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The influence of invasive aquatic plant removal on diets of bluegill in Minnesota lakes

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ABSTRACT

Invasive aquatic plants in U.S. lakes and reservoirs frequently require managers to implement plant control, yet little is known about how these management efforts alter habitat available to adult fish. We used a before–after, control-impact (BACI) design to study four Minnesota lakes (two treated lakes and two untreated control lakes) to evaluate the influence of plant management using herbicides (i.e., endothall/2,4-D) on diets of adult bluegill (*Lepomis macrochirus* Rafinesque) over the course of 4 yr. We hypothesized that removing plants would result in an immediate increase of prey items available to bluegill reflected in an increase in total items in the bluegill diet, and that an increase in prey items would affect diet breadth. Invasive Eurasian watermilfoil, *Myriophyllum spicatum* L., was eliminated following herbicide treatment; however, native plants immediately expanded and plant overall abundance in the littoral zone was not reduced. We found no significant treatment effects on number of prey items per stomach, stomach content mass, diet composition, or abundance of major diet groups. However, we found that diet breadth increased posttreatment in the fall season, as evidenced by a more even distribution of bluegill diet items in stomach contents. Bluegill diet composition varied across years and lakes (primarily due to changes in Cladocera), but not due to treatment. We concluded that early seasonal application of herbicides resulted in an immediate shift from invasive aquatic plants to a diverse native community, which had minor effects on diets of bluegill.

Key words: diet breadth, endothall/2,4-D, Eurasian watermilfoil, fish, invasive species.

INTRODUCTION

Aquatic plants provide many functions, including primary production, stabilizing sediments and maintaining water clarity, and habitat for zooplankton, macroinvertebrates, and numerous fish species (Dibble et al. 1996, Carpenter et al. 1998, Diehl and Kornijow 1998). Many juvenile and adult fish have been reported in habitats containing aquatic plants, often in greater densities than areas without plants (Killgore et al. 1989). Moreover, younger and smaller fish become more abundant as plant density increases (Barnett and Schneider 1974, Borawa et al. 1979, Moxley and Langford 1982). Macroinvertebrate abundances and diversity tend to increase with plant biomass and leaf complexity, because leaves and stems provide substrate for attachment and protection from predators (Gilinsky 1984, Keast 1984, Beckett et al. 1992). However, these relationships do not necessarily apply to habitats colonized by invasive plant species.

Motivated by the widespread biological invasions occurring in aquatic systems, researchers have long studied effects of invasive aquatic plants and their management on systems. Although complete plant removal can lead to increased turbidity and decreased fish populations (e.g., Mangas-Ramírez and Elías-Gutiérrez 2004, Parsons et al. 2009) as well as regime shifts in lakes (Scheffer and Carpenter 2003), researchers have shown that invasive plant removal followed by immediate reestablishment of native plants has neutral to positive short-term effects on fish and macroinvertebrate populations (Bremigan et al. 2005, Kovalenko et al. 2010).

Establishment of Eurasian watermilfoil, *Myriophyllum spicatum* L., can displace native aquatic plants (Madsen et al. 1991) and decrease macroinvertebrate biomass (Keast 1984, Cheruvelil et al. 2002). Eurasian watermilfoil is a highly dissected plant and has a relatively high surface-area to plant-mass ratio compared with submerged aquatic plants native to the Midwestern United States (Dibble and Thomaz 2009). Therefore, it could theoretically provide more habitats for macroinvertebrates than native communities on average (Krull 1970, Gilinsky 1984, Pardue and Webb 1985). However, despite its complexity, Eurasian watermilfoil generally supports fewer macroinvertebrates per gram of plant than native plant species, and macroinvertebrate density decreases with increasing cover of Eurasian watermilfoil (Dvorak and Best 1982, Keast 1984, Cheruvelil et al. 2002). Eurasian watermilfoil exudes allelopathic chemicals, and researchers have shown that epiphyton growth is negatively affected by the presence of Eurasian watermilfoil (Gross et al. 1996, Nam et al. 2008). Because epiphyton is a major food resource for primary consumers, allelopathic effects of Eurasian watermilfoil likely have an indirect negative effect on macroinvertebrate abundance and, as an extension, fish foraging.

Researchers have also found that the structure of Eurasian watermilfoil monocultures influences fish foraging (Valley and Bremigan 2002). When Eurasian watermilfoil forms extensive homogeneous beds throughout the littoral zone, aquatic plants act as barriers to fish movement (Keast 1984), and these barriers can reduce foraging success (Heck and Thoman 1981, Savino and Stein 1982, Dionne and Folt 1991). The reduction of foraging success is due to an

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Table 1. Information about the four lakes included in this study, including latitude, longitude, area, % of the area < 5 m in depth (littoral zone %), maximum water depth (max water depth) (Minnesota Department of Natural Resources 2015), water transparency depth, chlorophyll-a (chl-a), and total phosphorus (tp) (10-yr averages; Minnesota Pollution Control Agency 2014).

Lake	Latitude	Longitude	Area (ha)	Littoral Zone (%)	Maximum Depth (m)	Transparency (m)	Chl-a (ppb)	TP (ppb)
Auburn	44.86494	−93.6799	115	56.4	25.6	2	23	40.5
Bush	44.83747	−93.38246	75.3	59.1	8.5	3	7	17
Pierson	44.83348	−93.69801	120	40.1	12.2	3	8	25
Zumbra	44.88258	−93.66574	94.3	38.2	17.7	3	8	30

increase in search, encounter, and capture times (Anderson 1984, Diehl 1988). Crowder and Cooper (1982) found that fish in high aquatic plant densities (177 ± 10 stems m^{-2}) had reduced prey capture rates and slower growth rates compared with lower plant densities, despite the greater biomass of prey available. In another study, prey capture rates declined as a result of structural complexity, decreasing foraging efficiency as habitat became more spatially complex (Harrel and Dibble 2001).

Change in habitat complexity also affects fish diet, including the diversity and evenness of prey items consumed (i.e., diet breadth). The directionality of the relationship between habitat complexity and diet breadth is not clear cut, and depends on fish size, prey use of aquatic plants, and prey assemblage. Researchers have found evidence to support both that diet breadth widens (e.g., killifish, Vince et al. 1976) and narrows (e.g., pinfish, Stoner 1982) with increasing habitat complexity. Two distinct mechanisms could explain these results. An increase in habitat complexity can lead to a wider diet breadth when prey becomes less available and a fish has no choice but to eat the prey it finds. On the flip side, an increase in habitat complexity could lead to only certain prey species being available to fish or available in large numbers, therefore narrowing a fish's diet breadth (Spotte 2007).

Removal of aquatic plants can temporarily release prey in the environment, thus impacting fish populations (e.g., Bettoli et al. 1993, Trebitz et al. 1997, Bickel and Closs 2009). For example, Bickel and Closs (2009) found that macroinvertebrate biomass doubled with the mechanical removal of the invasive oxygen weed [*Lagarosiphon major* (Ridl.) Moss] and fish abundance increased by 150% in the treated areas. Zooplankton density, particularly Cladocera, has been shown to increase following plant removal; however, long-term population trends depended on trophic dynamics such as predation (Richard et al. 1985, Irvine et al. 1989). In studies of mechanized removal of Eurasian watermilfoil, bluegill (*Lepomis macrochirus* Rafinesque) growth was maximized when < 50% of plants remained (Trebitz and Nibbelink 1996, Trebitz et al. 1997, Olson et al. 1998). Researchers have suggested that this level of Eurasian watermilfoil removal increases edge habitat, which could increase the availability of macroinvertebrates, refuge from predators, or a combination of both (Trebitz and Nibbelink 1996). Pothoven et al. (1999) found that bluegill growth increased immediately following herbicide removal of up to 66% of plant cover and suggested that growth increased as a result of either reduced competition for food or increased utilization of different food sources. However, to our knowledge, researchers have not tried to tease apart these effects by investigating the impacts of Eurasian watermilfoil removal on adult bluegill diets or looked at effects of plant removal on a long-term scale.

We investigated the hypothesis that, as a result of Eurasian watermilfoil removal, there would be a temporary release of prey items into the environment, reflected by an increase in bluegill diet items and a change in diet breadth. We proposed two alternative hypotheses relative to a change in diet breadth as a result of herbicide removal of Eurasian watermilfoil: (1) a reduction in plant structure increases prey availability in general, leading to an increase in prey selection and a narrower diet breadth; and (2) a decrease in plant structure increases diet breadth as a greater diversity of prey becomes available. To test these hypotheses, we measured bluegill diet composition before and after herbicide removal of Eurasian watermilfoil and evaluated changes in bluegill diets immediately and up to 4 yr following Eurasian watermilfoil removal. Additionally, we evaluated the success of aquatic plant removal and the establishment of native plants.

MATERIALS AND METHODS

Our experiment constituted of four eutrophic lakes located in the Minneapolis, MN metropolitan area: Auburn, Pierson, and Zumbra (Carver County), and Bush (Hennepin County) (Table 1). These lakes ranged in area from 75 to 120 ha and had maximum depths from 8.5 to 25.6 m (Table 1). Lakes were all dominated by Eurasian watermilfoil with a surface coverage of at least 80% of the littoral zone (water depth $\leq$ 4.5 m), and had a fish assemblage dominated by bluegill (Skogerboe and Getsinger 2006). In terms of plant composition (besides Eurasian watermilfoil), the lakes also contained submergent plants including *Ceratophyllum demersum* (coontail), Potamogetonaceae spp. (pondweeds), *Elodea canadensis* L. (Canadian waterweed); as well as floating leaf species including *Nymphaea odorata* Aiton (white water lily) in 2003 (Skogerboe and Getsinger 2006). In spring of 2004, a low dose of endothall (1 mg/L) combined with 2,4-D (0.5 mg/L) was used to control the Eurasian watermilfoil and a small percentage of curly leaf pondweed (*Potamogeton crispus* L.) in Bush and Zumbra lakes annually from 2004 to 2007. Auburn and Pierson lakes were not treated with herbicide and represent the untreated controls.

Aquatic plant abundance prior to herbicide treatment was sampled in the last 2 wk of June and September of 2003 and posttreatment data were collected in the last 2 wk of June and September of 2004 to 2007 (Skogerboe and

Getsinger 2006). These sampling times were chosen to represent the variation in bluegill prey from early summer to early fall (Crowder and Cooper 1982). Plant samples were collected with the use of a 36-cm-wide rake on a 3-m pole at 30 to 35 randomly selected locations within a 50 by 50 m grid situated in the littoral zone of each lake. Each sample was separated by species and oven dried to a constant mass (Skogerboe and Getsinger 2006).

Bluegill were sampled in each lake, twice a year during the first 2 wk of June and September for 5 yr (2003 to 2007) with the use of a boat-mounted pulsed DC (250–350 V and 6–10 A) electrofishing unit. In each lake, four areas of the shoreline were sampled at night for a total of approximately 2 h of electrofishing time per lake in 15 to 20–min intervals. By using this collection method, we assumed that we would collect primarily adult bluegill (i.e., individuals > 75 mm) that had transitioned from feeding primarily in plants to open water. We randomly selected a minimum of 20 bluegill from the field collection, measured total length (TL) and body mass, and preserved the samples in 10% formalin. Specimens were transported to the laboratory at Mississippi State University where stomachs were removed and dissected, and contents preserved in 70% ethanol and stored until analysis (Bowen 1983). Macroinvertebrates, zooplankton, and all other stomach contents were enumerated during analysis and identified to order with the use of Merritt and Cummins (2008) and Thorp and Covich (2001). We also measured stomach-content mass as an additional estimate of foraging success because of the variation in size among taxonomic groups.

Diet breadth was calculated with the use of Levin's normalized B, which is a measure of specificity of resource use and has a standardized form, B_A (Levins 1968). Diet breadth is narrowest when only one resource was represented and broadest when equal proportions of each prey item was represented in the bluegill diet. B_A values are B values standardized to be between 0 and 1, 0 being only one resource represented and 1 being equal distribution of prey items.

Statistical analysis

We used a before–after, control-impact (BACI) sampling design and analysis to determine the effect of herbicide treatment on fish diets (composition and total items). We used a "beyond-BACI" approach because there were multiple sampling times representing both treatment periods and types. In other words, the mixed-effects ANOVA model we used included three fixed effects: treatment (control and impact) and time (before and after) and their interaction. Sampling time and site were designated as random effects (for details on the beyond BACI model specification see Underwood 1994). We calculated the individual BACI contrasts with the use of the LS Means Contrast function on the interaction factors (treatment × time) and recorded the estimate, standard error, F ratio, and P value with the program JMP 9 (SAS Institute 2010). This process was repeated for total invertebrates in the fish stomachs, fish stomach content mass, and for each of the diet components that made up at least 5% of the fish diets. Additionally, we analyzed the total plant abundance data from Skogerboe and Getsinger (2006) with the use of the beyond-BACI approach. Data that were not normally distributed were log-transformed. We chose $\alpha = 0.05$ as the cutoff for statistical significance and adjusted α for multiple tests with the use of the Bonferroni correction (e.g., five tests, $\alpha = 0.01$). To assess treatment effects on diet composition as a whole, we used multiresponse permutation procedures (MRPP), which calculate multivariate differences among predefined groups (in this case bluegill diets in each lake before and after treatment). We used the Sørenson coefficient as the distance measure in the MRPP. We tested significance of the null hypothesis that groups were not different with a Monte Carlo randomization procedure with 10,000 permutations, P values less than 0.05 represented no difference between pre- and posttreatment groups. We ran MRPP analyses with PC-ORD (version 5, MjM Software Design, Gleneden Beach, OR).

To describe differences in the composition of bluegill diets among treatments and years, we ran a nonmetric dimensional scaling (NMDS) analysis. This ordination technique conserves rank-order distances of the dissimilarity matrix and does not make assumptions about multivariate normality. Diet comparisons with the use of nonmetric dimensional scaling (NMDS) were based on the relative abundance of diet items in bluegill stomachs (n = 40) representing each year of sampling in each lake for a total of 20 fish sample groups. We included prey and other items present in > 5% of the bluegill stomachs in the NMDS analysis. We first standardized the data by lake totals in order to reduce the influence of outliers. The NMDS was conducted with the use of the autopilot method in PC-ORD (McCune and Mefford 1999). This method uses the Bray-Curtis distance measure, runs 250 iterations on real data, and then recommends a solution based on stress values, or "badness of fit," associated with each dimensionality and whether the stability criterion of 0.00001 is met. The analysis is then rerun with the best configuration found in the trial runs described above with 40 iterations on the real data.

RESULTS

Shift in vegetated habitat

Application of endothall/2,4-D was effective in the removal of Eurasian watermilfoil and curly-leaf pondweed. After the herbicide application in spring 2004, the biomass of invasive plant species decreased to a mean of 2% (± 1% SE) of pretreatment levels, whereas native plant biomass increased by a mean of 7.5% (± 16% SE) in the second and third years following treatment (Figure 1). Once invasive plants were removed from the lakes, native species such as *Chara* spp., *Elodea canadensis* Rich., *Najas flexilis* (Willd.) Rostk. & Schmidt, *Polygonom amphibium* L., *Potamogeton illinoensis* Morong., *Stuckenia pectinata* (L.) Börner, *Vallisneria americana* Michx., and *Heteranthera dubia* (Jacq.) MacMill. returned 1 yr after treatment (Skogerboe and Getsinger 2006). Untreated control lakes had a mean of 32 and 26 (± 5% SE) composition of invasive plants over the course of the sampling period (for details on species richness see Kovalenko et al. 2010). Total plant biomass (g DM per rake sample) did not change as a result of herbicide treatment in the treated lakes (Table 2).

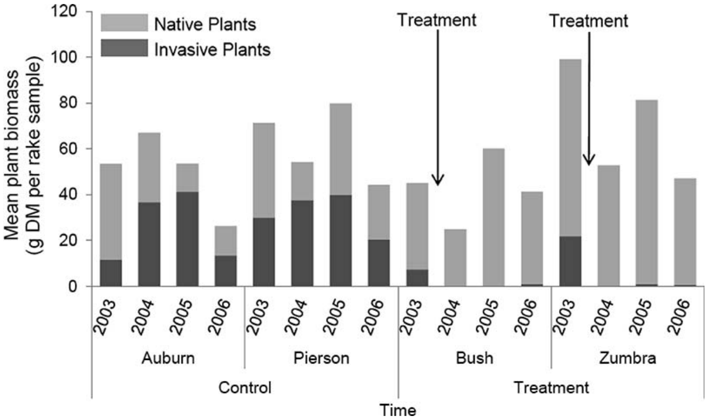

Figure 1. Abundance of native (light grey bars) and invasive plants (dark grey bars) in each of the study lakes pre- and posttreatment. Two lakes were not treated with herbicide and acted as untreated controls (Auburn and Pierson). Herbicide treatment occurred annually starting in the spring of 2004 in the treated lakes (Bush and Zumbra). Data from Skogerboe and Getsinger (2006).

Bluegill characteristics

We collected total length (TL) and body mass measurements from 522 bluegill collected via boat electrofishing from 2003 to 2007. Bluegill TL ranged from 50 to 191 mm with an average TL of 126 ± 1 mm. Body mass ranged from 1.9 to 169.5 g with an average mass of 43.9 ± 1.2 g. We collected 99% adult bluegill; only 12 individuals had a TL < 75 mm. Stomach contents were analyzed for a total of 842 bluegill; 28 or 3.3% of the stomachs were empty.

Short-term effects on diet

Across all four lakes we found 18 taxa in bluegill diets (Table 3). Two taxa orders (Cladocera and Diptera) comprised > 73% of diet items within treated and untreated control lakes and 11 were present in at least 5% of the bluegill samples. We did not find any effect of treatment on the number of prey in bluegill stomachs $F_{(1,\ 8)} = 1.09$, $P = 0.33$ (Table 2 Figure 2). Neither abundance of the dominant prey types nor the stomach content masses of bluegill in the treated lakes differed from before and after treatment such that the pattern was different from the change in untreated control lakes from the first to second year (Table 2). According to the MRPP analysis, there was also no difference between diet compositions before and after treatment in the treated lakes for either June or September the year after herbicide application, $P = 0.42$ and 0.45 for Bush and $P = 0.07$ and 0.07 for Zumbra for June and September, respectively.

Bluegill diet breadth, represented by the standardized Levin's B_A, broadened between September of 2003 and 2004 in the treated lakes (Table 4). During the same time period, diet breadth narrowed in the untreated control lakes. Diet breadth did not widen in the treated lakes because of an increase in richness of prey items, but rather a more even distribution of prey types represented in the diet. In contrast, diet breadth narrowed between June of 2003 and 2004 in the treated lakes; however, this diet breadth also narrowed in the untreated control lakes, and therefore was not a significant change due to herbicide treatment. Because diet breadth was calculated at the population level, both the treated and untreated control lakes were only represented by two data points before and after treatment; therefore we were unable to assess the statistical significance of these differences.

Long-term effects on diets

We found no long-term treatment effects on the number of prey items; stomach content mass; plant biomass; or abundance of Cladocera, Trichoptera, Ephemeroptera, Diptera, and Hymenoptera from 2005 until 2007 (Table 2).

Table 2. ANOVA least-square mean contrast values (before–after, control-impact [BACI] contrast) and standard errors (SE) for estimates of treatment effects on invertebrate abundance, the major food types represented in bluegill diets, and plant abundance for each year following treatment. BACI contrast estimates and standard errors were backtransformed for the log-transformed variables. F ratios and P values each year following treatment are also represented.

Parameter	BACI Contrast[1]	SE	F Ratio	P Value[2]
Year 1				
Total invertebrates (log)	2.13	2.06	1.09	0.33
Stomach mass (log)	1.07	1.09	0.60	0.46
Diptera (log)	1.16	1.54	0.12	0.74
Amphipoda (log)	−1.83	2.22	0.57	0.47
Cladocera (log)	3.04	3.10	0.96	0.36
Trichoptera (log)	−1.16	1.25	0.44	0.53
Plant material (log)	−1.77	1.64	1.34	0.28
Total plant abundance (g DM per rake sample)[3]	32.15	15.08	4.54	0.07
Year 2				
Total invertebrates (log)	1.17	1.63	0.10	0.76
Stomach mass (log)	1.06	1.08	0.64	0.45
Diptera (log)	1.46	1.61	0.64	0.45
Amphipoda (log)	−2.83	2.43	1.36	0.28
Cladocera (log)	1.73	2.13	0.53	0.49
Trichoptera (log)	1.13	1.41	0.12	0.74
Total plant abundance (g DM per rake sample)[3]	1.30	17.8	0.0053	0.94
Year 3				
Total invertebrates (log)	1.26	1.38	0.44	0.51
Stomach mass (log)	1.02	1.06	0.19	0.66
Diptera (log)	−0.94	1.13	0.32	0.58
Amphipoda (log)	−1.51	1.66	0.78	0.37
Plant material (log)	−1.20	1.38	0.34	0.56
Total plant abundance (g DM per rake sample)[3]	0.75	16.20	0.0021	0.96
Year 4				
Total invertebrates (log)	1.20	1.38	0.27	0.61
Stomach mass (log)	1.02	1.06	0.05	0.83
Amphipoda (log)	−2.63	1.59	4.26	0.04
Cladocera (log)	1.10	2.63	0.01	0.93
Plant material (log)	1.10	1.81	0.03	0.88

[1]BACI contrasts are calculated from the least-square means (μ) of the control (C) and treated (T) samples before (B) and after (A) treatment: BACI contrast = $(\mu_{CA} - \mu_{CB}) - (\mu_{TA} - \mu_{TB})$.
[2]Because of multiple comparisons, we used the Bonferroni correction, which reduced α values to 0.006 (Year 1), 0.006 (Year 2), 0.008 (Year 3), and 0.01 (Year 4).
[3]Data from Skogerboe and Getsinger (2006).

Table 3. Percent composition and frequency of diet items found in bluegill stomachs from 2004 through 2007 in treated ($N = 327$) and untreated control lakes ($N = 349$). Taxa printed in bold type represented $\geq 5\%$ of bluegill diet, calculated from bluegill during each year. Composition and frequency percentages were calculated with all bluegill in treated and untreated control lakes from 2004 through 2007.

	% Composition		% Frequency	
Taxa	Treated	Untreated Control	Treated	Untreated Control
Amphipoda[1]	3.6	2.7	29.9	39.4
Annelida[3]	0.0	0.0	0.9	2.0
Cladocera[1]	51.3	54.2	47.3	35.4
Coleoptera[1]	1.2	0.3	11.3	18.1
Copepoda[1]	0.2	0.0	2.7	1.1
Diptera[1]	21.4	19.6	86.9	87.5
Ephemeroptera[1]	1.3	2.1	23.2	39.4
Gastropoda[2]	0.2	0.1	5.8	5.1
Hemiptera[1]	0.1	0.1	6.4	7.1
Hydracarina[1]	1.3	0.5	31.7	28.3
Hymenoptera[1]	0.0	0.1	2.1	3.4
Nematoda[3]	0.2	0.1	4.9	4.0
Nematomorpha[3]	0.0	0.0	1.5	1.7
Odonata[1]	0.1	0.3	8.5	16.4
Ostracoda[1]	1.4	0.2	18.9	9.3
Pelecypoda[2]	0.1	0.1	0.9	0.8
Plecoptera[1]	0.0	0.0	0.9	1.1
Trichoptera[1]	1.1	1.8	24.4	33.4
Eggs	0.2	1.9	1.5	0.8
Fish parts	0.3	1.9	2.7	5.7
Other	0.1	0.1	1.5	3.1
Parasites	0.2	0.1	8.5	5.9
Plant material	15.0	13.3	60.7	72.0
Sand	0.0	0.0	0.9	0.6
Unknown	0.5	0.5	9.5	10.8

[1]Represents order.
[2]Represents class.
[3]Represents phylum.

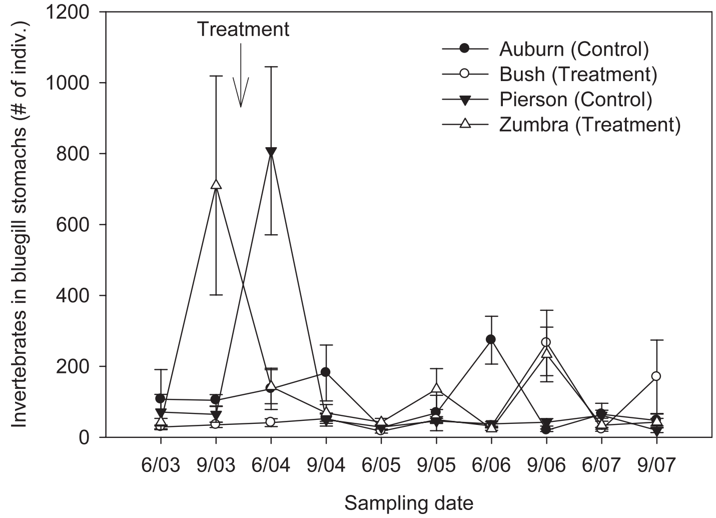

Figure 2. Average number of invertebrates in bluegill stomachs for each study lake for two sampling seasons prior to herbicide treatment (June and September 2003) and 4 yr following treatment (2004 through 2007). Treated lakes are represented by white markers (Bush, circle; Zumbra, triangle) and the untreated control lakes are represented by black markers (Auburn, circle; Pierson, triangle).

The stress value for the NMDS ordination on relative abundance of diet items in bluegill stomachs from 2003 to 2007 was 7.2 for the two-dimensional solution, which is considered a good fit according to Clarke (1993). In other words, the ordination explained 92.8% of the variance in the dissimilarity matrix of the diet samples. The analysis required 58 iterations, and the final stability was < 0.00001. The proximity of the points (fish samples) and triangles (diet items) on the NMDS ordination demonstrates how similar the diets of bluegill in each lake and year were with one another. A major difference in feeding variability of bluegill was the importance of Cladocera (Figure 3). Bluegill diets in each lake, independent of treatment type, were constituted primarily of Cladocera in at least 1 yr. Bluegill samples that were not associated with Cladocera had greater quantities of plant material and plant-dwelling macroinvertebrates (e.g., Odonata).

Table 4. Statistics describing diet breadth of bluegills June and September of the year preceding treatment and the year following for both the untreated control and treated lakes.

		June			September		
Parameter/Lake	Treatment	Pretreatment	Posttreatment	Difference	Pretreatment	Posttreatment	Difference
Number of diet taxa (n)							
Auburn	Untreated control	19	12	−7	19	16	−3
Pierson	Untreated control	19	12	−7	12	17	5
Bush	Treated	19	12	−7	24	16	−8
Zumbra	Treated	19	12	−7	18	15	−3
Diet breadth (Levin's B)							
Auburn	Untreated control	1.78	1.47	−0.31	2.31	1.27	−1.04
Pierson	Untreated control	1.94	1.08	−0.86	4.75	1.38	−3.37
Bush	Treated	3.57	1.99	−1.58	3.25	4.00	0.75
Zumbra	Treated	3.27	1.46	−1.81	1.11	2.83	1.72
Standardized diet breadth (B_A)							
Auburn	Untreated control	0.04	0.04	0.00	0.07	0.02	−0.05
Pierson	Untreated control	0.05	0.01	−0.04	0.34	0.02	−0.32
Bush	Treated	0.14	0.08	−0.06	0.10	0.20	0.10
Zumbra	Treated	0.13	0.04	−0.08	0.01	0.13	0.12

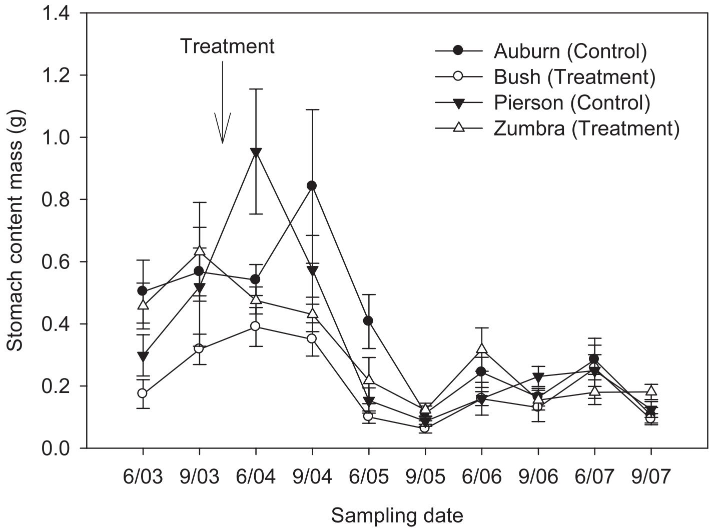

Figure 3. Average mass of bluegill stomach contents for each study lake for two sampling seasons prior to herbicide treatment (June and September 2003) and 4 yr following treatment (2004 through 2007). Treated lakes are represented by white markers (Bush, circle; Zumbra, triangle) and the untreated control lakes are represented by black markers (Auburn, circle; Pierson, triangle).

DISCUSSION

Prey abundance

We did not find evidence to support our hypothesis that abundance of prey items in bluegill stomachs would increase as a result of Eurasian watermilfoil control and a corresponding release of food items into the environment. This hypothesis was derived from the negative relationship typically found between fish foraging success and habitat complexity and the positive effect of Eurasian watermilfoil on habitat complexity. In our study, Eurasian watermilfoil was successfully controlled and biomass was reduced in treated lakes following herbicide treatment at the whole-lake scale to 2% of preherbicide levels (Skogerboe and Getsinger 2006). However, the littoral zone was immediately colonized by native plants, which is evident because of the lack of difference in plant biomass by treatment type, and habitat complexity likely was not reduced to the extent necessary to release enough prey items to observe a treatment effect. Because adult bluegill (> 75 mm TL) primarily feed in open-water habitats and on zooplankton (Werner et al. 1981), we would have expected an increase in zooplankton (e.g., Cladocera) importance in treated lakes if herbicide treatment had resulted in greater areas of open water. Although zooplankton was an important food item (Cladocera made up > 50% of diet items in both untreated control and treated lakes), the relative importance of zooplankton varied by season and year, irrespective of treatment. These dietary shifts within fish populations could be due to effects of bluegill consumption on zooplankton dynamics or differences in zooplankton dynamics among lakes (Vanni 1987, Mittelbach and Osenberg 1993). Our results are consistent with a study by Savino et al. (1992), who found that bluegill prey capture rates did not differ at plant densities greater than 100 stems m^{-2}, even though macroinvertebrate densities were greater at increasing plant densities.

Further, our findings contrast with research on largemouth bass response to the removal of *Hydrilla verticillata*, another invasive aquatic plant. Researchers found that number of prey in largemouth bass diets increased by 21% within 3 yr of invasive aquatic plant removal and the establishment of native plants (Sammons and Maceina 2006). The difference in effects could be attributed to the different foraging strategies of different-sized predators and the types of prey consumed by largemouth bass and bluegill. Furthermore, time required to establish native plants was different for southern reservoirs than for northern lakes in our study, which likely influenced the effect of aquatic plant removal on fish growth over time.

Diet breadth

Although we found that the overall number of prey items in bluegill diets was not affected by control of Eurasian watermilfoil, the diet breadth of bluegill increased in the fall sampling season following treatment. This result provides some evidence to support the hypothesis that certain types of prey become more available with a decrease in plant complexity following Eurasian watermilfoil control, and as a result, bluegill would consume a greater variety of prey and thus widen their diet breadth. Interestingly, the increase in diet breadth in the fall was not due to an increase in types of prey—types of prey actually decreased across both untreated control and treated lakes the year after treatment—but a more even distribution of prey in the bluegill diets. This result suggests that other types of desirable prey may have become more available to bluegill as plant structure changed from complex Eurasian watermilfoil to the simple stems of white water lily, for example. According to optimal foraging theory, diet breadths widen when the abundance of food items decreases, although this theory has been criticized for not accurately predicting behavior in many circumstances (see review by Pyke 1984). Our study was not designed to distinguish between the abundance of food items in the environment and diet selection. Therefore it is possible that the widening of diet breadth in the fall season was due to a decline in food abundance in the treated lakes; however, certain studies on fish have shown that diet breadth changes irrespective of food abundance (e.g., Hammerschlag et al. 2010). In our study, stomach content mass tended to be less in treated lakes than untreated control lakes in September 2004 (Figure 4); however, this difference was not statistically significant. An examination of macroinvertebrate abundance would have been necessary to evaluate what was driving the treatment effect on diet breadth.

Diets may have broadened as a result of treatment in the fall because of a shift in plant characteristics. Aquatic plants provide refuge and food sources for zooplankton and macroinvertebrates; however, these affiliations depend on the traits of aquatic plants. Eurasian watermilfoil has been shown to exude allelochemicals, which could have limited the diversity of species living in these plants and thus

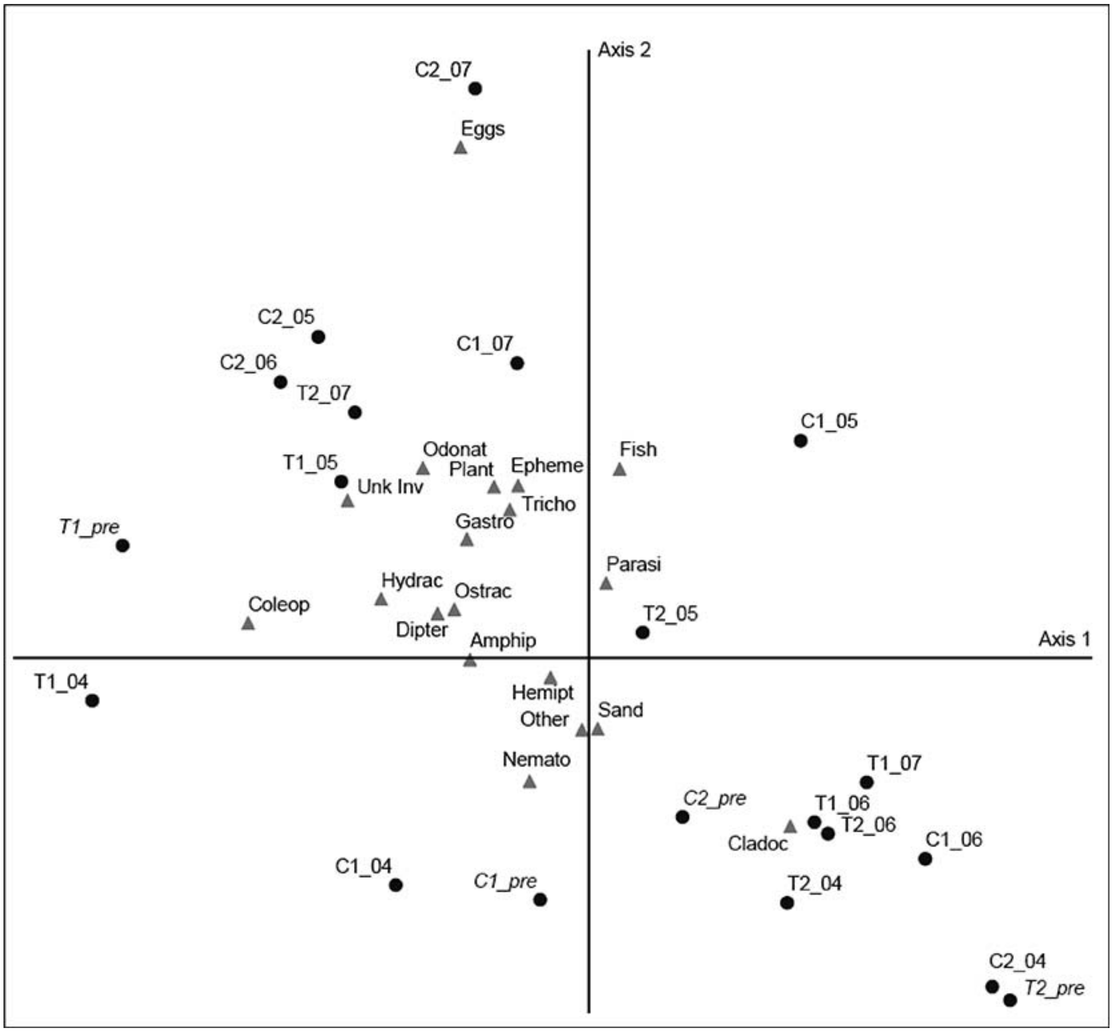

Figure 4. Nonmetric dimensional scaling (NMDS) ordination of relative abundance of items in bluegill stomachs that were found in a minimum of 5% of the bluegill samples. Bluegill samples ($n = 20$) are represented by black circles and are named by the lake treatment type and the year of sampling. C1 and C2 represent the two untreated control lakes (Auburn and Pierson) and T1 and T2 represent the two treatment lakes (Bush and Zumbra). "Pre" signifies samples taken the year prior to herbicide treatment (2003) and the successive years are numbered 04 through 07. Species and other stomach content items are represented by grey triangles and by the first six letters of the name listed in Table 2.

available for fish (Linden and Lehtiniemi 2005). Also, leaf complexity and patterns of senescence likely changed as a result of plant community shift to native plants, therefore altering the amount of refuge available, allowing fish greater access to a variety of species (for example: Amphipods, Ostacods, Copepods, and Cladocera). However, the abundance of prey in bluegill stomachs varied primarily by season and year rather than as a result of herbicide treatment. Similarly, in a study of six lakes, Cheruvelil et al. (2002) found that most of the variance in macroinvertebrate density and biomass was attributed site and seasonal effects. Also, in a concurrent study of juvenile fishes, Kovalenko et al. (2009) found that fish diets did not vary because of an herbicide treatment effect or habitat complexity, but rather by lake and season.

In terms of management, removing aquatic plants can increase fish growth; however, this depends on the establishment of native plants. Some instances of aquatic plant removal have resulted in virtually complete removal of vegetation, resulting in fish population declines as well as decreased water quality (e.g., Parsons et al. 2009). In our study, herbicide treatment was specific for Eurasian watermilfoil and did not hinder native plant establishment. However, because our study only included lakes with 11 and 27% invasive plant cover prior to treatment, our results may not be applicable to lakes being treated for higher levels of infestation. Species-specific herbicide treatment as well as targeted efforts to establish native plants following invasive species management could reduce negative impacts on the fish community. Future research is needed on the effects of herbicide treatment of lakes with greater coverage of invasive plants and subsequent native plant establishment on fish diets.

CONCLUSION

We rejected our hypothesis that Eurasian watermilfoil control would result in a temporary release of food items in the environment, thus increasing total prey in bluegill diets. However, we found evidence to support the hypothesis that a decrease in habitat complexity changes the availability of certain prey types, resulting in a more even distribution of prey items and an increase in bluegill diet breadth. This effect was only found in the fall season following herbicide treatment, suggesting that this is a temporary effect dependent on seasonal cycles of zooplankton and macroinvertebrates. Because variation in bluegill diets was mostly explained by seasonal and annual differences, plant removal does not appear to have a biologically significant impact on bluegill diets. Thus, when native plants replace invasive aquatic plants immediately, as in this restoration, there are relatively small changes to the system, including diet.

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