Beaver Dams Maintain Native Fish Biodiversity Via Altered Habitat Heterogeneity in a Coastal Stream Network: Evaluating Gear, Quantifying Fish Assemblages, and Testing Ecological Hypotheses

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A Dissertation Presented

by

JOSEPH M. SMITH

Submitted to the Graduate School of the University of Massachusetts Amherst in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY

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School of Marine Sciences
BEAVER DAMS MAINTAIN NATIVE FISH BIODIVERSITY VIA ALTERED
HABITAT HETEROGENEITY IN A COASTAL STREAM NETWORK:
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To my parents, Mike and Linda Smith, my sister, Julie Smith, and my brother, Luke Smith. Thanks for all of your help and support.
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ABSTRACT

BEAVER DAMS MAINTAIN NATIVE FISH BIODIVERSITY VIA ALTERED HABITAT HETEROGENEITY IN A COASTAL STREAM NETWORK: EVALUATING GEAR, QUANTIFYING FISH ASSEMBLAGES, AND TESTING ECOLOGICAL HYPOTHESES

FEBRUARY 2012

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Understanding the relationship between heterogeneity, biodiversity and ecosystem function is an active focus of ecological research that has direct applications to the formulation of sustainable, science-based, watershed conservation plans. Here, I applied ecological theory on heterogeneity to the expansion of North American beaver to test hypotheses about physical habitat and fish biodiversity at a riverscape scale. To test these hypotheses (Chapter 4), I first addressed two methodological issues (Chapter 2, 3). By evaluating three types of gear at three levels of effort in a randomized block design over 4 replicate days, I show that 10 minnow traps, 2 hoop nets and 20 m of electrofishing captured most fish species within a 30-m sampling area (Chapter 2). Multiple statistical measures provided similar information, therefore I used general indices (richness, diversity), ecological guilds (flow based), and select multivariate analyses (DCA) to
summarize fish communities (Chapter 3). I used these methodological insights to test ecological hypotheses by collecting habitat and fish data at all beaver dams \( n = 15 \) and select control sites \( n = 9 \) in Fish Brook, a coastal watershed in northeastern Massachusetts. From these data, I gained six basic and applied insights. First, beaver dams were distributed throughout the stream network. Second, at a local scale, beaver dams created more habitat heterogeneity than control sites. Specifically, beaver dams created four types of habitat alterations based on upstream-downstream differences in stream width, depth, velocity, and substrate. Third, richness and diversity of fish species around beaver dams were linked to habitat heterogeneity. Fourth, the mechanisms by which beaver dams altered fish biodiversity were mediated through habitat changes at the beaver dam patch boundary. Upstream of the dam macrohabitat guilds occupied the lentic areas, while below dams, fluvial fish guilds used shallow, faster water. Fifth, fluvial species responded the most dramatically to these habitat changes. Finally, in a system depauperate of lotic habitat, fluvial habitats created below beaver dams provided an important refuge for native stream fish. These source areas can increase resiliency and maintaining them may be useful for sustainable watershed conservation plans in these types of systems.
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CHAPTER 1

INTRODUCTION

Ecologists have been interested in the factors that drive biodiversity for over half a century (Hutchinson 1959). Biodiversity has been linked to ecosystem function (Hooper et al. 2005), and conserving biodiversity is currently a high priority (Sarkar et al. 2006). Biodiversity is declining worldwide (Dawson et al. 2011), therefore, understanding the drivers that influence biodiversity is a current focus for ecologists. Aquatic ecosystems are especially vulnerable to biodiversity loss (Malmqvist and Rundle 2002, Strayer and Dudgeon 2010). In aquatic systems, habitat heterogeneity is an important driver of biodiversity (Palmer and Poff 1997, Guégan et al. 1998, Palmer et al. 2010). For my dissertation, I build upon existing ecological theories concerning biodiversity, heterogeneity, and spatial scale. For this, I focused on a natural ecosystem engineer, North American beaver (*Castor canadensis*). To test ecological hypotheses regarding beaver dams, habitat heterogeneity, and fish biodiversity, I quantified instream habitat and fish assemblages directly above and below beaver dams and non-beaver dam control sites throughout an entire stream network (Chapter 4). In order to test the ecological hypotheses of interest, I first needed to address two methodological issues: a) how to sample fish assemblages in variable habitats above and below beaver dams throughout a stream network (Chapter 2), and b) which fish metrics best described the fish community adjacent to the patch boundary created by beaver dams (Chapter 3).

Identifying fish biodiversity patterns at large scales presents substantial sampling challenges. For example, different sampling gear catch different fish species and sizes
and their effectiveness varies in different habitats. Furthermore, different levels of effort may be required for different questions, systems, and fish communities. Thus, determining the type of gear and amount of effort that will provide a standard estimate of biodiversity across different habitats with different fish communities is difficult. In Chapter 2, I provide a process for determining the type of gear and amount of effort needed to sample fish biodiversity in small streams. Using a randomized block design, I compared the fish communities caught by three different gears (minnow traps, stream electrofishing, and hoop nets) at three levels of effort (one, two, and three mixed gear units) when these were randomly applied to blocks within a relatively homogeneous 90-m reach and replicated over 4 days. I found that a combination of 10 minnow traps, 20 meters of backpack electrofishing, and 2 hoop nets caught most species within 30-m stream reaches. Resampling simulations confirmed these results. This process guided my sampling of fish communities within 30-m habitat patches above and below beaver dams. Although, the type and amount of gear may be different for other studies and systems, the process I describe in Chapter 2 may be widely applied.

Fish assemblage data are complex and need to be simplified in an ecologically meaningful way. There are many ways to quantify assemblages including: general measures (e.g., species richness, abundance, biomass), diversity indices (e.g., Shannon’s $H'$), number and richness of ecological guilds, and multivariate statistical techniques such as cluster analysis (Haxton and Findlay 2009) and ordination (Kwak and Peterson 2007). Because only one or a few fish response metrics can be used within a statistical analysis, researchers must be parsimonious when deciding on fish metrics. My goal in Chapter 3 was to define a process to select defensible and ecologically interpretable statistical
simplifications of assemblage data in which I, and other researchers and managers, can have confidence. For this, I chose a suite of statistical methods, compared the groupings that resulted from these analyses, identified convergence among groupings, then I interpreted the groupings using species and ecological guilds. From this process, I determined that species richness, Shannon’s H’ diversity, detrended correspondence analysis, and fluvial fish guilds created useful fish assemblage metrics. I used these to test ecological hypotheses about beaver dams, habitat heterogeneity, and fish biodiversity.

I applied ecological theory on heterogeneity to the natural expansion of North American beaver to test hypotheses about physical habitat and fish biodiversity at a riverscape scale. I quantified physical beaver dam structure, adjacent instream habitat, and fish communities at all \((n = 15)\) beaver dams and select control sites \((n = 9)\) within Fish Brook, a low-gradient watershed in coastal Massachusetts. I start by examining the role of riverscape position for beaver dam characteristics and distribution. I then examine if beaver dams alter habitat and if there is variation in this alteration. I also categorize beaver dams into four types of habitat alterations based on differences in stream width, depth, current velocity, and substrate above and below dams. I then link the number and diversity of fish species around beaver dams to habitat heterogeneity, both locally and at the riverscape scale. I examine the importance of the impoundment above and fluvial habitat below beaver for fish species richness and fluvial fish guilds.

I close by discussing the implications of the shallow, high-velocity habitat created by beaver dams for riverscape biodiversity. Pockets of fluvial habitat created by beaver dams may be especially important in urbanized systems. River dynamics across the United States are becoming more homogenized due to anthropogenic impacts (Brooks et
Habitat alteration by beaver dams throughout a stream network may mitigate some of the homogenization due to anthropogenic impacts. In this Dissertation I give evidence that beaver dams increase limited fluvial habitat throughout the Fish Brook stream network, and that the niche partitioning that results from this diversification of habitats around beaver dams increases native fish richness and diversity. Because these lotic habitats are limited in this low-gradient, urbanized riverscape, they are important refuges for native fluvial fish species. Considering the dramatic decrease in biodiversity across the globe (Pimm et al. 1995), hotspots of biodiversity are a priority for conservation (Myers et al. 2000). Therefore, it may be useful to incorporate habitat heterogeneity created by beaver dams into sustainable, science-based, watershed conservation plans in low-gradient urbanized systems.
CHAPTER 2

PROCESS FOR EVALUATING THE COMBINATION AND AMOUNT OF SAMPLING GEAR NEEDED TO REPRESENTATIVELY SAMPLE FISH BIODIVERSITY IN STREAMS

2.1 Introduction

Functioning freshwater ecosystems provide goods and services for society (Baron et al. 2002; Strayer and Dudgeon 2010), but anthropogenic impacts and climate change threaten these services (Dudgeon et al. 2006, Geist 2011), and can facilitate biodiversity losses (Malmqvist and Rundle 2002; Rosales 2008; Dudgeon 2010). Identifying patterns of biodiversity (Vadeboncoeur et al. 2011; Jones et al. 2011), consequences of biodiversity (Tilman et al. 1996, Tilman 1999), drivers of these patterns (Palmer et al. 2000, Cardinale 2011), and causes of biodiversity loss (Allan and Flecker 1992, Díaz et al. 2006) are current priorities in ecology (Strayer and Dudgeon 2010, Dobrovolski et al. 2011). A general consensus is that large-scale, watershed-level research (Fausch et al. 2002, Tetzlaff et al. 2007) for restoration (Palmer et al. 2010, Stranko et al. 2011), conservation (Nelson et al. 2009, Bai et al. 2011), and management (Stohlgren et al. 1995; Manley et al. 2005) are needed. To effectively understand patterns, quantify drivers, and implement conservation actions at a large scale, researchers and managers must first be able to accurately quantify biodiversity in freshwater ecosystems using standardized sampling that allows comparison across a large number of sites with different physical habitats and different communities. Substantial challenges exist in
quantifying large-scale biodiversity patterns (Hughes and Peck 2008, Albert et al. 2010, Cao and Hawkins 2011). Consequently, determining what gear are effective for a range of different species and habitats (Cao et al. 2001, Kwak and Peterson 2007), standardizing gear and effort in order to make comparisons across sites (Bonar and Hubert 2002, Cao and Hawkins 2011), and determining effort, i.e., how much gear is needed (Jackson and Harvey 1997, Brashares and Sam 2005) are basic but vexing issues for large scale biodiversity sampling. I provide a process that can be used for addressing these concerns for fish communities in small, wadeable streams.

One of the issues that makes sampling stream fish biodiversity so difficult is that aquatic sampling gears function differently across habitats, and each gear is effective at catching a specific suite of fish species and sizes (Kwak and Peterson 2007). Specifically, each gear type has environmental constraints (Aadland 1993). For example, some gear requires depths that a sampler can walk (e.g., beach seine, backpack electrofishing), whereas other gear works in multiple depths (hoop net, minnow traps; Hayes et al. 1996, Hubert 1996, Reynolds 1996). Some gear requires a larger system (e.g., experimental gillnets, trawling), whereas other gear can work in a range of system sizes (minnow traps, hoop nets, electrofishing) (Hayes et al. 1996, Hubert 1996, Reynolds 1996). Some gear requires a smooth bottom (e.g., beach seine, trawling) whereas for other gear, bathymetry does not matter (e.g., hoop nets, minnow traps; Riha et al. 2008). In addition, different gear are better at capturing certain species and sizes (Jackson and Harvey 1997, Kwak and Peterson 2007). Active gear (e.g., seining, electrofishing) capture stationary and mobile fish whereas stationary gear (e.g., gillnets, hoop nets, minnow traps) only catch moving organisms (Portt et al. 2006). Furthermore, mesh size and trap/net openings will
affect the size and species of fish caught (Hubert 1996). Many studies have examined the selectivity of gear types (Myers and Hoenig 1997) including trap nets (Laarman and Ryckman 1982, Kraft and Johnson 1992), minnow traps (Clavero et al. 2006), and electrofishing (Larimore 1961, Reynolds 1996). Because different gears catch different sizes and species of fish in different habitats, determining the appropriate gear for community level sampling is challenging.

Previous studies have used and evaluated a variety of gear for use in small stream-river systems. In a literature review of ten aquatic journals (Canadian Journal of Fisheries and Aquatic Sciences, Fisheries, Fisheries Management, Fisheries Management and Ecology, Fisheries Research, Hydrobiologia, Journal of Freshwater Ecology, Journal of Fish Biology, North American Journal of Fisheries Management, Transactions of the American Fisheries Society) from 1984 to 2009, I evaluated 43 papers that sampled freshwater fish to determine the most common gear types for sampling stream fishes. From the literature review, the five most common gears were backpack electrofishing (42%), hoop nets (26%), gill nets (21%), seines (6%), and minnow traps (5%). Of these, only three types of gear (minnow traps, backpack electrofishing, and hoop nets) could be fished in the small, uneven-bottomed system that I studied. Although all of these gear can be used in small wadeable streams, whether one gear captures the full complement of resident species or whether combinations of gear are needed requires evaluation.

Determining the amount of sampling effort needed to adequately sample fish biodiversity is important. Species accumulation curves, in which the number of new species added when sampling units are aggregated, is a common way of determining effort (Jackson and Harvey 1997, Palmer 1990). These effort studies usually focus on the
number of sampling events or sections needed to reach a high level of species detection (Smith and Jones 2005), but some studies have examined increasing amounts of gear (Jackson and Harvey 1997). Resampling techniques have also been used to determine and evaluate sampling (Jackson and Harvey 1997, Dumont and Shlechte 2004) in marine (Kimura and Balsinger 1985, Stanley 1992) and freshwater (Angermeier and Smogor 1995, Paller 1995, Patton et al. 2000, Vokoun et al. 2001, Reynolds 2003). In this study I use both empirical and resampling techniques to evaluate varying levels of sampling effort.

Here, I present a process for determining the type of gear and amount of effort needed to adequately quantify fish biodiversity in small streams by addressing three specific questions: (1) What kind of sampling gear is effective? (2) What level of sampling effort (i.e., quantity of gear) adequately samples the fish community?, and (3) Can resampling simulations, based on empirical data, guide sampling decisions, especially related to the trade-offs between sampling effectiveness and time investment? Although different research locations and fish communities will require different types and amounts of gear, the process presented here can be adapted for use in many systems.

2.2 Materials and Methods

2.2.1 Study site

Fish sampling, designed to evaluate the type and amount of gear needed to compare fish biodiversity across sites, took place in Fish Brook, a fourth order tributary of the Ipswich River located in northeastern Massachusetts (Figure 2.1A). Within Fish Brook, a relatively homogenous 90-m reach was chosen to compare the number and
species of fish caught with different gears and levels of effort using a randomized block design (see study design section below). This 90-m reach of Fish Brook (42° 38' 39.94", 70° 59' 16.37 N) was small (mean width = 9.07 m, mean depth = 0.80 m), had a combination of gravel and silt substrate, was composed of primarily run macrohabitat, and was located within a watershed of 66% forested land.

2.2.2 Study design

To compare the fish community caught with three different types of gear using three different levels of sampling effort, this 90-m reach of Fish Brook was divided into three 30-m longitudinal blocks (A-C, Figure 2.1B). The block size was chosen because I needed an effective sampling design for a related study on fish communities 30-m above and below beaver dams. Each block was further divided into three 10-m sections (S1-S3; Figure 2.1B), resulting in 9 equal-sized sections. Within the 90-m reach, I evaluated two treatments (Figure 2.1C): (1) gear type [minnow traps \(n = 5\) and electrofishing \(n = 1\) 10-m section], hoop net \(n = 1\)], and (2) amount of sampling effort [1-3 mixed gear units (MGU)], where one MGU was defined as the combination of 5 minnow traps plus 1 hoop net plus 10-m of electrofishing. The two separate treatments of gear type and amount of sampling effort (Figure 2.1C) were tested in the three, 30-m blocks (A-C, Figure 2.1B) and were replicated over four days between June 24 - 29, 2009 (Figure 2.1D). Specifically, for each sampling day, each 30-m block (A-C) was first randomly assigned a level of effort (1, 2, or 3 MGUs). Next, each gear [minnow traps \(n = 5\) for 1 MGU, \(n = 10\) for 2 MGUs, \(n = 15\) for 3 MGUs ), electrofishing \(n = 1\) 10-m transect for 1 MGU, \(n = 2\) 10-m transects for 2 MGUs, \(n = 3\) 10-m for 3 MGUs], and hoop net \(n = 1\) for 1 MGU,
\( n = 2 \) for 2 MGUs, \( n = 3 \) for 3 MGUs) was randomly assigned to one of the three sections (S1-S3) within a block (A-C) in order to ensure that a single type of gear was not consistently set in the same location (Figure 4.1D). For the analysis, types of gear (minnow traps, electrofishing, and hoop nets) were compared across all sections, blocks, and days; the amount of effort (1-3 mixed gear units, MGU) was compared only across blocks and days. As a result of this design which compared fish (species and numbers) caught using three different gears (minnow traps, electrofishing, hoop nets) with three levels of sampling effort (1-3 MGUs), I was able to determine the best design (gear type and amount) given sampling trade-offs (e.g., additional species caught versus additional time required to sample).

2.2.3 Minnow traps and hoop nets

Hoop nets and minnow traps were set before dusk (about 18:00) and retrieved the next morning (about 6:00) for a total fishing time of 12 hours. Each hoop net (Memphis Net & Twine Co. Code: H9991-4, 61 cm diameter, 1.22 m long, 0.64 cm mesh) was placed in the stream thalweg. A mesh lead (Memphis Net & Twine Co. Code: WNG1, 3.0 m long, 1.8 m deep, 2.54 cm mesh) stretched from the net opening diagonally to an adjacent stream bank and was secured with rebar. Hoop nets were oriented downstream. In addition, five unbaited minnow traps (Gee brand, 22.9 cm diameter, 44.5 cm long, 0.64 cm mesh made of galvanized steel wire, opening 2.5 cm) were set within a 10-m section. Preliminary tests determined that baiting did not increase numbers or types of fish caught in the minnow traps. Each hoop net and each set of five minnow traps were randomly assigned to one of the three 10-m sections (S1-S3) within a block (A-C; Figure
2.1B, 2.1D). At the end of the sampling period, fish were placed in a water filled bucket, identified to species, measured (total length, mm), given a caudal fin-clip, and immediately returned to the stream. Fin clips were used to identify if fish were captured multiple times or in multiple types of gear.

2.2.4 **Backpack electrofishing**

Electrofishing was conducted in the afternoon between 13:00 and 16:00 using a Smith-Root LR-24 backpack electrofisher (300 to 500 volts, 60 Hz). Stream sections (10 m) were electrofished thoroughly in a serpentine pattern starting at the most downstream block. Fish caught while electrofishing were transferred to a water-filled bucket with a dipnet. After sampling, fish were processed as described above. As with hoop nets and groups of 5 minnow traps, each 10-m of electrofishing was randomly assigned to one of the three 10-m sections (S1-S3) within a 30-m block (A-C, Figure 2.1B, 2.1D) to ensure that electrofishing was not always done in the same location.

2.2.5 **Data summary and analyses**

To determine the type of gear needed to adequately sample fish biodiversity (*Question 1*), richness and abundance (mean and standard error) were calculated for each gear type using combined data from the four replicate days. Then the number and species of fish caught was statistically compared across gear types using a randomized block analysis of variance (ANOVA), followed by Tukey HSD multiple comparisons (Program R, ‘aov’ and ‘TukeyHSD’ functions, ‘stats’ package; R Core Development Team 2011). To assess if a single type of gear adequately sampled the fish community or if a
combination of gear was needed, I calculated and plotted how species accumulated with increasing types of gear (i.e., number of new species added per gear type). I started with the gear that caught the least number of species, then added the gear that caught the next most species, until all gear were included. The point of calculating species accumulation was not to identify the best or worst single gear but instead to determine if a combination of gear sampled the fish community best.

To determine effort, or the amount of gear, needed to adequately sample fish biodiversity (Question 2), for each level of effort (1-3 MGUs), I calculated six metrics: (1) total species richness for all days combined, (2) maximum daily species richness of all four sampling days, (3) percent of the total species pool that was caught by each level of effort, (4) species accumulations (i.e., new species added) for each level of effort for the entire sampling period, (5) richness (mean, standard error) using each day as a replicate, and (6) diversity (Shannon’s H’, mean, standard error,) using each day as a replicate. A randomized block ANOVA using effort as a treatment (1-3 MGUs) followed by Tukey HSD multiple comparisons was run on the last two measures. In addition, I used Non-metric multidimensional scaling (NMDS) to compare the similarity of fish assemblages among 1-3 MGUs. For the NMDS analysis, a two-dimensional analysis of a Bray-Curtis species abundance dissimilarity matrix for each day by gear unit was used (n = 12) (Program R, ‘metaMDS’ function, ‘vegan’ package; Oksanen et al. 2011). A subsequent Monte-Carlo permutation test determined if the amount of stress obtained by the NMDS was less than that expected by random processes.

Resampling simulations were used to test if the same patterns would occur if I added additional sampling days (n = 10, Question 3). Resampling simulations were
performed using the empirically-collected data from each gear type as the three species pools. Within each gear type, each individual fish was given a unique identifier. The mean abundance for each gear type (minnow trap mean abundance = 0.3, electrofishing mean abundance = 0.5, hoop net mean abundance = 3.7) was used to guide the number of individuals selected from each species pool for each resampling simulation. Random numbers determined which individuals were selected from each gear pool. Simulations were run ten times each for one, two, and three MGUs (i.e., sampling day replicates). The rules for resampling simulated the procedures I used for the empirical sampling. Mean and standard error of richness and Shannon’s H’ were calculated from the resampled data for each level of sampling effort and compared using a one-way ANOVA followed by Tukey HSD multiple comparisons. Percent detection was also calculated for each fish species.

Finally, I assessed the tradeoffs associated with the number of new species added compared to the amount of time required to complete additional sampling. For this, the mean number of species added per gear unit was divided by the number of MGUs to determine if increasing, decreasing, or uniform amount of new information was gained (additional species) per additional amount of sampling effort (MGU).

2.3 Results

Over the four days of the gear evaluation, 106 individuals and 11 species of fish were captured within the three 30-m blocks that were tested each day. Six species made up 94% of the individuals caught (fallfish *Semotilus corporalis*, yellow bullhead *Ameiurus natalis*, redfin pickerel *Esox americanus americanus*, American eel *Anguilla natalis*, redfin pickerel *Esox americanus americanus*, American eel *Anguilla natalis*).
rostrata, brown bullhead Ameiurus nebulosus, yellow perch Perca flavescens). Five species were rare for which only two individuals were captured for one species (pumpkinseed Lepomis gibbosus) and only a single individual was captured for four other species (golden shiner Notemigonus crysoleucas, brown trout Salmo trutta, chain pickerel Esox niger, largemouth bass Micropterus salmoides; Table 2.1).

2.3.1 Types of gear (Question 1)

Each individual gear type [e.g., 5 minnow traps (M), 10-m of backpack electrofishing (E), and 1 hoop net (H)] provided different estimates of fish species richness and mean fish abundance (Figure 2.2A, 2.2B). Hoop nets captured more species (Figure 2.2A) and more individuals (Figure 2.2B) than minnow traps and electrofishing, with no difference among blocks (richness ANOVA gear $P = < 0.0001$, block $P = 0.95$; abundance ANOVA gear $P = < 0.0001$, block $P = 0.81$). Only mixed gear units that combined all gear types (Minnow traps, Electrofishing, and Hoop nets (M+E+H)) captured the full range of freshwater fish species present in Fish Brook (Figure 2.2C).

2.3.2 Amount of gear (Question 2)

Two mixed gear units (MGUs, 10 minnow traps, 2 10-m sections of backpack electrofishing, and 2 hoop nets) adequately sampled fish biodiversity within a 30-m section of stream. Total richness (Figure 2.3A), maximum richness over all days (Figure 2.3B), and percentage of the species pool that was captured (Figure 2.3C) reached a maximum at two MGUs. Ten of the 11 species of fish detected over the entire sampling period (91%) were captured using two MGUs (Figure 2.3D). Only one species of fish,
largemouth bass (of which only a single individual was caught over the entire
evaluation), was not captured with two MGUs. Statistically, richness (Figure 2.3E) and
diversity (Figure 2.3F) were not different between two and three MGUs. Both two and
three MGUs, however, caught more fish than a single MGU (richness MGU ANOVA: \( P \\
= 0.02 \), block \( P = 0.45 \); Shannon’s H’ MGU ANOVA: \( P = 0.02 \), block \( P = 0.29 \)).
Furthermore, using an NMDS, fish assemblages were similar between two and three
MGUs [i.e., no clear separation between sites for 2-3 MGUs in ordination space (Stress =
0.001; \( P = 0.03 \); Figure 2.4].

2.3.3 Resampling simulations

Resampling using ten model simulations (i.e., 10 sampling days) for one, two, and
three MGUs captured a total of 451 individuals from the designated pool of 11 species. In
these simulations, the mean number of species and mean diversity were not different
between two and three MGUs (Figure 2.5A, 2.5B). As in the empirical sampling, both
two and three MGUs caught more fish than one MGU. In this resampling exercise in
which I could compare what I caught to what I knew was present (Appendix A), both two
and three MGUs sampled common species well (fallfish-FF, yellow bullhead-YBH,
redfin pickerel-RP; detection rates from 60 to 100%), sampled less common fish
moderately (American eel-AE, brown bullhead-BBH, and yellow perch-YP; detection
rates from 30 to 80% ), but performed poorly on rare species (pumpkinseed-PS, golden
shiner-GS, brown trout-BT, chain pickerel-CP, largemouth bass-LMB; detection rates
from 0 to 50%).
2.3.4 Trade-offs (Question 3)

One and two MGUs added > 1 species per unit of effort; whereas the species gained per effort was < 1 for three MGUs (Figure 2.6). These results suggest that two units of mixed gear were an appropriate amount of gear in this system when considering the trade-offs between information gained and the amount of effort expended.

2.4 Discussion

Biodiversity sampling at larger watershed and riverscape scales is increasingly common for both research and conservation. In ecological research, examining the relationship between biodiversity and ecosystem function (Loreau et al. 2001, Hooper et al. 2005, Dawson et al. 2011) often requires multiple samples at large scales. Effects of longitudinal discontinuities like human and beaver dams also need quantification at the larger riverscape scale (Burchsted et al. 2010). Current ecological concepts like networks (Eros et al. 2011, Jacobi et al. 2011), tributary confluences (Fernandes et al. 2004), and fragmentation (Dynesius and Nilsson 1994, Ward 1998, Nilsson et al. 2005), by definition, must sample fish communities at larger scales. In general, examining processes at the larger riverscape scale is a current priority (Schlosser 1991, Tetzlaff et al. 2007) and a well developed theme in aquatic ecology (Fausch et al. 2002, Allan 2004). In addition, larger-scale efforts are currently recommended for management and conservation. For example, restoration is being encouraged at the watershed scale (Palmer 2010, Stranko et al. 2011). Government agencies like U.S. Fish and Wildlife Service have made large-scale management a priority of their Landscape Conservation Cooperative program (http://www.fws.gov/science/SHC/lcc.html). The U. S. Forest
Service seeks to monitor ecoregional-scale biodiversity (Manley et al. 2005; Reeves et al. 2006). The Inventory and Monitoring Program of the National Park Service uses scientific knowledge to provide good stewardship of larger-scale park resources (http://science.nature.nps.gov/im/index.cfm, Stohlgren et al. 1995, Carey and Mather 2008).

Sampling that seeks to identify patterns of biodiversity at larger watershed and riverscape scales, however, represents substantial challenges. Increasingly, large-scale biodiversity sampling is undertaken to attain both a scientific understanding of how ecosystems function (Gorden et al. 2004, Anderson et al. 2011, Eros et al. 2011) and to implement effective conservation plans in the face of increasing human development (Tilman et al. 2002, Van Sickle et al. 2004, Hansen et al. 2005). These large scale assessments of biological communities differ from many traditional resource assessments, which often target single species or are undertaken repeatedly in a limited number of locations. Specifically, priorities for sampling used in larger-scale biodiversity research and conservation planning include sampling: (i) with a comparable (i.e., standardized) unit of effort (Bonar and Hubert 2002, Cao and Hawkins 2011) (ii) across a large number of sites (Brooks et al. 2006), (iii) that can be used in a robust statistical analysis (Worm et al. 2006). This sampling is typically undertaken (iv) at sites where an unknown species pool may differ across sites (Manley et al. 2005), (v) where sampling targets multiple species within the community that are differentially vulnerable to a single sampling gear (Kwak and Peterson 2007), and (vi) where physical conditions and related sampling effectiveness of any single gear differ (Diekmann et al. 2005). For this large-scale biodiversity sampling (vii) limited time can be allocated to any single sample (i.e.,
trade-off exists between information and time expended; Bailey et al. 2007). Therefore, researchers and environmental professionals that undertake fish biodiversity sampling in streams and rivers at larger scales (watersheds and riverscapes) need a process by which they can develop and evaluate an effective sampling plan.

Choosing the appropriate gear for sampling is critical for adequately sampling fish biodiversity. The five most common freshwater fish sampling gears (backpack electrofishing, hoop nets, gill nets, seines, minnow traps) are effective under different physical conditions and are often affected by depth (Dauwalter and Fisher 2007), bottom type (Riha et al. 2008), water quality characteristics (Reynolds 1996), system size (Diekmann et al. 2005), and benthic bathymetry (Riha et al. 2008). For example, beach seining and stream electrofishing both require a relatively shallow depth, walkable substrate (Hayes et al. 1996, Reynolds 1996), and beach seining further requires enough even-bottomed, snagless stream area to pull the seine for standardized sampling (Hayes et al. 1996). In my sampling, I eliminated seining as a sampling gear because the substrate at the sample location was difficult to walk in and the bottom was uneven with many tree snags in the stream. Backpack electrofishing requires a specific range of conductivity, temperature, and transparency (Reynolds 1996). Hoop nets and minnow traps work in a variety of depths as long as the opening of the net is submerged (Hubert 1996), whereas, gill nets are usually limited to larger river systems because of the frequent need for multiple panels of different sized mesh (Hubert 1996). Gill nets were also eliminated from my study because they required more space than was available in my small stream sections. This left me with three types of gear (minnow traps, electrofishing, and hoop nets) that combined active and passive gear, sampled a range of habitats, and caught a
range of fish species and sizes. Passive gear (hoop nets, minnow traps) catches actively swimming fish, whereas active gear (backpack electrofishing) can catch both stationary and mobile fish (Reynolds 1996). Minnow traps are restricted by mesh size, size of terminal openings, and capture small fish (Hubert 1996). Electrofishing can stun fish of a range of sizes, morphologies, physiologies, and behaviors (Reynolds 1996), although some sizes may be caught more than others. Hoop nets are also restricted by mesh size, but can capture both larger and smaller fish (Hubert 1996). In my sampling, hoop nets caught the largest number of fish species. However, electrofishing caught fish species that hoop nets did not (chain pickerel and largemouth bass). Minnow traps did not catch unique species compared to other gears, but because of their ability to catch small fishes and ease of use, I considered this gear a useful addition to the suite of gear. No single gear caught the full range of the fish assemblage. Thus, here and elsewhere (Carey and Mather 2008), a combination of gear sampled the most diverse fish assemblage.

The highest priority for any sampling program is to obtain an accurate assessment of the fish species that are present. Consequently, determining the amount of effort (or gear) is also an important consideration. Others have evaluated effort as the number of backpack electrofishing passes (Pusey et al. 1998, Reid 2009), the electrofishing reach length (Paller 1995), number of reaches (Angermeier and Karr 1986, Smith and Jones 2005), and area of stream (Smith and Jones 2005). Sampling multiple units to construct species accumulation curves, both empirical and estimations, is a common way to determine how many samples are needed (Smith and Jones, 2005, Kwak and Peterson 2007). In this approach, the effort needed to reach asymptotes of species richness (Palmer 1990, Soberon and Llorente 1993, De Silva and Medellin 2001) is assessed by
repeating the number of samples, reaches, or sampling days. My use of a homogeneous 90-m section with relatively uniform habitat, broken into three similar 30-m sample blocks, in which I randomly set 1, 2, or 3 MGUs, then repeated this randomized sampling for four separate days allowed me to assess the relationship between amount of effort (MGU) and species accumulation. In this small stream, two MGU provided complete physical coverage and three MGU was the maximum amount of gear that would fit into each block due to space limitations. Based on this highly controlled and replicated sampling, I concluded that two MGU adequately sampled fish richness and diversity within a 30-m reach of stream.

Because more gear likely will always catch a few more individuals and species, knowing at what gear level the majority of species are captured is also important. The randomized block design in this study provided a useful approach to determine the amount of gear that sampled fish biodiversity. In my sampling, one mixed gear unit only caught 6 species which comprised 54% percent of what was caught in all samples. Two mixed gear units caught 10 species which comprised 91% percent of what was caught in all samples. With any sampling regime, catching rare species is difficult (Fagan et al. 2005, Cucherousset et al. 2008). Increasing the effort increases the chance of catching rare species (Green and Young 1993, Reid 1998), however, even with increased effort detection can be low (Jackson and Harvey 1997). Here I had high detection rates for common species. Three mixed gear units only added one species of fish, suggesting that two mixed gear units captured the most information for the effort expended. For studies where the number of sampling units is important, understanding this trade-off is critical (Bailey et al. 2007, Guillera-Arroita et al. 2010).
Resampling can be a way of comparing sampling regimes (Angermeier and Smogor 1995, Jackson and Harvey 1997), providing confidence limits for sampling (Crowley 1992), and evaluating how well the sampling regime works when the number of species is known (Jackson and Harvey 1997). Because I had four estimates of each level of effort, I was able to calculate sample variability and evaluate sampling regimes with empirical data and resampling was not essential. Using resampling simulations, however, I was able to simulate 10 days of sampling and then compare the results to the empirical data. Others have used resampling to determine the amount of sampling needed to capture a minimum number of individuals or detection rates for different fish species (Dumont and Schlechte 2011), number of traps (Jackson and Harvey 1997, and number of reaches (Smith and Jones 2008). Although empirical sampling is critical, resampling can be a very useful tool in the general toolbox for researchers and managers who need to devise and test a biodiversity sampling regime, especially if based on good empirical estimates.

I have provided a process for determining the amount of gear necessary to quantify riverscape-level fish biodiversity in a variety of systems. Biodiversity evaluations present different sampling problems than those of traditional resource assessments. Biodiversity surveys typically sample a large number of locations a few times, target the entire range of species that dwell in a community whose composition is unknown, and require standardization among often widely different sample locations in order to make sample comparisons. My process can be divided into the following nine steps. First, determine the goal of the study. My goal was to quantify the fish community in small areas (30-m adjacent to beaver dams) in small streams when the habitat varied
and the fish community was unknown. Second, conduct a literature survey to determine which gears are appropriate for the systems being examined. I found that five gears were common for sampling in my type of system. Third, in the field, assess which of the gear from the literature survey is possible. I determined that beach seining and gillnetting were not feasible in my system. Fourth, make sure that the suite of gear under consideration samples a range of habitat types, sizes and species of fishes. With this suite of possible gear, determine a combination of mixed gear that samples a range of habitat types, sizes, and types of fishes (step 5). I was able to use three types of gear (minnow traps, backpack electrofishing, hoop nets) in my system that targeted different habitats, fish species, and sizes. In step six, use a randomized block design to evaluate the type and amount of sampling gear that adequately measures fish richness and diversity, defined as the leveling off of a species accumulation curve. Then use resampling to provide confidence in empirical data (step 7). By using a randomized block design sampling and resampling, I identified that two mixed gear units captured most of the fish community. Finally, choose the MGU treatment to use for the sampling locations (step 8). Based on the entire process used in my system, I used two mixed gear units (10 minnow traps, 20-m electrofishing, and 2 hoop nets) within each 30-m stream section above and below beaver dams and at damless control sites to explore how these alterations change physical habitat and fish biodiversity. Although different questions and different systems with different habitats and species pools will require different types of gear and different amounts of effort, the process I describe here has wide generality for researchers and managers sampling fish communities at a large number of previously unsampled sites.
**Table 2.1: Gear evaluation species list.**
For the 11 species caught during the four-day gear evaluation, shown are genus species, common name, abbreviation, and number of individuals caught (N).

<table>
<thead>
<tr>
<th>Genus species</th>
<th>Common name</th>
<th>Abbrev.</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>1  <em>Semotilus corporalis</em></td>
<td>Fallfish</td>
<td>FF</td>
<td>34</td>
</tr>
<tr>
<td>2  <em>Ameiurus natalis</em></td>
<td>Yellow bullhead</td>
<td>YBH</td>
<td>20</td>
</tr>
<tr>
<td>3  <em>Esox americanus americanus</em></td>
<td>Redfin pickerel</td>
<td>RP</td>
<td>17</td>
</tr>
<tr>
<td>4  <em>Anguilla rostrata</em></td>
<td>American eel</td>
<td>AE</td>
<td>10</td>
</tr>
<tr>
<td>5  <em>Ameiurus nebulosus</em></td>
<td>Brown bullhead</td>
<td>BBH</td>
<td>10</td>
</tr>
<tr>
<td>6  <em>Perca flavescens</em></td>
<td>Yellow perch</td>
<td>YP</td>
<td>9</td>
</tr>
<tr>
<td>7  <em>Lepomis gibbosus</em></td>
<td>Pumpkinseed</td>
<td>PS</td>
<td>2</td>
</tr>
<tr>
<td>8  <em>Notemigonus crysoleucas</em></td>
<td>Golden shiner</td>
<td>GS</td>
<td>1</td>
</tr>
<tr>
<td>9  <em>Salmo trutta</em></td>
<td>Brown trout</td>
<td>BT</td>
<td>1</td>
</tr>
<tr>
<td>10 <em>Esox niger</em></td>
<td>Chain pickerel</td>
<td>CP</td>
<td>1</td>
</tr>
<tr>
<td>11 <em>Micropterus salmoides</em></td>
<td>Largemouth bass</td>
<td>LMB</td>
<td>1</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td>106</td>
</tr>
</tbody>
</table>
CHAPTER 2 - FIGURE TITLES

**Figure 2.1:** (A) The study site located within Fish Brook a tributary of the Ipswich River in northeast Massachusetts. (B) Homogeneous 90-m stream section in which the gear evaluation was undertaken showing the three 30-m blocks (A, B, C) that were divided into three 10-m sections (S1, S2, S3). (C) Two treatments which included three gear types, and three levels of effort [1-3 mixed gear units (MGU)]. (D) Design of the gear evaluation showing the number of replicate days, blocks, the amount of effort per block (MGU), and random placement (indicated by an X) of gear types within each 10-m section of each block.

**Figure 2.2:** Mean and standard error of (A) species richness and (B) abundance in minnow traps (M, n = 24 [sets of 5]), 10-m sections of electrofishing (E, n = 24), and hoop nets (H, n = 24) (1, 2, 3, sets of gear per day for 4 days). (C) Species accumulation when combining gear types. P-values correspond to ANOVA results. Letters indicate similarity or difference based on Tukey HSD multiple comparisons.

**Figure 2.3:** (A) Total richness, (B) maximum richness per day, (C), total percent of the species pool, (D) species accumulation, (E) mean and standard error of species richness (n = 4) and, (F) mean and standard error of Shannon’s H’ diversity (n = 4) for 1, 2, and 3 mixed gear units (MGU) when days were used as replicates.
**Figure 2.4:** Non-metric multidimensional scaling (NMDS) ordination plot of two axis dimensions illustrating the similarity of 1, 2, and 3 MGUs in species assemblage. Numbers indicate the number of mixed gear units (MGU).

**Figure 2.5:** For resampling simulations, mean and standard error of (A) species richness \((n = 10)\) and, (B) Shannon’s H’ diversity \((n = 10)\) for each mixed gear unit (MGU). P-values correspond to results of the ANOVA. Letters indicate similarity or difference based on Tukey multiple comparison tests.

**Figure 2.6:** Mean number of species added divided by the amount of effort for each mixed gear unit (MGU). Values greater than one indicate a mean of more than one species added per effort, values less than one indicate less than one mean species added per effort.
Figure 2.1: Gear evaluation study design.
Figure 2.2: Evaluation of the type of gear needed to adequately sample fish biodiversity.
Figure 2.3: Evaluation of the amount of gear needed to adequately sample fish biodiversity.

- **A**: Total richness
- **B**: Maximum richness
- **C**: Percent of species pool
- **D**: Species accumulation
- **E**: Mean richness
- **F**: Mean Shannon's $H'$

**Legend:**

- **a**
- **b**

**Significance:**

- $P = 0.02$
Figure 2.4: Non-metric multidimensional scaling (NMDS) ordination plot of MGU.
Figure 2.5: Resampling simulations richness and diversity.
Figure 2.6: Number of species per unit of effort.
CHAPTER 3

USING ASSEMBLAGE DATA IN ECOLOGICAL INDICATORS: A COMPARISON AND EVALUATION OF COMMONLY AVAILABLE STATISTICAL TOOLS

3.1 Introduction

Scientists and managers need science-based methods to assess how human activities will impact resources. For example, environmental professionals are often asked to evaluate impacts of specific human activities on aquatic biota (Filipe et al., 2002; Anderson K. et al., 2006; Arthington et al., 2006). Ecological indicators that reflect the composition, structure, and function of ecosystems (Reza and Abdullah, 2011) can meet this need for science-based methods that aid impact assessment. Biological assemblage datasets are widely available and can potentially provide useful information on background ecosystem conditions and ecological responses to anthropogenic impacts. For example, the Environmental Protection Agency’s guidelines for ecological indicator suitability include conceptual relevance, feasibility of implementation, response variability, interpretation, and utility (Kurtz et al., 2001). Several impediments exist, however, to the use of assemblage datasets by environmental professionals. These complex data are composed of tens of species and hundreds of individuals so these data need to be simplified before they can be used in ecological indicator development and testing. In addition, the ideal data processing protocol should reduce the complexity of the assemblage data, yet still retain inherent ecological information. Finally, the output from statistical methods commonly used to process assemblage data are rarely compared
and evaluated, so little consensus exists on which approach works best. Consequently, field researchers and managers who construct and test ecological indicators could benefit from a practical guide to using assemblage data that includes a systematic comparison of commonly used statistical methods coupled with an evaluation of whether the resulting simplified statistical groupings reflect ecological patterns in the original dataset.

In the past, investigators have used a variety of statistical or ecological methods to process assemblage data. Commonly used multivariate statistical analyses that group species data include: cluster analysis (CL) (e.g., Orrego et al., 2009; Penczak et al., 2009), non-metric multidimensional scaling (NMDS) (e.g., Chick et al., 2006; Lorion and Kennedy, 2009), correspondence and detrended correspondence analyses (CA, DCA) (e.g., Falke and Gido 2006a, Humpl and Pivnička 2006), and principal components analysis (PCA) (e.g., Lamouroux and Cattaneo, 2006; Orrego et al., 2009 (Figure 3.1; Appendix B). Because multivariate statistics transform biological data into mathematical relationships, an effective processing protocol needs to include some validation that the simplified assemblage data reflect ecological trends. Guilds are a common ecological-based approach to grouping species (Welcomme et al., 2006; Noble et al., 2007). Concurrently using guild classifications, species information and quantitative approaches can provide insights into whether the simplified groupings that result from the multivariate and other grouping statistics reflect known ecological relationships.

Many researchers use exploratory analyses from biotic community datasets to develop ecological indicators (Podani and Csányi, 2010). How assemblage data are used in ecological indicators may influence the most appropriate statistical analysis. For example, assemblage data can be simplified to produce fewer, ecologically meaningful
multispecies groupings. In addition, these simplified assemblage groupings can be used to relate biota to environmental stressors of interest to managers or to identify influential species. Fish are often used as ecological indicators because of their links to environmental conditions (Kanno et al., 2009; Maceda-Veiga and De Sostoa, 2011). Here I used a statewide stream database as a case study to illustrate how common statistical methods can be used for these purposes. Specifically, I sought to provide a standardized framework for transforming raw data into usable ecological metrics by addressing the following objectives. First, I compared six common statistical grouping methods [i.e., cluster analysis (CL), non-metric multidimensional scaling (NMDS), principal components analysis (PCA), detrended correspondence analysis (DCA), logistic regression (Log), Poisson regression (Poisson)]. Although a number of novel statistical tools are currently being developed, I chose to compare well-developed statistical methods because these are readily available and most likely to be used by environmental professionals. I then evaluated the groupings that resulted from these statistical methods by comparing convergence, redundancy, and statistical similarity among methods, using guilds to interpret these groupings ecologically, and examining individual species to provide ecological validation. Second, I evaluated if the biotic groupings from these commonly used statistical methods could be related to environmental stressors. For this, I used low streamflow as an example of a stressor of interest in environmental management. However, any environmental variable of interest to regulators could be used. Third, I examined the distribution of individual species within each grouping across methods to identify influential taxa. Finally, I recommend a practical, step-by-step process that researchers and managers can use with other assemblage datasets. Many
excellent statistical treatments of multivariate analyses already exist in the literature; here, rather than duplicate these efforts, I seek to provide a user-friendly approach for field-oriented environmental professionals who want to use assemblage data.

3.2 Materials and Methods

3.2.1 Dataset

Fish were sampled at 344 sites throughout Massachusetts (Figure 3.2A). The sites were located within two U.S. Environmental Protection Agency (EPA) level III ecoregions, the Northeastern Highlands (58) and the Northeastern Coastal Zone (59; Figure 3.2A). Sites were small, wadeable streams with drainage areas from 0.04 to 262.93 km\(^2\), mostly \(\leq 10\) km\(^2\) (Figure 3.2B). All fish species sampled were present in both ecoregions. Fish were sampled from June to August, 1998 to 2005. All sample reaches were at least 30 times the width of the stream, a length within the range recommended for stream fish sampling (Simonson and Lyons, 1995). A single pass was made at all sites with one backpack electroshocker, a level of effort that has been shown to adequately characterize fish communities (Reid et al., 2009). Fish were identified to species, counted, measured, and returned to the stream. Species that were present in less than 5% of all samples were removed from the analyses to limit the undue influence of rare species (Gauch, 1982).

3.2.2 Create groupings that simplify assemblage data

We compared six statistical methods of which three used assemblage data only and three used assemblage plus environmental data (Table 3.1). As a result of each of
these statistical methods, one or more distinct "groupings" of multiple species were identified. Throughout, "groupings" refers to the species aggregations that result within and across multivariate analyses (e.g., CL-1, CL-2, NMDS-1, NMDS-2; Table 3.1). Most of these statistical methods can be calculated using the number of individuals (N) or the number of species (S). The first three methods that used assemblage data only included: cluster analysis (CL), non-metric multidimensional scaling (NMDS), and principal components analysis (PCA). I also chose three additional statistical tools that combined assemblage and environmental data: detrended correspondence analysis (DCA), logistic regression (Log), and Poisson regression (Poi).

Cluster analysis is a classification technique that places objects that are sufficiently similar into the same group while identifying distinctions between groupings (Legendre and Legendre, 1998). I used hierarchical agglomerative clustering with a Bray-Curtis resemblance matrix based on species presence-absence at each site (PRIMER 6.1.10 software; Clarke and Gorley, 2006). For this, I used a group average clustering algorithm (Legendre and Legendre, 1998). Species that were at least 30% similar were included in the cluster groups (CL-1, CL-2) and were calculated using species (S) and abundance (N) data (Table 3.1).

Non-metric multidimensional scaling (NMDS) is a non-eigenvector case of ordination that is used to provide a visual representation of dissimilarities in reduced-space ordination. I ran NMDS on a Bray-Curtis resemblance matrix of species presence-absence in two dimensions with PRIMER 6.1.10 software (Clarke and Gorley, 2006). The resulting NMDS scores for each species were plotted in two dimensional ordination space. Species that were >30% similar were retained as the NMDS groupings, NMDS-1,
NMDS-2, NMDS-3. These were based on both species (S) and abundance (N) data types (Table 3.1).

Principal components analysis (PCA) is an eigenvector-based multivariate analysis that transforms many correlated variables into a smaller number of uncorrelated principal components with a minimum loss of information (McGarigal et al., 2000). I used singular value decomposition with a correlation matrix of species abundance to reduce the dimensionality of fish species (“prcomp”; R Development Core Team, 2009). Each PC axis had an eigenvalue which indicated the amount of variation explained and an eigenvector which indicated the relative influence of each species. The first three PC site scores were retained as the PC-based groupings, PC-1, PC-2, PC-3 (Table 3.1).

Detrended correspondence analysis (DCA) is a variation of the eigenanalysis of a Chi-square distance matrix (also known as correspondence analysis or reciprocal averaging) and is used when a single long gradient appears as an arc in ordination (Hill and Gauch, 1980). I ran a DCA on presence-absence data to produce a two-dimensional ordination plot of site scores and species centroids over which a generalized additive model (GAM) spline of August median flow (AMF) was overlaid (“decorana,” “ordisurf” in the ‘vegan’ package; Oksanen et al., 2009; R Development Core Team, 2009). Species with centroids higher than 0.12 m$^3$ s$^{-1}$ AMF were included in the DCA grouping (Table 3.1). The threshold of 0.12 m$^3$ s$^{-1}$ AMF was chosen because it was where the GAM spline differentiated the upper 40% of AMF sites, however, other thresholds and other environmental variables could be used. All of the above statistical approaches are common ways to analyze assemblage data.
Finally, I used logistic and Poisson regression as additional grouping tools. Logistic regression is a generalized linear model that relates discrete response variables to one or more predictor variables by fitting data to a logistic curve (Quinn and Keough, 2002). Logistic regression was used to determine if AMF predicted presence-absence of each species (“glm” routine using the binomial family; R Development Core Team, 2009). If the logistic regression on an individual species produced a significant relationship with flow ($P \leq 0.05$), then that species was retained in the logistic grouping (Log) calculated as number of species (S) (Table 3.1).

Poisson regression is a generalized linear model that relates count data to one or more predictor variables (Quinn and Keough, 2002). I used Poisson regression to determine if AMF predicted the abundance of each species (“glm” routine using the Poisson family; R Development Core Team, 2009). The Poi (+) grouping included species that had a positive relationship ($P \leq 0.05$) with flow whereas the Poi (-) grouping included species that had a negative relationship with flow ($P \leq 0.05$; Table 3.1). Both Poi variables were calculated as abundance (N). My use of logistic and Poisson regression as ways to group species was not typical, but I think these methods provided innovative insights that were worth testing.

### 3.2.3 Evaluate groupings

I evaluated the groupings from these six analyses in several ways. First, I compared the similarity among groupings using two NMDS analyses. One NMDS compared groupings and guilds created as number of species (S); the other compared groupings and guilds calculated as abundance (N). A Bray-Curtis resemblance matrix of
Groupings was constructed for each data type. NMDS was then run on this resemblance matrix in two dimensions with PRIMER 6.1.10 software (Clarke and Gorley, 2006). The resulting NMDS scores were plotted in two dimensional ordination space. Groupings that were 20-80% similar were compared to assess convergence of statistical methods. Within these, I compared species across groupings and methods to assess redundancy. We also evaluated how these groupings compared to ecological flow guilds. Fish were classified into one of three ecological fluvial guilds based on fish life histories (e.g., Kinsolving and Bain, 1993). Fluvial specialists (FS) need flowing water at all life stages. Fluvial dependents (FD) need flowing water for at least one ontogenetic stage. Macrohabitat generalists (MG) never need flowing water and can live and reproduce in lentic systems. In other guild classifications, fluvial species were also categorized as lotic (Welcomme et al., 2006) or rheophilic (Aarts and Nienhuis, 2003). Alternate guild classifications for macrohabitat generalist species include lentic (Welcomme et al., 2006) and eurytopic (Aarts and Nienhuis, 2003).

3.2.4 Evaluate relationship among groupings and environmental stressor

Many environmental professionals are asked to evaluate specific environmental stressors, so understanding how biotic groupings are related to target environmental stressors may be another relevant use of assemblage data. I used linear regression models to evaluate how well my multispecies fish groupings, ecological flow guilds, and more tradition community measures (i.e., species richness and Shannon's H') explained variation in one example of an environmental variable of interest, low streamflow. Here, I used fish-based variables as the independent variable because I was interested in whether
these taxa could predict environmental conditions. Although relationships may not be completely linear (as with most biological phenomenon), linear approaches present more options for implementation and evaluation than nonlinear methods. Variables in any regression were limited to those groupings created by a single statistical method. I used simple linear regression (SLR) if a grouping method yielded only one grouping (e.g., Log) and multiple linear regression (MLR) if a method yielded multiple groupings (e.g., for the three PCA groupings, I compared seven models, three univariate, three bivariate, one trivariate) (SAS institute, 2008). From the candidate models within each method, I selected top models using Akaike Information Criteria (ΔAIC < 2; Burnham and Anderson, 1998). Then, I used the adjusted R² of the top model from each method to evaluate which methods and groupings explained the most variation in low streamflow. To compare the performance of individual groupings, individual regressors were evaluated by examining parameter estimates (β) and standard errors (SE). Linear regression assumes the data are independent observations with a normal distribution of errors and homogeneous variance in which the independent values are fixed (Quinn and Keough, 2002). As with most biological regression analyses, my independent variables were random not fixed (Quinn and Keough, 2002). After the response variable was log transformed, however, other statistical assumptions were met.

Researchers often want to validate statistical models, especially if they are used to make environmental decisions. Reliability was examined using training and test datasets on different discharge response variables (AMF, P₉₉, and PC flow; see Appendix C). After constructing fish variables, the fish dataset was randomly split in half. One half (N = 172) was used to develop models (training dataset) and the other half (N = 172) was
used to validate the models (test dataset). AMF was used as the dependent variable to
determine the best six models using the training dataset. Because many ways have been
suggested to quantify flow regimes, regressions for these top models were run on two
other measures of low flow (P99, and PC flow) as well as AMF using the test dataset.
Adjusted R² were compared for models using different datasets and flow measures.

3.2.5 Identify influential species

The importance of individual species within the groupings was explored using
hierarchical partitioning of variance (HP R²). Hierarchical partitioning of variance
quantified the explanatory power of each individual predictor variable within a regression
(Quinn and Keough, 2002). Across all groupings, I summed the number of times each
individual fish species was present in groupings with a HP R² > 0.10. A HP R² > 0.10
threshold was chosen because it is a reasonable amount of explained variation for a single
predictor, however, other thresholds could be used. The species most frequently present
within the most groupings with a high HP R² were judged influential species.

3.3 Results

3.3.1 Compare groupings that simplify assemblage data

Cluster analysis resulted in two clusters that were at least 30% similar (Figure
3.3A). CL-1 included eight species and CL-2 was composed of six species (Figure 3.3A;
Table 3.1). When species were plotted in two dimensional NMDS space (Stress = 0.14)
and clustered, three groupings emerged (Figure 3.3B). Five species occurred only in
NMDS-1; five species were unique to NMDS-2. NMDS-3 contained four species common to both NMDS-1 and NMDS-2 (Figure 3.3B; Table 3.1).

The first three PCs explained 26% of the variation in species abundance. Six, nine, and seven species had eigenvectors > 0.2 on PC1, PC-2, and PC-3 respectively (Table 3.1). The DCA fish variables included 10 species that had species centroids higher than 0.12 m³ s⁻¹ on the DCA ordination plot (Figure 3.4; Table 3.1). The Log grouping included 10 fish species that were present at more sites as AMF increased (Table 3.1). The Poi (+) grouping included 12 species that were more abundant as AMF increased (Table 3.1). The Poi (-) variable included seven species that were less abundant as AMF increased.

3.3.2 Evaluate groupings

Some of the groupings were more similar than others. For the variables measured as number of species (S), the Log, DCA, CL-1, and NMDS-1 groupings were ≥ 60% similar to each other (Figure 3.5A) with some subsets of these groupings being as much as 80% similar. These four groupings were most similar to the fluvial specialist ecological guild (FS) and contained mostly fluvial species (≥ 80%; Table 3.1). The NMDS-2 and CL-2 (Figure 3.5A) were also ≥ 80% similar to each other, most similar to the macrohabitat generalist guild (MG), and contained only macrohabitat generalists (Table 3.1). NMDS-3 was most similar to the fluvial dependent guild (FD; Figure 3.5A) and contained mostly (75%) fluvial species (Table 3.1).

Within groupings that were calculated as abundance (N), the NMDS-1, FS, CL-1, and Poi (+) variables were ≥ 80% similar (Figure 3.5B). The NMDS-3 and FD groupings were less similar (≥ 40%; Figure 3.4B). The MG, CL-2, and NMDS-2 groupings were ≥
60% similar to each other, but were not similar to other groupings (Figure 3.5B).

Although the arrangement of groupings was consistent for variables measured as species and individuals, groupings measured as species were more similar (≥ 40% similar; Figure 3.5A) than groupings measured as individuals (< 20% similar; Figure 3.5B).

3.3.3 Evaluate relationship among groupings and environmental stressors

Regression models using explanatory variables based on multispecies groupings derived from logistic regression, DCA, ecological guilds (FS, FG, MG), species richness (R), cluster analysis (CL-1, CL-2), and non-metric dimensional scaling (NMDS-1, NMDS-2, NMDS-3) explained 24-37% of the variation in low streamflow (Table 3.2; Figure 3.6). The regressors in these models were all positively related to streamflow (β=0.06-0.30; Figure 3.6A-F). Within these six regression models, at least one fish grouping regressor explained 11-37% of the variance in streamflow (Figure 3.6A-F). In multiple regressions, however, the influence of individual regressors varied. For example, in the ecological guild model, FS had a higher slope than FD, FS and FD explained a similar amount of variance, and MG had little effect (Figure 3.6C). In the cluster analysis model, CL-1 had both a higher slope and explained more of the variance than CL-2 (Figure 3.6E). In the NMDS model, all groupings had a similar slope but NMDS-1 and NMDS-3 explained more variation in flow than NMDS-2 (Figure 3.6F).

3.3.4 Test vs. training datasets

Regression models, developed with the training dataset, were similar to those obtained using the test dataset (adjusted R^2 within 3-8%; Table 3.2). Variation explained
using other measures of flow ($P_{99}$ and PC flow) were also similar, but slightly lower than those from the training dataset using AMF (Table 3.2).

### 3.3.5 Identify influential species

Twelve groupings explained at least 10% of the variation in their respective regression model using AMF (Table 3.3). With the exception of the summary variables ($R, H'$), which by definition included all species, these 12 groupings were dominated by species from the fluvial guilds (FS, FD). Brown trout (BT, *Salmo trutta*), white sucker (WS, *Catostomus commersoni*), and common shiner (CS, *Luxilus cornutus*) were in 10 of the 12 groupings that explained $\geq 10\%$ of the HP $R^2$ in flow in their respective regressions. Fallfish (F, *Semotilus corporalis*), tessellated darter (TD, *Etheostoma olmstedi*), and longnose dace (LND, *Rhinichthys cataractae*) were in nine of the groupings most related to flow (Table 3.3).

### 3.4 Discussion

Many researchers and managers use community field datasets to develop and tune ecological indicators. Here I compared statistical tools to help other environmental professionals translate field data into ecological indicators appropriate to their research question, regulatory need, or specific ecological system. My approach yielded four take-home messages. (1) Examining convergence and redundancy in the output of common statistical methods provided a process to evaluate statistical groupings. (2) The output from these common statistical methods can be used to assess relationships between biotic variables and environmental stressors. (3) Performance of metrics depended on whether
species or individual data were used. (4) These methods can be used to identify consistently influential species.

Similarities emerged in the composition of the groupings that resulted from the different statistical methods. Reliable groupings should be selected by examining convergence (i.e., similarity) across methods and groupings. Reliable groupings will also have redundancy (i.e., similarity) in species composition. Specifically, ecological flow guilds were essential for interpreting these statistically-based results. For example, four statistical methods (logistic regression, DCA, CL, and NMDS) created multispecies groupings that were > 60% similar. Groupings from these methods (Log, DCA, CL-1, NMDS-1) consistently grouped fluvial specialists together and often included the same set of species. Consequently, these groupings were statistically and ecologically justified as possible input to ecological indicators. These results contrasted with the PC-2, PC-3 and Poi (-) variables which did not provide consistent groupings compared to other methods, making them less credible as ecological indicators. For selection of the final metric, all of the convergent statistical methods are not needed. In environmental decision making, this convergence and redundancy can be useful in justifying the final methodological choice.

Regressing flow data against the groupings provided a quantitative criterion (adjusted R²) with which to compare groupings. Groupings created by logistic regression, DCA, cluster analysis, NMDS, and the ecological flow guilds were most related to low streamflow as was total species richness. Specifically, the Log, DCA, R, and CL-1 groupings, all measured as number of species, independently explained 19-37% of the variance in low streamflow in my dataset. With the exception of richness (R) which
contains all species, these groupings were consistently populated by species with a fluvial life history, a result that provides ecological credibility to the statistical results.

Overall, groupings that were calculated as number of species outperformed other data types. Species-based variables may be better indicators of flow at large spatial and temporal scales as they may not be as affected by year class strength and other year to year fluctuations. Although the methods I used were standardized, when examining fish communities for brief snapshots of time, presence-absence of species may be a more realistic metric of the fish community than number of individuals. For example, Poisson regression (i.e., species abundance vs. flow) performed worse than the logistic regression (i.e., presence-absence vs. flow). On the other hand, abundance may be a better indicator when examining mechanistic questions about fish communities at smaller scales.

* A priori choice of the appropriate statistical method will depend on type of data, assumptions of the analyses, options for post hoc analysis, and software packages. All of the methods calculated from assemblage only data (CL, NMDS, PCA) used a matrix of resemblance coefficients to examine the similarity or distance between objects. Cluster analysis and NMDS can use any resemblance matrix, however, PCA is restricted to a Euclidean distance matrix. The appropriate resemblance matrix depends on the data used. Legendre and Legendre (1998) and Gotelli and Ellison (2004) provide detailed criteria that environmental professionals can use for choosing resemblance coefficients. Cluster analysis (CL), a classification tool, is a popular multivariate grouping method because it has few assumptions, can be used on many types of data (using many types of distance matrices), can be visualized as a dendrogram, and the resulting relationships can be quantitatively evaluated with similarity measures.
The statistical tool NMDS is a specific case of ordination that creates axes that can be rotated arbitrarily and separated into dissimilar objects in ordination space for a specified number of dimensions and can be used with any distance measure (Legendre and Legendre, 1998). NMDS does not assume normality or require that variables change linearly along underlying gradients. NMDS uses a quantitative measure called Stress (the sum of squared differences between fitted values and the values forecasted by the regression of the fitted values on the empirical values) to assess goodness-of-fit. NMDS is also a popular multivariate grouping technique because it has few assumptions, can be used on many types of data (with many types of distance matrices), can be plotted as sites or species, and has a goodness-of-fit test that allows for quantitative evaluation of the results. Also, NMDS can be used in conjunction with cluster analysis to provide a spatial representation of clusters.

PCA has more restrictive assumptions than NMDS or cluster analysis, i.e., the data is multivariate normal, the samples are independent and random, there are no outliers in the data, and that variables change linearly along underlying gradients (McGarigal et al., 2000). Nevertheless, in some cases, PCA which uses Euclidean distance, can be plotted by sites, and can be evaluated with eigenvectors and eigenvalues, may be the preferred approach.

CA or DCA may be applied to any data table that is dimensionally homogenous and only contains positive integers or zeros (Legendre and Legendre, 1998). DCA uses a $\chi^2$ distance matrix which is appropriate when data are normally distributed across the environmental gradient and the environmental relationship is assumed to be unimodal (Gotelli and Ellison, 2004). There is debate on the usefulness of DCA because the
instability of solutions (Jackson and Somers 1991). However, I found that DCA produced a useful grouping, similar to other methods. CA and DCA can be quantitatively evaluated with eigenvectors and eigenvalues, and have an advantage over other ordination techniques in that they produce plots with a simultaneous representation of sites and species that can be overlain with a spline of environmental data.

Logistic and Poisson regressions are not common approaches for grouping species in assemblages. Nevertheless, I think these approaches are creative ways to explore the data, and, in the case of the logistic grouping, a very effective way to identify groups of species. These approaches use P-values as a quantitative decision tool. They do not require normality, but are based, of course, on specific ecological responses. Logistic regression assumes random error terms and a binomial distribution (Quinn and Keough, 2002). Poisson regression assumes a Poisson distribution where the mean equals the variance (Quinn and Keough, 2002).

By examining the output of all analyses together, select species were consistently identified. Although there was a general trend that fish with fluvial life histories outperformed generalist species, not all fluvial fish species were equally related to low streamflow. In my dataset, brown trout, white sucker, and common shiner were consistently present in groupings that explained variation in low streamflow. Brown trout, although not native, are often considered “naturalized.” These coldwater predators require highly-oxygenated water, use gravel substrate for spawning, and are intolerant of poor water quality (Hartel et al., 2002). White sucker are native, live in cold or warmwater, are trophic generalists that spawn in gravel, and are moderately tolerant of water quality. Common shiners are small bodied (≤ 18 cm), native, live in cold or
warmwater, are trophic generalists that spawn over gravel beds, and are moderately tolerant of water quality (Hartel et al., 2002). Although varied in their ecological requirements, these species were moderately common (present in 26.7%, 45.1%, and 16.9% of all sites, respectively) with a fairly broad distribution. All three require flowing water, need specific spawning substrates to complete their life cycle, and do not tolerate poor water quality. Once identified, these influential taxa can be used in a variety of ways by environmental professionals including potential indicator species in a multimetric index.

3.4.1 Step-by-step process for practitioners

Our case study provided a practical methodology to reduce complex assemblage datasets to simpler groupings that are statistically defensible and ecologically interpretable. Below, I summarize this methodology in a step-by-step process that identifies ecological trends in a suite of convergent statistical methods which practitioners can use to develop understandable multispecies groupings in which they have confidence (Figure 3.7).

The first step is to clarify the goals for processing the assemblage data (Step I, Figure 3.7) because the most appropriate type of grouping analysis can depend on the specific research questions being addressed. I processed assemblage data for three related objectives: (A) simplification of hundreds of individuals belonging to tens of species into a few multispecies groupings, (B) assessing the relationship of these groupings to environmental stressors of interest, and (C) identifying influential species. Step I (B) and (C) build on the process used for data simplification (A) (Step I; Figure 3.7). The second step in simplifying assemblage data for ecological indicators is to explore patterns in the
raw data (Step II; Figure 3.7). This will familiarize practitioners with patterns and problems in the data. For example, before simplifying assemblage data with multivariate and other statistical tools, practitioners need to identify common (species 2) and rare species (species 1) (Step II; Figure 3.7D, E) and assess if the underlying data is distributed normally (Step II; Figure 3.7F). Plots that examine the distribution of guilds or other ecological classifications (Step II, Figure 3.7G) will also aid data evaluation and interpretation after analyses are completed.

The third step is to identify candidate statistical analyses for simplifying assemblage data (Step III; Figure 3.7). Candidate analyses can be selected in a number of ways. I chose analyses that were cited frequently in the literature, were in common use, and for which I had statistical software (e.g. SAS, R, Primer), but other criteria are possible. In addition, choice of candidate analyses should be based on the type of statistical analysis (classification, ordination, or other), statistical assumptions (underlying data distribution, expected ecological response), characteristics of the analysis (distance measure, plots available, quantitative evaluation tools), or specific decision rules (Step III; Figure 3.7). Once the groupings are calculated using multiple techniques, the results should be evaluated and interpreted (Step IV; Figure 3.7). Using NMDS, I compared the similarity of the groupings derived from multiple statistical methods (to assess convergence). I also compared the similarity of the groupings to ecological criteria such as guilds (for interpretation) (Step IV, Figure 3.7H). I then compared species composition of the groupings (to assess redundancy) (Step IV, Figure 3.7I). After these steps, environmental professionals will have identified a number of convergent groupings with a similar species composition. From this redundancy,
practitioners will understand ecological trends behind the mathematical simplifications and can have confidence in their choice of a statistical grouping tool. Environmental professionals can then proceed using any one of the convergent methodologies. In summary, the process I have outlined here can be widely used to simplify assemblage datasets for a variety of research questions, regulatory needs, and ecological systems.
Table 3.1: Statistical methods, multispecies groupings, and associated fish species. Symbols indicate flow guilds: circle = fluvial specialist (FS), star = fluvial dependent (FD), triangle = macrohabitat generalist (MG).

<table>
<thead>
<tr>
<th>Statistical Methods</th>
<th>Groupings</th>
<th>FS</th>
<th>Species</th>
<th>FD</th>
<th>MG</th>
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<tr>
<td></td>
<td></td>
<td>Fallfish (F)</td>
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<td></td>
<td></td>
<td></td>
<td>Redfin pickerel (RP)</td>
<td>Golden shiner (GS)</td>
</tr>
</tbody>
</table>

| Assemblage          |           | CL-1                        |                   | *                           | ▲                            |
|                     |           | CL-2                        |                   | *                           | ▲                            |
|                     |           | NMDS-1                      |                   | *                           | ▲                            |
|                     |           | NMDS-2                      |                   | *                           | ▲                            |
|                     |           | NMDS-3                      |                   | *                           | ▲                            |
|                     |           | PCA-1                       |                   | *                           | ▲                            |
|                     |           | PCA-2                       |                   | *                           | ▲                            |
|                     |           | PCA-3                       |                   | *                           | ▲                            |

| Assemblage + Environmental |           | DCA                         |                   | *                           | ▲                            |
|                            |           | Logistic                    |                   | *                           | ▲                            |
|                            |           | Poisson Poi (+)             |                   | *                           | ▲                            |
|                            |           | Poisson Poi (-)             |                   | *                           | ▲                            |
Table 3.2: Top regression models.
Adjusted $R^2$ for each of the top six regression models (built with the training dataset) when used on the test dataset and with other flows as response variables. Presented are results for the training and test datasets. Shown are the groupings and adjusted $R^2$ for each flow variable: August median flow (AMF), $P_{99}$, and PC flow. $R =$ species richness. Other abbreviations are defined in the text.

<table>
<thead>
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<th>Test dataset</th>
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</table>
**Table 3.3: Ranked fish groupings.**

Groupings were ranked by HP $R^2$ to evaluate influential individual species. Only variables that explained at least 10% of the variation in August median flow in their respective regression are included. Columns include groupings, data type, species in each variable, and HP $R^2$. For data type S = species, N = abundance, D = diversity, SS = site scores. The bottom row shows the total number of groupings in which each fish species was present. See Table 1 for species abbreviations.

<table>
<thead>
<tr>
<th>Groupings</th>
<th>Data Type</th>
<th>FS</th>
<th>FD</th>
<th>MG</th>
<th>HP R²</th>
</tr>
</thead>
<tbody>
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<td>S</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>▲</td>
</tr>
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<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
</tr>
<tr>
<td>R</td>
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CHAPTER 3 - FIGURE TITLES

**Figure 3.1**: Percentage of papers that used common statistical grouping methods to summarize fish assemblages in a literature review of studies \( n = 101 \) from 2005-2010. The review was conducted using Web of Science. The terms “fish community(ies)” or “fish assemblage(s)” were searched in the journal article title, and the words “stream” or “river” within the topic field. Only papers that actively sampled fish in freshwater streams were included in the review. PCA = principal components analysis, CA = correspondence analysis, DCA = detrended correspondence analysis, NMDS = non-metric multidimensional scaling, and CL = cluster analysis. Papers are listed in Appendix B. These four analyses collectively comprise almost 60% of the analytical tools used in this database.

**Figure 3.2**: (A) Location of fish sample sites in Massachusetts, USA. Circles indicate the training dataset \( n = 172 \), and triangles indicate the test dataset \( n = 172 \). Training and test datasets were assembled randomly. Legend indicates EPA ecoregions 58, 59, and 84. All sample sites were in Northeastern highlands (58) and Northeastern coastal zone (59). (B) Histogram of drainage area (km\(^2\)) is shown for all sites \( n = 344 \).
**Figure 3.3:** (A) Results of a cluster analysis used to group species. Cluster 1 and 2 are > 30% similar. Each cluster of species was retained as a fish grouping variable (Cl-1, Cl-2; Table 3.1). (B) Ordination of multidimensional scaling in two dimensions with circles indicating 30% similarity. See Table 1 for a key to species abbreviations. Legend indicates flow guild. Arrows indicate groups of species that were retained as the groupings, NMDS-1, NMDS-2, NMDS-3, (Table 3.1).

**Figure 3.4:** Ordination plot of the first two axes of a detrended correspondence analysis (DCA). Circles are site scores, abbreviations are species centroids. See Table 3.1 for abbreviation key for species. Lines are GAM splines of August median flow. Bolded species abbreviations are the species that were retained in the DCA fish grouping variable, DCA (Table 3.1).

**Figure 3.5:** Non-metric multidimensional scaling (NMDS) of groupings from all statistical analyses measured as (A) number of species and (B) number of individuals. Circles indicate similarities between groupings considered in my analysis.

**Figure 3.6:** Top six regression models (A-F) from the training dataset ($n = 172$) that relate groupings to AMF (August Median Flow; natural log transformed). Variable symbols, $\beta$ (slope), SE of slope, and HP $R^2$ are indicated below each plot. The full model adjusted $R^2$ and regression line are indicated within each plot. Each of the fish grouping variables were calculated as number of species.
**Figure 3.7:** Step-by-step process for practitioners. The process starts by identifying objectives (Step I) and exploring the data (Step II). Then candidate analyses are determined (Step III), followed by evaluating and interpreting the data (Step IV). In Step III, EV = eigenvalues, % sim. = percent similarity, and % var. = percent variation explained. Step V represents a possible endpoint at which statistically defensible and ecologically interpretable groupings have been identified. Steps VI and VII are additional optional steps for developing ecological indicators. These steps summarize the process used for my case study.
Figure 3.1: Literature review of statistical analyses used to create fish groupings.
Figure 3.2: Study location and sample sites.
Figure 3.3: Cluster analysis and NMDS fish groupings.
Figure 3.4: DCA fish groupings.
Figure 3.5: NMDS of fish groupings.
Figure 3.6: Top regression models.
Figure 3.7: Step-by-step process for practitioners.
CHAPTER 4

BEAVER DAMS MAINTAIN NATIVE FISH BIODIVERSITY VIA ALTERED HABITAT HETEROGENEITY IN A COASTAL STREAM NETWORK

4.1. Introduction

Understanding the relationship between biodiversity and ecosystem function (Hooper et al. 2005, Cardinale 2011), especially the overall direction, strength, and shape of these relationships, is a current focus in ecology with direct applications to the formulation of sustainable watershed conservation plans. Most ecologists agree that high native biodiversity is a desirable trait (Tilman et al. 1996, Dawson et al. 2011), even though mechanisms by which biodiversity affects ecosystem function are poorly understood (Loreau et al. 2001, Hooper et al. 2005). Ecological theory suggests that the diversity of species in an ecosystem is related to habitat heterogeneity (Guégan et al. 1998, Dodds 2009, Munguia et al. 2011). To advance my understanding of how habitat heterogeneity affects biodiversity and guides sustainable watershed planning, I examine how a native ecosystem engineer, North American beaver (Castor canadensis), alters stream habitat and native fish assemblages at a riverscape scale.

Heterogeneity is a fundamental feature of ecological systems that alters the outcome of individual, population, community and ecosystem processes (Scheiner and Willig 2008). Heterogeneity has a rich history in theoretical and empirical ecology. In classic studies, mosaics of heterogeneous habitats change the outcome of species interactions (Gilinsky 1984, Power 1992) and stabilize predatory and competitive
interactions (Diehl 1992). Over the past quarter century, ecologists' views of heterogeneity have evolved into an array of specialized concepts. For example, specific patterns of habitat mosaics and resulting consequences play a key role in spatially-explicit ecological concepts such as the serial discontinuity concept (e.g., Ward and Stanford 1983, Stanford and Ward 2001), patch dynamics (e.g., Townsend 1989, Winemiller et al. 2010), landscape ecology (e.g., Turner 1989, 2010), the effect of confluences (e.g., Benda et al. 2004, Kiffney et al. 2006), the role of fragmentation (e.g., Fahrig 2003), and how metacommunities function (e.g., Leibold et al. 2004, Logue et al. 2011). In concept, ecological theory predicts that species richness increases with habitat heterogeneity (Guégan et al. 1998, Dodds 2009, Munguia et al. 2011), but in reality, the amount and configuration of heterogeneity that maintain intact functioning systems, especially at larger scales, is unclear.

Ecosystem engineers have the potential to alter physical heterogeneity of ecosystems and influence species diversity. North American beaver are a well studied ecosystem engineer (Rosell et al. 2005) that can dramatically modify aquatic landscapes (e.g., Naiman et al. 1988, Johnston and Naiman 1990). Specifically, beaver dams alter hydrology (e.g., Anderson and Shafroth 2010), biogeochemistry (e.g., Naiman et al. 1994), invertebrate assemblages (e.g., McDowell and Naiman 1986), and fish communities (e.g., Pollock et al. 2003, Rosell et al. 2005, Kemp et al. 2011). Although beaver dams have been broadly classified (Schlosser and Kellemeyn 2000), finer resolution of variation in individual dam structure and function has not been examined. Examining processes at the larger riverscape scale is a current priority in ecology (Schlosser 1991, Fausch et al. 2002; Tetzlaff et al. 2007), and a recognized need for
successful restoration (Palmer 2010, Stranko et al. 2011), but the role of beaver dams and other discontinuities have not been quantified at a larger riverscape scale (Burchsted et al. 2010).

Ecological tests about patterns, drivers, and consequences of habitat heterogeneity and biodiversity can provide science-based support for watershed planning and conservation. To provide a scientific basis for managing aquatic resources, here I applied ecological theory on heterogeneity to test hypotheses about how beaver dams might alter physical habitat and fish biodiversity throughout a stream network (Figure 4.1). I first asked about the spatial placement of the beaver dams within the watershed (Figure 4.1, Question 1), for example, was riverscape position the most important consideration (H$_{1a}$) or were local factors drivers (H$_{1b}$). Because beaver dams were not always located in a specific area of the watershed, I also asked how beaver dams altered instream habitat at a local scale (Figure 4.1, Question 2), especially whether dams had a uniform effect on physical habitat (H$_{2a}$) or if they introduced habitat heterogeneity through one (H$_{2b}$) or alternate pathways (H$_{2c}$). Next, I tested hypotheses about the relationship between habitat heterogeneity and fish diversity (Figure 4.1, Question 3, H$_{3a-3c}$), how beaver dams altered fish biodiversity (Figure 4.1, Question 4, H$_{4a-4b}$), and if individual fish species responded differently to habitat alterations (Figure 4.1, Question 5, H$_{5a-5b}$). Finally, I use these data to make inferences about the applied conservation consequences of beaver dams in order to help fish, wildlife, water, and land professionals manage the expansion of beaver and construct watershed conservation plans to protect native biodiversity (Figure 4.1, Question 6, H$_{6a-6b}$).
4.2 Materials and Methods

4.2.1 Study site

Hypotheses about the impact of beaver dams on instream habitat and fish biodiversity were tested in Fish Brook, a tributary of the Ipswich River, Massachusetts (Figure 4.2). The Ipswich River is a 72-km long, fifth-order, low-gradient (mean basin slope = 1.57 %) coastal river that drains a 404 km² watershed, dominated by residential, forest and wetland land use (Armstrong et al. 2001). Fish Brook, a fourth-order stream network, drains a 47 km² area and has similar physical features and land use as the Ipswich River watershed. During this study (June to October 2009), stream temperatures ranged from 10.0 to 15.7 °C (mean = 13.1, SE = 0.13) and the average discharge at the nearest gaging station (U. S. Geological Survey 01101500 Ipswich River at South Middleton, MA; http://waterdata.usgs.gov/usa/nwis/uv?01101500) was 1.88 m³ s⁻¹ (SE = 0.12, range = 0.28 to 6.65).

4.2.2 Beaver Dam Census and Architecture

All beaver dams in the Fish Brook drainage network were located and measured. The entire tributary was kayaked June 5-6, 2009 and the location of each beaver dam was identified (latitude, longitude) with a Garmin GPSmap 60C. Dams were again censused between September 30 and October 12, 2009 and dam architecture was assessed by measuring dam width (one width at mid-dam) and dam height (five equally-spaced distances between the downstream water surface and the top of the dam).
4.2.3 Approach and sampling units

I sampled instream physical habitat and fish biodiversity at both beaver dams \((n = 15)\) and control sites \((n = 9)\) that were located at least 100 m away from any beaver dam. Based on the serial discontinuity concept (Ward and Stanford 1983), I predicted that the greatest impact of beaver dams would be at the boundary between habitat patches that were immediately upstream and downstream of each beaver dam, and that the effect would be diluted with increasing distance from a beaver dam. Other studies that sample fish use rules of thumb for determining the length of a sample reach, such as 30 times the width of a stream to ensure that all habitat types are sampled (Rahel and Hubert 1991, Smith and Jones 2005). My intent was to capture the area of greatest impact while minimizing dilution. Therefore, I chose 30-m sample reaches directly upstream and downstream of beaver dams. My research unit was the site (dam or control) not the individual upstream and downstream habitat patches associated with each site. Statistical analyses (a) examined the physical differences between site-specific upstream and downstream habitat patches for all sites, (b) quantified patterns of physical habitat alteration for all beaver dams in Fish Brook, (c) compared fish in the combined upstream and downstream habitat patches across all sites, and (d) tested for site-specific differences in fish communities between upstream and downstream habitats throughout the stream network.

4.2.4 Physical habitat Measures in upstream and downstream patches

To compare physical habitat characteristics, stream width, stream depth, substrate, and current velocity were measured at transects 10-m, 20-m and 30-m upstream and
downstream of each beaver dam or control centerline (i.e., three transects per habitat patch, six transects per beaver dam or control site). Wetted stream width (m) was measured for each of the six transects at each site. Stream depth (m) and substrate were measured at 10 equally-spaced points along each transect. Substrate was categorized using a modified Wentworth scale (Cummins 1962) in which 5 = >256 mm, 4 = 32-256 mm, 3 = 2-32 mm, 2 = 0.125-2 mm, 1 = <0.125 mm. Stream velocity in m/s was measured at 60% of the total depth at 10 equally-spaced points (McMahon et al. 1996) along the 10 m transect, both above and below each dam or control site centerline. To examine if habitat changed through time, I measured upstream and downstream depths at ten equally-spaced locations along six transects (three upstream and three downstream) at a subset of five beaver dams (D9, D11, D16, D23, D24) on seven dates between July 31 to October 10, 2009 (July 31, August 1, August 4, September 30, October 1, October 9, October 10).

4.2.5 Fish sampling

Fish were sampled in the same upstream and downstream patches, as described above (n = 24 total, 15 beaver dams, 9 controls) over 12 days from August 5, 2009 to August 16, 2009. Two sites (i.e., two sets of upstream and downstream patches or four patches) were sampled in random order within each 24-h period. To sample fish, I used a combination of three sampling gears (backpack electrofishing, hoop nets, and minnow traps) in a sampling design that captured 100% of the total species pool (Chapter 1). In the afternoon between 14:00 and 16:00, fish were electrofished within each 30-m patch using a Smith-Root LR-24 backpack electrofisher (300 to 500 volts, 60 Hz). Starting
downstream, all wadeable areas of each upstream and downstream patch were
electrofished in a single pass, an effective fish collection method (Reid et al. 2009), for a
standard duration of 300 s. Fish were captured in dipnets and held in a water-filled bucket
until sampling was complete.

Two hoop nets and ten minnow traps were set in randomly determined locations
within each 30-m long habitat patch. These gear were set between 18:00 and 19:00 and
removed between 6:00 and 7:00 the next morning for a total fishing time of 12 h. Hoop
nets (Memphis Net and Twine Co., H9991-4, 61-cm diameter, 1.22-m long, 0.64 cm
mesh) were placed in the thalweg with a mesh lead (Memphis Net a Twine Co., WNG1,
3.0-m long, 1.8-m deep, 2.54-cm mesh) that connected the downstream net opening
diagonally to the opposite stream bank. Unbaited minnow traps (Gee Brand; 22.9-cm
diameter, 44.5-cm long, 0.64-cm mesh made of galvanized steel wire, with a 2.5 cm
opening) were randomly set around the hoop nets.

For all gears, fish were identified to species, measured (total length to the nearest
mm), fin clipped to assess if individuals were caught in multiple sections or gears, then
returned to the stream. Based on a statistical analyses from a larger stream fish dataset
(e.g., Smith and Mather 2011), I chose to analyze fish by abundance, species richness,
diversity indices, fluvial guilds, and select constrained and unconstrained multivariate
community metrics (redundancy analysis, RDA; detrended correspondence analysis,
DCA). For the fluvial guilds, macrohabitat generalists were defined as fish that can
occupy and reproduce in lentic or slow moving habitats whereas fluvial fish species (both
specialists and generalists) were classified as those fish that need flowing water or lotic
habitat for at least one ontogenetic life stage (Kingsolving and Bain 1993).
4.2.6 Data analyses

4.2.6.1 Spatial patterns

Many approaches exist for examining riverscape-scale patterns. I used three sets of simple tests to examine overall spatial patterns. First, I tested if the distances (km) between beaver dams \( n = 15 \) were equal using the ‘chisq.test’ function (R 2.13.0 software; R Development Core Team 2011). Next, I also used a Moran's \( I \) test (Wagner and Fortin 2005) to examine patterns of spatial autocorrelation for all independent and response variables (‘Moran.I’ function; R ‘ape’ package; Paradis et al. 2004). Finally, I regressed river km against dam height and width to assess if riverscape position affected dam architecture. I predicted that if local conditions were more important than riverscape position, the Moran's \( I \), chi-sq, and the regression analyses would not be significant (Figure 4.1, Question 1, H1b).

4.2.6.2 Habitat

To quantify how beaver dams altered differences in physical habitat characteristics between upstream and downstream patches, habitat data were analyzed in three ways. First, correlations among physical changes for a subset of dams, examined at multiple times from summer to fall, were examined to quantify seasonal patterns. The second habitat analysis created a heterogeneity index that ranked site-specific physical differences between upstream and downstream patches for all 24 sites in order to evaluate the impact of beaver dams on habitat complexity throughout the riverscape. The third habitat analysis used a k-means cluster analysis, followed by a principal components
analysis (PCA), to visualize patterns of differences in upstream and downstream patches. These three habitat analyses are described in detail below.

First, to examine if habitat changed throughout the summer-fall sampling season of 2009, a correlation matrix was constructed of upstream and downstream depths at five dam sites on seven sample dates. I predicted a high correlation across sampling times, a trend that would indicate that basic features of the beaver dams changed little within the sampling period. Second, to create a single value that integrated physical differences between upstream and downstream patches for the four habitat measures, a habitat heterogeneity index was calculated. For this, differences in means of the four habitat variables between each upstream and downstream patch were calculated at each site (stream depth based on 30 measures per patch; stream width based on three measures per patch, current velocity based on ten measures per patch, substrate based on 30 measures per patch). Next, for each habitat variable, sites were ranked based on the absolute value of the difference between upstream and downstream patches ($\Delta$ stream depth, $\Delta$ stream width, $\Delta$ current velocity, and $\Delta$ substrate). Finally, a single habitat heterogeneity index was calculated for each site by summing the ranks for the four habitat differences at each site. Sites with larger habitat heterogeneity index scores had higher habitat heterogeneity, defined as differences in habitat upstream and downstream at each site. Additive indices are common in ecology and other fields (Gerritsen 1995) and are useful for evaluating resources (Fore et al. 2011). An additive index was chosen over a multiplicative index because I assumed equal importance among habitat variables. My prediction (Figure 4.1, Question 2, H2b) that beaver dams would increase habitat heterogeneity compared to
control sites, regardless of their location within the watershed, was tested with a distribution-free Wilcoxon rank sum test.

Third, to examine if all beaver dams altered stream habitat similarly, I clustered differences in each habitat variable between upstream and downstream patches at both beaver dam and control sites using a nonhierarchical K-means cluster analysis ($n = 24$; R 2.13.0 software; R Development Core Team 2011). For this, a Euclidean distance matrix was calculated on the habitat difference variables. Using this matrix, I created clusters using the partitioning around medoids (‘pam’) function from the R ‘cluster’ package (Maechle et al. 2005). A break in a scree plot was used to determine the appropriate number of clusters. I tested the stability of the clusters using Jaccard means that were obtained from the bootstrap method within the ‘clusterboot’ function (‘fpc’ package; Hennig 2010). I tested my prediction that beaver dams have different types of effects (Figure 4.1, Question 2, H2c) by evaluating Jaccard values, i.e., >0.60 confirms cluster patterns, > 0.75 indicates stable clusters (Hennig 2010). These clusters, which represent different ways that beaver dams can change physical habitat, were displayed in ordination space with principal components using the ‘prcomp’ function. Kruskal-Wallis and subsequent Wilcoxon rank sum tests were run to test for differences in habitat variables ($\Delta$ stream depth, $\Delta$ stream width, $\Delta$ current velocity, and $\Delta$ substrate, habitat heterogeneity index) across clusters.

4.2.6.3 Fish

I also used three approaches to analyze the relationship between fish biodiversity, stream habitat, and beaver dams. These included: (1) heterogeneity index-diversity
regressions, (2) path analyses to understand how patterns emerged, and (3) constrained/unconstrained ordinations to examine relationships among individual species and habitat characteristics. The first fish analysis tested if beaver dams, in general, were associated with more diverse stream fish communities (Figure 4.1, Question 3, H3a-c). For this, I combined fish samples from both the upstream and downstream patches at each site and calculated total species richness and diversity, measured as Shannon’s H’ . These fish community indices (dependent variable) were then regressed against site-specific habitat heterogeneity index scores (independent variable) for all 24 sites to test my prediction that habitat alteration by beaver dams would increase fish diversity throughout the riverscape (Figure 4.1, Question 3, H3c).

Next, I used path analyses to test how specific patterns of fish diversity, measured as fish species richness (Δ richness) and fluvial fish abundance (Δ fluvial abundance), differed between upstream and downstream patches (Figure 4.1, Question 4, H4a-b). Path analysis examines both direct and indirect (mediated through other variables) relationships and is often used to understand how biotic patterns are established (Meyers et al. 2006). I used SPSS 14.0 software as an exploratory, hypotheses-generating tool. Three sets of exogenous (independent) variables included: landscape position, measured as river kilometers from the mouth of Fish Brook; beaver dam architecture, measured as mean dam height (m) and dam width (m); and stream habitat variables, measured as Δ stream depth (m), Δ stream width (m), Δ velocity (m/s), Δ substrate between upstream and downstream habitat patches.

I ran two separate path analyses to relate these exogenous variables to two (dependent) endogenous variables, Δ fish species richness and Δ fluvial fish abundance.
between upstream and downstream patches. Each path analysis used only beaver dam data \((n = 15)\) because there were no beaver dam characteristics at control locations. My sample size is comparable to that of other ecological studies (Wooten 1994). Although path analysis looks at all direct and indirect relationships between all exogenous and endogenous variables, I only show relationships that had a \(P\)-value <0.05. For these, solid lines in the path diagram indicated a positive relationship, and dotted lines indicated a negative relationship. For each relationship, I show slope (beta-coefficient), coefficient of variation \((R^2)\) and significance \((P\)-value). Assumptions of path analysis were tested and met (i.e., linear relationships between model variables, uncorrelated errors, recursive model, variables measured at an interval scale; Meyers et al. 2006).

The third set of fish analyses examined how individual fish species were related to habitat variables using constrained (redundancy analysis, RDA) and unconstrained ordination (detrended correspondence analysis, DCA) (Figure 4.1, Question 4, H\(_{4a-b}\)). For both analyses, I used the ‘vegan’ package in R on fish species that were present in at least five percent of sample sites (Oksanen et al. 2011). For the RDA, the constraining matrix included mean depth, width, velocity, and substrate for each sample patch; the response matrix used log transformed, chord-standardized abundance of each fish species for each sample patch. An ordination tri-plot was constructed that indicated the amount of constrained variation explained. On this triplot, upstream and downstream patches at each site were connected with a segmented line whose length indicated the relative difference in habitat characteristics based on Euclidean distance. Permutation tests indicated if the habitat variables explained more variation than chance alone. Only significant habitat vectors and fish species with > 5% variation explained are shown.
To examine the unconstrained variation in individual fish abundance among sites, I used a detrended correspondence analysis (DCA) in which site and species scores are shown on an ordination biplot of the first two DCA axes. To examine the response of individual species to one habitat variable, current velocity, a generalized additive model (GAM) spline of velocity differences (upstream patch – downstream patch) was overlaid on the ordination plot using the ‘ordisurf’ function in the R ‘vegan’ package.

4.3 Results

4.3.1 Spatial patterns (Question 1)

Landscape characteristics were not the primary determinant of beaver dam architecture or location as beaver dams occurred throughout Fish Brook (Figure 4.1, Question 1, H1b). A total of 15 dams were censused for the entire Fish Brook network (Figure 4.3A). Beaver dams were not limited to a single spatial location, nor did they conform to a single distributional pattern within the stream network. Stream slope at beaver dams did not differ from control sites (Wilcoxon rank sum test, \( P > 0.05 \)). Beaver dams occurred from river kilometer 2.8 to 16.5 and were found in both headwater and downstream portions of the drainage (mean = 8.64 rkm, SE = 0.84 rkm; Figure 4.3A). Beaver dams were interspersed throughout the drainage (\( X^2 = 8.75, P = 0.85 \)). Interestingly, all beaver dams but one (D21) were located on the mainstem of Fish Brook, probably because many tributaries had intermittent flow. Spatial patterns were not observed in \( \Delta \) current velocity (Moran’s \( I = -0.17, P = 0.25 \)), \( \Delta \) substrate (Moran’s \( I = -0.04, P = 0.99 \)), \( \Delta \) stream width (Moran’s \( I = -0.15, P = 0.32 \)), or \( \Delta \) stream depth (Moran’s \( I = -0.11, P = 0.57 \)). Beaver dams varied in height (mean = 0.38 m, SE = 0.07 m).
m, range = 0.91 m), and width (mean = 14.44 m, SE = 2.87 m, range = 35.41 m) (Figure 4.3B), but these dam characteristics were not related to rkm (rkm linear regressions \( P > 0.05 \)) or spatial patterns (dam width Moran’s \( I = -0.18, P = 0.42 \) and dam height Moran’s \( I = 0.02, P = 0.71 \)). Consequently, to understand the impact of beaver dams on physical habitat and fish biodiversity throughout the stream network, characteristics of physical habitat and fish communities above and below beaver dams first need to be examined at a local scale.

### 4.3.2 Patterns of beaver dam impact on physical habitat (Question 2)

Beaver dams altered local-scale patch boundaries and consequently increased physical habitat heterogeneity within the riverscape (Figure 4.1, H2b). Habitat heterogeneity at both beaver dams and control sites varied across the 24 locations sampled (Figure 4.4A). However, habitat heterogeneity was higher for beaver dams than for control sites \( (P = 0.003, \text{Wilcoxon rank sum test}; \text{Figure 4.4B}) \). Although habitat, measured as depth, at a subset of five beaver dams changed somewhat across seven sample dates (Figure 5.5A), these depths through summer and fall were highly correlated (Figure 5.5B), suggesting that variation among dams was more important than seasonal variation at any single location.

The impact of all beaver dams on physical habitat was not the same (Figure 4.1; H2c). Based on differences between upstream and downstream habitat characteristics at beaver dam and control sites, four clusters were identified (Figure 4.6A; Jaccards index = 0.64 to 0.82). The first two axes of the PCA accounted for 77% of the variation in habitat differences between sites (Figure 4.6B). These four clusters had unique combinations of physical features. Cluster 1 \( (n = 13) \) included the nine controls and four beaver dams
which had low habitat heterogeneity (Figure 4.7A). For this cluster, depth (Figure 4.7B), width (Figure 4.7C), velocity (Figure 4.7D) and substrate (Figure 4.7E) did not differ upstream and downstream. Beaver dams in clusters 2 \( (n = 4) \) and 3 \( (n = 5) \) created substantial habitat heterogeneity (Figure 4.7A). In these clusters, habitat above the beaver dam was deeper (Figure 4.7B), wider (Figure 4.7C), and slower (Figure 4.7D) than the habitat below the dam. Cluster 2 sites were a little deeper and wider above the dam (Figure 4.7B-C), a little faster below the dam (Figure 4.7D), and had larger substrate downstream (Figure 4.7E). Cluster 3 was considerably deeper above the dam (Figure 4.7B), somewhat wider above the dam (Figure 4.7C), with much faster velocities below the dam (Figure 4.7D), although substrate size varied little (Figure 4.7E). The beaver dams in cluster 4 included the two largest beaver dams sampled. These dams had the highest habitat heterogeneity (Figure 4.7A), were very deep and wide above the dam (Fig. 7B, C), had higher current velocity (Figure 4.7D), and larger substrate (Figure 4.7E) below the dam. Consequently, local conditions associated with beaver dams varied in predictable ways via multiple pathways.

4.3.3 Impact of changes in physical habitat on fish biodiversity (Question 3-Question 5)

Beaver dams increased fish diversity. Sixteen species of fish and 1,202 individuals were sampled in all sample sites combined (Table 4.1). Thirteen fish species were native. The three non-native species (bluegill *Lepomis macrochirus*; yellow bullhead *Ameiurus natalis*, and largemouth bass *Micropterus salmoides*) have been naturally reproducing in this region since 1917 (Hartel et al. 2002) and could be
considered naturalized. There was no spatial autocorrelation among any of the fish variables used in the analyses (Moran’s I tests, $P > 0.05$).

Habitat heterogeneity was positively related to both fish species richness ($R^2 = 0.19$, $P = 0.03$, Fig. 8A) and Shannon’s $H'$ diversity metric ($R^2 = 0.21$, $P = 0.02$, Figure 4.8B) (Figure 4.1, Question 3, H$_{3c}$). In general, species richness and diversity at the combined upstream and downstream patches were higher at locations with beaver dams compared to controls (Figure 4.8). The mechanisms by which upstream and downstream fish communities differed were mediated through multiple physical variables (Figure 4.1, Question 4, H$_{4b}$). Patterns of fish species richness at beaver dams were related to dam height and the difference in stream depth above and below the beaver dam (Figure 4.9A). Specifically, dam height was positively related ($\beta = 0.79$) to a difference in stream depth ($R^2 = 0.63$, $P = 0.0004$; Figure 4.9A). In general, patches above dams were deeper and the difference in stream depth above and below dams increased with dam height (Figure 4.9B). This difference in depth above and below a beaver dam was inversely related ($\beta = -0.52$) to $\Delta$ species richness ($R^2 = 0.27$, $P = 0.046$; Figure 4.9A). In other words, as the difference in stream depth above and below beaver dams increased, the distribution of fish species above and below the dam also changed because the number of fish species in downstream patches increased (Fig. 9B). Although dam height and dam width also affected stream width, these did not subsequently influence fish species richness (Fig. 9A).

Fluvial fish (i.e., species with life histories that require flowing water) were a critical component of the changes in fish communities that occurred as the size of beaver dams increased. This increase in fluvial fish species abundance was driven by differences
in current velocity above and below beaver dams ($R^2 = 0.48; P = 0.004$; Fig. 9D). Specifically, more individuals within the fluvial species guild ($\beta = 0.69$) occurred at sites that had the greatest difference in velocity above and below dams (Fig. 9D). Beaver dam sites had higher current velocity below dams compared to control sites ($P = 0.025$, Wilcoxon rank sum test, Fig. 9E). On the one hand, as the difference in stream depth above and below the dam increased, water depth above the dam got deeper but current velocity upstream changed little (gray line; Fig. 10B). On the other hand, as the difference in stream depth above and below the dam increased, water depths below the dam got shallower and current velocity downstream of the dam increased (black line; Fig. 10B). In general, larger dams created faster fluvial habitat downstream that attracted and retained in more fluvial fish (Fig. 7F; $R^2 = 0.48; P = 0.004$; Fig. 9F).

Predictable patterns also occurred between individual fish species and habitat variables (Q5, H5b; Fig. 1). Using an RDA, patch-specific habitat variables, especially stream depth and current velocity (RDA, $P = 0.01$), explained a significant amount of variation in fish abundance ($P = 0.005$, constrained variance = 0.20; Figure 11A). All habitat variables together explained variation in nine fish species including seven macrohabitat generalist species (Table 1). In addition, two fluvial fish species, fallfish (FF) and white sucker (WS), were significantly related to current velocity. The unconstrained ordination, DCA, supported the results of the path analysis and RDA. Specifically, species abundances varied among sites (Fig. 11B) with a positive relationship between velocity and the fluvial species, fallfish and white sucker.
4.4 Discussion

Understanding how stream alterations impact riverscape-scale biodiversity can provide science-based support for watershed conservation and restoration planning. I applied ecological theory on heterogeneity to the natural expansion of native North American beaver to test hypotheses about how beaver dams alter physical habitat heterogeneity and fish biodiversity within a stream network (Figure 4.1). My research yielded several insights that can help fish, wildlife, water, and land professionals manage the expansion of beaver and construct watershed conservation plans that protect biodiversity in the face of natural and anthropogenic stream alterations. Specifically, I found that beaver dams introduced physical heterogeneity into a stream network, but that the effect of beaver dams was not always the same. In addition, fish biodiversity, mediated through instream habitat changes, increased within the riverscape when beaver dams were present. Finally, both physical and biotic changes were detected at the local level but maintained at the riverscape scale. As a result, beaver dams in this low-gradient, rapidly-urbanizing watershed conserved limited fluvial habitats and provided a refuge for flow-dependent freshwater fish.

Beaver dams altered physical habitats at patch boundaries within Fish Brook, thereby increasing stream habitat heterogeneity (Figure 4.1, Question 2, H2b), especially through the creation of wider, deeper, slower pond habitat upstream and shallower, faster habitat below the dam. Many studies have examined the effects of beaver dams on physical conditions in streams (see reviews in Gurnell 1998, Collen and Gibson 2001, Pollock et al. 2003, Rosell et al. 2005). The creation of ponds or pool habitat upstream of beaver dams is well known. In fact, most beaver-related studies of physical changes in
the river focus on these upstream impoundments (Naiman et al. 1994, Anderson and Shafroth 2010). For example, beaver dams alter upstream pools hydrologically (Yeager and Hill, Rutherford 1955, Parker 1986), chemically (Smith et al. 1991, Alexander 1998), geomorphologically (Naiman et al. 1988, Meentemeyer and Butler 1999), and biogeochemically (Naiman and Melillo 1984). Few previous studies, however, have highlighted the importance of fluvial habitat downstream of beaver dams. In low gradient, urbanized systems, maintaining these limited pockets of fluvial habitat can have system-wide effects.

Although all beaver dams in Fish Brook consisted of aggregations of woody debris built across the stream, perpendicular to stream flow, they varied physically in height and width and consequently altered stream habitat in different ways. Beaver dams have been classified by major differences in location (e.g., lowland vs. upland dams) and condition (collapsed vs. rebuilt dams; Schlosser and Kellemeyn 2000), but functional variation within intact and topographically similar beaver dams within a drainage has not been previously described. This variation helped to identify how heterogeneity functions in stream ecosystems. Based on quantitative physical differences in upstream and downstream habitat, I classified beaver dams from a single riverscape into four clusters. One cluster of dams did not change the habitat at all compared to control sites (cluster 1). The three clusters of habitat-changing beaver dams (clusters 2, 3, 4) varied in the degree to which they modified the width and depth of the upstream pools and the depth and velocity of the downstream runs. Dam architecture (e.g., dam height) resulted in somewhat faster habitat below the dam for clusters 2 and 4 and much faster habitat below the dam for cluster 3. Stream geomorphology further influenced how much upstream
(width, depth) and downstream (depth) habitat could be altered. I think this functional variation across beaver dams is common in systems besides ours, but this variation could not be distinguished visually and required quantification of habitat characters.

Fish biodiversity increased throughout the stream network in the presence of beaver dams (Figure 1, Question 3, H3c), and was mediated through multiple habitat variables (Figure 1, Question 4, H4b). Fluvial species played an important role in this pattern (Figure 1, Question 5, H5b). Species richness in Fish Brook was positively related to habitat heterogeneity, which was greater at beaver dam sites than at damless controls. In Fish Brook, beaver dams created and maintained diverse habitats that provided both slow moving macrohabitats upstream of the dam and fast moving macrohabitats downstream. Slow moving macrohabitats such as pools and ponds supported lentic fish from the macrohabitat generalist guild whereas the faster water that primarily occurred in stream riffles and runs supported lotic fish from the fluvial specialist guild. Interestingly, in headwater streams, where pool habitat is generally limiting, beaver dam pools have been identified as sources of fish that can disperse throughout the stream drainage (Schlosser 1995).

Not all beaver dams affected fish communities equally. In Fish Brook, categories as well as a continuum of beaver dam characteristics (e.g., dam height) further altered upstream and downstream stream habitat and modified adjacent fish communities. Specifically, larger beaver dams increased the size (depth and width) of the pool habitat upstream, increased the difference in water depth between habitats upstream and downstream of the beaver dam, and increased velocity below the dam by reducing water depth. In Fish Brook, fluvial species (such as fallfish and white sucker) contributed to the
overall increase in species richness at larger dams and velocity was the key driver of this pattern.

The literature on how beaver dams affect fish is divided into studies that focus on either fish species or fish communities. Salmonids dominate species-centric studies (Kemp et al. 2011) and provide context-dependent insights which frequently differ with response, species, and system. Studies that look at fish community responses to the presence of beaver dams frequently find, as I did, that species richness increases (Snodgrass and Meffe 1998, Mitchell and Cunjak 2007); in addition, primary productivity and fish species richness can be higher in beaver ponds than in shallow, narrow, naturally-occurring stream pools (Hanson and Campbell 1963). With a few exceptions, (Hägglund and Sjöberg 1999), beaver-fish research has focused on the upstream pond, missing the important differences in fish communities that I found below beaver dams.

Beaver dams increased fish biodiversity through increased habitat heterogeneity at the riverscape scale, but this impact was only detected by sampling locally at every dam in the stream network. Riverscape scale is a current priority in ecology (Schlosser 1991, Tetzlaff et al. 2007), and a well developed theme in stream ecology (Fausch et al. 2002, Allan 2004). Using simple spatial metrics, I observed no relationship between watershed position and beaver dam characteristics. For examples, in Fish Brook, the stream slope at beaver dams did not differ from control sites, possibly because ours was a low gradient, coastal system. However, by examining local effects immediately adjacent to all beaver dams throughout the stream network, I were able to infer that beaver dams were a source of riverscape-scale heterogeneity. Many existing studies have looked at
broad scale changes to river reaches, but local conditions, such as I observed at patch boundaries, may be especially important for fish habitat selection. One current area of research in ecology, metacommunity theory, seeks to link local and regional scales (Leibold et al. 2004, Holyoak et al. 2005), yet often lacks specific examples and mechanisms (Logue et al. 2011). My local-scale observations made throughout an entire tributary network provide one example of how to relate local and regional patterns. Future efforts, of course, need to expand fish and habitat sampling to include reaches between dams.

Heterogeneity, the complexity and/or variability of a system property in space and/or time (Li and Reynolds 1995), is frequently linked to species richness (Guégan et al. 1998, Dodds 2009; Munguia et al. 2011). As is commonly predicted, I found that increased species richness resulted from increased habitat heterogeneity. A number of specialized spatial ecology concepts also seek to understand the relationship between complexity and species diversity. I drew on relevant aspects of these spatial concepts for my test of how one kind of habitat alteration affected adjacent patches throughout a river network and how those physical differences in habitat patches affected the associated biotic communities. For example, the patch dynamics concept seeks to link landscape ecology and the metacommunity perspective by examining both spatial and temporal relationships among aquatic habitat mosaics as well as how habitat patch structure is connected to population, community, and ecosystem patterns (Winemiller et al. 2010). I used aspects of patch dynamics to quantify habitat structure in two types of habitat patches (upstream and downstream of beaver dams) and to connect habitat and biotic structure in these two types of patches. Because I sought to compare adjacent upstream
and downstream patches at all beaver dams throughout a riverscape, I could not quantify patterns in all habitat patches throughout the network. An obvious next step is to link the patches associated with beaver dams to the entire mosaic of habitat patches throughout the riverscape. My decision to focus on the patches immediately upstream and downstream of beaver dams as the area of greatest impact was based on the serial discontinuity concept (Ward and Stanford 1983, Stanford and Ward 2001), which predicts that the impact of discontinuities will greatest at a local scale. I did not utilize the full range of metrics provided by landscape ecology, which uses a spatially-explicit approach to quantify the shape, size, and connectivity of habitat patches (Turner 2010) because many standard landscape ecology metrics are not as applicable to a bidirectional dendritic river network as they are for multidirectional mosaic of terrestrial patches.

My focus on limited types of patches throughout the riverscape enhanced my understanding of how increased heterogeneity promoted and maintained biodiversity. For example, adding natural functional heterogeneity provided additional niches that maintained native biodiversity. Understanding mechanisms responsible for patterns of biodiversity and identifying discrete groups or continuums that function differently are essential because structural heterogeneity, divorced from an understanding of how heterogeneity functions, does not necessarily increase biodiversity (Palmer 2010). Human impacts in a degraded system have substantial reduced heterogeneity such that any increase in functional heterogeneity will probably increase native species richness. However, in other systems, the relationship between heterogeneity and biodiversity may be more complex. In these systems, a detailed understanding of the full shape (e.g., slope, asymptote, etc.) of the relationship between heterogeneity and biodiversity is essential for
sustainable watershed planning, conservation, and restoration. My research has contributed to the development of this framework.

4.4.1 Summary

Many agency and watershed groups struggle with managing watersheds sustainably, yet little guidance exists on making science-based decisions on anthropogenic and natural alterations at both the local and regional scales. An issue that is especially challenging for local resource managers is how to formulate a plan for managing increasing populations of beaver, especially in the many locations in the world where they are native species experiencing a population resurgence. I show that the impact of beaver dams needs to be evaluated by putting local impacts in a regional, riverscape context that recognizes the functional diversity of beaver dams. In low gradient, urbanizing streams, the run or riffle habitat below beaver dams provides a repository for disappearing fluvial habitats and that can be a much needed refuge for native stream fish (Figure 4.1, Q6, H6b). Thus, similar to a national park or marine protected area, beaver dams can protect natural biodiversity by maintaining limited fluvial habitat, that acts as a source that protects native species that need flowing water to complete their life cycle.
Table 4.1: Beaver dam fish species list.
The scientific, common names, abbreviations, number of fish caught at all 24 sample sites with their corresponding Massachusetts flow guild and native status. MG = macrohabitat generalist, F = fluvial, NA = not available.

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<th></th>
<th>Genus species</th>
<th>Common name</th>
<th>Abbrev.</th>
<th>Number caught</th>
<th>MA flow guild</th>
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<td><em>Ameiurus nebulosus</em></td>
<td>brown bullhead</td>
<td>BBH</td>
<td>386</td>
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<td><em>Lepomis gibbosus</em></td>
<td>pumpkinseed</td>
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<td>3</td>
<td><em>Esox americanus americanus</em></td>
<td>redfin pickerel</td>
<td>RP</td>
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<tr>
<td>4</td>
<td><em>Notemigonus crysoleucas</em></td>
<td>golden shiner</td>
<td>GS</td>
<td>89</td>
<td>MG</td>
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<tr>
<td>5</td>
<td><em>Erimyzon oblongus</em></td>
<td>creek chubsucker</td>
<td>CCS</td>
<td>61</td>
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<td>6</td>
<td><em>Catostomus commersoni</em></td>
<td>American eel</td>
<td>AE</td>
<td>51</td>
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<td><em>Enneacanthus obesus</em></td>
<td>banded sunfish</td>
<td>BS</td>
<td>23</td>
<td>MG</td>
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<td><em>Ameiurus natalis</em></td>
<td>yellow bullhead</td>
<td>YBH</td>
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<td><em>Esox niger</em></td>
<td>chain pickerel</td>
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<td><em>Semotilus corporalis</em></td>
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CHAPTER 4 - FIGURE TITLES

**Figure 4.1**: Flow chart illustrating my six specific research questions and alternative hypotheses.

**Figure 4.2**: (A) Ipswich River Watershed located in northeastern Massachusetts, and (B) Fish Brook located with the Ipswich River Watershed.

**Figure 4.3**: (A) Beaver dams and control locations throughout Fish Brook, and (B) pictures of each of the 15 beaver dams.

**Figure 4.4**: (A) Habitat heterogeneity index scores for beaver dam and control sites, and (B) boxplot illustrating the difference in habitat heterogeneity between beaver dam and control sites. The P-value was derived from a Wilcoxon rank sum test.

**Figure 4.5**: (A) Difference in stream depth (upstream – downstream patches) through time, and (B) a correlation matrix of difference in stream depth through time. Dates range from July 31, 2009 to October 10, 2009.

**Figure 4.6**: (A) Silhouette widths for the sites \( n = 24 \) within four clusters created using cluster analysis and Jaccard bootstrap mean values for each cluster, and (B) sites presented in ordination space connected by lines according to their cluster.
Figure 4.7: Boxplots for (A) habitat heterogeneity index scores, (B) difference in stream depth, (C) difference in stream width, (D) difference in current velocity, (E) difference in substrate, and (F) natural log transformed fluvial abundance for each of the four clusters. P-values were derived from Kruskal-Wallis tests ($n = 24$).

Figure 4.8: (A) Species richness and (B) Shannon’s $H'$ plotted against habitat heterogeneity index scores. P-values and $r^2$ values derived from simple linear regression are presented.

Figure 4.9: Plots A-C examine path analyses for fish richness and plots D-F examine path analyses for fluvial abundance. (A) Path analysis that examined the relationship between riverscape position, beaver dam characteristics and stream habitat differences on difference in species richness. All possible relationships were examined, but only relationships with significant ($P < 0.05$) relationships are noted as lines within the plot. Solid lines indicate positive relationships. Segmented lines indicate negative relationships. The P-values, $R^2$ and beta coefficients are presented for each significant relationship. (B) Difference in stream depth vs. dam height. (C) Difference in species richness vs. difference in stream depth. (D) Path analysis that examined the relationship between riverscape position, beaver dam characteristics and stream habitat differences on fluvial fish abundance. (E) Boxplot showing the difference in current velocity for control and dam sites. The P-value was derived from a Wilcoxon rank sum test. (F) Change in fluvial fish abundance vs. difference in current velocity.
**Figure 4.10:** (A) Stream depth and (B) current velocity vs. the difference in depth \( (n = 15 \) upstream, \( n = 15 \) downstream).

**Figure 4.11:** (A) Constrained ordination plot of the first two RDA axes. The abundance of individual fish was constrained by stream depth, current velocity, substrate, and stream width. The dotted lines connect the upstream patch to the downstream patch for each sample site \( (n = 24) \). Gray arrows indicate significant habitat vectors of depth and velocity. Species abbreviations indicate species centroids. Only species with > 5% of their variation explained are presented in the plot. (B) Ordination plot of the first two DCA axes. Open circles indicate sample sites. Species abbreviations indicate species centroids. Contour lines indicate the gradient in the difference in current velocity (upstream patch – downstream patch). Species abbreviations can be found in Table 4.1.
Do beaver dams alter habitat heterogeneity and biodiversity in a stream network?

Q1. What is the role of location?
- H₁a. Riverscape position is paramount
- H₁b. Local factors are drivers

Q2. Do beaver dams alter habitat heterogeneity at local scales?
- H₂a. No effect of dams
- H₂b. Dams alter heterogeneity
- H₂c. Dams vary in function

Q3. Does habitat heterogeneity alter biodiversity?
- H₃a. Same
- H₃b. Reduced
- H₃c. Increased

Q4. How do beaver dams alter biodiversity?
- H₄a. No relationships
- H₄b. Via mediated relationships

Q5. How do individual fish species respond?
- H₅a. No response
- H₅b. Species respond differently to habitat

Q6. What are the ecological applications and conservation consequences of beaver dams?
- H₆a. No consequences
- H₆b. Via habitat heterogeneity, beavers conserve biodiversity

Figure 4.1: Flow chart illustrating my six specific research questions and alternative hypotheses.
Figure 4.2: Fish Brook study site.
Figure 4.3: Beaver dam locations and pictures.
Figure 4.4: Habitat heterogeneity index scores for beaver dam and control sites.
Figure 4.5: Difference in depth through time.
Figure 4.6: Beaver dam clusters.
Figure 4.7: Differences among clusters.
Figure 4.8: Linear regressions of species richness and diversity vs. habitat heterogeneity index.
Figure 4.9: Path analysis.
Figure 4.10: Stream depth and current velocity vs. difference in stream depth.
Figure 4.11: Individual species response to habitat alteration by beaver dams.
Appendix A.1: Percent detection rates with standard error bars for each species of fish from 10 resampling simulations for 1, 2, and 3 mixed gear units (MGUs). The percentages below fish abbreviations indicate the percent abundance from empirical data (dark gray = most common species, light gray = common species, white = rare species). A key to fish abbreviations can be found in Table 2.1.
**APPENDIX B**

**LITERATURE REVIEW OF STATISTICS USED TO GROUP FISHES**

**Appendix C Table:** Citations and corresponding fish species grouping methods used from a review of literature 2005-2010 conducted using Web of Science. These search phrases were used within the “Title” field: “fish assemblage” or “fish assemblages” or “fish community” or “fish communities”. Concurrently within the “Topic” field the words “river” or “stream” were searched. The following journals were searched independently: Canadian Journal of Fisheries and Aquatic Sciences; Copeia; Ecological Applications; Ecology of Freshwater Fish; Environmental Biology of Fishes; Fisheries Management and Ecology; Freshwater Biology; Hydrobiologia; Journal of Applied Ecology; Journal of Fish Biology; North American Journal of Fisheries Management; Oecologia; River Research and Applications; and Transactions of the American Fisheries Society. Only papers that actively sampled fish in freshwater streams or rivers were examined. There were 101 papers that met these criteria.

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<th>NMDS</th>
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| Total                     | 6   | 12     | 20    | 21     |
APPENDIX C

FLOW VARIABLES

At each site, stream discharge was measured in three ways: (1) August median flow \((m^3 \text{ s}^{-1})\); (2) \(P_{99} (m^3 \text{ s}^{-1})\), the amount of discharge that is exceeded 99\% of the time; and (3) PC flow, the site scores from the first principal component of the covariance distance matrix based on 13 StreamStats flow variables. StreamStats is a software program developed by the U.S. Geological Survey that can estimate multiple low streamflow discharge metrics for any given Massachusetts stream location. These estimates are based on nearby gauging stations, mean basin slope, catchment area of the upstream watershed, stratified drift per unit of total stream length, and region of the state (Ries and Friesz, 2000). StreamStats were developed from estimates of 37 gauging stations and 107 low-flow partial-record stations over a median of 27 years of record. The 13 StreamStats discharge estimates that were used included: \(P_{50}, P_{60}, P_{70}, P_{75}, P_{80}, P_{85}, P_{90}, P_{95}, P_{99}, Q_{7,2}, Q_{7,10}\), and August median flow. The \(P\) variables estimate the discharge at which flow is exceeded 50-99\% of the time. The \(Q_{7,2}\) and \(Q_{7,10}\) variables represent seven-day-two-year and seven-day-10-year low-flows, respectively. Consequently, the PC flow variable incorporated multiple discharge metrics that reflect the magnitude, duration, and timing of the flow regime. The flow statistics I used are examples chosen from the many possible measures of hydrological variation used in Canada and the United States to indicate low-flow (Tharme, 2003). At my sample sites, I estimated August median flows of 0.00005 to 0.79 \(m^3 \text{ s}^{-1}\) and \(P_{99}\) flows of 0.00 (no flow).
to $0.22 \text{ m}^3 \text{ s}^{-1}$. The first PC of the PC flow variable explained 98.4% of the variation among the 13 StreamStats discharge variables.


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