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Linking terrestrial and aquatic ecosystems: The role of woody habitat in lake food webs

Brian M. Roth^{a,c,*}, Isaac C. Kaplan^a, Greg G. Sass^a, Pieter T. Johnson^a,
Anna E. Marburg^b, Anthony C. Yannarell^a, Tanya D. Havlicek^a,
Theodore V. Willis^a, Monica G. Turner^b, Stephen R. Carpenter^a

^a Center for Limnology, University of Wisconsin, Madison, WI 53706, United States

^b Department of Zoology, University of Wisconsin, Madison, WI 53706, United States

^c Coastal Fisheries Institute, Louisiana State University, Baton Rouge, LA 70803, United States

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ABSTRACT

Trees that fall into lakes from riparian forest become habitat for aquatic organisms, and are potentially an important link between terrestrial and aquatic ecosystems. Coarse woody habitat (CWH) promotes the production of benthic invertebrate prey and offers refuge for prey fishes, which are in turn consumed by piscivorous fishes. We used a simulation model to explore responses of an aquatic food web to changes in CWH caused by lakeshore residential development and windstorm, as well as to harvest of adult piscivores. Residential development had a negative effect on fishes, and could lead to extirpation of benthivorous prey fish species. In contrast, pulsed addition of CWH following a windstorm had little effect on the aquatic food web. Our results suggest that CWH is more important as shelter for prey fishes than as a substrate for benthic invertebrate production. However, piscivore harvest can supersede the role of CWH as prey shelter, leading to piscivore collapse and prey persistence even when CWH levels are low enough to promote piscivore dominance. Thus, the effects of lakeshore residential development on fishes can be masked by angler harvest of top piscivores.

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1. Introduction

Worldwide, changes in land use and land cover during the past two centuries have been profound (Turner et al., 1996; Chapin et al., 2000; Dale et al., 2000). Housing density has increased in many rural areas that offer natural amenities such as mountains and lakes in the United States (Motzkin et al., 1996; Wear and Bolstad, 1998; Radeloff et al., 2001; Hansen et al., 2002; Schnaiberg et al., 2002; Scheuerell and Schindler, 2004) and Europe (Olin et al., 2002; Toivonen et al., 2004; Vail and Heldt, 2004). Ecological implications of rural development for local fauna have been investigated (Friesen

et al., 1995; Harrison, 1997; Odell and Knight, 2001), but many questions remain unanswered. In this study, we explore the implications of human activities associated with residential development in lake riparian zones for fish populations in a forested, rural lake district in northern Wisconsin, USA. Residential development in this area is associated with declines in the abundance of fallen trees in lakes (coarse woody habitat or CWH) (Christensen et al., 1996; Schindler et al., 2000; Jennings et al., 2003). These habitat changes are associated with adverse effects on fishes (Schindler et al., 2000; Scheuerell and Schindler, 2004) but the mechanisms of these effects are uncertain.

* Corresponding author at: Coastal Fisheries Institute, Baton Rouge, LA 70808, United States. Tel.: +1 225 578 9926; fax: +1 225 578 6513.

E-mail address: broth2@lsu.edu (B.M. Roth).

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Aquatic CWH is a prominent habitat in many lakes. CWH provides a substrate for primary and secondary production that supports fish populations (Angermeier and Karr, 1984; Benke et al., 1984; Vander Zanden and Vadeboncoeur, 2002). CWH also provides refuge from predation for juvenile fishes and increased prey availability for both juveniles and adults (Werner et al., 1981; Werner and Hall, 1983; Osenberg et al., 1988). Therefore, the loss of CWH concurrent with residential development could increase juvenile fish mortality, depress growth rates, and increase the probability of depensatory population growth dynamics or regime shifts (Schindler et al., 2000; Post et al., 2002; Carpenter, 2003).

Alternatively, within-lake processes such as angler harvest may mask negative effects of removing CWH. Angling is an especially strong driver of lake ecosystems (Cox and Walters, 2002; Post et al., 2002), with consequences at all trophic levels (Jeppesen et al., 1998; Jones and Tonn, 2004). Considering that increases in lakeshore residential development will likely be associated with increased angling pressure, the effects of angling and habitat changes should be considered jointly.

Comparative studies of CWH and fishes have shown strong trends but also raise many questions about the mechanisms through which CWH and fish dynamics interact. These mechanisms should be investigated with long-term, landscape-scale manipulations of riparian forests and fisheries. Such experiments will require extensive resource commitments, and must run for extensive time periods because trees, CWH and fishes turn over slowly. Before undertaking such costly field experiments, it is useful to consider the key mechanisms and their likely outcomes using models. Although models are artificial, simplified representations of terrestrial-aquatic systems, they are internally consistent, lead to clear predictions that can be falsified, and provide an arena for rapid, inexpensive experimentation.

The purpose of this paper is to explore the interactions of CWH and fishes using a model that explicitly couples riparian forest dynamics and harvest of piscivorous fish to responses of the lake food web. We developed the model to ask three specific questions. (1) Do changes in CWH mediated through lakeshore residential development affect lake food webs in a similar manner to natural disturbances such as windstorms? (2) How does harvest of piscivorous fishes change the response of the food web to riparian forest dynamics? (3) What is the role of CWH in these modeled interactions?

2. Methods

2.1. Study area

The Northern Highlands Lake District (NHLD) of northern Wisconsin, USA is a rural forested landscape characterized by many lakes and increasing development pressure (WDNR, 1996; Schnaiberg et al., 2002). Vilas County, the heart of the NHLD, contains over 1300 lakes ranging in size from 0.1 to >1500 ha that cover 16% of the county's surface area. Housing density in Vilas County has increased rapidly since the 1960s, and over half of new homes were built on lakeshores (WDNR, 1996; Schnaiberg et al., 2002). At the current building rate, all undeveloped lakes not in public own-

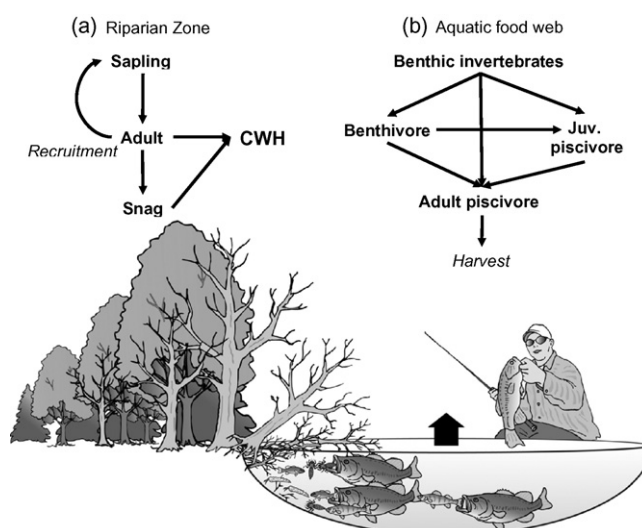


Fig. 1 – Diagram of model structure. Rates are designated in *italics*, pools in **bold font.**

ership could be developed within the next 20 years (WDNR, 1996).

2.2. Model overview

The model consists of a terrestrial module and aquatic food web module linked through CWH inputs to the lake (Fig. 1). Both terrestrial and aquatic aspects of the model are based largely on the riparian forest and food web of Little Rock Lake in Vilas County, Wisconsin. We used the metrics of Christensen et al. (1996) to quantify CWH and riparian forest abundance. CWH includes logs >10 cm in diameter, and is reported as the number per km of shoreline. The riparian forest is measured as the number of trees >5 cm dbh per ha. CWH and riparian forest tree densities in Little Rock Lake are intermediate compared to other undeveloped lakes in the region (Christensen et al., 1996; Marburg et al., *in press*). The terrestrial module produces CWH based on riparian forest dynamics which is then input into the fish food web module. In the aquatic food web, CWH acts as a refuge from predation and a source of food (benthic invertebrates) to the rest of the food web. Equations and parameter notes are presented in the Appendix A.

2.3. Riparian dynamics and CWH module structure

The terrestrial module is an adaptation of the Turner (2003) discrete-time model that simulated CWH production from northern Wisconsin riparian forests. We modified several details of the Turner (2003) model to approximate forest succession dynamics. Our purpose was not to model forest succession, but to create dynamic CWH inputs to the aquatic system based on riparian forest composition. The terrestrial aspect of the model tracks two major pools composed of 'early successional' trees, which represent fast-growing, shade-intolerant trees with higher rates of mortality and wood decomposition, and 'mid-late successional' trees, which represent slow-growing, shade-tolerant trees with lower rates

of mortality and wood decomposition. Within each pool, we tracked four state variables: saplings, adult trees, snags (standing dead trees), and CWH (Fig. 1). Sapling recruitment depended not only on the abundance of conspecific adults, but was also negatively affected by interspecific adult abundance. In this fashion, we were able to model shading of saplings by adult trees.

We simulated a 300-year time series of all state variables. During each one-year time step, state variables were updated according to a set of growth equations. Saplings graduated into adults, adult trees died and either fell immediately or became snags. Only snags and fallen adult trees contributed to the CWH pool. CWH was then used in the fish food web module to determine predator and prey functional responses and to provide a substrate for benthic invertebrate production.

2.4. Aquatic food web

The aquatic food web module tracked the response of fish biomass pools to CWH dynamics and fish harvest. The state variables represent the biomass pools of a general benthivore (parameterized as yellow perch *Perca flavescens*), a juvenile piscivore (parameterized as juvenile largemouth bass *Micropterus salmoides*), and an adult piscivore (parameterized as largemouth bass). These fish interact with each other in a simple three-tiered food web where invertebrates serve as food for the benthivore and both piscivore stages. Juvenile piscivores can be consumed by both the benthivore and adult piscivore (Fig. 1). Predation follows the functional response of Walters et al. (1997). This functional response implicitly apportions prey (juvenile piscivore and benthivore) between an invulnerable pool within CWH, and vulnerable pool outside of the CWH refuge. In the context of these functional response parameters, we were uncertain about whether benthivores or juvenile piscivores are more vulnerable to predation as CWH abundance decreases. Therefore, we considered two scenarios for the vulnerability parameters: one in which the benthivore was more vulnerable than the juvenile piscivore to CWH removal, and another where the benthivore was less vulnerable than the juvenile piscivore. This dichotomy allowed us to identify changes in the food web that resulted from differing susceptibility to predation.

2.5. Simulations

The effects of disturbances to the riparian forest were addressed by initiating either a severe windstorm or residential development at year 50 of the 300-year simulation. In the model, residential development entailed thinning of the riparian forest, as well as removal of CWH from the littoral zone. Following the onset of development, thinning of adult trees occurred at a constant rate per year and was indiscriminate with regard to tree type, i.e., whether it was an early successional or mid-late successional tree. Forest density was not allowed to decline below 800 trees ha⁻¹ (Christensen et al., 1996). Snags and CWH were removed in every time step following the onset of development regardless of the number of adult trees. We assumed that all saplings, adult trees, snags, and CWH lost to thinning were removed permanently.

The windstorm scenario was modeled as an instantaneous 65% windfall of adult trees and snags around a CWH-poor lake (70% less CWH than initial conditions in the development scenario). CWH produced from fallen adults and snags was then allowed to naturally dissipate from the littoral zone as a function of decay and movement into deep water. This percentage of riparian forest killed is large relative to natural events (Canham and Loucks, 1984; Frelich and Lorimer, 1991). Our attempt was to initiate a near-maximal response of the aquatic food web in order to compare this natural disturbance to anthropogenic disturbances.

To evaluate the influence of fishing on the food web response to CWH dynamics, we initiated piscivore harvest at year 100 in simulations of either residential development or windstorm. We implemented harvest on the adult piscivore by changing the catchability constant q from zero to the nominal value (see Appendix A, Eq. (5)). Thus, for each of the riparian perturbation scenarios, we ran two vulnerability and two fish harvest scenarios.

To evaluate the role of CWH as a substrate for benthic invertebrate production, we simulated a scenario with increased benthic invertebrate production. The logic for this test is as follows: if CWH is more important as substrate for benthic invertebrate production than as shelter for prey fishes, then increasing benthic invertebrate production should sustain elevated benthivore biomass in a situation where the benthivores would otherwise be suppressed by piscivores. We conducted this test by increasing benthic invertebrate production on CWH by 400% under conditions where residential development increased, the adult piscivore was not harvested, and the functional response dictated that the benthivore was more vulnerable than the juvenile piscivore as CWH decreased.

2.6. Sensitivity analysis

We conducted a numerical sensitivity analysis for both the fish module and the wood module. We changed each parameter $\pm 10\%$ and calculated the equilibrium biomass response in the benthivore and juvenile and adult piscivore. Parameters directly related to the perturbations – development and windstorm – were excluded from the sensitivity analysis and explored separately. Therefore, we ran this analysis with no development or windstorm. The vulnerability of the benthivore was varied $\pm 10\%$ from the average of its vulnerability in other scenarios. Harvest was set at an intermediate value ($q = 0.01$). Results of this analysis are presented in the Appendix A.

3. Results

3.1. Food web responses to natural and anthropogenic perturbations

Riparian forest disturbances influenced the aquatic food web, but the effects varied with vulnerability of the benthivore and juvenile piscivore. In the development scenario, all riparian forest and coarse wood stocks decreased, and CWH nearly disappeared in under fifty years (Fig. 2A). The decline in riparian forest stocks occurred concomitant with a switch in forest

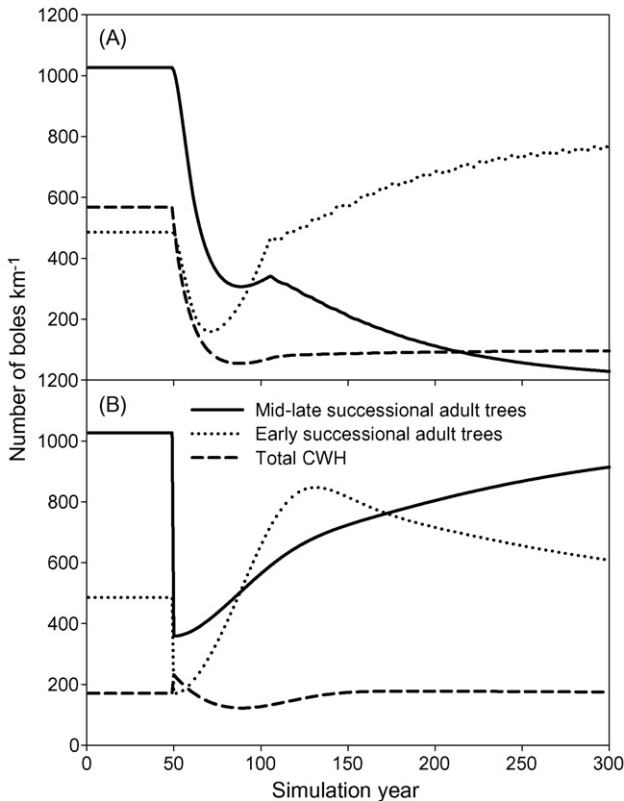


Fig. 2 – Simulation results for the riparian forest in the (A) residential development and (B) windstorm scenarios. Perturbations are initiated at year 50 of the simulation. Total CWH represents the combined contribution of CWH produced by mid-late successional and early successional trees.

dominance from mid-late successional trees to early successional trees. The loss of CWH initiated a decline in all three fish pools (Fig. 3A and B). When the benthivore was less vulnerable than the juvenile piscivore to changes in CWH abundance, benthivore biomass eventually recovered to near predevelopment levels owing to reduced piscivore abundance (Fig. 3A). However, when the benthivore was more vulnerable, residential development led to benthivore extirpation (Fig. 3B).

Similar to the residential development scenarios, aquatic food web responses to a windstorm in the riparian forest surrounding a CWH-poor lake depended on the respective vulnerabilities of the benthivore and the juvenile piscivore. Generally, the windstorm caused large-magnitude dynamics in the riparian forest. Adult trees decreased by 65% (as prescribed), and total CWH increased from 170 logs km⁻¹ to 240 logs km⁻¹ (Fig. 2B). However, these effects were tempered in the food web (Fig. 4A and B). With higher juvenile piscivore vulnerability, the model predicted that benthivore biomass would dominate the aquatic food web before and after the windstorm (Fig. 4A). When the benthivore was more vulnerable, piscivore biomass dominated (Fig. 4B). In this piscivore-dominated scenario, the reduction of CWH inputs to the littoral zone led to an extended period of very low benthivore biomass while the forest recovered from the windstorm.

3.2. The effect of angling on food web responses to riparian dynamics

Piscivore harvest generally had a much stronger effect on the aquatic food web than riparian perturbations in our model. However, this effect was not always unilateral and depended on how vulnerabilities to predation were apportioned between the juvenile piscivore and benthivore in each simulation. Generally, the addition of piscivore harvest uncoupled the relationship between CWH and the food web. In the residential development scenario, piscivore harvest led to benthivore recovery independent of benthivore or juvenile piscivore vulnerability (Fig. 5A and B). Similarly, the onset of piscivore harvest after the windstorm exaggerated benthivore recovery to decreased CWH, and the benthivores returned to their initial biomass in both vulnerability scenarios (Fig. 6A and B).

3.3. The dominant role of CWH in the model food web

Coarse woody habitat was more important as shelter than as substrate for benthic invertebrate production in our model. When compared to the nominal scenario presented in Fig. 3B, increasing benthic invertebrate production on CWH 400-fold did not prevent collapse of the benthivorous fishes (Fig. 7). The

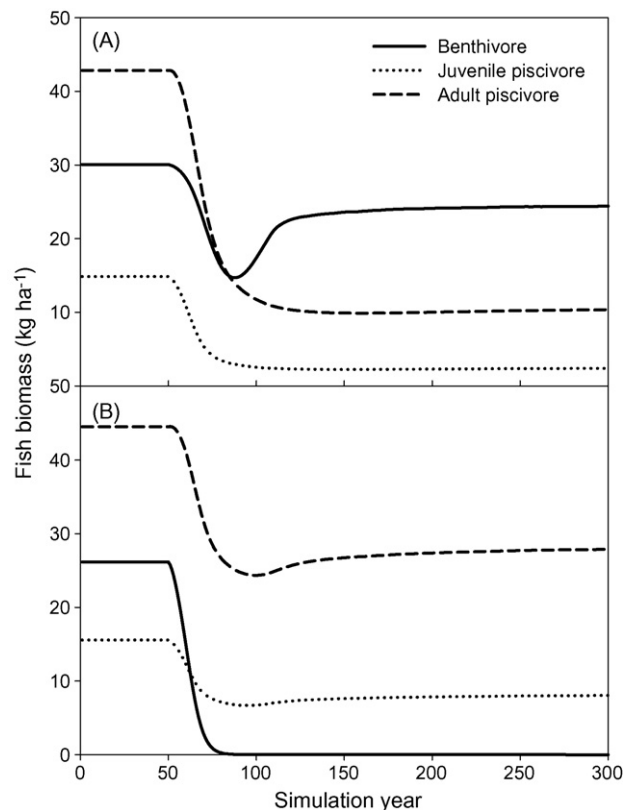


Fig. 3 – Aquatic food web dynamics during the residential development scenario without piscivore harvest when (A) the benthivore is less vulnerable to changes in CWH abundance compared to the juvenile piscivore, and (B) when the benthivore is more vulnerable.

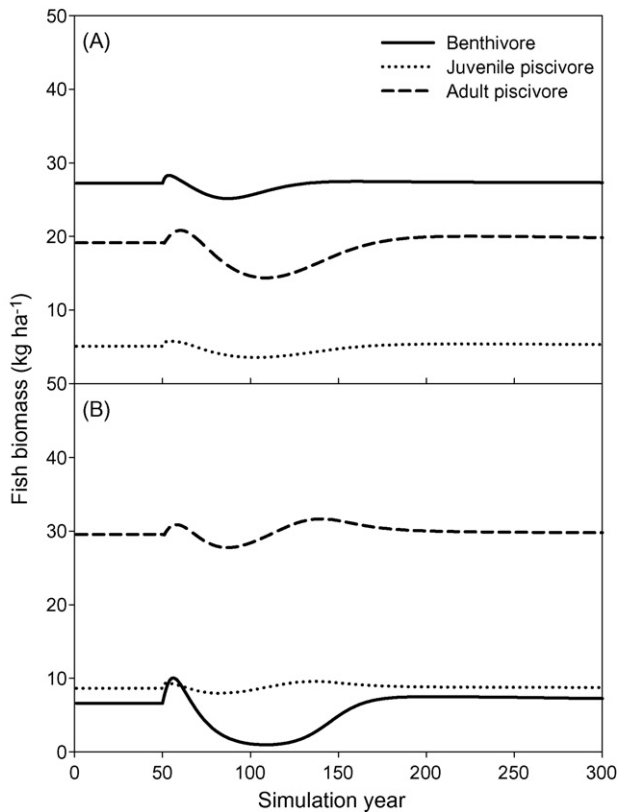


Fig. 4 – Aquatic food web dynamics during the windstorm scenario without piscivore harvest. In (A), the benthivore is less vulnerable to changes in CWH abundance compared to the juvenile piscivore, and in (B), the benthivore is more vulnerable.

manipulation did increase the initial biomass of all fish pools (Fig. 7). Much larger increases in benthic invertebrate production are implausible, and led to unrealistic growth rates in all food web components.

4. Discussion and conclusions

4.1. Response of aquatic food web to riparian zone perturbation and fishing

Residential development of the riparian forest of our simulated lake resulted in a long-term loss of adult trees, coarse woody habitat, and fish. However, piscivore harvest drastically altered the relationship between CWH and the aquatic food web. Angling allowed benthivore biomass to remain high in the development scenario, even when CWH and vulnerability values promoted benthivore collapse. Our model simulations are corroborated by evidence that even moderate angling pressure strongly influences aquatic ecosystems and their food webs (Carpenter et al., 1994; Cox and Walters, 2002; Post et al., 2002).

In contrast to the development scenario, the windstorm had little effect on the aquatic food web. Although the storm led to an initial increase in CWH levels, natural processes then gradually removed CWH from the littoral zone. With-

out adult piscivore harvest, benthivore and piscivore biomass responded positively to the CWH pulse, but only briefly. In contrast to the development scenario, benthivore biomass returned to near initial biomass after the windstorm in all vulnerability and harvest scenarios. The lack of long-term food web response following the windstorm suggests that adding wood to a CWH-poor lake has little positive effect on the fish community, but removing wood on a CWH-rich lake (as in the residential development scenarios) has large repercussions. In streams, adding CWH to depauperate systems increases total fish habitat and production (e.g. Roni and Quinn, 2001), but no analogous examples have been thoroughly examined in lakes at the whole-ecosystem scale.

CWH was important in our littoral food web primarily because it provided shelter for the juvenile piscivore and benthivore. In our model, increased benthic invertebrate production served to increase the biomass of all fish community members, which in turn led to no change in the relative abundance of the piscivore and benthivore. This supports the proposal that benthic invertebrate production may help to maintain top-down control in lakes (Vander Zanden et al., 2005). Consequently, food web composition and biomass dynamics owed largely to piscivore harvest and the vulnerability of each respective fish biomass pool to predation. For instance, the model suggests that when harvest is absent or CWH is uncommon, the food web could have two very different outcomes depending on the relative vulnerability of the

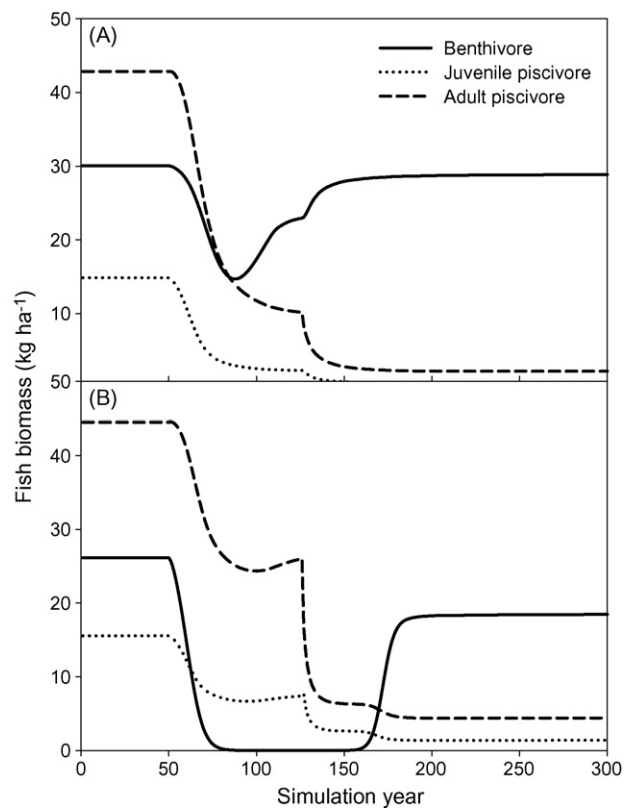


Fig. 5 – Aquatic food web dynamics during the residential development scenario with modest harvest of the adult piscivore. In (A), the benthivore is less vulnerable to changes in CWH abundance compared to the juvenile piscivore, and in (B), the benthivore is more vulnerable.

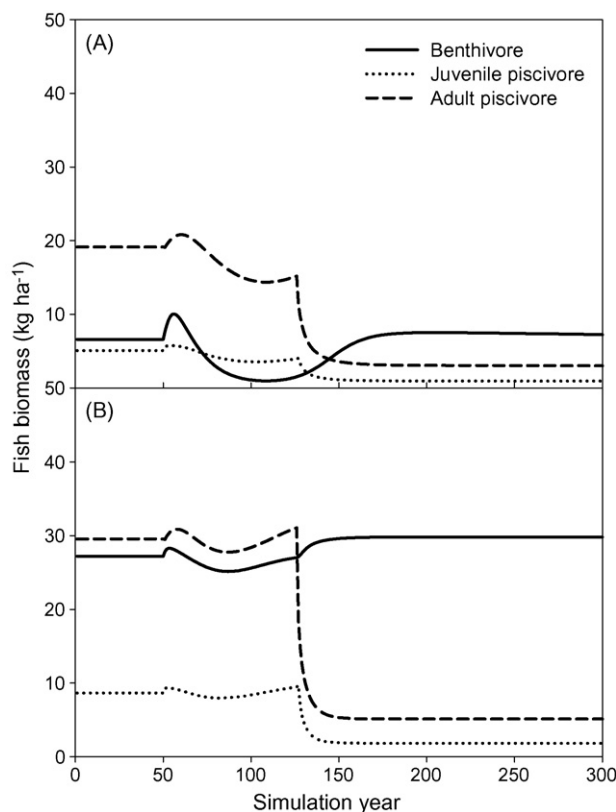


Fig. 6 – Aquatic food web dynamics during the windstorm scenario with piscivore harvest when (A) the benthivore is less vulnerable to changes in CWH abundance compared to the juvenile piscivore, and (B) when the benthivore is more vulnerable.

benthivore and the juvenile piscivore. This divergence should be explored further in field studies.

The composition of the model fish community was similar to that found in many northern Wisconsin lakes (Tonn, 1980; Rahel, 1982). In general, the piscivore was most abundant

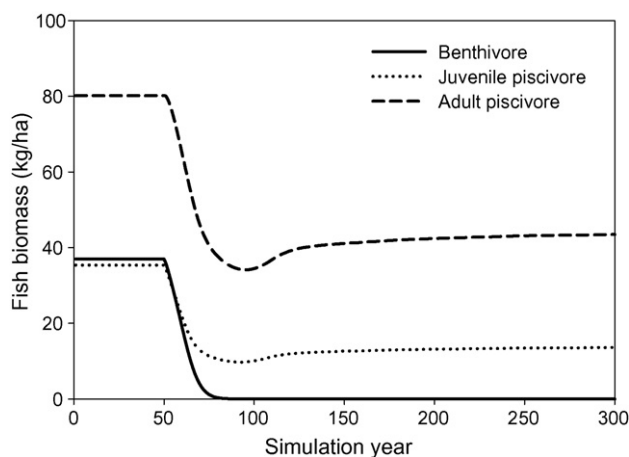


Fig. 7 – The aquatic food web in the development scenario, with the benthivore more vulnerable, with piscivore harvest, and benthic invertebrate production on CWH increased 400-fold compared to the nominal scenario.

and kept benthivore biomass low, except for two situations: (1) if the benthivore was less vulnerable and CWH was low, or (2) if fishing depressed piscivore biomass. Similar changes have been observed in natural lakes. For example, yellow perch dominated total fish biomass in Little Rock Lake under high exploitation rates of largemouth bass prior to fishery closure (Swenson, 2002). Following the cessation of angler harvest, largemouth bass came to dominance (Sass et al., 2006). Unexploited lakes in this region are generally piscivore dominated if physical-chemical conditions allow piscivores to survive (Carpenter and Kitchell, 1993). Thus, benthivores may be more vulnerable than juvenile piscivores in these lakes.

4.2. Model performance

Our model produced dynamics for a riparian forest, coarse woody habitat, and a simple aquatic food web that were generally consistent with the results of empirical studies on forest and fish community dynamics. The model is based largely upon parameters derived from the literature. Thus, it is likely that model results are logical consequences of currently available information about riparian forest dynamics and fish responses in northern temperate lakes.

We calibrated the riparian forest module to approximate typical dynamics during succession. The riparian forest pool drove the CWH pool of our model, contributing wood to the lake littoral zone in proportions that reflected both the composition of the forest canopy and the parameters that drive senescence. Changes in forest dynamics were apparent but dampened in the dynamics of CWH. Like other large perturbations such as fire (Hely et al., 2000), the windstorm event in our model produced a quick, large pulse of CWH, but in general CWH inputs occurred at rates comparable to those found in field studies (Stearns, 1951; Hodkinson, 1975; Harmon et al., 1986; Christensen et al., 1996; Bragg, 1997). The time scale of CWH response to forest perturbation and regrowth in the model is realistic (Hely et al., 2000). However, little information exists on CWH decay rates in northern lakes. We drew our decay parameters from work in streams in Washington State (Bilby et al., 1999), hardly the same environment as northern Wisconsin lakes. These rates are faster than those reported for slow-decaying white pine (*Pinus strobus*) in Ontario lakes (Guyette and Cole, 1999). However, natural CWH loss should be most important in the windstorm scenario, where natural loss has the potential to govern food web changes. This factor did not appear to have a strong effect in the simulations.

Benthivores in our model responded to changes in predation rates, competition with juvenile piscivores, and (to a much lesser extent) availability of invertebrate prey on CWH. All three factors can limit fish production in aquatic systems (Schindler et al., 2000). Abundant predators can also suppress fish production by confining vulnerable fishes to less productive habitats (Werner et al., 1983a,b; Werner and Hall, 1983), or by eliminating vulnerable size classes (Pine et al., 2000; De Roos et al., 2003; Persson et al., 2003). Littoral zones with high structural complexity reduce encounter rates between predatory and prey fish, in part by creating microhabitats with high visual interference for predators (Savino and Stein, 1989; Gotceitas and Colgan, 1990; Everett and Ruiz, 1993).

4.3. Conclusions

We advocate the use of modeling approaches that cross ecosystem boundaries and incorporate the movement of nutrients and biota across disparate habitats. For instance, allochthonous energy sources may drive dynamics in some unproductive ecosystems such as oligotrophic lakes and islands (Polis et al., 1997; Carpenter et al., 2005; Knight et al., 2005). As a result, within-ecosystem processes are difficult or impossible to understand without considering external energy sources (Polis et al., 1997; Loreau and Holt, 2004). Explicitly including external processes in modeling studies should yield additional insight in investigations of, for example, the implications of agricultural runoff on nutrient cycling in lakes (Bennett et al., 2001; Hu et al., 2006), and the effect of climate change on nutrient availability and microbial activity in terrestrial ecosystems (Mishra et al., 1979; Langeveld and Leffelaar, 2002; Schwalm and Ek, 2004). The effect of riparian dynamics on aquatic food webs represent another such example (Naiman et al., 2002; Francis and Schindler, 2006; Helfield and Naiman, 2006).

Residential development has the potential to drastically change the natural dynamics of woody habitat inputs and losses. Humans tend to simplify the littoral zone of developed lakes by removing CWH and macrophytes (Christensen et al., 1996; Radomski and Goeman, 2001; Jennings et al., 2003). In addition, humans alter natural CWH inputs by thinning or

removing source trees from their properties (Harmon et al., 1986; Maser and Sedell, 1994; Francis and Schindler, 2006). These changes may affect fishes adversely (Schindler et al., 2000; Scheuerell and Schindler, 2004; Sass et al., 2006).

Our model suggests that the effect of development on the lake shore extends into the lake itself, and may lead to large shifts in fish communities. These effects interact strongly with those of piscivore harvest. The combined effect of lakeshore development and fishing may produce surprises in fish population dynamics, including collapse of piscivore populations, or conversely, the persistence of benthivore populations. These forest and lake dynamics depend on slowly changing variables, including trees, fallen logs, and long-lived piscivorous fishes. Such slow changes may not be apparent to residents, anglers or managers who take a short-term view of the ecosystem. Fish managers must therefore look beyond the shoreline to maintain the habitat conditions necessary for long-term sustainability of lake fisheries.

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Table A1 – Values or and sources for riparian forest parameters that were fixed throughout model calibration

Parameter	Description	Value	Units	Source
K	Carrying capacity for tree density of riparian forest	1550	Number ha ⁻¹	Christensen et al. (1996); approximate average for undeveloped lakes
L _E , L _M	Proportion of recently killed trees that fall immediately	0.9	Year ⁻¹	Estimated based on Christensen et al. (1996) who observed few standing dead trees
f _E , f _M	Proportion of snags (standing dead trees) falling	0.15	Year ⁻¹	Christensen et al. (1996); Turner (2003)
A ₁₁	Decomposition rate for CWH of early successional trees	0.035	Year ⁻¹ estimated based on Bilby et al. (1999)	
A ₂₁	Proportion of CWH of early successional trees lost to deep water	0.01	Year ⁻¹ estimated based on Turner (2003)	
A ₁₂	Decomposition rate for CWH of mid-late successional species	0.025	Year ⁻¹ estimated based on Bilby et al. (1999)	
A ₂₂	Decomposition rate for CWH of mid-late successional trees	0.01	Year ⁻¹	Estimated based on Turner (2003)
m _E	Mortality rate for adult early successional trees	0.10	Year ⁻¹	Lorimer (1980); Romme and Knight (1981); Runkle (1982)
m _M	Mortality rate for adult mid-late successional trees	0.06	Year ⁻¹	Lorimer (1980); Romme and Knight (1981); Runkle (1982)
C _E , C _M	Rate of removal of adult trees with residential development	0 if no development; 0.01 if forest >799 trees/ha	Year ⁻¹	Christensen et al. (1996); Turner (2003)
c _E , c _M	Rate of removal of tree saplings during development	0 if no development; 0.2 if forest >799 trees/ha	Year ⁻¹	Estimated
a _E , a _M	Rate of CWH removal during development	0 if no development; 0.1 development occurs	Year ⁻¹	Turner (2003)
B	Proportion of trees affected by windstorm event	65	Percent	Estimated based on Frelich and Lorimer (1991)

Subscripts following parameter letters are E = early successional species and M = mid-late successional species.

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Appendix A

A.1. Equations for riparian forest dynamics

Riparian forest dynamics were simulated by representing saplings, adult trees, snags and coarse woody habitat for early successional and mid-late successional trees. Equations for the forest model's state variables are given below. Each equation applies to both early successional species and mid-late successional species (i.e. when i = early, j = mid-late).

Saplings were simulated by a logistic growth model that included competition with adult trees using the following equation:

$$J_i(t + 1) = J_i(t) + [r_i A_i(t)(1 - \alpha_{ii} A_i(t) - \alpha_{ij} A_j(t))] - g_i J_i(t) \quad (1)$$

where $J_i(t)$ is the sapling density of type i at time t , $A_i(t)$ the adult tree density of type i at time t , r_i the intrinsic rate of increase for sapling i , g_i the graduation rate of sapling i to the canopy, α_{ii} the effect of adult trees on saplings of the same tree-type, and α_{ij} is the effect of adult trees of type j on saplings of tree-type i , four saplings of early-successional species were given a higher intrinsic rate of increase (Table A1) than mid-late successional species ($r_{\text{early}} = 1$ and $r_{\text{mid-late}} = 0.5$) to reflect a higher reproductive potential. Early-successional saplings also graduated to the canopy faster than mid-late successional saplings ($g_{\text{early}} = 0.02$ and $g_{\text{mid-late}} = 0.01$), reflecting a higher growth rate. Logistic growth of saplings was simulated through the α_{ij} parameters. Extensive manipulation of the competition coefficients scaled relative to K identified a narrow range of values that would produce reasonable dynamics for adult trees.

Adult tree density, A_i , varied with the recruitment of new trees from the sapling pool and losses due to mortality according to the following equation:

$$A_i(t + 1) = A_i(t) + g_i J_i(t) - m_i A_i(t) \quad (2)$$

where $A_i(t)$ is the adult tree density of type i at time t , g_i the graduation rate of saplings J_i to the canopy and m_i is the mortality rate of adult trees. The mortality rate for early successional trees was set such that, in concert with competi-

tion coefficients, early successional trees would decline 60–80 years after a disturbance event. The lower mortality rate of mid-late successional species allowed them to dominate the older stands. Trees that died could remain as snags or fall directly to the forest floor and become CWH.

Standing snags were represented by the following equation:

$$S_i(t + 1) = S_i(t) + [(1 - L_i)m_i A_i(t) - f_i S_i(t)] \quad (3)$$

where $S_i(t)$ is the snag population at time t , L_i the proportion of recently killed adult trees that fall immediately (thus, $1 - L$ is the proportion that become snags), and f_i is the proportion of snags falling each year.

Coarse woody habitat dynamics varied with inputs from both recently killed trees and snags and losses to decomposition, transport away from the littoral zone, or removals by humans that were associated with lakeshore development. We modeled CWH dynamics using the following equation:

$$D_i(t + 1) = D_i(t) + [\gamma f_i S_i(t) + \gamma L_i m_i S_i(t)] - [(a + b)D_i(t)] \quad (4)$$

where $D_i(t)$ is the population of CWH at time t , γ the proportion of falling snags and dead adults that land in the lake, a the decay rate of CWH in the lake, and b is the rate of loss of CWH to deep water in lake. All parameter values are in Tables A1 and A2.

A.2. Fish biomass equations

For each species, we modeled the change in biomass with the following equation:

$$\frac{dB}{dt} = G - mB^2 - nB - P_2 - P_3 - qEB \quad (5)$$

where B is the biomass of the fish group of interest, G the growth in biomass per year (see below), m the mortality rate caused by density dependent interactions, n the mortality rate caused by density independent factors, P_2 the predation due to the juvenile piscivore (0, in this case), and P_3 is the predation due to the adult piscivore. E is the angling effort, which is proportional to B , and q is the catchability coefficient for fishing.

Table A2 – Parameter values used to simulate succession

Parameter	Description	Value	Units
r_e	Intrinsic rate of increase for early successional saplings	1.1	Number year ⁻¹
r_m	Intrinsic rate of increase for saplings of mid-late successional trees	0.4	Number year ⁻¹
g_e	Graduation rate of saplings to adults for early successional trees	0.009	Year ⁻¹
g_m	Graduation rate of saplings to adults for mid-late successional trees	0.005	Year ⁻¹
α_{eE}	Effect of adult mid-late successional trees on early successional saplings	0.9K ⁻¹	Unitless
α_{eE}	Effect of adult early successional trees on early successional saplings	1K ⁻¹	Unitless
α_{mE}	Effect of adult early successional trees on mid-late successional saplings	0.6K ⁻¹	Unitless
α_{mM}	Effect of adult mid-late successional trees on mid-late successional saplings	1K ⁻¹	Unitless
Γ	Proportion of boles that land in lake	0.2	Year ⁻¹

Most values were fit during model calibration to obtain the desired succession dynamics.

Table A3 – Fish food web parameters that were fixed during model calibration

Parameter	Description	Value	Units	Source
B_1	Biomass of benthivore	12	kg ha ⁻¹	Sass (2004)
B_2	Biomass of juv. piscivore	2	kg ha ⁻¹	Sass (2004)
B_3	Biomass of adult piscivore	28	kg ha ⁻¹	Sass (2004)
G_1	Growth rate of benthivore	<0.53 × biomass	(Year × ha) ⁻¹	Randall and Minns (2000)
G_2	Growth rate of juv. piscivore	<0.32 × biomass	(Year × ha) ⁻¹	Randall and Minns (2000)
G_3	Growth rate of adult piscivore	<0.32 × biomass	(Year × ha) ⁻¹	Randall and Minns (2000)
g_1	Conversion efficiency of fish prey by piscivore	0.1	unitless	Hanson et al. (1997)
g_2	Conversion efficiency of insect prey by fish	0.1	unitless	Hanson et al. (1997)
$n3f$	Piscivore fecundity	0.28	kg juv. kg adult Year ⁻¹	Sass (2004)
b	Density of invertebrates on CWH	0.00076	kg log ⁻¹	Bowen et al. (1998)
PB	Invertebrate production/biomass	6	kg (kg × ha) ⁻¹	Benke et al. (1984)
benthicBugDens	Invertebrate density on substrate	0.12	unitless	Benke et al. (1984)
g	Conversion efficiency of invertebrates by fish	0.1	unitless	Hanson et al. (1997)
pref	Diet preference for invertebrates	0.1	unitless	Sass (2004)
L	Length of shoreline	3.3	km	Sass (2004)
lakearea	Lake area	18	ha	Sass (2004)
E	Angling effort	αB_3	angler hours Year ⁻¹	
q	Catchability of piscivore	0 or 0.02	kg ⁻¹	

We compiled parameters for the fish biomass model from a wide range of sources, including the primary literature and unpublished data collected by coauthors. When possible, we used parameter values for northern Wisconsin; otherwise, we relied on data from north temperate and temperate lakes and streams.

Growth in biomass per year (G) can be calculated as

$$G = (\text{fishCons} \times g_1) + (\text{bugCons} \times g_2) \tag{6}$$

where g_i is a conversion efficiency and fishCons the biomass of fish prey consumed (see below) bugCons is bug prey consumed (see below). Growth in biomass is constrained to be less than $B_t \times (P/B)$. P/B is a value for the ratio of productivity to biomass, from Randall and Minns (2000). For instance, if a species can increase its biomass by 50% per year, its P/B is 0.5. All parameter values for the aquatic food web are presented in Tables A3 and A4.

The system of differential equations for all three groups was solved numerically using a variable-step Runge-Kutta method (Matlab v.6.0©, Mathworks, Natick MA). We could not solve over the entire simulation period at once, because the aquatic food web is driven by coarse woody habitat, an external forcing function. Instead, we iteratively solved over each

year using the previous year’s biomasses as initial conditions. We linked the adult and juvenile pools of piscivores by transferring all juveniles alive at the end of each year into the adult pool starting the next year. Adults had a constant per-capita fecundity that did not include density dependent effects on recruitment.

We incorporated habitat-mediated predator–prey interactions and fish behavior with the functional response model of Walters et al. (1997). This model allows prey to spend time in both a ‘foraging arena’ where they are vulnerable to predators, and a refuge where they are not vulnerable to predators. In many northern Wisconsin lakes, including Little Rock Lake, this refuge is coarse woody habitat. Only fish in the vulnerable habitat are available to predators. The terms v and h from Walters et al. (1997) equations are rate constants that affect equilibrium proportion of vulnerable and invulnerable fish. We assume that this equilibrium, which represents dynamics of fish behavior, is reached instantaneously. For each time step

Table A4 – Aquatic food web parameter values used in fish food web that were manipulated to produce results consistent with field observations and for alternative vulnerability scenarios

Parameter	Description	Value	Units
m_1	Dens-dependent mortality of benthivore	0.02	kg ⁻¹
m_2	Dens-dependent mortality of juv. piscivore	0.003	kg ⁻¹
m_3	Dens-dependent mortality of adult piscivore	0.002	kg ⁻¹
n_1	Dens-independent growth of benthivore	0.6	Unitless
n_3	Dens-independent mortality of piscivore	–0.2	Unitless
a_h	CWH at which hiding is 1/2 max	50,120 and 150	logs km shoreline ⁻¹
a_v	CWH at which v is 1/2 max	50,120 and 150	logs km shoreline ⁻¹
S_{vij}	Max vulnerability of prey fish i to piscivore j	1	Year ⁻¹
S_{hij}	Max hiding of prey fish i from piscivore j	1	Year ⁻¹
c_{12}	Consumption of benthivore by juv. piscivore	0.02	Year ⁻¹
c_{21}	Consumption of juv. piscivore by benthivore	0.06	Year ⁻¹
c_{13}	Consumption of benthivore by adult piscivore	0.03	Year ⁻¹
c_{23}	Consumption of juv. piscivore by adult	0.02	Year ⁻¹

of our model, the equilibrium biomass of vulnerable fish is calculated, and predation rate (P) is calculated based on this. For any given predator, fishCons is simply the total of its calculated P values each year. We selected functions to relate the rate constants v and h to CWH density. We choose sigmoidal functions because they allowed us to incorporate the fact that low densities of logs offer almost no refuge to fish. Thus,

$$v = S_v \left(1 - \frac{w^2}{a_v^2 + w^2} \right) \quad (7)$$

$$h = S_h \left(\frac{w^2}{a_h^2 + w^2} \right) \quad (8)$$

where S_v, S_h are scaling constants, w coarse woody debris density; a_v, a_h constants equal to the coarse woody debris density at which h and v are $1/2 S_h$ and S_v , respectively.

Fish growth in the model is also dependent on invertebrates, and invertebrate abundance is assumed to increase linearly with CWH abundance. In addition, there is some baseline level of invertebrates that live on benthic substrate rather than CWH (e.g. Benke et al., 1984). We calculated a standing stock as the sum of these invertebrate pools and assumed that all new invertebrate biomass produced by the standing stock was consumed by fish. Invertebrate prey is apportioned to a fish species proportional to the fish species' biomass relative to total fish biomass multiplied by a preference parameter. Invertebrates consumed by a fish group of biomass B_1 is:

$$\text{BugCons} = \left(\frac{L \times \text{CWH} \times b}{\text{lakearea}} + \text{benthicBugDens} \right) \text{PB} \\ \times \left(\frac{B_1 \text{pref}_1}{\sum_{\text{group}=1}^3 \text{biomass}_{\text{group}} \text{pref}_{\text{group}}} \right) \quad (9)$$

where L is the length of shoreline, CWH the logs per length of shoreline, b the invertebrate biomass per log, lakearea the area of the lake, benthicBugDens the density of invertebrates living on substrate other than logs, PB the production to biomass ratio of invertebrates, B_1 the biomasses of our fish species of interest, biomass the biomass of each fish group, and pref is the preference of species of interest for invertebrates. This simple relationship allowed us to model the effect of benthic invertebrate production on fish biomass dynamics, without explicitly tracking a dynamic pool of invertebrates. This is appropriate given the minimal impact of invertebrate production on fish (see Section 3.3 and Fig. A2).

A.3. Fish vulnerability equations

The vulnerability equations derive from Walters et al. (1997). From Fig. 2 in Walters et al. (1997) we determined that

$$\frac{dV_1}{dt} = v_1 \times (B_1 - V_1) - h_1(V_1) - c_{12}V_1B_2 \quad (10)$$

The equilibrium $dV_1/dt=0$ is reached rapidly, because prey movement in and out of refuge happens on a faster time scale than predation. Solving for V_1 , the biomass of prey

vulnerable, yields

$$V_1 = \left(\frac{v_1 B_1}{v_1 + h_1 + c_{12} B_2} \right) \quad (11)$$

Predation on species 1 by species 2 is $c_{12} B_2 V_1$, which is equivalent to

$$P_{12} = \left(\frac{c_{12} B_2 v_1 B_1}{v_1 + h_1 + c_{12} B_2} \right) \quad (12)$$

Total fish consumed by a predator can be calculated by summing these P terms. For example, total predation on fish by group 2, which eats groups 1 and 3, is simply

$$\text{fishCons} = P_{12} + P_{13} \quad (13)$$

Although there are several ways to model density-dependent mortality through the functional response (See Chapter 10 in Walters and Martell, 2004), including those that adjust predator foraging time based on predation risk, growth rates, and consumption rates, we chose a simple version of density-dependent mortality to maintain model simplicity and to ensure clear interpretation of model results. In addition, model runs using our simple functional response agreed qualitatively with field observations (Sass et al., 2006).

A.4. Sensitivity analyses

The sensitivity analysis revealed that fish biomass dynamics are not sensitive to the parameters controlling forest dynamics (Fig. A1). Ten percent changes in riparian forest parameters led to less than a 3% change in the biomass of any fish group.

As expected, fish biomass pools responded more strongly to parameters directly controlling fish dynamics (Fig. A2). Ten percent changes in benthivore growth parameter x_1 and density dependent mortality parameter m_1 led to slightly over 10% changes in biomass. Both adult and juvenile piscivore were highly sensitive to fecundity parameter n_{3f} , and to fishing targeting the adult piscivores (q).

In addition to the sensitivity analysis above, we also explored the equilibrium response of benthivore and adult piscivore to a broad range of CWH and fishing rates (Figs. A3 and A4, respectively). The results support conclusions stated in the main text: (1) Fish biomass tends to increase with CWH; (2) Piscivore biomass is more influenced by fishing than by CWH; (3) Benthivore biomass declines when CWH is depleted or fishing on the piscivore is absent, and this effect is strengthened when benthivores are more vulnerable; (4) Biomass of benthivores exceeds piscivores in cases where CWH is low (100–200 logs km^{-1}) and benthivores are more vulnerable than juvenile piscivores. This benthivore-dominated state occurs even when piscivores are not fished. The requisite 100–200 logs km^{-1} is comparable both to our windstorm scenario and empirical findings in northern Wisconsin lakes (Christensen et al., 1996; Marburg et al., in press). Overall, this exploration of the model dynamics suggests that these four observations are consistent consequences of the interaction between the fish functional response, CWH dynamics, and fishing.

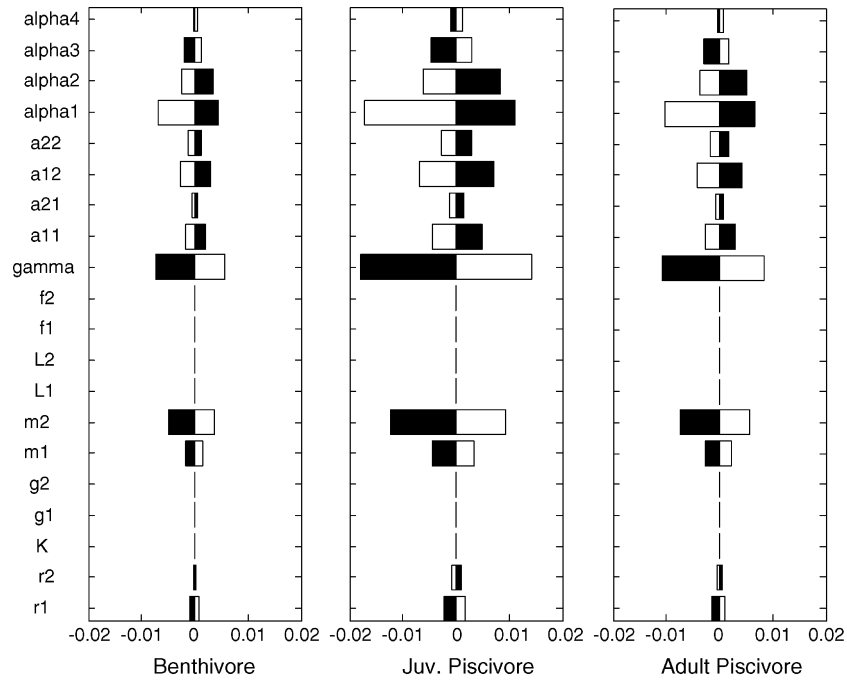


Fig. A1 – Sensitivity analysis of biomass pools to parameters that determine riparian forest dynamics. The x-axis represents proportional change in each fish biomass pool. White bars show the response when a parameter is increased 10%, and black bars show the response when a parameter is decreased by 10%. See the Appendix tables for parameter names and values.

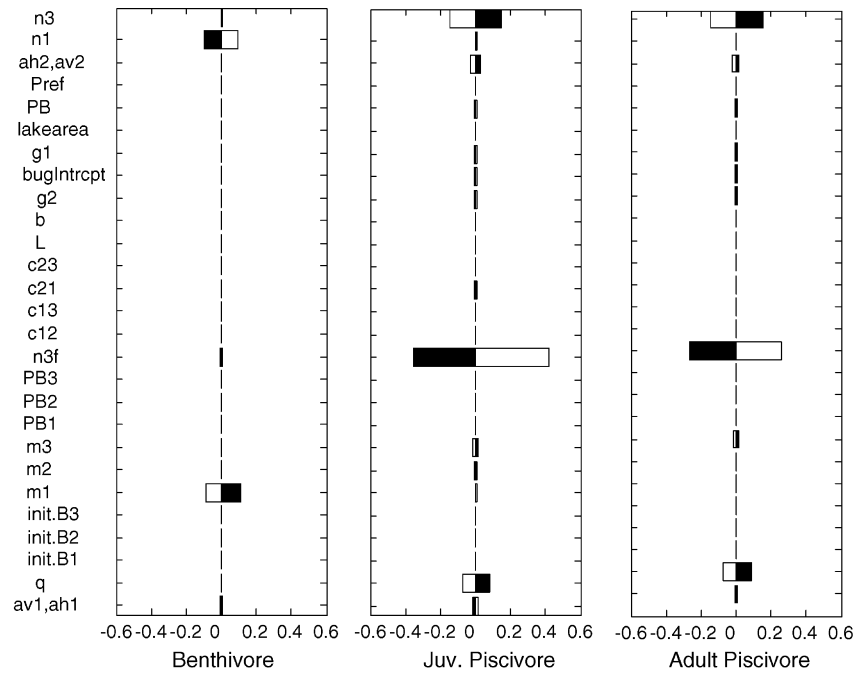


Fig. A2 – Sensitivity analysis of fish biomass pools to parameters within fish biomass and vulnerability equations. The x-axis represents proportional change in each fish biomass pool. White bars show the response when a parameter is increased 10%, and black bars show the response when a parameter is decreased by 10%. See Appendix tables for parameter names and values.

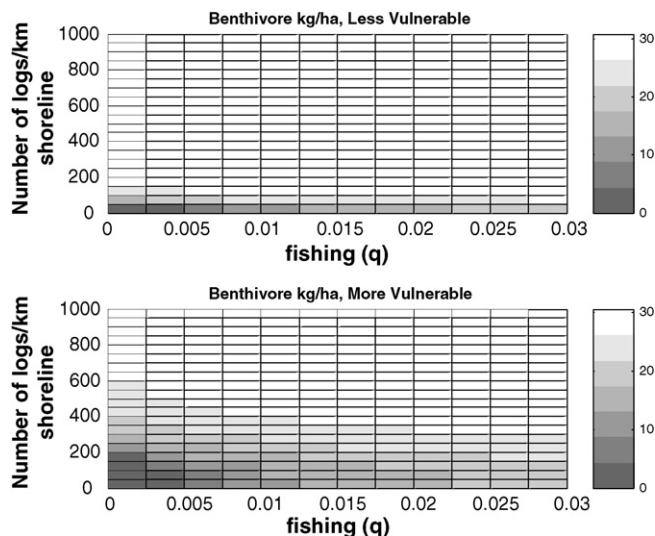


Fig. A3 – Equilibrium benthivore biomass (z-axis) along a gradient of CWH (y-axis) and fishing (x-axis).

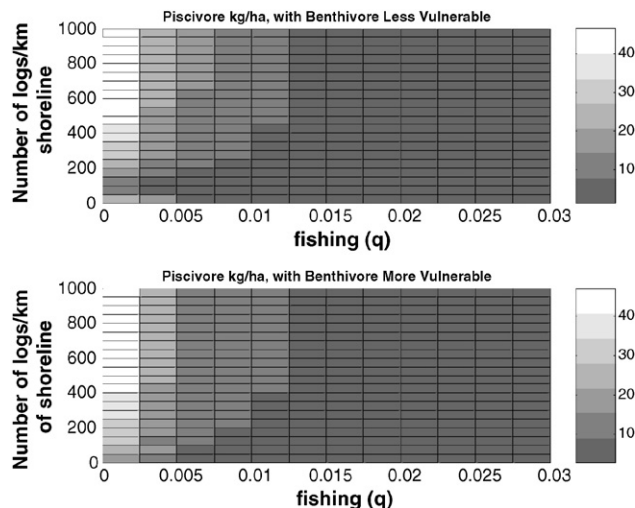


Fig. A4 – Equilibrium adult piscivore biomass (z-axis) along a gradient of CWH (y-axis) and fishing (x-axis).

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