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Predicting Eurasian watermilfoil's (*Myriophyllum spicatum*) distribution and its likely response to biological control in a spring-fed river

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ABSTRACT

Controlling invasive aquatic plants would benefit from development of predictive theories that can be used to set priorities for when, where, and how to manage these species. The invasion of Eurasian watermilfoil (*Myriophyllum spicatum* L.) into a northern California river provides an opportunity to apply predictive relationships for it and its management. To test a hypothesis (from the scientific literature) regarding habitat susceptibility to Eurasian watermilfoil invasion and evaluate prospects for its management, we collected water quality, temperature, and plant data from Fall River. During 2009 and 2010 we determined Eurasian watermilfoil abundance and distribution at 71 locations within the river from an upstream to downstream direction. We also determined water temperature and total phosphorus (P) concentration. Eurasian watermilfoil frequency increased in the river downstream from the confluence of Spring Creek. Based on measured total P concentrations and simulations from a physiologically based growth model, Eurasian watermilfoil should be able to grow upstream of this point as well. High water levels which prevent boats from passing under the bridge located at this point may limit the upstream spread of Eurasian watermilfoil. One proposal is to introduce the Eurasian watermilfoil weevil (*Euhryciopsis lecontei* Dietz) as a biological control agent. In other habitats the weevil has been most successful when 3 or more generations of weevils are produced each year. Degree-day calculations using Fall River water temperatures and 2 scenarios for weevil growth and development indicate that the weevil only achieves 3 or more generations per growing season at points downstream of the confluence of the Tule River. This represents the downstream one-third of the river. This information, in conjunction with simulations from a published model on the weevil/milfoil interaction, suggest that it is not likely that the milfoil weevil will reduce Eurasian watermilfoil biomass in Fall River.

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Key words: river plants, invasion, biological control, predictive aquatic plant management.

INTRODUCTION

Invasive aquatic plants may change aquatic habitats, modifying primary production, structure required for fish habitat, rates of ecosystem succession, and lake food chains (Sytsma 2008). Eurasian watermilfoil (*Myriophyllum spicatum* L.) is a significant and particularly troublesome invasive aquatic plant throughout North America (Smith and Barko 1990). Once established, Eurasian watermilfoil may quickly dominate freshwater habitats (Bayley et al. 1978, Aiken et al. 1979, Newroth 1985, Lillie 1986, Madsen et al. 1991). Most research on this plant has been conducted in lacustrine systems, and to our knowledge there are few published reports on Eurasian watermilfoil's distribution and spread within western North American rivers (Gibbons and Gibbons 1985, Rawson 1985, Getsinger et al. 1997, Alexander 1998, Spencer and Ksander 1999).

Fall River is a blue ribbon trout (*Oncorhynchus mykiss* Walbaum) stream located in northern California. In 1997 and 1998, it was characterized by 10 species of submersed aquatic plants: *Chara* sp., *Elodea canadensis* Michx., *Callitriche hermaphroditica* L., *Eleocharis acicularis* (L.) Roemer & Schultes, *Myriophyllum sibiricum* V. Komarov, *Potamogeton foliosus* Raf., *Ranunculus aquatilis* L., *Rorippa nasturtium-aquaticum* (L.) Hayek, *Sparganium emersum* Rehmann, and *Zannichellia palustris* L. *Zannichellia palustris*, *Elodea canadensis*, and *Callitriche hermaphroditica* were the dominant species (Spencer and Ksander 1998). In August 2003 a section of Fall River overflowed levees and flooded some 1,214 hectares (3,000 acres) of grazing lands (Fox 2003). A visit to Fall River within a week of this flood event revealed that large areas of the river were inhabited by Eurasian watermilfoil, a species that had not been observed in Fall River during the 1996 to 1997 surveys (Spencer and Ksander 1998). It appeared that Eurasian watermilfoil biomass had impeded the flow to such an extent that the flooding event resulted (Murphy et al. 1993). Eurasian watermilfoil has had other serious impacts on Fall River, and local groups interested in managing this aquatic weed requested answers to 2 questions likely to be posed by others faced with similar circumstances. One question concerned the potential for spread of Eurasian watermilfoil within Fall River. The 2nd question was what would likely be Eurasian watermilfoil's response to management using the biological control agent, the watermilfoil weevil (*Euhryciopsis lecontei* Dietz) (Sheldon and Creed 1995, Newman 2004). Our objective was to answer these questions using data on water quality, water temperature, and plant distribution from Fall River in conjunction with published quantitative information on the susceptibility of habitats to invasion by Eurasian watermilfoil (Madsen 1998) and temperature requirements for the watermilfoil weevil growth and development (Mazzei et al. 1999). This information will contribute to development of, and demonstrates the application of, predictive theories that can be used to set priorities for controlling invasive aquatic plants in this and other waterways (Rejmanek and Richardson 1996).

MATERIALS AND METHODS

Fall River is located in the northeastern corner of Shasta County, California [41°00′17″N; 121°26′18″W; elevation 1,014 m (3,327 f)] about 100 km northeast of Redding, CA (Figure 1). Fall River is a moderately sized, spring-fed, slow-flowing, meandering meadow stream. Being a spring-fed river means that Fall River does not fit in the standard river order classification system. Although Fall River originates from headwater springs, it does have 3 tributaries. Bear Creek joins the Fall River near the upper limit-to-navigation, Spring Creek enters at approximately 8 km downstream, and the Tule River joins Fall River at an additional 12 km downstream (Figure 1). Fall River's mean light extinction coefficient was 0.6 and a range of 0.4 to 0.8 for several sites on 25 August 2011 (D. F. Spencer, unpub. data). The shallow depths (< 6 m) mean that light penetrates to the sediment in most sections of the river.

We determined whether submersed aquatic plants were present or absent at 71 points in Fall River from the upstream limit-to-navigation to the downstream barricade at the power generating station (Figure 1) using a modification of the procedure described by Spencer and Ksander (1998). Although the points themselves were randomly selected, they were approximately 500 m apart within the river course that is approximately 35 river km (21 miles) long. On 31 August and 1 September 2009 and on 20, 21, and 22 July and 3 August 2010, we used a Global Positioning System digital camera and an underwater viewing device to collect images of the submersed plants and river sediments at these points. The underwater viewing device was held in place as a small boat powered with an outboard motor slowly traversed a rounded zigzag course downstream. In 2010, we collected a total of 9,037 images from the entire length of the river and in 2009, 4,268 images were collected from the upper 13 km of the river. Upon return to Davis, CA, the images were transferred to a desktop computer. As the images were viewed, the presence or absence of Eurasian watermilfoil was recorded. Using the distance formula (Batschelet 1973), we selected all images within a 100-m radius of each of the 71 sample points. Based on these images, the number of occurrences of Eurasian watermilfoil was divided by the total number of images within the 100-m radius to yield the frequency (proportion) which is a measure of relative abundance (Grieg-Smith 1983).

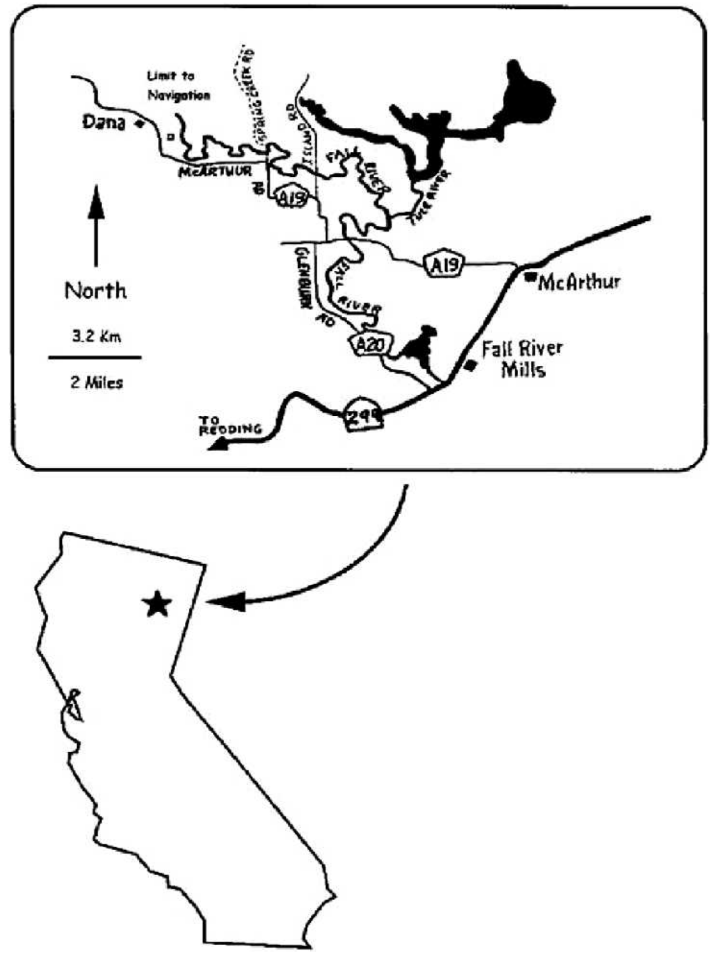

Figure 1. Map of Fall River, California, and vicinity.

On 15 dates between April 2010 and August 2011 (22 April 2010, 5 May 2010, 2 June 2010, 21 July 2010, 24 August 2010, 27 September 2010, 27 October 2010, 17 November 2010, 15 December 2010, 27 January 2011, 12 April 2011, 26 May 2011, 29 June 2011, 27 July 2011, and 25 August 2011), we collected 1-L (1.06 quarts) water samples at approximately 0.5-m depth at each of the 71 sites. The sites were arbitrarily designated as Sites 1 through 71, with Site 1 being the most downstream and Site 71 the most upstream location. Samples were placed in a portable cooler, returned to a field laboratory site where 250-mL aliquots were transferred to a smaller plastic bottle, and frozen. Frozen samples were stored and subsequently analyzed for total P using the alkaline persulfate digestion procedure described by Patton and Kryskalla (2003). A complete set of standards and deionized water blanks were run with each set of samples. Triplicate subsamples from each sample were analyzed and the mean value used in subsequent statistical and graphical analysis.

We deployed Hobo Pendant data loggers[1] at Sites 1, 8, 29, 36, 43, 50, 57, 64, and 71 between 6 June 2010 and 24 August 2011. Water temperature was recorded at 0.5-h intervals and stored within the data loggers, which were downloaded at irregular intervals. In order to have data equivalent to 1 calendar year, we treated the data from 25 August 2010 to 31 December 2010 as if it were recorded 1 yr later. Using the combined water temperature data from each location, we calculated degree-days for weevil development using the single-triangle method using equations described by Zalom et al. (1983). We used 9.8 C (49.6 F) as the lower temperature threshold and 31 C as the upper temperature threshold based on information from Mazzei et al. (1999). All calculations were done using SAS (SAS Institute Inc 2009). Using the degree-days calculated for each day, we examined 2 scenarios. In the midwestern United States, weevil oviposition does not begin until the water temperature is sustained above 15 C (Mazzei et al. 1999, Newman 2004); therefore, we first determined the accumulated degree-days between 1 June and 30 September and used these data to estimate the number of weevil generations for Scenario 1. This seems to be a reasonable scenario based on observations from Minnesota lakes that milfoil weevils begin to return to the water in May to June and move to the shore in September to November to overwinter (Newman et al. 2001). Since there is always the potential that weevil populations may evolve to more closely track the local environment or that milfoil weevils may respond differently to the Fall River environment than they do to those associated with lakes in Minnesota, we constructed a 2nd scenario for calculating the maximum number of weevil generations possible within a single year. Under this scenario (denoted Scenario 2) weevil oviposition and larval development were deemed to occur at any time throughout the year. While this is clearly very unlikely given winter snow cover and freezing conditions typical in this area, Scenario 2 may be said to represent the most favorable case scenario for weevil production along Fall River. Thus, the number of weevil generations estimated for Scenario 2 would be greater than the number of generations produced, if for example, weevils released in Fall River began oviposition 1 May instead of 1 June. For both scenarios the number of weevil generations produced was estimated by dividing the accumulated degree-days by 309 ± 18.8 (± SE), which is the measured level of accumulation required for a full weevil generation (Mazzei et al. 1999). To incorporate the standard error into these calculations, we performed 50 simulations where the standard error randomly varied between − 18.8 and + 18.8. These values were added to the mean value and the resulting sum was divided into the total number of accumulated degree-days.

We also used the Eurasian watermilfoil growth simulation model, MILFO (Best and Boyd 1999, Best et al. 2001), in conjunction with the water temperature data to estimate Eurasian watermilfoil biomass at 3 examples sites (Sites 1, 57, and 71) in Fall River. Site 1 was the most downstream sample location, Site 71 was the most upstream sample location, and Site 57 was the 1st temperature sampling location above the Spring Creek Bridge. MILFO simulates plant growth based on carbon uptake and respiration and includes the effects of a number of factors known to affect Eurasian watermilfoil biomass dynamics. Comparison of model simulations and actual Eurasian watermilfoil biomass values have been demonstrated to be in good agreement for scenarios that range from 1 to 5 growing seasons (Best et al. 2001).

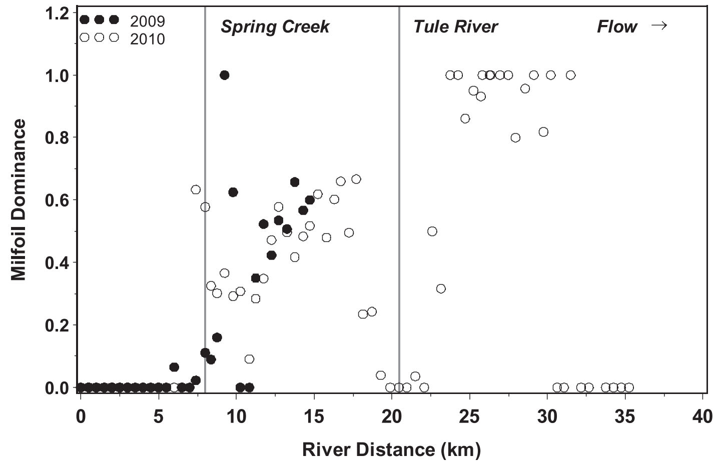

Figure 2. Dominance of Eurasian watermilfoil in Fall River, California, versus distance downstream from the limit-to-navigation in 2009 and 2010. The left vertical line represents the location of the confluence of Spring Creek with Fall River, and the right vertical line represents the location of the confluence of the Tule River with Fall River. These locations are indicated on the map of Fall River given in Figure 1.

RESULTS AND DISCUSSION

Eurasian watermilfoil was present in Fall River beginning 6 km downstream from the limit-to-navigation (Figure 2). Eurasian watermilfoil frequency generally increased from this initial point, until it decreased in the area of the confluence of the Tule River with Fall River. Below the confluence Eurasian water milfoil frequency was near 1 until a point about 3 km above the lower barricade.

The mean total P concentration across all sample sites and dates was 39 ± 21 μg L^{-1} (SD, $n = 1{,}018$). A total of 37 samples or 3.6% of the 1,018 measurements had total P concentrations < 10 μg L^{-1} (Figure 3). Thus, based on total P data and the information in Madsen (1998), Eurasian watermilfoil may be expected to occur throughout Fall River at locations from the upstream limit-to-navigation to the downstream barricade. Madsen (1998) examined 31 parameters associated with 102 North American lakes and reported that Eurasian watermilfoil dominance was most strongly related to total P in the water column. Madsen (1998) also reported that Eurasian watermilfoil dominance increased when total P values were > 10 μg L^{-1}. The fact that there is considerable evidence that rooted submersed plants obtain P required for growth from the sediment (Bole and Allan 1978, Barko et al. 1986) and the apparent relationship between total P concentration in the water and Eurasian watermilfoil dominance observed by Madsen (1998) may at first seem incongruous. However, Madsen (1998) pointed out that water total P may be an indicator of habitat fertility and this may explain the strong relationship between it and Eurasian watermilfoil abundance. This conclusion was also reached by Sager and Lachavanne (2009), who developed a trophic state index for predicting

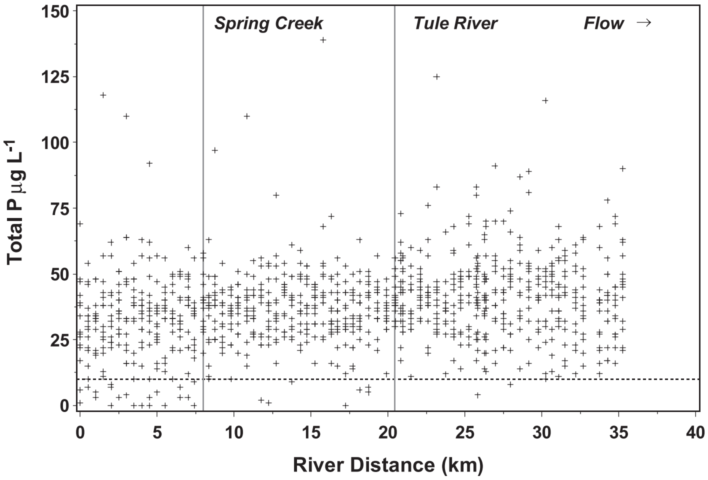

Figure 3. Total P concentration (μg L^{-1}) versus distance downstream for Fall River, California, between April 2010 and August 2011. The left vertical line represents the location of the confluence of Spring Creek with Fall River, and the right vertical line represents the location of the confluence of the Tule River with Fall River. These locations are indicated on the map of Fall River provided in Figure 1.

macrophyte occurrence in Swiss ponds. They evaluated several water quality parameters associated with macrophyte species in these ponds and found that total P concentrations in water samples were the best predictors of macrophyte species occurrence. Sager and Lachavanne (2009) concluded that while water column total P values did not represent all of the nutrients available for macrophyte growth, it was a reliable representative of the actual nutrient conditions prevailing in the pond and was thus useful for predicting macrophyte species occurrence.

There is evidence from other studies to support this interpretation as well. Bowes et al. (2005) reported that P and nitrogen were positively correlated in some English rivers that they examined. Haslam (1978) analyzed the distribution of plants in rivers in the United Kingdom in relation to water nutrient concentrations, and her findings indicated that Eurasian watermilfoil could be found in habitats with total P values of 0 to 3 mg L^{-1}. Dawson and Szoszkiewicz (1999) reported that Eurasian watermilfoil was frequently present in British rivers at locations where water column total P was high (> 1 mg L^{-1}). Sager and Lachavanne (2009) concluded that Eurasian watermilfoil occurrence was correlated with a trophic index based on the concentration of total P in pond water. According to Sager and Lachavanne (2009), Eurasian watermilfoil was associated with high levels of total P found in eutrophic conditions. Olson et al. (2012) analyzed the occurrence of Eurasian watermilfoil and water quality parameters for sites in a large Wisconsin reservoir. They reported that mean total P concentration was significantly ($P < 0.001$) related to the presence of Eurasian watermilfoil in sections of the reservoir. Similar findings were reported by O'Hare et al. (2010), who observed that biomass of the aquatic macrophyte *Ranunculus penicillatus* (Dumort.) Bab. in British rivers was strongly related to total P in the water column. Results from a field experiment also support the idea that water column total P is useful for predicting Eurasian watermilfoil

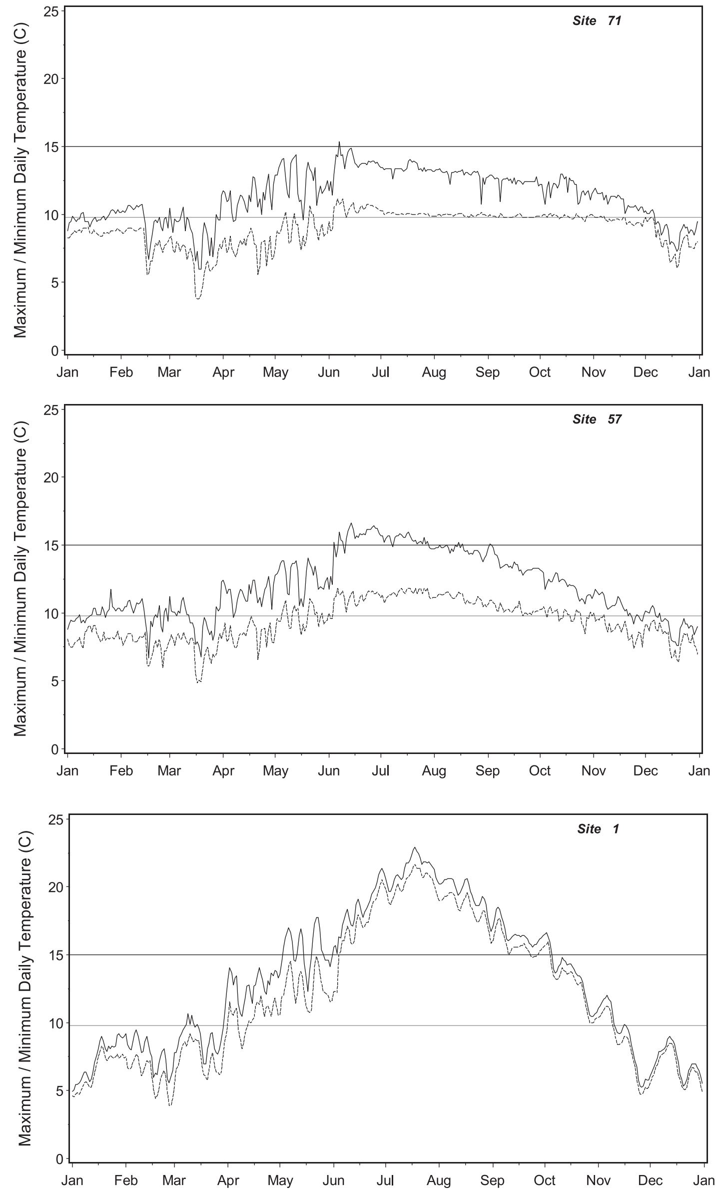

Figure 4. Minimum and maximum daily water temperatures over the course of 1 yr at 3 sites in Fall River, California. Site 1 is the most downstream sample location (distance 35.3 km), Site 71 is the most upstream sample location (distance 0), and Site 57 (distance 7 km) is the 1st temperature sampling location upstream of the Spring Creek Bridge near the confluence of Spring Creek with the Fall River. The lower horizontal line indicates 9.8 C, the lower temperature threshold for degree-day determinations. The upper horizontal line indicates 15 C, the threshold for initiation of Eurasian watermilfoil weevil oviposition.

occurrence. When total P concentrations in the water column of Conesus Lake, New York, was reduced, the Eurasian watermilfoil biomass declined by 30 to 50% (Bosch et al. 2009).

Simulated Eurasian watermilfoil biomass based on the physiologically based model, MILFO, increased with the distance downstream of the sampling site, likely reflecting increased water temperatures (Figures 4 and 5). Simulated Eurasian watermilfoil biomass at Site 1 was in the range of values reported from Fall River. Hunt (2009) sampled

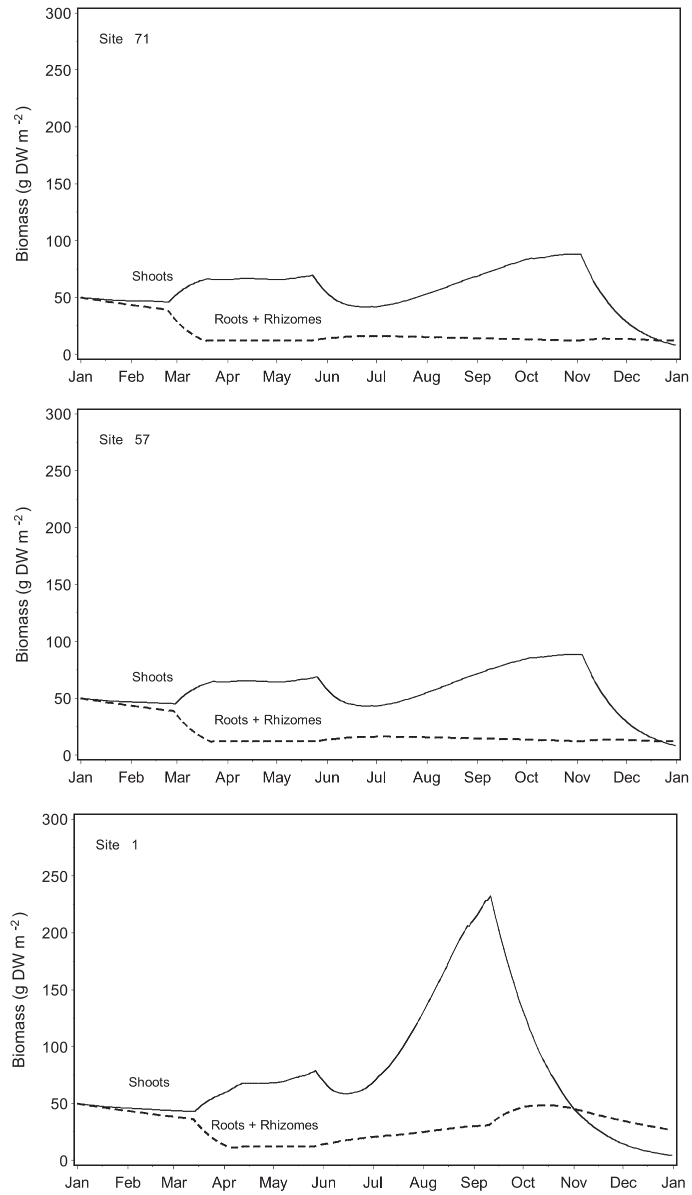

Figure 5. Simulated Eurasian watermilfoil biomass at 3 sites in Fall River, California, with differing annual water temperature patterns. Site 1 is the most downstream sample location, Site 71 is the most upstream sample location, and Site 57 is the 1st temperature sampling location upstream of the Spring Creek Bridge near the confluence of Spring Creek with the Fall River. These locations are indicated on the map of Fall River provided in Figure 1.

Eurasian watermilfoil biomass in 2005, 2006, and 2007, and reported that peak biomass at 2 sites that he designated as River Ranch and W1 was 437 g m^{-2} (318 to 556 g m^{-2}, 95% confidence limits) and 420 g m^{-2} (156 to 683 g m^{-2}, 95% confidence limits), respectively. Simulated biomass displayed maximum values in late summer/autumn. This agrees with Hunt (2009), who reported maximum biomass values in October in 2005, 2006, and 2007. This pattern is characteristic of Eurasian watermilfoil populations in lakes from more northerly U.S. locations (Adams and McCracken 1974, Perkins and Sytsma 1987) and likely reflects reduced growth at lower water temperatures. Interestingly, the simulated peak biomass occurred later in the year at more upstream sites characterized by cooler water temperatures. Simulation results indicate that while Eurasian watermilfoil biomass would be reduced at sites above Spring Creek Bridge, conditions were still favorable for Eurasian watermilfoil growth. The results of these simulations from a physiologically based growth model concur with the predictions made from total P values.

Thus, based on total P data and physiologically based growth simulations, Eurasian watermilfoil may be expected to occur in Fall River at locations from the upstream limit-to-navigation to the downstream barricade at the powerhouse. The likelihood of Eurasian water milfoil occurrence in areas upstream of Spring Creek Bridge is further supported by the occurrence of northern watermilfoil [*M. sibiricum* (V. Komarov)] in that portion of Fall River. In fact this is the only portion of Fall River inhabited by northern watermilfoil. Nichols and Buchan (1997) reported that Eurasian water milfoil was significantly positively associated with northern watermilfoil, occurring jointly in 24.4% of the habitats where northern watermilfoil occurred in Wisconsin lakes. Therefore, the conclusion that Eurasian watermilfoil could occur in that part of Fall River is supported by the occurrence of northern watermilfoil. It appears that the potential distribution for Eurasian watermilfoil is greater than its current actual distribution in Fall River. This conclusion agrees with results from experiments that compared the growth of Eurasian watermilfoil in sediments from a site above Spring Creek Bridge with those from a site below Spring Creek Bridge and showed that final dry weight did not differ between the 2 sediments (Hunt 2009).

The question arises then as to what may prevent Eurasian watermilfoil from achieving its potential distribution in Fall River. Aquatic plant distributions may be regulated by many factors, so it is risky to speculate about the importance of a single factor. However, it is quite common to observe that boats in Fall River create Eurasian watermilfoil fragments (Mumma et al. 1996) and transport a portion of them entangled with the propeller of the outboard/electric motors used to power boats traveling from one part of Fall River to another. This is likely to be a very important factor especially with regard to upstream movement. Thus, one barrier limiting Eurasian watermilfoil's distribution appears to be the bridge across Spring Creek Road. Due to the high water level, it is often not possible for a boat to pass under this bridge. This, in turn, greatly reduces the introduction of Eurasian watermilfoil fragments into the section of Fall River upstream of Spring Creek Bridge.

Fall River is rainbow trout (*Oncorhynchus mykiss*) habitat and as expected it is characterized by cool water temperatures most of the time with a mean temperature of 12 $\pm$ 4 C (SD $n = 187{,}075$). However, water temperature increases with distance downstream (Table 1). For Fall River, between the upstream limit-to-navigation and the confluence of the Tule River water temperature increased. Based on linear regression of mean daily water temperature versus distance downstream, the mean daily water temperature increased significantly ($P < 0.0001$) by 0.1 C km^{-1} of river distance.

TABLE 1. ACCUMULATED DEGREE-DAYS VERSUS DISTANCE DOWNSTREAM AT SELECTED SITES IN FALL RIVER, CALIFORNIA. SCENARIO 1 SHOWS ACCUMULATED DEGREE-DAYS ASSUMING THAT EURASIAN WATERMILFOIL WEEVIL OVIPOSITION AND DEVELOPMENT IS LIMITED TO THE INTERVAL BETWEEN 1 JUNE AND 30 SEPTEMBER. SCENARIO 2 SHOWS ACCUMULATED DEGREE-DAYS ASSUMING WEEVIL OVIPOSITION AND DEVELOPMENT MAY OCCUR AT ANY TIME THROUGHOUT THE YEAR. THE CONFLUENCE OF FALL RIVER AND TULE RIVER IS AT ABOUT 20 KM DOWNSTREAM. THE NUMBERS IN THE COLUMN LABELED "SITE" REFER TO SOME OF THE 71 SAMPLE SITES WHERE WATER SAMPLES WERE ALSO COLLECTED. ACCUMULATED DEGREE-DAYS WERE CALCULATED WITH A LOWER TEMPERATURE THRESHOLD OF 9.8 C AND AN UPPER TEMPERATURE THRESHOLD OF 31 C.

Site	Distance downstream (km)	Accumulated degree-days	
		Scenario 1	Scenario 2
71	0	220	317
64	3.5	334	466
57	7.0	374	483
50	10.3	484	610
43	13.8	537	677
36	17.3	654	815
29	21.0	1,005	1241
22	24.7	886	1121
15	27.0	961	1236
8	31.1	1,096	1377
1	35.3	1,055	1361

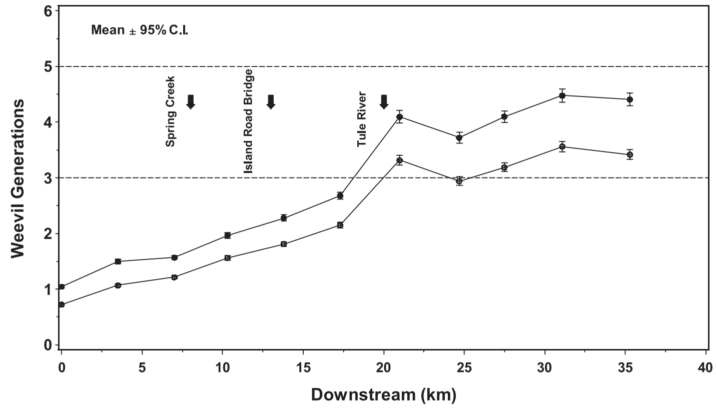

Figure 6. Estimated number of Eurasian watermilfoil weevil generations for a single growing season versus distance downstream from the limit-to-navigation in Fall River, California. The open dots represent values calculated assuming that weevil oviposition is limited to the interval between 1 June and 30 September, Scenario 1. The solid dots represent values calculated assuming that weevil oviposition may occur at any time, Scenario 2. A map of Fall River is provided in Figure 1.

The water temperature was noticeably warmer below the confluence with the Tule River, rising over 1 C on average. Below this point a similar linear regression of mean daily water temperature versus distance downstream indicated that the temperature did not increase significantly (0.001 C km^{-1}, $P = 0.7$). Water temperature was measured in locations between 1 and 2 m from the shoreline and in water that was 1 to 1.5 m deep. These temperatures are thought to be an accurate representative of those that occur along the length of Fall River. Differences in water temperatures across Fall River from one bank to the other would be expected to be small due to turbulent mixing (Moss 2010). Likewise, temperature stratification with depth has rarely been observed in rivers (Kalf 2002).

Temperature is thought to be an important factor driving the biological components of stream communities (Ward and Stanford 1982). Water temperature is especially important in determining the growth and development of aquatic insects (Brown and Fitzpatrick 1978, Sweeney 1978). Based on water temperatures at selected sites in Fall River, the number of accumulated degree-days for weevil development ranged from 220 to 1,096 under Scenario 1 and 317 to 1,377 under Scenario 2. Mazzei et al. (1999) reported that 309 ± 18.8 ($\pm$ SE) degree-days were required for the weevils to complete 1 generation (i.e., egg to adult). Combining this information with number of degree-days accumulated at the temperature measurement sites in Fall River indicates that the number of generations of weevils produced in Fall River would range from 0.7 yr^{-1} at the uppermost site to 3.6 yr^{-1} at the downstream sites for Scenario 1 (Figure 6). For Scenario 2, the number of generations would vary from a minimum of 1 at Site 71 to 4.5 at Site 8. In fact, for both scenarios the water temperature in Fall River is cool enough that fewer than 3 generations of weevils would be produced until a point 20 km below the limit-to-navigation (Figure 6). These results also agree with values calculated from other temperature data sets from Fall River. These data, collected at other sites and in different years, also indicate that 3 generations of weevils would not be achieved until a point below the confluence of the Tule and Fall rivers (Table 2). The number of generations possible in an area is useful for evaluating the likely effectiveness of a biological control agent (Mills 2005). Newman (2004) indicates that lakes in Vermont where the weevil has had an impact on Eurasian watermilfoil have produced at least 3 generations yr^{-1}, while those in similar Minnesota lakes produce up to 5 weevil generations yr^{-1}. Clearly the 3-generation threshold is not achieved upstream of the confluence of the Tule River under either Scenario 1 (the most biologically realistic scenario) or Scenario 2 (the scenario most favorable for weevil growth and development). This means that the weevil may not build up sufficient population density to noticeably impact Eurasian watermilfoil growing in Fall River upstream of that point. However, most of the area of Fall River where Eurasian watermilfoil occurs is upstream of this point. In fact, the portion of the river most heavily used by anglers is the section between Spring Creek Bridge and the confluence of the Tule River, so it is unlikely that stocking Fall River with watermilfoil weevils will improve the situation faced by anglers. If Eurasian watermilfoil successfully colonizes portions of Fall River upstream of Spring Creek Bridge and fully occupies its potential range in Fall River, then it is unlikely that the weevil will significantly impact it there due to the cooler water temperatures in this section of the river.

We may also be informed by a comparison of our results with simulations from a model of the interaction between Eurasian watermilfoil and the watermilfoil weevil. The model by Miller et al. (2011) is based on a growth model for Eurasian watermilfoil developed by Herb and Stefan (2006). Similarly with other models for this plant, this Eurasian watermilfoil growth model is driven by incident light and water temperature. For their simulations Miller et al. (2011) used light and water temperature data that are typical of a lake in southern Minnesota. Miller et al. (2011)

TABLE 2. MEAN NUMBER OF EURASIAN WATERMILFOIL WEEVIL GENERATIONS PER YEAR AT SITES IN FALL RIVER, CALIFORNIA. THE SITES ARE THOSE THAT CORRESPOND TO THE SITES USED IN THE PRESENT STUDY. THE NUMBER OF GENERATIONS WAS ESTIMATED USING THE SAME CONDITIONS AS WERE USED FOR SCENARIO 1 IN THIS STUDY. FOR REFERENCE THE TULE RIVER JOINS FALL RIVER AT APPROXIMATELY 20 KM DOWNSTREAM FROM THE LIMIT-TO-NAVIGATION.

Year	Distance downstream (km)	Scenario 1 (mean generations yr^{-1})	95% confidence limits	Site
2005[1]	2	0.66	0.65–0.67	67
2005[1]	8	0.93	0.92–0.95	55
1998[2]	9.8	1.18	1.08–1.13	51
2005[3]	9.8	1.27	1.24–1.29	51
2006[3]	9.8	1.22	1.20–1.24	51
2005[1]	13.3	1.48	1.45–1.50	44
2005[1]	19.9	0.87	0.85–0.88	31
2005[1]	25.7	2.95	2.89–3.01	20
2005[1]	30.2	3.11	3.05–3.16	10
2006[3]	30.2	3.14	3.08–3.20	10
2007[3]	30.2	2.44	2.40–2.47	10

[1]Sloat 2007.
[2]Spencer and Ksander 1998.
[3]Hunt 2009.

state that their model provided Eurasian watermilfoil biomass estimates that were within the reported range for natural stands of Eurasian watermilfoil. They also report that the model accurately reflected the phenology and seasonal variation in biomass that has been reported by others. Miller et al. (2011) conclude that the Eurasian watermilfoil/milfoil weevil model that they developed can be employed to optimize the utilization of the milfoil weevil as a biological control agent. Miller et al. (2011) base the age-structured population growth model of the milfoil weevil on information on reproductive and development rates and impacts provided by Mazzei et al. (1999) just as we did in this study.

Miller et al. (2011) reported that their model produced 6 weevil generations per growing season assuming conditions typical for a southern Minnesota lake. Under the various milfoil weevil stocking density scenarios (0, 10, 50, or 100 adult weevils m^{-2}) evaluated by Miller et al. (2011), the peak Eurasian watermilfoil biomass was 551, 433, 367, or 334 g m^{-2}, respectively. Thus, at the highest weevil stocking density (100 m^{-2}) Eurasian watermilfoil biomass was reduced to 61% of the levels attained when no weevils were stocked (i.e., 334 g m^{-2}/551 g m^{-2}). In other words, stocking 100 adult weevils m^{-2} resulted in a 39% reduction in predicted Eurasian watermilfoil biomass. This reduction is predicated on the production of 6 weevil generations per growing season. In the current study we found that water temperature data from Fall River implied that, at most, just over 4 generations of weevils would be produced at the most favorable site in Fall River under the most favorable scenario for weevil growth and development (Scenario 2). This site is upstream of the lower barricade that crosses Fall River just upstream of the powerhouse intake. Thus, the impact of the milfoil weevil on Eurasian watermilfoil biomass in Fall River may be expected to be less than the 39% reduction inferred from the model simulation reported by Miller et al. (2011). It is worth noting that the model developed by Miller et al. (2011) does not include the effect of fish predation on weevils even though it may be important in some habitats (Newman 2004). It is thus possible that the predictions from the Miller et al. (2011) model may actually overestimate the weevil's impact.

Spencer and Ksander (1999) observed that cool temperatures in another high-altitude California river, Truckee River, would only support production of 2 weevil generations, perhaps limiting the weevils' impact on Eurasian watermilfoil in this river. In Washington, weevils were found in lakes with average temperatures > 21 C and not found in lakes where the mean temperature was < 19 C (Tamayo et al. 2000). Newman (2004) concluded that weevil populations would not reach great enough densities in cold-water lakes (< 8 C) to control Eurasian watermilfoil. The extent to which weevil populations that may establish below the confluence of the Tule River with Fall River are likely to impact upstream Eurasian watermilfoil is difficult to gauge since the weevil's dispersal ability is unknown (Newman 2004).

There have been recent calls for the advancement of predictive aquatic plant management, including developing and evaluating models of aquatic plant invasions (Sytsma 2008). Increased understanding in this area would aid managers in setting priorities in where to begin management in a particular habitat and in determining which management techniques are most likely to be successful in a given habitat. Findings such as those reported here contribute to the development of these predictive capabilities by illustrating how they may be applied.

SOURCES OF MATERIALS

[1]Hobo Pendant data loggers, Onset Computer Corp., 470 MacArthur Blvd, Bourne, MA 02532.

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