INTRODUCTION

The use of integrated ecological and economic policy impact assessments is expanding (NRC 2004; Ruhl et al. 2007; Ranganathan et al. 2008; Koshel and MacAllister 2008), in part because the people who are affected by environmental policies and those who provide the resources for policy interventions are increasingly asking for evidence that environmental conditions and human well-being are in fact improved by the actions that are taken. Thus there is increasing demand for scientific analysis of the outcomes of environmental policies, using rigorous standards of data and modeling. On the supply side, the economics of ecosystem management is a fast-moving field of interdisciplinary science that is revealing new understanding of the interactions of people and nature (Kremen 2005; Barbier et al. 2008; Daily and Matson 2008; Maler et al. 2008). Yet many questions remain unanswered about the social, economic and ecological factors that determine the success or failure of environmental policies. In particular, there appears to be a growing gap between the theoretical/conceptual modeling of social-natural systems, and the data-driven application of these models to real-world systems. Such applications are at the core of induction about the general and specific features of coupled human-natural systems, and consequently serve as the basis for altering and refining environmental policies for these systems.

The effect of public policy on ecosystem services is complex (NRC 2002, 2004; MA 2005) not only for the obvious reason that ecosystems are complex, but also because a policy’s effect is filtered by the private decisions of individuals and households. In other words, the policy of the collective or the state is ultimately interpreted by the individual, often with unintended ecological consequences. It follows that good policy analysis –within coupled human-natural systems or otherwise—must correctly frame the effect of the policy on the behavior of individuals, and that induction about coupled human-natural systems must draw from quantitative empirical studies that carefully model the behavior of individuals actually using ecosystem services.

An important example is the problem of aquatic species invasions. Many invaders are spread among water bodies principally by boating, and so managing aquatic invasive species (AIS) requires close attention to how management policies affect boater behavior. We propose to develop a new approach to modeling the spatial dynamics of an aquatic species invasion that tightly integrates an empirical economic model of boater trip behavior with innovative research regarding invader dispersal, ecosystem suitability and economic and ecological impacts. The analysis focuses on the feedbacks within this coupled human-natural system, with particular focus on the effect of management activities to control/prevent an invasion on boater trip decisions and short-term boater welfare, and the subsequent impacts of changes in boater trip behavior on the spread of the invader and the consequent long-term welfare of boaters and other lake users. The analysis addresses a number of important policy questions that are summarized by the overarching question:

How do policy interventions intended to control or prevent harmful aquatic species invasions affect the decisions and economic welfare of individuals using the relevant resource, and the spatial dynamics of invasions on heterogeneous landscapes?

The model will be applied to aquatic species invasions in a region (the Northern Highland Lake District of Wisconsin and Upper Michigan) where species invasions are a pervasive driver of
ecosystem change (Magnuson et al. 2006; Carpenter et al. 2007). Although our analysis focuses on AIS in a particular lake district, the issue is far from a local problem. Globally, invasive species rank as a leading threat to native species and biodiversity (Wilcove et al. 1998; Sala et al. 2000), and are an important driver of global environmental change (Vitousek et al. 1996; Mack et al. 2000). Of all major ecosystems in the world, lakes are expected to be the most affected by species invasions (Sala et al. 2000; Claudi and Leach 2000), because the discrete boundaries of lakes create a landscape of small, closed systems sensitive to disruptions. Economic damages associated with invasive species and their control in the U.S. alone has been estimated at $120 billion/year (Pimentel et al. 2005), though there are few studies of the economic costs of aquatic species invasions; as noted by Lovell et al. (2006) in their review of the literature on the economics of aquatic invasive species, “[T]he literature is still in its infancy” (pg. 205).

MODEL OVERVIEW

An important aspect of AIS management is the role humans play in their dispersal. For the spread of AIS among inland lakes, the typical pathway for dispersal is boaters moving from lake to lake (Padilla et al. 1996; Johnson et al. 2001). We propose to develop and estimate a spatial dynamic model of species invasions within a freshwater lake system in which a set of managing agents is concerned with the inter-seasonal spread of invasive species across lakes (where a season is defined in this case as the annual boating season), and recreational boaters/anglers make a series of intra-seasonal trip decisions to maximize random utility during the course of the season, subject to the actions taken by the manager.

A schematic of the model is presented in Figure 1. Several aspects of the model are worth emphasizing. First, at the start of each season managing agents choose a set of controls (management actions) to solve a stochastic dynamic decision problem. These decisions are based on the spatial distribution of AIS within the lake district as well as the abundance of AIS within individual lakes. Controls may be chosen in anticipation of the reaction of both the invasive species and boaters to the controls. Possible controls include actions to reduce or eliminate invasive species on certain lakes (such as herbicide applications to control Eurasian watermilfoil), closing some lakes to boater access, charging an access fee at boat ramps to fund invasive species programs, and requiring boaters to wash their boats before entering or leaving the lake area. Second, boater trip decisions are captured by a random utility model in which, on each day of the season, a boater maximizes utility by choosing to boat on one of the lakes in the system, or stay home. Boater utility from a trip depends on lake attributes, including attributes affected by AIS, as well as the controls chosen by the manager. Importantly, the trip decision is stochastic from the perspective of the analyst (it is not possible to perfectly predict the trip decision of a boater). And third, boaters are inadvertent vectors for the spread of the invasive species. Thus, the spread of the species is a stochastic process that depends upon the life history of the invader, the suitability of the recipient ecosystem, management controls, and the decisions of boaters throughout the season. Adequately examining the range of management options requires modeling three stochastic events concerning the dispersal of the AIS: propagule uptake, transport to a new ecosystem, and establishment. Propagule uptake is the removal of a live propagule from an infested lake. The probability of this event depends on invader abundance in the lake, which itself depends on lake characteristics and control efforts on the lake. Transport is the movement of live propagules to an uninvaded lake. It depends on the ability of the propagule to survive out of the lake and the trip decisions of the boater. Establishment is the successful colonization of an uninvaded lake by live propagules transported to the lake. This depends on the frequency of live propagule introductions and the attributes of the lake. Each event is drawn
from a probability density function (PDF), and together these PDFs generate the probability of dispersal from an infested lake to an uninfested lake conditional on boater trip decisions.

The upshot is that the stochastic dynamics of the model take place on two time scales. An *intra*-seasonal portion of the model accounts for the intra-seasonal variability in abundance of AIS, the day-to-day decisions of boaters, and the implications of these decisions for the frequency of live propagule transport to uninvaded lakes. An *inter*-seasonal portion of the model accounts for the seasonal decisions of managers and the implications of these decisions for the spread of the invasive species across lakes. Manager decisions that may be harmful to boater welfare in the short run—that is, within the season affected by the decision—could be beneficial to boaters in the long run, via the long-term effects of the control on the spread of the invader.

![Figure 1. Schematic of the Model](image-url)
SCIENTIFIC CONTRIBUTION IN CONTEXT

Early literature highlighted the unpredictability of species invasions (Orians 1986; Pimm 1989). Fortunately, there has been significant progress in predicting invasions during the past decade (Kolar and Lodge 2001; Vander Zanden and Olden 2008), thus allowing managers to target monitoring and prevention efforts to species and vectors that are of greatest concern (Ricciardi and Rasmussen 1998; Kolar and Lodge 2002; Marchetti et al. 2004).

Two different approaches have been used to predict AIS invasions: those that focus on habitat suitability, and those that focus on propagule pressure. Very few studies have combined these aspects into the sort of integrated analysis proposed here (but see Leung and Mandrak 2007; Vander Zanden and Olden 2008). Ecological niche modeling has been used to model site suitability for specific invaders (Peterson and Vieglaís 2001; Peterson 2003). A simple approach is to classify lakes as suitable/unsuitable based on an environmental threshold for species survival. For example, zebra mussels require dissolved Ca\(^{+}\) concentrations above 15 mg/l (Sprung 1987; Ramcharan et al. 1992; Mellina and Rasmussen 1994). Studies more typically use statistical approaches such as logistic regression and classification and regression trees (CART) to relate species occurrence to environmental variables (Mercado-Silva et al. 2006). Those lakes with model false presences (i.e., species predicted, not observed) are considered ‘vulnerable’ to invasion based on environmental/habitat conditions.

Introduction of propagules to an ecosystem is necessary for an invasion, and it is generally accepted that the probability of establishment increases with propagule pressure or the number of propagule introduction events. Where boating and human activity are responsible for invasive species transport, variables that reflect the intensity of human activity (housing density, presence and number of roads and boat launches) have been used as indicators of invasive species propagule pressure (Johnson et al. 2008). Gravity models (GMs) currently dominate the ecological literature on forecasting the force of attraction between an origin (e.g., invaded lake) and a destination (e.g., noninvaded lake) (see Schneider et al. 1998; Bossenbroek et al. 2001; Leung et al. 2004; MacIsaac et al. 2004; Leung et al. 2006). Gravity models have provided great insight into the spread of invasive species. Unlike standard diffusion models, they can account for the “leapfrogging” of an invasive species that arises because the attractiveness of a lake to boaters depends on more than merely the travel distance to the lake, and in general they achieve higher accuracy and precision than diffusion models (MacIsaac et al. 2004). Moreover, they use relatively little data that is relatively inexpensive to obtain.

In this research we plan to develop a different type of model of boater movement to forecast the spread of invasive species, a model from the general class of models that environmental economists call travel cost models (TCMs). This departure is motivated by one of the main objectives of this research – to examine the net benefit of management policies to control aquatic species invasions. Because public policy is usually intended to improve human welfare, forecasting the net benefit of a policy is essential to evaluating the efficacy of the policy; the choice of control vs. prevention strategies, for instance, is usually framed in terms of relative net benefits (Finoff et al. 2006). To date, few theoretical and even fewer empirical studies rigorously model the economic impacts of AIS. The current literature concerning the economics of AIS focuses mostly on expenditures by local and state governments, commercial fisheries, sport fishers, power plants, and water treatment plants (Lovell, Stone, and Fernandez 2006; Lovell and Stone 2005). From an economic perspective, this focus on expenditures is only one side of the story – the cost side. The other side is the benefit derived by the people directly affected by a particular management policy. There has been very little empirical analysis of the magnitude of these benefits. The analyses that have been done indicate the benefits of invasive
species management could be large (see Lupi et al. 2003; Horsch and Lewis 2008). In our research we will focus on the benefits derived by boaters and shoreline property owners under different management policies, and compare these benefits to the costs of the management action, to obtain a measure of the net benefit of the policy.

Gravity models are silent on the economic benefits of a management policy, whereas TCMs were explicitly developed for the purpose of calculating the economic benefits derived from site-based recreation. Of course, if TCMs do a poor job of forecasting boater movement, then the predicted net benefits of a management policy will be poor as well. With this in mind, we plan to investigate the relative forecasting abilities of TCMs and GMs with regard to the effects of management policies on the spread of AIS. Our working hypothesis is that GMs are unmatched in forecasting marginal changes in the spread of invasive species across a lake system, and that they are probably unmatched as well at forecasting small-scale policy effects, but that TCMs will outperform GMs when forecasting away from the state of the system at which the models are fit to the data. This is an empirical issue that we plan to examine with out-of-sample forecasting. It is an important issue because it is entirely possible that management policies that are effective in achieving short run objectives are counterproductive in the long run, and thus good forecasting of long run effects is important. Our working hypothesis arises from the observation that, because TCMs model the individual behavior of boaters in response to changes in lake attributes, boating costs, and so on, they provide more realistic representations of boater adjustments to system policies than do GMs, and the importance of such realism becomes most evident as the coupled natural-human system evolves away from the original state to which the models are fitted.

We plan to investigate several formulations of travel cost models for which the base model is a random utility model (RUM). RUMs are widely used in the economic analysis of firm and household decisions and are ideally suited to modeling recreation site choice when there are many alternatives (e.g. Bockstael et al. 1987). Travel cost RUMs are econometrically estimated from the observed recreation choices of individuals, and model an individual’s choice of one site among many alternatives as a function of the characteristics of each site— including the travel cost of reaching the site. Examples of RUMs used to examine an angler’s choice of fishing site are found in Murdock (2006) and Parsons et al. (2000). Freeman (2003) provides a good overview and Phaneuf and Smith (2005) provide technical details of TCMs generally and RUMs in particular.

Among the RUM-based travel cost models that we plan to estimate are a corner solution model (Phaneuf et al. 2000) and a repeated RUM, in which each angler makes a decision on each day of the season about whether and where to take a boat trip. For applications of single-site repeated RUMs, see Provencher and Bishop (2004) and Baerenklau and Provencher (2005). The repeated RUM is the one that we describe in this proposal. It is the most data-intensive model, but it also provides the opportunity to separately identify the probabilities of the three stochastic events—uptake, transport, and establishment—that together constitute AIS dispersal. Separately identifying these probabilities would be unique in the literature on invasive species dispersal, and could prove important for accurate policy analysis because different policies intervene at different points in the dispersal of AIS.

Previous research that empirically models the spread of AIS characterizes the state of a lake invasion as present/absent (see, for instance, Mercado-Silva et al. 2006; MacIsaac et al. 2004; Leung et al. 2006). In the proposed research, we plan to estimate a lake-level model of AIS abundance as a function of lake attributes and the time elapsed since lake colonization. This model will be embedded in the larger model to relate AIS abundance to boater trip decisions (for
some AIS, abundance may affect the probability that a lake is visited by a boater), the spread of the invader, and the economic benefit of various management policies. Because estimating an abundance function is expensive in terms of the data required, we will explore the implications—for forecasting AIS dispersal and for estimates of the economic benefits of management policies—of using a lake-level AIS presence/absence model instead of an abundance model.

Finally, the proposed research builds on the nascent literature asserting the critical role of feedbacks in coupled-human natural systems in general, and in AIS management in particular. In the context of aquatic species invasions, Finoff et al. 2005 and Settle and Shogren 2002, and Macpherson et al. (2005) emphasize that relevant feedbacks induced by ecological change include not only the direct effects on the decisions of resource users, but also the indirect effects that arise because in many cases the policies that managers adopt to protect an ecosystem also affect the decisions made by resource users. In the proposed research we explore these feedbacks in considerable detail in a spatially-extensive lake district.

**REGION AND SPECIES TO BE USED IN THE ANALYSIS**

The geographic focus of this proposed project is the Northern Highlands Lakes District (NHLD) in northern Wisconsin, U.S.A. (See Figure 2). The NHLD is a 6400 km² area consisting of approximately 7,600 lakes that are the backbone of an important tourism economy. Housing density in riparian areas of the NHLD has increased 460% from 1940 to 2000 (Carpenter et al. 2007). The introduction and spread of AIS are among the most important drivers of ecological change in the NHLD (Carpenter et al. 2007). Understanding long-term regional change in the NHLD has been a goal of the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) program (Magnuson et al. 2006; Carpenter et al. 2007), and this proposed research builds upon previous and current research supported by NTL-LTER (see RESULTS OF PRIOR SUPPORT). Lakes in the district vary tremendously in terms of physical, biological, and chemical attributes, accessibility (i.e., boat launches), land ownership, and the extent and pattern of residential development. The sheer magnitude and variation of lakes makes this region ideal to develop a quantitative modeling framework to examine policy solutions to aquatic invasive species.

![North Temperate Lakes LTER Northern Highland Lakes District](image)

**Figure 2. Location of the Northern Highland Lake District in Wisconsin, USA. Inset: Detail showing high density of lakes and streams in a representative sector of the NHLD.**
We plan to apply the model first to Eurasian watermilfoil (EWM), for three reasons. First, it is present in a sufficient number of lakes in the NHLD—approximately 40 lakes and increasing by several lakes per year—to give us confidence that we can estimate model parameters concerning its uptake, transport, and establishment, while at the same time it is absent from the vast majority of lakes, so that policy simulations are economically and ecologically compelling. Second, it is widely regarded by residents in the NHLD as the most troublesome AIS. Our research in this region finds that the value of shoreline property on lakes invaded with EWM is 13% lower than similar property on uninvaded lakes (Horsch and Lewis 2008).

The general approach developed for EWM will be applied as is feasible to four other AIS of the NHLD: rainbow smelt, rusty crayfish, zebra mussel, and spiny water flea. Each of these species are established and spreading in the NHLD, and have undesirable ecological and economic impacts. Once the model is calibrated for EWM, we will test the ability of the model to make predictions for other species, and then test those predictions by collecting new data. At present, only EWM, rainbow smelt and rusty crayfish are sufficiently widespread in the NHLD to estimate parameters of our model. However, the other species are expanding and may become sufficiently widespread in the course of our research.

Research conducted by NTL-LTER PIs has examined the spread and impact of these five species in the NHLD, as well as at broader spatial scales (Wilson et al. 2004; Havel et al. 2005; Mercado-Silva et al. 2006; Johnson et al. 2008; Vander Zanden and Olden 2008). We currently have statewide presence/absence datasets for each of these five invasive species (Johnson et al. 2008). More detailed understanding of AIS dynamics and impacts for individual lakes derives from ongoing long-term studies in the core NTL-LTER lakes. Table 1 provides baseline information about these species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Native range</th>
<th>Occurrence in NHLD</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eurasian water-milfoil</td>
<td>Eurasia</td>
<td>About 40 lakes, expanding</td>
<td>WI DNR ; Johnson et al. 2008</td>
</tr>
<tr>
<td>Myriophyllum spicatum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rainbow smelt Osmerus mordax</td>
<td>East coast N. America</td>
<td>24 lakes, roughly 2% of potential habitat</td>
<td>Mercado-Silva et al. 2006; Johnson et al. 2008</td>
</tr>
<tr>
<td>Rusty crayfish Orconectes rusticus</td>
<td>Ohio River Valley</td>
<td>Widespread</td>
<td>Johnson et al. 2008</td>
</tr>
<tr>
<td>Spiny waterflea Bythotrephes longimanus</td>
<td>Eurasia</td>
<td>One lake</td>
<td>Johnson et al. 2008</td>
</tr>
<tr>
<td>Zebra mussel Dreissena polymorpha</td>
<td>Eurasia</td>
<td>A few lakes, but widespread in WI</td>
<td>WI DNR; Johnson et al. 2008</td>
</tr>
</tbody>
</table>

EXPLANATION OF KEY ASPECTS OF THE MODEL

Four aspects of the model require extended comment. The first is the economic model of boater behavior, the second is the linkage between boater behavior and AIS propagule dispersal, the third is the linkage between AIS propagule dispersal and subsequent colonization of lakes, and the fourth is intra-lake abundance of the AIS, which affects both propagule dispersal and the economic benefits of AIS management policies.

Economic model of boater behavior: We will analyze several types of travel cost models to describe boater trip behavior. Here we present the basic form of a repeated random utility
model. Once each day within season \( s \), the boater decides which lake within the system to visit, if any. Given \( J \) lakes in the system, there are \( J+1 \) choices, where the choice \( j=0 \) indicates the decision not to visit a lake in the system. Utility from choice \( j \) on day \( t \) takes the form,

\[
U_{jts} = V_{jts} + \varepsilon_{jts},
\]

where \( V_{jts} \) is the portion of utility captured by observable variables, and \( \varepsilon_{jts} \) is the portion treated as stochastic by the analyst (but known by the boater). The utility associated with taking no trip serves as the baseline utility, with \( V_{0ts} = 0 \), and otherwise we define,

\[
V_{jts} = V\left( X_{jts}, W_{jts}, Z_{its}, t_{c_j}; \alpha \right), \quad j = 1, \ldots, J,
\]

where \( X_{jts} \) is the abundance of the AIS on lake \( j \) in season \( s \); \( W_{jts} \) is a vector of observable lake attributes, such as lake size and fishing quality; \( Z_{its} \) is a vector of other trip-related variables, such as the weather on day \( t \), etc.; \( t_{c_j} \) is the trip cost, broadly defined to include such costs as the time cost of travel, the lake access fee, and the time cost of boat washing/inspection; and \( \alpha \) is a vector of utility parameters.

We assume that boaters make choices to maximize their utility. From the perspective of the analyst, these choices are stochastic because of the unobserved portion of utility, \( \varepsilon_{jts} \), and so for each lake there is an associated probability that the boater visits the lake on day \( t \), \( P_{jts} \). For instance, assuming that the unobserved component of utility is identically and independently Gumbel-distributed, the probability of choice \( j \) on day \( t \) in season \( s \) is given by

\[
P_{jts} = \frac{\exp(V_{jts})}{\sum_{i=0}^{J} \exp(V_{its})}.
\]

This stochastic characterization of boater behavior is the basic output of a random utility model.

**Linkage between boater behavior and invasive species dispersal:** At the start of each season, a lake system can be divided into two sets of lakes: those that are not invaded at the start of season \( s \), \( J_s^{N} \), and those that are invaded at the start of season \( s \), \( J_s^{I} \). We define the probability that a boat visiting an invaded lake \( j \), \( j \in J_s^{I} \), leaves the lake with a propagule of the invasive species by

\[
f_{jts} = f\left( X_{jts}, Y_{jts}; \eta \right),
\]

where \( X_{jts} \) is invader abundance on the lake, \( Y_{jts} \) is a vector of management actions taken for the lake, such as boat inspections, to reduce the probability of a boater leaving the lake with a propagule; and \( \eta \) is a vector of function parameters.

We denote by \( c_{ts} \) the event that a boat visiting an invaded lake becomes a propagule carrier on day \( t \) of season \( s \). The probability that a boat becomes a carrier on day \( t \) of season \( s \) depends on whether the boater visits an invaded lake on day \( t \) and picks up a propagule:

\[
\Pr[c_{ts}] = \sum_{j \in J_s^{I}} \left( f_{jts} \cdot P_{jts} \right).
\]

Focusing now on the probability that a live propagule is deposited in an uninvaded lake, we denote the probability that a propagule survives \( r \) days out of water by

\[
h_r = h(r; \theta),
\]

where \( \theta \) is a vector of parameters; and we denote by \( l_{kts} \) the event that on day \( t \) the boat enters uninvaded lake \( k \in J_s^{N} \) with a live propagule, and deposits the propagule. Assuming for
simplicity that a live propagule is deposited in the first lake visited after it is picked up, the probability that on day \( t \) the boat deposits a live propagule in uninvaded lake \( k \), conditional on the event that a propagule is picked up on day \( t-r \), depends on the probability that the propagule is still alive on day \( t \), the probability that lake \( k \) is visited on day \( t \), and the probability that the boater has not visited any other lake in the intervening days (the boater stays home on the intervening days). Formally,

\[
\Pr[l_{kts} | c_{t-r,s}] = \begin{cases} 
  h_r \cdot P_{kts} & \text{if } r = 1 \\
  h_r \cdot P_{kts} \cdot \prod_{n=1}^{r-1} P_{0,t-n,s} & \text{otherwise}
\end{cases}.
\]  

(6)

Building on (4) and (6), the unconditional probability of the boat depositing a live propagule in lake \( k \) on day \( t \) is the sum, over all previous days of the season, of the conditional probability (6) multiplied by the probability that a propagule is picked up on day \( t-r \),

\[
\Pr[l_{kts}] = \sum_{r=1}^{t-1} \Pr[l_{kts} | c_{t-r,s}] \cdot \Pr[c_{t-r,s}].
\]  

(7)

Linkage between AIS propagule dispersal and establishment of new colonies: The probability model in (7) forms the basis of a measure of propagule pressure in a stochastic environment. Define by \( L_{kts} \) the number of times a propagule is deposited by boaters in lake \( k \) on day \( t \) of season \( s \); it is the sum of \( l_{kts} \) across all boaters. The expected value of \( L_{kts} \) is the sum of (7) over the number of boaters in the system. Given a season of length \( T \), the seasonal frequency distribution of the deposit of live propagules in lake \( k \) is the vector \( L_{k} = (L_{k1s}, L_{k2s}, ..., L_{kTs}) \). This frequency distribution is a measure of propagule pressure, though it expands on the current literature to cast propagule pressure in terms of intra-seasonal patterns of trip frequency, thereby allowing examination of management policies with intra-seasonal variation.

Propagule pressure \( L_{ks} \) and relevant lake characteristics \( W_{ks} \), such as Ca+ concentration and conductivity, affect the probability that the invasive species becomes established in lake \( k \) by the end of season \( s \):

\[
g_{ks} = g(W_{ks}, L_{ks}; \lambda),
\]  

(8)

where \( \lambda \) is a vector of function parameters. Recent empirical studies have modeled the probability of presence/absence of AIS in a lake based on indicators of propagule pressure and lake ecological characteristics (see, for instance, Mercado-Silva et al. 2006; Leung and Mandrak 2007; Vander Zanden and Olden 2008). The estimation of \( g_{ks} \) would build on these studies to examine the probability of establishment in a given year. The general form of \( g_{ks} \) provides the flexibility to examine Allee effects (Leung et al. 2004, Kramer et al. 2008). Note too that it is possible to specify \( g_{ks} \) in such a manner as to allow for a baseline probability of invasion of a lake from outside of the system. The dynamics of AIS spread and the effectiveness of management policies to alter the spread arise from inter-seasonal changes in \( W_{ks} \) and \( L_{ks} \), both of which can be manipulated by management policies. Note in particular from tracing the relationships in (1)-(7) that management policies that affect boater utility from a visit to any lake in the system affects the probability of establishment on lake \( k \) via its effect on the propagule pressure vector \( L_{ks} \). As described below, \( g_{ks} \) would be estimated using panel data in a manner that is dynamically consistent with the full model.
The lake-level AIS abundance function – X_{jts}: Invader abundance, X_{jts}, plays an important role in our model. First, it determines the probability that invader propagules will be picked up by a boater (f). Second, it enters boater utility and thus affects the boater trip decision (see (1)). Third, because abundance is a good predictor of invasive species impact (Ricciardi et al. 1995; Parker et al. 1999; Ricciardi 2003), it typically affects the decisions of lake managers about how to allocate prevention/control resources (Y_{js}).

Abundance is influenced by variety of observable variables, and so correctly estimating the abundance function is critical to good forecasting of AIS dispersal and effective AIS management. To the extent possible we will model the lake-specific abundance of an invasion as a function of lake variables W_{js}, expenditures to control the invader E_{js}, the day of the season t (to capture intra-seasonal changes in abundance), and the years since colonization D_{js} (to capture the inter-seasonal evolution of abundance). Formally,

\[ X_{jts} = X(W_{js}, E_{js}, D_{js}, t, \tilde{\xi}_{jts}; \varphi) , \]  

where \( \tilde{\xi}_{jts} \) is the stochasticity of abundance, and \( \varphi \) is a vector of parameters to be estimated.

DATA COLLECTION AND MODEL ESTIMATION

Estimation of the model, and the data required for estimation, focuses on three elements: the RUM of boater trip decisions, the transmission probability density functions f, h, and g, and the AIS abundance function for a lake, X_{jts}. Table 2 at the end of this section summarizes the data required for estimation.

Estimation of the random utility model (RUM) of boater trip decisions: Estimates of the utility parameters \( \alpha \) involves a comparison of actual boater trip behavior to the probability of boater trips, \( P_{jts} \) (see (2)), as follows. Given a random sample of boaters, and the assumption of independence of \( \varepsilon_{jts} \) across boaters and days of the season, the relevant likelihood function of the observed daily trip decisions of boaters in the sample is simply the product of the associated trip probabilities \( P_{jts} \) over all observations of trip decisions. The set of utility parameters \( \alpha \) can be estimated by maximizing the likelihood function over \( \alpha \). If the independence assumption is relaxed, the likelihood function must be simulated, and maximization is over the simulated likelihood function (see, for instance, Provencher, Baerenklau, and Bishop 2002).

The sample data of boater trips required for this estimation will be collected during 2010 and 2011 via a web-based Internet survey of 800 anglers per season who indicate in a brief initial mail survey at least a 10% chance of fishing in the study area in 2010-2011. The survey sample will be drawn randomly from an electronic database of fishing license holders maintained by the state of Wisconsin Department of Natural Resources (WDNR).

The survey will take a quasi-diary form in which lake anglers are asked to record every two weeks the trip data for trips taken during the previous two weeks. Previous studies conducted by the PI’s indicate that a two-week interval is not too long for anglers to remember trip details, but long enough that anglers do not feel overly burdened by the demands of reporting data (Provencher, Baerenklau, and Bishop 2002; Provencher and Bishop 2004). The data collected from respondents will include the trip date and cost, lake choice, and fish catch for all trips taken during the season, as well as demographic characteristics, such as employment status and income.

Three other types of data will be gathered by the survey. First, as necessary to help estimate the model of boater trip behavior, stated-preference questions might be included. Such
questions might concern, for instance, an angler’s trip response to a new infestation of milfoil on
a favorite lake, or the angler’s trip response to management policies related to invasive species
control, such as inspections, fines, and educational campaigns, including signage at boat ramps.
These questions would be developed in such a manner as to allow quantitative integration in the
estimation of angler trip behavior, as done by previous studies integrating stated-preference and
revealed-preference data (see Bennett, Provencher and Bishop (2004), and citations therein), and
they would serve to resolve potential endogeneity bias in the RUM. Second, data concerning the
boater’s choice set—the lakes the angler actually considers in deciding where to fish—will be
obtained by querying respondents about their familiarity with lakes in the study area. Several
authors have noted the bias in the estimation of random utility models when the choice set is
misspecified (Haab and Hicks 1997, 1999). Third, the survey will query boaters about their
behavior to prevent invasive species dispersal, such as how much time they spend washing their
boats to prevent dispersal of an invasive species, how often they’ve found milfoil attached to
their boats, the care they believe other boaters take to prevent dispersal, and similar questions, to
supplement other data in the development of transmission probabilities ($f$, $h$, and $g$). Of course,
self-reports on such behavior may not be reliable, but when used with external data these self-
reports can be used to calibrate the variation in the dispersal prevention behavior of boaters in the
study area.

This survey strategy raises several issues, two of which concern sampling bias, and one
of which concerns “respondent fatigue”. The first is that the sample of anglers will not be
representative of all boaters in the study area; possibly the trip decisions of anglers are different
than those of non-angling boaters. To address this concern, we will take the following steps.
First, all anglers in the survey will be asked to record information for every boating trip,
regardless of whether the angler actually fished. Second, at a random sample of boat ramps
during the summer of 2009 we will ascertain the proportion of boaters in Vilas County who do
not actually hold a fishing license. If this proportion is small, as we suspect, we will take no
further action. If it is large, we will investigate ways to correct for the bias in estimation. Most
likely the bias correction would involve recruiting boaters without fishing licenses at boat ramps
in the study area during the summer of 2010, and asking them to participate in a parallel diary-
type survey during the summer of 2011, with a correction for the selection bias associated with
Alternatively, we may recruit the sample from the WDNR’s database of registered boat owners.

The second concern is that respondents completing the Internet survey will not be
representative of respondents overall. This is less of a concern now than even several years ago;
recent studies indicate that the percentage of households with Internet access will exceed 90% in
2009 (Leichtman Research Group 2008). Nonetheless, we will conduct 100 telephone calls with
boaters without Internet access (as determined from the initial mail contact) to determine
whether they are systematically different in their overall trip behavior than our sample anglers.

The third concern is that respondents will discontinue the survey partway through the
season, or will underreport their trips, due to “respondent fatigue”. To address this we will take
several steps, including periodic reminder emails, a survey “check-off” in which the angler, if so
inclined, can simply indicate that he does not wish to spend the time completing the survey data
for the previous two weeks (such a check-off avoids the problem of a response-fatigued angler
falsely claiming that he/she took no trips during the previous two weeks), and the inducement of
a $20 gift certificates to an online store (e.g. Amazon or Cabela’s) at the end of each season.
**Estimation of the probability density functions of species dispersal:** Modeling the spatial dynamics of an invasion under various management regimes requires understanding both boater trip behavior and the ecology of an invasion embodied in the transmission probability density functions $f$, $h$, and $g$ (respectively, propagule uptake, out-of-lake survival, and colony establishment). A primary empirical task of the research program is to approximate these functions statistically. Our approach is to estimate $f$ and $h$ directly using primary data we collect for the purpose, and to then use these estimated functions and the estimated RUM of boater trip behavior in a simulation algorithm to estimate $g$, as follows:

**Estimating the probability that a boat leaves with propagules ($f$):** We will randomly sample boats at landings as they are removed from selected invaded lakes. Each boat will be inspected to determine whether it is carrying any invasive species. Information will be recorded on the absence/presence of invasive species and other species and/or debris on the boat and trailer, the type of boat and trailer, boating activity (fishing, water skiing etc.), time of day, and day of the year. The value of recording the presence/absence of other species and debris on the boat/trailer is that it gives a general indication of the boater’s diligence in cleaning the boat after pulling it from the water. Boaters may be asked several related questions that may be important variables in estimating $f$, such as whether the boater lives on the lake or is destined for his home lake.

In order to accurately estimate the effect of management activities $Y_{ij}$ on $f$, the sample of lakes selected for inspections will be stratified to include lakes at different levels of invasive species management, such as lakes with extensive educational signage at the boat landing about invasive species control. Care will be taken to assure that boater behavior is not influenced by our presence at the landings—by, for instance, remaining inconspicuous at the ramps between inspections. To induce boaters to submit to an inspection, they will be given a $5 gas card, and assured that an inspection is for AIS research purposes only and that an inspection carries no negative consequence. We plan to sample 1200 boats in each of two seasons (2010 and 2011), for a total sample of 2400 inspections. Following the current literature, we will use this data, angler survey data, and our database for ecological characteristics of the lakes to fit $f$ as a logistic binomial model with over-dispersion (Gelman and Hill 2007).

**Estimating the probability of propagule survival ($h$):** We plan to estimate $h$ using both direct experiments and survey data. Survey data will come from an intercept sample similar to that used for estimating $f$, but in this case we approach boaters as they arrive at the boat landing and request permission to inspect the boat for invasive species and other species and debris. Specimens discovered will be analyzed for viability. All boaters in the sample will be asked about where and when they last had their boat in the water. As in the estimation of $f$, we will attempt to obtain a sample of 1200 boaters in each of two consecutive years (2010 and 2011) for a total sample of 2400, and we will use $5 gas cards as an incentive.

Direct experiments to estimate $h$ will be conducted by holding a small number of contaminated boats (owned by UW-Madison or volunteers) on land and sampling them daily for viable invasive species, until no viable individuals are found. Data from both the direct experiments and the surveys will be used to estimate survival probabilities by Poisson regression (Gelman and Hill 2007).

**Estimating the probability of colony establishment ($g$):** With both the RUM model of boater behavior and estimates of the probability functions $h$, and $f$, in hand, we plan to use a simulation algorithm to estimate $g$. The algorithm would compare the observed dispersal of the AIS over a historical calibration period to that predicted by the model, $g = g(W_{ks}, L_{ks}, \lambda)$ for
candidate values of $\lambda$, until the value of $\lambda$ that best fits the data is found. The algorithm contains the following elements:

- Data on the state of the invasion in the study area during a calibration period (e.g. 1990-2007);
- An objective function indicating the fit of the model given candidate values of $\lambda$. For instance, the objective function could be the sum of squared differences between the predicted probability of invasion and actual state of invasion (a (0,1) index function) for each lake in the study area in each year of the calibration period:

$$\sum_{s=1}^{S} \sum_{j=1}^{J} \left( g(W_{js}, L_{js}, \hat{\lambda}) - G_{js} \right)^2.$$  

(10)

where $G_{js}$ is the actual state of the invasion (presence/absence) on lake $j$ in year $s$, and $\hat{\lambda}$ is the candidate value of $\lambda$.
- A simulation routine that employs the estimated boater trip decision (RUM) model, the estimated probability density functions $f_{js}$ and $h_{rs}$, and the candidate probability density function $g_{ks}(\cdot; \hat{\lambda})$ to repeatedly calculate (10) for random draws of the stochastic elements of the model. From this routine the expected value of the objective function (10) is determined, and a gradient algorithm is used to search for the value of $\hat{\lambda}$ that minimizes this expected value.

Fundamental to this approach is observation of $G_{js}$, the presence/absence of the AIS on lake $j$ in season $s$ of the calibration period. The years in which invaded lakes in the NHLD were first known to be invaded is available from the Wisconsin Department of Natural Resources (WDNR). However, equating the first year of known invasion to the first year of actual invasion is problematic because lakes generally are not regularly sampled for AIS and so WDNR records of presence/absence are likely biased downwards. To address this concern we will supplement the WDNR data on presence/absence by strategically sampling ostensibly uninvaded lakes based on one or several ecological niche models developed in the ecology literature to predict presence/absence of an invader (Breiman et al. 1984; De’ath and Fabricius 2000; Vander Zanden et al. 2004; MacIsaac et al. 2000; Buchan and Padilla 2000).¹ Lakes for which these models indicate presence of the AIS, but existing data indicates absence, will be sampled in 2010. If this sampling discovers a fair number of new infestations then we will modify the simulation exercise to jointly estimate $g_{ks}$ and a hazard model (Lancaster 1990, Greene 2002) of the lag between AIS establishment and discovery in a lake.

Estimation of $g_{ks}$ requires a variety of lake characteristic variables $W_{js}$. The NHLD is among the most studied lake regions in the world, with lake data collected for many years by the University of Wisconsin Center for Limnology using a variety of funding sources, most recently NSF-LTER and an NSF Biocomplexity grant. Limnological and fisheries data are available for most lakes large enough to be of interest to boaters.

Several lake variables are available for most lakes large enough to be of interest to boaters, including lake area, lake depth, conductivity, boat access, and Secchi depth.

¹ For some species we will develop models using data from other regions that have been invaded, or from the species’ native range (Mercado-Silva et al. 2006).
**Estimation of the lake-level AIS abundance function (Xjts):** We will estimate the abundance function, \( X_{jts} = X(W_{jts}, E_{jts}, D_t, t, \xi_{jts}, \varphi) \), using data from a non-random survey of up to 100 invaded lakes. Depending on the availability of lakes for the particular AIS under investigation, some of the sampling may be conducted on non-NHLD lakes. For each lake, the survey will be repeated three times each summer for three consecutive summers (2010-2012), to allow examination of intra- and inter-seasonal variation in invader intensity. Methods for generating an index of abundance (CPUE) for each of these invaders have generally been developed for the NTL-LTER lakes, and will be used in this survey. We will focus our efforts on lakes for which invasive species, limnological, and habitat data are already available from previous surveys (http://lter.limnology.wisc.edu/). Using this dataset, we will develop statistical models predicting invader abundance using limnological and habitat predictors.

The above analysis assumes that invader abundance can be reasonably approximated for a lake. Yet there are several sources of variability that must be considered in the above analysis. First, invader abundance can fluctuate widely among years. This is demonstrated from NTL-LTER data for rusty crayfish and rainbow smelt. Second, within an invaded lake, there will be patchiness in terms of abundance: some areas may be highly invaded, while others may contain no evidence of the invader. Third, abundance may also vary seasonally, with the details depending on the life cycle and ecology of the species. For example, adult spiny water flea only appear in the water column in mid to late summer and remain into the fall. Both our modeling and our sampling of AIS abundance will take into account the above sources of spatial and temporal variability.

**Table 2. Summary of Key Data Necessary to Estimate the Model**

<table>
<thead>
<tr>
<th>Data</th>
<th>Purpose</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boater trips throughout the season, trip costs, boater-specific variables</td>
<td>Estimate RUM model</td>
<td>New boater diary survey to be administered in summer 2010, 2011</td>
</tr>
<tr>
<td>Propagule uptake, cleaning behavior, management activities</td>
<td>Estimate probability of uptake, ( f_{jts} )</td>
<td>New boater intercept survey in summer 2010, 2011</td>
</tr>
<tr>
<td>Propagule survival, conditions of boat transport and storage</td>
<td>Estimate probability of survival, ( h_r )</td>
<td>New boater intercept survey in summer 2010, 2011, and controlled experiments</td>
</tr>
<tr>
<td>Lake-level AIS presence/absence ( G_{js} ), year of AIS establishment</td>
<td>Estimate the probability of establishment, ( g_{ks} )</td>
<td>Existing WDNR data, additional lake sampling in summer of 2010 to check “false presences” as predicted by current models</td>
</tr>
<tr>
<td>Lake-level AIS abundance ( (X) )</td>
<td>Estimate the probability of uptake ( f_{jts} ); estimate the abundance function ( X_{jts} ), estimate the RUM model</td>
<td>Existing WDNR and LTER data; new survey of AIS abundance in 100 NHLD lakes, summer 2010-2012</td>
</tr>
<tr>
<td>Lake attributes ( W_{jts} )</td>
<td>Estimate the abundance function ( X_{jts} ), estimate the RUM model</td>
<td>Existing WDNR and LTER data, new survey of 100 lakes, summer 2010-2012</td>
</tr>
<tr>
<td>Management actions ( Y_{jts} ) and expenditures ( E_{jts} ) (both prevention and intra-lake control)</td>
<td>Estimate the probability of uptake ( f_{jts} ); estimate the probability of establishment ( g_{ks} ), estimate the abundance function ( X_{jts} )</td>
<td>Multiple external sources, new passive collection on lakes in NHLD, possibly some controlled experiments</td>
</tr>
</tbody>
</table>
FORECASTING AIS DISPERSAL AND SIMULATING MANAGEMENT POLICIES

The RUM will be used to simulate the effects of alternative management policies on the spatial dynamics of the species invasion. Importantly, due to the stochastic elements in the model (boater trip behavior and AIS uptake, transport, establishment and lake-level abundance are all stochastic), the output of the simulation is also stochastic. Thus the simulation does not give a deterministic spatial pattern for the AIS under a new policy, but rather generates for each lake a frequency distribution of the year of invasion under the policy. (See Lewis and Plantinga 2007 for a description of simulation in large-scale stochastic models).

In addition to the RUM, we will develop a production-constrained gravity model for the NHLD as an alternative means of modeling boater movement and the resulting invasive species spread (Bossenbroek et al. 2001). Gravity models can be developed from available GIS and boater registration data. The theory and application of this approach to modeling AIS propagule pressure is well developed (Leung et al. 2004, 2006; Leung and Mandrak 2007), including model assessment using survey data (Leung et al. 2006). The gravity model for the NHLD will serve as a benchmark for assessing the predictions of invasive species spread from the RUM.

In the AIS literature, a management policy is typically modeled as a fixed constraint, such as closing lakes X, Y, and Z (see, for instance, Schneider et al. 1998), but it can be a more complicated policy function, where the functional arguments reference the state of the invasion. For example, the policy function might be, “Charge a fee on lake X when invasion state Y is observed”, or it might be an objective function to be maximized or minimized, such as, “use lake closures to maximize boater consumer surplus”. In principle the simulation algorithm readily accommodates such objective functions, though given the scale of the model, maximization of objective functions must be done via approximation.

The policy simulation algorithm is the proximate instrument for addressing the overarching question posed in the introduction: How do policy interventions intended to control or prevent harmful aquatic species invasions affect the decisions and economic welfare of individuals using the relevant resource, and the spatial dynamics of invasions on heterogeneous landscapes? A wide range of specific policy questions can be addressed via the simulation algorithm, including the following:

- To what extent do different management objectives generate different temporal and spatial paths for the invasive? For instance, to what extent does the objective of maximizing economic net benefit from managing the invasion generate a different spread path than the objective of minimizing the rate of spread? What are the critical biological, ecological and economic parameters that cause different management objectives to lead to divergent paths of an invasion?
- How does a shift in management resources from control of a species in infected lakes to prevention of the spread of the invader from these lakes (control vs. prevention) affect the evolution of an invasion? What is the critical point in an invasion at which prevention should be abandoned for control? Given that a control policy reduces the probability of boats carrying the invasive species from infected lakes, is it possible that control is the most important feature of a prevention policy? Which type of policy –control or prevention –generates a higher economic benefit per management dollar?
- How do local management decisions affect the species invasion at the regional scale? For instance, suppose that a lake is invaded, and the lake manager decides to charge boaters an access (launch) fee on the lake as a means of defraying the cost of containing or
eradicating the invasive species. What would be the effect on the evolution of the species invasion? What would be the effect on boater welfare in the short run and the long run?

- How do related policies and/or economic and ecosystem changes affect AIS dispersal? For example, how do fish management policies such as walleye stocking affect the invasion?

CALCULATION OF NET ECONOMIC BENEFITS OF MANAGEMENT POLICIES

A major objective of the research is the calculation of the economic net benefits of various management policies that accrue to current and future lake users, namely boaters and shoreline property owners. The standard economic measure of the benefit of a policy change to consumers is the difference in money-measured utility with and without the policy change. In principle such calculations for boaters are easily done using the RUM model (see Haab and McConnell 2002, p. 220-236). In practice in the current context, the calculation is complicated by the dynamic stochastic elements of the model. These elements cause the predicted effect of a management policy on the lake system to be stochastic, and so the economic benefit of a policy is stochastic as well; a policy generates not a single value for the economic benefit, but rather a distribution of values. We will derive this distribution by embedding the usual calculation of net benefits from a RUM model in the policy simulation routine described in the previous section.

The net benefit of AIS management policies that accrues to shoreline property owners will be determined using hedonic models of property values and contingent valuation surveys currently being developed in LTER-funded research (see “Results of Prior Support” below). These methods are capable of generating the value to shoreline property owners of changes in lake attributes, such as presence/absence of AIS, and, as applicable, changes in fishing quality due to the presence of an AIS. Embedding these values in the policy simulation routines serves to capture the benefit of management policies that accrues to shoreline property owners via the impact of the policy on the dispersal of the AIS. An important issue to be addressed in the project is the double-counting of benefits that may arise because most shoreline property owners are also boaters.

EDUCATION PLAN

Our education plan includes outreach and continuing education for the public, policymakers, and resource managers, K-12 education, undergraduate education, and graduate training.

Outreach and continuing education: Aquatic invasive species are among the top natural resource concerns for the public in Wisconsin and other lake-rich places. For example, Wisconsin expenditures for “aquatic invasive species control grants” has increased dramatically, to a current level of $4.3 million/year, a sizable financial outlay for a state granting program. Much of the funding currently goes to application of herbicides to control Eurasian watermilfoil. The WDNR’s efforts to allocate these funds more effectively will benefit tremendously from research examining which lakes are most vulnerable to invasion, as well as the implications of alternative management regimes for the spread and economic impact of AIS.

Our project will greatly enhance ongoing outreach efforts. We will expand the scope and breadth of the science basis for public outreach, while at the same time providing the public with an integrated perspective on prevention and control of multiple invasive species. We will

---

2 There are well known caveats to using hedonic valuation in the calculation of the economic benefits of a change in environmental quality, as described in Champ et al. 2003, p. 360-377.
coordinate with the state and privately-funded “Smart Prevention” program operated by Vander Zanden and Maxted (Vander Zanden and Olden 2008; Vander Zanden and Maxted 2008). This proposed project will allow us to expand our work with homeowners’ groups and county invasive species coordinators in providing scientific information to guide local decision-making about aquatic invasive species. In addition, results from this project will be used in our recently-launched website on AIS research and prevention, which emphasizes the NHLD and the Great Lakes region (http://limnology.wisc.edu/personnel/jakevz/ais/).

Wisconsin policymakers and legislators are demanding evidence of the economic impacts of various legal measures to prevent invasive species dispersal, such as the currently proposed Assembly Bill NR40, which proposes various invasive species control requirements, prohibits certain activities, and prescribes specific enforcement actions. We will meet regularly with state agency personnel to share our findings, which are of interest to the resource management community. We will share our results to the general public through participation in various lake management workshops, and at the annual meeting of Wisconsin Association of Lakes. In addition, we will develop a web-based tool for education and planning. This tool will compute the effects of specific policy interventions on AIS dispersal and economic variables.

K-12 Education: This proposed project highlights some of the simple cause-and-effect relationships and feedbacks between human actions and ecological change on a lake rich landscape. As such, our research efforts will provide exciting new material and opportunity for broadening the scope of ongoing Schoolyard LTER programs offered by the NTL-LTER. Through Trout Lake Station, we have active collaborations with local private and public schools, including schools on the Lac du Flambeau reservation. We have found that the general topic of AIS is highly amenable to K-12 outreach programs, as well as teacher training. Our existing AIS outreach efforts focus on single lakes and organisms of interest to the public. The proposed research will allow us to add a regional, geographic perspective to our K-12 education. For example, we will be able to adapt mapping tools for students to explore the spread of invasive species.

Undergraduate education: Results of this project will be regularly used in undergraduate courses such as Limnology (165 students per year), Ecology of Fishes (75 students per year), Ecosystem Analysis and Concepts (20 students per year), Environmental Economics (120 students), and Natural Resource Economics (25 students). About 6 students will be employed as hourly workers on the project each summer, and these students will play a central role in data collection and social and biological surveys needed to estimate the model. The project will provide diverse opportunities for senior theses and directed studies projects for the many talented undergraduates whom we work with.

Graduate Training: This project will recruit a cohort of four Ph.D. students to be trained at the economics-ecology interface. Each PI will be the lead advisor for one graduate student, and each graduate student will be co-advised by both an economist (Provencher or Lewis) and an ecologist (Carpenter or Vander Zanden). All four Ph.D. students will take a mix of economics and ecology courses. From the onset, the PIs will foster a collaborative esprit de corps among the Ph.D. students, emphasizing the value of collaboration as a means of advancing interdisciplinary research. Teamwork will be promoted by regular meetings, annual retreats, and shared field facilities at Trout Lake Station.
MANAGEMENT PLAN

The PIs have a long history of successful work together. All of the PIs are physically housed at the University of Wisconsin-Madison, and all have collaborated extensively in the past via their involvement in NTL-LTER, an NSF biocomplexity grant (2000-2005), and other research grants. The ongoing NTL-LTER is a source of extensive intellectual support for addressing the emerging challenges that inevitably arise in the course of novel research.

Table 4 allocates modeling tasks across PIs, Research Scientists and graduate students. The entire research team (PIs, research scientists, graduate and undergraduate students) will meet monthly during the academic year to discuss progress of the research, and once a year the team will hold a retreat at UW’s Trout Lake Research Station. In each of the four years of the project a different PI will be assigned the role of project manager, whose tasks will include scheduling the retreat and meetings, coordinating the allocation of shared resources (such as student hourly labor used on several tasks), promoting the integration of graduate student training, and assuring that the project stays on schedule.

Table 3. Delegation of Project Activities

<table>
<thead>
<tr>
<th>Modeling Task</th>
<th>Primary/Secondary PI</th>
<th>Expected date of completion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimation of AIS presence/absence models, and subsequent sampling of “false presence” lakes</td>
<td>Vander Zanden, Lewis; Maxted, 2 grad and 2 undergrad students</td>
<td>Summer 2010</td>
</tr>
<tr>
<td>Data collection for RUM of boater trip behavior</td>
<td>Provencher, Carpenter; Anderson, 2 grad and 1 undergrad student</td>
<td>Fall 2011</td>
</tr>
<tr>
<td>Data collection for estimation of probability density functions f and h</td>
<td>Carpenter, Provencher; Maxted, 2 grad and 4 undergrad students</td>
<td>Fall 2011</td>
</tr>
<tr>
<td>Data collection for estimation of the AIS abundance function X</td>
<td>Vander Zanden, Carpenter; 2 grad and 2 undergrad students</td>
<td>Fall 2011</td>
</tr>
<tr>
<td>Estimation of the AIS abundance function X</td>
<td>Vander Zanden, Provencher; 1 grad student</td>
<td>Summer 2012</td>
</tr>
<tr>
<td>Estimation of the probability density functions f and h</td>
<td>Carpenter, Lewis; 1 grad student</td>
<td>Summer 2012</td>
</tr>
<tr>
<td>Estimation of the probability density function g</td>
<td>Lewis, Vander Zanden; 1 grad student</td>
<td>Summer 2012</td>
</tr>
<tr>
<td>Econometric estimation of RUM of boater trip behavior</td>
<td>Provencher, Lewis; Anderson and 1 grad student</td>
<td>Summer 2012</td>
</tr>
<tr>
<td>Simulation of policy scenarios</td>
<td>Lewis, Carpenter; Anderson and 1 grad student</td>
<td>Summer 2013</td>
</tr>
</tbody>
</table>

PROJECT SIGNIFICANCE

Research on coupled human-natural systems (CNHS) has twin motivations: fundamental scientific questions about social-ecological phenomena, and the need to address pressing human problems of environment and resources (Kates et al. 2001; Clark 2007; Liu et al. 2007). With regard to the first, there have been numerous bioeconomic analyses linking human and natural systems, but far fewer studies that recognize the feedbacks of these linkages that are the essence of CNHS research, and fewer yet that examine these feedbacks in an empirical, quantitative analysis. The proposed research is such a study. Its primary contribution is the integration of economic and ecological models in an empirical application to answer basic questions about aquatic species invasions and the role of system feedbacks in the management of the system.
These feedbacks are rich and complicated; both boaters and lake managers respond to the progress of the invasion in the lake system, and the decisions of both redirect the spatial dynamics of the invasion, with the decisions of managers acting directly on the progress of the invasion, for instance via lake-level control strategies, and indirectly via their effect on the decisions of boaters. Understanding these linkages is important for managing species invasions to preserve and protect a wide variety of ecosystem services, such as water quality, fishing quality, and biodiversity, that benefit lake users.

Economists and ecologists have collaborated in the development of a number of theoretical models examining optimal AIS management approaches (e.g. prevention vs. control) under a variety of conditions (e.g. Potapov et al. 2007; Finnoff et al. 2007). Meanwhile, ecologists have taken the lead in developing empirical models of invasive species spread, notably the extensive literature on gravity models (among others, Leung et al. 2006; Buchan and Padilla 1999; Maclsaac et al. 2004; Schneider et al. 1998; Bossenbroek et al. 2007). By its integration of economic models of boater movement with ecological models of aquatic ecosystems, the proposed analysis represents a significant advance in empirical collaborative economic-ecological modeling of aquatic species invasions. Comparing the comprehensive model that is the centerpiece of the analysis to models that make simplifying assumptions about human behavior, the ecology of invasive species, and/or the connections between them, should provide significant insight to identifying the features of models of AIS dispersal that are most critical to developing effective management strategies, and more generally should provide insights to the proper modeling of coupled natural-human systems. We expect to publish the conceptual and methodological contributions of the analysis and the general insights garnered from the approach in general science journals (e.g., Science, Nature, Bioscience), ecology and conservation biology journals (e.g., Ecological Applications, Conservation Biology), and economics journals (e.g., Land Economics, Journal of Environmental Economics and Management).

With regard to the second motivation for CNHS research—addressing pressing human problems of environment and resource—the analysis would make a significant contribution to the basic understanding of AIS ecology and how to manage a species invasion. Basic ecology questions about AIS out-of-lake survival, inter- and intra-seasonal abundance cycles, and colony establishment parameters will be answered.

Basic management questions will be answered as well. For instance, how should management resources be allocated between prevention and control? Historically, management resources have been directed primarily towards invasive species control, possibly because of the political economy of invasions, but recent work argues for rethinking the wisdom of such a strategy (Leung et al. 2005; Finnoff et al. 2007; Vander Zanden and Olden 2008). Yet only recently has there been quantitative theoretical research on managing species invasions to improve human welfare (Leung et al. 2005; MacPherson et al. 2005; Finnoff et al. 2007), and there has been little quantitative empirical research concerning the “correct” balance of management resources between control and prevention, the extent to which the correct balance depends on managers’ (and society’s) objectives with respect to aquatic invasive species management, and the relative role of the economic and biological variables affecting the correct balance. Moreover, both prevention and control are broad categories that must be parsed to develop an effective management policy: what kind of control action is warranted on invaded lake A vs. invaded lake B? Theoretical work in this area suggests that optimal policy is sensitive to a variety of factors, such as i) the economic damages from invasion, ii) the magnitude of the invasion, and iii) the planning horizon and the discount rate (Potapov et al. 2007). The research that we propose should provide a variety of insights to questions like these that are specifically
useful in the management of aquatic invasive species, and more generally useful to how researchers and managers think about invasive species control.

RESULTS OF PRIOR SUPPORT

The North Temperate Lakes Long-Term Ecological Research program (NTL-LTER; Grant DEB-0217533, Funding 2002-2008 = $6,720,000) has been operating continuously since 1981. A central goal is to develop an understanding of long-term regional change in the NHLD (Magnuson et al. 2006; Carpenter et al. 2007). NTL-LTER research has resulted in about 280 research articles and book chapters during the period 2002-2007. A full publication list, summary of research findings, and description of research sites is found at http://lter.limnology.wisc.edu.

NTL-LTER provides core data and a regional framework that comprises the basis for much of the work proposed here. Long-term studies of rainbow smelt (Hrabik et al. 1999) and rusty crayfish (Wilson et al. 2004) in three core LTER study lakes (Trout, Sparkling, and Crystal) provide a cornerstone for our understanding of the dynamics and impacts of these species. AIS research at NTL-LTER has also taken a more regional perspective, focusing on questions of spread and lake vulnerability (Mercado-Silva et al. 2006; Vander Zanden and Olden 2008; Johnson et al. 2008). In 1995, NTL-LTER received funding to further regionalize research efforts, and to expand collaborations to include the social sciences. Recent social science research funded in part by LTER and relevant to the proposed research include an examination of the emergence of panacea traps in rational adaptive management frameworks (Brock and Carpenter 2007), modeling of shoreline subdivisions (Lewis et al. 2009) and hedonic modeling of the effects of lakeshore zoning and Eurasian watermilfoil on property values (Spalatro and Provencher 2001; Horsch and Lewis 2008). On-going social science research is using hedonic modeling to estimate the value of lake attributes such as fishing quality, and contingent valuation surveys to develop estimates of shoreline property owners’ willingness to pay for management policies to prevent/control Eurasian watermilfoil, improve fishing quality, and preserve green frog populations.

Research proposed here will benefit directly from the information management system of NTL-LTER which serves many of the background datasets we will use, as well as the intellectual network of interdisciplinary scientists affiliated with the site. In the current grant cycle of NTL-LTER (2009-2014 field seasons) we will initiate a place-based survey focused on occupants of specific parcels of land. This survey, to be repeated each grant cycle in the future, provides the backbone for long-term social science research within NTL-LTER. This proposal centers on beliefs and behaviors of a highly mobile set of users of the NHLD, the boaters, in relation to dynamics of aquatic invasive species. The studies of boaters proposed here complement the LTER studies of households on parcels. Together, they will allow us to understand the dynamics of highly mobile boaters in the matrix of households and parcels, with specific reference to the expansion and management of aquatic invasive species.