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RETURN-ON-INVESTMENT FRAMEWORKS CAN INCREASE THE

EFFICIENCY OF RESTORATION EFFORTS TO IMPROVE FRESHWATER

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RETURN-ON-INVESTMENT FRAMEWORKS CAN INCREASE THE
EFFICIENCY OF RESTORATION EFFORTS TO IMPROVE FRESHWATER
CONNECTIVITY

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Abstract

With global declines in biodiversity and limited budgets, many conservation organizations are trying to increase the efficiency of conservation efforts. One method is the use of a return-on-investment (ROI) framework, which allows conservation actors to compare conservation projects based on the amount of ecological benefit achieved for a certain budget. Here I apply ROI frameworks to the challenge of directing the removal of dams and road-culverts in order to restore connectivity in freshwater ecosystems. In a first application, I examined the necessity of coordination of barrier removals between conservation actors. I found that a coordinated mixture of small, medium, and large barrier removals was necessary to achieve the greatest ROI. This result emphasizes the need for increased communication among different conservation organizations and the coordination of conservation efforts. In the second application, I used the ROI framework to evaluate the efficiency of using indicator species to guide barrier removals in the Great Lakes. Overall, I found that indicator species were able to guide barrier removals for the majority of native anadromous fishes. Both of these projects demonstrate the value in considering the ROI of a project and how conservation organizations could use similar applications to increase the efficiency of their projects.

Chapter 1: Introduction to Return-On-Investment Frameworks, Individual Based Models, and Indicator Species

Conservation practitioners worldwide face the challenge of combatting a global biodiversity crisis with limited conservation resources (Butchart et al. 2010). To efficiently direct conservation efforts, conservation organizations increasingly consider a project's potential return-on-investment (ROI; Murdoch et al. 2007), the project's potential net gain divided by its cost. An ROI framework allows conservation actors to quantify trade-offs between a range of conservation projects and how to implement those projects. Recent studies have shown the practicality and efficiency of ROI frameworks in selecting reserve sites (Ando et al. 1998), indicator species (Tulloch et al. 2011), and other conservation strategies (Auerbach et al. 2014, Possingham et al. 2012, Wintle et al. 2010). As an introduction to this thesis, I review three key components of my research: (1) the ROI framework and its conservation applications, (2) the history of ecological individual-based models, and (3) the use of indicator species and their potential to be a cost-effective approach for conservation efforts.

1.1 Return-On-Investment in Conservation

1.1.1 Introduction

Global biodiversity has continued to decline despite billions of dollars and person-hours dedicated to conservation efforts (Butchart et al. 2010). Over 10,000 species are currently listed as endangered or critically endangered by the International Union for Conservation of Nature (IUCN 2016), and the decline of many can be attributed to a combination of habitat loss, invasive species, poaching, pollution, and other human impacts on ecosystems. Due to limited budgets, conservation organizations are forced to

seek ways to "cut corners", "get the most bang for their buck", and in general determine the best ways to invest their money in order to slow or reverse human impacts (Bottrill et al. 2008, McCarthy et al. 2012). Within business and economic organizations the use of a return-on-investment (ROI) framework is often applied to accomplish these aims. An ROI framework weighs the cost of a project versus its net return. Recent studies have indicated the potential of an ROI approach to improve both ecosystem management decision making and monitoring programs (Murdoch et al. 2007, Auerbach et al. 2014). Here I review different ways in which ROI frameworks have been applied to conservation efforts, then demonstrate how an ROI framework can be applied to a restoration effort using fragmented river networks.

1.1.2 ROI definition

The benefit of an ROI framework is that it weighs the cost of a project against the predicted potential conservation benefit. In a conservation context, ROI measures the amount of conservation achieved (i.e., the "return", which may be the amount of land set aside, area surveyed, or population growth) for the amount of effort invested (i.e., the "cost", the investment of money, time, or people; see Naidoo et al. 2006 for cost examples) (Murdoch et al. 2007). As all conservation organizations are limited by financial resources, cost should be considered at some point when performing a conservation action.

Two general types of conservation efforts are management and monitoring programs, which can be used in concert to work towards more efficient conservation efforts (Possingham et al. 2012). Management programs include the creation of reserves, invasive species control, and habitat restoration projects. Management

programs rely on monitoring programs to improve conservation efforts and to guide

future management decisions. In comparison, conservation organizations use

monitoring programs to engage with the public, raise awareness of ecological and

environmental issues, and uncover previously unknown phenomenon, all of which can

be used to improve management efforts (Wintle et al. 2010, Possingham et al. 2012).

Possingham et al. (2012) suggests that monitoring programs have the greatest ROI for

the first 5-15 years when the chance of new discoveries is high. Continued monitoring

after the first decade is unlikely to result in new information and at that point it is more

cost-effective to spend funds on other monitoring or management programs. ROI

frameworks can be applied to both monitoring and management programs and

conservation studies (Ando et al. 1998, Murdoch et al. 2007) have emphasized that

including costs into any conservation planning can often increase the amount of

conservation done for a specified budget.

1.1.3 Conservation planning and management

One of the earliest conservation applications of an ROI framework was to the

problem of choosing a set of sites to serve as a nature preserve network (Ando et al.

1998). When systematically selecting reserve sites, Margule and Pressey (2000)

encourage conservation actors to consider both the acquisition cost of land and the

potential that same land has for commercial uses, and weigh these costs against

ecological gain. Recently ROI approaches have been applied to a greater range of

conservation management actions (Auerbach et al. 2014). To encompass the variety of

these actions, I define conservation management as an action performed by a

conservation actor to benefit a species, a group of species, or an entire ecosystem. These

actions include purchasing land, removing or renovating anthropogenic structures, and invasive species control. ROIs can allow conservation organizations to efficiently plan large scale management programs and incorporate a variety of social and biological factors into their analyses.

When planning reserve sites it is important to recognize that neither species distributions nor cost of land is constant across a large spatial range. Dobson et al. (1997) showed that the uneven distribution of endangered species created "hotspots" for different taxa and could be used to target areas of conservation. A follow-up study by Ando et al. (1998) demonstrated how the inclusion of land cost in the analysis resulted in a greater ROI. This combination of ecology and economics can be used to determine which areas conservation organizations should target in order to efficiently establish reserve sites. This approach also identified certain areas that had many species, but land was so expensive that reserve sites there would not be cost-effective. As a result, this approach selected against highly endemic species in areas with high land costs.

More recent studies have expanded upon Dobson et al. (1997) and Ando et al. (1998) by adding additional variables for evaluating both cost and benefit. Withey et al. (2012) preformed a similar set of analyses, but used high species richness and threat of land conversion to increase an area's importance, while land costs and well protected species decreased priority. They found that when these factors were taken into consideration for prioritization, both species loss and overprotection decreased compared to prioritizing areas based on species richness alone or richness/cost. In contrast, Torrubia et al. (2014) focused on restoring habitat connectivity to a single species (Washington ground squirrel, Urocitellus washingtoni), but included both the

cost of land and the cost of restoring the area by planting native vegetation. Both of these studies built on the ideas of Ando et al. (1998), but the increased complexity of their studies allowed for a more complete estimation of the costs and benefits of their respective conservation actions.

These studies emphasize how including cost in management decision making can produce drastically different plans of action then when cost is not included. However it is not clear to what extent conservation organizations have applied these ideas. Reserve selection is still approached as a piecemeal project with few examples of ROIs being used for large scale decision making (Murdoch et al. 2007, Auerbach et al. 2014). Costs are fundamental to any management action and it is necessary to include them in the decision making process.

1.1.4 Ecosystem monitoring

In contrast to conservation management actions, monitoring programs are conducted to repeatedly collect field-based measurements over a continuous time period (Lindenmayer and Likens 2010). Examples of monitoring projects include recording environmental variables and the size and health of species populations. These programs can be particularly useful for understanding the impact of management actions or detecting changes in the ecosystem, but many are implemented without a clear purpose or targeted goal (Possingham et al. 2012). While these actions do not incur the same type of costs that management programs do (such as cost of land), monitoring multiple species or implementing certain monitoring techniques can be quite expensive. Recent ROI studies involving monitoring programs have not only focused on what to monitor, but also which techniques to use and for how long.

When monitoring an ecosystem, the cost of surveying all or even several species can exceed a conservation organization's budget. Instead conservation actors must select a single or subset of species to represent a larger group of species. These "indicator" species can save resources for conservation organization by limiting the amount of resources that need to be spent on individual species surveying. However, no indicator species can perfectly represent the distributions and reactions to management strategies of another species. This leads to a trade-off between monitoring costs, which decreases with the number of indicator species employed, and ecological information, maximized when each species is individually surveyed. To address this trade-off, Tulloch et al. (2011) examined how incorporating cost of monitoring impacted the ranking of potential indicator species. While the rank of most species did not drastically change, the previously best indicator species was replaced by a more easily monitored species. This resulted in a trade-off between indicator effectiveness and cost of monitoring, but a more cost-efficient species meant that a greater area could be included in the survey or the saved funds could go towards other conservation programs (Tulloch et al. 2011).

ROI frameworks can also be used to compare between conservation programs, suggesting which ones organizations should choose to invest in. Monitoring programs range from targeted (or focused) monitoring, projects that are designed to answer a specific question, to surveillance monitoring, programs that collect a range of ecological or environmental data with the intention of being used in future research to detect trends over a long period of time (Wintle et al. 2010).

Critics of surveillance monitoring programs argue that the technique is inefficient and generally has no obvious management focus (Wintle et al. 2010). However there have been times when these records have been used to show ecologic change or other "unknown" unknowns (Wintle et al. 2010). Wintle et al. (2010) modeled the cost-efficiency of targeted and surveillance monitoring to determine when conservation organizations should invest in each method. They found that well-planned targeted monitoring had greater ROI than simple surveillance, unless there was a much greater chance of the surveillance program discovering unknown phenomena. This type of comparison allows conservation organizations to understand the tradeoffs between two traditional and contrasting methods, and to select the monitoring program will have the best ROI for their particular project.

Conservation organizations are often forced to choose between conservation projects to invest in because of limited budgets. This creates a trade-off between projects, in which funding one project may mean that other projects are never implemented. Due to these trade-offs, conservation organizations should choose to fund the project with the greatest ROI. Within a project there can also be trade-offs between the amount or quality of data and the spatial or temporal breath of the project. For example, Tulloch et al. (2011) found that choosing a slightly less effective indicator species, but was cheaper to monitor, could lead to substantial cost savings. In turn, these funds could be used to extend the size of the study region. Conservation actors can use the ROI framework to analyze these trade-offs in benefits and to choose between conservation projects.

1.1.5 Applying ROI frameworks to restoring river connectivity

To illustrate these ideas, I consider the application of an ROI framework to recent and ongoing efforts to restore freshwater ecosystem connectivity by removing dams and impassable road culverts from rivers. Highly fragmented freshwater ecosystems are an ideal system in which ROI frameworks can be utilized for making restoration decisions. The construction of thousands of dams and road-culverts across most large river systems restricts the movement of species throughout river networks and can lead to population declines or extirpations (Fagan 2002, Fischer and Lindenmayer 2007). Many of these structures have deteriorated over time to the point where they no longer serve their original purpose and can be dangerous to the surrounding human community (Grossman 2002). River systems are also ecologically complex, because they are made up of a wide variety of species that have differing habitat requirements, dispersal patterns, and life history strategies. Due to these ecological and social issues, removing these barriers has become a focus of both local and national conservation organizations attempting to restore freshwater ecosystems. An ROI framework enables these organizations to determine which of these many barriers to target in order to maximize accessible habitat for aquatic species. Furthermore, an ROI approach can also be used to identify the most cost-effective program for monitoring these newly restored areas.

Applying an ROI framework to barrier removals can be used to suggest a series of removals for a particular river system and to influence the way barrier removals are approached by conservation organizations. The first can be done by applying an optimization model to a particular region and the second can be accomplished by

changing the way the optimization model is applied. Neeson et al. (2015; see also O'Hanley 2011, O'Hanley et al. 2013) used an ROI framework to select barrier removals in the North American Great Lakes and demonstrated how the scale (county vs. basin) and time (yearly vs. all at once) conservation funds were allocated for barrier removals impacted the amount of upstream habitat made accessible to migratory fish species for a given budget. They found that ROI was greatest when allocated basin-wide instead of at smaller scales, such as by state or individual tributaries. There was also a temporal impact on the ROI of budgets, with single-pulse budgets being more efficient than annual allotments. Using an ROI framework can help conservation organizations justify where they are focusing their restoration efforts to policy makers and local communities.

To efficiently gauge the benefit of a barrier removal project, it is important to monitor species responses after the project has been completed. The construction of barriers and additional human impacts, such as increased run-off and changes to flow regimes, have led to changes in habitat throughout freshwater ecosystems (Bunn and Arthington 2002, Stanley and Doyle 2003, Graf 2006). While there may be historic records of species presence prior to the construction of a barrier, with these habitat changes there is no guarantee that these same species will return after the barrier has been removed. Because of this uncertainty, conservation actors should monitor which species return to these habitats to modify future restoration projects to increase benefit to target species. To monitor each species individually can be quite costly, but coordinating monitoring among species can potentially reduce this cost (Tulloch et al. 2011). To cost-efficiently monitor these species, conservation organizations should

consider the ROI for a variety of monitoring strategies, including the use of indicator species which reduces the number of species that are targeted for a monitoring program (Tulloch et al. 2011).

1.2 Individual-based models

All systems can be broken down to an individual level, whether it is an atom, cell, organism, or population. Each individual is thought to have its own properties and as such will uniquely respond to its environment. Individual or agent based models (IBMs or ABMs) reflect these characteristics by modeling each individual and its unique set of characteristics separately (although still influenced by) the rest of the individuals (DeAngelis and Mooji 2005). In contrast, classical models (also referred to as state-variable models; Huston et al. 1988, Grimm 1999) are a set of equations and model the population as a whole, effectively considering each individual to be the same. Within IBMs, individuals are objects that can have unique attributes and operate under a set of rules. By modeling individuals separately with different attributes, such as they appear in reality, we can gain a better understanding of natural systems.

1.2.1 Ecology and IBMs

IBMs are useful in ecology because they allow a modeler to explore the consequences of the interactions between individuals and their environment (DeAngelis and Grimm 2014). IBMs represent a "bottom-up" approach to ecology since they use variability at the individual level to understand processes at higher levels (i.e. population and community levels). These processes include, but are not limited to, population distributions (Neeson et al. 2012), habitat selection (Railsback et al. 2003), and responses to environmental changes (Shugart et al. 1992). In contrast, classical

models which take a "top-down" approach by modeling systems at a higher level of organization (e.g. population or community) to understand the processes at the individual level (e.g. behavior and movement). By combining both the "top-down" and "bottom-up" approaches, ecologists can approach ecologic questions from a variety of directions (Grimm 1999).

The first major use of an IBM for an ecological purpose is attributed to a 1972 study by Botkin et al. on the succession of forest communities in response to canopy gaps. Although it was not until the 1990s that IBMs became prevalent in other areas of ecology (DeAngelis and Grimm 2014). Presently, while IBMs have still not "unified ecological theory" as predicted by Huston et al. in 1988, they have become increasingly common in their applications, for both research and management purposes (Grimm 1999, DeAngelis and Grimm 2014). Conservation applications of IBMs have included the distribution of invasive species (Neeson et al. 2011, Neeson et al. 2012), understanding the responses of species to global environmental changes (Shugart et al. 1992), and the management of endangered species (Letcher et al. 1998). The increased publications of IBMs (DeAngelis and Mooji 2005, DeAngelis and Grimm 2014) and the creation of protocol for standardizing how to describe IBMs (Grimm et al. 2006, Grimm et al. 2010) suggest that ecologists are using IBMs to better understand complex ecological problems.

Many of the earliest applications of IBMs in ecology focused on freshwater fish populations (Grimm 1999, DeAngelis and Mooij 2005, DeAngelis and Grimm 2014). This was driven by the need to better understand the impact of human fishing on fish recruitment (DeAngelis and Grimm 2014). IBMs allowed for a better representation of

the harvested fishes' complex population dynamics than classical models (DeAngelis and Grimm 2014). Researchers found that simulating these poorly understood population dynamics (Grimm 1999) were best accomplished at the individual level, taking advantage of the "bottom-up" IBM approach (DeAngelis and Grimm 2014). For example, DeAngelis et al. (1979), considered to be the first application of IBMs to fish populations, used an individual approach to "take into account the size distribution within age classes" for largemouth bass. This "somewhat novel technique" allowed DeAngelis et al. (1979) to accurately simulate the cannibalism that they had observed in experimental fish populations.

1.2.2 Critiques of IBMs

When modeling populations and communities there are cases in which it is more appropriate to use an IBM than a classical model, particularly for systems where general assumptions about individuals cannot be made and when simulating interactions between individuals (Judson 1994). In contrast to classical models, IBMs suffer more from less consistent documentation and general unfamiliarity with the IBM modeling approach on the part of non-modelers. Like classical computer models, IBMs are limited by computing power, however recent technological advances have reduced this concern (Judson 1994). Similarly the more complex the model (either IBM or classical) the harder it can be to interpret the results (Judson 1994). However IBMs are typically more complex than classical models because they tend to be less mathematically transparent and consist of modeled individuals with a range of behaviors and potential interactions (Judson 1994, Grimm et al. 2006). In order to fully document an IBM, each of these components must be individually explained (Judson 1994, Grimm et al. 2006).

The lack of consistent documentation has led to IBMs with incomplete and ambiguous descriptions, making these studies difficult to understand and reproduce. Fortunately in 2006, Grimm et al. created a standard protocol for describing ecological IBMs that they called "ODD" (Overview, Design concepts, and Details; see Grimm et al. 2010 for a review and update). This purpose of this protocol is to organize the descriptions of IBMs to help readers better understand IBMs and associated research (Grimm et al. 2006).

Over the last forty years IBMs have been successfully applied to a range of ecological questions and their value to ecology is increasingly appreciated by non-modelers within the discipline (DeAngelis and Grimm 2014). IBMs offer ecologists a way to simulate ecological processes from the bottom (e.g. the individual) up (e.g. population, community, ecosystem), in contrast to top-down classical models. This increasingly common approach allows ecologists to gain new insights to ecological processes and paradigms from the perspective of the individual.

1.3 Indicator Species

There is an undeniable decline in global biodiversity (Butchart et al. 2010), and efforts by conservation organizations to halt extinctions arising from human impacts are woefully underfunded (McCarthy et al. 2012). These realities often force conservation organizations to rely on "shortcuts", methods that work in theory, but may be risky when applied to the real world scenarios. One such method is the reliance on surrogate species; species that conservation organizations use to represent other species or aspects of the environment (Caro 2010). While the type of surrogate species varies, conservation organizations use these species to "represent other species or aspects of the

environment" (Wiens et al. 2008). Surrogate species include indicator (Landres et al. 1988), flagship (Lorimer 2007), umbrella (Caro 2010), keystone (Power et al. 1996), and focal species (Lambeck 1996), all of which have been used interchangeably although there are ongoing efforts to define each separately (Caro 2010). I define the term "indicator species" as a surrogate species that is used to represent the presence of another species (Caro 2010). These species are typically grouped based on co-occurrence and may be directly or indirectly linked by habitat requirements, interspecific relationships, or life history traits.

1.3.1 Selection process

Many studies have focused on how to select an indicator species (Dufrene and Legendre 1997, Rice and Rochet 2005, Azeria et al. 2009, Tulloch et al. 2011). These studies range from relying strictly on the co-occurrence of species as the basis for choosing an indicator, to more complex approaches that incorporate multiple variables such as habitat use, life history traits, and public interest in the species. The detail of the method often indicates the amount of information known about an ecosystem and the species within it. Well documented species such as birds and mammals typically have more tailored methods (Tulloch et al. 2011), while other taxa, such as insects, tend to have more general methods due to a lack of information on life histories and species distributions (Azeria et al. 2009).

The selection and evaluation of indicator species is typically dependent on the amount of data available, with methods falling along a continuum from very limited data and simpler selection methods to complex datasets and methods. In cases where there is little to no information on a set of species, researchers often rely strictly on co-

occurrence data collected through surveys. For example Azeria et al. (2009) combined a null model and hierarchical clustering to group beetles and selected indicators for predicting species richness, which did not incorporate any additional information, but relied heavily on the data that was available. However since no other data is incorporated, the resulting clusters are left up to interpretation by the researcher. Dufrene and Legendre (1997) also attempted to create an indicator selection method using limited species data, but combined it with classifications of the habitats that the specimens were found in. They used a series of multivariate statistical methods to tease apart the relationship between different species and their sites. This method allowed for easily determined site variables to help with grouping and indicator selection to make up for a lack of additional species data.

When detailed data is available, it can be incorporated in a variety of ways for not simply ecologic efficiency, but also economic cost, societal benefits (i.e. ecosystem services), and public interest. Tulloch et al. (2011) proposed an indicator selection method for Australian mammals that includes ecologic, economic, and public interest criteria. These diverse criteria select for an indicator species that is ecologically efficient, cost-effective, and likely to be supported by public interests. While these factors require a complex dataset, these different dimensions of efficiency are all important for a conservation organization to consider when they invest in an indicator species strategy. These criteria reflect both the ecologic variables and societal and funding interests that influence conservation decision-making.

1.3.2 Costs and benefits

Persistent declines in global biodiversity put increased pressure on the inadequate budgets of conservation organizations (Butchart et al. 2010, McCarthy et al. 2012). McCarthy et al. (2012) estimated the cost of "downlisting" (reclassifying to one lower category, i.e. from "endangered" to vulnerable) each species on the IUCN Red List. It would cost U.S. $4.76 billion if conservation organizations considered each species separately (i.e. species-specific planning). However, it would only cost U.S. $3.41 billion if basic cost-sharing was achieved by considering overlaps in listed species distributions. Indicator species offer a way to target areas of overlapping habitat and save money by limiting the amount of surveying, planning, and monitoring to a subset of species. This money can then be directed towards additional conservation efforts.

Indicator species can decrease the financial burden of monitoring and managing many species, although this method can lead to trade-off in the accuracy of collected data or species benefit. A species-specific conservation plan will result in the most benefit for the target species based on that budget. An indicator-guided conservation plan, in contrast, will necessarily be less effective since the distribution of an indicator is an imperfect representation of the distribution of the other species. When considering whether to use indicator species, conservation organizations must weigh the expected differences between these two types of plans to determine "how good is good enough?" (Weins et al. 2008) While our confidence in an indicator species will increase with knowledge of the species and the ecosystem, neither the funds nor time to gather this data may be available.

While some studies have shown that indicator species can be used to effectively represent the presence of other species (Azeria et al. 2009), others have found that indicator species are ineffective for their study community (Cushman et al. 2010). Indicator species are also criticized for benefiting generalist or common species more than specialists and rare species (Lawler et al. 2003). This can result from a lack of information about the distributions of the rare species or because their habitat is restricted to few small areas that an indicator species will not select for unless they share the same habitat requirements (Lawler et al. 2003). These conflicting results and lack of clear definitions for indicator species (Caro 2010), can make it hard for conservation organizations to determine if and what type of indicator species is appropriate for their purposes. These critiques suggest that other approaches should be evaluated along with indicator-guided plans, in order to inform conservation actors of the possible tradeoffs of the method they choose to implement.

1.4 Summary and the structure for the remainder of the thesis

Return-on-investment frameworks allow conservation organizations to quantify and compare the cost-effectiveness between different conservation efforts. In the two following chapters I examine the ROI for management and monitoring programs focused on restoring connectivity to fragmented freshwater ecosystems. In the first chapter (chapter two overall), I compare the ROI of three common barrier removal strategies by using an IBM to model population distributions of fishes in response to these strategies. In the second chapter (chapter three overall), I examine the ecologic trade-offs in using indicator species to plan restoration efforts in lieu of optimizing conservation efforts for each individual species. I intend to publish both of these two

chapters as papers co-authored by T. Neeson (chapter two and three) and A. Moody, A. Milt, M. Diebel, M. Herbert, M. Khoury, E. Yacobson, J. Ross, P. Doran, M. Ferris, and P. McIntyre (chapter three). Both of these chapters demonstrate the strengths and challenges of applying an ROI framework to the selection of conservation and restoration projects.

Chapter 2: Aligning dam removals and road culvert upgrades boosts conservation return-on-investment

2.1 Abstract

Dams and road culverts fragment river ecosystems worldwide by restricting the movement of aquatic species. In many watersheds, a diverse set of actors coordinates the removal of these barriers. Non-governmental organizations often focus on small dams and road culverts, while large dam removal projects are coordinated by federal agencies or coalitions of partners. Here we evaluate the return-on-investment of these strategies by exploring a continuum of methods for selecting barrier removal projects, ranging from a focus on many small barrier removal projects to a few large ones. First, we used estimated removal costs of more than 100,000 barriers in the North American Great Lakes to construct economically realistic barrier removal scenarios. We then simulated the movement of stream-resident and anadromous fishes through river networks with a few large dam removals, many road culvert retrofits, or a mix of both. We found that the strategy of removing both dams and road culverts had the greatest potential to benefit both stream-resident and anadromous fishes, but only when projects were aligned longitudinally within the river network. Our results demonstrate the importance of allocating conservation resources to both small and large restoration projects, and highlight a need for increased coordination and communication among the many different organizations investing in barrier removals.

2.2 Introduction

Habitat fragmentation is a leading cause of global biodiversity decline (Fischer and Lindenmayer 2007, Perkin et al. 2015). The impacts of fragmentation are

particularly devastating for many freshwater fishes (Kanehl et al. 1997, Warren and

Pardew 1998, Catalano et al. 2007) because they are restricted to river networks and

cannot disperse over land (Fagan 2002); consequently, a single barrier in a river

network can completely block fish movements. In most fragmented watersheds, barriers

include dams and road crossings (Fig. 2.1), both of which are detrimental to stream

fishes (Warren and Pardew 1998, Nilsson et al. 2005, Bouska and Paukert 2010,

Januchowski-Hartley et al. 2013). To remedy this situation, local and national

conservation organizations are increasingly interested in restoring freshwater

connectivity by removing dams and retrofitting road culverts (Grossman 2002,

Magilligan et al. 2016). In most cases, completed barrier removal projects have been

selected by a process of strategic opportunism (Magilligan et al. 2016). This occurs

when local communities or barrier owners work with conservation organizations to

remove a barrier, typically one with a low economic cost (Magilligan et al. 2016).

In many watersheds, investments in restoring ecosystem connectivity are

coordinated by a diverse group of governmental natural resource management agencies

and non-governmental conservation organizations with varying budgets, focal

geographies, and species priorities (Neeson et al. 2015). Due to diverse institutional

constraints, different organizations often prefer to focus on different classes of barrier

removal projects, barrier removal strategies tend to exist along a continuum, ranging

from efforts to remove a small number of large dams, to a preference for many small

dam and road culvert projects. Large dam removals are often complex, costly, highly

politicized, and can take years of effort by conservation and government organizations

to be implemented (Grossman 2002, Wildman 2013). Notable examples include the

recently removed Elwha Dam in Washington (Service 2011) and the ongoing

deliberation concerning the Rodman Dam in Florida (Grossman 2002). Though

challenging to carry out, large dam removals can be particularly beneficial for

anadromous fish species, providing a dramatic increase in access to the river network

and upstream spawning habitat. At the opposite end of the spectrum, local watershed-

level organizations tend to focus on small dam removals and road culvert upgrades.

Although removing these structures can still be contentious depending on ownership

and location (Grossman 2002, Fox et al. 2016), they are typically much cheaper to

execute and less controversial. Barrier removals in small headwater streams will not aid

anadromous species if the mouth of the tributary remains blocked, but can still benefit

stream-resident species by reconnecting previously isolated sub-populations and

increasing accessible habitat (Bednarek 2001, Catalano et al. 2007).

Given the growing interest in restoring ecosystem connectivity and a general

lack of available funds for meeting conservation needs (McCarthy et al. 2012), it is

critical to identify strategies that enable a diverse set of natural resource managers to

collectively maximize return-on-investment (ROI; Murdoch et al. 2007) from barrier

removal projects. Although any barrier removal will improve connectivity, benefits may

vary dramatically depending on available habitat for beneficiary species, spatial context

of the barrier within the river network, and the set of other barrier removal projects

completed or planned within the watershed. Inefficiencies can arise from lack of

communication between agencies focused on different species or project classes

(O'Hanley et al. 2013), or from piecemeal planning of projects leading to missed

opportunities for aligning barrier removals (Neeson et al. 2015). Furthermore, if species

dispersal patterns, life history strategies, and habitats are not considered while planning a barrier removal, the benefits can be limited to only a few species.

Here, we calculate the ROI for three common conservation strategies: the removal a few large dams, the removal of many road culverts, and a mixed strategy, consisting of both dam and road culvert removals. To examine fish population response to barrier removals under each of these three strategies, we created an individual-based model (IBM) of stream-resident and anadromous fishes in a fragmented river network The IBM approach allows us to examine variability in restoration efficiency resulting from spatial alignment of barrier removals, as well as variability created by stochasticity in the spatial dynamics of the fish populations themselves. Focusing on this combined variability, we investigate the best-case, worst-case, and average outcomes in terms of population distributions for stream-resident and anadromous fishes under these three conservation strategies.

2.3 Methods

We created an IBM to simulate movement patterns of stream-resident and anadromous fishes through a fragmented river network. The model consists of three components: a river network, a fish population, and a set of barriers that block fish movements. The model is parameterized with barrier characteristics and estimated removal costs derived from a database of more than 100,000 barriers in the North American Great Lakes (Neeson et al. 2015). Thus, our barrier removal scenarios reflect the true range of project choices available to practitioners working in a large freshwater ecosystem. We modeled stream-resident and anadromous fishes separately, which enabled us to describe the response of each type of fish to the barrier removal strategies.

Our abstract approach is designed to be applicable to a wide range of real river networks, each uniquely ecologically and environmentally complex. While the exact benefit of any approach will vary from river to river, the general long-term trends that we find should be consistent for most river networks.

2.3.1 River network submodel

We used a symmetric, dendritic river network with fifteen reaches for all model runs (Fig. 2.2A). We define a reach as the section of river between two confluences, and assume that each reach in the network provides an equivalent amount of fish habitat (Fig. 2.2B). Each reach is directly connected to a maximum of three other reaches, one downstream and two upstream. In our model, we assume that a barrier, if present, completely blocks movement of fishes between reaches, and that barrier removal restores full movement between reaches (Fig. 2.2C). Following Perkin et al. (2013), barriers are placed directly between reaches. We refer to each barrier according to the Strahler order of the upstream reach, such that a barrier between a first-order and a second-order reach is a first-order barrier (Fig. 2.1C).

2.3.2 Fish submodel

We hypothesized that the way in which individual fish interact with the complex shape of a fragmented river network would play a key role in structuring fish distributions (Neeson et al. 2011, 2012). Accordingly, we chose an IBM approach because it allowed us to capture these individual interactions. The model uses a weekly time step, which approximates a month long migration from the mouth of our river network to the first-order headwaters (Okland et al. 2001). Though we recognize that movement rates vary considerably among species and individuals, our intent is to focus

on long-term impacts of barrier removals on equilibrium distributions of stream fishes, which will be insensitive to the speed at which individuals colonize recently-connected habitat.

We choose to model two general fish classes, stream-resident and anadromous, each of which includes a wide range of fish species with their own variations on the movement rules discussed here. Since most of the variation in the movement behaviors (e.g. natal homing, seasonal migrations, and movement rates) among these species tend to impact short-term population distributions, we feel that these simplified movement rules are sufficient to explore the long-term impacts of barrier removals for many of these species. Stream-resident fishes remain in the river network for their entire lifespan and move both downstream and upstream at will (Funk 1957). To represent this behavior in our model, at each time step, stream-resident fishes have an equal chance of moving to any neighboring upstream or downstream reach that is accessible (i.e., no barrier is present) or remaining in the reach they currently occupy. Anadromous fishes spend their lives in a large body of water (i.e. an ocean or large lake) and then migrate into the river network to spawn (Myers 1949). Our movement rules for anadromous fishes are similar to the ones for stream-resident fishes, except that they perform spawning runs and all movement is either upstream (prior to spawning) or downstream (post-spawning). The selection of a spawning site occurs probabilistically in any reach or with certainty when a fish reaches a point at which no further upstream travel is possible (i.e. when an individual fish reaches a first-order reach or further upstream movement is blocked by a barrier).

Anadromous fish always begin at the mouth of the river network and return there during downstream migrations. In the case of stream-resident fish, the entire population begins each run in a single reach; this represents a highly isolated stream-resident population constrained to a fraction of their historical habitat. We hypothesized that the benefits of a set of barrier removals for stream-resident fish would depend on both the location of barrier removals and the location of the isolated population within the river network. Accordingly, we performed separate runs with the entire stream-resident population beginning in each of the fifteen reaches.

In describing the effects of barrier removals on fishes, we focused on the evenness of the distribution of individuals across the entire river network. For the purposes of this study, we assumed that all reaches within the network had equal habitat and available resources, so that when no barriers were present stream-resident fishes would follow an ideal free distribution (Fretwell and Lucas, 1969) and distribute themselves equally throughout the river network. While habitat and resources are likely to vary across reaches in real river networks, their distribution is unlikely to vary systematically and will be specific to the targeted tributary. In fragmented river networks, fish distributions are often highly skewed because barriers inhibit dispersal of individuals towards an ideal free distribution (Perkin et al., 2015), which increases density-dependent effects and, at the population level, constitutes an underutilization of the total amount of suitable habitat available in the river network. To quantify the degree of aggregation of the fish population in each model run, we calculated the standard deviation of fish abundance among reaches either after the final time step (for stream-resident fish) or after the last step of the final upstream migration (for

anadromous fish). A high standard deviation was indicative of a tightly clustered

population with access to only one or a few reaches, while a standard deviation of zero

represents a perfectly even distribution of fish among all reaches in the river network.

2.3.3 Barrier removal scenarios

For both dams and road culverts, the size of a barrier and cost of removing it

generally increases with stream size. To determine in more detail how the cost of a

barrier removal depends on stream size, we analyzed a database of estimated removal

costs for 3 954 dams and 99 940 road-stream crossings in tributaries of the North

American Great Lakes (Neeson et al. 2015). Barriers on small streams (Strahler order 1

or 2) were primarily road-stream crossings (97%) and had an average removal cost of

US$ 125 073 (n = 86 541), including the cost of material and labor for removing the

road culvert and replacing it with a fully passable bridge. Barrier removal costs

averaged US$ 197 236 (n = 15 765) on medium streams (Strahler order 3 or 4) and

US$320 110 (n = 310) on large streams (Strahler order ≥ 5). In this data set, all barriers

on large streams were dams; all road-stream crossings on high order streams in this

dataset were bridges and fully passable to aquatic organisms, thus not candidates for

removal.

Using average prices as a starting point, we modeled the removal costs of small,

medium, and large barriers as US$ 100 k, US$ 200 k, and US$ 300 k, respectively. This

modest deviation from the true project costs enabled us to compare barrier removal

scenarios involving an integer number of barriers. For example, a budget of US$ 300 k

might be spent on one large, three small, or one medium and one small project.

Furthermore, given that 97% of barriers on small streams were road culverts, we

henceforth refer to all small barriers as road culverts. Similarly, we refer to all barriers on large streams as large dams given that road culverts do not occur on any large streams in the Great Lakes.

Using these estimates of barrier characteristics and costs, we compared three barrier removal strategies commonly used by conservation practitioners. In each case, we fully allocate a total budget of US$600 k. This budget represents the maximum budget that an organization would spend on removing large dams in this network, any additional funds would be directed to removing dams in another tributary. The first strategy entails removing both large dams near the mouth of the river network (Fig. 2.3A). The second is a mixed strategy, entailing the removal of one large dam, one road culvert, and one medium barrier (Fig. 2.3B). The final strategy involves the removal of six road culverts (Fig. 2.3C). For comparison, we completed an additional set of runs on a free-flowing river network without barriers (Fig. 2.1B).

Note that multiple permutations of the second (n = 64) and third (n =28) strategies are possible, and the benefits to stream fishes may differ dramatically among the permutations. For example, possible configurations of the mixed strategy include the spatial alignment of all three projects (Fig. 2.4A), the alignment of two projects (Fig. 2.4B), or of none (Fig. 2.4C). To understand the range of outcomes possible under each strategy, we modeled all possible permutations of each strategy throughout the network. Fig. 2.3 shows three examples of different configurations of the mixed removal strategy (Fig. 2.2B), in which all (Fig. 2.3A), two (Fig. 2.3B), or none (Fig. 2.3C) of the barrier removals are coordinated.

2.4 Results

We found clear differences in the average ROI of the three conservation

strategies, and between the best-case and worst-case outcomes for each strategy.

Considering the average outcomes, no single strategy was best for both stream-resident

and anadromous fishes. On average, the best strategy for stream-resident fishes was the

removal of six road culverts (Fig. 2.5A). However, anadromous fishes never benefitted

from this strategy because both large dams remained in place, blocking any upstream

migrations (Fig. 2.5B). The best strategy on average for anadromous fishes was the

removal of two large dams (Fig. 2.5B), but this strategy had low average benefit for

stream-resident fishes (Fig. 2.5A).

In contrast to these average outcomes, the best possible outcome for both

stream-resident and anadromous fishes occurred under the mixed strategy (i.e., the

removal of one small, one medium, and one large barrier; Fig. 2.5A, B). This single

strategy, when optimally executed, provided the maximum possible benefit to stream-

resident and anadromous fishes simultaneously. Worst-case outcomes for stream

resident fishes occurred under all three strategies, highlighting the broad range of

outcomes possible under each strategy.

For all three strategies, best-case outcomes depended on the spatial arrangement

of barrier removals. Benefits for stream-resident and anadromous fishes increased when

removals were aligned longitudinally in the river (i.e., directly up- or downstream of

each other), resulting in more continuous accessible habitat. The best-case scenario of

the mixed removal strategy heavily depended on the spatial alignment of the barrier

removals. When all three barrier removals were coordinated (as in Fig. 2.4A) both

stream-resident and anadromous fishes experienced the overall greatest benefit (peak a in Fig. 2.6A, B). If only two or none of the removals aligned (Fig. 2.4B, C) benefit decreased (peaks b and c in Fig. 2.6A, B). The removal of six road culverts was most effective for stream-resident species when both barriers upstream of the same second-order reach were removed (as in Fig. 2.3C). While the removal of large dams was not typically beneficial for stream-resident species, if the stream-resident population was located near the mouth of the river (3rd or 4th order reaches) they were able to benefit from the large dam removals along with the anadromous populations.

2.5 Discussion

Our results show clear differences in the ROI from three common conservation strategies: removing a few large dams, many road culverts, or a mix of both. The greatest benefit for stream-resident and anadromous fishes occurred under the mixed removal strategy, but only when the removals were aligned longitudinally within the river network. When barrier removals were not aligned, as if by piecemeal or individualistic planning, benefit decreased for both stream-resident and anadromous fishes. When the conservation strategies targeted a single class of barriers (i.e., the removal of two large dams or of six road culverts) only a single fish type benefited. On average, the large dam removal strategy was the most beneficial for anadromous fishes, but the least beneficial for stream-resident species. In contrast, removing road culverts was, on average, the best-case scenario for stream-resident fishes, but under this scenario anadromous fishes never benefited.

Though a mixed removal strategy can provide the greatest return-on-investment, effective implementation of this strategy requires the coordinated efforts of practitioners

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from many different organizations. It also provides an opportunity to leverage the expertise of each type of organization. Local organizations often have a good understanding of where fish populations have historically occurred and of the level of support from the local community for a particular project. As a result, local conservation organizations are often ideally positioned for detailed evaluation of the ecological, societal, and economic costs and benefits of a particular barrier removal (Grossman 2002, Fox et al. 2016). Conversely, large-scale planning initiatives may ignore cultural ties to dams, an error that can result in removals being delayed or stopped completely (Jorgensen and Renofalt 2012, Fox et al. 2016). At the same time, the regional perspective of federal agencies and national NGOs can enable these groups to identify high-priority watersheds and focal regions for investment.

Our model does not account for spatial variation in environmental factors such as habitat type and quality, sociopolitical factors like ownership and barrier degradation, or variation barrier impacts including passability. Consideration of these factors is known to be critical for evaluating the impact and feasibility of particular barrier removals (Poff and Hart 2002, Zheng and Hobbs 2013, Januchowski-Hartley et al. 2014, Fox et al., 2016). However, these factors are unlikely to vary in a systematic way across river networks; as a result, inclusion of these additional factors into our model is unlikely to alter our determination of the most cost-effective strategy.

Our results complement existing approaches for prioritizing barrier removals by providing conservation practitioners with general guidelines for project selection. For example, both federal agencies and local NGOs commonly use optimization models to identify high-priority barrier removal projects (Zheng et al., 2009, O'Hanley et al. 2013,

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Neeson et al. 2015). Though optimization models can identify a mathematically optimal set of projects, implementing these conservation plans at smaller scales is often complicated by local politics (Magilligan et al. 2016). Particularly with dams, ownership can be ambiguous and the dam itself may have historical significance for the surrounding community (Fox et al. 2016), but neither factor is accounted for by optimization models and can cause opposition to the removal among the local community. Future studies should be mindful of these factors and try to incorporate them, as they are likely to have a large impact on the implementation and success of barrier removal projects. Though optimization models are increasingly used to identify a set of high-priority projects, conservation practitioners in practice often implement an opportunistic strategy, in which organizations target barriers that already need to be replaced or have cooperating owners (Magilligan et al. 2016). As a result, the set of projects completed deviates from the one prescribed by an optimization model. Our study complements both barrier removal optimization studies and opportunistic approaches by providing conservation practitioners with a general strategy to follow to maximize conservation outcomes: when project selection must depart from the recommendations of an optimization model, conservation practitioners should seek a balance of large and small projects, and ensure that they are spatially aligned. Moreover, decision-makers could follow this general strategy while looking for opportunities to avoid known areas of socio-political contention.

2.6 Figures

Figure 2.1: Road culverts can block the upstream movement of fishes. The presence of an outlet drop (shown here) and increased water velocity are the two most common means by which road culverts block fish movement (Janchowski-Hartley et al. 2014). Photo credit: N. Sleight.
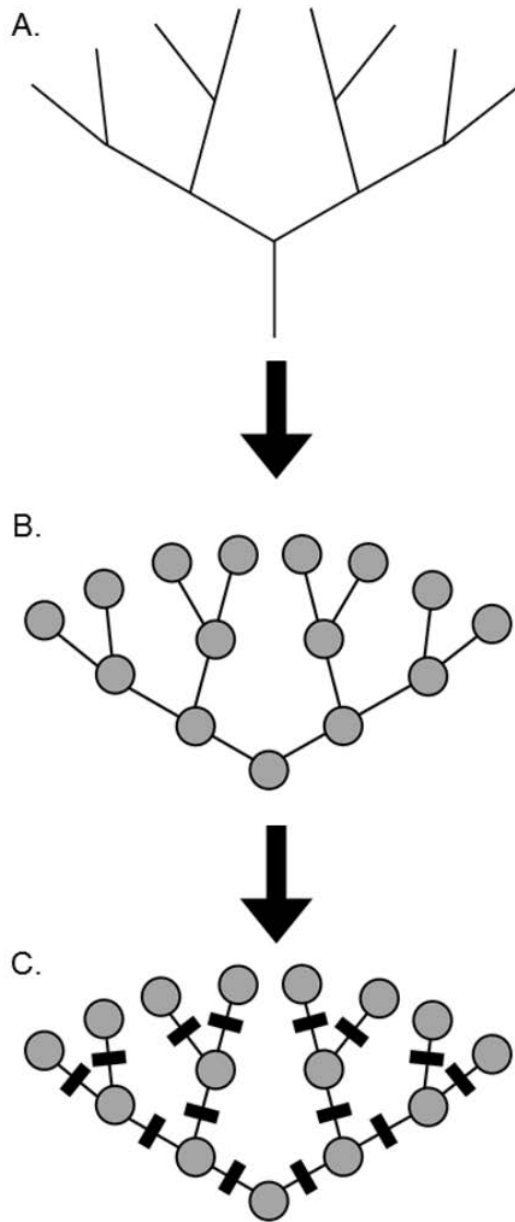
Figure 2.2: The river network (A) was transformed to a patch-based graph (B) by converting each reach into a node (grey circles); links represent connections between reaches (Eros et al. 2012). Impassable barriers (black bars) were added to represent dams and road culverts (C).
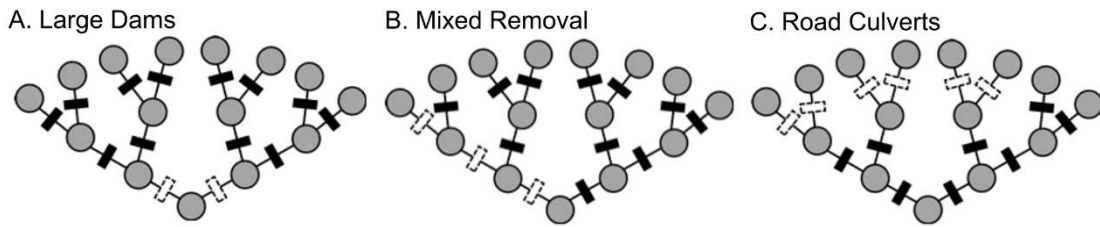
Figure 2.3: Three barrier removal strategies, each with a total cost of US$ 600 k. Black bars indicate barriers, white bars represent removed barriers. The large dams strategy (A) consists of removal of the two large third-order barriers, at a cost of US$ 300 k each. The mixed removal strategy (B) involves the removal of one large, one medium, and one small barrier at costs of US$ 300 k, US$ 200 k, and US$ 100 k, respectively. The road culverts strategy (C) consists of removing six of the first-order barriers at a cost of US$ 100 k each.
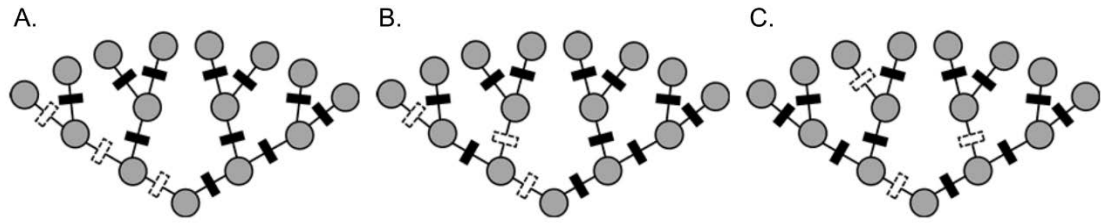
Figure 2.4: Three of the possible permutations of the mixed removal strategy (Fig. 2.3C). In (A), all three barriers are aligned longitudinally within the river network. In (B), only the largest two projects are aligned longitudinally. (C) represents a scenario in which none of the removals are aligned.
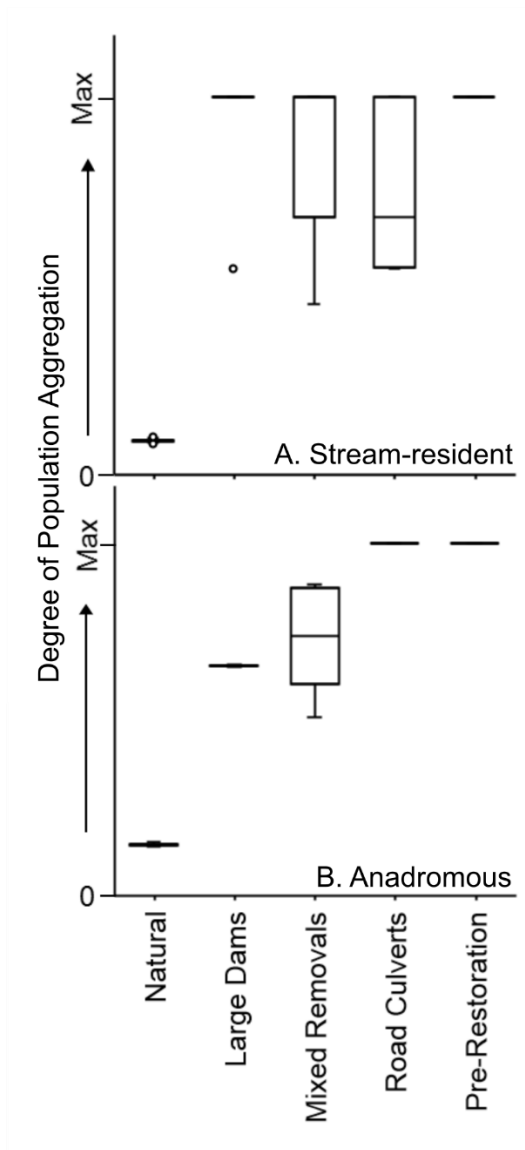
Figure 2.5: Degree of aggregation of stream-resident (A) and anadromous (B) fishes in river networks with no barriers (natural), under three barrier removal strategies (large dams, mixed removals, and road culverts), and with all barriers present (pre-restoration). Degree of population aggregation was calculated as the standard deviation of fish abundance between reaches. The maximum degree of aggregation occurs when the entire fish population is confined to a single reach, while 0 population aggregation indicates a population spread equally among all 15 reaches.
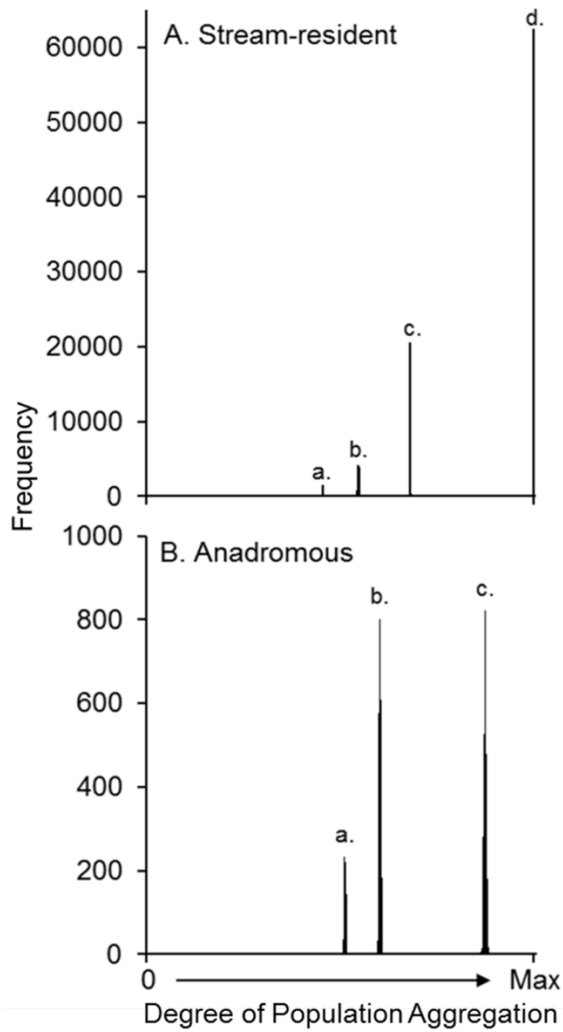
Figure 2.6: Histogram of stream-resident (A) and anadromous (B) population aggregation under all possible permutations of the mixed removal strategy. Peak 'a' occurs under barrier removal scenarios in which all three barrier removals are aligned longitudinally in the river network (as in Fig. 2.4A). Peak 'b' represents the alignment of two removals (as in Fig. 2.4B), and peak 'c' represents no alignment (as in Fig. 2.4C). Peak 'd' occurs when barrier removals occur in reaches that are inaccessible to stream-resident fishes and thus provide no benefit.

Chapter 3: Indicator species can successfully guide restoration efforts for migratory fishes in the Great Lakes

3.1 Abstract

Due to a lack of resources, conservation organizations often depend on a small group of species to indicate the presence of other species. Extensive research has gone into methods for selecting these "indicator" species, but few studies have directly measured the performance of indicator species in guiding conservation actions. Here, we evaluated whether a small number of indicator species could be used to select barrier removal projects to benefit the entire migratory fish community in the highly fragmented North American Great Lakes Basin. First, we compiled data on the historical distributions of 35 species of native anadromous fishes as well as upstream habitat and removals costs for over 100,000 dams and road culverts. Next we used k-means clusters to identify five groups of co-occurring species and selected an indicator species for each cluster based on within-group co-occurrence. To evaluate the utility of these five indicator species, we compared 1) the habitat gain that each of the 35 native migratory species could achieve if barrier removals were prioritized specifically for the benefit of that species, 2) the habitat gain that the 35 species could achieve if barrier removals were prioritized specifically for the benefit of their respective indicator species, and 3) total stream area. We found that under plans selected on the basis of indicator species, majority of species retained over 75% of the habitat they saw under their own prioritizations. However for a few species, prioritizing for indicator species resulted in very little habitat gain. Similar results from maximizing stream area, demonstrate the value of large species-specific distribution datasets in increasing

efficacy in conservation efforts for a wide range of species. Overall, our findings

revealed that indicator species could be an efficient means for planning restoration

efforts for most species of migratory fishes in the Great Lakes.

3.2 Introduction

Persistent decline of global biodiversity (Butchart et al. 2010) calls for an

increase in conservation and restoration efforts. Due to a lack of monetary and human

resources (McCarthy et al. 2012) it is impossible for conservation organizations to keep

an accurate and current inventory of all species in an ecosystem (the "Wallacean

shortfall"; Whittaker et al. 2005, Bini et al. 2006). Instead, conservation and wildlife

management practices often rely on certain species to indicate the presence of other

species within an ecosystem (hereafter indicator species; Caro 2010). Conservation

actors invest their resources towards benefiting and monitoring the indicator species and

act under the assumption that the indicator species accurately represents the other

species.

Though there is extensive literature on different ways to select indicator species

(Dufrene and Legendre 1997, Rice and Rochet 2005, Azeria et al. 2009, Tulloch et al.

2011), few authors have compared the relative efficiency (i.e., the return on

conservation investments) of using indicator species to guide conservation actions.

When conservation efforts are focused on a single species, that species is expected to

receive the maximum benefit possible for that budget (i.e., the greatest return-on-

investment). This benefit from species-specific planning can serve as a baseline to

which we can compare the return on investments for conservation actions selected on

the basis of indicator species. Plans guided by indicator species will necessarily be less

beneficial than the species-specific plans since an indicator species does not perfectly represent another species. However the difference between these two return-on-investments can represent how efficient an indicator species is at representing another species. A high relative efficiency would suggest that an indicator species is able to guide conservation actions for a species, while a low relative efficiency would suggest that conservation actors should consider a different approach in order to better benefit the represented species.

One area where indicators species could be a valuable way for directing conservation efforts is the North America Great Lakes. The Great Lakes are the largest freshwater ecosystem in the world and supports a $7 billion dollar recreational fishery industry (Southwick Associates 2012). In addition, the Great Lakes provide important ecosystem services for local communities (Allan et al. 2015) and support more than 35 species of native anadromous fishes. These fishes are ecologically diverse ranging in size classes, life history, and habitat requirements, making single basin-wide management strategies potentially inefficient. In order to efficiently manage these species, a suite of management strategies, such as a set of indicator species, is needed to benefit the ecosystem as a whole.

Growing interest in removing dams and road culverts from Great Lakes tributaries provides an opportunity to explore the relative efficiency of indicator species for directing conservation investments in the Great Lakes. The Great Lakes, along with over half of all large river systems globally (Nilsson et al. 2005), are heavily fragmented by dams and road culverts. Over half of the upstream habitat, including historic spawning habitat, is no longer accessible to anadromous fishes found in the Great Lakes

(Neeson et al. 2015). New conservation efforts are focusing on removing these barriers, but planning and evaluating these efforts can be difficult due to both the sheer number of barriers and species. Conservation organizations can use a set of indicator species to efficiently select barrier removal projects and to monitor areas after restoration.

Here, we use a return-on-investment framework to quantify the relative efficiency of using indicator species to guide the selection of dam removals and road culverts upgrades across the Great Lakes basin. We first used historical records of native anadromous fish distributions across the Great Lakes basin to identify clusters of species that typically co-occur. To investigate the biological basis for these clusters, we examined water temperature preferences and commonness and rarity of species in each cluster. We then chose an indicator species to represent each cluster by identifying the species with the highest mean co-occurrence with other species in its cluster. To explore the utility of these indicator species for guiding barrier removals, we compared habitat gains for each individual species when barrier removals were optimized for: the species itself, an indicator species, and total stream area. The comparison between optimizations for the species itself and an indicator species allowed us to quantify the relative efficiency of using indicator species, while total stream area served as a null model for indicator species.

3.3 Methods

3.3.1 Clustering and co-occurrence dataset

We compiled a data set of historical distributions of 35 native Great Lakes fishes to determine species co-occurrence. To create this data set, we compiled records from 12 different sources spanning the years 1823 to 2016 across the Great Lakes basin. In

total, our data set incorporates 942,045 individual point records of fish presences. For the purposes of our study, we spatially aggregated the data to the tributary level to account for all potential habitat in a tributary. Therefore if a species had been recorded anywhere within a tributary, we considered the entire tributary area as potential habitat for that species. If there was no record of a species within a tributary we considered that species to be absent.

To identify groups of species that historically co-occurred together, we used a k-means clustering algorithm. The k-means algorithm groups the species into a given k number of clusters based on the tributaries where species were historically present. We grouped the species into 5 clusters to provide a small enough subset of species that could be implemented for management and large enough for the clusters to be ecologically meaningful.

3.3.2 Selecting indicators

We selected an indicator species for each cluster based on which species had the greatest degree of co-occurrence with other species within their cluster. This insured that the indicator species well represented the distributions other species within the cluster. We measured co-occurrence using proportional similarity (PS; Schoener 1970), which accounts for both presences and absences and is the most robust method for measuring co-occurrence (Neeson et al. 2015). In our data set, one cluster contained only two species (Brook Trout and Longnose Dace). Because PS is necessarily equal for these two species (i.e., PS is a symmetric measure of co-occurrence), we selected Brook Trout to be the indicator species based on expert opinion.

3.3.3 Ecological basis for clusters

To explore whether there was an ecological basis for the five species clusters

that were identified, we quantified the commonness or rarity of each species and the

thermal preferences of each species. We chose to focus on commonness given that the

most common species, White Sucker, occurs in more than 100 times as many tributaries

as the rarest species, River Darter (Table 3.1). Since the most common species by

definition have low occurrence with the rarest species, we reasoned that commonness or

rarity would be a key driver in our clustering analysis. We chose to focus on thermal

preferences because stream temperature is a particularly strong determinate of species

occurrence (Wehrly et al. 2003, Lyons et al. 2009). Studies have often categorized

species "warmwater", "coolwater" or "coldwater" based on thermal requirements

(Lyons et al. 2009, Wehrly et al. 2003, Magnuson et al. 1979). We assigned each

species to a temperature guild based on the classification by David et al. (in prep.), and

assigned numerical values to these three guilds by giving the warm, cool, and coldwater

guilds a value of 1, 0, and -1, respectively (Table 3.1).

3.3.4 Conservation efficiency of indicator species

We evaluated the effectiveness of indicator species to guide conservation

investments in removing dams and road crossing to restore tributary access for native

migratory fishes. We used a data set of the location, removal costs and upstream

tributary area for more than 100,000 dams and road crossings across the Great Lakes

basin as input for a barrier removal optimization model (Neeson et al. 2015). This

model identifies the set of barrier removal projects that would provide the greatest

increase in accessible tributary area for a given budget. Tributary area (km2) was

calculated based on drainage area and tributary length. In this context, we define a single tributary as all of the river network that shares a common pour point or outlet into a Great Lake. We defined potential habitat for each species as the tributaries where a species had been historically present, if a species was not historically present in a tributary based on our dataset then that tributary was not considered to be potential habitat.

Using this optimization model, we compared each species' habitat gains under three prioritization strategies: when barrier removals were prioritized for that species itself (strategy "s1"); when barrier removals were prioritized to maximize gains for that species' indicator species (strategy "s2"); and when removals were prioritized to maximize accessible stream area without respect to species' distributions (strategy "s3"). We considered habitat gains when barrier removals were optimized for the species itself (s1) as a best case scenario, since this would be the maximum amount of habitat a species could possibly to gain for a particular budget. To calculate the relative efficiency of using indicator species to guide conservation investments, we compared habitat gains under s1 to the habitat gain a species would see when barrier removals were optimized for their respective indicator species (s2). When this ratio was close to 1 we considered a species to be well represented by its indicator species. When habitat gains under s1 were much larger than under s2, the indicator species was an ineffective basis for prioritizing barrier removals.

Our third prioritization strategy (choosing barrier removals to maximize stream area without respect to species' distributions; s3) serves as a null model in two ways. First, if species gained similar or more habitat when maximizing stream than under an

indicator species it would suggest that the selected indicator species is inefficient.

Second, our s3 strategy provides a means for assessing the value of our historical

species distribution data set. If habitat gains for each species under s1 are only

marginally better than under s3, our efforts to compile this species data added little

conservation value, in regards to selecting barrier removal projects, which could not

have been achieved simply by aiming to maximize accessible stream area. Conversely,

if habitat gains under s1 are much larger than under s3, this would indicate that

consideration of species' distributions is essential for cost-effective barrier removal

planning.

Since the species differed widely in historic distributions, and therefore amount

of potential habitat, comparing habitat gains alone would underrepresent trade-offs by

common species and over emphasize trade-offs for rare species. To account for

different distributions, we calculated a relative habitat gain for each species by dividing

the habitat gain under s1 by the habitat gain under s2. This gave us a percentage

(ranging from 0-100%) with lower values signifying greater trade-offs when indicator

species were optimized for than species with higher relative habitat gain values. For

comparison we also calculated relative habitat gain for maximizing stream area.

3.4 Results

We identified five clusters of co-occurring species (Table 3.1). Clusters ranged

in size from a single species (in the case of White Sucker) to 19 species (in the case of

cluster 5). Clusters also differed in the degree of co-occurrence of member species.

Brook Trout and Longnose Dace (cluster 2) had one of the highest PS between any two

species and the highest for a cluster (0.65; Table 3.1), while cluster 5 had the lowest

average co-occurrence between its species (mean PS: 0.21 ± 0.02; Table 1). Based on the greatest co-occurrence with other species in their respective clusters, Northern Pike, White Sucker, Brook Trout, Burbot, and Channel Catfish were selected as indicator species (Table 3.1).

Strong trends in commonness and thermal preferences within each of the clusters demonstrate that our clusters have an ecological basis (Fig. 3.1, Table 3.1). The most common species was White Sucker (1016 tributaries), so much so that it formed an individual cluster (Fig. 3.1, Table 3.1). In contrast, cluster 5 contained the rarest species which occurred, on average, in only 74 tributaries. Clusters were distinguished by the thermal guilds of their species, with all of the warmwater species in cluster 5 and the majority of coldwater species in cluster 3. Coolwater species were found in all of the clusters, but included all of the species in cluster 1. Although coolwater species were present in all of the clusters, cluster 1 was the only cluster entirely comprised of coolwater species.

Overall indicator species were fairly effective at coordinating barrier removals for the species they represented. Not including the indicator species themselves, 18 species had a relative habitat gain of 75% or greater for a budget of $25M (Fig. 3.2). With a single exception, all species in clusters 1, 2, 3, and 4 had relative habitat gains above 90% (Fig. 3.2A-C). Cluster 5 was the only cluster where large discrepancies were seen in the relative habitat gains (Fig. 3.2D). Two-thirds of the cluster were not well represented by Channel Catfish and had relative habitat gains of less than 75%. Six of these species had a relative habitat gain of less than 50%, with Channel Darter having the lowest relative gain at just 14.2% (Fig. 3.2D).

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Relative habitat gains were consistent across budgets when indicator species were used to direct barrier removals (s2), but varied when stream area was maximized (s3). Species only saw an average difference in relative habitat gain of 6.3% (± 1.1%) between a budget of $5M and $25M (Fig. 3.3) for s2. In contrast, for s3 there was 20.4% (± 3.7%) average difference in relative habitat gain between budgets of $5M and $25M (Fig. 3.4). While species tended to gain similar amounts of habitat when maximizing stream area as under indicator species, the greatest differences were seen in the fifth cluster, particularly at lower budgets (Fig. 3.5). For a budget of $5M, twice as many species had relative habitat gains of less than 50% under maximizing stream area then under indicator species (Fig. 3.5).

3.5 Discussion

Here we demonstrated strong support for using indicator species to guide conservation efforts for native anadromous fishes. We grouped the 35 species into 5 clusters, each of which were biologically supported by trends in thermal guilds and commonness, and selected an indicator species from each cluster based on greatest average co-occurrence with the other cluster species. Overall, we found that the indicator species were able to efficiently guide the removal of dams and road-culverts within Great Lakes tributaries for the majority of the species they represented. We also demonstrated that species distribution datasets, like the historic one used in these analyses, can increase the efficiency of conservation efforts.

We found strong trends in thermal guilds and commonness within each cluster, suggesting that there is a biological basis explaining why different species were grouped together. Both thermal preferences and commonness present key components of species

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distributions. Previous studies have shown that species distributions in Great Lakes tributaries are often characterized and limited by thermal preferences (Wehrly et al. 2003, Lyons et al. 2009). With species of similar thermal preferences (i.e. a thermal guild) often co-occurring, creating consistent species assemblages across streams with similar water temperatures (Wehrly et al. 2003, Lyons et al. 2009). Trends in commonness were evident across the clusters, however further research would be need to determine an underlying ecological explanation for the commonness of each species within the dataset.

Here we demonstrated that indicator species can effectively guide barrier removal projects in Great Lakes tributaries to increase freshwater connectivity for native anadromous fishes. While barrier removals were the only type of conservation effort that we considered, this set of indicator species may be effective for guiding a wide range of conservation projects, such as habitat restoration and species monitoring. Because we aggregated our historic distributions to the tributary level, these indicator species will be most effective for large scale (e.g. basin-wide) conservation planning. For conservation projects at smaller scales (e.g. selecting projects within a tributary), conservation organizations should consider choosing a new set of indicators, by using species distributions within their area of interest.

Our results showed that incorporating species distribution data into conservation planning can lead to increased conservation efficiency in comparison to when steam area alone is maximized. Under our maximizing stream area scenario (s3), there was a large range in efficiency among species, particularly at the smallest budget. Barrier removal projects vary in the amount of accessible upstream habitat that they would

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provide (Janchowski-Hartley et al. 2013, Neeson et al. 2015), such that barrier removal projects on tributaries with fewer barriers are likely to be selected for when maximizing stream area. However since barriers are not equally distributed across the Great Lakes (Janchowski-Hartley et al. 2013, Neeson et al. 2015), barrier removal plans that only consider increases in upstream habitat may indirectly target benefits to a subset or group of fishes (e.g. thermal guilds). Conservation actors should consider different species distributions when planning basin-wide conservation efforts to ensure efficiencies for a wide variety of fishes.

Indicator species can be an efficient way of planning barrier removal projects in the Great Lakes, additionally they may also be a cost-effective alternative to species-specific planning. To determine if indicator species are cost-effective, conservation actors would need to compare the cost of a basin-wide survey for an indicator species, to the cost of surveying the indicator species and all of the species it represents. The money that a conservation organization could save by just surveying the indicator species could then be invested into more barrier removals instead of additional species surveys. An indicator species could be considered cost-effective if plans selected on the basis of indicator species, including the potential money saved on species surveying, yielded greater habitat gains for the represented species than the species-specific plans.

3.6 Tables and Figures

Table 3.1: Cluster membership of fishes along with the average proportional similarly (PS) with other species in the cluster, which was used to measure species co-occurrence. To determine the biologic basis for each cluster, we considered species commonness (number of tributaries a species occurs in) and thermal preferences (thermal guild, minima, and maxima; David et al. in prep).

Cluster	Species Name	Common Name	Average PS	Commonness	Thermal Guild
1	*Esox lucius*	**Northern Pike**	0.571	500	coolwater
	Micropterus dolomieu	Smallmouth Bass	0.551	419	coolwater
	Notropis atherinoides	Emerald Shiner	0.525	414	coolwater
	Notropis hudsonius	Spottailed Shiner	0.563	445	coolwater
	Perca flavescens	Yellow Perch	0.542	633	coolwater
2	*Catostomus commersonii*	**White Sucker**	1.000	1016	coolwater
3	*Salvelinus fontinalis*	**Brook Trout**	0.653	539	coldwater
	Rhinichthys cataractae	Longnose Dace	0.653	547	coolwater
4	*Lota lota*	**Burbot**	0.398	200	coldwater
	Catostomus catostomus	Longnose Sucker	0.368	173	coldwater
	Coregonus artedi	Cisco	0.396	140	coldwater
	Coregonus clupeaformis	Lake Whitefish	0.320	82	coldwater

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Table 3.1: Continued.

Cluster	Species Name	Common Name	Average PS	Commonness	Thermal Guild
4	*Couesius plumbeus*	Lake Chub	0.330	232	coldwater
	Percopsis omiscomaycus	Trout-Perch	0.364	228	coldwater
	Salvelinus namaycush	Lake Trout	0.387	122	coldwater
	Sander vitreus	Walleye	0.354	239	coolwater
5	***Ictalurus punctatus***	**Channel Catfish**	0.316	114	warmwater
	Acipenser fulvescens	Lake Sturgeon	0.223	95	coolwater
	Anguilla rostrata	American Eel	0.161	60	coolwater
	Aplodinotus grunniens	Freshwater Drum	0.305	115	warmwater
	Carpiodes cyprinus	Quillback	0.279	80	coolwater
	Esox masquinongy	Muskellunge	0.234	85	warmwater
	Hiodon tergisus	Mooneye	0.102	14	coolwater
	Ichthyomyzon castaneus	Chestnut Lamprey	0.118	25	coolwater
	Ichthyomyzon unicuspis	Silver Lamprey	0.165	143	coolwater

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Table 3.1: Continued.

| Cluster	Species Name	Common Name	Average PS	Commonness	Thermal Guild
5	*Ictiobus cyprinellus*	Bigmouth Buffalo	0.181	34	warmwater
	Lepisosteus osseus	Longnose Gar	0.284	110	warmwater
	Morone chrysops	White Bass	0.297	98	warmwater
	Moxostoma anisurum	Silver Redhorse	0.310	114	coolwater
	Moxostoma macrolepidotum	Shorthead Redhorse	0.289	152	warmwater
	Moxostoma valenciennesi	Greater Redhorse	0.255	69	warmwater
	Percina copelandi	Channel Darter	0.097	23	warmwater
	Percina shumardi	River Darter	0.106	9	warmwater
	Prosopium cylindraceum	Round Whitefish	0.093	43	coldwater
	Sander canadensis	Sauger	0.138	25	coolwater
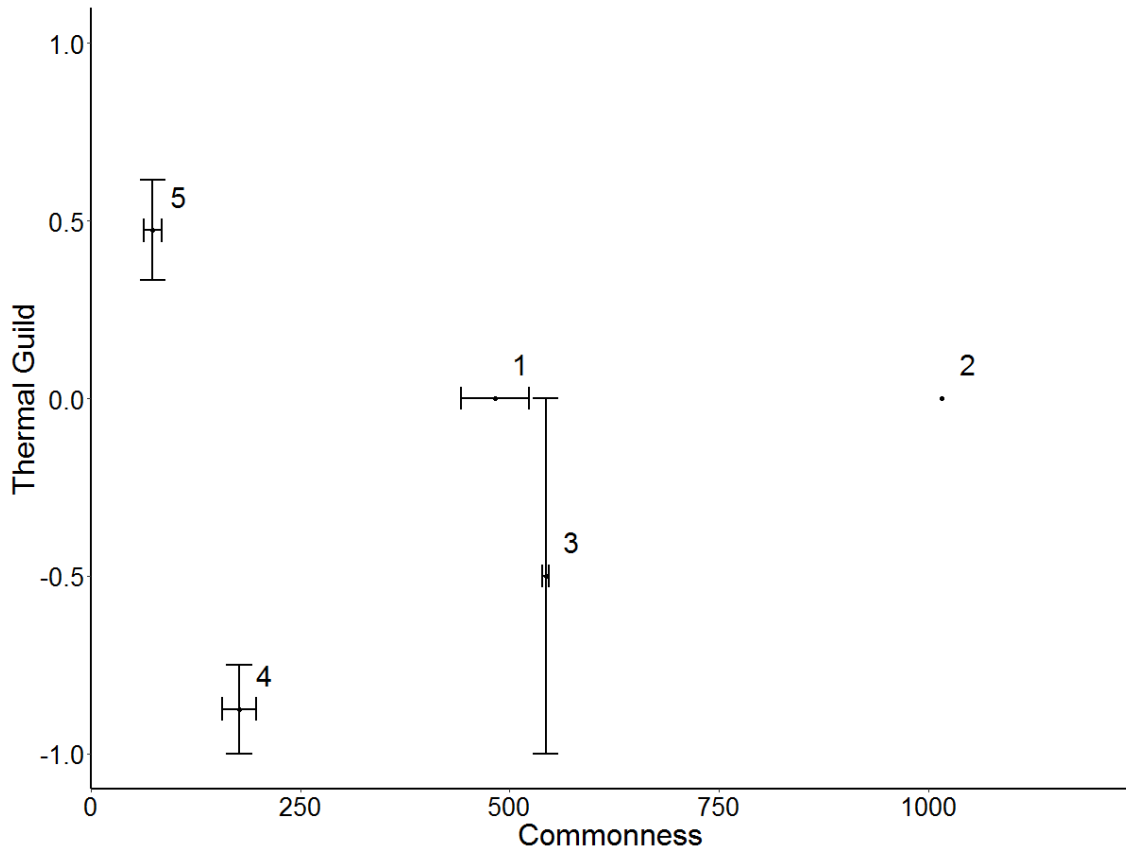
Figure 3.1: The average (±SE) commonness and thermal guild of each cluster. Commonness was defined as the number of tributaries where a species was present in the dataset. Thermal guilds were based on the work by S. David *(in prep)* which each species belonging to the cold (-1), cool (0), or warm (1) water guild.
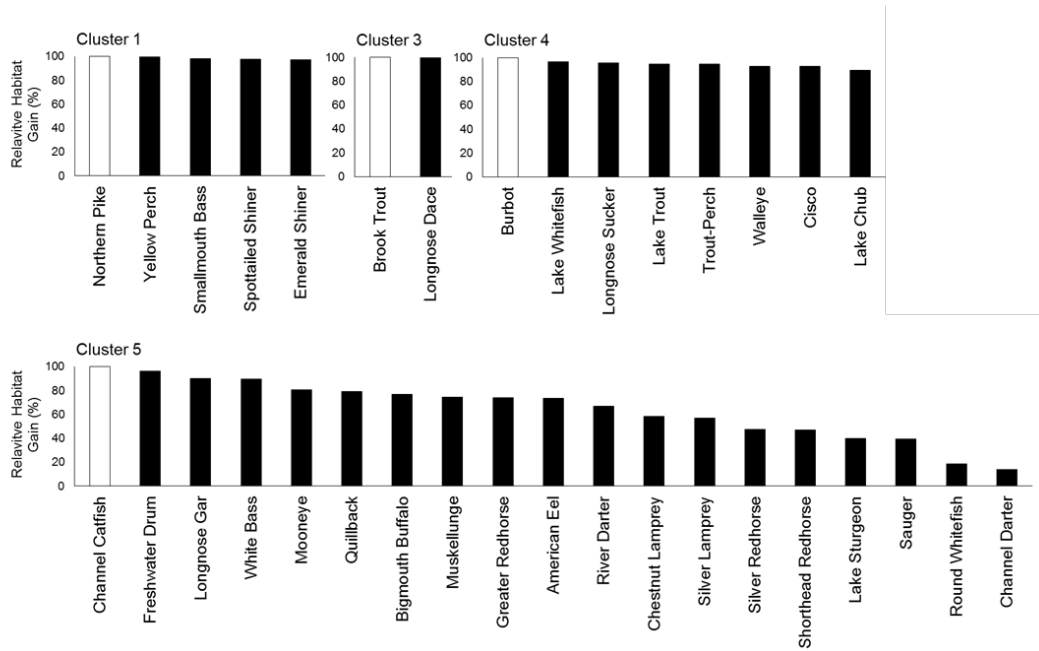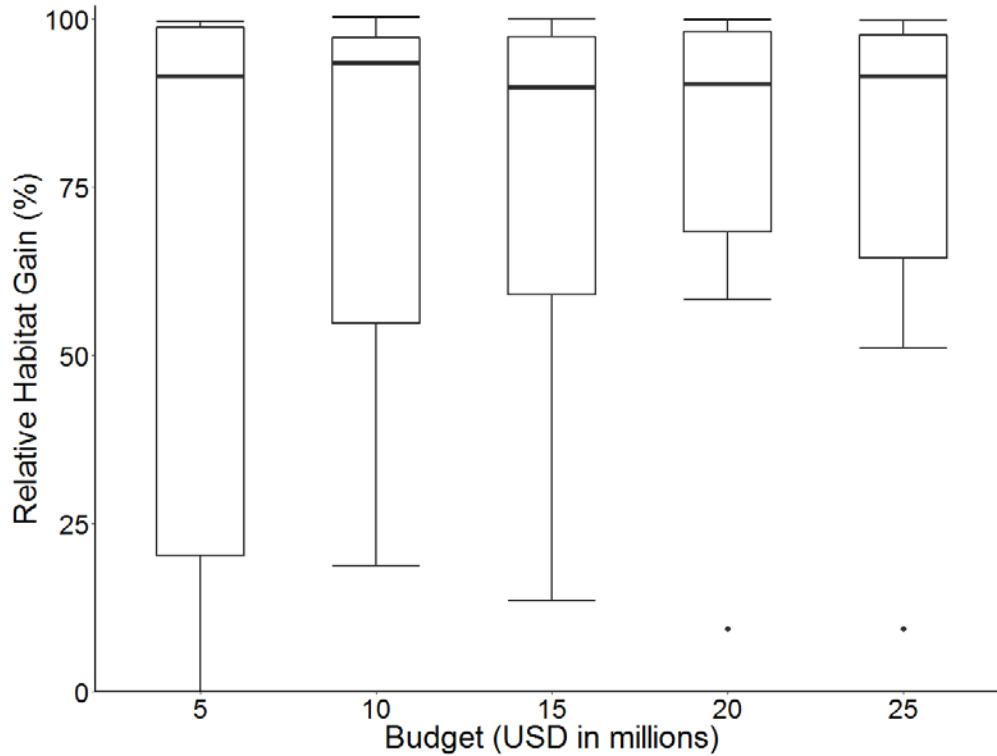
Figure 3.2: Percent habitat gains for species in clusters 1 (A), 3 (B), 4 (C), and 5 (D), when barrier removals are optimized for indicator species for a budget of 25M. Indicator species are listed first and are represented by white bars, while non-indicator species are represented by black bars. A habitat gain of 100% means a species gained an equal amount of habitat under its own optimization as it did under the indicator species. A low habitat gain signifies species that were not well represented by their indicator species. Cluster 2 is not included because it only includes one species (White Sucker).
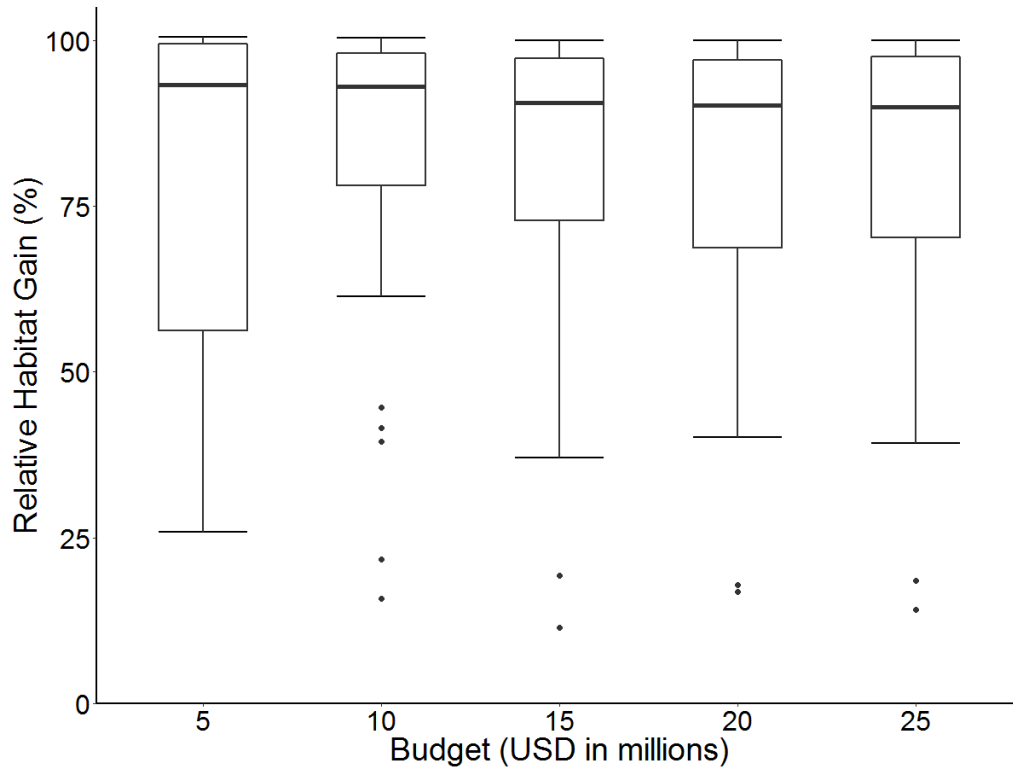
Figure 3.3: Percent habitat gains of species when barrier removals are optimized for their respective indicator species at five different budget levels (5-25M USD). A gain of 100% means that a species gained an equal amount of habitat under its own optimization as it does under the indicator species' optimization, while a gain of 0% means the species saw zero gain in habitat under the indicator species' optimization.

Figure 3.4: Percent habitat gains for species when barrier removals are optimized to maximize stream area. High percent gains represent species that gained similar amounts of habitat when stream area was maximize and when removals were optimized for their habitat. Low percent gains indicate species had minimal habitat gains when stream area was maximized.
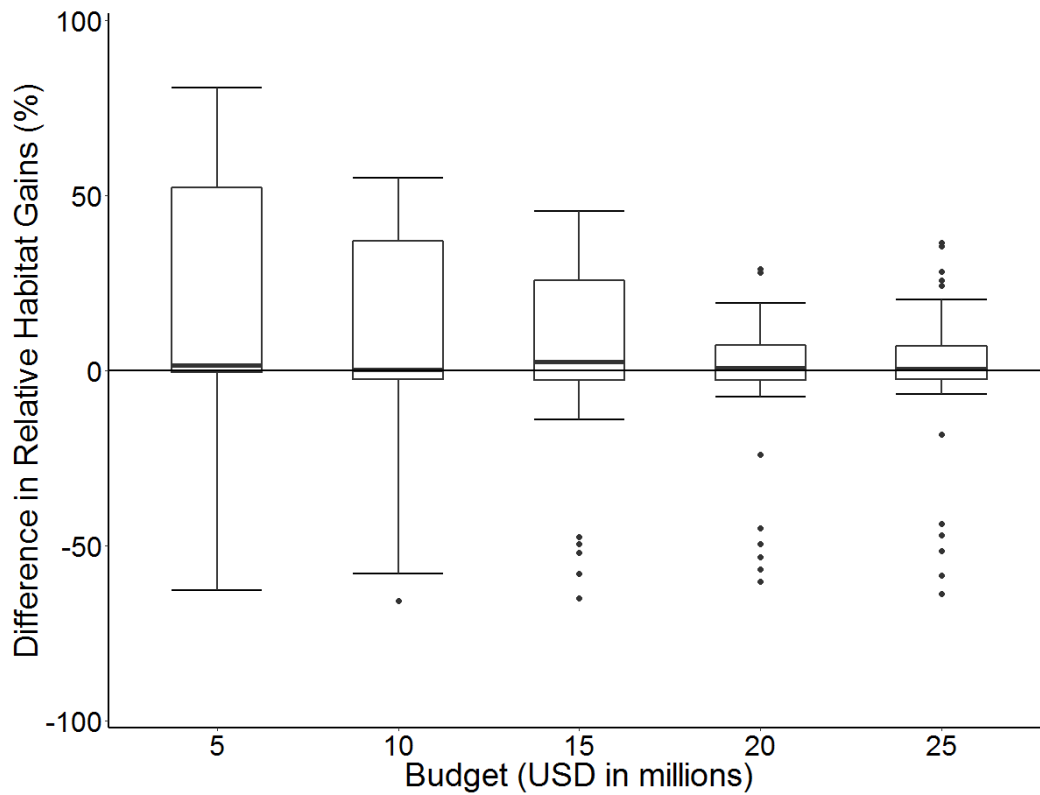
Figure 3.5: Difference in habitat gains for species when barrier removals are optimized for respective indicator species habitat and maximizing stream area. A difference of 0% represents species that gained equal amounts of habitat under the optimizations for their indicator and stream area. Values greater than 0% represent species that gained more habitat when their indicator species was optimized for, while species with values less than 0% gained more habitat when stream area was optimized.

Chapter 4: Conclusion

Return-on-investment (ROI) frameworks are powerful tools that conservation actors can apply to maximize their limited resources to obtain the greatest ecological benefit. Conservation actors should take full advantage of the ability to define both the costs and the benefits to fit their focal systems. Herein I demonstrated two applications of the ROI framework to cost-effectively increase connectivity in river networks.

Within my second chapter, I used an ROI framework to demonstrate the importance of funding and coordinating both small and large barrier removal projects. To calculate ROI, we used the cost of removing dams and road culverts and population distributions to represent benefit. We found that when conservation actors directed all of their funds towards removing either road-culverts or large dams only stream-resident or anadromous fishes typically benefited, respectively. To benefit both anadromous and stream-resident fishes, the coordinated removal of small, medium, and large barriers was necessary.

The third chapter utilizes an ROI framework to evaluate the use of indicator species for guiding barrier removals in the tributaries of the Great Lakes. We compared the ROI between species-specific plans for barrier removals and indicator-guided plans by calculating habitat gains over a range of budgets. We found that for most native migratory Great Lakes species, indicator-guided plans were highly efficient, meaning that these species gained similar amounts of habitat under both species-specific and indicator-guided plans. We also calculated the ROI of selecting projects to maximize stream area and compared these results to the ROI of the indicator guided plans. The

indicator-guided plans were more consistent across budgets, particularly when only a few barriers were removed. At these small budgets, the maximizing stream area method was unable to efficiently represent distributions of the wide range of species. The difference between the indicator-guided plans and maximizing stream area demonstrates the value of incorporating species distribution datasets into conservation planning.

The two example shown here demonstrate the value of incorporating the ROI framework into conservation efforts. These chapters highlight the need to prioritize projects that benefit multiple species; instead of considering these species or species types separately conservation actors can maximize their ROIs by selecting projects that benefit a large group of species. In addition to applying the ROI framework to a variety of conservation efforts, future studies should expand the included costs and benefits to consider and compare the outcomes of a variety of conservation efforts. The ROI framework can also be utilized by conservation organizations to clearly define the expected costs and goals of a project, allowing for transparency in conservation efforts (Possingham et al. 2012). Overall the budgets for conservation organizations are limited, and as such there should be an increased effort to calculate, consider, and compare the ROI for a variety of purposed conservation efforts. By comparing costs and benefits, conservation organizations can maximize the amount of ecological benefit for their limited budgets.

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