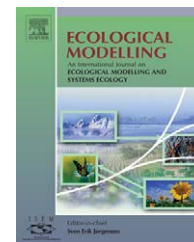


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Characterizing changes in maturity of lakes resulting from supplementation of walleye populations

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ABSTRACT

We constructed mass-balance models in two lakes to measure changes in community maturity associated with walleye stocking. Community maturity is related to stability. Stability, in terms of a particular community structure and total biomass, is a desirable characteristic. It is important to understand how management actions, such as fish stocking and fishery regulations, affect the stability of aquatic communities in order to effectively manage them. Walleye are stocked throughout North America and have the potential to dramatically affect aquatic ecosystems. We examined simulated changes in maturity, as measured by Finn's cycling index and relative overhead, associated with walleye stocking. We simulated three scenarios for each lake: (1) changes in angler effort associated with walleye stocking, (2) changes associated with the physical addition of juvenile walleyes, and (3) changes associated with both the physical addition of juvenile walleyes and changes in angler effort. For each scenario we also examined the role of prey vulnerability by varying the vulnerability parameter for each scenario. We found that expected increases in angler effort associated with walleye stocking generally acted to decrease community maturity and more than offset small increases associated with the physical addition of juvenile walleyes. Changes in maturity metrics were more dramatic when prey vulnerability was high (i.e. "top-down" control) than when they were low (i.e. "bottom-up" control). Walleye stocking may cause aquatic systems to be less stable due to expected increases in the amount of angler effort, particularly in systems controlled primarily through top-down mechanisms.

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In the past several decades there has been an increasing emphasis on ecosystem based fisheries management within natural resource agencies (e.g. NMFS, 1999; WDNR, 1999; Link, 2002; Christensen and Pauly, 2004). Considering fisheries management decisions from a multi-species or community perspective is critical to the long-term success of fisheries given the importance of species interactions and interactions of species with their environment (Link, 2002; Rochet and Trenkel, 2003). Quantifying effects of fisheries management

actions such as fisheries regulation changes and supplementation of fish populations on the aquatic community as a whole is an important step in determining the appropriateness of particular management actions.

One way to quantify the effects of management actions is to track changes in metrics that represent the state of communities. A number of metrics that characterize communities have been developed, and are based on such criteria as diversity, efficiency, stability, resilience, persistence, and maturity

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(e.g. Finn, 1976; Routledge, 1979; Karr, 1981; Ulanowicz, 1997; Perez-Espana and Arreguin-Sanchez, 1999, 2001). Useful measures of community or ecosystem characteristics should allow direct comparisons between different communities, be based on measurable variables, and be empirically and theoretically related to desirable community characteristics.

Stability of aquatic communities is a desirable characteristic. Although biotic communities are subject to continual change, relative temporal stability is beneficial from a fisheries and aquatic community management perspective because a stable system allows greater time to react to perturbations with appropriate management strategies while maintaining the current state of the community. Stability can be defined as a combination of the capacity of a community to: (1) return to its original state following a disturbance (resilience), (2) deviate minimally from its original state following a disturbance (resistance), and (3) continue without change after a disturbance (persistence) (Ulanowicz, 1997).

Relatively mature ecosystems may be more stable than immature ecosystems. Maturity is the final stage in the process of succession and is often measured based on Odum's (1969) attributes of ecosystem maturity. There is considerable discussion regarding whether ecosystem maturity or diversity are associated with stability (e.g. Odum, 1969; Christensen, 1995; Tilman, 1996; Ulanowicz, 1997; Christensen and Pauly, 1998; Perez-Espana and Arreguin-Sanchez, 2001; Cropp and Gabric, 2002). However, it is generally thought that more mature ecosystems exhibit greater temporal stability (Odum, 1969; Christensen, 1995; Christensen and Pauly, 1998; Vasconcellos et al., 1997; Cropp and Gabric, 2002; Brando et al., 2004; Manickchand-Heileman et al., 2004). Therefore, the maturity of a system may be a good measure of its expected stability over time.

Stocking of fish is a common management tool. Fish are stocked in every state and province in North America by federal, state, tribal, and local agencies. In general, the goal of fish stocking is to limit reductions of fish populations due to habitat limitations, fishing pressure or, in the case of depressed fish populations, to restore their populations to historic levels (see Schramm and Piper, 1995). While the effectiveness of these stocking programs with regard to the populations of the species being stocked is often well studied, the indirect effects of stocking on other fish species and aquatic communities are less well known. Since piscivores often determine the structure and dynamics of aquatic ecosystems (Carpenter et al., 1985; Lyons and Magnuson, 1987), determining the effects of their addition through stocking is important for successful management of the recipient community.

In particular, walleyes can play a large role in determining the population dynamics of individual sympatric populations of fishes (Lyons and Magnuson, 1987). Approximately 1 billion walleyes are stocked each year in the majority of states and provinces in North America (Fenton et al., 1996). In the state of Wisconsin alone, the Department of Natural Resources stocks almost 30 million walleyes each year (WDNR unpublished data) and similar numbers are stocked by other agencies.

Our objective was to quantify expected changes in the relative maturity of the aquatic communities as a result of walleye stocking. Walleye stocking has the potential to affect aquatic communities through changes in angler effort as

well as through biological interactions. Therefore, we separately examined effects on ecosystem status associated with changes in: (1) angler effort response to walleye stocking and (2) species interactions. Given the huge numbers of walleye and other fish species stocked throughout the world and their potential impacts on other fish species as well as on community maturity (and therefore possibly the stability of the system), it seems prudent to investigate these impacts further.

1. Methods

Food web models can quantify ecosystem attributes and how they are affected by various processes or stressors (Pauly and Christensen, 2002; Christensen and Pauly, 2004). In order to estimate the impact of walleye stocking on the relative maturity of aquatic communities we developed mass-balance models for two lakes in northern Wisconsin. One of these lakes, Crab Lake, had an entirely self-sustaining walleye population. The other, Whitefish Lake, had a walleye population that was stocked on a regular basis. Crab Lake and Whitefish Lake have similar physical characteristics and species compositions. Both lakes are located in the Northern Lakes and Forests ecoregion (Omernik et al., 2000). Crab Lake has a maximum depth of 20 m and an area of 384 ha and Whitefish Lake has a maximum depth of 33 m and an area of 318 ha. Although the two lakes are generally similar, Whitefish Lake is generally has a more developed shoreline and is slightly more productive than Crab Lake as evidenced by the mean summer Secchi depth in 2002 (Crab Lake = 4.5 m; Whitefish Lake = 4.2 m). We looked for similar patterns in measures of ecosystem maturity in these two models when we simulated the removal and initiation of walleye stocking.

We used Ecopath with Ecosim to construct mass-balance models for two lakes. Ecopath with Ecosim (Christensen and Walters, 2004) is a mass-balance model building tool that estimates balances of energy flow between organisms within a given system. Ecopath is used to establish mass-balance which allows analysis of flows between trophic levels and thereby the status of the ecosystem in general via goal functions such as relative overhead and Finn's cycling index. In general, Ecopath balances production and losses for each species or species group. In the form of an equation;

$$\text{Production} + \text{immigration} - \text{predation mortality} \\ - \text{other mortality} - \text{fishery harvest} = 0.$$

Or more specifically,

$$P_i = Y_i + B_i \times M_i + E_i + BA_i + P_i \times (1 - EE_i)$$

where P_i is the total production rate of group (i), Y_i the total fishery catch rate of (i), M_i the total predation rate for (i), B_i the biomass of (i), E_i the net migration rate (emigration – immigration) of (i), BA_i the biomass accumulation rate for (i), while $(1 - EE_i)$ is the 'other mortality' rate for (i).

In general, the model sets up a system with as many linear equations as there are species groups, and solves for one of four parameters (Christensen et al., 2000). Necessary model inputs for each group include biomass (B) in kg/acre, production/biomass ratio (P/B) per year, consumption/biomass ratio

(Q/B) per year, ecotrophic efficiency (EE), diet composition, and any associated fishing mortality per year. EE is the proportion of total production and mortality that is accounted for by the model. The opposite of EE (i.e. 1 – EE) is unexplained mortality. Although accurate estimates of all parameters for each functional species group lead to greater confidence in model outputs, only three of the four (B, P/B, Q/B, and EE) primary inputs are necessary. EE is generally not specified, but is often estimated during model balancing if reasonable estimates of the other three parameters (B, P/B, and Q/B) are available.

Ecosim propagates changes to the community through fishing or other predatory interactions. Ecosim uses a series of differential equations that demonstrate changes in biomass of each group as a function of time varying biomass and harvest rates.

1.1. Model inputs

We created balanced Ecopath models for two lakes in northern Wisconsin using: (1) lake specific diet information from the primary fish species in each lake and diet information from literature values for other species (Becker, 1983), (2) population estimates and electrofishing catch per effort estimates of relative abundance of each of the primary fish species in each lake in 2002, (3) production/biomass ratios based on literature values (Randall and Minns, 2000), (4) consumption/biomass ratios based on literature values (Rowan and Rasmussen, 1996), and (5) fishing mortality based on creel surveys completed on each lake in 2002. The Crab Lake model included 12 fish species groups (including an adult and a juvenile walleye group and an unidentified fish group), 1 detritus group, 1 phytoplankton group, 1 zooplankton group, 1 aquatic invertebrate group, and 1 crayfish group (Table 1). The Whitefish Lake model included all of the same groups but two additional fish species groups (largemouth bass *Micropterus salmoides* and black crappie *Pomoxis nigromaculatus*) were included (Table 1). We combined northern pike *Esox lucius* and muskellunge *Esox masquinongy* into one group (*Esox*) due to the small sample size of muskellunge and the relative similarity in their diet (Becker, 1983). Similarly, we combined pumpkinseeds *Lepomis gibbosus* and bluegills *Lepomis macrochirus* into one group (*Lep-*

omis) group due to the small sample of pumpkinseeds and the similarity of their diets (Becker, 1983).

1.1.1. Diet composition

We determined diet composition of each primary species or species group included in the models in Crab Lake and Whitefish Lake. Since many fish species are opportunistic predators (Becker, 1983), we used lake specific diet information whenever possible. Stomach samples were collected from the two lakes during both spring and fall using electrofishing and fykenetting sampling in both lakes to account for seasonal variation in diet composition. We split walleyes into juvenile and adult life-stages because substantial differences exist in diet composition (Becker, 1983) and because cannibalism is common among walleyes (Chevalier, 1973; Forney, 1976; Hansen et al., 1998).

Stomach contents were collected with a stomach flushing technique (Seaburg, 1957) and immediately preserved in 95% EtOH. The stomach contents were placed in a Number 60 sieve (250 µm mesh), examined under a dissecting scope, and identified to the lowest practical taxonomic classification (Pennak, 1978; Eddy and Hodson, 1982; Becker, 1983; Oates et al., 1993). Fish in advanced states of digestion were identified through the use of diagnostic bones such as the cleithrum, opercle, dentary, and vertebrae (Hansel et al., 1988). Each group of prey items was blotted dry on a paper towel and weighed to the nearest 0.01 g. Values of diet proportions for each species or species group are shown in Tables 2 and 3.

1.1.2. Biomass estimation

Abundance of walleyes, smallmouth bass, and largemouth bass (in Whitefish Lake only) were determined using Petersen mark-recapture population estimates. Fish of each species were captured using electrofishing and fyke netting and marked using a lake specific fin clip. Fish were recaptured using electrofishing equipment. Adult walleye population estimates were calculated based on electrofishing recapture results from approximately 1 week after marking in the spring. We converted the total number of adult walleye (Crab Lake = 2602; Whitefish Lake = 1244), juvenile walleyes (Crab Lake = 8516; Whitefish Lake = 3521), smallmouth bass (Crab Lake = 1648; Whitefish Lake = 682), and largemouth bass (Whitefish Lake = 946) into total biomass for each species by multiplying the estimated number in each population by the mean weight of each species (walleye = 0.5 kg, juvenile walleye = 0.08 kg, smallmouth bass = 0.5 kg, and largemouth bass = 0.4 kg).

We used catch per effort (CPE) from electrofishing to estimate relative biomass for species for which an acceptable mark-recapture estimate could not be made. Electrofishing CPE is generally proportional to population density (Serns, 1982; Beard et al., 1997; Edwards et al., 1997; Rogers et al., 2003). We used the ratio of adult walleye CPE values to adult walleye mark-recapture estimates to translate electrofishing CPE values into biomass estimates for other fish species in Crab Lake and Whitefish Lake. Indexing CPE values for other fish species using CPE and mark-recapture estimates for adult walleye assumes equal electrofishing catchability among fish species. However, since biomass values are altered during model balancing, they were simply used as reasonable starting values and were not expected to be precise point estimates.

Table 1 – Common and scientific names of fish species or species groups included in Crab Lake (C) or Whitefish Lake (W) Ecopath with Ecosim models

Common name	Scientific name	Model
Walleye	<i>Sander vitreus</i>	C, W
Pike	<i>Esox</i> spp.	C, W
Smallmouth bass	<i>Micropterus dolomieu</i>	C, W
Largemouth bass	<i>Micropterus salmoides</i>	W
Rock bass	<i>Ambloplites rupestris</i>	C, W
Black crappie	<i>Pomoxis nigromaculatus</i>	W
Sunfish	<i>Lepomis</i> spp.	C, W
Yellow perch	<i>Perca flavescens</i>	C, W
Iowa darter	<i>Etheostoma exile</i>	C, W
Logperch	<i>Percina caprodes</i>	C, W
Mottled sculpin	<i>Cottus bairdi</i>	C, W
Minnnows	<i>Cvovrinus</i> spp.	C, W

Table 2 – Diet proportions for fish or fish species groups in Whitefish Lake as determined by percent wet weight

Prey	Predator											
	Walleye (%)	Juvenile walleye (%)	Esox (%)	Smallmouth bass (%)	Largemouth bass (%)	Rock bass (%)	Yellow perch (%)	Black crappie (%)	Lepomis (%)	Aquatic invertebrates (%)	Zooplankton (%)	Crayfish (%)
Largemouth bass	1.0	0.0	31.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lepomis	27.4	0.0	1.0	48.9	6.7	0.3	3.4	3.4	0.0	0.0	0.0	0.0
Northern pike	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Smallmouth bass	0.0	0.0	27.5	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Walleye	0.1	0.0	0.1	8.2	4.8	0.0	0.0	6.5	0.0	0.0	0.0	0.0
Yellow perch	55.1	39.9	8.2	3.4	18.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Cyprinus	1.4	46.8	11.1	10.0	0.7	0.0	60.6	0.0	0.0	0.0	0.0	0.0
Iowa darter	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Logperch	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mottled sculpin	0.0	0.0	0.1	0.0	12.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified fish	7.7	13.2	3.8	7.5	0.1	1.3	12.0	4.7	0.1	0.0	0.0	0.0
Crayfish	0.0	0.0	14.6	1.3	43.1	77.3	0.0	0.0	29.0	0.0	0.0	0.0
Terrestrial invertebrate	6.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	28.4	0.0	0.0	0.0
Aquatic invertebrate	0.6	0.0	0.6	20.5	3.8	13.8	21.6	82.8	27.6	0.0	0.0	0.0
Zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.1	2.6	0.2	0.0	0.0	0.0
Phytoplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	100.0	0.0
Detritus	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	50.0	0.0	100.0
Other	0.0	0.0	0.0	0.1	7.7	6.9	1.4	0.0	14.7	0.0	0.0	0.0

Table 3 – Diet proportions for fish or fish species groups in Crab Lake as determined by percent wet weight

Prey	Predator										
	Walleye (%)	Juvenile walleye (%)	Esox (%)	Smallmouth bass (%)	Largemouth bass (%)	Rock bass (%)	Yellow perch (%)	Lepomis (%)	Aquatic invertebrates (%)	Zooplankton (%)	Crayfish (%)
Largemouth bass	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lepomis	0.0	3.6	36.8	0.4	0.0	0.0	1.0	0.0	0.0	0.0	0.0
Northern pike	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Smallmouth bass	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Walleye	4.2	1.3	48.9	3.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Yellow perch	13.3	0.5	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyprinus	4.1	0.0	1.2	0.1	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Iowa darter	17.7	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Logperch	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mottled sculpin	4.4	30.9	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified fish	37.5	0.0	4.2	2.7	50.0	0.3	1.1	0.0	0.0	0.0	0.0
Crayfish	0.1	0.0	3.1	58.2	0.0	19.8	21.9	0.7	0.0	0.0	0.0
Terrestrial invertebrates	0.0	0.0	0.0	0.0	0.0	13.4	0.0	49.1	0.0	0.0	0.0
Aquatic invertebrates	10.3	62.9	0.0	30.2	0.0	66.4	69.9	47.0	0.0	0.0	0.0
Zooplankton	0.0	0.7	0.0	0.1	0.0	0.0	5.9	0.4	0.0	0.0	0.0
Phytoplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	100.0	0.0
Detritus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	100.0
Other	0.0	0.0	0.0	1.1	0.0	0.1	0.1	2.8	0.0	0.0	0.0

1.1.3. Fishing mortality

Creel surveys were used to estimate angler harvest of fish species on both Crab Lake and Whitefish Lake. Creel surveys were based on a randomized stratified design (Pollack et al., 1994; Rasmussen et al., 1998). The surveys were stratified by month and day type (weekend and holidays or weekday). Information from angler counts and interviews was expanded over the appropriate strata to estimate total harvest and catch per effort of each fish species.

In addition to angler harvest, tribal members harvested walleyes from each lake because both lakes are located in the ceded territory of Wisconsin (Staggs et al., 1990). Each spring, tribal members harvest walleyes primarily through spearing during spring spawning. Each harvested walleye is measured and weighed as part of a creel census. Thus, the number of walleye harvested by tribal members in each of these lakes was a known value.

1.1.4. Model balancing

To achieve mass-balance in each model, a necessary step to obtain meaningful model outputs, we used an iterative

method based on certainty in model inputs developed by Kavanaugh et al. (2004). Ecopath with Ecosim includes the Kavanaugh et al. (2004) balancing method in a module and essentially perturbs biomass and diet proportions of groups with an EE value of greater than 1 according to specified criteria. EE values greater than one indicate that the model accounts for greater than 100% of the mortality of a given species or group, an obvious impossibility. We set the Kavanaugh et al. (2004) balancing routine to perturb values of biomass and diet proportions based on our level of confidence in the initial parameter values. In other words, while iteratively seeking to reduce EE values for all groups to one, only small changes were made to values that we felt were fairly accurate (such as the biomass of adult walleyes) but larger changes were made to parameter values that we felt were less accurate (such as biomass of phytoplankton). Confidence intervals for all starting parameter values used for the auto-balancing routine are shown in Table 4. Resulting model quality values as calculated by Ecopath with Ecosim (Christensen et al., 2000) was 0.524 for Whitefish Lake and 0.454 for Crab Lake and these values

Table 4 – Uncertainty values used for balancing Whitefish Lake and Crab Lake, Wisconsin Ecopath models. Numbers represent percent confidence intervals

Lake	Group	Ecopath parameter				
		Biomass	Production/biomass	Consumption/biomass	Diet	Catch
Whitefish	Aquatic invertebrates	80	70	70	80	–
	Zooplankton	80	70	70	80	–
	Largemouth bass	30	20	20	30	10
	Lepomis	50	20	20	30	–
	Esox	50	20	20	30	–
	Smallmouth bass	30	20	20	30	10
	Black crappie	50	20	70	30	10
	Rock bass	50	20	20	30	–
	Juvenile walleye	10	20	20	30	10
	Walleye	10	20	20	30	10
	Yellow perch	50	20	20	30	–
	Cyprinus	50	40	70	60	–
	Iowa darter	50	20	20	60	–
	Logperch	50	20	20	60	–
	Mottled sculpin	50	20	70	60	–
	Unidentified fish	80	40	70	80	–
	Crayfish	80	70	70	80	–
	Phytoplankton	80	70	–	–	–
Crab	Aquatic invertebrates	80	70	70	80	–
	Zooplankton	80	70	70	80	–
	Lepomis	50	20	20	30	–
	Esox	50	20	20	30	10
	Smallmouth bass	50	20	20	30	10
	Rock bass	50	20	20	30	–
	Juvenile walleye	10	20	20	30	10
	Walleye	10	20	20	30	10
	Yellow perch	50	20	20	30	–
	Cyprinus	50	40	70	60	–
	Iowa darter	50	20	20	60	–
	Logperch	50	20	20	60	–
	Mottled sculpin	50	20	70	60	–
	Unidentified fish	80	40	70	80	–
	Crayfish	80	70	70	80	–
	Phytoplankton	80	70	–	–	–

Uncertainty values reflect data collected in 2002.

are similar to other published models (Pinnegar and Polunin, 2004).

1.1.5. Modeling simulation methodology

Essentially, fish stocking can be viewed as immigration. In both cases, fish grow and consume resources outside of the system of interest. In order to estimate relative overhead and FCI values associated with walleye stocking, we treated stocking events as immigration of juvenile walleyes. We initially set the amount of immigration equal to the recommended stocking rate for small fingerling walleyes in Wisconsin (124 ha^{-1}). The mean weight of each of these fingerlings was 4 g (WDNR unpublished data). The biomass of the stocked walleyes was calculated accordingly.

In order to simulate the removal or addition of stocked walleye, we established a “fishing fleet” that “harvested” juvenile walleye. For example, we set up initial conditions in Crab Lake (no stocking) by simulating the immigration of juvenile walleyes and the immediate removal of the same biomass from the system through fishing. Then, to simulate the initiation of stocking in Crab Lake, we simulated a harvest of zero from the fleet that had been “harvesting” the juvenile walleyes. Similarly, to simulate the termination of stocking in Whitefish Lake, the harvest of the fishing fleet was increased until all stocked juvenile walleyes were “harvested”.

We used another fleet, labeled as “walleye anglers” to simulate changes in angler effort for walleyes based on their origin (i.e. stocked or natural). The amount of angler effort was altered according to the relationship between walleye density and angler effort in lakes with a daily walleye bag limit of two (Fayram et al., *in press*). Lakes stocked with walleyes had a constant directed effort of 23.15 h/ha (mean value of stocked lakes with a daily bag limit of two) and angler effort in lakes with self-sustaining walleye populations is predicted by the equation $\text{LN}(\text{angler effort/ha}) = -3.844 + 3.317 \text{ LN}(\#\text{walleye/ha})$. We changed angler effort for walleyes in Whitefish Lake, which is currently stocked, by multiplying the current level of angler effort by 0.09 (2.14 h/ha as predicted by the effort equation above divided by the directed effort in 2002 of 24.56 h/ha), to simulate the expected decrease in fishing effort if anglers believed that the walleye population (4.01 walleye/ha) was self-sustaining in origin. Similarly, we simulated an increase in the amount of angler effort in Crab Lake, which is not currently stocked, by multiplying the current level of angler effort by 13 (average directed effort/ha on stocked lakes of 23.15 h/ha divided by the estimated angler effort in 2002 of 1.78 h/ha), to simulate the increase in fishing effort if anglers believed that the walleye population was stocked. While the amount of effort directed at other fish species may change with walleye stocking, changes are small compared to the changes in effort directed at walleyes (Fayram et al., *in press*), therefore, we did not include effects of walleye stocking on directed effort at other species.

Potentially useful parameters describing the maturity, and therefore stability, of a given community are “relative ascendancy” and “relative overhead”. Ascendancy and overhead measures were developed by Ulanowicz (1986) and are based on information theory. The ascendancy value of ecosystems and communities is thought to increase during the process of ecosystem maturation. As ecosystems mature, they become

more energetically efficient and shed redundant and inefficient pathways. Ascendancy and similar measures (e.g. overhead, exergy, emergy, etc.) have been shown to be related to stability (Christensen, 1995; Cropp and Gabric, 2002), maturity (Christensen, 1995; Ulanowicz and Abarca-Arenas, 1997; Nielsen and Ulanowicz, 2000; Perez-Espana and Arreguin-Sanchez, 2001; Fath et al., 2001; Cropp and Gabric, 2002), eutrophication (Aoki, 1995), and human disturbance (Genoni and Pahl-Wostl, 1991; Ulanowicz, 1997). The focus of relative ascendancy is on the probability of energy flow in a system, rather than the standing stock biomass of predators and prey (Ulanowicz, 1997). Ascendancy quantifies ecosystem size and is essentially a measure of the degree of organization of a community. Ascendancy varies inversely with overhead. Overhead is a measure of the energy in an ecosystem that is available to resist perturbations (Christensen, 1995; Angelini and Petrere, 2000). Total system throughput is a measurement of the absolute size of a community, where size is gauged as the total amount of flows within the ecosystem, similar to measuring the size of an economic system. Ascendancy and overhead are measured in units of tonnes/km²/year \times bits, and throughput is measured in units of tonnes/km²/year. Relative overhead and relative ascendancy are simply measures of the amount of disorganized energy flow and organized energy flow, respectively, expressed as a percentage of the total capacity. Relative overhead and relative ascendancy must sum to one since capacity is defined as overhead plus ascendancy. Relative overhead is correlated with the maturity of aquatic communities (Christensen, 1995).

Another potentially useful measure of community maturity is the percentage of material that is recycled in a given system as measured by Finn’s cycling index (FCI) (Finn, 1976). Finn’s cycling index is a measurement of recycled energy flow in a given system. More specifically, FCI is the percent of the total system throughput attributed to the recycling of material within the system (Finn, 1976). Finn’s cycling index is positively correlated with maturity measures as defined by Odum (1969) (Vasconcellos et al., 1997; Christensen and Pauly, 1998).

In order to estimate approximate changes in relative overhead and FCI values due to changes in angler effort and biological interactions associated with walleye stocking, we examined six different model scenarios. The first two scenarios were meant to simulate situations where walleye stocking occurred and the community responses were exclusively biological (i.e. no changes in angler effort). The next two scenarios were meant to simulate effects of walleye stocking on angler effort only. Angler effort is expected to change to some degree based solely on the angler’s perceptions about whether the walleye population is supported through stocking or is self-sustaining. Essentially, the angler effort scenarios simulate a change in the expected amount of effort directed at walleyes if the walleye population changed from being supported through stocking to being supported through natural reproduction or vice versa with no actual change to the population density of walleyes. The final two scenarios were meant to characterize changes in the aquatic community due to the combined effects of changes in angler behavior due to stocking and changes in the community due to biological interactions with stocked walleyes. We changed parameters to reflect each scenario and used Ecosim to estimate expected community

composition and maturity indices after a simulated period of 100 years. To calculate maturity measures, we took relative species abundances derived from each of our Ecosim simulations and used Ecopath to calculate the associated relative overhead and FCI values.

Freshwater aquatic systems can be controlled to varying degrees by nutrient input (bottom-up) and predation (top-down) (e.g. Hunter and Price, 1992; Carpenter and Kitchell, 1993). The degree to which prey are vulnerable to predators plays a role in the population dynamics in a community. To determine how assumptions of prey vulnerability affected our results, we ran each of the six scenarios described above with various levels of prey vulnerability by altering the “*v*” parameter in Ecosim. We recorded relative overhead and FCI values for each scenario under top-down ($v = 3$), bottom-up ($v = 1$), and mixed control ($v = 2$).

To determine the sensitivity of FCI and relative overhead values to different intensities of walleye stocking and angler effort, we modeled a range of fishing pressure and stocking rates. We recorded estimated values for maturity metrics for models of both lakes at stocking rates of 0–20 times the recommended stocking rate of 124 small fingerling walleyes/ha. We also recorded estimated values for maturity metrics for models of both lakes at 1–20 times the current amount of angling harvest. Again, maturity indices were recorded after a simulated period of 100 years. We quantified the association between maturity and diversity metrics with stocking and fishing intensity through correlation analysis.

2. Results

Values of parameters describing the current state of the communities in each lake suggest that Whitefish Lake is a more active and mature system than Crab Lake. The throughput value for Whitefish Lake (16,886 tonnes/km²/year) is larger than Crab Lake (14,507 tonnes/km²/year). The greater throughput value in Whitefish Lake indicates that it is a “bigger” system in that a greater amount of material is processed by the

members of the aquatic community in each square kilometer in each year than in Crab Lake. Values for relative overhead and FCI are also substantially higher in Whitefish Lake than in Crab Lake (Table 5).

Model output from the biological effects of walleye stocking at the recommended rate of 124 walleyes/ha, in the absence of changes in angler behavior, showed some consistent effects. Simulated addition of walleyes to lakes seems to have no effect or result in very small increases of maturity measures. When we simulated the removal of walleye stocking in Whitefish Lake, FCI values decreased slightly in simulations with prey vulnerability values of two and three and remained the same in the simulation when the prey vulnerability value was set to one (Table 5). Relative overhead values also decreased slightly with prey vulnerability values of two and three but increased slightly when the prey vulnerability value was one. Similarly, when we simulated the initiation of walleye stocking in Crab Lake, the FCI value generally remained unchanged or increased slightly (Table 5).

Expected increases in angler effort associated with walleye stocking generally acted to decrease measures of community maturity. At estimated 2002 walleye densities in Crab Lake and Whitefish Lake, walleye stocking increased angler effort, which in turn decreased relative overhead and FCI values although the magnitude of these decreases was less in Whitefish Lake than in Crab Lake (Table 5). Increased angler effort in Crab Lake with the simulation of walleye stocking generally resulted in decreased relative overhead and FCI values (Table 5) although maturity metrics remained unchanged when vulnerability values were set to one. Similarly, decreased angler effort in Whitefish Lake expected with the removal of walleye stocking resulted in increased overhead and FCI values (Table 5).

When expected angler behavioral responses and biological responses to walleye stocking were combined, we found values of maturity metrics similar to those resulting from angler effort response alone. Both relative overhead and FCI values were lower and similar to those resulting from angler effort response alone in Crab Lake (Table 5). Maturity metric values

Table 5 – Output related to community maturity from Crab Lake and Whitefish Lake Ecopath with Ecosim models under different walleye stocking scenarios. Bold numbers indicate estimates from the balanced model

Lake	Metric	Scenario					
		Vulnerability	With stocking	Without stocking	Stocked fishing effort	Cease stocking fishing effort	Stocking and fishing
Whitefish	Relative overhead	1	61.0	61.1	×	61.1	61.0
		2	61.0	60.9	×	61.1	61.0
		3	61.0	60.9	×	61.4	61.5
	FCI	1	2.8	2.8	×	2.8	2.8
		2	2.8	2.7	×	2.8	2.8
		3	2.8	2.7	×	2.8	2.8
Crab	Relative overhead	1	40.9	40.9	40.9	×	40.9
		2	41.0	40.9	39.9	×	39.9
		3	41.0	40.9	36.4	×	36.5
	FCI	1	1.5	1.5	1.5	×	1.5
		2	1.5	1.5	1.2	×	1.2
		3	1.6	1.5	0.6	×	0.7

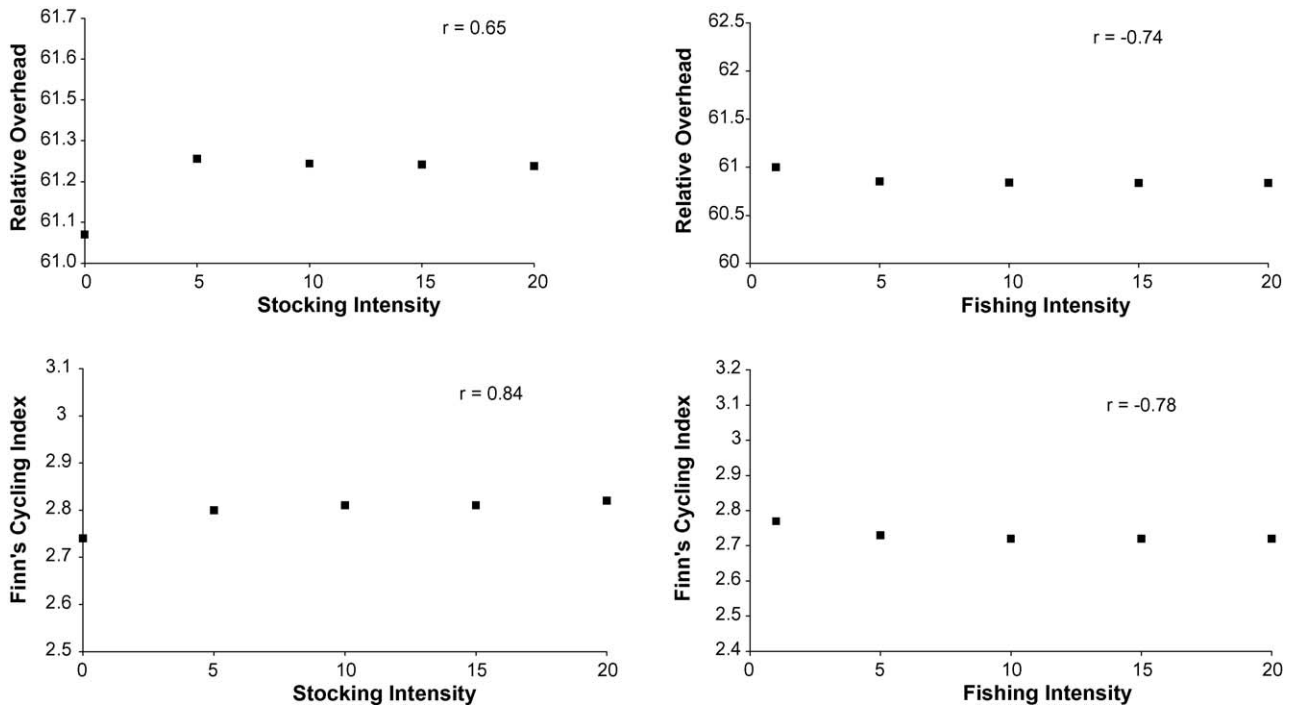


Fig. 1 – Simulated responses of relative overhead and Finn's cycling values to stocking or fishing intensity and associated correlation coefficients in Whitefish Lake.

were also similar to those found resulting from angler effort response alone in Whitefish Lake but the values were much more similar to values without any biological or angler effort response to stocking than in Crab Lake (Table 5).

Both relative overhead and FCI values were positively correlated to stocking rates and negatively related to angler effort (Figs. 1 and 2). However, FCI values were more highly correlated to simulated increases in walleye

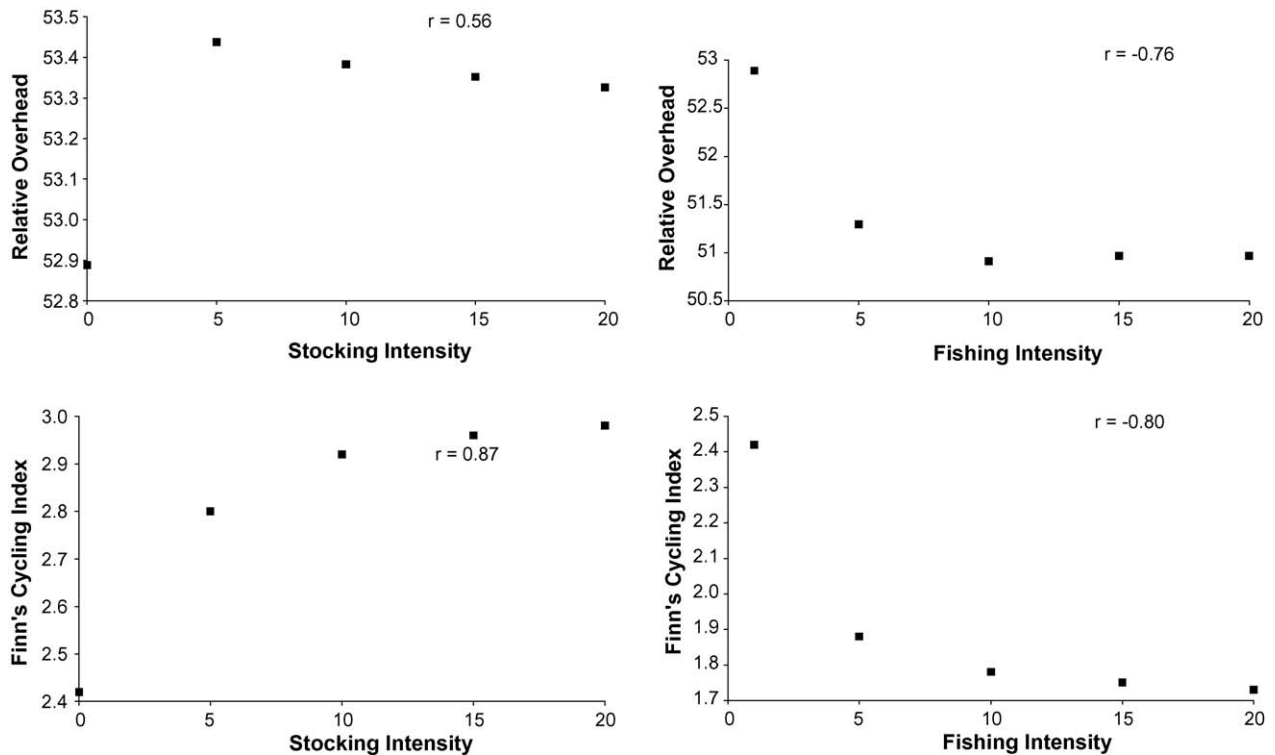


Fig. 2 – Simulated responses of relative overhead and Finn's cycling values to stocking or fishing intensity and associated correlation coefficients in Crab Lake.

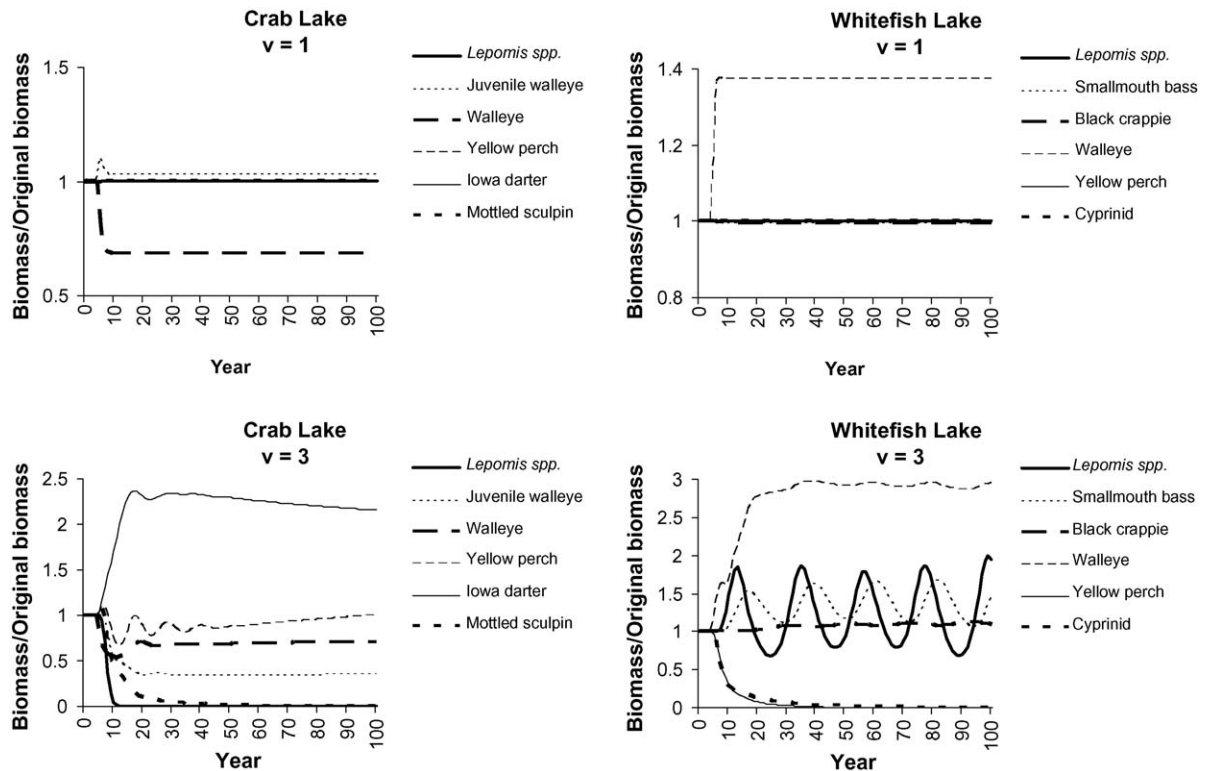


Fig. 3 – Predicted relative change in biomass of species in Crab Lake and Whitefish Lake resulting from both changes in angler effort and the physical addition of juvenile walleyes under “top-down” ($v = 3$) and “bottom-up” control ($v = 1$) assumptions. The six most abundant fish species, in terms of estimated biomass in Crab Lake and Whitefish Lake, are included in each figure.

stocking and angler effort than relative overhead values (Figs. 1 and 2).

Maturity metric values varied depending on whether the prey vulnerability parameter was set to simulate top-down or bottom-up control although the effects of vulnerability setting were more pronounced in Crab Lake (Table 5; Fig. 3). Effects of stocking and fishing were generally consistent across vulnerability levels but were dampened or eliminated when vulnerability values were low (bottom-up) and more pronounced when the vulnerability values were high (top-down) (Table 5; Fig. 3).

3. Discussion

Whitefish Lake is more mature than Crab Lake based on relative overhead and FCI values. The difference in relative overhead between the Crab Lake and Whitefish Lake was about 20% and the difference in FCI values was 1.3%. Whitefish Lake had relative overhead values similar to other aquatic systems that been considered “relatively mature” (Angelini and Agostinho, 2004; Manickchand-Heileman et al., 2004; Villanueva et al., 2004). Because high relative overhead and FCI values are thought to be associated with maturity (Christensen, 1995; Vasconcellos et al., 1997; Christensen and Pauly, 1998), and more mature communities may be more stable (Christensen, 1995; Vasconcellos et al., 1997; Christensen

and Pauly, 1998; Cropp and Gabric, 2002), Whitefish Lake may be a more stable system than Crab Lake.

The difference in maturity metrics between these two lakes is unlikely to have been caused solely by walleye stocking since the greatest difference we produced that was attributed to stocking in our simulations was 4.5% in relative overhead and 0.9% in FCI. However, it appears that walleye stocking can produce effects on maturity metrics similar effects attributed to other human disturbances. Ulanowicz (1997) suggested that a difference in relative overhead of 6% between the Baltic Sea and Chesapeake Bay indicated that Chesapeake Bay was more perturbed than the Baltic Sea. Similarly, relative overhead changed 10% in a marine upwelling system before and after the system was “severely stressed” by fishing (Heymans et al., 2004).

Although addition of fish through stocking can cause dramatic effects on a fish community (e.g. Evans and Loftus, 1987; Flecker and Townsend, 1994; Bronte et al., 2003; Mbabazi et al., 2004), supplementation of a species such as walleye, that are present in and generally adapted to a given type of system may cause less dramatic changes. Our findings suggest that changes in community maturity caused by biological interactions with walleyes, in the absence of changes in angling effort, were relatively small.

The presence or absence of fishing can dramatically alter the characteristics of a given aquatic community (Rochet and Trenkel, 2003; Perez-Espana, 2003; Sanchez and Olaso, 2004).

Our findings suggest that changes in angler behavior associated with walleye stocking caused changes in community maturity, but that effects differed between lakes. We found that although the addition of walleyes may slightly increase maturity, stocking induced a higher angler effort that offset any increases in maturity. Similarly, [Perez-Espana \(2003\)](#) suggested that increased fishing effort decreased stability of aquatic communities. Therefore, while the physical addition of walleyes may lead to a more mature and stable community, increased angling effort resulting from stocking is likely to cause the system to be less stable. It is important to note that angler behavior and perceptions of the quality of fishing opportunities often change over time ([Fayram, 2003](#)). Therefore, in the future, if angler's perception of walleye stocking changes such that stocking results in a decreased amount of angler effort, walleye stocking may act to increase community maturity.

Our results are consistent with [Vasconcellos et al. \(1997\)](#) assertion that FCI values will decrease in response to actions that decrease community maturity such as increased fishing effort ([Perez-Espana, 2003](#)). [Vasconcellos et al. \(1997\)](#) measured community maturity as the time necessary for a community to return to its original state after a disturbance, and found that FCI was positively related to the rate of recovery while relative ascendancy was not. Our findings suggest that relative overhead does in fact respond to actions that change the maturity of a community. Because we did not examine recovery time as a measure of maturity, relative overhead may reflect some aspect of maturity other than recovery time. [Christensen \(1995\)](#) found that relative ascendancy was negatively related to community maturity. Because relative overhead plus relative ascendancy must equal one, relative overhead should be positively related to maturity. Our results are consistent with relative overhead being positively associated with maturity.

In general, we found that increased angler effort associated with walleye stocking acts to decrease measures of community maturity and the decreases were more extreme under top-down control situations. Our results are consistent with [Gasalla and Rossi-Wongtschowski \(2004\)](#) who found that changes in biomass were more dramatic when prey vulnerabilities are set to simulate top-down rather than bottom-up control. The addition of juvenile walleyes to a system likely has a small impact on the total nutrient budget of a lake. Therefore, when lake communities are primarily driven by bottom-up processes, walleye stocking is may have little effect on maturity. However, stocked fish can have a dramatic role in structuring the community of a lake if they interact strongly with other organisms ([Carpenter and Kitchell, 1993](#)). Thus, changes in maturity due to stocking are likely to be more dramatic if the communities are structured primarily through top-down processes. While [Gasalla and Rossi-Wongtschowski \(2004\)](#) found that assumptions regarding prey vulnerability could result in opposite tendencies in biomass changes, we found consistent results in community measures regardless of whether the system was considered top-down or bottom-up. Only the magnitude of the changes in community measures was affected by the prey vulnerability, not the direction. The apparent disparity between directional change in biomass estimates found by [Gasalla and Rossi-Wongtschowski \(2004\)](#) and consistent results for maturity measures may result from

the fact that biomass estimates of individual species are much more variable and are more difficult to estimate than community level measures ([Peterson and Rabeni, 1995](#)).

Succession in lakes proceeds from nutrient poor oligotrophic lakes to nutrient rich hypereutrophic lakes ([Lampert and Sommer, 1997](#)). Maturity metrics suggest that Whitefish Lake is more mature than Crab Lake. This result is consistent with the fact that Secchi depth (a rough indication of trophic status) is lower in Whitefish Lake than in Crab Lake. Our results mirror [Aoki \(1995\)](#) who measured ascendancy and overhead values in three oligotrophic lakes (lower maturity) and one eutrophic lake (higher maturity). Although [Aoki \(1995\)](#) did not specifically calculate relative overhead values, calculations based on data presented in table form demonstrated that the eutrophic lake had higher relative overhead values than any of the oligotrophic lakes (62.3% versus 13.2%, 32.9%, and 51.4%). It follows that activities that decrease community maturity, such as increased fishing effort ([Perez-Espana, 2003](#)), may act to decrease stability and cause lakes to become more oligotrophic. Based on our model results, we expect walleye stocking, particularly the increased angler effort associated with stocking, to cause a decrease in lake maturity. As a result, a lake that is stocked with walleyes may be more oligotrophic than if it is not.

Fish stocking should be carefully considered prior to its implementation. Walleye stocking may have other important effects on aquatic communities (see [Schramm and Piper, 1995](#)). However, our results suggest that walleye stocking can also affect community maturity. It seems that more stable and mature communities may result from walleye stocking only in situations where there is no increase in angler effort. If fisheries managers seek stable communities, they should consider angler effort responses to stocking.

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