Coupling ecological and social network models to assess "transmission" and "contagion" of an aquatic invasive species

Danielle M. Haak[1*], Brian D. Fath[2,3], Valery E. Forbes[4], Dustin R. Martin[5], and Kevin L. Pope[6]

[1]Nebraska Cooperative Fish and Wildlife Research Unit, School of Natural Resources, University of Nebraska, Lincoln, 68583, dmhaak@uga.edu

[2]Advanced Systems Analysis Program, International Institute for Applied Systems Analysis, Laxenburg, Austria

[3]Department of Biological Sciences. Towson University, Towson, Maryland, bfath@towson.edu

[4]College of Biological Sciences, University of Minnesota, 55108, veforbes@umn.edu

[5]ReelSonar, Inc., Seattle, Washington, dustin@reelsonar.com

[6]U.S. Geological Survey, Nebraska Cooperative Fish and Wildlife Research Unit, School of Natural Resources, University of Nebraska, Lincoln, 68583, kpope2@unl.edu

*Corresponding author: Danielle Haak, University of Georgia, dmhaak@uga.edu

Abstract

Network analysis is used to address diverse ecological, social, economic, and epidemiological questions, but few efforts have been made to combine these field-specific analyses into interdisciplinary approaches that effectively address how complex systems are interdependent and connected to one another. Identifying and understanding these cross-boundary connections improves natural resource management and promotes proactive, rather than reactive, decisions. This research had two main objectives; first, adapt the framework and approach of infectious disease network modeling so that it may be applied to the socio-ecological problem of spreading aquatic invasive species, and second, use this new coupled model to simulate the spread of the invasive Chinese mystery snail (*Bellamya chinensis*) in a reservoir network in Southeastern Nebraska, USA. The coupled model integrates an existing social network model of how anglers move on the landscape with new reservoir-specific ecological network models. This approach allowed us to identify 1) how angler movement among reservoirs aids in the spread of *B. chinensis*, 2) how *B. chinensis* alters energy flows within individual-reservoir food webs, and 3) a new method for assessing the spread of any number of non-native or invasive species within complex, social-ecological systems.

Keywords: *Bellamya chinensis*, Chinese mystery snail, ecological network analysis, epidemiological network analysis, social network analysis, Ecopath with Ecosim, aquatic invasive species

Introduction

Ecologists and conservationists are challenged by the increasing, unintentional spread of species from one location to another. One method to quantify how a species interacts with and influences its environment is ecological network analysis (ENA). This method is particularly helpful for investigating potential effects before a species has been introduced, allowing managers to be proactive rather than reactive, and it acknowledges that ecosystems consist of complex networks of interactions and allows for a holistic examination of the system in question; we can use ENA to assess how energy flows throughout an entire food web are directly and indirectly affected (Fath *et al.* 2007). Ecosystem resilience can be assessed by adding or removing nodes and observing how the system reacts in a simulated future (Janssen *et al.* 2006), and the strong human component embedded in the problem of spreading aquatic invasive species naturally leads to a direct link with social network analysis.

Parallels exist between modeling the spread of invasive species and modeling the spread of infectious diseases (Byers 2009; Floerl *et al.* 2009; Meentemeyer *et al.* 2011). Infectious diseases spread through networks via physical contact of individuals (Meyers *et al.* 2005). The transmissibility of a disease is the average probability of an infected person transmitting the disease to a susceptible person through physical contact (Meyers *et al.* 2005). Network analysis allows scientists to calculate how many secondary cases are likely to occur as a result of contact with the primary host (Meyers *et al.* 2005), as well as the average number of connections an infected host has (Hethcote 2000). Using this same framework, we calculated the probability of a species (the freshwater, non-native Chinese mystery snail *Bellamya chinensis* [Reeve 1863]) from an "infected and contagious" primary host reservoir being "transmitted" (introduced) to a new reservoir as a result of human movement. Once *B. chinensis* "infected" a new lake, we then calculated how long it took for the population to become abundant enough so that the reservoir became “contagious” and was capable of acting as a source population. We also monitored how the introduction of *B. chinensis* affected biomass and energy flows among groups in the altered ecosystem.

Bellamya chinensis is native to Asia and was first recorded in North America in 1892 as an imported live food source (Wood 1892). The species has since spread to numerous lakes and slow-moving rivers throughout the USA, as well as southern Canada (Olden *et al.* 2013). This prosobranch, freshwater species is large, reaching shell lengths up to 70 mm, lives 4-5 years (Jokinen 1982), has an annual fecundity of 30 juveniles/female (Stephen *et al*. 2013), and can reach high population densities (Chaine *et al*. 2012) that fluctuate with environmental conditions (Haak *et al*. 2013).

All Chinese mystery snails graze on algae and periphyton, but adults > 43 mm are also capable of suspension feeding (Olden *et al*. 2013). When present alone, *B. chinensis* does not appear to reduce native snail abundance (Solomon *et al.* 2010); however, when present with the invasive rusty crayfish *Orconectes rusticus* [Girard 1852], native snail biomass decreases (Johnson *et al.* 2009).

Objectives

A geographically focused case study is used to demonstrate how social and ecological models can be used together to answer social-ecological questions. The objectives of this research study were twofold: 1) couple a social network depicting human movement among regional reservoirs with each reservoir’s individual ecosystem network model to assess how perturbations influence biomass and energy flows throughout the entire network, and 2) assess the specific impacts the non-native *Bellamya chinensis* could have on the region and estimate its introduction probability to individual reservoirs based on human activity.

Materials and methods

Study area

The Salt Valley region of southeastern Nebraska, USA comprises 19 reservoirs (near the City of Lincoln (40.8258 N, 96.6852 W) (Fig. 1). Reservoirs range from 0.048 to 7.28 km^2 in surface area and have variable fish communities and stocking regimes. Each reservoir has different established aquatic invasive species (Table 1). Salt Creek runs through the Salt Valley region and empties into the Platte River near Ashland, Nebraska (41.0393 N, 96.3683 W) (Martin 2013).

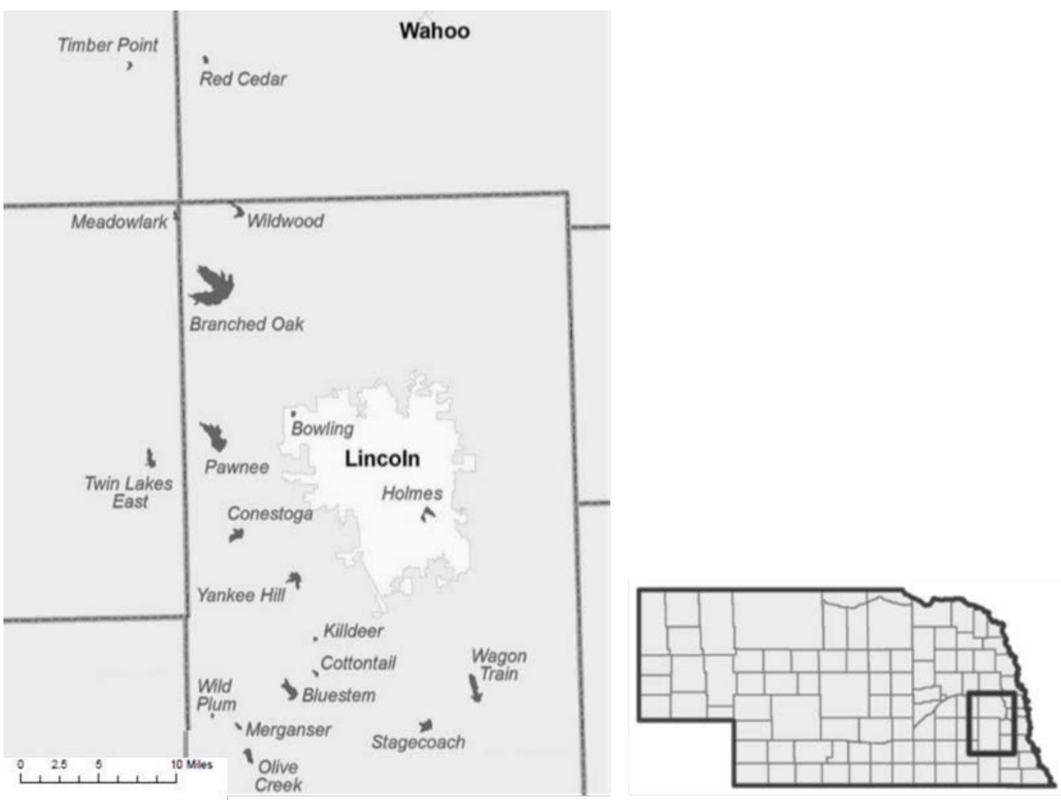

Figure 1. Reservoir locations in the Salt Valley region of southeastern Nebraska.

Table 1. Name, area, fish community, and established aquatic invasive species of each Salt Valley reservoir. Fish with (*) are species stocked at least once since January 2010.

Reservoir (year of last renovation)	Area (km^2)	Dominant fish community	Established aquatic non-native species
Bluestem	1.32	*Lepomis macrochirus*, *Micropterus salmoides*, *Sander vitreus*, *Pomoxis spp.*, *Pylodictis olivaris*, *Ictalurus punctatus*, *Cyprinus carpio carpio*	
Bowling (2007)	0.05	*L. macrochirus*, *M. salmoides**, *I. punctatus* *, *Oncorhynchus mykiss**	
Branched Oak	7.28	*L. macrochirus*, *M. salmoides**, *S. vitreus**, *Pomoxis spp.*, *P. olivaris*, *I. punctatus**, *Ictalurus furcatus*, *C. carpio carpio*, *Morone chrysops x Morone saxatilis**, *Morone americana*	*Corbicula fluminea* , *Bellamya chinensis*, *M. americana*
Conestoga	0.93	*L. macrochirus*, *M. salmoides*, *S. vitreus**, *Pomoxis spp.*, *P. olivaris*, *I. punctatus*, *C. carpio carpio*, *M. chrysops x M. saxatilis*, *Aplodinotus grunniens*	
Cottontail (2006)	0.12	*L. macrochirus*, *M. salmoides**, *I. punctatus**, *Lepomis cyanellus*	
East/West Twin	1.09	*L. macrochirus*, *M. salmoides*, *S. vitreus**, *Esox masquinongy*, *Pomoxis spp.*, *I. punctatus**, *Ameiurus spp.*, *C. carpio carpio*	
Holmes (2004)	0.40	*L. macrochirus*, *M. salmoides*, *S. vitreus**, *I. punctatus**, *O. mykiss**	*B. chinensis*
Killdeer	0.08	*L. macrochirus*, *M. salmoides**, *Pomoxis spp.*, *I. punctatus**, *Ameiurus spp.*	
Meadowlark (2007)	0.22	*L. macrochirus*, *M. salmoides*, *Pomoxis spp.*, *I. punctatus**	
Merganser	0.17	*L. macrochirus*, *M. salmoides*, *I. punctatus**, *Ameiurus spp.*	
Olive Creek	0.71	*L. macrochirus*, *M. salmoides*, *I. punctatus**	
Pawnee	3.00	*L. macrochirus*, *M. salmoides**, *Sander canadensis*, *S. vitreus**, *Morone chrysops*, *Pomoxis spp.*, *P. olivaris*, *I. punctatus*, *C. carpio carpio*, *A. grunniens*, *M. americana*	*B. chinensis*, *M. americana*
Red Cedar	0.20	*L. macrochirus*, *M. salmoides*, *Pomoxis spp.*, *P. olivaris*, *I. punctatus*	
Stagecoach	0.79	*L. macrochirus*, *M. salmoides*, *S. vitreus**, *Pomoxis spp.*, *I. punctatus*, *C. carpio carpio*, *M. chrysops x M. saxatilis**	
Timber Point (2005)	0.11	*L. macrochirus*, *M. salmoides*, *E. masquinongy**, *Pomoxis spp.*, *I. punctatus**	
Wagon Train	1.27	*L. macrochirus*, *Lepomis microlophus*, *M. salmoides*, *S. vitreus**, *E. masquinongy**, *I. punctatus**	*B. chinensis*
Wild Plum	0.06	*L. macrochirus*, *M. salmoides*, *I. punctatus*	*B. chinensis*
Wildwood (2003)	0.42	*L. macrochirus*, *M. salmoides*, *S. vitreus**, *I. punctatus**	
Yankee Hill (2007)	0.84	*L. macrochirus*, *M. salmoides*, *S. vitreus**, *I. punctatus**	

Five of the 19 Salt Valley reservoirs (Branched Oak, Pawnee, Wild Plum, Wagon Train, and Holmes) have established *B. chinensis* populations; however, no research has examined how the snails affect energy flows within these flood-control reservoirs. Despite some species causing extensive damage to their novel ecosystems, it is estimated that 90% of non-native species have minimal effects in their introduced ranges (Williamson 1996). The current lack of information on *B. chinensis* prompted its use in this research, as state resource managers are interested in learning more about its potential impact on local ecosystems.

Social network development

The Nebraska Game and Parks Commission (NGPC) and Nebraska Cooperative Fish and Wildlife Research Unit (NCFWRU) conducted in-person and mail-return angler surveys during 2009 – 2012. Data on number of anglers, angling methods, species sought, use of other Salt Valley reservoirs and demographics were collected and compiled, providing raw data for the social component of the current research project (Martin 2013). Experimental design, data collection and results are well-documented (Chizinski *et al.* 2014; Martin *et al.* 2014).

Data on reservoir substitutability and angler preferences on where and how to fish were obtained from the in-person angler interviews and analyzed using the iGraph package in R v3.1.1 (R Development Core Team 2014). Anglers were asked to identify a specific water body they would go to if their current reservoir was closed. Directed connections between nodes (reservoirs) were normalized to correct for different survey sizes and then weighted to depict the number of anglers who moved between two particular nodes. This provided a social network of how often anglers moved between and among reservoirs in the region. Boat anglers were also asked where they last fished (with their boat), enabling us to create a network depicting where anglers were coming from, including reservoirs and lakes outside of the current study area, a critical piece of information when studying aquatic invasive species that may be passively transported by humans.

The commonly used centrality measures of betweenness, closeness, and degree were calculated for each node in the network (Table 2). Betweenness is a measure of how a node lies on paths linking other reservoirs, closeness is the shortest path between two reservoirs, and degree is the total number of other nodes an individual node is connected to (Daly & Haahr 2007). Additionally, connectance index, transfer efficiency, system omnivory index, and Finn's Cycling Index values were also calculated (described in Christensen, Walters & Pauly 2005).

Ecological network development

If a snail is successfully transported from an infected reservoir to a susceptible reservoir, then what will happen to the newly infected ecosystem? Answering this question required developing ecosystem network models for each of the 19 study reservoirs. Using the dominant fish community as the basis for each network (Table 1), we were able to identify and compartmentalize species or functional groups critical to the trophic web of each reservoir.

Models were developed using the software Ecopath with Ecosim v6.4.2 (EwE) (Polovina 1984; Christensen & Pauly 1995). The first step was creating a static mass-balanced model of each reservoir in Ecopath, based on the ecosystem's current community composition, using previously identified inputs (Allen 1971; Walters, Christensen & Pauly 1997). These values, combined with the fishing pressure on species within each reservoir (from the NGPC and NCFWRU project), were used to develop a mass-balanced model based on Equation 1.

Eq. 1 $$B_i \times (P/B)_i \times EE_i = Y_i + \sum_{j=1}^{n} B_j \times (Q/B)_j \times DC_{ji}$$

where: B_i is the biomass of group i; $(P/B)_i$ is the production/biomass ratio of group i; EE_i is ecotrophic efficiency of group i; Y_i is the yield of group i, i.e., ($Y_i = F_i \times B_i$), where F_i is mortality due to fishing; B_j is the biomass of consumers or predators; $(Q/B)_j$ is food consumption per unit of biomass of predator *j*; and DC_{ji} is the proportion of prey *i* in the diet of predator *j*. Details on the development of this equation can be found in Christensen & Pauly (1992a, b).

Input data were collected from empirical studies on specific reservoirs when available; however, because much of this information has never been measured for these reservoirs, reported values were collected from the literature, using values from similar aquatic ecosystems when possible (i.e., reservoirs or small lakes in the Midwestern USA). After inputs were entered, models did not always mass-balance immediately. To manually balance each model, the diet composition matrix was adjusted (never exceeding ±10% of the initial value). If necessary, small adjustments were made to input variables for which we had the least confidence (also never exceeding ±10% of the initial value) until balanced models were achieved for each reservoir.

Once mass-balanced models were developed, Ecosim was used to create dynamic models by re-expressing Equation 1 as a set of differential equations as illustrated by Equation 2.

Eq. 2 $$\frac{dB_i}{dt} = f(B) - M_0 B_i - F_i B_i - \sum_{j=1}^{n} c_{ij}\left(B_i, B_j\right)$$

where: *f(B)* is a function of B_i if *i* is a primary producer or

$f(B) = g_i \sum_{j=1}^{n} c_{ji} \times (B_i, B_j)$ if *i* is a consumer (Walters, Christensen & Pauly 1997).

Ecosim reflects prey vulnerability when developing dynamic models, and adjusting vulnerability estimates dictates whether the model is donor-controlled or “joint limited.” In donor-controlled models, consumer abundance is ignored when calculating flow from source *(i)* to receiver *(j)*, and in joint-limited models, flows are adjusted based on prey and predator biomasses (Walters *et al.* 1997). Low vulnerability values create donor-controlled models, whereas high vulnerability values create joint-limited or “top-down” models with trophic cascades (Carpenter & Kitchell 1993). In the current research, we discuss results based on donor-controlled models only.

Dynamic models were developed under two scenarios: 1) *Bellamya chinensis* were introduced at a density of 0.0003 t km^{-2} and projected without biomass forcing or 2) *Bellamya chinensis* were introduced at a density of 0.0003 t km^{-2} and a biomass forcing function was loaded to simulate effects resulting from snail biomasses determined by logistic growth (de Vladar 2006) from the introduced density up to the carrying capacity. Carrying capacity was calculated for each reservoir (described in Langseth *et al.* 2012), using a conservative value of 10% (3.838 t km^{-2}) of the empirically calculated post-drought biomass of the *B. chinensis* population in Wild Plum of 38.58 t km^{-2} (Haak *et al.* 2013).

Coupling social and ecological network models

Within the framework for infectious disease modeling, we linked individual ecological reservoir models through the existing social network. We calculated the probability of *B. chinensis* from an "infected and contagious" primary host reservoir being "transmitted" (introduced) to a new "susceptible" reservoir as a result of human movement. Once *B. chinensis* "infected" a new lake, we then calculated how long it took for the population to become abundant enough so that the reservoir became "contagious" and was capable of acting as a source population. Once population size reached 10% of the estimated carrying capacity, it became a source population and the reservoir was categorized as "contagious" (Fogarty, Cote & Sih 2011). Finally, we combined this information to project an invasion timeline within this group of reservoirs while also evaluating how a system's structure (biomass values) and function (energy flows) were affected by the introduction of *B. chinensis*. Mass-balanced models were extracted at 10, 15, and 20 years after the simulated invasion. Variations in how a system responded to the disturbance of an added species in the network enabled us to estimate how resilient an individual reservoir is to stressors on the system.

We estimated that the maximum percentage of live snails that could successfully be introduced to a new lake via hitchhiking on macrophytes attached to boat trailers as 0.12% (i.e., infection rate) (Johnson, Ricciardi & Carlton 2001). This value gives us the propagule frequency but not the propagule size (Wittmann *et al.* 2014); propagule size is difficult to estimate. *Bellamya chinensis* females give live birth, and they may be carrying a number of viable juveniles at any given time (Jokinen 1982; Stephen *et al.* 2013). Thus, we assume the introduction of a single individual is adequate to establish a new population. Finally, we assumed angler movement, fishing pressure, and fish stocking were all constant over time.

Results

Social network analysis

Of the 4601 anglers interviewed, 3746 (81%) stated they would move to another reservoir within the Salt Valley region (Fig. 2a). Betweenness values for East and West Twin Lake and Bowling Lake are zero because no in-person interviews were collected from these two reservoirs. Additionally, though there are only 19 reservoirs, the highest possible degree is 38 due to the directed nature of the network. Boat anglers were asked an additional question about which water body they last fished with their boat; 2582 responses were recorded. Of these, 1908 (74%) had last fished at a Salt Valley reservoir (Fig. 2b).

a. b.

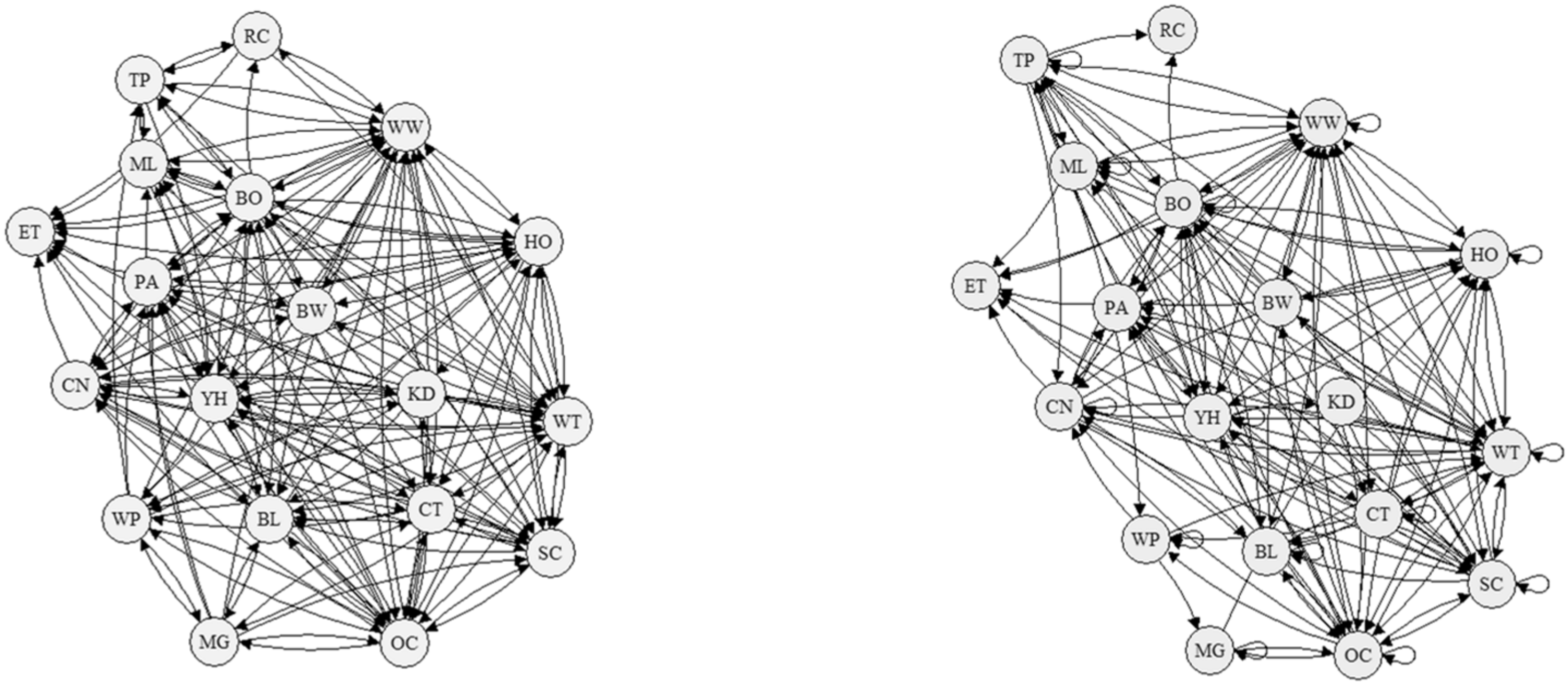

Figure 2. a. Reservoir substitutability of anglers and b. movement of anglers using boats in Salt Valley, Nebraska. Nodes represent individual reservoirs and weighted, directed edges depict the human movement between reservoirs. Reservoir codes: Bluestem (BL), Branched Oak (BO), Bowling (BW), Conestoga (CN), Cottontail (CT), East & West Twin (ET), Holmes (HO), Killdeer (KD), Meadowlark (ML), Merganser (MG), Olive Creek (OC), Pawnee (PA), Red Cedar (RC), Stagecoach (SC), Timber Point (TP), Wagon Train (WT), Wild Plum (WP), Wildwood (WW), Yankee Hill (YH).

Table 2. Betweenness, closeness, and degree values for each reservoir in the reservoir substitutability network and boater movement network.

	Betweenness		Closeness		Degree	
Reservoir	Reservoir suitability	Boater movement	Reservoir suitability	Boater movement	Reservoir suitability	Boater movement
Bluestem	37	0	0.83	0.02	19	15
Bowling	0	0	0.00	0.00	6	4
Branched Oak	8	36	0.72	0.04	25	26
Conestoga	23	20	0.89	0.03	22	21
Cottontail	15	8	0.60	0.03	19	13
East West Twin	0	0	0.00	0.00	11	8
Holmes	14	5	0.61	0.03	23	20
Killdeer	63	0	0.96	0.01	13	4
Meadowlark	21	0	0.63	0.03	15	12
Merganser	13	0	0.74	0.01	12	7
Olive Creek	21	46	0.64	0.03	27	26
Pawnee	20	17	0.48	0.04	21	19
Red Cedar	3	0	0.68	0.00	7	2
Stagecoach	3	18	0.55	0.04	23	25
Timber Point	36	29	0.68	0.03	12	18
Wagon Train	16	25	0.68	0.04	28	30
Wild Plum	93	0	0.98	0.02	15	9
Wildwood	42	28	0.79	0.04	31	27
Yankee Hill	14	28	0.59	0.04	25	25

Ecological network analysis

When no biomass forcing function was used, *B. chinensis* populations stayed equal to their initial density or even decreased. There were no significant differences among comparable flow values at model years 0, 10, 15, or 20 (ANOVA, P>0.5). When forcing biomass using a logistic growth model, mean flow values for consumption (P=0.0009), exports (P=0.001), respiration (P=0.00003), production (P=0.0001), flows to detritus (P=0.002), and total system throughput (P=0.0002) at simulation-year 20 were significantly greater than those of simulation year 0 (ANOVA followed by Tukey HSD, P<(0.01 for each)). Despite having significantly higher flows at simulation-year 20, there were no significant changes in network metrics of connectance index, transfer efficiency, or system omnivory index, even with biomass forcing (ANOVA, P>0.05), though total system biomass (excluding detritus) significantly increased at year 20 (ANOVA, P=0.006). In general, mid-trophic level fishes, such as *Pomoxis spp.*[Lesueur 1829, crappie], *Ictalurus punctatus* [Rafinesque 1818, channel catfish], and *Pylodictis olivaris* [Rafinesque 1818, flathead catfish] were negatively affected by the introduction of *B. chinensis* and showed reduced biomass values (Table 3). Piscivorous fish and terrestrial predators increased in biomass after an introduction, as did zooplankton and autotrophs.

Table 3. After the simulated introduction, a group's biomass within a lake increased, decreased, or had no change (column values are number of reservoirs that displayed each category).

Species/functional group	Increase	Decrease	No change
Ameiurus spp.	1	2	0
Aplodinotus grunniens	0	1	0
Autotrophs	12	0	2
Benthic macroinvertebrates	2	4	8
Cyprinus carpio carpio	2	0	2
Detritus	8	0	6
Esox masquinongy	2	0	0
Ictalurus punctatus	5	7	0
Lepomis macrochirus	4	3	7
Lepomis microlophus	0	1	0
Micropterus salmoides	12	2	0
Morone chrysops	0	0	1
Morone chrysops x Morone saxatilis	1	0	0
Oncorhynchus mykiss	0	0	1
Pomoxis spp.	3	7	1
Predatory birds	9	0	5
Pylodictus olivaris	1	2	0
Sander vitreus	4	2	0
Zooplankton	12	0	2

Coupled social and ecological network models

Using the infection rate of 0.12% (Johnson *et al.* 2001), the lag time was calculated for each reservoir, and a map of projected invasion over the next 25 years was developed. Through this method, primary host reservoirs critical to the spread of *B. chinensis* were identified. Wagon Train, Branched Oak and Pawnee reservoirs are the top three reservoirs in which managers should prevent the snail from being transported out. Wildwood and Stagecoach are the two most important reservoirs in which managers should prevent the snail from being introduced. Wildwood and Stagecoach act as secondary hubs and aid the snail's spread to peripheral, less-visited reservoirs in the network (Fig. 3). At the end of the 25-year simulation, seven additional reservoirs were infected and contagious, and an additional three were infected.

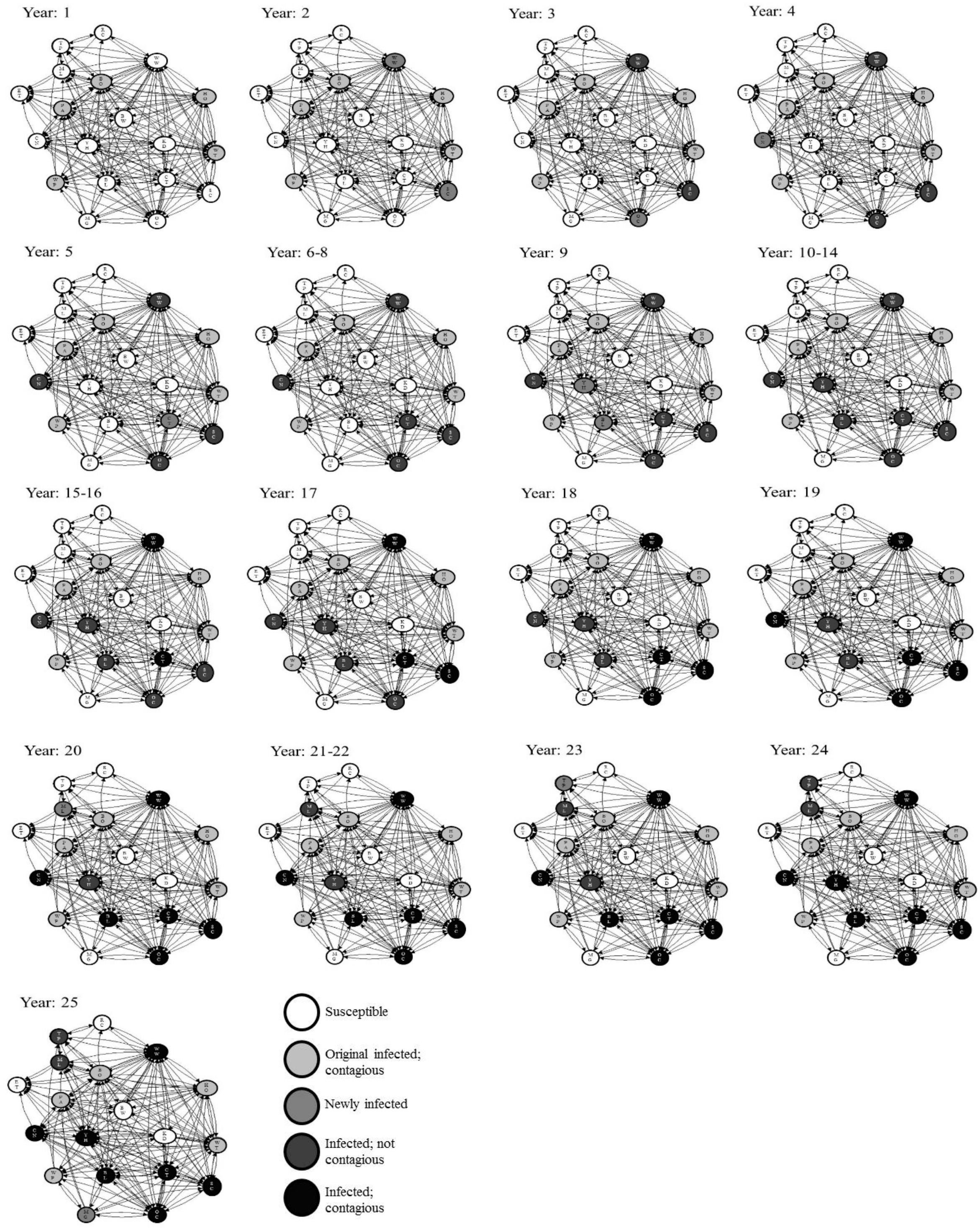

Figure 3. Simulated invasion of *Bellamya chinensis* in the Salt Valley, Nebraska reservoirs. Consecutive years when no changes take place are grouped together.

Discussion

Using ENA models to analyze the effects of invasive species is still a relatively new idea under development (Pinnegar, Tomczak & Link 2014). Miehls *et al.* (2009a, b) used ENA to compare ecosystems before and after a zebra mussel invasion, but because they had time series data spanning from pre- to post-invasion, they developed two static, mass-balanced models in Ecopath and compared the outputs. In contrast, Langseth, Rogers & Zhang (2012) used EwE to develop models that mirror species invasions in Great Lakes Michigan and Huron. They too had time-series data from pre- and post-invasions; however, they tested four different methods to determine which introduction method is best when employing Ecosim to model a species' introduction to a new ecosystem. Based on the quality of the data available to us, we followed their recommendation to use biomass forcing to assess hypothetical impacts of an invasive species introduction (Langseth *et al.* 2012). This group also tried introducing the invasive species at a low biomass, but found they had to control the species' dynamics with an artificial fishery, which may also explain why we did not see major changes to the system when we introduced *B. chinensis* at low biomasses without the use of biomass forcing.

Though the mean flow values of total system consumption, exports, respiration, production, flows to detritus, and total system throughput were significantly higher in simulation year 20, none of the connectivity metrics commonly used to compare ecosystems were significantly different. Additionally, certain fish species were more susceptible to population declines after the introduction of the snail, though not all fish within a calculated trophic level were negatively affected. It appears *B. chinensis* causes changes to the distribution of the community's biomass, but overall function remains relatively constant despite these changes.

Previous applications of epidemiological models to ecological research have been discussed in the literature. Mack *et al.* (2000) discussed the theoretical similarities between epidemiological models and invasive species models. Floerl *et al.* (2009) modeled the spread of a hypothetical invader by hull fouling on recreational yachts in New Zealand; though this study was based on a social network of boat movement, it did not incorporate ecological networks into the analysis. Meentemeyer *et al.* (2011) used spatio-temporal, stochastic epidemiological modeling and geographical modeling to predict the invasion of a forest pathogen. Ferrari, Preisser & Fitzpatrick (2014) also used epidemiology network theory to develop dynamic network models to simulate the spread of a terrestrial forest pathogen, though the pathogens in each of these examples spread independently and did not require a human network component for analyzing changes in distributions. To our knowledge, the present study is the first to apply the epidemiological model framework to an analysis including coupled social and ecological network models.

Network development

Ecopath with Ecosim has been consistently updated over the past 25 – 30 years and used in >150 peer-reviewed publications (Christensen & Walters 2004); however, as with any model, some limitations exist. Ecopath provides a static “snapshot” of a mass-balanced system; it does not necessarily represent equilibrium conditions. Ideally, long-term time series data are used to fit parameters, but such data did not exist in our case. Our models represent starting points based on best current information and can be adjusted as additional empirical data become available. In fact, these models can be used to identify where the largest gaps in critical data exist. For example, there were few published reports or available data with macroinvertebrate abundance or biomass. Thus, we selected macroinvertebrates most commonly reported in the limited fish-diet data that exist and used biomass estimates from similar Midwestern reservoirs with published data. As a result, the macroinvertebrate species or functional groups included are taxonomically broad and biased toward species that are consumed by fish species receiving study and analysis. Future research would benefit from individual lake assessments, but this would increase the amount of data necessary for this approach to work.

Diet composition matrices are extremely important inputs for the development of Ecopath models, yet these proportions are estimates based on the species and functional groups included in the model. Including age stanzas to account for ontological diet changes would be beneficial but could not be included due to the uncertainty of the input data. This is another example of an existing information gap where future research could be focused to improve the current model.

In Ecosim, the vulnerability values are critical to how the model is structured. Lower vulnerability values simulate a network based on bottom-up control, and higher vulnerability values simulate a network based on top-down control (Christensen & Pauly 1998; Ahrens, Walters & Christensen 2012). The vulnerability values used in the present study were estimated by the software and provide results of a donor-controlled model. Converting the Ecopath models to dynamic models in Ecosim is also complicated by temporal variation. Most likely, actual values of input parameters change over the course of a year, especially in temperate climates, but for simplicity a single value is entered for a period of one year.

The developers of EwE have actively identified strengths and weaknesses of the software as it continues to be developed (Walters *et al.* 1997; Pauly *et al.* 2000; Christensen & Walters 2004), and reviews on the strengths and weaknesses of EwE, as well as comparisons with other ecological network models, have been published by other groups. The major strength of ecosystem network modeling, in general, is the ability to look at the system as a whole rather than limiting investigation to single-species effects; however, some caveats have been provided. When using EwE, accepting the default values provided by the software should be discretionary, and users should not use the software as a “black-box” modeling tool, especially when confidence in the data is limited (Plaganyi & Butterworth 2004). Link *et al.* (2008) compared Ecopath with another software, EcoNetwrk, and found the results to be similar despite the differences underlying the models. Fath, Scharler & Baird (2013) compared Ecopath with the software NEA (Fath & Borrett 2006) and found discrepancies in results between the two models, particularly with the calculated Finn's Cycling Index. In the current study, we heeded these warnings as much as possible (for example, by not including Finn's Cycling Index in the analyses).

The 25-year simulations that did not force *B. chinensis* biomass resulted in the snail either staying at a very low biomass or disappearing all together. One possibility is that we did not include all of the vital compartments specific to the functioning of that reservoir in the analysis. Nutrient concentrations and the microbial community were both excluded due to extremely low confidence in available data. Little (if any) data exist on macroinvertebrate biomass, and we could not conduct individual lake surveys for each species. This affects our ecological models because we had less confidence in biomass estimates for the lower trophic levels. However, it may also be that the reservoirs had enough functional redundancy allowing changes to ecosystem structure without changing ecosystem function.

Coupled social and ecological network models

To couple the social and ecological models, a number of assumptions were required. First, we assumed the transmission rate of 0.12% from Johnson, Ricciardi & Carlton (2001) applied to *B. chinensis* movement on macrophytes attached to boat trailers. Aquatic invasive species are commonly moved by commercial and recreational boating (Schneider, Ellis & Cummings 1998; Muirhead & Macissac 2005). This estimate is conservative because it does not take into account other means of introduction, such as movement on wildlife or fishing gear, and it does not include intentional aquarium dumping (Padilla & Williams 2004) or "merit releases" by people who wish to establish a harvestable population as a food source (Vidthayanon 2005).

Using this transmission rate, it is assumed snails will be introduced at boat landings, and subsequent populations will be found around these points in a reservoir (Rothlisberger *et al.*

2010). Once a lake is infected, there is a lag time before the population density is large enough to begin acting as a contagious source population.

Admittedly, this coupled approach is difficult to implement due to the data-intensive nature of the method. Collecting long-term data available on the movement of humans within a region and on the biotic community composition is a difficult task, particularly in an era of budget cuts and limited resources. In the present study, the survey data used to develop the social networks and the data on fishing pressure were collected over a four-year period as part of a PhD thesis (Martin 2013), and not all lakes were included in each aspect of data collection, providing some limitations in the analysis. Stocking records were collected from the NGPC online database. Input data for the ecological networks were collected from empirical research on specific reservoirs, when possible, but many of the inputs were collected from research on other Midwestern USA reservoirs reported in the literature. Site-specific input data for each reservoir simply do not exist, but we tried to include values from as ecologically similar systems as possible. The resulting models are believed to be as accurate as possible with the constraints of current data availability.

Conclusions and management implications

We demonstrated that network coupling is possible and allows for the assessment of ecological resilience at a regional scale, as recommended by Pope, Allen & Angeler (2014). Our coupled social and ecological network approach enabled us to rank reservoirs in order of prioritization, both in terms of where invasive species management should focus on preventing individuals from leaving and where management should focus on preventing individuals from being introduced.

Based on simulations, three of the reservoirs that currently have *B. chinensis* populations and high levels of boating traffic, Wagon Train, Branched Oak, and Pawnee, are the most important source populations; preventing outgoing snails from these reservoirs will greatly limit, or at least slow, the spread of *B. chinensis* in the region. In contrast, despite having the largest population of *B. chinensis*, Wild Plum's population is of little importance in the spreading of snails through the network. If *B. chinensis* spreads in the manner suggested by simulations, then two reservoirs, Wildwood and Stagecoach, are the two invasion hubs, connecting peripheral, less-visited reservoirs to the infected and contagious reservoirs. This is indicated by their high betweenness and degree values, both for reservoir substitutability and boater movement. Additionally, these two reservoirs have high fishing pressure and close proximity to source populations. In the current model, anglers from Branched Oak infect Wildwood and anglers from Wagon Train infect Stagecoach, both in simulation year two. This is a tangible output agencies can use to ensure their efforts are as effective as possible.

This framework was implemented using *B. chinensis* as a study species, but it has the potential to be applied to other aquatic invasive species that spread via anthropogenic movement. It also helps managers identify how humans may be affecting the landscape by creating a visual representation of connection patterns that may not otherwise be apparent. Finally, this approach may be useful in determining regional effects of intentional (e.g., stocking) and unintentional (e.g., invasive species, natural disasters) disturbances.

Acknowledgments

This research was supported in part by an NSF IGERT grant, DGE-0903469, as well as the International Institute for Applied Systems Analysis (IIASA) as part of the Young Scientists Summer Program. We thank Bruce Stephen for helpful comments on earlier drafts of this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The Nebraska Cooperative Fish and Wildlife Research Unit is jointly supported by a cooperative agreement among the U.S. Geological Survey, the Nebraska Game and Parks Commission, the University of Nebraska, the U.S. Fish and Wildlife Service, and the Wildlife Management Institute.

References

Ahrens, R.N.M., C.J. Walters & Christensen, V. (2012) Foraging arena theory. *Fish and Fisheries*, **13**, 41-59.

Allen, K.R. (1971) Relation between production and biomass. *Journal of the Fisheries Research Board of Canada*, **28,** 1573-1581.

Byers, J.E. (2009) Competition in marine invasions. *Biological Invasions in Marine Ecosystems: Ecological, Management, and Geographic Perspectives* (eds G. Rilov & J.A. Crooks), pp. 245-260. Springer-Verlag, Herdelberg.

Carpenter, S.R. & Kitchell, J.F. (1993) *The Trophic Cascade in Lakes*, Cambridge University Press, New York.

Chaine, N.M., Allen, C.R., Fricke, K.A., Haak, D.M., Hellman, M.L., Kill, R.A., Nemec, K.T., Pope, K.L., Smeenk, N.A., Stephen, B.J., Uden, D.R., Unstad, K.M. & VanderHam, A.E. (2012) Population estimate of Chinese mystery snail (Bellamya chinensis) in a Nebraska reservoir. *BioInvasions Records*, **1**, 283-287.

Chizinski, C.J., Martin, D.R., Pope, K.L., Barada, T.J. & Schuckman, J.J. (2014) Angler effort and catch within a spatially complex system of small lakes. *Fisheries Research*, **154,** 172-178.

Christensen, V. & Pauly, D. (1992a) Ecopath II – a software for balancing steady-state models and calculating network characteristics. *Ecological Modelling*, **61**, 169-185.

Christensen, V. & Pauly, D. (1992b) A Guide to the ECOPATH II Program (version 2.1). ICLARM Software 6. Manila: ICLARM.

Christensen, V. & Pauly, D. (1995) Fish production, catches and the carrying capacity of the world oceans. *NAGA, the ICLARM Q*, **18**, 34-40.

Christensen, V. & Pauly, D. (1998) Changes in models of aquatic ecosystems approaching carrying capacity. *Ecological Applications*, **8 (Supplement),** S104-S109.

Christensen, V. & Walters, C.J. (2004) Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling*, **172**, 109-139.

Christensen, V., Walters, C.J. & Pauly, D. (2005) Ecopath with Ecosim: user's guide. Fisheries Centre, University of British Columbia, Vancouver, 154 p.

de Vladar, H.P. (2006) Density-dependence as a size-independent regulatory mechanism. *Journal of Theoretical Biology,* **238,** 245-256.

Fath, B.D. & S.R. Borrett. (2006) A Matlab function for network environ analysis. *Environmental Modelling & Software*, **21**, 375-405.

Fath, B.D., Scharler, U.M., Ulanowicz, R.E. & Hannon, B. (2007) Ecological network analysis: network construction. *Ecological Modelling,* **208**, 49-55.

Fath, B.D., Scharler, U.M. & Baird, D. (2013) Dependence of network metrics on model aggregation and throughflow calculations: demonstration using the Sylt-Romo Bight Ecosystem. *Ecological Modelling,* **252**, 214-219.

Ferrari, J.R., Preisser, E.L. & Fitzpatrick, M.C. (2014) Modeling the spread of invasive species using dynamic network models. *Biological Invasions,* **16**, 949-960.

Floerl, O., Inglis, G.J., Dey, K. & Smith, A. (2009) The importance of transport hubs in stepping-stone invasions. *Journal of Applied Ecology*, **46**, 37-45.

Fogarty, S., Cote, J. & Sih, A. (2011) Social personality polymorphism and the spread of invasive species: a model. *The American Naturalist*, **177**, 273-287.

Haak, D.M., Chaine, N.M., Stephen, B.J., Wong, A. & Allen, C.R. (2013) Mortality estimate of Chinese mystery snail, *Bellamya chinensis*, (Reeve, 1863) in a Nebraska reservoir. *BioInvasions Records*, **2**, 137-139.

Daly, E. & Haahr, M. (2007) Social network analysis for routing in disconnected delay-tolerant MANETs. *Proceedings of the 8th ACM international symposium on Mobile ad hoc networking and computing*, 32-40.

Hethcote, H.W. (2000) The mathematics of infectious diseases. *Society for Industrial and Applied Mathematics*, **4**, 599-653.

Janssen, M.A., Bodin, O., Anderies, J.M., Elmqvist, T., Ernstson, H., McAllister, R.R.J., Olsson, P. & Ryan, P. (2006) Toward a network perspective of the study of resilience in social-ecological systems. *Ecology and Society*, **11**, 15-35.

Johnson, L.E., Ricciardi, A. & Carlton, J.T. (2001) Overland dispersal of aquatic invasive species: a risk assessment of transient recreational boating. *Ecological Applications*, **11**, 1789-1799.

Johnson, P.T.J., Olden, J.D., Solomon, C.T. & Vander Zanden, M.J. (2009) Interactions among invaders: community and ecosystem effects of multiple invasive species in an experimental aquatic system. *Oecologia*, **159**, 161-170.

Jokinen, E.H. (1982) *Cipangopaludina chinensis* (Gastropoda: Viviparidae) in North America, review and update. *Nautilus*, **96**, 89-95.

Langseth, B.J., Rogers, M. & Zhang, H. (2012) Modeling species invasions in Ecopath with Ecosim: an evaluation using Laurentian Great Lakes models. *Ecological Modelling*, **247**, 251-261.

Link, J., Overholtz, W., O'Reilly, J., Green, J., Dow, D., Palka, D., Legault, C., Vitaliano, J., Guida, V., Fogarty, M., Brodziak, J., Methratta, L., Stockhausen, W., Col, L. & Griswold, C. (2008) The Northeast U.S. continental shelf Energy Modeling and Analysis exercise (EMAX): ecological network model development and basic ecosystem metrics. *Journal of Marine Systems*, **74**, 453-474.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecological *Applications*, **10**, 689-910.

Martin, D.R. (2013) *Spatial and temporal participation in recreational fishing*. PhD thesis, University of Nebraska-Lincoln.

Martin, D.R., Chizinski, C.J., Eskridge, K.M. & Pope, K.L. (2014) Using posts to an online social network to assess fishing effort. *Fisheries Research*, **157**, 24-27.

Meentemeyer, R.K., Cunniffe, N.J., Cook, A.R., Filipe, J.A.N., Hunter, R.D., Rizzo, D.M. & Gilligan, C.A. (2011) Epidemiological modeling of invasion in heterogeneous landscapes: spread of sudden oak death in California (1990-2030). *Ecosphere*, **2**, art17. http://dx.doi.org/10.1890/ES10-00192.1.

Meyers, L.A., Pourbohloul, B., Newman, M.E.J., Skowronski, D.M. & Brunham, R.C. (2005) Network theory and SARS: predicting outbreak diversity. *Journal of Theoretical Biology*, **232**, 71-81.

Miehls, A.L.J., Mason, D.M., Frank, K.A., Krause, A.E., Peacor, S.D. & Taylor, W.W. (2009a) Invasive species impacts on ecosystem structure and function: a comparison of Oneida Lake, New York, USA, before and after zebra mussel invasion. *Ecological Modelling*, **220**, 3194-3209.

Miehls, A.L.J., Mason, D.M., Frank, K.A., Krauses, A.E., Peacor, S.D. & Taylor, W.W. (2009b) Invasive species impacts on ecosystem structure and function: a comparison of the Bay of Quinte, Canada, and Oneida Lake, USA, before and after zebra mussel invasion. *Ecological Modelling*, **220**, 3182-3193.

Muirhead, J.R. & Macisaac, H.J. (2005) Development of inland lakes as hubs in an invasion network. *Journal of Applied Ecology*, **42**, 80-90.

Olden, J.D., Ray, L., Mims, M.C. & Horner-Devine, M.C. (2013) Filtration rates of the non-native Chinese mystery snail (*Bellamya chinensis*) and potential impacts on microbial communities. *Limnetica*, **32**, 107-120.

Padilla, D.K. & Williams, S.L. (2004) Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Frontiers in Ecology and the Environment*, **2**, 131-138.

Pauly, D., Christensen, V. & Walters, C. (2000) Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science: Journal du Conseil*, **57**, 697-706.

Pinnegar, J.K., Tomczak, M.T. & Link, J.S. (2014) How to determine the likely indirect food-web consequences of a newly introduced non-native species: a worked example. *Ecological Modelling*, **272**, 379-387.

Plaganyi, E.E. & Butterworth, D.S. (2004) A critical look at the potential of Ecopath with Ecosim to assist in practical fisheries management. *African Journal of Marine Science*, **26**, 261-287.

Polovina, J.J. (1984) Model of a coral reef ecosystem I. the Ecopath model and its application to French Frigate Shoals. *Coral Reefs*, **3**, 1-11.

Pope, K.L., Allen, C.R. & Angeler, D.G. (2014) Fishing for resilience. *Transactions of the American Fisheries Society*, **143**, 467-478.

R Development Core Team. (2014) R: *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rothlisberger, J.D., Chadderton, W.L., McNulty, J. & Lodge, D.M. (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.

Schneider, D.W., Ellis, C.D. & Cummings, K.S. (1998) A transportation model assessment of the risk to native mussel communities from zebra mussel spread. *Conservation Biology*, **12**, 788-800.

Solomon, C.T., Olden, J.D., Johnson, P.T.J., Dillon Jr, R.T. & Vander Zanden, M.J. (2010) Distribution and community-level effects of the Chinese mystery snail (*Bellamya chinensis*) in northern Wisconsin lakes. *Biological Invasions*, **12**, 1591-1605.

Stephen, B.J., Allen, C.R., Chaine, N.M., Fricke, K.A., Haak, D.M., Hellman, M.L., Kill, R.A., Nemec, K.T., Pope, K.L., Smeenk, N.A., Uden, D.R., Unstad, K.M., VanderHam, A.E. & Wong, A. (2013) Fecundity of the Chinese mystery snail in a Nebraska reservoir. *Journal of Freshwater Ecology*, **28**, 439-444.

Vidthayanon, C. (2005) Aquatic alien species in Thailand (Part 1): biodiversity. *International Mechanisms for the Control and Responsible Use of Alien Species in Aquatic Ecosystems: Report of an Ad Hoc Expert Consultation, Food and Agriculture Organization* (ed Bartley, D.M.), pp. 1-195.

Walters, C., Christensen, V. & Pauly, D. (1997) Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries*, **7**, 139-172.

Williamson, M. (1996) *Biological Invasions*, Chapman and Hall, London.

Wittmann, M.J., Metzler, D., Gabriel, W. & Jeschke, J.M. (2014) Decomposing propagule pressure: the effects of propagule size and propagule frequency on invasion success. *Oikos*, **123**, 441-450.

Wood, W.M. (1892) *Paludina japonica* Mart. for sale in the San Francisco Chinese markets. *The Nautilus*, **5**, 114-115.