

The Weevil-Watermilfoil Interaction at Different Spatial Scales: What We Know and What We Need To Know

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ABSTRACT

The North American weevil (*Euhrychiopsis lecontei* (Dietz)) is being considered as a biological control agent for Eurasian watermilfoil (*Myriophyllum spicatum* L.). This native insect damages watermilfoil plants and is frequently associated with declining watermilfoil populations. Weevils and watermilfoil interact over at least four different spatial scales—1) the level of the individual plant, 2) the level of beds within lakes, 3) lakes within geographic regions and 4) geographic regions—and we still have much to learn about the interaction at these different scales. For example, at the level of the individual plant, we have a good idea of how weevil herbivory influences plant growth but we still need to determine whether or not weevils can cause plant death. At the level of beds, we do not know how long it takes a weevil population to reach a density that will result in a significant reduction in watermilfoil biomass. Finally, at the level of lakes within geographic regions, we do not know if differences in lake productivity influence the weevil-watermilfoil interaction. It is my hope that addressing these questions and filling in the gaps in our knowledge will lead to a better understanding of the interactions between these two species and to more efficient use of the insect in watermilfoil control projects.

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

INTRODUCTION

Eurasian watermilfoil (*Myriophyllum spicatum* L.), hereafter referred to as watermilfoil, is a nuisance aquatic plant that is widely distributed throughout North America (Couch and Nelson 1986, Smith and Barko 1990, Creed 1998). Unlike other nuisance aquatic plants in North America where biological control programs have focused on the use of introduced insects (i.e., classical biological control), much of the control research for watermilfoil has focused on native or naturalized insects as potential control agents (Painter and McCabe 1988, Kangasniemi et al. 1993, Creed and Sheldon 1995, Sheldon and Creed 1995, Newman et al. 1996, other papers in this issue). The majority of research has examined the impact the native watermilfoil weevil (*Euhrychiopsis lecontei* (Dietz)), hereafter referred to as weevil, has on watermil-

foil. This weevil has had a significant negative impact on watermilfoil in a variety of experiments (Creed et al. 1992, Creed and Sheldon 1993, 1994a, 1995, Sheldon and Creed 1995, Newman et al. 1996) and has been found associated with several declines of watermilfoil populations in North America (Creed 1998). This insect clearly shows promise as a biological control agent. However, many unanswered questions remain with respect to the interaction between the weevil and watermilfoil. In this paper I will briefly review what we know about this interaction and then suggest what I believe are some of the questions we need to answer about the interaction in general, and specifically about the use of the weevil as a biological control agent. I will examine the weevil-watermilfoil interaction at four different spatial scales: the individual plant, beds within a lake, lakes within a region, and geographical regions.

THE INDIVIDUAL PLANT

Weevil larvae, pupae and adults attack watermilfoil plants. Larvae initially destroy meristems and later tunnel through the stem consuming vascular tissue (Creed and Sheldon 1993, 1994a, Newman et al. 1996). Pupation occurs in the stem; vascular tissue is destroyed during the construction of the pupal chamber (Creed and Sheldon 1993). Adults feed on stems and leaves (Creed and Sheldon 1993).

Weevil larvae probably have the greatest impact on watermilfoil growth. By destroying the meristems they largely halt stem elongation (Creed and Sheldon 1993, 1995). By consuming vascular tissue they sever the connection between the canopy and the roots which has an impact on root production (Creed and Sheldon 1995) and the translocation of nonstructural carbohydrates (Newman et al. 1996, Newman and Biesboer 2000). With little or no translocation of nonstructural carbohydrates to the roots, root growth may slow or even stop. Reduced root production could influence nutrient uptake from the sediments which in turn could slow the production of above sediment biomass (John D. Madsen, pers. comm.). Penetration of the stem epithelium by larvae results in stored gases being lost from stem tissue. These gases are important for maintaining stem buoyancy; without them watermilfoil stems sink out of well-lit surface waters (Creed et al. 1992, Creed and Sheldon 1995) which should result in reduced rates of photosynthesis. The loss of stored gases, especially stored CO₂, should also affect plant growth. Thus, weevils can influence watermilfoil growth in a variety of ways. However, watermilfoil is a notoriously resilient plant. A common means of managing nuisance watermilfoil popu-

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WATERMILFOIL BEDS WITHIN A LAKE

lations is harvesting. Harvesters cut the plants 1-2 m below the surface, i.e., the stem epithelium is breached and the canopy tissue is lost. Why are watermilfoil plants usually able to tolerate harvester cutting and rapidly grow back to the surface and yet exhibit little or no growth (or even death) after the attack of this minuscule weevil?

Weevil larvae differ from harvesters in that individual larvae continually damage the stem for approximately two weeks. Therefore, the wound can not heal as it does after harvesting and the canopy remains disconnected from the roots which should inhibit growth. Furthermore, multiple generations of weevils may attack a plant over the course of a summer. With repeated weevil attacks there will be little or no accumulation of carbohydrates in the lower shoot and root crown which could ultimately result in plant death (John D. Madsen, pers. comm.).

A curious behavior of weevil larvae may suggest another mechanism by which watermilfoil plants are severely damaged or even die after being attacked by weevils. Weevil larvae rarely burrow continuously through a watermilfoil stem. Instead they will burrow for a distance, exit the tunneled stem, move down the stem and start another tunnel. I find this behavior quite puzzling. Why should the relatively vulnerable larvae leave the comparable safety of the tunnel and expose themselves to predators? Close inspection of the tunnels suggests an explanation for this behavior. A larva eats its way through a stem removing vascular tissue at one end and producing a mass of frass (insect excrement) at the other. The accumulation of frass in a tunnel with relatively poor water flow may make conditions intolerable for the larva (e.g., low dissolved oxygen concentrations, accumulation of toxins etc.) resulting in the larva exiting the burrowed stem and starting a new tunnel. The accumulated frass may also provide a suitable culturing medium for various bacteria and fungi. These may in turn produce a systemic infection of the damaged plant, penetrating the vascular system where it has been damaged by the weevils. Indeed, watermilfoil stems turn brown or black in the vicinity of weevil tunnels which suggests death of adjacent tissues. Therefore, it is possible that weevils create the appropriate conditions that result in plant death by pathogen attack. More research is needed that examines this potentially important interplay between weevils and aquatic bacteria and fungi. Specifically, we need to know if the rate of pathogen attack increases when weevils damage plants and if these pathogens can produce infections that can kill entire watermilfoil plants.

Another area that needs to be investigated is the effect of plant nutrient content on the ability of the weevil to control a watermilfoil population. Plant nutrient content does affect interactions between aquatic plants and herbivorous insects (Room 1990, Newman et al. 1998). For example, plants with low nitrogen concentrations may not provide adequate nutrition for herbivorous insects with the result that their populations increase slowly, if at all, and there is little or no impact on the plant population (Room 1990, Newman et al. 1998). We need to know if there is a similar impact of nitrogen content in watermilfoil on weevil population dynamics. If there is then introductions and augmentations of weevils in lakes containing plants with low nitrogen concentrations may result in little or no control of watermilfoil.

Watermilfoil beds attacked by the weevil can actually disappear. This was observed in Brownington Pond, VT (Creed and Sheldon 1994b, 1995). The South Bed largely disappeared during the winter of 1991-1992; only a few small plants remained. Interestingly, the northern half of the West Bed also disappeared but the southern half of the bed was still present. Most of the remaining plants in this part of the West Bed were small (<50 cm tall). Why was there only a partial disappearance of the West Bed? Was it due to differences in concentrations of sediment nutrients? Limited sampling of pond sediments revealed that only the concentration of ammonium was higher in the West Bed sediments (Creed and Sheldon 1994b). The higher concentration of ammonium in West Bed sediments may have promoted a more rapid regrowth of this watermilfoil bed in 1992 following the decline. However, we need more experimental data to determine if there is an effect of sediment nutrient concentration on the rate of watermilfoil regrowth following a decline; specifically, will watermilfoil populations rebound more rapidly on sediments with higher concentrations of certain nutrients.

The small plants that were present in the West Bed following the 1991-1992 decline had eggs and larvae on them but no pupae. Creed and Sheldon (1995) hypothesized that the stem diameter of these small plants may have been too narrow for the weevils to construct a complete pupal chamber. There are alternative explanations for why no pupae were found on these plants. The shorter plants were farther from the surface of the water. As this could possibly affect the chemical environment inside the stem it is possible that conditions inside the stem (e.g., oxygen concentration) were not conducive for completion of the pupal stage. If this is true then you would expect to see dead pupae in the stem. Alternatively, these plants may have had lower nutrient concentrations or they were deficient in a particular nutrient with the result that the larvae never pupated. This is consistent with the observation that no pupae were found. I should note that we did not see damage indicative of incomplete puparia. Knowing why many weevils were unable to complete their life cycle is important and we need to determine why there appeared to be a decrease in the number of weevils that successfully pupated even though plants were present. Being able to predict when this decline in pupation rate should occur could influence weevil stocking programs. For example, if the majority of watermilfoil plants remaining in a lake are small the frequency of stocking or augmentation should be reduced as the existing weevil population will probably decline naturally.

Other questions need to be answered at this scale. For example, what density of weevils is required to cause the collapse of a bed? Data presented in Creed and Sheldon (1995) and Newman and Biesboer (2000) suggest that weevil densities >1.5 weevils per stem (entire plant) may be sufficient to produce a decline. On an areal basis, Newman and Biesboer suggest that a density greater than 100 weevils/m² could produce a decline. More data are needed from other lakes to see if similar densities of weevils result in declines. We also need to know how long it takes a population of weevils to reach the density at which the collapse of a watermilfoil bed occurs.

This will obviously be a function of several variables including weevil population size after a previous decline (or at time of stocking), overwinter mortality of weevils, the size of the bed, the density of plants etc. We need a better understanding of weevil demography. We also need models that incorporate weevil population dynamics and watermilfoil bed characteristics if we wish to make predictions about when declines might occur.

LAKES WITHIN REGIONS

A variety of factors that frequently differ among lakes within a region may influence the weevil-watermilfoil interaction, specifically the rate at which a decline occurs or if one occurs at all. These include, but are not limited to, the types of predators present and the productivity of the habitat. In this paper my discussion of habitat productivity will focus on the concentration of sediment nutrients. While other factors can also influence macrophyte production (e.g., light transparency, concentration of dissolved carbon) I will not discuss their impacts here.

Predators (fishes and invertebrates) may influence weevil abundance. At present, it is unclear what effect predators have on weevil populations and if they indirectly influence the rate at which a watermilfoil decline could occur. In Brownington Pond, the dominant fish predator on littoral macroinvertebrates was the yellow perch (*Perca flavescens* (Mitchill)). In order to assess the effect of perch predation on weevil abundance two fish exclusion experiments were conducted in Brownington Pond (Creed and Sheldon 1992, Creed et al. 1993). In the first experiment, a two month exclusion experiment that was terminated in August of 1991, there was no effect of perch on weevil abundance across treatments. Examination of perch guts in August found that they were feeding primarily on zooplankton. In a second, shorter (two weeks in late June-early July 1992) experiment, conducted at a time when perch feed heavily on littoral invertebrates, more weevils were observed in the fish enclosures. However, no weevils were found in the stomachs of perch collected in the immediate vicinity of the experiment. This suggests that the higher densities of weevils in the enclosures in the second experiment were not due to a numerical reduction in weevil abundance by perch but to weevils aggregating in areas with reduced predation risk (Creed et al. 1993).

Fish species that feed more heavily on littoral zone invertebrates than perch may have a greater impact on weevil abundance. Sutter and Newman (1997) did find weevils in the stomachs of bluegill sunfish (*Lepomis macrochirus* (Rafinesque)) collected in MN. These authors suggested that bluegill predation could influence weevil densities in some lakes. Can bluegills and other sunfish prevent declines from occurring? Possibly. However, watermilfoil declines have occurred in lakes containing bluegills and other sunfish species (e.g., Lake Memphremagog, VT, McCullom Lake, IL, Cenai-ko Lake, MN). In addition, no significant effect of bluegills on weevil abundance was observed in an enclosure experiment in VT (Newbrough 1993). It is possible that bluegill densities in these lakes were below the density that can have a significant impact on a weevil population. We need to know the density of sunfish that might be critical in influencing weevil population size and thus influencing the likelihood of

a decline. There is a clear need for more experimentation in this area. I should point out that we have no information on what impact other predators, particularly invertebrate predators like damselflies and dragonflies, have on weevil populations. While adult weevils do not appear to be vulnerable to most invertebrate predators (Robert Creed, pers. obs.) larvae may well be very vulnerable.

Recently, ecologists have begun considering how ecological interactions might vary across gradients in environmental productivity (e.g., Oksanen et al. 1981, Mittelbach et al. 1988). For the weevil-watermilfoil interaction a potentially important measure of environmental productivity is the concentration of nutrients in the sediments. Variation in the concentration of sediment nutrients could influence the weevil-watermilfoil interaction in various ways but the outcome is difficult to predict. At present we can not even predict the outcome of the interaction *at one point* on a gradient of sediment productivity. To illustrate this point I present some of the possible outcomes of the weevil-watermilfoil interaction on sediments with low concentrations of nutrients critical to watermilfoil growth. It is conceivable that a decline would be *more* likely to occur on sediments with lower nutrient concentrations because watermilfoil growth would be fairly slow relative to the rate at which the weevils damage the plant, i.e., the weevil damage rate is greater than the production of new watermilfoil tissue. Alternatively, declines could be *less* likely to occur on these sediments because the watermilfoil is less nutritious to the weevil and the weevil population growth rate is slow, i.e., the production of watermilfoil tissue exceeds the rate of weevil damage (see discussion above). Finally, declines might be *more* likely to occur in lakes with less productive sediments. These less productive lakes may support fewer fish that consume macroinvertebrates. With few fish there would be lower losses of weevils to predators and therefore a higher rate of weevil damage on watermilfoil, i.e., the weevil damage rate is greater than the production of new watermilfoil tissue. In this last scenario, herbivores would be largely unregulated by carnivores with the result that the herbivores could have a dramatic impact on the primary producers. Oksanen et al. (1981) and Mittelbach et al. (1988) describe the underlying theory for the third scenario in greater detail. As you can see, there is no straightforward prediction as to how the weevil-watermilfoil interaction will respond at a single level of sediment productivity, let alone along a gradient in sediment productivity. Since we are interested in controlling watermilfoil in lakes that differ in productivity I suggest that we devote a significant amount of research effort towards seeing how the interaction will vary along gradients in environmental productivity.

GEOGRAPHIC REGIONS

Lake productivity, predators and climate should differ across geographic regions. I have already covered productivity and predators in the previous section; the same argument for lakes within regions should apply to lakes across regions with respect to these two factors. My discussion here will focus on the potential impact of climate on the weevil-watermilfoil interaction.

In a recent paper on the distribution of watermilfoil declines in North America (Creed 1998), I found that the vast majority of declines occurred in the northern United States

and in southern Canada. All of the northern declines occurred in the range of the weevil. If the weevil becomes approved as a biological control agent for watermilfoil then there is a possibility that it might be released on southern populations of watermilfoil. Will weevils be able to control watermilfoil farther south or will they only have an effect in northern lakes? It is possible that weevils are able to cause watermilfoil declines in northern lakes because at cooler temperatures the weevil damage rate exceeds the production rate of new watermilfoil tissue. In southern lakes the production of new watermilfoil tissue could exceed the rate at which weevils are capable of damaging it. Moreover, there may be thermal limitations on the weevil. This species may not be able to survive in waters above a certain temperature (e.g., 34 to 35C, see Sheldon 1997). Preliminary answers to these questions could be obtained from greenhouse experiments. We should conduct these experiments prior to releasing the weevil in the southern United States. Finally, the phenology of watermilfoil is influenced by water temperature (John D. Madsen, pers. comm.). In warmer, southern lakes, watermilfoil biomass peaks in the spring, declines during the summer and a second biomass peak is observed in the fall. Will weevils be able to adjust to this change in watermilfoil phenology or will it preclude them from having an appreciable impact on the plant? We need to know if weevil phenology can adapt to changes in watermilfoil phenology.

CONCLUSIONS

Over the last ten years we have learned a great deal about the weevil-watermilfoil interaction. This is one of the best studied interactions between an herbivorous insect and a submersed aquatic macrophyte. Nevertheless, we still have a lot to learn about this interaction. Determining the answers to the questions posed in this paper will improve our understanding of this interaction. Moreover, this additional research should improve our ability to predict the conditions under which weevils will cause a watermilfoil decline to occur and when it will occur. Knowing the answers to these questions should lead to a more efficient use of this insect as a biological control agent for watermilfoil.

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