. 3. Four press perturbations used to manage a focal predator (A1). Black lines with arrows extending from the press perturbation box point to species components that are pressed in model experiments. Press perturbations were applied to the adult of the target predator PA1 (increase), the juvenile of the target predator PJ1 (increase), the adult of a non-target predator PA2 (decrease), and the juvenile of the non-target predator PJ2 (decrease). Circles represent species components of the model food web. Within the food web arrow heads indicate positive effect and circles negative effects. [Color figure can be viewed at wileyonlinelibrary.com]

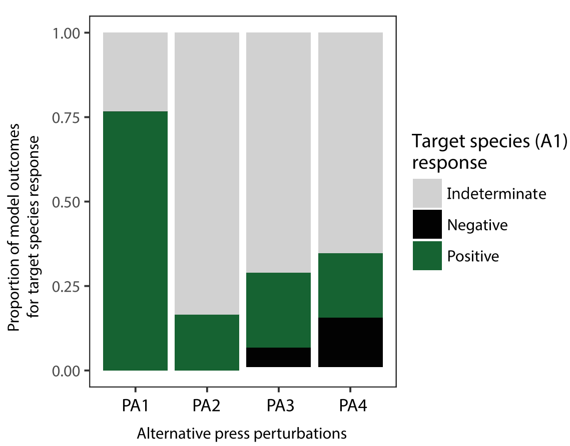


FIG. 4. Consistency of the focal species response to four different press perturbations. Sustained perturbations were applied to the adult of the target predator PA1 (increase), the juvenile of the target predator PJ1 (decrease), the adult of a non-target predator PA2 (increase), and the juvenile of the non-target predator PJ2 (decrease) in 193 different food web topologies. The colored bars show the proportion of adult target species responses that were positive (green), negative (black), and indeterminate (gray). Each perturbation outcome is assessed with a weighted prediction matrix (weighted value > 0.5) using a net feedback value with 90% expectation that the sign of the response (+,–) can be predicted, i.e., <0.5 indicates an indeterminate result (Dambacher et al. 2003*a*).

positive response in the target predator, while 5% resulted in the negative undesirable response.

Directional consistency was low for non-target predator perturbations (PA2, PJ2). The target predator response was not consistent with the desired outcome in 75% of food webs when the non-target adults (PA2) and 79% of the non-target juveniles (PJ2) perturbations (Fig. 3). Moreover, these non-target predator press perturbations resulted in three qualitative responses. Manipulating the non-target predator produced desirable outcomes but also resulted in outcomes that were opposite the intended outcome, as well as indeterminate outcomes. In comparison, press perturbations of the target predator (PA1, PJ1) produced only desirable outcomes for the target species and indeterminate responses (Fig. 4).

Despite the low directional consistency across all press perturbations for all food web topologies, our analysis reveals that alternative press perturbations differed in the consistency of their outcomes. Most importantly, direct perturbation of the target predator (PA1) had the highest consistency. This management perturbation resulted in an increase in the target predator in 77% of food web topologies. The remaining 23% were indeterminate (Fig. 4). In contrast, increasing the abundance of the targeted predator's juvenile stage (PJ1) produced the highest percentage of indeterminate outcomes (83%) with few sign determined outcomes (0% negative, 17% positive).

Multiple management perturbations are sometimes applied simultaneously under the expectation of increasing the chances of achieving a desirable outcome. We found that single perturbations on average had fewer indeterminate responses and therefore, responses were more consistent than combinations of two, three, and four perturbations (Fig. 5). This result was largely attributable to the low number of indeterminate responses when the target predator was directly manipulated alone (77% were determined). Generally, the number of indeterminate responses increased with the number of management perturbations. Application of all four press perturbations at the same time produced an equivalent number of indeterminate responses as the worst single species perturbation option (Fig. 5).

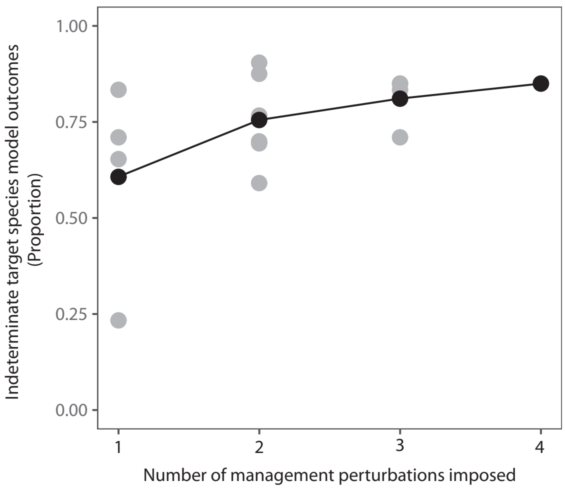


FIG. 5. Indeterminate focal species responses to management perturbations. Management perturbations are presented in four categories beginning with single species perturbations, then combinations of two, three, and finally all four management perturbations applied simultaneously. Gray circles represent the proportion of focal species responses to each management action (i.e., single or combination of species). Black circles represent the mean response for each management perturbation category. Each perturbation outcome is assessed with a weighted prediction matrix (weighted value > 0.5) using a net feedback value with 90% expectation that the sign of the response (+, −) can be predicted, i.e., <0.5 indicates an indeterminate result (Dambacher et al. 2003*a*).

DISCUSSION

Predicting species responses to press perturbations is a long standing goal of ecology with important implications for ecosystem conservation and management. Inland lake walleye fisheries in the Midwestern United States exemplify a common problem in managed ecosystems (e.g., Grubbs et al. 2016). Species abundance changes have been observed, and timely management actions are required (Hansen et al. 2015*a*, 2015*b*). Yet, food web data are scarce, research capacity is limited, and there are many food webs to manage (>1,000 walleye lakes in Wisconsin, USA). Therefore, the occurrence of particular food web linkages and their strengths are largely unknown to decision makers. In the face of this food web uncertainty, we addressed the question of whether some press perturbations have more directionally consistent outcomes. Four common management perturbations were applied to a set of food webs represented by qualitative community matrices (Dambacher et al. 2003*a*). The outcomes of these perturbations for the targeted species were mostly indeterminate across food web topologies. However, despite high indeterminacy, we also found certain perturbations produced the desired outcome more consistently than others.

Interestingly, we found that limiting adult mortality for the target species had the most consistent outcomes of the four press perturbations. If decision makers are averse to uncertainty (Epstein 1999), then a perturbation that directly effects the target species is a good option. On the other hand, adding more juveniles in our model food webs resulted in a high number of indeterminate responses in the target adult. These findings parallel previous theoretical work, which found that direct press perturbations produced fewer indeterminate responses than indirect perturbations in community matrices with plausible parameter values included (Yodzis 1988). Recent qualitative analysis suggests that the predicted outcomes of a range of management and environmental perturbations are more likely to produce the desired outcome when the set of food web models is constrained (Hosack et al. 2008, Dambacher et al. 2015, Marzloff et al. 2016).

Direct target predator manipulation had a relatively consistent positive response, and yet some responses (23%) were found to be indeterminate. That human actions can potentially have unanticipated impacts is a classic ecological idea. For example, the "paradox of enrichment" argued that the well-intentioned practice of trying to increase ecological production through nutrient enrichment could destabilize population dynamics and lead to unwanted extinctions (Rosenzweig 1971). Another closely related example that runs counter to initial expectations is the idea that under some conditions increased mortality or harvest can potentially increase the abundance of a population ("hydra effects"; Ricker 1954, Abrams 2009). In food webs, increasing the growth rate of target species has a direct component and an indirect component that together sum to the net effect of a change in abundance (Yodzis 1988). Therefore, a direct increase in a target species can lead to an unanticipated or opposite outcome when negative indirect feedbacks are numerous and/or have a summed magnitude that is larger than positive direct and indirect effects.

The outcome of manipulating the non-target species is difficult to predict because perturbation effects transfer among species via a network of links that are not well known. Yet management may attempt to control species through removal of their predators or competitors, even when food web interactions are uncertain (Pine et al. 2009). Given our current knowledge of the food web, our results argue against this approach as a way of addressing the recent walleye population declines that motivate our research. In our analysis, removal of the non-target predator (bass) produced responses in the target predator (walleye) that were sensitive to topology. For topologies in which walleye responses were determinant, bass reductions resulted in model outcomes where walleye adults both increased and decreased. Managers may want to avoid perturbations that can potentially decrease the target species if a better option exists.

Multiple perturbations are sometimes applied at the same time in attempt to increase the magnitude of a management perturbations impact. Previous modelling research has argued that in some cases such practices are predicted to produce more desirable management outcomes compared to single perturbations (Marzloff et al.

2016). However, in our study, increasing the number of press perturbations applied simultaneously generally decreased the consistency of the direction of the target species response. As the number of perturbations applied increased so did the proportion of indeterminate responses. Translated in terms of loop analysis, combining multiple perturbations tended to decrease the ratio of net feedback to total feedback. This suggests that in data poor situations it is important to consider food web uncertainty when individual and combined management perturbations are compared. If achieving a management goal requires that multiple perturbations are applied to increase the magnitude of a desirable outcome, then managers may want to apply press perturbations that are predicted to be directionally consistent when combined.

Much of the research on predicting species dynamics with uncertainty in food webs focuses on the parameter values of the community matrix (links strengths) that govern interaction strengths (Yodzis 1988, Montoya et al. 2009, Novak et al. 2011). It is important to recognize that changes in link strength can reverse the direction of a press perturbation outcome. Our results that show a high number of indeterminate responses certainly support this idea. Yet some directional predictions are consistent, even though we had no information on parameter values. Interestingly, the outcomes of management perturbations can also change among food webs with different topological wiring. If determining precise values for the magnitude of key interactions is an important step in predicting species responses to perturbations, then establishing the presence and absence of key interactions is perhaps the first step.

In the Midwestern walleye fishery, there is no single true food web to manage and the topology of every real food web on the landscape can never be fully known. Nonetheless, the same type of perturbation is often applied to many lakes. Our analysis focused on a single target species that was embedded within a set of key food web interactions. This kind of intermediate food web module is well suited to loop analysis (Dambacher et al. 2015). Yet, it is important to remember that the real food webs that contain walleye are more complex in their entirety than the eight-species webs examined here. The relatively fewer species and linkages in our models potentially limit the impact of indirect effects compared to real walleye lake ecosystems. For example, our models contain few long indirect feedback loops, which may alter perturbation outcomes. Further the real landscape of food webs will contain some distribution of link patterns where some topologies are more prevalent than others. This landscape may include food web motifs that are not considered here. However, we argue that given our starting point, the use of intermediate complexity food webs provides insights that are well suited to our question and provide knowledge that is useful to inform management decisions.

Moving forward requires that future research attempt to reduce food web uncertainty and thereby improve management. Recent qualitative analysis has been used as a means to prioritize key topological uncertainties (Hosack et al. 2008, Dambacher et al. 2015, Marzloff et al. 2016). A cursory examination of the models used in our analysis suggests that some inconsistency in the bass reduction perturbation can be reduced if more is known about the occurrence of predation links between bass and walleye (Appendix S1). To rapidly procure empirical data on food web linkages, recent advances in DNA barcoding promise to improve the ability to resolve species diet contents (Bartley et al. 2015, Kelling et al. 2016), and isotope tracers provide insights into changes in food web structure (Tunney et al. 2014). Perturbation experiments, whether natural or through planned manipulation, are a promising way to probe the kinds of uncertainty identified in our study (Walters and Holling 1990, Carpenter and Kitchell 1996). Additions or removals of predators at meaningful scales are needed to expose the causal linkages that affect target species in the food web.

Feasibility and public palatability are important components to consider moving from conceptual models to on-the-ground management. Stocking juveniles is a common management practice in fisheries that is often supported by the public. In practice, adding juveniles to increase adult abundance has had mixed results (Pine et al. 2009) and the potential for this inconsistency was apparent in our analysis. For fishery management in Midwestern lakes, increasing bass harvest to improve walleye stocks might be palatable to some stakeholders. Managers may remove harvest restrictions to increase bass mortality. But even with reduced restrictions, it is hard to predict whether anglers will change their behavior and harvest enough bass to have the desired effect. A planned bass removal is another feasible option, but requires large investments of time and resources. A whole-lake bass reduction experiment is underway in Wisconsin, and is currently in a public consultation process. Directly controlling mortality of the adult population is widely used by management agencies through imposing limits on the number and the size of fish that can be legally harvested. For species like walleye, however, reducing harvest is perhaps the least palatable action to the public.

Uncertainty is prevalent in many human-managed ecosystems, but management actions to protect organisms and maintain human benefit are required nonetheless (Essington 2004, Tallis et al. 2010, Schindler and Hilborn 2015). We do not suggest that assessing the direction of a species response using loop analysis and the weighted prediction matrix is all that needs to be known to understand the outcome of a press perturbation. Instead, this kind of analysis may be useful in the many situations where data are scarce, but comparisons of management perturbations are immediately required (Walters and Martell 2004). In these situations, qualitative food web interpretation is a useful way to rapidly gain insights into the consistency of species responses to different management perturbations.

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