

Short Communication

Eurasian watermilfoil fitness loss and invasion potential following desiccation during simulated overland transport

Christopher L. Jerde^{1*}, Matthew A. Barnes¹, Elise K. DeBuysser¹, Anna Noveroske¹,
W. Lindsay Chadderton² and David M. Lodge¹

¹ Center for Aquatic Conservation & Environmental Change Initiative, Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, USA

² The Nature Conservancy, Department of Biological Sciences, University of Notre Dame, PO Box 369, Notre Dame, IN 46556, USA

E-mail: cjerde@nd.edu (CLJ), mbarnes3@nd.edu (MAB), ecochick@stanford.edu (EKD), annanov@comcast.net (AN),
lchadderton@nc.org (WLC), dlodge@nd.edu (DML)

*Corresponding author

Received: 22 April 2011 / Accepted: 31 July 2011 / Published online: 19 September 2011

Handling editor: Thomas Therriault, Fisheries and Oceans Canada, Canada

Abstract

Vegetative reproduction promotes human-mediated dispersal of aquatic invasive plants as fragments “hitchhike” between water bodies on boats and trailers. However, desiccation of plant fragments may also reduce fitness, decreasing the likelihood of fragment survival as transport distances increase. Current inter-lake invasive species spread models do not directly consider fitness loss due to desiccation and mechanical damage of the transport pathway. Here, we estimate survival as a function of desiccation exposure for Eurasian watermilfoil (*Myriophyllum spicatum*). Following desiccation treatments, we monitored survival and root formation of individual fragments and assessed the differences between treatments. Highest survival rates occurred for short (< one hour) air exposures and coiled fragments with root production for the coiled treatment occurring in less than two weeks, irrespective of fragment length. In contrast, fragments that experienced desiccation for more than 24 hours had little risk of surviving. Our results emphasize the threat posed by same-day overland movements of boats from invaded to uninvaded waterways, and provide managers with a surveillance radius to inform delimitation surveys arising from the discovery of a new invasion.

Key words: Survival analysis; establishment; secondary spread; macrophyte

Introduction

Recreational boaters can unintentionally transport species (Johnstone et al. 1985; Johnson et al. 2001), including the seeds, fruits, or other reproductive structures of aquatic plants between lakes (Smith and Barko 1990), which can lead to new aquatic invasions. This pathway is particularly problematic when a clonal reproductive mode makes it possible for fragments, fouled on boat hulls and trailers, to initiate new invasions (Johnstone et al. 1985). However, overland transport will cause desiccation, and plants trapped between boats and their trailers may be crushed, presumably resulting in some loss of fitness. Importantly, fragments in bunches, or wrapped layers, may benefit from insulation to environmental

stressors and remain viable. Understanding the fitness loss caused by variable desiccation, crushing, and coiling of aquatic invasive plant fragments in the introduction pathway is critical for defining a “surveillance radius” around an invaded water body based on the likely maximum distances a plant could survive travel (Wilson et al. 2009).

Here, we present a study of the fitness loss of overland transport due to desiccation and mechanical damage of Eurasian watermilfoil, *Myriophyllum spicatum* (Linnaeus, 1753), an aquatic invasive plant commonly spread by fragmentation. Invasion by Eurasian watermilfoil (hereafter milfoil) has resulted in considerable negative consequences around the globe (Smith and Barko 1990), especially for native vegetation because milfoil colonizes rapidly and forms

dense canopies that limit light availability (Madsen et al. 1991). Although milfoil can reproduce and be spread by means of seeds through sexual reproduction (Hartleb et al. 1993), vegetative propagation and spread is considered the dominant mode by which milfoil has become widespread and invasive (Aiken et al. 1979; Hartleb et al. 1993).

In this study, we evaluated the change in survival and establishment potential of milfoil as a function of the environmental conditions fragments experienced during simulated overland transport. This evaluation will inform management efforts by aiding the identification of a “surveillance radius” around invaded lakes (i.e. lakes that are potential candidates to receive viable fragments via overland dispersal or lakes that could have acted as the sources of the original invasion). Additionally, we assess the change in survival due to variation of fragment length and the insulative effects of fragment coiling that is experienced when plant material wraps around a propeller shaft or is collected on anchors and nets.

Materials and methods

All milfoil specimens in this study were collected from the St. Joseph River in South Bend, Indiana (42°N, 86°W). Samples were collected between 8 July 2008 and 12 August 2008 from high-density (> 10 plants m⁻²) populations. Plants were transported to the lab and held in a cooler of river water, and all experiments were conducted within 24 hours of collection. No flower spikes were included, and branching segments were removed.

Anemometer readings taken at multiple locations where macrophytes potentially foul on the back of vehicles and trailers indicated that a vehicle traveling at 55 mph could expose fragments to average wind speeds of less than 10 mph. For conservative inferences, we targeted the minimum wind exposure recorded at the vehicle’s trailer hitch. For all experiments, a fan, which mimicked the airspeed exposure of approximately 7.5 MPH (SD 1.5), was used to desiccate the fragments. All experiments were conducted in a climate-controlled solarium. The average daily relative humidity was 40.1% (SD 8.33%), and the average ambient air temperature was 25°C (SD 1.01°C). Temperature and humidity settings reflect summer averages in northern Indiana.

We used four milfoil stem lengths (5, 10, 20, and 40 cm), each with 15 replicates (n = 60 fragments) to estimate desiccation rate. Trials began by blotting dry each fragment and recording the initial (wet) mass. We then positioned the fragments on a drying apparatus consisting of a mesh screen elevated eight inches above a table. We recorded the mass of each fragment every 15 minutes over four hours. Fragments were systematically rotated in proximity to the fan (0.25 m to 1 m). After 4 hours, fragments were oven-dried (40°C SD 3.2°C) for a minimum of one week to obtain a dry mass.

We fit the data to an exponential decay curve of the form $y(t) = a \exp(bt) + c$, where $y(t)$ is the mass of the fragment at time t , a is the initial wet mass, and c is the final dry mass. The desiccation rate parameter, b , was estimated by performing linear regression with a forced intercept through the origin under the transformation $\ln[(y(t) - c)/a] = bt$. We used one-way ANOVA to test for a difference in desiccation rate between the four fragment lengths.

For a separate group of milfoil fragments, we quantified how the weekly probability of establishment was affected by the degree of desiccation experienced. Here we considered milfoil established when the fragment produced roots that could ultimately allow for persistence of the individual. It is important to note that from a broader perspective, establishment of invasive populations is influenced by factors beyond the viability of individual propagules (e.g. habitat suitability, sufficient propagule pressure to overcome Allee effects in sexual species) (Jerde and Lewis 2007; Jerde et al. 2009) that are beyond the scope of our analysis. In the current study, after applying a desiccation treatment to a group of fragments, each individually labeled fragment was placed in a one-quart, glass canning jar with 2 mm² nylon mesh screen so fragments could be individually tracked and handled while being exposed to the same environment. Jars were submerged in 900L plastic troughs with circulating water. Two troughs were used during the experiment, and jars were moved within and between the troughs randomly after weekly inspections. Troughs were filled with well water, and water levels were maintained approximately 10 cm above the lids. The well water chemistry was pH=7.6, nitrates=5.7 ppm, orthophosphate=0.09 ppm, and total alkalinity=300 ppm. Water temperature fluctuated between 19.5°C (min) and 25.2°C

Table 1. Desiccation treatments, sample sizes, and fate of milfoil fragments. Times in the Treatment column indicate length of desiccation period. Over the course of the experiment, no fragments died after forming roots, so we consider root formation as an “alive” absorbing state.

Experiment		Fate	
Treatment	Sample size	Dead	Alive
Control	100	20	80
1 hour	100	71	29
3 hour	50	50	0
5 hour	100	100	0
24 hour	100	100	0
Crushed Control	30	29	1
Coiled Control	14	0	14
Coiled 1 hour	30	0	30
Coiled 3 hour	30	2	28
Coiled 5 hour	30	23	7

Table 2. Models, hypotheses, number of parameters, log-likelihood values, and the corresponding p-value of the likelihood ratio test with reference to the null model (m_0).

Model	Hypothesis	No. Of Parameters	Log-Likelihood	LRT (m_0) p-value
$m_0: g(x)=\beta_0$	No effect of length or treatment	1	-175.719	--
$m_1: g(x)=\beta_0 + \beta_1(\text{Treatment})$	Treatment effect only	2	-175.519	0.53
$m_2: g(x)=\beta_0 + \beta_2(\text{Length})$	Length effect only	2	-175.709	0.89
$m_3: g(x)=\beta_0 + \beta_1(\text{Treatment}) + \beta_2(\text{Length})$	Length and treatment effects	3	-175.518	0.81

(max), mimicking the daily summer water temperature fluctuations in shallow backwaters. We monitored the fate of each fragment over a maximum of 8 weeks.

Ten treatments were applied to milfoil fragments (Table 1). “Control” fragments (no desiccation) were only removed from water to measure the length of the fragment, ranging in 1-cm increments from 3-22 cm. Fragment lengths in this study were selected based on lengths and weights reported in Rothlisberger et al. (2010), which surveyed the macrophytes fouled on recreational boats. Additional un-crushed treatments were one, three, five, and twenty-four hour desiccation. “Crushed” control treatments of 5, 10, and 15 cm length fragments, were pressed between boards covered with the marine cloth commonly used to cover the slide and bumper rails of boat trailers. We applied approximately 180 kg across a 0.5 meter surface to the fragments for 5 minutes – this simulated the pressure experienced between a 4.25 m aluminum jon boat (flat bottomed) with a boat motor loaded onto a trailer with two static bumpers. The crushed fragments were not

desiccated. In addition, “coiled” fragments between 25 and 65 cm in length were wrapped around one-inch PVC tubing to simulate being encircled around a boat’s propeller. The length of the segment ensured at least three overlapping strands of the milfoil fragment. We ran a control (i.e. quickly wrapped, with minimal time out of water) and 1, 3, and 5-hour desiccation treatments for coiled fragments. Environmental conditions were the same as those experienced during the desiccation rate measurements.

At weekly intervals, each plant fragment was categorized as having root growth, dying, or exhibiting no change. Death was determined by the absence of discernable plant morphology (i.e. leaves or stem) and chlorophyll (i.e. green appearance). During the experiment, no plants growing roots subsequently died. Consequently, we considered root formation and dying as absorbing states (a state from which the fragment cannot transition from).

The objective of the survival study was to estimate the weekly transition probabilities of fragments going from no change to roots, no change to death, and no change to no change. A

multinomial distribution described the transition from the initial fragments to next week observations,

$$\Pr(X_1 = x_1, X_2 = x_2, X_3 = x_3) = \frac{n!}{x_1!x_2!x_3!} p_1^{x_1} p_2^{x_2} p_3^{x_3}$$

where X_1 is the number of fragments observed to set roots, X_2 is the number of fragments observed to die, X_3 is the number of fragments observed to have no change, n is the total number of fragments in the experiment, p_1 is the probability of a fragment forming roots, p_2 is the probability of a fragment dying, and $(1-p_1-p_2)=p_3$ is the probability of a fragment demonstrating no change. Only fragments that have no observed change in state can transition to the next time step. The likelihood estimates are found by maximizing a conditional probability chain (Appendix 1).

For treatments with variable fate (survival or death), we evaluated if fragment length was a significant explanatory variable. We used logistic regression for each treatment and performed a likelihood ratio test (LRT) for significance. The area under the curve (AUC) was also calculated as a diagnostic measure of the model robustness (Hosmer and Lemeshow 2000). Fragment length may influence the timing (week) during which roots form. Therefore, we used a geometric distribution to model the waiting time (T) until roots were produced with a logit link function such that,

$$\Pr(T = t) = \theta(1 - \theta)^{t-1}$$

$$\theta = \frac{\exp[g(x)]}{1 + \exp[g(x)]}$$

where θ is the weekly probability of establishing roots and $g(x)$ denotes the linear covariate models used to assess treatment and length effects. Models and hypotheses are listed in Table 2. LRT was used to evaluate the significance of the covariates. Small sample size of the coiled fragments precluded similar analysis.

All established fragments from the survival experiment were removed after 8 weeks. New growth was dissected away from the original fragment and desiccated in a drying oven, and the final dry mass was recorded. Dividing the dry mass by the time since root establishment gives an estimate of the weekly rate of growth for all treatments for which roots were produced.

Results

The relationship between fragment mass and drying time resembled an exponential decay curve, with mass loss occurring quickly at first and slowing over time as fragments approached their final dry mass (Figure 1A). Indeed, we observed that milfoil leaves became brittle after as little as 15 minutes of air exposure. Generally, stems became brittle within an hour, but there was noticeable variability depending on the diameter of the stem. Over 85% of water loss occurred within 3 hours. Fragment desiccation rate was independent of the length of the fragment (Figure 1B, p-value=0.17).

All individual fragments in 3, 5, and 24-hour desiccation treatments died, as did all but one crushed fragment (Table 1). In contrast, 80% of non-crushed control and 29% of the 1-hour desiccation fragments established roots (Figure 2A). The fates of all fragments were determined within 8 weeks, and control fragments had a significantly higher weekly probability of root establishment than one-hour desiccation fragments (LRT, p-value<0.01). Of the coiled treatments, all control and 1-hour desiccation fragments survived and established roots (Table 1). Additionally, coiled fragments that received 1 hour of desiccation were found to establish roots more quickly than control fragments (Figure 2B). Although coiled 3 and 5-hour desiccation treatments demonstrated higher mortality, some fragments did establish roots (Figure 2C).

Of the treatment groups, only the control fragments, 1-hour desiccation fragments, and 5-hour desiccation of the coiled fragments had variability in fate sufficient to explore the influence of fragment length. For both the control (p=0.013) and the 1-hour desiccation (p<0.01), fragment length was a significant explanatory variable (LRT). In both cases, smaller fragments (<5 cm) had reduced survival. However, the AUC for the control was 0.674 and for the 1-hour desiccation was 0.705, indicating there is not a clear threshold below which all small fragments die. The 5-hour coiled treatment did not have a significant effect of fragment length (p=0.20, AUC=0.658). Treatment and length effects did not significantly explain the timing of root production (Table 2). For all surviving fragments, the mean time of root establishment from the null model (m_0) was 2.4 weeks with 93.6% of the roots establishing by the end of the fifth week.

Desiccation of milfoil in simulated overland transport

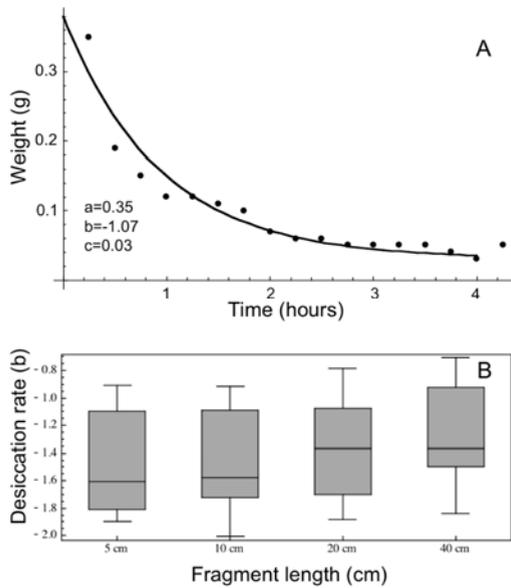


Figure 1. Desiccation of milfoil fragments. (A) For a 5 cm fragment of milfoil the wet mass was 0.35g (a) and the dry mass was 0.03g (c). The estimated desiccation rate parameter (b) was -1.07. After two hours of desiccation, the fragment lost over 90% of its wet mass. (B) Across the four different fragment lengths, no significant difference existed in the desiccation rate (ANOVA, $p=0.17$).

Average dry mass growth between the six groups of fragments that established roots was similar, excluding coiled fragments that received 1 hour of desiccation (Figure 3). All of the 1-hour desiccated coils set roots within 2 weeks (Figure 2B).

Discussion

Understanding the spatial patterns of human-mediated dispersal of invasive species is fundamental to the development of management strategies to prevent further spread (Wilson et al. 2009). For effective management, early detection and delimitation surveys are needed to evaluate the extent or identify the source of an invasion (Lodge et al. 2006). Coupling survival to distance traveled by a boater can determine a surveillance radius from which a fragment likely arrived from or dispersed to. Plants that desiccate quickly, resulting in increased probabilities of death, would intuitively require smaller search radii than plants that can resist desiccation (Panetta and Lawes 2005). For fragmenting plants, desiccation rate is likely a critical indicator of spread potential and

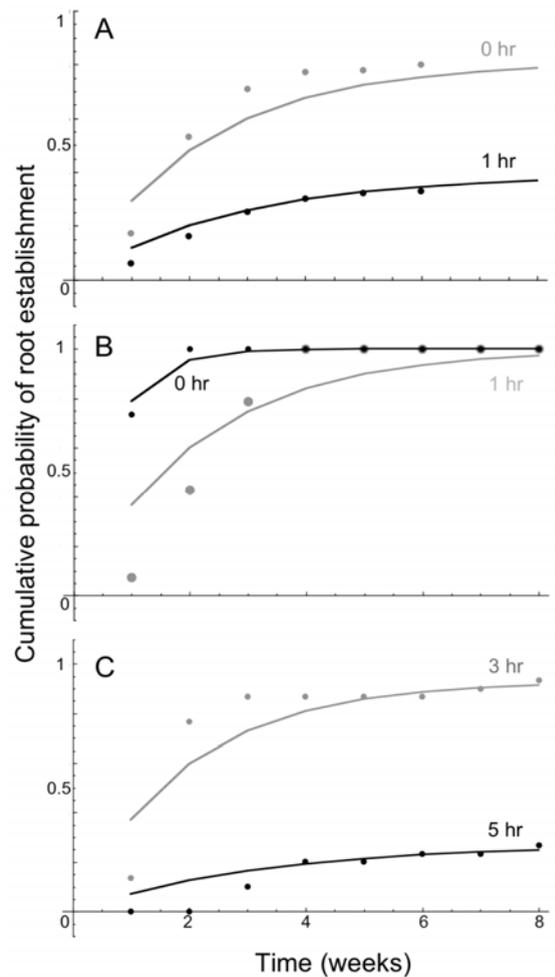


Figure 2. Establishment curves as a function of time for desiccation treatments of Eurasian watermilfoil fragments. Solid lines are from the maximum likelihood estimates of the survival analysis, and points are proportions observed from the experiment. (A) The gray line is the weekly cumulative survival of control fragments and the black line is the weekly cumulative survival of fragments desiccated for one hour. Lines for 3, 5, and 24 hour desiccation treatments are not shown as there was no survival. (B) Control (gray) and one hour desiccation (black) treatments for coiled fragments. All fragments survived and eventually established roots, although the one hour desiccation treatment established earlier. (C) There was increasing mortality of coiled fragments desiccated for three (gray) and five hours (black) but surviving fragments did establish roots.

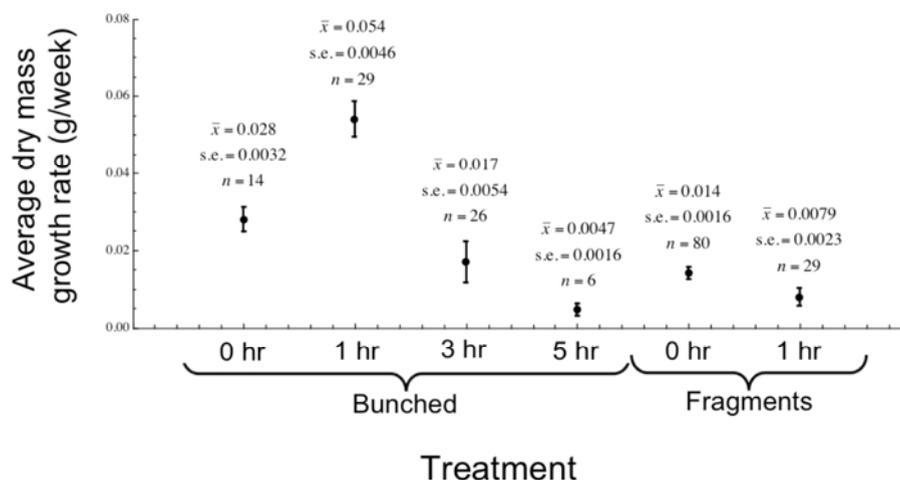


Figure 3. Average dry mass growth rate for the six treatments in the survival analysis with viable fragments. All treatments resulted in average dry mass growth rates less than 0.04 grams per week with the exception of coiled (bunched) fragments that were desiccated for one hour. These fragments also established roots much earlier than the coiled control fragments (Figure 2). Bars indicate standard errors of the estimate.

invasiveness that, when measured and related to boat movement patterns, can inform conservation managers as to the distance (time) traveled from a source to a new incursion. This approach would provide an additional management consideration for preventing or containing the secondary spread of invasive species (Johnstone et al. 1985, Vander Zanden and Olden 2008)

The results of our study suggest that milfoil desiccation during transport significantly reduces the viability of plant fragments and is a mechanism that may explain why boater movement alone does not predict milfoil spread (Rothlisberger and Lodge 2010). For single fragments, we demonstrated significant fitness loss after one hour of desiccation, although even small fragments (<5 cm) were capable of surviving air exposure and setting roots. Indeed, Rothlisberger et al. (2010) found that the majority of plant fragments recovered from trailered boats are small (<10 cm). Other research has shown that the distance to the nearest invaded lake is the strongest predictor of milfoil invasion (Roley and Newman 2008), a pattern consistent with the impacts of desiccation demonstrated in our study. Additionally, root setting and growth appeared to be stimulated in coiled plant fragments by short (i.e. one hour) desiccation. This response enhances establish-

ment potential and further emphasizes the invasion risk posed by short overland boat movements.

Our results suggest that singular fragments attached to boats and trailers are unlikely to be responsible for the invasion of distant lakes. Instead, the “fat tail” of the redistribution kernel, which is the driver of fast spreading non-indigenous species (Kot et al. 1996), is most likely due to fragments that remain insulated during transport, either because of the mass of material being transported or because plants are coiled or bunched in nets, traps, around anchors, propellers or in live wells and bait buckets. Alternatively these jump dispersal events may result from introductions through other pathways, such as contamination in horticultural trade (Maki and Galatowitsch 2004).

Johnstone et al. (1985) conducted similar desiccation experiments on a number of aquatic plants, but not Eurasian watermilfoil. Their experimental procedure did not include simulated overland transport of fragments, but rather 25 cm fragments were exposed to shaded conditions at 20°C and 50% humidity. Nevertheless, milfoil fragments in our study showed the same trend of decreasing survival probability as the plant becomes more desiccated. In contrast to Johnstone et al. (1985),

we did not see a significant effect of fragment length on survival. However, both studies support the general conclusion that short distance, or duration, movements of recreational boaters represent a threat to spread and establishment of aquatic weeds.

Our experiments considered a single set of environmental conditions, and we expect that different temperatures and humidity levels would change the outcome of our treatments. For instance, higher temperatures and lower humidity levels would probably yield faster desiccation rates and lower probability of fragment survival across all treatments. Along this line of thinking, seasonal conditions may be worth considering when thinking about aquatic plant invasion management practices. We would expect that cooler, humid periods would increase the likelihood of hitchhiking plant survival as well as the distance fragments could travel compared to hot, dry periods. Similarly, rainy days may allow plant fragments to travel long distances, regardless of temperature. Additionally, depending how the fragment is insulated during transport, the wind exposure and resulting desiccation rate will vary. Fragments that are protected in anchor and live wells, covered by boat tarps, or otherwise shielded from desiccation will remain viable for longer periods of out of water exposure. This is exemplified by the increased survival of coiled fragments. Depending on the occurrence of such desiccation protected boat fouling, the radius of surveillance for milfoil, or any other aquatic hitchhiker, will need to be increased.

Nevertheless, the success of some (and sometimes many) fragments in our study bolsters the value of adopting containment strategies (e.g. boat washing facilities) at invaded lakes and uninvaded neighboring lakes within short (e.g. 1 hour) travel distances (Rothlisberger et al. 2010). However at larger scales, effective prevention of long distance invasion events relies on inspecting and intercepting boaters carrying macrophytes that are insulated from desiccation effects (Johnson et al. 2001).

In developing predictions of the spatial patterns of invasions, it is important to consider life history attributes of an invading species, the nature of the receiving environment, and propagule pressure (Vander Zanden and Olden 2008). Our results reinforce the need to better understand how species respond to the stresses imposed by different invasion pathways. We have demonstrated the type of basic life history

research needed to develop a delimitation (surveillance) radius and other practical management strategies for Eurasian watermilfoil. Future studies should explore the fitness costs of overland dispersal in other macrophyte species and invasive aquatic invertebrates. Furthermore, evaluation of the extent to which fragmentation represents the dominant dispersal pathway will also help us understand the secondary spread of aquatic invasive species (Vander Zanden and Olden 2008).

Acknowledgements

This work was supported by the U.S. Army Corps of Engineers (W912HZ-08-2-0014), the National Fish and Wildlife Foundation (2008-0063-011), and NOAA CSCOR (#NA09NOS4780192). MAB was partially supported by a Center for Aquatic Conservation fellowship. Thank you to J McNulty.

References

- Aiken SG, Newroth PR, Wile I (1979) The biology of Canadian weeds 34. *Myriophyllum spicatum* L. *Canadian Journal of Plant Science* 59: 201–215, <http://dx.doi.org/10.4141/cjps79-028>
- Hartleb CF, Madsen JD, Boylen CW (1993) Environmental factors affecting seed germination in *Myriophyllum spicatum* L. *Aquatic Botany* 45: 15–25, [http://dx.doi.org/10.1016/0304-3770\(93\)90049-3](http://dx.doi.org/10.1016/0304-3770(93)90049-3)
- Hosmer DW, Lemeshow S (2000) Applied Logistic Regression, 2nd Edition. Wiley Inter-Science, New York, 373 pp, <http://dx.doi.org/10.1002/0471722146>
- Jerde CL, Lewis MA (2007) Waiting for invasions: A framework for the arrival of non-indigenous species. *American Naturalist* 170: 1–9, <http://dx.doi.org/10.1086/518179>
- Jerde CL, Bampfyld CJ, Lewis MA (2009) Chance establishment of semelparous, sexual species: Overcoming the Allee effect. *American Naturalist* 173: 734–746, <http://dx.doi.org/10.1086/598496>
- Johnson LE, Ricciardi A, Carlton JT (2001) Overland dispersal of aquatic invasive species: A risk assessment of transient recreational boating. *Ecological Applications* 11: 1789–1799, [http://dx.doi.org/10.1890/1051-0761\(2001\)011\[1789:ODOAIS\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2001)011[1789:ODOAIS]2.0.CO;2)
- Johnstone IM, Coffey BT, Howard-Williams C (1985) The role of recreational boat traffic in interlake dispersal of macrophytes: A New Zealand case study. *Journal of Environmental Management* 20: 263–279
- Kot M, Lewis MA, van den Driessche P (1996) Dispersal data and the spread of invading organisms. *Ecology* 77: 2027–2042, <http://dx.doi.org/10.2307/2265698>
- Lodge DM, Williams SL, MacIsaac H, Hayes K, Leung B, Reichard S, Mack RN, Moyle PB, Smith M, Andow DA, Carlton JT, McMichael A. (2006) Biological invasions: recommendations for U.S. policy and management. *Ecological Applications* 16: 2035–2054, [http://dx.doi.org/10.1890/1051-0761\(2006\)016\[2035:BIRFUP\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2006)016[2035:BIRFUP]2.0.CO;2)
- Madsen JD, Sutherland JW, Bloomfield JA, Eichler LW, Boylen CW (1991) The decline of native vegetation under dense Eurasian watermilfoil canopies. *Journal of Aquatic Plant Management* 29: 94–99

- Maki K, Galatowitsch S (2004) Movement of invasive aquatic plants into Minnesota (USA) through horticulture trade. *Biological Conservation* 118: 389–396, <http://dx.doi.org/10.1016/j.biocon.2003.09.015>
- Panetta FD, Lawes R (2005) Evaluation of weed eradication programs: The delimitation of extent. *Diversity and Distributions* 11:435–442, <http://dx.doi.org/10.1111/j.1366-9516.2005.00179.x>
- Roley SS, Newman RM (2008) Predicting Eurasian watermilfoil invasions in Minnesota. *Lake and Reservoir Management* 24: 361–369, <http://dx.doi.org/10.1080/07438140809354846>
- Rothlisberger JD, Chadderton WL, McNulty J, Lodge DM (2010) Aquatic invasive species transport via trailered boats: what is being moved, who is moving it, and what can be done. *Fisheries* 35: 121–132, <http://dx.doi.org/10.1577/1548-8446-35.3.121>
- Rothlisberger JD, Lodge DM (2010) Limitations of gravity models in predicting the spread of Eurasian watermilfoil (*Myriophyllum spicatum*). *Conservation Biology* 25: 64–72, <http://dx.doi.org/10.1111/j.1523-1739.2010.01589.x>
- Smith CS, Barko JW (1990) Ecology of Eurasian watermilfoil. *Journal of Aquatic Plant Management* 28:55–64
- Vander Zanden MJ, Olden JD (2008) A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic Science* 65: 1512–1522, <http://dx.doi.org/10.1139/F08-099>
- Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: Dispersal pathways affect invasion success. *Trends in Ecology & Evolution* 24: 136–144, <http://dx.doi.org/10.1016/j.tree.2008.10.007>

Supplementary material

The following supplementary material is available for this article.

Appendix 1. The likelihood function for survival analysis.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2012/Supplements/AI_2012_1_Jerde_etal_Supplement.pdf