HOW BIG OF AN EFFECT DO SMALL DAMS HAVE?: USING ECOLOGY AND GEOMORPHOLOGY TO QUANTIFY IMPACTS OF LOW-HEAD DAMS ON FISH BIODIVERSITY

by

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Abstract

In contrast to well documented adverse impacts of large dams, little is known about how smaller low-head dams affect fish biodiversity. Over 2,000,000 low-head dams fragment United States streams and rivers and can alter biodiversity. The spatial impacts of low-head dams on geomorphology and ecology are largely untested despite how numerous they are. A select review of how intact low-head dams affect fish species identified four methodological inconsistencies that impede our ability to generalize about the ecological impacts of low-head dams on fish biodiversity.

We tested the effect of low-head dams on fish biodiversity (1) upstream vs. downstream at dams and (2) downstream of dammed vs. undammed sites. Fish assemblages for both approaches were evaluated using three summary metrics and habitat guilds based on species occurrence in pools, riffles, and runs. Downstream of dams vs. undammed sites, we tested if (a) spatial extent of dam disturbance, (b) reference site choice, and (c) site variability altered fish biodiversity at dams. Based on information from geomorphic literature, we quantified the spatial extent of low-head dam impacts using width, depth, and substrate.

Sites up- and downstream of dams had different fish assemblages regardless of the measure of fish biodiversity. Richness, abundance and Shannon's index were significantly lower upstream compared to downstream of dams. In addition, only three of seven habitat guilds were present upstream of dams. Methodological decisions about spatial extent, and reference choice affected observed fish assemblage responses between dammed and undammed sites. For example, species richness was significantly different when comparing transects within the spatial extent of dam impact but not when transects outside the dam footprint were included. Site variability did not significantly influence fish response.

These small but ubiquitous disturbances may have large ecological impacts because of their potential cumulative effects. Therefore, low-head dams need to be examined using a contextual riverscape approach. How low-head dam studies are designed has important ecological insights for scientific generalizations and methodological consequences for interpretations about low-head dam effects. My research provides a template on which to build this approach that will benefit both ecology and conservation.

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Preface

The contents of this thesis represent ideas and approaches developed in collaboration with my major professor and members of my dissertation committee. Although the work is my own, the chapters are presented in third person for the sake of peer-reviewed publication. Chapter 1 is formatted for publication in the journal *PLOS ONE* with Martha Mather, Katie Costigan and Melinda Daniels as coauthors. Chapter 2 is formatted similarly with Martha Mather, Joseph Smith and Sean Hitchman as coauthors.

Chapter 1 - How Big of an Effect Do Small Dams Have?; Using Geomorphological Footprints to Quantify Spatial Impact of Low-Head Dams and Identify Patterns of Across-Dam Variation

Abstract

Longitudinal connectivity is a fundamental feature of streams and rivers that can be broken by dams. Over 2,000,000 low-head dams (<7.6 m high) potentially fragment United States streams and rivers and can alter biodiversity. Despite potential adverse impacts of these ubiquitous disturbances, the spatial impacts of low-head dams on geomorphology and ecology are largely untested. Progress for research and conservation is impaired by not knowing how low-head dams affect natural systems or the magnitude of their impact. Based on the geomorphic literature, we refined a methodology that allowed us to quantify the spatial extent of low-head dam impacts (herein dam footprint), assessed variation in dam footprints across individual low-head dams within a single subbasin, and identified select aspects of the ecological context of this variation. We quantified width, depth, and substrate profiles upstream and downstream of six low-head dams within the Upper Neosho River, Kansas, United States of America. Dam footprints, with respect to substrate size, averaged 6.7 km upstream (range 2.2 – 13.7), 1.2 km downstream (range 0.2 to 1.6), and 7.9 km total (3-15.3) footprint per dam. Altogether the six low-head dams in this subbasin impacted 47.3 km (about 17%) of the stream network. Despite differences in size, location, and original function, the geomorphic footprints of the six low-head dams in the Upper Neosho subbasin were relatively similar. The number of upstream dams and proximity to upstream dams, but not dam height, affected the spatial extent of dam footprints. In summary, ubiquitous low-head dams individually and cumulatively altered lotic ecosystems. Both characteristics of individual dams and the ecological context of neighboring dams affected

low-head dam impacts within and across watersheds. For these reasons, low-head dams require a different, more integrative, approach for research and management than the individualistic approach that has been applied to larger dams.

Introduction

Large dams can are known to alter native aquatic biodiversity in aquatic ecosystems by modifying geomorphic, hydrological, and ecological connectivity [1, 2]. Large dams fragment riverscapes within the Great Plains [3] by regulating streamflows and dampening floods [4]. For small, low-head dams, however, the potential impacts on geomorphic and ecological impacts are infrequently examined and poorly understood. Although the effect of low-head dams likely extends beyond the immediate vicinity of the dam structure, the spatial extent of low-head dam impacts has not been previously measured, only estimated (e.g. [5,6,7]). Unless scientists and managers can distinguish impacted from unimpacted areas adjacent to dams, environmental professionals will be unable to undertake appropriate research or propose effective management actions to evaluate, understand, and remedy potential fragmentation by low-head dams. Here, we use geomorphic paradigms and metrics to test predictions about the longitudinal extent of low-head dam impacts (hereafter the dam footprint) within the Upper Neosho subbasin, KS, United States of America. The resulting insights on the size of geomorphic impacts, across-dam variation, and ecological context of this variation will fill important information gaps about these small, but abundant, ecological disturbances.

In addition to the 87,000 large dams listed in the US Army Corps of Engineers National Inventory of Dams [8], 2,000,000 low-head dams (< 7.6 m high) are estimated to block United States streams and rivers [9]. A large body of literature documents how large dams alter stream and river ecosystems (e.g. [10, 11]), but data on low-head dams are limited [12]. Low-head dam studies have also typically only sampled at one or two dams [13]. By virtue of their numerical abundance, these small dams may substantially impact flowing water ecosystems either alone or as a basin-wide cumulative impact. Alternatively, if the footprint is small or the physical recovery is rapid, the isolated or cumulative spatial impacts of low-head dams could be negligible.

Geomorphic paradigms may provide guidance on metrics that can be used to quantify the spatial extent of dam impact. A Web of Science search (17 Feb 2015) on the keywords "geomorph*" and "low-head dam," "low head dam," "lowhead dam," "small dam," or "run-of-river dam" identified only 32 peer-reviewed publications (Table A.1). Half of these papers on geomorphology and low-head dams (*N*=16) were not considered further because they addressed issues other than physical conditions adjacent to dams (Fig. 1.1). The remaining papers (*N*=16) documented geomorphic changes occurring around low-head dams (e.g., width, extent of channel widening, bar formation, depth, and substrate size) on which we based predictions about the spatial extent of dam footprints. Specifically, stream width is greater in the impoundment upstream of dams compared to downstream of dams [14] (Fig. 1.2A). Channel widening and bar formation occur immediately downstream of low-head dams [15, 16, 17] (Fig. 1.2B). Water is deeper in the upstream impoundment compared to downstream of dams [14, 17] (Fig. 1.2C). Substrate size increases immediately below low-head dams, but gradually returns to the pre-dam local equilibrium [17, 18] (Fig. 1.2D).

If researchers and managers could quantify the size of geomorphic dam footprints, variation in footprint size across dams, and ecological context of this variation, they could better understand fragmentation, minimize dam impacts, and conserve aquatic biodiversity**.** Links between geomorphic and ecological recovery are largely untested but are assumed to be related to one another [19]. Here, we modified and evaluated a method to detect geomorphic changes adjacent to low-head dams, then used this approach to ask three questions. First, we asked if low-head dams have an impact on stream habitat, as measured by width, depth, and substrate size. Relative to this first question, at least two outcomes are possible: (H_{1a}) low-head dams may alter stream habitat upstream and downstream; alternatively (H_{1b}) low-head dam impacts might be negligible because these structures are small and recovery is rapid. The outcome of this first question is widely assumed but rarely tested. Second, we asked if low-head dams differ in footprint size as (H_{2a}) individual dam characteristics may cause differences in the spatial extent of low-head dam impacts, or (H_{2b}) small low-head dams may be so similar in structure that they exhibit no among-dam geomorphic variation. Third, we tested if characteristics of the individual dam (height) and neighboring dams (e.g., number of upstream dams, proximity to neighboring dams, size of neighboring dam) affected footprint size. Relative to this last question, (H_{3a}) each low-head dam may operate as an independent unit or (H_{3b}) numbers and locations of neighboring dams may change the impact of individual dams. Our aim is to quantitatively evaluate both the spatial and cumulative extents of low-head dam impacts, and so we fill a critical gap in our understanding of anthropogenic controls on fragmented river network ecosystems.

Materials and Methods

Study site

The Neosho River basin, located in the Great Plains ecoregion, flows southeast 756 km through Kansas, Arkansas, Missouri, and Oklahoma [20] and drains 32,789 km^2 of mesic grasslands before joining the Arkansas River in Oklahoma (Fig. 1.3A). The drainage area includes the Flint Hills upland and Osage Cuestas physiographic regions which are characterized by gently rolling hills and escarpments [21]. The native vegetation is tallgrass prairie dominated by perennial warm-season grasses. The current land use is primarily agriculture, forest, and range [22]. The study area has a mean annual precipitation of 910 mm [23].

The Upper Neosho River subbasin is located within the 7,000 km^2 Upper Neosho River basin and includes the 5th order Upper Neosho River and 6th order Lower Cottonwood River systems [24] (Fig. 1.3B). This study area is characterized by low gradient dendritic stream networks (channel slopes of 0.00023 to 0.00057; [25], well-defined banks ranging from 1 to 10 m in height, and channel beds composed of gravel, boulders and some exposed bedrock. The hydrologic regime is characteristic of the highly variable intercontinental climate, with relatively low mean annual flow and highly variable annual peak flow, typically occurring between April and June [Upper Neosho River: mean annual discharge, 8.7m^3s^{-1}; annual peak flows, 124.6 – 4,927.3 m^3s^{-1} (1963-2012; USGS gage 07179730); Lower Cottonwood River: mean annual discharge, 24.4 m^3s^{-1}; annual peak flows, 146.7 – 26,306.5 m^3s^{-1} (1963-2012; USGS gage 07182250)[26]]. The entire Neosho River basin has high aquatic biodiversity including over 100 species of fish [27, 28] and approximately 35 species of mussels [29]. Many of these aquatic species have life histories adapted to perennial flashy streams (*sensu* [30]).

We quantified stream widths, depths, and substrate size at six low-head dams (height 1.2-3 m) and two undammed sites within Upper Neosho subbasin (Fig. 1.3B). Four low-head dams (Riverwalk, Correll, Ruggles, Emporia) were located on the Upper Neosho River and two low-head dams (Cottonwood Falls and Soden) were located on the Lower Cottonwood River. The two undammed locations (Undammed-1, 2) were located on the Upper Neosho River; > 8 km from the nearest dam). Except for a mill dam downstream of Marion Reservoir on the Upper Cottonwood River, our study included all low-head dams on the Upper Neosho and Lower Cottonwood Rivers between three large U. S. Army Corps of Engineer dams (Marion, Council

Grove, John Redmond) (Fig. 1.3B). The six low-head dams that we sampled were built between the 1860s and 1995 for recreation [31, 32], water supply on the Upper Neosho River [33, 34], and as mills on the Lower Cottonwood River [35, 36] (Table 1.1).

Dam impacts

Width and depth

Width and depth were quantified using field surveys. Sampling extended 3 km upstream and downstream of dams or until we reached the end of the upstream impoundment (e.g., Riverwalk > 2.2 km), could not obtain landowner permission (Correll downstream > 1 km), or were logistically unable to sample (Emporia upstream).

We compared width and depth upstream and downstream of each dam at transects spaced every 200 m for the first kilometer and 500 m thereafter, starting at 200 m (N=9 transects). In the field, width was determined using a laser range finder (< 1 m accuracy, range 3-200 m). Depth was measured at five regularly-spaced points along each transect with a meter stick (< 1 m depth) or a depth finder (Lowrance X-4) attached to a kayak (> 1 m depth). The difference in width and depth between upstream and downstream reaches was evaluated using a non-parametric Wilcoxon rank sum statistic (W) and a Bonferroni family-wise error rate of 0.01 (0.05/5 corresponding to the five dam comparisons).

Quantifying the geomorphic dam footprint

Substrate sizes were characterized in the field following a careful evaluation of potential individual sampler bias in substrate size selection (*sensu* [37]). We evaluated variation in substrate size selection by the four individual members of our sampling team using two separate approaches in order to establish that no statistically-significant bias existed in our protocol. In the first evaluation, we tested if substrate size selection by four different individuals was more variable than repeated selection of substrate by a single individual at the same location. For this, we used a randomized block design in which substrate size (response) selected by four individual samplers (treatment) at three points within a riffle (blocks) was replicated ten times. Each individual walked to a marked point, placed a rebar perpendicular to the channel bed at the marked point, averted his or her eyes from the substrate, picked up the substrate particle abutting the upstream edge of the rebar, measured the particle with a gravel template (gravelometer, 4 - 362 mm) or metric tape (> 310 mm), then replaced the particle. The other three samplers replicated this procedure 10 times for each of three preselected points. The order in which individuals selected a substrate particle was randomized at each point. In conjunction with a Kruskal-Wallis test of individual sampler effects, a Bonferroni family-wise error rate of 0.016 (0.05/3 corresponding to three riffle points) was applied. In this first evaluation of individual sampler effects, mean substrate size selected by individuals did not differ (Fig. 1.4A; $\alpha \leq 0.016$). All individual samplers selected similar-sized substrates (+/- one size class of the gravelometer) at predetermined locations along a transect [location 1 (*Chi-sq*=0.72, *df* =3, *P*=0.87), location 2(*Chi-sq*=1.31, *df*=3, *P*=0.73), location 3 (*Chi-sq*=7.25, df=3, P=0.06); α = 0.016].

In the second evaluation of individual sampler effects, we tested if substrate size characterization over an entire riffle was more variable between individuals than for each individual. The same four individuals selected 100 particles from 10 equally spaced points along 10 equally spaced transects (i.e., Wolman pebble count [38]) for three replicate riffles. For this second method, each individual created a 100 point grid in each riffle by using their paces and riparian marker flags to identify 10 equally spaced transects and 10 approximately equally spaced points across each transect. Each point along each transect was at least twice the *b*-axis length (i.e. intermediate axis) of the largest observed substrate (with the exception of bedrock), to reduce overrepresentation of larger clasts [39]. At these 100 points, each individual sampler selected and measured one substrate particle. We compared D_{50} (the median sediment size, e.g. [18]) across individual samplers with a Kruskal-Wallis nonparametric analysis. For the second evaluation of individual sampler effects, D_{50} was marginally different among the four individuals (*Chi-sq*=6.55, *df*=3, *P*=0.09; Fig. 1.4B).

Because our standard protocols controlled individual sampler effects satisfactorily, next, we used a Wolman pebble count (evaluation method 2 above) to quantify substrate size three km downstream of six dams and at two undammed sites (a distance approximately 100 times wetted width). We sampled at standard geomorphic units (i.e. riffles) to prevent local sorting of sediment from confounding longitudinal patterns in substrate sizes [40]. All riffles downstream of each dam were sampled the same day and reference sites were sampled within 24 h to ensure comparable flow conditions. When a large distance separated riffles (> 1 km), we measured channel depths along a longitudinal transect to ensure that no riffle was missed. The end of the downstream dam footprint was defined as the downstream location at which median (D_{50}) substrate particle size leveled off for two consecutive riffles. D_{16}, D_{50}, and D_{84} were determined and plotted along the cumulative substrate distribution curves. A two-sample Kolmogorov-Smirnov test was used to determine if the cumulative distribution curves from the first riffle downstream of a dam was statistically different from a riffle outside the downstream dam footprint [41].

We supplemented field surveys with aerial imagery to help locate the extent of impoundments and channel widening. Upstream, we quantified the extent of the upstream dam impoundment by identifying the first gravel bar or riffle upstream of the dam, and then groundtruthed this location in the field. The end of the upstream footprint was defined as the location of the first riffle or gravel bar above the dam. Downstream of dams, we measured the longitudinal distance of channel widening from the dam spillway to the point where channel width returned to the average width of that site using aerial images [42] and transect measurements.

Patterns of Variation in Dam Footprints

We examined patterns of variation in geomorphic footprints across dams in three ways. First, we compared size of dam footprints across individual dams within the Upper Neosho subbasin. Second, to understand variation in footprints across dams, we tested if dam height, number of nearby upstream dams within 50 km, distance to nearest upstream dam, and size of the nearest upstream dam were related to the size of the dam footprint (downstream, upstream, and total) using univariate regression (N=6 dams) [41]. We chose dams within 50 km to constrain the geographic area at which an across dam impact could realistically occur (however, results were similar whether all dams or just dams within 50 km were included). The total footprint was the sum of the upstream and downstream substrate footprints. Each dam's position in the subbasin, relative to other dams, was measured along the river flowline [42, 44].

Results

Widths and Depths

Stream width was not consistently different between upstream impoundments (range 20-45 m) and downstream of dams (range 7-47 m). Although mean width was greater upstream at all sites (Fig. 1.5 – Y axis arrow), upstream reaches were significantly wider than downstream reaches at only two of our five dams for which we had upstream and downstream data [Ruggles dam (P=0.0006, Fig. 1.5C); Soden dam (P<0.0001, Fig. 1.5F)]. Riverwalk and Cottonwood Falls were not statistically different (Fig. 1.5A and 1.5E). Correll was marginally different using the Bonferroni- corrected α = 0.01 (0.05/5 dams; Fig 1.5B).

Depth also was not consistently different between upstream impoundments (82 to 330 cm) and downstream (range 3 to 216 cm) of dams. At all sites, mean depths upstream of dams (Y axis arrows) were greater than mean depths downstream of dams, but significantly different at only four of the five dams for which we had upstream and downstream data [Correll, P=0.0079, Fig. 1.6B; Ruggles, P<0.004; Fig. 1.6C; Cottonwood Falls, P<0.0006; Fig. 1.6E; Soden, P<0.0001; Fig. 1.6F). Riverwalk depths were not significantly different at the Bonferroni-corrected critical α (0.05/5 = 0.01; Fig 1.6A). Transect measurements for neither width nor depth revealed consistent longitudinal trends with increasing distance from the dam.

Substrate Size

Substrate size consistently detected dam effects and a longitudinal recovery. Riffles at the undammed reference sites (Undammed-1; Fig. 1.7A; Undammed-2; Fig. 1.7B) had a D_{50} from 22.5 to 45 mm (Fig. 1.7B). Immediately downstream of all dams, D_{50} was larger than at reference sites (Fig. 1.7A-F), decreased below all dams, and leveled off to 22.5 mm at 0.21-1.2 km downstream of Upper Neosho R. dams (Fig. 1.7A, 1.7C, and 1.7D – vertical arrow), and to 32 mm at 1.4 and 1.6 km downstream of both Cottonwood River dams (Fig. 1.7D and 1.7E). Substrate size increased downstream of tributary junctions (Fig. 1.7A and 1.7D).

Cumulative distribution curves of riffles displayed fining in which riffles closest to the dam (1st riffle) had the largest substrate sizes (Fig. 1.8A-F). Riffles farthest from the dam had higher percentages of small substrates (unless a tributary joined the mainstem). The substrate distribution curves of the riffles closest to the dam were significantly different from those of riffles outside the dam footprint (Fig. 1.8A-F). As with D_{50}, patterns of D_{16} and D_{84} particle size fractions were largest immediately downstream of dams [Upper Neosho R ($D_{16:}$ 22.5-32 mm; $D_{84:}$ 45-256 mm); Lower Cottonwood R (D_{16}: 22.5-122; D_{84}: 362-618)]. Undammed sites had consistent and overlapping substrate size distributions (Fig. 1.8G and 1.8H).

Geomorphic low-head dam footprint

The spatial extent of the downstream dam substrate footprint ranged from 0.2 to 1.6 km with a mean of 1.2 km (Fig. 1.9, Table 1.3). The downstream geomorphic footprints of all our low-head dams were relatively similar (1.2 – 1.6 km) with the exception of Emporia's smaller (0.2 km) downstream footprint. At all dam sites, downstream impact of channel widening (0.050 - 0.250 km) extended a shorter distance than the downstream substrate footprint (t=-4.84, 5, P=0.0047) (Table 1.2).

The upstream dam footprints extended 2.2 to 13.7 km with a mean of 6.7 km (Fig. 1.9). Upstream footprints were larger than downstream footprints at all sites (t=3.50, df=5, P=0.017). Total dam footprints (upstream plus downstream) averaged 7.9 km and varied from 3.5- 15.3 km (Table 1.3). A total of 47.3 km of stream habitat in the Upper Neosho subbasin was altered by these six intact low-head dams (Table 1.3).

Patterns of Variation in Dam Footprints

Number of upstream dams was inversely related to downstream footprint size and explained 44% of variation in the downstream footprint [Y = -0.405 (0.183) X + 1.567 (0.236); P< 0.09, $R^{2\text{-}adj}$=0.44; Fig. 1.10A]. On the Lower Cottonwood River, Cottonwood Falls and Soden were not within 50 km of any other dams. On the Upper Neosho, Riverwalk and Ruggles had one upstream dam < 50 km, and Emporia and Correll had two dams upstream < 50 km (Fig. 1.2; Table 1.3).

Distance to the nearest dam was positively related to upstream [Y = 0.124 (0.040) X + 2.562 (1.618); P=0.03; $R^{2(adj)}$ = 0.66; Fig. 1.10B] and total footprint sizes [Y = 0.133 (0.04) X + 3.402 (1.750); P=0.03; $R^{2(adj)}$ = 0.66; Fig. 1.10C). Footprint size increased with distance to nearest dam. For Riverwalk, a large USACE dam (29.3 m high) was only 2.9 km upstream. For Emporia and Ruggles, the upstream low-head dams were quite close (10.1-13.5 km). Whereas for Correll, the nearest dam was about 42 km away, and for Cottonwood Falls and Soden the nearest upstream dam was located at a much greater distance (65-69 km). Models with dam size and size of nearest dam were not significant for upstream, downstream, or total footprints (Table A.2).

Discussion

We were able to quantify geomorphic dam footprints at six low-head dams. Our field surveys of substrate particle size distributions documented increased substrate size immediately below dams, a consistent longitudinal decrease in substrate size downstream of dams, and a return to baseline substrate size along a longitudinal recovery trajectory at each of our study sites. Past geomorphic research [13, 16-18], has concluded that coarsening of substrate occurs immediately downstream of low-head dams, but previous research has not found that larger substrate particle sizes downstream of dams are significantly different from upstream reference sites [16, 17]. In contrast, our results showed significantly larger particle sizes downstream of dams compared to riffles outside the footprint. Use of regularly spaced transects [16, 17], rather than repeating geomorphic units (as we used), may confound dam effects with those related to local sorting of sediment [40]. Consequently, methodological difference may explain discrepancies between our results and previous studies.

Substrate is an ecologically valuable indicator of the dam footprint because substrate can affect the structure of invertebrate communities and survival and reproductive success of fishes (e.g. [45, 46]). Measuring the dam footprint explicitly measures habitat characteristics (e.g. substrate, hydraulic habitat regime) on which aquatic biodiversity depends (e.g. [10]). Many stream organisms are adapted to the lateral and longitudinal connectivity of geomorphic, hydrologic, and ecological processes in flowing water ecosystems [1-2, 47]. This relationship makes the spatial frame of dam induced habitat changes (single or cumulative) relevant to patterns in biodiversity. Maintaining biodiversity is a priority for environmental science and management because biodiversity can affect ecosystem function [48, 49], act as a useful indicator of anthropogenic stress, and provide a foundation for effective conservation practices. Without knowing where the geomorphic dam footprint ends, downstream dam impacts on biodiversity and individual variability across dams will be difficult to assess, interpret, and generalize.

Many of our results, though not all, were consistent with previous findings regarding the geomorphic impact of low-head dams. As reported in other studies, we found that upstream dam impoundments are variable and not consistently, statistically deeper or wider than downstream of low-head dams (e.g. [14, 16, 17]. The lack of clear longitudinal patterns in the downstream trajectory of width and depth channel geometry parameters reduce the usefulness of width and depth as indicators of low-head dam footprint zones. Although channel widening has been frequently documented [15-17], the spatial extent of channel widening did not correlate well with our other measured geomorphic parameter - substrate particle size. For example, at Ruggles dam, channel widening extended 0.2 km downstream of the dam, while particle size did not return to the 22.5 mm baseline until 1.232 km downstream. The dam-related process of altered sediment supply-transport capacity leading to channel adjustments is well understood (e.g. [50]) but, to our knowledge, ours is the first study to evaluate the longitudinal pattern and extent of this phenomenon at low-head dams.

Low-head dams are capable of altering and fragmenting large sections of river networks, especially when multiple low-head dams are present within a network. Our spatially extensive data sets reveal that the total spatial extent of low-head dam footprints can be quite substantial (7.9 km per dam on average). The average downstream component of this geomorphic dam footprint for the six dams in the Upper Neosho subbasin averaged 1.2 km. Although smaller than the reported spatial impact downstream of large dams (> 7.6 m high), which may extend up to hundreds of kilometers (e.g. [51]), this downstream geomorphic footprint for low-head dams is greater than what has been predicted from channel widening or assumed previously [<100 m (e.g. [7]); < 500 m (e.g. [6])]. When examined cumulatively from a network perspective, 47.3 km of the Upper Neosho subbasin or about 17% of the study area were physically altered by low-head dams.

The individual and cumulative extents of low-head dam footprints may be affected by a dam's geographic location/geology, position in a watershed, position relative to other dams higher in a watershed, and sediment supply [13]. In the Upper Neosho subbasin, the distance to the nearest upstream dam and the number of nearby upstream dams affected the size of upstream and downstream dam footprints, respectively. Because we are the first to quantify these effects, the underlying processes are still unclear. The downstream dam footprint was negatively correlated with the number of dams upstream, i.e., more upstream dams often resulted in a smaller footprint. The number of upstream dams is important because sediment storage by upstream dams can limit sediment delivery to downstream dams [13]. For example, Emporia dam had the smallest downstream footprint at 0.213 km, and was located below four dams in the subbasin and two dams within 50 km. The dams above Emporia dam (Correll, Ruggles), are close together in the study site (13 and 10 km apart). Sediment starvation below their impoundments, and limited recovery distance for the input of coarse substrates from tributaries likely exacerbated substrate fining at Emporia. Thus, the substrate below Emporia dam returned to baseline sizes quickly, causing a smaller footprint, because the sediments upstream of Emporia had not recovered from the impacts of upstream dams. Thus, many dams close together may have more of an impact than fewer dams further apart. The upstream dam footprint was positively correlated with distance to the nearest dam. The underlying processes of this is unclear (e.g., ratio of dam height to channel slope [13]) and requires further examination. Our results clearly suggest that, in addition to the characteristics of the dam itself, the context (e.g. proximity to and number of neighboring dams) should to be included in any future evaluations of low-head dam impacts.

The next steps for testing low-head dam effects are critical for research and conservation, but also challenging. More samples across watersheds are necessary to draw generalities about the spatial extent of low-head dam impacts. However, increasing sample size for testing low-head dam effects, especially in a watershed context, will not be easy because incorporating dams from other watersheds to ensure a desirable sample size will also add additional sources of variation. Thus, increasing sample size of comparable dams will always be a problem. Although we had a limited number of samples (i.e., six dams), they were all within the same subbasin and had comparable basic stream characteristics. Furthermore, our sample size exceeded other low-head dam studies which typically have sampled at only one or two dams [13].

Dam size, appropriate undammed references, and a limited understanding of the link between hydrologic, geomorphic and ecological recovery present future research and management challenges for understanding the effects of low-head dams. Research that has shaped our thinking about dam impact largely has been undertaken on large dams with strong, impacts [12]. Low-head dams may be relatively small but there are many, many more of them [9]; by number, they may dominate the fragmentation problem (e.g. [52]), but, as our sampling demonstrates, in a variable, complex, and difficult to interpret manner. Thus, quantifying cumulative effects and the spatial context of low-head dams within watersheds will require a fundamentally different approach to studying low-head dams than the isolated approach that has been applied to larger dams. This neighborhood context is particularly unique to low-head dams because their high abundance makes their effects different from large dams. Finally, we assume geomorphic recovery and ecological recovery are linked [19], but these complex and highly variable relationships are rarely tested.

A quantitative measure of dam footprint facilitates testing how dams interface with a wide range of ecological concepts (e.g., thresholds, disturbance, and edge-effects). For example, dams or their footprints may create habitat edges producing behavioral responses that may help explain observed phenomenon in species distributions (*sensu* [53]). Differences in width and depth between upstream and downstream could function as breakpoints (*sensu* [54]) where dams separate habitats (lentic upstream vs lotic downstream) which are important determinants of macroinvertebrate (e.g. [55]), mussel (e.g. [56]), and fish (e.g. [5]) distributions. However, comparable breakpoint research that relates geomorphic (e.g., habitat structure) and ecological (e.g. organismal) patterns of low-head dam impacts has not been undertaken in geomorphology [13] and rarely in stream ecology (but for example see [3]).

Understanding dam footprints also provides a foundation for more effective conservation planning (e.g., establishing baseline data before dam removals or quantifying recovery trajectories) [57]. It is imperative that aquatic scientists use a holistic and interdisciplinary perspective when studying and managing low-head dams. Interest in and literature about low-head dams is growing because many dams are reaching the end of their lifespan and being considered for removal for safety and other reasons [58]. A call exists for the formal classification of all dams [12] because limited guidance exists about how to manage dams. Our novel approach to quantifying spatial extent of dam footprints to detect low-head dam effects and individual variability across dams can guide ecological research, restoration, and environmental evaluation related to anthropogenic impacts of fragmentation.

In summary, our standardized and generalizable methodology quantified changes in riffle substrate size and channel geometry, documented the spatial extent of these impacts and explored their variability within the network context of the Upper Neosho subbasin. This research approach can easily be applied elsewhere to consistently detect geomorphic dam footprints and longitudinal recovery trajectories and to better inform ecologists and environmental professionals as they seek knowledge to guide management of low-dams within riverscapes.

Tables

Table 1.1 Dam Information. Primary purpose and date of construction for dams in the study site of the Upper Neosho and Lower Cottonwood Rivers.

River	Dam name	Built	Purpose
Upper Neosho	Riverwalk	1995	Recreation
	Correll	1920s	Water supply
	Ruggles	1920s	Water supply
	Emporia	1890s	Water supply
Lower Cottonwood	Cottonwood Falls	1860s	Mill
	Soden	1860s	Mill

Table 1.2 Channel Widening, Downstream, Upstream, and Total Footprint for Each Dam. Downstream footprints were determined by measuring the distribution of median substrate size (D50) from riffles downstream of dam (see Figs. 1.7 and 1.8). Extent of channel widening, and upstream footprints were determined using aerial photography.

Subbasin	Site	Channel widening (km)	Downstream footprint (km)	Upstream footprint (km)	Total footprint (km)
Upper Neosho	Riverwalk	0.05	1.3	2.2	3.5
	Correll	0.25	1.2*	6.6	7.8
	Ruggles	0.21	1.232	6.5	7.7
	Emporia	0.20	0.213	2.8	3.0
Lower Cottonwood	Cottonwood Falls	0.22	1.595	13.7	15.3
	Soden	0.21	1.436	8.6	10.0
	Mean (km)	0.2	1.2	6.7	7.9
	Total (km)	1.1	6.9	40.4	47.3
	Range (km)	0.05, 0.25	0.2, 1.6	2.2, 13.7	3.0, 15.3

* footprint is estimated based on available data

Table 1.3 Variables for Univariate Regressions. Dam size and subbasin context relative to other dams in the subbasin (number of upstream dams < 50 km, distance to nearest upstream dam, and height of 1st upstream dam). These variables were used as the inputs for univariate regressions.

River	Dam name	Dam height (m)	Number of upstream dams < 50 km	Distance to nearest upstream dam (km)	Height of 1st upstream dam (m)
Upper Neosho	Riverwalk	1.2	1	2.9	29.3
	Correll	2.3	2	42.2	1.2
	Ruggles	2.4	1	13.5	2.3
	Emporia	3	2	10.1	2.4
Lower Cottonwood	Cottonwood Falls	3	0	65.0	3
	Soden	3	0	69.0	3

Figures

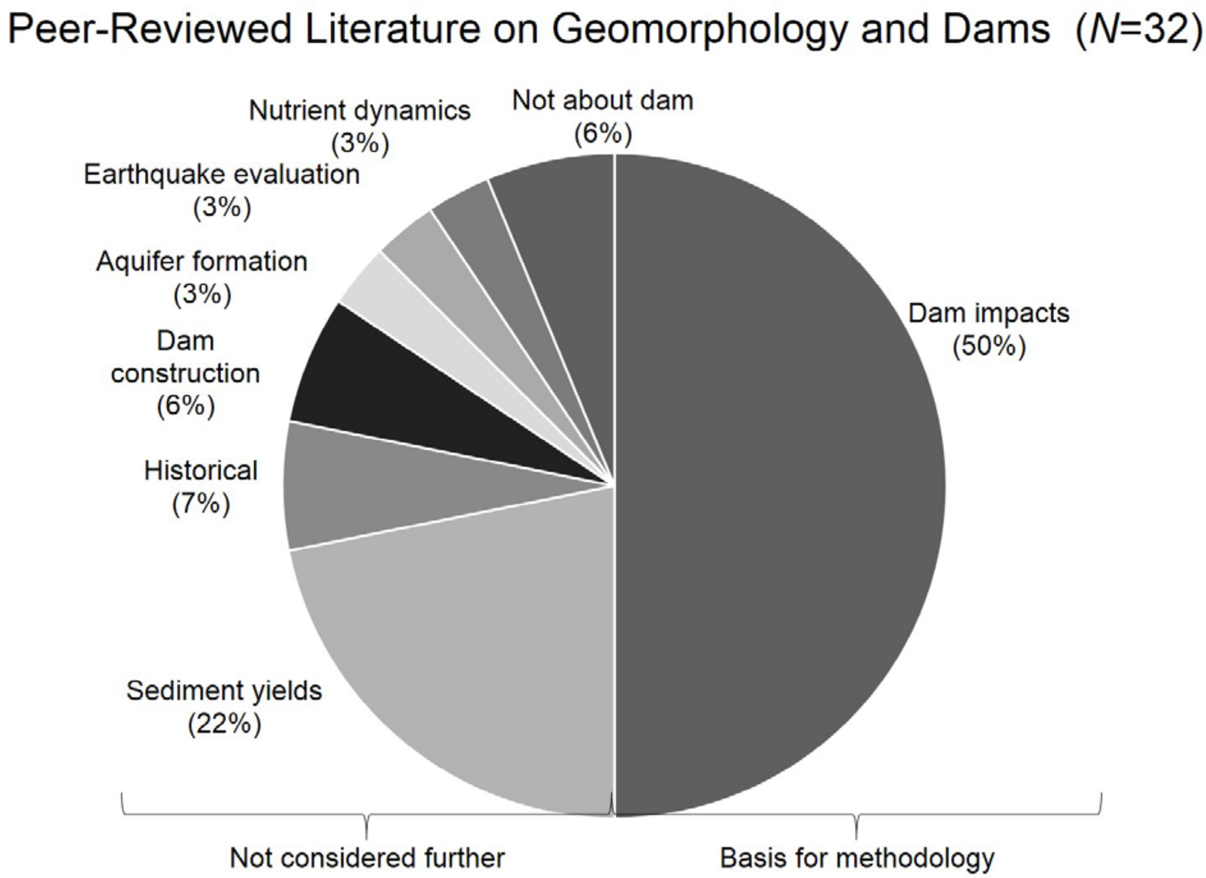

Figure 1.1 Peer-Reviewed Literature on Geomorphology and Dams. Peer reviewed papers on geomorphology and low-head dams organized by topics accessed 17 Feb 2015. We based our research design on the studies that examined physical conditions at low-head dams (N=16).

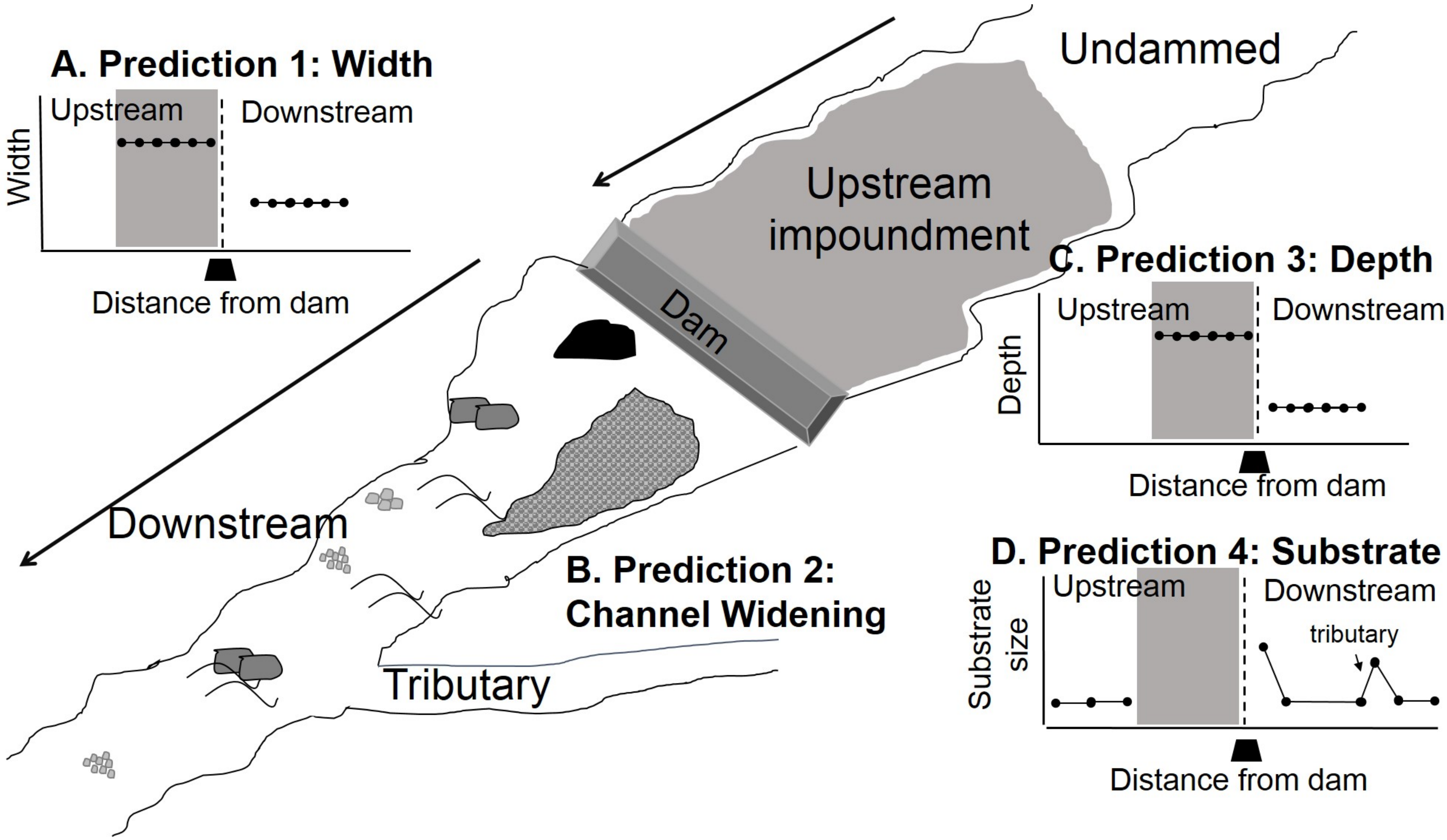

Figure 1.2 Predictions About Dam Impacts. Predictions of geomorphic effects caused by low-head dams on (A) width, (B) channel widening, (C) depth, and (D) substrate size from the geomorphic literature on low-head dams (Fig. 1.1). On all prediction plots, the X axis is the distance from the dam, where the black trapezoid represents dam position with left of the dashed line representing habitat upstream of the dam and right of the dashed line representing habitat downstream of the dam. The impoundment is represented by grey shading.

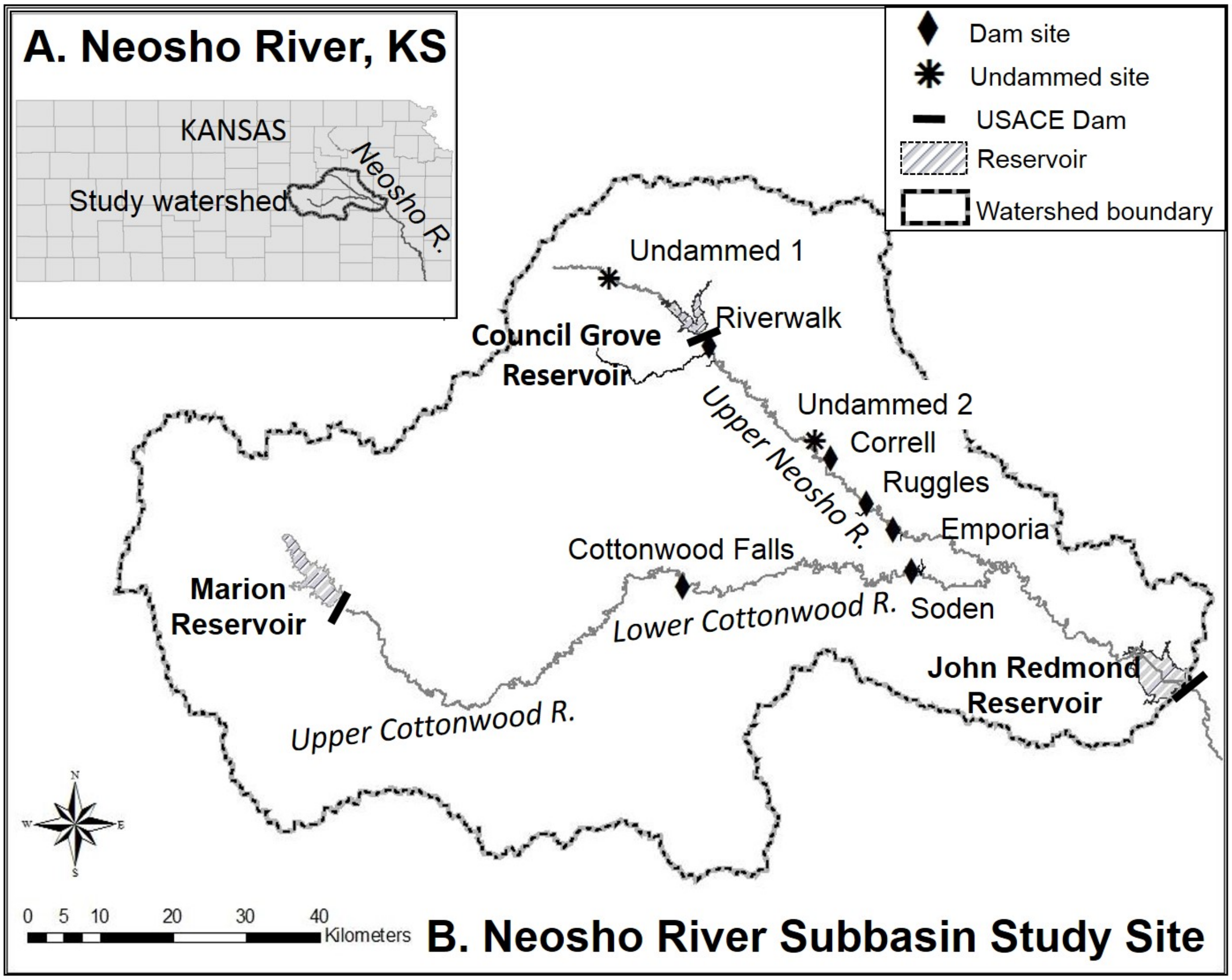

Figure 1.3 Study Area Map. Map of our study area in the Upper Neosho subbasin (A) located in Kansas. Also shown are (B) six dam sites and two undammed reference sites along the Upper Neosho River and Lower Cottonwood Rivers. Major Army Corp of Engineers (USACE) reservoirs in the study subbasin are labeled for reference.

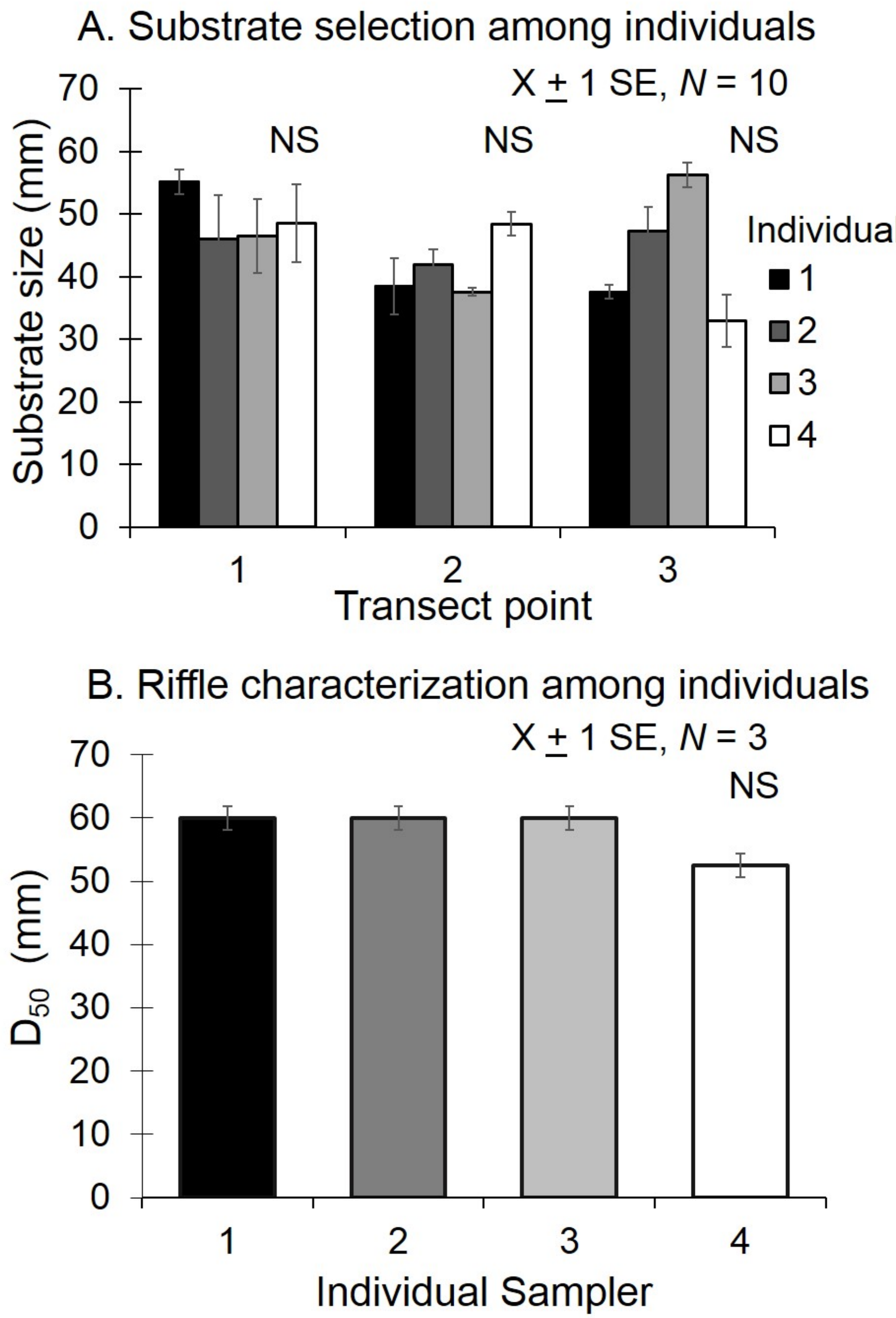

Figure 1.4 Individual Variation in Substrate Selection. Comparison of (A) mean substrate particle size picked by four individuals at three randomly chosen points along a transect with ten replicates for each point and (B) average D50 of three Wolman pebble counts of one riffle. NS indicates no significant difference between individuals. Statistics are the result of a Kruskal-Wallis test of sampler effect using (A) a Bonferroni family-wise error rate at 0.05/3 = 0.016 = α and (B) critical α = 0.05

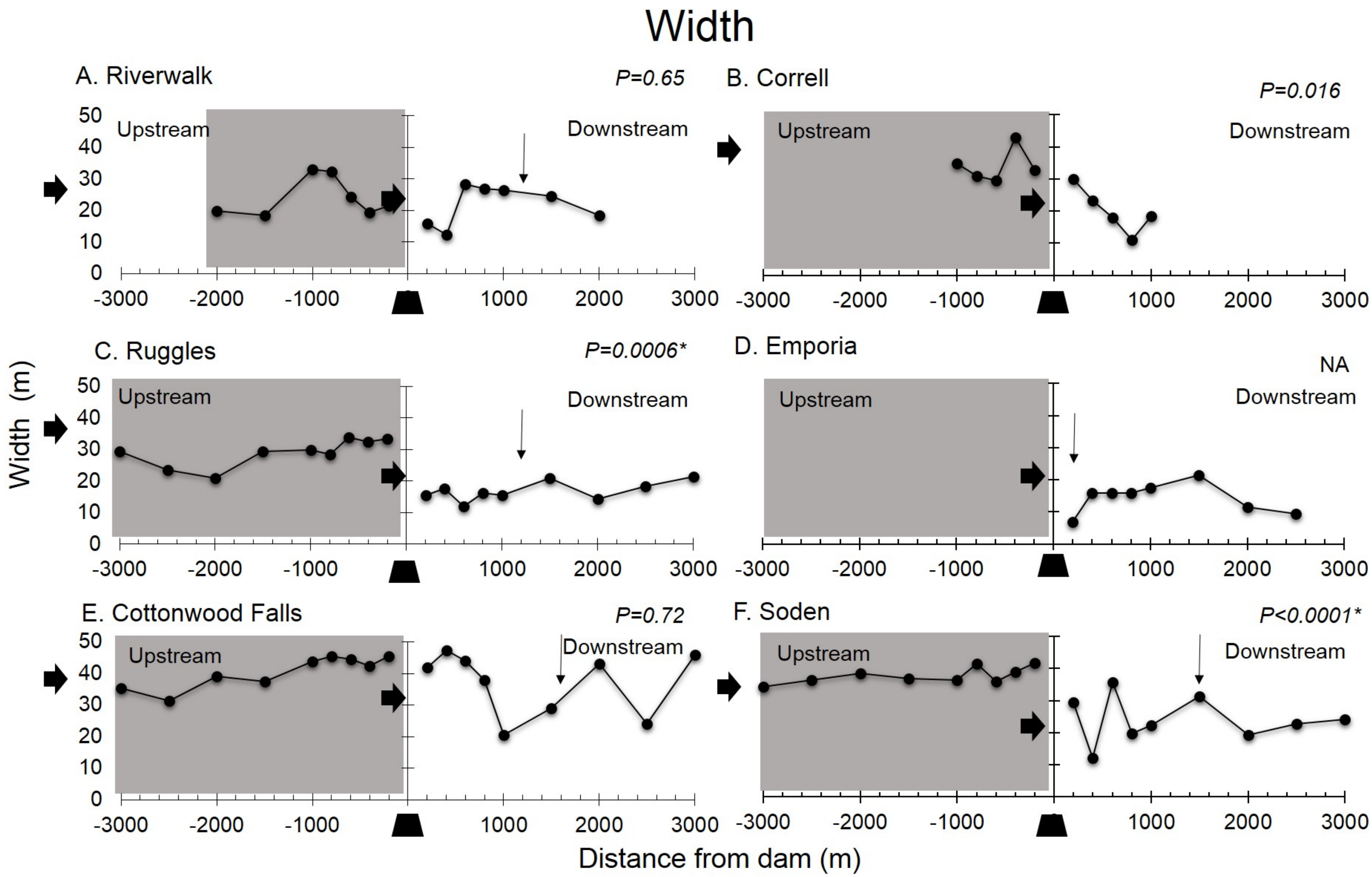

Figure 1.5 Wetted Widths Upstream and Downstream of Dams. Longitudinal profiles of width for the six dams in the study reach showing upstream (left) and downstream (right) samples for our six study dams (black trapezoid); (A) Riverwalk, (B) Correll, (C) Ruggles, (D) Emporia, (E) Cottonwood Falls, and (F) Soden. Y axis arrows indicate mean width. Small arrows in

panel indicate footprint based on substrate profiles (Fig. 1.7). P-values from Wilcoxon rank sum test for mean differences between upstream and downstream transects are shown. Asterisk indicates significance with Bonferroni family-wise error rate at 0.05/5 = 0.01 = α.

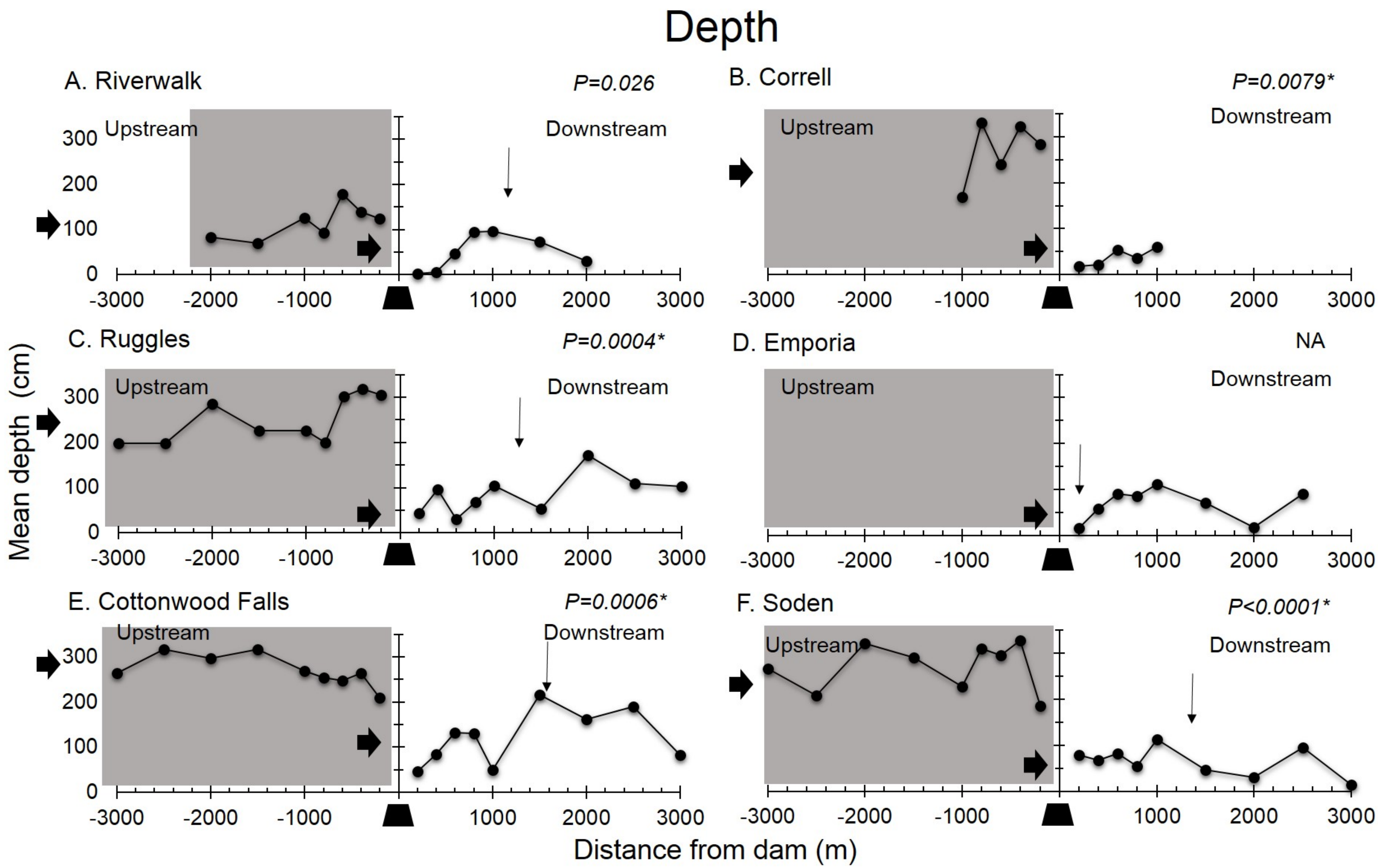

Figure 1.6 Average Depths Upstream and Downstream of Dams. Longitudinal profiles of depth for the six dams in the study reach showing upstream (left) and downstream (right) samples for our six study dams (black trapezoid). (A) Riverwalk, (B) Correll, (C) Ruggles, (D) Emporia, (E) Cottonwood Falls, and (F) Soden. Y axis arrows indicate mean depth. Small arrows in

panel indicate footprint based on substrate profiles (Fig. 1.7). P-values from Wilcoxon rank sum test for mean differences between upstream and downstream transects are shown. Asterisk indicates significance with Bonferroni family-wise error rate at 0.05/5 = 0.01 = α.

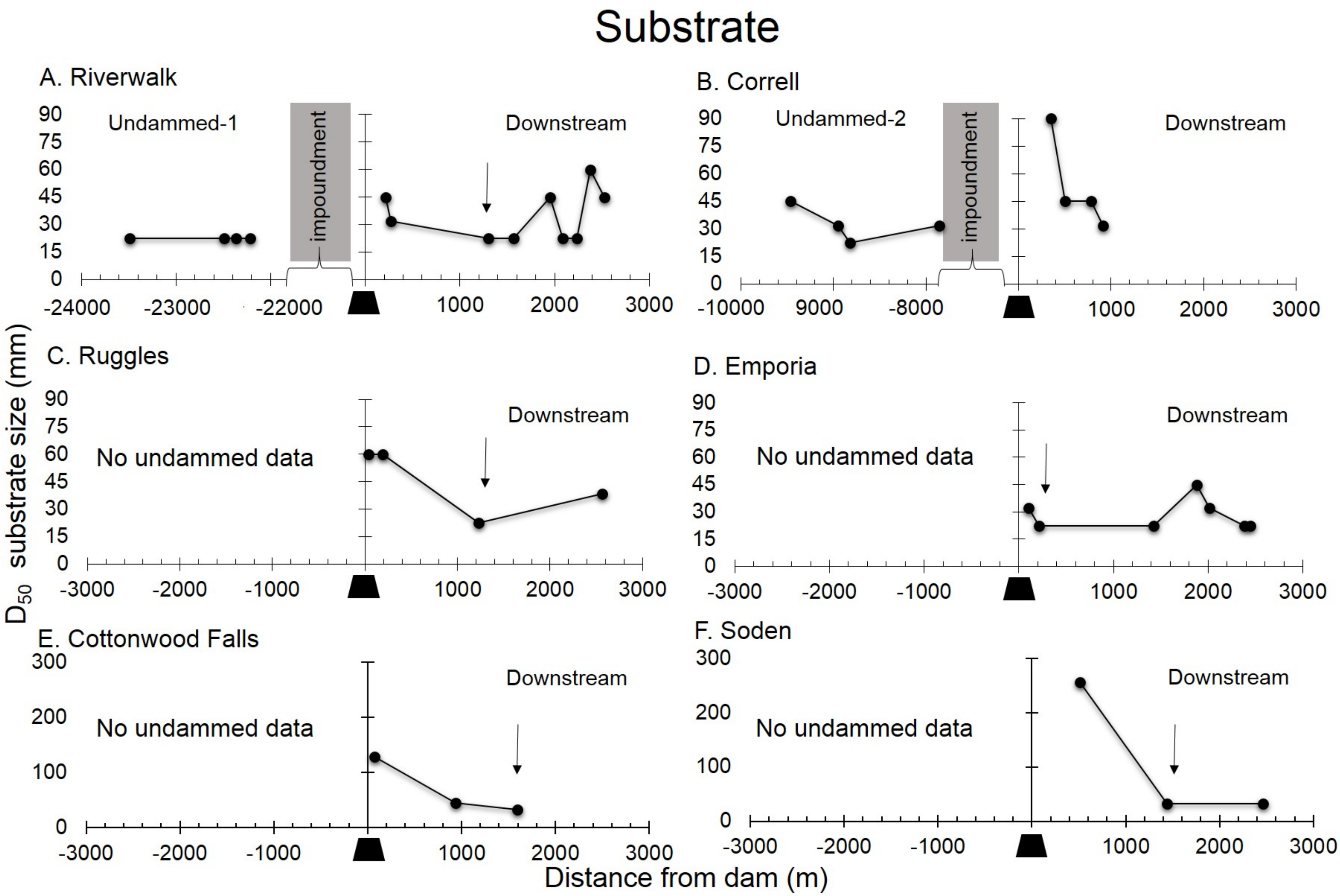
Substrate
A. Riverwalk
Undammed-1
impoundment
Downstream
B. Correll
Undammed-2
impoundment
Downstream
C. Ruggles
No undammed data
Downstream
D. Emporia
No undammed data
Downstream
E. Cottonwood Falls
No undammed data
Downstream
F. Soden
No undammed data
Downstream
D50 substrate size (mm)
Distance from dam (m)

Figure 1.7 Median Substrate Size at Riffles. Longitudinal profiles of substrate size for the six dams in the study reach showing upstream undammed sites as available (left) and downstream (right) samples (black trapezoid). Each point represents a riffle's location in relation to its distance from the dam. The end of the dam footprint is indicated by an arrow, where applicable, and was considered where substrate size leveled off for two-consecutive riffles or was within the reference baseline condition. (A) Riverwalk, (B) Correll, (C) Ruggles, (D) Emporia, (E) Cottonwood Falls, and (F) Soden. The longitudinal profile for the two reference sites, Undammed-1 and Undammed-2 are plotted in the upstream panel for their corresponding dam sites, Riverwalk and Correll, respectively.

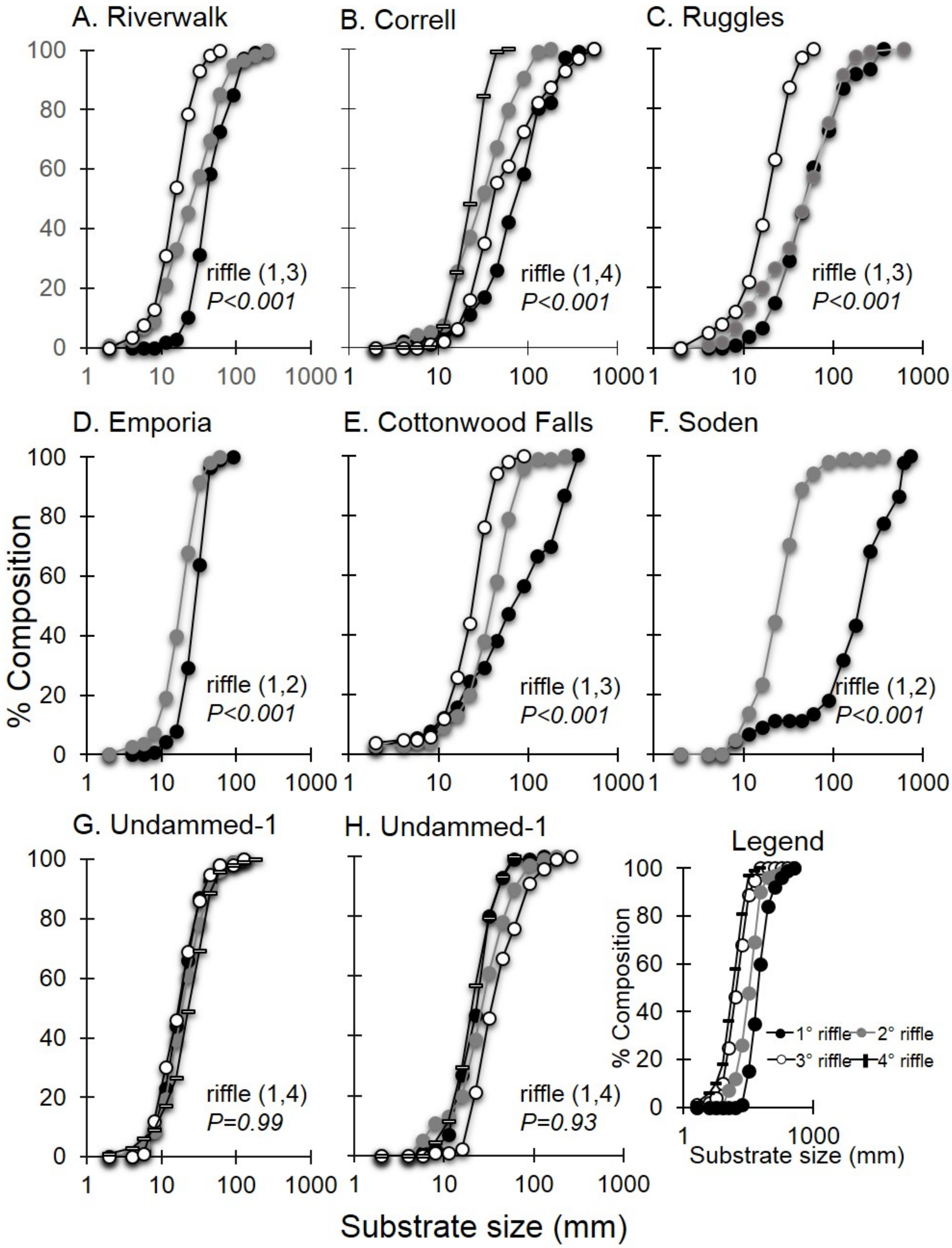

Figure 1.8 Substrate Cumulative Distribution Curves Upper panels display substrate particle size composition changes with increasing distance from dams for (A) Riverwalk, (B) Correll, (C) Ruggles, (D) Emporia, (E) Cottonwood Falls, (F) Soden, and undammed

sites (G) Undammed-1 and (H) Undammed-2. Consecutive riffles below the dam are displayed until median particle size (D50) returned to 22.5 mm for Neosho River or 32 mm for Cottonwood River. For comparison, lower panels display particle size compositions for riffles at reference sites located away from dams where distributions remain similar. Note: reference sites with riffles were not available for four of the six dams. P-values in the figures are based on Kolmogorv-Smirnov test of the distribution curves comparing the two riffles indicated in parentheses. See panel I for the legend - 1° riffle indicates the first riffle downstream of a dam, 2° riffle indicates the second riffle downstream of a dam, 3° riffle indicates the third riffle downstream of a dam.

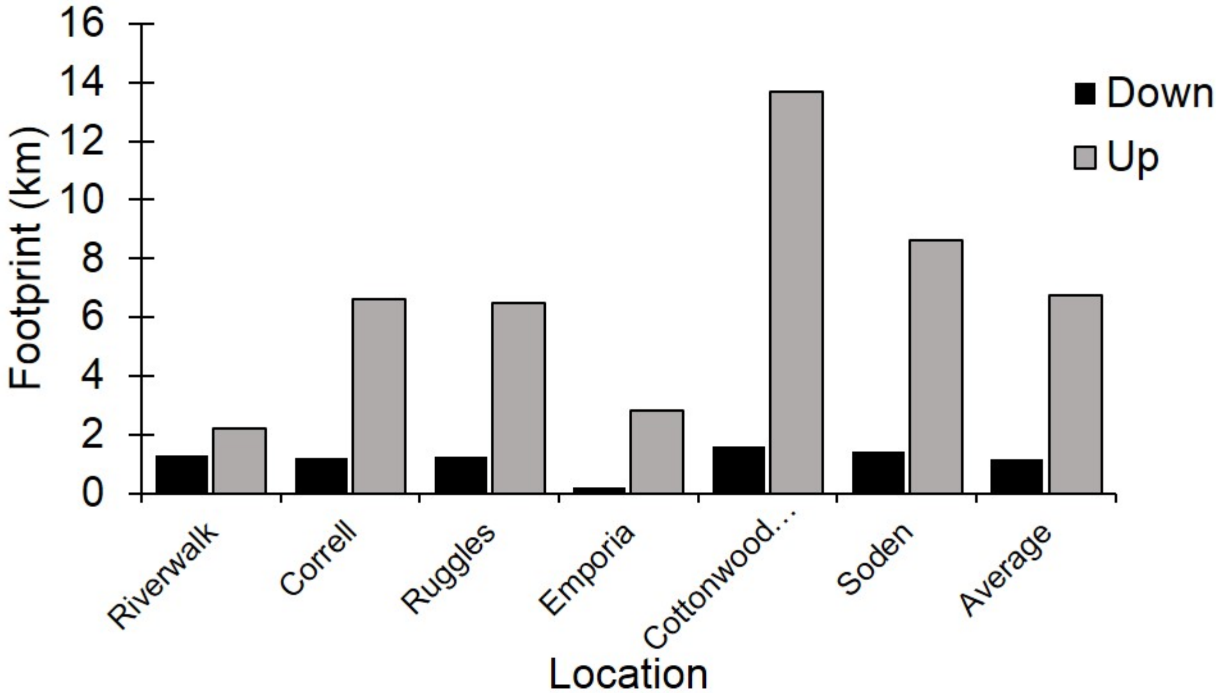

Figure 1.9 Low-head Dam Footprints Downstream (black bars) and upstream (gray bars) footprints of six dam sites and the average downstream and upstream footprints in the Neosho River subbasin.

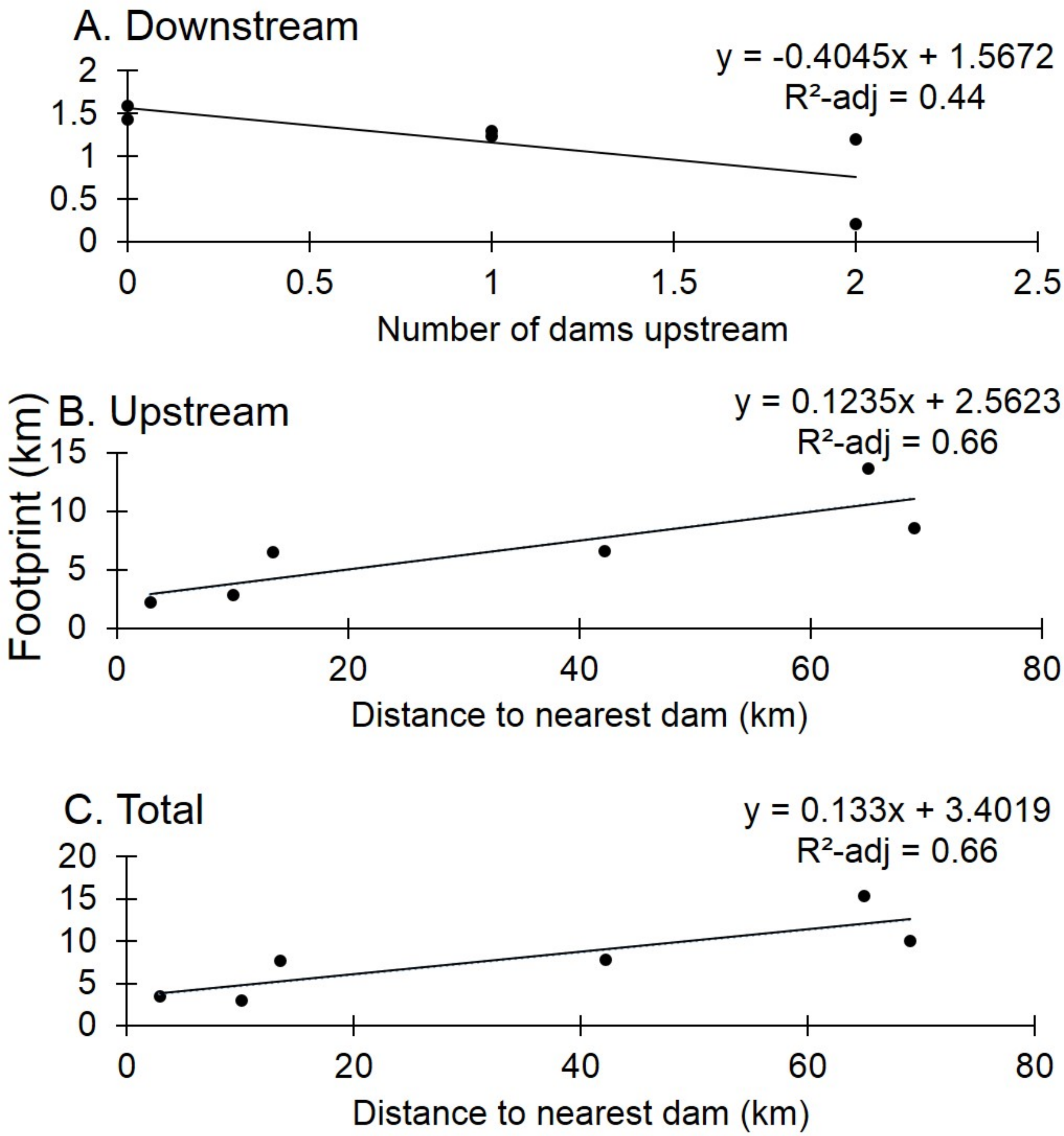

Figure 1.10 Univariate Regressions of Downstream, Upstream, and Total Footprint. Univariate regressions for environmental correlates of (A) downstream, (B) upstream, and (C) total dam footprints. The relationship shown corresponds to the top model amongst competing univariate regressions testing dam height, distance to nearest upstream dam, number of upstream dams within 50 km, and height of nearest upstream dam (S2 for details). The corresponding equation and correlation (adjusted R-sq) between the dam footprint and the corresponding explanatory variable are indicated in each panel.

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Chapter 2 - Low-head Dam Impacts on Fish Assemblages: Methodological Decisions Affect Observed Ecological Outcomes

Abstract

In contrast to well documented adverse impacts of large dams, little is known about how smaller low-head dams affect fish biodiversity. Less than 1% of peer-reviewed papers on dams and fish focused on fish at low-head dams. A select review of how intact low-head dams affect resident fish species identified four methodological inconsistencies that impede our ability to generalize about the impacts of low-head dams on fish biodiversity. The four inconsistencies included different measures of fish assemblages, spatial recovery from dam disturbance, reference comparisons, and site variability. The peer-review was used to inform our study to test the effect of low-head dams on fish biodiversity with two approaches: (1) upstream compared to downstream at dams and (2) downstream of dammed compared to undammed sites. Both approaches were evaluated with six variables including three summary metrics: species richness, abundance, Shannon's diversity index (H') and three habitat guild metrics. For downstream of dammed versus undammed site comparisons, we also tested if variation in methodological decisions corresponding to the inconsistencies present in the literature affected the observation of fish responses to low-head dam impacts. Species richness, abundance, Shannon's diversity index, habitat guild richness were all consistently, significantly higher upstream of dams compared to downstream of dams. We observed higher species and guild richness downstream of dams compared to undammed sites but no significant differences in abundance or Shannon's diversity index. Our ability to observe low-head dam impacts on species richness downstream of dams was sensitive to methodological decision of sampling distance from the dam, and reference site choice. Site variability did not significantly influence overall trends. Our research reveals

new insights about the subtle and complex effects of low-head dams on fish assemblages. These new ecological insights should inform methodological decisions when investigating low-head dam impacts on fish assemblages in future studies.

Introduction

Adverse effects of large dams on lotic ecosystems have been well documented. Large dams alter longitudinal connectivity, a fundamental characteristic of flowing water ecosystems (e.g. Vannote et al. 1980). Over 50% of the world's largest rivers are fragmented by large dams (Nilsson et al. 2005, Liermann et al. 2012) and over 87,000 large dams are listed on the US Army Corps of Engineers National Inventory of Dams (NID 2014). Large dams alter biodiversity in at least three ways, 1) as barriers to movement and dispersal of aquatic organisms (e.g. spawning migrations in fish) which affects population and community dynamics and organisms' responses to disturbances (e.g. Fagan 2002, Landeiro et al. 2011, Auerbech and Poff 2011), 2) by altering habitat and modifying distributions of species with different life history traits (Mims & Olden 2013), and 3) by impacting native stream biota through more complex changes in natural sediment variability, flow alterations, temperature differences, and exotic species (Baron et al. 2002, Power et al. 1996). In contrast to these well documented adverse impacts of large dams, little is known about how smaller low-head dams affect biodiversity.

Over two million small (<7.6 m high), low-head dams have been estimated to fragment U.S. rivers and streams (Graf 1993). Of 10,614 Web of Science peer-reviewed papers on keywords "dams" and "fish", less than 1% focused on "fish" at "low-head dams" (108 of 10,614; Fig. 2.1A - I). From the 108 papers, a selective literature review focused on papers about how intact low-head dams affect resident fish assemblages (N=12). From the review, we identified four methodological inconsistencies that may impede our understanding and ability to generalize about the impacts of low-head dams (Fig. 2.1A- II; Table 2.1). First, the variables used to measure fish assemblage response are inconsistent. In the existing literature on fish and low-head dams, research has examined species richness (e.g. Helfrich et al. 1999, Cumming 2004, Yan et al. 2013), assemblage composition (e.g. Gillette et al. 2005, Yan et al. 2013), distribution of species from downstream to upstream of multiple barriers (e.g. Porto et al. 1999, Santucci 2005), relative abundance or evenness (e.g. Helfrich et al. 1999, Tiemann et al. 2004), and/or trait groups (e.g. Helms et al. 2011) (Table 2.1). The inconsistent use of fish assemblage metrics among studies examining the same question (i.e. low-head dam effects), complicates the identification, quantification, and generalization of low-head dam impacts on fish biodiversity.

Second, the distance from and extent of sampling at low-head dams affect the evaluation of spatial recovery of fish assemblages to low-head dam disturbance (Fig. 2.1B- I). The spatial extent of physical and biological recovery from low-head dam disturbance may be short for low-head dams and consequently hard to detect, especially because researchers are inconsistent in the longitudinal distance from the dam at which they sample fish assemblages. In the existing literature on fish and low-head dams, the spatial extent of assumed ecological dam disturbance (impact zones) is highly variable with downstream impact zones defined in the existing study designs as <0.1 km (e.g. Yan et al. 2013), <0.5 km (e.g. Helms et al 2011), <1 km (e.g. Santucci 2005), or <2 km (Gillette et al. 2005), or not considered (e.g. Cumming 2004, Chick et al. 2006, Rolls 2011) (Table 2.1). Upstream sampling distance is equally variable with studies either sampling (e.g. Santucci 2005, Yan et al. 2013) or not sampling the dam impoundment (e.g. Tiemann et al. 2004, Helms et al. 2011). Inconsistency in distance that constitutes as an impact zone in one's sampling regime may have methodological implications that impede scientific advances in our ability to generalize about spatial recovery or ecological impacts of low-head dams.

Third, the choice of a reference comparison with which to examine fish biodiversity can affect the evaluation of fish responses to low-head dams (Fig. 2.1B- II). Finding references sites to compare dam impacts is challenging. Because low-head dams are so numerous, unimpacted sites are rare (but see Porto et al. 1999, Dodd et al. 2003, Rolls 2011) (Table 2.1). Many studies compare low-head dams to reaches within the same watershed that may be >1 km from the dam (e.g. Santucci 2005), >5 km from the dam (e.g. Tiemann et al 2004, Gillette et al. 2005), or in headwater streams (e.g. Yan et al. 2013), although some studies do not use reference sites, per se (e.g. Helfrich et al. 1999, Cumming 2004, Chick et al. 2006). The lack of an adequate reference comparison and variation in the unimpacted condition across existing research is problematic for generalizing ecological impacts of low head dam research in a way that advances basic research and provides a foundation for management.

Lastly, site variability can affect the evaluation of fish responses to low-head dams (Fig. 2.1B- III). Multiple low-head dams on river systems may be a major concern to lotic ecosystems because of potential cumulative impacts of fragmentation. Some studies conclude there are little to no cumulative impacts and attribute most of the variation in fish species composition to local habitat changes or regional characteristics of the watershed (Cumming 2004, Chick et al. 2006). However, other observational and modeling studies of connectivity in stream networks indicate interaction among sites in that fish species are significantly influenced by fragment length and permeability of barriers (Bourne et al. 2011, Perkin and Gido 2012, Roberts et al. 2013). The number and selection of sites is also inconsistent across existing low-head dam research (Table 2.1). Most studies examine one to three dams within the same watershed (e.g. Gillette et al. 2005, Rolls 2011). Few examine more than 15 dams across multiple watersheds (e.g. Helms et al. 2011) unless they are trying to determine potential cumulative effects of dams at a regional scale (e.g. Cumming 2004).

Thus, the existing low-head dam literature shows that research downstream of dams is variable in ecological response at least partly because of inconsistent data collection and design. These methodological inconsistencies obscure impacts of low-head dams and impede our ability to generalize. A better ecological understanding of and improved methodological standardization for low-head dam effects is needed (Fig. 2.1C). To address this information gap, here we asked four questions. First, do fish assemblages differ above and below low-head dams? We hypothesized that differences in fish assemblages between sites in upstream impoundments and downstream of dams would be large and consistent (Fig. 2.2A) because of the large differences in habitat. Second, do fish assemblages differ downstream of dammed and undammed sites? We hypothesized that effects downstream of dams would be more subtle, complex and variable since habitats are more similar (Fig. 2.2C). Third, for both upstream-downstream and downstream dammed-undammed comparisons, does the measure of the fish assemblage change conclusions about low-head dam effects on fish biodiversity? Fourth, for the downstream comparisons, we examined if methodological decisions associated with extent of spatial recovery, reference comparison, and site variability alter the perceived ecological outcome of low-head dam impacts (Fig. 2.1B). For questions 3-4, we hypothesized that differences in how low-head dams affect fish biodiversity (Y axis) might vary with the how the fish assemblage, spatial recovery, reference comparison, and site variability is conceptualized and measured (X axis; (Fig. 2.2C). Of course, low-head dams might have a consistent impact (Fig. 2.2A) or no impact regardless of the ecological conceptualization and methodological approach (Fig. 2.2B). Insights from our four specific research questions should advance scientific understanding of the impact of low-head dams on biodiversity, promote methodological standardization, and increase the ability to generalize from individual research studies.

Materials and Methods

Study site

The Neosho River is a major tributary of the Arkansas River located in the Central Prairie Freshwater Ecoregion (Abell et al. 2000). Our study site, the Upper Neosho subbasin, was located in the upper third of the Neosho River basin and included the Upper Neosho and Lower Cottonwood Rivers (Fig. 2.3). These rivers originate in the Flint Hills upland and continue into the Osage Cuestas physiographic regions (Schoewe 1949). The Upper Neosho and Lower Cottonwood Rivers are 5th and 6th order meandering rivers with low to moderate flows and large seasonal fluctuations of discharge [Upper Neosho River: mean annual discharge, 8.7m^3s^{-1}; annual peak flows, 124.6 – 4,927.3 m^3s^{-1} (1963-2012; USGS gage 07179730); Lower Cottonwood River: mean annual discharge, 24.4 m^3s^{-1}; annual peak flows, 146.7 – 26,306.5 m^3s^{-1} (1963-2012; USGS gage 07182250)]. The terrestrial landscape is tallgrass prairie and current land use is primarily agriculture, forest, and range (Wilson 2003).

We examined effects of low-head dams on fish assemblages at six low-head dams. Four low-head dams were located on the Upper Neosho River and two low-head dams were located on the Lower Cottonwood River (Fig. 2.3B). Except for a mill dam downstream of Marion Reservoir on the Upper Cottonwood River, our study included all low-head dams on the Upper Neosho and Lower Cottonwood rivers between three large U.S. Army Corps of Engineer dams (Marion, Council Grove, John Redmond) (Fig. 2.3B). The dams were all permanent, concrete run-of-river dams 1.2 – 3 m high that spanned the entire width of the channel. The dams were built between 1860 and 1995 for recreation, water supply (Upper Neosho River), and to power mills (Lower Cottonwood River) (Table 2.2). Because our study included all intact low-head dams within a single subbasin, we were able to examine individual, multiple, and cumulative dam effects.

Research Design

We tested the effect of low-head dams on fish biodiversity using two approaches (1) upstream versus downstream comparisons at dams, and (2) downstream of dammed versus undammed site comparisons. For both approaches, a transect represented a single fish sample and a site represented a dammed or undammed location with multiple transect samples (Fig. 2.4). Fish were sampled for a standardized distance along each transect using a 2.4 m mini-Missouri trawl (Herzog et al. 2009) with 35 mm outer mesh and 3.2 mm inner mesh. The mini-Missouri trawl can be used in a variety of depths and habitats to sample both above and below dams in wadeable and non-wadeable streams. In a gear comparison, the mini Missouri trawl caught the same numbers of species as a beach seine and more fish species than backpack electrofishing and hauls of 100 and 40 m upstream and downstream, respectively, caught the same number of species as longer hauls (Fig. B.1). The mini-Missouri trawl was chosen over seining because it allowed us to sample deeper habitats than would not be accessible with a seine. Throughout, our goal was to assess if dams affected fish biodiversity (Fig. 2.2) for both approaches. Fishes were enumerated, identified to species, when possible, and returned to the stream.

Differences in fish assemblages at low-head dams, for both approaches, were evaluated with six variables (Fig. 2.5). First, we used three summary metrics: species richness, abundance, and Shannon’s diversity index (H’). In addition, we explored which kinds of fishes, based on habitat guilds, were present and changed with dam presence. Because habitat characteristics are important in structuring fish communities (e.g. Schlosser 1982), habitat based classifications of species can be useful to describe trends in fish assemblages (Welcomme 2006). Fishes were categorized into seven habitat guilds based on the proportion of time they spent in riffle, run, and pool habitats in the Neosho River (Hitchman et. al in preparation; Table 2.3). Here, we focused on three Neosho habitat guild measures (number of guilds, number of riffle specialists, and number of pool specialists) in detail. Number of habitat guilds represented trait group richness. Number of species in the riffle and pool specialist guilds discriminated distinct lotic and lentic habitat types. Paired t-tests were performed on all six measures of fish assemblages in R (R Core Team 2014). Critical $\alpha=0.05$ was used throughout. In addition, to determine which species contribute to possible differences (downstream of dammed vs undammed sites only), we examined the frequency of occurrence and relative abundances of species through Dufrene-Legendre Indicator Species Analysis (Dufrene and Legendre 1997, Roberts 2013).

In the second approach, for downstream of dammed versus undammed site comparisons, we tested if variation in methodological decisions in spatial recovery, reference comparison and site variability affected the observation of fish responses to low-head dams. We use the term 'decisions' to address issues that might affect observed dam effects (Fig. 2.1 and Fig. 2.5). We use the term 'variable' to describe the different ways each decision can be measured and tested (Fig. 2.5). For all three decisions, our objective was to identify if the variables within each decision altered the outcome of dam comparisons (Fig. 2.2).

Upstream vs. Downstream Comparisons at Dams

For upstream vs. downstream comparisons, we sampled fish assemblages within a 3 km reach both above and below the six dams. For this first approach, samples were collected at five to nine transects in both directions, starting 0.2 km from the dam for safety (Fig. 2.4A). Sample transects were spaced every 0.2 km m for the first kilometer and every 0.5 km thereafter until we reached the end of the 3 km reach, the end of the impoundment (Riverwalk, 7 transects), could not procure landowner permission (Correll, 5 transects), or encountered an obstruction in the impoundment (Emporia, 8 transects). The same number of transects were compared upstream and downstream of dams.

Upstream, two individuals deployed the mini-Missouri trawl off the bow of a 3 m Jon boat with a lead length of 8 m, as the driver reversed the boat downstream at about 6 km hr^{-1} for 0.1 km. Downstream, while wading, two individuals pulled the trawl in an upstream to downstream direction faster than the current for 45 m. A GPS was used to record the start and stop position and track the distance of each trawl haul both upstream and downstream. Both upstream and downstream tows were standardized to fish per 5 m^{-1}. Fish assemblages were analyzed as described above.

Downstream of Dammed Versus Undammed Site Comparisons

For downstream of dammed versus undammed site comparisons, we sampled fish assemblages within a 3 km reach downstream of five of the six dams described above and at five corresponding undammed sites (Fig. 2.3B). Undammed sites were between 5 and 24 km away from dam sites. For this downstream sampling, we used a slightly different arrangement of transects that provided more resolution along the spatial trajectory. Between June and August, 2013, at each site, samples were collected at 14 transects starting 0.1 km below the dam every 0.1 km for the first kilometer and every 0.5 km thereafter until we reached 3 km downstream (Fig. 2.4B). Fish collection methods and the six biodiversity responses were the same as described above for downstream (wadeable) samples.

Decision I – Spatial recovery (Fig. 2.1 and Fig. 2.5)

Spatial recovery trajectories from potential ecological disturbances such as dams must be evaluated. To examine if distances from the dam changed the interpretation of low-head dams impacts on fish assemblages, we quantified patterns at four distances (Fig. 2.1-I; Fig. 2.5-IB i-iv). These four distances were the first transect downstream of a dam (N=1 per site), channel widening transects (N=1-2 per site), footprint transects (N=2 – 11 per site) or whole site transects (N=14 per site). Each comparison was matched with the same number of transects for the nearest undammed site (Table 2.4). Channel widening and footprint transects were determined using geomorphological characteristics measured downstream of the six dams (Chapter 1). Comparisons between dammed and undammed sites were analyzed using paired t-tests. Channel widening was the default impact zone for the evaluation of the other two methodological decisions and overall characterization of fish assemblages.

Decision II – Reference comparison (Fig. 2.1 and Fig. 2.5)

Dam impacts must be evaluated relative to some reference measure of undammed effects. For reference-comparisons, we compared four variables that included undammed sites along the main channel and distant transects at dam sites (Fig. 2.3 and Fig. 2.5-IIB i-iv) as no equivalent dam-free watersheds existed in the geographic region. First, we compared all dam sites to all undammed sites using a Welch's t-test, which accounted for the potential of unequal variances between samples (Welch 1947). Second, we used a pairwise t-test to compare each dam to each undammed site, assuming all else being equal, that sites near each other would be identical. Third, we compared the first three transects adjacent to the dam to the last three transects at each dam site. Fourth, we determined if the difference between the first and last three transects at a dam site was different from differences between first and last transects at undammed sites. Comparisons between dammed and undammed transects were analyzed using paired t-tests.

Undammed sites were the default reference comparison for the evaluation of the other two methodological decisions.

Decision III – Site variability (Fig. 2.1 and Fig. 2.5)

Site variability may be an influential covariate on fish assemblages and the cumulative ecological context of dam impacts. In the third methodological decision, we examined if site specific variability in fish assemblages affects the interpretation of low-head dam impacts in downstream dam vs. undammed comparisons (Fig. 2.1 and Fig. 2.5-IIIB i-iii). For this option, we examined three models. The first model was a linear model with dam (categorical: dammed or undammed) as an explanatory fixed effect and no site variable. The second model for testing was a linear mixed effect model with dam (categorical: dammed-undammed) as the explanatory fixed effect and site (i.e. location) included as a random effect. Third, we examined linear model with site as a fixed effect. Models were fitted by restricted maximum likelihood estimation (REML) in R (Pinheiro et al. 2013). The two models with dam (dammed-undammed) as a fixed effect were compared using AIC model selection in which the model selected had a change in AIC > 2 (Burnham and Anderson 2002). No site effect was the default condition for the evaluation of the other two methodological decisions.

Results

Upstream vs. Downstream Comparisons at Dams

In this first approach, we caught a total of 3,372 fish representing 31 species, 19 genera, and nine families over 94 samples. Our six upstream sites had a total of nine species and 262 individuals, whereas the corresponding six sites downstream of dams had a total of 30 species and 3,110 individuals (Table B.1).

Sites that were upstream and downstream of dams had different fish assemblages no matter which measure of fish biodiversity was used. Species richness (Fig. 2.6A), abundance (Fig. 2.6B), and Shannon's diversity index (Fig. 2.6C) were significantly lower upstream compared to downstream of dams ($P < 0.001$). On average, transects at downstream sites had 3.3 more species (t=9.77, df=46, Fig. 2.6A), 5.1 more individuals per 5 m (t=4.56, df=46, Fig. 2.6B), and a 0.69 higher Shannon's index value (t=8.28, df=46, Fig. 2.6C) downstream compared to upstream of dams. More habitat guilds were represented downstream of dams than upstream of dams, on average 3.1 per transect (t=12.11, df=46, P<0.001, Fig. 2.6D). All seven guilds were found downstream of dams, but only three guilds occurred upstream (pool specialists, pool-run generalists, and generalists) (Fig. 2.7). No species representing the riffle specialist guild was found upstream (t=5.08, df=46, P<0.001, Fig. 2.6E). The pool specialist guild was represented by fewer species upstream of dams (t=3.2, df=46, P=0.002, Fig. 2.6F). Only five of thirteen pool specialist species occurred upstream of dams: Freshwater Drum (*Aplodinotus grunniens*), Gizzard Shad (*Dorosoma cepedianum*), Orangespotted Sunfish (*Lepomis humilis*), Longear Sunfish (*Lepomis megalotis*), and White Crappie (*Pomoxis annularis*) (Table B 2.2).

Downstream of Dammed Versus Undammed Site Comparisons

In our second approach, we caught a total of 10,279 fish representing 37 species, 20 genera, and nine families in 140 samples. Sites downstream of dams had a total of 36 species and 4,563 individuals, whereas undammed sites had a total of 32 species and 5,716 individuals (Table B.2).

Fish biodiversity

The interpretation of whether a low-head dam affected downstream fish biodiversity depended on how the fish assemblage was conceptualized and measured. Species richness was higher downstream of dams compared to undammed sites by a mean difference of two species (t=2.68, df=8, *P*=0.028, Fig. 2.8A). Abundance did not differ between sites (t=0.28, df=8, *P*=0.79, Fig. 2.8B). Shannon's diversity index was marginally higher downstream of dams compared to undammed sites (t=01.89, df=8, *P*=0.096, Fig. 2.8C). Although more species were present downstream of dams, the individual species varied across sites. Number of habitat guilds was significantly higher below dams compared to undammed sites (t=2.68, df=8, *P*=0.028, Fig. 2.8D), again with a change in the identity of the individual species causing this difference across sites. The number of riffle specialists was marginally higher below dams compared to undammed sites (t=1.79, df=8, *P*=0.110; Fig. 2.8E). Central Stoneroller (*Campostoma anomalum*), a riffle specialist, was a marginally significant indicator species of downstream dam effects (*P*=0.08, Table 2.5). The riffle generalist guild was not represented at any undammed sites (Fig. 2.9, Table 2.5). The riffle generalist, Bluntnose Minnow (*Pimephales notatus*), was a significant indicator species (*P*=0.02, Table 2.5) of dam effects due to their high abundance and increased frequency of occurrence below dams. Other species that were not represented at undammed sites included the Gizzard Shad [(*Dorosoma cepedianum*), pool specialist], Western Mosquitofish [(*Gambusia affinis*), pool specialist], Channel Catfish [(*Ictalurus punctatus*), pool-run generalist], Fathead Minnow [(*Pimephales promelas*), pool-run generalist], and Redhorse [(*Moxostoma spp*), generalist] (Table 2.5). Species that occurred at undammed sites but not below dammed sites were the Longnose Gar (*Lepisosteus osseus*) and Redfin Shiner (*Lythrurus umbratilis*), both pool specialists.

Decision II – Spatial recovery

Observed differences in fish assemblages downstream of dams compared to undammed sites depended on the decision of which fish samples were included relative to distance from the dam. Differences in species richness between the first transect at dammed and undammed sites were marginally significant (t=2.27, df=4, *P*=0.086 Fig. 2.10A). The mean for the first transects was higher below dams compared to undammed sites, but variation was also high, masking dam-related differences. Channel widening and footprint transects showed significantly more species at dammed sites compared to undammed sites (t=2.68, df=8, *P*=0.028; t=2.16, 42, *P*=0.037, Fig. 2.10 B & C, respectively). The observed difference in the number of species for channel widening transects (mean difference = 2) was greater than footprint transects (mean difference = 1.3; Fig. 10 B & C, respectively). The identity of species responsible for these differences was similar to patterns described above. No significant differences in species richness was observed between dammed and undammed sites when the whole 3 km site (14 transects) was examined (t=1.15, df=69, *P*=0.25, Fig. 2.10D).

Decision III – Reference comparison

Choice of the reference comparisons influenced whether fish assemblages appeared to differ below dams compared to undammed sites. Dams, as a treatment, had significantly higher species richness both when evaluated against all undammed sites, as a treatment (t=2.27, df=11.32, *P*=0.044, Fig. 2.11A). Dams also differed from undammed reference sites when dam sites were paired with undammed sites (t=2.68, df=8, *P*=0.028, Fig. 2.11B). Species richness between the first and last three transects at a dam site were marginally different from one another (t=1.55, df=14, *P*=0.14, Fig. 2.11C). Select transects near and far from sites did not differ between dammed and undammed locations (t=1.06, df=4, *P*=0.35, Fig. 2.11D). Thus, comparisons of dams to undammed reference sites, both pooled and paired, were significantly different, but transects near and far from dams at the same site were not.

Decision III – Site variability

Site variability did not alter the overall pattern about fish biodiversity downstream of dams compared to undammed sites. When a fixed dam effect was included in the linear model, dammed sites had about two more species than undammed sites (Fig. 2.12A, P=0.04). When site was incorporated as a random effect, species richness remained higher at dammed compared to undammed sites but was marginally significant (Fig. 2.12B, P=0.11). When site was tested as a fixed effect, site was a marginal predictor of species richness (P=0.063, Fig. 2.12C), primarily because of one reference site, Neosho-2 (NE2). The best of these three-models was dam with no site effect (ΔAIC < 2; *weight* = 0.80; Table 2.6).

Discussion

Our research revealed distinct differences in fish assemblages downstream compared to upstream of dams but more complex patterns downstream of dammed compared to undammed sites. We showed that the experimental design of low-head dam studies has important ecological ramifications for and methodological consequences for how we interpret and generalize about the science of low-head dam effects. Species richness is a popular measure of fish assemblages, but knowing which species are contributing to species richness is equally important. Small dam effects can impact riverscape-scale fish biodiversity by fragmenting river reaches and causing impoundments that extend many kilometers upstream. We showed that the spatial recovery in fish assemblages downstream of low-head dam disturbances may be underestimated by some studies since the greatest differences in fish assemblages between dammed and undammed sites were in transects less than 1 km from the dam. We showed that reference sites should probably be located more than 3 km away from a dam since we did not observe any significant differences comparing transects within this distance. Changes in fish assemblages may be somewhat gradual with increasing distance from dams, because some species may be more sensitive to the disturbance than others. Hence thoughtful choice of and consistency in the choice of reference sites with which to compare dam effects is key. We showed that site variability in fish assemblages exists. Even though this across dam variation did not change the outcome of our conclusions, it will be important to test for this variability in future low-head dam studies so that more sites can be thoughtfully included.

Upstream vs downstream fish biodiversity

Our hypothesis that the lentic vs lotic difference in upstream impoundment vs downstream free-flowing sites was supported by the absence of flow associated habitat guilds upstream of dams including riffle specialists, riffle generalists, run generalists, and riffle-run generalists. Low-head dams can have a large upstream effect because they create lentic habitat with slower flow and deeper water. Changes in habitat characteristics upstream of dams include greater channel width and depth, lower current velocities, and smaller substrate sizes (Dodd et al. 2003, Santucci et al. 2005, Yan et al. 2013). These changes in conditions upstream of dams create more favorable habitat for lentic species that resulted in lower species richness here and elsewhere (Santucci et al. 2005, Yan et al. 2013). However, many native stream fish use natural stream pools (not dam reservoirs) and these pool specialists were also reduced upstream of dams. When many low-head dams co-occur within a single watershed, the lentic impact of dams may accumulate. For example, non-native zebra mussels (*Dreissena polymorpha*) have colonized in low-head dam impoundments and multiple dams have facilitated their progressive invasion downstream (Smith et al. *in press*). Streams with multiple low-head dams have truncated distributions of fishes (Helfrich et al. 1999, Porto et al. 1999, Santucci 2005). Pelagic spawning fishes in the Great Plains are affected by stream fragment lengths related to multiple dam disturbances (Perkin et al. 2014). In summary, fish assemblages upstream of low-head dams are dramatically and consistently different and can have adverse impacts throughout the length of a river.

Downstream dammed vs undammed site fish biodiversity

Differences in fish assemblages downstream of dammed sites and undammed sites were usually determined by one or a few potentially ecologically important species such as Central Stonerollers (Taylor et al. 2012). We observed that species richness was higher downstream of dams compared to undammed sites. Elsewhere, sites immediately downstream of dams have higher species richness compared to sites farther downstream (Dodd et al. 2003, Gillette et al. 2005) or reference streams (Dodd et al. 2003, Rolls 2011). This higher species richness below low-head dams may be related to three different mechanisms. First, species richness may be highest immediately downstream of dams because species from the upstream impoundment of influence swim, are washed downstream, or otherwise spillover low-head dam structures. For example, Gizzard Shad, pool specialists, were present in channel widening transects downstream of dams, but not at undammed sites. Second, habitat alterations downstream of dams may create favorable habitat heterogeneity for native stream fish species (Smith and Mather 2013). The surface release of water over low-head dams creates a plunge pool immediately downstream that scours the bed material thereby armoring the channel bed, leaving behind coarser substrates, and perhaps increasing the amount of riffles directly downstream (Csiki and Rhoads 2010). We found that the Bluntnose Minnow (riffle generalist) and Central Stoneroller (riffle specialist), both native stream species that need fluvial habitat, were more common below dams compared to undammed sites. The coarse substrate downstream of dams likely provides the cavity spawning Bluntnose Minnow with ideal spawning habitat on which to deposit eggs on the flat underside of rocks (Pflieger 1997). Central Stonerollers (*Campostoma anomalum*) typically occur in riffles (Eberle 2014), and were more common below dammed compared to undammed sites (Table 2.5). Similarly, Helms et al. (2011) found that algivores, such as *Campostoma spp*. were most abundant immediately below intact dams and Tiemann et al. (2004) found higher abundances of benthic specialists downstream of dams. Furthermore, pool specialists such as Longnose Gar and Redfin Shiner were absent immediately below dams (Table 2.5), but did occur at other transects downstream of dams and at undammed sites (S 2.2). Third, aggregations of species and individuals occur below dams because dams may cause accumulation via a 'traffic jam' (Dodd et al. 2003, Rolls 2011) to individuals attempting to disperse upstream. However, we did not see higher numbers of individuals below dams. Consequently, the higher species richness below the dams we examined could be the result of two of three possible mechanisms, upstream spillover or increased below dam habitat heterogeneity, but not downstream accumulation.

Spatial recovery

To our knowledge, no other study has examined what the potential spatial recovery of fish assemblages is using different subsets of transects based on proximity and geomorphological characteristics below low-head dams. Most studies assume the extent of spatial impact. Sometimes this impact is determined to be anywhere less than 100 m (e.g. Helms et al. 2011, Yan et al. 2013), 1 km (Porto et al. 1999, Dodd et al. 2003, Bean et al. 2007, Santucci et al. 2005) or 2 km from the dam (Tiemann et al. 2004, Gillette et al. 2005). In developing our study, we were particularly interested in longitudinal trends, and our goal was to sample far enough to make sure to observe ecological recovery from low-head dam disturbance. We learned that, in fact, it is better to have more replicates closer to dams although the full scope of the trajectory needs to be mapped for each new site. When we examined transects close to the dam (channel widening, footprint transects) we found richness was significantly higher downstream of dams compared to undammed sites. Examining the first downstream transect was only marginally significant, but we believe that more replicates would increase the power of this result. Examining all 14 transects, from 0.1 km to 3 km downstream, revealed no differences in species richness between dammed and undammed sites. Fish assemblages had a rapid recovery from the downstream disturbance of low-head dams so it's possible that some studies have not incorporated the disturbance downstream of dams.

Reference comparison

Choosing a reference site is important to correctly interpret effects of potential ecological disturbances. Our study system is sandwiched by large reservoirs, so the results we observe now are probably influenced by the legacy of large reservoirs and smaller low-head dam impacts. Any differences in fish assemblages between dam and reference sites in this study are probably conservative compared to what would have been observed when the dams were first constructed over 50 years ago. Ideally one would use an unimpacted free-flowing reference stream, which is possible in a few watersheds (e.g. Porto et al. 1999, Dodd et al. 2003, Rolls 2011) but not most. Most studies that examine reference sites use a site within a few kilometers of their impact site (e.g. Santucci et al. 2005, Helms et al. 2011, Yan et al. 2013). Choosing a reference site within a few kilometers of a dam is convenient in coordinating sampling logistics, but is probably too close. We found that differences in species richness between the first three (≤0.3 km) and last three transects (≥2 km) at dam sites were greater compared to the same comparison at undammed sites, but not significantly different. This is most similar to the comparisons of Helms and colleagues (2011) at intact dams and Yan et al (2013), from our review of the low-head dam literature. Neither Helms et al. (2011) nor Yan et al. (2013) found significant differences in species richness immediately downstream of dams (<0.1 km) compared to their reference sites (>

1 km). However, both found the general trend that species richness was highest immediately below dams. In our study, looking at undammed sites at a larger distance between 5 and 25 km away did show significant differences in dammed and undammed sites, whether or not a paired test was performed. To our knowledge, no one has compared dam impacts to references at different distances from low-head dams before. Based on our results, we recommend looking at reference sites no closer than 5 km from any dam or its impoundment. If reference sites are too close to dams ecologically important differences in fish assemblages may be missed, causing misguided assessments toward conservation and management implications such as assessments of dam removal.

Site variability

We wanted to know if sites are replicates of each other, or if they are a unique 'element' in the river system (*in sensu* Poole 2002). The value of looking at multiple sites is to account for more variation and be able to generalize about emergent statistical outcomes. We used six sites in the same watershed. Generally, this is not considered a big enough sample size statistically, but it is more sites than most studies which have examined one to three low-head dams (e.g. Tiemann et al. 2004, Gillette et al. 2005, Porto et al. 1999, Bean et al. 2007, Yan et al. 2013). The challenge of looking at multiple sites is that natural variation exists and it takes more effort in the amount of time and manpower so it may not always be feasible. In systems like ours, there is also the additional challenge of acquiring landowner permission for multiple sites. Incorporating a variable that accounts for geographic location may be important in studies where dams are examined across multiple watersheds (e.g. Cumming 2004, Helms et al. 2011). Studies which examine a much longer profile of the river (e.g. Santucci et al. 2005, Chick et al. 2006) may also need to account for geographic location because of natural ecological changes along a river continuum (Vannote et al. 1980) but should be cautious that observed structural changes in fish assemblages may be confounded by cumulative dam effects. The sites in our study were variable, but not significantly different from each other, and our generalized linear model did not change much when site variability was accounted for as a random effect. Therefore, we can be confident that the differences in dammed and undammed sites were not skewed by high variability in one or a few sites.

Summary

Scientists and managers alike have interest in creating ecologically meaningful characterizations of low-head dams (e.g. Poff and Hart 2002). Because low-head dams are so numerous, with over 2,000,000 estimated to fragment rivers in the U.S. alone (Graf 1993), understanding their individual and cumulative impacts is important. Even though any one dam may not have as large of an impact as large reservoir dams, the addition of each small dam may be to a watershed like the death of a thousand cuts. How low-head dams have been measured in the literature is inconsistent. We showed that differences in how we measured fish biodiversity, the spatial recovery trajectories, reference comparisons and site variability could lead to different results and interpretation. For managers and scientists who work with aquatic systems to move forward on the science of low-head dams, all should consider these things in study design and explicitly describe how these challenges were addressed.

Tables

Table 2.1 Literature Review. Literature review of fish and low-head dam papers, narrowed to include papers about entire fish assemblages at run-of-river type low-head dams. Literature was reviewed for study design complexities that may affect interpretation of low-head dam impacts on fish biodiversity including the ways fish response, spatial recovery, reference choice, and sites were chosen. Grey boxes indicate the chosen measurement of each inconsistency and are used to indicate the upstream downstream comparisons in studies for reference.

				Fish Response							Spatial recovery (km)		Reference Site						Site (dam)	
Citation	Up vs down (impoundment)	Up vs down (no impoundment)	Dist. not explicit	Richness	Abundance	Diversity/Evenness	Species composition	Guild/Trait group	Length/size reltshps	Distribution	Upstream	Downstream	< 1 km from dam	> 1 km from dam	> 5 km from dam	Reference streams	Headwater site	None	Within watershed	Across watersheds
1. Helfrich 1999	■			■	■		■		■	■	<5	<5						■	3	
2. Porto et al. 1999		■		■					■	■	<1	<1				■			2	
3. Dodd et al. 2003		■		■	■		■				<1	<1				■				24
4. Cumming 2004			■	■							--	--						■		>1000
5. Tiemann et al. 2004		■		■	■	■	■				<5	<2			■				2	
6. Gillette et al. 2005		■		■			■				<5	<2			■				2	
7. Santucci 2005	■			■				■		■	<1	<1		■					15	
8. Chick et al. 2006			■	■			■				--	--						■	6	
9. Helms et al. 2011		■		■				■			--	<0.1	■							20
10. Rolls 2011			■	■	■		■	■			--	--				■			1	
11. Bean et al. 2007	■						■				<1	<1		■					3	
12. Yan et al. 2013	■			■	■		■				<0.1	<0.1		■			■		3	

Table 2.2 Dam Characteristics. Primary purpose and date of construction for dams in the study site of the Upper Neosho and Lower Cottonwood Rivers.

River	Dam name	Height (m)	Built	Purpose
Upper Neosho	Riverwalk	1.2	1995	Recreation
	Correll	2.3	1920s	Water supply
	Ruggles	2.4	1920s	Water supply
	Emporia	3.0	1890s	Water supply
Lower Cottonwood	Cottonwood Falls	3.0	1860s	Mill
	Soden	3.0	1860s	Mill

Table 2.3 Guild Classifications. Each species was classified into one of seven guilds based on the proportion of capture in three habitat types: pool, riffle, run

Guild	Guild classification	Species in guild
Riffle specialist	Species are caught in riffle habitats greater than 75% of the time	Central Stoneroller, Fantail Darter, Suckermouth Minnow, Orangethroat Darter, Bluntface Shiner, Freckled Madtom, Neosho Madtom, Slender Madtom
Pool specialist	Species are caught in pool habitats greater than 75% of the time	Longear Sunfish, Orangespot Sunfish, Western Mosquitofish, Freshwater Drum, Redfin Shiner, Brook Silverside, Gizzard Shad, Spotted Bass, Bluegill Sunfish, Channel Darter, Longnose Gar, Shortnose Gar, White Crappie, Largemouth Bass, Smallmouth Bass
Riffle generalist	Species is caught in riffle habitat greater than 50% of the time	Bluntnose Minnow
Run generalist	Species is caught in run habitat greater than 50% of the time	Sand Shiner
Riffle-run generalist	Species is caught in riffle and run habitats greater than 33% of the time	Red Shiner
Pool-run generalist	Species is caught in pool and run habitats greater than 33% of the time	Carmine Shiner, Ghost Shiner, Mimic Shiner, Fathead Minnow, Slim Minnow, Logperch, Channel Catfish, River Carpsucker
Generalist	Species is not caught greater than 33% in any two habitats nor greater than 50% of the time in any habitat	Slenderhead Darter, Bullhead Minnow, Redhorse spp.

Table 2.4 Spatial Trajectory Transects Transects chosen based on geomorphological classification of channel widening and substrate (footprint), for each dammed site and its corresponding undammed site

Site Dam/Control	Channel widening transects (total per site)	Footprint transects (total per site)
Riverwalk (RW) /Neosho-1 (NE1)	100 m (1)	100 – 1000 m (10)
Ruggles (RU) /Neosho-2 (NE2)	100, 200 m (2)	100 – 1000 m (10)
Emporia (EM) /Neosho-3 (NE3)	100, 200 m (2)	100, 200 m (2)
Cottonwood Falls (CF) /Control (CC)	100, 200 m (2)	100 – 1500 m (11)
Soden (SO) /Neosho-4 (NE4)	100, 200 m (2)	100 – 1000 m (10)

Table 2.5 Indicator Species Analysis. Relative abundance and frequency of occurrence of each species based on Dufrene-Legendre indicator species analysis. Data includes the default channel widening transects downstream of dammed and undammed sites. Guilds are included for reference. Species are listed under the heading of which group (dammed or undammed) they were assigned to by the analyis, and p-value indicates if that assignment is significant.

			Dammed		Undammed	
Species	**IndVal (max)**	***P-value***	**RelAbu**	**FreOcc**	**RelAbu**	**FreOcc**
Dammed						
Riffle specialist						
Central Stoneroller	0.43	*0.08*	0.78	0.56	0.22	0.11
Bluntface Shiner	0.15	*0.72*	0.69	0.22	0.31	0.22
Fantail Darter	0.11	*1*	0.5	0.22	0.5	0.11
Suckermouth Minnow	0.35	*0.35*	0.78	0.44	0.22	0.22
Riffle generalist						
Bluntnose Minnow	0.56	*0.02*	1	0.56	--	--
Run generalist						
Sand Shiner	0.3	*0.7*	0.53	0.56	0.47	0.33
Riffle-run generalist						
Red Shiner	0.52	*0.83*	0.52	1	0.48	1
Generalist						
Redhorse	0.11	*1*	1	0.11	--	--
Slenderhead Darter	0.51	*0.49*	0.65	0.78	0.35	0.89
Pool-run generalist						
Channel Catfish	0.11	*1*	1	0.11	--	--
Carmine Shiner	0.19	*0.49*	0.83	0.22	0.17	0.11
Logperch	0.09	*1*	0.4	0.22	0.6	0.11
Fathead Minnow	0.33	*0.2*	1	0.33	--	--
Slim Minnow	0.06	*1*	0.5	0.11	0.5	0.11
Pool specialists						

Species	IndVal (max)	*P-value*	Dammed RelAbu	Dammed FreOcc	Undammed RelAbu	Undammed FreOcc
Gizzard Shad	0.11	*1*	1	0.11	--	--
Western Mosquitofish	0.22	*0.47*	1	0.22	--	--
Brook Silverside	0.1	*1*	0.89	0.11	0.11	0.11
Orangespotted Sunfish	0.22	*0.78*	0.59	0.22	0.41	0.56
Spotted Bass	0.09	*1*	0.8	0.11	0.2	0.11
Undammed						
Generalist						
Bullhead Minnow	0.63	*0.43*	0.19	0.78	0.81	0.78
Pool-run generalist						
Mimic Shiner	0.17	*0.88*	0.26	0.22	0.74	0.22
Pool specialists						
Longear Sunfish	0.31	*0.78*	0.31	0.44	0.69	0.44
Longnose Gar	0.11	*0.69*	--	--	1	0.11
Redfin Shiner	0.11	*1*	--	--	1	0.11

Table 2.6 Site Variability Evaluation. Site variability evaluation using linear and linear mixed effect models. The effect of site variability on species richness (Richness) was tested either by including or not including site as a random effect in dammed and undammed comparisons. The intercept (B0), standard error of the intercept (SE(B0)), and slope (B1) and standard error (SE(B1)) of the explanatory variable as well as degrees of freedom (dfe) test statistic (F-stat) p-value (P) and criteria information from AIC model selection are included. The third model tests site as a fixed effect

Model	B0	SE(B0)	B1	SE(B1)	dfe	*F-stat*	*P*	*ΔAIC*	AICc	weight
Richness ~Dam (fixed)	5.7	0.62	2	0.88	16	5.14	0.04	0	77.56	0.80
Richness~Dam (fixed) + site (random)	5.8	0.74	1.88	1.05	8	3.20	0.11	2.83	80.39	0.20
Richness~Site (fixed)	--	--	--	--	8	3.10	0.06	22.48	100.04	<0.01

Figures

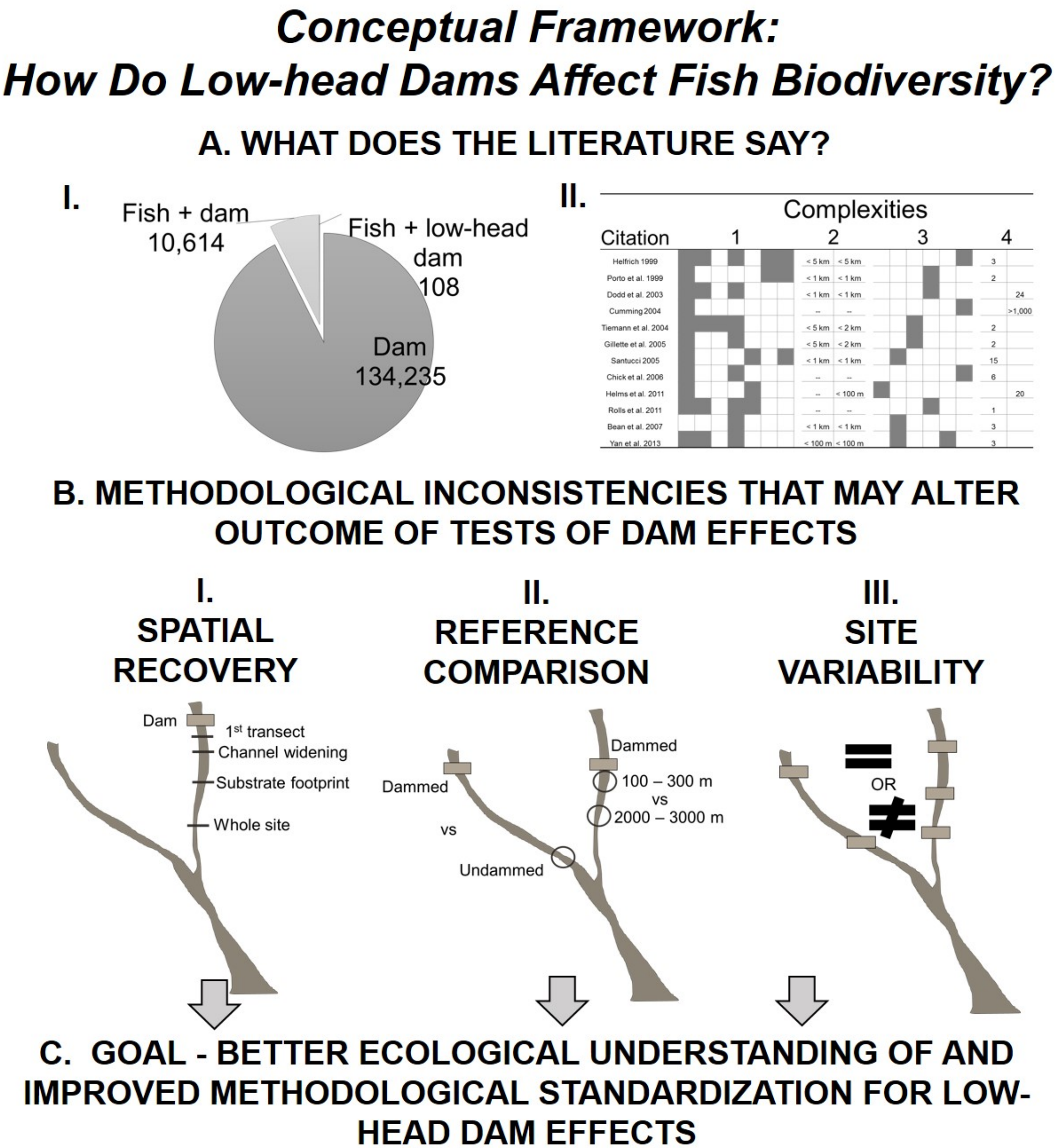

Figure 2.1 Conceptual Framework. Conceptual diagram of the methodological inconsistencies of low-head dam impacts on fish assemblages. A) Literature review found less than 1% of papers were about fish and low-head dams, and that the study designs of this literature was variable B) Four methodological inconsistencies in study design from literature review found that may alter the outcome of tests of dam effects (Table 2.1).

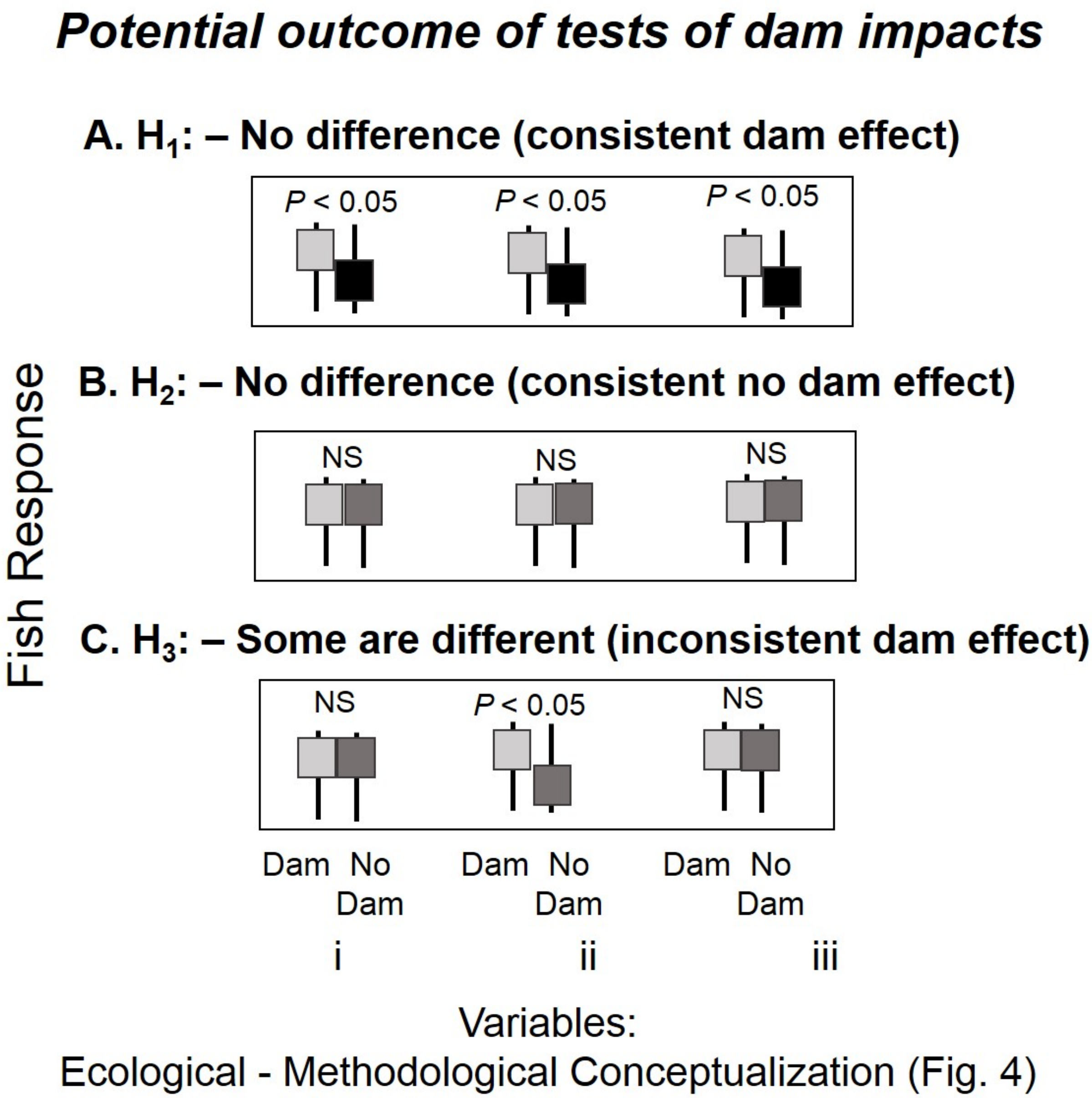

Figure 2.2 Conceptual Hypotheses. Potential outcome of tests of dam impacts for each of four complexities tested downstream of dammed and undammed sites. A) Representation of a consistent dam effect B) inconsistent dam effect C) no dam effect at dammed (D) and undammed (U) sites between three different variables (I, II, III) used to measure the same methodological decision

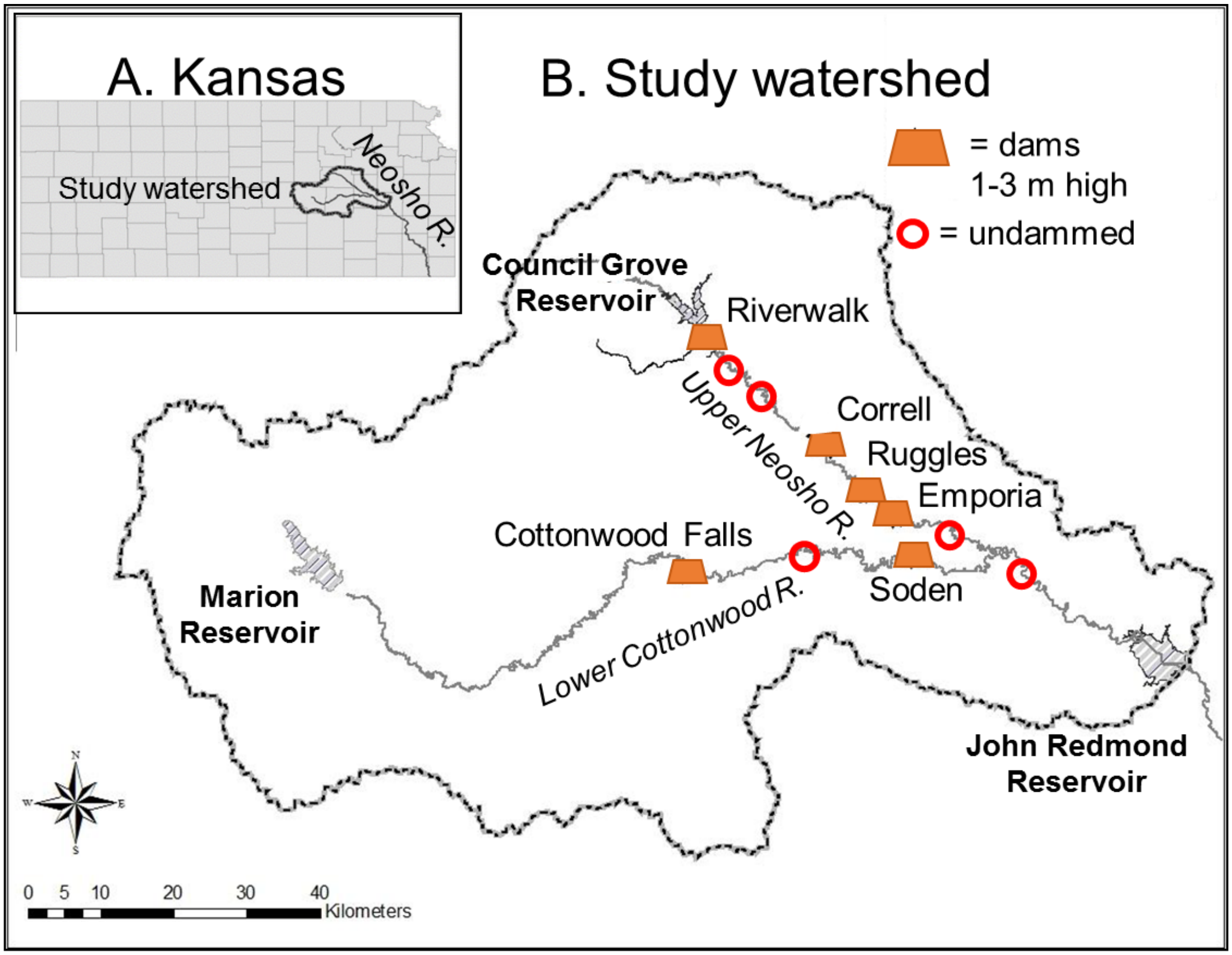

Figure 2.3 Study Site. Map of our study area in the Upper Neosho subbasin A) located in Kansas. Also shown are B) six dam sites (orange trapezoids) and five undammed reference sites (red open circles) along the Upper Neosho River and Lower Cottonwood Rivers. Major Army Corp of Engineers (USACE) reservoirs in the study subbasin are labeled for reference.

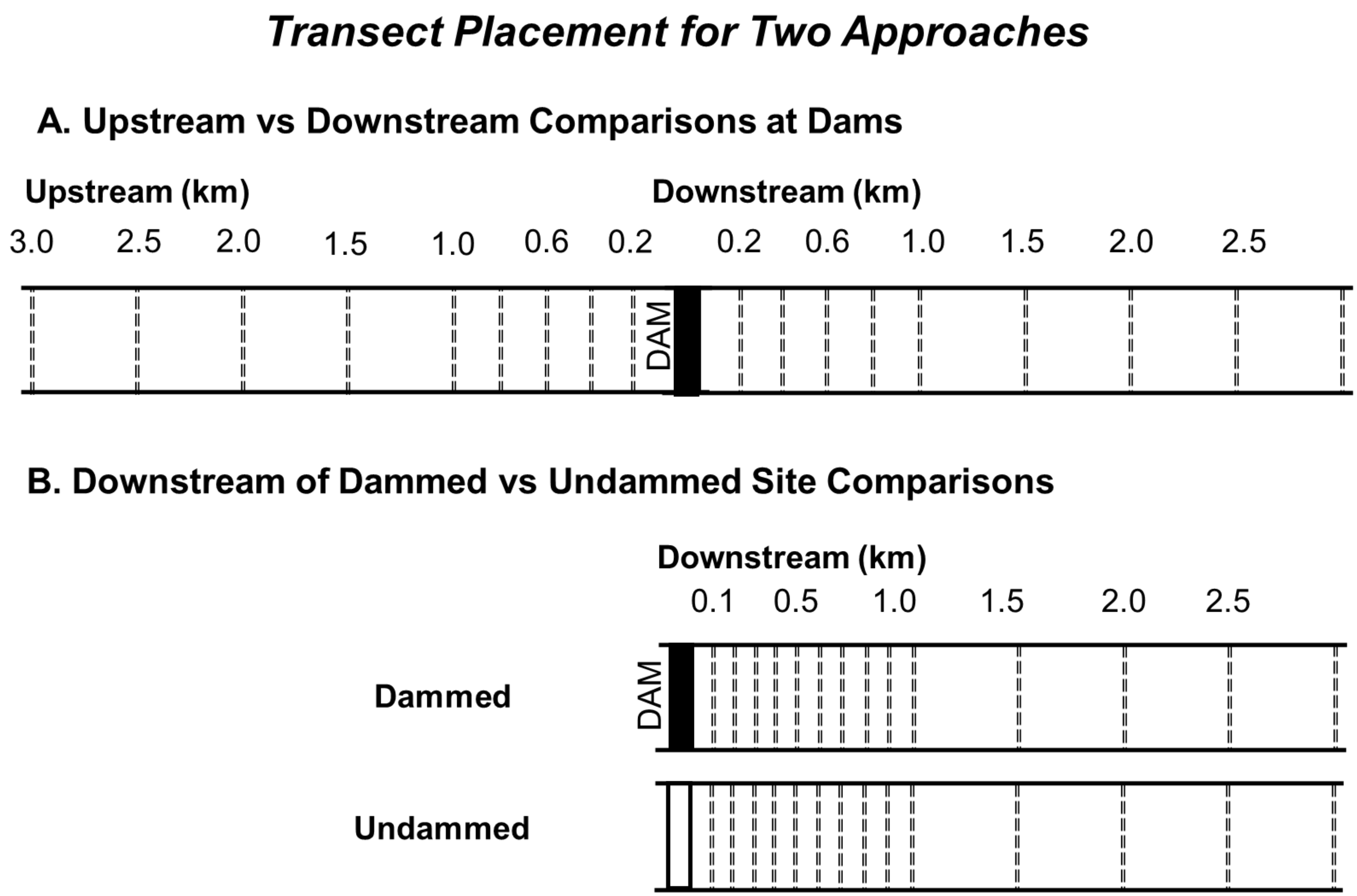

Figure 2.4 Transect Placement. Transects sampled per site for Upstream vs Downstream and Downstream vs Undammed transects with distances given in meters. A) Upstream (left of black rectangle) and downstream (right of black rectangle) sample transects (double dashed line). B) Downstream of dams (black rectangle) and undammed site (white outlined rectangle) sample transects (double dashed line).

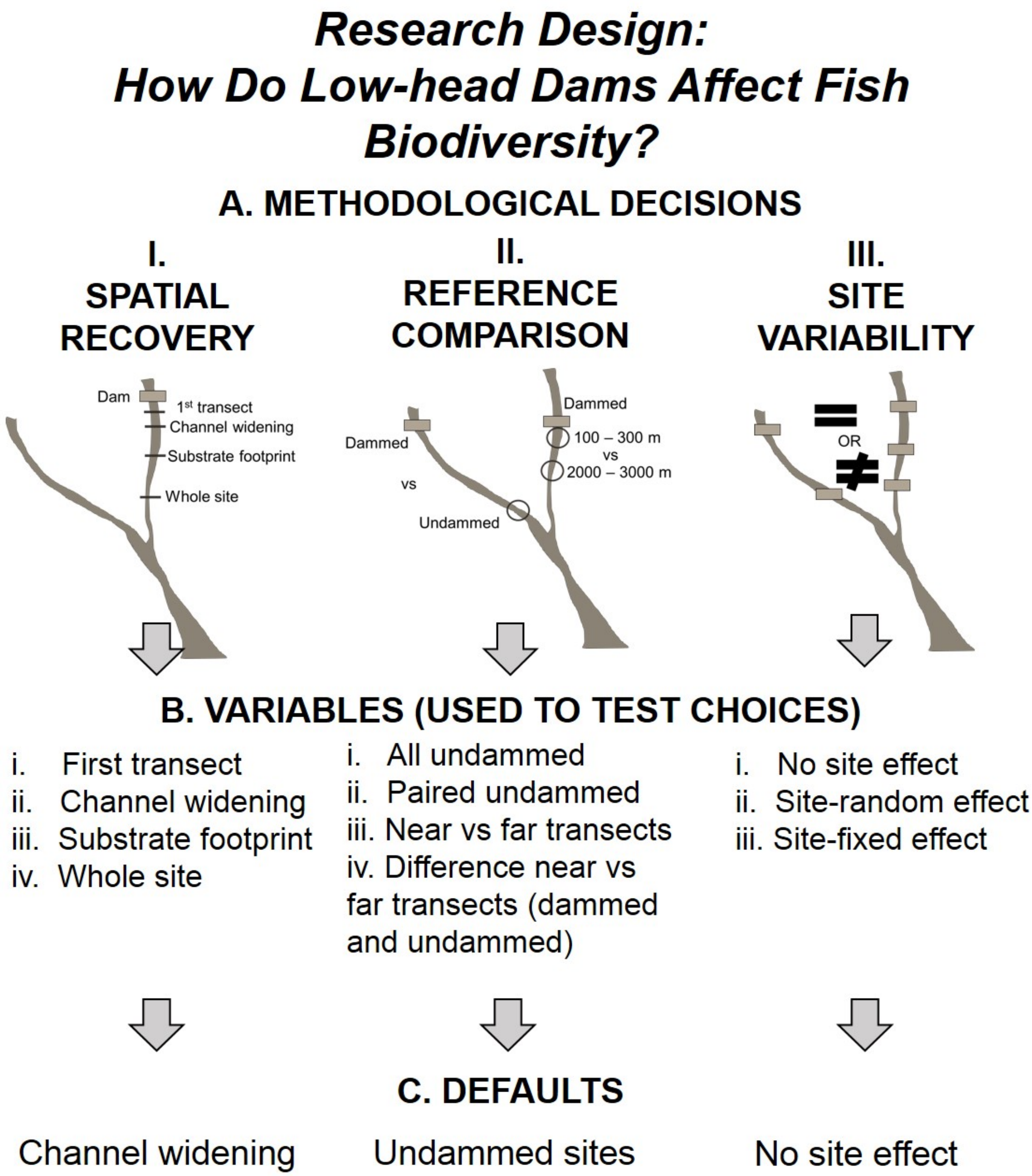

Figure 2.5 Research Design. Complexities that may affect low-head dam impacts on fish biodiversity. A) Complexities explored in this study, B) variables used to test complexities, and C) defaults used in other tests.

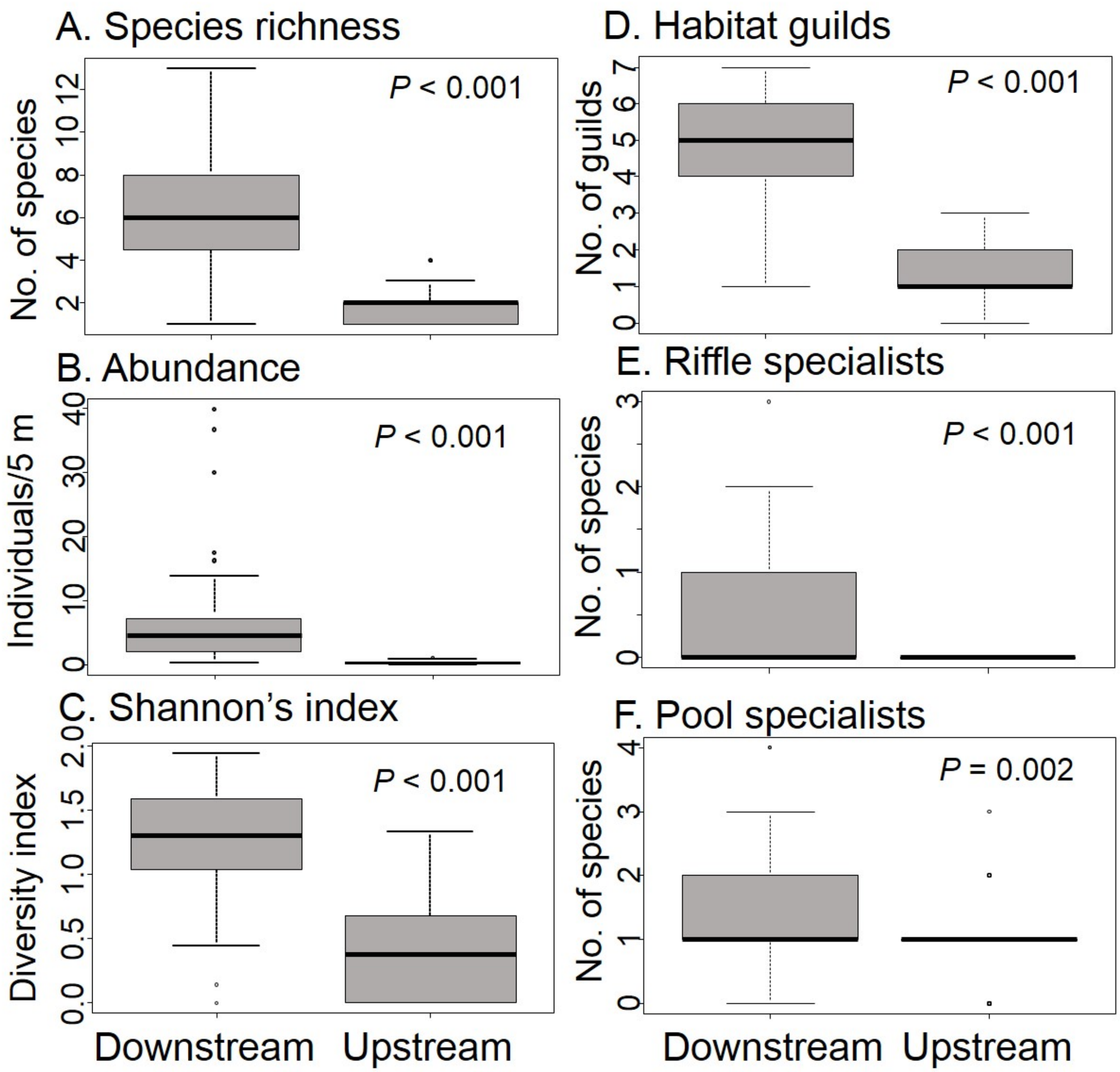

Figure 2.6 Upstream vs Downstream Fish Assemblages. Upstream and downstream measures of fish assemblages including A) species richness B) abundance per 5 m trawl haul C) Shannon's index of diversity, D) number of habitat guilds E) number of riffle specialists F) number of pool specialists. P-values are based on paired t-tests.

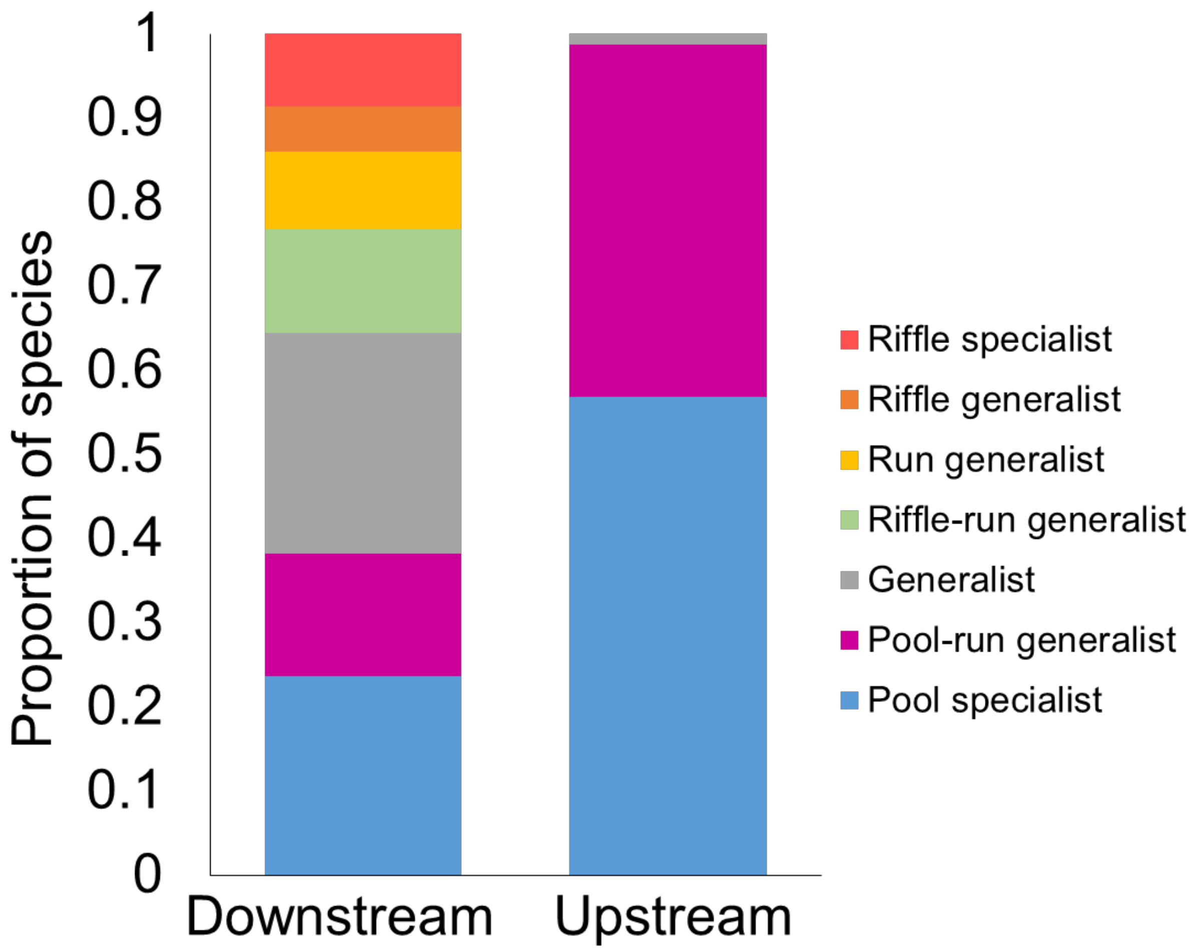

Figure 2.7 Upstream vs Downstream Habitat Guilds. Proportion of seven habitat guilds at upstream and downstream sites respectively.

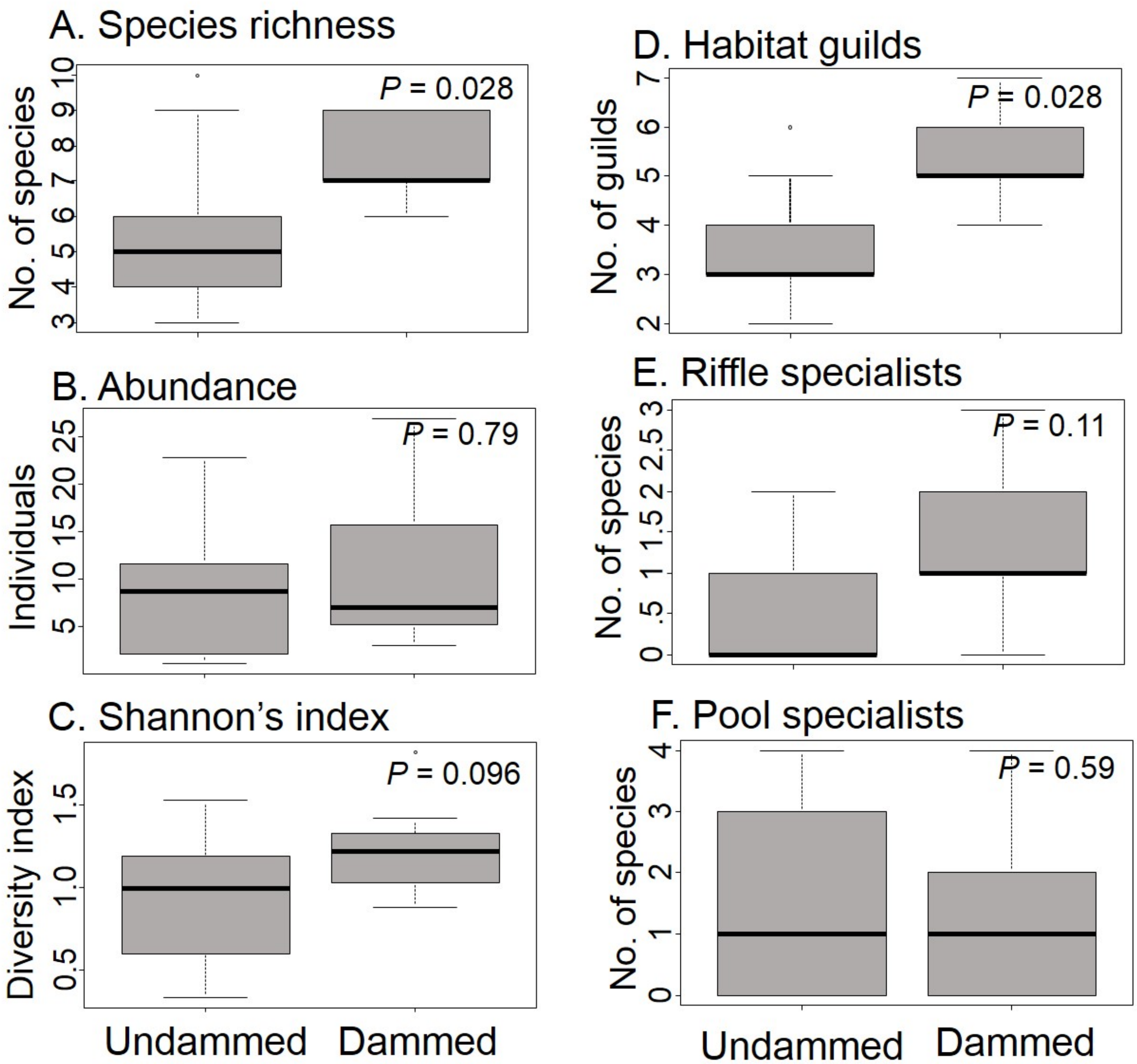

Figure 2.8 Downstream Dammed vs. Undammed Fish Assemblages. Dammed and undammed measures of fish biodiversity. Testing variables of A) species richness B) abundance per 5 m trawl haul C) Shannon's index of diversity, D) number of habitat guilds E) number of riffle specialists F) number of pool specialists. P-values are based on paired t-tests.

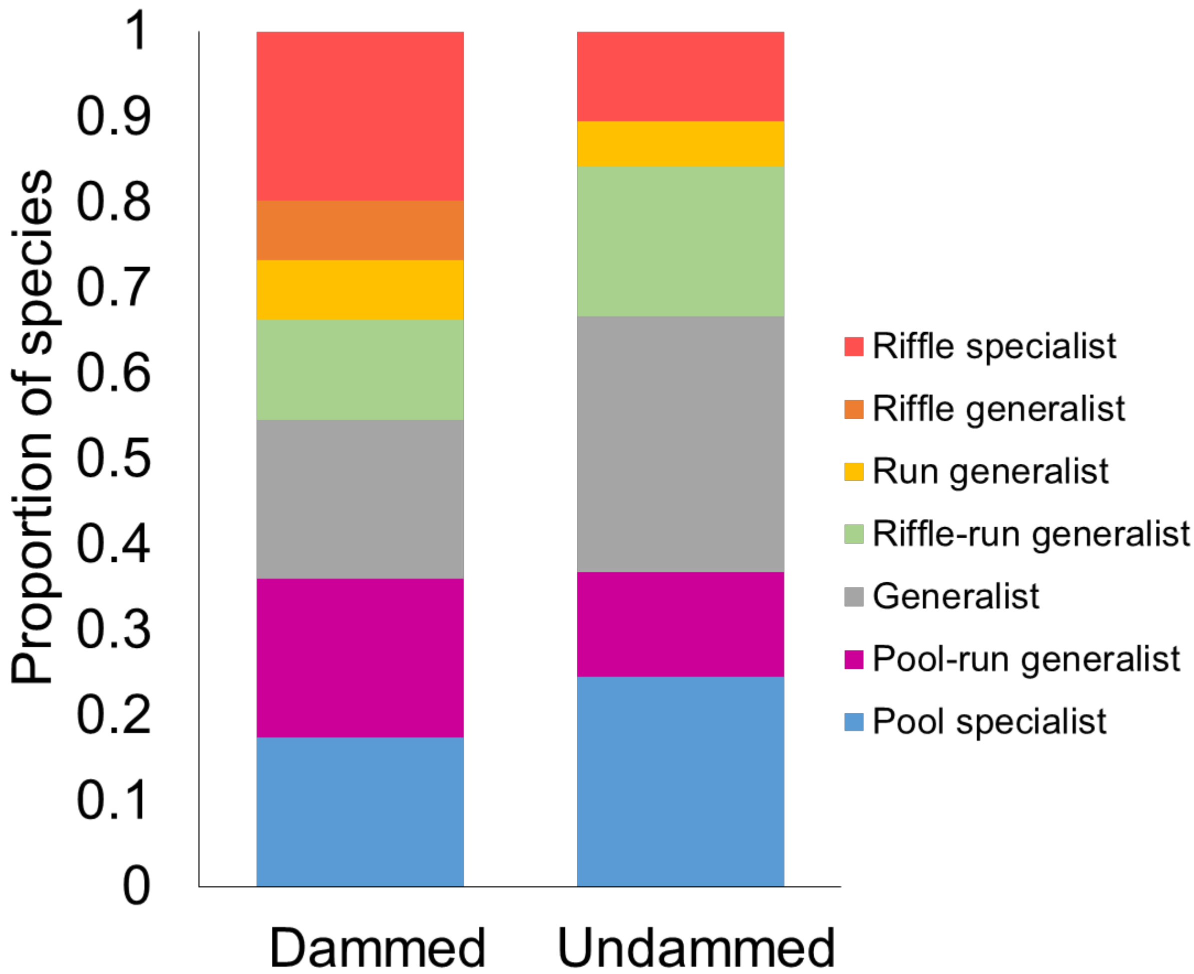

Figure 2.9 Downstream Dammed vs. Undammed Habitat Guilds. Proportion of seven habitat guilds at dammed and undammed sites respectively.

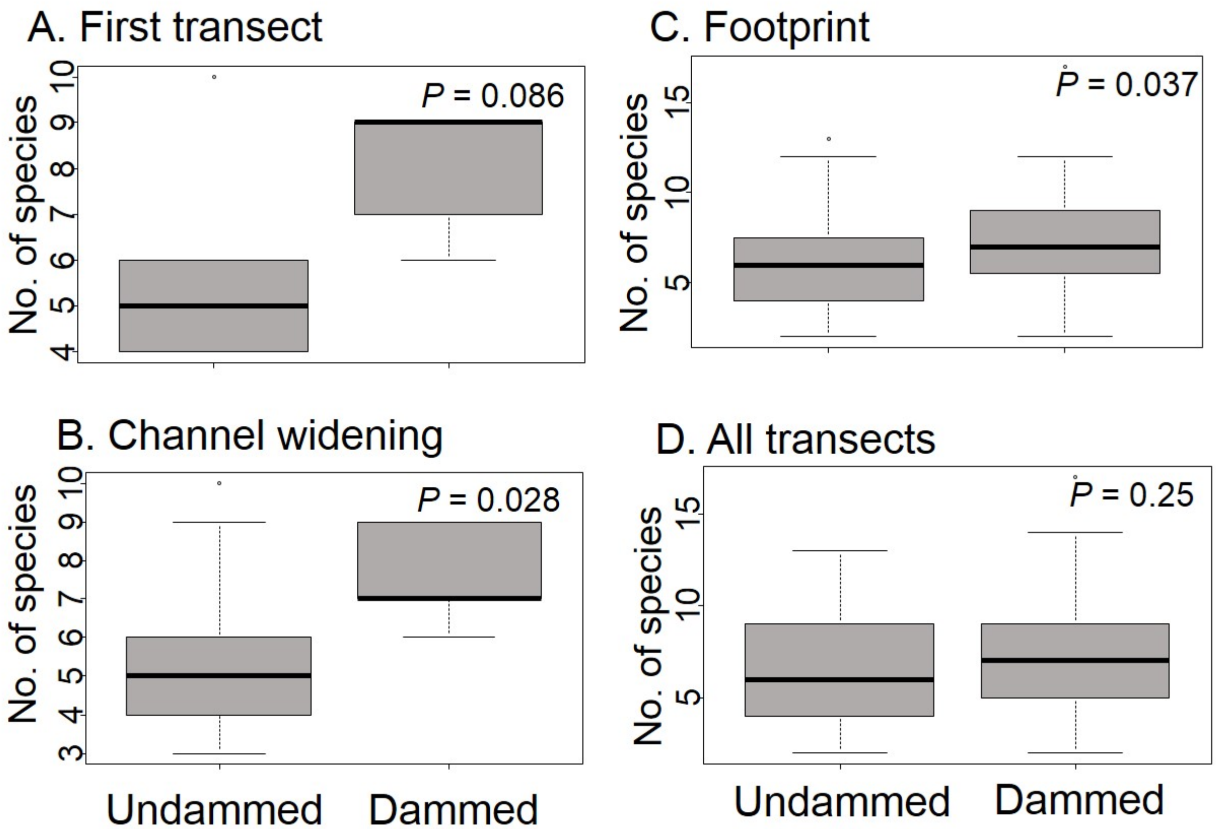

Figure 2.10 Spatial Trajectory. Spatial trajectory from potential ecological disturbance methodological decision based on proximity to dam and geomorphological criteria. Testing variables of A) the first transect below dams B) channel widening transects C) footprint transects D) all transects. See Table 4 and text for details.

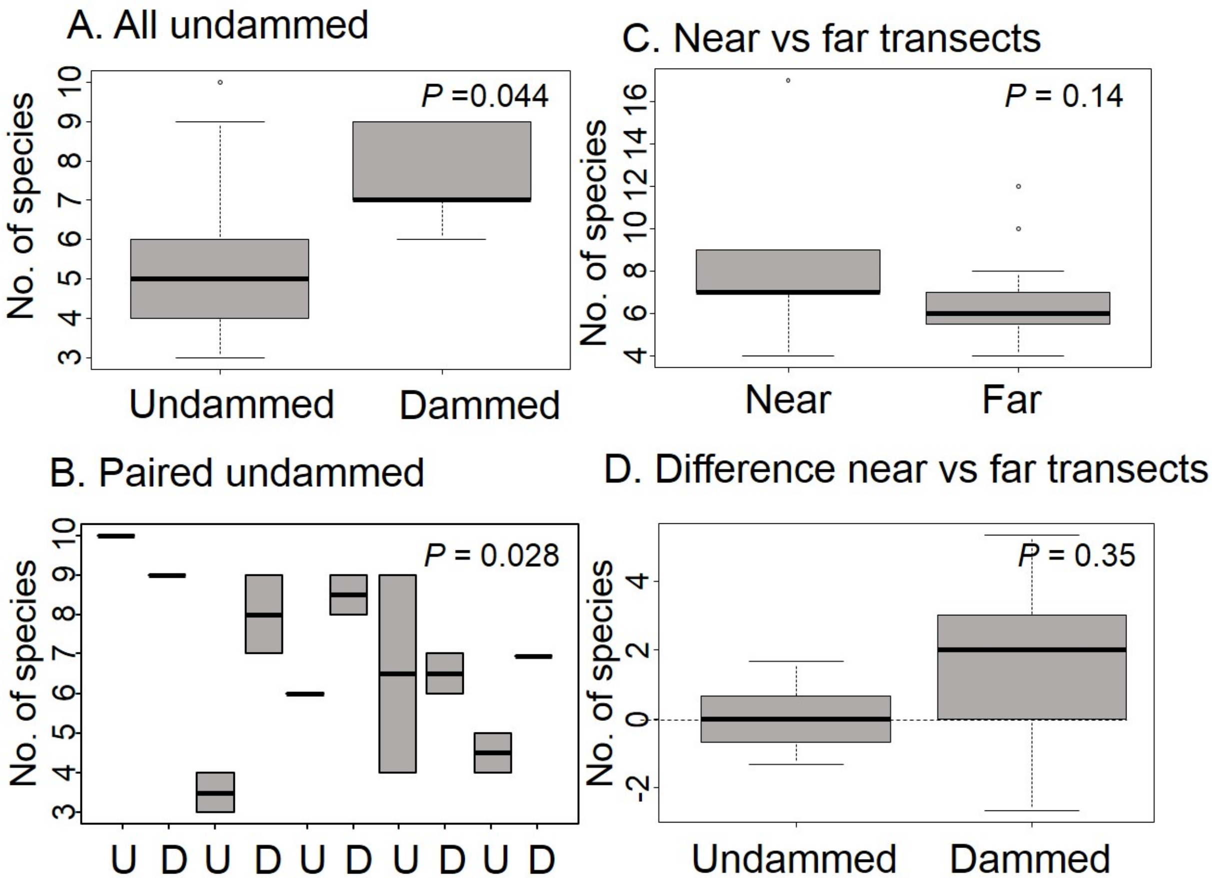

Figure 2.11 Reference Comparison. Reference comparison methodological decision. Testing variables of A) Difference between all dammed and undammed sites B) Difference between paired dammed and undammed sites C) Difference between the first (near-impact) and last (far-reference) three transects downstream of dammed sites D) Comparison of difference between the near and far transects at dammed and undammed sites

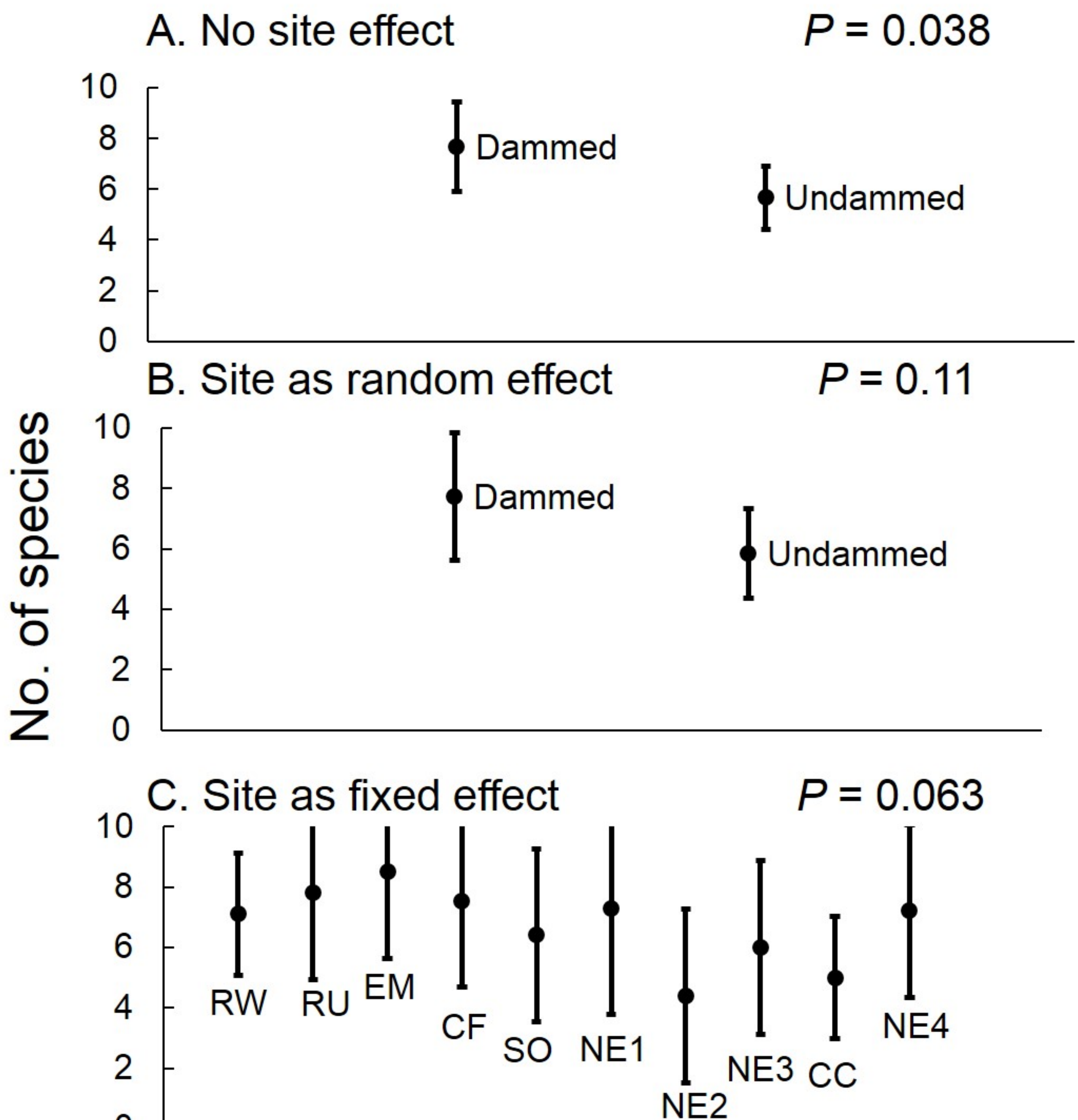

Figure 2.12 Site Variability. Testing variables of linear models and linear mixed effect models on dammed and undammed comparisons with A) no site effect B) site as a random effect C) testing site as a fixed effect, only.

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Appendix A - Chapter 1 Supplemental Information

Table A.1 Literature Review

Categorization	References
Sediment yield	(1) Barendregt RW, Ongley ED. Piping in the Milk River Canyon, southeastern Alberta - a contemporary dryland geomorphic process. IAHS Publication 1977;(122):233-243.
Not about dam	(2) Bhagat VS, Sonawane KR. Use of Landsat ETM plus data for delineation of water bodies in hilly zones. J Hydroinf 2011;13(4):661-671.
Sediment yield	(3) Boardman J, Foster IDL. The potential significance of the breaching of small farm dams in the Sneeuberg region, South Africa. Journal of Soils and Sediments DEC 2011;11(8):1456-1465.
Dam impact	(4) Csiki SJC, Rhoads BL. Influence of four run-of-river dams on channel morphology and sediment characteristics in Illinois, USA. Geomorphology FEB 1 2014;206:215-229.
Dam impact	(5) Csiki S, Rhoads BL. Hydraulic and geomorphological effects of run-of-river dams. Prog Phys Geogr DEC 2010;34(6):755-780.
Historical	(6) Cubizolle H, Tourman A, Argant J, Porteret J, Oberlin C, Serieyssol K. Origins of European biodiversity: palaeo-geographic signification of peat inception during the Holocene in the granitic eastern Massif Central (France). Landscape Ecol APR 2003;18(3):227-238.
Dam impact	(7) Doyle MW, Stanley EH, Orr CH, Selle AR, Sethi SA, Harbor JM. Stream ecosystem response to small dam removal: Lessons from the Heartland. Geomorphology OCT 1 2005;71(1-2):227-244.
Nutrient dynamics	(8) Doyle MW, Stanley EH. Exploring potential spatial-temporal links between fluvial geomorphology and nutrient-periphyton dynamics in streams using simulation models. Ann Assoc Am Geogr DEC 2006;96(4):687-698.
Dam impact	(9) Evans JE, Huxley JM, Vincent RK. Upstream channel changes following dam construction and removal using a GIS/remote sensing approach. J Am Water Resour Assoc JUN 2007;43(3):683-697.

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Sediment yield	(10) Feiznia S, Ahmadi H, Jalili SY, Fatahi MA, Abbasi M. Investigation on volume and statistical parameters of sedimentology in upstream channels of Tehran - Qazvin highway located in Khor-Sefidarak Basin. Iranian Journal of Range and Desert Research 2012;19(2):244-263.
Not about dam	(11) Feld CK, Birk S, Bradley DC, Hering D, Kail J, Marzin A, et al. From Natural to Degraded Rivers and Back Again: A Test of Restoration Ecology Theory and Practice. Advances in Ecological Research, Vol 44 2011;44:119-209.
Dam impact	(12) Finn D, Walter C, Tullos D, Pandit M. Geomorphic and Ecological Disturbance and Recovery from Two Small Dams and Their Removal. PLoS ONE 2014;9(9):e108091.
Dam impact	(13) Gangloff MM, Hartfield EE, Werneke DC, Feminella JW. Associations between small dams and mollusk assemblages in Alabama streams. J N Am Benthol Soc DEC 2011;30(4):1107-1116.
Dam construction	(14) Henschel S. The involvement of the private sector to ensure sustainability of systems. Water Practice & Technology 2010;5(4):111-111.
Historical	(15) Herget J. Holocene development of the River Lippe Valley, Germany: A case study of anthropogenic influence. Earth Surf Process Landforms MAR 2000;25(3):293-305.
Aquifer formation	(16) Hiller T, Romanov D, Kaufmann G, Epting J, Huggenberger P. Karstification beneath the Birs weir in Basel/Switzerland: A 3D modeling approach. Journal of Hydrology JUL 2 2012;448:181-194.
Sediment yield	(17) James LA. Sediment from hydraulic mining detained by Englebright and small dams in the Yuba basin. Geomorphology OCT 1 2005;71(1-2):202-226.
Earthquake evaluation	(18) Kamanbedast MI, Azmoudeh AAE, Hossein M. Dynamic analysis of concrete dam due to seismic forces. World Applied Sciences Journal 2012;17(8):1046-1053.
Dam impact	(19) Kibler K, Tullos D, Kondolf M. Evolving Expectations of Dam Removal Outcomes: Downstream Geomorphic Effects Following Removal of a Small, Gravel-Filled Dam. J Am Water Resour Assoc APR 2011;47(2):408-423.

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Sediment yield	(20) Mahmoudzadeh A, Erskine WD, Myers C. Sediment yields and soil loss rates from native forest, pasture and cultivated land in the Bathurst area, New South Wales. Australian Forestry 2002;65(2):73-80.
Not about dams	(21) Marsden JE, Evans JE, Gottgens JF. Dam removals and river channel changes in northern Ohio: implications for Lake Erie sediment budgets and water quality. J Great Lakes Res 2007;33(SI2):87-193.
Sediment yield	(22) Mousavi SF, Samadi-Boroujeni H. Evaluation of sedimentation in small dam reservoirs in Chaharmahal-Bakhtiary region. Iranian Journal of Science and Technology 1998;22(4):421-429.
Sediment yield	(23) Ndomba PM. Validation of PSIAC model for sediment yields estimation in ungauged catchments of Tanzania. International Journal of Geosciences 2013;4(7):1101-1115.
Dam impact	(24) Orr CH, Rogers KL, Stanley EH. Channel morphology and P uptake following removal of a small dam. J N Am Benthol Soc SEP 2006;25(3):556-568.
Dam impact	(25) Reid HE, Brierley GJ, Mcfarlane K, Coleman SE, Trowsdale S. The role of landscape setting in minimizing hydrogeomorphic impacts of flow regulation. International Journal of Sediment Research MAR 2013;28(2):149-161.
Dam impact	(26) Roberts SJ, Gottgens JF, Spongberg AL, Evans JE, Levine NS. Assessing potential removal of low-head dams in urban settings: an example from the Ottawa River, NW Ohio. Environ Manage 2007;39(1):113-124.
Dam construction	(27) Salih SA, Kadim LS, Qadir M. Hydrochemistry as indicator to select the suitable locations for water storage in Tharthar valley, Al-Jazira Area, Iraq. Journal of Water Resource and Protection 2012;4(8):648-656.
Dam impact	(28) Sawaske SR, Freyberg DL. A comparison of past small dam removals in highly sediment-impacted systems in the U.S. Geomorphology MAY 15 2012;151:50-58.
Dam impact	(29) Skalak K, Pizzuto J, Hart DD. Influence of Small Dams on Downstream Channel Characteristics in Pennsylvania and Maryland: Implications for the Long-Term Geomorphic Effects of Dam Removal. J Am Water Resour Assoc FEB 2009;45(1):97-109.

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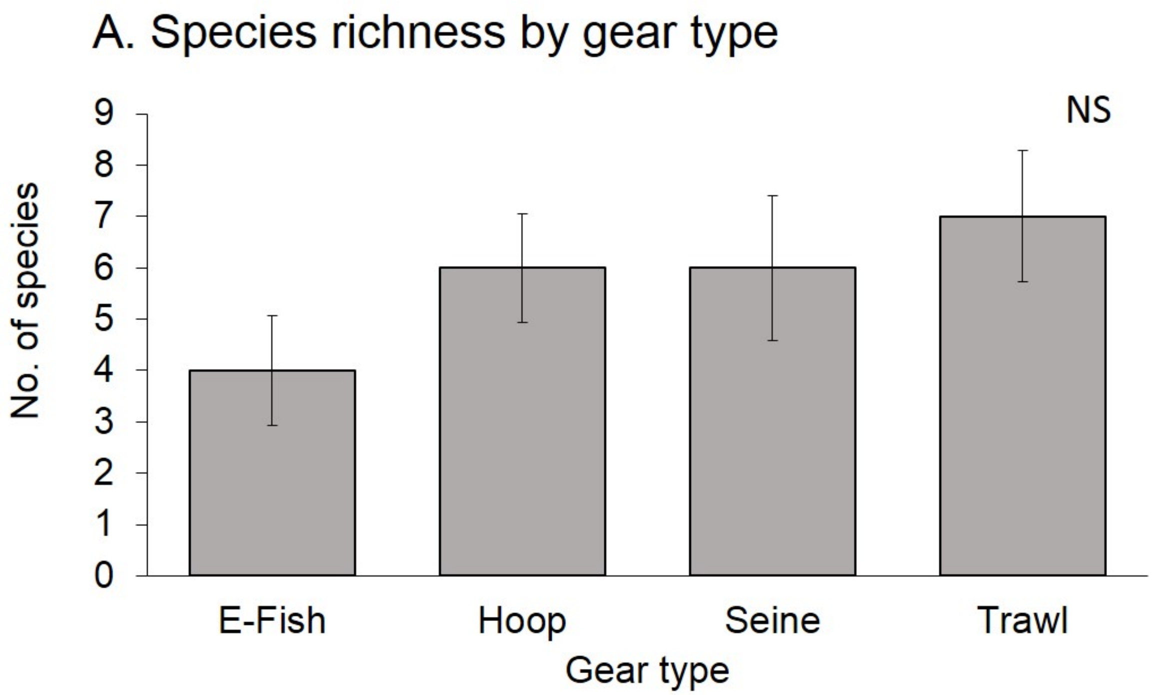
Dam impact	(30) Stanley EH, Luebke MA, Doyle MW, Marshall DW. Short-term changes in channel form and macro invertebrate communities following low-head dam removal. J N Am Benthol Soc MAR 2002;21(1):172-187.
Dam impact	(31) Tullos DD, Finn DS, Walter C. Geomorphic and Ecological Disturbance and Recovery from Two Small Dams and Their Removal. Plos One SEP 18 2014;9(9):e108091.
Not about dam	(32) Woo H, Han MS, Kim CW. Situation and Prospect of Ecological Engineering for Stream Restoration in Korea. KSCE Journal of Civil Engineering 2005;9(1):19-27.

Table A.2 Competing Models of Univariate Regressions of Downstream, Upstream, and Total Footprint. Parameters for the model include intercept (B0), slope of the explanatory variable (B1) and their corresponding standard errors (SE).The best model from AIC selection is highlighted in grey,

Footprint	Variable	B0	SE(B0)	B1	SE(B1)	*F*	*P*	*R2*	*R2-adj*	*AIC*
Downstream	Dam height	1.477	0.872	-0.127	0.340	0.14	0.73	0.03	-0.21	108.002
	Dist. to nearest upstream dam	0.840	0.297	0.00001	0.00001	1.92	0.24	0.32	0.16	105.856
	No. upstream dams within 50 km	1.567	0.236	-0.405	0.180.003	4.90	0.09	0.55	0.44	103.406
	Height of nearest upstream dam	1.117	0.266	0.007	0.022	0.09	0.77	0.02	-0.22	108.067
Upstream	Dam height	-1.643	6.288	3.373	2.451	1.89	0.24	0.32	0.15	131.716
	Dist. to nearest upstream dam	2.562	1.618	0.00012	0.00004	10.74	0.03	0.73	0.66	126.217
	No. of upstream dams within 50 km	9.958	2.201	-3.225	1.705	3.58	0.13	0.47	0.34	130.208
	Height of nearest upstream dam	8.053	2.004	-0.192	0.165	1.36	0.31	0.25	0.07	132.283
Total	Dam height	-0.166	7.103	3.247	2.769	1.38	0.31	0.26	0.07	133.178

Footprint	Variable	B0	SE(B0)	B1	SE(B1)	*F*	*P*	*R2*	*R2-adj*	*AIC*
	Dist. to nearest upstream dam	3.402	1.750	0.00013	0.00004	10.65	0.03	0.27	0.66	127.163
	No. of upstream dams within 50 km	1.153	2.278	-3.630	1.765	4.23	0.11	0.51	0.39	130.622
	Height of nearest upstream dam	9.169	2234	-0.186	0.184	1.02	0.37	0.20	0.00	133.587

Appendix B - Chapter 2 Supplemental Information



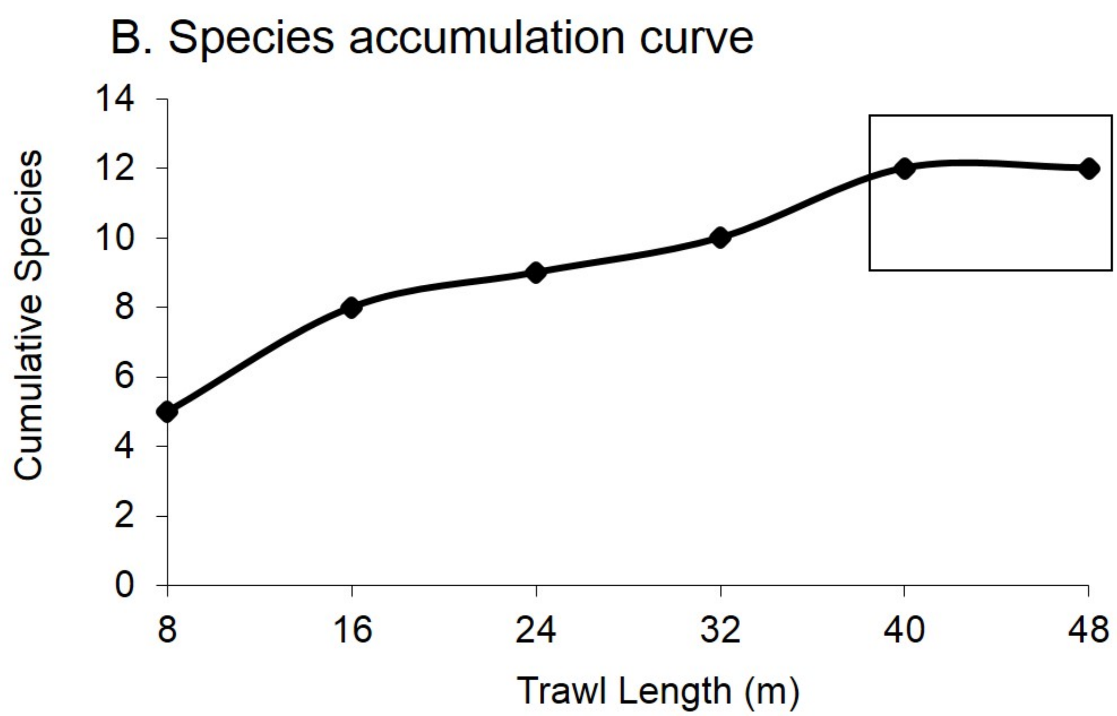


Figure B.1 Gear Experiment Data

Table B.1 Abundances of Species Upstream and Downstream of Dams

Family	Scientific Name	Common Name	Upstream	Downstream
Sciaenidae	*Aplodinotus grunniens*	Freshwater Drum	12	2
Cyprinidae	*Campostoma anomalum*	Central Stoneroller		15
Cyprinidae	*Cyprinella camura*	Bluntface Shiner		4
Cyprinidae	*Cyprinella lutrensis*	Red Shiner		1275
Clupeidae	*Dorsoma cepedianum*	Gizzard Shad	2	2
Percidae	*Etheostoma flabellare*	Fantail Darter		3
Poecilidae	*Gambusia affinis*	Western Mosquitofish		15
Ictaluridae	*Ictalurus punctatus*	Channel Catfish	14	4
Atherinopsidae	*Labidesthes sicculus*	Brook Silverside		53
Centrarchidae	*Lepomis humilis*	Orangespotted Sunfish	114	271
Centrarchidae	*Lepomis macrochirus*	Bluegill		2
Centrarchidae	*Lepomis megalotis*	Longear Sunfish	1	39
Lepisosteidae	*Lepisosteus osseus*	Longnose Gar		2
Cyprinidae	*Lythrurus umbratilis*	Redfin Shiner		23
Centrarchidae	*Micropterus punctulatus*	Spotted Bass		3
Centrarchidae	*Micropterus salmoides*	Largemouth Bass		1
Cyprinidae	*Moxostoma species*	Redhorse		6
Cyprinidae	*Notropis buchanani*	Ghost Shiner	1	36
Cyprinidae	*Notropis rubellus*	Carmine Shiner		9
Cyprinidae	*Notropis stramineus*	Sand Shiner		320
Cyprinidae	*Notropis volucellus*	Mimic Shiner	117	91
Ictaluridae	*Noturus placidus*	Neosho Madtom		1
Percidae	*Percina caprodes*	Logperch		9
Percidae	*Percina copelandi*	Channel Darter		4
Percidae	*Percina phoxocephala*	Slenderhead Darter		194
Cyprinidae	*Phenacobius mirabilis*	Suckermouth Minnow		54
Cyprinidae	*Pimephales notatus*	Bluntnose Minnow		141
Cyprinidae	*Pimephales promelas*	Fathead Minnow		1

Family	Scientific Name	Common Name	Upstream	Downstream
Cyprinidae	*Pimephales tenellus*	Slim Minnow		3
Cyprinidae	*Pimephales vigilax*	Bullhead Minnow	1	527
Centrarchidae	*Pomoxis annularis*	White Crappie	3	1
		Total abundance	265	3111
		Total species	9	31

Table B.2 Abundances of species at dammed and undammed sites, including all transects

Family	**Scientific Name**	**Common Name**	Dammed	Undammed
Sciaenidae	*Aplodinotus grunniens*	Freshwater Drum	1	1
Cyprinidae	*Campostoma anomalum*	Central Stoneroller	25	64
Cyprinidae	*Carpiodes carpio*	River Carpsucker	1	
Cyprinidae	*Cyprinella camura*	Bluntface Shiner	25	12
Cyprinidae	*Cyprinella lutrensis*	Red Shiner	1873	2806
Clupeidae	*Dorsoma cepedianum*	Gizzard Shad	12	10
Percidae	*Etheostoma flabellare*	Fantail Darter	20	58
Percidae	*Etheostoma spectabile*	Orangethroat Darter	14	
Poecilidae	*Gambusia affinis*	Western Mosquitofish	113	87
Ictaluridae	*Ictalurus punctatus*	Channel Catfish	4	14
Atherinopsidae	*Labidesthes sicculus*	Brook Silverside	18	24
Centrarchidae	*Lepomis humilis*	Orangespotted Sunfish	532	300
Centrarchidae	*Lepomis macrochirus*	Bluegill	9	2
Centrarchidae	*Lepomis megalotis*	Longear Sunfish	87	95
Lepisosteidae	*Lepisosteus osseus*	Longnose Gar	2	7
Lepisosteidae	*Lepisosteus platostomus*	Shortnose Gar	1	
Cyprinidae	*Lythrurus umbratilis*	Redfin Shiner	26	9
Centrarchidae	*Micropterus dolomieu*	Smallmouth Bass	1	
Centrarchidae	*Micropterus punctulatus*	Spotted Bass	9	3
Centrarchidae	*Micropterus salmoides*	Largemouth Bass	1	
Cyprinidae	*Moxostoma species*	Redhorse	4	4
Cyprinidae	*Notropis buchanani*	Ghost Shiner	29	18
Cyprinidae	*Notropis rubellus*	Carmine Shiner	13	3
Cyprinidae	*Notropis stramineus*	Sand Shiner	356	587
Cyprinidae	*Notropis volucellus*	Mimic Shiner	160	292
Ictaluridae	*Noturus exilis*	Slender Madtom		1
Ictaluridae	*Noturus nocturnus*	Freckled Madtom	1	4
Ictaluridae	*Noturus placidus*	Neosho Madtom	1	1

Family	**Scientific Name**	**Common Name**	Dammed	Undammed
Percidae	*Percina caprodes*	Logperch	17	10
Percidae	*Percina copelandi*	Channel Darter	7	3
Percidae	*Percina phoxocephala*	Slenderhead Darter	235	299
Cyprinidae	*Phenacobius mirabilis*	Suckermouth Minnow	47	76
Cyprinidae	*Pimephales notatus*	Bluntnose Minnow	217	121
Cyprinidae	*Pimephales promelas*	Fathead Minnow	7	8
Cyprinidae	*Pimephales tenellus*	Slim Minnow	16	10
Cyprinidae	*Pimephales vigilax*	Bullhead Minnow	677	785
Centrarchidae	*Pomoxis annularis*	White Crappie	2	2
		Total abundance	4563	5716
		Total species	36	32