Social-ecological interactions in inland recreational fisheries

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Abstract

The goal of this PhD thesis is to better understand prominent social-ecological interactions in inland recreational fisheries to inform practical local level management that helps maintain inland recreational fisheries and the benefits they provide. Using a coupled social-ecological model I synthesize current hypotheses in inland recreational fisheries related to lakeshore development and stock enhancement to determine social-ecological outcomes as people both develop shorelines and stock fish when they become dissatisfied with catch rates. I demonstrate that increased development near lakes can lead to a dependency on stock enhancement to maintain recreational fisheries. Therefore, increased management costs could threaten the ability of managers to continue to supply future fishing opportunities. In the remainder of the dissertation, I present potential ecological and institutional approaches to maintaining inland recreational fisheries in highly developed areas. I first follow up on a widely-held ecological hypothesis from my first chapter that littoral structure reduces young of year mortality and improves recruitment of fish populations. My results show that there is no support for this hypothesis for largemouth bass and highlight the need for a basic understanding of the determinants of early life mortality of other freshwater fish species. I then focus on improving stock enhancement decisions in open access inland recreational fisheries by using bio-economic theory to help guide optimal investments under both formal and informal management institutional arrangements. Despite a hypothesis within natural resource management that communities will not invest in a resource under open access, I show that informal management groups do have incentives to voluntarily invest in maintaining their fish populations through stock enhancement even under open access. Finally, I determine whether stakeholders – those carrying out management of and affecting fish populations – view their fisheries as coupled social-ecological systems, by comparing their mental models to a prominent academic framework for understanding social-ecological systems. I show that stakeholders emphasize the number, diversity, and influence of actors and resource systems, and focus less on governance systems and broader environmental settings. Based on strong empirical evidence that the number and diversity of governance system attributes are positively correlated with social-ecological fisheries success, I suggest approaches for improving the role of governance systems in local management of recreation fisheries. Overall, this thesis demonstrates that a social-ecological perspective of inland recreational fisheries can improve our understanding and ability to maintain recreational fisheries, but also identifies important knowledge gaps currently limiting our ability to effectively manage these fisheries and the benefits they provide.

Résumé

L'objectif de cette thèse de doctorat est de mieux comprendre les principales interactions socio-écologiques dans les pêcheries récréatives à l'intérieur des terres afin d'éclairer une gestion pratique au niveau local qui aide à maintenir la pêche récréative dans les eaux intérieures et les avantages qu'elles fournissent. En utilisant un modèle socio-écologique couplé, je synthétise les hypothèses actuelles de la pêche récréative à l'intérieur des terres liées au développement des lacs et au réapprovisionnement des lots ('stocks') afin de déterminer les résultats socio-écologiques du développement et du réapprovisionnement des stocks à cause des prises peu satisfaisantes. Je démontre que le développement accru et le nombre d'habitants près des lacs peuvent entraîner une dépendance vis-à-vis du réapprovisionnement des stocks pour maintenir les pêches récréatives. Par conséquent, une augmentation des coûts de gestion pourrait menacer la capacité des gestionnaires à continuer à fournir des possibilités de pêche futures. Dans le reste de la thèse, je présente des approches écologiques et institutionnelles potentielles pour maintenir la pêche récréative dans les zones très développées. J'examine d'abord une hypothèse écologique largement répandue, discutée dans mon premier chapitre, selon laquelle la structure du littoral réduit la mortalité des jeunes de l'année et améliore le recrutement des populations de poissons. Mes résultats ne soutiennent pas cette hypothèse au cas de l'achigan à grande bouche, et soulignent la nécessité d'une compréhension de base des déterminants de la mortalité précoce chez d'autres espèces de poissons d'eau douce. Je me concentre ensuite sur l'amélioration des décisions du réapprovisionnement des stocks dans les pêcheries récréatives intérieures en libre accès en utilisant la théorie bioéconomique pour aider à orienter les investissements optimaux dans les arrangements institutionnels de gestion formels et informels. Malgré une hypothèse de gestion des ressources naturelles selon laquelle les communautés n'investiront pas dans une ressource en accès libre, je montre que les groupes de gestion informels sont incités à investir volontairement pour maintenir leurs populations de poissons, même en accès libre. Enfin, je détermine si les parties prenantes - celles qui gèrent et affectent les populations de poissons - considèrent leurs pêcheries comme des systèmes socio-écologiques couplés en comparant leurs modèles mentaux à un cadre académique important pour comprendre les systèmes socio-écologiques. Je montre que les parties prenantes mettent l'accent sur le nombre, la diversité et l'influence des acteurs et des systèmes de ressources, et se concentrent moins sur les systèmes de gouvernance et les paramètres environnementaux généraux. Sur la base de preuves empiriques solides montrant que le nombre et la diversité des attributs du système de gouvernance sont positivement corrélés au succès socio-écologique de la pêche, je suggère des approches pour améliorer le rôle des systèmes de gouvernance dans la gestion locale des pêches récréatives. Dans l'ensemble, cette thèse démontre qu'une perspective socio-écologique de la pêche récréative à l’intérieur des terres peut améliorer notre compréhension et notre capacité à maintenir la pêche récréative, mais identifie également d'importantes lacunes dans les connaissances qui limitent actuellement notre capacité à gérer efficacement ces pêcheries et leurs avantages.

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I would like to thank: my supervisor Chris Solomon for his exceptional mentorship and guidance during my PhD; Elena Bennett for her generous support as my committee member and acting supervisor in the latter half of my program; Stuart Jones for his intellectual input and guidance throughout my program; all past and current members of the Solomon, Bennett, and Jones labs for making my PhD such a beneficial experience; Lauren Chapman for her guidance as a member of my committee; the University of Wisconsin Extension Wisconsin Lakes Convention, Vilas County Lakes and Rivers Association, Julia Solomon, and everyone involved in my fourth chapter, they have helped shape and further my understanding of recreational fisheries; the graduate student communities of the Biology and Natural Resource Sciences Departments at McGill University for such a positive and fun community; friends and family that supported me throughout my program; and all members of the MFE team for always assisting with and making fieldwork so enjoyable. I am exceptionally grateful to the Wisconsin Department of Natural Resources and the Northern Temperate Lakes Long Term Ecological Research Database for data used in some of my manuscripts. I would also like to thank S.A. Wolf, D.J. Lewis, D.T. de Kerckhove, E.M. Bennett, and anonymous reviewers for comments on early versions of manuscripts, they have substantially improved my work. My research was supported by grants from NSERC Graduate Scholarships Doctoral (475586-2015) and GRIL EcoLac Programme to J.P. Ziegler, NSERC (402530-2011) and National Science Foundation (1716066) to C.T. Solomon and S.E. Jones, and the 2017 McNALMS and MLSA Lake Research Grants Program, as well as finical and research support from the University of Notre Dame Environmental Research Center.

Contribution to Original Knowledge

In Chapter 1 I demonstrated that there is an interaction between lakeshore development and reliance on stock enhancement to maintain inland recreational fisheries. Not only does this advance our understanding of recreational fisheries as coupled social-ecological systems but it demonstrates that as lakes become more developed the costs for recreational fisheries management are increased which can threaten the ability of people to maintain inland recreational fisheries and the benefits they provide.

In Chapter 2 I provided the first (to the best of my knowledge) empirical in-situ estimates of fresh water fish young of year mortality along an environmental gradient. My results do not support a widely-held hypothesis that littoral structure reduces young of year mortality. These findings are valuable because they suggest that changes in littoral structure (removal or addition) may not have the strong effects on recruitment and fish population stability that are often assumed by fisheries scientists and managers. My results also suggest that open-water season young of year mortality, while seldom quantified by fisheries scientists, is as or more important in determining recruitment success of fish as over-winter mortality. Empirical estimates of young of year mortality are valuable parameters for fisheries models, which are sensitive to young of year mortality estimates. From a purely applied perspective, my results suggest that investing in improving littoral structure may not reduce the reliance on stock enhancement for supplying fishing opportunities for anglers.

In Chapter 3 I developed theory for guiding efficient stock enhancement investment decisions in open access recreational fisheries to help maintain the benefits of these fisheries while limiting the costs of management. I am the first (to the best of my knowledge) to consider the role of local organizations in stock enhancement of open access recreational fisheries and disprove a widely-held assumption that community organizations do not have incentives to invest in maintaining an open access common resource.

In Chapter 4 I demonstrate that stakeholders who conduct and are most affected by recreational fisheries management do view recreational fisheries as social-ecological systems but they emphasize the role and effects of actors and resource systems over governance systems and broader environmental settings. These results are important because there is empirical evidence that the number and diversity of features of governance systems are strongly, positively related to successful fisheries management. This highlights the opportunity for governance systems, that address large scale issues at local scales, to play a larger role in inland recreational fisheries management.

Contribution of Authors

This thesis is in a manuscript format and I am the primary author of all manuscripts. Below I describe the contribution of authors for each manuscript.

Chapter 1

- Jacob P. Ziegler co-developed the model presented in the manuscript, analyzed the model, and wrote the manuscript.
- Elizabeth J. Golebie collected data from the literature to parameterize the economic portion of the model and provided feedback on manuscript drafts.
- Stuart E. Jones co-developed the model presented in the manuscript and provided feedback and intellectual input on the manuscript.
- Brian C. Weidel provided feedback and intellectual input on the manuscript.
- Christopher T. Solomon co-developed the model presented in the manuscript provided intellectual input and guidance on all aspects of the study and manuscript.

Chapter 2

- Jacob P. Ziegler designed and conducted the field study, analyzed the results, and wrote the manuscript.
- Colin Dassow provided intellectual input on study design, helped conduct fieldwork, and provided feedback on the manuscript.
- Stuart E. Jones provided intellectual input on study design and provided feedback and intellectual input on the manuscript.
- Alexander J. Ross provided intellectual input on study design, helped conduct fieldwork, and provided feedback on the manuscript.

- Christopher T. Solomon provided intellectual input and guidance on all aspects of the study and manuscript.

Chapter 3

- Jacob P. Ziegler co-developed the bio-economic model presented in the manuscript, analyzed the model, and wrote the manuscript.
- Sunny L. Jardine co-developed the bio-economic model presented in the manuscript and provided intellectual input and feedback on the manuscript.
- Stuart E. Jones provided intellectual input and feedback on the manuscript.
- Brett T. van Poorten provided intellectual input and feedback on the manuscript.
- Christopher T. Solomon co-developed the bio-economic model presented in the manuscript and provided intellectual input and guidance on all aspects of the study and manuscript.

Chapter 4

- Jacob P. Ziegler designed and conducted the field study, analyzed the results, and wrote the manuscript.
- Stuart E. Jones provided intellectual input and feedback on the study and manuscript.
- Christopher T. Solomon provided intellectual input and guidance on all aspects of the study and manuscript.

Introduction

Recognition that people have rapidly and extensively changed global ecosystems in the past 50 years more so than any other point in human history has led to the idea that people and ecosystems are tightly coupled social-ecological systems (Holling 2001, Westley et al. 2002, Steffen et al. 2007). Anthropogenic changes to ecosystems are happening at a novel and rapid pace, which threatens the ability of ecosystems and institutions managing them to adapt (Steffen et al. 2011, Steffen et al. 2015). While the behavior of people and institutions will dictate future trajectories of ecosystems, natural resource management has only recently begun to investigate the interactions of ecosystems and societies as coupled social-ecological systems (Kates et al. 2001, Alberti et al. 2003).

Inland waters support many ecosystem services, including recreational fisheries. In Canada alone approximately 3.3 million people partook in recreational fishing in 2010, representing 10% of the Canadian population, and contributed an estimated 8.3 billion dollars to provincial and territorial economies (Department of Fisheries and Oceans Canada 2010). Similarly, in the USA 35.8 million people partook in recreational fishing in 2016, representing 11% of the US population, and contributed an estimated 46.1 billion dollars to state economies (U.S. Census Bureau 2016). The threats to inland recreational fisheries are well documented (Post et al. 2002, Cooke and Cowx 2004, Post 2013) but our understanding of these fisheries has been mostly limited to biological interactions and individual human behaviors and has not taken a holistic social-ecological view (Arlinghaus et al. 2013, Arlinghaus et al. 2017).

In this thesis, my goal is to better understand prominent social-ecological interactions in inland recreational fisheries to inform practical local level management that helps maintain inland recreational fisheries and the benefits they provide. In the section that follows I review the relevant literature on management of shared natural resources and how it has evolved to consider social-ecological interactions. I then conclude with an outline of my thesis and specific objectives for each chapter.

Overview of relevant literature

The old paradigm of management of shared natural resources

There is a long-standing view that shared resources are notoriously difficult to manage because there are incentives for people to overuse and collapse the resource. Common resources (also known as common property resources or common pool resources) are one type of shared resource that has two defining characteristics: it is difficult or impossible to exclude people from consuming the resource, and the use of the resource by one person inhibits its use by another (Gordon 1954, Ostrom 1986, Fortmann and Bruce 1988, Berkes 1989, McGinnis 1999). Fish are often used as a classic example of common resources; controlling harvest on the oceans or inland waters is difficult and the removal of fish reduces harvest opportunities for others (Gordon1954, Ciriacy-Wantrup and Bishop 1975). Open access occurs when there are no institutions regulating access to or withdrawal of a common resource (Feeny et al. 1990). Gordon (1954) pioneered work on outcomes of common resources under open access and found that these resources are prone to over-exploitation. He showed that new fishers will continue to enter into a fishery until the cost of entry is greater than the perceived benefit of doing so; the net result is an exploitation rate that is often beyond what is socially or ecologically desirable (Gordon 1954).

Since Gordon (1954) there was a common misconception within the academic literature that all common resources not under government control were open access (Hardin 1968, Berkes et al. 1989, Feeny et al. 1990). Instead, there is an important distinction between an open access common resource – whose access and withdrawal is unregulated – and one that is under the ownership of a community that has the ability to limit access and withdrawal of the resource (Ostrom 1986, Fortmann and Bruce 1988, Berkes 1989, McGinnis 1999). This seemingly small misconception framed research and policy recommendations for several decades but was later proved false, spurring a paradigm shift in shared natural resource management that has come to shape our current understanding of how to sustainably manage publicly held common resources (Kates et al. 2001, Dietz et al. 2003).

Prior to the 1980's the academic recommendation for maintaining common resources was either government ownership or privatization. Scott (1955) furthered the work of Gordon (1954) on open access systems and argued that sole ownership of a common resource can lead to optimal outcomes because it removes incentives for overexploitation. However, Hardin (1968) conflated open access with common property and extended the research of Gordon (1954) and Scott (1955) to community owned resources. He suggested that all common resources not under government or private control were destined to collapse due to over exploitation and lack of incentives for individuals to voluntarily invest in maintaining the shared resource. This led to a popularization of the "tragedy of the commons" within ecological research and resulted in high-profile research suggesting that communities were trapped in a negative state unable to effectively manage their shared resources (Platt 1973, Costanza 1987). Hardin's (1968) analysis only considered the resource and individual human behaviors but failed to consider property rights and associated rules (collectively referred to as institutional arrangements) of common resources (Berkes 1989, Feeny et al. 1990).

Property rights grant authority to individuals or communities to undertake enforceable actions (defined by rules) related to a given resource (McGinnis 1999). Examples of property rights are rights to access, withdraw, manage, determine access to, and transfer rights for a given resource (Table 1).

The new paradigm of management of shared resources

Natural resource management in general neglected institutional arrangements until a paradigm shift towards considering coupled social-ecological systems occurred around the 1980's. In a critical review, Holt and Talbot (1978) suggested that the primary goal of natural resource management should be to manage the ecological system to maintain desirable outcomes and only secondarily mentioned institutional arrangements. But by the 1980's managers became aware of the complexity that arises from interactions between people and ecology and moved away from considering management outcomes as ecological in nature towards an understanding that most ecosystem outcomes were the result of exogenous factors including human actions and institutional arrangements (Mangel et al. 1996, Kates et al. 2001). The shift in natural resource management paradigm was characterized by a sense of high ecological uncertainty; managers questioned their ability to control ecological systems and meet consumptive and even non-consumptive management goals (Mangel et al. 1996). The heightened uncertainty resulted in a need to understand basic interactions between ecology and society and society's ability to direct ecosystems along desirable trajectories (Kates et al. 2001, Clark and Dickson 2003). Academic researchers responded with a proliferation of studies in ecology and environmental sciences that considered coupled social-ecological systems as opposed to only ecological systems (Fig. 1).

With increased research, one view of social-ecological systems that has emerged is that social-ecological interactions lead to complexity and uncertainty. Scholars argued that social-ecological systems can never be fully understood, much less directed in desirable ways, due to the innate complexity of coupled and interacting systems (Rittel and Webber 1973, Roe 1988, Ludwig et al. 1993, Ludwig 2001). However, Holling (2001) and Walker et al. (2006) argued an alternative view, that social-ecological systems are complex but they can be understood and explained by a handful of controlling processes and variables. These arguments have been supported by extensive empirical studies.

Fikret Berkes and Elinor Ostrom analyzed empirical examples of communities managing common resources to determine social and ecological variables that helped avoid the pessimistic predictions of Hardin's (1968) tragedy of the commons. Berkes (1989) identified successful examples of communities self-managing their common resources through devising rules of access and limiting exploitation. 2018-11-05 2:35:00 PM furthered these ideas in a review of diverse community based common resource management. She developed a set of design principals of institutions that proved successful for preventing freeriding, translating the status of the resource into action by users, addressing conflicts, and building legitimacy for rules (Ostrom 1990, Anderies et al. 2004). The work of Berkes and Ostrom suggested that when communities had the property right of exclusion (Table 1) they were able to successfully devise rules that led to sustainable resource use and avoid tragedy of the commons outcomes. They highlighted the need to consider institutional arrangements in explaining real world outcomes of shared resources, something previously ignored in the old view of natural resource management (Platt 1973, Costanza 1987, Hardin 1968, Ludwig et al. 1993).

Ostrom later formalized her findings into the Social Ecological Systems Framework for understanding social-ecological systems with application for local natural resource management (Ostrom 2009). She defined social-ecological systems as interacting subsystems or components that included resource users, resource systems, resource units, and governance systems (institutional arrangements). Similar to Holling (2001) she considered the complexity of social-ecological systems to be tractable and defined by key variables that interact within and among social-ecological system components to generate outcomes.

Since the contributions of Berkes and Ostrom, there have been calls to move beyond simply understanding social-ecological interactions to providing practical solutions for sustainability issues (Miller et al. 2014). Current natural resource management theory has widely recognized that understanding individual components of social-ecological systems is insufficient for understanding real-world outcomes and has begun to focus on the dynamic interactions between ecology and society (Clark and Dickson 2003, Miller 2013). However, sustainability scholars have argued that social-ecological research must move beyond simply understanding social-ecological interactions to offering practical, policy relevant solutions for sustainability problems (Clark and Dickson 2003, Wiek et al. 2012, Miller et al. 2014). Wiek et al. (2012) and Miller et al. (2014) recommended that social-ecological research can strengthen its real-world impact by understanding stakeholder views of sustainability problems and identifying implementation gaps. Fisheries management is one field that has begun to translate social-ecological theory into practical natural resource management.

Fisheries management, from ecological to social-ecological

The field of fisheries management has followed a path similar to that of the general theory of shared natural resource management. At the beginning of the century several high-profile studies suggested that global marine commercial fisheries were collapsing with as much as 70% of global stocks collapsed in 2005 (Pauly et al. 1998, Jackson et al. 2001, Myers and Worm 2003, Worm et al. 2006). These studies seemed to support a tragedy of the commons hypothesis that common resources are destined to collapse (Hardin 1968). However, Hilborn et al. (2005) argued that these studies only focused on fish populations and failed to consider the many examples under various institutional arrangements where fisheries were sustainable. He later summarized three main tenets established within marine fisheries management by these high-profile biologically focused studies, and presented alternative tenets using examples from successful local management of fisheries (Hilborn 2007). Hilborn et al. (2005) found that characteristics of institutional arrangements were the primary determinant of a fishery's success and recommended that fisheries management should focus on understanding the interactions between institutions and fisheries that lead to sustainable outcomes (Hilborn 2007). More accurate data on the state of global marine fish stocks has since been compiled and suggested that approximately 75% of stocks were at a sustainable biomass or were being used at a sustainable rate (Worm et al. 2009). This study highlighted that institutional arrangements like local management have contributed to the sustainable use and recovery of global fish stocks.

Similar to marine fisheries, there has been a prevailing view in inland recreational fisheries that they too are prone to collapse. Historically, inland recreational fisheries in North America were truly open access, with little to no regulation (Lester et al. 2003). But by the 1960's reports that fish populations were declining resulted in centralized government control over inland fisheries and establishment of angling seasons, harvest limits, and penalties for infractions (Lester et al. 2003). Despite increased government regulation, a series of papers suggested that North American inland recreational fisheries were prone to collapse and provided empirical examples and theory of fishery collapses (Post et al. 2002, Cooke and Cowx 2004, Allan et al. 2005, Post 2013). These papers concluded that North American inland recreational fisheries were still open access because government led effort control is often ineffective and user access is not restricted (see also Cox et al. 2002). Hardin's predictions would therefore hold true under open access and suggest that North American inland recreational fisheries are prone to collapse. However, a broader social-ecological understanding of the responses of actors to changes in the resource system, the incentives people face under various institutional arrangements, and gaps in stakeholder implementation of a social-ecological approach to inland recreational fisheries management, may help understand the conditions that create vulnerability to collapse versus resilient recreational fisheries (Post 2013).

An attempt to understand inland recreational fisheries as social-ecological systems has begun (Johnston et al. 2010, Hunt et al. 2013) but so far studies have largely focused on ecology or individual human behaviors and not on an understanding of how all the components of social-ecological systems, including institutional arrangements, interact to create outcomes in inland recreational fisheries (Arlinghaus et al. 2013, Arlinghaus et al. 2017).

Thesis Outline and Specific Objectives

In this thesis, I present four original research projects that are focused on understanding prominent social-ecological interactions in inland recreational fisheries in North America and providing results that can inform practical local level management that helps maintain inland recreational fisheries and the benefits they provide. The objective of my first chapter was to understand a potential social-ecological interaction between two prominent behaviours in inland recreational fisheries using Ostrom's Social Ecological System Framework. Specifically, I asked if lakeshore development and stock enhancement interact and what the implications would be for maintaining inland recreational fisheries in highly developed areas. In my second chapter I follow up on the findings of my first chapter to test a widely held ecological hypothesis that littoral structure improves fish recruitment, which could reduce management costs and reliance on stock enhancement. In my third chapter I develop theory for improving stock enhancement decisions in open access inland recreational fisheries and investigate how different institutional arrangements for stocking could affect recreational fisheries outcomes. In my fourth chapter I determine if stakeholders, those conducting and most affected by recreational fisheries management, view their recreational fisheries as social-ecological systems and I discuss how their system understanding can inform recreational fisheries management through incorporating results from previous social-ecological research.

Tables and figures

Table 1. Examples of institutional arrangements (also known as the governance system in Ostrom 2009) in inland recreational fisheries applied to my study region of northern Wisconsin. Institutional arrangements are composed of property rights that grant authorization for certain actions and rules that enforce and define these actions. Rules can be operational (set by a government) or collective (set by a community). This table was adapted from McGinnis (1999).

Institutional arrangements			
Property right	**Description**	**Rule type**	**Example**
Access and withdrawal	Ability to access and harvest a resource	Operational	Any individual who holds a fishing license is authorized by state government to harvest fish from public waters
Management	Ability to alter and improve a resource	Collective	Members can authorize lake organizations to appropriate money for use by non-profits to undertake conservation efforts on or around a lake
Exclusion	Ability to change access and withdrawal rights of users	Operational	Government organizations set catch and harvest limits for fish species but do not limit access
Alienation	Ability to transfer rights to individuals or groups	Operational	Government organizations grant lake associations management rights

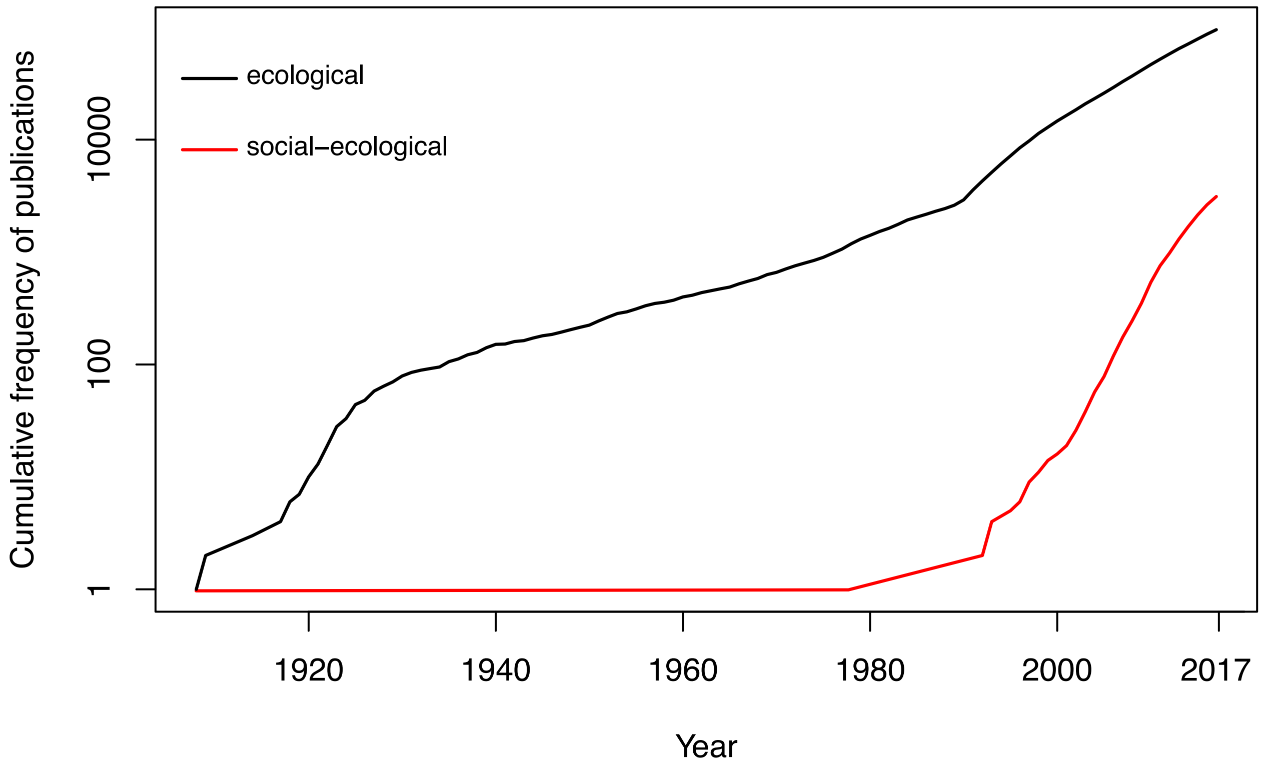

Figure 1. The phrase “ecological” is more commonly used than the term “social-ecological within the fields of Ecology, Environmental Sciences, and Environmental Studies. However, publications that use the term “social-ecological” have proliferated since the 1980’s when a paradigm shift occurred within natural resource management towards considering social factors like institutional arrangements. Results are from an ISI Web of Science literature search with “ecological” and “social-ecological” as search terms within Ecology, Environmental Sciences, and Environmental Studies fields of study. Note the y-axis is in logarithmic scale.

Chapter 1

Social-ecological outcomes in recreational fisheries: the interaction of lakeshore development and stocking

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Abstract

Many ecosystems continue to experience rapid transformations due to processes like land use change and resource extraction. A systems approach to maintaining natural resources focuses on how interactions and feedbacks among components of complex social-ecological systems generate social and ecological outcomes. In recreational fisheries, residential shoreline development and fish stocking are two widespread human behaviors that influence fisheries, yet emergent social-ecological outcomes from these potentially interacting behaviors remain under explored. We applied a social-ecological systems framework using a simulation model and empirical data to determine whether lakeshore development is likely to promote stocking through its adverse effects on coarse woody habitat and thereby also on survival of juvenile and adult fish. We demonstrate that high lakeshore development is likely to generate dependency of the ecosystem on the social system, in the form of stocking. Further, lakeshore development can interact with social-ecological processes to create deficits for state-level governments, which threatens the ability to fund further ecosystem subsidies. Our results highlight the value of a social-ecological framework for maintaining ecosystem services like recreational fisheries.

1.1 Introduction

Many ecosystems continue to experience rapid transformations due to processes like land use change and resource extraction often with significant gains in human well-being, which exemplifies the persistent problem of maintaining natural resources in continually human dominated landscapes (Halpern et al. 2008, Jentoft and Chuenpagdee 2009, Raudsepp-Hearne et al. 2010). A systems approach to maintaining natural resources focuses on how interactions and feedbacks among variables of complex social-ecological systems generate social and ecological outcomes (Berkes and Folke 1998, Ostrom 2009). Generalized frameworks aid in the difficult task of dealing with the complexity of diverse social-ecological systems because they facilitate the development of models to explain processes and predict outcomes (McGinnis and Ostrom 2014).

For example, the McGinnis and Ostrom (2014) social-ecological system framework (SESF) is an interdisciplinary diagnostic tool to determine which variables interact in a given social-ecological system and how these interactions can affect the sustainability of that system (Hinkel et al. 2014, Bots et al. 2015). The SESF is a multi-teired framework of variables that can be collapsed or expanded to describe a social-ecological system as needed. At the most general level (first tier variables) the framework describes a social-ecological system as natural resources units embedded in resource systems that are affected by interactions of actors and governance systems to create outcomes that can feedback to determine future contextual variables (Ostrom 2009, McGinnis and Ostrom 2014). The SESF is particularly useful compared to other prominent social-ecological frameworks when considering reciprocal social and ecological interactions that occur on the micro (i.e. individual actions) to macro (i.e. group and societal actions) scale (Binder et al. 2013). The purpose of the SESF is to organize knowledge on diverse social-ecological systems to facilitate shared understanding of how to maintain natural resources (McGinnis and Ostrom 2014). However, shared understanding cannot be achieved without testing the framework through applying it to diverse social-ecological systems and action situations (McGinnis and Ostrom 2014, Bots et al. 2015). Despite the popularity of the SESF (combined ISI web of science citations for Ostrom 2009 and updated McGinnis and Ostrom 2014 = 995) it is seldom applied to case studies and tested in a quantiative manner (Leslie et al. 2015).

Inland recreational fisheries are salient examples of prominent social-ecological systems (Carpenter and Brock 2004, Liu et al. 2007, Lorenzen, 2008, Hunt et al. 2013, Schlüter et al. 2014). In North America lake resource systems are widely used for the recreational benefits they provide resulting in preferential human development on or near lakes (Walsh et al. 2003). Lakefront property owners typically use lakes for swimming, boating, and aesthetic appeal, which often favors removal of littoral structure in the form of aquatic vegetation and coarse woody habitat (CWH). Removal of riparian trees for viewing corridors and landscaping can lead to decreased inputs of CWH into a lake (Sass et al., 2006a). Therefore, both aquatic vegetation and CWH are often present at very low densities with increased lakeshore development (defined as the number of buildings km^{-1} shoreline) (Jennings et al. 2003, Francis and Schindler 2006, Hicks and Frost 2011). Removal of littoral structure is hypothesized to affect fish, the focal resource unit in recreational fisheries, through a reduction in refuge for juveniles, which can determine recruitment success and stock rebuilding (Schindler et al. 2000, Walters and Kitchell 2001, Sass et al. 2006a, Sass et al. 2006b). Walleye (*Sander vitreus*), a commonly sought after and stocked sport fish, can experience reduced young of the year (YOY) survival with loss of CWH through predation, competition, and benthic siltation (Appendix A Table A1). Lakeshore development can also affect adult mortality as proximity of human development increases fishing pressure and harvest of adult fish, which can lead to a collapse of targeted fish populations (Appendix E, Post et al. 2008).

When the ecosystem service of recreational fishing declines, resource users and managers tend to stock lakes with fish to maintain adult populations (van Poorten et al. 2011). The institutional arrangements that determine stocking decisions are diverse and can be structured into operational rules, collective choice rules, and external arrangements (see Lorenzen 2005 and

Lorenzen 2008 for a detailed discription). However, a structured decision making process that includes stakeholder input on stocking decisions is recommended and often employed (WDNR 2014, Arlinghaus et al. 2015). Stocking has become the most dominant management panacea for recreational fisheries worldwide (Eby et al. 2006, van Poorten et al. 2011), and it has implications for nearly every aspect of aquatic food webs including trophic interactions, nutrient cycling, cross ecosystem linkages, and genetic and species diversity (Eby et al. 2006). Stocking also influences the economic state of a social-ecological system, as rearing and stocking costs can be high, especially for extended growth fingerlings which are larger and have higher survival rates than smaller fingerlings (Santucci Jr. and Wahl 1993, Szendrey and Wahl 1996).

As this background and SESF suggest, common interactions in inland recreational fisheries may lead to outcomes that then feed back to determine further social-ecological contexts (Ostrom 2009, Hunt et al. 2013, McGinnis and Ostrom 2014). We consider the SESF applied to recreational fisheries in a well-studied lake region to determine if lakeshore development interacts with stocking and what potential implications may be for maintaining recreational fisheries with increased lakeshore development. We used a social-ecological model and empirical data to explore these dynamics. Our model contained a stage-structured fish population of hatchery and wild individuals with stocking based upon structured decision making and recruitment based upon lakeshore development dependent habitat (Fig. 1.1). We compared our model output to empirical data on stocking rates and fishery-related economic costs and benefits in our study region. We hypothesized that lakeshore development would increase resource extraction and alter recruitment dynamics that would then feed back to reinforce stocking and create emergent ecological and socioeconomic outcomes.

1.2. Methods

1.2.1 Social-ecological model formulation

Our social-ecological fisheries model follows McGinnis and Ostrom's (2014) framework of a generalized social-ecological system (see Appendix B for a detailed description of our study system and application of Hinkel et al. 2015 diagnostic procedure for applying the SESF). We based our model on van Poorten et al. (2011) and Roth et al. (2007) with a few important modifications (see Appendices C and D). The ecological portion of the model defines dynamics of a stage-structured walleye population, from which people harvest adult walleye and to which they stock fingerlings to the YOY stage or extended growth fingerlings to the juvenile stage (Fig. 1.1). The survival of YOY fish depends on availability of littoral structure, which is negatively related to the density of lakeshore housing development. The social portion of the model defines a structured discussion making process, whereby, loss of natural recruitment and decreased adult densities lead to stocking of fingerlings or extended growth fingerlings. High post stocking mortality due to predation leads to stocking extended growth fingerlings, while a decline in adult densities between stock assessments and the responsiveness of management influences the amount of fingerlings or extended growth fingerlings stocked. Similar to van Poorten et al. (2011) we used a Ricker stock recruitment model, which assumes density dependence through decreased per capita recruitment with increasing size of the spawning stock. We increased harvest rates of adult walleye as a function of increased lakeshore development. This assumption was supported by empirical analysis relating angling effort and lakeshore development (see Appendix E).

1.2.2 Model simulation

We parameterized our social-ecological model to reflect walleye stocking and stage specific processes in Vilas County lakes in the Northern Highlands Lake District of Wisconsin, USA. This area is a well-studied system where recreational fishing is very important socially, economically, and ecologically (Liu et al. 2007). We focused on walleye, as this is a commonly stocked and sought after fish species in this region. A structured decision making process is used in Wisconsin to determine whether a lake will be stocked with walleye by the Wisconsin Department of Natural Resources (WDNR) (WDNR 2014). Adequate natural recruitment to support a walleye population and fishery, adult densities, and the likelihood of recruitment success based on physio-chemical predictors are the three greatest concerns when prioritizing lakes for stocking in Wisconsin (see Appendix C for further details, WDNR 2014, Hansen et al. 2015).

To determine ecological outcomes of lakeshore development on our walleye population we simulated lakes along a lakeshore development gradient. Our dependent variables were adult and YOY wild and hatchery fish densities obtained once simulations reached dynamic equilibria after 150 years. We used mean output values from 50 time steps to capture inter annual variation and our lake gradient of lakeshore development was 0 to 50 by an increment of 1.

1.2.3 Empirical walleye data

We compared model output of walleye stage-specific densities and stocking outcomes to a dataset from 158 Vilas County lakes spanning a gradient of lakeshore development. All lakes in our dataset had walleye present, were > 20 ha, and had publically available satellite images taken in 2013 or 2015, from which we determined lakeshore development (number of buildings km^{-1} shoreline). To test model-predicted walleye densities with empirical data we obtained walleye YOY and adult densities, determined using fall shoreline electrofishing and mark recapture in 29 and 58 of our lakes respectively, from the WDNR. YOY densities were estimated between 2011 and 2013 and adult densities were estimated between 1990 and 2014.

We modeled YOY counts (number of YOY walleye per kilometer of shoreline) using zero-inflated Poisson regression. Zero-inflated Poisson regression can account for two separate processes generating zeros in count data. In our application, zeros can be generated when YOY were present in a lake but failed to be detected by electrofishing or when YOY were actually absent from the lake. Known predictors of YOY catch per kilometer of shoreline in Wisconsin are lake surface area and shoreline complexity (defined as shoreline development factor or the ratio of lake perimeter to the perimeter of a circle with an area equal to the lake; Hansen et al. 2015). Therefore, we included lake surface area and shoreline complexity in candidate models and compared them using Akaike Information Criterion corrected for small sample sizes (AICc). Because shoreline complexity and lake surface area were highly correlated we did not consider both predictors in the same model. Lake surface area and shoreline complexity were unrelated to lakeshore development in our 29-lake dataset (R-squared = 0.02, p = 0.43, n = 29 and R-squared = 0.01, p = 0.66, n = 29, respectively). We related adult densities to lakeshore development using ordinary least squares regression.

To test stocking outcomes, we collected records of walleye stocking since 1972 for all lakes in our dataset from the WDNR and by collecting records of approved permits for stocking by all lake associations and angling clubs in Vilas County. Lakes that have adequate natural recruitment to sustain a walleye fishery are not stocked in Wisconsin (WDNR 2014), therefore, we estimated the odds that a lake had substantial walleye natural recruitment by using a logistic regression relating presence or absence of walleye stocking to lakeshore development in all 158 of our lakes (Fig. 1.3a). We could not test if a switch to stocking extended growth fingerlings occurred as a function of lakeshore development because we did not have lakeshore development data over time for our lakes. Instead, we relied on illustrating an increasing trend of stocking extended growth fingerlings in recent years by determining the average length of walleye stocked in our lakes between 1972-2014. While the mechanisms in our social-ecological model that cause a shift from stocking fingerlings to extended growth fingerlings closely mimic the decision process that the WDNR uses (Appendix C, Simonson 2010), an increased reliance on stocking extended growth fingerlings over time does not provide definitive evidence that the mechanism underlying this trend is driven solely by lakeshore development. However, we feel it is a useful trend to illustrate as lakeshore development within Vilas County has increased substantially over the timeframe considered (Schnaiberg et al. 2002).

1.2.4 State and municipal government costs and revenues

To determine economic outcome metrics associated with lakeshore development we used economic estimates of state and municipal government costs and revenues based on our model output and parameter estimates relevant to Vilas County. We corrected all economic estimates for inflation to 2004 to allow comparison across estimates. We determined the average cost of rearing and stocking fingerlings and extended growth fingerlings from the Wisconsin Legislative Audit Bureau summary of fish stocking activities in Wisconsin (WLAB 1997, Appendix G). We determined the property tax generated for an average lakefront building using assessments of lakefront property values, including renovation valuations, from lakefront properties sold between 1997 and 2004 in Vilas County (see Appendix F for details). We calculated the sales tax generated per fish harvested using estimates of total statewide expenditures by anglers, total fish harvested, and the sales tax rate in Wisconsin (US Department of the Interior 2001, McClanahan and Hansen 2005). We scaled revenue from property and sales taxes and costs from stocking to US dollars lake^{-1} year^{-1} using the average lake perimeter and area of the 158 lakes we considered in our empirical dataset.

1.3. Results

1.3.1 Social-ecological model

Results from our social-ecological model suggested that high lakeshore development eliminated natural recruitment and led to a reliance on stocking extended growth fingerlings to sustain the walleye population and fishery. Natural recruitment failed because higher lakeshore development led to decreased survivorship for YOY walleye via the loss of CWH refuge. This loss of refuge affected wild YOY and stocked fingerling survival, such that wild YOY densities declined and remained low above 15 buildings per km of shoreline and low fingerling survival led to extended growth fingerling stocking (Fig. 1.2a). At high lakeshore development, wild adult stocks were extirpated and were replaced by hatchery individuals that were maintained by extended growth fingerling stocking (Fig. 1.2c).

1.3.2 Empirical walleye data

Empirical data on YOY and adult walleye densities supported our model hypotheses that lakeshore development can influence stocking through increased YOY mortality (Fig. 1.2b and 2d). A zero-inflated Poisson regression model that predicted the number of YOY per kilometer of shoreline as a function of lakeshore development and shoreline complexity had the greatest predictive power (ΔAIC of a model with lakeshore development alone = 13). Only lakeshore development had a significant effect on the odds that a lake had no YOY present (odds ratio = 1.17, p value = 0.01). Specifically, an additional building per kilometer of shoreline increased the odds that a lake had no YOY present by 17%. Among lakes where YOY were present both lakeshore development and shoreline complexity had a significant negative effect on the number of YOY per kilometer of shoreline. An additional building per kilometer of shoreline decreased the expected number of YOY by 9%, while a unit increase in shoreline complexity decreased the expected number of YOY by 1%. These results are congruent with our model predictions of high predation pressure and lack of refuge at high lakeshore development leading to high YOY mortality and loss of natural recruitment (Fig. 1.2a). Decreased YOY densities could also be caused by reduced adult densities due to increased fishing pressure. However, despite increased fishing pressure with lakeshore development in our study region (see Appendix E) there was no significant decline in adult walleye density with lakeshore development (Fig. 1.2d), likely because highly developed lakes were more reliant on stocking (Fig. 1.3a), which effectively decouples fishing pressure and adult walleye density (Post and Parkinson 2012).

Empirical data on stocking in 158 Wisconsin lakes further supported our model results of reduced natural recruitment in lakes with high lakeshore development and a need for stocking extended growth fingerlings. Our logistic regression model determined that the odds that a walleye population and fishery were maintained by stocking increased significantly with lakeshore development (Fig. 1.3a, odds ratio = 1.1, p value < 0.001). At 0 houses per km of shoreline the odds of stocking were 50%, whereas, at 40 houses per km of shoreline the odds of stocking were 90% (Fig. 1.3a). The length of walleye stocked over time in the above mentioned lakes provided some support for our social-ecological model results that stocking practices tend to rely more on extended growth fingerlings than fingerlings as development increases (Fig. 1.2a). Stocking records from 1972 to 2014 indicated an increase in the average size of walleye stocked in recent years (Fig. 1.3b). 1999 marked the onset of a trend of stocking larger walleye because regional biologists began requesting more extended growth fingerlings, which are used when post-stocking mortality is high due to predation pressure (Simonson 2010).

1.3.3 State and municipal government costs and revenues

Economic outcome metrics from our model results suggested that lakeshore development can have unintuitive effects on government revenue at the state level through its effects on stocking, harvest, and tax revenue. Below ~18 buildings per kilometer of shoreline, sales tax generated from recreational fisheries outweighed the cost of stocking (Fig. 1.4). However, by approximately 18 buildings per kilometer of shoreline the cost of stocking for a lake was one order of magnitude greater than the revenue generated by sales tax. Stocking costs were increased further once stocking switched to extended growth fingerlings at approximately 20 buildings per km of shoreline, despite the decrease in number of fish stocked (Fig. 1.4, Fig. D1). Stocking costs at 50 buildings per kilometer of shoreline were 2 orders of magnitude greater than sales tax revenue. Municipal revenue from property tax when development was present was high in comparison with state level stocking costs and sales tax revenue (Fig. 1.4). Even at one building per kilometer of shoreline property tax revenue was one order of magnitude greater than sales tax and by 50 buildings per kilometer of shoreline property tax revenue was three orders of magnitude greater (Fig. 1.4). See Appendix H for sensitivity of results to model parameters.

1.4. Discussion

Management that successfully maintains natural resources despite intensive land use change and resource extraction requires developing policy that is robust to possible future scenarios (Schindler et al. 2015). Emergent outcomes from social-ecological interactions often lead to surprises in natural resource management (Holling et al. 2002). Therefore, developing a paradigm that incorporates emergent social-ecological outcomes is key to creating possible future scenarios that capture some of these surprises. For example, there has been an increasing call for incorporating human decisions and behaviors of anglers, managers, and stakeholders into recreational fisheries management (Hunt et al. 2013, Arlinghaus et al. 2013). Lakeshore housing development and stocking are two of the most prominent behaviors by users and managers of lake ecosystems (Schnaiberg et al. 2002, Eby et al. 2006). We illustrate how a SESF can be applied to recreational fisheries to determine emergent ecological and socio-economic outcomes. Our results suggest that at low to moderate lakeshore development, a lake in our study region can produce positive state revenues, positive and quite substantial municipal revenues, and fishing opportunities, all while maintaining wild fish stocks. At higher development, the state makes modest investments in sustaining the fishery (and native stocks may be sacrificed) in order to maintain fishing, local economies, and local municipal revenue.

Loss of natural recruitment at high lakeshore development results in the need for funding structures to be in place to sustain constant stocking regimes or to fund initiatives to improve recruitment success if recreational fisheries are to be maintained. A government-financed payment for ecosystem services is based on the beneficiary-pays principal and seeks to internalize the cost for maintaining an ecosystem service by charging users of the resource (Engel et al. 2008). This approach is employed in the United States, where revenue from taxes on gas and other expenditures by anglers fund recreational fisheries research, stocking, and maintenance costs (Buck 2009). However, our results suggest that revenue from sales tax generated by angler expenditures is two orders of magnitude lower than the cost of stocking on highly developed lakes. We note that our estimates of sales tax attributable to angler expenditure may be biased low because we used fish harvest instead of fishing effort to model these estimates, however, given the magnitude of stocking cost relative to sales tax revenue at high lakeshore development we feel our results are robust to this assumption. Therefore, a government financed payment for ecosystem services is only applicable at low lakeshore development where revenue from fisheries sales tax attributable to angler expenditure outweighs stocking costs. As lakeshore development increases an alternative funding structure is needed. One alternative funding structure is a third-party redistribution of costs, where government payment for stocking or habitat restoration comes from sources of revenue external to those generated by the resource users (Mauerhofer et al. 2013). In 2013 legislation was passed in our study area which used revenue from income tax and general sales tax, but not property tax, to fund stocking initiatives (Wisconsin Act 20 2013). Our results suggest that shoreline property tax revenue could be an alternative or additional source of funding for fisheries management in highly developed areas, as we demonstrate a strong relationship between lakeshore development and natural recruitment. However, our simple cost benefit analysis is a first examination of potential socio-economic outcomes and more in-depth economic valuations are required.

Managing development at the landscape level to promote heavily developed lakes while also conserving undeveloped lakes could represent a balance between state costs and local revenue in lake rich regions. Highly developing some lakes can provide substantial local revenue through property tax. However, stocking costs are reduced by natural recruitment and revenue from sales tax attributable to angler expenditure at low lakeshore development, therefore, conserving some lakes below the lakeshore development threshold where natural recruitment is lost could minimize state costs of maintaining recreational fisheries. A similar approach to natural resource management is used in forestry. The triad approach for forest management divides forests into zones of intensive use, extensive management, and reserve zones (Seymour and Hunter 1992). Managers often use assessments for protecting forested land for conservation or reassigning it for other human uses like food production (Lin and Trianingsih 2016). The concept of Environmentally Sensitive Areas is also used in natural resource management to guide land use and zoning on landscapes where heavy pressure from tourism and development occur (Dai et al. 2011, Leman et al. 2016). For lakes, creating landscape level diversity in the form of policy can result in fisheries that are resilient to angler over-exploitation (Carpenter and Brock 2004). Our results provide a new cost-benefit perspective to this issue by suggesting that zoning some lakes for heavy development and others for no development may limit state costs while still benefiting municipal governments.

Our social-ecological model predicted no stocking at low lakeshore development but our empirical data showed a 50% chance of stocking even at no lakeshore development (Fig. 1.3a), which could be due to heavy use of some lakes by non-residents, factors affecting natural recruitment other than lakeshore development, or stakeholder input in stocking decisions. Increased access to a lake through proximity to towns or roads, the reputation of a lake for fishing, and angler aversion to crowding could all result in higher than expected fishing pressure given the lakeshore development of a lake (Post et al. 2008, Hunt et al. 2011, Beardmore et al. 2014). Therefore, fishing effort on some low development lakes with high use could result in decreased adult densities and a need for supplementary stocking. Alternatively, some low development lakes may not have physio-chemical characteristics that allow for substantial natural recruitment. Hansen et al. (2015) found that lake surface area, water temperature degree-days, shoreline complexity, and conductivity were all predictors of walleye natural recruitment in Wisconsin lakes. Therefore, low development lakes that cannot support natural recruitment may be stocked especially if stakeholders have an interest in augmenting these fisheries. Stakeholder input from businesses owners, Native American tribes, and lake associations also influence stocking decisions in Wisconsin.

Although stakeholder input has substantially less weight for stocking decisions in our study area than natural recruitment and adult densities, there is an increasing call for co-management in natural resource management. Co-management in fisheries through stakeholder involvement in setting regulations is recommended to overcome "wicked" problems, which are defined as having many stakeholders with conflicting perspectives, unknowns, and no clear right/wrong solutions (Jentoft and Chuenpagdee 2009). Specifically, in regard to habitat and stocking regulations in recreational fisheries a stakeholder inclusive approach is recommended (Arlinghaus et al. 2015).

Although we did not consider interactions between lakeshore development and management techniques like catch-related regulations, our results suggest that increasing adult fish survival will not curb a reliance on stocking expensive extended growth fingerlings at high lakeshore development. Management regulations like catch-and-release in highly developed lakes may increase the adult fish population if post-hook mortality rates are not too high (Muoneke and Childress 1994), however, lack of natural recruitment will inevitably lead to loss of the population without expensive inputs of extended growth fingerlings (Arlinghaus et al. 2015). Therefore, if a management goal is to reduce reliance on stocking in highly developed lakes a focus should be placed on improving natural recruitment as opposed to altering catch regulations (Arlinghaus et al. 2015).

In our social-ecological model stocking of fish may have further exacerbated loss of natural recruitment with lakeshore development due to density dependent recruitment. Similar to van Poorten et al. (2011) we used a Ricker stock recruitment model, which assumes density dependence through reduction of per capita recruitment with increasing size of the spawning stock. Therefore, increasing the spawning stock through stocking extended growth fingerlings may have exacerbated loss of natural recruitment if adult densities were high enough to cause declines in YOY. Given that stocking only occurred when YOY densities were low to begin with and that the amount of fingerlings and extended growth fingerlings stocked were constrained to approximately 150 and 15 fish per hectare, respectively, it is unlikely that stocked adult densities had a noticeable effect on YOY densities through decreased per capita recruitment. However, our model did not take into account other community level effects like emergent Allee effects, emergent facilitation, or predator exclusion which can occur as a result of differential juvenile and adult mortality (Carpenter and Brock 2004, Persson and de Roos 2013, Schröder et al. 2014).

In a broader sense our results provide an example of how individual human behaviors can have large-scale outcomes that potentially threaten persistence of an ecosystem service without appropriate management of thresholds and social-ecological feedbacks. A review of prominent social-ecological frameworks by Binder et al. (2013) determined frameworks that predict macro-scale outcomes from micro-scale interactions and explicitly consider ecological, social, and reciprocal social-ecological dynamics are rare. Here we show behaviors of individual anglers and property owners (i.e. harvest and habitat removal) can have reciprocal large-scale ecological and socio-economic outcomes. Specifically, our application of a general social-ecological systems framework (McGinnis and Ostroms 2014) to recreational fisheries determined that a well-known threshold of fish habitat loss with lakeshore development (Marburg et al. 2006, Liu et al. 2007) can lead to a reliance on stocking. Stocking can then feed back to determine economic states, which threaten persistence of recreational fisheries if lakeshore development is not adequately managed and funding structures put in place to maintain stocking and habitat restoration initiatives. These results are congruent with resilience planning approaches to maintaining ecosystem services, which highlight the need to manage thresholds and feedbacks (Bennett et al. 2005, Biggs 2015).

While the SESF has been applied to recreational fisheries in Germany our application builds on this by considering a region with formal management oversight of stocking. Schlüter et al. (2014) and Hinkel et al. (2015) applied the SESF to recreational fisheries in Western Germany where informal institutions in the form of angling clubs and associations are in charge of managing the fishery. Our results suggest that harvest and habitat removal are more likely to have large-scale socio-economic outcomes in a formal management context than an informal one. For example, in Western Germany clubs and associations collect fees to conduct stocking, which limit management costs to resource users and would be less likely to have large-scale socio-economic outcomes observed in our study region through government payment for stocking programs using sources of revenue external to resource users (Schlüter et al. 2014). In a formal management context, the number of resource systems considered is much larger (i.e. all lakes within a region) making it difficult to monitor and create resource system specific regulations (Carpenter and Brock 2004). The number of resource systems is not considered in McGinnis and Ostrom (2014) as a second tier variable of resource systems but our application suggests that it is likely to interact with governance systems and affect both appropriation and provisioning action situations (Appendix B). While the size of a resource system is included in the list of second teir variables this implies one resource system and ignores the hetergonity of many discrete resource systems.

Ecosystems and the people that interact with them are diverse; therefore, ecological and economic outcomes are likely to differ among social-ecological systems. Simple models, like the one presented in this manuscript, do not fully characterize all social-ecological systems and implementation of management panaceas based on simplified models is sure to fail (Ostrom et al. 2007 and associated special issue). Our goal is to illustrate the utility of applying a social-ecological systems framework to help determine emergent social-ecological outcomes using recreational fisheries as a model system. We demonstrate that a social-ecological systems framework can provide useful insights of emergent social and ecological outcomes to inform future studies and policy that seeks to maintain ecosystem services.

Figures

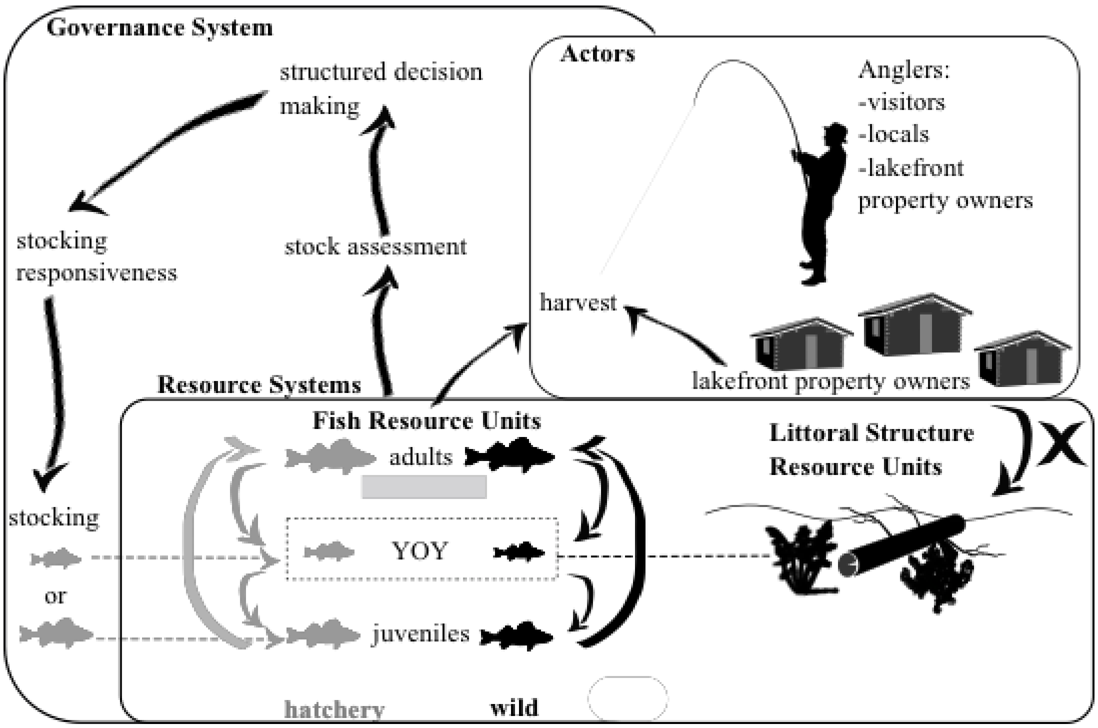

Figure 1.1. Social-ecological fisheries model based on van Poorten et al. (2011) and Roth et al. (2007). The resource system in the model includes resource units that are described by the dynamics of a stage-structured walleye fish population. Actors in the form of anglers and lakefront property owners interact with the resource system via harvest of adult walleye and removal of littoral structure, which decreases survival of young-of-year (YOY) walleye. A government organization maintains the resource units (fish) through stocking walleye fingerlings or extended growth fingerlings to the YOY or juvenile stage respectively. Stock assessments by the government organization inform structured decision making that determines if stocking occurs and the degree of stocking. See Appendices B, C, and D for more detail on our study system, model formation, equations, and parameters.

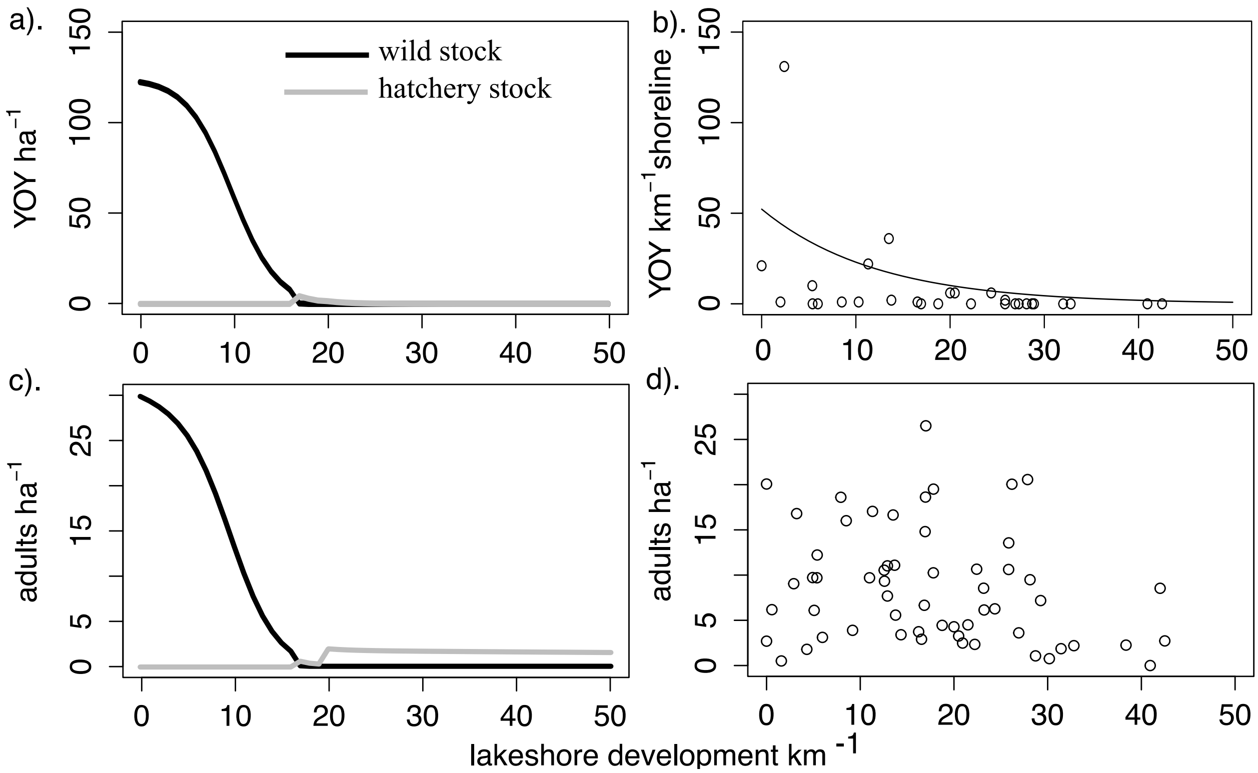

Figure 1.2. Social-ecological model output (a and c) and empirical data (b and d) illustrating ecological outcomes of adult and young of the year (YOY) walleye densities with lakeshore development. a). Wild YOYs declined to zero at approximately 20 buildings per kilometer of shoreline due to increased YOY mortality from loss of CWH related refuge. b). Catch per kilometer of shoreline of walleye YOY significantly declined with lakeshore development in 29 Vilas County Wisconsin, USA lakes (odds ratio = 1.17, p value = 0.01). c). Below 20 buildings per kilometer of shoreline adult walleye densities were determined by wild stocks but above 20 buildings per kilometer of shoreline only extended growth fingerlings determined densities. Adult densities were low but constant when the population was maintained only by stocking. d). There was no significant effect of lakeshore development on adult walleye densities, determined by mark recapture, in 58 Vilas County lakes despite higher fishing pressure with lakeshore development in this region (Appendix E).

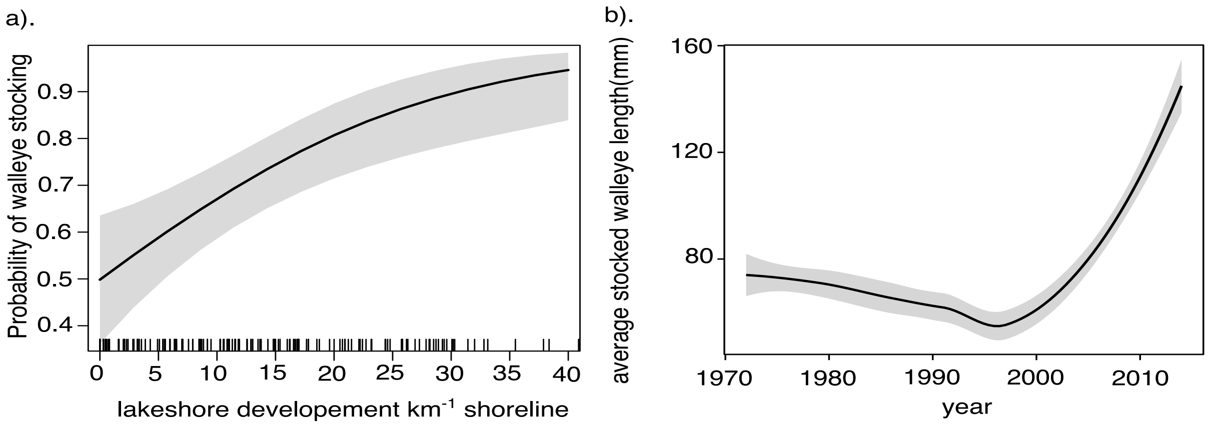

Figure 1.3. Empirical walleye stocking data for Vilas County Wisconsin. a). The probability that a walleye population and fishery were maintained by stocking increased significantly with lakeshore development in 158 Vilas County Wisconsin, USA lakes (odds ratio = 1.1, p value < 0.001). Vertical black marks on x-axis represent lakes observed at a given lakeshore development. 95% confidence intervals are plotted in grey. b). Of the 158 lakes 109 were stocked, in these stocked lakes the mean length of walleye stocked increased over time from stocking fingerlings (~50mm) to extended growth fingerlings (~150mm). We fit a moving average smoother to the data and 95% confidences intervals are plotted in grey.

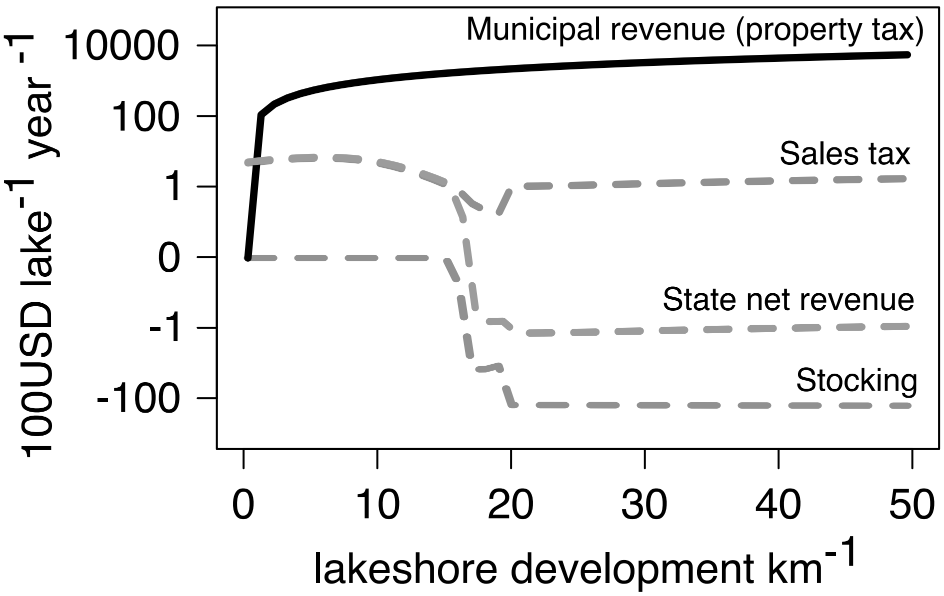

Figure 1.4. Municipal and state revenues with lakeshore development. Local municipal government revenue from property tax is plotted in black, while state net revenue is plotted in grey. State net revenue was comprised of sales tax attributable to angler expenditures and costs of stocking, depicted in dashed lines. Parameters relevant to Vilas County Wisconsin, USA and output from our social-ecological model results suggested that sales tax generated from recreational fisheries outweighed the cost of stocking below ~18 buildings per kilometer of shoreline but once a switch to stocking extended growth fingerlings occurred at approximately 20 buildings per km of shoreline, stocking costs were up to 2 orders of magnitude greater than sales tax revenue. Property tax revenue when development was present was one to three orders of magnitude greater than sales tax and stocking costs.

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Preface to Chapter 2

In Chapter 1 I found that lakes with higher development densities (and therefore less littoral structure) had a greater reliance on stock enhancement to maintain recreational fisheries. In Chapter 2 I further investigate the relationship between young of year fish mortality and littoral structure to determine if littoral habitat additions could reduce reliance on stock enhancement. The economic outcomes in Chapter 1 suggested that management costs may become too high to effectively maintain recreational fisheries through stock enhancement if lakes are heavily developed. However, if recruitment of fish populations in heavily developed lakes could be improved this might reduce reliance on stock enhancement.

In Chapter 1 I focused on walleye populations, in Chapter 2 I focus on largemouth bass because their behaviour, high population densities within small waterbodies, and hypothesized reliance on littoral structure make them an ideal model species to test the hypothesis that young of year morality is reduced at higher littoral structure densities.

Chapter 2

Coarse woody habitat does not predict largemouth bass young of year mortality during the open-water season

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Abstract

Littoral structure is often assumed to provide refuge to young of year (YOY) freshwater fish species but empirical *in situ* tests of this relationship are lacking. We estimated mortality rates of YOY largemouth bass (*Micropterus salmoides*) over the open-water season in 13 lakes in northern Wisconsin and Michigan, using repeated snorkel surveys. Our goal was to test the hypothesis that mortality rate is negatively related to the abundance of littoral coarse woody habitat, which ranged from 3-1500 pieces of wood per km of shoreline in these lakes. Instantaneous mortality rates were well-constrained and ranged from 0.04 to 0.19 among the 13 lakes. Mortality was not related to coarse woody habitat abundance. Our results suggest that the relationship between coarse woody habitat and YOY mortality might not be as strong or universal as is often assumed.

2.1 Introduction

Young of year (YOY) mortality is an important determinant of population dynamics, and managing to minimize YOY mortality can increase productivity and resilience of fish populations. Literature reviews of experiments focused on mortality in stage-structured populations provide empirical evidence that changes in YOY mortality have significant and often counterintuitive effects on population abundance (Zipkin et al. 2009; Schröder et al. 2014). In a theoretical study, Carpenter and Brock (2004) illustrated that reducing YOY mortality in lakes had the combined effect of increasing the level of harvest a fish stock can withstand before collapsing and decreasing the benefits anglers receive from overfishing. Additional theoretical studies have demonstrated that freshwater fish species with higher YOY mortality require larger population sizes to persist (Velez-Espino and Koops 2012) and population growth rates for most freshwater fish species are more sensitive to YOY mortality than adult mortality (Van der Lee and Koops 2015). Population level outcomes of YOY mortality can affect community level outcomes through Allee, emergent facilitation, predator exclusion, and cultivation effects (Walters and Kitchell 2001; Persson and de Roos 2013). However, YOY mortality estimates of freshwater fish species are rare and those that span environmental gradients, which build intuition of how YOY mortality might vary with environmental change, do not exist.

Much of the research to date on controls of early-life mortality and recruitment of freshwater fish species has ignored mortality during the open-water season, instead focusing on body size and the advantages it confers for overwinter survival. Early studies investigating controls of YOY mortality were conducted in systems without top predators (Ludsin and DeVries 1997, Post et al. 1999, Pine et al. 2000) or only considered overwinter mortality (Post and Evans 1989; Miranda and Hubbard 1994a; Miranda and Hubbard 1994b). These studies provided evidence that YOY with larger body sizes had lower overwinter mortality, likely due to an increased foraging ability and higher fat stores (although see Rogers and Allen 2009 who did not detect an effect of size-dependent overwinter mortality). However, body size is largely determined by hatch date and growth rates (Miller et al. 1988), variables that are difficult for fisheries managers to control.

Open-water season YOY mortality has been largely ignored in studies but there is some evidence that it is a determinant of recruitment success in largemouth bass. Like research on YOY mortality in general, much of the focus of largemouth bass YOY mortality has been on the potential for increased body size to decrease overwinter mortality (Miranda and Hubbard 1994a; Miranda and Hubbard 1994b; Olson 1996; Garvey et al. 1998; Miller and Storck 2011; Miranda and Muncy 2011; Pine et al. 2000). During the open-water season however, Rogers and Allen (2009) found no effect of body size on largemouth bass YOY mortality. While Rogers and Allen

(2009) were unable to compare the relative importance of overwinter mortality to open-water season mortality, Post et al. (1998) found that the open-water season represented a more extreme bottleneck for largemouth bass YOY survival than overwinter survival. In addition, Post et al. (1998) found that estimates of YOY predation during the open-water season explained 98% of the variation in observed initial YOY densities, suggesting that nearly all YOY mortality during the open water season was due to predation.

Coarse woody habitat is generally assumed to reduce YOY predation and mortality rates in temperate lakes by providing refuge from predators, but empirical tests of this hypothesis have yielded mixed results. Fish species are frequently found in littoral structure like coarse woody habitat and submerged macrophytes during their early-life stages (Hall and Werner 1977; Wallus and Simon 2008; Lewin et al. 2004), which has led to the assumption that this habitat is used as refuge (MacRae and Jackson 2001; Wallus and Simon 2008; Roth et al. 2007; Wallus and Simon 2008; Biggs et al. 2009; Ziegler et al. 2017). However, DeBoom and Wahl (2013) found no effect of coarse woody habitat abundance on predation of YOY of two species in mesocosm experiments and Klecka and Boukal (2014) found that littoral structure can be used as an ambush site by some predators. Alternatively, in an overwinter pond experiment Miranda and Hubbard (1994a) found that coarse woody habitat provided refuge from mortality for the smallest of four size classes of YOY largemouth bass, indicating an interaction between starvation and predation vulnerability, and Sass et al. (2006a) found that yellow perch experienced a recruitment failure after a whole lake removal of coarse woody habitat. They attributed the recruitment failure to increased predation pressure on YOY yellow perch and lack of spawning substrate.

The assumption that littoral structure is refuge for YOY has led aquatic and fisheries researchers to suspect that a threshold of coarse woody habitat exists, below which fish populations experience adverse effects from increased YOY mortality (Carpenter and Brock 2004; Liu et al. 2007). Coarse woody habitat is sensitive to human development and often completely absent when there are more than 7 houses per kilometer of shoreline (Marburg et al. 2006; Liu et al. 2007). The assumption that YOY mortality is affected by coarse woody habitat and in turn by housing development has been included in many studies of littoral species (Brock and Carpenter 2007; Biggs et al. 2009; Ziegler et al. 2017). However, there have been no comparisons of YOY mortality among lakes across gradients of coarse woody habitat density. *In situ* mortality estimates can provide insights into factors regulating recruitment success to help guide sustainable development and fisheries management.

In this study, we tested for a relationship between littoral habitat structure and YOY mortality during the open-water season by estimating largemouth bass YOY mortality rates in 13 lakes that varied in coarse woody habitat density. Based on the prevalent hypothesis that coarse woody habitat reduces predation pressure on YOY, we predicted that coarse woody habitat would be negatively correlated to YOY mortality.

2.2 Methods

2.2.1 Study sites

We selected 13 small lakes in northern Wisconsin and the Upper Peninsula of Michigan USA that had largemouth bass as the dominant piscivore, and which spanned previously documented coarse woody habitat gradients (Table 2.1). Development in this lake-rich forested region has been rapid since the 1940s and is often concentrated around lakes (Carpenter et al. 2007). As a result, there are various degrees of lakeshore development in the region resulting in a range of coarse woody habitat in lakes. Littoral coarse woody habitat has been observed to vary from 0 to 965 pieces of wood per kilometer of shoreline in this region (Christensen et al. 1996;

Marburg et al. 2006). Our study lakes extended this gradient to 3 – 1520 pieces of wood per kilometer of shoreline (Table I).

2.2.2 Young of year mortality

We estimated YOY largemouth bass instantaneous mortality rates in each lake using the decline in YOY relative abundance over the open-water season, following the methods of Essig and Cole (1986) and Miranda and Hubbard (1994b). We estimated relative abundance on at least 4 occasions in each lake, at approximately biweekly intervals from the beginning of June (just after swim-up) until late August or early September of 2016 or 2017 (Table 2.1). In both years largemouth bass successfully produced cohorts, and when we returned in 2017 to lakes that had been sampled in 2016 we did not observe major differences in bass recruitment between the two years. There were no notable events that would cause recruitment failures during our study period (e.g. anoxia, algal blooms, or large decreases in water level or temperature). We used line-transect snorkel surveys similar to Weidel et al. (2007) and Chamberland et al. (2013) to quantify relative abundance. We determined through a pilot study in our lakes that electrofishing was not effective at capturing YOY in the spring and early summer, while snorkel surveys allowed for consistent quantification of YOY throughout their first open-water season and did not affect YOY mortality unlike electrofishing and rotenone sampling (Chamberland et al. 2013). Numerous studies have shown strong correlations (R^2 between 0.88 and 0.99) between snorkel survey counts and absolute abundances of littoral fish in both lakes and rivers (Mullner et al. 1998; Pink et al. 2007; Weidel et al. 2007; Chamberland et al. 2013) and Brind'Amour and Boisclair (2004) found no difference between relative abundance estimates of lake littoral fish when measured using snorkel surveys or beach seines.

Relative abundance estimates are an accurate measure of the decline in YOY if detectability of YOY does not change within a lake over time. We controlled for and estimated habitat related detectability in our sampling and we tested for potential biases in YOY detection due to changes in water clarity. We always returned to the same sites and transects in each lake to maintain the same littoral structure density on transects over the sampling period. Within lakes we tested for an effect of coarse woody habitat on YOY detection probability using well-developed theory from species occupancy modeling (MacKenzie et al. 2002). We calculated the site level detection probability of YOY using logistic regression with 8 observations of YOY presence or absence on transects at each of the 6 sites per lake and sampling day (see Mollenhauer et al. 2018 for spatial re-sampling method of MacKenzie et al. 2002). Transect level coarse woody habitat density was included as a predictor of site level variation in YOY detection probability. We compared logistic regression models that allowed the effect of coarse woody habitat on YOY detection probability to remain constant or vary among sites and over time using AICc. Similar to Toft et al. (2007) we measured water clarity at the time of sampling as a covariate of visual detectability to determine if it changed over time. We measured water clarity as horizontal Secchi distance, vertical Secchi depth, and percent cloud cover. We also looked for changes in behavioural responses of YOY largemouth bass to divers over the study period and we considered potential biases in our results related to increased fish length over time (Appendix K and L).

On each lake visit we conducted snorkel surveys at six littoral sites located at the north, northeast, east, south, southwest, and west edges of the lake. At each site we sampled eight 10 m transects that extended perpendicular from shore because YOY largemouth bass are littoral (Wallus and Simon 2008) and transect orientation should be perpendicular, rather than parallel, to the density gradient of the object of interest (Buckland et al. 1993). We marked the end of transects on the shoreline with flagging tape and the start from a boat using a buoy and a range finder, being careful never to disturb transects. Two divers entered the water approximately 30m from transects, approached each transect slowly and calmly, swam in parallel at a constant rate of 10m per minute, and recorded on underwater tablets the number of YOY largemouth bass within their line of sight. It is common methodology to estimate school size when there are more fish than divers can count; we improved on this methodology by using video analysis to provide reproducible, unbiased, and more accurate counts of YOY when there were more than 5 YOY present on a transect (Buckland et al. 1993). Each underwater transect was filmed using a GoPro Hero 4 (GoPro Inc., San Mateo, California) and in instances where more than 5 YOY were encountered on a transect all YOY were captured on video and then video frames were used to count individuals using the cell counter plugin on ImageJ 1.x (Schneider et al. 2012; De Vos 2010). While using video counts might change the detection probability of YOY compared to only using snorkel counts, any bias introduced here is likely to be much smaller than simply estimating school size as is standard practice in snorkel surveys. Videos typically had good visibility allowing for easy counting of YOY present in video frames.

We conducted additional line-transect samples in pelagic habitat in each lake to confirm the absence of significant ontogenetic habitat shifts that could have biased the mortality rates that we estimated from our littoral sampling. We sampled at three sites per visit just offshore of littoral sites. The total amount of pelagic sampling varied per lake but was conducted at least twice (once early in the season and once later in the season) and on average three times per lake over the sampling period. We set 40 m pelagic transects parallel to shore at 30 m and 40 m from shore, using a thin white nylon line set at half the thermocline depth. If the thermocline depth was greater than two meters scuba divers swam along the transect line at a speed of 10 m per minute, and recorded YOY largemouth bass in the same manner as littoral transects. If the thermocline depth was less than two meters and divers could see past two meters in the water column (judged by vertical Secchi depth) the pelagic transects were snorkeled in the same manner as littoral transects.

2.2.3 Littoral structure

We determined the density of coarse woody habitat, the structural complexity of coarse woody habitat, and the density of macrophytes, another form of littoral structure, in each of our study lakes. Coarse woody habitat density was previously estimated for eight of our study lakes by Marburg et al. (2006) and we estimated coarse woody habitat in our other five lakes following their methods. We also estimated coarse woody habitat density in all thirteen lakes by quantifying the number of pieces of wood present on our littoral transects from video footage. Our video-derived estimates of coarse woody habitat density were strongly correlated with the estimates from Marburg et al. (2006) ($r=0.92$, $p<0.01$, $n=6$), so we present only the latter here. We used video footage to estimate the mean branchiness of woody habitat (following the methods of Marburg et al. 2006) and percent macrophyte cover.

2.2.4 Statistical analyses

The expected size of a population *X* at time *t* undergoing a random death process is given by a negative exponential model with initial abundance X_0 and mortality rate *z* (Bailey 1990), with errors that might be distributed with Poisson or negative binomial distributions (Bolker 2008):

$$X_t \sim Poisson(X_0 e^{-zt}) \qquad \text{Equation 1}$$

Or

$X_t \sim Negative\ Binomial(X_0 e^{-zt}, k)$ Equation 2

We estimated the initial abundance (X_0), mortality rate (z), and the dispersion parameter (k, Equation 2 only) along with their 95% confidence intervals for all 13 lakes by fitting our count data over time to Equation 1 and 2 using maximum likelihood (Table 2.1 and Fig. 2.1). We compared the predictive power of fitted models with the small-sample version of Akaike's information criterion (AICc). All statistical analyses were conducted in R using packages MASS and AICcmodavg (Venables and Ripley 2002; R Core Team 2017; Mazerolle 2017).

To test for potential effects of coarse woody habitat density, coarse woody habitat complexity, and the density of macrophytes on YOY mortality we used ordinary least squares regression (OLS) and weighted least squares regression (WLS) with mortality estimates (z in Equation 1 and 2) as the dependent variable and coarse woody habitat and littoral structure as the predictor variables (Fig. 2.3). In WLS we weighted mortality estimates by the inverse of their squared standard errors (Chatterjee and Hadi 2015). For simplicity, all results presented in figures are from models that had a single predictor of YOY mortality, however, we tested all predictor variables individually and in combination with each other, including interactions (Table M1). When an estimated dependent variable (EDV) is used in regression it can violate assumptions of heteroscedasticity due to variation in the EDV's 95% confidence intervals (Hanushek 1974; Williams and Lewis 2008). Two approaches are frequently used to deal with EDV regression: ordinary least squares and weighted least squares (Williams and Lewis 2008; Chatterjee and Hadi 2015). Ordinary least squares regression (OLS) allows some of the error in the regression model to be unexplained by predictor variables but does not account for known variation in measurement error when estimating regression parameters and standard errors. Weighted least squares regression (WLS) does not allow unexplained variation from predictor variables (i.e. it assumes all of the error in the regression model is due to measurement error and R^2 would be 1 if the EDV were directly observable) but accounts for measurement error in the EDV when fitting regression parameters and standard errors. Therefore, we report both OLS and WLS results as recommended by Williams and Lewis (2008). In all instances, we plotted the 95% confidence intervals from the WLS regression fits as they accounted for uncertainty in mortality parameter estimates.

When testing for an effect of littoral structural complexity on YOY mortality we could not include coarse woody habitat density and mean coarse woody habitat branchiness in the same model because they were positively correlated ($r = 0.84$ $p < 0.01$). Therefore, to characterize total littoral structure we ran a principal component analysis, which explained 94% of the variation in coarse woody density, coarse woody branchiness, and macrophyte cover in two principal components (PC1 and PC2 in Table 2.2). We then used the principal components, which corresponded to coarse woody habitat complexity (PC1) and macrophyte cover (PC2), as predictor variables of YOY mortality following the same methods as above.

Our hypothesis assumes that predation pressure is a strong control of YOY mortality in our lakes, as has been demonstrated in previous studies (Anderson 1988; Duarte and Alcaraz 1989; Post and Evans 1989; Ludsin and DeVries 1997; Post et al. 1998; Post et al. 1999; Post and Parkinson 2001). We used historical data on predator densities in a subset of our lakes to corroborate this assumption (Appendix I).

2.3. Results

2.3.1 Young of year mortality

Young of the year counts significantly and exponentially declined over the study period in all lakes (Fig. 2.1). On average, we sampled 4.6 km of transect per lake and observed 4,400 YOY per lake over the study period. For all lakes, a negative exponential-negative binomial model fit our observed count data better than a negative exponential-Poisson model (in all instances $\Delta AIC > 100$). Young of the year largemouth bass mortality estimates in the thirteen lakes ranged from 0.04 to 0.19 with a mean of 0.11 and a standard deviation of 0.04, and had reasonably well-constrained confidence intervals (Table 2.1).

Our ability to detect YOY was, for the most part, unrelated to coarse woody habitat density and water clarity did not significantly vary over time. There was no significant effect of CWH on YOY detection probability in 11 of our 13 lakes (Fig. 2.2). In one lake, the effect of coarse woody habitat significantly varied by site and had a significant positive effect on detection probability in two sites (West Long in Fig. 2.2, $\Delta AICc$ from a model with constant site effect > 2). Coarse woody habitat had a significant negative effect on YOY detection probability in only one lake but this lake had the lowest coarse woody habitat density of all lakes (Fig 2.2, Johnson Lake). Therefore, it is likely that the decline in detection probability with coarse woody habitat observed in Johnson Lake was ecologically driven rather than determined by a diver's reduced ability to see YOY when coarse woody habitat was present. In all lakes, the effect of coarse woody habitat on site level YOY detection probability did not vary over time as our best model predicting site detection probability included a constant coarse woody habitat effect over time for all lakes (Fig. 2.2, $\Delta AICc > 50$ compared to model with coarse woody habitat effect varying by lake, site, and time). Water clarity in each lake at the time of sampling did not significantly change over the study period when measured as horizontal Secchi distance (p values for the day of year effect in a regression model with lake as a blocking factor were all greater than 0.05 for all lakes) and vertical Secchi depth (all $p > 0.05$). Cloud cover at the time of sampling did not significantly change over the study period (all $p > 0.05$).

The declines in YOY counts were not due to ontogenetic shifts from littoral to pelagic habitats. We did not detect YOY largemouth bass on pelagic transects in 9 of our 13 lakes, despite an average 740m of pelagic transect line sampling per lake over the study period. In two lakes, young of the year were present on pelagic transects only where those transects were as shallow or more shallow than the littoral transects (i.e. not representative of pelagic habitat but rather additional littoral habitat). In the remaining two lakes, a negative exponential, negative binomial model described the decline in pelagic YOY counts over the open-water season and the pelagic mortality estimates did not significantly differ from littoral mortality estimates (mortality parameter estimate and 95% CI for pelagic YOY counts: $z = 0.05 \pm 0.02$ and $z = 0.07 \pm 0.03$, mortality parameter estimate and 95% CI for littoral YOY counts: $z = 0.05 \pm 0.02$ and $z = 0.08 \pm 0.02$, respectively). Therefore, it is unlikely that movement of YOY to pelagic habitat could account for the significant decline in littoral YOY counts in our lakes as pelagic YOY were either not present or, when they were present, declined at the same rate in both habitats.

2.3.2 Littoral structure and young of year mortality

In our 13 lakes, which spanned a large coarse woody habitat gradient (3 – 1500 pieces of wood per km of shoreline), YOY mortality was unrelated to coarse woody habitat, coarse woody habitat complexity, and macrophyte cover (Fig. 2.3 and 2.4, Table M1). Mortality was not significantly related to coarse woody habitat in WLS or OLS models (Fig. 2.3A, Table M1). Our data constrained the effect of coarse woody habitat on YOY mortality to near zero (Fig. 2.4). Coarse woody structural complexity and macrophyte cover (Table 2.2 PC1) were also poor predictors of YOY mortality during the open-water season and were not significant in any WLS or OLS models (Fig. 2.3B and C, Table M1).

2.4 Discussion

Our results are, to our knowledge, the first to compare *in situ* YOY mortality along an environmental gradient in lakes, and suggest that the relationship between coarse woody habitat and YOY mortality might not be as strong or universal as is often assumed. Although our results are limited in sample size and only consider one freshwater fish species they suggest that littoral structure variations alone may not lead to decreased YOY mortality as is often assumed in the literature (MacRae and Jackson 2001; Carpenter and Brock 2004; Wallus and Simon 2008; Brock and Carpenter 2007; Roth et al. 2007; Wallus and Simon 2008; Biggs et al. 2009; Allen et al. 2011; Ziegler et al. 2017). Our results also advance our understanding of early-life mortality of largemouth bass over the open-water season and provide an example that can be used to better understand early-life mortality and its determinants in other species through well-constrained estimates of YOY mortality.

Our estimates of open-water season YOY mortality are comparable to the few estimates that exist for largemouth bass and suggest that open-water season mortality is greater than overwinter mortality. There are only three published estimates of YOY largemouth bass open-water season mortality that we are aware of (Miranda and Hubbard 1994a; Shirley and Andrews 1977; Rogers and Allen 2009). Only two studies provided instantaneous mortality estimates: Shirley and Andrews (1977) provided one without an error estimate ($z = 0.0028$) making it difficult to compare with our estimates, while Rogers and Allen (2009) had 6 estimates with a range of 0.019 to 0.12. Our instantaneous mortality rates were well-constrained and ranged from 0.04 ± 0.02 to 0.19 ± 0.09 among 13 lakes, which is similar to the range observed by Rogers and

Allen (2009) (0.019 to 0.12). Rogers and Allen (2009) found that open-water season mortality alone was as high or higher than overwinter mortality. Our range in estimates of open-water season mortality are higher than those reported for largemouth bass overwinter mortality (range in estimates from Garvey et al. 1998 and Miranda and Hubbard 1994a = 0.00008 to 0.04). Despite the focus in the literature on overwinter mortality and its implications for recruitment success, our results suggest that open-water season mortality should be as great or greater a concern for recruitment success than overwinter mortality in largemouth bass.

High open-water season YOY mortality in largemouth bass could have a compensatory effect at the population level, especially when cannibalism is high, by reducing density-dependent competition of YOY for resources. A Ricker stock-recruitment relationship predicts that recruitment should decline at higher adult population densities if there is cannibalism by adults (Ricker 1954). Despite cannibalism accounting for the majority of largemouth bass YOY mortality in Post et al. (1998) they found no relationship between adult density and recruitment success. One explanation of this is that self-thinning through cannibalism may remove density dependent mortality that YOY might otherwise experience and compensate for increased predation pressure at higher adult densities. Based on our range of mortality rates (0.04 ± 0.02 to 0.19 ± 0.09) and study duration, largemouth bass populations can lose between 68% and 99% of their YOY populations over the open-water season. These large declines in abundance would reduce competition among the remaining YOY for resources and improve their chance for successful recruitment to older life stages.

While littoral structure may not serve as refuge for YOY largemouth bass, researchers have hypothesized it is refuge to other freshwater species. For example, YOY rainbow trout (Tabor and Wurtsbaugh 1991), yellow perch (Eklöv 1997), and walleye (Pratt and Fox 2001) have been assumed to use littoral structure to reduce predation pressure. However, few empirical tests have provided evidence for this (Savino and Stein 1982; Tabor and Wurtsbaugh 1991; Sass et al. 2006b). Behavioural differences in boldness of species may explain why largemouth bass do not receive refuge from littoral structure but species like bluegill, that adapt their behaviour to predators, do (Savino and Stein 1982; Turner and Mittelbach 1990). There is a known trade-off of boldness in largemouth bass, bold juveniles experience increased predation mortality but bold adults experience higher fitness and pass on their heritable behavioural traits (Ballew et al. 2017). Other known predictors of recruitment success among species are climate change, lake morphometry, overharvesting, and spawning substrate (Walters and Kitchell 2001, Nash et al. 2001, Hansen et al. 2015) but without well controlled studies estimating YOY mortality, the relative importance of these predictors and their interactions remains unclear.

Our analysis demonstrates how well-constrained mortality estimates can advance our understanding of determinants of freshwater fish early-life mortality and recruitment success. Our approach, while time intensive (65 days of snorkel surveys for 13 mortality estimates) might be useful in similar studies of littoral species in small lakes. Our approach might also be powerfully combined with large-scale experiments; for instance, one could manipulate wood levels and measure YOY mortality response in a whole-lake, before-after control-impact design. Other promising approaches for understanding determinants of YOY mortality in multiple systems include using marked stocked YOY (Shirley and Andrews 1977), standardized long term monitoring of YOY over the open-water season among multiple lakes (Post et al. 1998), and metaanalyses.

Fisheries management focused on maintaining productive fish stocks requires knowledge of critical variables like YOY mortality and how they might change with habitat modifications like removal or addition of littoral structure. Thresholds of critical variables that can lead to undesirable changes in social-ecological systems are a key concept in resilience thinking (Folke 2016). Understanding where these critical thresholds lie and avoiding trajectories that cross them is the role of responsible natural resource management. The concept of a safe operating space bounded by critical thresholds has recently been applied to fisheries management and illustrates the necessity of understanding which critical variables a manger can control and how best to allocate effort in managing them (Carpenter et al. 2017). For example, federal fisheries management in Canada has shifted from protecting fish habitat to protecting fish productivity, which requires a better understanding of the effects that habitat alterations have on critical variables for fish productivity like YOY mortality (Rice et al. 2015). Our results provide useful but rare estimates of *in situ* YOY mortality along a littoral structure gradient and suggest that littoral structure may not be as strong or universal a control on open-water season YOY mortality as is often assumed.

Figures and tables

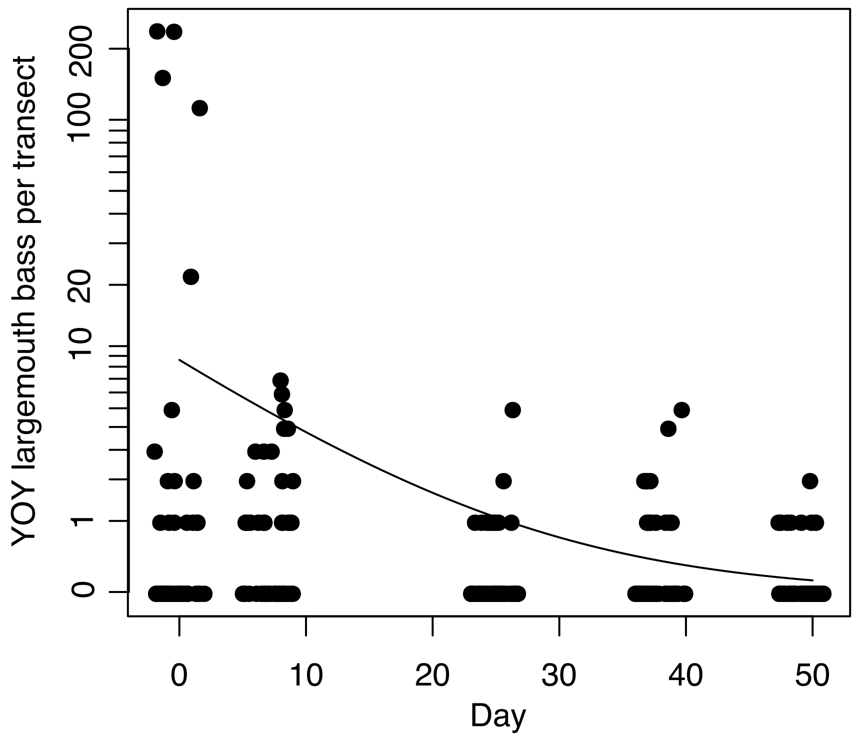

Figure 2.1. An example of young of year (YOY) largemouth bass counts per 10m transect line over the study period for a single lake (see Appendix J for plots from all lakes). Individual points represent total number of YOY present on a 10m transect line and are jittered to prevent over plotting (sampling days were 0, 7, 25, 38, and 49). The solid line shows the fit of the model used to estimate YOY mortality (a negative exponential model with negative binomial errors). Note that the y-axis is in logarithmic scale.

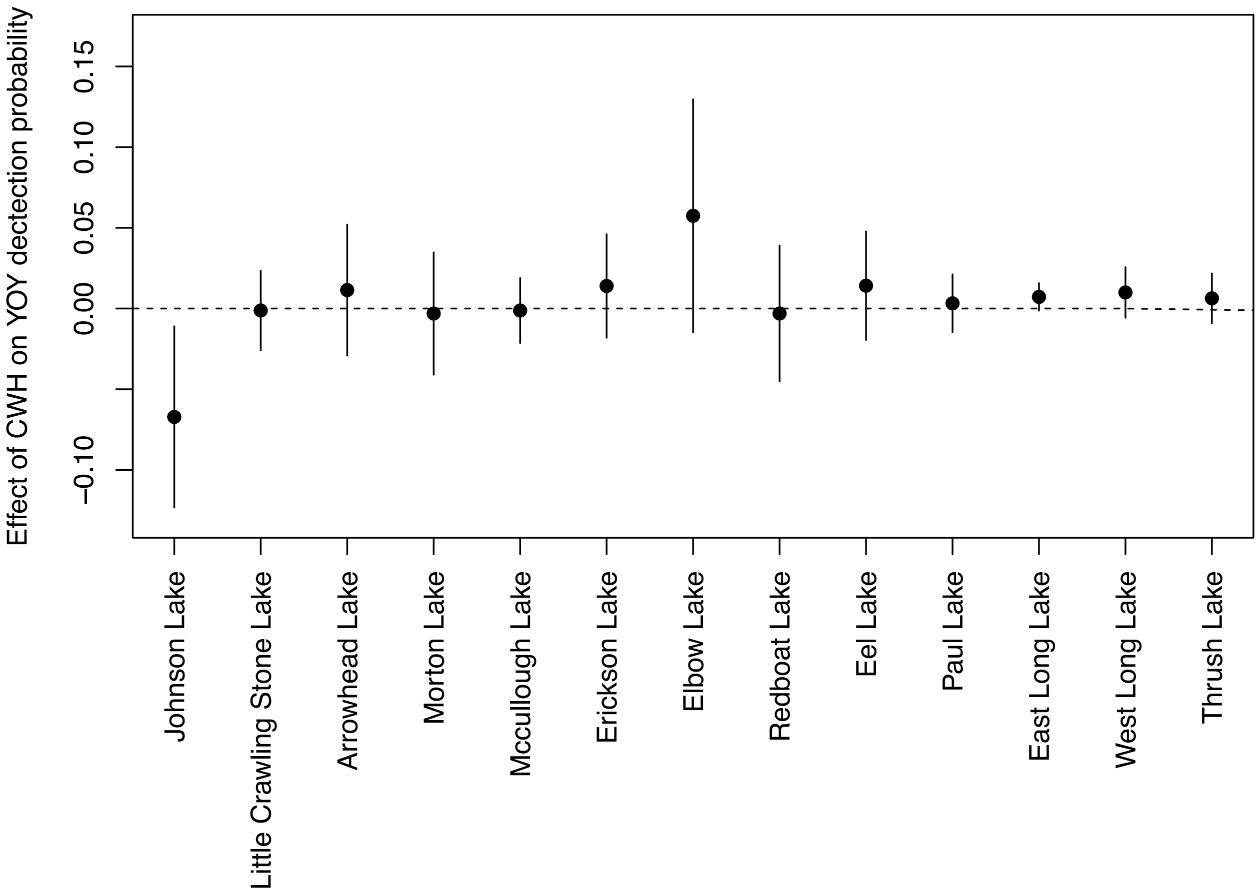

Figure 2.2. Detection probability of young of year (YOY) was unrelated to coarse woody habitat (CWH) on transects in 11 of our 13 lakes. In two lakes (Johnson and West Long) there were significant effects but these were weak and in opposite directions. Note, the best model explaining West Long YOY detection probability included an effect of CWH that varied by site (two sites had significantly positive effects while the rest were not significant) but here we display the lake level effect. In all lakes the best model included a constant CWH effect over time.

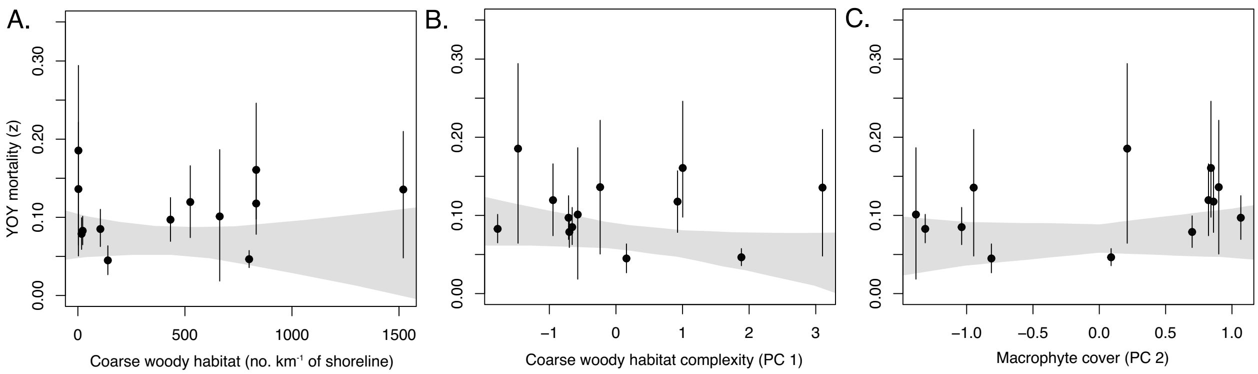

Figure 2.3. Young of year (YOY) largemouth bass mortality was not significantly related to coarse woody habitat density (A) coarse woody habitat complexity (B) or macrophyte cover (C). The first principal component (PC 1) from a principal component analysis describing littoral structural complexity was positively correlated to coarse woody habitat density and branchiness, while the second principal component (PC 2) was positively correlated to macrophyte cover (Table 2.2). Models were fit with weighted least squares) regression and ordinary least squares regression. Vertical lines represent 95% confidence intervals for mortality estimate fits (z parameter in Equation 2). The shaded area is the 95% confidence interval from a WLS regression models.

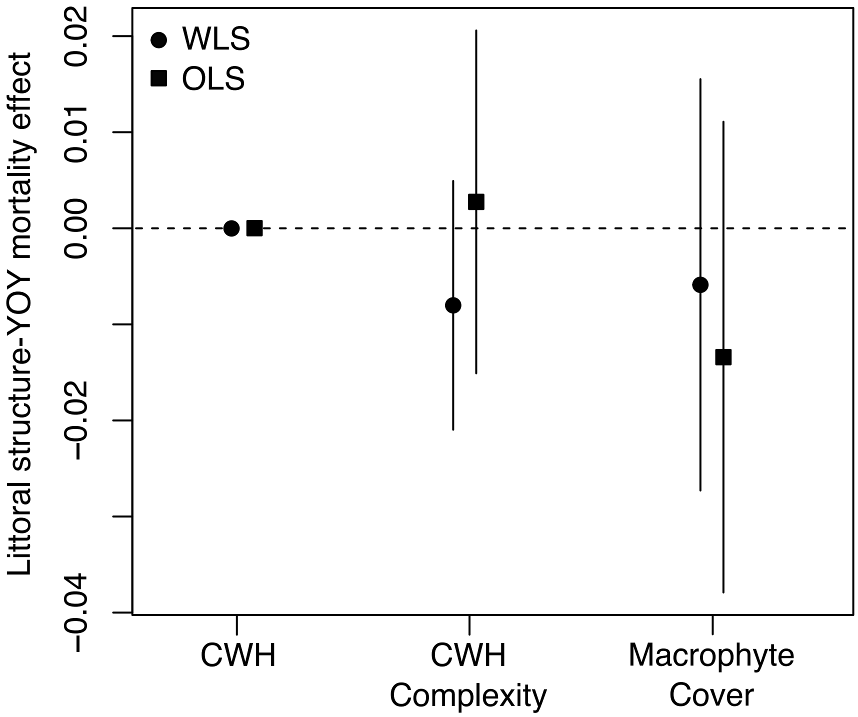

Figure 2.4. The effect of coarse woody habitat (CWH) on YOY mortality was near zero, while CWH complexity and macrophyte cover had more variable effects on YOY mortality but were not significantly different from zero. The effects fit with weighted least squares (WLS) regression and ordinary least squares (OLS) regression were similar. Vertical lines represent 95% confidence intervals (the lines for CWH are indistinguishable from the size of points).

Table 2.1. Study lake information and young of the year mortality model estimates. 95% confidence intervals are provided in parentheses, YOY = young of the year, CWH = coarse woody habitat, inst. daily mort. = instantaneous daily mortality, ab. = abundance, and neg. binom. = negative binomial. Note initial YOY abundances reported in natural log. Littoral area was calculated as shoreline perimeter × average length from shore where sediment light was 1% surface light (determined from littoral slope and Secchi depth).

Lake	**Year**	**Lat.**	**Long**	**CWH (no. km^{-1} of shoreline)**	**Area (km^2)**	**Littoral area (km^2)**	**z (YOY inst. daily mort.)**	**X_0 (ln initial YOY ab.)**	**k (Neg. Binom. dispersion)**
Johnson	2017	45.90	-89.72	2.5	35	0.21	0.19 (± 0.09)	3.55 (± 1.01)	0.010 (± 0.009)
Little Crawling Stone	2017	45.92	-89.90	2.5	47	0.34	0.14 (± 0.09)	3.09 (± 3.78)	0.010 (± 0.007)
Arrowhead	2017	45.91	-89.69	17	40	0.30	0.08 (± 0.02)	4.90 (± 0.76)	0.10 (± 0.02)
Morton	2016	46.19	-89.58	23	70	0.50	0.08 (± 0.02)	2.17 (± 0.54)	0.16 (± 0.04)
McCullough	2016	46.20	-89.57	100	93	0.31	0.09 (± 0.03)	2.63 (± 0.56)	0.05 (± 0.02)
Erickson	2017	45.95	-89.62	140	47	0.30	0.04 (± 0.02)	1.18 (± 0.32)	0.7 (± 0.3)
Elbow	2017	46.35	-89.78	430	11	0.14	0.10 (± 0.03)	4.40 (± 0.63)	0.16 (± 0.04)
Redboat	2017	46.34	-89.77	530	11	0.13	0.12 (± 0.05)	5.12 (± 0.96)	0.020 (± 0.008)
Eel	2017	46.30	-89.76	660	23	0.48	0.10 (± 0.09)	5.33 (± 2.76)	0.010 (± 0.004)
Paul	2016	46.25	-89.50	800	1.6	0.03	0.05 (± 0.01)	2.87 (± 0.27)	0.21 (± 0.05)
East Long	2016	46.24	-89.50	830	3.3	0.02	0.16 (± 0.08)	2.07 (± 1.97)	0.02 (± 0.01)
West Long	2016	46.24	-89.50	830	5.4	0.07	0.12 (± 0.04)	3.39 (± 3.91)	0.02 (± 0.01)
Thrush	2017	46.32	-89.79	1500	32	0.13	0.14 (± 0.06)	4.99 (± 0.84)	0.020 (± 0.007)
Range									

Table 2.2. Description of littoral structure principal components. Correlations show the relationship of the number of pieces of wood per km of shoreline, mean branchiness of coarse woody, and percent macrophyte cover with two principal components from a principal component analysis that explains 92% of the variation in these three variables. Significant correlations are highlighted in bold.

Littoral structure	PC 1	PC 2
Coarse woody habitat complexity		
Number per km of shoreline	**r = 0.93 p < 0.001**	r = 0.10 p = 0.75
Mean Branchiness	**r = 0.85 p < 0.001**	r = 0.40 p = 0.17
Macrophyte cover		
Percent cover	r = 0.51 p = 0.07	**R = 0.85 p < 0.001**
Variance explained		
	0.62	0.30

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Preface to Chapter 3

The results of Chapter 2 do not support a widely-held hypothesis that littoral structure reduces young of year mortality. These findings are valuable because they suggest that changes in littoral structure (removal or addition) may not have the strong effects on recruitment and fish population stability that are often assumed by fisheries scientists and managers. However, my results highlight a need for future work on determinants of open-water season young of year mortality, which is seldom considered by fisheries scientists but as important as over-winter mortality.

From a practical stand point, I did not find support for an ecological approach to reducing reliance on stock enhancement through improving littoral structure. In Chapter 3 I investigate an institutional approach to improving stock enhancement activities. I use bio-economic theory to determine stock enhancement allocations that efficiently maximize angler net benefits. I also evaluate outcomes if stocking were under centralized government versus devolved management control. Improving stocking allocations that limit the costs of management will allow for further research on improving recruitment success of fish populations to occur while still maintaining the benefits recreational fisheries provide.

Chapter 3

Optimal stock enhancement in inland recreational fisheries: who should stock and how much?

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Abstract

Stock enhancement – the release of hatchery fish to augment a wild population – has become a dominant management panacea in inland recreational fisheries. Stock enhancement has typically been under government control in North America, but increasingly there are calls for, and experiments with, co-management or outright devolvement of stocking authority to local stakeholders, to capture the potential benefits of polycentric management for maintaining shared resources like fisheries. To better understand the conditions under which government versus devolved management of stock enhancement might lead to beneficial outcomes for anglers in open access inland recreational fisheries, we present a bio-economic investment analysis of optimal stocking allocations and apply it to an inland recreational fisheries landscape. We find that there are incentives for both government and local organizations to invest in stock enhancement, that lake associations in our study region stock at approximately optimal rates, and that government stocking rates may not be maximizing angler net benefits. Our results suggest that stocking by local organizations can be an effective way to maintain harvest benefits at low fish population densities, while stocking by government can maintain positive economic spillover effects of non-local anglers but can lead to higher effort on lakes and negative social welfare at low fish population densities. We provide a flexible and structured way of thinking about stock enhancement in recreational fisheries that can be applied by local or government managers to guide stocking decisions that meet their management objectives.

3.1 Introduction

There is an increasing push for governments to provide local organizations more control over management of shared natural resources, like fisheries. Some form of co-management has become a recommended approach for long-term maintenance of the benefits these resources provide (Armitage et al. 2008). In the 1960's there was a pervasive idea in natural resource management that either centralized government oversight or private property institutional arrangements were the only way to effectively maintain shared resources (Gordon 1954, Scott 1955, Hardin 1968, Feeny et al. 1990, Dietz et al. 2003). However, by the 1990's the ability of centralized governance to sustainably and equitably manage shared resources was called into question (Berkes 2010) and numerous empirical examples of local organizations effectively managing shared resources were recognized (Berkes et al. 1989, Ostrom 1990, Feeny et al. 1990, McGinnis 1999, Dietz et al. 2003). Since then, community based management has gained in popularity (Agrawal and Gibson 1999, Meynen and Doornbos 2002, Ambus and Hoberg 2011). For example, Kooiman et al. (2005) recommended that fisheries management adopt the subsidiarity principle, which states that management responsibilities should rest with the most local competent organization possible (Berkes 2010). This approach is thought to be beneficial because it ensures that management decisions are made by those most affected by the decisions, it promotes experimentation through community participation in problem solving, it can lead to more efficient use of resources, and it incorporates local knowledge, which allows for adaptive responses to changes in the fishery (McGinnis 1999, Lebel et al. 2006, Berkes 2010). In reality, devolving management away from government control toward local organizations has worked well in some cases but not in others (Kellert et al. 2000, Berkes 2010). Understanding the incentives and actions of resource users under devolved governance can help predict when these management approaches work well and how they can be improved.

Research into the institutional arrangements of fisheries has shown that the incentives organizations face, the actions they take, and the outcomes that result are dependent on the rights they hold (De Alessi 1980, McGinnis 1999). Operational rules constrain and determine what rights anglers have and therefore, which actions they are allowed to take in a fishery (McGinnis 1999). For example, rules of access define which anglers have access to a certain location (e.g. a lake), while rules of withdrawal define how, when, and how much an angler can harvest from a location. Community based natural resource management is concerned with granting collective rights to local organizations of resource users that allow them to change the operational rules of a fishery. Collective rights can include exclusion and management rights, which allow organizations to change anglers' access and withdrawal rights respectively. Management rights also allow communities to improve a fishery through collective action, like releasing hatchery fish to augment a wild population (stock enhancement). However, this second component of management rights is rarely the primary focus of research because it is generally assumed that local organizations do not have incentives to improve their fishery without limiting access or withdrawal rights of outside anglers (Gordon 1954, Scott 1955, McGinnis 1999, Goffe and Salanié 2005, Lorenzen 2008).

In the context of stock enhancement in inland recreational fisheries, it is generally assumed that government and not local organizations, like lake associations, have incentives to invest in stock enhancement. In North America housing development is preferentially clustered around lakes (Gonzalez-Abraham et al. 2007), which can result in dedicated angler populations and the formation of lake associations interested in improving and maintaining lake fisheries (Korth and Klessig 1990, Carpenter and Brock 2004). Lakes also experience fishing pressure from mobile roving anglers that travel from nearby urban centers to fish (Carpenter and Brock 2004, Hunt et al. 2011). Given the nature of recreational fisheries in North America, limiting access or withdrawal rights of angler groups is often not an attainable or desirable goal (Cox et al. 2002, Cox et al. 2003). Gordon (1954) and Scott (1955) theorized that fisheries without effort control would generate no economic rent, consequently, the fishery would be of little value to local users and would lead to no investment in the resource unless it was under the control of a sole-owner (e.g. a local or centralized government). These predictions have been extended to investment in the form of stock enhancement in inland recreational fisheries (Goffe and Salanié 2005, Lorenzen 2008). Therefore, it is generally assumed that only governments have incentives to partake in stock enhancement while local organizations, like lake associations, behaving rationally to optimize their own net benefits should not invest in stock enhancement due to exogenous fishing pressure from roving anglers (McGinnis 1999, Goffe and Salanié 2005, Lorenzen 2008). However, in reality lake associations do frequently invest in stock enhancement without the ability to control outside fishing effort.

Government and local organizations make large investments in stock enhancement in inland recreational fisheries but there is little guidance for these institutions on how to make efficient investments that benefit anglers. Stocking has become the most dominant management panacea in inland recreational fisheries (Arlinghaus et al. 2002, Eby et al. 2006, van Poorten et al. 2011). In our study region of Wisconsin USA, records indicate 1,912 waterbodies received stock enhancement between 2008 and 2017 (data from Wisconsin Department of Natural Resources). In 57% of these lakes only state government performed stocking while local organizations like lake associations contributed to or conducted all of the stocking in the remaining 43% of lakes. While data on stock enhancement decisions by local organizations are not widely available, community stocking frequently occurs in other states and provinces in North America (Rahel 2004, Kerr 2006, Johnson et al. 2009). The majority of past research on indicators of stock enhancement success have focused on biological variables like fish survival and biomass (McWilliams and Larscheid 1992, Santucci and Wahl 1993, Szendrey and Wahl

1996, Buynak et al. 1999, Quiros 1999, Wahl 1999, Skov et al. 2003, Sugunan and Katiha 2004, Buckmeier et al. 2005, Fayram et al. 2005, Colvin et al. 2008, Kampa and Hatzenbeler 2009, Hansen et al. 2015). Despite recognition that stock enhancements are made into coupled natural-human systems (Garaway et al. 2006), far fewer studies have considered socio-economic indicators of stock enhancement success, like net benefits to anglers (although see: Anderson 1983, Botsford and Hobbs 1984, Fenichel et al. 2010, Rogers et al. 2010, Askey et al. 2013, Camp et al. 2014, Mee et al. 2016, Hunt et al. 2017). To our knowledge no studies have explicitly considered the role of devolved management in stock enhancement in open access fisheries to determine if there are incentives for local organizations to behave in ways that lead to beneficial outcomes for anglers compared to government oversight of stock enhancement. Bio-economics can help inform stocking investments and provide a framework that considers both biological and socio-economic variables in clearly defined objective functions that are flexible for various institutional arrangements and management goals (Clark 2005).

To better understand the conditions under which government versus devolved management of stock enhancement might lead to beneficial outcomes for anglers in inland recreational fisheries, we present a bio-economic investment analysis for determining optimal stocking allocations (Clark 2005). We illustrate the effect of ecological and socio-economic conditions on optimal stocking allocations under government and lake association control by presenting equilibrium results from an application of our bio-economic model and then compare these results to empirical data on stock enhancement in our study region.

3.2 Modelling optimal stock enhancement for government and local managers

3.2.1 Stock enhancement dynamics in a fisheries model

Fish stocking can increase maximum equilibrium harvest of a fish population and its resilience against collapse in response to fishing pressure (Fig. 3.1). Several models have been developed to describe the dynamics of fish populations under stock enhancement (Botsford and Hobbs 1984, Lorenzen 1995, Lorenzen 2005, Rogers et al. 2010, van Poorten et al. 2011, Askey et al. 2013, Camp et al. 2014, Taylor 2017) and more elaborate models have included negative feedbacks of hatchery stocks on wild stocks and stage structured processes (Lorenzen 2005, Camp et al. 2017, van Poorten et al. 2011, Ziegler et al. 2017). For simplicity and tractability, we use a common and well-studied fish population model to illustrate the effects of stocking on fish populations

$$\dot{X} = rX(1 - \frac{X}{k}) - H + S, \text{ where } \quad H = qEX \qquad \text{Eq. 1}$$

where X = fish density, H = harvest, r = growth rate, k = carrying capacity, q = catchability coefficient (proportion of the fish stock removed with one unit of effort), E = total fishing effort, and S = stocking rate (note we are using Newton's notion for differential equations where $\dot{X} = \frac{dX}{dt}$, all state variables are in uppercase, and parameter values are in lowercase). This model assumes that hatchery derived fish have similar survival as wild fish and that they have the same value to anglers as wild fish. These assumptions are supported by empirical evidence of high survival of older and larger stocked fingerlings (Santucci Jr. and Wahl 1993, Szendrey and Wahl 1996) and no significant effect of the relative abundance of wild versus hatchery derived fish on the utility anglers gain from fishing (Arlinghaus et al. 2014). Solving $\dot{X} = 0$ for H provides harvest at equilibrium (Fig. 3.1). When the equilibrium stocking rate is zero maximum equilibrium harvest is less than when the stocking rate is non-zero (vertical lines in Fig. 3.1).

When there is no stocking there is a point at high angler effort where equilibrium harvest is zero because the fish stock is completely collapsed but this does not occur when there is stocking at equilibrium (open circles in Fig. 3.1).

3.2.2 Open access angler effort from multiple user groups

One challenge when choosing a stocking rate over time is considering dynamic effort from multiple angler groups that responds to fishing quality. Open access dynamics, where the access to and level of exploitation of a natural resource cannot be well controlled, have long been studied in natural resource management (Smith 1968). Despite use of bag limits and other attempts of harvest control, recreational fisheries are often open access fisheries in North America (Cox et al. 2002, Cox et al. 2003). The net result of open access dynamics is hypothesized to be a homogenization of fishing quality (relative to travel costs) in a region as angling pressure is attracted to areas of higher fishing quality and leaves areas of lower quality (Parkinson et al. 2004, Askey et al. 2013, Baer et al., 2007, Mee et al. 2016). Bio-economic theory in open access fisheries describes this process as effort responding myopically to current average net benefits of fish harvest (Smith 1968). While these models were developed to describe commercial fisheries, we follow Horan et al. (2011) and assume angler utility is linear in benefits from fishing, so effort dynamics are similar to the Smith (1968) model and follow:

$$\dot{E}_i = \delta E_i[p_i q X - c_i] \qquad \text{Eq. 2}$$

where δE_i = the sluggishness of the response of fishing effort from angler group i to average net benefits of harvest (Clark 1990), p_i = the marginal willingness to pay for fish harvest by angler group i, and c_i = marginal cost of fishing effort for angler group i. Here we chose to focus on the net benefits of harvest to anglers because harvest related benefits are often higher than catch related benefits (Wilson et al. 2016).

We explicitly incorporated angler heterogeneity in our model by including two typical angler groups in inland recreational fisheries, lakeshore residents and roving anglers. In our hypothetical but plausible scenario, any angler who is not a resident on a focal lake is a roving angler, including for example residents of distant urban centers and of nearby neighboring lakes. Angler heterogeneity in bio-economic models is often ignored, despite it changing optimal regulations and measures of social utility (Johnston et al. 2010; although see: Fenichel et al. 2013, Fenichel and Abbott 2014). Travel time and distance are negatively related to effort allocation in inland recreational fisheries (Clawson 1959, Brown and Mendelsohn 1984), therefore, when considering a single fishing trip roving anglers have higher costs associated with fishing than lake-shore residents due to longer travel times and distances. Here we allowed the marginal costs of effort and marginal value attached to fishing to vary between the resident and roving angler populations.

We modeled lake-shore resident effort (E_{res}) and mobile roving effort (E_{rov}) using Equation 2. Setting $\dot{E}_i = 0$ provides two solutions at equilibrium where effort from user group i is either greater than or equal to zero,

$$0 = \delta E^*_{rov}[p_{rov}qX^* - c_{rov}] \text{ if } \begin{cases} p_{rov}qX^* = c_{rov}, \ E^*_{rov} > 0 \\ E^*_{rov} = 0 \end{cases} \qquad \text{Eq.3}$$

$$0 = \delta E^*_{res}[p_{res}qX^* - c_{res}] \text{ if } \begin{cases} p_{res}qX^* = c_{res}, \quad E^*_{res} > 0 \\ E^*_{res} = 0 \end{cases} \qquad \text{Eq.4}$$

where asterisks represent equilibrium values of state variables.

We consider only the case where both resident and roving effort are present at equilibrium, therefore, the following condition must be met,

$$\frac{c_{rov}}{p_{rov}q} = \frac{c_{res}}{p_{res}q} = X^* \; ; \; p_{rov} = \frac{c_{rov}p_{res}}{c_{res}} \qquad \text{Eq.5}$$

suggesting that for roving angler marginal cost of effort to be higher than that of residents, the rovers' marginal willingness to pay for harvest must also be higher with $p_{rov} = \frac{c_{rov}p_{res}}{c_{res}}$, assuming catchability of the two groups to be approximately equivalent. This is similar to effort sorting, whereby, only anglers with certain attributes are present at equilibrium and selected for from a population of potential anglers with a range in attributes (van Poorten et al. 2016). We assumed that there was high latent resident and roving fishing effort in the fishery such that the number of potential anglers never limited realized fishing effort, which can occur in fisheries near large urban centers (Hunt et al. 2011, Wilson et al. 2016).

3.2.3 Optimal stocking decisions by government and local management groups

By varying the amount of stocking through time a rational government manager might try to maximize the net benefits of harvest for all anglers while a rational local management group, like a lake association, might try to maximize the net benefits of harvest for its members. Although we focus on the net benefits of harvest to anglers in our objective functions we recognize that the goals of government and local managers are diverse and can include maintaining biological diversity, increasing non-catch related fisheries benefits, or increasing the spillover economic effects of fishing; these goals would have different objective functions. We define our objective functions for government and lake associations using present value of net benefits (PVNB) to anglers,

$$PVNB_{Government} = \int_{t=0}^{\infty} e^{-\rho t}(p_{res}qE_{res}X - c_{res}E_{res} + p_{rov}qE_{rov}X - c_{rov}E_{rov} - \gamma S^2)\, dt$$

Eq.7

$$PVNB_{Lake\ Asc.} = \int_{t=0}^{\infty} e^{-\rho t}(p_{res}qE_{res}X - c_{res}E_{res} - \gamma S^2)\, dt \qquad \text{Eq.8}$$

where, ρ = the discount rate, γ is proportional to the marginal cost of stocking, and the terms in parentheses represent the net benefits of harvest for anglers less the cost of stocking. The integral of net benefits of harvest adds up the net benefits over time, with future benefits weighted less through the discount term $e^{-\rho t}$. We modeled the cost of stocking as a non-linear function to represent the increased production costs associated with the need to increase the production capacity of hatcheries or buying hatchery fish from exogenous sources at high stocking rates (Askey et al. 2013).

Optimal control theory and the maximum principal provide an optimal stocking rate over time that maximizes a defined objective function (Clark 2005). The optimal stocking rate is expressed as a function of shadow prices (μ_i, also known as adjoint variables) that are determined from constructing a Hamiltonian ($\mathcal{H}$) of the optimal control problem (Clark 2005, Appendix N). Applying optimal control theory to Equations 1 and 2 and our objective functions (Equations 7 and 8) provides the stocking rate over time that maximizes the PVNB defined by our objective functions,

$$\dot{S} = \frac{\dot{\mu}}{2\gamma} \qquad \text{Eq. 9}$$

where μ = the current value shadow price of the stock (the increase to the objective function with a 2 unit increase in the stock) and 2γ = the marginal cost of stocking. See Appendix N for the application of optimal control theory to our problem and derivation of Equation 9.

3.2.4 Model solutions

To compare optimal stocking rates under government and lake association control and to determine how stocking rates changed as a function of parameter values we used analytical solutions at equilibrium conditions. Setting our model differential equations equal to zero and solving for stocking provided the optimal stocking rate at equilibrium (see full solution in Appendix N). Similar to van Poorten et al. (2011) we compared the sensitivity of equilibrium stocking rates to changes in model parameters between government and lake association controlled stocking using elasticity estimates that describe the percent change in optimal stocking rate to a 1% increase in a parameter value while all other parameters were held constant (see Table O1 default values of parameters). Elasticity estimates are useful when comparing the effects of model parameters that are measured on different scales.

To compare social welfare (the combined harvest benefits to all anglers, less the costs of stocking) under government and lake association controlled stocking we used numerical solutions of our model, which allowed us to sum the net benefits accrued over time. The numerical solutions of the boundary value problem were calculated in Mathematica (Wolfram Research 2018). Our metric of social welfare under each management scenario was calculated as the combined present value of net benefits of each angler group less the cost of stocking (Equation 7). Because PVNB is an integral of the trajectory of the system over time it is dependent on starting conditions of the state variables in the model, therefore, we present the results as contour plots over large ranges of starting conditions of state variables to compare the social welfare of government and lake association controlled stocking.

For both analytical and numerical solutions, we parameterized the biological component of our model to reflect walleye and used socio-economic parameters to reflect Wisconsin USA (Table O1). This area is a well-studied system where recreational fishing is socially, economically, and ecologically important (Liu et al. 2007). We focused on walleye, as this is a commonly stocked and sought after fish species in this region.

3.2.5 Empirical stocking data

We compared our model output to empirical data on government and local organization stocking rates and relative angling pressure of resident and roving anglers for 46 lakes in Vilas and Oneida Counties in Wisconsin USA. We obtained records of all government and local organization stocking of walleye in these lakes between 2008 and 2017 from the Wisconsin Department of Natural Resources. We only considered stocking events of fingerlings, which have higher survival rates compared to fry (Santucci Jr. and Wahl 1993, Szendrey and Wahl 1996). We calculated the relative use of our study lakes by resident and roving anglers using creel survey data obtained from the Wisconsin Department of Natural Resources, all lakes had public access. Creel clerks surveyed anglers on lakes between 1995-2017 and recorded if they used the boat landing to launch a boat (roving anglers) or if they came from a lakeshore residence or walked to the lake (resident anglers). The number of anglers interviewed per lake ranged from 79 to 5,548 with a median of 1,108.

We tested if empirical relationships between percent resident fishing effort and stocking conducted by government and lake associations were similar to those predicted by our bio-economic model. We used ordinary least squares regression to quantify the relationship between observed percent resident fishing effort and stocking rates by government and lake associations. Our bio-economic model suggested that optimal government stocking was determined by an interaction between percent resident fishing effort and roving angler value of harvest, therefore, we considered multiple regression models that included both predictors and compared models using small sample size corrected Akaike Information Criteria (AICc, Table 3.1).

We parameterized our bio-economic model to our 46 study lakes and tested if predicted optimal stocking rates were correlated with observed stocking rates under both government and lake association controlled stocking. We calculated lake-specific per-trip costs for roving anglers (c_{rov}) using the round-trip distance of a lake to the nearest urban center, the average operational cost of a sport utility vehicle ($0.11 USD per km, American Automobile Association 2016), and the average operating cost of a boat for a freshwater angler in the USA (6.22 USD per trip, US Census Bureau 2016). We then empirically estimated the value of fish harvest for roving anglers using per trip costs for roving anglers and Equation 5 (Table O1). The sluggishness of effort in response to average net benefits of harvest (δ) and the rate of future discounting (ρ) were the only two parameters for which we did not have empirical estimates of model parameters (Table O1), therefore, we presented correlation results over large ranges of δ and ρ.

3.3 Results

3.3.1 Model solutions of optimal stock enhancement

The contribution of residents to total fishing effort at equilibrium (α^*) was dependent on the initial fishing effort of each angler group and on whether government or lake associations controlled stocking (Fig. 3.2A). A higher initial resident fishing effort led to a higher contribution of residents to total fishing effort at equilibrium because it reduced harvest benefits for rovers and attracted less of their effort. This was true in reverse for roving anglers as well.

Government control also led to less resident angler effort relative to roving effort at equilibrium (Fig. 3.2A). This was due to higher optimal stocking rates under government control when roving anglers had higher travel costs and associated value of harvest (Fig. 3.2B), which attracted more roving angler effort. The contribution of residents to total effort at equilibrium was similar between government and lake association controlled stocking when initial roving effort was low and resident effort was high (Fig 3.2A black line) because stocking rates became similar between the two management scenarios (Fig. 3.2B and 3.2C greater than 80% resident fishing effort at equilibrium).

There was an interaction between the value of harvest for roving anglers and the relative abundance of resident effort at equilibrium for determining optimal stocking rates under government control (Fig. 3.2B). Because roving anglers have higher travel costs than residents, they are present at equilibrium only if the value that they place on harvest increases in proportion to their travel costs (Equation 5). When roving and resident anglers had similar travel costs and value of harvest, government optimal stocking rates did not vary with the relative abundance of each angler group at equilibrium because both angler groups were interchangeable in the objective function (Fig. 3.2B, $p_{rov} \sim 22$). However, when roving anglers had higher travel costs and therefore valued harvest more than residents, government stocking rates decreased when there was more resident effort at equilibrium (Fig. 3.2B $p_{rov} > 30$). This was because roving anglers with higher travel costs and value of harvest had higher net benefits per unit of effort compared to residents before equilibrium was reached (see Appendix N for proof). Therefore, one percent increases in the contribution of residents to total fishing effort at equilibrium (α^*) and the cost (c_{rov}) or value (p_{rov}) of harvest for roving anglers led to a 0.2% decrease and 0.5% increase in optimal government stocking rates respectively (Fig. 3.3).

Lake association optimal stocking rates were positively related to the contribution of residents to total fishing effort at equilibrium but only weakly to the cost and value of roving angler harvest (Figures 3.2C and 3.3). A one percent increase in the contribution of residents to total fishing effort at equilibrium resulted in a one percent increase in the optimal equilibrium stocking rate under lake association control (Fig. 3.3). Lake association optimal stocking rates decreased by 0.04% when roving angler costs or value of harvest increased by one percent (Fig. 3.3).

Optimal stocking rates were also sensitive to the cost and value of harvest for residents and characteristics of the fish population but relatively insensitive to sluggishness of effort in response to harvest benefits, the future discounting rate, and the marginal cost of stock enhancement (Figures 3.3). The value of harvest for resident anglers and the cost of resident fishing effort directly affected government and lake association objective functions and influenced optimal stocking rates in predictable ways (Fig. 3.3, Equations 7 and 8). Attributes of the fish population (r, k, and q) were positively related to optimal stocking rates. Higher intrinsic growth rates (r) allowed for the fish stock to recover quicker after harvest, higher carrying capacities (k) prevented fish growth from declining due to competition, and higher catchabilities (q) allowed anglers to benefit from a larger proportion of the fish stock, resulting in anglers having higher benefits from stock enhancement. Optimal stocking rates were less sensitive to the sluggishness of effort in response to harvest benefits, future discounting of harvest benefits, and the marginal cost of stock enhancement (Fig. 3.3; see Figure O1 for the direction of these relationships). Over large ranges in model parameters, the optimal stocking rate under both management scenarios were always greater than zero (Figures 3.2B, 3.2C, and O1).

3.3.2 Empirical data on stock enhancement

Empirical data on government and lake association stocking rates showed similar relationships with percent resident fishing effort as our bio-economic model but were unrelated to the value of harvest for roving anglers. Government stocking rates were weakly, negatively related to percent resident fishing effort (Table 3.1, Fig. 3.4A) and lake association stocking rates were more strongly, positivity related to percent resident fishing effort (Table 3.1, Fig. 3.4B). However, unlike optimal stocking rates predicted by our bio-economic model, government controlled stocking was unrelated to the value of harvest for roving anglers (Table 3.1, Fig. 3.4C).

Model predicted optimal stocking rates were positively correlated to observed lake association stocking rates but unrelated to observed government stocking rates (Fig. 3.5). Correlation results were robust to parameters for which we did not have empirical estimates (δ and ρ, Fig. 3.5). Similar to our bio-economic model output, observed government stocking rates were on average higher than lake association stocking rates (mean of 30 and 4 fish per hectare per year for government and lake association stocking respectively, $t = 5.3$, p-value < 0.0001) but in reality, government stocking rates were much higher than model predicted optimal stocking rates; average differences between observed and predicted optimal stocking rates among δ and ρ estimates ranged from 25 – 30 fish per hectare per year for government stocking and 2 – 4 for lake association stocking. Three of our study lakes had greater than 80% resident fishing effort, a level where predicted optimal stocking rates become similar under both management scenarios; two of these were stocked by lake associations at a rate of 9 fish per hectare per year while one was stocked by government at a rate nearly double that (16 fish per hectare per year).

3.3.3 Social welfare under optimal stock enhancement

Numerical solutions of our bio-economical modeled showed that high initial angling effort led to negative social welfare for both management scenarios, but social welfare was positive over a larger range in initial roving effort when stocking was under government as opposed to lake association control (Fig. 3.6C). Initial angling effort above the solid line in Fig. 3.6A and 3.6B led to negative social welfare even with optimal stock enhancement, suggesting that alternative management approaches like effort control would be more beneficial than beginning stocking programs on lakes with high total effort. The initial effort that maximized PVNB corresponded to the effort that maximized economic yield (red regions in Fig. 3.6A and 3.6B), which occurs at a lower level than equilibrium effort in open-access fisheries (Scott 1955, Christensen 2010, dotted lines in Fig. 3.6A and 3.6B). Government controlled stocking maintained positive social welfare at higher initial roving angler effort (area under the solid black curve below ~10 on the x-axis is larger in Fig. 3.6A than 3.6B) because roving anglers had greater net benefits than resident anglers before equilibrium was reached (Appendix N) and government controlled stocking increased in this region (Fig. 3.2B). At lower initial roving angler effort, lake association controlled stocking led to similar or higher social welfare as government controlled stocking (Fig. 3.6C).

Initial stocking rates near optimal equilibrium stocking rates led to the highest social welfare under both management scenarios and social welfare was positive over a larger region of initial fish densities when stocking was under lake association as opposed to government control (Fig. 3.6F). Social welfare increased up to and then decreased beyond initial stocking rates that maximized PVNB (dotted lines in Fig. 3.6D and 3.6E). The highest social welfare occurred when fish densities began at carrying capacity and anglers could obtain high harvest benefits for a period of time until the fish population reached a lower equilibrium. When the fish population began at low densities, as is often the case during stock rebuilding in an over-exploited fishery, lake association controlled stocking provided higher social welfare compared to government controlled stocking (Fig. 3.6F, area under the solid black curve in Fig. 3.6E is greater than in 3.6D). This was likely caused by lower equilibrium effort when stocking was under lake association control (dotted line in Fig. 3.6B is lower than in 3.6A), which maintained higher harvest benefits for anglers at low fish population sizes compared to when stocking was under government control.

3.4 Discussion

3.4.1 What is the optimal stocking rate under centralized and devolved management?

Bell et al. (2006) and Lorenzen (2008) suggested that stock enhancement should only be conducted when it adds value to a fishery. While there have been studies investigating the added value of stock enhancement for commercial fisheries (Lorenzen 2005, Amoroso et al. 2017), bio-economic theory has rarely been applied to recreational fisheries to determine what amount of stock enhancement adds socio-economic value (although see Anderson 1983). Our results suggest that stock enhancement under government and lake association control can increase the net benefits of harvest for anglers, as optimal stocking rates predicted by our bio-economic model were non-zero over large parameter ranges. However, socio-economic and biological factors affect the amount of stock enhancement that is optimal and these effects vary under centralized or devolved management. In general, optimal stocking rates were highest under both management scenarios when: resident angler populations had high value of harvest and low cost of effort; and when fish populations had high rates of reproduction, carrying capacity, and catchability. Under government control, optimal stocking rates were positively related to the relative abundance and cost of roving effort; under lake association control, optimal stocking rates were negatively related to these variables.

Our model and empirical results suggest that lake associations do have incentives to invest in stock enhancement and that they stock at approximately optimal rates, despite the common assumption that only governments have incentives to do so. Lake association stocking was non-zero in our bio-economic model and supported both resident and roving angler harvest (Figures 3.2B, 3.2C, and O1). Our empirical data on lake association stocking rates demonstrated that local management groups do voluntarily invest in their fishery through stock enhancement, the investment increased as residents made up more of the angling effort on the lake, and that stocking rates were correlated with predicted optimal stocking rates. While there are other empirical examples of communities voluntarily maintaining common pool resources (Berkes et al. 1989, Ostrom 1990, Feeny et al. 1990, McGinnis 1999, Dietz et al. 2003) these examples have been limited to cases where resources are not open access. Our results indicate that voluntary local management can occur even when communities are not granted exclusion and withdrawal rights.

Heterogeneity in the angler population changed the optimal stocking rate when under government control. Diversity in angler groups is known to affect which policies are predicted to be socially optimal by bio-economic models (Johnston et al. 2010). Stocking rates that maximized social welfare under government control responded to increased costs and value of harvest for roving anglers. However, our empirical data suggested that government stocking rates were only weakly related to the relative abundance of roving angler effort on a lake and unrelated to increased costs for roving anglers. This led to predicted optimal government stocking rates being uncorrelated with observed stocking rates. Observed government stocking rates were often higher than model predicted stocking rates, which suggests that overstocking may be occurring or government managers are meeting objectives other than maximizing angler net benefits.

Different management goals and considering non-catch related benefits would lead to changes in optimal stocking rates (Lorenzen 2008). The discrepancy in predicted optimal stocking rates and observed government stocking rates might reflect government managers stocking to meet objectives other than maximizing angler welfare. Objective functions can be defined based on other management goals. For example, given our formulation of the objective function, stocking when there were low initial fish densities led to negative social utilities due to open access effort (Fig. 3.6D and 3.6E). However, this is a recommended action for rebuilding previously collapsed fish stocks (Lorenzen 2008); optimal stock rebuilding could be achieved through including costs of effort control and stock enhancement in an objective function (Anderson 1983). Stock rebuilding through release of hatchery fish is a common conservation goal, particularly when hatchery reared fish are able to reproduce and are viewed in a similar fashion as wild stocks (Camp et al. 2017). Other conservation goals like maintaining biodiversity might seem at odds with stocking (Camp et al. 2017), but there are examples where stocking can be used to direct fishing effort away from native fish stocks (Lorenzen et al. 1998). Maintaining the genetic integrity of locally adapted populations where stocking occurs may be difficult (Lorenzen 2005, Cowx et al. 2010, van Poorten et al. 2011) and could be represented as a cost in the objective function to penalize stocking as a management tool in certain applications. While we only considered one simplistic value of stock enhancement (harvest benefits for anglers), in reality anglers derive different benefits from a bundle of catch and non-catch related attributes of fishing trips (Hunt 2005, Johnston et al. 2010, Beardmore et al. 2014). Considering non-catch related benefits could change optimal stocking outcomes if they cause effort to be unresponsive to fishing quality or if there are increased crowding costs on lakes where stocking occurs (Goffe and Salanié 2005).

Summary

Generally, stock enhancement does make sense within open access fisheries to improve the net benefits of harvest for multiple angler groups when under government and lake association control. How much stocking is beneficial to anglers depends on characteristics of the angler and fish populations. Optimal stocking rates are likely to change under different management objectives but our bio-economic approach with clearly defined objective functions can be applied to fisheries with a diversity of biological and socio-economic conditions and allows for comparisons among management objectives and institutional control over stocking.

3.4.2 Who should hold the management right of stock enhancement?

In the following sections we consider the broader conditions under which local organizations versus government controlled stocking is likely to lead to desirable or undesirable outcomes in inland recreational fisheries.

Local organizations

Increasing angler benefits while also preventing excessive angler effort is a desirable outcome of stocking programs (Askey et al. 2013). Our results suggest that lake association controlled stocking may reduce the total amount of fishing effort in the fishery (dotted line in Fig. 3.6B is lower than in 3.6A) but this is mostly at the expense of roving angler effort. In recreational fisheries with low excludability of outside anglers, any improvement in the quality of a fishery through stock enhancement is likely to draw in more effort and dissipate gains in harvest benefits (Anderson 1983, Baer et al. 2007, Mee et al. 2016). Consequently, Askey et al.

(2013) suggested that the primary role of stocking should be to manage for sustainable fishing effort because fishing quality cannot be improved in an open access fishery. Lower stocking rates under lake association control drew less effort into the fishery but tended to support less roving angler effort than government stocking (dotted lines in Fig. 3.6A and 3.6B).

Lake association controlled stocking is likely to reduce benefits for roving anglers and may not be appropriate near urban centers. In some places in Europe and Asia, communities hold stocking rights and the ability to restrict access to fisheries (Lorenzen et al. 1998, Daedlow et al. 2011), which can improve harvest benefits if residents cooperate to limit the effort of their own members and outside anglers (Anderson 1983, Lorenzen et al. 1998, Arlinghaus 2006, Arnason 2008). However, restricting angler access contrasts with the traditional approach to fisheries management in North America, where inland recreational fisheries are viewed as public goods that are available to all. While devolved stocking management does not explicitly restrict access to outside anglers it may implicitly devalue non-local anglers, especially for anglers for whom travel costs are high or burdensome. Formal management could correct for inequalities that arise in devolved management through incentives and taxes prompting more optimal outcomes for non-local anglers (Arnason 2008). Devolved stocking management should be considered in light of other options particularly near urban centers where heavy historic use of lakes by roving anglers may limit resident fishing effort and interest in the fishery (Fig. 3.2A).

Our results suggest that local organizations performing stock enhancement can lead to greater social welfare when fish stocks are low and could allow for funding otherwise spent on stocking by government managers to be used for other forms of fisheries management. Lake association controlled stocking led to larger regions of positive social welfare at low initial fish densities compared to government stocking. Therefore, removing the substantial cost of stocking by relying on informal management when fish stocks are imperiled would allow for more resources to support actives like fish population monitoring, recovery efforts for fish species, ecological research, and enforcement of regulations (Cooke et al. 2013). Our results suggest that if government mangers were to stop stocking, local organizations would have incentives to take on the role. Nonetheless, the transition from centralized to devolved management in inland recreational fisheries may be prevented by influential stake holders (Daedlow et al. 2013). With more resources, government managers could also divert funding to enhance non-catch related benefits for anglers by investing in facilities on lakes, improving the aesthetics of a lake, or reducing congestion at boat landings (Hunt 2005).

Devolved management control of stock enhancement could also promote the ability of lake associations to learn from one another through a diversity of stocking approaches, allow for rapid feedback from changes in stocking rates, and include local level knowledge in decision making (Berkes 2010). Experimentation by local organizations with various stocking rates combined with knowledge transfer among lake associations and academics could lead to social learning and improve stocking outcomes on the landscape (Berkes 2009, Cooke et al. 2013, Fujitani et al. 2017). Stock enhancement in systems where there is little responsiveness to ecological conditions or local knowledge can lead to unintended outcomes (Lorenzen et al. 1998). Stocking conducted by lake associations is likely to be more responsive and adaptive to changes in the fishery than government management (Lebel et al. 2006). Stocking decisions would also incorporate local knowledge and be tailored to how much fishing is valued by its members. However, the value of fishing and associated travel costs of outside angler groups would likely be neglected if stocking were under lake association control. Formal management could correct for this through incentives and taxes prompting more optimal outcomes for anglers outside of lake associations (Arnason 2008).

Government

Our results suggest that government controlled stocking is responsive to outside anglers who highly value the fishery and can have positive spillover effects on local economies (Bergstrom et al. 1990). Optimal stocking under government control was highest when non-local anglers that highly valued fish harvest made up the majority of the fishing pressure at equilibrium, but the opposite occurred when stocking was under lake association control. In the USA in 2011, fishing trip related expenditures by freshwater anglers were greater than 25 billion USD (U.S. Department of the Interior et al. 2011). In addition, 21% of all recreational anglers fished outside of their state of residence, leading to positive spill over economic effects of fishing for local economies. Under lake association controlled stocking, fewer outside anglers are likely to be drawn to an area due to lower optimal stocking rates compared to when stocking is under government control.

Higher optimal stocking rates under government control can lead to higher total fishing effort and negative social welfare at low fish densities. Our results indicate that total equilibrium fishing effort on lakes tends to be higher when stocking is under government control and this can lead to negative social welfare when initial fishing densities are low even if stocking allocations are optimal. Controlling fishing effort on lakes with high total effort and low fish densities is likely to lead to more beneficial outcomes than beginning government run stocking programs on these lakes.

Summary

Local organizations can play a beneficial role in maintaining harvest related benefits in inland recreational fisheries through stocking particularity when fish stocks are low but the costs and values of non-local anglers are likely to be ignored under this management scenario. Government controlled stock enhancement can promote and maintain fishing opportunities for non-local anglers and the positive economic effects they have on local economies but can lead to higher effort on lakes and negative social welfare at low fish densities.

3.4.3 Future directions

Our model had several simplifying assumptions that allowed for generality and tractability while solving for optimal stocking rates but future research will be required to determine when it is important to relax these assumptions. Our model did not assume a stage structured fish population with stage specific mortality. Lorenzen (2005) did consider stage structured dynamics in the context of stock enhancement and similar to our results, he found that optimal stocking rates increased as a function of marginal value from harvest and decreased with the marginal cost of stocking. Our optimal control model could be extended to include a stage structured dynamics similar to Botsford and Wainwright (1985). In addition to simplified biological interactions, we assumed that there was high latent fishing effort from both residents and roving anglers but in areas far away from high population densities there might be an upper limit to fishing capacity (Wilson et al. 2016). In cases where there is not a high degree of latent effort, probability density distributions can be parameterized to the potential angler population and used to describe entry into the fishery (Fenichel et al. 2010). Our model of effort dynamics assumed linear benefits in harvest but future work is required to determine if this is an accurate representation of recreational angler preferences.

Our model, which explicitly considered angler travel costs, can be extended to consider how landscape stocking decisions can distribute fishing effort among lakes. Travel costs are a key predictor of effort allocation by anglers but have not been explicitly considered in previous model applications of stocking allocations (Parkinson et al. 2004, Askey et al. 2013, but see Matsumura et al. 2010). While we focused on a single lake, our approach can be expanded to a landscape context to determine how stocking and effort decisions interact under government or lake association controlled stocking (see Anderson 1993 for an example). Strategic stocking decisions by neighboring lake associations may direct roving effort on landscape (Sumaila 1995, Copeland 1990) in predictable and potentially desirable ways. Alternatively, government managers could choose stocking rates on lakes to direct landscape effort in a way that meets their management objectives (Askey et al. 2013).

3.4.4 Conclusion

The assumption that local organizations do not have incentives to invest in improving their fishery when they do not have control over outside fishing pressure has likely limited the adoption of devolved management approaches to stock enhancement in inland recreational fisheries in North America. We suggest that there are incentives for local organizations to invest in stock enhancement and that they stock at approximately optimal rates. Devolved management can maintain fishing benefits when fish population densities are low, promote social learning among local organizations through experimentation with a diversity of stocking rates and incorporates local knowledge that is responsive to changes in the fishery (McGinnis 1999, Berkes 2010). However, for devolved management of stock enhancement to be successful it will require government managers to oversee wider management goals, correct inequalities or unfavorable outcomes that arise from decentralized control of stocking, provide quality information to local management groups, and promote social learning through networks of local management groups and academics (Lane and McDonald 2005, Berkes 2009, Cooke et al. 2013, Fujitani et al. 2017).

Tables and figures

Table 3.1. Regression models of empirical stocking data. Percent resident angling effort = α and roving angler marginal willingness to pay for harvest = p_{rov}.

Model	Government			Lake association		
	AICc	Parameter estimates	R^2	AICc	Parameter estimates	R^2
1. $Stocking\ rate \sim \beta_0 + \beta_1\alpha$	409	$\beta_0 = 43*$ $\beta_1 = -40*$	0.10	68	$\beta_0 = 1.0$ $\beta_1 = 6.8*$	0.48
2. $Stocking\ rate \sim \beta_0 + \beta_1\alpha + \beta_2 p_{rov}$	412	$\beta_0 = 44*$ $\beta_1 = -40*$ $\beta_2 = -.02$	0.10	69	$\beta_0 = 6.0$ $\beta_1 = 6.6*$ $\beta_2 = -.16$	0.54
3. $Stocking\ rate \sim \beta_0 + \beta_1\alpha + \beta_2 p_{rov} + \beta_3\alpha \cdot p_{rov}$	413	$\beta_0 = -15$ $\beta_1 = 161$ $\beta_2 = 2.1$ $\beta_3 = -7.3$	0.13	72	$\beta_0 = -1.2$ $\beta_1 = 28$ $\beta_2 = 0.1$ $\beta_3 = -0.8$	0.58

*estimate is significantly different from zero

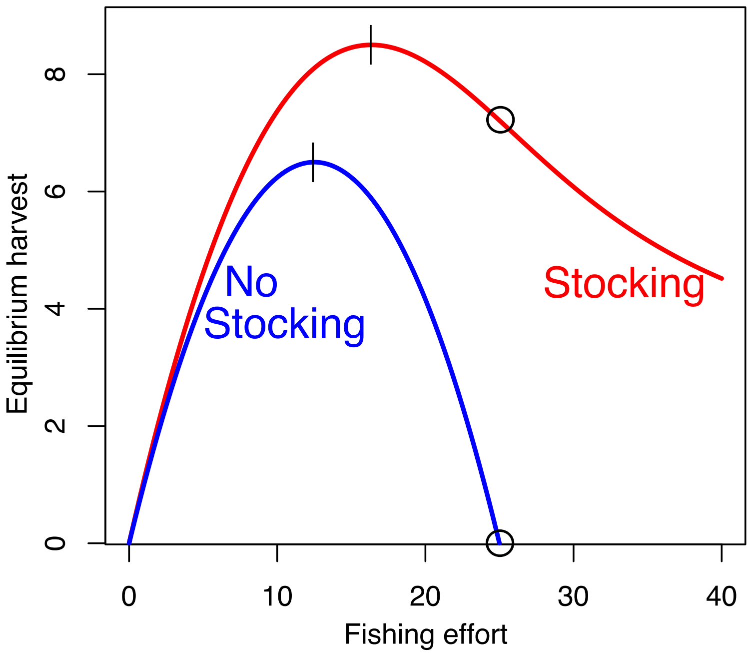

Figure 3.1. Equilibrium harvest and fishing effort of a fish population with (red) and without (blue) a constant stocking rate at equilibrium. The maximum equilibrium harvest (vertical lines) is higher when there is stock enhancement. When there is no stock enhancement there is a point at high fishing effort where equilibrium harvest is zero because the fish stock is completely collapsed but this does not occur when there is stocking at equilibrium (open circles).

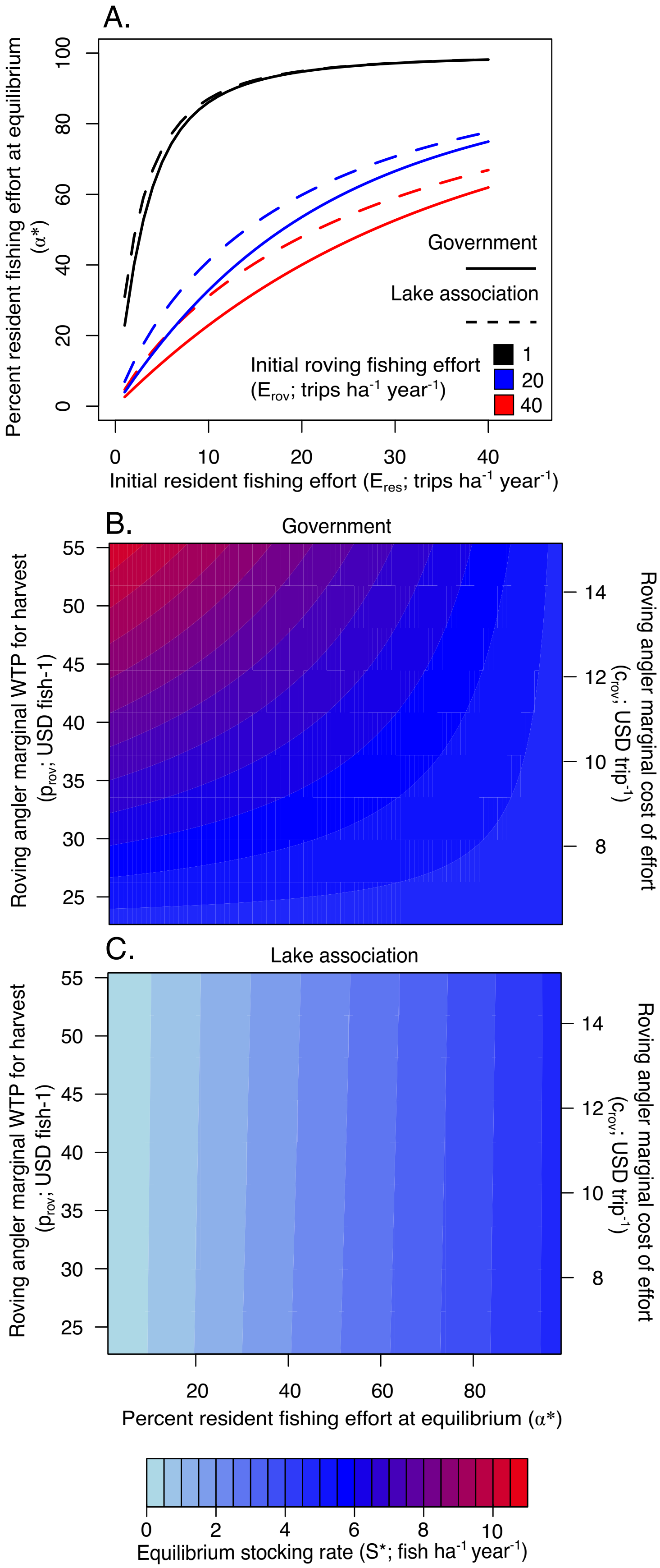

Figure 3.2. (A) The contribution of residents to total fishing effort at equilibrium (α^*) was dependent on the initial fishing effort of residents and rovers . Resident effort was lower under government controlled stocking when residents were less than ~80% of equilibrium effort due to higher stocking rates attracting higher roving angler effort. The travel cost for roving anglers was held constant at 10 USD trip^{-1}. (B and C) Optimal equilibrium stocking rates across a range in roving angler marginal willingness to pay for harvest (WTP) and percent resident fishing effort at equilibrium when stocking was under government (B) and lake association (C) control. Government stocking rates increased at higher willingness to pay and associated travel costs because rovers had higher net benefits per unit effort compared to residents (Appendix N). See Table O1 for parameter values.

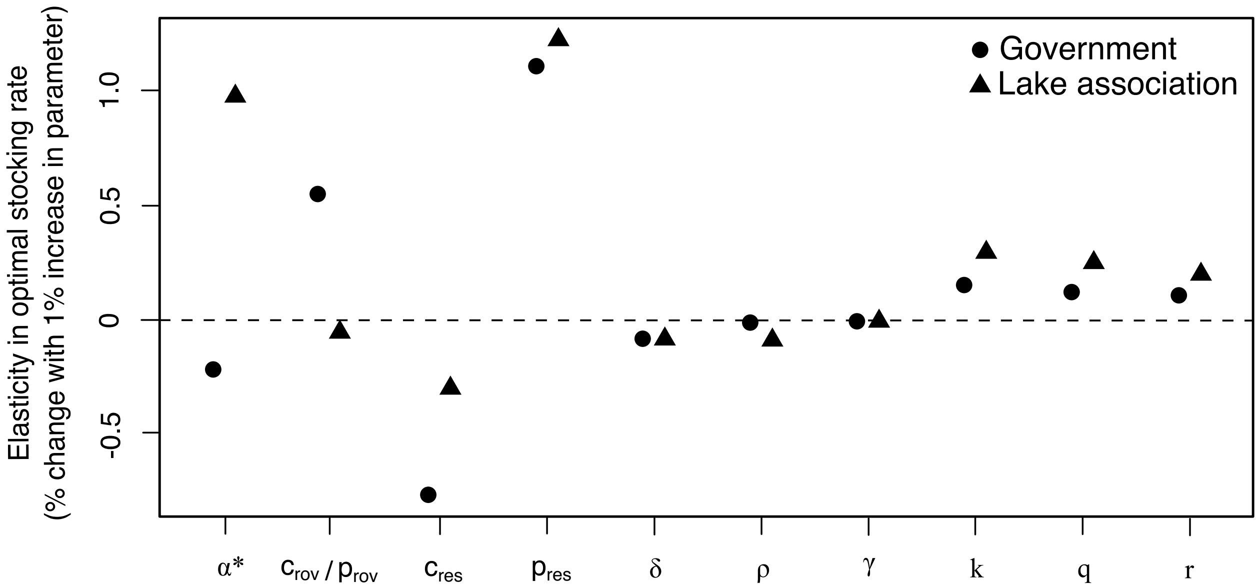

Figure 3.3. Sensitivity of government and lake association optimal equilibrium stocking rates to a one percent increase in model parameters. Individual parameters (indicated on the x-axis) were varied while all other parameters were held constant at default values. See Table O1 for default parameter values and definitions.

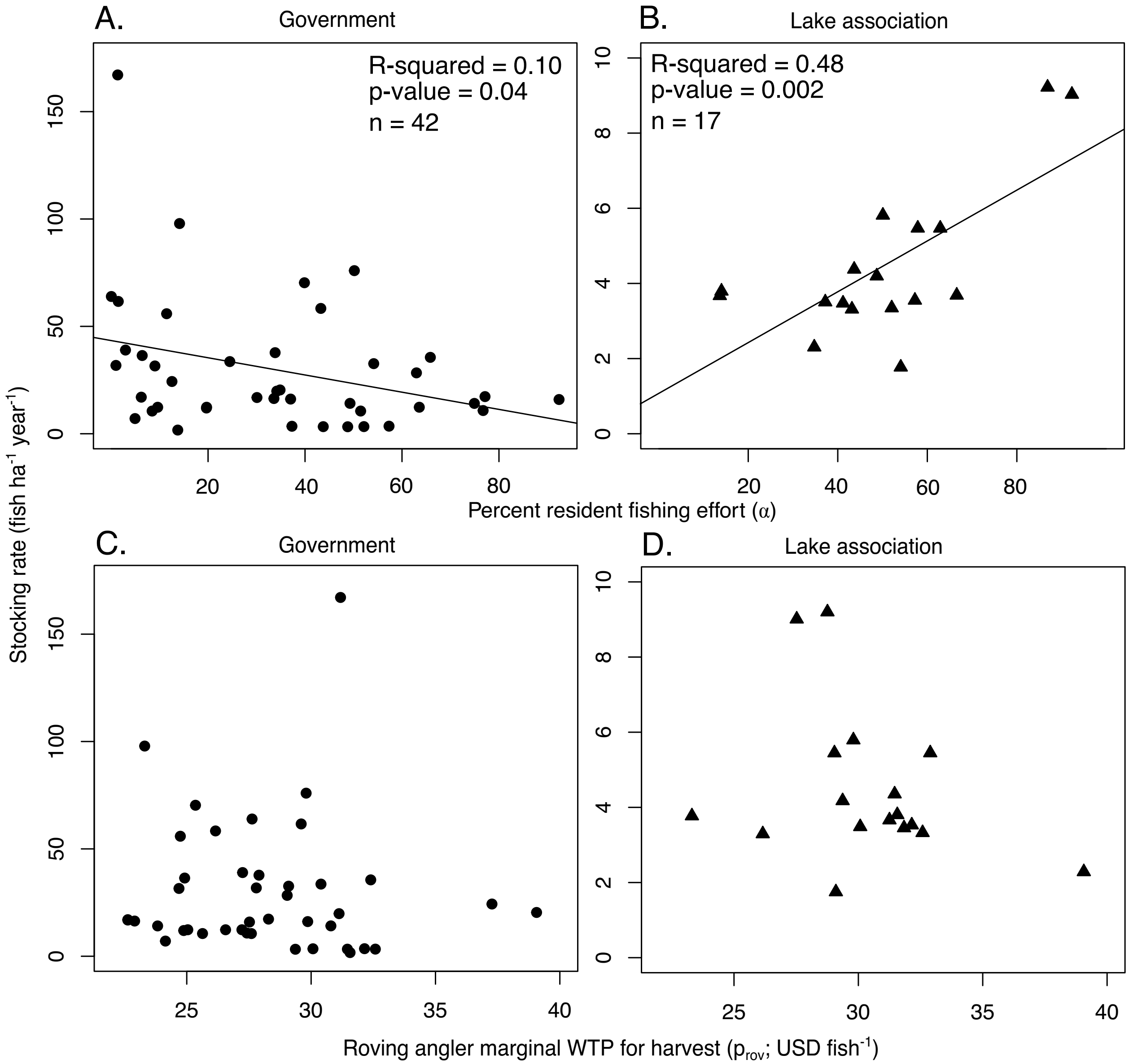

Figure 3.4. Observed government stocking rates of walleye fingerlings significantly declined with increased resident fishing effort relative to roving angler effort in our study lakes (A) but were unrelated to calculated roving angler marginal willingness to pay (WTP) for walleye harvest (C). Observed lake association stocking rates of walleye fingerlings significantly increased with increased resident fishing effort relative to roving angler effort in our study lakes (B) but were unrelated to calculated roving angler marginal willingness to pay (WTP) for walleye harvest (D, Table 3.1). Roving angler marginal willingness to pay was calculated for each lake using Equation 5, round trip travel costs to the lake, and boat operating costs (Table O1).

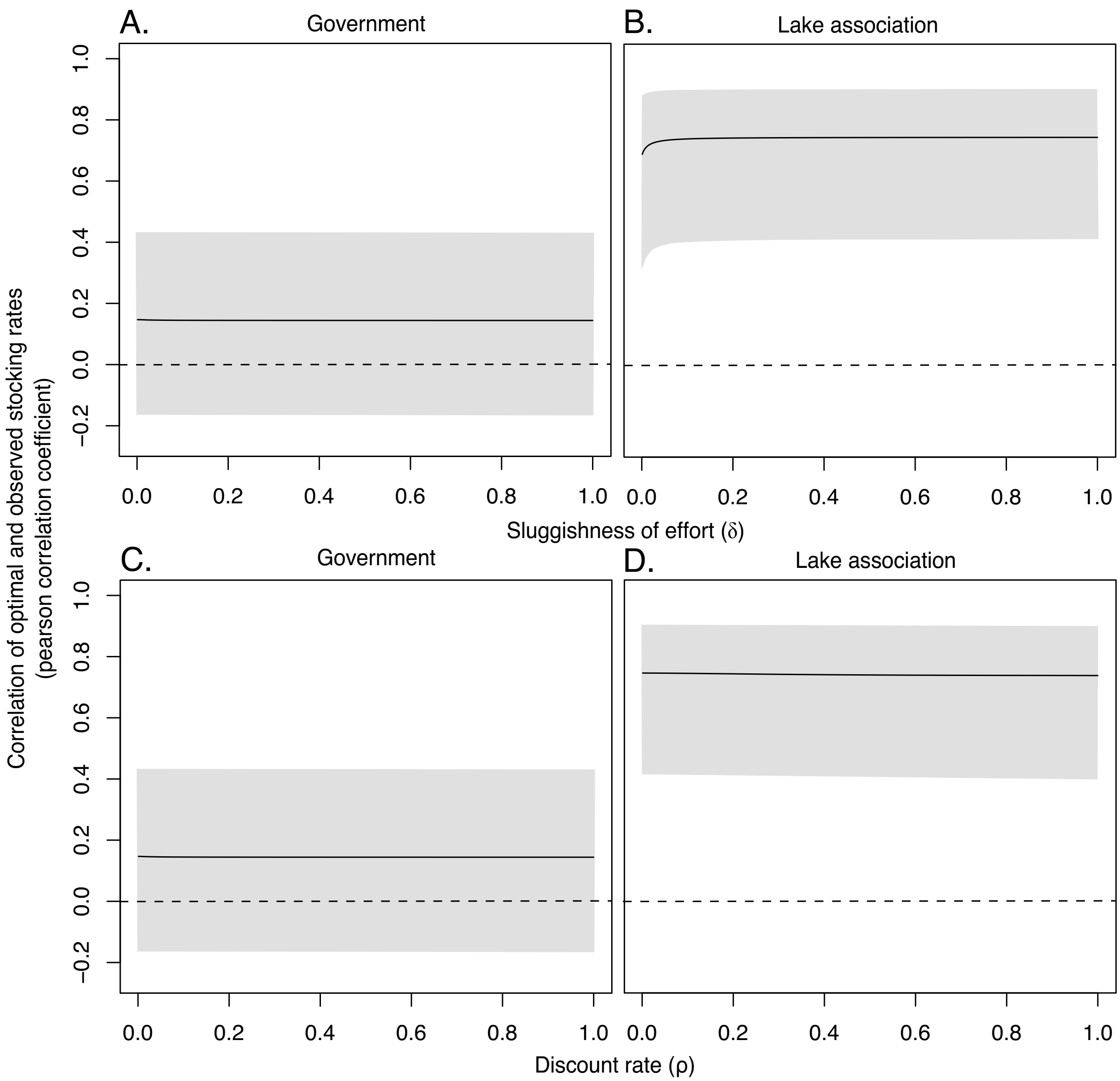

Figure 3.5. Observed government stocking rates of walleye fingerlings in 42 lakes we not significantly correlated to predicted optimal stocking rates for each lake, which was robust to changes in the sluggishness of effort (A) and future discount rate (C) parameters used in model predictions. Observed lake stocking rates of walleye fingerlings in 17 lakes we significantly positively correlated to predicted optimal stocking rates for each lake, which was robust to changes in the sluggishness of effort (A) and future discount rate (C) parameters used in model predictions. See Table O1 for model parameters. Solid lines represent Pearson correlation coefficient estimates and shaded regions represent 95% confidence intervals.

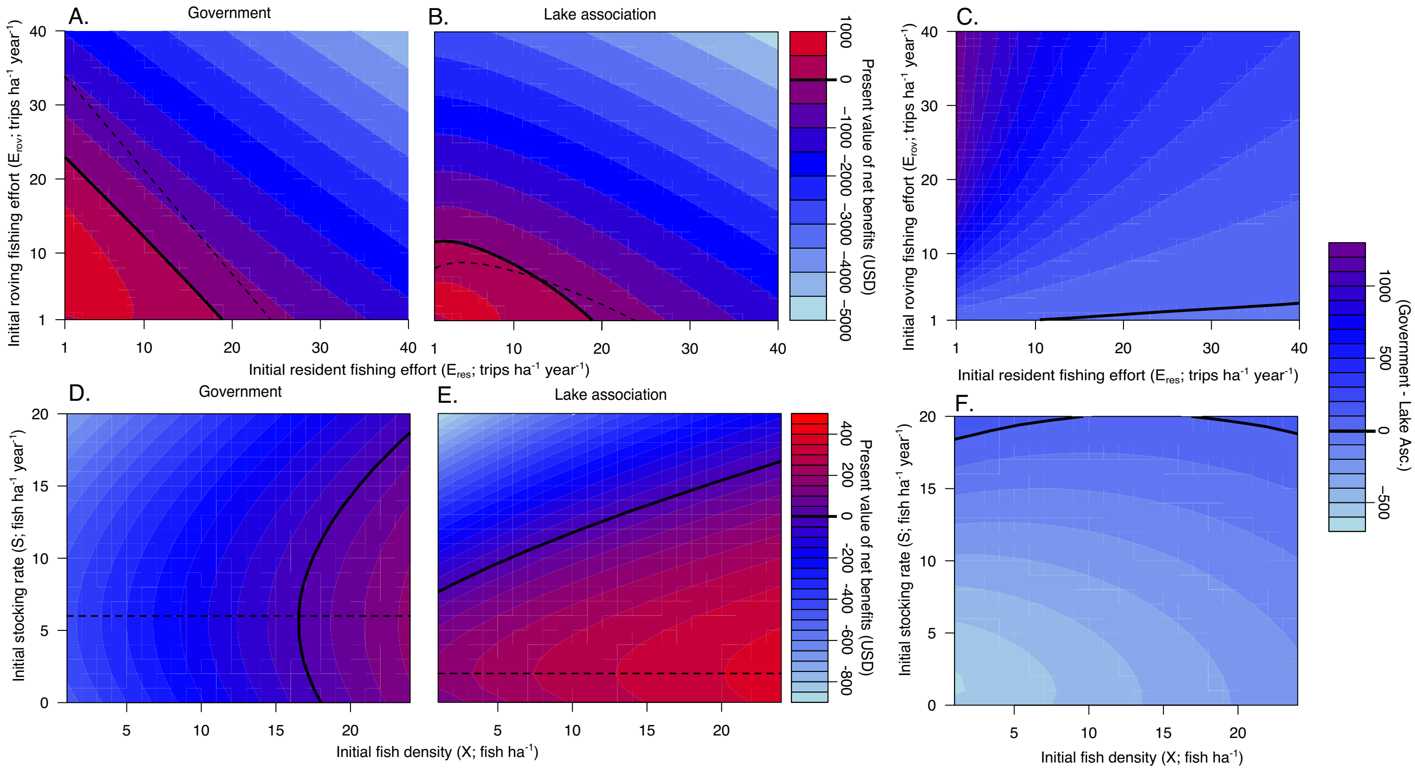

Figure 3.6. (A, B, C): Numerical solutions of our bio-economical modeled showed that high initial angling effort led to negative social welfare (present value of net benefits of all anglers less the cost of stocking) for both management scenarios but social welfare was higher over a larger range in initial roving effort when stocking was under government (A) as opposed to lake association (B) control as seen by the difference in social welfare between government and lake association controlled stocking (C). Equilibrium effort (dotted line in the top panel) was higher under government controlled stocking. (D, E, F): Initial stocking rates near equilibrium optimal stocking rates (dotted line in bottom panel) led to the highest social welfare under both management scenarios and social welfare was positive over a larger region of initial fish densities when stocking was under lake association (E) as opposed to government control (D) as seen by the difference in social welfare between government and lake association controlled stocking (F).

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Preface to Chapter 4

In the previous chapters I applied a social-ecological systems paradigm to an inland recreational fishery and demonstrated how it can inform our understanding and approaches to recreational fisheries management. While a social-ecological systems paradigm is widely viewed as beneficial in the academic community, unless it is employed in practice it remains an ivory tower theory without much real-world impact. In Chapter 4 I determine if stakeholders within an inland recreational fishery landscape understand their system as social-ecological in nature. Conducting this study allowed me to apply theory from other studies of successful shared resource management to inform paths forward for improving inland recreational fisheries management.

Chapter 4

Local stakeholders do understand their systems as social-ecological in nature but are actors playing a larger role than governance systems? Insights from an inland recreational fishery.

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Abstract

Recognition that there are often social and ecological components to problems that arise from management of shared resources has led to a dominant paradigm among academics that natural resource management should consider coupled social-ecological systems. For academic theory to have real-world impact it must be taken up and understood by stakeholders at the local scale. However, it is unclear if stakeholders view their systems as coupled social-ecological systems. We interviewed key stakeholders in an inland recreational fishery to solicit their mental models of system dynamics in the context of Ostrom's Social-Ecological Systems Framework. We found that stakeholders in aggregate considered all components of the Social Ecological Systems Framework (actors, resource systems, environmental settings, and governance systems) in their view of recreational fisheries but that they viewed actors and resource systems as more diverse and influential than governance systems and broader environmental settings. Given strong empirical evidence of positive relationships between the number and diversity of governance system attributes and successful fisheries outcomes, our results suggest that governance systems could play a larger role in local level management of inland recreational fisheries.

4.1 Introduction

A social-ecological approach to natural resource management has become the dominant paradigm among academics. In a critical review of natural resource management goals Holt and Talbot (1978) suggested that the primary goal of management should be to maintain a resource system in a desirable state despite environmental and socio-political changes. However, during the 1980's there was recognition that solutions to natural resource management problems were often composed of ecological, economic, and social components (Mangel et al. 1996, Mace 2014). Since the 1980's a new form of natural resource management has emerged, which focuses on understanding the many complex interactions among social and ecological systems (Kates et al. 2001, Mace 2014). These interactions among system components produce dynamics like feedbacks and thresholds that can only be explained by considering coupled social-ecological systems (Costanza et al. 1993). Considering social-ecological interactions can also improve our ability to predict outcomes of shared resource use (Berkes et al. 1989, Dietz et al. 2003).

An example of the shift in natural resource management paradigm can be seen in inland recreational fisheries, where research was initially focused on fish and their immediate environment but has since moved towards a social-ecological perspective. Prior to the 1980's inland recreational fisheries research was within the realm of ecological and physical sciences (Arlinghaus et al. 2008). However, since the 1980's there have been increasing calls to correct for the lack of social research and embrace a social-ecological paradigm within recreational fisheries (Fulton et al. 2011, Beard et al. 2011, Arlinghaus et al. 2013, Arlinghaus et al. 2017). Researchers have begun to understand inland recreational fisheries as coupled social-ecological systems (Johnston et al. 2010, Hunt et al. 2013) but so far studies have largely focused on ecological dynamics and individual human behaviors and have not focused on understanding other components of social-ecological systems, like governance systems, and the outcomes of interactions among social-ecological components (Arlinghaus et al. 2013, Arlinghaus et al. 2017).

The complexity of interacting systems poses a challenge for understanding and defining social-ecological systems (Rittel and Webber 1973, Roe 1988, Ludwig et al. 1993, Ludwig 2001). However, empirical data and theory have suggested that social-ecological complexity can be understood and defined by a handful of controlling processes and variables (Ostrom 1990, Holling 2001, Walker et al. 2006). Ostrom (2009) formalized findings from extensive fieldwork on social-ecological systems into a Social Ecological Systems Framework (SESF) designed for understanding local social-ecological systems and use in natural resource management. She identified variables for understanding a social-ecological system that she organized into system components. The components she originally defined included resource systems, resource units, actors, governance systems, environmental and socio-political settings, and related ecosystems. The SESF has become one of the most widely used frameworks for understanding complex social-ecological systems (Ostrom 2009 has been cited over 2,000 times, see also past and more recent versions of the SESF in (Ostrom 2007, Ostrom 2009, McGinnis and Ostrom 2014, Hinkel et al. 2014).

While the SESF has been applied at local scales by researchers, including in inland recreational fisheries, it is unclear if stakeholders – those managing and acting within these systems – understand their systems in a similar manner as the SESF. To date, studies applying the SESF at a local scale have focused on determining which of the variables proposed by Ostrom (2009) were present in a given system. These studies have ranged from no stakeholder involvement in applying the SESF by relying on researcher knowledge and literature reviews (Meinzen-Dick 2007, Basurto and Ostrom 2009, Santos and Thorne 2010, Madrigal et al. 2010, Bal et al. 2011, Blanco 2011, Gutiérrez et al. 2011, Amblard 2012, Schlüter and Madrigal 2012, Nagendra and Ostrom 2014) to including stakeholders in applying the SESF through questionnaires, interviews, and focus groups (Blanco and Fedreheim 2011, Dumyahn and Pijanowski 2011, Begossi et al. 2012, Cinner et al. 2012, Falk et al. 2012, Baur and Binder 2013, Risvoll et al. 2014, Naiga et al. 2015). However, studies applying the SESF rarely allow stakeholders to define their understanding of the system and which variables they view as important (although see Delgado-Serrano and Ramos 2015).

While a social-ecological paradigm in natural resource management has become dominant in academic circles, if those carrying out and informing management at local scales do not share a similar understanding then there is little real world impact of academic theory. Shared mental models among diverse stakeholders is often necessary for successfully implementing natural resource management (Biggs et al. 2011). There is strong empirical evidence that fisheries outcomes are often dependent on SESF components like governance systems and environmental and socio-political settings (Pollnac et al. 2010). However, past focus within academia on ecological dynamics and individual human behaviour, as observed in inland recreational fisheries management (Salas and Gaertner 2004, Fulton et al. 2011, Murray and Ings 2015), may result in stakeholder understanding not capturing the full extent of social-ecological systems.

Our objective was to understand how stakeholders conceptualized a shared resource, specifically how important they perceived Ostrom's SESF components to be relative to and interacting with each other. We characterized stakeholder understanding of an inland recreational fishery landscape using mental models that we then represented within the SESF. We compared the importance of SESF components in stakeholder mental models and discuss how previous studies applying the SESF can help inform inland recreation fisheries management.

4.2 Methods

4.2.1 Representing stakeholder mental models within the Social Ecological Systems Framework

Fuzzy cognitive maps (FCMs) are an effective method of representing individuals' mental models of how a complex social-ecological system operates (Özesmi and Özesmi 2004, Kok 2009, Papageorgiou 2013, Vasslides and Jensen 2016). They depict key system variables (things that take on specific values at different time points) and concepts (groupings of variables with similar attributes) along with their direct relationships to one another (Bernard and Bernard 2012, see Fig. P1 for an example). When FCMs are conducted with local experts they can provide detailed depictions of local social-ecological systems (Vasslides and Jensen 2016).

We used FCMs to characterize stakeholder understanding of an inland recreational fishery landscape and coded FCM variables and concepts into Ostrom's Social-Ecological Systems Framework. While the SESF was developed to classify concepts and variables to allow for generalizations among diverse social-ecological systems, its application is often difficult and inconsistent (Thiel et al. 2015). Hinkel et al. (2014) improved ease and consistency of application of the SESF at the local scale by formalizing methods for adding concepts into the SESF. They reorganized the SESF into a nested hierarchy of four components of a social ecological system: 1. actor – defines the social entities that act within the system, 2. resource system – defines the ecological and biological context of the resource, 3. governance system – defines the rules and rights of actors, and 4. environment – defines related systems that affect the resource and actors. Hinkel et al. (2014) did not highlight the action situation, which is featured prominently in an updated version of the SESF (McGinnis and Ostrom 2014) and is composed of interactions among the SESF components that result in outcomes. Each variable and concept that arose in stakeholder FCMs was categorized as a feature of the actor, resource system, governance system, or environment, and the direction and strength of relationships between concepts was used to describe the action situation using the methods described in the following sections.

4.2.2 Study region and Fuzzy Cognitive Map collection

We focused on recreational fisheries in Vilas County Wisconsin USA, a 2,600 km^2 sparsely populated area in Northern Wisconsin where recreational fisheries represent prominent coupled social-ecological systems (Liu et al. 2007). Based on our knowledge working within this study area we selected 15 individuals who had expert knowledge of the four components of the SESF (actor, resource system, governance system, and environment). We interviewed experts on the actor and governance system components of the SESF (n=8), who were heads of lake organizations, state fisheries managers, and avid anglers in the county. We collectively refer to this group as managers & anglers. We interviewed experts on the resource system and environment components (n=7), who were fisheries and aquatic ecology academic researchers in in the study region. We collectively refer to this group as researchers. We used a standard method of accumulation curves to ensure that we conducted enough sampling to thoroughly represent the concepts deemed important by stakeholders for recreational fisheries in our study region (Vasslides and Jensen 2016). We computed the accumulation curve of the number of unique concepts with additional FCMs (added at random) using the Specaccum function in the Vegan package in R (Oksanen et al. 2018).

We followed standard methods for creating FCMs through one-on-one in-depth interviews with informants (Özesmi and Özesmi 2004, Vasslides and Jensen 2016). The same interviewer conducted all interviews during the summers of 2016 and 2017. Interviews began with an overview of the project and an explanation of how to draw a FCM using a simple unrelated example of traffic flow on a road (Fig. P1). The interviewer then asked informants to list which variables, concepts, or things came to mind when thinking about recreational fisheries in the study region and the interviewer recorded this list. Informants then diagramed the relationships among the concepts listed by drawing each as a node and connecting the nodes with arrows to represent directional relationships between concepts. Informants scored the direction of each relationship (positive or negative) and its strength (high, medium, or low). Once all concepts and variables from the list were diagramed, informants were given the opportunity to review and revise their maps until they confirmed that it accurately depicted their understanding of the system. Interviews ranged from 45 min to 105 min, with a mean of 60 min. In accordance with federal regulations, this research was reviewed and approved by an Institutional Review Board and the interviewer received "Protecting Human Research Participants" certification from the National Institutes of Health (IRB no. 130-2016).

4.2.3 Coding fuzzy cognitive map concepts into the Social Ecological Systems Framework

We used the methods of Hinkel et al. (2014) to add concepts from FCMs into the SESF using attribution and subsumption relationships. Attribution and subsumption relationships are sometimes referred to as "has-a" and "is-a" relationships respectively. For example, a concept X has an attribution relationship with a variable Y if the sentence "X has a Y" is meaningful for all instances of X and Y. Conversely, a concept X has an subsumption relationship with Z if the sentence "all X's are Z's but not vice versa" is true. We followed these methods when coding concepts from FCMs into the four nested components of the SESF that Hinkel et al. (2014) developed. We provide an overview of how all concepts present in FCMs were classified into the SESF using Hinkel et al.'s (2014) visual representation of the SESF with attribution and subsumption relationships (Fig. 4.2) and a list of the original terms used in FCMs along with how they were classified (Table P1).

4.2.4 Testing importance of SESF components for stakeholder understanding

We tested the relative importance of SESF components for stakeholder understanding of their recreational fishery using the percentage and frequency of concepts in FCMs that we categorized within the four components of the SESF. We used Analysis of Variance to test for differences in the mean percentage and frequency of concepts in FCMs categorized into the four

SESF components (R Core Team 2017). We then tested for pairwise differences among means using Tukey Honest Significant Differences. Given our a priori selection of stakeholder groups we expected that researchers would have higher importance of resource system and environment components in their FCMs and managers and anglers would have higher importance of actors and governance systems. Therefore, we fit models that did and did not allow means to differ by stakeholder group (i.e. managers and anglers vs. researchers). We present results from models that included stakeholder group if it had a significant effect.

Although Hinkel et al.'s (2014) enhanced SESF did not focus on the action situation, FCMs have standard quantitative methods that allowed us to compare differences in the action situation among SESF components. The action situation of the SESF is composed of interactions among SESF components and the resulting outcomes (McGinnis and Ostrom 2014).

Interactions in the SESF are defined as process relationships where one concept influences another (Hinkel et al. 2014, Schlüter et al. 2014). Fuzzy cognitive maps explicitly describe these relationships with the size and direction of effects between concepts or variables. Two standard metrics used to describe these relationships in FCMs are the outdegree and indegree of a given concept. An outdegree is the cumulative strength (absolute value) of the effects a concept has on others, while an indegree is the cumulative strength of the effects other concepts have on a given concept (Özesmi and Özesmi 2004, Vasslides and Jensen 2016).

Outcomes, the other component of the action situation, are the result of all the interactions within a social-ecological system (Hinkel et al. 2014). Outcomes in the context of FCMs can be quantitatively calculated by expressing FCM concepts and relationships among concepts in an adjacency matrix and iterating out the relationships to an equilibrium state from initial conditions (see Dickerson and Kosko 1994). We made these calculations following the methods of Vasslides and Jensen (2016), who used an initial value of one for each state variable and a logistic transformation to bound state variable output between zero and one before each iteration. We expressed outcomes as the percent change in state variables at equilibrium from initial conditions.

We tested for differences in interactions and outcomes among the SESF components using hierarchical linear models where indegree, outdegree, and percent changes from initial conditions were our response variables measured at the concept level nested within FCMs nested within SESF components. We tested models that allowed means to differ by interviewee type (i.e. managers and anglers vs. researchers) against models that did not. We present results from the best performing model as judged by small sample size corrected Akaike Information Criteria (AICc).

4.3 Results

The average number of unique concepts among maps declined with additional informants (Fig. 4.1). There were 60 unique concepts among the 15 maps (Fig. 4.1A); this included both concepts (bolded) and their attributes (non-bolded) in Figure 4.2 but did not include the four SESF components themselves (i.e. actor, resource system, governance system, and environment) as these were never explicitly included in FCMs. The rate at which new concepts and variables were added to our understanding of the social-ecological system with additional informants interviewed declined from ~10 to 1 by 15 informants, as most concepts were already represented in previous FCMs (Fig. 4.1B).

In aggregate, stakeholder mental models captured the four components of the Social Ecological Systems Framework (Fig. 4.2). Individually, just over two thirds of mental models captured all four SESF components but to varying degrees (Fig. P2, Fig. 4.3). All concepts and variables present in FCMs fit into the four components of the SESF through either attribution or subsumption relationships (closed and open arrows, respectively, in Fig. 4.2). The majority of nodes present in FCMs were attributes of a concept in the SESF (e.g. the ability of an angler, Fig. 4.2) and not subsumption relationships.

Both stakeholder groups emphasized actor concepts in their mental models, and researchers emphasized resource system concepts more than managers and anglers did (Fig. 4.3). As expected from our a priori group choices, managers and anglers emphasized actor concepts and did not identify many features of the resource system or the environment in their FCMs (p-values < 0.001 for all pairwise comparisons, Fig. 4.3), while researchers emphasized resource systems compared to managers and anglers (p-value < 0.01, Fig. 4.3). However, what differed from our expectations was that all stakeholders emphasized actor concepts over environment and governance system concepts. Further, researchers did not identify many features of the environment compared to the resource system (p-value < 0.01, Fig. 4.3). On average, researchers' maps included 5 actor concepts (38% of all concepts in the average researcher map), 4 resource system concepts (35%), 3 governance system concepts (17%), and 2 environment concepts (10%). For managers and anglers, the average map included 7 actor concepts (49%), 3 resource system concepts (16%), 2 governance system concepts (17%), and 3 environment concepts (17%).

All stakeholders emphasized the influence of actors and resource systems in the social-ecological system compared to environment and governance system (Fig. 4.4A). On average, the cumulative effect of an actor or resource system concept on other concepts was significantly larger than the cumulative effect of a governance system or environment concept (p-values $<$ 0.05 for all pairwise comparisons, Fig. 4.4A). The average effect of a resource system concept on other concepts was larger than that of actors but they were not significantly different from one another (Fig. 4.4A).

Despite a higher number and influence of actor and resource concepts in FCMs, they did not disproportionately affect concepts in any one SESF component, therefore, outcomes did not differ among SESF components. The cumulative effects that other concepts had on a given concept (indegree) did not significantly differ among the SESF components (Fig. 4.4B). Consequently, the larger representation of actor and resource system concepts and their influence on other concepts did not lead to significant differences in equilibrium outcomes among SESF components (Fig. 4.5). All equilibrium outcomes of mental models converged on a steady state within 25 iterations of the model.

4.4 Discussion

Our results suggest that stakeholders do view inland recreational fisheries as social-ecological systems but that actor and resource system components of the SESF are emphasized more than governance system and environment components in stakeholder mental models. This may have been because governance and environment concepts were underrepresented in our study region, or because fuzzy cognitive maps underrepresented government and environment concepts. We discuss these two possibilities below and their implications for inland recreational fisheries management.

4.4.1 Hypothesis 1: Governance and environment concepts were underrepresented in our region

There is strong empirical evidence that the success of local fisheries management is positively related to the number of attributes of well-functioning governance systems. There has been a long history of research into the effects of governance systems on management of shared resources that have highlighted property rights, collective choice rights, co-management, and strong institutions as having large effects on the success of shared resource management (Hilborn et al. 1995, Dietz et al. 2003, Ostrom 2007, Berkes 2009, Worm et al. 2009, Horan et al. 2011). In a global meta-analysis of 130 locally managed fisheries Gutiérrez et al. (2011) found that the social-ecological success of a fishery was positively correlated to attributes of well-functioning governance systems. Social-ecological success increased linearly above eight governance system attributes but when fisheries had eight or less attributes their social-ecological success was near zero; informants in our study identified 9 attributes of the governance system in aggregate. Leslie et al. (2015) scored the importance of governance systems in local fisheries based on the presence of rules within local management and access rights of anglers and found that fisheries with higher governance system scores had greater fish abundance. However, Cinner et al. (2012) found no effect of the governance system on ecological conditions but strong effects on fisheries livelihood and compliance outcomes. Gutiérrez et al. (2011) also found that governance system attributes were more correlated with social-ecological success of a fishery than actor attributes.

Evidently, the number and diversity of governance system attributes are important for successful fisheries management yet stakeholders reported less diversity and influence of the governance system in our study region compared to actor and resource system components. Incorporating attributes of the governance system that are known to improve outcomes for shared resources could aid inland recreational fisheries management. One promising approach would be to incorporate a diversity of attributes of governance systems that are likely to lead to social-ecological success of shared resource management (Ostrom 1990, Anderies et al. 2004). Based on empirical studies of local institutions managing a shared resource, Ostrom (1990) hypothesized a set of design principle for governance systems that lead to successful management of a resource. Of the eight design principles proposed by Ostrom there were six that were not explicitly included in the mental models of stakeholders in our system.

Stakeholders did not include the first three of Ostrom's design principles in their mental models. These three design principles help prevent free riding by identifying who should receive benefits from and pay costs for the resource, distributing benefits in proportion to the costs people pay for the resource, and allowing for collective choice to set rules of resource use (Anderies et al. 2004). In the context of inland recreational fisheries these design principles could be incorporated by rewarding user groups, like lake associations, who invest in stewardship of fish populations by granting them higher catch quotas to match the investments they make. While community based management rights were included in one FCM, none of the mental models contained rules that defined community management rights or their collective choice rights (Fig. 4.2).

Stakeholders did not include two other design principles that establish a feedback about the state of the system into management and user actions (Anderies et al. 2004). Enforcing rules through graduated sections along with rapid and accessible ways of dealing with conflicts that arise over the interpretation and understanding of the rules were not explicitly mentioned by stakeholders. These design principles ensure resource users follow the rules and help support stakeholder agreement (Anderies et al. 2004). Stakeholders mentioned frequent monitoring of fish populations by state government which informed harvest rules. However, rule enforcement, communication, and widely solicited stakeholder feedback could help ensure the information on the state of the fish stock is translated into user actions. Interestingly, Pollnac et al. (2010) found a correlation between community led monitoring and compliance with regulations but did not find a correlation between enforcement of regulations and compliance.

Like the governance system, stakeholders identified fewer environment concepts compared to actor and resource system concepts. The environment concepts they did identify tended to be larger scale concepts like climate (global to national level) and social and political settings (national to state level). In addition, all rules in use identified by stakeholders were operational rules set by the state government (Fig. 4.2). Ostrom (1990) suggested that nested institutions could help ensure that large scale problems are considered and addressed at the local scale. Allowing local institutions like lake districts and lake associations to set regulations through devolved management (Berkes 2010) might allow state government to consider and address larger scale issues and take actions at the local scale to offset variables they cannot control at larger scales (Carpenter et al. 2017). Allowing for multiple organizations to set regulations on a landscape of recreational fisheries can also improve the social and ecological resilience of the system (Carpenter and Brock 2004).

4.4.2 Hypothesis 2: FCMs underrepresented government and environment concepts

Our method of fuzzy cognitive maps may have underrepresented governance system and environment concepts because FCMs can capture variables that have clear agency that act within the system but may not be able to capture features of the governance system and environment if informants viewed them as fixed contextual settings. Governance and environmental concepts tend to be slower moving processes than actor or resource system concepts (e.g. regulations and climate change vs. fish harvest and fish reproduction). The temporal scale of drivers within recreational fisheries may have influenced the way stakeholders viewed the system; fast moving processes are often viewed as variables and can be captured by FCMs, while slower moving processes are often viewed as parameters or contextual settings that are fixed and may not be as easily captured by FCMs (Carpenter and Turner 2000, Cumming et al. 2006). However, there were several slow-moving governance and environment concepts within FCMs (e.g. political setting, climate change, regulations, legislation, etc.; Fig. 4.2 and Fig. P2) and informants consistently reported them as having less influence within the social-ecological system (Fig. 4.4).

Similar results have been observed in previous academic applications of the SESF to recreational fisheries that have not used FCMs. In an application of the SESF to inland recreational fisheries Hunt et al. (2013) emphasized the complexity within the actor component of the SESF. Similarly, Hinkel et al. (2014) applied the SESF to a recreational fishery and categorized most variables and concepts in the actor component (11), followed by the resource system (7), the environment (4), and the governance system (1). Our approach of using stakeholder mental models in application of the SESF resulted in a more complex view of recreational fisheries with more concepts and variables identified but the distribution of those concepts among SESF components was similar.

Use of mixed methods for elucidating if FCMs underrepresent government and environment concepts and promoting a view of actor agency within inland recreational fisheries represent future directions for research. Use of mixed methods like semi structured interviews (Cinner et al. 2012, Leslie et al. 2015) and content analysis from local management reports (Gutiérrez et al. 2011), could help test if FCMs underrepresent governance and environmental concepts in stakeholder mental models. Promoting a view of actor agency that includes active participation in shaping the governance system and environment components could reduce the perception that these components are fixed and could expand their role in inland recreational fisheries management (Larsen et al. 2011).

4.4.3 Understanding social-ecological systems with stakeholder mental models

Our use of stakeholder mental models can aid in applications of the SESF at a local level. Social-ecological systems are notoriously hard to delineate spatially, temporally, and institutionally (Carpenter et al. 2009) and guidance on applying frameworks to specific systems or research questions is scarce or non-existent (Binder et al. 2013). In a review of empirical applications of the SESF Thiel et al. (2015) found that authors were not consistent in their application of the framework. The advantages of using FCMs to help apply the SESF at a local scale are that they follow standardized methods that allow for quantitative testing, they are easy to understand and conduct for both the interviewer and the interviewee (Papageorgiou and Kontogianni 2012), and they involve stakeholders, which often promotes policy relevant results (Walker et al. 2002, Posner et al. 2016, Bennett 2016). However, the use of FCMs in combination with other methods like semi-structured interviews and content analysis of management reports could aid in revealing potential biases associated with FCMs. Our application of FCMs in combination with the SESF highlighted the opportunity for the governance system and local level actions addressing larger scale environment concepts to play an increased role in recreational fisheries management.

Figures

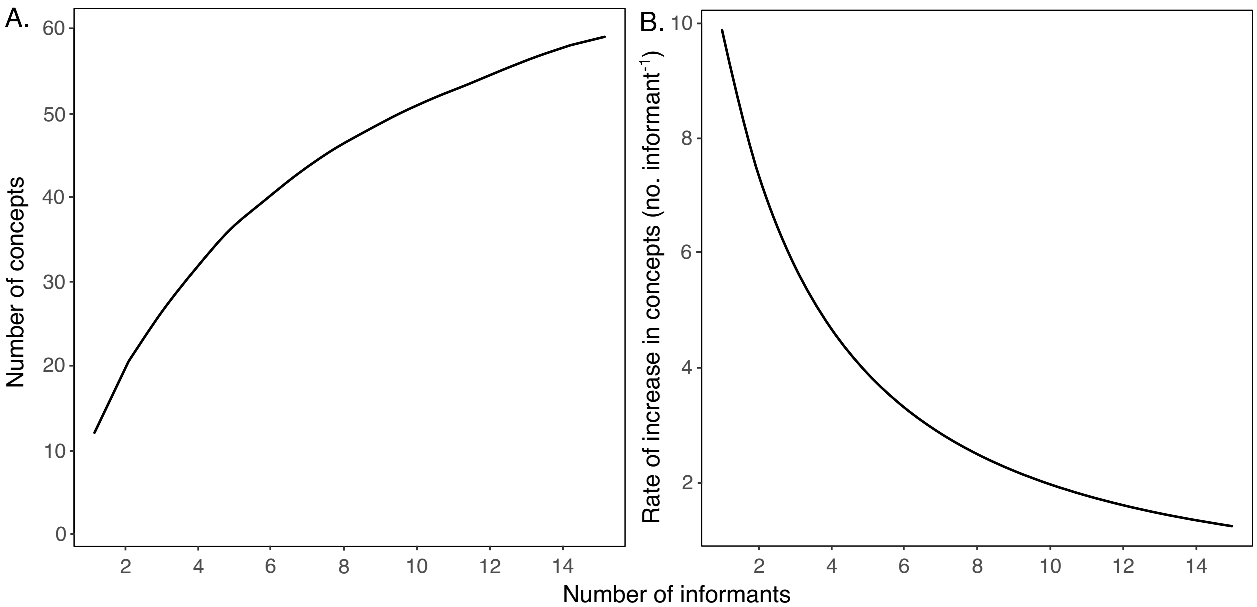

Figure 4.1. The average number (A) and rate (B) of new concepts and variables added to our understanding of the social-ecological system declined as the number of informants interviewed increased. The lines represent means from a rarefaction analysis that added informants at random.

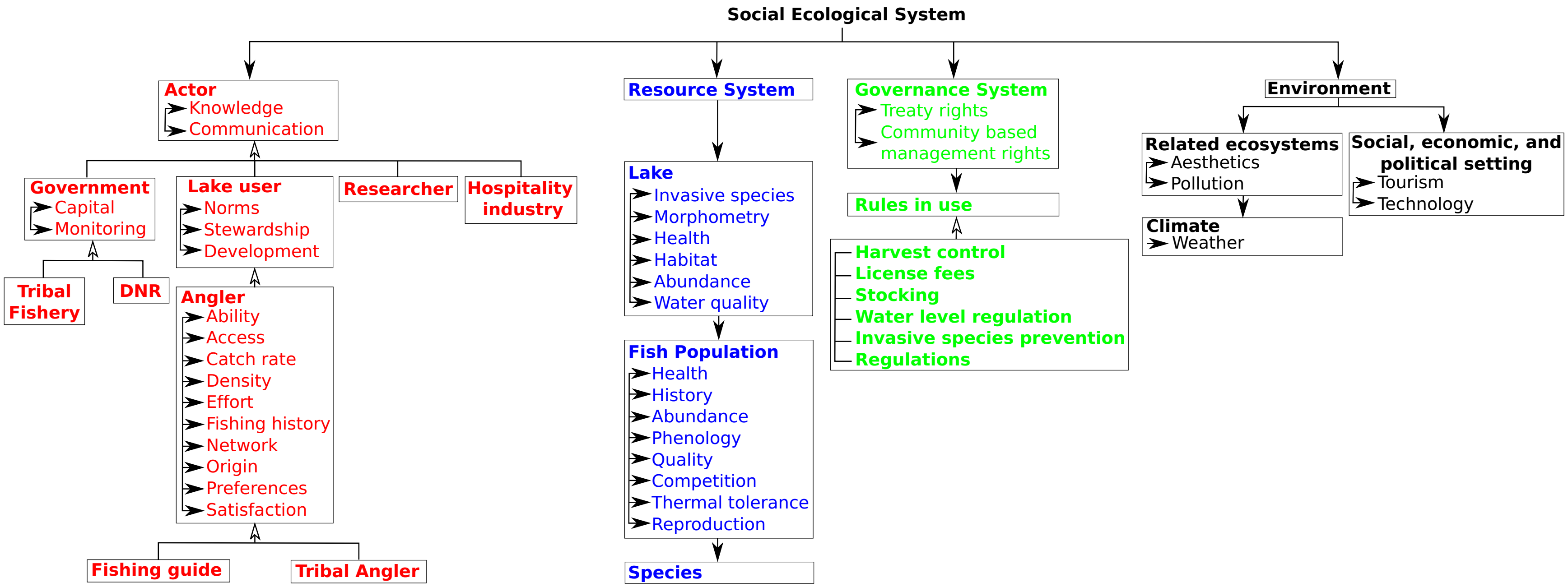

Figure 4.2. All concepts present in stakeholder mental models coded into the Social Ecological Systems Framework (SESF) using attribution (closed arrows) or subsumption (open arrows) relationships (see Hinkel et al. 2014). See Table P1 for how concepts from FCMS were coded in the SESF.

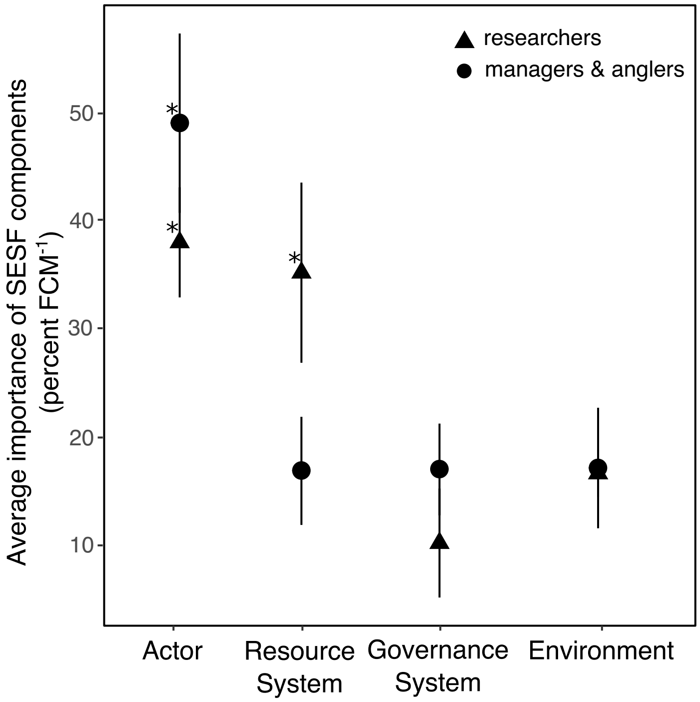

Figure 4.3. Stakeholders consistently included more actor concepts in their mental models compared to governance and environment concepts and researchers included more resource system concepts than managers and anglers. Mean values highlight with asterisks indicates that they are significantly different from those without asterisks.

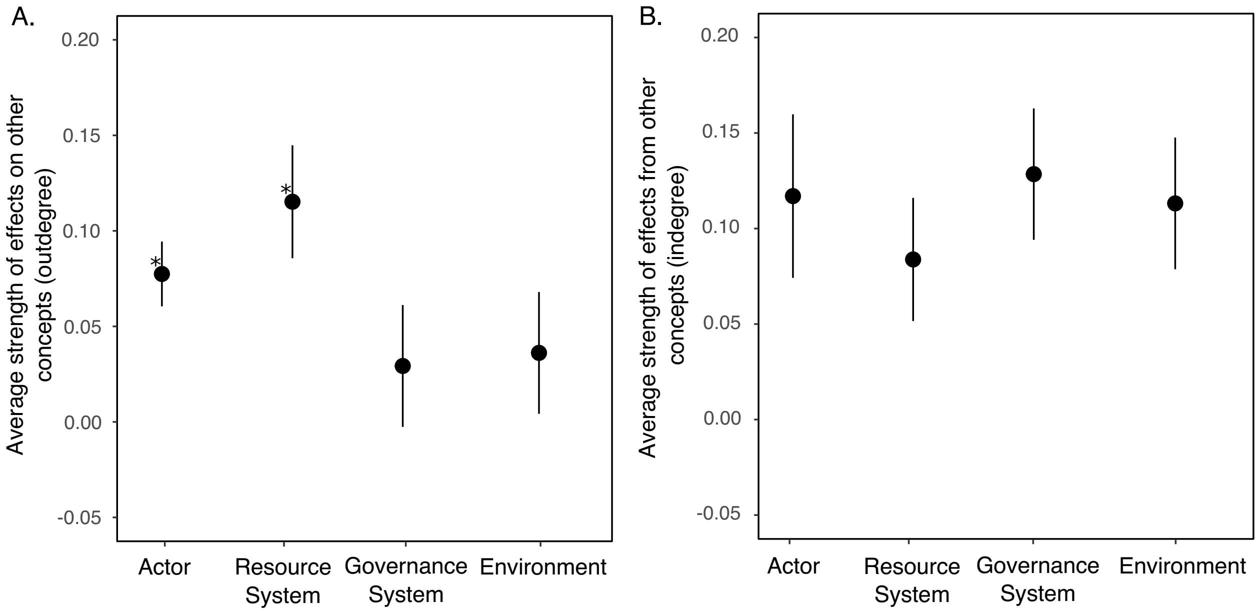

Figure 4.4. (A) Stakeholders consistently reported larger influences of actor and resource system concepts on other concepts (outdegree) compared to governance and environment concepts. However, (B) The cumulative effects that other concepts had on a given concept (indegree) did not significantly differ among the SESF components.

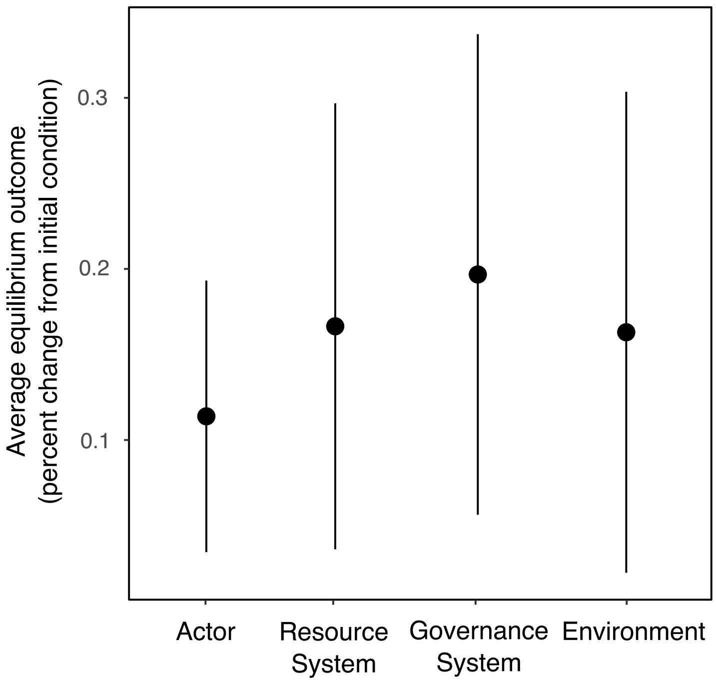

Figure 4.5. The larger representation of actor and resource system concepts and their influence on other concepts did not lead to significant differences in equilibrium outcomes among Social Ecological System Framework components. Average equilibrium outcomes were calculated as the average percent change of state variables within the four Social Ecological System Framework components at equilibrium from initial conditions. Equilibrium conditions were determined from adjacency matrices that iterated out the relationships described in fuzzy cognitive maps to an equilibrium state.

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General Conclusions and Summary

In the section that follows I discuss, in the context of the broader literature, how the results of my four chapters have met my goal of understanding prominent social-ecological interactions in inland recreational fisheries to inform practical local level management.

In Chapter 1 I improved understanding of social-ecological interactions in inland recreational fisheries by demonstrating that lakeshore development and stock enhancement are likely to interact to generate dependency of fisheries on stock enhancement. Ecosystem services can be viewed on a continuum of varying levels of natural and human capital required for co-production of a given ecosystem service (Palomo et al. 2016, Díaz et al. 2015). My results suggested that lakeshore development increases the reliance on human capital to provide recreational fishing opportunities. Trade-offs and synergies often occur from combinations of human and natural capital that affect the resilience, quantity, and quality of ecosystem service co-production (Palomo et al. 2016). Stock enhancement in inland recreational fisheries is often negatively framed (Lorenzen et al. 2012, Cooke and Cowx 2004, Post 2013) because of the potential for it to reduce resilience of fish populations to environmental conditions through loss of genetic diversity and inbreeding depression (Laikre et al. 2010, Fraser et al. 2011, van Poorten et al. 2011). On the other hand, stock enhancement can provide benefits too (Gerdeaux 2004, Hunt et al. 2017). These have often been overlooked, perhaps due to a historic focus on ecological dynamics in natural resource management (Holt and Talbot 1978), and to the fact that open access fishing effort homogenizes the quantity and quality of fishing opportunities in lake rich regions (Lorenzen 2008, Askey et al. 2013, Mee et al. 2016).

Understanding the interaction between lakeshore development and stock enhancement can inform inland recreational fisheries management by emphasizing increased management costs at high lakeshore development. The results of Chapter 1 demonstrated that stock enhancement can prevent the collapse of inland recreational fisheries with increased lakeshore development but that there is a trade-off of increased management costs associated with stock enhancement, which threatens the ability of managers to supply future fishing opportunities. Limited budgets exist for government managers particularly in lake rich regions (Lester et al. 2003), therefore, the ability to stock fish to meet the demand for catch benefits in some regions or through time might be inadequate. Reduced catch rates of walleye and limited ability to supply more through hatchery programs in our study region suggests that this is already occurring (Hansen et al. 2015). As I highlight in Chapter 1, one of the difficulties in managing increased management costs with higher lakeshore development is that revenue generated by lakeshore development (property tax) occurs at a different level of government (municipal) than the level that manages and pays for stock enhancement (state level). As state level management costs increase they may not be offset by state level revenue associated with angling. Therefore, reducing the role of human capital (stock enhancement) and increasing the role of natural capital (natural recruitment) in providing catch benefits is a desirable goal to maintain inland recreational fishing opportunities.

In Chapter 2 I improved understanding of social-ecological interactions in inland recreational fisheries by providing evidence against a widely-held hypothesis that littoral structure increases largemouth bass natural recruitment through reducing predation on young of year. Increasing natural recruitment of fish populations requires understanding where thresholds of critical variables like young of year mortality lie and avoiding behaviours that cross these thresholds (Folke 2016). The results of Chapter 2 provided useful but rare estimates of *in situ* young of year mortality along a littoral structure gradient and suggested that littoral structure may not be as strong or universal a control on open-water season young of year mortality as is often assumed.

The results of Chapter 2 identified how a better understanding of determinants of early life mortality can inform management of fish natural recruitment. Lorenzen (2008) suggested that increasing natural recruitment of fish populations through habitat improvement should be considered in replacement of stock enhancement. My results in Chapter 2 suggested that investing in littoral structure restoration or augmentation may not be an effective substitute for stock enhancement. Instead, a basic understanding of the determinants of open water season young of year mortality of freshwater fish species is necessary before reducing mortality can be used as an effective management tool. This includes testing if littoral structure reduces young of year mortality for other freshwater fish species that are hypothesized to use littoral structure as refuge (Tabor and Wurtsbaugh 1991, Eklöv 1997, Pratt and Fox 2001), characterizing effects of human development on the productivity of fish populations beyond lakeshore development and young of year mortality (Rice et al. 2015), and understanding the effect of climate change on recruitment success of freshwater species with varying thermal tolerances (Sharma et al. 2007, Hansen et al. 2016) in order to compensate for large scale changes at a local level (Carpenter et al. 2017).

In Chapter 3 I improved understanding of social-ecological interactions in inland recreational fisheries by considering the role of centralized and devolved institutional arrangements for managing stock enhancements and the social-ecological outcomes they generate. Berkes et al. (1989) and Ostrom (1990) demonstrated that a social-ecological perspective was necessary for understanding why resource collapses predicted under open access do not always occur. They demonstrated that communities often develop rules that negated open access; however, they concluded this will only occur if communities possess exclusion property rights. My research furthers their results by demonstrating that community held management rights alone (i.e. without the ability to limit access or withdrawal rights of others) can prevent resource collapse under open access. In Chapters 1 and 3 I demonstrated that although there is no effective limit on fishing capacity in inland recreational fisheries in North America (i.e. open access), investment in maintaining a fish stock through stock enhancement by formal and informal management groups is widespread because there are incentives (increased benefits to anglers) for both groups to invest. In Chapter 3 I found that lake associations in our study region stocked at approximately optimal rates, while government stocking rates were likely not maximizing angler net benefits.

The results of Chapter 3 can inform inland recreational fisheries management through improving stocking programs that efficiently maintain the benefits that inland recreational fisheries provide while limiting the costs of supplying fishing opportunities. I found that local organizations can effectively maintain harvest benefits at low fish population densities, while stocking by government is likely to maintain positive economic spillover effects of non-local anglers but can lead to higher effort on lakes and negative social welfare at low fish population densities. I provide a flexible and structured way of thinking about stock enhancement in recreational fisheries that can be applied by local organizations or government managers to guide stocking decisions that meet management objectives while minimizing the cost of management.

Stock enhancement decision making by formal and informal management groups can be further improved by considering increased ecological and angler behavioural complexity in future bio-economic models. The ontogenetic development of fish populations leads to a delay in stock enhancement payoff (Lorenzen 2005) and can create development bottlenecks due to density dependent competition for resources (Osenberg et al. 1992, Abrams 2009, Persson and de Roos 2013). These processes could change the optimal stock enhancement approach by formal and informal management groups. Developing stock enhancement models that can capture increased ecological complexity will help inform efficient species specific stock enhancement programs. Inland recreational fisheries are unique in that they represent multiple fisheries linked by mobile anglers that allocate their effort across the landscape (Parkinson et al. 2004, Hunt et al. 2011). Including fishery landscape dynamics of angler effort allocation in stock enhancement models could improve decision making of formal and informal management groups by attempting to allocate effort in a desirable way across the landscape (Askey et al. 2013) or by considering strategic behavior of neighboring lake associations (Sumaila 1995, Copeland 1990).

In my final chapter I moved beyond simply understanding social-ecological interactions to beginning to identify potential implementation gaps of a social-ecological approach to inland recreational fisheries management. For academic theory to have real-world impact it must be taken up and understood by stakeholders at the local scale. There have been calls for social-ecological research to produce practical results that have highlighted the importance of stakeholder understanding of sustainability problems for translating knowledge into action (Wiek et al. 2012, Miller et al. 2014). Taking a social-ecological approach to natural resource management requires a shared vision among stakeholders and social-ecological researchers (Biggs et al. 2011). In Chapter 4 I found that stakeholders in aggregate considered all components of social-ecological systems (defined by the Social Ecological Systems Framework) in their view of recreational fisheries but that they viewed actors and resource systems as more diverse and influential than governance systems and broader environmental settings. Given strong empirical evidence of positive relationships between the number and diversity of governance system attributes and successful fisheries outcomes, my results suggested that governance systems could play a larger role in local level management of inland recreational fisheries.

Governance systems could be improved in inland recreational fisheries by incorporating design principals or by identifying novel approaches to resource management. Wiek et al. (2012) recommended using design principals to generalize insights on sustainability solutions beyond case specific research. While I provided examples of how Ostrom's (1990) design principals could improve the role of governance systems in inland recreational fisheries management, another promising approach is identifying characteristics that define "bright spots" of local management. Bright spots are communities that manage social-ecological systems in a way that leads to more beneficial outcomes than expected (Bennett et al. 2016). This approach would allow for discovery of novel innovations developed by diverse institutions that could be shared with other local organizations once identified. Novel innovations can be identified through determining which lakes have better observed social-ecological fisheries outcomes than predicted based on known bio-physical predictors (see Frei et al. 2018). In-depth institutional analyses of local management groups like lake associations could then be conducted to determine which institutional arrangements predict above average social-ecological outcomes in inland recreational fisheries.

Summary

Using simulation, statistical, and semi qualitative models supported by field studies and empirical data I have advanced knowledge on social-ecological interactions in inland recreational fisheries with research that has direct implications for local level management of inland recreational fisheries and other shared natural resources. My research has demonstrated that lakeshore development and stock enhancement are likely to interact to generate dependency of fisheries on stock enhancement. This interaction can both prevent recreational fisheries collapses at higher lakeshore development and increase the vulnerability of recreational fisheries to funding limitations of state level management. While littoral structure restorations and improvements may not increase fish natural recruitment through providing refuge to young of year, transitioning stock enhancement from centralized government control to devolved management could maintain the benefits that recreational fisheries provide while limiting management costs. Translating academic knowledge on social-ecological interactions into action requires stakeholders share a similar understanding of recreational fisheries as social-ecological researchers. My research suggests that stakeholders do view their recreational fisheries as social-ecological systems but that they are likely to emphasize actors and resource systems more than governance systems and broader environmental settings. My results highlight the opportunity for governance systems that address large scale problems at a local scale to play a larger role in maintaining inland recreational fisheries and the benefits they provide.

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Appendices

Appendix A: Supplemental information for Chapter 1

Table A1. Mechanisms for increased walleye young of the year mortality with loss of coarse woody habitat.

Mechanism	Citation
Increased predation by largemouth bass	
i. YOY select cover for refuge	Pratt and Fox 2001
ii. YOY frequently preyed on by largemouth bass	Santucci and Wahl 1993, Fayram et al. 2005
iii. Observed negative relationships between largemouth bass densities and YOY densities	Inskip and Magnuson 1983, Nate at al. 2003
Increased time spent foraging in high risk areas	
i. Fish aggregate in CWH for refuge and forage within or near it to maximize survival	Walters and Juanes 1993, Scheuerell and Schindler 2004, Sass et al. 2006
ii. Reduced CWH increases competition within and near remaining CWH leading to more time spent by YOY foraging in areas with increased predation	Walters and Juanes 1993, Walters and Kitchell 2001
Suspended sediment can asphyxiate YOY	
i. Removal of CWH from riparian systems increases erosion and siltation of benthic habitats	Schindler and Scheuerell 2002, Jennings et al. 2003
ii. Suspended sediment leads to high YOY mortality	Cordone and Kelley 1961, Mion et al. 1998

YOY = young of the year walleye, CWH = coarse woody habitat

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Appendix B. Application of social-ecological diagnostic procedure to our study system

While other procedures for applying the social-ecological systems framework to a case study exist, Hinkel et al. (2015) was well suited for our application as it assists in analyzing and diagnosing potential interactions in social-ecological systems and considers provisioning action situations. We applied Hinkel et al. (2015) procedure using our knowledge of the social-ecological system, literature review, and empirical data.

What is the research question?

For our research question we consider recreational fisheries in Northern Wisconsin lakes and ask does lakeshore development interact with stocking and if it does what are potential implications for maintaining recreational fisheries with increased lakeshore development? This question reduces our focus to lake resource systems (RS) and their associated resource units (RU) of fish populations and littoral structure. It focuses the action situation of interest on provisioning.

Which actors (A) obtain which benefits from the social ecological system?

The A relevant to our research question include lakefront property owners and local and visiting anglers, which obtain benefits from lakes in the form of recreation. Activities of lakefront property owners often include swimming, boating, angling, and enjoying the aesthetics of the lake. Visiting and local anglers' activities also include angling and enjoying the aesthetics of the lake.

Which collective goods are involved in the generation of these benefits?

Different collective goods generate benefits for lakefront property owners and anglers. Locations used for swimming and boating by lake front property owners are usually characterized by low dead tree fall (coarse woody habitat) and macrophytes abundance. The aesthetics valued by lakefront property owners can vary. For example, some lakefront property owners value lawns and the ability to view the lake from their cabin or home. This leads to removal of riparian trees, which prevents coarse woody habitat entering the lake. Other lakeshore property owners prefer more naturalized and forested lakeshores, which leaves the riparian community intact. In general, however, macrophytes and coarse woody habitat (CWH) are often absent in develop lakes (Jennings et al. 2003, Francis and Schindler 2006, Hicks and Frost 2011), which speaks to the overall preference of lakefront property owners to remove these forms of littoral and riparian structure. Collective goods that generate angler (including lakefront property owners, locals, and visitors) benefits include catching fish and locations to fish that are aesthetically pleasing (i.e. not overly crowded or lacking in natural beauty). Empirical evidence from our study area indicates that angling pressure increases with lakeshore development (Appendix S5), which suggests that lakeshore development is not a deterrent for overall angling pressure.

Are any of the collective goods obtained subtractable?

Fish resource units are partially subtractable because both harvest and catch and release practices are used, while littoral structure in the form of coarse woody habitat (CWH) is highly subtractable. Rates of harvest and catch and release for walleye in our study region are 33% and 67% respectively (Gaeta et al. 2013). Here we focus only on the subtractable aspect of recreational fisheries (harvest) as this action directly affects our research question of maintaining recreational fisheries. Lakeshore development is a subtractive practice through the removal of littoral structure and riparian trees.

What are the biophysical and/or technological processes involved in the generation of the stock of RU?

The biophysical and technological processes that affect the generation of the focal resource unit stock (fish population) are natural recruitment and stocking of fish. A biophysical process affecting natural recruitment that is of particular interest for our research question is refuge for juvenile fish provided by CWH (Francis and Schindler 2006, Sass et al. 2006a, Sass et al. 2006b, Roth et al. 2007). Refuge affects recruitment success and stock rebuilding through reducing predation mortality on juveniles (Schindler et al. 2000, Walters and Kitchell 2001). Lakes can have other biophysical properties that determine their ability to support natural recruitment in our study region. For example, the ability of a lake to support walleye natural recruitment increases with lake surface area, lower water temperatures, shoreline complexity, and decreases with water conductivity (Hansen et al. 2015). Therefore, we controlled for these other variables as much as possible within our dataset to focus on the effect that lakeshore development might have on walleye natural recruitment. The technological process of fisheries enhancement also affects the fish stock through stocking of fish. Therefore, our resource system includes the processes of littoral structure removal, juvenile predation pressure, and stocking of hatchery reared fish.

How do the variables of RS and RU characterize the appropriation-related governance challenges?

Second tier RS/RU variables that characterize the challenges of governing appropriation of fish in our study region are the number of RS (this variable is not included in second tier variables listed in McGinnis and Ostrom 2014 but we feel it is an important consideration in our context) and the mobility of resource units. Because there are many lakes in our study area with discrete fish populations that are mobile, monitoring the state of all the stocks is difficult.

What kind of institutional arrangements have emerged as a response to the appropriation action situation governance challenge?

The institutional response to the appropriation action situation challenge is that a governmental organization (Wisconsin Department of Natural Resources) sets regulations that limit appropriation through bag limits, size limits, and seasonal fishing restrictions. They conduct stock assessments on lakes but it can be years before they revisit the same lake to reassess regulations. Therefore, prioritization, structured decision making, and extrapolation from other fish populations often determine regulations.

Which actors contribute to the provision, maintenance, or improvement of the RS and by what input?

The Wisconsin Department of Natural Resources (WDNR) contributes to the provisioning of the fish stock through stocking of fish. Stocking additions can be made in the form of small fingerlings, which contribute to future year classes but also experience high predation mortality (Santucci Jr. and Wahl 1993, Brooks et al. 2002, Kampa and Hatzenbeler 2009) or in the form of extended growth fingerlings when predation pressure is high, because they experience very little post stocking mortality (Santucci and Wahl 1993, Szendrey and Wahl 1996, Simonson 2010). The WDNR relies on a structured decision making process to set regulations and prioritize lakes for stocking (see Appendix S3).

How do variables of RS characterize the provisioning action situation related governance challenge?

This question is the focus of our study, specifically we are interested in how lakeshore development might interact with stocking through removal of littoral refuge that increases juvenile mortality, reduces natural recruitment, and subsequently leads to the need to stock a lake. Here the second tier RU variable economic value presents a governance challenge as stocking can be expensive, especially for extended growth fingerlings that require more energy to rear but are less prone to predation.

What kind of institutional arrangements have emerged as a response to the provisioning action situation governance challenge?

Changes in funding structures that allow for stocking to persist despite increased costs with lakeshore development have emerged in our study region (see Discussion paragraph two).

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Appendix C. Model formulation

We based our model structure on van Poorten et al. (2011), with three notable modifications that allowed us to accurately model stocking in our study area and consider the interaction between stocking and lakeshore development:

We incorporated a habitat sub-model that reduced coarse woody habitat as a function of lakeshore development and young of the year survival as a function of coarse woody habitat. We did this following the methods of Roth et al. (2007).

2. We altered the stocking decision process of van Poorten et al. (2011) to reflect the structured decision making process used by the Wisconsin Department of Natural Resources (WDNR) to determine stocking. Natural recruitment and adult densities are the two main considerations of the WDNR when prioritizing stocking in Wisconsin. Typically, stock assessments of walleye natural recruitment and adult densities occur every five years in our study area. This information is then used to reassess and set regulations for walleye stocking in a lake (WDNR 2014).

The structured decision making process is as follows:

First, lakes that have adequate natural recruitment to support a walleye population and fishery are not stocked. A definition of adequate natural recruitment based on expert opinion in our study area is a catch per unit effort >6.2 YOY walleye per km of shoreline (Hansen et al. 2015) or a density of approximately 8 YOY per hectare (i.e. the mid point of the range listed in Hansen et al. 2004). Second, lakes with declining adult walleye densities have high priority for stocking. Third, the likelihood that a lake can support natural recruitment, determined by physio chemical characteristics like lake surface area, water temperature degree-days, shoreline development factor, and conductivity, increases a lake's priority for stocking. We consider lakes in our model that have uniform surface area, latitude, perimeter, and conductivity, thus all lakes have the same priority for stocking under this third consideration. Fourth, stakeholder input from businesses owners and state and tribal anglers is taken into consideration. This fourth consideration influences stocking to a lesser degree than the above considerations, therefore, we have ignored this consideration in our model.

To reflect the structured decision making process outlined above we simulated walleye populations at an annual time scale and stock assessments at a five-year time scale. Stock assessments of YOY and adult densities determined the size and abundance of fish stocked to the population for the following five-year interval. New information on adult and YOY densities after each stock assessment were then used to reassess stocking. We ran the model until dynamic equilibrium was reached. We used 8 YOY per hectare as our indication of loss of natural recruitment. If YOY dropped below this cutoff, stocking additions were initially made as walleye fingerlings to the YOY age class until YOY mortality due to lack of CWH resulted in very low YOY densities (defined here as <2 YOY per hectare). Fingerlings are a commonly stocked size class that contribute to future year classes but also experience high predation mortality (Santucci Jr. and Wahl 1993, Brooks et al. 2002, Kampa and Hatzenbeler 2009). WDNR regional biologists use extended growth fingerlings when post-stocking predation mortality is high (Simonson 2010), therefore, when YOY densities fell below 2 per hectare, extended growth fingerlings, which experience very minimal post stocking and predation mortality, were stocked to the juvenile age class (Santucci and Wahl 1993, Szendrey and Wahl 1996). The number of fish stocked was determined by the change in adult densities relative to the density at the last stock assessment (i.e. five years previous) and the stocking responsiveness of management, which was specific for fingerlings and extended growth fingerlings and parameterized to our study system (see Appendix S4).

3. We increased harvest rates of the adult population as a function of increased LD density (equation S1.14). This assumption was supported by analysis of angling effort and LD in 16 Vilas County lakes (see Appendix S5). Modeled increases in harvest rates with LD (0.05 - 0.35) corresponded to levels observed in Wisconsin, with 0.35 representing the target maximum harvest set by the Wisconsin Department of Natural Resources (Cichosz 2012).

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Appendix D. Model parameters and equations

We modeled stocking based on the structured decision making process used by Wisconsin Department of Natural Resources (see Appendix C) and walleye dynamics based on a stage-structured fish population using the methods of van Poorten et al. (2011) described in equations D1-14. We used parameters relevant to walleye in our stage structured fish population because walleye is a socially and economically important fish species in our study region of Vilas County Wisconsin, USA. A steepness value for walleye was used to estimate a compensation ratio described (Table D1). We chose an unfished spawner density that reflected the higher end of walleye densities in Wisconsin (Beard et al. 1997) and adult survival, juvenile survival, and maturation rates reflective of an unfished walleye population (Kocovsky and Carline 2001).

Because management practices and responsiveness place constraints on the amount of stocking that can occur, we calibrated our social-ecological model to a realistic range of walleye stocking densities in our study region using separate estimates of d for fingerlings and extended growth fingerlings (Fig. D1). Stocking densities predicted by our social-ecological model when d = 9 and 0.1 for fingerlings and extended growth fingerlings, respectively, fell within the 95% confidence interval of predicted size dependent stocking densities of a regression model that explained 60% of the variation in walleye stocking densities in 102 Vilas County lakes. The regression model predicted walleye stocking densities based on length of walleye stocked and controlled for multiple stocking events in lakes by including lake as a blocking factor (i.e. ln stocked walleye $ha^{-1}{}_{\text{Lake } L} \sim \beta_L + \beta_1 \times$length of walleye $\text{stocked}_L + \varepsilon$; $\beta_1 = -0.02$ $p < 0.0001$, $R^2 = 0.60$).

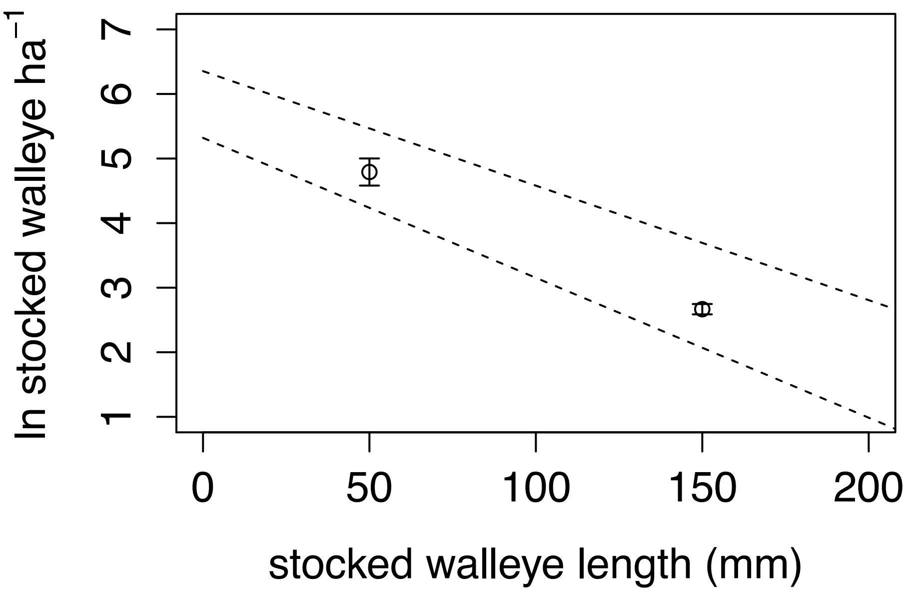

Fig. D1. Calibration of d used in social-ecological model. Circles with error bars represent mean and 95% confidence intervals of walleye fingerling (50mm) and extended growth fingerling (150mm) stocking densities predicted by our social-ecological model when d = 9 and 0.1 for fingerlings and extended growth fingerlings respectively. These stocking densities fall within the 95% confidence interval (dotted lines) of a regression model that explained 60% of the variation in walleye stocking densities in 102 Vilas County lakes using length of walleye stocked as a predictor variable and controlled for multiple stocking events in lakes by including lake as a blocking factor (i.e. ln stocked walleye $\text{ha}^{-1}{}_{\text{Lake } L} \sim \beta_L + \beta_1 \times$length of walleye stocked$_L + \varepsilon$; $\beta_1 = -0.02$ $p < 0.0001$, $R^2 = 0.60$).

Stocking determined in a stock assessment year (every 5 years)

$$A_t = z_{1,t} + z_{2,t}$$
$$U_t = A_t \square A_{t=i} \tag{D1}$$

$$S_{Fin,t+1} = \max\left(0, S_{Fin,t} - d_{Fin} U_t\right) \tag{D2}$$

$$S_{EG,t+1} = \max\left(0, S_{EG,t} - d_{EG} U_t\right) \tag{D3}$$

Stocking in a non-stock assessment year

$$S_{Fin,t+1} = S_{Fin,t=i} \tag{D4}$$

$$S_{EG,t+1} = S_{EG,t=i} \tag{D5}$$

Early young of the year

$$\begin{aligned} j_{1,t+1} &= (1-c)z_1\alpha e^{-\beta(z_1+rz_2)} \\ j_{2,t+1} &= (cz_1+rz_2)\alpha e^{-\beta(z_1+rz_2)} \end{aligned} \tag{D6}$$

Late young of the year

$$x_{1,t+1}\begin{cases} \dfrac{refuged \cdot r_0\left[j_{1,t}\right]}{1+k\left[j_{1,t}+j_{2,t}\right]} & \left(\left[x_{1,t=i}+x_{2,t=i}\right]>8\right) \\ \dfrac{refuged \cdot r_0\left[j_{1,t}\right]}{1+k\left[j_{1,t}+j_{2,t}+uS_{Fin,t}\right]} & \left(8 \geq \left[x_{1,t=i}+x_{2,t=i}\right]>2\right) \\ \dfrac{refuged \cdot r_0\left[j_{1,t}\right]}{1+k\left[j_{1,t}+j_{2,t}\right]} & \left(\left[x_{1,t=i}+x_{2,t=i}\right]\leq 2\right) \end{cases} \tag{D7}$$

$$x_{2,t+1}\begin{cases} \dfrac{refuged \cdot r_0\left[j_{2,t}\right]}{1+k\left[j_{1,t}+j_{2,t}\right]} & \left(\left[x_{1,t=i}+x_{2,t=i}\right]>8\right) \\ \dfrac{refuged \cdot r_0 s_3\left[j_{2,t}+uS_{Fin,t}\right]}{1+k\left[j_{1,t}+j_{2,t}+uS_{Fin,t}\right]} & \left(8 \geq \left[x_{1,t=i}+x_{2,t=i}\right]>2\right) \\ \dfrac{refuged \cdot r_0\left[j_{2,t}\right]}{1+k\left[j_{1,t}+j_{2,t}\right]} & \left(\left[x_{1,t=i}+x_{2,t=i}\right]\leq 2\right) \end{cases} \tag{D8}$$

Juveniles

$$y_{1,t+1}\begin{cases} s_1\left[x_{1,t}+(1-\mu)y_{1,t}\right] & \left(\left[x_{1,t=i}+x_{2,t=i}\right]>8\right) \\ s_1\left[x_{1,t}+(1-\mu)y_{1,t}\right] & \left(8\geq\left[x_{1,t=i}+x_{2,t=i}\right]>2\right) \\ \dfrac{s_1\left[x_{1,t}+(1-\mu)y_{1,t}\right]}{1+k\left[y_{1,t}+y_{2,t}+uS_{EG,t}\right]} & \left(\left[x_{1,t=i}+x_{2,t=i}\right]\leq 2\right) \end{cases} \tag{D9}$$

$$y_{2,t+1}\begin{cases} s_4 s_1\left[x_{2,t}+(1-\mu)y_{2,t}\right] & \left(\left[x_{1,t=i}+x_{2,t=i}\right]>8\right) \\ s_4 s_1\left[x_{2,t}+(1-\mu)y_{2,t}\right] & \left(8\geq\left[x_{1,t=i}+x_{2,t=i}\right]>2\right) \\ \dfrac{s_4 s_1\left[x_{2,t}+(1-\mu)y_{2,t}+uS_{EG,t}\right]}{1+k\left[y_{1,t}+y_{2,t}+uS_{EG,t}\right]} & \left(\left[x_{1,t=i}+x_{2,t=i}\right]\leq 2\right) \end{cases} \tag{D10}$$

Adults

$$\begin{aligned} z_{1,t+1} &= s_2\left[\mu\cdot y_{1,t}+\left(1-h\right)z_{1,t}\right] \\ z_{2,t+1} &= s_5 s_2\left[\mu\cdot y_{2,t}+\left(1-h\right)z_{2,t}\right] \end{aligned} \tag{D11}$$

Coarse woody habitat

$$CWH_{development}=b\cdot\exp^{e\cdot development} \tag{D12}$$

Refuge provided by coarse woody habitat

$$refuged=\frac{CWH^2}{\left(a^2+CWH^2\right)} \tag{D13}$$

Harvest

$$h_{development}=0.05+0.007\times development \tag{D14}$$

where,

t = current time step,

i = the time step of the previous stock assessment,

subscript 1 = wild stock,

subscript 2 = hatchery derived stock,

Fin = fingerlings

EG = extended growth fingerlings

$$\alpha = \kappa \frac{R_0}{S_0},$$

$$\beta = \frac{\ln\left(\alpha \frac{S_0}{R_0}\right)}{S_0},$$

and

$$k = \frac{\left(r_0 \frac{R_0}{j_0} - 1\right)}{R_0}$$

Table D1 Social-ecological model parameters. CWH = coarse woody habitat.

Term	Explanation	Value	Unit
st	Steepness	0.67*	Recruits/spawner
κ	Compensation ratio	9.5	
S_0	Equilibrium spawner density in an unexploited population	30	fish ha^{-1}

R_0	Equilibrium recruit abundance in an unexploited population	1,250	fish ha^{-1}
μ	Maturation rate	0.33	y^{-1}
r	Relative recruitment success for hatchery fish	0.9	
Juvenile survival			
u	Immediate survival for stocked fish	0.9	
j_0	Equilibrium young of the year abundance at the end of the first year in an unexploited population	125	Fish
s1	Constant survival of wild juveniles	0.36	y^{-1}
s3	Relative density-dependent survival of young of the year to juveniles	0.9	
s4	Relative survival of extended growth fingerlings	0.9	
Adult survival			
s2	Constant survival of wild adults	0.625	y^{-1}
s5	Relative survival of hatchery adults	0.9	
Harvest			
Development	Number of shoreline buildings	0-50	buildings km^{-1} shoreline
Stocking decisions			

A	Total adult density	NA	fish ha^{-1}
U	Discrepancy in adult density from previous stock assessment	NA	fish ha^{-1}
S	Stocking addition	NA	fish ha^{-1}
d_{Fin}**	Fingerling stocking response as a multiple of the change in adult density	9	Fish ha^{-1}
d_{EG}**	Extended growth fingerling stocking response as a multiple of the change in adult density	0.1	Fish ha^{-1}
Coarse woody habitat and refuge			
a	CWH at which hiding is ½ max	120	logs km shoreline^{-1}
b	CWH density in an undeveloped lake	812	logs km shoreline^{-1}
e	Exponential coefficient of CWH loss with shoreline development	-0.2	logs km shoreline^{-1} building^{-1}

*Following the methods of van Poorten et al. (2011) we used this estimate of steepness that was then converted to a compensation ratio for walleye, see (Myers et al., 1999)
**Calibrated from stocking densities of walleye in Wisconsin, see above text in Appendix S4. EG = extended growth

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Appendix E. Relationship between angling effort and lakeshore development in Vilas County

We used empirical data to determine how angling effort in Vilas County lakes varied as a function of lakeshore development to inform input into our social-ecological model. We estimated angler effort as a function of lakeshore development using creel surveys conducted by the Wisconsin Department of Natural Resources on 16 of the lakes in our dataset. Creel survey estimates of angler effort included but did not differentiate between resident and non-resident anglers. Our goal was not to imply a causal relationship between lakeshore development and effort, given that many anglers might be non-residents, but instead to make use of the phenomenological pattern observed. Angler effort (angler hours) was standardized to lake surface area (hectares). The effect of lakeshore development density on angler effort lake^{-1} area was linear and significantly positive (slope estimate with 95% confidence interval 7.11±5.7, R^2=0.31).

Appendix F. Calculation of property tax based on property valuations

We calculated average property tax for a lakefront house in 2004 in Vilas County using Equation F1. We based this equation on the criteria used to calculate property taxes in Vilas County Wisconsin. Where, P is the calculated average property tax in 2004 ($1,580 USD), A is the assessed property value for a property sold in year i, R is the assessed renovation value for that property in year i, T is the total number of lakefront properties sold between 1997 and 2004 (A, T, and R were obtained from Residential Lakeshore Property Sales in Vilas County 1997 – 2004, North Temperate Lakes Long Term Ecological Research program (http://lter.limnology.wisc.edu), NSF, Robert Provencher, Center for Limnology, University of Wisconsin-Madison), 0.0101 is the 1.01% property tax rate in Vilas County Wisconsin, IR is the cumulative inflation rate from year i to 2004.

$$P = \frac{\sum_{t=1}^{T}\left[\left(A_i + R_i\right) IR_i \times 0.0101\right]}{T}$$ Equation F1

The argument could be made that property value should decrease with increased lakeshore development due to limitation of property frontage. Therefore, a decreasing function of property tax revenue with lakeshore development would model lake level property tax revenue better than an average. However, we found no effect of lakeshore development on property value within our data (slope and 95% confidence interval = -830 ± 1685), therefore, an average value was used.

Appendix G. Cost estimates for fingerling and extended growth fingerlings

We determined the average cost of rearing and stocking fingerlings and extended growth fingerlings from the Wisconsin Legislative Audit Bureau summary of fish stocking activities in Wisconsin (WLAB 1997). We used \$0.07 USD fish^{-1} for our fingerling cost estimate and \$2.74 USD fish^{-1} for our extended growth fingerling cost estimate, which was an average of large and extended growth fingerling cost estimates as these two terms were used interchangeably to refer to the size range that we defined in our manuscript as extended growth fingerlings of walleye (~150mm).

References

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Appendix H. Sensitivity analysis of model results

We assessed the sensitivity of our social-ecological model to parameter values by calculating model results with a 10% increase and decrease in each parameter value while all other values were held at baseline values (Fig. H1 and H2). Parameters varied included κ, S_0, R_0, μ, r, u, j_0, s1, s2, s3, s4, s5, $d_{Fingerlings}$, $d_{EG\ Fingerlings}$, sales tax generated per fish harvested, annual property tax for an average lake front building in Wisconsin, and cost of raising and stocking a walleye fingerling and extended growth fingerling. Changes in model parameter values led to little change in our model results of walleye densities and government costs and revenues (Fig. H1 and H2).

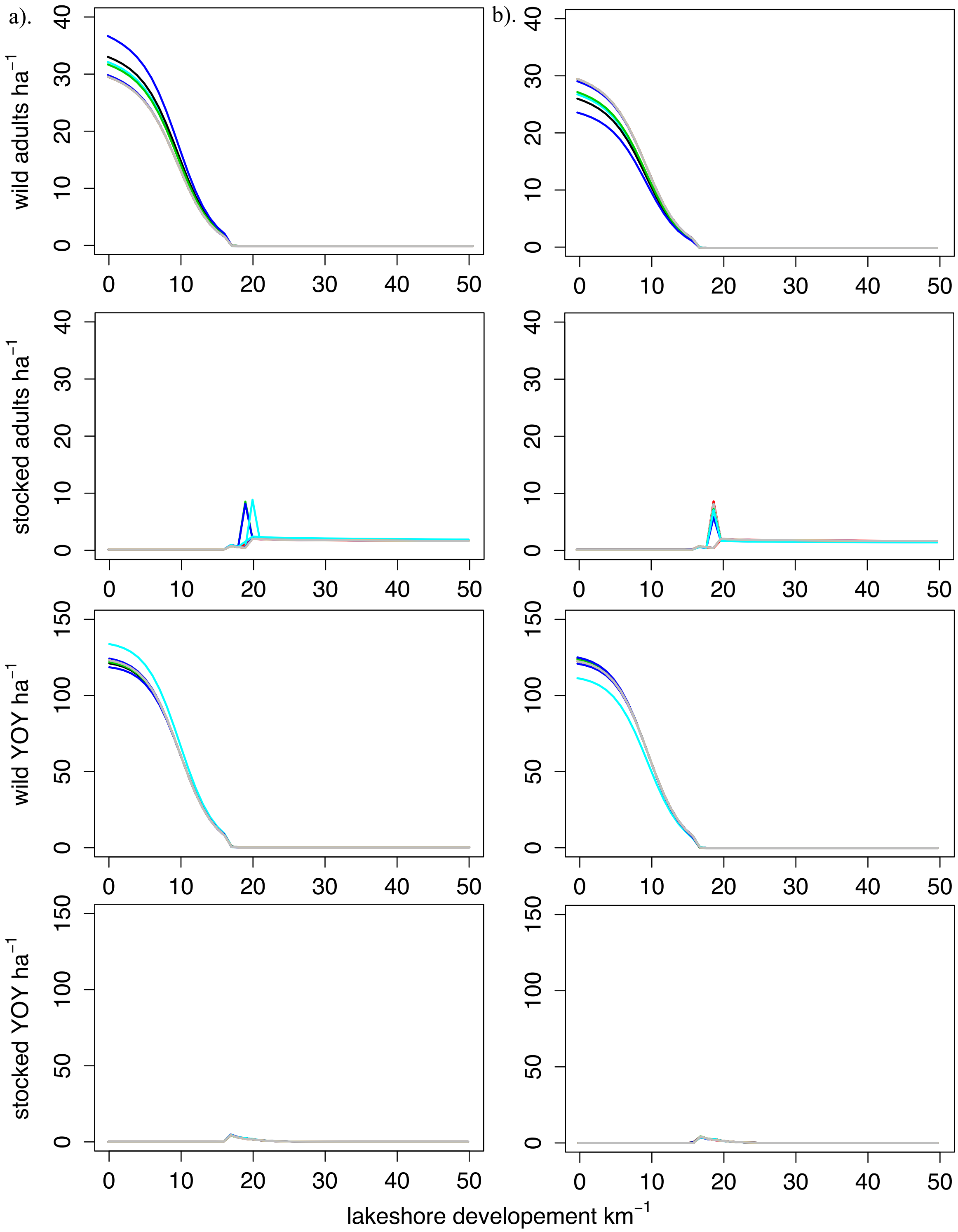

Figure H1. Sensitivity of walleye density model results to a). a ten percent increase and b). a ten percent decrease in each model parameter. Colored lines represent results after each parameter was varied and included κ, S_0, R_0, μ, r, u, j_0, s1, s2, s3, s4, s5, $d_{Fingerlings}$, $d_{EG\ Fingerlings}$, sales tax generated per fish harvested, annual property tax for an average lake front building in Wisconsin, and cost of raising and stocking a walleye fingerling and extended growth fingerling. Results presented in manuscript are also plotted in black (mostly covered by colored lines).

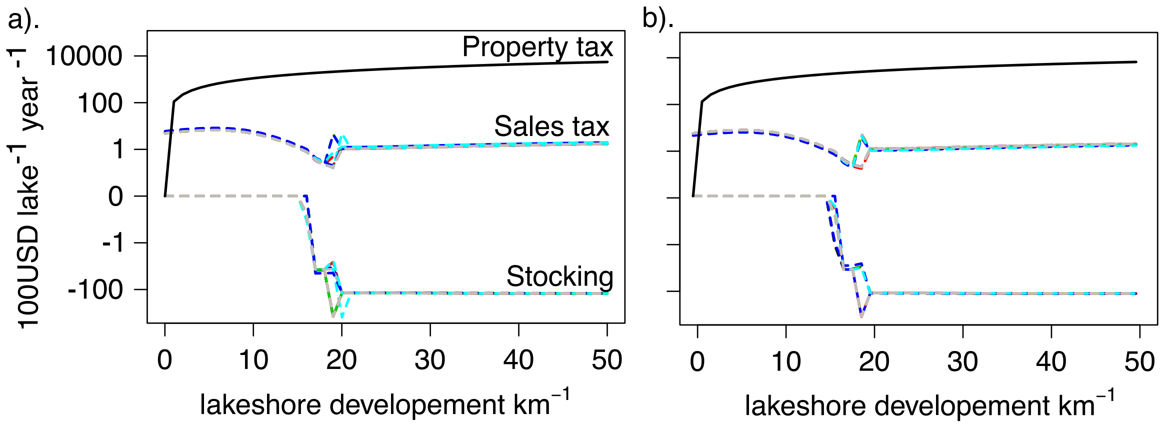

Figure H2. Sensitivity of government costs and revenues to a). a ten percent increase and b). a ten percent decrease in model parameters. Colored lines represent results after each parameter was varied. Parameters varied included κ, $S_{0,}$ $R_{0,}$ μ, r, u, $j_{0,}$ s1, s2, s3, s4, s5, $d_{Fingerlings}$, $d_{EG\ Fingerlings}$, sales tax generated per fish harvested, annual property tax for an average lake front building in Wisconsin, and cost of raising and stocking a walleye fingerling and extended growth fingerling. Results presented in manuscript are also plotted in black (mostly covered by colored lines).

Appendix I. Predation pressure and young of year mortality in our study lakes

We wanted to test our underlying assumption that predation was regulating YOY mortality in our lakes and were able to estimate predator densities in eight of our thirteen study lakes from boat electrofishing surveys conducted previously by the North Temperate Lakes Long-Term Ecological Research network (https://lter.limnology.wisc.edu/data) and Koizumi et al. (2018). In two of the eight lakes boat electrofishing surveys were conducted twice in the spring and twice in the fall from 2011 to 2016 and biomass caught per unit of effort for all species in did not vary significantly over the five years or by spring or fall sampling. In the remaining six lakes surveys from the North Temperate Lakes Long-Term Ecological Research database were conducted once per lake in July and August between 2002 and 2004. Ideally, we would have multiple survey dates from these lakes closer in time to our current study (2016-2017), therefore, we caution readers that predator densities in these lakes may have changed. We assume that catchability did not vary greatly among lakes so that catch per unit effort is an accurate measure of relative abundance among lakes. To standardize between the two datasets, we used predator biomass per meter of shoreline as a combined metric of predation pressure in each lake and we calculated it by summing the wet weight of all individuals of species caught for which we had direct diet or visual evidence of predation on YOY largemouth bass in our lakes (yellow perch, bluegill, pumpkinseed, rock bass, smallmouth, and largemouth bass). Not all fish from the North Temperate Lakes Long-Term Ecological Research database were weighed and in these instances, we used length weight relationships specific for each species and lake to determine wet weight from length.

In the 8 lakes where we knew predator densities, which spanned a large coarse woody habitat gradient (3 – 830 pieces of wood per km of shoreline), YOY mortality was positively related to predator biomass but unrelated to coarse woody habitat (Fig. I1). Predator biomass explained 60 and 83% of the variation in mortality in unweighted and weighted least squares regressions (Fig. I1A). Coarse woody habitat density did not explain residual variation in YOY mortality once the effect of predator biomass was controlled for (Fig. I1C).

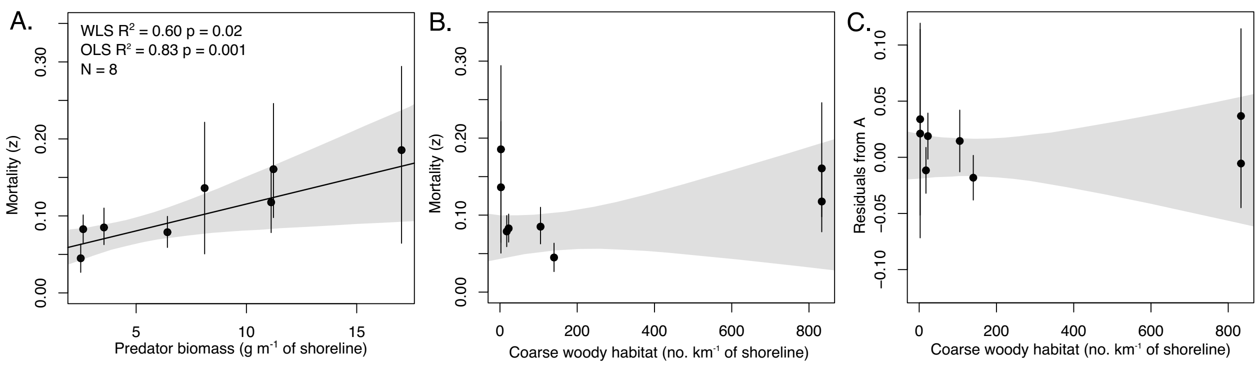

Figure I1. Young of year (YOY) largemouth bass mortality in the eight lakes where we knew predator densities was positively related to predator biomass (A). Neither YOY mortality, nor the residual variation from the mortality-predator relationship in panel A, were significantly related to the density of coarse woody habitat (B and C). Vertical lines represent 95% confidence intervals for mortality estimates (z parameter in Equation 2). The shaded area is the 95% confidence interval from a weighted least squares (WLS) regression. Results from ordinary least squares (OLS) and WLS regression are displayed for A but not for B and C, where p values were greater than 0.30.

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Appendix J. Young of year counts with day of sampling

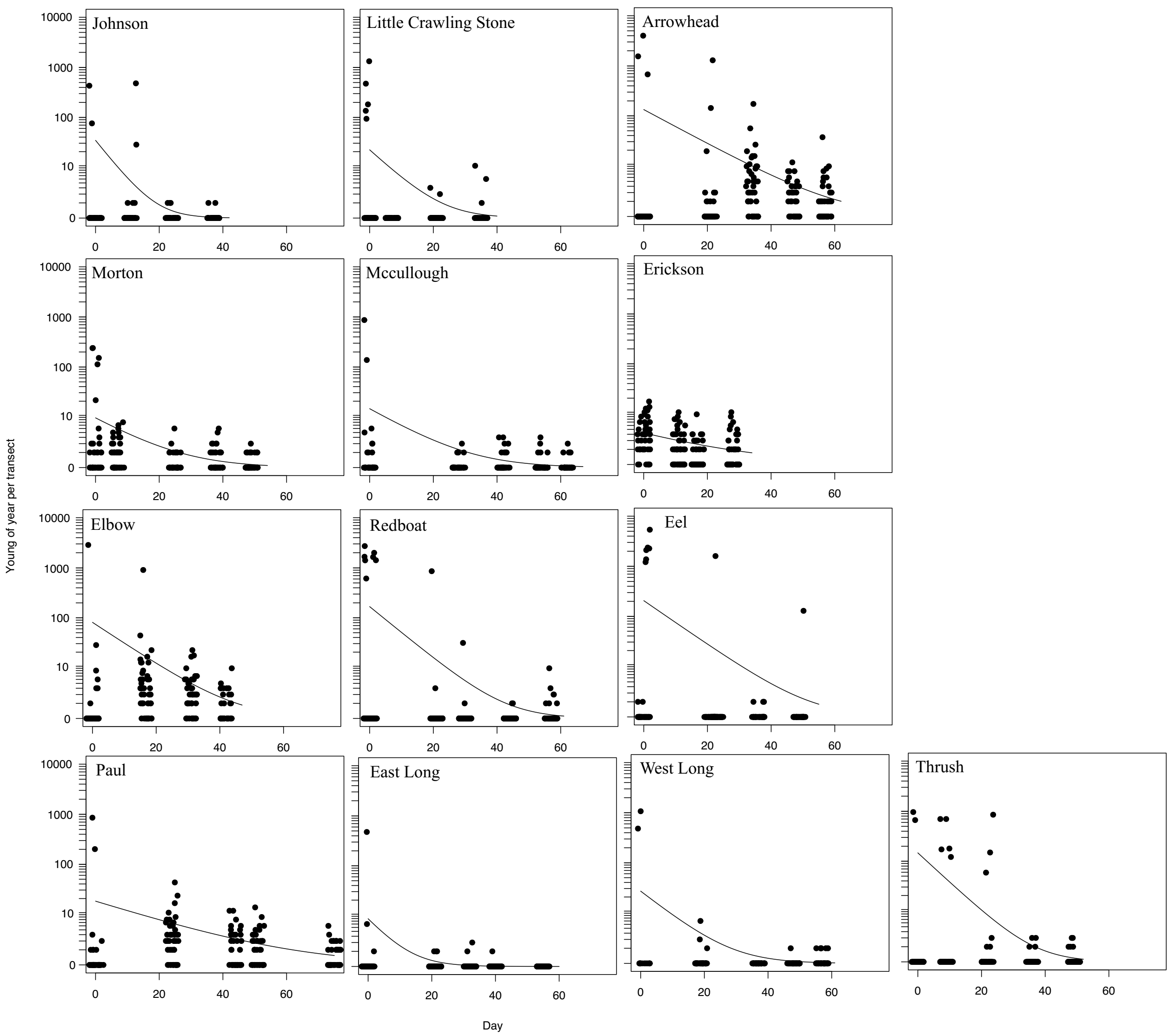


Figure J1. Young of year (YOY) largemouth bass counts per 10m transect line over study period for all 13 lakes. Individual points represent total number of YOY present on a 10m transect line and are jittered along the x-axis to prevent over plotting. Solid lines show the fit of the model used to estimate YOY mortality (a negative exponential model with negative binomial errors Table 2.1). Note that the y-axes are in logarithmic scale.

Appendix K. Young of year behavioural responses to divers and effects of fish length on results

Neither behavioural responses of YOY to divers nor increased YOY length over time were likely to have biased our results. Young of year typically exhibited indifference (did not swim away from nor toward divers) or curiosity (swam towards divers) at first detection of divers and there were no notable changes in these behaviours throughout the study period. The size of fish varied significantly with day of year and because lakes were not sampled on the same day we compare fish size among lakes using the slope of mean size of YOY on date (Fig. K4 and Fig. K5). Lakes differed significantly in their slope of mean size of YOY on date (Fig. K3, we note that this is not equal to growth rate as we did not look at individual fish growth over time) but there was no relationship between the slope of mean size of YOY on date and YOY mortality (Fig. K4A). Within lakes, we did not see a significant effect of transect level coarse woody habitat on YOY size (effect of coarse woody habitat on size = -4.02 p-value > 0.6). Among lakes, coarse woody habitat at the lake level was unrelated to the slope of mean size of YOY on date (Fig. K4B).

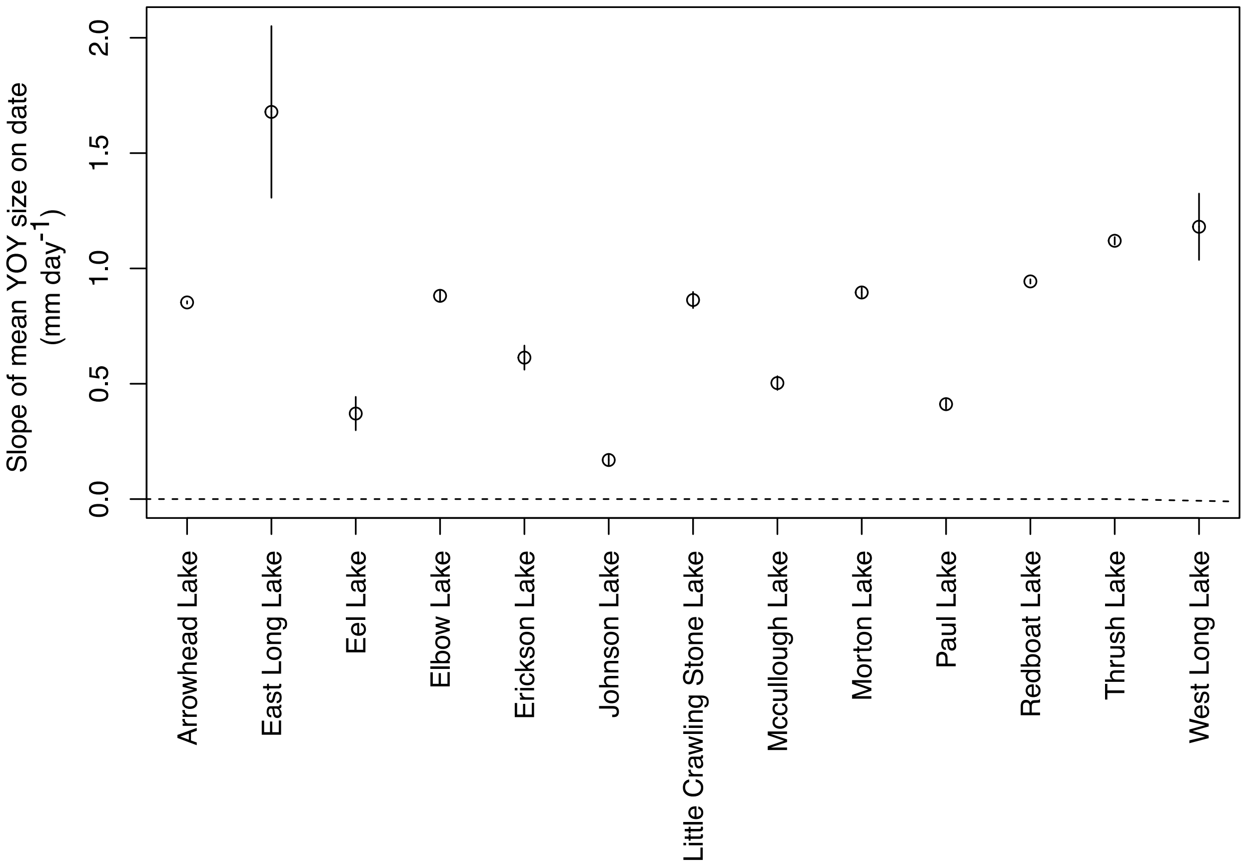


Figure K3. The effect of day of year (DOY) on observed young of year (YOY) fish length varied among our 13 study lakes. Results are from an ordinary least squares regression model with lake as a blocking factor. Vertical lines represent 95% confidence intervals.

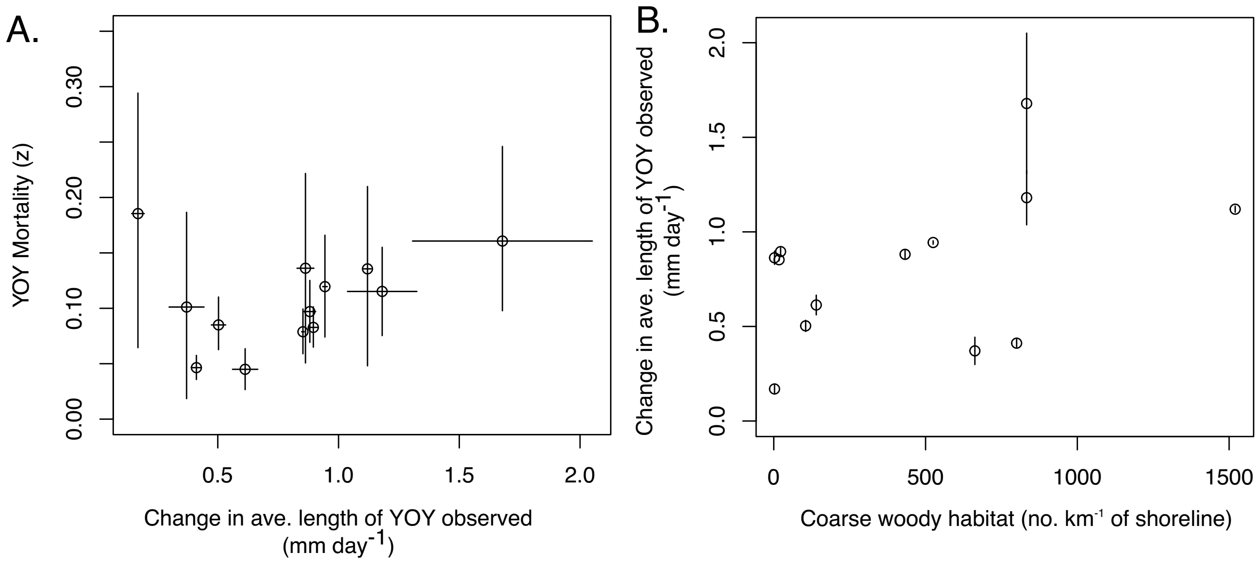
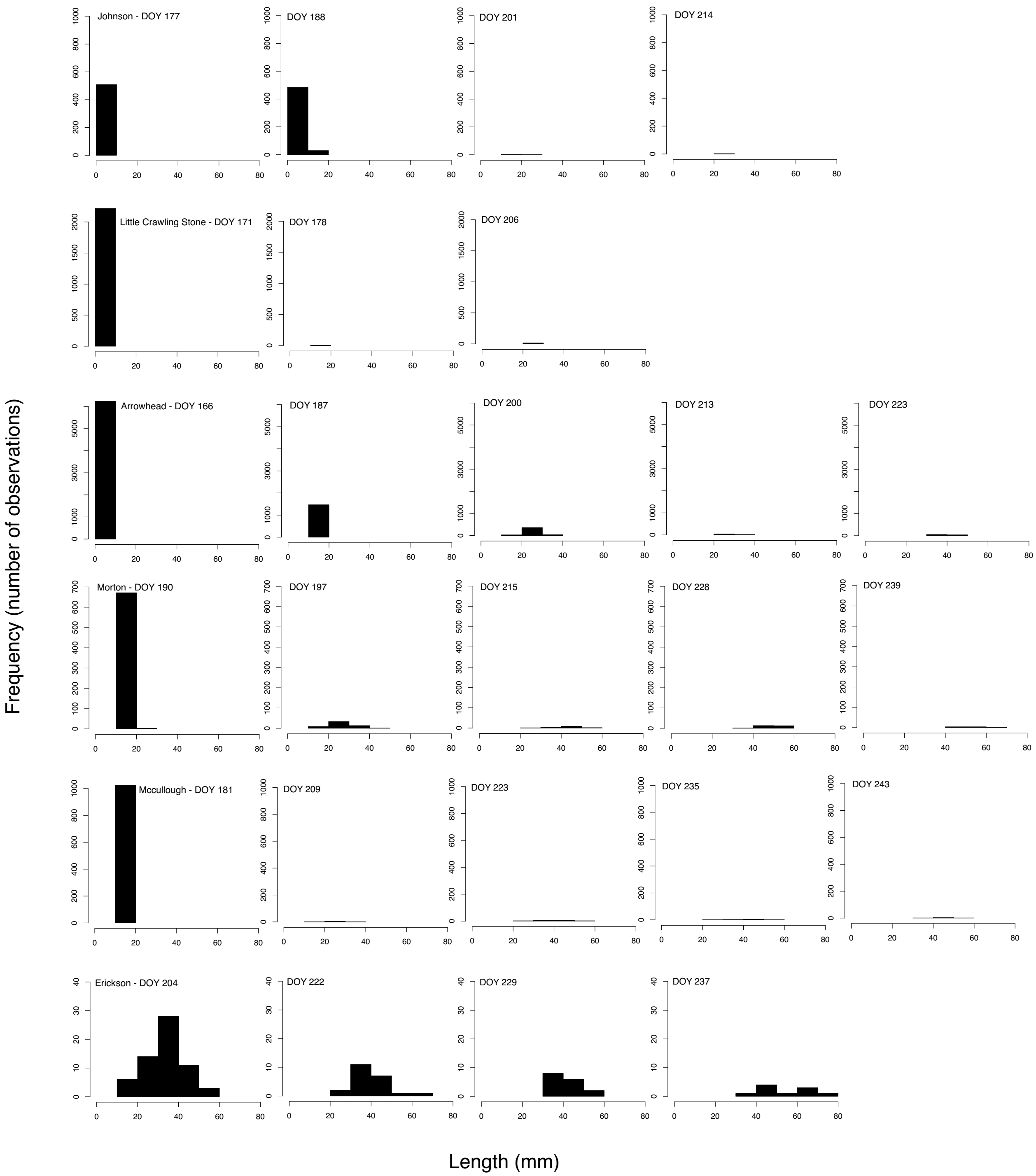


Figure K4. The slope of mean size of young of year (YOY) on date was unrelated to YOY mortality (A) and coarse woody habitat (B) in our 13 study lakes (both p values > 0.05)

Appendix L. Young of year length frequencies with day of year



(Figure continued on next page)

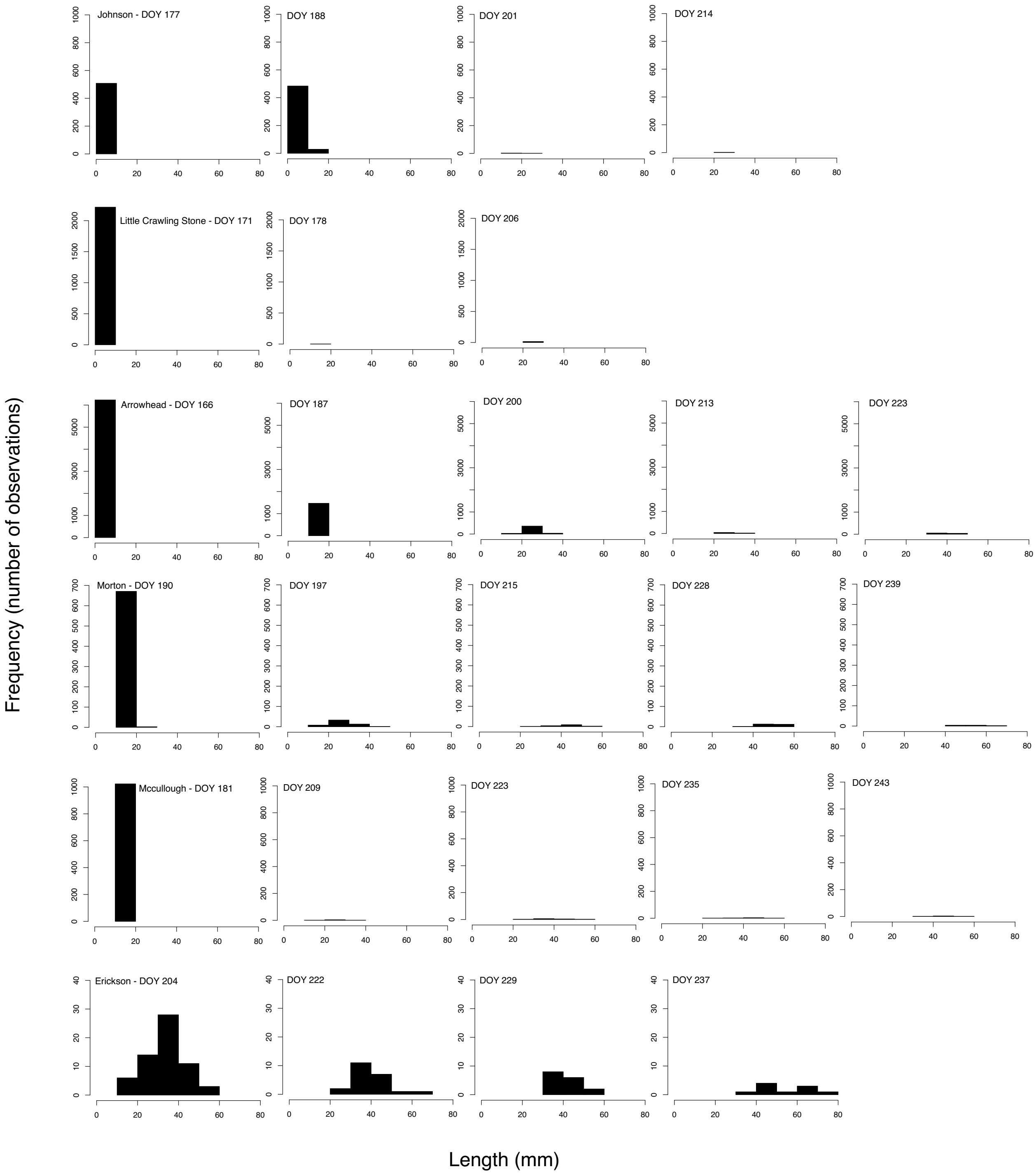


Figure L5. Length frequencies for each sampling day of year (DOY) when young of year (YOY) were observed in the 13 study lakes. Lengths were estimated visually by divers into 10mm categories (0-10mm, 10-20mm, 20-30mm, etc.). Estimates were validated by capturing individuals with dip nets to confirm sizes.

Appendix M.

Table M1. Models predicting young of year largemouth bass mortality in 13 lakes (*l*). WLS = weighted least squares regression, we weighted mortality estimates by the inverse of their squared standard errors. OLS = ordinary least squares regression. See Table 2.2 for details on principal component scores (PC Sores).

		WLS			***OLS***		
	Model	**R^2**	**P-value, Effect**	**AICc**	**R^2**	**P-value, Effect**	**AICc**
1.	$z_l \sim \beta_0 + \beta_{P1} \cdot PC1Score_l$	0.11	$\beta_{P1} = 0.26$, -0.008	-38.8	0.01	β_{P1} 0.76, 0.03	-38.4
2.	$z_l \sim \beta_0 + \beta_C \cdot CWH_l$	0.03	β_C 0.54, -0.00001	-37.7	0.02	β_C 0.62, 0.00001	-38.6
3.	$z_l \sim \beta_0 + \beta_{P2} \cdot PC2Score_l$	0.03	β_{P2} 0.59, 0.006	-37.6	0.01	β_{P2} 0.30, 0.013	-39.7
4.	$z_l \sim \beta_0 + \beta_{P1} \cdot PC1Score_l + \beta_3 \cdot PC2Score_l$	0.21	β_{P1} 0.16, -0.011 β_{P2} 0.30, 0.012	-35.9	0.11	β_{P1} 0.76, 0.003 β_{P2} 0.32, 0.013	-35.5
5.	$z_l \sim \beta_0 + \beta_{P1} \cdot PC1Score_l + \beta_{P2} \cdot PC2Score_l + \beta_{P1P2} \cdot PC1Score_l \cdot PC2Score_l$	0.24	β_{P1} 0.15, -0.013 β_{P2} 0.50, 0.009 β_{P1P2} 0.57, -0.007	-30.8	0.18	β_{P1} 0.71, -0.005 β_{P2} 0.33, 0.013 β_{P1P2} 0.40, -0.011	-31.0

Appendix N. Optimal control theory solution for optimal stocking

Objective functions

We are looking to maximize the objective functions below using a dynamic stocking rate over time. The functions describe the present value of net harvest benefits considered by a government manager and a lake association. Taking the integral of net benefits over time sums the net benefits at each *t*, with future net benefits discounted by the term $e^{-\rho t}$.

Government objective function:

$$max_{with\ respect\ to\ S} \int_0^\infty e^{-\rho t}\{p_{RES}qE_{RES}X - c_{RES}E_{RES} + p_{ROV}qE_{ROV}X - c_{ROV}E_{ROV} - c_S S^2\}\, dt$$

Lake association objective function:

$$max_{with\ respect\ to\ S} \int_0^\infty e^{-\rho t}\{p_{RES}qE_{RES}X - c_{RES}E_{RES} - c_S S^2\}\, dt$$

State Equations

$$\dot{X} = rX - bX^2 - qEX + S \qquad \text{N1}$$

$$\dot{E}_{RES} = \delta E_{RES}[p_{RES}qX - c_{RES}] \qquad \text{N2}$$

$$\dot{E}_{ROV} = \delta E_{ROV}[p_{ROV}qX - c_{ROV}] \qquad \text{N3}$$

where,
r = intrinsic growth rate,
k = carrying capacity,
$b = \frac{r}{k}$
q = catchability coefficient (proportion of the fish stock removed with one unit of effort)
E_{RES} = resident fishing effort
E_{ROV} = roving fishing effort
$E = E_{ROV} + E_{RES}$
δ = the sluggishness of fishing effort in response to average net benefits of harvest
p_i = the marginal willingness to pay for fish harvest by angler group *i*
c_i = marginal cost of effort for user group *i*
ρ = rate of discount

Current Value Hamiltonian

Optimal control theory and the maximum principal provide an optimal stocking rate over time that maximizes the objective function. The optimal stocking rate is expressed as a function of shadow prices (λ_l or current value shadow prices μ_l; also known as adjoint variables) that are determined from constructing a Hamiltonian ($\mathcal{H}$) of the optimal control problem (Clark 2005).

Government Hamiltonian:

$$\mathcal{H} = e^{-\rho t}(p_{RES}qE_{RES}X - c_{RES}E_{RES} + p_{ROV}qE_{ROV}X - c_{ROV}E_{ROV} - \gamma S^2) \quad \text{N4}$$
$$+\lambda_1(rX - bX^2 - qEX + S)$$
$$+\lambda_2(\delta E_{RES}[p_{RES}qX - c_{RES}]) + \lambda_3(\delta E_{ROV}[p_{ROV}qX - c_{\ OV}])$$

Lake association Hamiltonian:

$$\mathcal{H} = e^{-\rho t}(p_{RES}qE_{RES}X - c_{RES}E_{RES} - \gamma S^2) \quad \text{N5}$$
$$+\lambda_1(rX - bX^2 - qEX + S) + \lambda_2(\delta E_{RES}[p_{RES}qX - c_{RES}])$$
$$+\lambda_3(\delta E_{ROV}[p_{ROV}qX - c_{ROV}])$$

where,

The current value Hamiltonian $\widetilde{\mathcal{H}} = e^{\rho t}(\mathcal{H})$

The current shadow price $\mu_l = e^{\rho t}(\lambda_l)$

γ = the marginal cost of stocking

The Maximum Principal

$$\frac{\partial\widetilde{\mathcal{H}}}{\partial s} = 0 \quad \text{N6}$$

and

$$\frac{\partial\mu_l}{\partial t} = \rho\mu_l - \sum_{j=0}^{n}\mu_j\frac{df^j}{dv^l} \quad \text{N7}$$

where,

f^j = term j in $\widetilde{\mathcal{H}}$, with the first term being $j = 0$ and $\mu_0 = 1$

v^l = state variable l ($v^1 = X, v^2 = E_{RES}$, and $v^3 = E_{ROV}$)

n = number of state vairables

Current shadow prices (adjoint equations)

Lake association:

$$\dot{\mu_1} = -p_{RES}qE_{RES} - 2\gamma S \quad \text{N8}$$
$$(r - 2bX - q(E_{ROV} + E_{RES}) - \rho)$$
$$-\delta q(\mu_2 p_{RES}E_{RES} + \mu_3 p_{ROV}E_{ROV})$$

Government:

$$\dot{\mu_1} = -q(p_{\ OV}E_{ROV} + p_{RES}E_{RES}) - 2\gamma S \quad \text{N9}$$
$$(r - 2bX - q(E_{ROV} + E_{RES}) - \rho)$$
$$-\delta q(\mu_2 p_{RES}E_{RES} + \mu_3 p_{ROV}E_{ROV})$$

$$\dot{\mu_2} = \mu_2(\rho - \delta p_{RES}qX + \delta c_{RES}) + qX(2\gamma S - p_{RES}) + c_{RES} \quad \text{N10}$$

Lake association:

$$\dot{\mu_3} = 2\gamma SqX - \mu_3(\delta p_{ROV}qX - \delta c_{ROV} - \rho) \quad \text{N11}$$

Government:

$$\dot{\mu_3} = \mu_3(\rho - \delta p_{ROV}qX + \delta c_{ROV}) + qX(2\gamma S - p_{ROV}) + c_{ROV} \quad \text{N12}$$

Optimal Stocking

By Equation 6, $\frac{d\widetilde{\mathcal{H}}}{dS} = -2S\gamma + \mu_1 = 0$, therefore, $\mu_1 = 2S\gamma$. Taking the derivative of both sides of this equation with respect to time and solving for $\dot{S}$ gives,

$$\dot{S} = \frac{\dot{\mu_1}}{2\gamma} \quad \text{N13}$$

Equilibrium solutions to effort state equations

By Equations 2 and 3,

$$\delta E^*_{ROV}[p_{ROV}qX^* - c_{ROV}] = 0 \;\text{ if } \begin{cases} p_{ROV}qX^* = c_{ROV}, \; E^*_{ROV} > 0 \\ E^*_{ROV} = 0 \end{cases} \quad \text{N14}$$

$$\delta E^*_{RES}[p_{RES}qX^* - c_{RES}] = 0 \;\text{ if } \begin{cases} p_{RES}qX^* = c_{RES}, \quad E^*_{RES} > 0 \\ E^*_{RES} = 0 \end{cases} \quad \text{N15}$$

By Equations 14 and 15, if E^*_{ROV} & $E^*_{RES} > 0$,

$$\frac{c_{ROV}}{p_{ROV}} = \frac{c_{RES}}{p_{RES}} = qX^*$$

let $\frac{c_i}{p_i} = d$

$$X^* = \frac{d}{q} \quad \text{N16}$$

Equilibrium solution to fish population state equation

Setting Equation N1 equal to 0 and solving for X^* gives,

$$X^* = \frac{\left(r - E^*q + \sqrt{(r - E^*q)^2 + 4bS^*}\right)}{2b} \quad \text{N17}$$

Equilibrium solution to total effort

Setting Equation N16 equal to Equation N17 and solving for E^* gives,

$$E^* = \frac{-bd^2 + rdq + q^2S^*}{dq^2} \quad \text{N18}$$

Equilibrium solution to current value shadow prices

Setting Equations N10 – 12 equal to 0 gives,

$$\mu_2^* = \mu_3^* = \frac{-2dS^*\gamma}{\rho} \qquad \text{N19}$$

Setting Equations N8 (lake association) & N9 (formal management) equal to 0, substituting in equations N16, N18, and N19, and solving for S^* provides the optimal stocking rate at equilibrium. Given the size of the equation for S^* we do not provide it here but describe which parameters it is a function of, $S^*(c_{rov}, c_{res}, p_{res}, q, \gamma, \delta, r, k, \rho, \alpha)$ (see Table O1 for parameter descriptions).

Net benefits of harvest per unit of fishing effort

$$NB_i = p_i qX - c_i \qquad \text{N20}$$

Where *NB* = the net benefits of harvest per unit of effort from user group *i*, *p* = marginal willingness to pay for harvest for user group *i*, *q* = catchability coefficient, *X* = fish stock density, and *c* = marginal cost of fishing effort for user group *i*.

By Equation N5 the marginal willingness to pay for harvest by roving anglers must increase if they have higher marginal costs of fishing effort and are present at equilibrium. Substituting Equation N5 into Equation 20 demonstrates open access "rent" dissipation at equilibrium because the marginal net benefits for each user group are equal to 0,

$$NB_{res}^* = p_{res}qX^* - c_{res} = \cancel{p_{res}q}\frac{c_{res}}{\cancel{p_{res}q}} - c_{res} = 0 \qquad \text{N21}$$

$$NB_{rov}^* = p_{rov}qX^* - c_{rov} = \frac{c_{rov}\cancel{p_{res}}}{\cancel{c_{res}}}\cancel{q}\frac{\cancel{c_{res}}}{\cancel{p_{res}q}} - c_{rov} = 0 \qquad \text{N22}$$

However, when the fish stock is not at equilibrium and is at density *X*, the marginal net benefits of resident anglers is less than roving anglers when $c_{res} < c_{rov}$:

$NB_{res} < NB_{rov}$,
$p_{res}qX - c_{res} < p_{rov}qX - c_{rov}$,
$p_{res}qX - c_{res} < \frac{c_{rov}p_{res}}{c_{res}}qX - c_{rov}$,
$p_{res}qX - c_{res} + c_{rov} < \frac{c_{rov}}{c_{res}}p_{res}qX$,
$1 - \frac{c_{res}+c_{rov}}{p_{res}qX} > \frac{c_{rov}}{c_{res}}$,
$c_{res} - \frac{2c_{res}+c_{res}c_{rov}}{p_{res}qX} < c_{rov}$,
$-\frac{2c_{res}+c_{res}c_{rov}}{p_{res}qX} < c_{rov} - c_{res}$,

is true given $c_{res} < c_{rov}$ (i.e. $c_{rov} - c_{res} > 1$) and $X \neq 0$

Appendix O

Table O1. Parameter values for bio-economic stocking model

Parameter	Definition	Value	Unit	Reference
p_{res}	Resident angler marginal willingness to pay for harvest	22.63	USD per walleye	Johnson et al. (2006)
p_{rov}	Roving angler marginal willingness to pay for harvest	$\frac{c_{ROV}p_{RES}}{c_{RES}}$	USD per walleye	Equation 5
c_{res}	Boat operating costs	6.22	USD per trip	U.S. Census Bureau (2016)
c_{rov}	Round trip travel cost plus boat operating costs	Calculated; 10 was used as a default value	USD per trip	See Methods
γ	Proportional to the marginal cost of stocking a walleye (i.e. 2γ)	2.35	USD	WLAB (1997)
δ	Sluggishness of fishing effort to average net benefits of walleye harvest	0.001	Unitless	Clark (1990)*
r	Walleye intrinsic growth rate	0.34	Per year	Hunt et al (2011)
q	proportion of the fish stock removed with one unit of effort	0.04	Angler per trip	Hunt et al (2011)
k	Walleye carrying capacity	24	Walleye per hectare	Hunt et al (2011)
ρ	Discount rate of net benefits of harvest	10	Percent	Fenichel (2010)*
α	Percent resident angling effort	Calculated; 50 was used as a default value	Percent	See Methods

*Does not provide an empirical estimate of model parameter

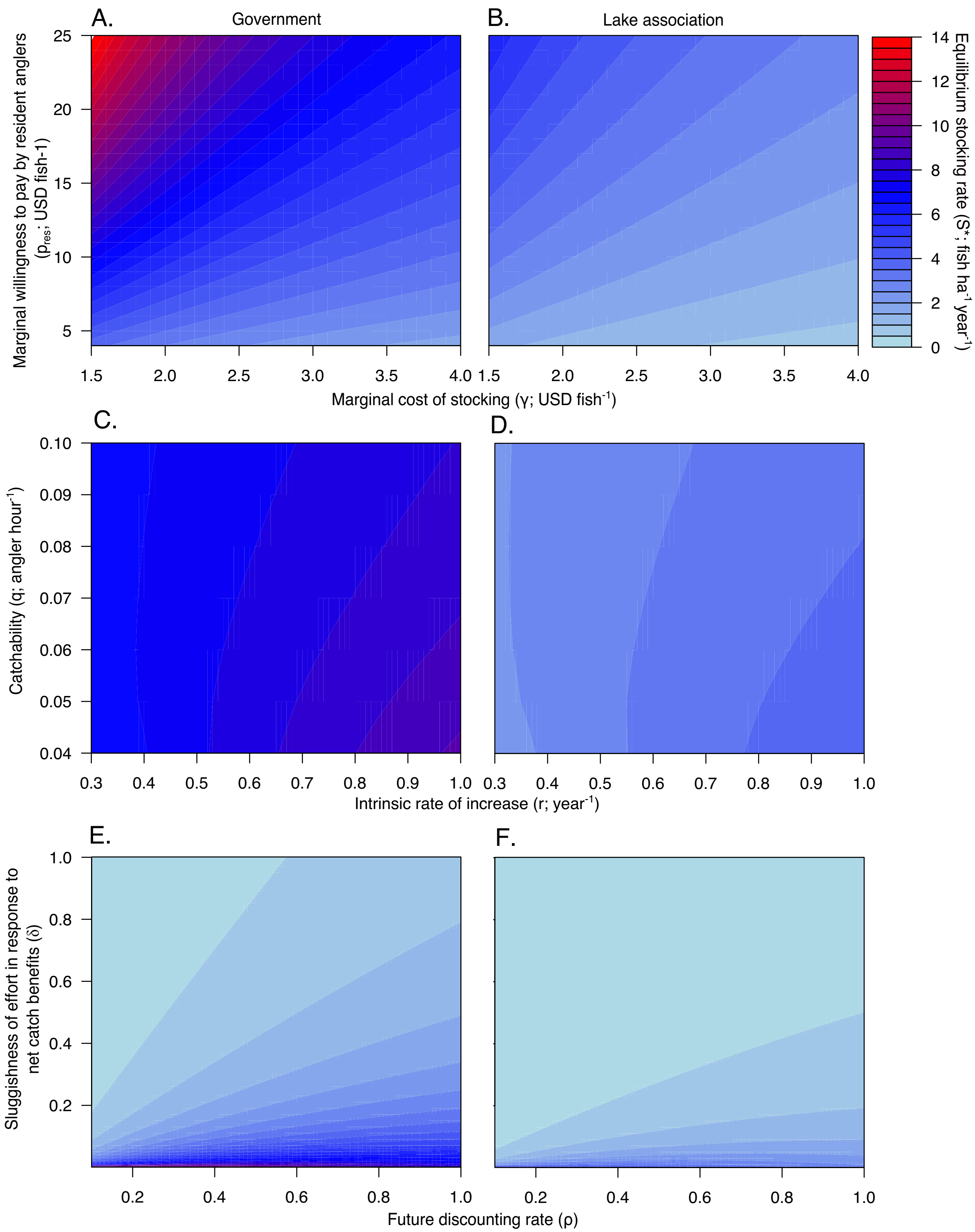


Figure O1. Optimal stocking at equilibrium was negatively related to the marginal cost of fish stocking (A and B) and the future discounting of harvest benefits (E and F). It was positively related to the marginal value of fish harvest (A and B), the intrinsic rate of increase of the fish population, the catchability coefficient of harvest (C and D), and the sluggishness of effort in response to net harvest benefits (E and F). Stocking under government control (left panel) had higher optimal equilibrium stocking rates than under lake association control (right panel). See Table O1 for default model parameters.

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Appendix P

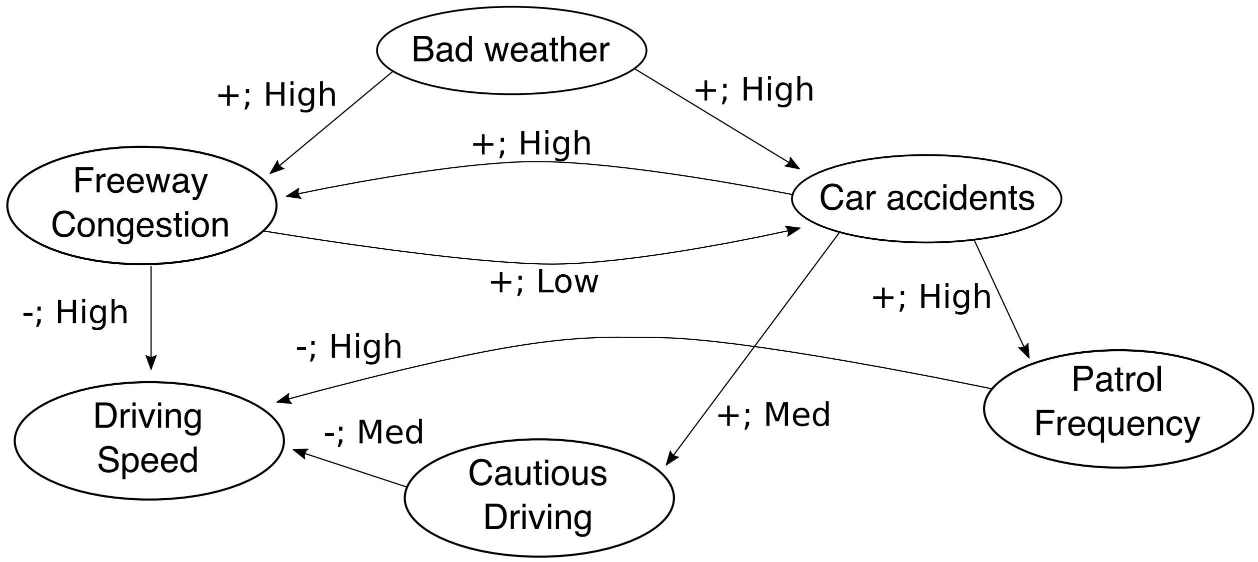


Figure P1. Example of a fuzzy cognitive map depicting traffic flow. Arrows represent direct relationships between concepts and variables that have a positive or negative correlation with a subjective strength of high, medium, or low.

Table P1. Original terms used in Fuzzy Cognitive Maps and how they were coded

SESF component	Attribution relationship	Subsumption relationships	Term used in FCM
Actor	Angler/Ability	Angler/Lake user/Actor	Ability
Actor	Angler/Ability	Angler/Lake user/Actor	Catchability
Actor	Angler/Access	Angler/Lake user/Actor	Accessibility
Actor	Angler/Catch rate	Angler/Lake user/Actor	Catch rate
Actor	Angler/Density	Angler/Lake user/Actor	Number of anglers per lake
Actor	Angler/Effort	Angler/Lake user/Actor	Effort
Actor		Tribal Angler/Angler/Lake user/Actor	Spearing of walleye
Actor	Angler/Fishing history	Angler/Lake user/Actor	History
Actor	Actor/Knowledge	Angler/Lake user/Actor	Knowledge
Actor	Actor/Communication	Angler/Lake user/Actor	Communication
Actor	Angler/Origin	Angler/Lake user/Actor	Local anglers
Actor	Angler/Origin	Angler/Lake user/Actor	Proximity to fishery
Actor	Angler/Origin	Angler/Lake user/Actor	Resident
Actor	Angler/Origin	Angler/Lake user/Actor	Tourists
Actor	Angler/Origin	Angler/Lake user/Actor	Visiting anglers
Actor	Angler/Preferences	Angler/Lake user/Actor	Aesthetics
Actor	Angler/Preferences	Angler/Lake user/Actor	Harvest
Actor	Angler/Preferences	Angler/Lake user/Actor	Catch and release
Actor	Angler/Preferences	Angler/Lake user/Actor	Mental aspect of fishing
Actor	Angler/Preferences	Angler/Lake user/Actor	Trophy fishing
Actor	Angler/Satisfaction	Angler/Lake user/Actor	Angler satisfaction
Actor	Angler/Satisfaction	Angler/Lake user/Actor	Angst with other anglers
Actor	Angler/Satisfaction	Angler/Lake user/Actor	Angst with tribal spearing
Actor	Angler/Satisfaction	Angler/Lake user/Actor	Positive experience
Actor		Angler/Lake user/Actor	Angler
Actor		Fishing guide/Angler/Lake user/Actor	Guide
Actor		Hospitality industry/Lake user/Actor	Hospitality industry
Actor	Lake user/Development	Lake user/Actor	Development
Actor	Lake user/Development	Lake user/Actor	Loss of shoreline buffer
Actor	Lake user/Development	Lake user/Actor	Real-estate purchasing
Actor	Lake user/Development	Lake user/Actor	Removal of aquatic habitat
Actor	Lake user/Norms	Lake user/Actor	Norms
Actor	Lake user/Norms	Lake user/Actor	Self-policing
Actor	Lake user/Stewardship	Lake user/Actor	Lake shore stewardship
Actor	Lake user/Stewardship	Lake user/Actor	Stewardship
Actor	Lake user/Stewardship	Lake user/Actor	Preserving lakes mindset
Actor		Lake user/Actor	Cabin owners
Actor		Lake user/Actor	Jet skier
Actor		Lake user/Actor	Other uses of lakes

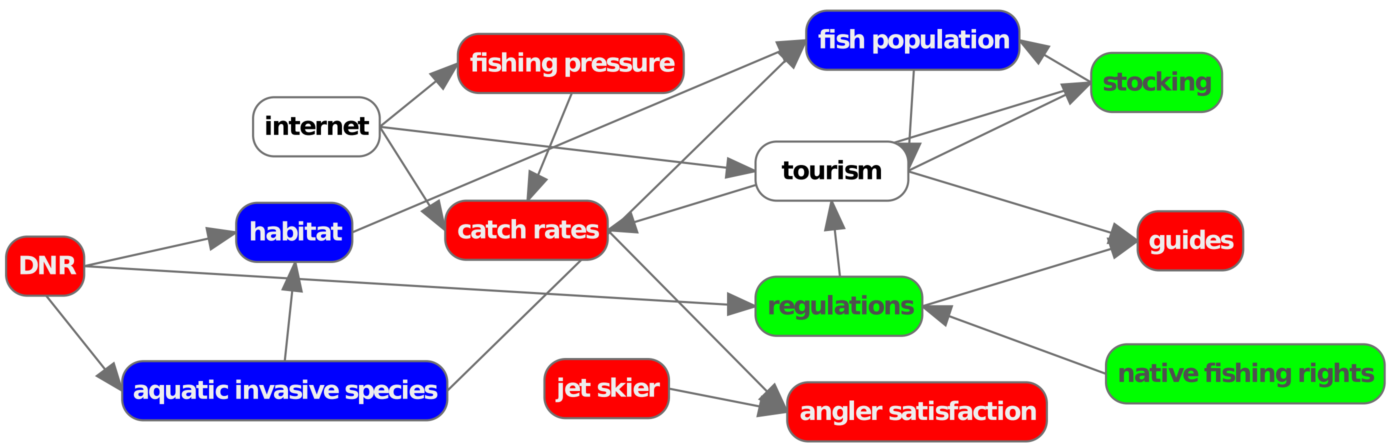
Actor		Government/Actor	Management
Actor		DNR/Government/Actor	DNR
Actor	Government/Capital	Government/Actor	Transportation infrastructure
Actor	Government/Capital	Government/Actor	Boat landing quality
Actor	Government/Capital	Government/Actor	Infrastructure for recreational fisheries
Actor	Government/Capital	Government/Actor	DNR funding
Actor	Government/ Monitoring	Government/Actor	Monitoring by DNR
Actor		Researcher/Actor	Researcher
Actor		Tribal fishery/Government/Actor	Tribal fishery
Resource System	Resource System/Lake/Fish Population/Health		Health and sustainability of fishery
Resource System	Resource System/Lake/Fish Population/History		Fishery history
Resource System	Resource System/Lake/Fish Population/Abundance		Abundant fish population
Resource System	Resource System/Lake/Fish Population/Abundance		Fish abundance
Resource System	Resource System/Lake/Fish Population/Phenology		Phenology
Resource System	Resource System/Lake/Fish Population/Quality		Quality
Resource System	Resource System/Lake/Fish Population/Competition		Replacement of species
Resource System	Resource System/Lake/Fish Population/ Reproduction		Natural reproduction
Resource System	Resource System/Lake/Fish Population/Thermal Tolerance		Warm water species
Resource System	Resource System/Lake/Fish Population/Species		Smallmouth bass, Species, Walleye, Pan fish, Piscivore
Resource System	Resource System /Lake/Invasive Species		Aquatic invasive species

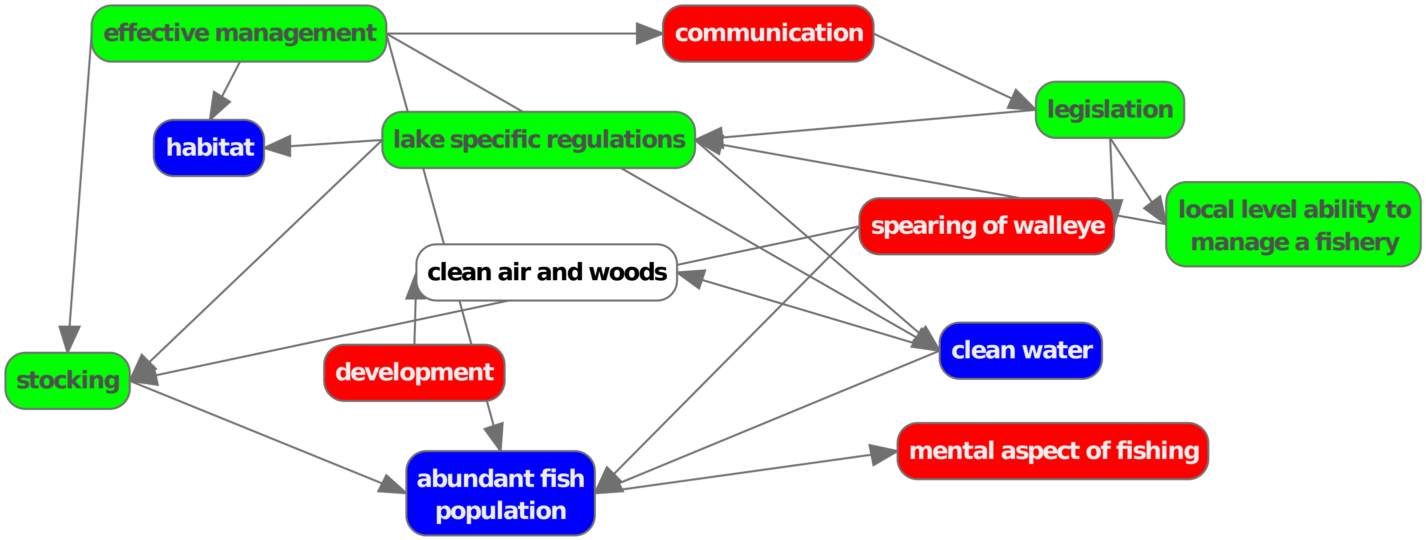
Resource System	Resource System/Lake/ Morphometry		Morphometry
Resource System	Resource System/Lake/Fish Population		Fish Population
Resource System	Resource System/Lake/Habitat		Fish habitat
Resource System	Resource System/Lake/Habitat		Habitat
Resource System	Resource System/Lake/Health		Healthy ecosystem
Resource System	Resource System/Lake/Health		Lake health
Resource System	Resource System/Lake/ Abundance		Number of lakes
Resource System	Resource System/Lake/ Water Quality		Water quality
Environment	Environment/Related Ecosystems/Aesthetics		Clean air and woods
Environment	Environment/Related Ecosystems/Aesthetics		Wildlife
Environment	Environment/Related Ecosystems/Climate		Climate change
Environment	Environment/Related Ecosystems/Climate		Average weather trends
Environment	Environment/Related Ecosystems/Climate		Seasons
Environment	Environment/Related Ecosystems/Climate/Weather		Good weather for anglers
Environment	Environment/Related Ecosystems/Climate/Weather		Local weather patterns
Environment	Environment/Related Ecosystems/Climate/Weather		Regional weather patterns
Environment	Environment/Related Ecosystems/Climate/Weather		Temperature
Environment	Environment/Social, economic, and political setting		Economy
Environment	Environment/Social, economic, and political setting		Local economy

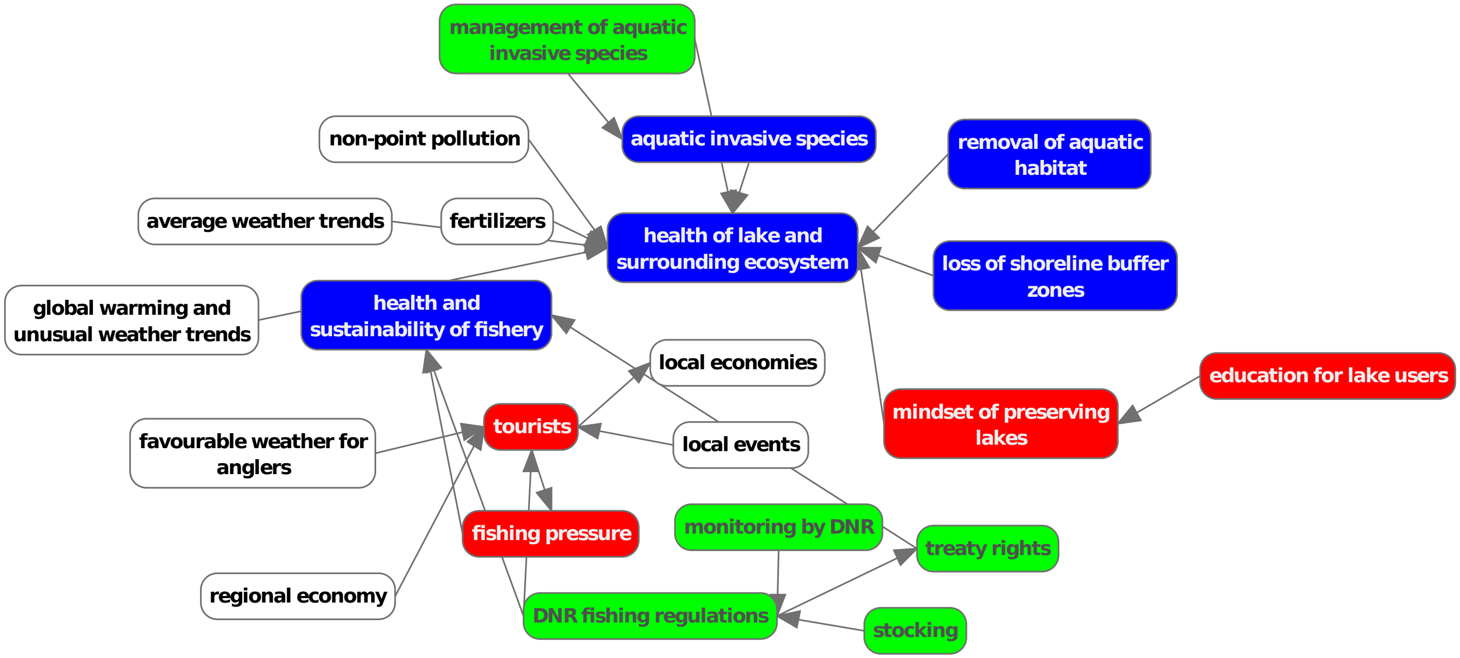
Environment	Environment/Social, economic, and political setting		Revenue
Environment	Environment/Social, economic, and political setting		Government budget
Environment	Environment/Social, economic, and political setting		Politics
Environment	Environment/Social, economic, and political setting/Technology		Social media
Environment	Environment/Social, economic, and political setting/Technology		Internet
Environment	Environment/Social, economic, and political setting/Technology		Technology
Environment	Environment/Social, economic, and political setting/Tourism		Local events
Environment	Environment/Social, economic, and political setting/Tourism		Tourism
Governance System	Governance System/Rules In Use	Invasive species prevention/Rules In Use	Management of aquatic invasive species
Governance System	Governance System/Rules In Use	Community based management/Collective choice/Rules In Use	Local level ability to manage a fishery
Governance System	Governance System/Community Based Management Rights		Local level ability to manage a fishery
Governance System	Governance System/Community Based Management Rights		Public pressure
Governance System	Governance System/Treaty Rights		Treaty rights
Governance System	Governance System/Rules In Use	Harvest control/Operational Rule/Rule in Use	Bag Limit
Governance System	Governance System/Rules In Use	Harvest control/Operational Rule/Rule in Use	Harvest regulations
Governance System	Governance System/Rules In Use	License fees/Operational Rule/Rule in Use	License fee

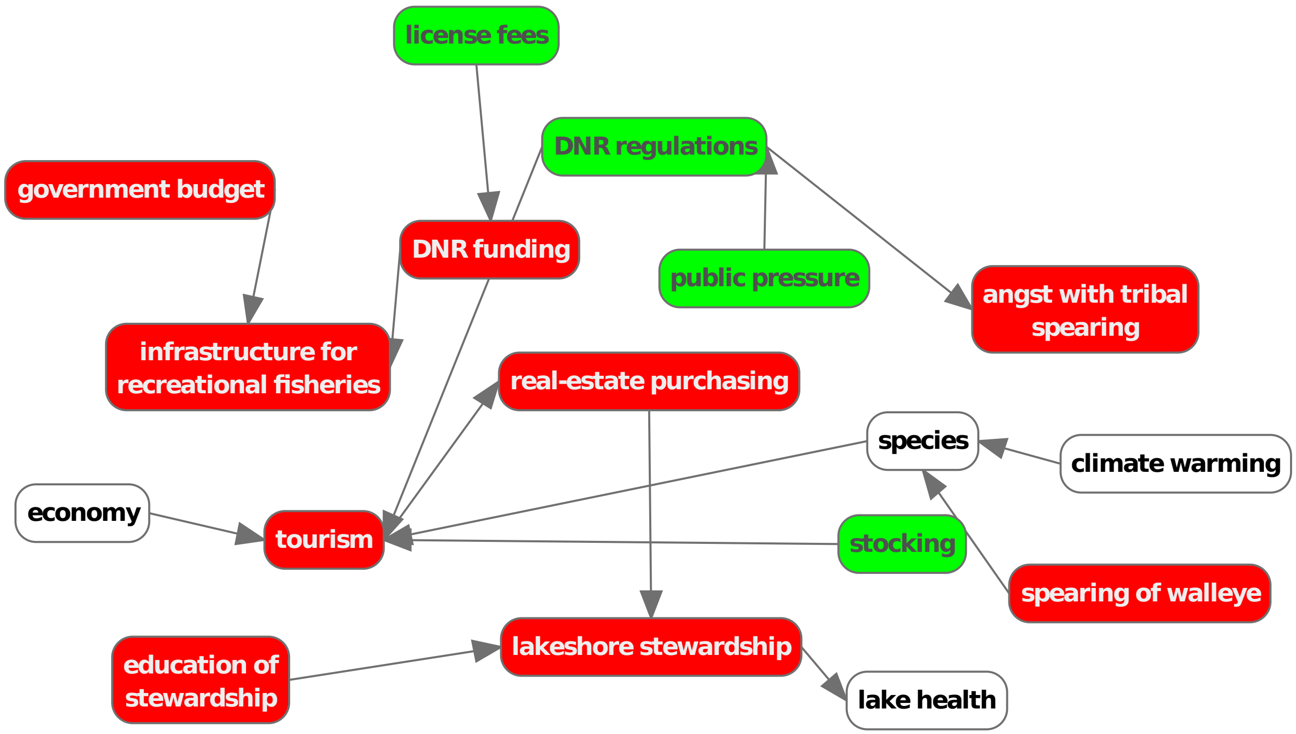
Governance System	Governance System/Rules In Use	Stocking/Operational Rule/Rule in Use	Stocking
Governance System	Governance System/Rules In Use	Water Level Regulation/Operational Rule/Rule in Use	Water level management
Governance System	Governance System/Rules In Use		Regulations

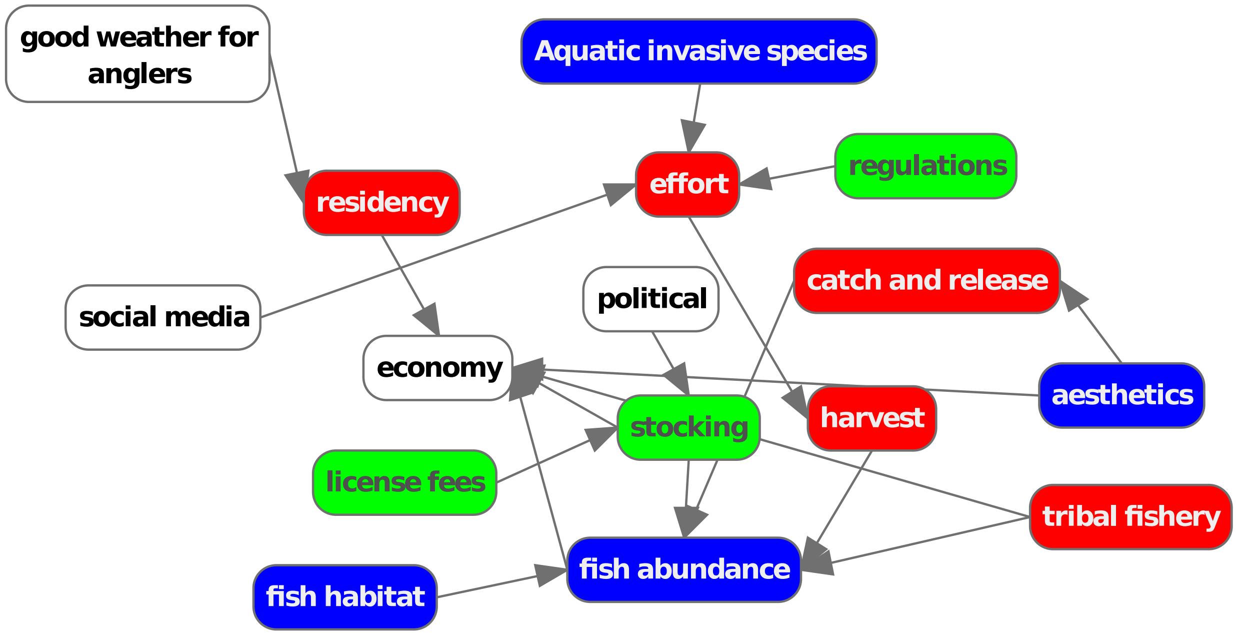
Figure P2. Concepts in individual fuzzy cognitive maps and how they were coded into Ostrom's Social-Ecological Systems Framework components; each concept that arose in the mental models was categorized as a feature of the actor (red), resource system (blue), governance system (greed), or environment (white), see Table P1.

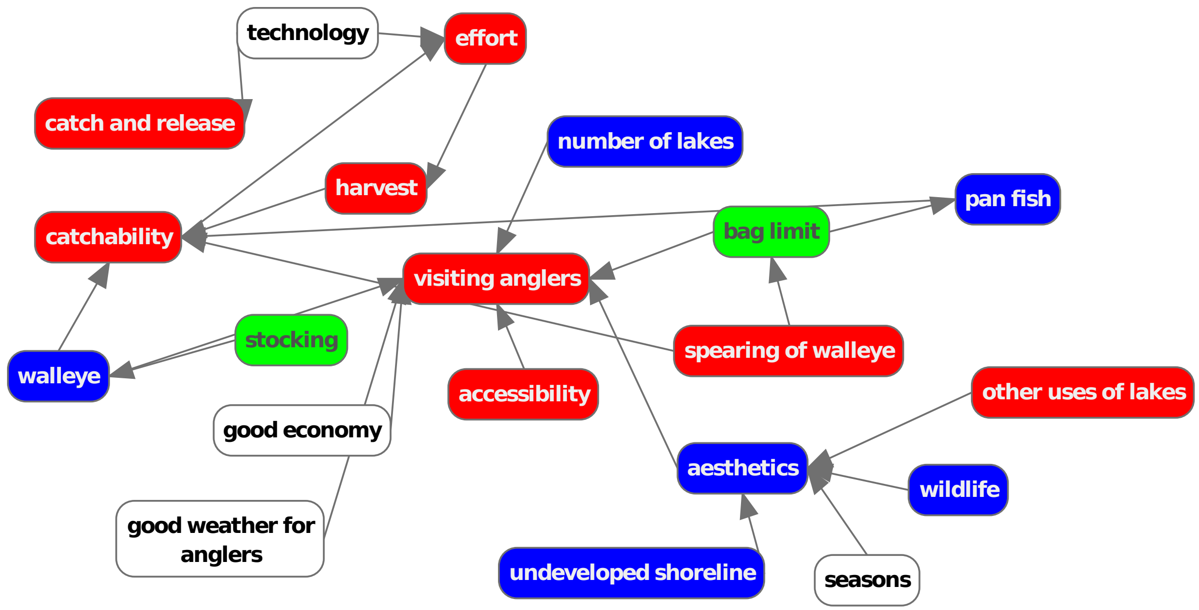


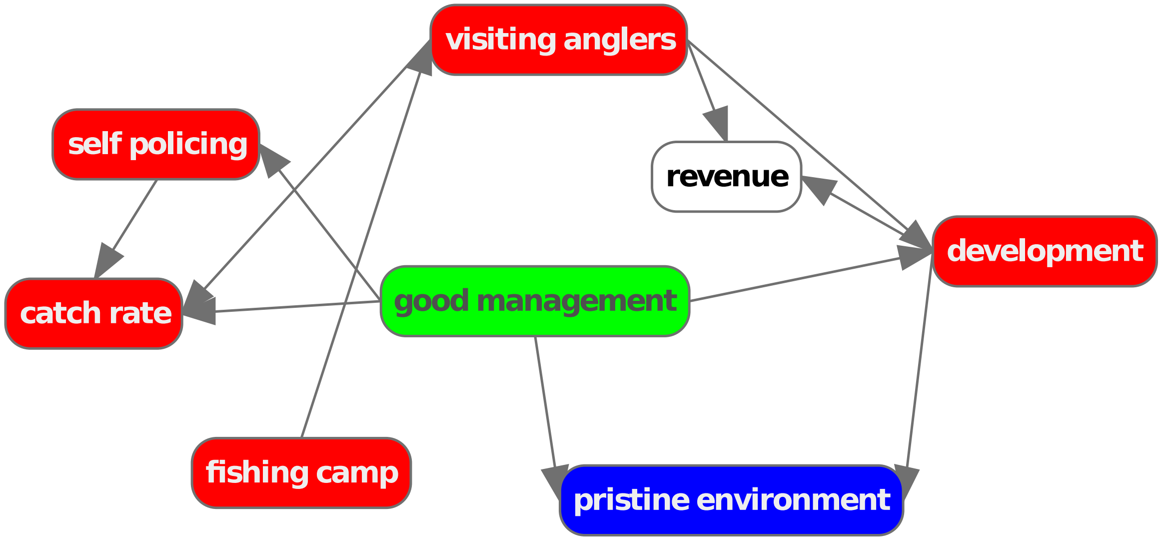

effective management
communication
legislation
habitat
lake specific regulations
local level ability to manage a fishery
spearing of walleye
clean air and woods
clean water
stocking
development
mental aspect of fishing
abundant fish population

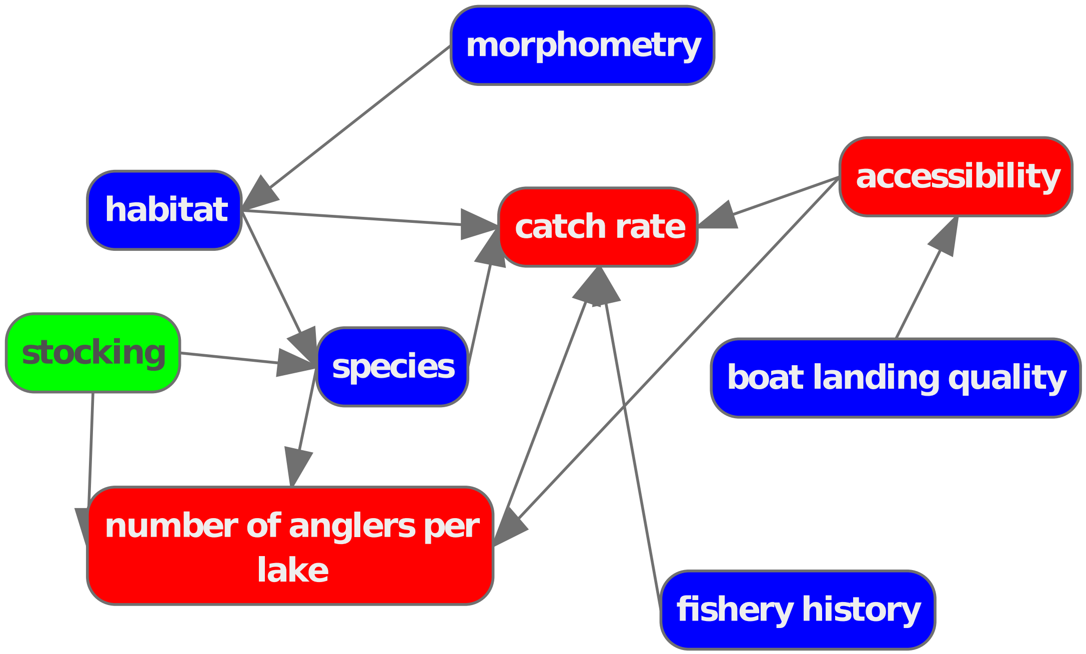

management of aquatic invasive species
aquatic invasive species
non-point pollution
removal of aquatic habitat
average weather trends
fertilizers
health of lake and surrounding ecosystem
loss of shoreline buffer zones
global warming and unusual weather trends
health and sustainability of fishery
local economies
education for lake users
tourists
local events
mindset of preserving lakes
favourable weather for anglers
fishing pressure
monitoring by DNR
treaty rights
regional economy
DNR fishing regulations
stocking

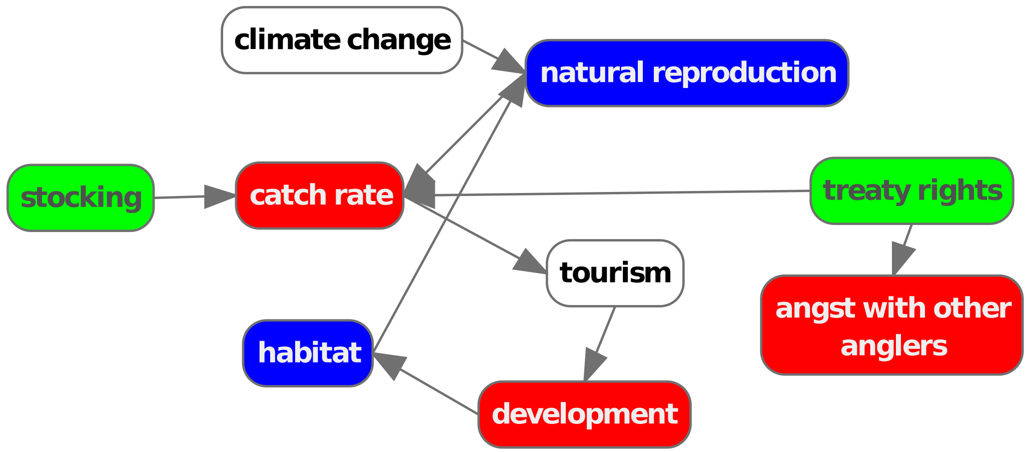

license fees
DNR regulations
government budget
DNR funding
public pressure
angst with tribal spearing
infrastructure for recreational fisheries
real-estate purchasing
species
climate warming
economy
tourism
stocking
spearing of walleye
lakeshore stewardship
education of stewardship
lake health


good weather for anglers
Aquatic invasive species
regulations
effort
residency
social media
political
catch and release
economy
aesthetics
stocking
harvest
license fees
tribal fishery
fish abundance
fish habitat

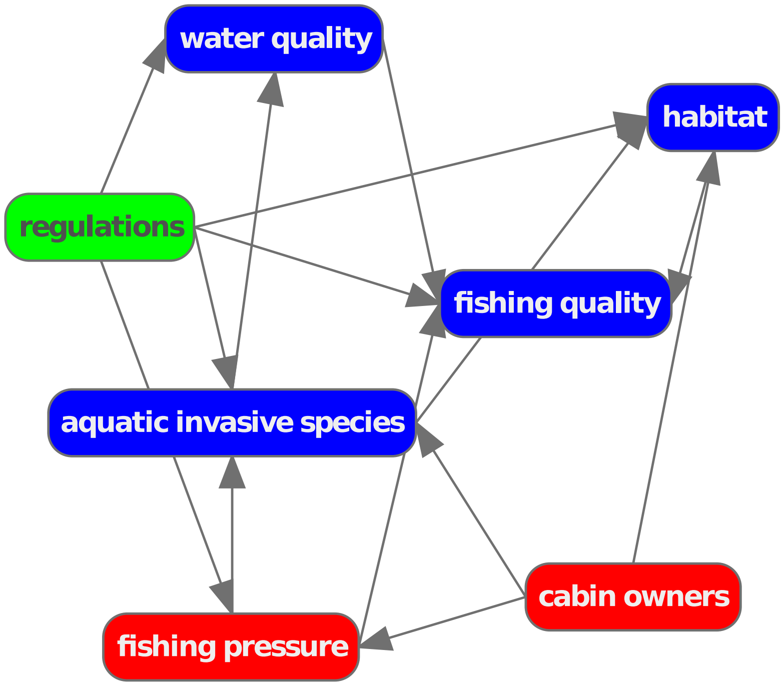

technology
effort
catch and release
number of lakes
harvest
pan fish
catchability
bag limit
visiting anglers
stocking
spearing of walleye
walleye
accessibility
other uses of lakes
good economy
aesthetics
wildlife
good weather for anglers
undeveloped shoreline
seasons

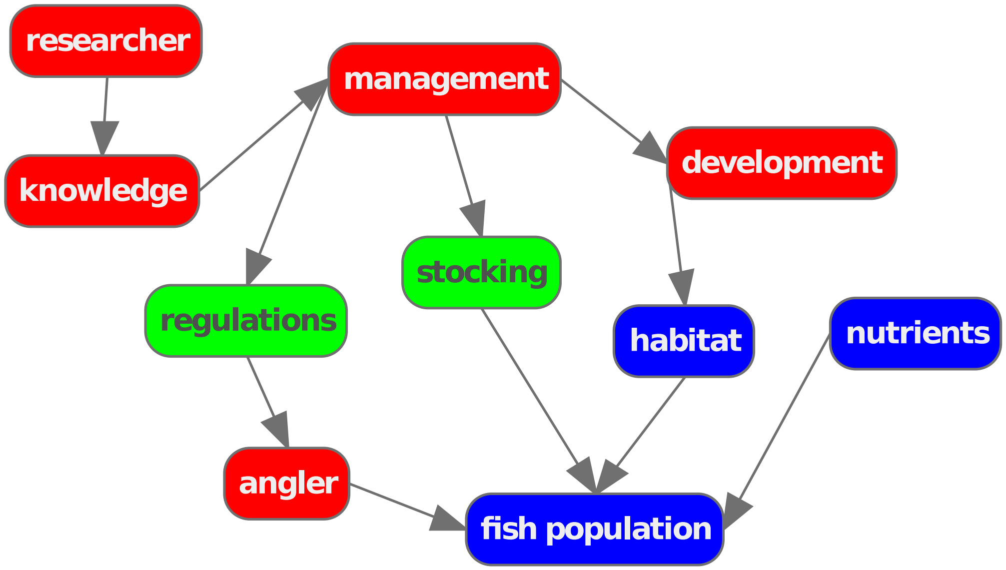

visiting anglers
self policing
revenue
development
catch rate
good management
fishing camp
pristine environment

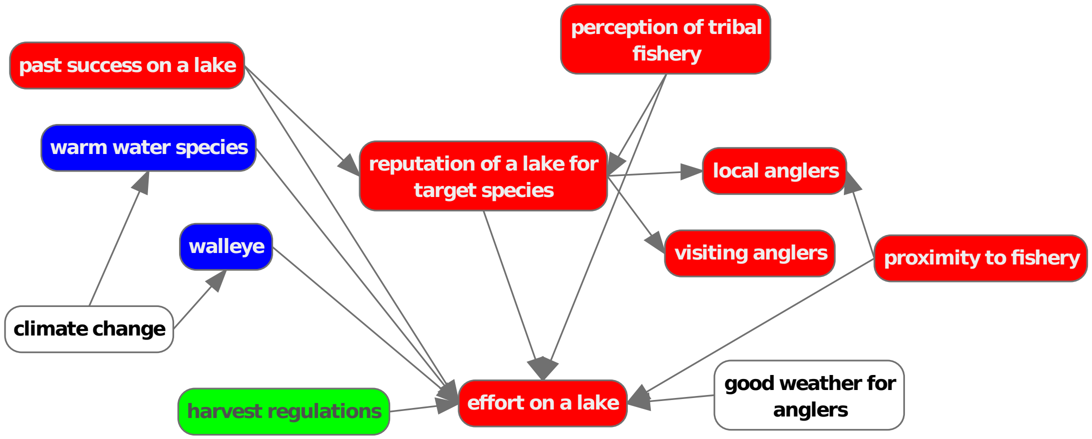

morphometry
habitat
catch rate
accessibility
stocking
species
boat landing quality
number of anglers per lake
fishery history


climate change
natural reproduction
stocking
catch rate
treaty rights
tourism
angst with other anglers
habitat
development

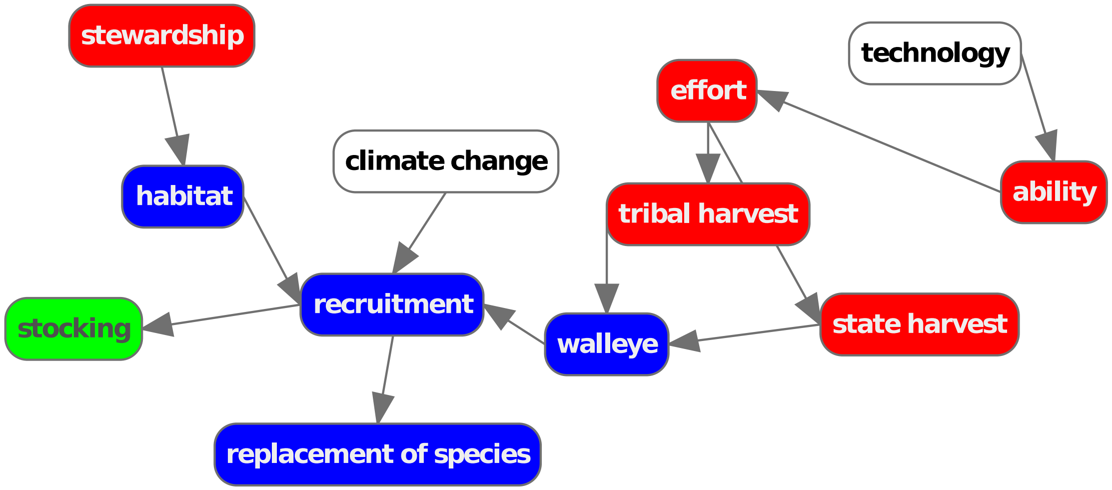
\

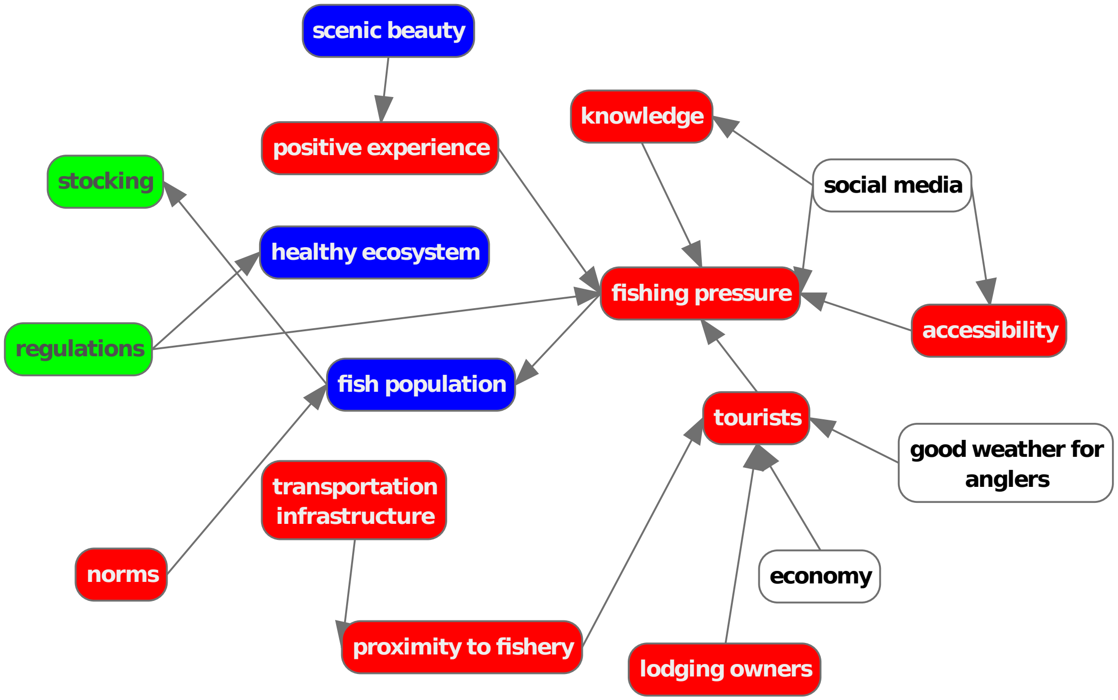

water quality
habitat
regulations
fishing quality
aquatic invasive species
cabin owners
fishing pressure

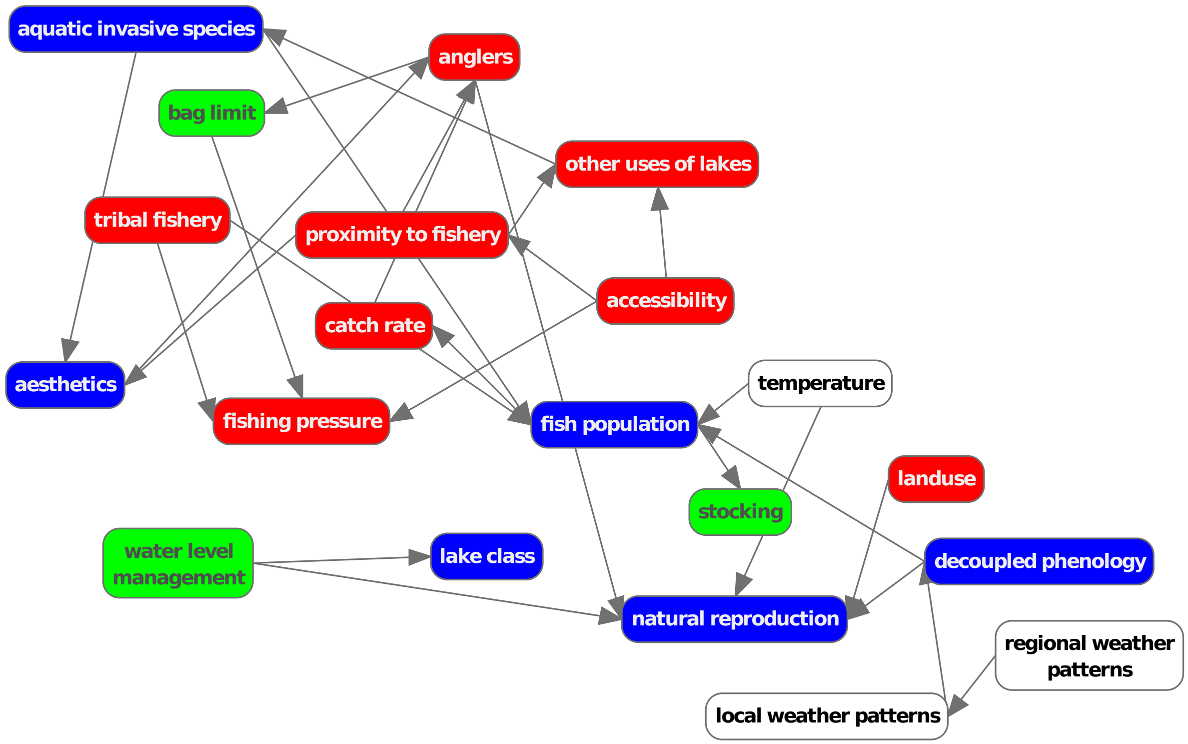

researcher
management
knowledge
development
stocking
regulations
habitat
nutrients
angler
fish population



past success on a lake
perception of tribal fishery
warm water species
reputation of a lake for target species
local anglers
walleye
visiting anglers
proximity to fishery
climate change
harvest regulations
effort on a lake
good weather for anglers


stewardship
technology
effort
climate change
habitat
tribal harvest
ability
recruitment
stocking
walleye
state harvest
replacement of species


scenic beauty
positive experience
knowledge
social media
stocking
healthy ecosystem
fishing pressure
accessibility
regulations
fish population
tourists
good weather for anglers
transportation infrastructure
economy
norms
proximity to fishery
lodging owners


aquatic invasive species
anglers
bag limit
other uses of lakes
tribal fishery
proximity to fishery
accessibility
catch rate
aesthetics
temperature
fishing pressure
fish population
landuse
stocking
water level management
lake class
decoupled phenology
natural reproduction
regional weather patterns
local weather patterns