Changes in Diet and Food Consumption of Largemouth Bass Following Large-scale Hydrilla Reduction in Lake Seminole, Georgia

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2 authors:

Steven M. Sammons
Auburn University

Michael J Maceina
Auburn University

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Primary Research Paper

Changes in diet and food consumption of largemouth bass following large-scale hydrilla reduction in Lake Seminole, Georgia

Steve M. Sammons* & Michael J. Maceina
Department of Fisheries, Auburn University, Auburn, AL, 36849, USA
*(*Author for correspondence: Tel: 334-844-4058; Fax: 334-844-9208; E-mail: sammosm@auburn.edu)*

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Abstract

Largemouth bass *Micropterus salmoides* Lacepède growth (in length) increased an average of 14% and bioenergetics modeling predicted a 38% increase in total annual food consumption following a large-scale reduction of hydrilla *Hydrilla verticillata* L.f. Royle in Spring Creek, a 2,343-ha embayment of Lake Seminole, Georgia. Coverage of submersed aquatic vegetation (SAV) declined from 76% to 22% in 1 year due to a drip-delivery fluridone treatment. In contrast, largemouth bass growth only increased an average of 4% and bioenegetics modeling predicted a 13% increase in total food consumption over the same time period in the Chattahoochee River embyament, where SAV coverage naturally declined from 26% to 15%. Diets were collected from a total of 4,409 largemouth bass over a 2.5-year period in the two embayments; the primary diet item (by weight) for largemouth bass in both embayments was sunfish (mostly *Lepomis* spp.). Diets before and after SAV reduction were generally similar for fish greater than stock-size (≥203 mm) in the Spring Creek arm; however, fewer invertebrates were consumed after SAV reduction. Low diet similarity was observed in smaller fish, caused by a decline in consumption of grass shrimp and sunfishes and an increase in use of damselflies, shiners *Notropis* spp., and topminnows *Fundulus* spp. after SAV reduction. Diets were similar between the same time periods for all sizes of fish in the Chattahoochee River arm. These results agreed with many laboratory results describing the effects of aquatic plant density on largemouth bass food consumption and growth, and demonstrated that increased predation efficiency resulting from decreased plant abundance was likely a stronger factor determining growth rates than any potential diet shift that may occur as a result in vegetation decline.

Introduction

Submersed vegetation can mediate trophic food webs in aquatic communities, providing both foraging opportunities for predators and refuge from predation for prey (Anderson, 1984; Rozas & Odum, 1988; Dionne & Folt, 1991). The nature of the predator–prey dynamics present within such a community depends on both density (Savino & Stein, 1989; Hayse & Wissing, 1996) and species composition (Dionne & Folt, 1991; Dibble & Harrel, 1997) of submersed aquatic vegetation (SAV). Dense SAV restricts feeding of largemouth bass *Micropterus salmoides* Lacepède (Savino & Stein, 1982; Gotceitas & Colgan, 1989), leading to reduced growth and condition (Colle & Shireman, 1980; Cailteux et al., 1998; Pothoven et al., 1999; Brown & Maceina, 2002). Similarly, a shift in SAV communities to species with more complex growth forms also can decrease fish feeding efficiency (Dionne & Folt, 1991; Dibble & Harrel, 1997).

Because prey species can exhibit different behaviors within SAV communities, changes in SAV density can result in differing effects on prey vulnerabilities (Schramm & Zale, 1985; Savino &

Stein, 1989; Dionne & Folt, 1991). Also, large shifts in SAV density can affect recruitment of phytophilic species, leading to changes in prey population composition (Anderson, 1984; Bettoli et al., 1991, 1993). The combination of these two factors can lead to large diet shifts in largemouth bass when SAV suddenly increases or decreases (Bettoli et al., 1992; Miranda & Pugh, 1997; Cailteux et al., 1998; Unmuth et al., 1999). Changes in diet can also affect fish growth, if food consumption and/or diet energetic content differs (Adams et al., 1982; Anderson, 1984; Bettoli et al., 1992). Thus changes in both density and species composition of the SAV community can affect largemouth bass growth through changes in feeding efficiency and/or diet.

Lake Seminole is an impoundment of the Chattahoochee and Flint Rivers on the Georgia–Florida border. Hydrilla *Hydrilla verticillata* L.f. Royle was discovered in the reservoir in 1967, and since then has dominated the SAV community, particularly in Spring Creek, a 2,343-ha embayment (the U.S. Army Corps of Engineers (USACE), 1998). An areal survey in 1997 indicated that coverage of SAV, primarily hydrilla, was 76% in Spring Creek, compared to 26% in the Chattahoochee River, a 5,143-ha embayment that typically has higher river inflows and greater turbidity than Spring Creek, providing a natural control on hydrilla (USACE, 1998). To partially reduce hydrilla in Lake Seminole, the USACE initiated a drip delivery fluridone system (Fox et al., 1994) in Spring Creek in May 2000 to reduce hydrilla in Spring Creek to levels similar to those found in other areas of the reservoir. Hydrilla coverage in Spring Creek declined from over 70% in August 2000 to 22% in August 2001; 1,800 ha of hydrilla in Spring Creek was eliminated (J. Staigl, USACE, unpublished data). Some native plant species began recolonizing areas that were formerly monotypic hydrilla stands, including tape-grass *Vallisneria americana* Michaux, spatterdock *Nuphar luteum* L., muskgrass *Chara* sp. L., Illinois pondweed *Potamogeton illinoensis* Morong, and small pondweed *P. pusillus* L. These plants covered less than 100 ha in 2001 in Spring Creek, but abundance increased rapidly in 2002, reaching a coverage of almost 30% of the entire embayment (D. Morgan, USACE, personal communication). In contrast, SAV coverage remained similar (26% coverage) from 1997 to 2000 in the Chattahoochee River arm, and declined to 15% by September 2001 because of high-riverine flows in the winter of 2000–2001.

Previous work had found that largemouth bass growth and condition in the Spring Creek embayment was considerably lower than in the Chattahoochee River embayment (Brown & Maceina, 2002). The authors assumed that the dense SAV in Spring Creek inhibited predation efficiency of largemouth bass, leading to reduced growth and condition. Thus, when hydrilla was reduced in that system, we expected commensurate changes in food consumption as predation efficiency increased, and possibly a diet shift as new prey items became available. The purpose of this study was to quantify diet composition in largemouth bass in the Spring Creek and Chattahoochee River arms of Lake Seminole over a 3-year period during the operation of the herbicide drip system in Spring Creek. In addition, we used a bioenergetics model to predict food consumption changes based on growth data before and after hydrilla reduction in the Spring Creek arm. Although largemouth bass predation efficiency has been shown experimentally to decline at high SAV densities (Gotceitas & Colgan, 1989; Savino & Stein, 1989), this mechanism has rarely been examined at large spatial scales.

Methods

Diet collection and analysis

To determine if diets changed during SAV reduction, we sampled largemouth bass approximately once every 3 months in the Chattahoochee and Spring Creek arms of Lake Seminole during August 2000 through March 2003 using electrofishing boats. The Chattahoochee River arm was sampled to serve as a control to diminish the possibility that our results would be confounded by temporally confounding factors such as weather events (i.e., similar to a BACI design; Cloutman & Jackson, 2003). Approximately 200 largemouth bass were collected in each arm during each sampling period. Ten fish per 25-mm group were collected up to 281 mm total length (TL); all fish over 281 mm TL were collected until the requisite sample size was reached in each embayment. Fish under 281 mm TL were placed in a 300 mg/L solution of MS-222 until expired, then placed on ice and stomachs were excised from these fish in the lab. Stomach contents were removed from larger fish using clear acrylic tubes and the fish were released (Van Den Avyle & Roussel, 1980).

Food items were identified to the lowest practical taxonomic level (order or suborder for invertebrates, family, genus, or species for fishes). TLs and weights of consumed fishes were estimated from standard lengths, vertebrae lengths, or otolith radius using regression equations from this study or from literature sources (Carlander, 1969, 1977a, 1997b; Irwin, 2001). All invertebrates were measured for TL; weights were predicted from TL using regression equations from Irwin (2001) and Slaughter (2002). Mean lengths of all diet items were calculated for each largemouth bass length group-sampling date combination and used in cases where accurate lengths of diet items could not be obtained. Diet items were grouped into broad categories for comparison (Table 1); composition was described using percent by weight, as this measure has been found to closely approximate caloric contribution of stomach contents (Pope et al., 2001).

To quantify diets, we divided largemouth bass into four length groups: substock (<203 mm TL), stock (203–303 mm TL), quality (304–380 mm TL), and preferred (381–507 mm TL) as described by Anderson and Neumann (1996). We considered two time periods to examine changes in largemouth bass diet and feeding due to the reduction in SAV. Based on hydrilla coverage in Spring Creek, samples collected in August and November of 2000 and February 2001 were chosen to represent conditions before the major reduction of hydrilla; whereas samples collected in August and December 2002 and March 2003 were chosen to represent conditions after hydrilla reduction. Since we expected seasonal effects on diet composition, we used samples collected during approximately the same months for this analysis. Changes in diet composition between these time periods were assessed using the Percent Resource Overlap Index (PROI) developed by Schoener (1970); values over

Table 1. Classification of diet items used for PROI analysis

Items (order, family, genus, species)	Category
Anisoptera	Dragonflies (larvae and adults)
Zygoptera	Damselflies (larvae and adults)
Ephemeroptera	Mayflies (larvae and adults)
Cambaridae	Crayfish
Palaemonidae	Grass shrimp
Enneacanthus gloriosis Holbrook, *E. obesus* Girard, *Lepomis gulosus* Cuvier, *L. macrochirus* Rafinesque, *L. marginatus* Holbrook, *L. microlophus* Günther, *L. punctatus* Valenciennes, *Pomoxis nigromaculatus* Lesueur	Sunfish
M. salmoides	Largemouth bass
Notropis maculatus Hay, *Notropis petersoni* Fowler, *Notropis texanus* Girard	Minnows
Fundulus chrysotus Günther, *F. escambiae* Bollman, *Gambusia holbrooki* Girard, *Heterandria formosa* Agassiz, *Lucania goodei* Jordan	Killifishes
Erimyzon sucetta, Notimigonus chrysoleucas	Large Cypriniformes
Esox niger	Chain pickerel
Alosa chrysochloris Rafinesque, *Dorsosoma cepedianum* Lesueur, *D. petenense* Günther	Shad
Ameiurus nebulosus Lesueur, *Ictalurus punctatus* Rafinesque, *Pylodictis olivaris* Rafinesque	Catfish
Elassoma zonatum Jordon, *Etheostoma fusiforme* Girard, *Strongylura marina* Walbaum, unidentified fish	Other fish

Diet items were grouped to reflect their approximate taxonomic relationship whenever possible. However, items that could be easily mistaken for each other were grouped based on morphology and maximum adult size. The ‘fish’ category consisted of unidentified fish and rarely eaten species that did not fit into other categories.

60 were considered to indicate high overlap (Wallace, 1981). Changes in relations between lengths of largemouth bass and their fish prey were examined between time periods using covariance analysis (SAS Institute, 2000). To determine changes in percent empty stomachs, numbers of fish prey per stomach for all sizes of fish, and relative weight, all diet samples were divided into pre- (August 2000–February 2001) and post-time periods (May 2001–March 2003). Differences in percent empty stomachs between treatment periods were assessed for each embayment using *Z*-tests; differences in numbers of fish prey per stomach were examined using *t*-tests (SAS Institute, 2000). Mean relative weight was used as a surrogate to examine changes in relative food consumption and growth throughout the study (Guy & Willis, 1995), and was compared between treatment periods in each embayments for two groups of fish: substock and stock-sized fish and quality and preferred-sized fish. All data sets were tested for the assumption of normality prior to analyses using Shapiro–Wilk *W*-tests; if this assumption was violated, the data were then transformed until normality was achieved. Significance for all statistical tests was set at $p \leq 0.10$. A *p*-value of 0.10 was chosen because we considered Type-II error to be important (Peterman, 1990). The large scale of this study precluded replication in this study, thus we expected high variability and low power.

Bioenergetics modeling

Food consumption by largemouth bass was estimated by combining measured growth and a generalized bioenergetics model (Hanson et al., 1997) for both the Chattahoochee River arm and the Spring Creek arm of Lake Seminole. Two simulations were run for each area, using growth data collected in 1998 (Brown & Maceina, 2002) and 2003 (from Sammons, 2004). Largemouth bass diet composition (percent by weight) was quantified from the quarterly diet samples described above. Diet samples from August 2000 to May 2001 were used with the 1998 growth data and were assumed to reflect conditions before hydrilla reduction in Spring Creek. Diet samples from August 2001–May 2002 were used with the 2003 growth data and were similarly assumed to reflect conditions after hydrilla reduction in Spring Creek. Mean daily water temperature for each area was obtained from the U.S. Geological Survey (L. Torak, unpublished data). Since bioenergetics models are extremely dependent on water temperature, models for each area were run with the same water temperature regime for each year of growth data to minimize the chance that any differences in consumption would be due to changes in water temperature. Prey items were grouped into broad categories based on taxonomy and relative caloric density (Table 2). Caloric density of diet items was determined by bomb calorimetry or obtained from published literature (Table 3). Potential prey fish were collected using electrofishing in May and August 2001 from the Chattahoochee River and Spring Creek arms. Samples ($N = 30$ for each prey fish species) were prepared following the methods of Slaughter (2002) and ignited in a bomb calorimeter (Parr Instrument Company, Model 1425, semi-micro bomb calorimeter) to measure calorimeter content. Mean caloric content (cal/g) was calculated for each prey group, pooling between areas (Table 3). All metabolic variables for the mass balance equations were the default values in the Wisconsin model (Rice et al., 1983), which have been validated for largemouth bass (Rice & Cochran, 1984; Whitledge & Hayward, 1997).

Annual daily food consumption was estimated for an individual fish for each age class in each of the two areas using starting and ending weights predicted from von Bertalaffy (1938) models using empirical data from 1998 and 2003 (Sammons, 2004). Fish age was determined from otoliths using the methods described in Maceina (1988). Diet composition was calculated for three size groups of fish in each area (<200 mm TL, 200–379 mm TL, and ≥380 mm TL) to simulate ontogenetic shifts in diet; age-classes were assigned diet composition for the size group that they were in for the majority of the year. Spawning was simulated for mature fish; percent body mass spawned was estimated using gonadosomatic index values obtained in a related study (Sammons, 2004). Food consumption was summed for each year for each age class and compared between areas (Spring Creek and Chattahoochee River) and years (1998 and 2003).

Table 2. Classification of diet items used for bioenergetics analysis

Items (order, family, genus, species)	Category
Odonata, Ephemeroptera, Diptera, Hemiptera, Coleoptera	Invertebrates
Cambaridae	Crayfish
Palaemonidae	Grass shrimp
Elassoma zonatum, Enneacanthus gloriosis, E. obesus, Lepomis gulosus, L. macrochirus, L. marginatus, L. microlophus, L. punctatus, Pomoxis nigromaculatus	Sunfish
M. salmoides	Largemouth bass
Erimyzon sucetta, Fundulus chrysotus, F. escambiae, Gambusia holbrooki, Heterandria formosa, Lucania goodei, Notemigonus chrysoleucas, Notropis maculatus, Notropis petersoni, Notropis texanus	Cypriniformes and Cyprinodontiformes
Alosa chrysochloris, Dorsosoma cepedianum, D. petenense	Shad
Ameiurus nebulosus, Esox niger, Etheostoma fusiforme, Ictalurus punctatus, Pylodictis olivaris, Strongylura marina, unidentified fish	Other fish

Diet items were grouped according to their approximate taxonomic relationship and relative caloric value, except for ‘other fish’, which consisted of unidentified fish and rarely eaten species that did not fit into other categories.

Results

Food habits

A total of 4,409 largemouth bass was examined for food habits, 2,158 in the Chattahoochee River arm and 2,251 in the Spring Creek arm. Sunfish were the primary diet item in both embayments, usually composing more than 50% of the diet by weight and often composing more than 60% of the diet for stock size and larger fish (Tables 4 and 5). In contrast, shad composed less than 10% of the diet of all size class of fish in both embayments, but usually composed a higher percentage in the Chattahoochee River arm than in the Spring Creek arm (Tables 4 and 5). Large cypriniformes were important components in the diets of preferred-sized fish, but their importance progressively decreased as largemouth bass size decreased. Grass shrimp, mayflies, and odonates were important components of stock and substock-sized fish in both embayments (Tables 4 and 5). Crayfish constituted approximately equal proportions of largemouth bass diets in both embayments in each size class of fish.

Table 3. Caloric densities of prey fish used for bioenergetics modeling of largemouth bass in Lake Seminole

Category	Caloric density (cal/g)	Source
Cypriniformes and Cyprinodontiformes	1063	Present study
Shad	1444	Present study
Other fish	1154	Present study
Sunfish	1160	Miranda and Muncy (1990)
Crayfish (corrected)	828	Irwin (2001)
Invertebrates	875	Slaughter (2002)
Grass shrimp	818	A. Peer, Auburn University, unpublished data
Largemouth bass	1160	Miranda and Muncy (1990)

Diet similarity between pre- and post-treatment periods was generally high for all sizes of fish in the Chattahoochee River arm (Table 4). The only appreciable difference in diet occurred in preferred-sized fish, which appeared to increase their use of large cypriniformes and decrease their use of sunfishes during the later periods of the study. Similarly, diet overlap was high between these periods for fish greater than stock-size in the Spring Creek arm; however, stock-sized and larger largemouth bass consumed less invertebrates after SAV reduction (Table 5). In contrast, low diet overlap was observed in smaller substock fish, caused by a decline in use of grass shrimp and sunfishes and an increase in use of damselflies, minnows, and killifishes after SAV reduction.

Percent empty stomachs declined 20% after hydrilla reduction in the Spring Creek arm ($Z = 3.77$; $p < 0.10$; Fig. 1); whereas, percent empty stomachs were similar between time periods in the Chattahoochee River arm ($Z = 0.83$;

Table 4. Percent contribution by weight of 14 diet items for four size groups of largemouth bass collected in the Chattahoochee River arm of Lake Sole

	Size groups							
	Preferred		Quality		Stock		Substock	
Food	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Dragonflies	<0.1	0.0	<0.1	0.1	0.4	1.5	3.1	4.9
Damselflies	0.0	0.2	<0.1	0.3	0.3	2.7	0.7	6.6
Mayflies	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0.1	3.3
Grass shrimp	<0.1	0	<0.1	0.2	0.6	0.6	10.5	5.1
Crayfish	10.3	6.5	18.4	24.0	28.9	8.7	–	–
Catfish	0.6	0	0.2	0.0	0.1	1.2	–	–
Shiners	3.9	0	3.3	0.2	1.7	0.7	9.0	5.6
Killifishes	–	–	0.3	0.0	0.7	0.3	0.6	10.3
Large Cypriniformes	0	39.7	2.2	0.0	0.9	0.0	–	–
Sunfishes	80.7	46.3	66.7	57.1	51.1	75.4	50.4	43.7
Largemouth bass	1.3	0	2.4	4.1	2.8	3.2	1.0	0.0
Chain pickerel	0	<0.1	0.0	2.1	0.9	0.0	–	–
Shad	3.0	3.0	2.8	4.9	5.8	1.1	4.7	0.0
Fish	0.2	4.2	3.7	6.9	5.3	4.5	19.9	20.4
PROI	56		84		71		79	

PROI values are for overlap between two time periods, before d after the major collapse of hydrilla in the Spring Creek arm.

Table 5. Percent contribution by weight of 14 diet items for four size groups of largemouth bass collected in the Spring Creek arm of Lake Seminole

	Size groups							
	Preferred		Quality		Stock		Substock	
Food	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Dragonflies	–	–	0.1	<0.1	0.8	<0.1	4.0	2.0
Damselflies	0.1	0.0	<0.1	<0.1	0.1	1.3	0.2	19.9
Mayflies	0.0	<0.1	<0.1	0.0	<0.1	<0.1	<0.1	0.6
Grass shrimp	<0.1	0.0	<0.1	<0.1	0.9	0.1	9.1	0.8
Crayfish	7.3	3.8	29.3	10.1	22.0	8.8	–	–
Catfish	0.5	0.0	–	–	–	–	–	–
Shiners	0.0	0.1	1.0	0.8	1.5	1.9	7.7	24.8
Killifishes	–	–	<0.1	0.0	0.5	0.2	6.2	11.5
Large Cypriniformes	12.6	30.8	–	–	0.8	2.4	4.3	0.0
Sunfishes	75.9	53.4	58.9	84.5	68.4	80.7	49.8	11.5
Largemouth bass	1.0	2.2	3.2	0.5	1.8	0.7	–	–
Chain pickerel	0.3	0.0	4.3	0.0	–	–	–	–
Shad	1.8	0.0	1.7	2.8	0.8	0.0	–	–
Fish	0.4	9.6	1.3	1.3	2.5	3.8	18.6	29.0
PROI	71		73		83		47	

PROI values are for overlap between two time periods as in Table 4.

$p < 0.10$; Fig. 1). In contrast, number of fish prey per stomach increased 21% after hydrilla reduction in the Spring Creek arm ($t = 1.86$; $p < 0.10$; Fig. 1), but did not change in the Chattahoochee River arm ($t = -1.19$; $p > 0.10$; Fig. 2). Fish prey-length-to-predator-length ratios did not change among pretreatment and post-treatment periods in Spring Creek (Covariance; $F = 0.03$; $df = 1$; 1021; $p = 0.86$). Adjusted mean length of fish prey consumed by largemouth bass was higher in the post-treatment period compared to the pre-treatment period in the Chattahoochee River arm (Covariance; $F = 4.46$; $df = 1{,}878$; $p < 0.05$); however, the difference was only 3 mm, which is not likely biologically significant.

Relative weight of substock and stock-sized largemouth bass was lower before hydrilla reduction in Spring Creek ($t = 8.13$; $df = 584$; $p < 0.05$); however, no difference was found in relative weight between the two time periods in the Chattahoochee River arm ($t = 0.58$; $df = 548$; $p < 0.05$; Fig. 2). Similarly, relative weight of quality and preferred-sized largemouth bass was lower in Spring Creek before hydrilla reduction in Spring Creek ($t = 5.81$; $df = 529$; $p < 0.05$); however, relative weight was also lower in the pre-hydrilla treatment period in the Chattahoochee River arm ($t = 2.16$; $df = 939$; $p < 0.05$; Fig. 2).

Bioenergetics modeling

Growth rates (in length) of largemouth bass increased 6–18% from 1998 to 2003 in the Spring

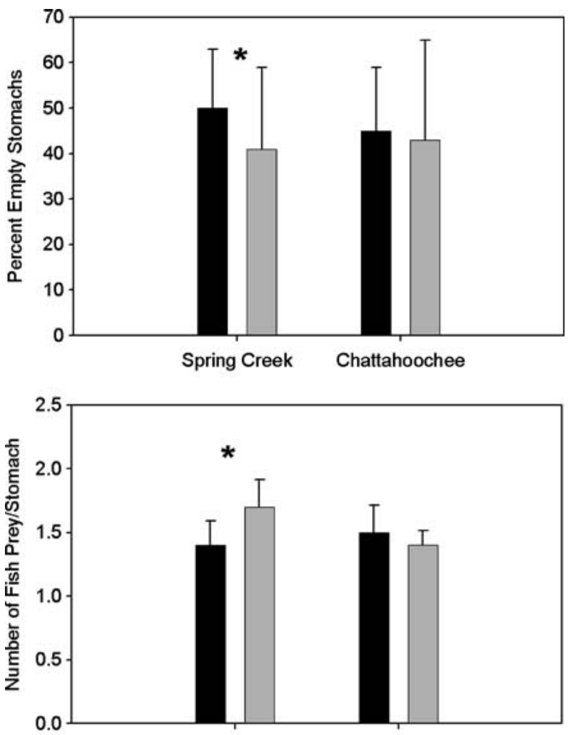

Figure 1. Percent empty stomachs (top) and number of fish prey per stomach (bottom) of all sizes of largemouth bass collected from two areas of Lake Seminole, Georgia, before (dark bars) and after (gray bars) major collapse of hydrilla in the Spring Creek arm. Vertical lines show one standard deviation. Asterisks denote significant differences between time periods ($p < 0.10$).

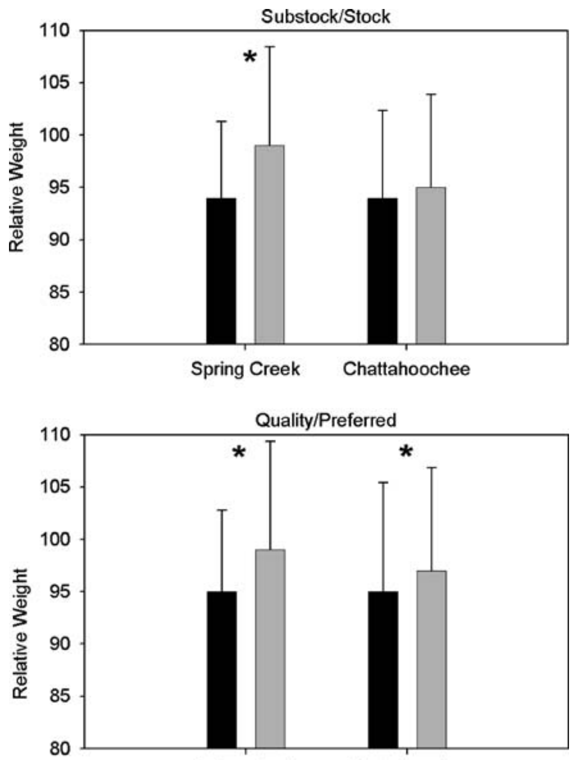

Figure 2. Mean relative weight of two size groups of largemouth bass collected from August 2000 through March 2003 from two areas of Lake Seminole, Georgia, before (dark bars) and after (gray bars) major collapse of hydrilla in the Spring Creek arm. Vertical lines show one standard deviation. Asterisks denote significant differences between areas (t-test, $p < 0.10$).

Creek embayment; whereas, growth rates declined 11% and 1% for ages 2 and 3 fish, respectively, and increased only 3–7% for age 4 and older fish in the Chattahoochee River arm over the same time period (Table 6). Bioenergetic modeling predicted that total food consumption increased 6–21% (mean = 13%) across all age classes in the Chattahoochee River arm from 1998 conditions to 2003 conditions (Fig. 3). Greatest increases were predicted for 4–6 year-old fish. Predicted total food consumption increased 18–49% (mean = 38%) across all age classes in the Spring Creek arm over the same duration. Similar to the Chattahoochee River arm, the greatest increases were predicted for 4–6 year-old fish; however, food consumption in 2003 increased much more over 1998 conditions for all age classes (Fig. 3).

Discussion

The drip-delivery fluridone application in the Spring Creek arm of Lake Seminole constituted the largest herbicide treatment of its kind (W. Haller, University of Florida, personal communication), and successfully eliminated over 1,800 ha of hydrilla. This treatment resulted in an almost complete change of habitat for the fish community living in Spring Creek, from one dominated for many years by dense monotypic stands of hydrilla to a more open, dynamic SAV community composed of a variety of native species. Dense SAV has been shown to obstruct feeding by largemouth bass in a variety of experimental systems (Savino & Stein, 1982, 1989; Anderson, 1984; Gotceitas & Colgan, 1989), and largemouth bass growth and condition has been shown to decrease in areas of high SAV density (Colle & Shireman, 1980; Wiley et al., 1984; Wrenn et al., 1996; Brown & Maceina, 2002). However, diet composition changed little over time in Spring Creek and largemouth bass consumed similar items in both the herbicide-treated and untreated periods. Percent empty stomachs declined 20% and number of prey consumed per largemouth bass stomach increased 21% in Spring Creek over the three-year period. In contrast, percent empty stomachs and number of prey per

Table 6. Predicted mean length at age (mm) from von Bertalanffy models for age 2–12 largemouth bass in two areas of Lake Seminole, Georgia, before and after hydrilla reduction occurred in Spring Creek

	Chattahoochee			Spring Creek		
Ages	Pre	Post	% change	Pre	Post	% change
2	288	255	−11	263	280	6
3	338	332	−1	304	343	13
4	380	391	3	339	394	16
5	415	438	6	371	435	17
6	444	474	7	398	468	18
7	469	502	7	423	494	17
8	490	524	7	444	515	16
9	507	541	7	463	532	15
10	522	554	6	479	546	14
11	534	564	6	494	557	13
12	545	572	5	506	565	12
mean % change			4			14

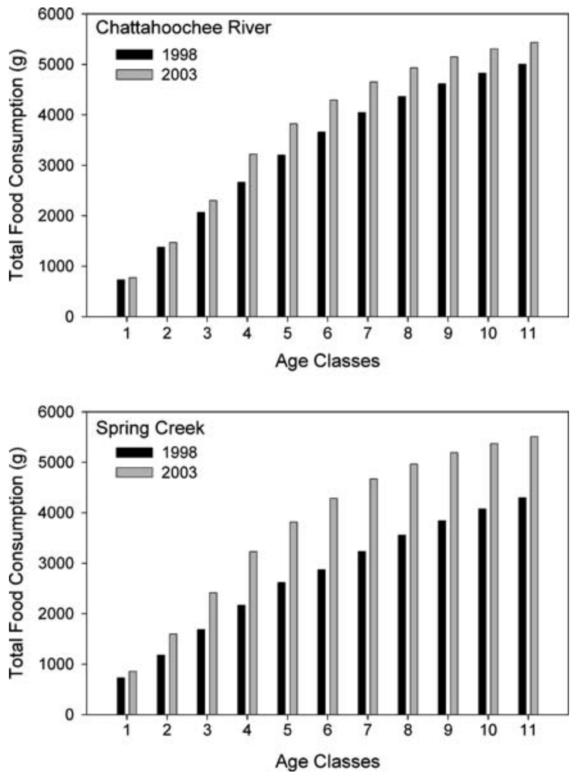

Figure 3. Total food consumption predicted by bioenergetic models for largemouth bass collected from August 2000 through March 2003 from two areas of Lake Seminole, Georgia. Models were based on growth data collected in 1998 and 2003.

stomach did not change over time in the Chattahoochee River arm. Cailteux et al. (1998) reported that percent empty stomachs was greater in vegetated Florida lakes than in unvegetated Florida lakes, which they inferred to indicate that food consumption was higher in unvegetated lakes.

Largemouth bass are generally opportunistic predators, and have been found to consume a wide variety of prey types depending on prey availability (Summers, 1981; Maceina & Murphy, 1989). Bettoli et al. (1992) found that stock size and smaller largemouth bass changed their diets and became more piscivorous after total elimination of hydrilla in Lake Conroe, Texas. Largemouth bass in that system primarily consumed shad once hydrilla was gone, concomitant with a large decrease in sunfish and increase in shad populations (Bettoli et al. 1993). However, largemouth bass diet remained similar before and after hydrilla reduction in Spring Creek, consisting primarily of sunfish in both reservoir arms. Shad densities typically are low in heavily vegetated systems such as Lake Seminole, and sunfish are usually the primary prey item for largemouth bass in these systems (Summers, 1981; Cailteux et al., 1998; Pothoven et al., 1999). Largemouth bass in Spring Creek did appear to consume less invertebrates after SAV reduction, which has been linked to increased growth (Bettoli et al., 1992).

Although only little change was observed in largemouth bass diet composition, the rapid decline in hydrilla in the Spring Creek arm of Lake Seminole resulted in dramatic changes in characteristics of the largemouth bass population. Relative weight of smaller largemouth bass in Spring Creek increased compared to those fish in the Chattahoochee River arm, corresponding to the large reduction of hydrilla. Relative weight of larger fish increased in the post-treatment period in both embayments; however, the increase in Spring Creek was more than twice as great as that observed in the Chattahoochee River arm. Relative weight has often been used as a surrogate of food consumption and growth rates of fish (Parrish et al., 1986; Guy & Willis, 1990, 1995), although the relationship does not always hold true (Liao et al., 1995). However, in this study, relative weight and food consumption both increased following hydrilla reduction, resulting in greater growth.

The predicted increase in total food consumption and the observed trends in fewer empty stomachs and more prey consumed in Spring Creek were likely caused by the decline in SAV. Many authors have found that dense SAV constrains largemouth bass feeding (e.g., Savino & Stein, 1982; Anderson, 1984; Gotceitas & Colgan, 1989) by providing refugia for prey to escape predation (Gotceitas & Colgan, 1987; Rozas & Odum, 1988; Werner & Hall, 1988). This decline in feeding efficiency has resulted in decreased growth and condition of largemouth bass in heavily vegetated systems (Colle & Shireman, 1980; Hayse & Wissing, 1996; Miranda & Pugh, 1997; Cailteux et al., 1998). When SAV is reduced, largemouth bass growth and condition increase, presumably because they have improved access to prey (Bettoli et al., 1992; Wrenn et al., 1996; Pothoven et al., 1999; Unmuth et al., 1999). Declines in SAV can result in a diet shift to prey with greater energy densities, which also leads to higher growth (Bettoli et al., 1992; Miranda & Pugh, 1997; Cailteux et al., 1998; Unmuth et al., 1999).

Similarly, largemouth bass growth and condition in the Spring Creek arm increased. However, these results were achieved without a major diet shift to a more energy-rich prey, but simply through increased consumption of relatively similar diet items. Bioenergetics modeling predicted that food consumption in Spring Creek increased an average of 38% after hydrilla reduction, which resulted in an increase of 14% in growth (in length) across age groups. The decline in SAV likely enhanced largemouth bass predation in two ways. First, overall coverage of SAV in Spring Creek declined from 76% in 2000 to 22% in 2001. Many authors have found that moderate coverages of SAV (20–40%) maximizes largemouth bass production by providing adequate habitat for prey fish recruitment while still allowing for successful predation (Wiley et al., 1984; Moxley & Langford, 1983; Maceina, 1996; Wrenn et al., 1996). Gotceitas and Colgan (1989) found that foraging success of largemouth bass was lower when stem density increased above 350 stems/m^2 and predicted that a stem density of at least 276 stems/m^2 would be required to decrease foraging success. Second, the decline in SAV and subsequent regrowth of native species likely changed the architecture of the SAV community (Valley & Bremigan, 2002), increasing the amount of interstitial spacing and decreasing the amount of complexity, both of which could lead to increased predation efficiency (Dionne & Folt, 1991; Dibble & Harrel, 1997). Thus the initial decrease of hydrilla allowed SAV density to fall below the predation inhibition threshold, while the regrowth of natives allowed these benefits to remain longer than they would have if the regrowth had been another monoculture of hydrilla.

Our results are in agreement with numerous laboratory studies, and demonstrated the effects of SAV on largemouth bass food consumption and growth at a large spatial scale. This study also demonstrated that increased predation efficiency resulting from decreased SAV density and structural complexity was likely a stronger factor influencing growth rates than any potential diet shift that may have occurred. Although the lack of a true control and replication in this study does hinder attribution of causation, our results have been supported by numerous experimental studies performed at smaller scales. Dense SAV communities can mediate largemouth bass growth and condition by restricting access to prey. When that constraint is lifted, largemouth bass populations can respond quickly, resulting in dramatic changes in food consumption and increased growth. Most aquatic communities in densely vegetated systems likely contain ample prey for largemouth bass to grow rapidly, if these predators gain access to the prey. When excessive densities of SAV (particularly exotic species) are reduced, largemouth bass feeding efficiency and subsequent growth will likely increase.

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