

A Biogeographic Perspective on Eurasian Watermilfoil Declines: Additional Evidence for the Role of Herbivorous Weevils in Promoting Declines?

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ABSTRACT

Recent research suggests that a native, herbivorous weevil (*Euhrychiopsis lecontei* (Dietz)) may play a major role in promoting or causing Eurasian watermilfoil (*Myriophyllum spicatum* L.) declines in North America. When the locations of all unexplained (i.e., not related to a specific management practice) North American Eurasian watermilfoil declines were plotted there was a non-random distribution of declines. The majority of declines have occurred in northern states in the USA and some Canadian provinces which is the original range of *E. lecontei* and its native host, northern watermilfoil (*Myriophyllum sibiricum* Komarov (= *M. exalbescens* Fernald)). If other factors were important in producing declines (e.g., competition with native species, accumulation of toxins, changes in water clarity or sediment chemistry) one would not expect to see such a latitudinal bias in the location of declines. This pattern of declines supports the hypothesis that *E. lecontei* is an important agent in promoting or causing Eurasian watermilfoil declines. Alternative factors (e.g., climate, other herbivores) that could have produced this pattern were also considered.

Key words: *Myriophyllum spicatum*, *Euhrychiopsis lecontei*, biological control, insect herbivory.

INTRODUCTION

Eurasian watermilfoil (hereafter referred to as watermilfoil) is an exotic, aquatic macrophyte that has become a considerable nuisance in rivers, lakes, ponds, and estuaries throughout North America (e.g., Bayley et al. 1968, Grace and Wetzel 1978, Aiken et al. 1979, Newroth 1979, Kangasniemi 1983, Nichols and Shaw 1986, Smith and Barko 1990, Carter and Rybicki 1994). Watermilfoil appears to have been introduced into North America in the early to mid-1940's (Couch and Nelson 1986). According to Couch and Nelson (1986), the few watermilfoil populations that were present in North America in the 1940's were widely distributed (MD, OH, AZ and CA). By the 1960's, watermilfoil populations were found in 21 states and 2 Canadian provinces (Couch and Nelson 1986). At present, watermilfoil is found in 44

states and 3 Canadian provinces (Nonindigenous Aquatic Species Database 1997, also see Figure 1A).

Beginning in the 1960's unexplained declines in watermilfoil populations were observed and reported; the first unexplained decline occurred in the Chesapeake Bay (Bayley et al. 1968). Eleven more declines occurred in the 1970's including one in Lake Wingra, WI, a lake that had been intensively studied for a decade (Carpenter 1980). Carpenter (1980) described the increase in watermilfoil abundance in Lake Wingra and the subsequent decline, and evaluated a number of factors that may have produced this decline. These included toxin accumulation, cumulative effects of harvesting and herbicides, climatic changes, nutrient depletion, overgrowth by epiphytes, competition with native macrophytes, pathogens and parasites. Carpenter (1980) concluded that no single factor produced the Lake Wingra watermilfoil decline. Instead, he hypothesized that a combination of some or all of these factors was responsible. In the 1980's and 1990's, a number of researchers suggested that various herbivorous insects also should be considered as possible causes of watermilfoil declines based on field observations and experiments (e.g., Kangasniemi 1983, Painter and McCabe 1988, Creed et al. 1992, Creed and Sheldon 1993, Creed and Sheldon 1995, Sheldon and Creed 1995, Newman et al. 1996).

The purpose of this paper is to examine the distributional pattern of all reported, unexplained watermilfoil declines that have occurred to date in North America from a biogeographic perspective. I consider declines to be unexplained if their occurrence does not appear to be directly related to any particular management practice. Specifically, my objective is to demonstrate that the distribution of these watermilfoil declines in North America is not random but instead that the majority are confined to the range of the herbivorous, North American weevil *Euhrychiopsis lecontei* (hereafter referred to as either *E. lecontei* or weevil). This non-random pattern lends additional support to the idea that *E. lecontei* is playing an important role in promoting or causing watermilfoil declines.

MATERIALS AND METHODS

Information on the distribution of watermilfoil in North America was compiled from the literature, personal communication with colleagues, and personal observations. I relied entirely on Couch and Nelson (1986) for data on the distri-

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bution of watermilfoil through the mid-1980's. For more recent information I relied on other published information (e.g., Engel 1995, Newman and Maher 1995, Sheldon and Creed 1995), data compiled by the Nonindigenous Aquatic Species Program, U.S. Geological Survey in Gainesville, FL, personal communications with colleagues, and personal observations. If a state or province was reported to have at least one watermilfoil population the entire state/province was considered to have watermilfoil (see Figure 1A).

Information on watermilfoil declines was compiled from the published literature, personal communications with colleagues, and personal observations (see Appendix 1). Admittedly, this may not be a complete record of all declines in North America but I believe that it includes the majority of them. Any information on additional, unexplained watermilfoil declines in North America would be greatly appreciated. Lakes having multiple declines (e.g., Brownington Pond, VT (Creed and Sheldon 1995)) were only recorded once in this data set; the decade in which their first decline occurred was the one recorded in the figures.

Weevil distribution data were obtained from the published literature (e.g., Kissinger 1964, Hatch 1971, O'Brien and Wibmer 1982, Kangasniemi 1983, Lillie 1991, Creed and Sheldon 1994b, Newman and Maher 1995), personal communication with colleagues, and personal collections from various locations in North America.

The data for the distribution of watermilfoil declines with respect to the range of the weevil and weevil presence/absence were analyzed using a G test (Sokal and Rohlf 1981).

RESULTS AND DISCUSSION

The number of reported watermilfoil declines has increased since the 1960's (Figure 2). An additional 53 declines have been reported during the intervening years. Both the cumulative number of declines and the number of new declines appeared to be increasing in an exponential fashion since the 1970's (Figure 2). These may indicate a real increase in the frequency of declines or simply be due to the fact that more unexplained declines have been reported in recent years. The persistence of the declines listed here was variable; while some declines only lasted one season the abundance of watermilfoil in other lakes has remained low for several years following the initial decline.

Significantly more declines have occurred within the range of *E. lecontei* than would be expected by chance ($G = 20.0828$, $p < 0.001$) (Figures 1B and 3A). When I examined only declines that occurred within the range of the weevil, using the assumption that weevils were not present in the lakes for which we have no weevil data (Big Green Lake, Lake Mendota, Lake Monona, Lake Waubesa, Lake Wingra, Cayuga Lake, Seneca Lake, Austin Lake, Park Lake, Watkins Lake - see Appendix 1 for the location of these lakes), there were significantly more declines in lakes in which *E. lecontei* was present ($G = 12.8222$, $p < 0.001$) (Figure 3B). This is clearly a conservative analysis since some of the ten lakes for which we have no weevil data may well have contained *E. lecontei* when the declines occurred.

Correlative data such as these do not demonstrate that weevils caused the declines that occurred within their range. However, when considered in conjunction with the observa-

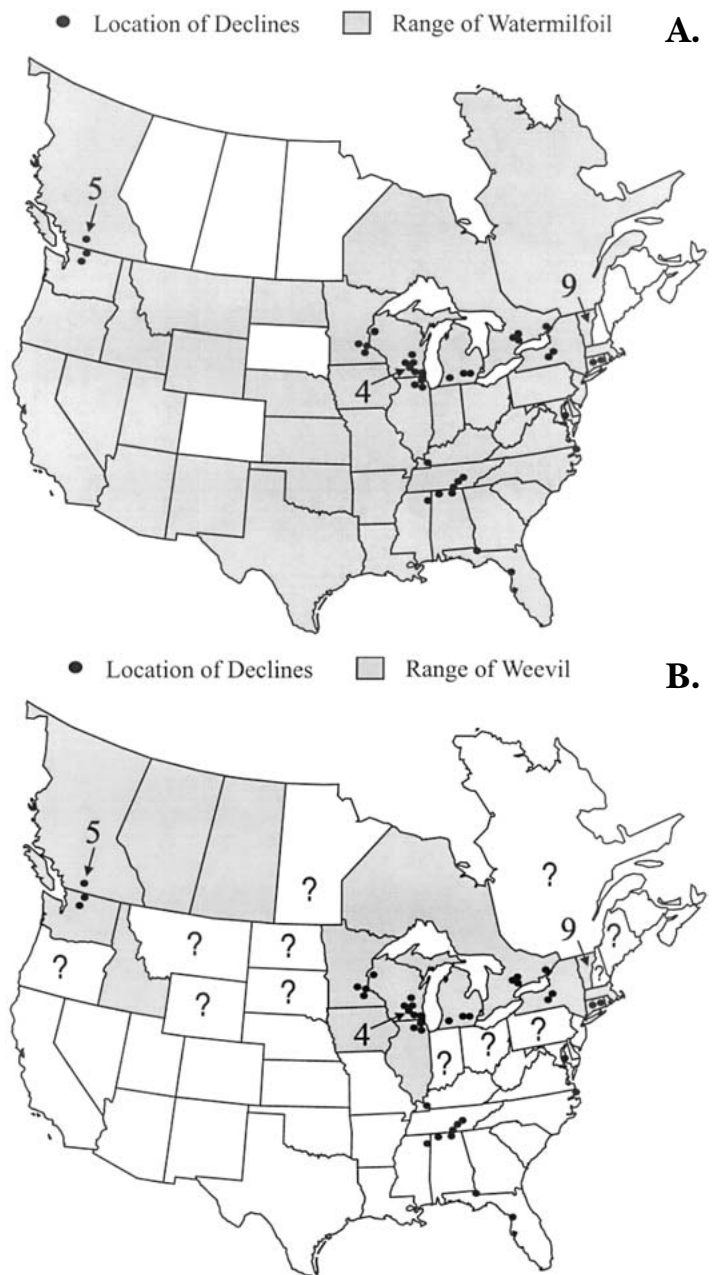


Figure 1. **A.** The distribution of Eurasian watermilfoil and watermilfoil declines in the United States and Canada. The figure is based on information in the published literature, personal communications and personal observations (see methods). The dots give the approximate location of the watermilfoil declines. The number 9 pointing to Vermont indicates that 9 declines have occurred in that state. The number 4 pointing to the dot in southern Wisconsin represents the declines that occurred in the four Yahara Lakes and the number 5 pointing to the dot in British Columbia refers to declines that have occurred in the 5 major lakes in the Okanogan Valley. **B.** The range of the weevil (*E. lecontei*) and watermilfoil declines in North America. This map is also based on information in the published literature, personal communications and personal observations. The question marks refer to areas where the weevil's native host (Northern watermilfoil - *M. sibiricum*) is reported to occur but for which we have no data on weevil presence.

tional and experimental evidence accumulated to date (e.g., Creed et al. 1992, Creed and Sheldon 1993, 1994a, 1995, Sheldon and Creed 1995, Newman et al. 1996, Lillie 1996)

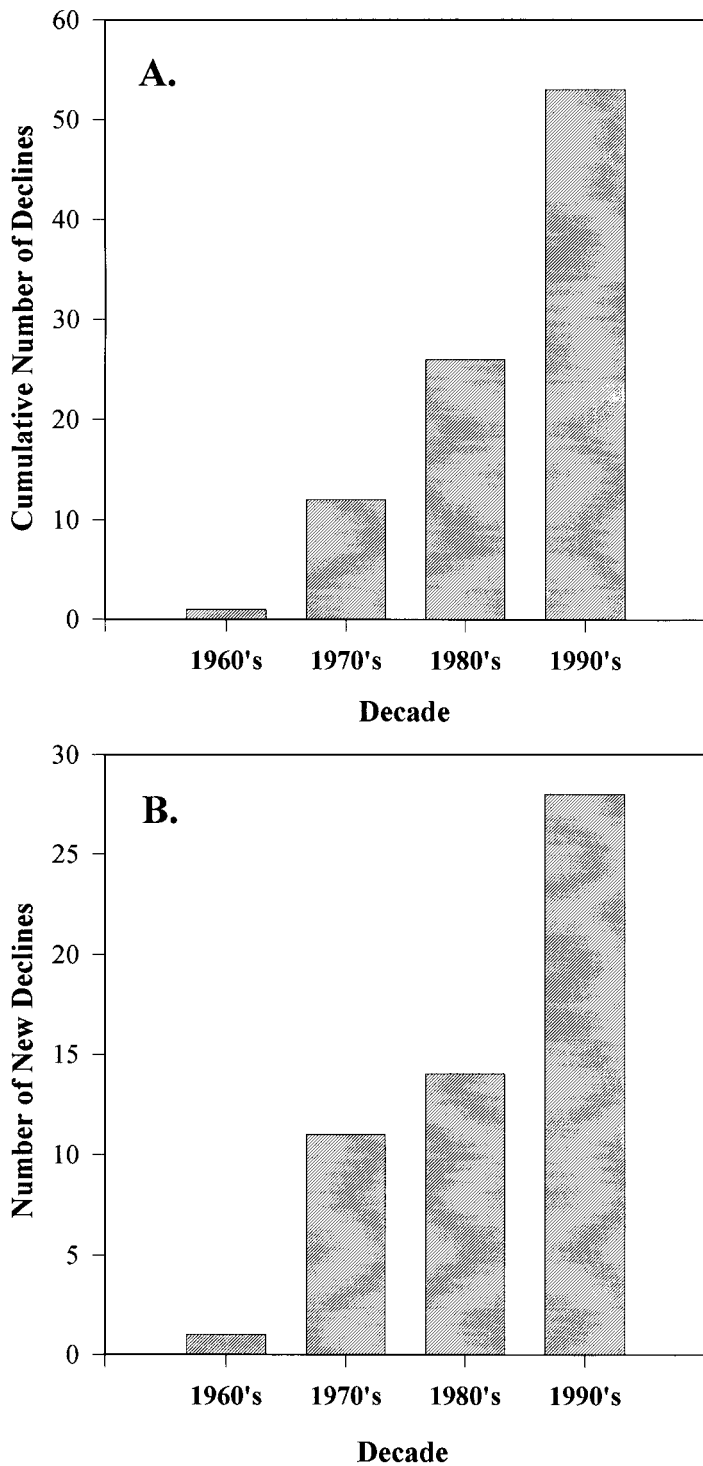


Figure 2. **A.** The cumulative number of unexplained, watermilfoil declines that have occurred in North America since the 1960's. **B.** The number of new watermilfoil declines that have occurred each decade since the 1960's.

they are consistent with the hypothesis that the weevil did play a role in promoting or causing many of these watermilfoil declines. The geographic pattern of declines was not consistent with most of the mechanisms proposed by Carpenter (1980) to explain the Lake Wingra decline. If factors such as nutrient depletion, overgrowth by epiphytes, compe-

tion with native macrophytes, and harvesting were important causes of declines we would expect to see declines occurring throughout much of North America, i.e., declines resulting from nutrient depletion or competition with native macrophytes should be just as likely to occur in the south (note: competition with the exotic macrophyte *Hydrilla verticillata* (L.F.) Royle may have caused some watermilfoil declines in the southern USA). The latitudinal pattern in declines does suggest that climate may be an important factor, i.e., that watermilfoil populations in the northern part of its range are more susceptible to declines than southern populations. Declines may be more likely to occur at cooler temperatures in northern lakes or with more overcast days. Carpenter (1980) rejected climate change as being important in producing the Lake Wingra decline. Smith and Barko (1996), however, considered climatic change that resulted in reduced light availability to have been important in causing some watermilfoil declines in eastern North America in the late 1980's. Watermilfoil coverage increased in several Tennessee Valley Authority (TVA) lakes during the drought of 1988. Heavy rains in subsequent years increased water flow and turbidity, with the result that light availability was reduced at many sites and watermilfoil coverage decreased (Smith and Barko 1996). Considering the data presented here, if climatic fluctuations were the primary factor producing declines then we would not expect to see more declines in lakes containing weevils. Moreover, if climatic fluctuations were important then we would expect to see declines occurring simultaneously in several adjacent lakes. With the exception of the TVA lake declines reported by Smith and Barko (1996) this does not appear to have been the case.

Other herbivores (the midge *Cricotopus myriophylli* (Oliver) and the caterpillar *Acentria ephemerella* (Denis and Schiffermüller)) have been implicated in watermilfoil declines (e.g., Kangasniemi 1983, Painter and McCabe 1988)^{2,3}. While these insects can damage watermilfoil plants (Painter and McCabe 1988, MacRae et al. 1990, Creed and Sheldon 1994a), the range data point to *E. lecontei* as the primary herbivore promoting or causing declines. Watermilfoil declines have occurred outside the apparent ranges both of *A. ephemerella* (this species has not been collected in western North America) and *C. myriophylli* (this species has been collected in British Columbia, MN, WI and southern Ontario (Newman and Maher 1995, Don Oliver, pers. comm.) but has not been collected in eastern North America). Of these two insects, more declines have occurred in areas where *A. ephemerella* was found (eastern and central North America). *A. ephemerella* larvae damage the upper portion of watermilfoil stems. They consume leaf tissue and also cut the stem to make retreats (Creed and Sheldon 1994a). They can have a significant effect on small watermilfoil fragments (Painter and McCabe 1988) and small, rooted plants (Creed and Sheldon 1994a); there are no experimental data documenting their effect on

²Johnson, R. 1995a. Monitoring Aquatic Vegetation in Tompkins County. Aquatic Vegetation Control Program. Project Completion Report SFY1993-1994. Report to Tompkins County Planning Department. 38 pp.

³Johnson, R. 1995b. Monitoring Aquatic Vegetation in Seneca County. Aquatic Vegetation Control Program. Project Completion Report 1994. Report to Seneca County Soil and Water Conservation District. 30 pp.

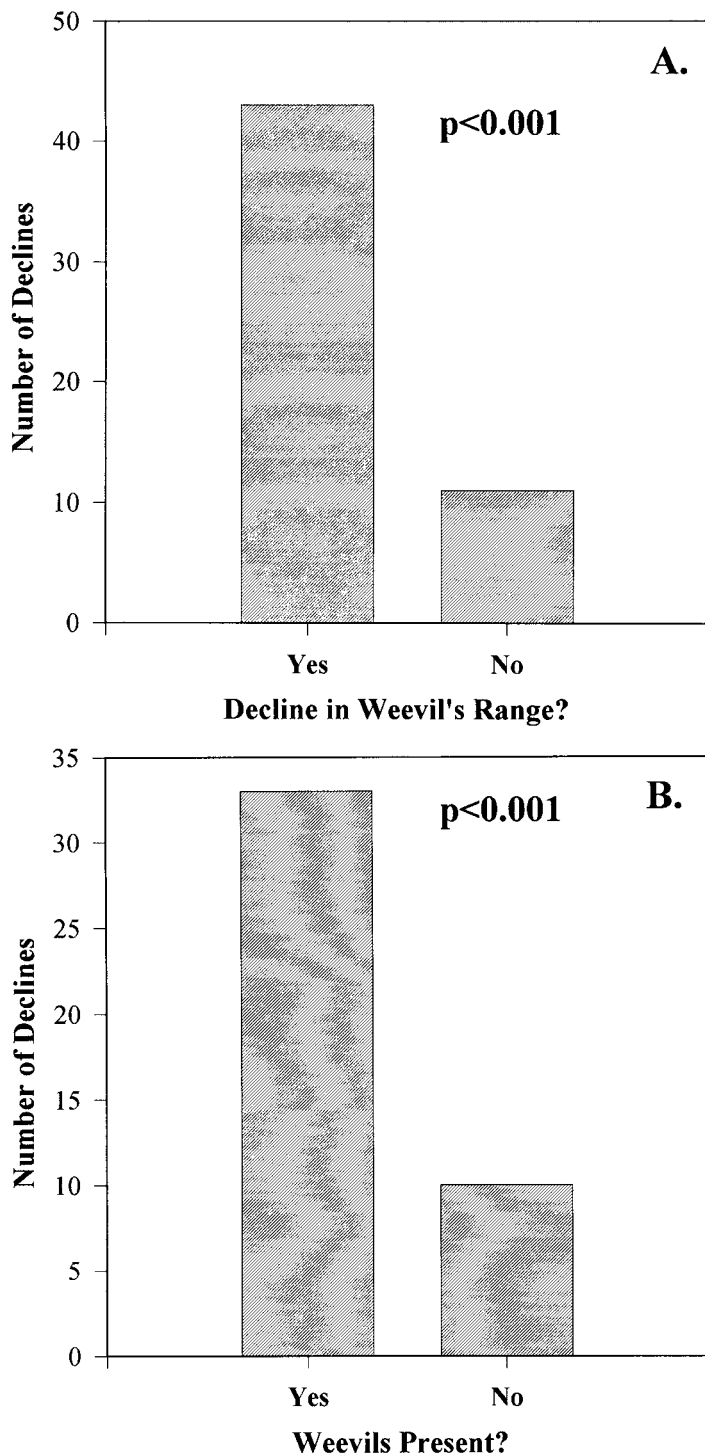


Figure 3. **A.** The number of watermilfoil declines that have occurred in the range of the weevil. **B.** The number of watermilfoil declines that occurred in the range of the weevil where the weevil was collected. The significance values in each figure are from G tests. The null hypothesis for the first figure was that equal numbers of declines occurred inside and outside of the weevil's range. The null hypothesis for the second figure was that equal numbers of declines occurred with and without weevils.

larger plants. Field observations suggest that this species does not have as great an effect on watermilfoil plants as the weevil (Creed and Sheldon 1994a)⁴. Nevertheless, it is possible that

watermilfoil populations attacked by both *A. ephemera* and *E. lecontei* may decline faster than those attacked by just the weevil. At present, it is not clear that a watermilfoil population attacked by just *A. ephemera* will decline although a decline in Cayuga Lake, NY has been attributed to this insect^{2,3} (note: *E. lecontei* appears to have been present in the lakes with declines documented by Painter and McCabe (1988) and attributed to *A. ephemera*, see Appendix 1).

If *E. lecontei* is important in promoting or causing watermilfoil declines then why were declines not observed sooner? Based on the data in Couch and Nelson (1986), watermilfoil was not common in the range of the weevil until the mid-1960's; most of these watermilfoil populations were in the north-central Midwest. Watermilfoil populations were not common in eastern and western North America until the 1970's. It is interesting that some of the early declines (The Yahara Lakes (Mendota, Monona, Wingra and Waubesa), Big Green Lake, Chemung Lake, etc.) occurred in the part of the weevil's range first invaded by watermilfoil, the north-central Midwest and central Canada. Like many herbivorous insects, *E. lecontei* is highly host specific (Sheldon and Creed 1995, Solarz and Newman 1996). The native host appears to be northern watermilfoil (Creed and Sheldon 1994b). Despite the presence of the exotic watermilfoil in its range it may have taken 5-10 years (or more) before *E. lecontei* underwent a host shift and began feeding largely on the introduced watermilfoil species (the data of Solarz and Newman (1996) suggest that the shift may have occurred more rapidly). Additional time would have been required for weevil population size to increase to a level where it might significantly affect a watermilfoil population. The lag in a weevil effect would be especially pronounced if a watermilfoil population in a lake was rapidly expanding. The apparent lag in a weevil effect could also have been a result (at least in part) of human interference. Weevil population growth may have been inhibited by other control measures that either reduce total abundance of watermilfoil (e.g., herbicides) or reduce specific plant parts required by the weevils to complete their life cycle (e.g., harvesting removes the apical portions of watermilfoil stems which is where much of the weevil life cycle takes place (Creed and Sheldon 1993, Sheldon and O'Bryan 1996)). Even other herbivores may have a negative impact on *E. lecontei* abundance. The midge *C. myriophylli* also feeds on watermilfoil meristems; when this herbivore is abundant there may be few meristems available to weevils for oviposition.

The geographic distribution of the watermilfoil declines that have occurred since Carpenter (1980) published his discussion of the Lake Wingra decline allows us to consider further the relative importance of various factors in promoting these declines. The pattern of watermilfoil declines is consistent with the hypothesis that *E. lecontei* has promoted or caused the majority of these declines. However, it is premature to completely rule out effects of other herbivores, pathogens or climate. Examination of the effects of multiple herbivores on watermilfoil populations and their interaction with climatic factors may be important avenues for future research into the control of this nuisance aquatic plant.

⁴but see footnotes 2 and 3.

ACKNOWLEDGMENTS

I want to thank all of my colleagues who graciously and generously shared unpublished information on watermilfoil distribution, watermilfoil declines, and weevil distribution. I would also like to thank Holly Crosson, Ray Newman and three anonymous reviewers for valuable comments on an earlier draft of this manuscript. Finally, my thanks to Lori Felix for drafting the maps.

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APPENDIX 1. NORTH AMERICAN LAKES (PLUS CHESAPEAKE BAY AND CURRITUCK SOUND) IN WHICH WATERMILFOIL DECLINES HAVE OCCURRED AS OF 1996. THE STATE/PROVINCE IN WHICH THE LAKE IS LOCATED IS PROVIDED, ALONG WITH WHETHER OR NOT THE WEEVIL (*E. LECONTEI*) WAS FOUND IN THE LAKE WHEN THE DECLINE WAS OBSERVED. OTHER CONTROL MEASURES REFERS TO WHETHER OR NOT WATERMILFOIL WAS BEING MANAGED BY PHYSICAL (E.G., HARVESTING) OR CHEMICAL MEANS AT THE TIME OF THE DECLINE.

	Lake	Weevil Present?	Other Control Measures?	Source of Information
United States				
Alabama				
	Guntersville Lake	#	Yes	1
	Wheeler Lake	#	Yes	1
Connecticut				
	Beseck Lake	Yes	?	2
	Wannonskopomic Lake	Yes	Yes	3, 4
Florida				
	Crystal River	No	Yes	5
	Lake Seminole	No	Yes	5
Illinois				
	Cedar Lake	Yes	No	6
	Druce Lake	Yes	No	4, 6
	McCullom Lake	Yes	No	4, 6
Kentucky				
	Kentucky Lake	No	?	1, 7
Maryland				
	Chesapeake Bay	#	Yes	8
Michigan				
	Austin Lake	#	No	7, 9
	Park Lake	#	Yes	9
	Watkins Lake	#	Yes	9
Minnesota				
	Cenaiko Lake	Yes	No	10
	Otter Lake	Yes	?	10
	Smith's Bay (Lake Minnetonka)	Yes	?	10
Mississippi				
	Tennessee-Tom Bigbee Canal	#	?	11
New York				
	Cayuga Lake	#	Yes	11, 12, 13
	Seneca Lake	#	?	11
North Carolina				
	Currituck Sound	No	?	14
Tennessee				
	Chickamauga Lake	#	Yes	1
	Nickajack Lake	#	Yes	1
	Watts Bar Lake	#	Yes	1
Vermont				
	Arrowhead Mountain Lake	Yes	No	15
	Berlin Pond	Yes	No	15
	Brownington Pond	Yes	No	16
	Glen Lake	Yes	No	4, 15
	Memphremagog	Yes	No	4, 15
	N. Montpelier Pond	Yes	No	15
	Lake Paran	Yes	No	15
	Round Pond	Yes	No	15
	Winona Lake	Yes	No	15
Washington				
	Columbia River (at Brewster, WA)	# ¹	No	4, 17

#- No weevil data.

#¹- No weevil data. However, weevils had been collected upstream of the site on the Okanogan River and approximately 20 km downstream of it on the Columbia River in 1993, three years before the decline. (R. P. Creed, unpubl. data).

#²- Weevils were collected in this lake in 1996; the decline occurred in 1993.

?- No data on other control measures.

*- *E. lecontei* appears to have been misidentified as *Phytobius (Litodactylus) leucogaster* since the larvae of *Phytobius* are not aquatic (see Painter and McCabe 1988, p. 5) but found on flower spikes.

Sources: 1 Smith and Barko (1996); 2 Charles Lee, Connecticut Department of Environmental Conservation, pers. comm.; 3 James Morrill, Hotchkiss School, pers. comm.; 4 Robert Creed, Department of Biology, Appalachian State Univ., pers. obs.; 5 William Haller, Center for Aquatic Plants, pers. comm.; 6 Robert Kirchner, Northern Illinois Planning Commission, pers. comm.; 7 Shearer (1994); 8 Bayley et al. (1968); 9 Douglas Pullman, Aquest, Flint, Michigan, pers. comm.; 10 Raymond Newman, Department of Fisheries and Wildlife, Univ. of Minnesota, pers. comm.; 11 Craig Smith, Aquest, Flint, Michigan, pers. comm.; 12 see footnote 2; 13 see footnote 3; 14 Carter and Rybicki (1994); 15 Holly Crosson, Vermont Department of Environmental Conservation, pers. comm.; 16 Creed and Sheldon (1995); 17 Kathy Hamel, Washington Department of Ecology, pers. comm.; 18 Kangasniemi (1983); 19 Nichols (1994a); 20 Stanley Nichols, Wisconsin Geological and Natural History Survey, pers. comm.; 21 Lillie and Barko (1990); 22 Lillie (1996); 23 Laura Jester, Univ. of Wisconsin, Stevens Point, pers. comm.; 24 Nichols (1994b); 25 Dan Helsel, Wisconsin Department of Natural Resources, pers. comm.; 26 Carpenter (1980); 27 Painter and McCabe (1988).

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	Lake	Weevil Present?	Other Control Measures?	Source of Information
	Osoyoos Lake	Yes	No	4, 17, 18
Wisconsin	Big Green Lake	#	Yes	19, 20
	Devil's Lake	Yes	No	10, 21
	Fish Lake	Yes	No	10, 22
	Longtrade Lake	Yes	No	23
	Lake Mendota	#	Yes	19, 20, 24
	Lake Monona	#	Yes	19, 20, 24
	Lake Waubesa	#	Yes	19, 20, 24
	Whitewater Lake	# ²	Yes	25
	Wind Lake	Yes	Yes	25
	Lake Wingra	#	Yes	19, 20, 24, 26
Canada				
British Columbia	Kalamalka Lake	Yes	Yes	18
	Okanogan Lake	Yes	Yes	18
	Skaha Lake	Yes	Yes	18
	Vaseux Lake	Yes	Yes	18
	Wood Lake	Yes	Yes	18
Ontario	Buckhorn Lake	Yes*	?	27
	Chemung Lake	Yes*	Yes	27
	Lake Opinicon	Yes*	?	27
	Lake Scugog	Yes*	?	27

#- No weevil data.

#¹- No weevil data. However, weevils had been collected upstream of the site on the Okanogan River and approximately 20 km downstream of it on the Columbia River in 1993, three years before the decline. (R. P. Creed, unpubl. data).

#²- Weevils were collected in this lake in 1996; the decline occurred in 1993.

?- No data on other control measures.

*- *E. lecontei* appears to have been misidentified as *Phytobius (Litodactylus) leucogaster* since the larvae of *Phytobius* are not aquatic (see Painter and McCabe 1988, p. 5) but found on flower spikes.

Sources: 1 Smith and Barko (1996); 2 Charles Lee, Connecticut Department of Environmental Conservation, pers. comm.; 3 James Morrill, Hotchkiss School, pers. comm.; 4 Robert Creed, Department of Biology, Appalachian State Univ., pers. obs.; 5 William Haller, Center for Aquatic Plants, pers. comm.; 6 Robert Kirchner, Northern Illinois Planning Commission, pers. comm.; 7 Shearer (1994); 8 Bayley et al. (1968); 9 Douglas Pullman, Aquest, Flint, Michigan, pers. comm.; 10 Raymond Newman, Department of Fisheries and Wildlife, Univ. of Minnesota, pers. comm.; 11 Craig Smith, Aquest, Flint, Michigan, pers. comm.; 12 see footnote 2; 13 see footnote 3; 14 Carter and Rybicki (1994); 15 Holly Crosson, Vermont Department of Environmental Conservation, pers. comm.; 16 Creed and Sheldon (1995); 17 Kathy Hamel, Washington Department of Ecology, pers. comm.; 18 Kangasniemi (1983); 19 Nichols (1994a); 20 Stanley Nichols, Wisconsin Geological and Natural History Survey, pers. comm.; 21 Lillie and Barko (1990); 22 Lillie (1996); 23 Laura Jester, Univ. of Wisconsin, Stevens Point, pers. comm.; 24 Nichols (1994b); 25 Dan Helsel, Wisconsin Department of Natural Resources, pers. comm.; 26 Carpenter (1980); 27 Painter and McCabe (1988).