EFFECTS OF DAMS ON STREAMS OF THE CONTERMINOUS UNITED STATES: CHARACTERIZING PATTERNS IN HABITAT FRAGMENTATION NATIONALLY AND FLUVIAL FISH RESPONSE IN THE MIDWEST

By

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ABSTRACT

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Dams can exert great influence on fluvial habitats through a variety of mechanisms, however spatial measures representing dam locations throughout river networks, along with their attributes (e.g. reservoir storage), are not available in a consistent, comparable manner for the conterminous U.S. In this study, spatial metrics are developed that account for fragmentation and alteration of river networks by large dams throughout the conterminous U.S., allowing for the examination of river network fragmentation patterns by stream size and ecoregion. Results show that streams in the conterminous U.S. have been heavily fragmented by dams, with the greatest dam influence tending to occur in large and great rivers due to cumulative dam effects along river networks. Using a subset of fragmentation metrics generated in this study, fish species considered to be most sensitive to dam influences were identified for streams in Michigan, Wisconsin, and Minnesota. Of the sensitive species identified, those that were positively associated with greater dam effects were predominantly fishes associated with warm water temperatures, large river habitats, and/or lentic habitats, while species negatively associated with greater dam effects were cold and coolwater lotic species, suggesting a combination of downstream thermal effects and upstream influences from impoundments generated by dams. With dams representing an aging infrastructure leading to likely increases in habitat restoration and dam management opportunities, it will be essential to further reveal the spatial influence of dams along the river network.

This work is dedicated to my wife Rebecca and sons Gabriel and Maxwell, and to my parents Marion Bradford and Raymond Cooper.

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CHAPTER 1

FRAGMENTATION BY DAMS: SPATIAL MEASURES OF DAM EFFECTS ON STREAMS OF THE CONTERMINOUS U.S.

ABSTRACT

Dams can have wide-ranging effects on fluvial habitats including fragmentation of river networks, flow modification, and conversion of streams to lentic-like impoundments. Further, efforts to represent the various effects of dams in river networks over very large geographic extents, including the conterminous U.S., are lacking, highlighting the need for diverse spatial measures to account for dam influences throughout large landscapes. In this study, multiple types of metrics were assembled to characterize dams throughout nine large ecoregions of the conterminous U.S using ~50,000 georeferenced dams from the 2012 National Anthropogenic Barrier Dataset and 2.3 million stream reaches from the National Hydrography Dataset Plus Version 1. Metrics occur in three groups: 1) individual dam characteristics (e.g. age, height), 2) stream segment-level descriptors of fragmentation (e.g. distances-to-dams, cumulative reservoir storage), and 3) patch-level descriptors of fragmentation, summarized by adjacent sets of stream segments and catchments that account for dam locations. Comparison of dam characteristics and spatial measures shows great variability in dam characteristics and fragmentation patterns by stream size and ecoregion. Examination of segment-level spatial measures across stream size classes suggests that most prominent dam influences occur in large and great rivers due to cumulative dam effects along the river network. Overall, streams in the conterminous U.S. have been heavily fragmented by dams, with the number of patches increasing between 700-1200% depending on stream size when compared to undammed conditions. Understanding, and accounting for, the variability in the individual, cumulative, and patch-level dam influences will be important in national studies and assessments of fishes. Dams constitute an aging infrastructure, further underscoring the importance of integrating multiple spatial measures in assessing habitat restoration opportunities associated with dams.

INTRODUCTION

Dams constitute a complex and highly variable form of disturbance to fluvial habitats, including altering hydrology, stream temperature, channel morphology, water chemistry, and multiple aspects of hydrologic connectivity. In particular, dams have an enormous capacity to affect connectivity throughout stream networks and with adjacent habitats including lateral, vertical, temporal, and longitudinal components of connectivity (Ward and Stanford 1983, Ward 1989), with longitudinal fragmentation of river networks being one of the most commonly cited impacts resulting from dams. This type of fragmentation has significant implications for stream fishes that use disparate habitats for reproduction, growth, and survival (Schlosser and Angermeier 1995, Fausch 2002), including impeding fish movement and migration and changing species assemblage structure, genetic variation, and population abundance (e.g. Morita and Yamamoto 2002, Guenther and Spacie 2006, Heggenes and Roed 2006, Alo and Turner 2005). Ultimately, indirect or direct changes to the habitat factors which fish depend on (e.g., Maddock 1999) can lead to population declines, potentially leading to localized extirpation or even extinction of species (Dunham et al. 1997, Fagan 2002, Morita and Yamamoto 2002, Perkin and Gido 2011).

Characterizing dam effects from a landscape scale

Although dams can negatively influence the well-being of fishes, very few studies of fishes have incorporated spatial measures that characterize dam effects across large geographic regions (e.g., tens of thousands of square kilometers). In addition, most studies have chronicled the effect of dams on fishes only at relatively localized scales (e.g. above or below a dam, or before and after a single dam removal), with few having investigated the cumulative effects of multiple dams within the river network or having addressed fragmentation across large regions

(Wang et al. 2011a). The paucity of studies involving spatial measures of dams along river networks is due in part to a lack of available data on spatially consistent dam locations across large regions and to the dendritic nature and resulting spatial complexity of river systems that make them inherently difficult to study from a connectivity standpoint at large spatial scales (Fullerton et al. 2010, Steel et al. 2010). As a result, most spatial measures of dams over large geographic regions have been coarse in nature (e.g., density of dams within an entire river basin; Graf 1999, Esselman et al. 2011), providing limited utility for understanding their effects on stream fishes and for informing management.

Recently, a few studies have begun to incorporate spatial and temporal measures of dams into analyses characterizing dam influences on fishes, including metrics generated through use of geographic information systems (GIS). In general, these studies have focused on the fragmentation of either river basins (catchment-based approach) or the stream network itself. For example, Fukushima et al. (2007) identified catchment sub-basins isolated by dams for a regional analysis of the presence/absence of fishes on the island of Hokkaido, Japan, finding that fragmentation by downstream dams, and subsequent duration of isolation, had an influence on 11 of 41 species studied. Similarly, Hall et al. (2011) used dam construction dates obtained from historical records to create a fragmentation timeline for watersheds in Maine, using this information to describe current and historic fragmentation patterns of lake and stream habitat accessible for two species of anadromous river herring. Lastly, Wang et al. (2011a) developed multiple spatially-explicit measures of fragmentation by dams along stream networks for the states of Michigan and Wisconsin, including distances from a given stream reach to the nearest upstream and downstream dam along the mainstem of the river network, total number and density of dams along all flow paths upstream, and total number and density of dams along the downstream mainstem. These measures were used to partition the relative influence of dams from other environmental covariates (non-dam measures that included both natural and anthropogenic variables) using selected biotic integrity metrics and groups of fish summarized by habitat and social preferences as response variables. Results showed that dam influences accounted for 16% and 19% of the total variation for the two groups respectively. Findings from this paper suggest that stream fish assemblages are responsive to a variety of dam influences, including localized (proximity to individual dams) and cumulative (dam counts/densities within catchments) factors originating in both an upstream and downstream direction.

Although the fragmentation of fluvial systems into discrete subsections, or patches, based on the locations of dams has been evaluated in a number of studies pertaining to fishes, these studies have typically only included one overall measure of stream fragmentation. These measures have included either catchment-based approaches (e.g. Fukushima et al. 2007), lengths of stream networks including tributaries (e.g. Bain and Wine 2010, Hall et al. 2011) or free-flowing mainstem lengths (e.g. Perkin and Gido 2011). Defining patch-based measures that account for fragmentation of all three components – catchments, stream networks including tributaries, and stream mainstems – would provide a more thorough examination of the fragmentation effects of dams across large regions.

In this study, we consider effects of dams on streams of the conterminous U.S. by characterizing stream network fragmentation and other dam influences in nine large ecoregions. Specifically, we describe fragmentation and dam influence patterns at three different levels: 1) individual dam characteristics (age, height, reservoir storage, and degree of regulation) for nearly 50,000 dams, 2) segment-level metrics encompassing distance-based measures to dams and measures integrating cumulative dam effects for approximately 2.3 million stream segments, and

3) patch-level fragmentation metrics of river networks that account for fragmentation of catchments, stream networks with tributaries, and stream mainstems. Lastly, we discuss the potential uses of these dam measures in the management and conservation of fishes.

METHODS

Study area and spatial framework

Study area.—The study region includes the conterminous U.S., an area varying widely in its physiographic, climatic, and anthropogenic settings with respect to stream environments (Wang et al. 2011b). Due to broad regional differences in these factors, we used nine aggregated ecoregions to stratify our analyses (Figure 1.1, Herlihy et al. 2008). The nine aggregated ecoregions, hereafter called ecoregions, include: Northern Appalachians (NAP), South Appalachians (SAP), Upper Midwest (UMW), Coastal Plain (CPL), Temperate Plains (TPL), Northern Plains (NPL), Southern Plains (SPL), Western Mountains (WMT), and Xeric (XER). In addition, a stream size stratification based on catchment area (A) was employed which includes six classes (Esselman et al. 2011, Wang et al. 2011b); headwaters (HW; $A \leq 10$ km^2), creeks (CR; $10 < A \leq 100$ km^2), small rivers (SR; $100 < A \leq 1{,}000$ km^2), medium rivers (MR; $1{,}000 < A \leq 10{,}000$ km^2), large rivers (LR; $10{,}000 < A \leq 25{,}000$ km^2), and great rivers (GR; $A >$ 25,000 km^2).

Stream network data.—The spatial framework used for this study is based on the 1:100,000 scale National Hydrography Dataset Plus Version 1 (NHDPlusV1; USEPA and USGS 2005), a GIS dataset that includes stream reaches, lake/reservoir polygons, and local catchment boundaries encompassing the land area draining directly to a given stream reach. To facilitate generation of measures of fragmentation by dams along the stream network, modifications were made to the NHDPlusV1. Dam locations were used to split stream reaches (Figure 1.2) when dam locations did not already coincide with a reach break (node) in the NHDPlusV1. Reaches were subdivided using polyline split functions available with ArcMap GIS software (ESRI 2006). The subsequent subdivided reaches accounting for dam locations, hereafter referred to as segments, were given a new unique identifier, and those situated immediately above or below a dam were assigned the corresponding dam ID from the dataset used in this study (described below). Using the elevation data available with the NHDPlusV1 and the Watershed function in ArcMap, local reach catchments of the NHDPlusV1 were subdivided for dams that were greater than 100 m away from an existing reach break in the NHDPlusV1, resulting in segment catchments corresponding to dam locations (Figure 1.2).

Dam data.—Dams from the National Anthropogenic Barrier Dataset (NABD) were used for this study (USGS 2013). The NABD consists of spatially-verified dam locations and attributes (e.g. age, height, reservoir storage volume) derived from the 2009 National Inventory of Dams (NID; USACE 2009) developed by the U.S. Army Corps of Engineers. Dams are included in the NABD if they meet the following criteria: 1) the dam is classified as having a high or significant hazard potential (dam failure would lead to a possible loss of life) or 2) the dam is classified as a low hazard potential and either exceeds 25 ft in height and 15 acre-feet of storage or exceeds six ft in height and 50 acre-feet of storage (USACE 2009). As a final criterion, dams in NABD were required to be located on the NHDPlusV1 network, removing off-stream dams. The spatial location (coordinates) of dams in the NABD were manually verified by using streams from the NHDPlusV1, satellite imagery available in Google Earth(TM), and attributes of the dams (dam name, reservoir name, etc.). As necessary, dam locations represented in the NID were moved to align with stream reaches of the NHDPlusV1 using

Google Earth to create the NABD, ensuring that dams were linked with the correct stream reaches in the NHDPlusV1. Additionally, dams greater than 25 ft in height from the USFWS fish passage decision support system (USFWS 2008) dataset were verified against dam locations in NABD, ensuring a full coverage of large dams within NABD. Currently, NABD includes 49,468 dams mapped to stream reaches represented by the NHDPlusV1 throughout the conterminous United States (Figure 1.1).

Fragmentation metrics.—To generate the fragmentation metrics used in this study (Table 1.1), extensive programming using the Python programming language (Python v 2.7, www.python.org) was developed to characterize spatial relationships between dam locations and stream segments throughout the United States. This program managed a wide range of conditions found within the NHDPlusV1, such as divergences, loops, and highly braided stream networks. Using the topology of the stream network and the location of dams along the network, the program identified total number of dams upstream of each stream segment, both along the mainstem flow path and along all upstream flow paths in the river network. We defined the upstream mainstem flow path as the longest navigable upstream pathway above each stream segment. Similarly, the program also identified the number of dams along the downstream mainstem flow path, which was defined as the shortest pathway below each segment to an ocean, Great Lake, or terminal node in the case of disconnected stream networks. These dam counts were used to generate both upstream (mainstem and total network) and downstream (mainstem only) dam densities calculated using either network catchment area or mainstem/network stream length (Table 1.1). Using the upstream and downstream mainstem pathways identified for each segment, the program was also used to calculate the distance to the nearest mainstem dams if they were present along the upstream and/or downstream mainstem pathways. These distance values were then used to generate the total mainstem distance between dams, as well as the proportion of upstream, downstream, and total mainstem distances free of dams for each stream segment in the region. Lastly, the program calculated the cumulative upstream normal reservoir storage volume (acre/ft) above each segment, which resulted in storage metrics expressed per unit network stream length, network catchment area, or as a percentage of estimated annual stream discharge volume (hereafter referred to as "degree of regulation" *sensu* Lehner et al. 2011) derived from the NHDPlusV1 (Table 1.1). Since reaches of the NHDPlusV1 were subdivided at dam locations (including locations near the middle of a reach; Figure 1.2) and due to occasional discrepancies in catchment areas defined between the NHDPlusV1 and the Python program used in this study to develop the fragmentation metrics, only segments with catchments ± 25% the size of initial NHDPlusV1 reach catchment size were assigned degree of regulation percentages.

Artificial habitat patches.—An additional unit of analysis for this study, artificial habitat patches (AHPs), were delineated to account for the role of dams in the fragmentation of stream networks and their catchments. AHPs are defined as an adjacent set of stream segments, and their associated catchments, that are bounded by dams (Figure 1.3). With respect to AHPs, dams were identified as bounding individual AHPs in either the upstream direction or downstream direction, or in limited cases, were classified as internal to AHPs in situations where alternate flow paths allowed for stream connectivity around dams. AHPs were assigned to a stream size strata based on the total upstream catchment area of the most downstream stream segment, and two measures of AHP size were calculated, total network length and catchment area. In addition, the total mainstem length within AHPs was generated by summing the length of segments for the largest size strata represented within the AHP (e.g. total length of large river segments with a large river AHP).

Metric reduction and description of fragmentation patterns.— Due to the number of segment-level metrics calculated (Table 1.1) and the redundancy of certain metrics, a principal component analysis (PCA) was conducted to reduce the initial set of segment-level metrics to a subset of five metrics used to represent and describe fragmentation patterns. For the PCA, count-based metrics were removed from the analysis in favor of density-based metrics, as count-based metrics can be highly correlated with network catchment area and length (see Chapter 2), resulting in a total of 14 metrics that were used in the analysis. PCAs were performed for the conterminous U.S. and two example ecoregions, NAP and SPL, using fish community survey locations obtained for use in the 2015 National Fish Habitat Partnership (NFHP; http://fishhabitat.org/) river assessment for the conterminous U.S., allowing for results to inform fragmentation metric selection for future analyses. The NAP and SPL ecoregions were selected due to their widely varying conditions with respect to both natural conditions (climate, hydrology, etc.) and relative dam density (Figure 1.1). Total sample sizes were 37,060 for the conterminous U.S., 8,148 for NAP, and 2,391 for SPL, respectively. For the PCA, factors with eigenvalues of 1 or greater were retained and a Varimax rotation was performed to aid interpretation. SPSS software was used to run the PCAs (IBM SPSS Statistics 20 2011).

Based on the results of the PCAs (described in Results), a subset of five metrics were chosen for summarization including upstream mainstem openness, upstream network dam density, cumulative upstream degree of regulation, distance to downstream mainstem dam, and downstream mainstem density. First quartile, median, and third quartile statistics were calculated for ~ 2.3 million stream/river segments nationally, and segments representing flow paths through lakes and reservoirs were removed from analysis. In characterizing fragmentation and dam effects in this study, emphasis was placed on comparing and contrasting patterns in the individual, segment-level, and patch-level dam measures both among ecoregions and as a function of stream size class, utilizing statistics such as the first quartile, median, and third quartile to characterize metric distributions. In addition, results were reported for the conterminous U.S., allowing for comparison between ecoregions and broader conterminous U.S.

RESULTS

Patterns in dam characteristics

Dam count and density.—Among stream size classes, headwaters and creeks contained the greatest number of dams both at conterminous U.S. and ecoregion scales, with many fewer dams found on larger rivers (Table 1.2). Although dam counts were lower with increasing stream size class, dam densities (as a function of stream length within each size class) had highly variable distributions among ecoregions (Figure 1.4) showing left-skewed (e.g. UMW), right-skewed (e.g. CPL), and bi-modal (e.g. SAP) patterns. For the conterminous U.S., dam densities ranged from a high of 1.2 dams/100 km of stream within headwaters to a low of 0.5 dams/100 km of stream within great rivers. Overall, the NAP ecoregion had the highest dam densities for four of the six size classes, while the lowest densities were found in the XER ecoregion for smaller size classes and the NPL/CPL ecoregions for larger size classes.

Dam age and height.—For the conterminous U.S., 56% of dams are at least 50 years old (Figure 1.5). Median dam age increased from a low of 50 years for headwaters to high of 87 years for large rivers, then dropped for great rivers to a median age of 62 (Table 1.2; Figures 1.6-1.8). The headwater size class had the youngest median dam age for all ecoregions except WMT where the creek size class was the youngest. Similarly, the oldest median age occurred in the large river size class with the exception of the NAP and NPL ecoregions where the great river size class was the oldest. Across ecoregions, the NAP ecoregion had the oldest median age among size classes and was substantially older (by ~30-40 years) and had a larger interquartile range than other ecoregions for headwater and creek size classes, while the youngest median ages for dams within a given size strata tended to occur in the four plains ecoregions (CPL, TPL, NPL and SPL). For dam height, the first quartile and median height were similar across the headwater to large river size classes for the conterminous U.S., however the third quartile increased across these size classes (Table 1.2). Dam height measures were largest for the great river size class at the national scale. Dam height was the greatest in the WMT ecoregions for the large and great river size classes with median heights exceeding 200 ft. In the NAP and TPL ecoregions, median dam heights ranged from only 15 – 25 ft and 13 - 34 ft, respectively across all size classes.

Dam storage and degree of regulation.—As expected, reservoir storage tended to increase with increasing size class both for the conterminous U.S. and among ecoregions (Table 1.2). Although storage within the headwater and creek size classes was comparable across ecoregions, there were large differences among the ecoregions in storage in the small to great river size classes. Both for the conterminous U.S. and for a number of ecoregions, first quartile, median, and third quartile reservoir storage increased by an order of magnitude when moving from the large to great river size classes. In the SAP, SPL, and WMT ecoregions, median reservoir storage exceeded 100,000 acre-feet, with third quartile storage exceeding 1,000,000 acre feet for the NPL and WMT ecoregions. Comparing the total amount of storage by size strata, dams on great rivers collectively store the largest amount as a percentage of total storage in the conterminous U.S., followed by medium-sized rivers (Figure 1.9). Total storage on large and small rivers is comparable, while creeks and headwaters combine for a relatively small amount (~6%) of overall storage in the conterminous U.S. For several ecoregions (SAP, UMW, CPL, and WMT), storage on medium-sized rivers surpassed storage on great and large rivers. Across ecoregions, storage on great rivers showed the greatest variability.

Cumulative degree of regulation at dam locations was the lowest within the small river size class with a median value of 11% and the highest for great rivers at 40% for the conterminous U.S (Table 1.2). The UMW ecoregion was consistently among the lowest in median degree of regulation with values ranging from 6 - 25% across size classes. Overall, the highest median degree of regulation at dam locations occurred in the headwater size class for the TPL ecoregion at 295%, or nearly three years of estimated discharge volume being stored in upstream reservoirs.

Dam purpose.—The main dam purpose varied widely across size classes and ecoregions (Table 1.3). In the eastern ecoregions of NAP, SAP, UMW, and CPL, recreational use was the dominant purpose among the headwater and creek size classes, ranging from 38 to 70% of dams for these size classes, with flood control and water supply being major contributors depending upon the ecoregion. For these regions, recreational use tended to decline, while hydroelectric and/or navigation uses were greater with increasing stream size for the small to great river size classes. In the more central ecoregions of TPL, NPL, and SPL, flood control and fire protection/farm ponds were most prevalent within the headwater and creek size classes with recreation, water supply, irrigation and flood control being main uses in the larger size classes. Irrigation dominated (46 - 55%) for headwaters and creeks in the western ecoregions (WMT and XER), and irrigation remained the primary purpose in the XER. In contrast, hydroelectric use increased in prevalence with increasing size for the WMT ecoregion. For the conterminous U.S., recreation was the leading use within the headwater to small river sizes, while hydroelectric and navigation uses were dominant among the larger size classes. Levels of irrigation and water supply use were relatively steady across size classes ranging from 8 -15% and 6 – 12%, respectively.

Patterns in stream segment fragmentation metrics

Principal component analysis results.—The principal component analysis of 14 segment-level fragmentation metrics resulted in two axes for the conterminous U.S. and NAP ecoregion and four axes for the SPL ecoregion, with total variation explained ranging from 79-91% by region (Table 1.4). For the conterminous U.S. and NAP ecoregion, the first axis represented all upstream-oriented metrics and was interpreted as a combination of all upstream dam influences. The second axis for these regions was comprised of downstream mainstem and total mainstem metrics. Since the total mainstem metrics grouped closely with downstream mainstem metrics, this axis was interpreted as a combined set of downstream dam influences. For the SPL ecoregion, the first and third axes accounted for upstream dam metrics, with the first axis representing cumulative, network-based dam influences whereas the third axis was interpreted as representing upstream mainstem dam effects. The second and fourth axes for the SPL ecoregion were characterized by downstream mainstem and total mainstem metrics, respectively. As before, this combination was interpreted as representing largely downstream-oriented dam influences, with the second axis representing downstream habitat availability, while the fourth axis represented downstream dam density.

Select metric statistics.—Based on the PCA results, a subset of fragmentation metrics were selected for summarization that represented a diversity of dam influences, including upstream and downstream habitat availability (upstream mainstem openness and distance to downstream mainstem dam) and cumulative effects (upstream network dam density, upstream degree of regulation, and downstream mainstem density). For the upstream mainstem openness metric, all ecoregions were characterized by having maximum openness values (100%) for the first quartile, median, and third quartile statistics for headwaters and creeks, with high levels of openness also occurring in the small river and even medium river strata for some ecoregions (e.g. CPL and NPL; Table 1.5). Openness values typically declined with increasing size among the strata, with great rivers having a first quartile range of only 1 - 12% and median range of 2 - 28%. For the conterminous U.S., median values remained high through the medium river size strata at 91%, dropping to 30% for large rivers and 16% for great rivers, respectively.

Among headwater and creek size strata, upstream network densities were zero for virtually all three statistics (Table 1.5). For the remaining size strata, densities tended to increase slightly with increasing size for most ecoregions. Among the medium to great river size strata, densities were the lowest in WMT and XER ecoregions, with median values ranging 0 - 0.3 dams/100 km and highest for the CPL and NAP ecoregions, with values ranging from 0.6 - 3.6 dams/100 km. At the national level, densities also increased slightly when moving from the small to great river size classes, with median values ranging from 0.3 - 0.8 dams/100 km. Similarly to upstream network densities, cumulative degree of regulation values were minimal for headwater and creek strata within ecoregions, continuing to remain very low (median <=1%) for the small river stratum with exception of the TPL ecoregion with a median of 8%. Within all ecoregions, degree of regulation values increased when moving from the medium to great river strata, with the lowest values tending to occur in the SAP and UMW ecoregions, while XER and SPL values were among the highest. The great river strata had a wide degree of variation across ecoregions (Figure 1.10), with median values ranging from 6 - 69%, and third quartile values exceeding

100% in the TPL, SPL, and XER ecoregions. For the conterminous U.S., great river values had a large inter-quartile range, with a median value of 44%.

Although distance to downstream dam values increased with size across the first quartile, median, and third quartile statistics for the conterminous U.S., patterns among ecoregions tended to differ, with some having the greatest distances for the smaller strata (e.g. TPL), while others showed the opposite trend (e.g. SPL, Table 1.5). Within some ecoregions, distances across the various size strata were comparable, as occurred in the NAP and WMT ecoregions. Overall, segments in the NAP and UMW ecoregions had the closest distances (generally less than 50 km) to downstream mainstem dams, while distances to downstream dams were relatively long within the NPL ecoregion with median values ranging 285 - 511 km across size strata. Downstream dam densities were the highest in the NAP ecoregion for the headwater to large river size strata, where median values were nearly double of those in the UMW ecoregion, which had the next highest density values. For the great river stratum, the UMW and WMT had the highest median densities at ~1 dam/100 km, while values were very low (<=0.1 dam/100 km) for several ecoregions. The NPL and CPL had the lowest median densities among ecoregions, with values ranging from 0 to 0.4 dams/100 km across size strata.

Artificial habitat patches

For the conterminous U.S., a total of 54,120 AHPs were identified (Table 1.6, Figure 1.11), with the highest degree of fragmentation occurring in the NAP ecoregion (Figure 1.12). When compared to the 6,007 individual non-dam patches (Figure 1.11 top), defined by contiguous stream networks that are not subdivided at locations of dams, this represents a total increase of 801% in the number of patches. Across size strata, the percentage increase in the number of patches was very high, ranging from 703 – 1188%. In comparing median network length, AHP network length declined from 23 - 94%, with the lowest occurring in the creek stratum, while influences on large and great river strata were the highest. A similar pattern occurred for both median catchment size values and median mainstem length, with greater declines when moving from the smaller to larger size strata. For all three size measures, there tended to be a large decline when moving from the small to medium river size strata.

DISCUSSION

This study aimed to characterize fragmentation and dam influence patterns across the conterminous U.S. within nine large ecoregions, specifically describing individual dam characteristics (age, storage, etc.), segment-level distance-to-dam and cumulative dam effects, and patch-level fragmentation of river networks. Results within all three levels show a highly variable pattern in dam characteristics and dam effects across the U.S., both by ecoregion and stream size. For instance, among individual dam characteristics some regions contain a high density of dams and relatively low degree of regulation (e.g. NAP and UMW), while other ecoregions, such as XER, had opposite characteristics, with a low dam density and a high degree of regulation. In many ecoregions, main dam purposes changed considerably as stream size increased. Understanding how dams vary in terms of their specific characteristics, including their purpose and how they may be fragmenting river networks, can provide insight into their ecological impacts (Poff and Hart 2002), particularly when accounting for influence of network position and stream size (Ward and Stanford 1983).

Larger rivers, in particular, appear to have the greatest degree fragmentation as indicated by both segment and patch-level measures for the large and great river size strata. This observation is likely a function of stream network structure, as conditions in larger rivers are associated with cumulative effect of all upstream tributaries. A study by Lehner et al. (2011)

suggested a level of 2% degree of regulation for flow impairment by dams, a level which would encompass 91% of large river segments and 97% of great river segments in this study for the conterminous U.S. This suggests an incredibly high degree of potential flow alteration to the Nation's rivers resulting from dams. The increase in degree of regulation with stream size in this study is consistent with the findings of Lehner et al. (2011), which found a similar pattern of increases by stream size in a global study of reservoir storage by dams. This pattern demonstrates the pervasive, cumulative effects of reservoir storage along the river network, culminating in a high degree of regulation in larger rivers. Similar to the segment-level results, larger rivers were highly affected at the patch level, sustaining the highest amount of fragmentation according to AHP size measures when compared to non-dam conditions. This pattern likely arise from the "pruning" effect of dams within the stream network, as larger rivers are influenced not only by dams on mainstems but also by dams along major tributaries. Overall, the presence of dams in the conterminous U.S. has greatly increased the number of river patches of all size classes.

Implications for fisheries management and conservation

As a result of the great variability in dam measures across the U.S., careful consideration of the metrics used in future studies involving dam effects will be required. Selecting a subset of metrics that capture a variety of influences, such as localized (resulting from effects of individual dams), cumulative (resulting from multiple dams located throughout a river network), and patch-level connectivity metrics will be vital in order to capture the range of dam effects. Using a single metric (e.g. network density) would likely fail to adequately represent dam influences in most ecoregions. The results of the PCAs suggest the selection of multiple segment-level metrics for analyses incorporating the influence of dams on fishes, including two metrics for the NAP ecoregion, one each representing upstream and downstream influences, and four metrics in the SPL ecoregion, representing upstream cumulative, upstream mainstem, downstream habitat availability, and downstream density dam influences. The ability to discern between various effects (localized, cumulative, and patch-level) and reveal any changes in their relative influences along the river network, would yield a much broader understanding of the complex landscape-scale effects that dams have on fishes. Perhaps the development of a multi-metric dam index, driven by fish taxa responses in each ecoregion, could help ensure that the proper metrics were selected.

Data generated in this study could also be used to identify and conserve relatively unfragmented and unimpacted river networks. For instance, due to the effects of climate change, habitats within river networks may become unsuitable for some fish species. As a consequence of these changes and potential movement limitations imposed by barriers, the future range of certain species may be restricted due to localized extinctions within habitat patches (e.g. coldwater fishes). Several studies have predicted the future distributions of individual fish species (Rieman et al. 2007) or assemblages (Buisson et al. 2008, Buisson and Grenouillet 2009) by factoring climate change impacts on habitat suitability (e.g. changes in both stream temperature and precipitation), but in each case colonization of suitable habitat was allowed regardless of the presence of dams as barriers to dispersal. While these studies can give us a general sense of the potential range contraction or expansion of certain fish species or assemblages under various climate change scenarios, they may offer limited practical use. By incorporating measures of longitudinal fragmentation and dam influences along the river network, future studies forecasting climate change impacts on fish habitat and potential for species distribution would generate projections that better matched on-the-ground conditions, providing greater utility to aquatic resource managers and decision makers.

Although dams are generally viewed as being detrimental to the existence of native stream fishes, some have argued that dams can provide utility in certain circumstances, by protecting native species, improving water quality (Jackson and Pringle 2010), or by offering unique opportunities for flow and thermal regime improvements. For instance, in some situations, dams can prevent the establishment of non-native fishes by limiting their movement and dispersal (Novinger and Rahel 2003, Peterson et al. 2008, Fausch et al. 2009). Fausch et al. (2009) provide two examples from the western U.S. where barriers have isolated remnant populations of a native salmonid from introduced salmonid species, likely preventing their extirpation. By combining fragmentation data with the known distributions of native and non-native fishes, river networks that are free of non-native fishes can be identified and conserved.

Implications for restoration

Although dam influences can be difficult to isolate due to the complex and varied impacts that dams can have on river systems (connectivity, hydrology, geomorphology, etc.), they also represent a unique restoration opportunity. While other forms of human disturbance, such as urbanization, can be mitigated to a certain extent, dam removals can offer dramatic cases of restoration, with the initial re-establishment of connectivity after dam removal to the gradual "resetting" of river geomorphology. Dams have limited life spans, typically resulting from sediment accumulation that restricts water storage capabilities and a physical infrastructure that weakens over time, presenting safety concerns (Poff and Hart 2002). With an aging set of dams in the conterminous U.S. (nearly 75% of dams used in this study will be at least 50 years old by 2020), managers will increasingly be confronted with decisions on whether to remove a dam or cope with continued repairs and maintenance. While these decisions are likely based in part on social and economic considerations (Doyle et al. 2008), the dam measures presented here can provide an ecological component to the decision-making process by identifying the types of habitat which will be connected after a dam removal, determining if there will be increased connectivity to known source populations, and providing a landscape context for the potential dam removal project. For instance, the information gathered in this study can help guide dam removal priorities by integrating other measures of anthropogenic disturbance (e.g. agriculture, urbanization, point source pollutant locations; Esselman et. al 2013), allowing for the potential to identify longitudinal connections between higher quality, relatively undisturbed habitats.

Physical habitat restoration projects are at risk for failure if the full scope of human-induced changes to river systems are not considered (Palmer et al. 2005), with restoration activities being potentially unsuccessful due to historical and ongoing disturbances occurring at larger, regional scales (Bond and Lake 2003). For instance, the presence of a large dam above a restoration site, and the associated flow regime alterations, could supersede any local habitat enhancements, making them ineffective (Bond and Lake 2003). By considering dam effects in a larger regional context when evaluating restoration opportunities, overriding factors related to dams can be avoided. This is particularly true regarding stream connectivity, where fragmentation of the stream network can impede colonization from source populations, potentially limiting the biotic response to restoration activities (Bond and Lake 2003). A study of six restored stream sites by Riley and Fausch (1995) found that dispersal was instrumental in the increased abundance of three trout species, even though all three species were already present at the restored sites, and concluded that survival and recruitment were relatively less important factors in the abundance increases. From an ecological standpoint, the restoration of stream network connectivity is a key motivation for dam removal (Bednarek 2001), emphasizing the need for a spatial accounting of stream fragmentation and dam influences across large regions and at multiple scales.

Potential improvements

The dams used in this study represent ~50,000 of largest dams in the U.S. that are georeferenced to a modified 1:100,000 NHDPlusV1 stream network. As result, small dams are underrepresented in this study. For instance, Wang et al. (2011a) identified 5,215 dams connected to a modified version of the 1:100,000 NHD (precursor to the NHDPlusV1) for the states of Michigan and Wisconsin, which compares to 1,612 dams found in the NABD dataset for the two respective states. An analysis of dams in the NID (which forms the basis of the NABD dataset) for the state of Texas found that smaller dams were greatly underrepresented when compared to dams identified from digital orthoquads (DOQs) and the number of water bodies found in the NHD (Chin et al. 2008). Inclusion of smaller dams from state databases and other sources would improve connectivity-based measures, particularly in the fragmentation of headwater and creek size classes. Development of a holistic barrier layer that includes other potential anthropogenic sources of connectivity disruption such as road crossings (Januchowski-Hartley et al. 2013) and water diversions, along with cases of natural fragmentation (e.g. waterfalls, endorheic basins) would provide a broader overall view of fragmentation in the conterminous U.S.

The annual stream flow estimates used in this assessment, obtained from the NHDPlusV1, are derived from a relatively coarse flow model. Better segment-level annual flow estimates at national or even regional scales would likely provide improved degree of regulation estimates. In this study, degree of regulation was calculated from normal reservoir storage volume, however NABD attributes also include a maximum storage volume as well. A comparison of the ratio between maximum and normal degree of regulation could provide a metric related to the flood attenuation capacity of individual dams, perhaps providing a better measure of seasonal flow impacts.

Conclusion

The spatially-explicit study of human impacts on hydrologic connectivity is an emerging topic (Fullerton et al. 2010), one which provides many opportunities for advancing our knowledge of the effects of dams and fragmentation on aquatic organisms. Continued research and exploration will be needed in order to fully address and integrate the varied, multi-scale effects of dams into the restoration, conservation, and management activities pertaining to fishes and other aquatic organisms.

APPENDICES

APPENDIX A

TABLES

Table 1.1.— Dam metric descriptions, units, direction of metric indicating increasing levels of fragmentation, and sign of individual species/metric relationship to indicate positive response of species to increased fragmentation (indicated by increasing catch per unit effort). For the principal component and canonicial correspondence analyses, distance-based metrics were given the maximum value for that metric within the entire database in cases where upstream and/or downstream mainstem dams were absence for a given record.

Metric	Description	Units	Higher values result in:	Positive species response:
UMCT	Upstream mainstem dam count	#	Greater fragmentation	+
UMD[1,2,3]	Upstream mainstem dam density per unit upstream river mainstem length	#/100 km	Greater fragmentation	+
UM2D[2]	Distance to upstream mainstem dam	km	Less fragmentation	-
UMO	Proportion of open upstream mainstem	proportion	Less fragmentation	-
UNCT	Total upstream dam count	#	Greater fragmentation	+
UNDR[1,2]	Upstream mainstem dam density per unit river network length	#/100 km	Greater fragmentation	+
UNDC	Upstream mainstem dam density per unit network catchment area	$\#/km^2$	Greater fragmentation	+
USR[1,2,3]	Upstream reservoir storage volume per unit river length[a]	acre feet/100 km	Greater fragmentation	+
USC	Upstream reservoir storage volume per unit catchment area[a]	acre $feet/km^2$	Greater fragmentation	+
USF	Proportion of estimated annual discharge stored in upstream reservoirs[a,b]	proportion	Greater fragmentation	+
DMCT	Downstream mainstem dam count	#	Greater fragmentation	+
DMD[1,2,3]	Downstream mainstem dam density along the river network	#/100 km	Greater fragmentation	+
DM2D[1,2,3]	Distance to downstream mainstem dam	km	Less fragmentation	-
DMO[2]	Proportion of open downstream mainstem	proportion	Less fragmentation	-

Table 1.1 (cont'd).

Metric	Description	Units	Higher values result in:	Positive species response:
TMCT	Total mainstem dam count	#	Greater fragmentation	+
TMD[2]	Total mainstem dam density per unit downstream river mainstem length	#/100 km	Greater fragmentation	+
TM2D[2]	Total mainstem distance between upstream and/or downstream mainstem	km	Less fragmentation	-
TMO[1,2,3]	Total proportion of open mainstem	proportion	Less fragmentation	-

[1] Dam metrics selected for headwater and mid-size strata change point and Spearman correlation analysis.

[2] Dam metrics selected for large size strata change point and Spearman correlation analysis.

[3] Dam metrics selected for CCA analysis.

[a] Normal reservoir storage volumes taken from the National Anthropogenic Barrier Dataset (NABD)

[b] Annual flow estimates from the National Hydrography Dataset Plus Version 1 (NHDPlusV1) unit runoff method.

Table 1.2.—Descriptive statistics (first quartile, median, and third quartile) for dam characteristics for the conterminous U.S. (CONUS) and by ecoregion. Dam densities were calculated per 100 km of network length within a given stratum and region. Degree of regulation (UDOR) was calculated using cumulative upstream reservoir storage divided estimated mean annual stream flow and had a total sample size of 34,175. Based on the available information within the NABD dataset, a total sample size of 43,658 was used for age, 49,356 for height, and 49,468 for storage.

				Age (years)			Height (feet)			Storage (acre feet)			UDOR (%)		
Region	Stratum	Count	Density	Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75
CONUS	HW	32351	1.2	40	50	60	18	24	31	31	58	120	7	23	81
	CR	11851	0.8	44	55	78	15	24	40	60	165	554	3	12	56
	SR	3259	0.6	50	75	98	14	22	47	91	479	5895	2	11	46
	MR	1411	0.7	54	82	100	15	27	67	216	1500	24943	4	16	49
	LR	314	0.9	62	87	104	16	26	72	450	4588	28000	8	20	53
	GR	282	0.5	46	62	78	35	66	124	4334	80000	388800	20	41	100
NAP	HW	2662	2.0	50	78	110	11	15	23	40	91	263	3	10	24
	CR	1711	2.3	64	93	113	12	16	25	51	180	975	2	6	19
	SR	729	3.1	72	96	113	13	19	31	60	220	2255	2	9	23
	MR	280	3.7	79	97	107	16	23	39	203	892	3303	5	12	27
	LR	30	2.2	92	100	107	19	25	36	1150	3939	16600	13	20	20
	GR	1	0.3	188	188	188	18	18	18	10744	10744	10744	30	30	30
SAP	HW	7000	1.6	42	50	59	21	26	35	32	60	124	4	11	28
	CR	1493	0.9	43	50	67	25	39	56	98	248	1071	2	5	15
	SR	341	0.6	48	73	95	19	40	73	92	910	13430	1	8	25
	MR	210	1.0	56	84	103	20	51	129	310	4700	97000	5	10	37
	LR	68	1.8	61	87	113	21	55	104	3586	13000	119925	6	8	16
	GR	52	1.2	44	57	81	53	78	110	37850	161900	420450	9	18	45
UMW	HW	644	0.6	39	46	52	11	18	28	15	45	147	2	6	17
	CR	697	0.9	44	57	83	9	12	19	42	150	832	1	4	16
	SR	452	1.4	74	83	113	10	15	22	120	645	3875	1	5	21
	MR	195	2.0	84	94	106	18	25	40	600	2483	8958	2	9	18
	LR	31	2.5	76	100	118	24	30	50	1815	8170	23250	12	15	19
	GR	24	1.6	76	76	78	32	43	46	10450	52700	98600	23	25	39

Table 1.2 (cont'd).

Region	Stratum	Count	Density	Age (years)			Height (feet)			Storage (acre feet)			UDOR (%)		
				Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75
CPL	HW	6004	1.6	40	50	58	14	19	25	28	60	116	2	9	27
	CR	1763	0.9	48	59	83	12	15	24	54	127	333	1	3	7
	SR	256	0.4	48	59	80	13	19	35	190	787	9100	1	4	32
	MR	79	0.2	43	52	75	23	43	71	1475	31500	144500	3	21	58
	LR	26	0.3	47	63	87	20	41	70	1300	8800	60400	11	37	53
	GR	31	0.3	38	45	51	49	79	108	43000	70500	212500	24	41	47
TPL	HW	6116	1.8	31	42	51	24	28	35	28	49	93	18	49	135
	CR	1074	0.6	35	45	60	21	36	48	99	253	1000	7	24	105
	SR	308	0.5	46	74	91	12	17	39	100	469	3974	3	17	66
	MR	216	0.9	67	78	91	10	13	27	150	449	3807	3	13	36
	LR	67	1.4	74	79	98	11	16	21	231	1690	9808	10	25	63
	GR	43	0.6	55	75	80	14	34	48	764	55000	184000	11	18	22
NPL	HW	2750	1.4	49	57	64	17	21	26	30	46	72	80	295	812
	CR	1516	1.2	50	59	73	15	20	27	40	75	161	30	118	359
	SR	228	0.5	50	63	76	15	20	30	55	190	626	8	33	125
	MR	30	0.2	53	63	75	13	20	38	135	390	7010	5	19	111
	LR	4	0.1	53	58	83	29	115	200	325	65250	548660	25	102	319
	GR	18	0.4	56	84	98	45	107	210	1710	38926	1725000	46	47	134
SPL	HW	5313	2.2	41	48	54	19	25	32	34	55	100	24	59	204
	CR	2049	1.1	41	49	55	24	34	45	80	174	287	15	31	105
	SR	303	0.5	43	53	74	16	26	53	64	192	2085	3	18	83
	MR	167	0.6	44	57	79	15	28	86	112	560	39545	4	35	172
	LR	41	0.8	62	93	103	10	13	27	197	285	808	36	138	435
	GR	34	0.3	50	62	72	35	98	140	280	124067	505381	76	137	253

Table 1.2 (cont'd).

				Age (years)			Height (feet)			Storage (acre feet)			UDOR (%)		
Region	Stratum	Count	Density	Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75
WMT	HW	1231	0.3	46	60	87	17	26	36	58	130	380	9	35	104
	CR	896	0.4	47	59	84	21	33	58	84	347	1720	3	18	76
	SR	315	0.6	49	64	89	30	70	149	311	5750	38755	5	32	89
	MR	112	0.6	50	64	88	31	89	202	480	13984	166531	13	39	66
	LR	24	1.0	49	68	89	53	201	249	2150	32900	211524	13	37	84
	GR	14	0.7	53	58	73	125	203	330	58386	137300	1153000	30	33	48
XER	HW	631	0.1	36	52	68	22	32	49	40	115	411	23	85	317
	CR	652	0.2	44	58	83	20	31	50	69	200	1047	4	28	133
	SR	327	0.4	45	59	85	20	40	82	171	960	9010	4	28	101
	MR	122	0.4	46	60	94	23	60	164	222	3300	87500	26	67	156
	LR	23	0.4	64	96	99	23	95	225	850	4765	65540	7	31	52
	GR	65	0.6	45	63	80	37	87	208	500	50130	516000	33	53	108

Table 1.3.—Main dam purpose both for the conterminous U.S. (CONUS) and by ecoregion with values expressed as a percentage. Flood = Flood control and stormwater management; Hydro = Hydroelectric power generation; Supply = Water supply; Fire/Farm = Fire protection, stock, and small farm ponds; Fish/Wild = Fish and wildlife ponds; Debris = Debris control.

Region	Stratum	Flood	Hydro	Irrigation	Navigation	Supply	Recreation	Fire/Farm	Fish/Wild	Debris	Tailings	Other
CONUS	HW	19	0	8	0	9	39	18	2	0	1	4
	CR	22	2	12	0	12	35	9	3	0	0	4
	SR	12	16	15	1	13	27	4	2	0	0	9
	MR	12	41	9	3	12	13	2	3	0	0	5
	LR	7	37	12	19	6	13	0	2	0	0	4
	GR	9	26	10	36	9	6	0	1	0	0	3
NAP	HW	6	1	1	0	16	70	2	2	0	0	3
	CR	8	6	1	1	16	58	2	2	0	0	5
	SR	13	39	0	1	10	25	1	1	0	0	8
	MR	3	82	0	8	2	2	1	0	0	0	1
	LR	3	70	0	27	0	0	0	0	0	0	0
	GR	0	0	0	0	0	100	0	0	0	0	0
SAP	HW	13	0	4	0	6	67	5	1	0	1	3
	CR	33	1	1	0	17	45	0	1	0	1	2
	SR	17	20	0	0	27	31	0	1	0	1	3
	MR	25	49	0	4	11	9	0	0	0	0	2
	LR	6	41	0	29	1	21	0	0	0	0	1
	GR	2	31	0	56	2	6	0	0	0	0	4
UMW	HW	22	0	1	0	0	38	11	7	3	2	15
	CR	7	2	4	0	2	61	1	7	1	1	16
	SR	2	16	2	0	2	45	0	2	0	0	29
	MR	1	65	0	1	2	17	0	1	0	0	14
	LR	0	90	0	0	0	7	0	0	0	0	3
	GR	0	17	0	75	4	4	0	0	0	0	0

Table 1.3 (cont'd).

Region	Stratum	Flood	Hydro	Irrigation	Navigation	Supply	Recreation	Fire/Farm	Fish/Wild	Debris	Tailings	Other
CPL	HW	12	0	7	0	3	65	7	2	0	1	3
	CR	13	0	5	0	4	69	3	1	0	1	4
	SR	13	2	6	2	16	50	1	2	0	0	7
	MR	21	15	0	8	22	24	5	0	0	0	5
	LR	8	19	0	58	0	8	0	0	0	0	8
	GR	13	0	7	67	7	0	0	0	0	0	7
TPL	HW	26	0	3	0	4	21	35	1	1	0	8
	CR	40	0	1	0	9	31	6	4	1	0	7
	SR	21	3	1	1	14	42	2	5	0	0	11
	MR	21	10	3	2	16	29	2	9	0	0	8
	LR	12	12	3	23	9	28	2	11	0	0	0
	GR	9	5	0	58	16	2	0	5	0	0	5
NPL	HW	1	0	13	0	36	3	42	3	0	0	1
	CR	3	0	25	0	17	9	40	5	0	0	1
	SR	2	0	37	0	7	19	25	7	0	0	2
	MR	3	0	34	0	3	24	14	17	0	0	3
	LR	0	0	100	0	0	0	0	0	0	0	0
	GR	29	47	24	0	0	0	0	0	0	0	0
SPL	HW	46	0	5	0	6	7	31	1	0	0	4
	CR	56	0	9	0	11	8	12	1	0	0	3
	SR	17	0	25	0	25	12	13	0	0	0	7
	MR	12	3	19	0	35	21	6	1	0	0	2
	LR	11	3	36	0	28	6	0	0	0	0	17
	GR	19	19	6	0	34	16	0	0	0	0	6

Table 1.3 (cont'd).

Region	Stratum	Flood	Hydro	Irrigation	Navigation	Supply	Recreation	Fire/Farm	Fish/Wild	Debris	Tailings	Other
WMT	HW	4	4	55	0	12	13	4	4	0	2	2
	CR	4	7	46	0	12	18	4	5	0	1	2
	SR	8	22	39	0	14	10	2	2	1	0	2
	MR	9	46	25	1	11	3	1	1	0	0	2
	LR	0	70	10	0	10	0	0	0	0	0	10
	GR	0	93	0	0	7	0	0	0	0	0	0
XER	HW	15	1	48	0	9	3	8	3	4	4	5
	CR	17	1	51	0	10	4	6	4	2	2	4
	SR	17	2	55	0	8	5	3	4	1	0	4
	MR	12	17	51	0	8	3	1	5	2	0	1
	LR	9	27	64	0	0	0	0	0	0	0	0
	GR	8	37	34	8	3	7	0	0	2	0	0

Table 1.4.—Principal component analysis results for the conterminous U.S. and for the NAP and SPL ecoregions with fragmentation metric weights by axes. Weights with an absolute value of 0.7 or greater, shown in bold, were used in the axis interpretation found at the top of each axis column. Cumulative percentage of variation explained is located at the bottom of each axis column.

Region	Metric	Axis 1	Axis 2	Axis 3	Axis 4
		Upstream Combined	Downstream Combined		
CONUS	UMD	**0.89**	-0.10		
	UM2D	**-0.84**	0.13		
	UMO	**-0.87**	0.11		
	UNDR	**0.92**	-0.02		
	UNDC	**0.91**	-0.01		
	USR	**0.96**	0.00		
	USC	**0.95**	0.00		
	USF	**0.82**	0.03		
	DMD	-0.03	**-0.89**		
	DM2D	-0.04	**0.87**		
	DMO	0.04	**0.86**		
	TMD	0.17	**-0.86**		
	TM2D	-0.07	**0.91**		
	TMO	-0.04	**0.85**		
C. Var. Exp.		47.19	79.15		
		Upstream Combined	Downstream Combined		
NAP	UMD	**0.93**	-0.10		
	UM2D	**-0.90**	0.12		
	UMO	**-0.90**	0.11		
	UNDR	**0.95**	-0.06		
	UNDC	**0.95**	-0.05		
	USR	**0.97**	-0.06		
	USC	**0.97**	-0.05		
	USF	**0.85**	-0.08		
	DMD	-0.06	**-0.91**		
	DM2D	-0.10	**0.86**		
	DMO	0.06	**0.91**		
	TMD	0.21	**-0.88**		
	TM2D	-0.20	**0.91**		
	TMO	-0.09	**0.91**		
C. Var. Exp.		52.67	84.78		

Table 1.4 (cont'd).

Region	Metric	Axis 1 Upstream Network	Axis 2 Downstream Availability	Axis 3 Upstream Mainstem	Axis 4 Downstream Density
SPL	UMD	0.48	0.09	**0.81**	-0.03
	UM2D	-0.35	-0.01	**-0.89**	0.04
	UMO	-0.40	-0.07	**-0.86**	0.01
	UNDR	**0.93**	0.04	0.21	0.00
	UNDC	**0.93**	0.02	0.18	0.01
	USR	**0.90**	0.13	0.35	0.00
	USC	**0.91**	0.12	0.33	0.01
	USF	**0.79**	0.06	0.37	-0.08
	DMD	-0.05	-0.28	-0.11	**0.94**
	DM2D	0.07	**0.92**	0.05	-0.11
	DMO	0.02	**0.93**	0.11	-0.16
	TMD	0.03	-0.20	0.05	**0.97**
	TM2D	0.14	**0.92**	-0.02	-0.16
	TMO	0.06	**0.94**	0.03	-0.14
C. Var. Exp.		45.60	72.51	82.90	90.57

Table 1.5.—Descriptive statistics (first quartile, median, and third quartile) for a subset of segment-level fragmentation metrics, including upstream mainstem openness (UMO) expressed as a percentage, upstream river network density (UNDR), cumulative upstream degree of regulation (UDOR), downstream distance to mainstem dam (DM2D), and downstream mainstem dam density (DMD).

		UMO (%)			UNDR (#/100 km)			UDOR (%)			DM2D (km)			DMD (#/100 km)		
Region	Stratum	Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75
CONUS	HW	100	100	100	0.0	0.0	0.0	0	0	0	31	93	226	0.1	0.3	0.8
	CR	100	100	100	0.0	0.0	0.0	0	0	0	36	100	249	0.1	0.4	0.8
	SR	100	100	100	0.0	0.3	1.3	0	0	2	42	109	264	0.1	0.4	0.8
	MR	33	91	100	0.2	0.6	1.3	1	4	20	44	119	274	0.1	0.4	0.8
	LR	10	30	70	0.4	0.7	1.2	6	17	47	44	123	385	0.1	0.4	0.8
	GR	5	16	38	0.3	0.8	1.1	21	44	112	56	200	544	0.1	0.3	0.6
NAP	HW	100	100	100	0.0	0.0	0.0	0	0	0	8	25	60	0.8	1.7	4.1
	CR	100	100	100	0.0	0.0	3.0	0	0	1	8	25	60	0.8	1.8	4.1
	SR	23	98	100	0.3	1.1	2.8	0	1	5	8	25	63	0.8	1.8	3.9
	MR	4	21	60	0.7	1.2	1.9	2	6	17	6	23	57	0.8	2.1	4.2
	LR	3	8	22	0.8	1.5	2.1	7	10	20	10	31	142	1.1	1.5	3.3
	GR	1	3	30	3.1	3.6	3.6	30	30	30	0	0	0	0.0	0.0	0.0
SAP	HW	100	100	100	0.0	0.0	0.0	0	0	0	31	73	141	0.3	0.5	0.8
	CR	100	100	100	0.0	0.0	0.0	0	0	0	36	77	144	0.3	0.5	0.8
	SR	94	100	100	0.0	0.8	2.1	0	0	2	40	80	146	0.3	0.5	0.8
	MR	19	62	100	0.4	0.8	1.7	1	3	10	40	90	183	0.2	0.4	0.8
	LR	3	12	37	0.6	0.9	1.3	5	8	14	13	44	100	0.3	0.5	0.9
	GR	2	4	9	0.8	1.0	1.2	8	9	44	19	43	78	0.3	0.4	0.7
UMW	HW	100	100	100	0.0	0.0	0.0	0	0	0	19	44	83	0.5	0.9	1.2
	CR	100	100	100	0.0	0.0	0.0	0	0	0	16	39	79	0.6	1.0	1.4
	SR	50	100	100	0.0	0.4	1.4	0	0	2	15	38	75	0.7	1.0	1.5
	MR	9	32	72	0.5	0.9	1.4	1	4	13	12	34	80	0.8	1.1	2.0
	LR	3	8	21	1.1	1.3	1.4	5	16	25	18	53	88	0.8	1.0	1.1
	GR	1	2	8	0.8	0.9	0.9	22	23	25	13	24	45	0.8	1.0	1.0

Table 1.5 (cont'd).

Region	Stratum	UMO (%)			UNDR (#/100 km)			UDOR (%)			DM2D (km)			DMD (#/100 km)		
		Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75
CPL	HW	100	100	100	0.0	0.0	0.0	0	0	0	19	81	159	0.0	0.0	0.4
	CR	100	100	100	0.0	0.0	0.0	0	0	0	30	90	172	0.0	0.0	0.4
	SR	100	100	100	0.0	0.6	1.9	0	0	1	55	106	185	0.0	0.0	0.4
	MR	71	100	100	0.5	1.0	1.9	0	1	7	53	124	230	0.0	0.0	0.4
	LR	13	39	64	0.9	1.2	2.5	6	14	51	30	71	116	0.0	0.0	0.3
	GR	9	18	28	1.1	1.6	2.6	24	41	83	73	167	291	0.0	0.0	0.2
TPL	HW	100	100	100	0.0	0.0	0.0	0	0	0	41	112	270	0.1	0.2	0.5
	CR	100	100	100	0.0	0.0	0.0	0	0	0	49	118	288	0.1	0.2	0.6
	SR	100	100	100	0.0	0.6	1.7	0	0	4	55	124	341	0.1	0.2	0.6
	MR	22	71	100	0.4	0.7	1.7	1	5	16	33	96	260	0.1	0.3	0.7
	LR	4	13	30	0.5	0.7	1.2	5	10	23	18	59	189	0.1	0.5	0.8
	GR	2	6	24	0.8	0.9	1.2	10	32	125	29	82	486	0.0	0.1	0.4
NPL	HW	100	100	100	0.0	0.0	0.0	0	0	0	77	285	558	0.1	0.1	0.1
	CR	100	100	100	0.0	0.0	0.0	0	0	0	84	307	604	0.1	0.1	0.1
	SR	83	100	100	0.0	0.8	1.7	0	8	47	138	350	612	0.1	0.1	0.1
	MR	64	100	100	0.5	0.9	1.4	4	19	49	156	430	692	0.1	0.1	0.1
	LR	56	93	100	0.5	0.7	0.9	17	38	52	126	328	586	0.1	0.1	0.1
	GR	11	28	100	0.3	0.7	0.9	20	41	76	302	511	793	0.1	0.1	0.1
SPL	HW	100	100	100	0.0	0.0	0.0	0	0	0	42	172	404	0.1	0.3	0.7
	CR	100	100	100	0.0	0.0	0.0	0	0	0	51	166	384	0.1	0.4	0.7
	SR	94	100	100	0.0	0.5	1.8	0	1	11	73	199	418	0.1	0.3	0.7
	MR	36	88	100	0.3	0.8	1.7	1	8	31	76	200	570	0.1	0.3	0.6
	LR	15	35	72	0.4	0.8	1.3	7	45	104	82	341	590	0.1	0.3	0.7
	GR	12	22	56	0.5	0.8	1.1	27	59	123	179	360	1171	0.0	0.1	0.7

Table 1.5 (cont'd).

Region	Stratum	UMO (%)			UNDR (#/100 km)			UDOR (%)			DM2D (km)			DMD (#/100 km)		
		Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75	Q25	Median	Q75
WMT	HW	100	100	100	0.0	0.0	0.0	0	0	0	39	101	226	0.2	0.5	1.0
	CR	100	100	100	0.0	0.0	0.0	0	0	0	40	103	235	0.2	0.5	1.0
	SR	100	100	100	0.0	0.0	0.4	0	0	0	41	99	231	0.2	0.6	1.0
	MR	45	100	100	0.1	0.2	0.4	0	3	18	51	112	241	0.3	0.5	1.0
	LR	11	32	72	0.1	0.2	0.4	3	15	45	62	113	164	0.3	0.7	1.3
	GR	5	30	100	0.1	0.3	0.3	2	18	32	38	102	183	0.3	0.9	1.0
XER	HW	100	100	100	0.0	0.0	0.0	0	0	0	46	150	361	0.0	0.4	0.8
	CR	100	100	100	0.0	0.0	0.0	0	0	0	53	166	398	0.0	0.4	0.7
	SR	100	100	100	0.0	0.0	0.2	0	0	0	56	173	403	0.0	0.5	0.8
	MR	45	100	100	0.1	0.2	0.4	0	7	41	68	172	417	0.2	0.5	0.8
	LR	19	32	92	0.2	0.3	0.5	7	25	47	77	184	475	0.3	0.5	0.8
	GR	6	18	44	0.2	0.3	0.3	42	69	146	45	152	377	0.5	0.6	1.0

Table 1.6.—Patch count, median size characteristics, and percent increase (Inc.)/decrease (Dec.) in metrics by siza strata for the conterminuous U.S. when comparing patches in the absence of dams (No Dam; Figure 8 top) and when considering dam locations as artificial habitat patch (AHP) boundaries (Dam; Figure 8 bottom).

	Patch Count			Network Length (km)			Catchment Area (km^2)			Mainstem Length (km)		
Stratum	No Dam	Dam	% Inc.	No Dam	Dam	% Dec.	No Dam	Dam	% Dec.	No Dam	Dam	% Dec.
HW	3810	35017	819	2.4	1.7	30	2.3	2.1	8	2.4	1.7	30
CR	1535	13280	765	15.3	11.8	23	23.0	17.9	22	6.4	4.4	31
SR	456	3661	703	134.7	87.9	35	221.5	145.7	34	17.4	11.0	37
MR	147	1531	941	1362.3	349.6	74	2206.5	691.3	69	56.8	20.9	63
LR	26	335	1188	9918.2	553.0	94	13982.7	844.8	94	91.1	20.2	78
GR	33	296	797	28049.4	2445.4	91	42015.7	3561.9	92	281.6	71.2	75

APPENDIX B

FIGURES

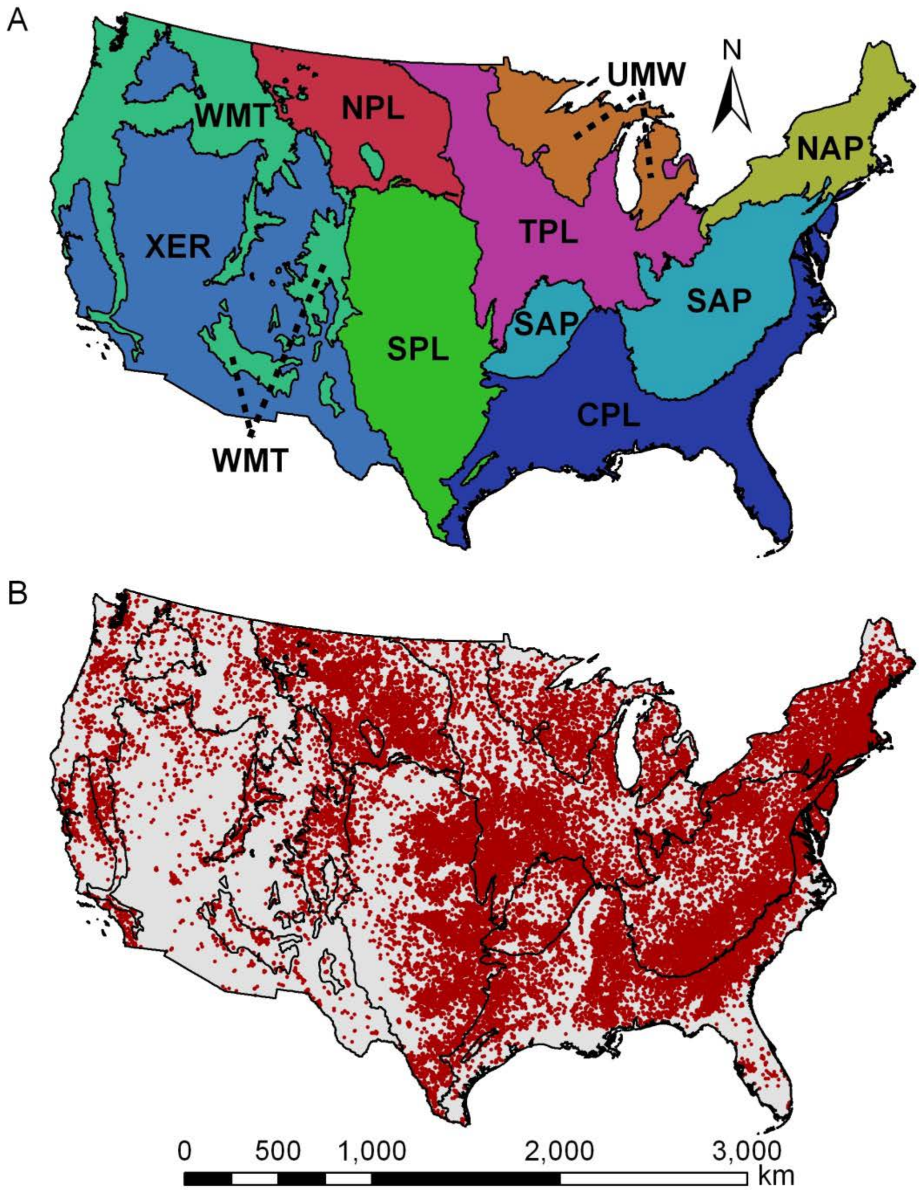

Figure 1.1.—Distribution of the nine aggregated ecoregions (A) and dam locations (B; N = 49,468) of the conterminous U.S. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

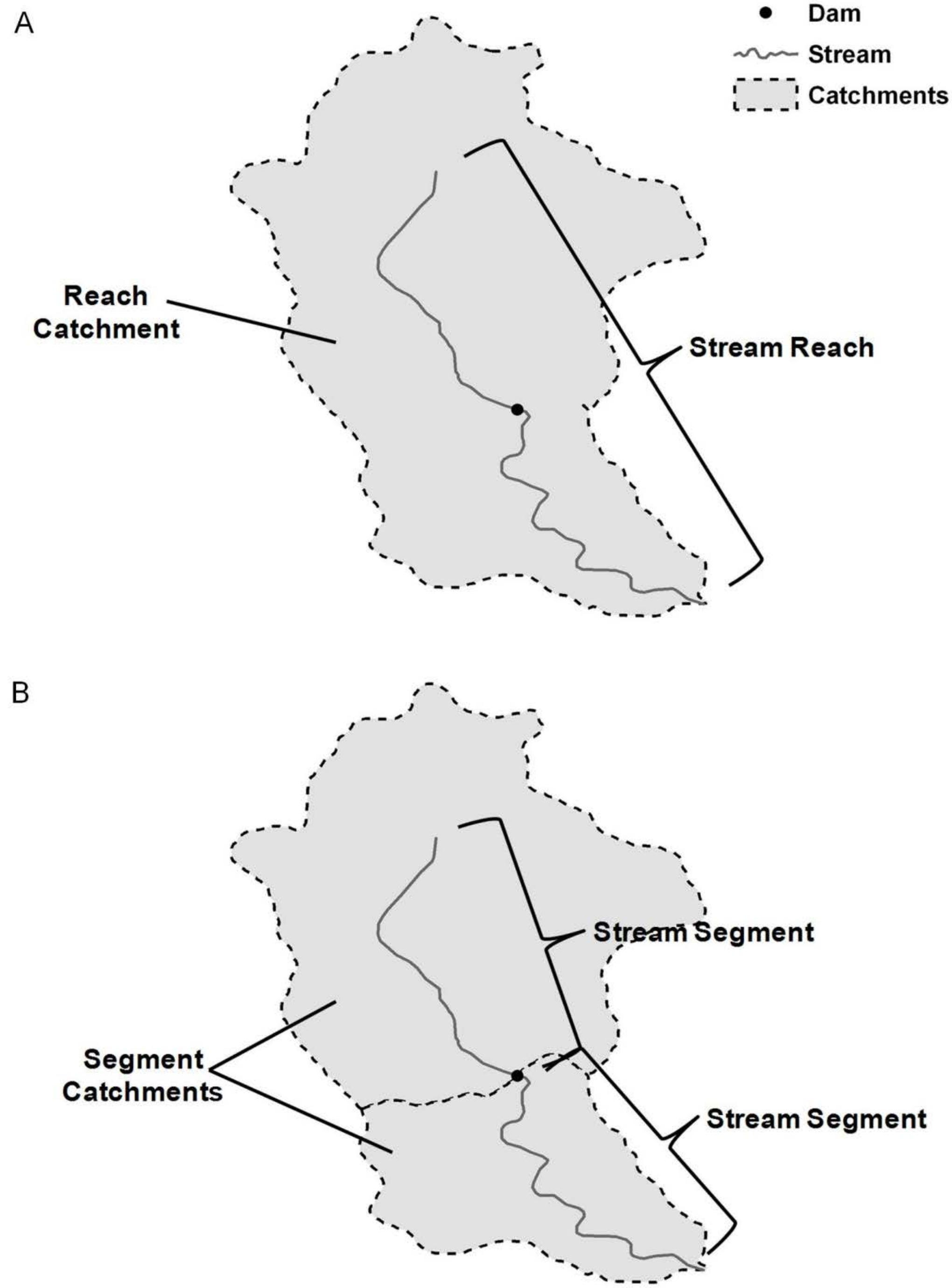

Figure 1.2.—Example depiction of an NHDPlusV1 stream reach and catchment (A) and its subdivision into stream segments with subsequent delineation of segment catchments (B) for dams occurring greater than 100 m from an existing node in the NHDPlusV1.

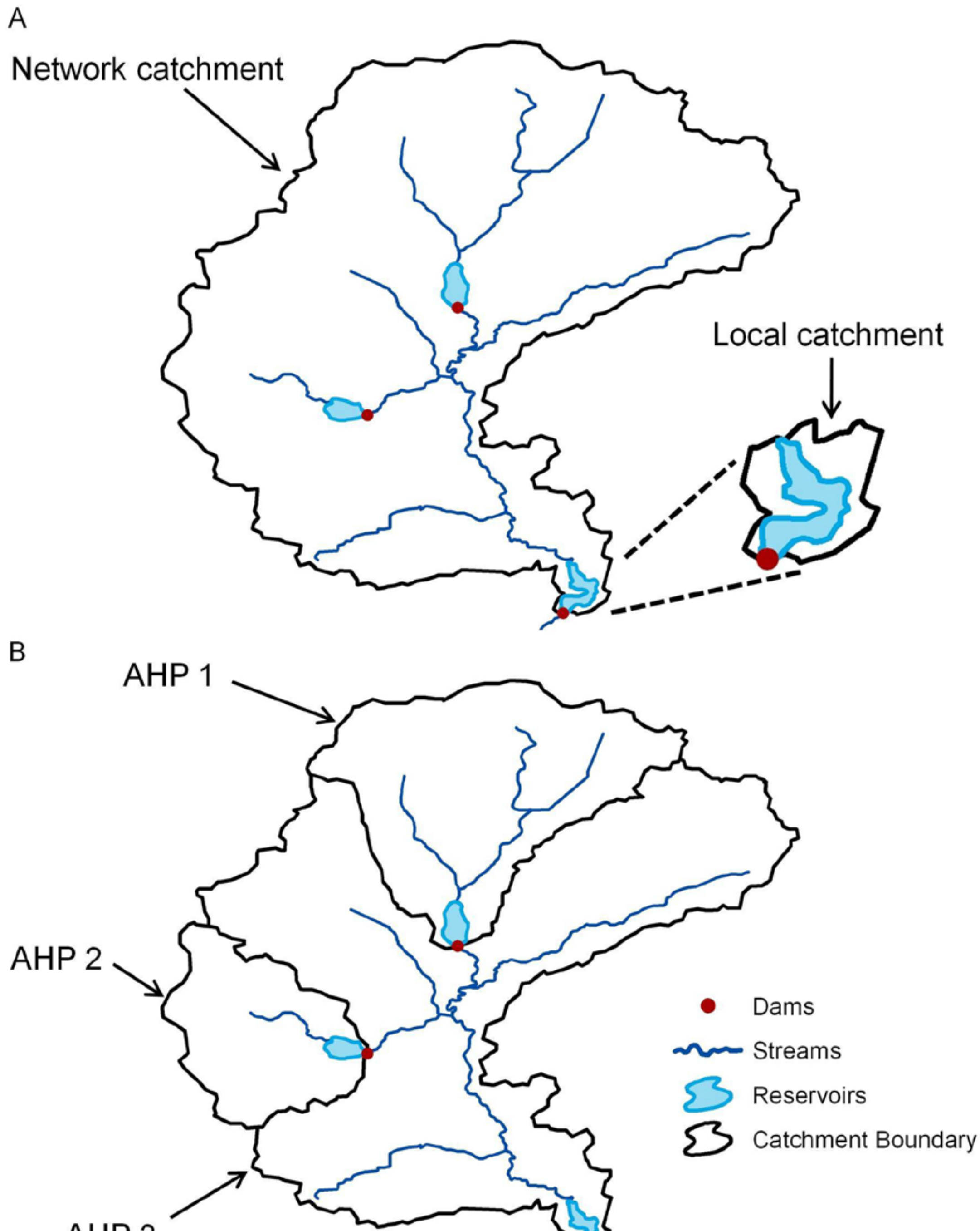

Figure 1.3.—Depiction of the traditional scales of catchment delineation (A), consisting of local catchments (land area draining directly to a stream reach or water body) and network catchments (cumulative upstream drainage area, including the local catchment of the target stream reach or water body). In contrast, an alternative set of catchments for artificial habitat patches (AHPs) are defined by the locations of dams (B).

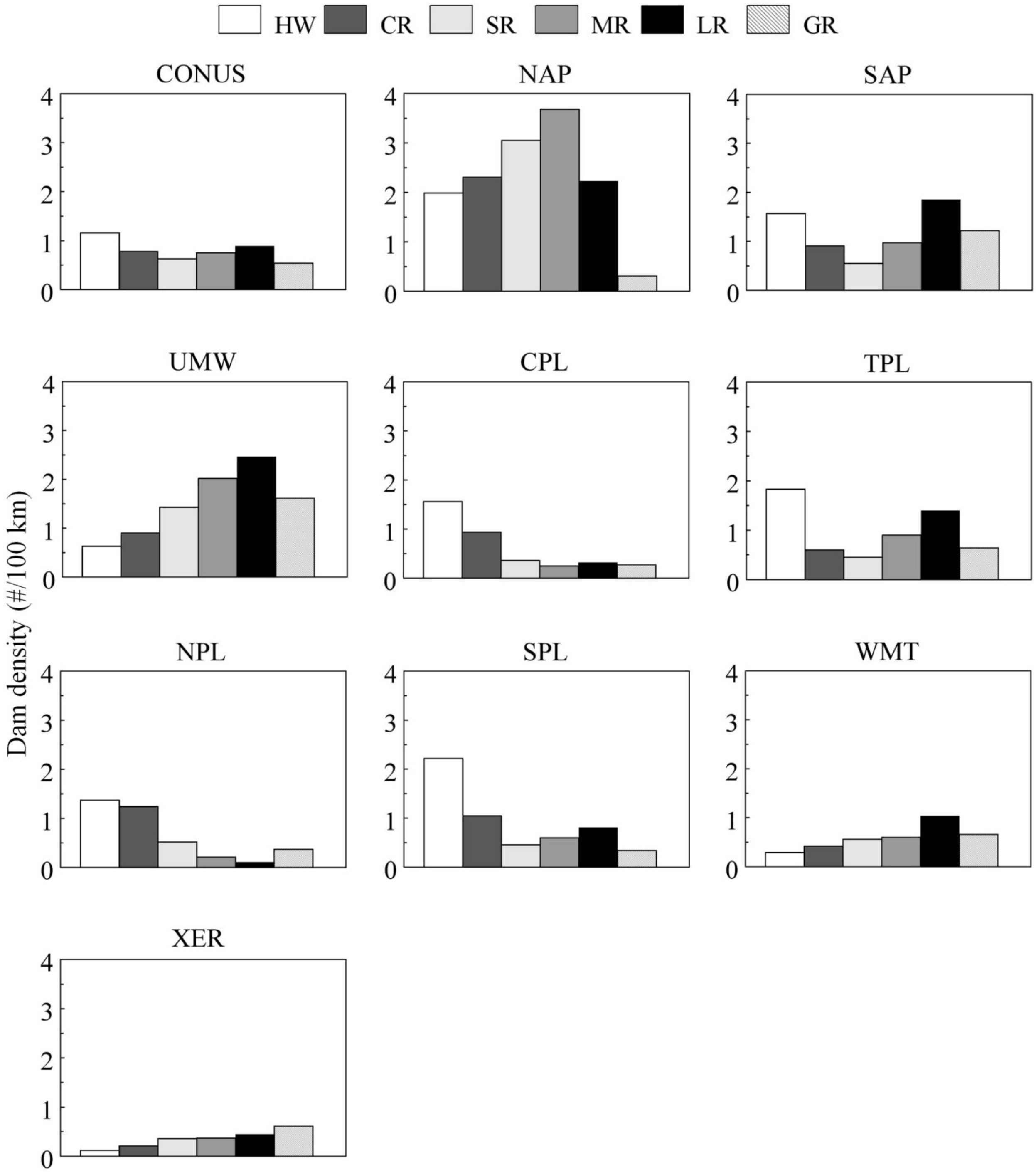

Figure 1.4.—Dam density distributions by size strata for the conterminous U.S (CONUS) and by ecoregion. Dam densities were calculated per 100 km of network length within a given stratum and region.

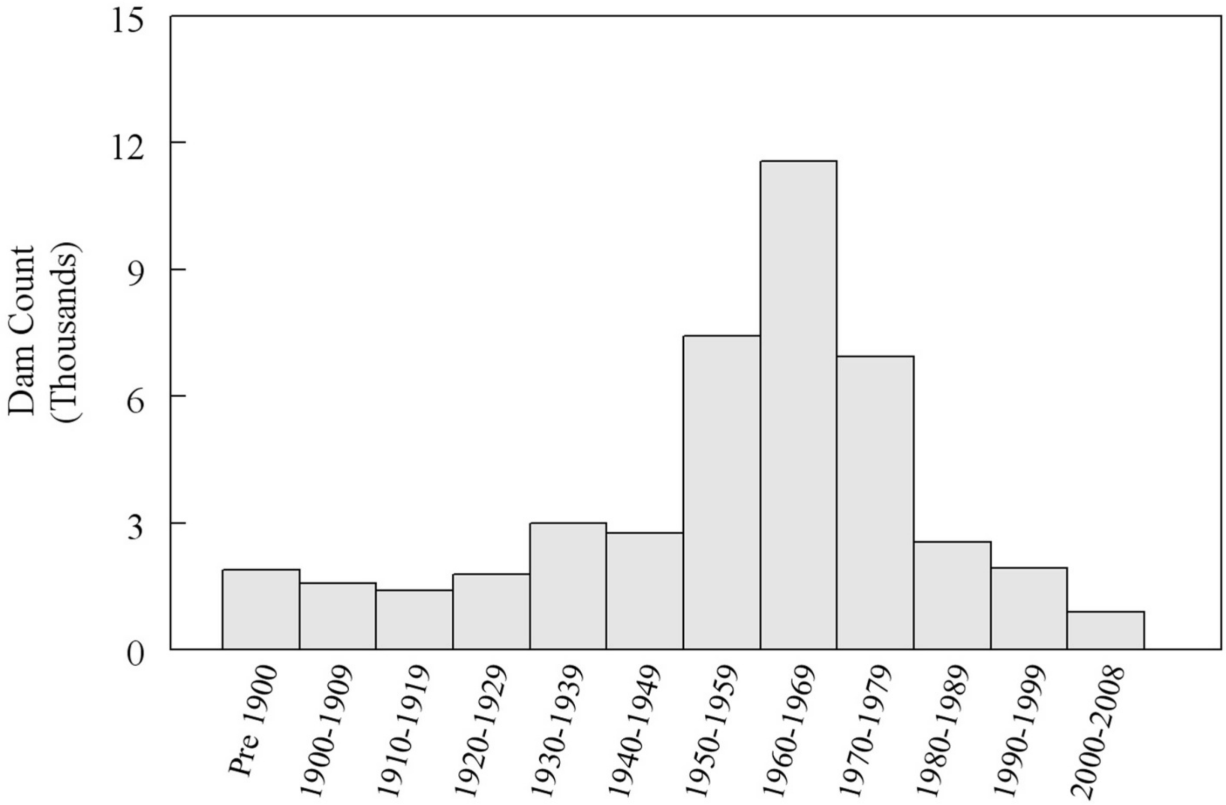

Figure 1.5.—Number of dams constructed by decade (source NABD).

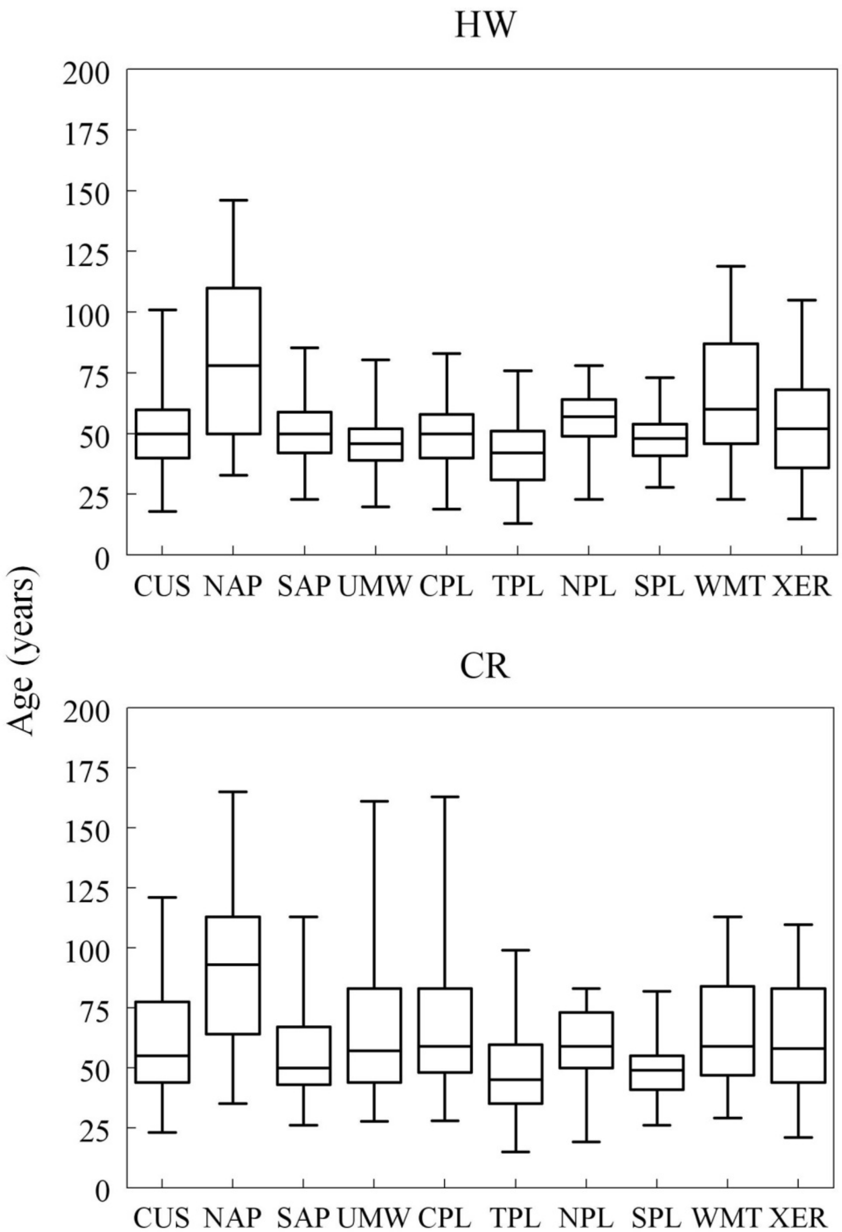

Figure 1.6.—Distribution of dam age in years for headwater (HW) and creek (CR) size strata for the conterminous U.S. (CUS) and ecoregions. Box plot whiskers represent the 5th and 95th percentiles.

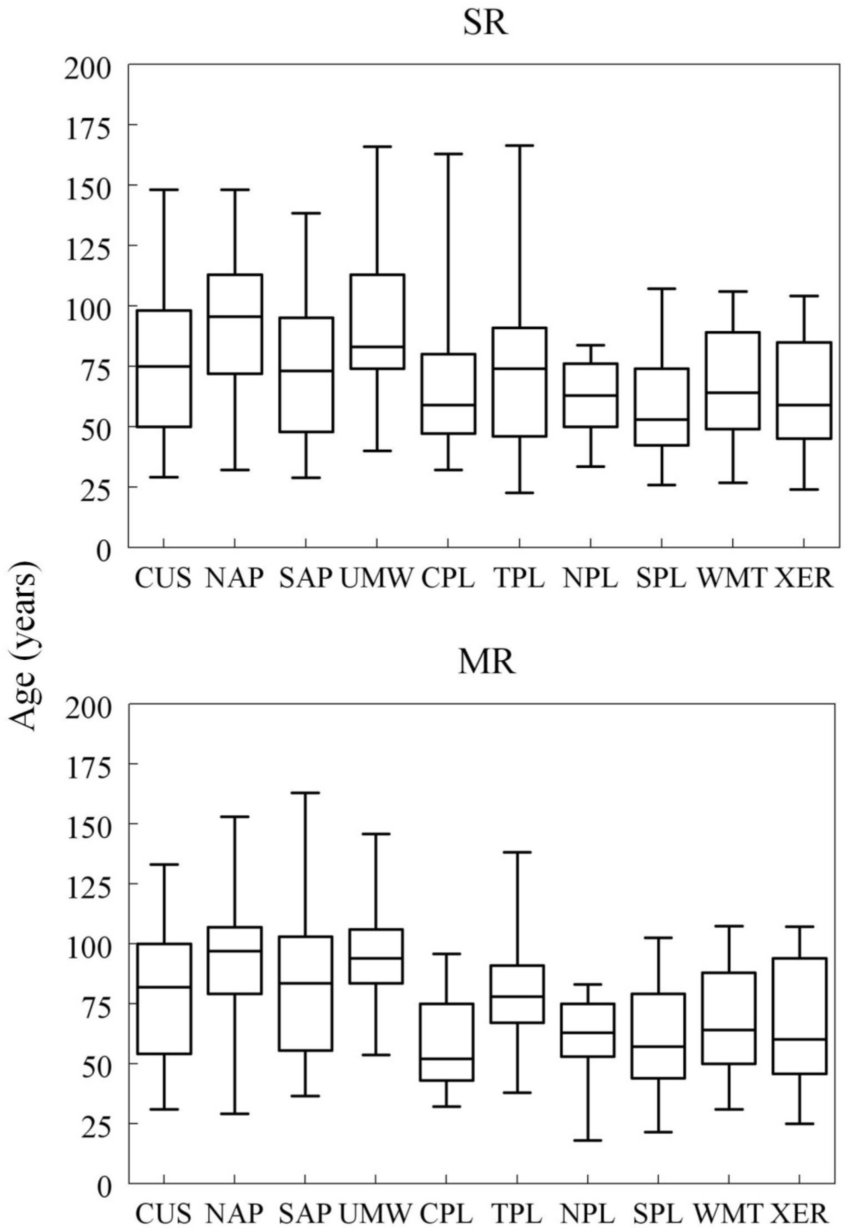

Figure 1.7.—Distribution of dam age in years for small river (SR) and medium river (MR) size strata for the conterminous U.S. (CUS) and ecoregions. Box plot whiskers represent the 5th and 95th percentiles.

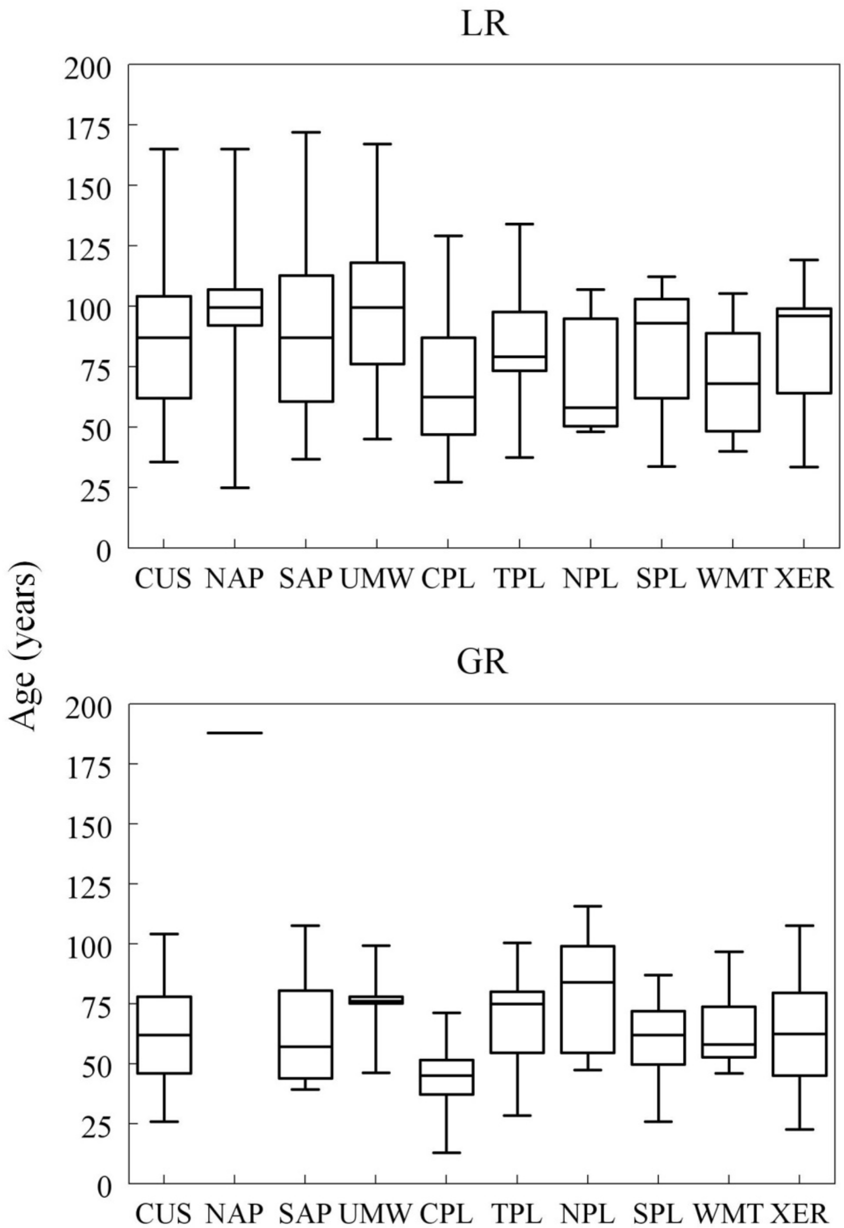

Figure 1.8.—Distribution of dam age in years for large river (LR) and great river (GR) size strata for the conterminous U.S. (CUS) and ecoregions. Box plot whiskers represent the 5^{th} and 95^{th} percentiles.

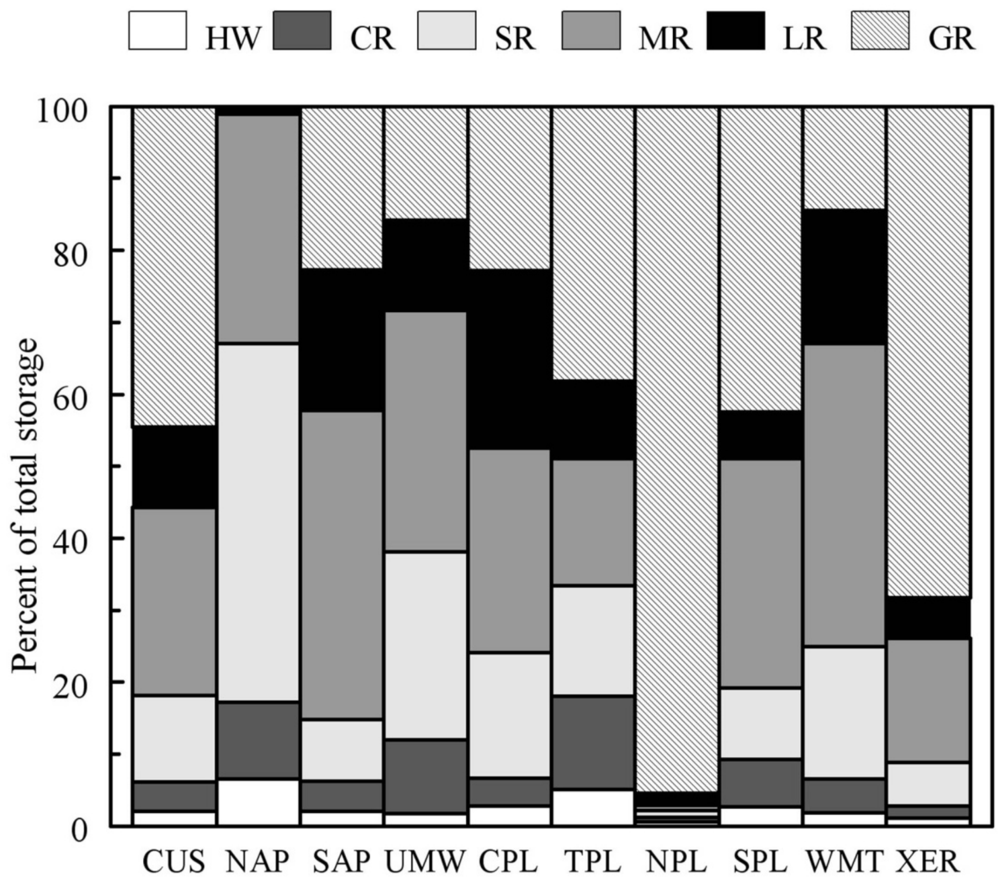

Figure 1.9.—Stacked bar graph of overall reservoir storage showing total contribution of each size stratum for the conterminous U.S. (CUS) and ecoregions.

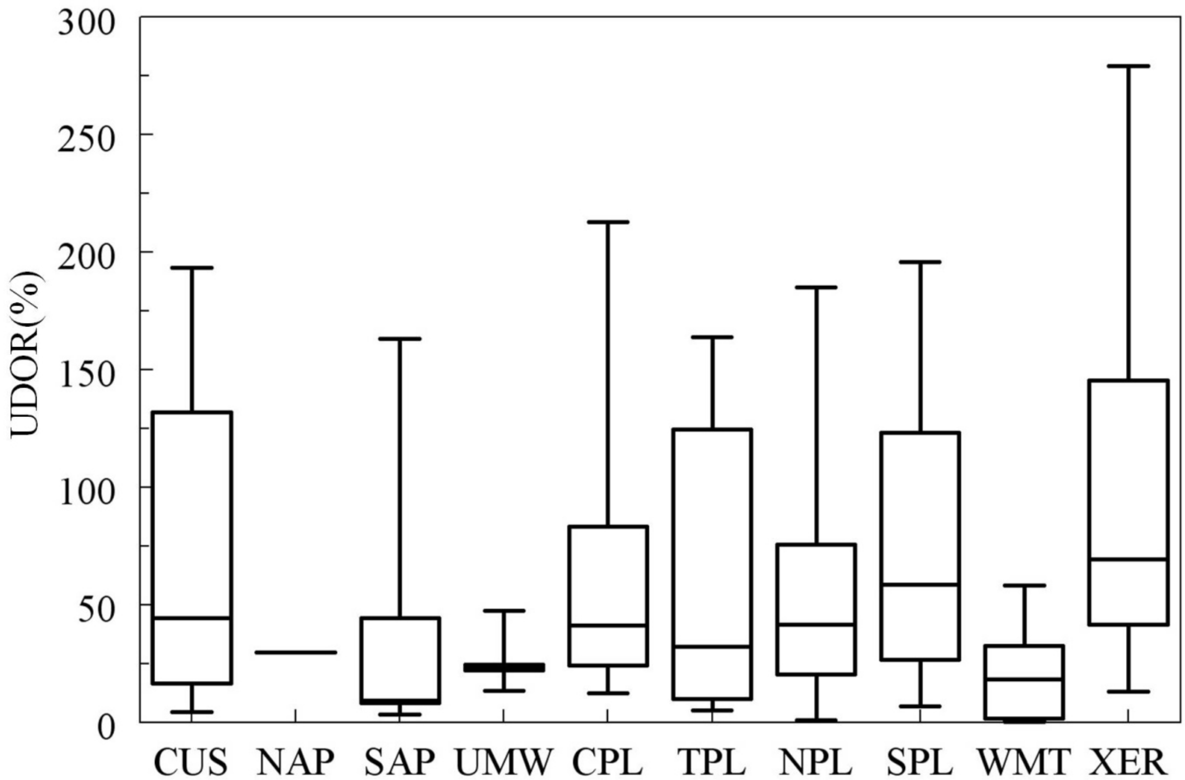

Figure 1.10.—Cumulative upstream degree of regulation (%) for great river segments for the conterminous U.S. (CUS) and by ecoregion (total N = 18,752). Box plot whiskers represent the 5th and 95th percentiles.

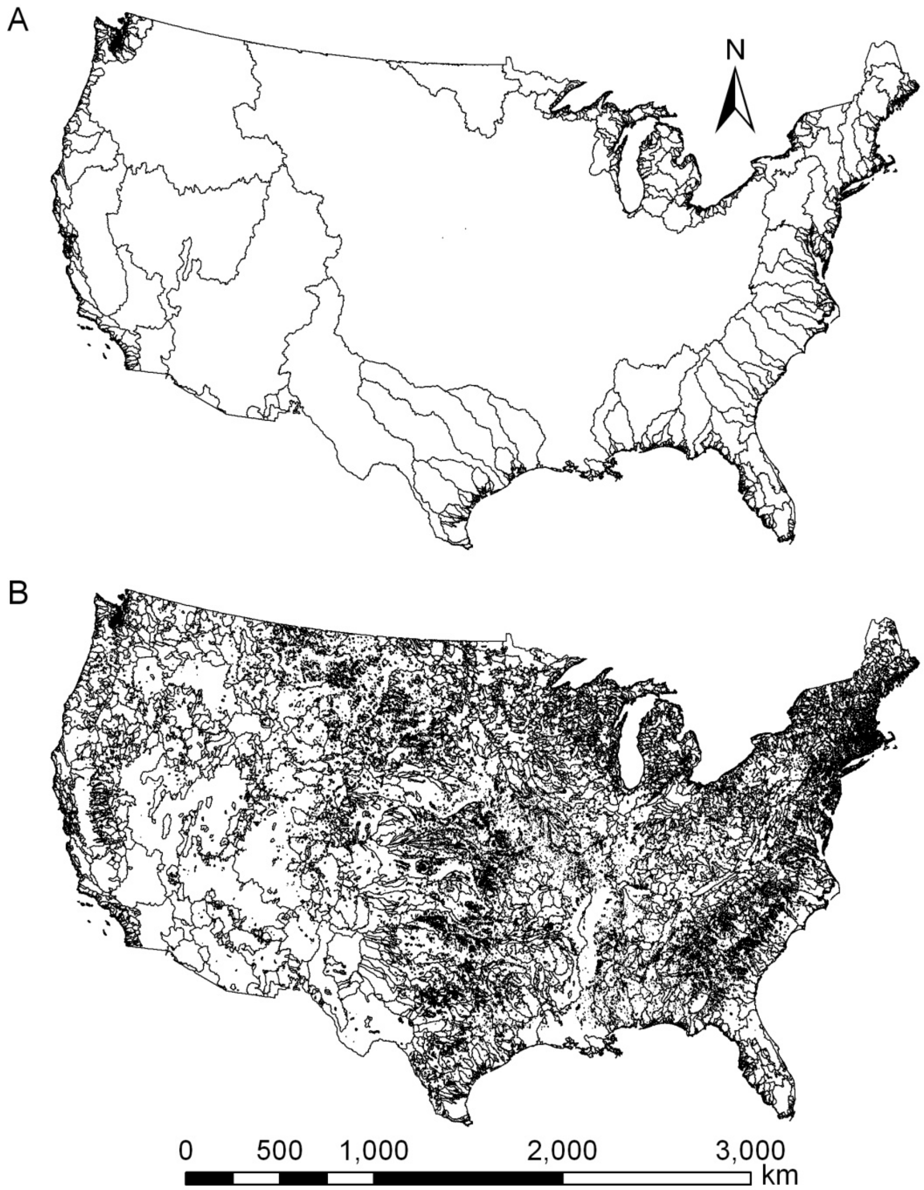

Figure 1.11.—Individual patches in the absence of dams (A; N = 6,037) and the resulting set of artificial habitat patches when accounting for dams (B, N = 54,120).

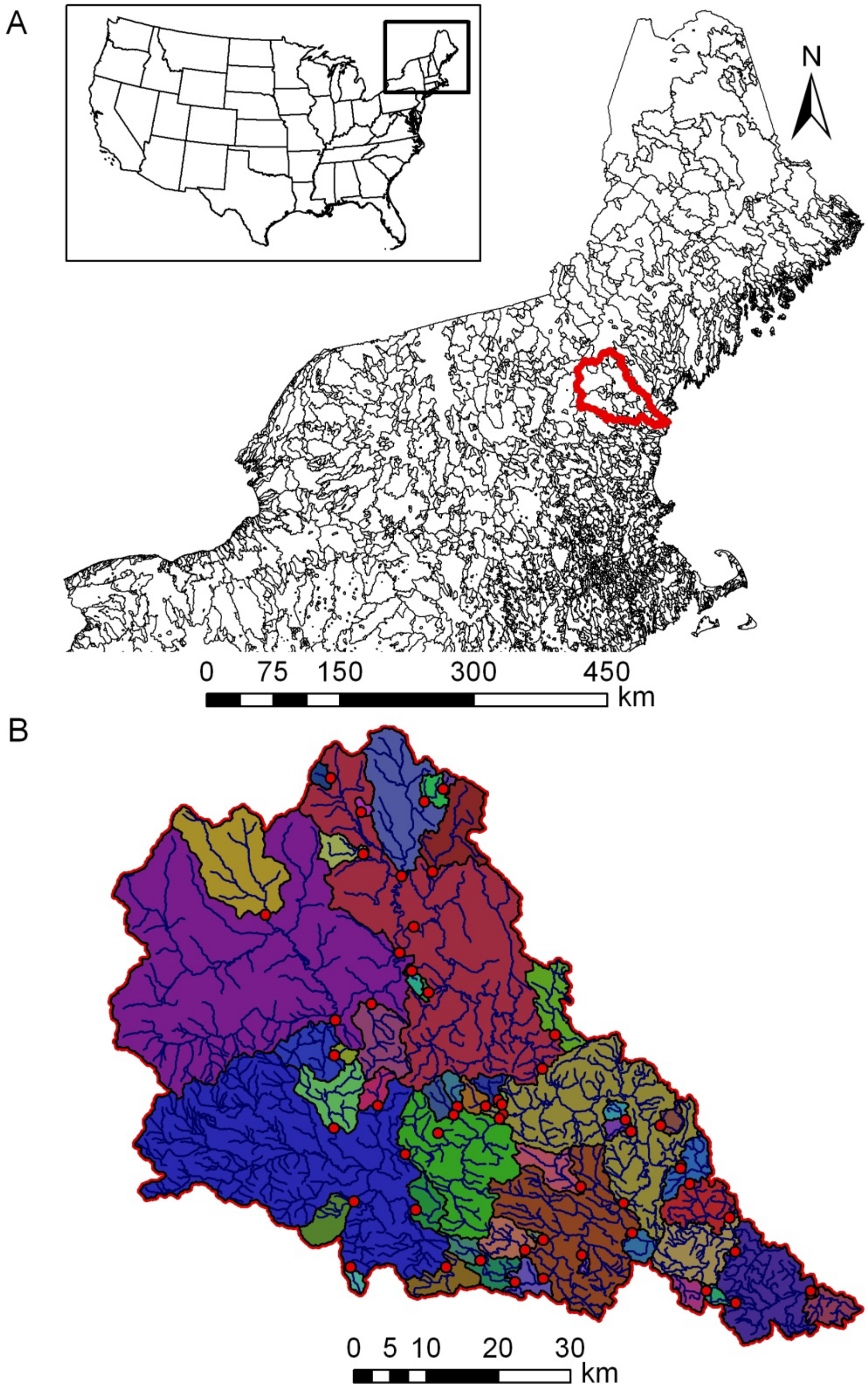

Figure 1.12.—Artificial habitat patches (AHPs) for the northeast U.S. with inset of AHPs for the Saco River (basin highlighted in red in top view). For the bottom view, individual AHPs are given a unique color, with dam locations represented as red points and streams as blue lines.

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CHAPTER 2

EFFECTS OF DAMS ON FLUVIAL FISH ASSEMBLAGES IN MICHIGAN, WISCONSIN, AND MINNESOTA: CONSIDERATION OF MULTIPLE MEASURES OF FRAGMENTATION AND DAM INFLUENCE

ABSTRACT

While the site-specific and localized effects of dams on stream fish assemblages have been relatively well-studied, little is known about dam effects on fishes across much larger geographic scales such as entire river basins, ecoregions, and states. Uncovering patterns in these influences would provide useful information for a variety of management activities, including dam operation and dam removal prioritization. This study evaluated multiple network-based dam measures representing proximity-based (distance-to-dams) and cumulative (e.g. reservoir storage) dam influences for streams of Michigan, Wisconsin, and Minnesota, identifying the species considered to be most sensitive to dam effects. Using change point and correlation analyses, responses of stream fishes indicated by change in catch per unit effort in relation to various dam metrics were analyzed using a total of ~2,000 fish survey sites stratified by stream size, thermal regime, and ecoregion. Of the identified sensitive species, those that were positively associated with greater dam influences were predominantly warmwater, large river, and/or lentic species, while species negatively associated with greater dam influences were cold and coolwater lotic species, suggesting a combination of downstream thermal effects and upstream influences from impoundments generated by dams. A variance partitioning analysis using sensitive species as indicators revealed a transition from upstream-dominated dam influences in headwaters to a mixture of upstream/downstream influences in mid-sized streams. Overall, a combination of proximity-based and cumulative metrics as well as both upstream and downstream-oriented measures were influential in species' responses, emphasizing the importance of selecting a variety of dam measures when assessing the effects of dams on stream fishes. Dams represent unique opportunities for the conservation and management of fishes, which can be aided through the identification of large-scale dam influences on fish assemblages.

INTRODUCTION

Dams represent a complex form of human disturbance to riverine systems, altering habitat both above and below the location of the dam within the stream network. Often these alterations involve multiple facets of abiotic habitat including hydrology, stream temperature, channel morphology, water chemistry, and multiple aspects of hydrologic connectivity throughout river networks. In addition, individual dam influences often vary with factors such as their position within the stream network (Ward and Stanford 1983), the way in which they are managed (Poff et al. 1997), and the length of time that they have been in operation (Poff and Hart 2002). Multiple dams along the stream network can have cumulative effects (e.g. Pringle 2001, Bosch 2008). The complex set of influences that dams can have on stream systems highlights the need to account for dams both spatially and temporally in studies attempting to characterize effects of dams on fluvial habitat and biota. Ultimately, understanding individual and cumulative influence of sources of stream habitat degradation like dams depends on characterizing the location and intensity of each degradation source, as well as the regional context in which disturbances may be occurring (Utz et al. 2010).

Numerous studies have documented the effects of dams on stream fishes, typically by sampling fish or abiotic habitat above and below dams, by comparing surveys between dammed and undammed streams, or by sampling along individual stream networks containing a series of dams. Such studies highlight localized effects of dams, including thermal shifts resulting in decreased abundance of coldwater species, increased prevalence of lentic species above reservoirs, and overall species composition changes (e.g., Lessard and Hayes 2003, Guenther and Spacie 2006, McLaughlin et al. 2006, Slawski et al. 2008). In some cases, studies have observed fish assemblage changes by surveying before and after dam removals (Catalano et al. 2007, however see Stanley et al. 2007). Largely missing are a complimentary set of studies incorporating spatial measures to investigate the influences of dams on fishes across large geographic regions, such as entire river networks, ecoregions, or multi-state regions. Studies such as these could identify patterns of dam influences not observable at smaller scales, or alternatively, could determine if observations made in smaller field-based studies are evident across larger regions. Information provided by large-scale studies could be utilized for prioritizing dam management actions, benefiting fisheries conservation and management.

Recently, studies have begun investigating dam influences on fishes over large-scale regions, often through use of geographic information systems. For example, Fukushima et al. (2007) identified catchment sub-basins isolated by dams for a regional analysis of the presence/absence of fishes on the island of Hokkaido, Japan. Using species-specific generalized linear models, the authors found that fragmentation by downstream dams had an influence on 11 of 41 species studied, with eight migratory species predicted to have decreased occurrences and three non-migratory species predicted to have increased occurrences resulting from greater fragmentation. The authors also created a variable representing the duration of isolation using the year when the dam was built, which was found to be a significant indicator variable in the occurrence models for eight of the 11 impacted species. Similarly, Hall et al. (2011) used dam construction dates obtained from historical records to create a fragmentation timeline for watersheds in Maine. This information was used to calculate the percentage of lake and stream habitat accessible to two species of anadromous river herring, alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), at various time steps. This data allowed the authors to describe current and historic fragmentation patterns, identifying trends in the loss of access to lake and stream habitat through time.

Other studies have focused on how dams alter free-flowing stream lengths, exploring the relationship between stream segment size and fish response. A study by Bain and Wine (2010) analyzed the influence of stream fragment length on fish species diversity, abundance, and size for 31 locations in the Hudson River basin, New York. As expected, species diversity increased as a function of fragment size, however larger fragments did not contain a greater overall fish abundance or wider range of fish sizes as the authors expected, possibly due to the confounding influence of the stocking of the two dominant species in the study area, brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*). The authors found that fragments containing naturally produced brown trout and brook trout were significantly larger than those that did not support reproduction. Perkin and Gido (2011) analyzed river fragment length (largely bounded by dams and reservoirs) for pelagic spawning fishes in the Great Plains region under multiple population status conditions (extirpated, declining, and stable). The authors found significant differences in effect of fragment length both for individual species and for all species combined, with a general pattern of increased fragment length resulting in species moving from extirpated to declining to stable population conditions. The authors also estimated fragment length thresholds associated with the localized extirpation of each species, which together explained 67% of the variation in population persistence among the species studied.

Lastly, Wang et al. (2011a) developed multiple spatially-explicit measures of fragmentation by dams for the states of Michigan and Wisconsin, including distances from a given stream reach to the nearest upstream and downstream dam along the mainstem of the river network, total number and density of dams along all flow paths upstream, and total number and density of dams along the downstream mainstem. These measures were used in a multivariate statistical analysis that partitioned the relative influence of dams from other environmental covariates (non-dam measures that included both natural and anthropogenic variables) using selected Index of Biotic Integrity (IBI) and habitat/social preference fish metrics as response variables. While dam influences only accounted for 16% and 19% of the total variation explained for groups of IBI-based metrics and habitat/social preference metrics respectively, the authors did find that dams had a significant impact (both positive and negative) on fish metrics evaluated in the study. For instance, overall IBI varied with multiple dam measures, including distance-to-dam measures (upstream, downstream, and total free mainstem) and cumulative measures (upstream dam count, downstream dam count and density). These results suggest that key measures of stream fish assemblages are responsive to dam influences 1) in both the upstream and downstream direction, and 2) in both a localized (proximity to individual dams) and cumulative (dam counts/densities within catchments) context.

Despite such advancements in our understanding of dam influences on fish, measuring fragmentation by dams, and river connectivity as whole, continues to present challenges to stream ecologists and managers (Wang et al. 2006, Steel 2010). Although many studies have chronicled the effect of dams on fishes at localized scales (e.g. above or below a dam or before or after a dam removal), few studies have investigated the individual and cumulative effects of dams within river networks across large regions. The ability to discern between localized (resulting from effects of individual dams) and cumulative (resulting from multiple dams located throughout a river network) dam effects, for example, and revealing any changes in the relative influence of such factors throughout the river network would yield a much broader understanding of the complex landscape-scale effects that dams have on fishes. Despite the pervasive threat of dams to lotic systems, dams represent a unique restoration opportunity, one that would be informed by understanding individual species-specific responses to multiple dam measures as a function of network position.

This study addresses these needs through a detailed evaluation of individual fish species responses to network-based dam metrics in the states of Michigan, Wisconsin, and Minnesota. The main objectives of this study are to: 1) Determine which fish species are most sensitive to dam influences, 2) Identify the most influential dam measures as they relate to species responses, and 3) Examine the relative influence of dams on identified sensitive fish species as a function of stream network position (i.e. stream order).

METHODS

Study area and spatial framework

Study area.—The study area occurs throughout the states of Michigan, Wisconsin, and Minnesota, USA, a land area encompassing 514,000 km^2 with approximately 262,000 km of streams (as represented by the 1:100,000 NHDPlusV1; USEPA and USGS 2005). This region has been heavily influenced by glaciation and lacustrine deposition (e.g., Farrand and Bell 1982), leading to a diverse series of surficial geology deposits that vary widely in texture (e.g. coarse vs. fine) and landform (e.g. moraine, outwash plain, lake plain). This geologic and topographic complexity results in highly variable groundwater discharge regimes throughout the region, including streams receiving large amounts of groundwater with relatively stable flow and thermal regimes (commonly draining areas with coarse-textured land forms) to streams driven primarily by surface runoff with "flashy" flow regimes and variable water temperatures (e.g. silt/clay lake plain landform; Seelbach et al. 1997, Zorn et al. 2002).

In addition to highly variable natural features, this region also contains a range of landscape-based anthropogenic disturbances, including human land use, roads, and point-source pollution sites. In general, this gradient has a north/south distribution, from the relatively least-disturbed northern areas dominated by forest and wetlands to highly disturbed areas that are typical of the southern portions of the study region, which contain high levels of agricultural and urban land uses (e.g., Wang et al. 2008).

Spatial data.—The 1:100,000 scale National Hydrography Dataset Plus Version 1 stream network (NHDPlusV1; USEPA and USGS 2005) was used in this study (Chapter 1 Methods). Network catchments (i.e. the cumulative upstream land area draining to a reach, including a reach's local catchment) are not represented as a spatial data layer in the NHDPlusV1, however network catchment attributes can be generated by the upstream aggregation of local catchment data using stream network topology information (Tsang et al. in prep.). This study utilized pre-existing network catchment attributes summarized within a national spatial framework (Wang et al. 2011b), which includes a suite of variables representing both natural and anthropogenic data layers (Table 2.1).

In total, 2,303 dams from the National Anthropogenic Barrier Dataset (NABD; USGS 2013; Chapter 1) were identified as being connected to stream networks within the study region (Figure 2.1). Dam spatial location along the stream network, as well as attributes of individual dams (e.g. reservoir storage), were used to develop a set of 18 metrics describing fragmentation by dams within the study region (Chapter1 Methods; Table 1.1).

Fish data.—Fish survey data were acquired for Michigan, Wisconsin, and Minnesota from respective state natural resource agencies as well as a federal program (U.S. Geological Survey, National Water-Quality Assessment Program). Survey site coordinates were verified against the NHDPlusV1 streams using similar methodology applied for dam site verification, ensuring that survey sites were spatially referenced to the correct stream reach. Any survey locations that could not be ascertained using available site information were not included in this study. A subset of the survey sites were then selected to produce a dataset with comparable survey methodology which covered the time period from 1995 to 2010. These included surveys that targeted community assemblages. We limited the fish data to surveys conducted using either single-pass electrofishing methods (primarily boat, barge, or backpack electrofishing gear), or used only the first pass results from multiple-pass electrofishing surveys. Distances over which surveys were conducted allowed for calculation of individual species catch per unit effort standardized by survey length (#/100 meters of stream length). For survey sites that were sampled more than once, the most recent survey data were used. As a last step, survey sites that had greater than 10% urban and/or greater than 60% agricultural land uses in their network catchments were excluded from analysis, following a previous study of Midwestern streams that identified high levels of anthropogenic land use related to declining fish index of biotic integrity (IBI) scores (Wang et al. 1997). Removing these sites reduced potential influences of highly altered upstream landscapes on stream fish assemblages, which could confound analyses intended to detect relationships between dam metrics and fish responses (Wang et al. 2011a). This process resulted in the initial selection of 442 survey sites for Michigan, 834 survey sites for Wisconsin, and 835 survey sites for Minnesota. We also used Lyons et al. (2009) to characterize the thermal preferences of individual fish species (cold vs. warm) within the study region.

Site stratification.—To account for the large degree of natural variation within the study region and to account for large-scale biogeographic shifts in taxa distribution across the region, a multi-level stratification approach was employed to separate fish sites into distinct groups for analysis. The first level of the stratification consisted of freshwater ecoregions developed by Abell et al. (2008), which were largely determined through analyzing geographic patterns in fish taxa distributions. Ecoregions reflect the influence of large scale "filters" (e.g. Tonn et al. 1990, Poff 1997), including ecological and evolutionary processes, that have shaped contemporary fish biogeography across large regions. The study area included three primary ecoregions: Laurentian Great Lakes (LGL), Upper Mississippi (UM), and English-Winnepeg Lakes (EWL) (Figure 2.1). A fourth ecoregion, Middle Missouri, occurred in southwest Minnesota, however only one fish site was located within this ecoregion after site selection screening process due to high levels of agricultural land use in this area. As a result, this ecoregion was dropped from analysis. The second level of the stratification was stream size, with known influences on distributions of fish species (Lyons 1996, Zorn et al. 2002, Goldstein and Meador 2004). We used Strahler stream order (Straher 1957) to generate three stream size groups: headwater (HW; 1^{st} and 2^{nd} order streams), mid-size (MS; 3^{rd} and 4^{th}), and large size (LS; 5^{th} and 6^{th}). Lastly, sites were classified into two thermal groups, warmwater and coldwater, using stream temperature estimates by Krueger et al. (in prep) for stream reaches throughout Michigan, Wisconsin, and Minnesota that were assigned to a thermal classification first developed in Michigan and Wisconsin by Lyons et al. (2009). Of the 16 resulting strata, 13 had sample sizes deemed large enough for statistical analysis (sample size > 30; e.g., Utz et al., 2010; Table 2.2) resulting in the final selection of 2,067 fish survey sites across the study region (Figure 2.1).

Statistical approaches

Data preparation and variable reduction.—Prior to evaluating the normality of the fragmentation metrics, metrics were transformed using natural log (X + 0.01) for density and storage metrics, arc-sine square root for proportion metrics, and square root for count metrics. The distributions of fragmentation metrics were then evaluated by visually inspecting P-P plots (IBM SPSS Statistics 20 2011). Some fragmentation metrics had highly skewed distributions even after transformation, resulting in use of Spearman correlation (a rank-based non-parametric correlation approach) to evaluate interrelationships between transformed variables. As a first step in metric reduction, dam density metrics were selected over dam count metrics (UMCT, UNCT, DMCT, and TMCT) to better control for the influence of stream size. Next, correlation coefficients among fragmentation metrics were examined for each stratum using SPSS (IBM SPSS Statistics 20 2011), with the least-correlated (typically < 0.8) set of upstream and downstream-oriented metrics being retained to facilitate comparisons among size classes. Of the 14 metrics initially considered, six metrics were retained for the headwater and mid-size classes, while 10 metrics were selected for the large size class, respectively (Table 1.1).

Detecting fish relationships with fragmentation metrics.—Change point analysis was conducted to identify distinct, step function responses of individual fish species to dam fragmentation metrics within each stratum using threshold indicator taxa analysis (TITAN) methodology (Baker and King, 2010). This approach was selected due to its ability to test for step function responses of individual taxa (as opposed to threshold approaches that are used only for pooled, community responses), including those that occur at relatively low frequencies or have highly variable abundance (Baker and King 2010) and for its ability to detect associations between taxa and environmental factors. TITAN employs a rigorous multi-step significance screening process to identify responses. This screening process includes testing for significant p-values from indicator species analysis results (Dufrene and Legendre 1997) using random permutations of the environmental variable. For this study, we chose to use 250 permutations and a p-value of 0.05 for the indicator species analysis cutoff. Next, TITAN uses bootstrap replicates (N = 500 for this study) to provide measures of purity, the proportion of replicates matching the direction of the observed species response (positive or negative), and reliability, the proportion of bootstrap-derived thresholds that result in indicator species analysis p-values that fall below a defined probability level (Baker and King 2010). In this study, we selected species with purity values >=0.95 (i.e., 95% or more of bootstrap replicates matched the observed response direction) and reliability values of >=0.95 at the 0.05 probably level (i.e. 95% of replicates had indicator values resulting in p-values <= 0.05) and >=0.5 for the 0.01 probability level, respectively. Prior to analysis, species catch per unit effort data were log transformed (log (x + 1)) to reduce the effect of species of with highly variable abundances on species indicator analysis results (Baker and King, 2010). Species with less than 20 occurrences for a given fragmentation metric (including 'conditional' metrics, such as distances-to-dam measures) within a stratum were removed from the analysis to eliminate rare and underrepresented species. The untransformed fragmentation metrics were used as the environmental variables in the threshold analysis. TITAN threshold analysis was performed using the TITAN package available for R statistical software (R 2.15 2012).

Because relationships between species distributions and fragmentation metrics may not necessarily show abrupt transitions that could be characterized by point change analysis, we also evaluated relationships of species distributions with fragmentation metrics using Spearman correlation analysis. Correlation was performed only on individual species/metric combinations that failed to show a threshold response using the screening process from the change point analysis for each stratum in R statistical software (R 2.15 2012).

Canonical correspondence analysis.—To estimate the relative influences of fragmentation metrics on selected fish species variables, we used the partial canonical correspondence analysis (CCA; e.g. Borcard et al. 1992). We partitioned the total variance explained in fish species indicators (identified in Results) into four variable groupings; natural, non-dam anthropogenic, upstream-oriented fragmentation, downstream-oriented fragmentation using CANOCO 4.5 software (ter Braak and Smilauer 2002). This analysis was performed to investigate overall dam influences when compared to other variables (natural and non-dam anthropogenic) and to identify any changes in the relative orientation (upstream vs. downstream) of dam influences as a function of size and thermal regime across the study region. Although we were primarily interested in assessing dam influences, we also treated natural and non-dam anthropogenic factors as separate variable groups to compare the relative influences of dams to other anthropogenic sources. Based on a regional set of sensitive species (identified using results from steps above), fish indicator variables were chosen for the CCA analysis, emphasizing species that responded similarly within the cold headwater, warm headwater, cold mid-size, and warm mid-size thermal/size classes (see Table 2.2 for sample sizes). The warm large-size class had only one candidate sensitive species and was subsequently dropped from the analysis. We conducted an *a priori* variable reduction by identifying variable pairs with Pearson correlation coefficients > 0.8, retaining the variable among the correlated pair that was deemed more easily interpretable (see Table 2.1 for selected natural and non-dam anthropogenic variables). To account for potential differences in species responses among ecoregions, ecoregion was added as a categorical variable and included in the natural variable group. This process resulted in the selection of six natural variables, five non-dam anthropogenic variables, and five dam metrics, with the dam metrics separated into two upstream-oriented metrics, UMD and USR, and three downstream-oriented fragmentation metrics, DMD, DM2D, and TMO (Tables 1.1 and 2.1).

RESULTS

Site landscape characteristics

Natural landscape characteristics.—Catchment area ranged from one to 93,000 km^2 across sites, with mean catchment areas tending to increase by an order a magnitude when moving from headwaters to mid-size to large size classes (Table C1). While mean catchment areas were similar across all three ecoregions within a given size/temperature class, catchments in coldwater strata were smaller on average than their warmwater counterparts. Overall, sites in the EWL ecoregion had colder mean annual air temperatures with less annual precipitation and base flow than those in the LGL and UM ecoregions. While EWL ecoregion sites had greater mean elevations than those in the LGL and UM ecoregions, they also had lower mean slope with each size/temperature class. Catchment soil permeability was similar across most strata, with the exception of coldwater headwater and mid-size coldwater sites in the UM ecoregion, which had lower permeability than corresponding coldwater EWL and LGL sites. Within mid-size and large size sites, the EWL ecoregion had a lower proportion of coarse-textured lithography than the LGL and UM ecoregions. Average forest land cover varied from 38-59%, with similar values occurring across strata within the same size/temperature class. In general, LGL and UM sites had comparable natural catchment conditions for a given size/temperature class, including mean annual air temperature, annual precipitation, and base flow.

Non-dam anthropogenic landscape factors.—Among non-dam anthropogenic variables, EWL ecoregion sites had lower densities of roads and human population than the LGL and UM ecoregions (Table C1). Average percentage of urbanization and imperviousness was low overall (due to the site selection criteria of <10% urbanization), but tended to be highest in the LGL ecoregion and lowest for the EWL ecoregion. For the EWL ecoregion, the average percentage of agriculture increased within catchments when moving from headwater to mid-size to large size classes. For the LGL ecoregion, coldwater classes had less overall agriculture than corresponding warmwater size classes, however the opposite trend occurred for the UM ecoregion.

Dam metrics.—Upstream mainstem and upstream total river network dam densities ranged from 0.4 to 2.4 dams/100 river km across strata, with the lowest densities found in the EWL ecoregion and highest fluctuating between the LGL and UM ecoregions by stratum (Table C2). Headwaters and mid-size classes were characterized by a high proportion of upstream mainstem openness (~ 0.7 and higher), which dropped for large size classes (range of 0.3-0.5). In general, upstream reservoir storage (per unit catchment area or river network length) tended to increase as a function of increasing size class. Average mainstem lengths (upstream, downstream, and total) were typically longest in the EWL ecoregion for a given stratum and comparable for the LGL and UM ecoregions.

Fish species response to fragmentation

Interpretation of results.—The number of fish species analyzed for each strata ranged from 11 to 40 (Table 2.3) with a total of 59 species in 13 families across all strata. Species were selected that had significant relationships with at least two of the six dam metrics in the headwater and mid-size classes or at least three of 10 dam metrics for the large size class. This led to the identification of a subset of species that were considered sensitive to fragmentation. Within each stratum, relationships (hereafter referred to as “associations”) between each species and dam measure were defined as positive, negative, or mixed through summary of individual species’ responses to multiple dam metrics (Table 1.1 provides examples of how to interpret species responses to each metric). For species associated with two or three metrics, we required unanimous direction among metric responses to assign an association (i.e., for a given species, all responses indicated increasing catch per unit effort with increasing or decreasing fragmentation). For species associated with four or more fragmentation metrics, we required 75% of metric responses to be in agreement. Finally, species not meeting the conditions above were classified as showing a mixed response to fragmentation (Table 2.3). The results below are described for each thermal/size class, with emphasis placed on consistent species responses among strata and the identification of key fragmentation metrics as they relate to the most species responses.

Cold headwaters.—Overall there were 8, 19, and 23 associations identified for the EWL, LGL, and UM ecoregions, respectively (Table 2.3). Within the EWL and LGL ecoregions, there was a relatively even number of positive and negative species associations with few mixed associations, whereas species associations in the UM ecoregion were predominately positive or mixed. No species responded consistently across all three ecoregions, however five species had positive responses to fragmentation in both the LGL and UM ecoregions, including hornyhead chub (*Nocomis biguttatus*) and three centrarchids: rock bass (*Ambloplites rupestris*), bluegill (*Lepomis macrochirus*), and largemouth bass (*Micropterus salmoides*) (Table 2.4). In contrast, two species were negatively associated with fragmentation across two ecoregions, including brook stickleback (*Culaea inconstans*) and pearl dace (*Margariscus margarita*). Three other species, including white sucker (*Catostomus commersonii*), had opposite responses across two or more ecoregions.

For individual dam metrics, a majority of species were associated with downstream-oriented metrics (DM2D, DMD, and TMO) in the LGL and UM ecoregions, compared to the EWL ecoregion, where species' response was mixed between upstream and downstream metrics.

Overall, fish were generally positively associated to upstream metrics in all three ecoregions, while the downstream-oriented metrics tended to have more of a mixture of positive/negative species response.

Warm headwaters.—Compared to other strata, there were relatively few associations detected for species in warm headwaters (Table 2.3). Three species with positive associations with fragmentation in cold headwaters (LGL & UM), bluegill, largemouth bass, and hornyhead chub, also had positive associations in the UM warm headwaters (Table 2.5). Similarly, brook stickleback, negatively associated to fragmentation in cold headwaters (LGL & UM), also had a negative association in the UM warm headwaters. Due to the limited number of associations occurring in the warm headwaters, no trends in species-metric relationships were interpreted.

Cold mid-size.—There were 17 species associations in both the LGL and UM ecoregions, with a majority of associations being positive overall (i.e., species catch per unit effort increased with fragmentation, Table 2.3). Several species with positive associations to fragmentation in cold headwaters also showed positive associations for cold mid-size streams, including rock bass, bluegill, largemouth bass, and hornyhead chub (Table 2.6). Three additional centrarchid species, green sunfish (*Lepomis cyanellus*), pumpkinseed (*Lepomis gibbosus*), and smallmouth bass (*Micropterus dolomieu*) also had positive associations with fragmentation in one or both ecoregions. No species had a consistent negative response to fragmentation across both ecoregions.

For dam metrics, downstream mainstem density (DMD), total mainstem openness (TMO; LGL only) and two upstream-oriented metrics (UNDR & USR) had the greatest number of species-metric relationships (Table 2.6). For both ecoregions, upstream species-metric relationships were predominately positive as was also the case for the cold headwater strata.

Among the upstream-oriented variables, cumulative network metrics (UNDR & USR) tended to have a higher number of associations than the upstream mainstem metric (UMD) for both ecoregions. Overall, there were a comparable number of the upstream and downstream oriented species-metric relationships in both ecoregions.

Warm mid-size.—Total associations identified for warm mid-size strata varied from 13 in the EWL ecoregion to 19 in both the LGL and UM ecoregions, respectively (Table 2.3). Similarly to cold mid-size strata, most species associations were positive across all ecoregions. Two species, bluegill and hornyhead chub, had positive associations to fragmentation in all three ecoregions (Table 2.7). Four additional species had positive associations among two ecoregions, including pumpkinseed, largemouth bass, yellow perch (*Perca flavescens*), and bluntnose minnow (*Pimephales notatus*). In total, six species had negative associations to dam metrics across two ecoregions, which included brassy minnow (*Hybognathus hankinsoni*), burbot (*Lota lota*), and longnose dace (*Rhinichthys cataractae*), the latter two species also having a negative association in the cold mid-size strata.

The dominant dam metrics varied among ecoregions, with influential upstream-oriented metrics varying from largely cumulative upstream metrics (UNDR & USR) in the EWL, to the upstream mainstem metric (UMD) in the LGL ecoregion to a combination of cumulative and mainstem metrics for the UM ecoregion (Table 2.7). In contrast to cold mid-size strata, upstream oriented species-metric relationships in the warm mid-size strata were a mixture of positive and negative species responses (instead of mainly positive only in cold mid-size strata). Among downstream-oriented metrics, there were several relationships observed for the distance to downstream mainstem dam metric (DM2D) metric in the LGL and UM ecoregions (particularly for centrarchids), while none were identified for the EWL ecoregion. Overall, a majority of species-metric relationships were linked to upstream-oriented metrics for all three ecoregions (Table 2.7).

Warm large size.—Within this strata, the number and direction of species associations was highly variable (Table 2.3). Species associations ranged from being entirely positive in the EWL ecoregion to a mixture of responses in the LGL ecoregion to largely negative associations for the UM ecoregion. Of the 18 species associations identified in the UM ecoregion, only two had positive associations to increased fragmentation (Table 2.8). One species, shorthead redhorse (*Moxostoma macrolepidotum*) had a similar response between the LGL and UM ecoregions, while several additional species had conflicting responses among ecoregions.

Overall, fragmentation influences in the EWL and UM ecoregions were a mixture of downstream, upstream, and total mainstem metrics, whereas in the LGL ecoregion species-metric relationships were associated with upstream-oriented fragmentation, namely upstream mainstem density (UMD) and upstream reservoir storage (USR; Table 2.8). For downstream-oriented metrics, most species-metric relationships were associated with the downstream mainstem dam density (DMD) metric and relatively few were linked to the downstream mainstem openness (DMO) metric, particularly for the UM ecoregion.

Region-wide trends.—By evaluating species associations across strata, an overall list of general species sensitive to fragmentation was determined by examining patterns in associations (Table 2.9). Species were selected that had a consistent response direction (either positive or negative) for at least two strata within a thermal/size class. While there were numerous mixed associations identified for some species, the variable nature of their relationship with individual dam metrics (mixture of positive and negative responses) suggests that they do not respond to fragmentation in the same manner.

Across the study region, species associations for warmwater species were largely positive in nature while coldwater species tended to respond negatively to dam influences. In particular, hornyhead chub, yellow perch, and multiple centrarchid species had positive associations to fragmentation across multiple strata despite differences in thermal class and/or stream size (Table 2.9). The majority of species responding negatively to fragmentation were found in the mid-size class, which included six species from five different families. Only two species, pearl dace and brook stickleback, had negative associations in the headwaters while one species, shorthead redhorse, was selected in the large size class due to the lack of consistent species responses across strata. A few species that are among the most ubiquitous across the study region, white sucker, common shiner (*Luxilus cornutus*), and creek chub (*Semotilus atromaculatus*), also had the most variable responses to dams across strata (mixture of positive, negative, mixed, and no associations; Table 2.9).

Both within and across size/thermal classes, there was variation in the key fragmentation metrics. The orientation of these metrics (upstream vs. downstream) tended to differ between coldwater and warmwater strata. For coldwater strata, there appeared to be a transition from downstream-oriented metrics in headwaters to both upstream and downstream metrics for mid-size streams. In contrast, there was greater upstream-oriented dam influence for warm mid-size streams. For the large size class, there was high degree of variability in the key upstream and downstream metrics among ecoregions.

Canonical correspondence analysis results.—Overall, CCA explained between 15 to 28% of the total variation in fish response variables within the four thermal/size classes (Table 2.10). Of the explained variation, natural factors accounted for a majority of the variation in three of four classes, with interaction effects representing a highly variable influence across classes (Figure 2.2). Fragmentation accounted for 10 to 19% of the variation explained across classes while non-dam anthropogenic factors ranged from nine to 29% of variation explained. In the cold headwater and cold mid-size classes, fragmentation accounted for as much or more of the explained variation than non-dam anthropogenic factors, whereas non-dam anthropogenic influences explained twice or more variation than fragmentation in the warm headwater and warm mid-size classes (Table 2.10). Among the variation uniquely explained by fragmentation effects on fish response variables, upstream-oriented influences accounted for more variation within the cold headwater and warm headwater classes, at 63 and 64% of variation, respectively (Table 2.10). In contrast, downstream-oriented fragmentation accounted for a majority of variation attributed to fragmentation in the cold mid-size and warm mid-size classes at 54 and 60%, respectively.

Plots from the CCA analyses showed strong associations between individual species and the natural, dam, and non-dam anthropogenic variables (Figures 2.3-2.6). Among dam variables, TMO and DM2D were strongly positively associated with multiple species depending upon the size/thermal class, including pearl dace, central mudminnow (*Umbra limi*), brook stickleback, yellow perch, and brassy minnow. Conversely, bluegill and largemouth bass tended to be negatively related to the TMO and DM2D variables indicating an association with shorter stream mainstems and closer proximity to downstream dams. In the cold thermal classes, cumulative upstream storage (USR) was positively associated with hornyhead chub and yellow bullhead in the headwaters and bluegill and largemouth bass in mid-size streams (Figures 2.3 and 2.5). Overall, bluegill tended to be associated with a mixture of dam and non-dam anthropogenic influences.

DISCUSSION

This study used landscape-based dam fragmentation measures to explore influences of dams on fish species within the states of Michigan, Wisconsin, and Minnesota, with three main objectives; first to identify a core set of sensitive fish species with respect to stream habitat alterations by dams, secondly to identify key fragmentation metrics related to species responses, and lastly to investigate the relative influence of dams (including upstream vs. downstream influences) on sensitive species when compared with other covariates such as natural and non-dam human disturbance variables. There are three main findings in this study. First, among sensitive species, there was a strong positive association between warmwater species and greater dam effects, while cold/cool water species were negatively associated with dam measures. Secondly, both proximity-based measures to individual dams (e.g. distance to dams, available mainstem length) and cumulative dam measures (e.g. total upstream storage) were influential in changes to the catch per unit effort for sensitive species. Lastly, irrespective of stream temperature class (cold or warm), dam influences on sensitive species transitioned from predominantly upstream-oriented influences in headwaters to greater downstream-oriented influences in mid-size streams.

Overall, a total of 18 sensitive species (out of potential pool of 40 species) were selected due to having consistent responses within one or more size/thermal classes. This level is similar to those found by McLaughlin et al. (2006) (albeit with different study design and response measures) which examined fish species sensitivity to low-head lamprey barriers in the Great Lakes basin by matching streams with barriers to undammed reference streams. Of the 48 species analyzed, the authors considered between 8-19 species as sensitive to dams depending upon the type of sensitivity measure being used (catch per unit effort and two types of ratio measures comparing taxon abundance above and below barriers). One key difference in the results of McLaughlin et al. (2006) and those of the current study is that the authors found a majority of the sensitive species to be underrepresented above barriers (exhibiting a negative response), whereas most species associations in this study were positive in nature (resulting in catch per unit effort with greater fragmentation and dam influence). In examining the thermal preferences for the 18 total species considered sensitive to dams in this study, many of the species with a negative association to dams are considered cold or coolwater species (e.g. mottled sculpin, brook stickleback, burbot, brassy minnow; Lyons et al. 2009) whereas species with positive associations inhabit warmer streams (e.g. black bullhead, bluntnose minnow, yellow perch, hornyhead chub, and multiple centrarchid species; Lyons et al. 2009). This result suggests the potential for wide-scale thermal influence of dams within the study region, as site-specific studies of the impacts of dams on fishes have also observed. For instance, Slawski et al. (2008) detected a transition in coolwater/specialist fish species to warmwater/generalist fish species along dammed mainstem tributaries of the Des Plaines River along the Illinois/Wisconsin border. A study of ten surface-releasing hydropowered dams on coldwater streams in Michigan found increased summer stream temperatures below dams, resulting in decreased densities in three of the four coldwater species studied (Lessard and Hayes 2003). In a related study, Hayes et al. (2008) concluded that when temperature increases substantially (> 2° C) below hydroelectric dams, thermal alterations had a much greater impact on fish communities in coldwater streams than the effects of habitat fragmentation by dams. A study analyzing primary dam purposes of the NABD (dataset used in this study) found that 16% of dams on small rivers in the upper Midwest are hydro-powered, increasing substantially to 65% and 90% for medium and large-sized rivers, respectively (Chapter 1). The thermal influence of surface-releasing dams on cold/coolwater streams could serve as an explanation for the observed increase in catch per unit effort of warm water species, while cold and coolwater species may have reduced catch per unit effort as observed in this study.

In addition to potential downstream thermal effects of dams, conversion of fluvial habitats to the lentic-like impoundments above dams has known consequences on upstream habitat (Pringle 1997) and fish assemblages (Falke and Gido 2006, Sreekantha and Ramachandra 2008). In the current study, centrarchid species were associated with relatively short distances to downstream dams (DM2D and/or TMO metric). A study by Guenther and Spacie (2006) yielded a similar result, finding an increase in the abundance of several centrarchids in streams located above impoundments when compared to undammed streams in the upper Wabash River, Indiana. Despite being commonly associated with lentic and large river habitats (Trautman 1981), the centrarchid species in this study were indicative of fragmentation in headwater (first and second order) systems. An analysis of dam purposes in the upper Midwest, found that a majority of dams on headwaters, creeks, and small rivers are primarily used for recreational purposes (Chapter 1). These headwater recreational dams could be playing a role in this observed pattern, particularly if maintained (and potentially stocked) for warm water sport fishes such as largemouth bass, bluegill, and other centrarchids. In addition, another species, hornyhead chub, exhibited an overwhelmingly positive response to fragmentation across the size and thermal classes in which it occurred. This is consistent with the findings of McLaughlin et al. (2006), who found hornyhead chubs to be abundant above dams when compared to undammed reference streams. Overall, these results suggest that proximity to downstream dams, and the impoundments they form, are playing a role in the increased abundance of certain species, including those typically associated with warm, lentic or large river environments.

While many previous studies have looked at the influence of individual dams on fish assemblages by sampling above and below a dam or by comparing dammed streams to undammed reference streams, few have explored the cumulative effects of dams. The results of this study demonstrate the importance of network-based cumulative dam measures, which aligns with other studies that have found cumulative dam effects on fishes in both upstream and/or downstream directions (Cumming 2004, Slawski et al. 2008, Wang et al. 2011a; however see Santucci et al. 2005). For instance, Cumming (2004) found that fish species richness in headwater streams of Wisconsin was reduced significantly with an increasing number of downstream dams, however other factors related to water volume and temperature were more instrumental in the observed pattern. Slawksi et al. (2011) found a cumulative effect of dams in the Des Plaines River along Illinois/Wisconsin border, as an accumulation of mainstem dams resulted in decreased in fish diversity. Lastly, Wang et al. (2011a) found that a combination of distance-to-dam measures and cumulative measures (e.g. upstream and downstream dam density) were influential for numerous fish indicators, including biotic integrity and habitat/social preference metrics. These studies, along with the current findings, underscore the importance of considering the cumulative effects of dams on fish assemblages in addition to the influence of individual dams, such as connectivity loss.

Results of the variance partitioning analysis showed that natural variables tended to have a greater influence than either dams or other anthropogenic disturbances in all size/thermal classes. This result is not unexpected given the role of natural variables, such as drainage area, stream flow, and temperature regime, in the distribution of fishes within the study region (Lyons et al. 1996, Zorn et al. 2002, Wehrly et al. 2003). Overall, dam influences uniquely contributed between 10-19% of variation explained in sensitive species, which compares closely to variance explained by dam measures in Wang et al. (2011a), at 16% for biotic integrity and 19% habitat and social preference fish indicators, respectively. Although this level might appear to be modest, it is important to view these results in regional context given the multi-scale influences on fish assemblages, including large-scale zoogeographic factors (e.g. historic connectivity, climate, etc.; Wang et al. 2011a). Also, outside of the unique variation attributed to dams, there can be additional interaction effects between dams and other covariates. While the relative influence of dams was comparable between studies, the overall amount of variation explained was much higher for Wang et al. (2011a). There are two likely reasons for this difference. First, a substantial amount of variation was likely accounted for *a priori* in the current study through the size and thermal class stratification employed, whereas Wang et al. (2011a) conducted the analysis across streams of all sizes and thermal regimes in Michigan and Wisconsin. Secondly, Wang et al. (2011a) integrated more overall explanatory variables (23 vs. 16), including reach-level flow and temperature estimates that were unavailable across the current study region. In comparing the relative influences of dams and other anthropogenic factors across thermal classes, dam effects tended to be more prevalent in coldwater streams than warmwater streams. A comparison of non-dam anthropogenic variables between size classes (e.g. MS cold vs. MS warm) shows similar levels (Table C1). As levels of non-dam anthropogenic variables are not appreciably higher in warmwater size classes, these results provide additional support to the importance of thermal influence of dams in coldwater streams. The finding that dams can be a greater influence on fish assemblages than other anthropogenic disturbances in certain cases was shown by Slawski et al. (2008), who found dams had a greater influence on fish composition than urbanization in dammed tributaries of the Des Plaines River. Lastly, variance partitioning showed a transition in upstream vs. downstream influences, with upstream dam measures dominating in the headwaters moving to a slight downstream-oriented majority in mid-size streams in both coldwater and warmwater systems. No other studies have explored the relative landscape-scale effects of upstream vs. downstream dam influences within a region of this size. These results demonstrate the importance of accounting for both upstream and downstream-oriented dam influences, and that other factors, such as the spatial position within the stream network and thermal regime, can play important role in the relative influence of dams at a landscape scale.

Potential improvements

The spatial measures presented in this study aim to broadly represent dam effects across large regions, however they fail to characterize temporal variability in dam effects. For instance, while the cumulative upstream reservoir storage metric used in this study can provide a coarse indication of overall flow alteration, it does not capture within-year flow variability that occurs due to the storage and managed release of water from reservoirs. In addition, measures that incorporate the influence of dams at other spatial scales, such as the size, age, and location within the stream network of river habitat patches formed by the locations of dams (described in Chapter 1), could elucidate additional dam influences not accounted for in the current study. Also, individual fish species catch per unit effort, the response variable used in this study, can undergo a high degree of seasonal variability in studies of the impacts of dams on fishes (Gillette et al. 2005, Buckmeier et al. 2013). Additional analyses accounting for seasonal variability in fish responses may yield insight into the influence of dams on specific life history traits. In addition, certain species may be responding to dams in other ways not adequately measured by their abundance. For instance, numerous studies have documented the genetic influences of river fragmentation by dams, resulting in intrapopulation homogeneity and interpopulation heterogeneity (e.g., Yamomoto et al. 2004, Heggenes and Roed 2006). Ultimately, accounting for the full effect of dams on stream fishes would likely involve both the use of additional types of data (e.g. patches, seasonal sampling) and multiple response measures in addition to those used in the current study.

Conclusion

While there have been a number of studies analyzing the effects of dams on fishes, few have incorporated cumulative measures, particularly across large geographic areas. Landscape-scale analyses of the effect of dams on fishes can complement smaller scale field studies by determining if results extend beyond the particular stream system studied to a larger region, or identify patterns of dam influence occurring at larger, regional scales. The findings in this study underscore the importance of accounting for not only the downstream effect of upstream dams, but also the upstream effect of downstream dams. In addition, a mixture of metrics capturing both individual (proximity-based) and cumulative influences will be required in order to gain the full breadth of the effects of dams on fishes.

APPENDICES

APPENDIX A

TABLES

Table 2.1.— Source datasets for the natural and non-dam anthropogenic variables summarized for network catchments of stream reaches.

Variable	Description	Units	Source	Dataset	Scale/Resolution	Currentness
AREA[1]	Catchment area	km^2	EPA/USGS	National Hydrography Dataset Plus v. 1	1:100,000	2006
PPT[1]	Mean annual precipitation	mm	EPA/USGS	National Hydrography Dataset Plus v. 1	4 km	1960-1990
MAAT	Mean annual air temperature	degrees celsius	EPA/USGS	National Hydrography Dataset Plus v. 1	4 km	1960-1990
BFIC[1]	Baseflow index	%	USGS	Base-flow Index Grid for the Conterminuous United States	1 km	2003
ELEV	Mean catchment elevation	masl	EPA/USGS	National Elevation Dataset	30m	2006
SLP[1]	Catchment slope	degrees	EPA/USGS	Derived from National Elevation Dataset	30m	2006
SOIL	Soil permeability	inches/hour	USGS	Soils Data for the Conterminuous United States	1:250,000	1995
FINE	Fine-textured surficial lithography	%	USGS	Surficial Lithography	1 km	2004
CRSE[1]	Coarse-textured surficial lithography	%	USGS	Surficial Lithography	1 km	2004

Table 2.1 (cont'd).

Variable	Description	Units	Source	Dataset	Scale/Resolution	Currentness
URB[2]	Developed low intensity, developed medium intensity, and developed high intensity	%	MRLC[a]	National Land Cover Database	30 m	2001
AG[2]	Pasture/hay and cultivated crops	%	MRLC[a]	National Land Cover Database	30 m	2001
FRST	Deciduous forest, evergreen forest, and mixed forest	%	MRLC[a]	National Land Cover Database	30 m	2001
IMP	Imperviousness	%	MRLC[a]	National Land Cover Database	30 m	2001
POP[2]	Population density	$\#/km^2$	NOAA	U.S. Population 2000	1 km	2000
RDC[2]	Road crossing density,	$\#/km^2$	US Census	Census 2000 TIGER Roads	1:100,000	2000
RDL[2]	Road length density	km/km^2	US Census	Census 2000 TIGER Roads	1:100,000	2000

[1] Variable included in natural variable grouping for CCA analysis.

[2] Variable included in non-dam anthropogenic variable grouping for CCA analysis.

[a] Multi-Resolution Land Characteristics Consortium

Table 2.2.—Number of sites for each ecoregion, stream size, and temperature class grouping. Numbers shown in bold indicate groupings used in the univariate threshold and correlation analyses. For the multivariate CCA analysis, sites used in the univariate analyses were grouped across ecoregions within a given size/temperature stratum indicated by the CCA Total. A dash (-) indicates that there were no sites for a given stratum or grouping.

Ecoregion	Size/Thermal Class					
	HW		MS		LS	
	Cold	Warm	Cold	Warm	Cold	Warm
EWL	**68**	19	7	**95**	-	**34**
LGL	**348**	**70**	**200**	**102**	1	**50**
UM	**582**	**89**	**255**	**122**	2	**67**
Total	998	178	462	319	3	151
CCA Total	998	159	455	319	-	-

Table 2.3.—Number of species associations by strata. Overall association of species with greater levels of fragmentation are summarized as positive, negative, or mixed (See Results for definitions).

Size/Thermal Class	Ecoregion	Sites	Species	Assoc.	Positive	Negative	Mixed
HW Cold	EWL	68	13	8	3	4	1
	LGL	348	29	19	10	7	2
	UM	582	40	23	12	3	8
HW Warm	LGL	70	11	2	1	1	0
	UM	89	12	4	3	1	0
MS Cold	LGL	200	27	17	12	4	1
	UM	255	32	17	12	2	3
MS Warm	EWL	95	29	19	12	7	0
	LGL	102	24	13	7	6	0
	UM	122	36	19	12	6	1
LS Warm	EWL	34	11	5	5	0	0
	LGL	50	10	6	2	1	3
	UM	67	27	18	2	13	3

Table 2.4.—Significant change point threshold (t) and Spearman correlation analysis (s) results characterizing relationships between fish species catch per unit effort and selected dam metrics (Table 1.1). For Spearman correlation, significance was determined by $p<0.05$; see Methods for criteria used to determine significance of threshold results. Overall association of species with greater levels of fragmentation are summarized as positive (P), negative (N), or mixed (M). Asterisks (*) indicate an insufficient number of species occurrences to perform analyses for a given metric. Results shown are for the cold headwater strata in the EWL, LGL, and UM ecoregions.

					Fragmentation Metric						
Ecoregion	Family	Genus and Species	Common Name	Assoc.	DM2D	DMD	TMO	UMD	UNDR	USR	Count
	Catostomidae										
		Catostomus commersonii	white sucker	N	+ s	- t	+ t				3
	Cyprinidae										
		Luxilus cornutus	common shiner	P	*	- s		+ s	+ s	+ s	4
		Margariscus margarita	pearl dace	N	*	- t	+ s				2
		Notropis heterolepis	blacknose shiner	P	*			+ s	+ s	+ s	3
EWL		*Rhinichthys atratulus*	eastern blacknose dace	P	*			+ s	+ s	+ s	3
	Percidae										
		Etheostoma nigrum	johnny darter	M	*	- t	+ t	+ s	+ s	+ s	5
		Percina maculata	blackside darter	N	*	- t	+ t				2
	Umbridae										
		Umbra limi	central mudminnow	N	+ t	- s	+ t				3
				Met. Cnt	2	6	5	4	4	4	
	Catostomidae										
		Catostomus commersonii	white sucker	P		+ t	- t		+ s	+ s	4
	Centrarchidae										
		Ambloplites rupestris	rock bass	P	*		- s	+ s	+ t	+ t	4
LGL		*Lepomis cyanellus*	green sunfish	P	- t		- t		+ s	+ s	4
		Lepomis macrochirus	bluegill	P	*		- t	+ s	+ s	+ s	4
		Micropterus salmoides	largemouth bass	P	- s	+ t	- t		+ s	+ s	5
	Cottidae										
		Cottus bairdii	mottled sculpin	M		+ t		- s			2

Table 2.4 (cont'd).

Ecoregion	Family Genus and Species	Common Name	Assoc.	DM2D	DMD	TMO	UMD	UNDR	USR	Count
				Fragmentation Metric						
LGL	Cyprinidae									
	Luxilus cornutus	common shiner	P	+ t	+ s	- t	+ s			4
	Margariscus margarita	pearl dace	N	+ t		+ t				2
	Nocomis biguttatus	hornyhead chub	P	*		- t	+ s	+ s	+ s	4
	Phoxinus eos	northern redbelly dace	N	+ t		+ t				2
	Phoxinus neogaeus	finescale dace	N	*	- t	+ t				2
	Rhinichthys cataractae	longnose dace	N	+ t	- s	+ t				3
	Semotilus atromaculatus	creek chub	P				+ s	+ t		2
	Gasterosteidae									
	Culaea inconstans	brook stickleback	N		- t	+ s	- s	- s	- s	5
	Ictaluridae									
	Ameiurus melas	black bullhead	P		+ t	- t				2
	Salmonidae									
	Oncorhynchus mykiss	rainbow trout	N	*	- t	+ t				2
	Salmo trutta	brown trout	P		+ t	- t		+ s	+ s	4
	Salvelinus fontinalis	brook trout	N		- s	+ t				2
	Umbridae									
	Umbra limi	central mudminnow	M	+ s	+ s	- t				3
			Met. Cnt	7	12	17	7	9	8	
UM	Catostomidae									
	Catostomus commersonii	white sucker	M		+ t	+ t				2
	Centrarchidae									
	Ambloplites rupestris	rock bass	P		+ t		+ t	+ t	+ t	4
	Lepomis macrochirus	bluegill	P		+ s		+ t	+ t	+ t	4
	Micropterus salmoides	largemouth bass	P		+ t		+ s	+ s	+ s	4
	Cottidae									
	Cottus bairdii	mottled sculpin	N	+ t	- t	+ t				3

Table 2.4 (cont'd).

Ecoregion	Family	Genus and Species	Common Name	Assoc.	Fragmentation Metric						Count
					DM2D	DMD	TMO	UMD	UNDR	USR	
UM	Cyprinidae										
		Campostoma anomalum	central stoneroller	N	+ s	- t	+ s				3
		Clinostomus elongatus	redside dace	P	- t	+ t					2
		Hybognathus hankinsoni	brassy minnow	M	+ s	+ t	+ s		+ s	+ s	5
		Luxilus cornutus	common shiner	M	+ s	+ t	+ t		+ s	+ t	5
		Margariscus margarita	pearl dace	M	+ s	+ t	+ s				3
		Nocomis biguttatus	hornyhead chub	P	- t	+ t		+ s	+ t	+ t	5
		Phoxinus eos	northern redbelly dace	M	+ t	+ t					2
		Phoxinus neogaeus	finescale dace	M	+ t	+ t	+ t				3
		Pimephales promelas	fathead minnow	P		+ t		+ s	+ t	+ t	4
		Semotilus atromaculatus	creek chub	M	+ t	+ t	+ t		+ s	+ s	5
	Gadidae										
		Lota lota	burbot	M	+ t	+ t	+ t		+ s	+ s	5
	Gasterosteidae										
		Culaea inconstans	brook stickleback	N	+ t	+ t		- s	- s		4
	Ictaluridae										
		Ameiurus melas	black bullhead	P		+ t				+ s	2
		Noturus gyrinus	tadpole madtom	P	- t	+ t	- t		+ s	+ t	5
	Percidae										
		Etheostoma exile	Iowa darter	P		+ t			+ s	+ s	3
		Perca flavescens	yellow perch	P		+ t		+ s	+ s	+ s	4
		Percina caprodes	logperch	P	- t	+ t		+ t	+ t	+ t	5
		Percina maculata	blackside darter	P		+ t			+ s	+ s	3
				Met. Cnt	14	23	10	8	15	12	

Table 2.5.—Significant change point threshold (t) and Spearman correlation analysis (s) results characterizing relationships between fish species catch per unit effort and selected dam metrics (Table 1.1). For Spearman correlation, significance was determined by $p<0.05$; see Methods for criteria used to determine significance of threshold results. Overall association of species with greater levels of fragmentation are summarized as positive (P), negative (N), or mixed (M). Asterisks (*) indicate an insufficient number of species occurrences to perform analyses for a given metric. Results shown are for the warm headwater strata in the LGL and UM ecoregions.

					Fragmentation Metric						
Ecoregion	Family	Genus and Species	Common Name	Assoc.	DM2D	DMD	TMO	UMD	UNDR	USR	Count
LGL	Salmonidae										
		Salvelinus fontinalis	brook trout	P		+ t	- t				2
	Umbridae										
		Umbra limi	central mudminnow	N					- s	- s	2
				Met. Cnt	0	1	1	0	1	1	
UM	Centrarchidae										
		Lepomis macrochirus	bluegill	P				+ s	+ t	+ t	3
		Micropterus salmoides	largemouth bass	P	- s		- t	+ s	+ t	+ t	5
	Cyprinidae										
		Nocomis biguttatus	hornyhead chub	P		+ s			+ s	+ s	3
	Gasterosteidae										
		Culaea inconstans	brook stickleback	N	+ t		+ t				2
				Met. Cnt	2	1	2	2	3	3	

Table 2.6.—Significant change point threshold (t) and Spearman correlation analysis (s) results characterizing relationships between fish species catch per unit effort and selected dam metrics (Table 1.1). For Spearman correlation, significance was determined by $p<0.05$; see Methods for criteria used to determine significance of threshold results. Overall association of species with greater levels of fragmentation are summarized as positive (P), negative (N), or mixed (M). Asterisks (*) indicate an insufficient number of species occurrences to perform analyses for a given metric. Results shown are for the cold mid-size strata in the LGL and UM ecoregions.

					Fragmentation Metric						
Ecoregion	Family	Genus and Species	Common Name	Assoc.	DM2D	DMD	TMO	UMD	UNDR	USR	Count
	Catostomidae										
		Catostomus commersonii	white sucker	P		+ t	- t		+ s		3
		Hypentelium nigricans	northern hog sucker	P			- t		+ t		2
	Centrarchidae										
		Ambloplites rupestris	rock bass	P			- t	+ t	+ s	+ t	4
		Lepomis cyanellus	green sunfish	P		+ t	- t	+ s	+ t	+ s	5
		Lepomis macrochirus	bluegill	P	*	+ s	- t	+ s	+ s	+ t	5
		Micropterus dolomieu	smallmouth bass	P	*			+ s		+ s	2
		Micropterus salmoides	largemouth bass	P		+ s	- s		+ t	+ t	4
LGL	Cyprinidae										
		Nocomis biguttatus	hornyhead chub	P			- t	+ t	+ t	+ t	4
		Rhinichthys cataractae	longnose dace	N		- t	+ t				2
	Gadidae										
		Lota lota	burbot	N	*	- s	+ t				2
	Gasterosteidae										
		Culaea inconstans	brook stickleback	M	+ t	+ t					2
	Percidae										
		Etheostoma nigrum	johnny darter	P			- s		+ s		2
		Perca flavescens	yellow perch	P		+ s				+ s	2

Table 2.6 (cont'd).

Ecoregion	Family Genus and Species	Common Name	Assoc.	Fragmentation Metric DM2D	DMD	TMO	UMD	UNDR	USR	Count
LGL	Salmonidae									
	Oncorhynchus mykiss	rainbow trout	N		- t	+ t				2
	Salmo trutta	brown trout	P		+ t	- t	+ s	+ t	+ t	5
	Salvelinus fontinalis	brook trout	N					- t	- s	2
	Umbridae									
	Umbra limi	central mudminnow	P		+ t	- s				2
			Met. Cnt	1	11	13	6	10	9	
UM	Catostomidae									
	Moxostoma macrolepidotum	shorthead redhorse	P					+ s	+ t	2
	Centrarchidae									
	Ambloplites rupestris	rock bass	P		+ t				+ s	2
	Lepomis gibbosus	pumpkinseed	P	*			+ s	+ s	+ t	3
	Lepomis macrochirus	bluegill	P		+ t		+ t	+ t	+ t	4
	Micropterus dolomieu	smallmouth bass	P		+ t			+ t	+ t	3
	Micropterus salmoides	largemouth bass	P		+ t		+ t	+ t	+ t	4
	Cottidae									
	Cottus bairdii	mottled sculpin	M	+ t		+ t		+ t	+ s	4
	Cyprinidae									
	Cyprinella spiloptera	spotfin shiner	P		+ t			+ s	+ t	3
	Hybopsis dorsalis	bigmouth shiner	P	- s	+ t					2
	Nocomis biguttatus	hornyhead chub	P	- s	+ t					2
	Rhinichthys cataractae	longnose dace	M		+ t		- s			2
	Semotilus atromaculatus	creek chub	N			+ t	- s			2
	Esocidae									
	Esox lucius	northern pike	P	- t	+ t	- t			+ t	4

Table 2.6 (cont'd).

Ecoregion	Family Genus and Species	Common Name	Assoc.	Fragmentation Metric DM2D	DMD	TMO	UMD	UNDR	USR	Count
	Ictaluridae									
	Noturus gyrinus	tadpole madtom	P		+ t				+ s	2
	Percidae									
UM	*Etheostoma nigrum*	johnny darter	M		+ t			- t		2
	Perca flavescens	yellow perch	P		+ t				+ s	2
	Salmonidae									
	Salmo trutta	brown trout	N	+ t	- t					2
			Met. Cnt	5	13	3	5	7	10	

Table 2.7.—Significant change point threshold (t) and Spearman correlation analysis (s) results characterizing relationships between fish species catch per unit effort and selected dam metrics (Table 1.1). For Spearman correlation, significance was determined by p<0.05; see Methods for criteria used to determine significance of threshold results. Overall association of species with greater levels of fragmentation are summarized as positive (P), negative (N), or mixed (M). Asterisks (*) indicate an insufficient number of species occurrences to perform analyses for a given metric. Results shown are for the warm mid-size strata in the EWL, LGL, and UM

					Fragmentation Metric						
Ecoregion	Family	Genus and Species	Common Name	Assoc.	DM2D	DMD	TMO	UMD	UNDR	USR	Count
	Catostomidae										
		Catostomus commersonii	white sucker	P		+ s	- s				2
		Moxostoma anisurum	silver redhorse	P	*				+ s	+ s	2
		Moxostoma erythrurum	golden redhorse	P	*	+ t	- s	+ t	+ t	+ t	5
		Moxostoma macrolepidotum	shorthead redhorse	P	*				+ t	+ t	2
	Centrarchidae										
		Lepomis macrochirus	bluegill	P	*	+ s				+ s	2
	Cottidae										
		Cottus bairdii	mottled sculpin	N	*	- t	+ t		- t		3
	Cyprinidae										
EWL		*Hybognathus hankinsoni*	brassy minnow	N	*			- s	- s	- t	3
		Hybopsis dorsalis	bigmouth shiner	P	*	+ s			+ s	+ s	3
		Luxilus cornutus	common shiner	P		+ s	- s				2
		Margariscus margarita	pearl dace	N	*			- s	- t	- t	3
		Nocomis biguttatus	hornyhead chub	P		+ t	- t		+ t	+ s	4
		Phoxinus eos	northern redbelly dace	N	*			- s	- t	- t	3
		Pimephales promelas	fathead minnow	P		+ t	- t				2
		Rhinichthys atratulus	eastern blacknose dace	P		+ t	- s				2
		Semotilus atromaculatus	creek chub	P		+ t	- s				2
	Gasterosteidae										
		Culaea inconstans	brook stickleback	N					- s	- s	2

Table 2.7 (cont'd).

Ecoregion	Family Genus and Species	Common Name	Assoc.	Fragmentation Metric DM2D	DMD	TMO	UMD	UNDR	USR	Count
EWL	Percidae									
	Perca flavescens	yellow perch	P		+ s	- s		+ s	+ s	4
	Percina maculata	blackside darter	N		- t	+ t				2
	Umbridae									
	Umbra limi	central mudminnow	N				- s	- s	- s	3
			Met. Cnt	0	12	10	5	12	12	
LGL	Centrarchidae									
	Lepomis cyanellus	green sunfish	P	- t	- t		+ s	+ t		4
	Lepomis gibbosus	pumpkinseed	P	- t			+ t	+ t		3
	Lepomis macrochirus	bluegill	P	- t			+ s			2
	Micropterus salmoides	largemouth bass	P	- t		- t	+ t	+ t	+ t	5
	Cottidae									
	Cottus bairdii	mottled sculpin	N				- t	- t	- s	3
	Cyprinidae									
	Nocomis biguttatus	hornyhead chub	P	- s			+ s			2
	Pimephales notatus	bluntnose minnow	P				+ s	+ s		2
	Rhinichthys cataractae	longnose dace	N	+ t		+ t	- s	- s		4
	Semotilus atromaculatus	creek chub	N		- t				- t	2
	Gadidae									
	Lota lota	burbot	N	+ t		+ t	- t	- t		4
	Ictaluridae									
	Noturus flavus	stonecat	P	*		- t	+ t		+ t	3
	Percidae									
	Etheostoma nigrum	johnny darter	N		- t	+ s				2

Table 2.7 (cont'd).

Ecoregion	Family Genus and Species	Common Name	Assoc.	Fragmentation Metric DM2D	DMD	TMO	UMD	UNDR	USR	Count
	Umbridae									
LGL	*Umbra limi*	central mudminnow	N			+ s	- s		- t	3
			Met. Cnt	7	3	6	11	7	5	
	Centrarchidae									
	Lepomis gibbosus	pumpkinseed	P	- s		- t				2
	Lepomis macrochirus	bluegill	P	- t	- t	- t	+ t	+ t	+ s	6
	Micropterus dolomieu	smallmouth bass	N			+ t	- t			2
	Micropterus salmoides	largemouth bass	P	- t		- t	+ t	+ s	+ t	5
	Pomoxis nigromaculatus	black crappie	P	- t		- s		+ s	+ s	4
	Cyprinidae									
	Cyprinella spiloptera	spotfin shiner	P		- t		+ t	+ s	+ t	4
	Hybognathus hankinsoni	brassy minnow	N				- t	- s	- s	3
UM	*Nocomis biguttatus*	hornyhead chub	P	- t	+ s	- s		+ s	+ s	5
	Pimephales notatus	bluntnose minnow	P	- s		- s	+ s	+ t	+ t	5
	Rhinichthys atratulus	eastern blacknose dace	M		+ t			- s	- s	3
	Rhinichthys cataractae	longnose dace	N	+ t		+ t	- t		- s	4
	Gadidae									
	Lota lota	burbot	N	+ t		+ t	- t			3
	Ictaluridae									
	Ameiurus melas	black bullhead	P				+ s		+ s	2
	Ameiurus natalis	yellow bullhead	P			- s	+ t	+ s	+ t	4
	Noturus gyrinus	tadpole madtom	P		+ s		+ s		+ t	3

Table 2.7 (cont'd).

Ecoregion	Family	Genus and Species	Common Name	Assoc.	Fragmentation Metric						Count
					DM2D	DMD	TMO	UMD	UNDR	USR	
	Percidae										
		Etheostoma nigrum	johnny darter	N			+ t	- s	- t	- t	4
UM		*Perca flavescens*	yellow perch	P		+ t	- t	+ t	+ t	+ t	5
		Percina caprodes	logperch	P					+ s	+ s	2
		Percina phoxocephala	slenderhead darter	N	+ t	- t	+ t	- t	- t	- t	6
				Met. Cnt	9	7	13	14	13	16	

Table 2.8.—Significant change point threshold (t) and Spearman correlation analysis (s) results characterizing relationships between fish species catch per unit effort and selected dam metrics (Table 1.1). For Spearman correlation, significance was determined by p<0.05; see Methods for criteria used to determine significance of threshold results. Overall association of species with greater levels of fragmentation are summarized as positive (P), negative (N), or mixed (M). Asterisks (*) indicate an insufficient number of species occurrences to perform analyses for a given metric. Results shown are for the warm large size strata in the EWL, LGL, and UM ecoregions.

				Fragmentation Metrics										
Eco.	Fam. Genus and Species	Common Name	Assoc.	DM2D	DMD	DMO	TM2D	TMD	TMO	UM2D	UMD	UNDR	USR	Cnt
	Catostomidae													
	Catostomus commersonii	white sucker	P	*				+ t	- t	- t	+ t	+ t	+ t	6
	Moxostoma erythrurum	golden redhorse	P	*	+ t	- s	*	*		*		+ t		3
	Centrarchidae													
	Ambloplites rupestris	rock bass	P	*				+ s	- t				+ s	3
EWL	Cyprinidae													
	Luxilus cornutus	common shiner	P	*	+ t	- t			- t			+ t		4
	Esocidae													
	Esox lucius	northern pike	P	*			- t	+ t		*	+ t			3
			Mt. Cnt	NA	2	2	1	3	3	1	2	3	2	
	Catostomidae													
	Catostomus commersonii	white sucker	P		+ t	- t					- s		+ s	4
	Hypentelium nigricans	northern hog sucker	P	*					- s		+ t	+ t	- t	4
	Moxostoma erythrurum	golden redhorse	M	*	- s						+ t	+ t	- t	4
	Moxostoma macrolepidotum	shorthead redhorse	N	+ t			+ t			+ t		- t	+ s	5
LGL	Cyprinidae													
	Cyprinus carpio	common carp	M	*	- t			+ t	- s		+ t		- s	5
	Percidae													
	Percina caprodes	logperch	M	*	+ s		+ s		*		- t		+ t	4
			Mt. Cnt	1	4	1	2	1	2	1	5	3	6	

Table 2.8 (cont'd).

Eco.	Fam. Genus and Species	Common Name	Assoc.	DM2D	DMD	DMO	TM2D	TMD	TMO	UM2D	UMD	UNDR	USR	Cnt
				Fragmentation Metrics										
	Catostomidae													
	Catostomus commersonii	white sucker	N		+ t		+ t		+ t		- t	- t		5
	Hypentelium nigricans	northern hog sucker	N		- t			- t				+ t	- t	4
	Moxostoma anisurum	silver redhorse	N	+ s	- t	+ s		- t				+ s	- t	6
	Moxostoma erythrurum	golden redhorse	N	+ t	- t	+ t	+ t	- t	+ s			+ t	- t	8
	Moxostoma macrolepidotum	shorthead redhorse	N				+ t	- t	+ t	+ t		+ t	- t	6
	Moxostoma valenciennesi	greater redhorse	N						+ t	+ t			- t	3
	Centrarchidae													
	Ambloplites rupestris	rock bass	N		+ t		+ t		+ t		- t			4
	Micropterus dolomieu	smallmouth bass	M					- s				+ t	- s	3
	Micropterus salmoides	largemouth bass	M		+ t		+ s				- t		+ t	4
UM	Cyprinidae													
	Cyprinella spiloptera	spotfin shiner	N	+ s		+ s	+ t		+ t					4
	Cyprinus carpio	common carp	P		- t		- t	+ t	- t	- t	+ t			6
	Luxilus cornutus	common shiner	N		+ t		+ t		+ t	+ t	- t			5
	Notropis atherinoides	emerald shiner	P		- t		- t		- t	- t	+ t			5
	Notropis stramineus	sand shiner	N		- t			- t				+ t	- t	4
	Notropis volucellus	mimic shiner	N		- t		+ t	- t	+ t			+ t	- s	6
	Percidae													
	Etheostoma nigrum	johnny darter	N		+ t		+ t		+ t	+ t	- t			5
	Perca flavescens	yellow perch	M		+ t		+ t		+ s		- t		+ t	5
	Percina maculata	blackside darter	N		- t			- t		+ s		+ t	- s	5
			Mt. Cnt	3	14	3	12	9	12	7	8	9	11	

Table 2.9.—Overall set of sensitive species (highlighted in gray) within the study region with species associations expressed as positive (P), negative (N), mixed (M), and no association (#) by stratum. Blanks indicate that no analyses were run either due to species absence within a strata or an insufficient number of species occurrences. Species selected for CCA analysis are shown with numeric superscripts.

			HW Cold			HW Warm		MS Cold		MS Warm			LS Warm		
Family	Genus and Species	Common Name	EWL	LGL	UM	LGL	UM	LGL	UM	EWL	LGL	UM	EWL	LGL	UM
Catostomidae															
	Catostomus commersonii	white sucker	N	P	M	#	#	P	#	P	#	#	P	P	N
	Moxostoma macrolepidotum	shorthead redhorse							P	P		#	#	N	N
Centrarchidae															
	Ambloplites rupestris [1,3]	rock bass		P	P			P	P	#	#	#	P	#	N
	Lepomis gibbosus [4]	pumpkinseed		#	#			#	P		P	P			
	Lepomis macrochirus [1,2,3,4]	bluegill		P	P		P	P	P	P	P	P			#
	Micropterus dolomieu [3]	smallmouth bass						P	P	#	#	N	#	#	M
	Micropterus salmoides [1,2,3,4]	largemouth bass		P	P	#	P	P	P		P	P			M
Cottidae															
	Cottus bairdii [4]	mottled sculpin		M	N	#	#	#	M	N	N	#			
Cyprinidae															
	Hybognathus hankinsoni [4]	brassy minnow			M				#	N		N			
	Luxilus cornutus	common shiner	N	P	M	#	#	#	#	P	#	#	P		N
	Nocomis biguttatus [1,2,3,4]	hornyhead chub		P	P		P	P	P	P	P	P			#
	Pimephales notatus [4]	bluntnose minnow		#	#			#	#		P	P			#
	Margariscus margarita [1]	pearl dace	N	N	M					N					
	Rhinichthys cataractae [4]	longnose dace		N	#		#	N	M	#	N	N			
	Semotilus atromaculatus	creek chub	#	P	M	#	#	#	N	P	N	#			

Table 2.9 (cont'd).

Family Genus and Species	Common Name	HW Cold EWL	HW Cold LGL	HW Cold UM	HW Warm LGL	HW Warm UM	MS Cold LGL	MS Cold UM	MS Warm EWL	MS Warm LGL	MS Warm UM	LS Warm EWL	LS Warm LGL	LS Warm UM
Gadidae														
Lota lota [4]	burbot		#	M			N	#		N	N			#
Gasterosteidae														
Culaea inconstans [1,2]	brook stickleback	#	N	N	#	N	M	#	N		#			
Ictaluridae														
Ameiurus melas [1]	black bullhead		P	P						#	P			
Percidae														
Etheostoma nigrum [4]	johnny darter	N		#	#	#	P	M	#	N	N	#		N
Perca flavescens [3,4]	yellow perch		#	P			P	P	P	#	P		#	M
Umbridae														
Umbra limi [2,4]	central mudminnow	N	M	#	N	#	P	#	N	N	#			

[1] Species selected as an indicator variable in CCA analysis for the cold headwater class.

[2] Species selected as an indicator variable in CCA analysis for the warm headwater class.

[3] Species selected as an indicator variable in CCA analysis for the cold mid-size class.

[4] Species selected as an indicator variable in CCA analysis for the warm mid-size class.

Table 2.10.—Percentage of variation explained in selected fish response variables by thermal/size class using CCA, subdivided into the percentage of variation explained attributed to natural, non-dam anthropogenic, fragmentation, and interaction components. Fragmentation effects are further separated into the relative upstream and downstream variation explained (Up Frag./Down Frag.) and percentage of overall dam influence (% Up Frag/% Down Frag).

Class	Sites	Total Var. Exp.	Natural	Non-dam Anthro.	Fragmentation	Interaction	Up Frag.	Down Frag.	% Up Frag.	% Down Frag.
HW Cold	998	15.4	42.5	9.3	15.6	32.6	9.9	5.7	63.5	36.5
HW Warm	178	28.2	38.2	29.0	15.2	17.6	9.6	5.6	63.1	36.9
MS Cold	462	18.7	54.9	23.2	19.1	2.8	8.7	10.4	45.7	54.3
MS Warm	319	23.2	27.8	25.7	9.6	36.9	3.9	5.7	40.4	59.6

APPENDIX B

FIGURES

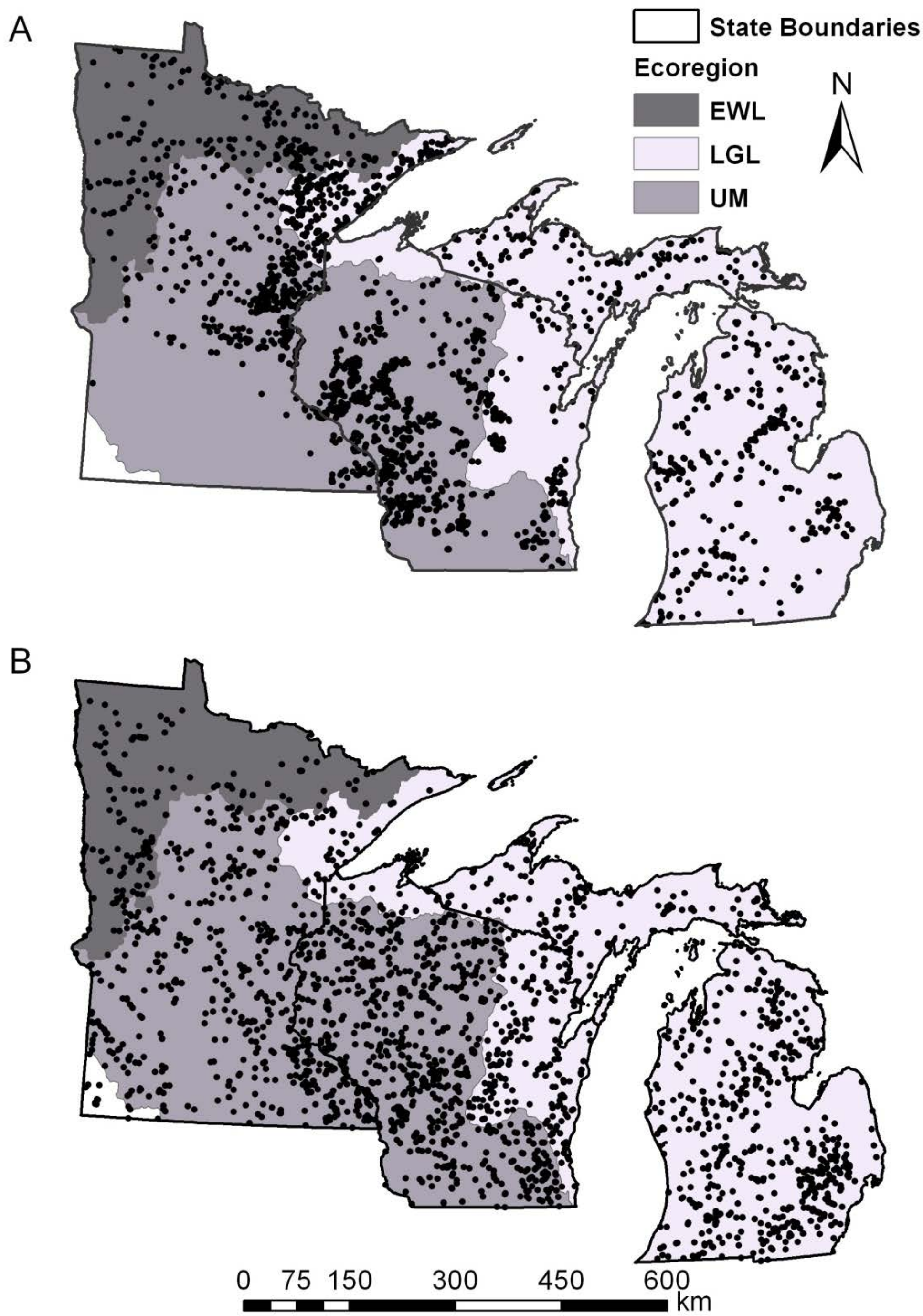

Figure 2.1.—Locations of fish survey sites (N = 2,067; A) and dam locations (N = 2,303; B) within ecoregions of the study region.

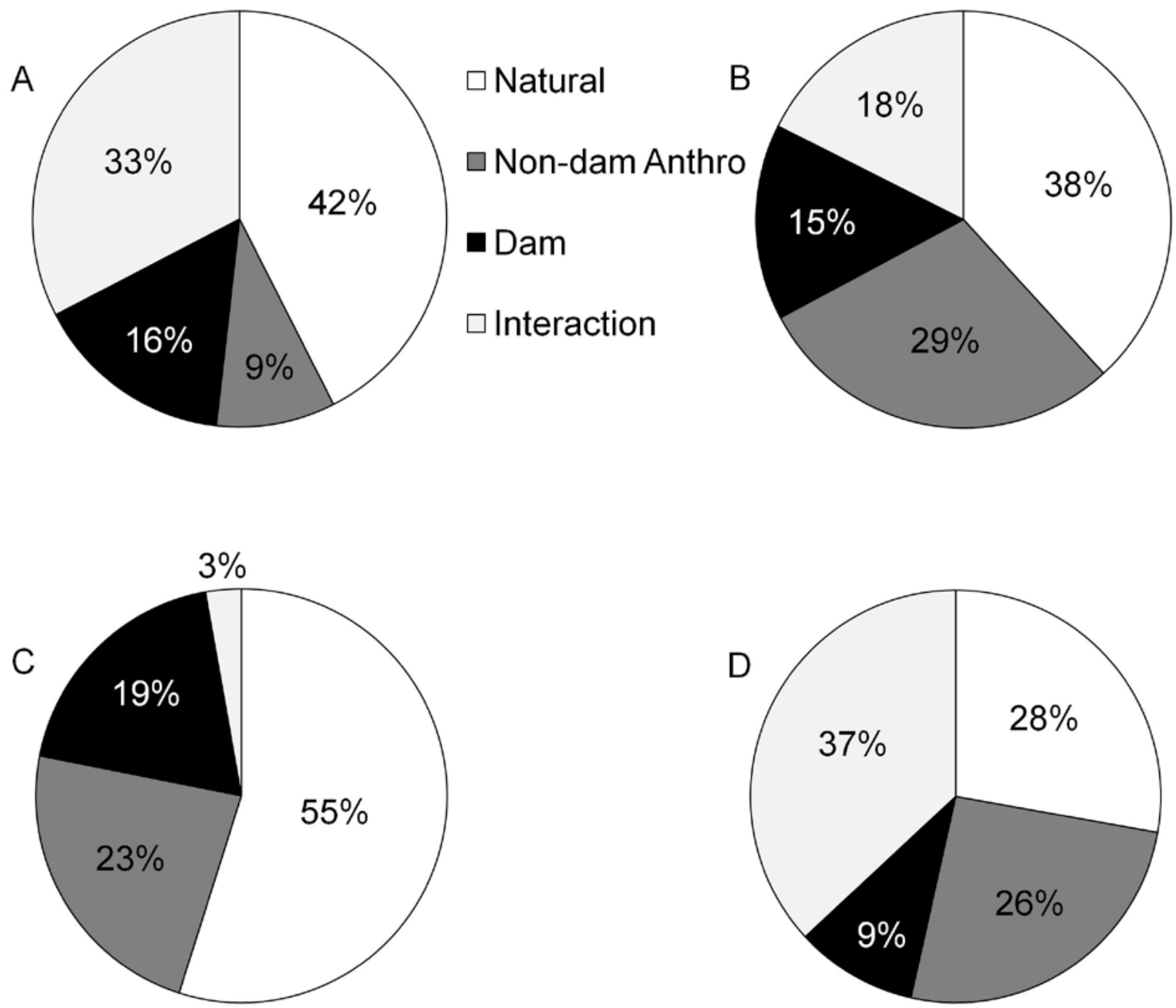

Figure 2.2.—Percentage of variation explained in selected fish indicators partitioned into natural, non-dam anthropogenic, fragmentation by dams, and interaction components using canonical correspondence analysis for cold headwaters (A), warm headwaters (B), cold mid-size (C), and warm mid-size (D) classes.

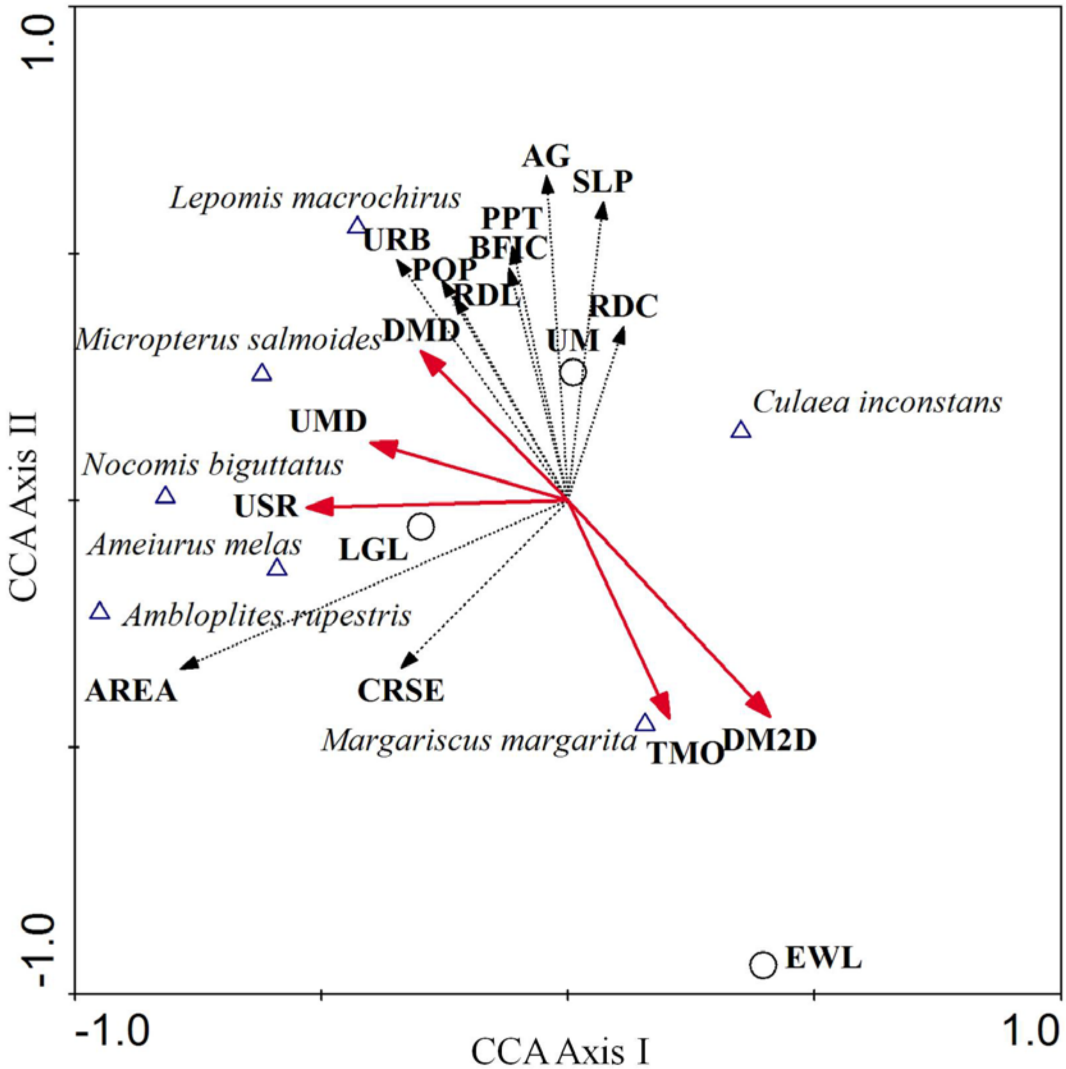

Figure 2.3.—Plot of canonical correspondence axis I vs. axis II for cold headwaters. Abbreviations for natural, non-dam anthropogenic, and dam variables are found in Tables 1.1 and 2.1. Species common names are found in Table 2.9.

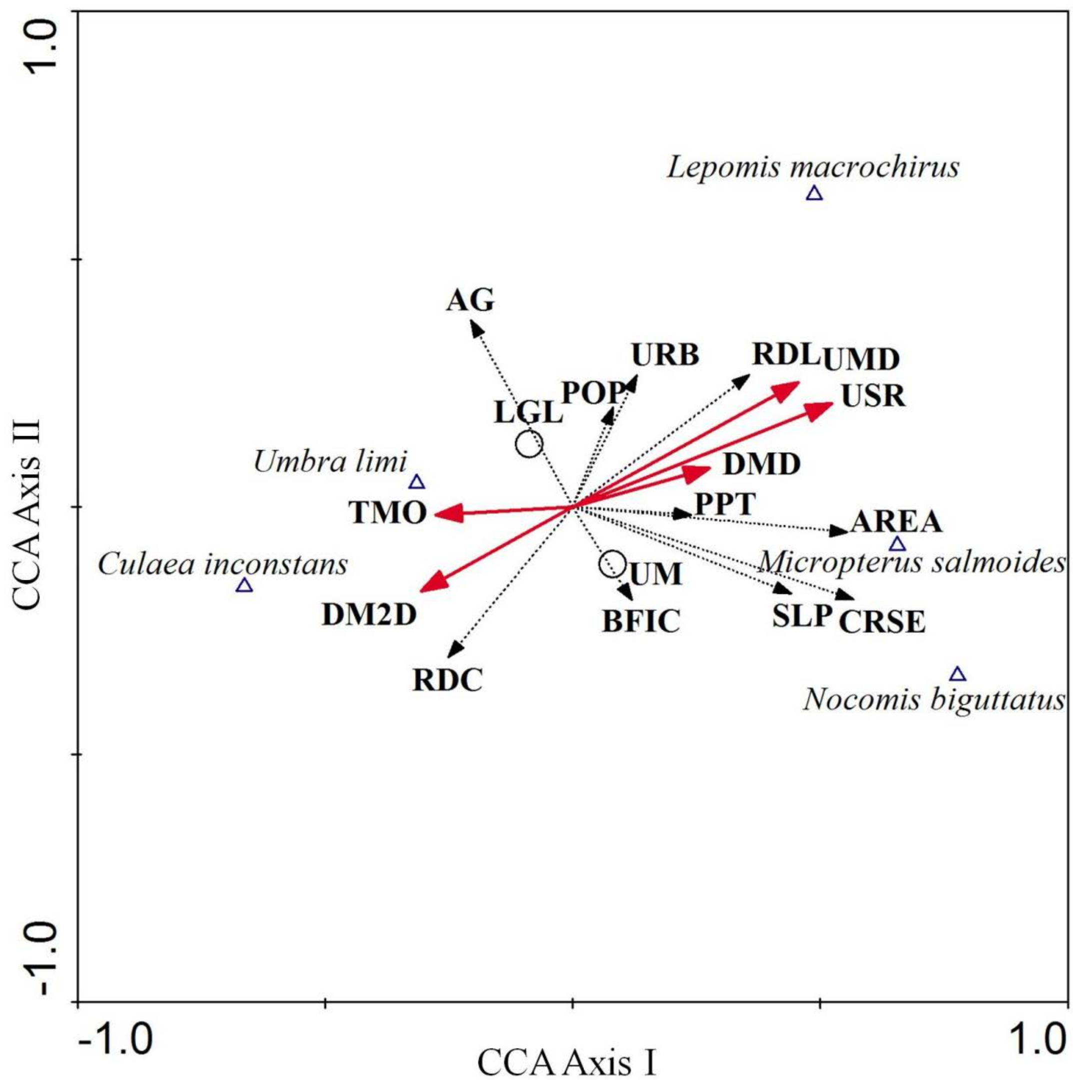

Figure 2.4.—Plot of canonical correspondence axis I vs. axis II for warm headwaters. Abbreviations for natural, non-dam anthropogenic, and dam variables are found in Tables 1.1 and 2.1. Species common names are found in Table 2.9.

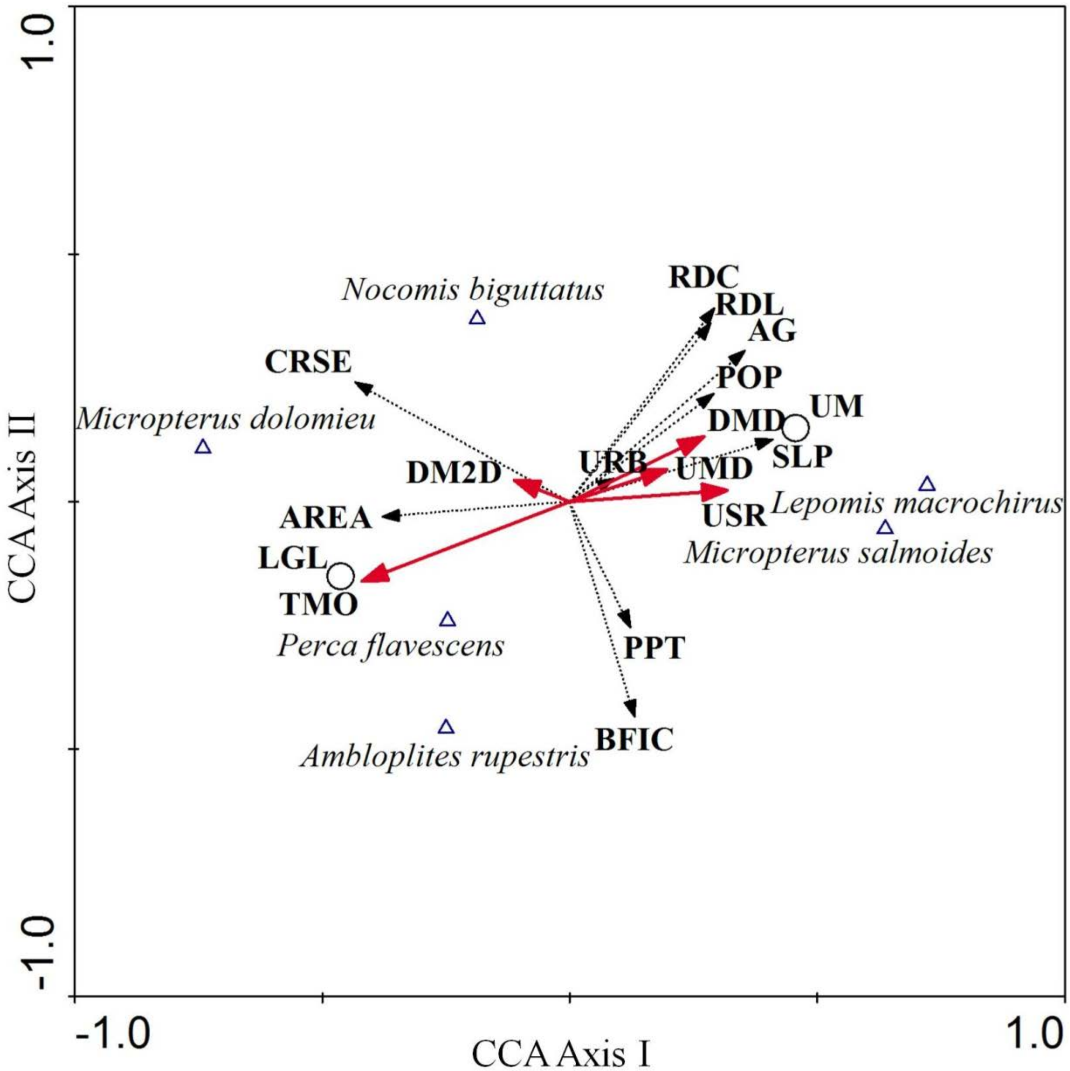

Figure 2.5.—Plot of canonical correspondence axis I vs. axis II for cold mid-size streams. Abbreviations for natural, non-dam anthropogenic, and dam variables are found in Tables 1.1 and 2.1. Species common names are found in Table 2.9.

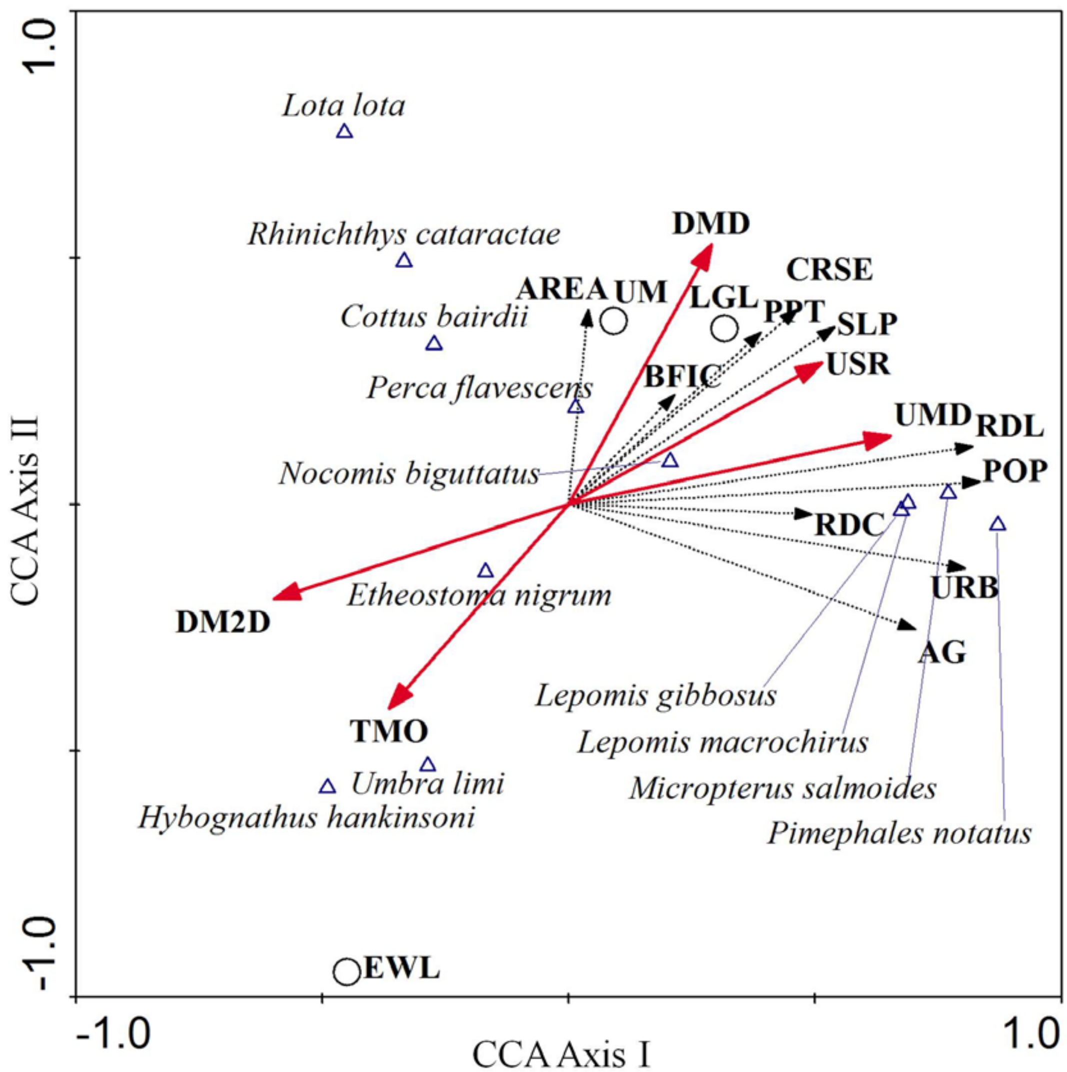

Figure 2.6.—Plot of canonical correspondence axis I vs. axis II for warm mid-size streams. Abbreviations for natural, non-dam anthropogenic, and dam variables are found in Tables 1.1 and 2.1. Species common names are found in Table 2.9.

APPENDIX C

SUPPLEMENTAL TABLES

Table C1.—Descriptive statistics for natural and non-dam anthropogenic reach network catchment variables (Table 2.1) by stratum.

Stratum	Variable	Minimum	Maximum	Mean
EWL HW Cold	AREA	2.6	446.3	58.8
	PPT	478.5	760.8	654.7
	MAAT	2.2	5.1	3.3
	BFIC	27.5	69.5	52.2
	ELEV	305.5	566.5	431.1
	SLP	0.0	5.2	1.2
	SOIL	1.3	11.0	5.1
	FINE	0.0	100.0	14.3
	CRSE	0.0	100.0	76.0
	URB	0.0	4.5	0.3
	AG	0.0	59.4	12.4
	FRST	9.8	95.6	58.3
	IMP	0.0	3.0	0.2
	POP	0.0	19.2	1.9
	RDC	0.0	0.6	0.2
	RDL	0.0	2.4	8.6
LGL HW Cold	AREA	1.7	217.9	37.9
	PPT	643.2	997.7	801.8
	MAAT	2.1	9.7	5.5
	BFIC	43.6	87.6	62.6
	ELEV	193.7	601.0	340.9
	SLP	0.0	7.7	1.8
	SOIL	0.9	13.0	6.0
	FINE	0.0	100.0	14.3
	CRSE	0.0	100.1	81.1
	URB	0.0	9.9	1.3
	AG	0.0	59.7	13.4
	FRST	6.7	99.1	55.9
	IMP	0.0	5.2	0.7
	POP	0.0	200.5	10.9
	RDC	0.0	1.3	0.3
	RDL	0.0	2.9	1.3

Table C1 (cont'd).

Stratum	Variable	Minimum	Maximum	Mean
UM HW Cold	AREA	1.3	247.9	26.0
	PPT	615.2	896.4	794.0
	MAAT	3.1	8.3	6.2
	BFIC	30.8	74.9	57.5
	ELEV	256.2	533.9	337.4
	SLP	0.0	12.5	4.4
	SOIL	0.8	12.4	3.4
	FINE	0.0	100.0	1.8
	CRSE	0.0	100.0	57.8
	URB	0.0	10.0	0.9
	AG	0.0	59.9	36.0
	FRST	10.1	94.2	48.5
	IMP	0.0	7.3	0.6
	POP	0.2	198.0	7.6
	RDC	0.0	2.3	0.4
	RDL	0.0	3.4	1.2
LGL HW Warm	AREA	5.5	3254.7	78.7
	PPT	687.6	870.6	790.4
	MAAT	2.8	9.0	6.5
	BFIC	35.4	74.1	57.3
	ELEV	186.5	495.4	308.2
	SLP	0.0	3.1	1.3
	SOIL	0.6	10.5	5.1
	FINE	0.0	100.0	19.0
	CRSE	0.0	100.0	78.8
	URB	0.0	8.2	1.8
	AG	0.0	59.9	34.1
	FRST	2.8	81.7	35.6
	IMP	0.1	3.6	0.9
	POP	0.2	194.2	20.2
	RDC	0.0	1.0	0.3
	RDL	0.5	2.8	1.5

Table C1 (cont'd).

Stratum	Variable	Minimum	Maximum	Mean
UM HW Warm	AREA	4.9	607.1	51.5
	PPT	608.6	868.0	805.5
	MAAT	3.4	8.3	5.8
	BFIC	33.7	71.0	56.8
	ELEV	246.5	527.2	378.9
	SLP	0.0	11.3	1.8
	SOIL	0.6	12.4	5.3
	FINE	0.0	100.0	6.8
	CRSE	0.0	100.0	76.7
	URB	0.0	9.5	1.2
	AG	0.0	58.3	22.0
	FRST	8.4	75.9	45.8
	IMP	0.0	4.5	0.7
	POP	0.3	154.7	12.1
	RDC	0.0	0.8	0.2
	RDL	0.4	3.3	1.3
LGL MS Cold	AREA	17.1	2696.7	227.0
	PPT	647.4	990.2	806.7
	MAAT	2.1	9.2	5.3
	BFIC	43.8	87.6	64.9
	ELEV	205.4	583.0	366.5
	SLP	0.2	6.3	1.9
	SOIL	1.2	12.5	6.4
	FINE	0.0	99.2	8.5
	CRSE	0.8	100.0	89.4
	URB	0.0	7.9	1.3
	AG	0.0	59.9	10.0
	FRST	11.6	97.1	58.6
	IMP	0.0	3.8	0.7
	POP	0.0	57.6	7.4
	RDC	0.0	1.6	0.2
	RDL	0.2	3.1	1.3

Table C1 (cont'd).

Stratum	Variable	Minimum	Maximum	Mean
UM MS Cold	AREA	8.9	766.2	96.4
	PPT	683.1	847.4	808.5
	MAAT	4.2	8.4	6.7
	BFIC	30.0	73.9	60.3
	ELEV	265.8	443.3	323.3
	SLP	0.1	12.0	5.8
	SOIL	0.8	11.0	3.3
	FINE	0.0	65.6	1.6
	CRSE	0.0	100.0	38.3
	URB	0.0	8.1	1.2
	AG	0.0	59.9	42.9
	FRST	8.4	89.7	44.6
	IMP	0.1	4.1	0.7
	POP	0.7	101.8	9.1
	RDC	0.0	0.9	0.4
	RDL	0.5	2.4	1.3
EWL MS Warm	AREA	51.2	4382.1	558.3
	PPT	489.1	750.1	643.7
	MAAT	2.4	4.8	3.3
	BFIC	28.1	65.8	52.3
	ELEV	327.2	560.8	408.7
	SLP	0.0	2.9	0.9
	SOIL	1.4	8.0	4.4
	FINE	0.0	80.4	18.4
	CRSE	0.7	100.0	63.2
	URB	0.0	1.2	0.3
	AG	0.0	59.9	13.6
	FRST	15.1	87.4	48.9
	IMP	0.0	0.9	0.3
	POP	0.0	24.7	2.2
	RDC	0.0	0.5	0.1
	RDL	0.1	1.6	0.7

Table C1 (cont'd).

Stratum	Variable	Minimum	Maximum	Mean
LGL MS Warm	AREA	29.8	1935.6	358.0
	PPT	647.0	995.7	782.1
	MAAT	2.7	9.7	5.9
	BFIC	35.7	78.3	56.3
	ELEV	202.1	539.2	347.4
	SLP	0.1	2.5	1.1
	SOIL	1.7	10.3	4.6
	FINE	0.0	100.0	17.3
	CRSE	0.0	100.0	75.7
	URB	0.0	9.1	2.0
	AG	0.0	59.2	26.5
	FRST	3.4	93.0	42.8
	IMP	0.0	4.4	1.0
	POP	0.2	87.0	15.9
	RDC	0.0	1.4	0.3
	RDL	0.2	2.4	1.3
UM MS Warm	AREA	21.0	91043.8	1132.7
	PPT	600.3	917.9	751.2
	MAAT	3.3	8.7	5.1
	BFIC	32.7	71.6	54.9
	ELEV	242.6	531.9	382.8
	SLP	0.2	4.7	1.1
	SOIL	0.6	11.4	3.8
	FINE	0.0	100.0	2.8
	CRSE	0.0	100.0	87.6
	URB	0.0	9.5	0.9
	AG	0.0	59.8	23.6
	FRST	1.2	82.3	48.1
	IMP	0.0	4.7	0.5
	POP	0.5	93.6	7.4
	RDC	0.0	0.7	0.2
	RDL	0.2	3.3	1.1

Table C1 (cont'd).

Stratum	Variable	Minimum	Maximum	Mean
EWL LS Warm	AREA	529.5	48662.7	9996.6
	PPT	527.8	713.9	626.2
	MAAT	2.7	4.2	3.4
	BFIC	31.2	56.5	50.0
	ELEV	337.9	430.5	392.2
	SLP	0.1	2.3	0.7
	SOIL	2.7	7.7	4.3
	FINE	0.7	41.8	16.3
	CRSE	24.8	99.3	59.6
	URB	0.1	4.5	0.8
	AG	0.1	58.1	21.4
	FRST	22.8	67.7	38.4
	IMP	0.1	3.9	0.7
	POP	0.7	2.7	1.6
	RDC	0.0	0.2	0.1
	RDL	0.1	1.2	0.7
LGL LS Warm	AREA	700.2	15755.8	4681.3
	PPT	694.8	917.5	784.4
	MAAT	2.9	9.1	6.0
	BFIC	36.9	84.2	61.6
	ELEV	230.8	510.5	339.8
	SLP	0.4	2.2	1.1
	SOIL	2.5	11.2	5.8
	FINE	0.0	51.4	16.8
	CRSE	36.9	100.0	77.9
	URB	0.1	9.9	3.0
	AG	0.1	60.0	20.7
	FRST	9.8	86.4	43.7
	IMP	0.1	5.0	1.5
	POP	0.8	87.7	21.8
	RDC	0.1	0.6	0.3
	RDL	0.6	2.2	1.5

Table C1 (cont'd).

Stratum	Variable	Minimum	Maximum	Mean
UM LS Warm	AREA	748.8	34020.2	11284.7
	PPT	640.1	823.6	745.0
	MAAT	3.4	7.1	4.7
	BFIC	48.5	69.2	58.1
	ELEV	335.8	480.1	375.7
	SLP	0.5	8.6	1.3
	SOIL	1.7	7.4	4.9
	FINE	0.0	14.8	4.0
	CRSE	0.0	99.7	86.1
	URB	0.4	1.6	0.9
	AG	3.5	58.3	18.6
	FRST	26.0	70.4	52.8
	IMP	0.3	0.9	0.5
	POP	2.7	12.7	5.7
	RDC	0.1	0.5	0.2
	RDL	0.9	1.4	1.2

Table C2.—Descriptive statistics for fragmentation metrics (Table 1.1) by stratum.

Stratum	Variable	N	Minimum	Maximum	Mean
EWL HW Cold	UMCT	68	0.0	3.0	0.1
	UMD	68	0.0	8.0	0.4
	UM2D	4	0.0	8.1	2.0
	UMO	68	0.0	1.0	0.9
	UNCT	68	0.0	3.0	0.1
	UNDR	68	0.0	7.6	0.4
	UNDC	68	0.0	3.3	0.1
	USR	68	0.0	506.5	8.2
	USC	68	0.0	146.9	2.4
	USF	68	0.0	2.2	0.0
	DMCT	68	0.0	24.0	2.8
	DMD	66	0.0	2.7	0.5
	DM2D	36	3.7	294.8	82.6
	DMO	68	0.0	1.0	0.6
	TMCT	68	0.0	27.0	2.9
	TMD	68	0.0	2.9	0.5
	TM2D	38	15.3	423.8	107.9
	TMO	68	0.0	1.0	0.6
LGL HW Cold	UMCT	348	0.0	4.0	0.1
	UMD	348	0.0	49.7	1.0
	UM2D	25	0.0	16.3	4.5
	UMO	348	0.0	1.0	0.9
	UNCT	348	0.0	4.0	0.1
	UNDR	348	0.0	49.7	1.1
	UNDC	348	0.0	20.3	0.4
	USR	348	0.0	7711.6	26.5
	USC	348	0.0	1395.8	5.7
	USF	348	0.0	5.1	0.0
	DMCT	348	0.0	16.0	2.7
	DMD	327	0.0	21.5	2.3
	DM2D	221	0.0	167.1	44.9
	DMO	348	0.0	1.0	0.6
	TMCT	348	0.0	16.0	2.8
	TMD	348	0.0	17.1	1.9
	TM2D	226	4.7	191.1	59.2
	TMO	348	0.0	1.0	0.6

Table C2 (cont'd).

Stratum	Variable	N	Minimum	Maximum	Mean
UM HW Cold	UMCT	582	0.0	2.0	0.1
	UMD	582	0.0	40.6	0.6
	UM2D	29	0.0	19.6	3.3
	UMO	582	0.0	1.0	1.0
	UNCT	582	0.0	4.0	0.1
	UNDR	582	0.0	40.6	0.7
	UNDC	582	0.0	34.1	0.5
	USR	582	0.0	566.5	3.9
	USC	582	0.0	253.8	1.9
	USF	582	0.0	1.5	0.0
	DMCT	582	0.0	46.0	28.3
	DMD	579	0.0	1.4	1.0
	DM2D	578	0.0	278.0	57.9
	DMO	582	0.0	1.0	0.0
	TMCT	582	0.0	46.0	28.3
	TMD	582	0.0	1.4	1.0
	TM2D	578	4.1	285.1	69.3
	TMO	582	0.0	1.0	0.0
LGL HW Warm	UMCT	70	0.0	5.0	0.2
	UMD	70	0.0	19.9	0.9
	UM2D	6	0.0	3.7	0.8
	UMO	70	0.0	1.0	0.9
	UNCT	70	0.0	25.0	0.5
	UNDR	70	0.0	19.9	0.8
	UNDC	70	0.0	8.8	0.3
	USR	70	0.0	173.0	7.2
	USC	70	0.0	52.1	2.5
	USF	70	0.0	20.3	0.3
	DMCT	70	0.0	13.0	6.2
	DMD	67	0.0	8.6	3.8
	DM2D	58	0.2	155.1	33.4
	DMO	70	0.0	1.0	0.3
	TMCT	70	0.0	13.0	6.3
	TMD	70	0.0	7.2	3.4
	TM2D	60	1.7	172.0	47.3
	TMO	70	0.0	1.0	0.4

Table C2 (cont'd).

Stratum	Variable	N	Minimum	Maximum	Mean
UM HW Warm	UMCT	89	0.0	2.0	0.3
	UMD	89	0.0	30.1	2.0
	UM2D	18	0.0	9.3	2.7
	UMO	89	0.0	1.0	0.8
	UNCT	89	0.0	4.0	0.4
	UNDR	89	0.0	30.1	2.2
	UNDC	89	0.0	13.5	1.0
	USR	89	0.0	2996.0	69.4
	USC	89	0.0	1049.1	24.5
	USF	89	0.0	3.8	0.1
	DMCT	89	0.0	46.0	31.7
	DMD	87	0.4	1.4	1.1
	DM2D	87	0.0	138.2	33.0
	DMO	89	0.0	1.0	0.0
	TMCT	89	0.0	47.0	32.0
	TMD	89	0.0	1.4	1.1
	TM2D	87	7.0	157.9	46.1
	TMO	89	0.0	1.0	0.0
LGL MS Cold	UMCT	200	0.0	4.0	0.3
	UMD	200	0.0	11.1	0.7
	UM2D	39	0.0	63.7	12.6
	UMO	200	0.0	1.0	0.9
	UNCT	200	0.0	9.0	0.7
	UNDR	200	0.0	13.1	0.7
	UNDC	200	0.0	6.7	0.3
	USR	200	0.0	475.6	16.6
	USC	200	0.0	246.0	8.0
	USF	200	0.0	1.1	0.0
	DMCT	200	0.0	14.0	2.0
	DMD	186	0.0	11.1	1.8
	DM2D	111	0.2	164.5	49.3
	DMO	200	0.0	1.0	0.7
	TMCT	200	0.0	14.0	2.3
	TMD	200	0.0	5.7	1.4
	TM2D	123	6.2	231.7	74.9
	TMO	200	0.0	1.0	0.7

Table C2 (cont'd).

Stratum	Variable	N	Minimum	Maximum	Mean
UM MS Cold	UMCT	255	0.0	4.0	0.2
	UMD	255	0.0	22.6	1.3
	UM2D	43	0.0	73.0	8.3
	UMO	255	0.0	1.0	0.9
	UNCT	255	0.0	11.0	0.7
	UNDR	255	0.0	10.1	1.0
	UNDC	255	0.0	9.8	0.8
	USR	255	0.0	1330.5	10.5
	USC	255	0.0	470.2	5.5
	USF	255	0.0	5.2	0.0
	DMCT	255	0.0	40.0	25.2
	DMD	253	0.0	1.3	0.9
	DM2D	249	0.0	239.8	53.6
	DMO	255	0.0	1.0	0.0
	TMCT	255	0.0	42.0	25.5
	TMD	255	0.0	1.3	0.9
	TM2D	249	4.3	243.5	72.4
	TMO	255	0.0	1.0	0.0
EWL MS Warm	UMCT	95	0.0	20.0	0.6
	UMD	95	0.0	7.3	0.4
	UM2D	18	0.0	105.1	38.0
	UMO	95	0.0	1.0	0.9
	UNCT	95	0.0	38.0	1.5
	UNDR	95	0.0	6.6	0.6
	UNDC	95	0.0	2.9	0.2
	USR	95	0.0	1188.0	71.7
	USC	95	0.0	296.4	24.7
	USF	95	0.0	4.4	0.3
	DMCT	95	0.0	17.0	1.5
	DMD	95	0.0	2.1	0.3
	DM2D	39	6.5	282.5	100.9
	DMO	95	0.0	1.0	0.7
	TMCT	95	0.0	27.0	2.0
	TMD	95	0.0	2.9	0.3
	TM2D	41	23.6	353.5	155.4
	TMO	95	0.0	1.0	0.7

Table C2 (cont'd).

Stratum	Variable	N	Minimum	Maximum	Mean
LGL MS Warm	UMCT	102	0.0	6.0	0.9
	UMD	102	0.0	24.2	2.4
	UM2D	41	0.0	82.4	13.1
	UMO	102	0.0	1.0	0.7
	UNCT	102	0.0	15.0	2.0
	UNDR	102	0.0	18.1	1.7
	UNDC	102	0.0	13.4	0.9
	USR	102	0.0	691.4	41.5
	USC	102	0.0	258.1	19.1
	USF	102	0.0	0.9	0.1
	DMCT	102	0.0	12.0	4.2
	DMD	101	0.0	14.5	3.0
	DM2D	87	0.0	171.2	46.2
	DMO	102	0.0	1.0	0.4
	TMCT	102	0.0	13.0	5.1
	TMD	102	0.0	8.1	2.7
	TM2D	88	2.8	187.4	80.4
	TMO	102	0.0	1.0	0.5
UM MS Warm	UMCT	122	0.0	15.0	0.8
	UMD	122	0.0	20.1	1.6
	UM2D	46	0.0	68.3	12.0
	UMO	122	0.0	1.0	0.7
	UNCT	122	0.0	293.0	4.1
	UNDR	122	0.0	8.4	1.3
	UNDC	122	0.0	4.8	0.5
	USR	122	0.0	1444.1	86.5
	USC	122	0.0	479.4	32.0
	USF	122	0.0	48.2	0.6
	DMCT	122	10.0	46.0	33.1
	DMD	122	0.4	1.4	1.1
	DM2D	122	0.4	217.9	61.0
	DMO	122	0.0	0.1	0.0
	TMCT	122	11.0	47.0	33.9
	TMD	122	0.4	1.5	1.1
	TM2D	122	11.7	234.1	96.0
	TMO	122	0.0	0.1	0.0

Table C2 (cont'd).

Stratum	Variable	N	Minimum	Maximum	Mean
EWL LS Warm	UMCT	34	0.0	4.0	1.6
	UMD	34	0.0	2.3	0.6
	UM2D	25	0.0	149.4	71.2
	UMO	34	0.0	1.0	0.5
	UNCT	34	2.0	27.0	8.7
	UNDR	34	0.1	1.2	0.4
	UNDC	34	0.0	0.5	0.2
	USR	34	1.6	2704.9	391.9
	USC	34	0.8	627.0	99.8
	USF	34	0.0	5.0	0.9
	DMCT	34	0.0	6.0	1.4
	DMD	34	0.0	1.0	0.3
	DM2D	17	2.2	214.0	135.6
	DMO	34	0.0	1.0	0.7
	TMCT	34	0.0	6.0	3.0
	TMD	34	0.0	1.1	0.5
	TM2D	26	88.0	301.6	202.2
	TMO	34	0.1	1.0	0.5
LGL LS Warm	UMCT	50	0.0	15.0	4.6
	UMD	50	0.0	7.9	2.1
	UM2D	42	0.0	135.4	39.3
	UMO	50	0.0	1.0	0.3
	UNCT	50	0.0	98.0	23.2
	UNDR	50	0.0	3.0	1.0
	UNDC	50	0.0	1.6	0.5
	USR	50	0.0	428.7	71.3
	USC	50	0.0	177.7	34.1
	USF	50	0.0	0.5	0.1
	DMCT	50	0.0	8.0	2.0
	DMD	48	0.0	6.9	2.1
	DM2D	28	0.1	125.6	39.2
	DMO	50	0.0	1.0	0.7
	TMCT	50	0.0	15.0	6.5
	TMD	50	0.0	4.3	2.1
	TM2D	46	8.2	192.2	87.3
	TMO	50	0.0	1.0	0.4

Table C2 (cont'd).

Stratum	Variable	N	Minimum	Maximum	Mean
UM LS Warm	UMCT	67	0.0	26.0	5.3
	UMD	67	0.0	5.5	1.6
	UM2D	57	0.0	231.2	51.1
	UMO	67	0.0	1.0	0.3
	UNCT	67	3.0	160.0	54.4
	UNDR	67	0.3	1.8	1.1
	UNDC	67	0.1	0.9	0.5
	USR	67	1.1	855.4	172.2
	USC	67	1.0	248.3	64.0
	USF	67	0.0	654.5	14.3
	DMCT	67	21.0	42.0	32.5
	DMD	67	0.8	1.3	1.1
	DM2D	67	0.0	274.7	70.0
	DMO	67	0.0	0.1	0.0
	TMCT	67	21.0	47.0	37.7
	TMD	67	0.8	1.4	1.1
	TM2D	67	2.4	274.9	134.1
	TMO	67	0.0	0.1	0.0

LITERATURE CITED

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