

Eurasian Watermilfoil Biomass Associated with Insect Herbivores in New York

ROBERT L. JOHNSON¹, PETER J. VAN DUSEN², JASON A. TONER³, AND NELSON G. HAIRSTON, JR.¹

ABSTRACT

A study of aquatic plant biomass within Cayuga Lake, New York spans twelve years from 1987-1998. The exotic Eurasian watermilfoil (*Myriophyllum spicatum* L.) decreased in the northwest end of the lake from 55% of the total biomass in 1987 to 0.4% in 1998 and within the southwest end from 50% in 1987 to 11% in 1998. Concurrent with the watermilfoil decline was the resurgence of native species of submersed macrophytes. During this time we recorded for the first time in Cayuga Lake two herbivorous insect species: the aquatic moth *Acentria ephemerella*, first observed in 1991, and the aquatic weevil *Euhrychiopsis lecontei*, first found in 1996. Densities of *Acentria* in southwest Cayuga Lake averaged 1.04 individuals per apical meristem of Eurasian watermilfoil for the three-year period 1996-1998. These same meristems had *Euhrychiopsis* densities on average of only 0.02 individuals per apical meristem over the same three-year period. A comparison of herbivore densities and lake sizes from five lakes in 1997 shows that *Acentria* densities correlate positively with lake surface area and mean depth, while *Euhrychiopsis* densities correlate negatively with lake surface area and mean depth. In these five lakes, *Acentria* densities correlate negatively with percent composition and dry mass of watermilfoil. However, *Euhrychiopsis* densities correlate positively with percent composition and dry mass of watermilfoil. Finally, *Acentria* densities correlate negatively with *Euhrychiopsis* densities suggesting interspecific competition.

Key words: *Myriophyllum spicatum*, *Acentria ephemerella*, *Euhrychiopsis lecontei*, biological control, herbivory, Cayuga Lake.

INTRODUCTION

The invasive submersed macrophyte Eurasian watermilfoil (*Myriophyllum spicatum* L.) was first recorded in Cayuga Lake and other Finger Lakes in central New York State during the mid-1960s (R. L. Johnson, pers. observ.). On June 21, 1972, Tropical Storm Agnes caused the surface of Cayuga Lake to rise above flood level where it remained for several weeks. Muddy waters and flood conditions cut off light to, and buried many aquatic plant species at a critical time in their growth cycle (Oglesby et al. 1976). The watermilfoil biomass

reported in 1970, before the storm, was 74 g dry mass m⁻² in southern Cayuga Lake (Vogel 1973, Oglesby et al. 1976). An increase in Eurasian watermilfoil growth followed this major disturbance within the southern end from 17 g dm m⁻² in August of 1972 to 166 g dm m⁻² in 1973 (Oglesby et al. 1976). Peverly et al. (1974) and Oglesby et al. (1976) report even greater biomass of watermilfoil after the storm for the northwest corner of Cayuga Lake in 1973 (349 g dm m⁻²) and 1974 (763 g dm m⁻²). Eurasian watermilfoil continued to dominate the plant community at the shallow northern and southern ends of the lake until the early 1990s. Annual monitoring of aquatic plant biomass in Cayuga Lake from 1987 through 1996 displayed a marked decline in Eurasian watermilfoil (Johnson et al. 1998). The first report of the aquatic Pyralid moth *Acentria ephemerella* Denis and Schiffermuller (= *Acentria nivea* Olivier, Passoa, 1988) in Cayuga Lake was in 1991 (Johnson et al. 1998) within a large Eurasian watermilfoil bed in the northwestern corner. We did not look for watermilfoil herbivores before 1991 and only happened upon *Acentria* after observing a chlorotic appearance of a watermilfoil bed. This area, mechanically harvested twice annually for the previous five years, went undisturbed in 1991 allowing the watermilfoil to grow toward the surface. The entire watermilfoil bed showed chlorosis of the apical meristems just under the surface. Upon closer inspection, we found late instar *Acentria* caterpillars inhabiting most apical meristems. These moth larvae first found in Cayuga Lake in 1991 were likely in the watershed since 1946. At that time, Munroe (1947) records a single *Acentria* moth in Varna, NY along a tributary approximately 5.5 km from the lake.

Results from our previous herbivore surveys show that *Acentria* and *Euhrychiopsis lecontei* Dietz (= *Euhrychiopsis lecontei*), an aquatic weevil, are widespread throughout New York State (Johnson et al. 1998). We observe these two herbivores in many New York lakes, along with the midge *Cricotopus myriophylli* Oliver, abundantly on Eurasian watermilfoil where they often cause extensive damage. Although we document long-term suppression of watermilfoil only in association with *Acentria* in Cayuga Lake (Johnson et al. 1998), we routinely observe in many other lakes the mining and breakage of watermilfoil caused by *Euhrychiopsis*. A summer decrease or "crash" in watermilfoil is most evident during July and August in New York. Nevertheless, unlike the declines in Cenatico Lake, Minnesota reported by Newman and Biesboer (2000, this issue) and Brownington Pond, Vermont (Creed and Sheldon, 1994), we do not find *Euhrychiopsis*-induced declines that persist in New York lakes. In our survey of lakes for watermilfoil herbivores (Johnson et al. 1998), we observed that either *Acentria* or *Euhrychiopsis* usually dominated with co-dominance being rare.

¹Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853, rlj5@cornell.edu. Received for publication April 14, 1999 and in revised form December 13, 1999.

²Department of Biological Sciences, 740 Dow, Michigan Technological University, Houghton, MI 49931.

³Department of Environmental and Forest Biology, 1 Forestry Drive, College of Environmental Science and Forestry, Syracuse, NY 13210.

Here, we present twelve consecutive years of macrophyte biomass data (1987-1998) from the northwest and southwest ends of Cayuga Lake, with three years of concurrent *Acentria* densities (1996-1998) from the southwest end of this lake. We consider the relationship between herbivore populations and associated Eurasian watermilfoil production. A comparison is made of aquatic plant biomass and associated herbivore abundance among Cayuga, Dryden, Keuka, Lamoka, and Waneta Lakes from two sites within each lake.

MATERIALS AND METHODS

Cayuga Lake Plant Biomass

Cayuga Lake is a glacially-scoured mesotrophic lake 61 km long, 2.8 km wide, and 54.4 m mean depth (Birge and Juday 1914, Oglesby 1978). It is the second largest of the Finger Lakes in central New York and supports important macrophyte communities within the littoral zones of the northern and southern basins. Our study areas include sites sampled in previous investigations (Johnson et al. 1998). Miller (1988, 1989, 1990) reported wet plant biomass from the northwestern part of the lake for 1987-1989, which we transformed by multiplying his reported wet weights by 0.1 to obtain dry weight estimates. This conversion falls within the range given by Wetzel (1983), who cites a value of 88% mean water content and a range of 85% to 92% for submersed macrophytes.

The collection time for submersed aquatic plant biomass ranged between August 1 and September 15 of each year for the southwest end in 1987-1998 and the northwest end in 1990-1998. All previous researchers reporting data on Cayuga Lake macrophytes collected at a comparable time of the year, between the last week of July and the end of August (Vogel 1973, Peverly et al. 1974, Oglesby et al. 1976, Miller 1988, 1989, 1990). Our long-term program of macrophyte sampling for plant biomass and species diversity determination includes eleven sites in the southwestern corner and two sites in the northwestern corner of the lake. All sites were 100 by 100 m plots with mean water depths of 2-3 meters. We sampled submersed macrophytes from the southwestern corner by hand-harvesting five randomly selected 1 m² quadrats from each site during 1987-1992, and 20 randomly selected 0.25 m² quadrats from each site during 1993-1998. Divers hand-harvested two northwestern corner sites using 20 randomly selected 0.25 m² quadrats at each site, for each year.

At each selected quadrat, a diver hand-harvested plant biomass above the sediment. This diver placed each sample in a separate plastic bag for transport to the laboratory for immediate analysis or frozen for later separation and dry mass determination. This analysis requires the plant material to have the sediment and epibiota removed from the plant surface by washing and then separate the plants by species for each plot. We then oven-dried the separated plant species at 105C for 48 h and recorded the dry mass.

Cayuga Lake Herbivore Surveys

In the southwest end of Cayuga Lake, we sampled four separate sites for insect herbivores during the summers of 1996, 1997, and 1998. We haphazardly collected plants with a garden rake or grapple hook from a boat where we randomly

selected twenty-five watermilfoil stems from each of the four sites. We then removed the top 25 cm of each selected stem and immediately placed this 25 cm section in a separate plastic bag. Next, we placed the 100 separately bagged apical meristems in a cooler and on return to our laboratory refrigerated the samples until analysis that occurred within two weeks. We refer to this 25 cm section of the stem as the apical meristem, which could include side shoots and multiple growing tips.

We inspected each apical meristem for signs of herbivory and herbivores, along with the type and extent of watermilfoil damage using a stereoscopic dissecting microscope. We recorded all life stages of *Euhrychiopsis* and *Acentria*, including eggs, found on each individual apical meristem. These counts result in the number of herbivores per apical meristem, which determined our mean herbivore densities. Our reported herbivore densities are minimum densities per watermilfoil stem since we collected and analyzed only the top 25 cm.

Five-lake Surveys

The intent of these surveys was to explore the relationship between lake size, abundance of watermilfoil and watermilfoil herbivore numbers in the summer of 1997. In each of five lakes: Cayuga, Dryden, Keuka, Lamoka, and Waneta we compare data collected from two sites. Methods to determine plant biomass and herbivore density followed the same protocol as the Cayuga Lake sampling previously described. We collected biomass and herbivore densities in each lake within three weeks of the other measurement. The two sites chosen in Cayuga and Dryden Lakes for this analysis represented the average watermilfoil composition for their respective lakes. In Waneta and Lamoka Lakes, the two sites selected were the only sites where we collected both biomass and herbivore numbers in 1997. At Keuka Lake, the two sites selected are within our previously described depth range of 2-3 meters. The Spearman's rank order correlation coefficient (r_s) for data not normally distributed tests the associations from 10 sites in five lakes. We calculated the Spearman's correlation to determine whether significant relationships existed among lake size, watermilfoil abundance, and herbivore numbers of these five lakes in 1997.

RESULTS

Eurasian watermilfoil biomass declined markedly in Cayuga Lake since the middle 1970s. The relative biomass of watermilfoil in Cayuga Lake ranged between 58% and 95% in the 1970s and 1980s (Johnson et al. 1998), and declined to 11.3% in the southwest end and 0.4% in the northwest end in 1998. Eurasian watermilfoil almost disappeared completely from the study locations at the northwest end by 1996. Biomass peaks of 763 g dm⁻² in 1974 (Peverly et al. 1974) and 325 g dm⁻² in 1988 fall to 0.34 g dm⁻² in 1998 (Figure 1A). Watermilfoil biomass declined at the southwest end from 166 g dm⁻² in the 1970s (Oglesby et al. 1976, Johnson et al. 1998) to 17.7 g dm⁻² in 1998 (Figure 1B). Native plant species were low in abundance throughout the Eurasian watermilfoil invasion of the 1970s and 1980s. An increase in native macrophyte abundance in the 1990s (Johnson et al. 1998, Figure

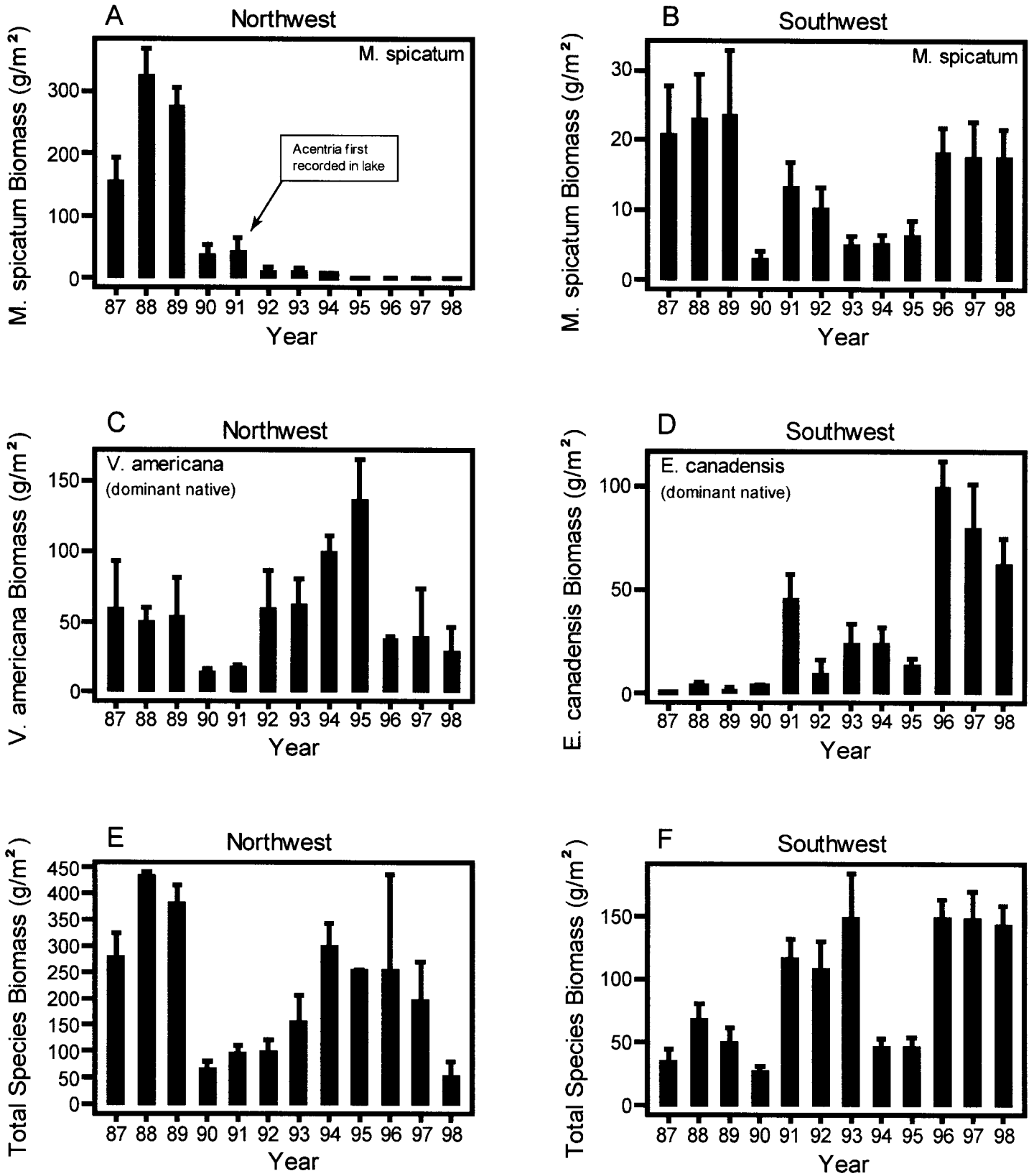


Figure 1. The dry biomass (g dm⁻²) of *Myriophyllum spicatum* (A and B) and two currently dominant native plant species *Vallisneria americana* and *Elodea canadensis* (C and D) shown with dry biomass (g dm⁻²) of all submersed macrophytes (E and F) for both the northwest and southwest ends of Cayuga Lake 1987-1998. Error bars indicate +1SE, based on the mean of two study locations sampled at the northwest end and the mean of eleven study locations sampled at the southwest end. See Materials and Methods section for number and size of samples collected at each site. Note the important difference in scaling of y-axis for all graphs.

1C, 1D), follows the Eurasian watermilfoil decline in Cayuga Lake (Figure 1A, 1B). At the northwest end of the lake, *Vallisneria americana* is a dominant plant that increased as a percentage of total biomass from 24% or 60.0 g dm⁻² in 1987 to 54% or 29.5 g dm⁻² in 1998 (Figure 1C). *Elodea canadensis*, the dominant macrophyte in the southwest end of the lake, increased from 0.7 g dm⁻² in 1987 to 62.5 g dm⁻² in 1998 or from 3% to 50% of the total biomass respectively (Figure 1D). The total biomass including all macrophytes varies annually in Cayuga Lake without a trend (Figure 1E, 1F), in spite of the substantial and long-lasting decline in watermilfoil's relative abundance from 1989 to 1998.

The abundance of *Acentria* ranged from 0.7 to 1.4 individuals per apical meristem from 1996 to 1998 in Cayuga Lake's southwest end (Table 1). Over the same time, *Euhrychiopsis* was present at extremely low densities, ranging from 0.0 to 0.03 individuals per apical meristem in the southwest end (Table 1). This enormous difference in the densities of these two herbivores on Cayuga Lake watermilfoil where we associate *Acentria* with a long-term decline of watermilfoil (Johnson et al. 1998) leads us to investigate other lakes.

Our examination of five lakes in New York State shows considerable variation among water bodies, watermilfoil, and herbivore densities. We identify relationships between lake surface area (Swart and Bloomfield 1987), average lake depth (Sander 1988), relative densities of each herbivore species, percent watermilfoil, and dry mass watermilfoil (Table 2). Lakes chosen by us cover a wide range of morphological characteristics, with surface area varying from 41.4 ha (Dryden Lake) to 17,326 ha (Cayuga Lake) and mean lake depth from 1.5 m (Dryden Lake) to 54.4 m (Cayuga Lake). The percentage of Eurasian watermilfoil in the sampled plant biomass ranged from 6.6% to 99.9% (Table 2). Dry mass of Eurasian watermilfoil increased from 4.3 g dm⁻² to 190 g dm⁻² (Table 2). Densities of *Euhrychiopsis* varied from 0.0 to 3.8 individuals per tip, while densities of *Acentria* ranged from 0.0 to 2.4 individuals per apical meristem (Table 2). Within this group of lakes, *Acentria* densities correlate negatively with *Euhrychiopsis* densities and positively with lake surface area and mean depth. In contrast, *Euhrychiopsis* densities correlate negatively with lake surface area and mean depth. The abundance of Eurasian watermilfoil correlates positively with *Euhrychiopsis* density but negatively with *Acentria* density (Table 3).

DISCUSSION

The substantial and sustained decline of Eurasian watermilfoil's relative abundance in relation to the increase in the relative abundance of native macrophyte species in both the northern and southern basins of Cayuga Lake since 1989

TABLE 1. THE MEAN NUMBERS OF *ACENTRIA* AND *EUHRYCHIOPSIS* (\pm 1SD) FOUND ON INDIVIDUAL 25 CM APICAL MERISTEMS OF EURASIAN WATERMILFOIL FROM THE SOUTHWEST END OF CAYUGA LAKE (1996-1998).

Date	Total number of apical meristems	<i>Acentria</i> per apical meristem	<i>Euhrychiopsis</i> per apical meristem
8/01/96	101	0.74 \pm 0.59	0.00 \pm 0.00
8/27/97	100	1.40 \pm 0.67	0.03 \pm 0.04
7/22/98	100	1.02 \pm 0.40	0.02 \pm 0.04

needs to be looked at closely. In the 1970s watermilfoil reached high biomass, well within the range of dense watermilfoil beds observed elsewhere (280-1150 g dm⁻², Grace and Wetzel 1978). We did not collect data between 1974 and 1987, and it is more than likely that during the latter part of this period watermilfoil already started its decline. It was, however, still the dominant macrophyte at both ends of the lake between 1987 and 1989 (Figure 1A, 1B). Corresponding with this watermilfoil decline is the resurgence of native macrophyte species (Johnson et al. 1998, Figure 1C, 1D). The dominant species present in 1998 were *V. americana* and *E. canadensis* for the northwest and southwest ends of the lake, respectively. Watermilfoil persists at low levels without increasing above 14% of the total biomass since 1990 in our southwestern and 1992 in our northwestern sampling sites in Cayuga Lake. The persistence of watermilfoil at a low density in the southern end of the lake may be due to stochastic events in the Cayuga Lake southern basin where several major tributaries enter the lake. These events create disturbances that contribute to high rates of sediment deposition and periods of extended turbidity following storm events. These in turn may encourage watermilfoil growth (Oglesby et al. 1976, Smith and Barko 1990, Mataraza et al. 1999).

Although nutrient limitation could cause a reduction in watermilfoil density, it cannot explain the events in Cayuga Lake since total macrophyte biomass was not affected (Figure 1E, 1F). Similarly, Painter and McCabe (1988) excluded nutrient impacts as a reason for the watermilfoil decline in the Kawartha Lakes, Canada. Newman and Biesboer (2000 this issue), report a decline in Cenaiko Lake in Minnesota accompanied by an increase in native plant abundance similar to what we see in Cayuga Lake. These authors also discount nutrient limitation as the causal agent of their watermilfoil decline. A likely explanation for these watermilfoil declines is the feeding on this plant by the herbivorous insects *Acentria* and *Euhrychiopsis*.

Our data show that *Acentria* is the dominant watermilfoil herbivore in Cayuga Lake (Table 1). In Cayuga and Seneca Lakes, the two largest of the Finger Lakes in New York State, we report high densities of *Acentria* since 1994 (Johnson et al. 1998, Table 1). *Euhrychiopsis*, first identified during 1996 in Cayuga Lake, remains at extremely low densities (Table 1). Unlike *Acentria*, which overwinters within the lake, *Euhrychiopsis* overwinters on shore. The low abundance of *Euhrychiopsis* in Cayuga Lake may then be due to stressful overwintering conditions along the shore of this large lake both from wave action during winter storms and from shoreline development (Johnson et al. 1998). The sustained, long-term decline in watermilfoil, and the continuing high densities of *Acentria* in Cayuga Lake, suggests that *Acentria* contributed to the watermilfoil decline and may be preventing its rebound. *Acentria*'s preferred feeding at the apical meristem appears to limit elongation of watermilfoil toward the lake surface (Johnson et al. 1998).

Acentria is associated with watermilfoil declines in other lakes as well. In the Kawartha Lakes Painter and McCabe (1988), report that watermilfoil declined by 95%. They found *Acentria* larvae present in approximately the same abundance (6 larvae per 10 watermilfoil apical meristems 25 cm long) as we observed in Cayuga Lake in 1996. The decline of water-

TABLE 2. THE COMPARISON OF LAKE SIZE, *ACENTRIA*, AND *EUHRYCHIOPSIS* NUMBERS PER APICAL MERISTEM AND ABUNDANCE OF EURASIAN WATERMILFOIL FOR FIVE NEW YORK LAKES IN 1997.

Lake-site	Lake surface area (ha)	Lake mean depth (m)	<i>Acentria</i> per apical meristem	<i>Euhrychiopsis</i> per apical meristem	Percent watermilfoil in plant community	Dry mass of watermilfoil (g dm m ⁻²)
Dryden Lake-C	41.4	1.52	0.21	1.20	99.3	87.5
Dryden Lake-D			0.12	2.40	78.8	82.2
Waneta Lake-A	316	4.57	0.00	1.08	97.7	92.1
Waneta Lake-B			0.00	3.80	99.9	190
Lamoka Lake-B	334	6.10	0.00	2.36	100	114
Lamoka Lake-D			0.04	1.96	70.3	66.7
Keuka Lake-A	4740	30.8	0.72	0.00	57.9	80.8
Keuka Lake-B			0.88	0.21	27.8	60.1
Cayuga-132	17300	54.4	2.40	0.00	6.57	4.30
Cayuga-149			1.08	0.04	17.1	37.5

milfoil in Brownington Pond, Vermont reported by Creed and Sheldon (1994) may also be attributable, at least in part, to *Acentria* larvae. In Brownington Pond, they report finding from 1 to 2 *Euhrychiopsis* per stem. However, they also report *Acentria* in densities of generally less than 1 larva per meristem, but occasionally more than 2 *Acentria* per stem. It seems likely that the density of *Acentria* larvae reported in Brownington Pond lies within the range associated with the watermilfoil declines reported for Cayuga and the Kawartha Lakes (Johnson et al. 1998, Painter and McCabe 1988). Creed (1998) reports another watermilfoil decline in Lake Memphremagog, Vermont where Creed and Sheldon (1993) reported *Acentria* abundant. Creed and Sheldon (1994) further report that *Acentria* caused more damage to Eurasian watermilfoil plants than *Euhrychiopsis* in concomitant laboratory experiments. These observations, along with our data, suggest that *Acentria* may have played a larger role in these watermilfoil declines than previously considered.

The observation from our survey of five lakes that *Acentria* densities have a highly significantly negative correlation with percent composition and total dry mass of watermilfoil (Table 3), and the *Acentria* associated decline in Cayuga Lake (Johnson et al. 1998) suggests that *Acentria* may be an effective long-term biological control agent. In these same lakes, *Euhrychiopsis* correlates positively with both watermilfoil variables (Table 3), reveals an association of high watermilfoil abundance with a high *Euhrychiopsis* abundance prompting questions about this positive relationship between *Euhrychiopsis* and watermilfoil. However, Jester (1998) found a non-significant correlation between *Euhrychiopsis* densities and watermilfoil biomass in Wisconsin lakes. These associations

of high *Acentria* densities to low watermilfoil abundance, a negative relationship, and high *Euhrychiopsis* densities to high watermilfoil abundance, a positive relationship, deserve further investigation. Aquatic plant communities with higher naturally occurring *Acentria* densities (Cayuga and Keuka Lakes) also have greater species diversity and native macrophyte abundance than lakes with low *Acentria* densities (Dryden, Waneta, and Lamoka Lakes, Table 2). This suggests that *Acentria* may indirectly have a beneficial effect on native macrophyte communities. We found significant positive correlations between *Acentria* densities and lake surface area and mean depth (Table 3). *Euhrychiopsis* densities correlate significantly, but negatively, with lake surface area and mean depth in our study. Jester (1998) reported a non-significant correlation of *Euhrychiopsis* densities with lake size and mean depth for selected Wisconsin lakes. We sampled lakes with a wider range of mean lake depths (1.5 to 54 m) than Jester (1998) did (0.6 to 7.6 m), possibly explaining why the correlation between *Euhrychiopsis* densities and lake size were significant in our study, but not in the shallower Wisconsin lakes.

The significant negative correlation between the densities of *Euhrychiopsis* and *Acentria* for the five lakes we sampled implies that competition between these two herbivores may be important. Newman et al. (1998) reported that competition between two insect herbivores might be an equal or greater source of herbivore mortality than natural enemies or host plant resistance. In our survey of lakes for watermilfoil herbivores (Johnson et al. 1998), we observed that one or the other of these herbivores typically dominated with co-dominance being rare. This may indicate competitive exclusion (Hardin 1960), since both herbivores are competing for the

TABLE 3. THE SPEARMAN'S RANK CORRELATION COEFFICIENTS (R_s) FOR THE ASSOCIATION OF LAKE SIZE, HERBIVORE NUMBERS PER APICAL MERISTEM AND ABUNDANCE OF EURASIAN WATERMILFOIL FOR FIVE NEW YORK LAKES IN 1997.

Variable	Lake surface area (ha)	Lake mean depth (m)	<i>Acentria</i> per apical meristem	<i>Euhrychiopsis</i> per apical meristem
<i>Acentria</i> per apical meristem	0.673*	0.673*		
<i>Euhrychiopsis</i> per apical meristem	-0.753*	-0.753*	-0.775**	
% watermilfoil in plant community	-0.763***	-0.763**	-0.890***	0.790**
Dry mass watermilfoil (g dm m ⁻²)	-0.739*	-0.739*	-0.902***	0.736*

*p < 0.05, **p < 0.01, ***p < 0.001.

same resource (the apical meristem). This may also help explain why *Acentria* densities tend to be greater in larger lakes that have low *Euhrychiopsis* populations. We observed in Dryden Lake that the timing of *Acentria* pupation, egg-laying, and consequent hatching of larvae in 1997 and 1998 coincided with the annual watermilfoil "crash," resulting from *Euhrychiopsis* damage⁴. Availability of green, metabolically active watermilfoil may be critical for the survival of both *Acentria* pupae (Buckingham and Ross 1981) and newly hatched larvae. Besides damage to the plant by *Euhrychiopsis*, Dryden Lake's watermilfoil often develops a thick epiphyte growth as *Euhrychiopsis* damage increases. This further decreases the palatability of the plant (Batra 1977, Buckingham and Ross 1981), likely increasing the mortality of young *Acentria* larvae at a critical point in their life history. In addition, another possible important New York watermilfoil herbivore, the midge *Cricotopus myriophylli* might compete with *Euhrychiopsis* for plant resources (Creed 1998).

The encouraging macrophyte growth trends in Cayuga Lake and elsewhere, indicate a strong inference for biological control of Eurasian watermilfoil. However, the interspecific interactions between Eurasian watermilfoil herbivores raise important questions that bear on the task of developing successful biological control strategies for this plant. The inhospitable shorelines of many large lakes or large bays within lakes may limit the overwintering habitat required for *Euhrychiopsis* while smaller lakes with vegetation or manmade structures at the shoreline would aid winter survival of this herbivore. *Acentria* overwintering on submersed aquatic plant material may have the competitive advantage in many large lakes. These relationships between lake size, herbivore densities, and Eurasian watermilfoil together with interspecific competition warrant further investigation.

ACKNOWLEDGEMENTS

We thank E. Mulligan, R. Schindelbeck, K. Switzer, D. Corson, T. Groman, J. Shaffer, K. Thomas, E. Thomas, N. Thomas, J. Howell, J. Riggs, R. Riggs, and K. Hester for help with the field collections and attention to detail during hundreds of hours at the microscope and separating plant species. R. E. Hoebeke, Cornell Insect Collection, Ithaca, NY confirmed the identification of *Acentria ephemera* and *Euhrychiopsis lecontei*. R. W. Bode, NY State Museum, Albany, NY, verified the identification of adults and larvae of *Cricotopus myriophylli*. A special thanks to Dr. E. M. Gross, Limnological Institute, University of Konstanz, Konstanz, Germany; Dr. D. R. Bouldin Department of Soil, Crop, and Atmospheric Science Cornell University; Dr. J. E. Skaley of the Tompkins County Planning Department and J. Malý with the Seneca County Soil and Water Conservation District for their support and encouragement throughout this study. We also thank the editor of this journal John D. Madsen and anonymous reviewers for helpful comments and suggestions. Funds from Hatch Project (NYC-1837402) USDA, the Aquatic Vegetation Control Program of the Tompkins County Planning Department, the Aquatic Veg-

etation Control Program of the Seneca County Soil and Water Conservation District the Finger Lakes-Lake Ontario Watershed Protection Alliance formerly the Aquatic Vegetation Control Program of the Water Resources Board and the New York State Legislature supported this research work.

LITERATURE CITED

- Batra, S. W. T. 1977. Bionomics of the aquatic moth *Acentropus niveus* (Oliver), a potential biological control agent for Eurasian watermilfoil and *Hydrilla*. N. Y. Entomol. Soc. 85: 143-152.
- Birge, E. A. and C. Juday. 1914. A limnological study of the Finger Lakes of New York. US Bureau Fish Bulletin 32: 523-609.
- Buckingham G. R. and B. M. Ross. 1981. Notes on the biology and host specificity of *Acentria nivea* (= *Acentropus niveus*). J. Aquat. Plant Manage. 19: 32-36.
- Creed, R. P., Jr. 1998. A biogeographic perspective on Eurasian watermilfoil declines: additional evidence for the role of herbivorous weevils in promoting declines? J. Aquat. Plant Manage. 36: 16-22.
- Creed, R. P., Jr. and S. P. Sheldon. 1993. The effect of feeding by a North American weevil, *Euhrychiopsis lecontei*, on Eurasian watermilfoil (*Myriophyllum spicatum*). Aquat. Bot. 45: 245-256.
- Creed, R. P., Jr. and S. P. Sheldon. 1994. The effect of two herbivorous insect larvae on Eurasian watermilfoil. J. Aquat. Plant Manage. 32: 21-26.
- Grace, J. B. and R. G. Wetzel. 1978. The production biology of Eurasian watermilfoil (*Myriophyllum spicatum* L.): a review. J. Aquat. Plant Manage. 16: 1-11.
- Hardin, G. 1960. The competitive exclusion principle. Science 131: 1292-1298.
- Jester, L. L. 1998. The geographic distribution of the aquatic milfoil weevil (*Euhrychiopsis lecontei*) and factors influencing its density in Wisconsin lakes. College of Natural Resources, University of Wisconsin. Stevens Point, WI. 78 pp.
- Johnson, R. L., E. M. Gross and N. G. Hairston, Jr. 1998. Decline of the invasive submersed macrophyte *Myriophyllum spicatum* (Haloragaceae) associated with herbivory by larvae of *Acentria ephemera* (Lepidoptera). Aquat. Ecol. 31: 273-282.
- Mataraza, L. K., J. B. Terrell, A. B. Munson and D. E. Canfield, Jr. 1999. Changes in submersed macrophytes in relation to tidal storm surges. J. Aquat. Plant Manage. 37: 3-12.
- Miller, G. L. 1988. Effects of mechanical control of aquatic vegetation on community structure in Cayuga Lake. Department of Environmental Studies. University of North Carolina, Asheville, NC. 57 pp.
- Miller, G. L. 1989. Second annual review of the effects of mechanical control of aquatic vegetation on community structure in Cayuga Lake. Department of Environmental Studies University of North Carolina, Asheville, NC. 71 pp.
- Miller, G. L. 1990. Third annual review of the effects of mechanical control of aquatic vegetation on community structure in Cayuga Lake. Department of Environmental Studies University of North Carolina, Asheville, NC. 65 pp.
- Munroe, E. G. 1947. Further North American records of *Acentropus niveus* (Lepidoptera, Pyralidae). Can. Ent. 79: 120.
- Newman, R. M. and D. D. Biesboer. 2000. A decline of Eurasian watermilfoil in Minnesota associated with the milfoil weevil, *Euhrychiopsis lecontei*. J. Aquat. Plant Manage. this issue.
- Newman, R. M., D. C. Thompson and D. B. Richman. 1998. Conservation strategies for the biological control of weeds. In: P. Barbosa, ed. Conservation biological control. Academic Press, New York, NY. pp. 371-396.
- Oglesby, R. T., A. Vogel, J. H. Peverly and R. L. Johnson. 1976. Changes in submerged plants at the south end of Cayuga Lake following tropical storm Agnes. Hydrobiologia. 48: 251-255.
- Oglesby, R. T. 1978. The limnology of Cayuga Lake. In: J. A. Bloomfield, ed. Vol. I: Lakes of New York. Academic Press, New York, NY. pp. 1-120.
- Painter, D. S. and K. J. McCabe. 1988. Investigation into the disappearance of Eurasian watermilfoil from the Kawartha Lakes, Canada. J. Aquat. Plant Manage. 26: 3-12.
- Peverly, J. H., G. Miller, W. H. Brown and R. L. Johnson. 1974. Aquatic weed management in the Finger Lakes. Technical Report 90. Cornell University. Water Resources and Marine Science Center. Ithaca, NY. 24 pp.
- Sander, J. M. 1988. Sanders fishing guide 2: Finger Lakes Region Edition. Sanders Fishing Guide and Service Directory, Inc. Amherst, NY. 323 pp.

⁴Van Dusen, P. J., J. A. Toner, and R. L. Johnson. 1998. Aquatic Vegetation Control Program Tompkins County, NY. Division of Biological Sciences, Section of Ecology and Systematics. Cornell University. Ithaca, NY. 37 pp.

- Smith, C. S. and J. W. Barko. 1990. Ecology of Eurasian watermilfoil. *J. Aquat. Plant Manage.* 28: 55-64.
- Swart, J. M. and J. A. Bloomfield. 1987. Characteristics of New York State Lakes Gazetteer of Lakes, Ponds, and Reservoirs. Third Edition. Lakes Assessment Section of Division of Water. New York State Department of Environmental Conservation Publication. October 1987. 82 pp.
- Vogel, A. 1973. Changes in the submerged aquatic flora at the south end of Cayuga Lake between 1929 and 1970. Department of Natural Resources. Cornell University. Ithaca, NY. 113 pp.
- Wetzel, R. G. 1983. *Limnology*. 2nd Ed. Saunders College Publishing, New York. 743 pp.