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Diet of Invasive Adult White Perch (*Morone americana*) and their Effects on the Zooplankton Community in Missisquoi Bay, Lake Champlain

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ABSTRACT. *White perch* (Morone americana) *became established in Missisquoi Bay, Lake Champlain in the mid 1990s. Since that time, cyanobacteria blooms have become common in summer. Although introduced planktivorous fish often impact plankton communities through a reduction in* Daphnia *density, such effects can be difficult to predict in an opportunistic species such as white perch. In this study, we examined the extent of zooplanktivory exhibited by adult white perch in Missisquoi Bay. Adult white perch were collected from Missisquoi Bay on ten dates in spring and summer of 2005. White perch diet consisted of large numbers of* Daphnia *on dates when* Daphnia *densities exceeded 20 individuals/L and when* Daphnia *comprised more than 50% of the zooplankton assemblage. When* Daphnia *densities were below these threshold values, adult white perch diet consisted predominantly of benthic prey. Our results show that white perch feed on large numbers of* Daphnia *in Missisquoi Bay and select* Daphnia *over other zooplankton taxa when they are abundant. It is likely that adult white perch grazing in Missisquoi Bay has contributed to a reduction in* Daphnia *density which in turn may be contributing to summertime cyanobacteria dominance in this bay.*

INDEX WORDS: *White perch,* Morone americana*, diet composition, trophic cascade,* Daphnia.

INTRODUCTION

The northernmost extension of Lake Champlain, Missisquoi Bay, is shallow ($\leq$ 5 m), eutrophic, and in the past decade, has undergone significant ecological change. One major change is the establishment of an abundant and thriving population of white perch, *Morone americana* (Hawes and Parrish 2003, Bilodeau *et al.* 2004). In August of both 1994 and 1995, Hawes and Parrish (2003) found that white perch had a less than 5% occurrence rate in bottom trawls in Missisquoi Bay. Just 8 years later Bilodeau *et al.* (2004) found that white perch made up more than 50% of gill net catches and 9% of shoreline seine catches in Missisquoi Bay.

Although originally an estuarine species, the opportunistic white perch has increased its range to many freshwater systems throughout the Great Lakes region and eastern United States and Canada (Boileau 1985, Prout *et al.* 1990). Previously absent planktivorous fish species can have great impacts on the plankton communities of temperate freshwater systems (Brooks and Dodson 1965, Hambright 1994). Often, newly established planktivorous fish deplete large cladocerans such as *Daphnia* through direct grazing (Pont *et al.* 1991). This depletion of *Daphnia* has been hypothesized to be one of the steps in the pathway to cyanobacteria dominance in temperate lakes (Elser 1999). Since 2000, Missisquoi Bay has been dominated by cyanobacteria in the summer (Myer and Gruendling 1979, Boyer *et al.* 2004, Watzin *et al.* 2006), a fact that led us to hypothesize that the newly established white perch population had contributed to observed changes in the trophic structure of Missisquoi Bay through direct grazing on *Daphnia*. This hypothesis seemed especially intriguing because phosphorus concentrations have not changed significantly in 15 years (Medalie and Smeltzer 2004, Lake Champlain

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TABLE 1. Mean length (± SE), mean weight (± SE), mean indices of stomach fullness (± SE) among white perch containing food in their stomachs (N) captured in Missisquoi Bay, Lake Champlain, on various dates in 2005. Stomach fullness on dates sharing the same letter was not significantly different (p > 0.05). Fish were collected with a seine in April and May at Sandy Point, in the southeast bay, and from June-July fish were collected with a combination of gillnet and hook and line in Highgate Cliffs, in the northeast bay.

		Total Length (mm)		Weight (g)		Stomach Fullness		
Date	N	Mean	(SE)	Mean	(SE)	Mean	(SE)	Significant Difference
23 April	10	226	(8)	191.54	(26.49)	2.68	(0.31)	ABC
30 April	10	235	(7)	205.30	(21.54)	1.89	(0.28)	BC
8 May	9	226	(9)	189.26	(25.74)	1.51	(0.14)	BCD
17 June	25	224	(5)	174.98	(10.61)	1.39	(0.11)	CD
24 June	25	218	(4)	157.56	(9.13)	1.42	(0.11)	CD
30 June	25	218	(6)	169.78	(14.92)	4.34	(0.39)	A
8 July	25	229	(5)	189.22	(12.13)	0.93	(0.10)	D
14 July	25	224	(4)	174.68	(8.98)	1.03	(0.08)	D
22 July	25	216	(5)	158.01	(9.77)	1.03	(0.10)	D
27 July	25	191	(8)	121.30	(16.30)	1.54	(0.20)	CD

Steering Committee 2005) nor have zebra mussels, *Dreissena polymorpha*, invaded Missisquoi Bay (Vermont Agency of Natural Resources 2005).

Because white perch is an opportunistic species, diet composition is greatly influenced by the habitat in which it is found (Stanley and Danie 1983). Although young-of-year white perch are known to be planktivorous (Parrish and Margraf 1990), adult white perch have a more cosmopolitan diet, frequently switching to piscivory (Moring and Mink 2002), but they have also been observed to select large epibenthic invertebrates in the James River, VA (Rudershausen and Loesch 2000), zooplankton and other fish species in Lake Superior (Sierszen *et al.* 1996), and amphipods in the Hackensack River, NJ (Weis 2005). White perch also often switch preferred prey seasonally between insects and plankton. This opportunistic and variable feeding by adult white perch makes it difficult to predict white perch diet in recently invaded waterbodies. Therefore, the objective of this research was to determine the diet of adult white perch in Missisquoi Bay to make inferences about possible trophic effects of their establishment.

To test our hypotheses that white perch feed on *Daphnia* in Missisquoi Bay, we collected adult white perch from Missisquoi Bay to examine their diet, stomach fullness, and selectivity for zooplankton. In addition, plankton samples were taken at the time of fish collection to document changes to the zooplankton community and to determine zooplankton availability for white perch.

MATERIALS AND METHODS

In Situ Diet and Zooplankton Availability

Fish and plankton samples were collected from Missisquoi Bay, Lake Champlain on ten dates over the spring and summer of 2005. On three dates in April and May, fish were collected by seine in conjunction with a Vermont Department of Fish and Wildlife survey along the southeast shore of the bay. On the subsequent seven sampling dates in June and July (Table 1), white perch were collected by hook and line and gillnet approximately 500 m from the eastern shore of the bay, in a depth of about 4 m. A 30.5-m × 1.5-m gillnet with 3.8-cm bar mesh was set perpendicular to shore approximately 1 hour after sunrise and collected 2 hours later to minimize digestion of stomach contents. During this 2-hour period, fish were also collected using hook and line in a location near the gillnet. White perch collected by all three methods were immediately frozen on dry ice and transferred to the lab for stomach content analysis.

To assess density and composition of the zooplankton community available to white perch on each date, two vertical zooplankton tows were taken from the bottom to the surface with a 0.175-m diameter 64-µm mesh net in the same vicinity and at the same time as fish collection. Filtering efficiency was assumed to be 100%, and the volume was calculated using the distance towed and net diameter. Plankton samples were preserved in 70% ethanol for later identification and enumeration of zooplankton taxonomic groups.

In the lab, white perch were thawed partially, measured for total length (nearest mm), and weighed (nearest 0.01 g). After removing the stomach contents, each empty stomach was blotted dry and weighed with the rest of the fish in order to obtain wet weight of the fish without stomach contents for calculation of the Index of Stomach Fullness (ISF) (Okach and Dadzie 1988) where

$$\mathrm{ISF} = \frac{(\text{weight of fish-}\ \text{weight of fish and empty stomach})}{(\text{weight of fish})} \quad (1)$$

Fish with empty stomachs were excluded from this analysis. Mean ISF was calculated for each sampling date.

To determine the diet of white perch, stomach contents were identified to major taxonomic group. Copepods and cladocerans in the stomach contents were further identified to the taxonomic levels of calanoid copepods, cyclopoid copepods, *Daphnia* spp., *Bosmina* spp., Sididae, and Leptodoridae. After sorting stomach contents by taxonomic group and counting individual prey items, dry weights were determined by drying at 80°C for 24 hours and weighing to the nearest 0.01 g. Percent diet composition by number (%N) and by dry weight (%W) were calculated for each date (Hyslop 1980).

To estimate zooplankton density and community composition, plankton samples were suspended in a known volume of water and subsampled using a 5-mL Henson-Stemple pipette. This volume was selected to yield at least 200 organisms in each of two subsamples. Zooplankton were identified and enumerated using an Olympus CK2 optical microscope at 40X. The resulting duplicate counts were averaged, and *in situ* densities (number of individuals/L) were estimated for total zooplankton (excluding copepod nauplii and rotifers), calanoid copepods, cyclopoid copepods, *Daphnia*, *Bosmina*, Sididae, and Leptodoridae. Mean total zooplankton density and percent composition of the total zooplankton community by each zooplankton group were also calculated for each date.

The Manly-Chesson index of selectivity for zooplankton prey was calculated by comparing the proportion of zooplankton prey groups in each stomach to the proportion available in the environment when *m* prey groups are available (Chesson 1983). Mean α selectivity values were calculated for each prey item and date. Neutral selection was considered m^{-1} where

$$m^{-1} = \frac{1}{(\text{number of prey groups available in the environment})} \quad (2)$$

Selection was interpreted as neutral if the 95% confidence interval for α at a particular date included m^{-1}. Selection was interpreted as either positive or negative if the mean of α was higher or lower than m^{-1} and the 95% CI of the mean did not include the value of m^{-1} (Fulford *et al.* 2006).

The ISF values were log transformed to meet homogeneity of variance and normality assumptions. After first testing for a significant gear effect in ANCOVA and finding none, ISF values were analyzed with a one-way ANOVA in the Statistical Analysis System (SAS) program (SAS Systems 2001). Tukey tests were used to make all pair-wise comparisons between dates. All reported means are back-transformed.

Missisquoi Bay zooplankton density was analyzed for differences across the ten dates using the nonparametric Kruskal-Wallis test in SAS because homogeneity of variance assumptions were not met; however, means rather than medians are still reported in the text due to their relevance to other aspects of the study. One sample T-tests were conducted for each mean Chesson α selectivity value versus the calculated neutral selection value (m^{-1}) for each date (Fulford *et al.* 2006) using SAS.

RESULTS

In Situ Diet and Zooplankton Availability

Reflecting our targeted sampling effort at least in part, white perch was the predominant species captured (approximately 70% of catch 17 June–27 July) in Missisquoi Bay by both hook and line and gillnet. Mean total length (± SE) by date of capture ranged from 191 ± 8 mm on 27 July to 235 ± 7 mm on 30 April and mean total weight ranged from 121 ± 16 g on 27 July to 205 ± 21 g on 30 April (Table 1). The number of fish analyzed for diet was nine or ten in April and May and 25 thereafter (15 fish captured by gillnet and 10 fish captured by hook and line). Kruskal-Wallis tests comparing median number of each prey item in stomach contents showed no significant differences in the four major prey types between the fish caught by gillnet and those caught by hook and line.

TABLE 2. Percent diet composition by number (%N) and by weight (%W) for white perch collected on various dates in 2005 in Missisquoi Bay, Lake Champlain.

	23 April		30 April		8 May		17 June		24 June	
Food Type	%N	%W	%N	%W	%N	%W	%N	%W	%N	%W
Copepoda	0.0	0.0	0.0	0.0	0.0	0.0	10.6	1.6	0.5	0.6
Cladocera	0.0	0.0	0.0	0.0	0.0	0.0	87.6	17.8	85.1	13.2
Fish	0.2	13.1	0.2	6.5	0.0	0.0	0.3	54.0	0.3	46.9
Chironimidae	39.6	4.8	63.6	6.0	61.5	17.1	1.2	12.0	13.5	24.0
Ephemeroptera	21.6	63.0	21.4	75.1	14.1	51.8	0.0	0.0	0.0	0.3
Trichoptera	0.2	0.1	0.2	0.1	2.1	3.7	0.0	0.3	0.1	4.5
Amphipoda	21.2	6.9	2.9	0.9	4.8	1.0	0.1	0.2	0.1	0.7
Isopoda	11.2	4.6	4.1	2.2	9.3	9.1	0.1	0.9	0.0	0.1
Oligachaetae	3.0	5.0	7.0	6.0	7.9	15.1	0.0	0.1	0.0	0.0
Megaloptera	1.5	1.4	0.2	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera	0.0	0.0	0.2	0.0	0.3	0.0	0.0	0.1	0.4	1.4
Odonota	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mussel	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.2	0.0	3.0
Snail	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Eggs	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified		1.0		2.7		2.1		2.9		5.1

	30 June		8 July		14 July		22 July		27 July	
Food Type	%N	%W	%N	%W	%N	%W	%N	%W	%N	%W
Copepoda	0.1	0.1	0.1	0.1	0.2	0.1	0.0	0.1	0.6	0.1
Cladocera	95.5	20.6	3.0	0.5	10.6	0.9	19.5	1.4	4.0	0.2
Fish	0.3	70.1	2.3	40.8	2.9	50.0	0.6	14.5	4.4	66.0
Chironimidae	1.5	2.7	80.5	36.5	64.4	33.7	75.8	72.4	86.0	28.4
Ephemeroptera	0.0	0.2	0.4	2.5	0.3	0.5	0.0	0.0	0.4	1.4
Trichoptera	0.0	0.2	0.7	1.5	1.0	1.7	0.5	1.0	0.2	0.1
Amphipoda	2.5	5.1	10.5	2.4	18.3	4.4	1.5	0.9	0.0	0.0
Isopoda	0.0	0.0	0.1	0.2	0.2	0.4	0.2	0.2	0.2	0.1
Oligachaetae	0.0	0.2	0.0	0.0	0.2	0.8	0.0	0.0	0.0	0.0
Megaloptera	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera	0.0	0.1	0.4	0.6	1.6	1.6	0.3	0.2	0.1	0.0
Odonota	0.0	0.5	0.0	0.0	0.0	0.0	1.3	4.0	0.2	0.9
Mussel	0.0	0.0	1.3	4.7	0.2	0.7	0.2	2.0	2.0	1.5
Snail	0.0	0.0	0.6	0.5	0.0	0.0	0.1	1.3	0.4	0.4
Eggs	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.1
Unidentified		0.1		9.7		5.3		2.0		0.7

The diet composition of white perch changed substantially across sampling dates (Table 2). The major food items in the diet of white perch in this study (by both % abundance and mass) were cladocerans, fish, chironomids, and Ephemeroptera. Chironomids and Ephemeroptera (by % mass) dominated the diets of white perch collected on 23 April, 30 April, and 8 May. Fish (by % mass) and cladocerans (by % abundance) made up the greatest proportion of the diet on 17 June, 24 June, and 30 June. Fish (by % mass) and chironomids (both % mass and % abundance) comprised the greatest proportion of prey items in white perch diet on the four sampling dates in July (Table 2).

Stomach fullness of white perch differed across sampling dates. Mean ISF (± SE) ranged from 0.93 ± 0.10 on 8 July to 4.34 ± 0.39 on 30 June. ISF differed significantly between dates ($F = 21.7$, $p < 0.0001$). The ISF on 30 June was significantly higher than on all other dates ($p < 0.05$) except 23 April (Table 1).

Zooplankton density in Missisquoi Bay was low in April, increased throughout June, and declined again in July (Fig. 1A). Differences in zooplankton

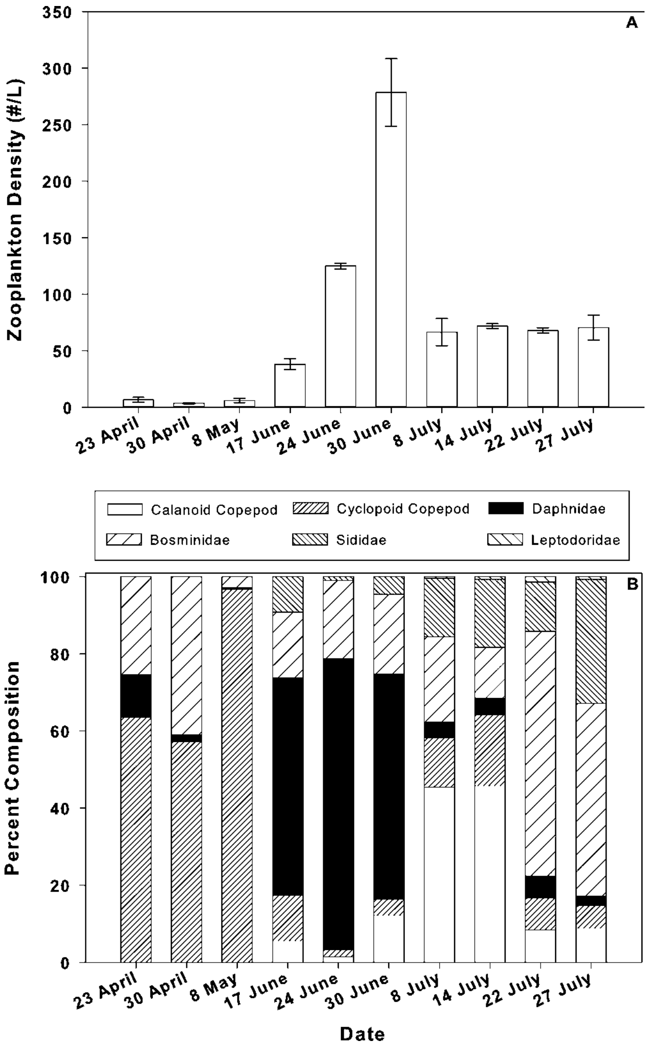

FIG. 1. (A). Mean (±SE) density of zooplankton (without rotifers and copepod nauplii) in Missisquoi Bay, Lake Champlain on various dates in 2005, and (B) Percent composition of zooplankton community by six zooplankton groups in Missisquoi Bay, Lake Champlain on various dates in 2005.

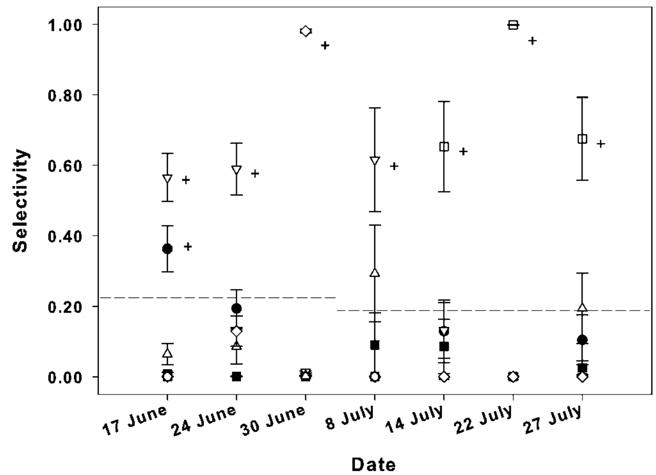

FIG. 2. Mean Selectivity (Manly/Chesson index α ± SE) for all zooplankton groups present on various dates when white perch were foraging in Missisquoi Bay, Lake Champlain in 2005. Broken lines indicate the neutral selection value (m^{-1}; 0.20 in June, 0.17 in July). Zooplankton groups (Calanoida ●; Cyclopoida ■; Daphnididae ▽; Bosminidae △; Sididae ◇; Leptoridae □) that were significantly positively selected are marked with +.

density between dates were significant (H = 17.69, df = 9, p = 0.039). Mean zooplankton density was the highest on 30 June (Fig. 1A). Cyclopoid copepods dominated the zooplankton community on the first three sampling dates (ranging from 57% to 97% of the total zooplankton assemblage; Fig. 1B).

Differences in *Daphnia* density between dates were also significant (H = 18.21, df = 9, p = 0.033), and *Daphnia* density was highest on 30 June. *Daphnia* dominated the zooplankton assemblage on all three dates in June, making up 56%, 76%, and 58% of the total assemblage on 17 June, 24 June, and 30 June, respectively (Fig. 1B). The most abundant zooplankton group on 8 July and 14 July was calanoid copepods (Fig. 1B). Finally, *Bosmina* was the most abundant group for the last two sampling dates of 22 July and 27 July at 63% and 50% (Fig. 1B).

For all dates, α selection values showed some type of cladoceran as the most positively selected zooplankton prey group. Mean α selectivity values were not calculated for the first three sampling dates in April and May because no zooplankton prey were found in the stomach contents of any fish collected on these dates. Chesson α values of each prey category for June were compared to the neutral selectivity value of 0.20 (m^{-1}) because only five zooplankton prey categories were present in June (*Leptodora* was not present), whereas Chesson α values of each prey category for the four dates in July were compared to the neutral selection value 0.17 (m^{-1}) because six zooplankton prey categories were present in July. *Daphnia* and *Leptodora* were both positively selected for on three dates (Fig. 2). White perch positively selected for Sididae (primarily *Diaphanosoma bergei*) on 30 June (Fig. 2).

DISCUSSION

In Situ Diet and Zooplankton Availability

In Missisquoi Bay, large numbers of *Daphnia* and other large cladocerans were consumed by white perch in June when these prey items were abundant in the zooplankton assemblage. Our observations of overall zooplanktivory along with selection of *Daphnia* are consistent with previous findings for adult white perch from Lake Erie (Parrish and Margraf 1990, 1994), which ate some plankton; but our results differ from those in other freshwater systems where adult white perch were much less planktivorous (Hergenrader and Bliss 1971, Stanley and Danie 1983, Danehy *et al.* 1991, Moring and Mink 2002, St-Hilaire *et al.* 2002).

When zooplankton densities were lowest in spring, white perch relied on benthic macroinvertebrates such as chironomids and Ephemeroptera. In early summer, when zooplankton densities were highest, white perch switched to planktonic prey items, such as cladocerans and small fish. In midsummer, when zooplankton densities declined, white perch again relied on chironomids and fish. Other studies have shown similar variability in the adult white perch diet. In three Maine lakes, white perch were piscivorous (Moring and Mink 2002). In Lake Ontario, they relied more on benthic amphipods and fish eggs (Danehy *et al.* 1991), while in Lake Erie their diet contained both chironomids and *Daphnia* (Parrish and Margraf 1990).

White perch have also been shown to switch between benthic and planktonic prey when it is advantageous (Parrish and Margraf 1990, 1994). Fish eggs were found to constitute nearly 100% of white perch diet in May–June in the Sandusky River, OH, except on one date when a different prey item (the shiner *Notropis*) was locally abundant and constituted 97% of the stomach contents by volume (Schaeffer and Margraf 1987). In Lake Ontario, white perch fed on amphipods during spring, switched to alewife (*Alosa pseudoharengus*) eggs as they became available, and returned to relying on amphipods in late summer (Danehy *et al.* 1991). A similar switch was observed in our study when *Daphnia* density rose to a level > 20/L, and when *Daphnia* made up at least 50% of the zooplankton assemblage. On dates when these threshold values were reached, white perch shifted from consuming benthic prey to consuming planktonic prey almost exclusively, and *Daphnia* was a major prey item.

On two dates white perch selected cladocerans other than *Daphnia* spp. in Missisquoi Bay. However, the high α selectivity value for Sididae on 30 June may be an artifact of our zooplankton sampling method, which probably underestimated the density of *Diaphanosoma bergei*. *Diaphanosoma* density estimates have been shown to differ greatly depending on time of sample collection, with much higher densities recorded at dusk and dawn (Nurminen and Horppila 2002). Stomachs from fish collected on 30 June contained thousands of *Diaphanosoma* along with many *Daphnia*. White perch selected *Leptodora* on 14 July, 22 July, and 27 July, although smaller cladocerans such as *Bosmina* were much more abundant on these dates. The larger size of *Leptodora* may have made them more easily detectable and therefore more highly selected by white perch. Our results are similar to those of Gliwicz *et al.* (2006) who observed relatively more *Leptodora* present in roach (*Rutilus rutilus*) stomachs than expected based on the low densities of *Leptodora* observed in zooplankton samples.

Stomach fullness in white perch captured in Missisquoi Bay remained relatively constant except for 30 June when the mean ISF was significantly higher than on any other date. This date corresponds to the time when both mean zooplankton and mean *Daphnia* density were highest (278 individuals/L and 163 individuals/L, respectively), suggesting that white perch rely on *Daphnia* and other large zooplankton as a major source of food when these zooplankton are abundant.

Mean zooplankton densities in Missisquoi Bay during the summer of 2005 were within the range of densities found in other recent studies there. The taxonomic composition of the zooplankton community exhibited a seasonal pattern similar to that found by Hawes *et al.* (1998) in the 1990s, with dominance by cyclopoid copepods and bosminids in April and May, a shift in mid June to an assemblage dominated by *Daphnia* and increasing diversity in July, as *Bosmina*, calanoid copepods, Sididae, and Leptodoridae became relatively more abundant.

The midsummer decline of *Daphnia* observed in Missisquoi Bay in our study is commonly seen in temperate lakes (Demott 1983, Sommer *et al.* 1986, Hulsmann 2003) and may have many causes. Some of the proposed mechanisms behind this decline in *Daphnia* include predation by fish (Mills and Forney 1983), predation by other zooplankton (Hoffman *et al.* 2001), starvation due to a decrease in food availability or food quality (Lampert *et al.* 1986), and interspecific competition between *Daphnia* species. However, when competition and zooplankton life history mechanisms are responsible for the decline in certain *Daphnia* species, there is usually an increase in another *Daphnia* species (Threlkeld 1979, Rettig *et al.* 2006). Such a pattern was not observed in our study. The reduction in *Daphnia* density observed in Missisquoi Bay is of a similar magnitude and pattern to that seen in other temperate lakes with planktivorous fish (Threlkeld 1979, Luecke *et al.* 1990, Hulsmann 2003). Although the decline of *Daphnia* observed in Missisquoi Bay may not be solely the result of grazing by white perch and other planktivorous fish, it is likely that grazing contributed to the sudden and significant depletion of *Daphnia*.

Significance of White Perch Grazing on *Daphnia*

Other introduced fish have had significant impacts on zooplankton in lakes (Hutchinson 1971, Siegfried 1987, Johannsson and O'Gorman 1991, Rudstam *et al.* 1993, Persson *et al.* 2004) and in enclosure experiments (Pont *et al.* 1991, Angeler *et al.* 2002, Stephen *et al.* 2004) imposing top-down control on the food web. It is possible that the selective grazing on *Daphnia* by white perch in June in Missisquoi Bay is reducing the density of *Daphnia* in a similar way. Couture (2006) found that *Daphnia* was the only zooplankton group that was significantly reduced by white perch feeding in a laboratory mesocosm study using Lake Champlain plankton communities, suggesting that white perch can change zooplankton communities by their foraging choices. Our results show white perch diet in Missisquoi Bay consisted of large numbers of *Daphnia*, and *Daphnia* were positively selected for over other zooplankton groups on a number of dates. By extension, we suggest that the presence of large numbers of white perch in Missisquoi Bay could lead to a shift in the zooplankton assemblage with many fewer daphnids in the summer zooplankton community.

Paralleling our research results, zooplankton monitoring data from Missisquoi Bay also suggest that the invasion of white perch may be one factor contributing to declines in *Daphnia* in the summer. In 1977, prior to the establishment of white perch, the Missisquoi Bay zooplankton community was comprised of 70–80% large cladoceran species such as *Daphnia retrocurva* in summer (Myer and Gruendling 1979). Zooplankton monitoring data from Missisquoi Bay in 2003, after the white perch population was established, still showed the presence of large-bodied cladocerans, but copepods and smaller cladocerans comprised a greater proportion of the zooplankton community than in 1977 (Mihuc 2007).

The extent to which adult white perch in Missisquoi Bay were planktivorous when it was advantageous is an important finding of this study. Although white perch young-of-year are known to feed primarily on zooplankton and *Daphnia* (Prout *et al.* 1990, Parrish and Margraf 1991), zooplankton are typically a much smaller part of the adult white perch diet (Parrish and Margraf 1990, 1994; Sierszen *et al.* 1996). Young-of-year fish feeding alone can be an important regulator of freshwater zooplankton (Devries and Stein 1992). In a meta-analysis of 18 studies examining the effect of feeding of young-of-year versus older juvenile fish of various species, zooplankton communities were often structured differently depending on the dominant age class of fish present (Mehner and Thiel 1999). Ontogenetic diet shifts are common in ruffe (*Gymnocephalus cernuus*), yellow perch (*Perca flavescens*), and white perch, with older fish switching from diets almost entirely of zooplankton to diets consisting of benthos and other fish (Parrish and Margraf 1990, Rezsu and Specziar 2006). Our results suggest that although adult white perch in Missisquoi Bay feed on larger benthic prey and fish, they remain heavily reliant on zooplankton when the density of large zooplankters is high. Therefore, the increased grazing pressure on the summer zooplankton community of Missisquoi Bay resulting from the establishment of a white perch population likely includes the combined effects of significant predation by the young-of-year as well as the opportunistic adult white perch.

In other lakes, zooplanktivorous fish density has been associated with changes in both zooplankton and phytoplankton community composition (Kurmayer and Wanzenbock 1996, Hunt *et al.* 2003, Van De Bund *et al.* 2004). The opportunistic switch we observed to zooplankton in mid-summer, as well as the strong positive selection for *Daphnia* and other cladocerans throughout the month of June, may have significant implications for the entire plankton community of Missisquoi Bay. In June, water temperature and phytoplankton biomass (including cyanobacteria) are increasing in Missisquoi Bay. If, at this crucial time, white perch feeding can deplete *Daphnia*, the cascading changes in the food web could facilitate cyanobacteria dominance through release from grazing (Elser 1999, Nandini 2000, Kurmayer 2001, Gustafsson *et al.* 2005) and changes in the nitrogen:phosphorus ratios (Elser 1999, Elser *et al.* 2000). Cyanobacteria have been observed to dominate the summer phytoplankton community of Missisquoi Bay from 2000 through 2006 (Watzin *et al*. 2006, 2007). Diet plasticity and opportunistic feeding, the very traits that often allow introduced fish species such as white perchto become established, also make predictions about the diet of these species in a new system challenging. Consequently, it is also difficult to predict possible trophic shifts. Our results demonstrate the importance of separately analyzing the diet of introduced species in new systems to more accurately assess possible trophic shifts and ecological change.

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