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WALLEYE STOCKING AS A TOOL TO SUPPRESS FATHEAD MINNOWS AND IMPROVE HABITAT QUALITY IN SEMIPERMANENT AND PERMANENT WETLANDS IN THE PRAIRIE POTHOLE REGION OF MINNESOTA

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EXECUTIVE SUMMARY

1. In the absence of winterkill or predators, fathead minnows *Pimephales promelas* often reach very high densities, and influence both aquatic invertebrate abundance and community structure in Minnesota's prairie pothole wetlands. Furthermore, reductions in herbivorous zooplankton by fathead minnows may modify water transparency contributing to turbidity shifts and loss of aquatic vegetation. We stocked walleye *Sander vitreus* in a group of Prairie Pothole Region wetlands in western Minnesota to test the efficacy of "biomanipulation" to suppress fathead minnow populations, to enhance invertebrate populations, and to improve habitat quality by inducing shifts from turbid, phytoplankton-dominance to clear water, macrophyte-dominance.

2. We evaluated two separate treatments using either larval (fry) walleye, or age-1 and older (advanced) walleye. We stocked larval walleye into 6 wetlands (walleye fry treatment) and age-1 and older walleye into 6 additional wetlands (advanced walleye treatment) in May 2001 and 2002. Six other wetlands served as reference sites during both study years (reference treatment).

3. We observed a significant reduction in fathead minnow abundance in our walleye fry treatment during 2001 and 2002. This included larval fathead minnows, and was likely due to a combination of direct predation and decreased reproduction by adult fish. Concurrently, higher abundances of *Daphnia* spp. and most macroinvertebrate taxa, including amphipods, were also observed. Phytoplankton abundance and turbidity decreased, but not until the second year. In 2001, we did not observe a decrease in phytoplankton, despite a pronounced increase in large cladocerans later during the growing season. In 2002, both phytoplankton abundance and turbidity decreased, perhaps indicating that presence of a robust zooplankton population during early summer was critical for the switch to a clear water state. Submerged aquatic vegetation showed continued improvement in the walleye fry treatment throughout the study, although this response developed rather gradually following the initial manipulation. Zooplankton populations, and water transparency remained high in 2003 despite the reestablishment of fathead minnow populations in most wetlands. We hypothesize that this is due to the stabilizing influence of submerged aquatic vegetation in maintaining the clear water conditions.

4. Positive responses by invertebrate populations were maintained in the walleye fry treatment despite dietary dependence of walleye on invertebrate prey once prey fish were eliminated. One important group of invertebrates that may have been affected by walleye fry was benthic chironomids. Although this trend was not significant, chironomids were less abundant in the walleye fry treatment in 2002 relative to the other treatments.

5. We observed very few improvements in our advanced walleye treatment, except for some modest suppression of fathead minnows in 2002. Increases in amphipods and benthic chironomids were evident in 2002, but we saw no increases in other invertebrate taxa.

6. Our results indicate that biomanipulation via walleye fry stocking may be useful to suppress fathead minnow populations and improve habitat quality in Minnesota wetlands, at least over short time periods. To ensure persistent clear water and macrophyte-dominated conditions, we recommend that fry stocking be conducted as needed to control fathead minnows as they have prolific recruitment potential, and exhibit strong predation effects on invertebrate taxa. In some wetlands, this may require stocking walleye fry at least every other year. To minimize predation on invertebrates, we recommend that as many walleye fingerlings as possible be removed during fall. We also recommend that walleye fry not be stocked in wetlands with intermittent surface water connections. Efforts should be made to select sites that are isolated from other surface waters because the success of biomanipulation efforts will be lower in systems where flooding and fish immigration frequently occur.

7. Stocking of advanced walleye (age-1 and older) was not successful in producing desired food web responses in our study wetlands. Here, consumption rates were simply not high enough to reduce fathead minnow abundance. We acknowledge that our stocking rate was low compared to other biomanipulation studies using adult piscivorous species.

8. Logistically it was very difficult to obtain the numbers/biomass of advanced walleye needed in this study. Obtaining numbers of these older walleye necessary for a successful biomanipulation is probably not practical in a wetland management context.

Background

Fathead minnows *Pimephales promelas* are common residents of semipermanent and permanently-flooded wetlands throughout much of the Prairie Pothole Region (PPR) in North America (Stewart and Kantrud 1971; Peterka 1989). Aquatic invertebrates are also abundant in these wetland habitats, and comprise an important link between primary producers and vertebrate consumers, especially birds and amphibians, known to rely on these habitats as foraging areas (Euliss et al. 1999). Recent evidence indicates that fathead minnows influence aquatic invertebrate abundance and community structure in prairie wetlands (Zimmer et al. 2000; 2001). Furthermore, reductions in herbivorous zooplankton may modify water transparency, contributing to turbidity shifts consistent with predictions of recent models describing community dynamics within shallow lakes (Scheffer et al. 1993; Scheffer 1998).

Wetland managers are interested in methods to increase wetland quality and wildlife food available in wetlands. Meanwhile, fisheries managers are interested in using wetlands to rear walleyes for stocking into lakes as part of their annual walleye-stocking program. Our study evaluated whether stocking walleyes in wetlands could be used to meet both objectives without negative impacts, and details potential wetland habitat benefits associated with this technique.

Study Design and Data Analysis

We stocked walleye *Sander vitreus* to test the efficacy of biomanipulation in PPR wetlands in western Minnesota. Our goal was to assess whether walleye predation was useful to suppress fathead minnow populations, thus facilitating 1) increases in abundance of large-bodied *Daphnia,* 2) reduced phytoplankton biomass, 3) improved water transparency, and 4) shifts toward a clear-water state. We apportioned 18 study wetlands among three treatment groups. We stocked larval walleye (hereafter referred to as “walleye fry”) at a rate of 12,000/ha in 6 wetlands (walleye fry treatment) in May 2001 and 2002; similarly, age-1 and older walleye (130 + mm; hereafter referred to as “advanced walleye”) were stocked at a rate of 5.6-6.7 kg/ha in 6 additional wetlands (advanced walleye treatment) in May 2001 and 2002; 6 wetlands served as reference sites and received no walleye stockings (reference treatment). Walleye fry stocking rate and removal methods used in our study were similar to that used by DNR Fisheries to rear walleyes for their annual stocking program. In September and October of the treatment years, DNR Fisheries personnel removed walleye fingerlings from the walleye fry treatment wetlands using established wetland-harvesting techniques (primarily via trap netting). Harvested walleye fingerlings were subsequently stocked into area lakes as part of the DNR Fisheries stocking program. Study wetlands ranged in size from 4.4-27.6 ha, and maximum wetland depths were 1.7-3.3 m. All study sites were permanently-flooded wetlands that contained antecedent populations of fathead minnows, but initial population densities of fathead minnows were variable. To account for variable fathead minnow densities, treatments were randomly assigned to one of three blocks corresponding to either high, medium, or low fathead minnow density based on population surveys conducted in April 2001, just prior to start of the study.

Response variables of greatest interest included populations of adult fathead minnows, macroinvertebrates and zooplankton, phytoplankton (indexed by chlorophyll *a*), water transparency, concentrations of major nutrients, and submerged aquatic vegetation. These characteristics and parameters were sampled once per month from May to September 2001 and 2002, except for submerged aquatic vegetation and benthic macroinvertebrates, which were surveyed once annually, in late July and early August, respectively. In 2002 only, additional sampling for larval fathead minnows was conducted once per month from May to September to assess more fully the impacts of predatory walleye on entire fathead minnow populations, including fathead minnow recruitment dynamics within the study wetlands. Diets of fathead minnows and walleye were assessed concurrently with monthly sampling to help clarify the direct and relative impacts of these predators on invertebrate populations. We continued to monitor a selected set of response variables in the study wetlands throughout 2003 to assess additional potential changes (either improvements or deteriorations) after cessation of walleye stocking. Response variables monitored during 2003 included populations of fathead minnows and zooplankton, concentrations of chlorophyll *a* and major nutrients, water transparency, and submerged aquatic vegetation. Several response variables (e.g., fathead minnows, macroinvertebrates) were measured as catch-per-unit-effort (CPUE), which we interpreted as an index of abundance, and refer to as “abundance”.

Methodological details for fish community, aquatic invertebrate, macrophyte, and water quality sampling can be found in Potthoff (2003). Similarly, field and laboratory methods for the walleye diet analyses can be found in Ward (2003). Fathead minnow diet analyses were also conducted for one wetland from each treatment group. Up to 20 fathead minnows from each of three size classes (<20 mm, 20-40 mm, and >40 mm) were collected from each wetland three times throughout 2001 and 2002 (early, middle, and late in the summer) using an ichthyoplantkon net or shoreline seine. Collected fish were anesthetized with a lethal dose of MS-222™, and preserved in a 10% formalin solution. Fathead minnows were later transferred to a solution of 95% ethanol. Diets from up to 10 fathead minnows from each size class were analyzed to determine gut contents. Only the anterior 1/3 of the intestinal tract was dissected and analyzed because items lower in the intestinal tract are severely masticated and difficult to identify (Duffy 1998). Diet items were identified to the lowest feasible taxon, measured, and length-weight regressions applied to estimate the biomass of each taxon. Detritus was filtered directly onto a 0.7 µm glass-fiber filter to obtain both wet and dry weights. Diets were expressed as mean percent by wet weight.

Potential data trends were assessed using repeated-measures ANOVA (Proc Mixed procedure; Littell et al. 1996). For each response variable, we first fit our data against several candidate covariance structure models. Model fit was assessed using AIC values and we selected models based on the lowest AIC values (Littell et al. 1996). Time was treated as a categorical variable. We used the Kenward-Roger (KR) method to estimate degrees of freedom; this method has been found to perform well in situations with fairly complex covariance structures, when sample sizes are small and the designs are reasonably balanced (Schaalje et al. 2002). Data sets were ln (n+1) transformed to satisfy assumptions of the normality and to stabilize variance . Type 1 error rate was 5%. Once a treatment effect was identified, differences were assessed using LSMEAN comparisons (SAS Institute 1999). We also used planned contrasts to determine which treatments differed on each sampling date. To control our comparison-wise error rate, we used sequential Bonferroni adjustments (Rice 1990). Blocks were included in the analysis of the 2001 data, but were not included in the 2002 and 2003 analysis because, in later years, fathead minnow populations were unrelated to initial densities. Initial fathead minnow densities at the outset of our study did not influence our results. This was evidenced by lack of block effect ($p>0.05$) for all response variables, except fathead minnows. A significant block effect for fathead minnows was expected because initial fathead minnow abundance was included as the block in our initial study design; however, as time progressed fathead minnow abundances converged across wetlands. Block was not a significant source of variation, therefore, we did not subsequently report block effects. Because initial minnow densities differed markedly among years, data gathered each year were analyzed separately.

Results

Walleye survival

Survival of age-0 walleye stocked as fry in 2001 was high in three of six wetlands (Hagstrom, Reisdorph 1, and Cuba wetlands), as evidenced by the removal of greater than 24 kg/ha of fingerlings in the fall 2001 (Table 1). Lower survival of age-0 walleye was observed in Froland, Morrison, and Mavis East wetlands in 2001, based on the removal of less than 9 kg/ha of walleye fingerlings from each of these wetlands in fall 2001. Survival of walleye fry stocked in 2002 was generally lower, and was confirmed only in Froland, Cuba, Reisdorph 1, and Morrison wetlands. Fall removal of the 2002 walleye fingerlings from these sites ranged from 0.07-1.04 kg/ha, except for Froland wetland that was not trap netted (Table 1). In Froland wetland, age-0 walleye from the 2002 fry stocking were sampled only for diet analysis, where 0.34 kg/ha of age-0 walleye were removed via seining and electrofishing. No age-0 walleye were captured in 2002 in either Mavis East or Hagstrom wetlands. Complete removal of the 2001 cohort was not achieved in any of the wetlands, consequently variable numbers of age-1 walleye remained in the wetlands in 2002 as evidenced by the additional removal of walleye from the 2001 cohort throughout 2002 (Table 1).

Total estimated cumulative mortality associated with sampling walleye for diet information (i.e., the estimated walleye population size/cumulative number of walleye killed during the process of collecting diet samples) in the advanced walleye treatment ranged from 5.8-27.6% during the study (Table 2). Consistently high catch rates of walleye (to obtain diet information) suggest that natural mortality was low in Rolland Lake, Bellevue, State Hospital, and Lunde Lake wetlands, and comparatively lower catch rates in Reisdorph 2 and Weigers wetlands indicates higher natural mortality rates in these wetlands (Table 2).

Adult fathead minnows

Introductions of walleye were associated with reduced biomass of fathead minnows in the walleye fry treatment during the first year of our study (2001) (Figure 1a; F=3.72, p=0.0479). Following walleye introduction, fathead minnow biomass declined by June 2001 in all three treatments. However, recruitment by fathead minnows resulted in significantly higher fathead minnow biomass in the reference treatment compared to the walleye fry treatment during August (p=0.014). By September 2001, fathead minnow biomass remained significantly lower in the walleye fry treatment relative to either the reference (p<0.002), or advanced walleye treatments (p=0.0325).

Repeated measures ANOVA indicated a significant treatment effect in 2002 (F=49.19, p<0.0001) and planned contrasts indicated all treatments were significantly different from each other on each sampling date (p<0.05) with the following exceptions: advanced walleye and reference treatments in June and July, and advanced walleye and walleye fry treatments in August and September. Fathead minnow biomass remained low (<19 grams fathead minnows/ trap) in the walleye fry treatment throughout 2002 (Figure 1b). In contrast, mean fathead minnow CPUE was consistently higher (>450 grams fathead minnows/trap) in the reference treatment. Fathead minnow biomass in the advanced walleye treatment was always intermediate between the walleye fry and reference treatments; however, biomass levels in August and September were similar to those in the walleye fry treatment.

Fathead minnow CPUE was not significantly different among the three treatments during 2003 (F=2.76, p=0.0946); one year after the final treatment (stocking) was applied to the study wetlands (Figure 1c). By July, and in subsequent months, the walleye fry and reference treatments had similar fathead minnow densities (>200 grams fathead minnows/trap), while mean fathead CPUE in the advanced walleye

Table 1. Estimated cumulative number of walleye removed/ha and biomass (kg) of walleye removed/ha from walleye fry treatment wetlands in 2001 and 2002.

Wetland	Cohort	Time period removed	Method of removal	Estimated cumulative number/ha removed	Estimated kg/ha removed
Cuba	2001	6/15/01-9/15/01	Seining/Electrofishing	6.42	0.06
	2001	Fall 2001	Trap netting	1410.45	29.62
	2001	Spring 2002	Electrofishing	1413.41	0.17
	2001	5/15/02-9/15/02	Seining/Electrofishing	1417.58	0.38
	2002	5/15/02-9/15/02	Seining/Electrofishing	1423.79	0.04
	2001	Fall 2002	Trap netting	1431.60	1.28
	2002	Fall 2002	Trap netting	1436.24	0.07
Froland	2001	6/15/01-9/15/01	Seining/Electrofishing	25.32	0.40
	2001	Fall 2001	Trap netting	149.00	5.64
	2001	Spring 2002	Electrofishing	223.45	4.62
	2001	5/15/02-9/15/02	Seining/Electrofishing	239.05	3.55
	2002	5/15/02-9/15/02	Seining/Electrofishing	257.20	0.34
Hagstrom	2001	6/15/01-9/15/01	Seining/Electrofishing	14.36	0.17
	2001	Fall 2001	Trap netting	1154.52	32.22
	2001	Spring 2002	Electrofishing	1388.24	15.94
	2001	5/15/02-9/15/02	Seining/Electrofishing	1397.93	0.74
	2001	Fall 2002	Trap netting	1508.60	9.31
	2001	Fall 2002	Electrofishing	1582.38	6.21
Mavis East	2001	6/15/01-9/15/01	Seining/Electrofishing	6.67	0.05
	2001	Fall 2001	Trap netting	357.26	8.47
	2001	5/15/02-9/15/02	Seining/Electrofishing	362.31	0.52
	2001	Fall 2002	Trap netting	415.94	10.64
Morrison	2001	6/15/01-9/15/01	Seining/Electrofishing	11.79	0.08
	2001	Fall 2001	Trap netting	302.00	6.29
	2001	Spring 2002	Electrofishing	370.62	8.14
	2001	5/15/02-9/15/02	Seining/Electrofishing	380.20	1.22
	2001	Fall 2002	Trap netting	395.23	2.65
	2002	Fall 2002	Trap netting	401.68	0.14
Reisdorph I	2001	6/15/01-9/15/01	Seining/Electrofishing	11.31	0.05
	2001	Fall 2001	Trap netting	3203.24	23.52
	2001	Spring 2002	Trap netting	3263.93	4.12
	2001	5/15/02-9/15/02	Seining/Electrofishing	3270.99	0.83
	2002	5/15/02-9/15/02	Seining/Electrofishing	3277.91	0.10
	2001	Fall 2002	Trap netting	3283.95	1.21
	2002	Fall 2002	Trap netting	3314.30	1.04

Table 2. Summary of collection methods for walleye in advanced walleye treatment wetlands throughout 2001 and 2002, including number of walleye collected for stomach content analysis and CPUE using various sampling gears.

Wetland	Sample date	Gear type	Minutes set	Number collected	Number per minute	Number of observed mortalities	Estimated percentage of stocked walleye remaining
Bellevue	6/14/01	electrofishing		40	0.51	12	97.81
	7/13/01	electrofishing		36	0.26	5	96.89
	8/13/01	4 gill nets	30	35	0.29	15	94.15
	9/23/01	5 gill nets	30	41	0.27	5	93.24
	5/13/02	4 gill nets	30	29	0.24	24	96.53
		electrofishing		18	1.20		
	6/14/02	electrofishing		58	2.64	2	96.41
	7/23/02	3 gill nets	30	31	0.34	6	96.07
	8/15/02	3 gill nets	30	59	0.66	60	92.66
	9/17/02	3 gill nets	30	82	0.91	59	89.30
Lunde	6/17/01	electrofishing		20	0.31	10	97.00
	7/12/01	electrofishing		32	0.22	15	92.54
	8/20/01	6 gill nets	30	45	0.25	16	87.76
	9/14/01	3 gill nets	30	39	0.43	7	85.67
	5/16/02	electrofishing		48	0.67	22	95.01
	6/15/02	electrofishing		54	2.85	15	93.94
	7/19/02	3 gill nets	30	29	0.32	9	93.30
	8/18/02	3 gill nets	30	52	0.58	24	91.59
	9/19/02	3 gill nets	30	40	0.44	10	90.88
Reisdorph II	6/18/01	electrofishing		2	0.02	0	100.00
	7/16/01	2 gill nets	120	41	0.17	18	93.23
	8/14/01	6 gill nets	30	20	0.11	7	90.60
	9/15/01	5 gill nets	30	23	0.15	5	88.72
	5/15/02	4 gill nets	30	32	0.27	23	95.69
		electrofishing		12	0.67		
	6/18/02	electrofishing		29	0.95	12	94.72
	7/24/02	9 gill nets	30	7	0.03	2	94.55
	8/14/02	9 gill nets	30	2	0.01	0	94.55
	9/14/02	3 gill nets	300	11	0.01	4	94.23
Rolland	6/19/01	electrofishing		31	0.22	11	98.48
	7/15/01	electrofishing		9	0.08	5	97.79
		2 gill nets	30	15	0.25		
	8/15/01	4 gill nets	30	26	0.22	7	96.48
	9/16/01	4 gill nets	30	24	0.20	5	96.15
	5/12/02	electrofishing		41	1.28	21	97.67
	6/13/02	electrofishing		47	1.03	0	97.67
	7/25/02	3 gill nets	30	27	0.30	1	97.62
	8/11/02	3 gill nets	30	44	0.49	44	95.52
	9/20/02	3 gill nets	30	78	0.87	33	93.95

Table 2. Continued.

Wetland	Sample date	Gear type	Minutes set	Number collected	Number per minute	Number of observed mortalities	Estimated percentage of stocked walleye remaining
State Hospital	6/15/01	electrofishing		19	0.12	10	97.30
	7/23/01	3 gill nets	45	19	0.14	6	95.68
	8/19/01	5 gill nets	30	44	0.29	12	92.43
	9/21/01	7 gill nets	30	37	0.18	13	88.92
	5/14/02	4 gill nets	30	22	0.18	21	93.81
		electrofishing		26	0.63		
	6/12/02	electrofishing		45	1.03	1	93.71
	7/21/02	3 gill nets	30	47	0.52	8	92.91
	8/13/02	3 gill nets	30	32	0.36	12	91.72
	9/15/02	3 gill nets	30	22	0.24	11	90.62
Weigers	6/16/01	electrofishing		25	0.15	10	92.54
	7/14/01	electrofishing		11	0.31	8	86.57
		6 gill nets	45	10	0.04		
	8/16/01	12 gill nets	30	22	0.06	12	77.61
	9/22/01	4 gill nets	30	8	0.07	7	72.39
	5/17/02	4 gill nets	30	10	0.08	2	89.82
		electrofishing		21	0.23		
	6/17/02	electrofishing		21	0.76	3	89.03
	7/22/02	6 gill nets	30	14	0.08	6	87.47
	8/17/02	5 gill nets	60	14	0.05	3	86.68
	9/16/02	3 gill nets	240	15	0.02	8	84.60

treatment remained consistently lower (<200 grams fathead minnows/trap).

Larval fathead minnows

Walleye fry stocking resulted in decreased densities of larval fathead minnows in 2002 (Figure 2; F=3.24, p=0.0492). Larval fathead minnow densities were significantly lower in the walleye fry treatment relative to the advanced walleye (p=0.0359) and reference (p=0.0302) treatments. Mean density of larval fathead minnows in the walleye fry treatment remained <0.5 fish/m^3 throughout the summer, except for August when larval density peaked at 1.8 fish/m^3. In contrast, larval fathead minnow density peaked at nearly 12 fish/m^3 in the advanced walleye treatment and 5.6 fish/m^3 in the reference treatment. However, in August and September larval fathead minnow populations were similar among all three treatments (p>0.05).

Zooplankton

Robust populations of large cladocerans characterized the walleye fry treatment. We observed lower densities of large cladocerans (including *Daphnia* spp.) in the reference and advanced walleye treatments during the period of June - September 2001 (Figure 3a; p<0.05). The density of large cladocerans averaged >100/l in the walleye fry treatment, but remained <50/l in both the reference and advanced walleye treatments throughout this period (Figure 3a). Means separation (LSMEANS) indicated zooplankton were more abundant in the walleye fry treatment than both the advanced walleye (p=0.0021) and reference (p=0.0361) treatments.

Densities of large cladocerans were significantly higher in the walleye fry treatment than either the advanced walleye or reference treatments from May-July 2002 (Figure 3b, p<0.05). The mean density of large

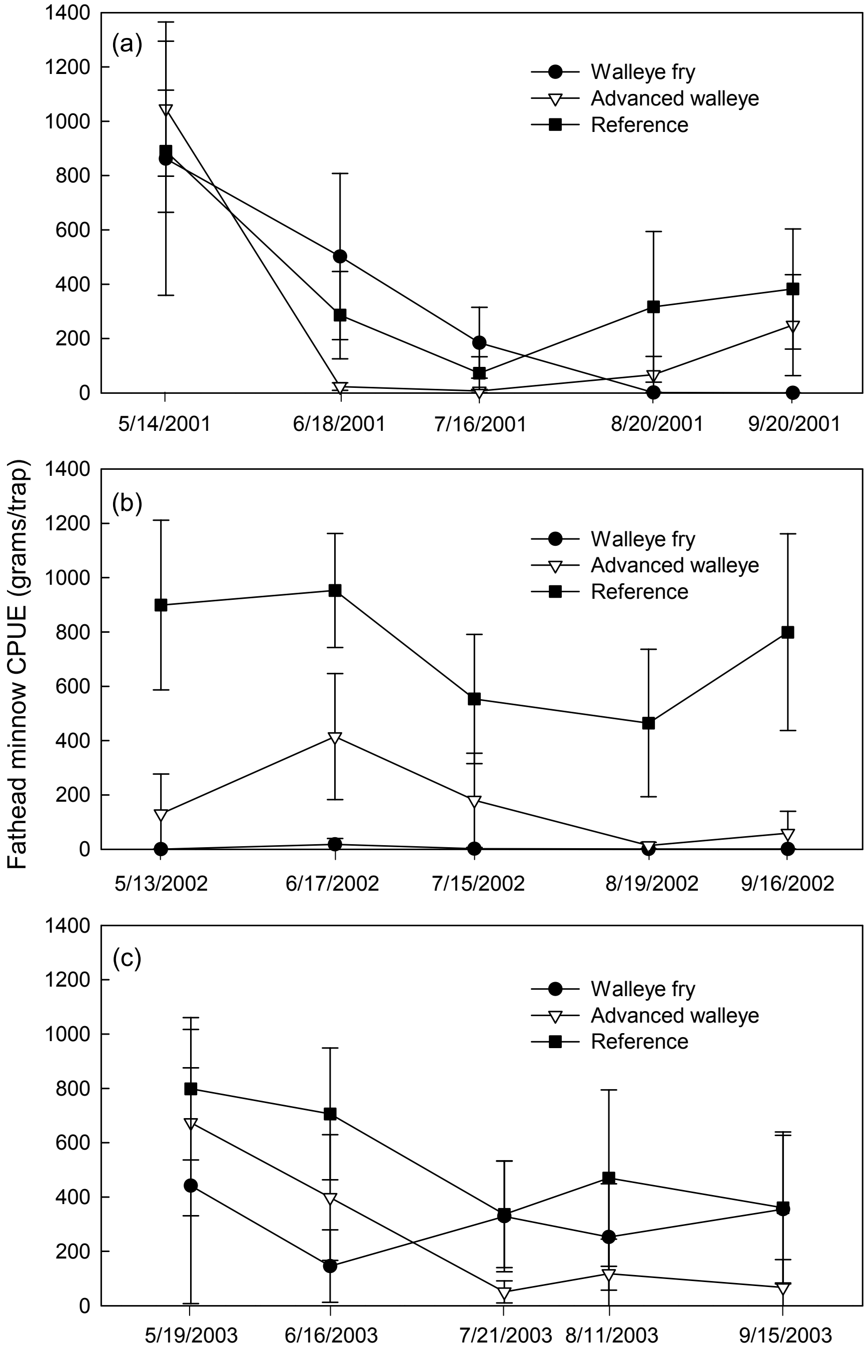

Figure 1. Fathead minnow catch-per-unit-effort (treatment mean ± 1 SE) from minnow trap sampling conducted during (a) 2001, (b) 2002, and (c) 2003.

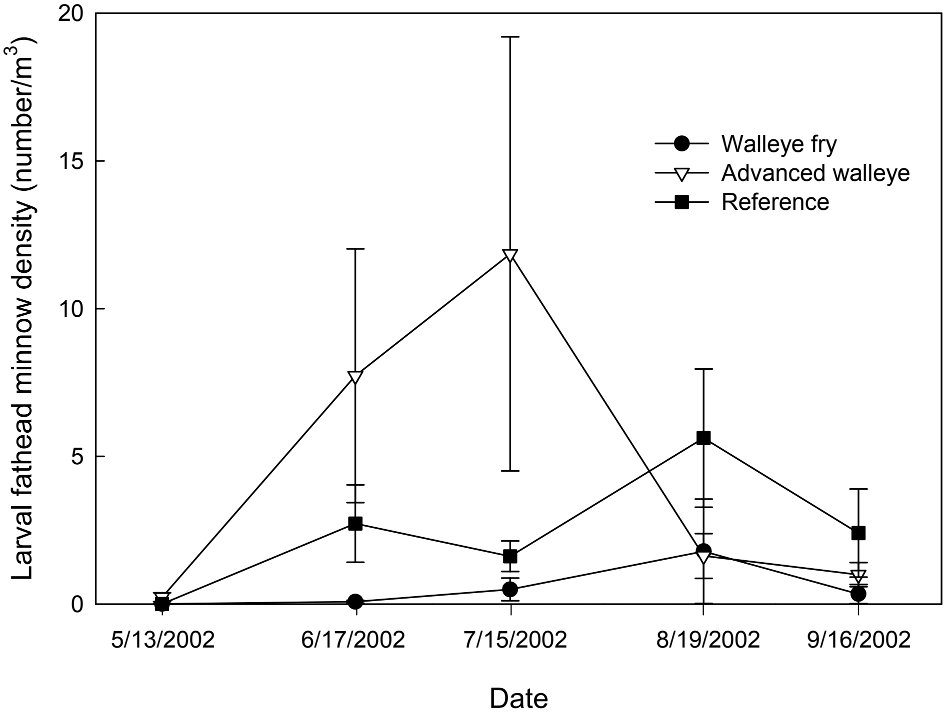

Figure 2. Larval fathead minnow population trends for each treatment (mean ± 1 SE) during 2002.

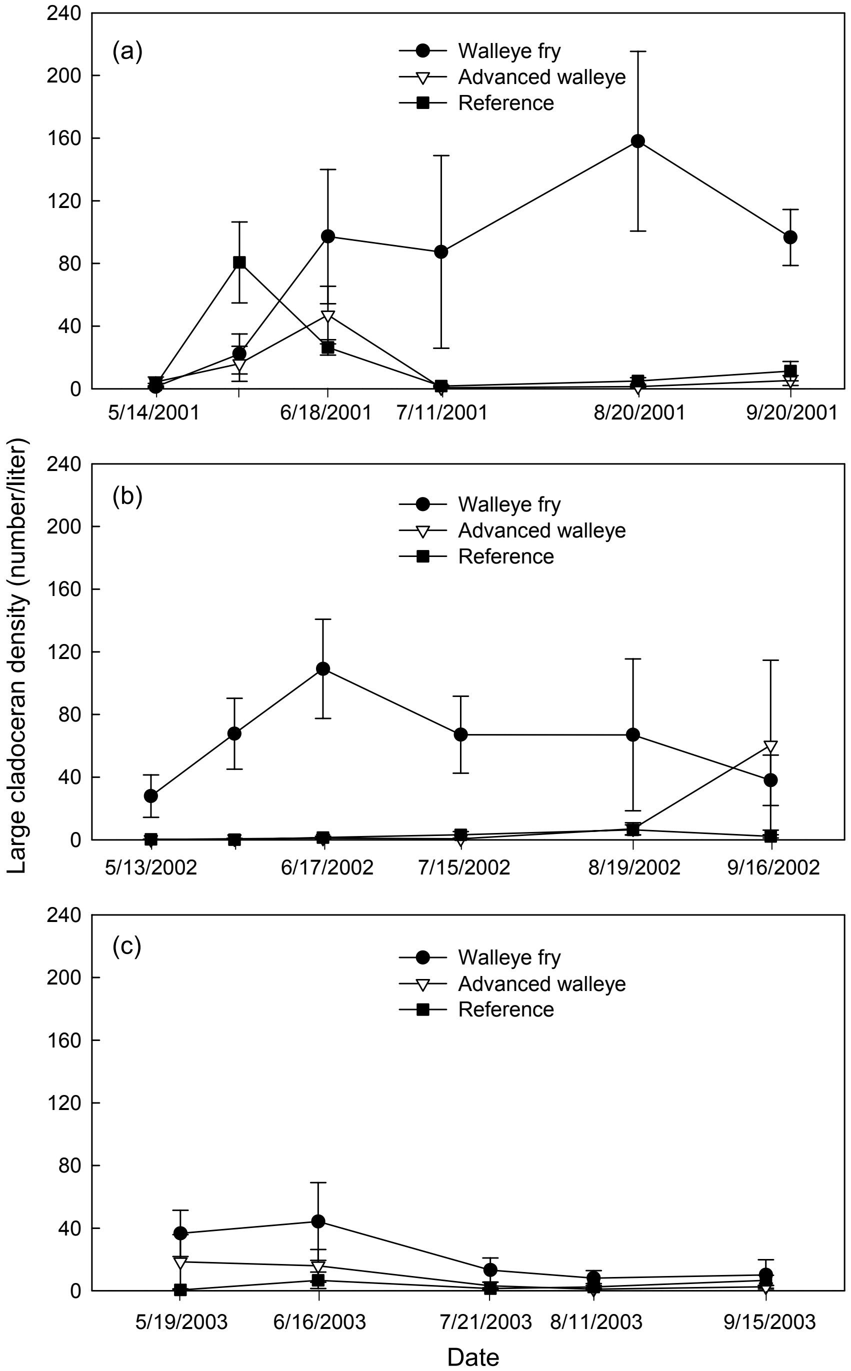

Figure 3. Densities of large cladoceran zooplankton (treatment mean ± 1 SE) calculated from vertical column samples collected during (a) 2001, (b) 2002, and (c) 2003.

cladocerans in the walleye fry treatment peaked at 109/l in June, that was >75 times higher than observed in the other two treatments (Figure 3b). By August and September, densities of large cladocerans were no longer significantly different among treatments. Although variable, by September 2002, the mean density of large cladocerans in the advanced walleye treatment exceeded that observed in the walleye fry treatment (Figure 3b).

Populations of large cladocerans remained higher in the walleye fry treatment than either the advanced walleye or reference treatments during May - June 2003 ($p<0.05$), approximately one year after walleye stocking was discontinued (Figure 3c). By July, all three treatments had few large cladocerans (<15/l), and densities were similar among all treatments ($p>0.10$).

Amphipods

Wetlands stocked with either walleye fry or advanced walleye had a higher abundance of amphipods than those containing only fathead minnows in 2001 (Figure 4a; $F= 6.58$, $p=0.0106$). During May - July 2001, amphipod CPUE was markedly higher in the advanced walleye treatment relative to the reference treatment, but amphipod abundance was higher in the walleye fry than reference treatment during August and September (Figure 4a). The reference treatment differed significantly from both the advanced walleye ($p=0.0056$) and walleye fry ($p=0.0016$) treatments; however, the advanced walleye and walleye fry treatments were not different ($p=0.7117$). High densities of amphipods observed in the advanced walleye treatment in July were not indicative of patterns observed in most of these wetlands, but reflected extremely high amphipod abundance in two wetlands.

In 2002, amphipod abundance was highest in the walleye fry treatment, intermediate in the advanced walleye treatment, and lowest in reference treatment (Figure 4b; $F=20.12$, $p<0.0001$). Amphipod CPUE was significantly higher in the walleye fry treatment than either the advanced walleye ($p=0.0132$) or reference treatments ($p<0.0001$). The advanced walleye treatment was also significantly higher than the reference treatment ($p<0.0031$).

Macroinvertebrates

Several macroinvertebrate taxa sampled with vertically deployed activity traps were grouped, forming an aggregate response variable (hereafter referred to as "macroinvertebrates") that included: the order Coleoptera (adults and larvae), which included the families DYTISCIDAE, HALIPIDAE, STAPHYLINIDAE, GYRINIDAE, CHRYSOMELIDAE, CURCULIONIDAE and HYDROPHILIDAE; the order Hemiptera, which included the families NOTONECTIDAE, PLEIDAE and BELOSTOMATIDAE; the order Ephemeroptera; the order Trichoptera; the order Odonata, which included the suborders of Anisoptera and Zygoptera; the order Diptera, which included the families CHIRONOMIDAE, CHAOBORIDAE, CULICIDAE, CERATOPOGONIDAE, SIMULIIDAE, ATHERICIDAE and TIPULIDAE; the suborder Trombidiformes (Hydracarina); the order Collembola; the phylum Nematoda; and the class Oligochaeta.

Macroinvertebrate abundance in the advanced walleye treatment was consistently lower than either of the other two treatments during 2001 (Figure 5a). During May 2001, macroinvertebrate abundance in the walleye fry treatment was similar to the reference treatment, but steadily increased through August, reaching a mean peak level nearly three times that observed in the reference treatment. Although overall treatment effects were evident ($F=4.73$, $p=0.0285$), means comparison tests did not indicate a significant separation between the walleye fry and reference treatments ($p=0.4032$), despite higher macroinvertebrate catches on the last three sampling dates. The advanced walleye and reference treatments also were not significantly different ($p=0.053$), but macroinvertebrates were significantly more abundant in the walleye fry versus advanced walleye treatment ($p=0.0104$).

Populations of macroinvertebrates were also significantly different among treatments in 2002 (Figure 5b; $F=9.12$, $p=0.0026$). Macroinvertebrate abundance remained higher in the walleye fry treatment than either the advanced walleye ($p=0.0043$) or reference

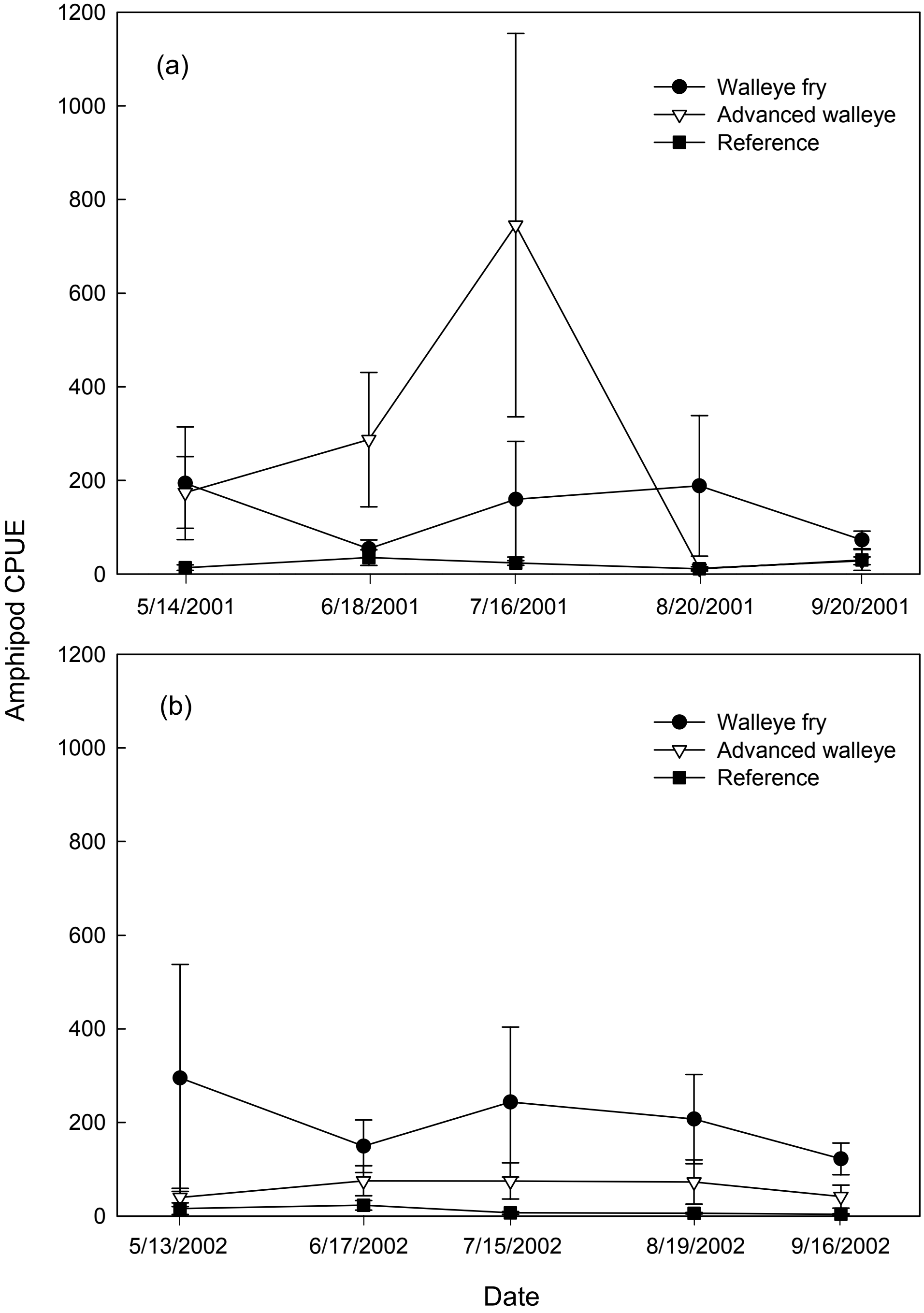

Figure 4. Amphipod abundance (mean ± 1 SE) for each treatment calculated from activity trap samples collected during (a) 2001 and (b) 2002.

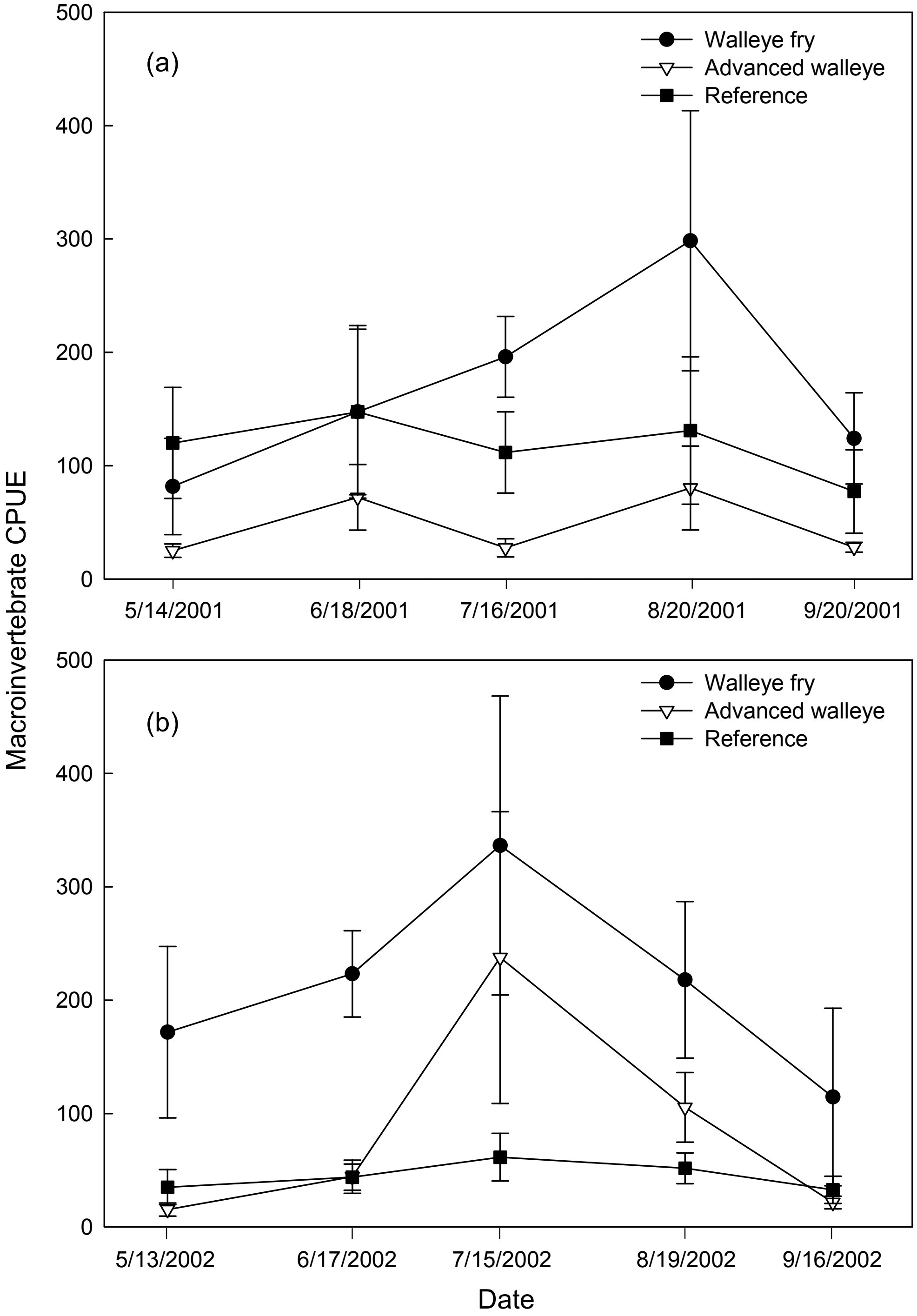

Figure 5. Macroinvertebrate abundance among treatments (mean ± 1 SE) during (a) 2001 and (b) 2002 calculated from activity trap samples.

(p=0.0013) treatments. Macroinvertebrates were three to six times more abundant in the walleye fry treatment than in the reference treatment throughout 2002 (Figure 5b). In July and August, the advanced walleye treatment had a higher abundance of macroinvertebrates than the reference treatment, but decreased to low levels by September.

Benthic chironomids

Density of chironomids sampled with an Ekman sampler was similar in the walleye fry and reference treatments in 2001, but chironomid biomass was almost two times higher in the walleye fry treatment than in the reference treatment (Figure 6a). However, due to extreme variability, a significant treatment effect was not identified for either density (F=0.56, p=0.5812) or biomass (F=1.13, p=0.3481). Chironomid biomass was comparable between the advanced walleye and reference treatments even though, on average, the advanced walleye treatment had approximately 600 fewer chironomids/m^2. During 2002, chironomid density and biomass was lowest in the walleye fry treatment, intermediate in the reference treatment, and highest in the advanced walleye treatment (Figure 6b). Similar to 2001, no treatment effects were observed for either chironomid density (F=0.39, p=0.6830) or biomass (F=0.00, p=0.9983).

Phytoplankton

Phytoplankton biomass, as indexed by concentrations of chlorophyll *a*, did not differ among treatments in 2001 (Figure 7a; F=0.63, p=0.5473). Chlorophyll *a* was low in May and increased throughout the summer in all three treatments. During the second year of our study, lower concentrations of chlorophyll *a* were observed in the walleye fry treatment relative to both the advanced walleye (p=0.0281) and reference treatments (p=0.0260). Similar to 2001, chlorophyll *a* steadily increased throughout the 2002 sampling season in the advanced walleye and reference treatments, achieving a level approximately double that observed in the walleye fry treatment by September (Figure 7b). Chlorophyll *a* concentrations increased in all three treatments throughout 2003, but phytoplankton abundance was significantly lower in the walleye fry treatment than either the advanced walleye (p=0.0092) or reference treatments (p=0.0236). By September, chlorophyll *a* was 2.1 times higher in the advanced walleye treatment, and 2.8 times higher in the reference treatment than the walleye fry treatment (Figure 7c).

Turbidity

Turbidity data collected during 2001 were incomplete due to equipment failure; therefore, there are no turbidity relationships to report for 2001. However, we identified a strong positive relationship between chlorophyll *a* and turbidity in the study wetlands (simple linear regression: R^2=0.6864, p<0.0001), thus trends for turbidity reflected those observed for chlorophyll *a*.

Turbidity, as indexed by Nephelometric Turbidity Units (NTUs), was significantly lower in the walleye fry treatment than either advanced walleye (p=0.0258) or reference treatments (p=0.0091) during 2002. Turbidity increased in all three treatments throughout the summer, but mean turbidities never exceeded 20 NTUs in the walleye fry treatment (Figure 8a). This contrasts with the reference treatment, in which mean turbidity exceeded 45 NTUs. Turbidity levels in the advanced walleye treatment were intermediate between the other two treatments during most of 2002 (Figure 8a).

Water transparency remained high in the walleye fry treatment throughout 2003 (Figure 8b). Despite lower mean turbidity in the walleye fry treatment throughout the summer, turbidity levels were significantly lower than both the advanced walleye (p=0.0135) and reference (p=0.0406) treatments only during June. Similar to 2002, water clarity was generally poor and decreased throughout the summer months in both the advanced walleye and reference treatments.

Concentrations of major nutrients

Total nitrogen (TN) and total phosphorus (TP) generally increased in all three treatments

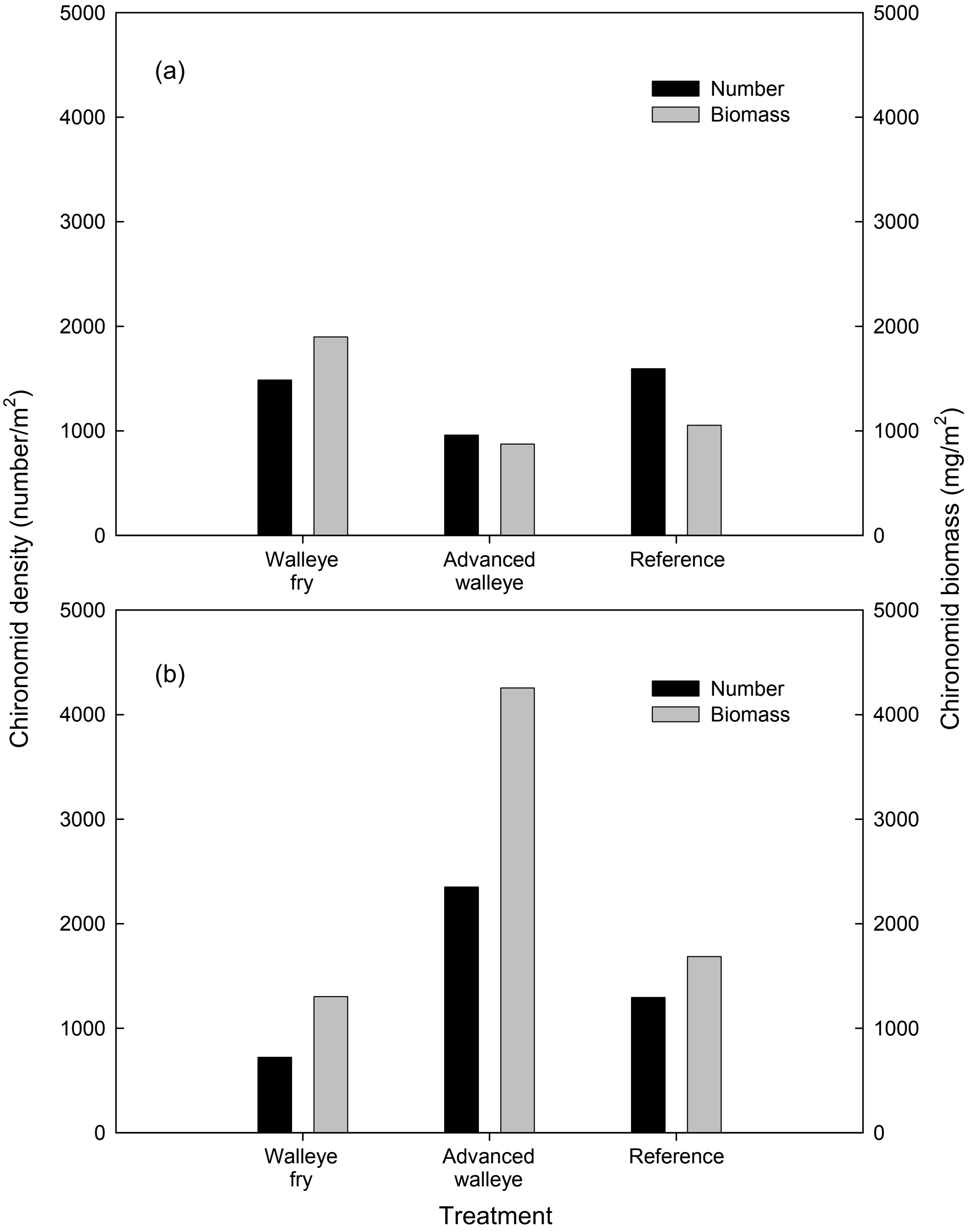

Figure 6. Estimates of mean density and biomass of chironomid larvae in each treatment based on Ekman samples taken of surficial sediments in late summer (a) 2001 and (b) 2002.

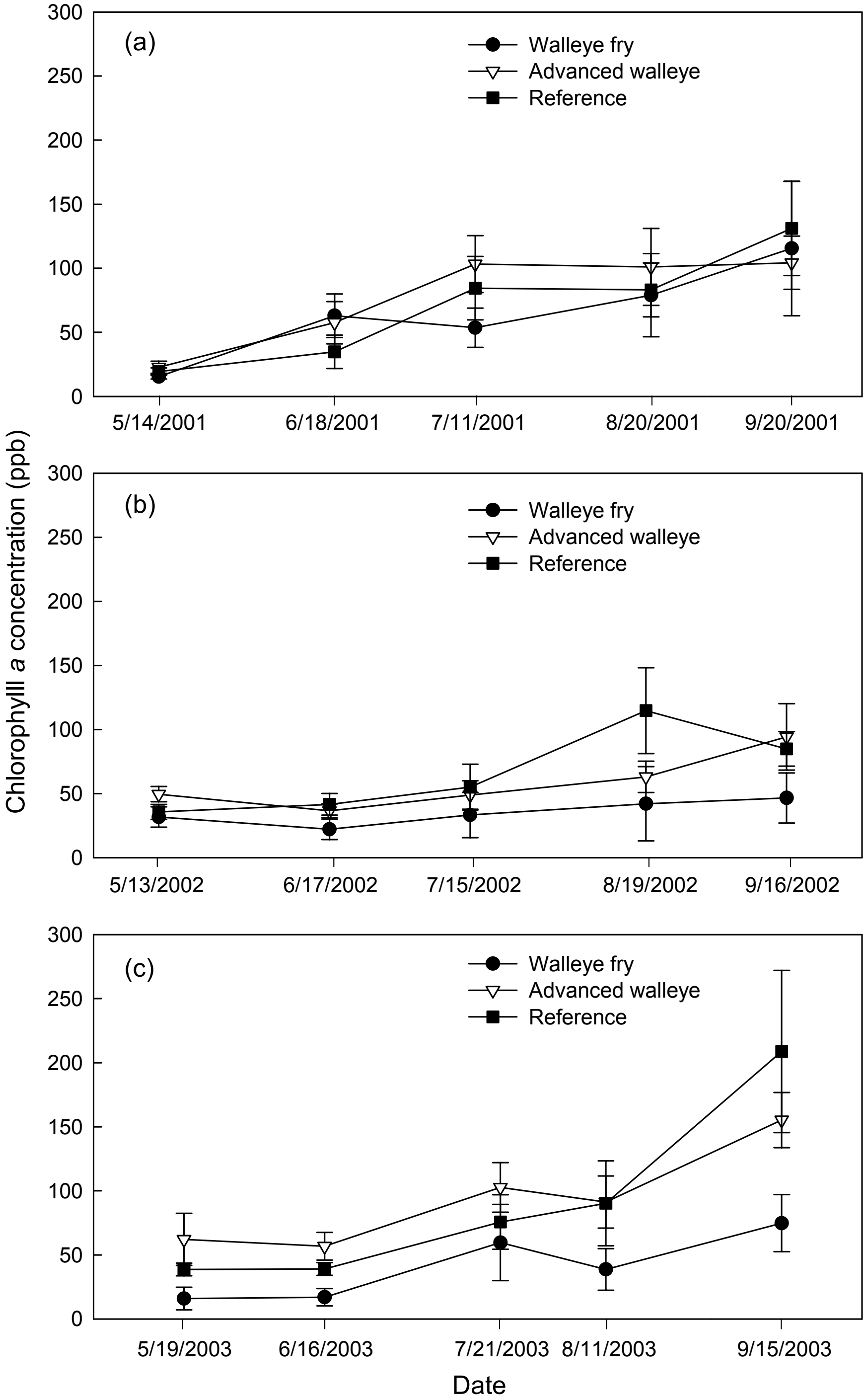

Figure 7. Phytoplankton abundance (indexed by chlorophyll *a*) in each treatment (mean ± 1 SE) during (a) 2001, (b) 2002, and (c) 2003.

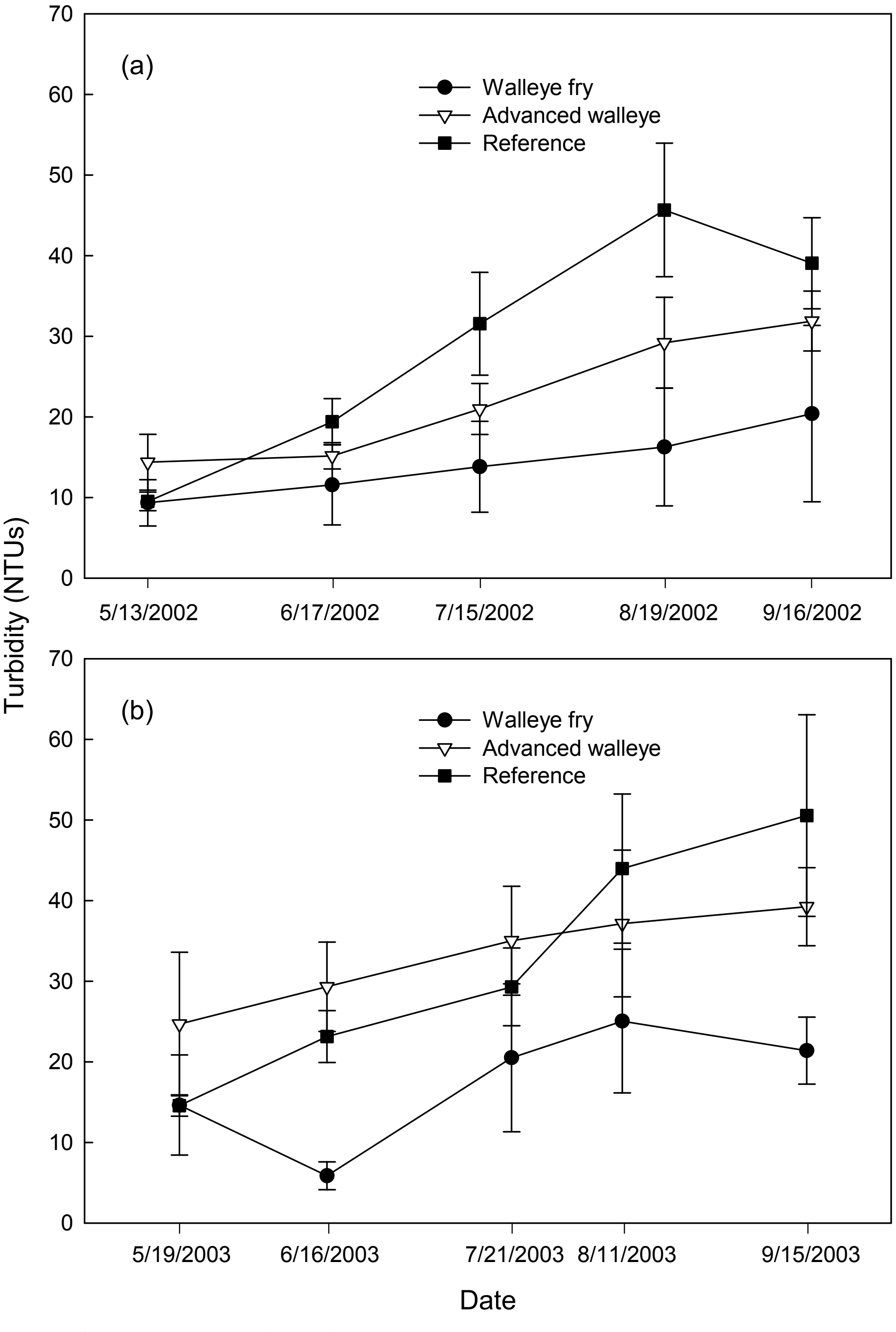

Figure 8. Comparison of water transparency among treatments (mean ± 1 SE) during (a) 2002 and (b) 2003.

throughout 2001, although no significant treatment effects were evident (Figure 9a). In general, nutrient concentrations tended to be higher in the advanced walleye treatment and increased most during the early summer (Figure 9). Mass ratios of TN:TP (hereafter N:P) were relatively high in May, but declined to lower levels by June, although no statistical differences were detected among treatments (Figure 9a).

Concentrations of TN and TP were relatively stable and similar in all three treatments during 2002 (Figure 9b; $p>0.05$). Although no significant treatment effects were evident, N:P ratios started at similar levels in May, increased in the walleye fry and reference treatments in June and July, but subsequently decreased (Figure 9b). By September, N:P was again comparable among the treatments.

In 2003, TN increased in all three treatments, but no treatment effects were detected (Figure 9c). TP varied among sampling dates for each of the treatments, but all remained within a similar range throughout the summer (Figure 9c; $p>0.05$). The N:P ratio remained relatively high and stable in the reference treatment, stable and low in the advanced walleye treatment, but switched from low to high (nearly doubled) between June and July in the walleye fry treatment (Figure 9c). N:P remained high in the walleye fry treatment for the balance of the summer. While temporal patterns were again evident for this response, we did not detect any significant treatment effects.

Submerged aquatic vegetation

Coverage by submerged aquatic vegetation (SAV) did not differ among treatments in any year, perhaps due to the high variability in our data (Figure 10a-c). Mean submerged plant abundance was especially similar in all three treatments in 2001. We observed a consistent increase in mean plant scores in the walleye fry treatment over the time series, nearly doubling between 2001 and 2003 (Figure 10a-c). Mean SAV abundance in the advanced walleye treatment was similar in 2001 and 2002, but decreased sharply in 2003. In contrast, SAV abundance in the reference treatment remained consistent among years.

Fathead minnow diets

Larval fathead minnow (<20mm) diets in Stammer wetland (reference treatment) consisted of zooplankton and rotifers in early summer, but changed to mostly detritus in late summer 2001 (Figure 11a). In 2002, larval fathead diets were comprised almost entirely of detritus in early June, zooplankton and rotifers in mid-July, and macroinvertebrates and detritus in early September (Figure 11a). Juvenile fathead minnow (20-40 mm) diets consisted primarily of macroinvertebrates (>70%), some detritus, and a small amount of zooplankton in mid-June 2001 (Figure 11b). By late summer, juvenile diets were comprised of detritus (>70%) and macroinvertebrates (<30%). In 2002, detritus was prominent in the diet of juvenile fathead minnows, with macroinvertebrates composing an equivalent proportion of the diet in late-July and some zooplankton observed in the diet in late summer (Figure 11b). Adult fathead minnow (>40 mm) diets consisted exclusively of macroinvertebrates in early-June 2001 (Figure 11c). Macroinvertebrates remained an important component of diet (30-69%) on subsequent dates, but detritus (late-August), and detritus and zooplankton (late-June) were also important. The diet of adult fathead minnows consisted almost entirely of detritus (>90%) throughout 2002 (Figure 11c).

Larval fathead minnow diets in Froland wetland (walleye fry treatment) consisted exclusively of zooplankton throughout the summer of 2001 (Figure 12a). This pattern continued in early-June 2002, but by mid-July larval diets were comprised predominantly of detritus (>80%), with lesser amounts of zooplankton and rotifers (<20% of total). During 2001, juvenile diets contained mostly macroinvertebrates (>50%), some zooplankton (4-27%), and detritus (19-38%; Figure 12b). In 2002, detritus dominated the diet of juvenile fathead minnows (>60%), and either zooplankton or macroinvertebrates made up the balance of the diet (Figure 12b). Macroinvertebrates comprised about 70% of the diet of adult fathead minnows throughout 2001 (Figure 12c). Detritus constituted the remainder of diet in early and late summer, while

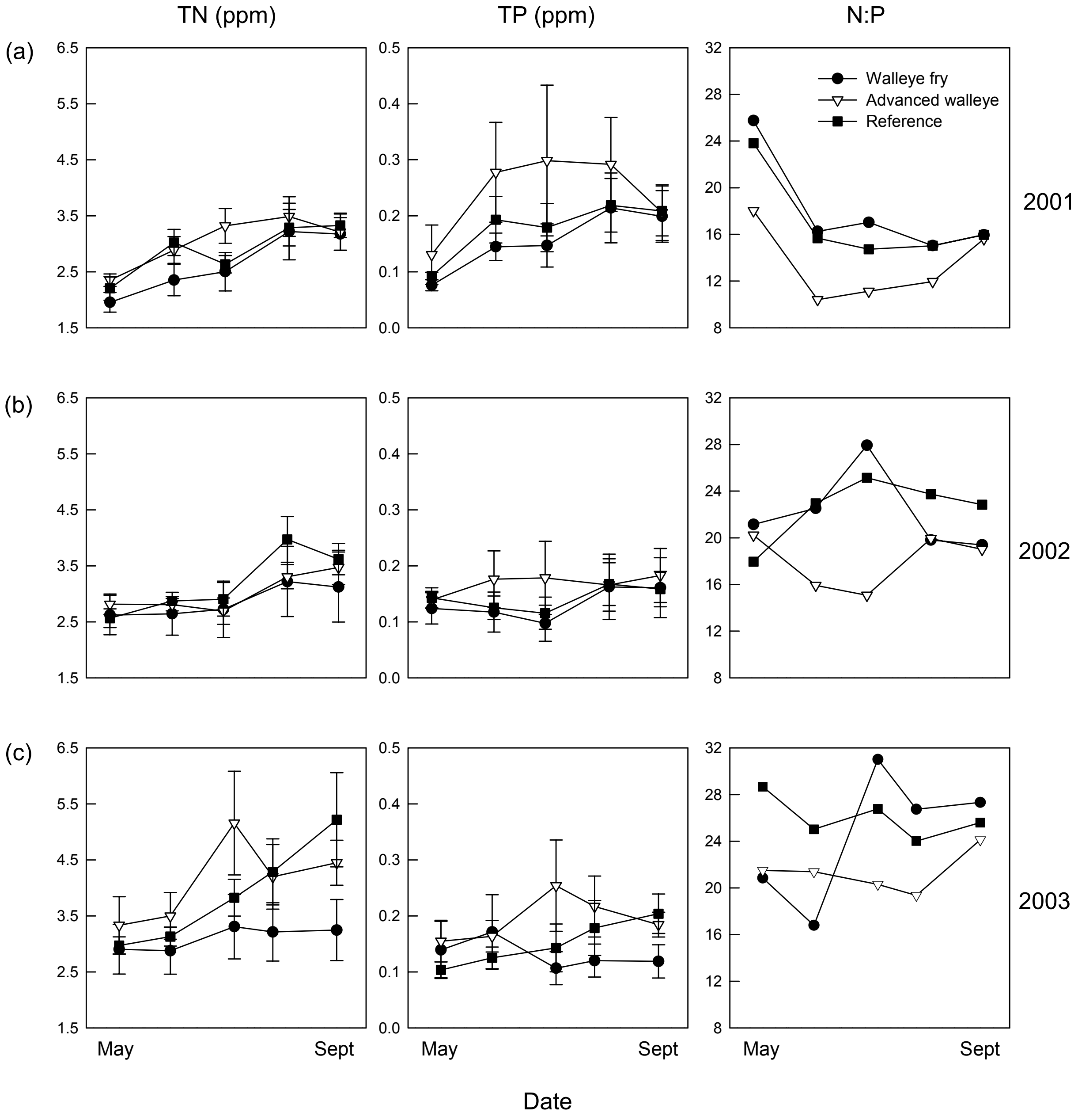

Figure 9. Concentrations of major nutrients (mean ± 1 SE) and the N:P ratio for each treatment from monthly samples collected from May - September during (a) 2001, (b) 2002, and (c) 2003. Total nitrogen (TN) is plotted on the left, total phosphorus (TP) is plotted in the center, and the mass ratio of TN:TP is plotted on the right side of each panel.

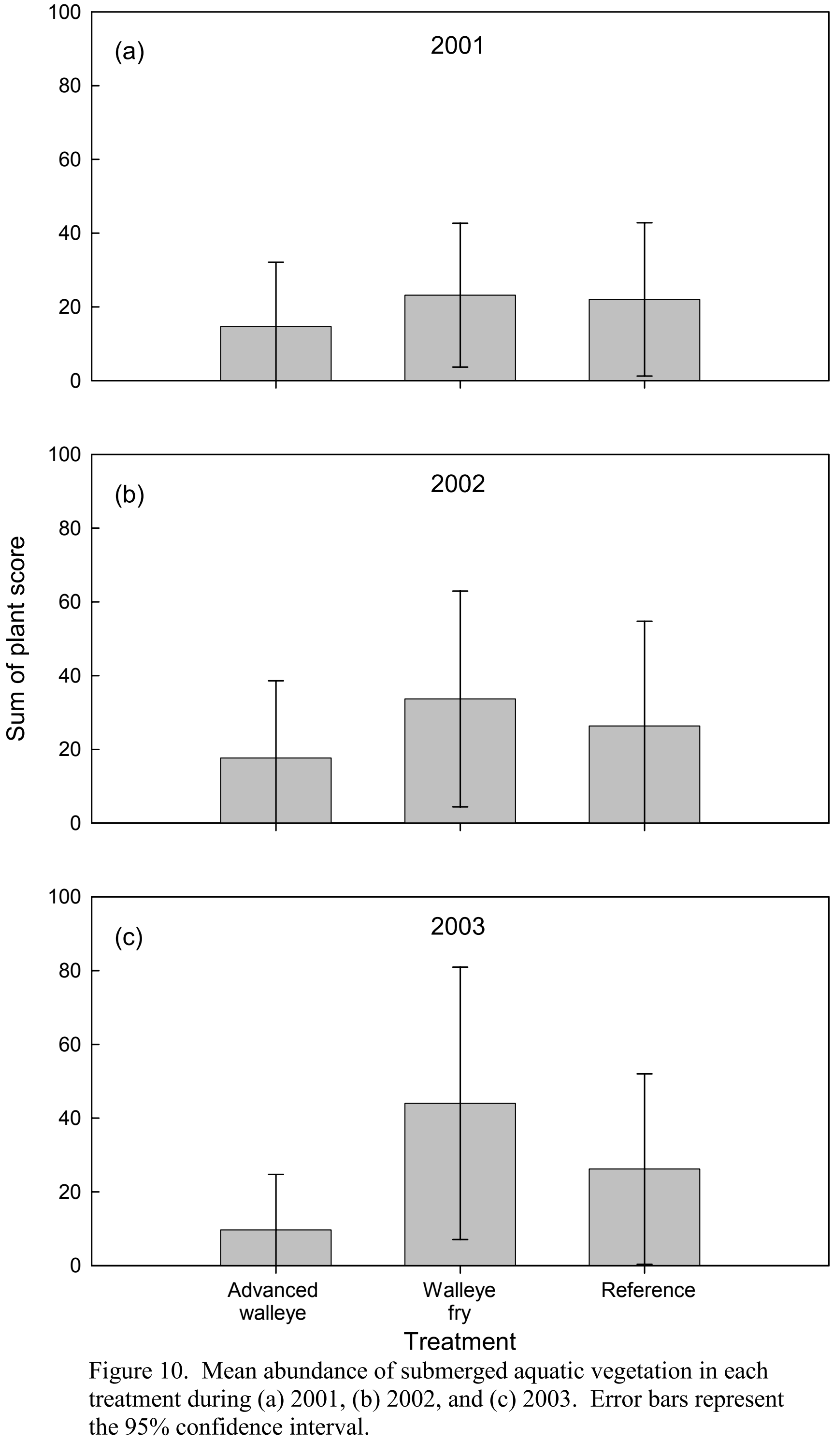

Figure 10. Mean abundance of submerged aquatic vegetation in each treatment during (a) 2001, (b) 2002, and (c) 2003. Error bars represent the 95% confidence interval.

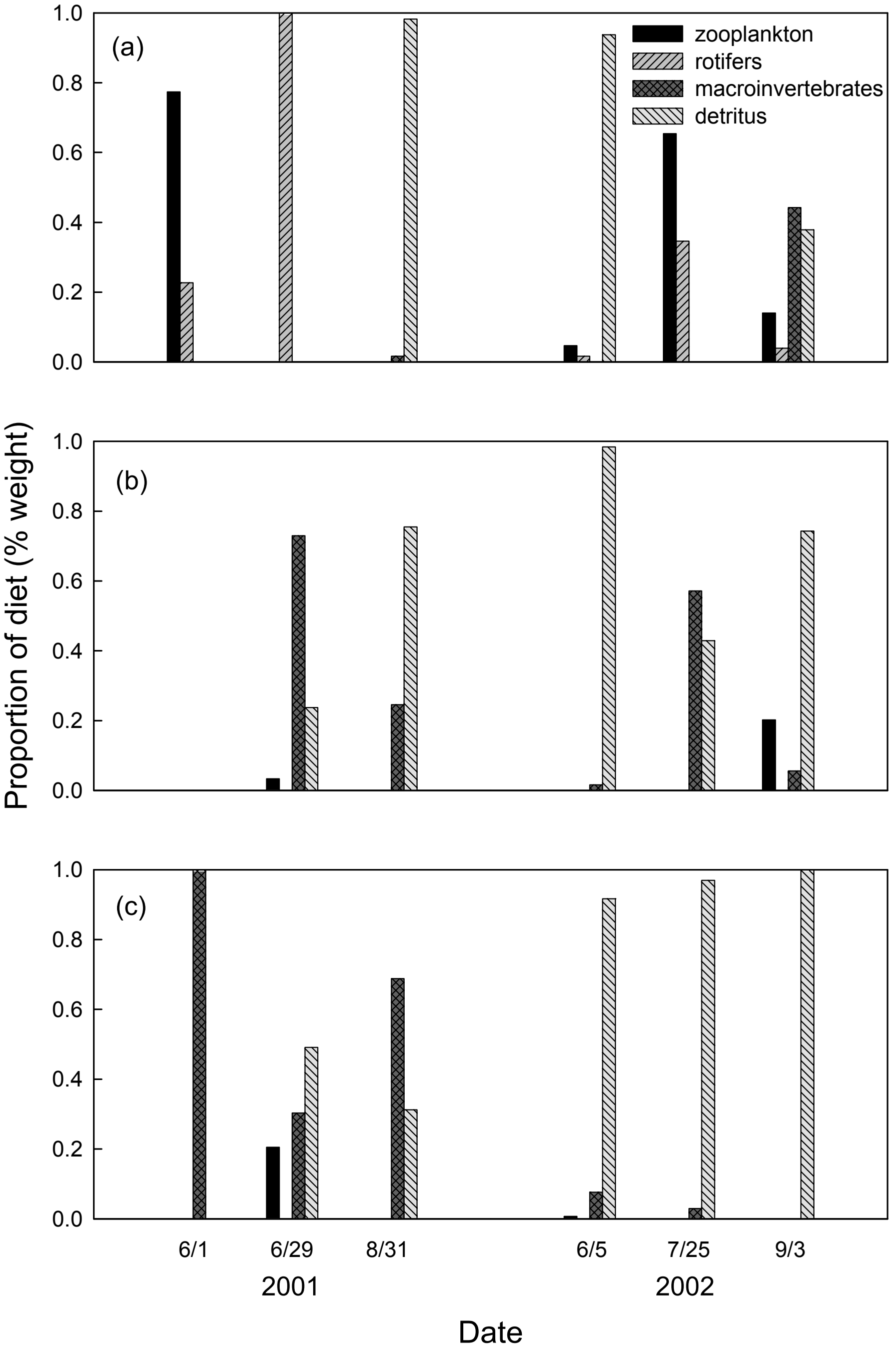

Figure 11. Proportion of major food resources in diets of fathead minnows for three dates throughout the summer of 2001 (left side of panel) and 2002 (right side of panel) for (a) larval (< 20 mm), (b) juvenile (20-40 mm), and (c) adult (> 40 mm) fathead minnows in Stammer (a reference treatment wetland).

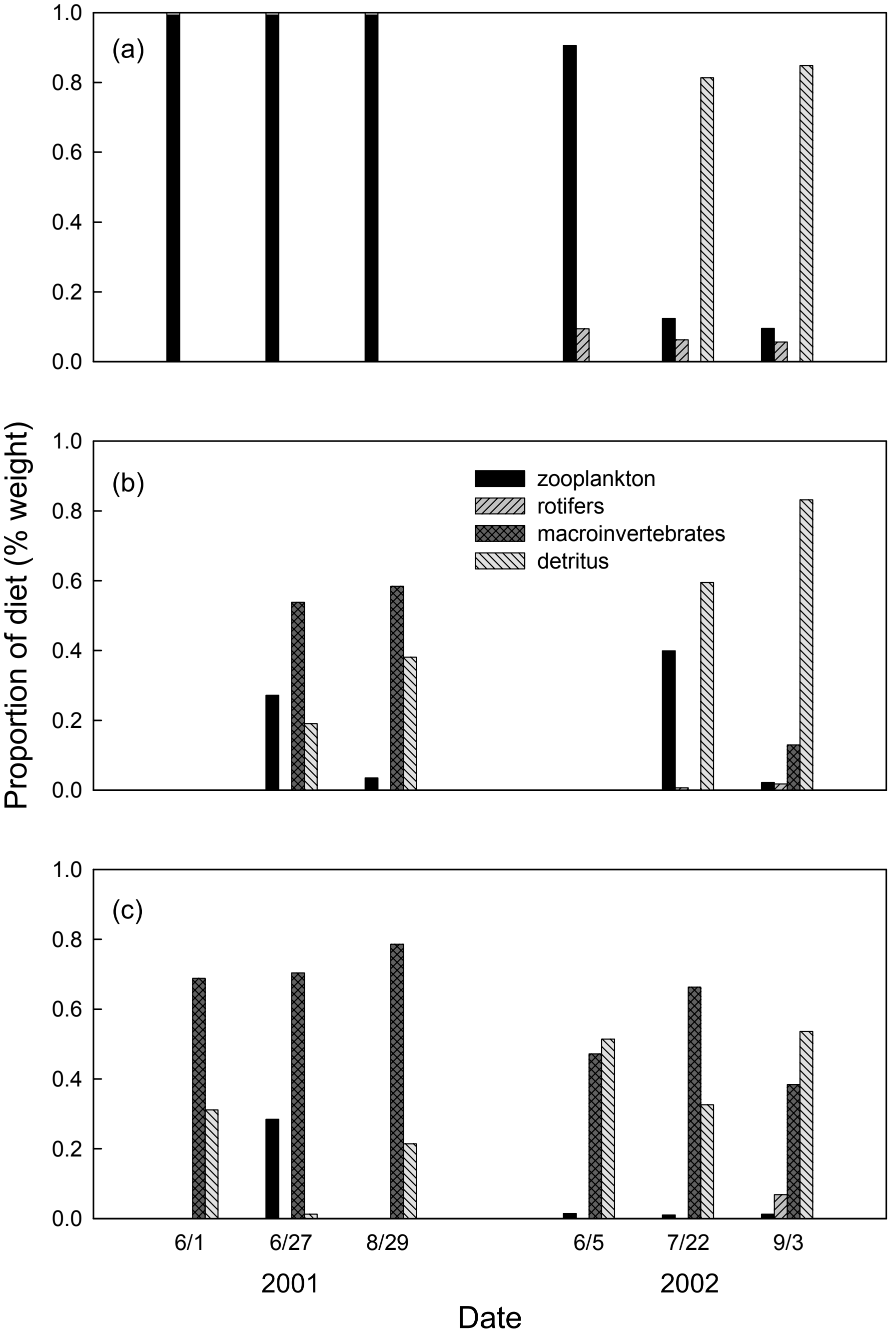

Figure 12. Proportion of major food resources in diets of fathead minnows for three dates throughout the summer of 2001 (left side of panel) and 2002 (right side of panel) for (a) larval (< 20 mm), (b) juvenile (20-40 mm), and (c) adult (> 40 mm) fathead minnows in Froland (a walleye fry treatment wetland).

zooplankton were important in mid-summer. In 2002, the diet of adult fathead minnows was split between detritus and macroinvertebrates, with these two items composing at least 92% of the diet (Figure 12c). Zooplankton and rotifers made up the remaining 1-7% of adult diets. In general, the diet patterns observed in Froland wetland during 2001 were very different from those observed in both years in Stammer wetland (Figures 11 and 12). During 2001, invertebrate prey dominated the diets of fathead minnows in Froland wetland, while detritus was more important in 2002 (Figures 11 and 12).

Walleye diets

Diets of walleye stocked as fry in wetlands

A generalized diet transition from zooplankton to fish to macroinvertebrates was observed for the 2001 walleye cohort throughout 2001 and 2002. Diets of age-0 walleye in 2002 were similar to age-1 walleye diets in 2002, and both were comprised primarily of macroinvertebrates, although considerable variation in diet composition was observed among wetlands (Tables 3 and 4). No diet samples were collected for the 2002 walleye cohort in Mavis East, Hagstrom, and Morrison wetlands because of the low walleye survival observed in these wetlands.

Zooplankton comprised substantial, but variable portions (up to 92% of weight) of the age-0 walleye diets in Reisdorph 1, Morrison, Cuba, Hagstrom, and Mavis East wetlands throughout 2001 (Table 3). Zooplankton were not observed in the diet of age-0 walleye in Froland wetland in 2001. Dominance of *Daphnia* spp. versus copepods (zooplankton portion of the diet) varied among wetlands in 2001; however, *Daphnia* spp. dominated this portion of the diet for both age-0 and age-1 walleye in 2002 (Tables 3 and 4). Overall, zooplankton were much less important proportionately to the diet in 2002 compared to 2001.

Fathead minnows and brook stickleback also comprised substantial portions of walleye diets in the walleye fry treatment during 2001 and 2002 (Tables 3 and 4). Piscivory among age-0 walleye was first demonstrated by a 27-mm walleye, which consumed a 6-mm larval fathead minnow (Table 3). Larval fathead minnows from 7 to 10 mm (TL) were commonly observed in the stomach contents of walleye from 30 to 40 mm. Mean lengths of fathead minnows consumed by age-0 and age-1 walleye ranged from 6 to 72 mm throughout 2001 and 2002 (Tables 3 and 4).

Fish comprised up to 93% of age-0 walleye diets in 2001 (Table 3). In general, the percentage of fish in the diet peaked in June or July, and then declined. Age-0 walleye diets (all samples) in 2002 consisted of <43% fish in Reisdorph 1 wetland, and <10% fish in Cuba wetland (Table 4). Fish comprised >56% of age-0 walleye diets on all sample dates in Froland wetland in 2002. During 2002, fish never comprised >30% of the diet of age-1 walleye in Reisdorph 1, Morrison, and Cuba wetlands (Table 3). Brook stickleback comprised <51% of the diet of age-1 walleye at times in Hagstrom and Mavis East wetlands, and were the predominant prey fish in the diet. In Froland wetland, fathead minnows comprised >95% of age-1 walleye diets throughout 2002.

Cannibalism by age-0 walleye was observed in several sites in 2001 (Morrison, Reisdorph 1, Hagstrom, and Mavis East wetlands; Table 3). Cannibalism was most evident in samples from the mid-June and mid-July periods in 2001, and walleye comprised up to 36% of age-0 walleye diets at this time. Cannibalism was observed only once in the diets of age-0 and age-1 walleye in 2002 (Tables 3 and 4).

Macroinvertebrates were frequently consumed by age-0 and age-1 walleye throughout 2001 and 2002. Macroinvertebrates comprised >48% of the food consumed by the 2001 walleye cohort in Hagstrom, Morrison, Reisdorph 1, Mavis East, and Cuba wetlands, on all sample dates from mid-September 2001 through mid-September 2002 (Table 3). Food habits of the 2002 walleye cohort in Reisdorph 1 and Cuba wetlands were also comprised of >58% macroinvertebrates on all sample dates in 2002 (Table 4). Although macroinvertebrates comprised >95% of age-0 walleye diets in Froland wetland from mid-July through mid-September 2001, macroinvertebrates comprised <6% of age-1 walleye diets,

Table 3. Bi-monthly mean percent by weight for stomach contents of walleye stocked as fry in 2001 in each of the fry treatment wetlands throughout the summers of 2001 and 2002. Standard error of the mean is reported in parentheses. Sample size (N), percentage of empty stomachs (% empty), and mean length(length (mm)) of walleye are reported, and mean size of fathead minnows consumed (FHM len cons (mm)) on each sampling date is indicated. Abbreviations are as follows: BSB = brook stickleback, CMM = central mudminnow, FHM = fathead minnow, WAE = walleye, CHI (L) = chironomid larva, CHI (P) = chironomid pupa, AMP = amphipod/scud, LEEC = leech, EPH= mayfly larva, TRI = caddisfly larva, NOT = backswimmer, COR = water boatman, ANIS = dragonfly larva, ZYG = damselfly larva, CHAO = phantom midge, DYT = predaceous diving beetle, CRAY = crayfish, WORM = earthworm, COPE = copepod, DAPH = *Daphnia* spp.

Cuba Wildlife Management Area

Date	**6/17/01**	**6/27/01**	**7/12/01**	**7/25/01**	**8/20/01**	**8/29/01**	**9/14/01**	**5/16/02**	**6/15/02**	**7/19/02**	**8/18/02**	**9/16/02**
N	25	29	30	21	23	23	26	20	20	27	23	25
% empty	0	10	30	29	9	30	38	0	0	22	9	4
length (mm)	30 (0)	46 (0)	74 (2)	112 (5)	106 (3)	128 (6)	131 (3)	186 (3)	192 (3)	188 (4)	227 (5)	264 (5)
FHM len cons (mm)	7.29	14.00	19.40	38.80	33.00	66.00	n/a	n/a	n/a	n/a	n/a	n/a
	% Weight											
FISH	**12 (6)**	**8 (5)**	**67 (11)**	**53 (13)**	**14 (8)**	**6 (6)**	**0**	**0**	**0**	**0**	**0**	**4 (4)**
FHM	12 (6)	8 (5)	67 (11)	53 (13)	14 (8)	6 (6)	0	0	0	0	0	0
WAE	0	0	0	0	0	0	0	0	0	0	0	4 (4)
INVERT	**1 (1)**	**0**	**5 (5)**	**27 (12)**	**86 (8)**	**94 (6)**	**87 (7)**	**100 (0)**	**100 (0)**	**100 (0)**	**100 (0)**	**96 (4)**
CHI (L)	0	0	0	0	6 (5)	0 (0)	8 (6)	0	0 (0)	0 (0)	0	0
CHI (P)	1 (1)	0	0	20 (11)	9 (5)	2 (2)	1 (1)	0	0	8 (5)	17 (8)	0
AMP	0	0	5 (5)	7 (7)	43 (9)	73 (11)	69 (11)	4 (1)	1 (0)	0 (0)	33 (8)	51 (10)
LEEC	0	0	0	0	9 (6)	6 (6)	0	96 (1)	90 (4)	45 (10)	27 (8)	32 (9)
EPH	0	0	0	0	14 (7)	0	0	0	1 (1)	0	7 (4)	0
TRI	0	0	0	0	1 (1)	0	0	0	0	0	0	0
NOT	0	0	0	0	0	12 (8)	0	0	0	2 (2)	6 (3)	13 (6)
COR	0	0	0	0	4 (3)	0	5 (3)	0	0	0	0	0
ANIS	0	0	0	0	0	0	0	0	0	0	3 (3)	0
ZYG	0	0	0	0	0	0	0	0	0	0	5 (3)	0
CHAO	0	0	0	0	0	0	5 (3)	0	7 (3)	44 (9)	4 (4)	0
DYT	0	0	0	0	0	0	0	0	1 (1)	0	0	0
ZOO	**88 (6)**	**92 (5)**	**29 (10)**	**20 (11)**	**0**	**0**	**13 (7)**	**0**	**0**	**0**	**0**	**0**
DAPH	18 (5)	7 (5)	0	0	0	0	13 (7)	0	0	0	0	0
COPE	70 (7)	85 (7)	29 (10)	20 (11)	0	0	0	0	0	0	0	0

Table 3. Continued

Froland Waterfowl Production Area

Date	**6/13/01**	**6/26/01**	**7/16/01**	**7/28/01**	**8/12/01**	**8/28/01**	**9/15/01**	**5/21/02**	**6/16/02**	**7/20/02**	**8/12/02**	**9/12/02**
N	21	26	21	23	21	22	25	21	10	9	41	17
% empty	24	15	5	0	5	0	4	5	10	11	49	12
length (mm)	36 (0)	61 (0)	94 (1)	110 (1)	129 (2)	147 (2)	166 (2)	185 (2)	226 (6)	282 (4)	301 (2)	331 (4)
FHM len cons (mm)	9.09	7.15	n/a	n/a	n/a	34.00	77.00	47.30	49.17	52.14	34.33	32.92
	% Weight											
FISH	**89 (8)**	**89 (8)**	**0**	**0**	**0**	**4 (4)**	**4 (4)**	**95 (5)**	**100**	**100**	**100**	**100**
FHM	89 (8)	89 (8)	0	0	0	4 (4)	4 (4)	95 (5)	100	100	100	100
INVERT	**11 (8)**	**11 (8)**	**100**	**100**	**100**	**96 (4)**	**96 (4)**	**5 (4)**	**0**	**0**	**0**	**0**
CHI (L)	0	0	59 (8)	56 (6)	27 (5)	6 (5)	0 (0)	0	0	0	0	0
CHI (P)	0	0	16 (7)	9 (3)	40 (7)	61 (9)	1 (1)	0	0	0	0	0
AMP	0	0	6 (3)	8 (3)	10 (6)	8 (5)	10 (4)	0	0	0	0	0
LEEC	0	0	9 (6)	8 (5)	9 (6)	9 (6)	73 (8)	5 (5)	0	0	0	0
EPH	11 (8)	11 (8)	9 (5)	11 (3)	1 (1)	2 (1)	0	0	0	0	0	0
NOT	0	0	1 (1)	6 (4)	13 (7)	10 (5)	5 (4)	0	0	0	0	0
COR	0	0	0	0	1 (1)	0	0	0	0	0	0	0
ANIS	0	0	0	2 (2)	0	0	0	0	0	0	0	0
ZYG	0	0	0	0	0	0	7 (5)	0	0	0	0	0
ZOO	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**

Hagstrom Waterfowl Production Area

Date	**6/15/01**	**6/26/01**	**7/17/01**	**7/29/01**	**8/13/01**	**8/27/01**	**9/15/01**	**5/20/02**	**6/16/02**	**7/15/02**	**8/10/02**	**9/12/02**
N	24	26	23	24	26	23	26	20	20	26	25	25
% empty	42	35	44	17	27	39	15	0	0	19	8	16
length (mm)	34 (0)	58 (1)	86 (3)	96 (2)	120 (3)	139 (5)	151 (3)	197 (3)	204 (4)	207 (3)	227 (3)	227 (2)
FHM len cons (mm)	n/a	n/a	n/a	n/a	37.00	n/a	62.00	64.00	n/a	n/a	n/a	n/a
	% Weight											
FISH	**14 (10)**	**93 (6)**	**85 (10)**	**35 (11)**	**79 (10)**	**21 (11)**	**36 (10)**	**19 (9)**	**3 (2)**	**51 (11)**	**26 (9)**	**36 (10)**
FHM	0	0	0	0	4 (4)	0	5 (5)	5 (5)	0	0	0	0
BSB	7 (7)	93 (6)	62 (14)	15 (8)	39 (11)	7 (7)	32 (10)	9 (6)	3 (2)	51 (11)	22 (8)	36 (10)
CMM	0	0	23 (12)	20 (9)	35 (11)	14 (8)	0	5 (5)	0	0	4 (4)	0
WAE	7 (7)	0	0	0	0	0	0	0	0	0	0	0
INVERT	**7 (7)**	**7 (6)**	**4 (4)**	**3 (3)**	**21 (10)**	**79 (11)**	**64 (10)**	**81 (9)**	**97 (2)**	**49 (11)**	**74 (9)**	**64 (10)**

Table 3. Continued

Date	**6/15/01**	**6/26/01**	**7/17/01**	**7/29/01**	**8/13/01**	**8/27/01**	**9/15/01**	**5/20/02**	**6/16/02**	**7/15/02**	**8/10/02**	**9/12/02**
N	24	26	23	24	26	23	26	20	20	26	25	25
% empty	42	35	44	17	27	39	15	0	0	19	8	16
length (mm)	34 (0)	58 (1)	86 (3)	96 (2)	120 (3)	139 (5)	151 (3)	197 (3)	204 (4)	207 (3)	227 (3)	227 (2)
FHM len cons (mm)	n/a	n/a	n/a	n/a	37.00	n/a	62.00	64.00	n/a	n/a	n/a	n/a
	% Weight											
CHI (L)	0	0	4 (4)	0	2 (1)	0 (0)	1 (1)	2 (1)	3 (3)	0	2 (1)	0
CHI (P)	7 (7)	0	0	0	0	0	0	0	0	5 (5)	1 (1)	2 (1)
AMP	0	0	0	0	0	0	10 (5)	0	1 (1)	14 (8)	5 (3)	13 (5)
LEEC	0	0	0	0	0	0	5 (5)	20 (7)	0	0	9 (6)	0
EPH	0	0	0	3 (3)	16 (8)	78 (11)	48 (10)	54 (9)	1 (1)	11 (7)	26 (8)	39 (9)
COR	0	7 (6)	0	0	0	0	0	0	0	0	2 (2)	4 (3)
NOT	0	0	0	0	4 (4)	1 (1)	0	0	0	1 (1)	4 (3)	5 (4)
ANIS	0	0	0	0	0	0	0	0	0	0	22 (9)	0
ZYG	0	0	0	0	0	0	0	5 (3)	91 (5)	17 (8)	0	0
CRAY	0	0	0	0	0	0	0	0	0	0	3 (3)	0
ZOO	**79**	**0**	**11 (8)**	**62 (11)**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
DAPH	79	0	11 (8)	62 (11)	0	0	0	0	0	0	0	0

Mavis East Waterfowl Production Area

Date	**6/16/01**	**6/25/01**	**7/15/01**	**7/27/01**	**8/15/01**	**8/29/01**	**9/16/01**	**5/20/02**	**6/17/02**	**7/16/02**	**8/10/02**	**9/12/02**
N	24	25	24	23	23	23	2	20	20	21	22	26
% empty	4	8	21	43	4	0	0	0	0	0	0	8
length (mm)	38(0)	57(1)	96(2)	115(3)	111(3)	132(4)	147(3)	158 (4)	202 (4)	213 (5)	243 (4)	278 (3)
FHM len cons (mm)	n/a	8.86	28.50	27.00	31.00	31.00	37.00	n/a	n/a	n/a	n/a	n/a
	% Weight											
FISH	**74 (9)**	**87 (7)**	**42 (12)**	**38 (14)**	**5 (5)**	**9 (6)**	**50 (50)**	**5 (5)**	**5 (5)**	**37 (9)**	**51 (10)**	**37 (10)**
FHM	0	14 (7)	11 (7)	8 (8)	5 (5)	9 (6)	50 (50)	0	0	0	0	0
BSB	43 (10)	60 (10)	32 (11)	31 (13)	0	0	0	5 (5)	5 (5)	37 (9)	51 (10)	37 (10)
WAE	31 (9)	13 (7)	0	0	0	0	0	0	0	0	0	0
INVERT	**0**	**0**	**37 (11)**	**62 (14)**	**18 (8)**	**48 (10)**	**50 (50)**	**95 (5)**	**95 (5)**	**63 (9)**	**49 (10)**	**63 (10)**
CHI (L)	0	0	9 (6)	5 (3)	0	6 (5)	0	0	5 (5)	0	0	0
CHI (P)	0	0	10 (7)	12 (9)	0	9 (6)	0	30 (8)	0	0	15 (6)	0
AMP	0	0	8 (6)	15 (10)	0	10 (6)	0	0	13 (7)	1 (1)	0	0

Table 3. Continued.

Date	**6/16/01**	**6/25/01**	**7/15/01**	**7/27/01**	**8/15/01**	**8/29/01**	**9/16/01**	**5/20/02**	**6/17/02**	**7/16/02**	**8/10/02**	**9/12/02**
N	24	25	24	23	23	23	2	20	20	21	22	26
% empty	4	8	21	43	4	0	0	0	0	0	0	8
length (mm)	38(0)	57(1)	96(2)	115(3)	111(3)	132(4)	147(3)	158 (4)	202 (4)	213 (5)	243 (4)	278 (3)
FHM len cons (mm)	n/a	8.86	28.50	27.00	31.00	31.00	37.00	n/a	n/a	n/a	n/a	n/a
	% Weight											
LEEC	0	0	5 (5)	7 (7)	0	9 (6)	50 (50)	14 (8)	59 (10)	61 (9)	27 (9)	44 (10)
EPH	0	0	0	23 (12)	18 (8)	11 (6)	0	43 (8)	0 (0)	0	1 (1)	0
COR	0	0	5 (5)	1 (1)	0	0	0	0	0	0	0	0
NOT	0	0	0	0	0	3 (3)	0	0	0	1 (0)	0	0
ANIS	0	0	0	0	0	0	0	0	0	1 (1)	5 (5)	10 (5)
ZYG	0	0	0	0	0	0	0	0	19 (7)	0	0	8 (6)
CHAO	0	0	0	0	0	0	0	8 (3)	0	0	0	0
ZOO	**26 (9)**	**13 (7)**	**21 (10)**	**0**	**77 (9)**	**43 (10)**	**0**	**0**	**0**	**0**	**0**	**0**
DAPH	21 (8)	11 (6)	21 (10)	0	77 (9)	43 (10)	0	0	0	0	0	0
COPE	5 (3)	2 (2)	0	0	0	0	0	0	0	0	0	0

Morrison Waterfowl Production Area

Date	**6/16/01**	**6/25/01**	**7/15/01**	**7/27/01**	**8/15/01**	**8/29/01**	**9/16/01**	**5/20/02**	**6/16/02**	**7/16/02**	**8/10/02**	**9/12/02**
N	27	24	25	24	26	21	29	31	23	31	34	24
% empty	11	8	8	25	19	52	17	35	13	32	32	13
length (mm)	34 (0)	48 (1)	77 (1)	83 (1)	93 (1)	102 (5)	118 (6)	232 (2)	221 (7)	220 (8)	258 (4)	274 (3)
FHM len cons (mm)	6.35	9.00	n/a	6.80	n/a	n/a	57.00	36.17	72.00	70.00	n/a	n/a
	% Weight											
FISH	**25 (9)**	**17 (8)**	**0**	**17 (9)**	**0**	**0**	**21 (8)**	**30 (11)**	**5 (5)**	**5 (5)**	**0**	**0**
FHM	25 (9)	3 (3)	0	11 (8)	0	0	13 (7)	30 (11)	5 (5)	5 (5)	0	0
BSB	0	14 (7)	0	5 (5)	0	0	0	0	0	0	0	0
WAE	0	0	0	0	0	0	8 (6)	0	0	0	0	0
INVERT	**5 (4)**	**31 (10)**	**61 (10)**	**14 (8)**	**75 (9)**	**100 (0)**	**57 (10)**	**70 (11)**	**95 (5)**	**95 (5)**	**100**	**100**
CHI (L)	4 (3)	0	32 (9)	0	10 (5)	18 (11)	0	0 (0)	7 (5)	1 (1)	0	0
CHI (P)	1 (1)	0	0	0	37 (10)	46 (15)	0	0	10 (5)	6 (5)	0	10 (5)
AMP	0	0	12 (6)	9 (6)	15 (8)	16 (10)	26 (8)	45 (11)	20 (8)	49 (11)	85 (7)	46 (10)
LEEC	0	0	0	0	0	0	15 (7)	15 (8)	35 (10)	22 (9)	0	5 (3)
NOT	0	0	0	0	0	0	0	0	0	13 (7)	4 (4)	39 (10)
EPH	0	0	0	0	9 (6)	10 (10)	5 (4)	0	0	0	0	0
COR	0	0	17 (8)	6 (6)	5 (5)	10 (10)	0	0	0	0	2 (1)	0

Table 3. Continued.

Date	**6/16/01**	**6/25/01**	**7/15/01**	**7/27/01**	**8/15/01**	**8/29/01**	**9/16/01**	**5/20/02**	**6/16/02**	**7/16/02**	**8/10/02**	**9/12/02**
N	27	24	25	24	26	21	29	31	23	31	34	24
% empty	11	8	8	25	19	52	17	35	13	32	32	13
length (mm)	34 (0)	48 (1)	77 (1)	83 (1)	93 (1)	102 (5)	118 (6)	232 (2)	221 (7)	220 (8)	258 (4)	274 (3)
FHM len cons (mm)	6.35	9.00	n/a	6.80	n/a	n/a	57.00	36.17	72.00	70.00	n/a	n/a
	% Weight											
ANIS	0	0	0	0	0	0	0	0	0	5 (5)	9 (6)	0
CHAO	0	31 (10)	0	0	0	0	12 (7)	5 (5)	23 (8)	0	0	0
WORM	0	0	0	0	0	0	0	5 (5)	0	0	0	0
ZOO	**71 (9)**	**53 (11)**	**39 (10)**	**69 (11)**	**25 (9)**	**0**	**22 (8)**	**0**	**0**	**0**	**0**	**0**
DAPH	14 (6)	29 (9)	0	0	12 (7)	0	22 (8)	0	0	0	0	0
COPE	57 (9)	24 (9)	39 (10)	69 (11)	13 (7)	0	0	0	0	0	0	0

Reisdorph 1 Wildlife Management Area

Date	**6/18/01**	**6/26/01**	**7/16/01**	**7/26/01**	**8/14/01**	**8/28/01**	**9/15/01**	**5/21/02**	**6/18/02**	**7/17/02**	**8/14/02**	**9/14/02**
N	25	22	28	21	29	24	24	20	25	20	13	30
% empty	52	50	54	67	59	71	17	0	40	0	23	3
length (mm)	34 (0)	45 (1)	67 (1)	71 (2)	75 (2)	110 (6)	102 (1)	200 (3)	196 (7)	228 (6)	241 (10)	270 (5)
FHM len cons (mm)	6.00	n/a	n/a	n/a	43.33	n/a	n/a	n/a	n/a	32.00	36.00	37.75
	% Weight											
FISH	**16 (11)**	**55 (16)**	**8 (8)**	**14 (14)**	**25 (13)**	**0**	**0**	**0**	**0**	**3 (3)**	**10 (10)**	**21 (8)**
FHM	7 (7)	0	0	0	25 (13)	0	0	0	0	3 (3)	10 (10)	16 (7)
BSB	0	18 (12)	0	14 (14)	0	0	0	0	0	0	0	5 (4)
WAE	8 (8)	36 (15)	8 (8)	0	0	0	0	0	0	0	0	0
INVERT	**6 (6)**	**0**	**15 (10)**	**29 (18)**	**50 (15)**	**43 (20)**	**81 (8)**	**100 (0)**	**87 (9)**	**97 (3)**	**90 (6)**	**79 (8)**
CHI (L)	0	0	8(8)	0	0	0	35 (7)	0	6 (4)	1 (1)	0	2 (2)
CHI (P)	0	0	0	0	0	17 (14)	32 (6)	49 (9)	71 (10)	14 (7)	22 (13)	0 (0)
AMP	0	0	0	0	0	0	4 (2)	16 (5)	0	0	0	3 (2)
LEEC	0	0	8(8)	0	0	0	5 (5)	1 (1)	0	25 (9)	34 (15)	55 (8)
EPH	0	0	0	0	0	14 (14)	5 (5)	0	0	44 (10)	20 (11)	1 (1)
NOT	0	0	0	29 (18)	50 (15)	12 (12)	0	0	6 (6)	4 (3)	0	4 (3)
COR	6(6)	0	0	0	0	0	0	0	0	0	0	0
ZYG	0	0	0	0	0	0	0	0	0	0	5 (5)	14 (5)
CHAO	0	0	0	0	0	0	0	34 (9)	5 (5)	4 (3)	7 (7)	0
CRAY	0	0	0	0	0	0	0	0	0	5 (5)	0	0
ZOO	**78 (12)**	**45 (16)**	**77 (12)**	**57 (20)**	**25 (13)**	**57 (20)**	**19 (8)**	**0**	**13 (9)**	**0**	**1 (1)**	**0**
DAPH	8 (8)	3 (3)	26 (12)	14 (14)	17 (11)	57 (20)	19 (8)	0	13 (9)	0	1 (1)	0
COPE	70 (13)	42 (15)	51 (14)	43 (20)	8 (8)	0	0	0	0	0	0	0

Table 4. Bi-monthly mean percent by weight for stomach contents of walleye stocked as fry in 2002 in Cuba, Froland, and Reisdorph 1 study sites throughout the summer of 2002. Standard error of the mean is reported in parentheses. Sample size (N), percentage of empty stomachs (% empty), and mean length (length (mm)) of walleye are reported, and mean size of fathead minnows consumed (FHM len cons (mm)) on each sampling date is also indicated. Abbreviations are as follows: BSB = brook stickleback, FHM = fathead minnow, CHI (L) = chironomid larva, CHI (P) = chironomid pupa, AMP = amphipod/scud, LEEC = leech, EPH= mayfly larva, NOT = backswimmer, CHAO = phantom midge, COPE = copepod, DAPH = *Daphnia* spp.

Cuba Wildlife Management Area

Date	**6/15/02**	**7/19/02**	**8/18/02**	**9/16/02**
N	38	58	39	36
% empty	0	0	13	3
length (mm)	28 (0)	76 (1)	112 (1)	130 (1)
FHM len cons (mm)	n/a	13.82	24.00	n/a
	% Weight			
FISH	**0**	**9 (4)**	**3 (3)**	**0**
FHM	0	9 (4)	3 (3)	0
INVERT	**88 (5)**	**69 (5)**	**97 (3)**	**89 (5)**
CHI (L)	0 (0)	19 (4)	0	0
CHI (P)	0 (0)	11 (3)	50 (8)	0 (0)
AMP	0	0 (0)	6 (4)	65 (7)
LEEC	0	1 (1)	3 (3)	0
EPH	0	5 (2)	28 (7)	3 (2)
NOT	0	1 (1)	8 (5)	21 (6)
CHAO	88 (5)	32 (5)	1 (1)	0
ZOO	**12 (5)**	**22 (5)**	**0**	**11 (5)**
DAPH	3 (3)	22 (5)	0	11 (5)
COPE	9 (4)	0 (0)	0	0

Froland Waterfowl Production Area

Date	**6/14/02**	**7/16/02**	**8/14/02**	**9/12/02**
N	46	26	8	34
% empty	13	4	0	12
length (mm)	33 (0)	83 (1)	143 (3)	182 (4)
FHM len cons (mm)	5.57	14.69	29.50	32.90
	% Weight			
FISH	**57 (8)**	**78 (7)**	**100**	**100 (0)**
FHM	57 (8)	78 (7)	100	100 (0)
INVERT	**3 (2)**	**22 (7)**	**0**	**0 (0)**
CHI (P)	1 (1)	0	0	0 (0)
EPH	0	22 (7)	0	0
NOT	3 (2)	0	0	0
ZOO	**40 (8)**	**0**	**0**	**0**
DAPH	25 (6)	0	0	0
COPE	15 (5)	0	0	0

Table 4. Continued.

Reisdorph 1 Wildlife Management Area

Date	**6/18/02**	**7/17/02**	**8/14/02**	**9/14/02**
N	44	0 Sampled	24	38
% empty	9		0	5
length (mm)	36 (0)		112 (2)	160 (2)
FHM len cons (mm)	n/a		21.50	37.54
		% Weight		
FISH	**0**		**36 (10)**	**42 (8)**
FHM	0		36 (10)	38 (8)
BSB	0		0	4 (3)
INVERT	**82 (6)**		**64 (10)**	**58 (8)**
CHI (L)	5 (3)		0	6 (3)
CHI (P)	33 (7)		21 (8)	9 (4)
AMP	0		0	2 (2)
LEEC	0		0	3 (2)
EPH	0		42 (10)	28 (7)
NOT	3 (3)		0	9 (4)
CHAO	41 (7)		1 (0)	0
ZOO	**18 (6)**		**0 (0)**	**0**
DAPH	18 (6)		0 (0)	0

and <23% of age-0 walleye diets in Froland wetland in 2002 on all sample dates (Tables 3 and 4). Chironomids, amphipods, leeches, ephemeropterans, *Chaoborus* spp., corixids, and notonectids were the most commonly consumed macroinvertebrates, although dytiscids, anisopterans, zygopterans, trichopterans, lepidopterans, crayfish, and worms were also present in the walleye diets at times.

Diets of age-1 and older walleye stocked in wetlands

Fish comprised >82% of walleye diets in the advanced walleye treatment on all sample dates throughout 2001 and 2002, except one (Table 5). Fathead minnows were present in walleye diets in all wetlands. Brook stickleback were present in walleye diets in Reisdorph 2, Bellevue, and Lunde Lake wetlands. The mean length of fathead minnows consumed was approximately 60 mm at the onset of this study, and generally decreased to approximately 40 mm by September 2002 (Table 5).

Macroinvertebrates comprised <18% of walleye diets (all dates) in the advanced walleye treatment throughout 2001 and 2002, except in Bellevue wetland in mid-September 2002 when macroinvertebrates comprised 42% of walleye diets (Table 5). Leeches were the most frequently consumed macroinvertebrate, although amphipods, corixids, chironomid pupae, and dragonfly larvae were also found in walleye stomachs.

Only four tiger salamanders were present in the stomachs of the 1,359 walleye that contained prey items in the advanced walleye treatment in 2001 and 2002, and tiger salamanders were always <6% of the walleye diets (Table 5).

Discussion

Previous studies have illustrated the potential of piscivorous fish to limit fathead minnow densities and improve water quality (Walker and Applegate 1976; Spencer and King 1984; Elser et al. 2000). Our results also indicated that predation by walleye stocked as fry has potential to suppress fathead minnow populations, resulting in a series of sequential cascading interactions that include increases in herbivorous zooplankton (especially *Daphnia* spp.), decreases in phytoplankton, and improved water transparency. These results are consistent with both the trophic cascade hypothesis (Carpenter et al. 1985) and lake biomanipulation theory (Hrbáček et al. 1961; Shapiro et al. 1982; Shapiro and Wright 1984), which emphasize the roles of food web structure and top-down control on lake primary production (Figure 13).

Table 5. Monthly mean percent by weight for stomach contents of walleye stocked in each of the advanced treatment wetlands throughout the summer of 2001 and 2002. Standard error of the mean is reported in parentheses. Sample size (N), percentage of empty stomachs (% empty) of walleye are reported and mean size of fathead minnows consumed (FHM len cons (mm)) on each sampling date is also indicated. Abbreviations are as follows: BSB = brook stickleback, FHM = fathead minnow, CHI (P) = chironomid pupa, AMP = amphipod/ scud, LEEC = leech, NOT = backswimmer, ANIS = dragonfly larva, SALAM = tiger salamander.

Bellevue Waterfowl Production Area

Date	**6/14/01**	**7/13/01**	**8/13/01**	**9/23/01**	**5/13/02**	**6/14/02**	**7/23/02**	**8/15/02**	**9/17/02**
N	40	36	35	41	47	58	31	59	57
% empty	34	17	43	12	11	31	19	56	30
FHM len cons (mm)	54.84	40.89	36.00	44.22	21.54	36.14	24.88	33.20	37.49
					% Weight				
FISH	**100**	**100**	**100 (0)**	**85 (6)**	**98 (1)**	**85 (5)**	**95 (4)**	**83 (7)**	**58 (7)**
FHM	100	100	100 (0)	85 (6)	98 (1)	85 (5)	95 (4)	83 (7)	57 (7)
BSB	0	0	0	0	0	0	0	0	1 (1)
INVERT	**0**	**0**	**0 (0)**	**12 (5)**	**2 (1)**	**15 (5)**	**5 (4)**	**17 (7)**	**42 (7)**
LEEC	0	0	0 (0)	12 (5)	1 (1)	10 (5)	5 (4)	0	5 (3)
AMP	0	0	0	0	1 (0)	4 (3)	0	10 (5)	25 (6)
CHI (P)	0	0	0	0	0	0	0	4 (2)	3 (3)
ANIS	0	0	0	0	0	0	0	4 (3)	0
NOT	0	0	0	0	0	0	0	0	8 (4)
VERT	**0**	**0**	**0**	**3 (3)**	**0**	**0**	**0**	**0**	**0**
SALAM	0	0	0	3 (3)	0	0	0	0	0

Lunde Lake Wildlife Management Area

Date	**6/17/01**	**7/12/01**	**8/20/01**	**9/14/01**	**5/16/02**	**6/15/02**	**7/19/02**	**8/18/02**	**9/19/02**
N	20	32	45	39	48	54	29	52	40
% empty	10	29	31	5	15	31	3	46	18
FHM len cons (mm)	58.95	57.13	43.60	45.75	35.71	49.17	37.31	34.56	39.33
					% Weight				
FISH	**85 (8)**	**100 (0)**	**100**	**99 (0)**	**92 (4)**	**89 (5)**	**86 (4)**	**84 (6)**	**93 (4)**
FHM	63 (10)	67 (7)	42 (8)	29 (6)	69 (7)	50 (8)	29 (7)	59 (8)	53 (8)
BSB	22 (8)	33 (7)	58 (8)	71 (6)	23 (6)	39 (8)	57 (7)	25 (8)	40 (8)
INVERT	**12 (8)**	**0**	**0**	**1 (0)**	**8 (4)**	**11 (5)**	**14 (4)**	**16 (6)**	**7 (4)**
LEEC	12 (8)	0	0	1 (0)	8 (4)	11 (5)	14 (4)	16 (6)	7 (4)
VERT	**3 (3)**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
SALAM	3 (3)	0	0	0	0	0	0	0	0

Reisdorph 2 Wildlife Management Area

Date	**6/18/01**	**7/16/01**	**8/14/01**	**9/15/01**	**5/15/02**	**6/18/02**	**7/24/02**	**8/14/02**	**9/14/02**
N	2	41	20	23	44	29	7	2	11
% empty	0	43	10	9	9	7	0	0	36
FHM len cons (mm)	58.00	40.44	40.23	45.27	37.40	44.37	47.00	24.48	52.00
					% Weight				
FISH	**100**	**100**	**100**	**100**	**97 (2)**	**99 (1)**	**100**	**100**	**100**
FHM	68 (32)	100 (0)	92 (4)	60 (10)	97 (2)	99 (1)	100	100	40 (19)
BSB	32 (32)	0	8 (4)	40 (10)	0	0	0	0	60 (19)
INVERT	**0**	**0**	**0**	**0**	**3 (2)**	**1 (1)**	**0**	**0**	**0**
LEEC	0	0	0	0	3 (2)	1 (1)	0	0	0
VERT	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**

Table 5. Continued.

Rolland Lake Waterfowl Production Area

Date	**6/19/01**	**7/15/01**	**8/15/01**	**9/16/01**	**5/12/02**	**6/13/02**	**7/25/02**	**8/11/02**	**9/20/02**
N	31	24	26	24	41	47	27	44	47
% empty	26	33	19	17	2	13	0	10	15
FHM len cons (mm)	59.20	36.03	34.65	35.09	40.67	46.51	31.10	24.04	34.47
					% Weight				
FISH	**84 (7)**	**92 (6)**	**100 (0)**	**96 (3)**	**97 (2)**	**97 (2)**	**100 (0)**	**93 (4)**	**96 (2)**
FHM	84 (7)	92 (6)	100 (0)	96 (3)	97 (2)	97 (2)	100 (0)	93 (4)	96 (2)
INVERT	**16 (7)**	**2 (2)**	**0**	**4 (3)**	**3 (2)**	**3 (2)**	**0 (0)**	**7 (4)**	**4 (2)**
LEEC	16 (7)	2 (2)	0	4 (3)	3 (2)	3 (2)	0	7 (4)	0
AMP	0	0	0	0	0	0	0	0	3 (2)
ANIS	0	0	0	0	0	0	0	0	1 (1)
VERT	**0**	**6 (6)**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
SALAM	0	6 (6)	0	0	0	0	0	0	0

State Hospital Wildlife Management Area

Date	**6/15/01**	**7/23/01**	**8/19/01**	**9/21/01**	**5/14/02**	**6/12/02**	**7/21/02**	**8/13/02**	**9/13/02**
N	19	19	44	37	48	45	47	32	22
% empty	37	21	18	14	17	11	13	19	9
FHM len cons (mm)	65.25	37.93	48.71	47.99	45.67	48.55	43.96	44.89	49.27
					% Weight				
FISH	**100 (0)**	**100 (0)**	**100 (0)**	**97 (3)**	**100**	**100 (0)**	**97 (2)**	**91 (5)**	**100**
FHM	100 (0)	100 (0)	100 (0)	97 (3)	100	100 (0)	97 (2)	91 (5)	100
INVERT	**0**	**0**	**0**	**3 (3)**	**0**	**0**	**3 (2)**	**9 (5)**	**0**
LEEC	0	0	0	3 (3)	0	0	3 (2)	9 (5)	0
VERT	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**

Weigers Waterfowl Production Area

Date	**6/16/01**	**7/14/01**	**8/16/01**	**9/22/01**	**5/17/02**	**6/17/02**	**7/22/02**	**8/17/02**	**9/16/02**
N	25	21	22	8	31	21	14	14	15
% empty	28	38	18	38	3	5	0	7	20
FHM len cons (mm)	53.04	33.13	40.35	55.67	43.75	50.19	43.02	29.56	24.58
					% Weight				
FISH	**100 (0)**	**87 (9)**	**94 (6)**	**100**	**100 (0)**	**100 (0)**	**93 (7)**	**100 (0)**	**100**
FHM	100 (0)	87 (9)	94 (6)	100	100 (0)	100 (0)	93 (7)	100 (0)	100
INVERT	**0**	**13 (9)**	**6 (6)**	**0**	**0**	**0**	**7 (7)**	**0**	**0**
LEEC	0	13 (9)	6 (6)	0	0	0	7 (7)	0	0
VERT	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**

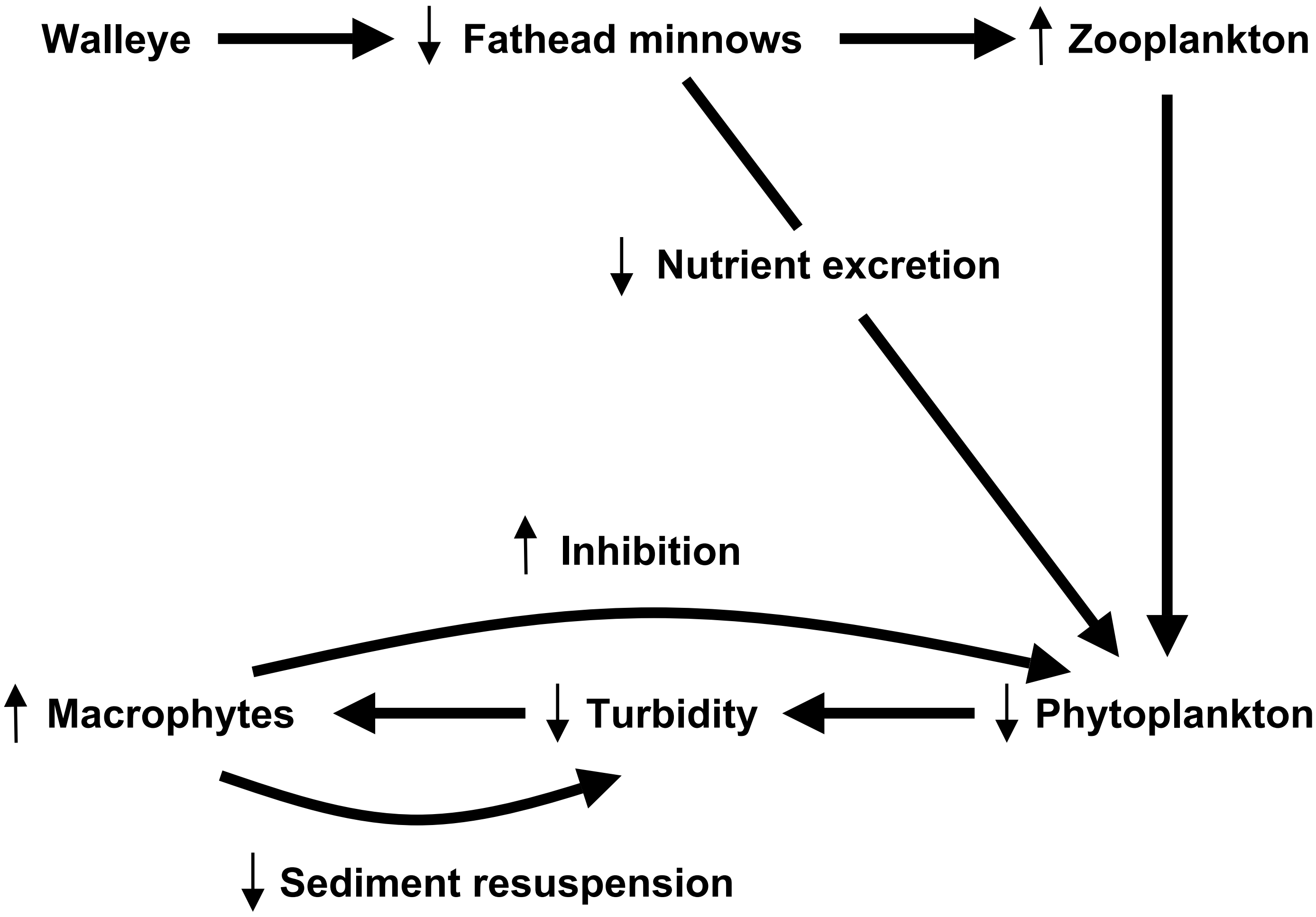

Figure 13. Predicted interactions resulting from biomanipulation involving the addition of walleye to turbid wetlands. The trophic cascade hypothesis predicts that a reduction in planktivorous fish (fathead minnows in this example) will result in a decrease in phytoplankton abundance, once predation pressure on large zooplankton grazers by fish is sufficiently reduced. The lower part of the diagram partially depicts the concept of alternative equilibria in shallow lakes. In this model, over a range of nutrient concentrations, shallow lakes can exist in either a turbid, phytoplankton-dominated state, or clear-water, macrophyte-dominated state. In the context of our study, the goal of the biomanipulation was to "switch" the wetlands to the clear water state, and improve macrophyte coverage. Submerged aquatic vegetation is postulated to stabilize the clear water state through the positive feedback mechanisms outline above.

Success of shallow-lake biomanipulation is largely dependent upon shifting a lake from a turbid, phytoplankton-dominated state to a clear-water, macrophyte-dominated state. This typically requires three key responses: 1) a dramatic reduction in the biomass of planktivorous fish; 2) an increase in large-bodied zooplankton grazers (especially *Daphnia* spp.); and 3) the development of submerged aquatic vegetation (Scheffer et al. 1993). Once SAV communities are established, they stabilize the associated clear water state and buffer the influences of future fish populations (Scheffer et al. 1993; Zimmer et al. 2001).

In our study, notable reductions in fathead minnow abundance were evident in the walleye fry treatment during 2001, and continued throughout 2002. This included larval fathead minnows, which were likely reduced through a combination of direct predation by walleye and diminished recruitment resulting from a decreased adult fathead minnow population. Such joint suppression of adult planktivorous fish and young of year has been cited as a key element in successful biomanipulation efforts (Hansson et al. 1998). The reduction in planktivore abundance subsequently resulted in significant increases in large cladocerans (primarily *Daphnia* spp.). *Daphnia* spp. have much higher filtering rates than small-bodied zooplankton, and therefore, far greater impacts on phytoplankton biomass (McQueen et al. 1986; Carpenter et al. 1987; Scheffer et al. 2001). Both zooplankton grazers and nutrients influence phytoplankton populations, and high nutrient levels tend to dampen, or even prohibit, trophic cascades (Scheffer et al. 1993; Moss et al. 1996). We did not observe a decrease in phytoplankton in 2001 despite a sharp increase in large cladocerans. It is plausible that high nutrient levels in late summer 2001 sustained high phytoplankton growth rates. In early-summer 2002, when nutrient concentrations were lower, both phytoplankton abundance and turbidity decreased, suggesting that the timing of the zooplankton response relative to temporal nutrient dynamics was critical for the switch to a clear water state. SAV showed continued improvement in the walleye fry treatment throughout the study, although no significant differences were achieved, thus we urge a cautious interpretation of the SAV response. Phytoplankton and water clarity responses persisted in 2003 despite the reestablishment of fathead minnow populations in all but Cuba and Hagstrom wetlands. We attribute this to the stabilizing influence of SAV in maintaining the clear water state (Scheffer et al. 1993; Moss et al. 1996). As fathead minnow populations continue to reestablish in study wetlands, it remains unclear whether SAV will remain of sufficient abundance to buffer a switch back to a turbid state, or how long it might take for this change to occur.

We suspect that Froland wetland (walleye fry treatment) received a large influx of adult fathead minnows sometime prior to the 2002 sampling season via seasonal flows from an adjacent wetland. Prior to this event, fathead minnows were at low abundance, presumably due to predation by walleye. However, due to a combination of this colonization event and low survival of walleye fry in this wetland in both years, food-web mediated responses were never observed in this wetland. This illustrates that the relative success of biomanipulation efforts will be decreased in systems with a high disturbance regime, such as periodic flooding and associated fish immigrations (see review by Angeler et al. 2003).

In June and July of 2001, we observed blue-green algae (cyanobacteria) blooms in several wetlands. This corresponded to a strong decline in the N:P (mass ratio) in all treatments, especially in the advanced walleye treatment. Decreases in N:P have been shown to favor cyanobacteria over non-cyanobacterial forms of algae in lakes (Schindler 1977; Smith 1983). N:P ratios increased and cyanobacteria eventually disappeared from the advanced walleye and reference treatment wetlands. However, cyanobacteria persisted to varying degrees throughout the study in four of the walleye fry treatment wetlands. N:P ratios varied considerably in the walleye fry treatment throughout 2002 and 2003, but were typically comparable to ratios observed in the reference treatment. With very few exceptions N:P ratios for all wetlands were < 29:1 (N:P mass ratio), the threshold below which cyanobacterial forms of algae are favored in lakes (Smith 1983). The preponderance of cyanobacteria in some of the wetlands stocked with walleye fry may also represent a shift from small, grazable forms of algae to large, inedible (sometimes toxic) cyanobacteria, which may negatively influence growth, reproduction, and body condition in *Daphnia* spp. (reviewed in Gliwicz 1990). In spite of cyanobacteria blooms in walleye fry treatment, water transparency still remained very high in comparison to the advanced walleye and reference treatments.

Very few ecosystem-scale changes were observed in association with our advanced walleye treatment, despite some suppression of adult fathead minnows in 2002. This may indicate that suppression of adult fathead minnows here was not sufficient to limit recruitment by the remaining population. In fact, larval fathead minnow densities peaked at levels nearly double those observed in the reference treatment; however, they declined to levels similar to the walleye fry treatment in August and September. Larval fathead minnow production may have increased in the advanced walleye treatment, perhaps due to reduced competition with adult minnows or the preference for larger-sized fathead minnows in the diets of advanced walleye. One advantage of this treatment was that advanced walleye were highly piscivorous throughout the study. Despite the affinity for fathead minnows in the diet, consumption rates by walleye were simply not high enough to induce the desired zooplankton, water transparency, or plant responses.

Advanced walleye were stocked at a rate of 5.6-6.7 kg/ha in the present study, resulting in walleye densities between 65 and 130 walleye/ha throughout the study. Other biomanipulation studies that have successfully used piscivorous adult fish to suppress fathead minnow populations stocked at rates much higher than our study. Largemouth bass *Micropterus salmoides* were stocked at 3,000/ha in a Michigan pond (Spencer and King 1984), northern pike *Esox lucious* at 26 kg/ha in a 5 ha Ontario lake (Elser et al. 2000), and walleye fingerlings at 62/ha for 6 consecutive years in a Michigan lake (Schneider 1983). Time lags of up to three years preceded responses in these studies, the same time scale over which responses were monitored in our study. This may indicate that our stocking rate was less than ideal for suppressing fathead minnow populations and inducing trophic cascades. Furthermore, advanced walleye do not prey substantially on larval fathead minnows. Unless advanced walleye can drive adult fathead minnows to extinction, and prevent recruitment of larval fish to the population, biomanipulation attempts are likely to be less successful (Hansson et al. 1998).

Macroinvertebrate populations are an important consideration for managers charged with managing wetlands for waterfowl. This is due to the importance of invertebrates as waterfowl food, and the relationships between invertebrates and egg production, as well as duckling survival (reviewed in Bouffard and Hanson 1997; Cox et al. 1998). Most macroinvertebrate taxa, including amphipods, benefited from the biomanipulation using walleye fry stocking, exhibiting significant population increases in the walleye fry treatment when compared to the reference treatment (see Potthoff 2003 for additional details). One exception was benthic chironomids, which appeared to be enhanced in the walleye fry treatment during the first year of the study, but declined in 2002. We attribute these patterns to interacting influences of reduced predation by fathead minnows, and the increasing use of invertebrates by walleye late in 2001 and throughout 2002. Previous studies have demonstrated strong influences of fathead minnow populations on invertebrate production (Duffy 1998) and community structure (Zimmer et al. 2000). When fathead minnows are suppressed it is likely that macroinvertebrates will respond positively, although there may be a time lag before strong responses develop due to the longer generation time for some species.

Macroinvertebrates and amphipods both responded positively in the walleye fry treatment in the first year of the study. Furthermore, the ratio of biomass:density for benthic chironomids in sediment samples was higher in the walleye fry versus reference treatment, indicating that the size-structure was shifted toward larger individuals. We interpret this as a response to relaxed size-selective predation by fathead minnows. In the second year of the study, most invertebrate taxa exhibited additional increases, with populations ending at significantly higher levels in the walleye fry treatment, suggesting additional relaxation of predation by fathead minnows. Chironomid densities and biomass decreased appreciably in the walleye fry treatment during the second year of the study, although no significant differences were detected. We attribute this pattern to increased predation by walleye, as chironomids and other macroinvertebrates became a more important component of walleye diets. The contribution of chironomids to walleye diets was highly variable among wetlands, but was among the most common diet items found in walleye stomachs.

Macroinvertebrate responses were generally more limited in the advanced walleye treatment than in the walleye fry treatment, and most taxa showed no improvement. One notable exception was amphipod populations, which were higher in the advanced walleye than reference treatment in the second year of the study. This group may be more sensitive to predation by adult fathead minnows because of their smaller body size (easier to handle and consume); therefore, increases in amphipods may reflect relaxed predation associated with the reduction in adult fathead minnows that occurred during 2002.

Zooplankton, macroinvertebrates (especially chironomids and amphipods), and detritus have all been found to be important components of fathead minnow diets at various times of the year (Held and Perterka 1974; Price et al. 1991). We also found that fathead minnows used all of these food sources at various times of the year, but there were some trends among life stages. Zooplankton was most common in the diet of larval fathead minnows; macroinvertebrates and detritus dominated the diets of adult fathead minnows, and juvenile fathead minnows used a combination of all three major food resources. Detritus use was considerable among all life stages, and was probably a function of low invertebrate abundance (e.g., Froland and Stammer wetlands in 2002). Detritus has usually been considered a supplemental food source that allows fathead minnows to survive when other more nutritional food sources are low (Held and Peterka 1974; Price et al. 1991). More recently, detritus, which is deficient in protein, but relatively high in energy, in combination with difficult-to-catch invertebrate prey (high in protein) has been suggested as a mechanism supporting rapid growth in fathead minnows (Lemke and Bowen 1998). In addition to higher nutrient recycling resulting from intense fish predation on zooplankton (Carpenter and Kitchell 1993; Attayde and Hansson 2001), high rates of consumption on detritus and benthic invertebrates by fathead minnows may also represent a significant source of additional water column nutrients, generated during excretion, which may further promote phytoplankton populations. We are currently working on research that explores these processes, and developing estimates for invertebrate consumption by fathead minnows.

A generalized shift in diet from zooplankton to fish, and subsequently to macroinvertebrates was observed for walleye in the walleye fry treatment throughout 2001, while macroinvertebrates dominated the diet throughout 2002. This switch toward macroinvertebrates likely reflects elimination of preferred fish prey. Despite the predominance of macroinvertebrate prey in walleye diets, most macroinvertebrate populations were higher in the walleye fry treatment than either the advanced walleye or reference treatments, suggesting that consumption of invertebrates by fathead minnows outweighs that by walleye. We estimated consumption of macroinvertebrates and zooplankton by walleye to range from 40-300 kg/ha in 2001 and 1-31 kg/ha in 2002 (see Ward 2003 for details). In contrast, Duffy (1998) estimated the consumption of prey by fathead minnows to range from 333-1,104 kg/ha in South Dakota wetlands. These estimates illustrate, and our invertebrate data supports, the view that potential for fathead minnows to impact invertebrate populations exceeds that of walleye at densities used in our study. Stocking walleye fry at densities similar to ours indicates that achieving suppression of fathead minnows outweighs the impacts associated with the consumption of invertebrates by walleye in wetlands containing fathead minnow populations.

Recent evidence suggests that fathead minnows are the most ubiquitous fish species in west-central Minnesota wetlands (Hanson et al. 2004). Moreover, the prevalence of fathead minnow populations in PPR wetlands in Minnesota may have actually increased in recent years due to: 1) reduced winter anoxia resulting from above average precipitation and associated increases in wetland depth (Hanson et al. 2004); 2) increased watercourse connectivity due to drainage and tiling (Leibowitz and Vining 2003); and 3) unintentional and intentional stocking (Ludwig and Leitch 1996; Carlson and

Berry 1990). In addition, there is an increasing propensity for intermittent surface water connections, and therefore, fish invasions towards the eastern part of the PPR because of the natural east-west gradient in precipitation and relief (Hanson et al. 2004). In addition to these landscape and anthropogenic influences, numerous life history characteristics (omnivory – Held and Perterka 1974; Price et al. 1991; present study; low oxygen tolerance – Klinger et al. 1982; rapid growth – Held and Perterka 1974; robust recruitment – Payer and Scalet 1978) make fathead minnows well adapted to shallow wetland habitats, and contribute to their widespread distribution in Minnesota. When present, fathead minnows have been shown to strongly influence habitat quality in prairie wetlands, including reduced macroinvertebrate and zooplankton populations, high phytoplankton biomass, low water transparency, and reduced submerged aquatic vegetation (Zimmer et al. 2000; 2001; 2002). As a result, waterfowl managers need innovative, effective techniques to mitigate influences of abundant fathead minnow populations.

Attempts to control fathead minnow populations with chemical treatment and physical removal have met with very limited success. Elimination of fathead minnow populations in wetlands using fish toxicants has failed in most cases. In a study that evaluated the use of the rotenone in 11 Minnesota wetlands, fathead minnows were eliminated from only 1 wetland (Zimmer et al., unpublished data). Among freshwater fish, fathead minnows are among the most resistant to rotenone (Marking and Bills 1976). Use of rotenone is also costly. Average cost per treatment in the Minnesota study was $1,100.00 per wetland. Further complicating the use of rotenone is the public opposition to the use of chemicals. Duffy (1998) reported that simulated commercial harvest of fathead minnows in two South Dakota wetlands had little influence on density, mortality rates, or size distribution of populations. He estimated fishing mortality to be <1% of total mortality, and suggested that predation had greater influences on the populations than did harvest pressure.

Biomanipulation using walleye fry stocking produced many desirable benefits in our study wetlands, including enhanced invertebrate populations and increased water clarity. We also observed a weak trend toward increased development of submerged aquatic vegetation. This technique avoids both chemical treatments and labor-intensive physical removals of small planktivorous fish, and may represent an innovative tool for wetland managers when the goal is short-term suppression of fathead minnow populations to improve habitat quality in Minnesota wetlands. Wildlife and fish managers working together to manage wetlands similar to those used in this study could both meet their needs for producing better resources for ducks as well as producing walleye fingerlings for stocking. Our results indicate that by limiting populations of fathead minnows, walleye predation has the potential to increase densities of macroinvertebrates and zooplankton, and reduce phytoplankton biomass in semipermanent and permanent PPR wetlands. We caution that walleye addition to previously fishless wetlands is likely to invoke very different responses (Reed and Parsons 1999). Our diet analysis demonstrated potential for walleye to consume littoral, benthic, and planktonic invertebrates in absence of fathead minnow prey. Thus, adverse influences of walleye stocking in fishless wetlands seem likely and should be avoided.

Management Implications

1. Walleye fry stocking

Walleye fry stocking in wetlands supporting antecedent populations of fathead minnows resulted in suppression of fathead minnow populations and subsequent improvements in many other wetland features during our three-year study. These secondary responses included increased densities of large zooplankton, increased abundances of many invertebrate groups (including amphipods), reduced phytoplankton, increased water transparency, and muted increases in submerged aquatic vegetation (SAV) coverage. Most responses did not develop until the second year of the study, suggesting that more than one year of fry stocking may be necessary to induce shifts to a clear water state. Current walleye culture practice in Minnesota involves stocking walleye fry in wetlands during the spring, and based on our results, appears to be compatible with managing wetland habitats for both invertebrate and duck production, and subsequent waterfowl use in permanently-flooded wetlands with dense populations of fathead minnows. We recommend that wetland managers consider the possible benefits of walleye fry/fingerling culture if short-term wetland remediation is a management goal. We observed poor walleye survival in most wetlands during the second year of the study, indicating that most of the positive responses resulted from the initial manipulation. Walleye fry were not stocked in the third year and fathead minnows repopulated four of the six wetlands. We recommend that fry stocking be conducted as needed to facilitate persistent clear water and macrophyte-dominated conditions, which on many basins will require stocking at least every other year. Fathead minnows have prolific recruitment potential and exhibit strong predation pressure on invertebrates, thus sites with persistent minnow populations may require continued treatments to sustain clear water. We emphasize that we are not advocating the establishment of permanent walleye populations, and expect that occasional winterkill in shallow wetlands will periodically eliminate advanced stage walleye populations. Instead, we emphasize that periodic walleye fry stocking will likely be necessary to favor persistent clear water conditions in the absence of frequent winterkill or management activities designed to limit fish invasions because of the propensity for fathead minnows to repopulate prairie wetlands. Our data, and trends towards high-density fathead minnow populations within Minnesota's PPR, suggest that biomanipulation will be a useful tool over a range of fathead minnow abundances.

Once fathead minnows were reduced, walleye shifted to a diet high in invertebrates. Consistent with Reed and Parsons (1999), we recommend that walleye stocking not occur in fishless wetlands. In wetlands supporting dense populations of fathead minnows, we suggest that the degree of diet overlap between walleye and waterfowl for shared invertebrate foods is ecologically significant; however, the consequences are mitigated by the food preferences, relatively low density, and ephemeral nature of walleye populations within wetlands. Our data indicates that predation on invertebrates by fathead minnows far outweighs that of walleye, at least at our stocking densities. However, to minimize predation on invertebrates, we recommend that as many walleye fingerlings as possible be removed during fall harvest. Our results also illustrate the dynamic nature of wetland fish communities, thus highlighting challenges for management. We recommend that when fathead minnow suppression is the primary management goal, that sites be selected that are isolated from other surface waters because the relative success of biomanipulation efforts will be limited where periodic flooding and fish invasions occur (see review by Angeler et al. 2003). For wetland complexes with frequent surface water connections, biomanipulation efforts will likely be most successful when the entire complex is stocked with walleye, because stocking only one or two basins within a complex may result in an insufficient predator density, or re-colonization by fathead minnows.

Low survival of stocked walleye fry would obviously impact the success of a wetland biomanipulation. This could be due to either a mismatch with appropriate food sources (i.e., zooplankton), or possibly weather-related events (i.e., cold fronts). In this situation, it is recommended that fry stocking be repeated in subsequent years until a successful stocking is achieved. In consultation with Fisheries staff, wetlands should also be selected that are of appropriate depth to support a walleye population, so that probability of summer anoxia is minimized, thereby ensuring survival of walleye throughout the summer. Finally, prior to all walleye fry stocking, wetlands should be monitored to allow managers to assess effectiveness of the biomanipulation efforts and to ensure that walleyes are not added to fishless wetlands.

2. Stocking of age-1 and older walleye

For the most part, advanced walleye stocking was not successful in producing desired food web responses in our study sites. This treatment was advantageous in that advanced walleye were highly piscivorous, but consumption rates were simply not high enough to sufficiently reduce fathead minnows to induce a trophic cascade. We acknowledge that our stocking rate was low compared to other biomanipulation studies using adult piscivorous species, but logistically it was very difficult to even obtain the numbers/biomass of advanced-stage walleye used in this study. Given the numbers of older walleye necessary for a successful biomanipulation, we suggest that manipulation via advanced walleye is probably not practical.

3. Submerged aquatic vegetation

According to current shallow lake theory, a strong submerged plant response is required for long-term persistence of clear water conditions (Scheffer et al. 1993). Plants are thought to stabilize the clear water state through a variety of mechanisms including: 1) reduced sediment suspension; 2) competition with phytoplankton for nutrients; and 3) providing refuges from predation for zooplankton. This suggests that long-term success of biomanipulation may be higher in systems with large littoral areas where a good coverage of aquatic macrophytes can be achieved. While it is possible that stocking of piscivorous fish can be discontinued once a strong plant response is achieved, it is unclear whether SAV can sufficiently buffer against influences of recurrent fish populations, especially fathead minnows. Additional long term monitoring is needed to understand these dynamics and to develop specific management guidelines.

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