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THE IMPACT OF LOW-HEAD DAMS ON FISH SPECIES RICHNESS IN WISCONSIN, USA

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Abstract. Communities that live in linear systems such as streams or riparian zones may be particularly sensitive to changes in habitat connectivity. I examined the relationship between environmental variables, the number of low-head dams downstream of each reach, and fish species richness in first-order streams in Wisconsin, USA. The analysis was based on an extensive database of 13 628 localities and ~180 000 individual collection records. The environmental variables included climate, elevation, distance from nearest town, and network-specific measures such as link number (the number of first-order tributaries upstream of the current reach), downstream link number, stream order, and fractal dimension. The link number of the downstream reach was the strongest broad-scale correlate of fish species richness in first-order streams. Path analysis of a simple directed graph suggested that, although downstream dams have a significant effect on fish species richness, this effect is small by comparison to the influence of water quantity and summer maximum temperatures. From a management perspective, the results imply that modifications of water volume and temperature are greater threats to fish communities than the decrease in connectivity that results from low-head dams.

Key words: *biodiversity; connectivity; conservation; corridor; fishes; gradient; impoundment; path analysis; streams; Wisconsin, USA.*

INTRODUCTION

The long-term persistence of many species depends on access to the necessary quality and quantity of habitat. The problem of maintaining habitat access for far-ranging species (the ''functional landscapes'' of Poiani et al. 2000) is particularly acute in freshwater systems, where the linear nature of streams and the potentially high dependence of aquatic fauna on connectivity may mean that habitat gains made through preservation or restoration efforts in one part of the catchment are doomed to failure by activities occurring elsewhere in the same network. Linear habitats such as streams, riparian zones, and hedgerows are easily fragmented, and are potentially made even more vulnerable by virtue of the way that they cut across a variety of other habitat types.

Uncertainty over the importance of connectivity in streams is of high current relevance, with a number of low-head dams in the Midwest and eastern areas of the USA due for relicensing or possible removal (Bushaw-Newton et al. 2002, Stanley et al. 2002). The effects of large dams on downstream aquatic habitats and communities have been documented by a number of studies (Poff et al. 1997, Rosenberg et al. 2000, Poff and Hart 2002). Less research has been undertaken on the impacts of low-head dams (i.e., those of head height <15 m [Poff and Hart 2002]), and very little is known about the impacts of low-head dams on upstream communities. Dams can in theory affect upstream nutrient cycling and primary productivity (Pringle 1997), implying that they may influence fish communities even where fish dispersal through the network is relatively unimportant. At the same time, dams differ in their location, construction, and management. Although small-scale studies suggest that low-head dams have a negative influence on upstream fish species richness (e.g., Porto et al. 1999), it has not been established whether such effects have a cumulative effect on local species richness at a regional scale, or if they are sufficiently variable (or sufficiently local) that no broad-scale pattern emerges. Hierarchy theory predicts that the directions and magnitudes of relationships may change with changes in the grain and extent of analysis (Turner et al. 2001). Without support from broad-scale analyses, the logical assumption that dams alter connectivity and hence should have substantial cumulative effects on upstream fish biodiversity at a regional scale cannot be taken for granted. Furthermore, the relative impact of downstream dams on fish species richness has not been compared to other threats, such as climate change, invasive species, and reductions in water quantity and quality.

Since the most severe environmental impacts usually affect more than just one species, measures of species richness are frequently used to select priority areas for conservation efforts. This approach is epitomized by the ''hot spot'' approach to conservation (Myers et al. 2000), which focuses conservation expenditure on ar-

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TABLE 1. Summary of variables considered as potential correlates of fish species richness in first-order streams.

Variable	Description	Source
Arbolate sum	Total length of water upstream	Calculated from 1:100 000 RF3 files and a 1-km point coverage
No. dams	Number of dams downstream of collection locality	Calculated from 1:100 000 RF3 files and WiDNR dams database
D_mstem	Distance of collection locality from either the Mississippi or one of the Great Lakes	Calculated from 1:100 000 RF3 files
Dist_Town	Distance to the nearest town	Calculated at 200 × 200 m resolution from 1:24 000 coverage of urban regions
DLink	Link number of downstream reach	Calculated from 1:100 000 RF3 files
Elevation	Elevation	Extracted from USGS 75 m DEM
Fractal_D	Fractal dimension of containing watershed	Calculated by block method on by-watershed basis using DNR map of 334 subcatchments
GLB(01–19)	Growing day and temperature data (19 variables; see Table 2 for details)	Canadian Forestry Service; interpolated from weather data using BIOCLIM
GLS(01–16)	Precipitation and temperature data (16 variables; see Table 2 for details)	Canadian Forestry Service; interpolated from weather data using BIOCLIM
Gradient	Rise/run	Calculated using USGS 75 m DEM and reach length from 1:100 000 RF3 files
Link	Number of upstream tributaries	Calculated from 1:100 000 RF3 files
Log_Arbsum	Log of the arbolate sum	
Log_Gradient	Log of gradient	
Loglink	Log of link number	
St_order	Strahler stream order	Calculated from 1:100 000 RF3 files
Wshd_km2	Contributing area of upstream watershed	Calculated from 1:100 000 RF3 files and a 1-km point coverage

Notes: References for each data set are given in *Methods*. Fractal dimension was calculated by watershed, variables calculated from the RF3 database were obtained on a reach-by-reach basis, and the upstream contributions of land cover and geology to particular reaches were calculated; all other variables take the value of the base map at the point of collection. Further details of individual variables are given in Table 2 and *Methods*. Abbreviations used: RF3, Reach files version 3; USGS, United States Geological Survey; DNR or WiDNR, Wisconsin Department of Natural Resources; WEXGNHS, University of Wisconsin-Extension Geology and Natural History Survey; BIOCLIM, Bioclimatic Analysis and Prediction System; DEM, Digital Elevation Model.

eas of high diversity and endemism. Despite its potential weaknesses, the use of species richness as a metric that influences conservation efforts remains widespread. Consequently, it is important for both our understanding of ecology and our ability to undertake successful conservation that the different influences affecting species richness in different habitats are understood and described.

There is strong evidence to suggest that regional processes can play an important role in determining local patterns of fish species richness (Hugueny and Paugy 1995, Griffiths 1997), implying that assumptions that are central to the conservation of freshwater species must be considered at both local and regional scales. Lyons (1996) has shown that the fish communities of Wisconsin fall into several distinct groups based on their habitat preferences, further supporting the need for a regional approach in this system. It is widely accepted that human activities are the main cause of the currently unsustainable global extinction rate (Purvis and Hector 2000), and that the loss of biodiversity, if unchecked, will have severe implications for human survival (Chapin et al. 2000). Linking biodiversity and the broad-scale drivers that determine it (such as anthropogenic factors, climate, and geomorphology [e.g., Gotelli and Graves 1996, Burnett et al. 1997, Gaston 2000]) is a critical step in the definition of natural ‘‘ecoregions’’ (e.g., Bailey 1995) and other approaches to conservation.

I undertook a study of the environmental correlates of fish species richness in first-order streams, at the grain of a 1:100 000 map and the extent of the state of Wisconsin, USA. In addition to describing the broad-scale correlations between species richness, latitude, climate and the landscape context of different reaches, I asked whether the presence of numerous small- to medium-sized dams across the state has a general, directional effect on upstream species richness that is strong enough to detect at this scale of observation. The results suggest that although low-head dams may impact upstream fish species richness, their relative importance as a threat to fish species richness is low by comparison to climate change and decreases in water quantity.

METHODS

The extent of the study was the whole state of Wisconsin. Statewide data for environmental variables were obtained directly from different sources or calculated from existing data layers (Table 1).

Fish data

The fish data were provided by the Wisconsin Department of Natural Resources (WiDNR) (Fago 1984,

FIG. 1. Localities in Wisconsin at which fish were sampled. The black dots indicate sampling localities; the fine lines are the 1:100 000 streams map for the state.

1992). An extensive, statewide sampling effort using standardized netting and electroshocking procedures was undertaken between 1974 and 1986 at 10 841 stations. These data were added to 3635 earlier records (mostly from 1960–1972) to produce the WiDNR's master fish file (Fago 1992). Species distribution maps and full details of the methods used in the study have been published by Fago (1992). After removing errors such as inadequate locations and ambiguous species names, the data set contained a total of 13 628 unique localities (Fig. 1) from which a total of >180 000 individual fish were identified. Species richness was calculated from the master fish file for each locality.

Although the fish data undoubtedly have some weaknesses, including (1) the lack of repeated samples through time in the same locations, and (2) a tendency for sampling locations to be situated at obvious access points, they represent an unusually good resource for broad-scale analysis. Very few fish sampling efforts of this magnitude have been undertaken, and local biases in collection sites do not generally translate to regional biases. We are also faced with the choice of learning something from analysis of the data or learning nothing at all, since superior data sets for this region do not currently exist. It should be kept in mind when interpreting the results that the estimates of fish diversity are likely to be low as a consequence of their lack of temporal depth, making the conclusions less strong than they might otherwise have been. On the positive side, the extremely large sample size compensates for many of the potential biases in the data.

Environmental correlates

A wide range of potential environmental correlates of species richness was considered (Table 1). The climatic data (Table 2) were provided by the Canadian Forestry Service (D. McKenney, *personal communication*); values for each collection locality were derived from the modelling package BIOCLIM, which uses weather station data and a digital elevation model (Nix 1986, McKenney et al. 1999, 2001). Climate influences water temperature and food availability in streams.

Growing-day periods were also included in the analysis on the grounds that they act as surrogate measures for spatiotemporal variation in primary production, temperature, rainfall, and fertilizer use. The growing-

TABLE 2. Summary of climatic data.

Variable	Interpretation
GLB01	Annual mean temperature
GLB02	Mean diurnal range (mean [maximum minus minimum])
GLB03	Isothermality 2/7
GLB04	Temperature seasonality (coefficient of variation)
GLB05	Max. temperature of warmest period
GLB06	Min. temperature of coldest period
GLB07	Temperature annual range (5–6)
GLB08	Mean temperature of wettest quarter
GLB09	Mean temperature of driest quarter
GLB10	Mean temperature of warmest quarter
GLB11	Mean temperature of coldest quarter
GLB12	Annual precipitation
GLB13	Precipitation of wettest period
GLB14	Precipitation of driest period
GLB15	Precipitation seasonality (coefficient of variation)
GLB16	Precipitation of wettest quarter
GLB17	Precipitation of driest quarter
GLB18	Precipitation of warmest quarter
GLB19	Precipitation of coldest quarter
GLS01	Day of year for start of growing season (day 1 = 1 January)
GLS02	Day of year for end of growing season
GLS03	Number of days of growing season
GLS04	Total precipitation for period 1
GLS05	Total precipitation for period 2
GLS06	Total precipitation for period 3
GLS07	Total precipitation for period 4
GLS08	Growing days above base temperature for period 1
GLS09	Growing days above base temperature for period 2
GLS10	Growing days above base temperature for period 3
GLS11	Growing days above base temperature for period 4
GLS12	Annual mean temperature
GLS13	Annual minimum temperature
GLS14	Annual maximum temperature
GLS15	Mean temperature for period 3
GLS16	Temperature range for period 3

Notes: Each of these variables was estimated on a point-by-point basis using weather station data and the interpolation program BIOCLIM (Bioclimatic Analysis and Prediction System; Nix 1986). A quarter is a fixed three-month block of time, while climatic periods are three-month blocks that may have different starting dates. Growing day periods 1–4 are defined as follows: period 1 is three months prior to the start of the growing season; period 2 is the first six weeks of the growing season; period 3 is the growing season; and period 4 is the difference between periods 3 and 2.

day periods are defined as follows: Period 1 is three months prior to the start of the growing season, period 2 is the first six weeks of the growing season, period 3 is the entire growing season, and period 4 is the difference between periods 3 and 2. The periods are not the same as the quarters that are typically defined in BIOCLIM applications. The growing season was defined as starting when mean daily temperature was ≥5°C for five consecutive days, beginning 1 March, and ending when the minimum temperature reached <−2°C, on or after 1 August. Further details can be found in Mackey et al. (1996).

A 75-m Digital Elevation Model (DEM) was obtained from the USGS (1999; also on Geodisc 3.0 [WiDNR 1998]). Elevation influences stream flow rates and volumes as well as determining the locations at which dams can be built. Most of the stream-specific data were calculated using the alpha version of the third reach file data set (RF3) developed by the United States Environmental Protection Agency (EPA 1994). The RF3 data set was developed from the United States Geological Survey (USGS) Digital Line Graph data set at a scale of 1:100 000. The files contain a variety of fields that can be used, in combination with the appropriate software, to navigate along river networks.

Sampling localities were restricted to those for which complete data could be obtained for each variable. The RF3 data set is based on a division of drainages into subunits, the smallest of which is a reach. Individual reaches in Wisconsin vary in length from 8 m to 36 km; the mean length is 2.208 km. Reaches terminate at any point where a connection to another stream occurs. I assumed that attributing reach-level data to specific localities would not cause significant errors, because of the broad scale of the study, the large sample sizes involved, and the random distribution of collection localities within reaches.

Database and GIS routines provided by staff of The Nature Conservancy's Freshwater Initiative (TNC 2000) were used to calculate most of the landscape-position variables used in the study. These included arbolate sum (total upstream channel length as measured on a 1:100 000 map), link number (number of first-order tributaries upstream of the reach) and downstream link number (number of first-order tributaries upstream of the downstream reach, a surrogate measure of position within a drainage network), Strahler stream order (Strahler 1957), contributing watershed area, and gradient. The routines can be obtained from the web site of The Nature Conservancy's Freshwater Initiative (TNC 2000). Stream orders for these data ranged from 1 to 7, with a mean of 2.73 and a standard deviation of 1.51. Link numbers ranged from 0 to 11 423, with a mean of 171 and a standard deviation of 827. Naturally, neither of these data sets has a normal distribution.

The Wisconsin DNR has developed a coverage that divides the three major drainages in the state (Mississippi, Superior, and Michigan) into 334 subcatchments. To obtain a measure of local network complexity, I calculated the fractal dimension of each subcatchment using the box method (Tarboton et al. 1988). Fractal dimensions provide an estimate of the space-filling properties of a stream network. Streams that are branchier (not just more sinuous) will have higher fractal dimensions. Theoretical analyses suggest that the complexity of a stream network can influence population sizes and habitat colonization rates (Cumming 2002), and hence may have an influence on community composition. In Wisconsin, the fractal dimensions of

PLATE. 1. Fish sampling near a typical low-head dam in Wisconsin. Photo credit: T. Pellatt of the Wisconsin DNR.

different catchments also serve to distinguish between the driftless zone (unglaciated) and the northern and eastern regions of the state that were glaciated ~18 000 years ago.

To calculate the fractal dimension, grids composed of squares at resolutions of 800, 1700, 2300, 3000, 5000 and 10 000 m, respectively, were overlayed on the stream network and the number of squares intersecting the 1:100 000 stream coverage for each different grid size was calculated. A plot of the log of grid dimension against the log of the number of intersecting squares produces a straight line that is steeper for more complex catchments; the gradient of this line gives the catchment's fractal dimension (Tarboton et al. 1988). Lakes and reservoirs, with the exception of Lake Winnebago, were removed from the coverage prior to these calculations. Some catchments are not naturally defined (for example, Lake Winnebago is defined as a single region; and in a few cases, the lower portion of a single catchment is defined as a catchment of its own). In a few instances, the influence of larger lakes resulted in a value for fractal dimension that was lower than one. The range of fractal dimensions obtained was from 0.52 to 1.62 with a mean of 1.29.

Towns were defined by their outlines on a 1:24 000 map (WiDNR 1998). The distance to the nearest town was mapped using a square grid at a resolution of 200 m, from which data were extracted for each collection locality. Towns may impact fish populations through their impacts on water quality. Streams near to towns are likely to receive higher use for recreation and cattle farming, and may consequently have an elevated number of exotic species. (The data show that this effect holds for carp in Wisconsin.)

Dam localities were obtained from a database developed by the Wisconsin DNR Bureau of Watershed Management (WiDNR 2000) that included all dams in the state regardless of their size (Fig. 2). The inventory is based on the 1:24 000 GIS hydrography layer and includes locations for >4600 large and small dams in Wisconsin. Dams were assigned to the nearest reach; the RF3 database was then used to count the number of dams downstream of each collection locality.

Data analysis

The first step in the analysis was to look at correlates of species richness for all first-order streams (i.e., terminal reaches that are large enough to appear on the map) over the full extent of Wisconsin. Many of the dams in Wisconsin are low-head structures that can be crossed by fish during high flows (see Plate 1), and so I tested for the cumulative impacts of multiple dams on diversity rather than merely looking at the presence or absence of dams downstream. When interpreting the results it is important to note that not all ''first-order'' streams will be truly first order, since many true first-order streams are too small to map. Despite this weakness, the data do provide a solid distinction between small and large streams to a degree of accuracy that is appropriate for this scale of analysis.

The environmental data are highly intercorrelated, and the distribution of dams in the state is spatially nonrandom with respect to environmental gradients (E. H. Stanley, G. S. Cumming, M. W. Doyle, and H. A. Livingston, *unpublished manuscript*); dams in Wisconsin have been built selectively on reaches that have definite characteristics. The correlations between different variables were weak for a data set of this size, and scatterplots of the data were inconclusive about the form of relationships, making it inappropriate to attempt to statistically correct for the effect of any single variable through the use of residuals. Because of these problems, I initially adopted a gradient-based analysis by cumulatively selecting localities in ''first-order'' streams with increasing numbers of dams downstream. For each threshold (number of downstream dams <1, number of downstream dams <2, and so on up to <39), the means and standard deviations of species richness

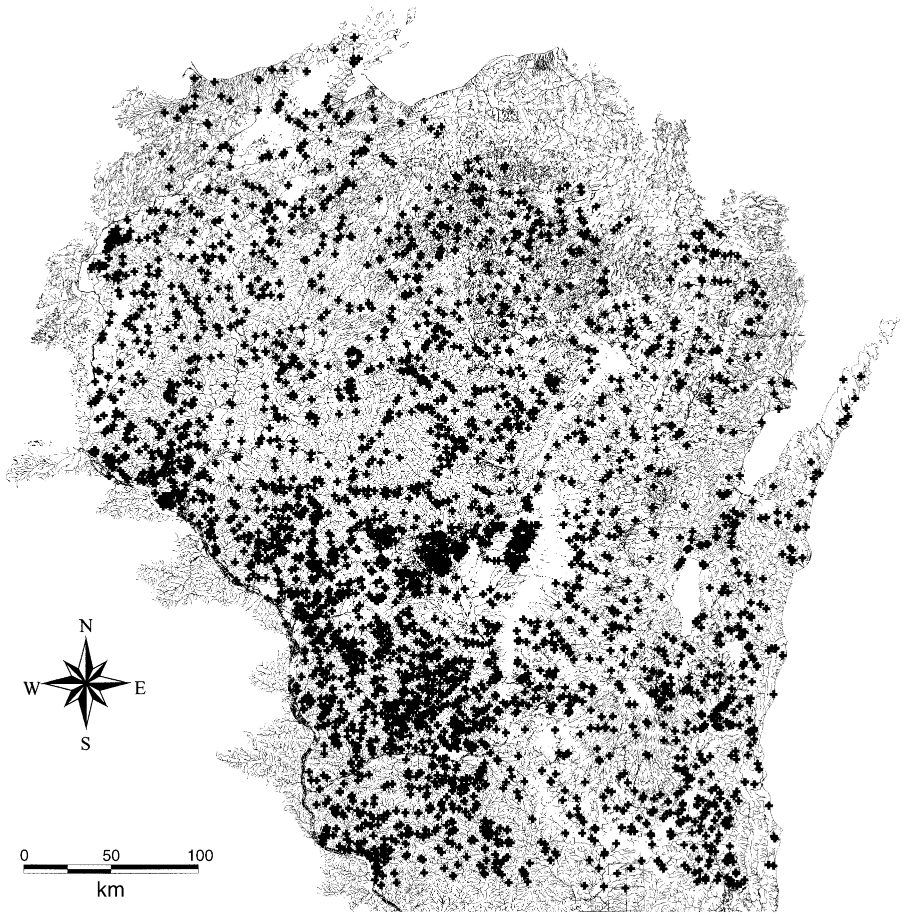

FIG. 2. Localities of dams in Wisconsin. Each black cross indicates a dam; the fine lines are the 1:100 000 streams map for the state.

and its potential correlates were calculated. These data were then plotted and inspected by eye to establish which variables showed obvious similarities with the strong trend exhibited by species richness. This procedure identified a much smaller set of key variables (elevation, downstream link number, distance from town, and northing/*y* coordinate) as potential confounding factors in considering correlations between dams and species richness. To establish whether there were significant differences in the trends shown by these variables, I first standardized the data (subtracting the mean and dividing by the standard deviation for each variable) and then compared them using a Friedman two-way analysis of variance (Siegel and Castellan 1988). The Friedman two-way ANOVA tests for overall differences in variance within the set of potential confounding factors according to their relationship to the number of downstream dams and species richness.

As the Friedman test shows, any signal created by the influence of dams on fish species richness was swamped by noise from other variables. To better cope with the complexity of the problem, I developed a parsimonious system model that captured the main elements of the problem. I then used the software program AMOS 5 (Arbuckle 2003) to undertake path analysis of the model, using maximum likelihood to estimate the strengths of interactions between different variables. For the uninitiated reader, an excellent treatment of path analysis and its utility for testing causal hypotheses can be found in Shipley (2002). Path analysis uses partial regressions together with insights from graph theory to establish the strengths of interactions between pairs of variables, while compensating for other relationships within the data set. It can be used to quantify both direct effects (immediate interactions of one variable with another) and indirect effects (interactions of two variables via a third intermediary, for example the interaction of elevation and fish species richness as mediated by impoundments). I ran the path analysis on the same model using (1) all reaches in the data set, and (2) only first-order streams, to compensate for confounding effects from upstream dams.

Since many of the variables in the analysis are not distributed normally, I performed 20 randomizations to

TABLE 3. Results of Pearson's product-moment correlations of different predictor variables with species richness for collection localities on all first-order streams in Wisconsin and for collection localities with no downstream dams.

Variable	All first-order streams (n = 4174)		First-order streams with no downstream dams (n = 2304)	
	Pearson's r	P	Pearson's r	P
Arbolate sum	0.0958	***	0.1242	***
DLink	0.3199	***	0.3787	***
D_mstem	−0.0407	**	−0.0477	**
Dist_Town	−0.1113	***	−0.1635	***
Elevation	−0.1107	***	−0.1582	***
No. dams	−0.0813	***	…	
Fractal_D	−0.0152	NS	0.0401	NS
GLB01	0.1656	***	0.2281	***
GLB02	−0.1180	***	−0.0893	***
GLB03	−0.0372	*	0.0039	NS
GLB05	0.0775	***	0.1831	***
GLB06	0.1480	***	0.1729	***
GLB07	−0.0978	***	−0.0828	***
GLB08	0.1793	***	−0.2579	***
GLB09	0.1768	***	0.2287	***
GLB10	0.1484	***	0.2432	***
GLB11	0.1762	***	0.2290	***
GLB12	0.1661	***	0.2327	***
GLB13	0.0070	NS	0.0403	NS
GLB14	0.1007	***	0.0922	***
GLB15	−0.0775	***	−0.0467	*
GLB16	0.0085	NS	0.0689	***
GLB17	0.0980	***	0.0701	***
GLB18	0.0309	*	0.1007	***
GLB19	0.0980	***	0.0702	***
GLS01	−0.1668	***	−0.2552	***
GLS02	0.1638	***	0.2037	***
GLS03	0.1781	***	0.2457	***
GLS04	0.0826	***	0.0620	**
GLS05	0.1188	***	0.2010	***
GLS06	0.1514	***	0.2474	***
GLS07	0.1509	***	0.2442	***
GLS08	−0.0367	*	−0.0380	NS
GLS09	−0.0018	NS	0.0716	***
GLS10	0.1670	***	0.2546	***
GLS11	0.1736	***	0.2589	***
GLS12	0.1745	***	0.2501	***
GLS13	0.1747	***	0.2344	***
GLS14	0.1575	***	0.2488	***
GLS15	0.1388	***	0.2348	***
GLS16	0.0954	***	0.1965	***
Gradient	−0.1726	***	−0.1615	***
Link	−0.0225	NS	−0.0009	NS
Log_Arbsum	0.0562	***	0.0868	***
Log_Gradient	0.0920	***	0.0366	NS
X coordinate	0.0277	NS	−0.0109	NS
Y coordinate	−0.1707	***	−0.2426	***
Wshd_km2	0.1375	***	0.1097	***

Notes: The Pearson's r statistics for the two columns are significantly different (Wilcoxon signed-ranks $Z = -3.862$, $P \leq 0.001$). For abbreviations, see Table 1. Other variables are defined as follows: X coordinate, easting; Y coordinate, northing; n, sample size. Definitions of climate-related variables generated using BIOCLIM (GLB and GLS) are given in Table 2 and in *Methods*. Significance levels of the correlation coefficients are * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; NS, not significant at the $P \leq 0.05$ level.

test whether the model fit was better than would be expected from chance correlations between data with the same distributions. In each randomization, I randomly reshuffled all of the numbers in each column of data before repeating the path analysis to derive an estimate of model fit.

As a word of caution, the size of the data set is such that statistical power is extreme. This has the effect of inflating P values and biasing the results of the chi-square statistic in the path analysis. When interpreting the results it is more appropriate to focus on the r values of individual correlations (the amount of variance ex-

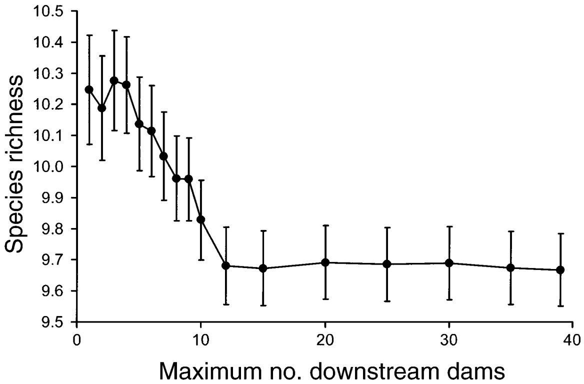

FIG. 3. Species richness (mean ± 1 SE) relative to the number of dams downstream of a given collection locality. Values on the x-axis indicate the maximum number of dams below first-order streams that were included in estimating each data point. Taken out of context, the plot suggests that increasing the number of downstream dams results in a net decrease in species richness.

plained by each correlation) and the weightings of the relationships between individual pairs of variables in the path analysis.

RESULTS

Correlative analysis

The correlation between stream order and species richness for all collection localities was significant (Pearson's $r = 0.341$, $P \leq 0.0001$). When only localities on first-order streams were considered, many of the variables in the study showed weak but significant correlations with species richness (Table 3). The strongest correlate of species richness in first-order streams was downstream link number (Pearson's $r = 0.32$, $P \leq 0.001$). Several climatic variables were also significant correlates of species richness ($P \leq 0.001$), including GLB08 (mean temperature of the wettest quarter; Pearson's $r = 0.26$), GLS11 (growing days above base temperature for period 4; Pearson's $r = 0.26$) and GLS12 (annual mean temperature; Pearson's $r = 0.25$). The correlation between species richness and the number of downstream dams was weak, but negative and significant (Pearson's $r = -0.08$, $P \leq 0.001$). The correlation between the number of downstream dams and the residuals of the regression of species richness on downstream link number was also weak but significant (Pearson's $r = -0.066$, $P \leq 0.001$); the residuals follow a roughly normal distribution. The correlations of different variables with species richness showed a general improvement when collection localities with downstream dams were excluded from the analysis, despite the resulting decrease in sample size (Table 3).

Consideration of species richness relative to dams suggested initially that dams might have a negative effect on local species richness (Fig. 3). However, this trend must be compared to those for other covariates (Fig. 4), which cast a different light on the results. The Friedman two-way analysis of variance did not show a significant difference between northing, distance to town, downstream link number, and elevation as defined by the maximum number of downstream dams (Friedman chi-square = 0.4, $P \leq 0.98$, $n = 14$).

Path analysis

Assessment of the overall fit of path models can be biased by large sample sizes and departures from normality (Bollen and Long 1993). This data set has both of these properties. The models had high chi-square values (all streams, chi-square = 412 914 036; first-order streams, chi-square = 46 838 128; 11 degrees of freedom; $P < 0.001$; $n = 17\,272$ and 2629 respectively), suggesting significant deviations of the data from the model predictions. Despite the poor overall fit, however, the weightings of all interaction terms in the path analysis were highly significant ($P < 0.001$). In 20 randomizations the lowest chi-square value for the all-streams data was 489 294 711. Since this is 76 380 675 greater than the chi-square value for the actual model, we can safely infer that the data fit the model considerably better than expected by chance. A multiple regression using the same six variables as predictors also gave a significant result for the overall model ($r = 0.4$, $F = 544$, $P < 0.001$, $n = 17\,272$) and all coefficients were again significant ($P < = 0.001$), implying that the choice of variables to include in the model is adequate (multivariate regression is a special case of path analysis, in which each variable interacts with every other variable).

In light of these results and given the technical uncertainties associated with assessing the fit of path models that do not meet stringent assumptions (Shipley 2002), I concluded that the specified model was adequate for the purposes of this analysis. The overall fit of the model could have been improved by removing parameters that have little influence on species richness; but the aim of the analysis was to establish the relative importance of interactions between variables that had already been identified as potential covariates. The path coefficients associated with each interaction indicate the relative strength and significance of the interaction between the variables that the arrow (''edge'') links. One of the advantages of path coefficients over standard regression coefficients is that path coefficients can incorporate asymmetrical (one-directional) interactions explicitly, for example in the instance where elevation affects temperature but temperature has no impact on elevation. A second major advantage of path coefficients is that they compensate for other interactions within the data, holding them constant, and hence their relative weightings do not show the high sensitivity of regression coefficients to the other variables that are included in the model.

Consideration of direct effects within the model (the immediate interactions between pairs of variables; Fig. 5) yielded several valuable insights. In the broader data

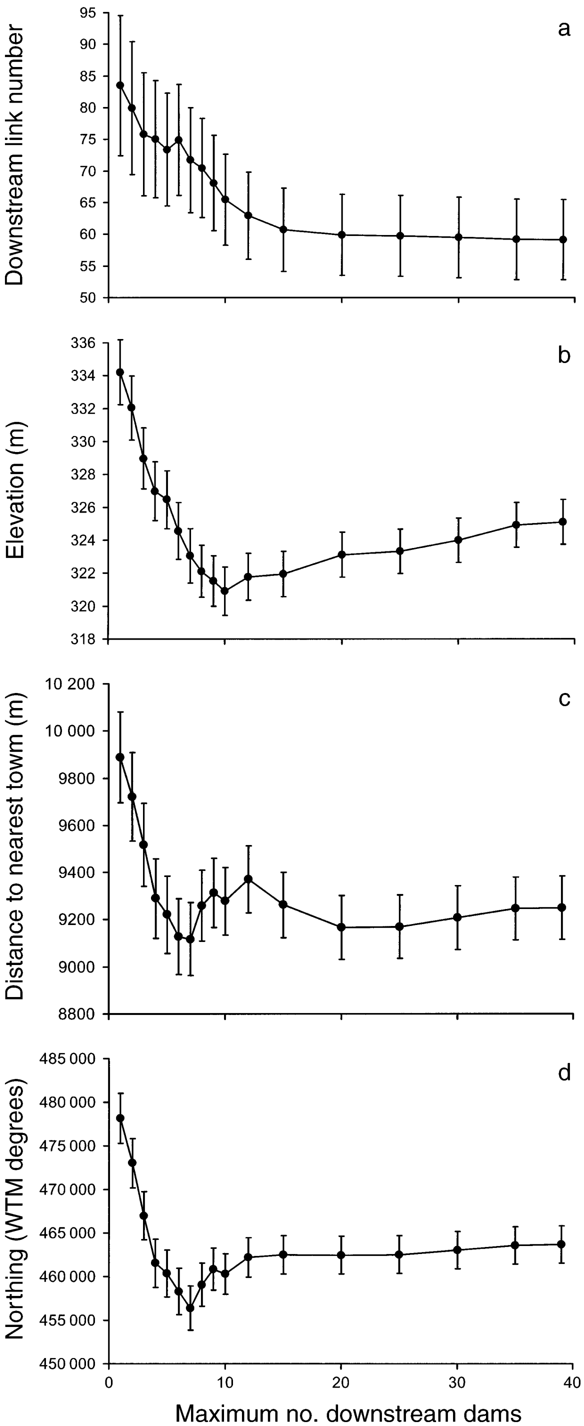

FIG. 4. Plots of environmental variables (mean ± 1 SE) that show a similar trend to species richness in relation to the number of downstream dams. Values on the *x*-axis indicate the maximum number of dams below first-order streams that were included in estimating each data point. (a) Downstream link number; (b) elevation; (c) distance to nearest town; and (d) northing/*y* coordinate (Wisconsin Transverse Mercator [WTM] projection).

set the dominant effect is the influence of water volume (as represented by the arbolate sum) on species richness (direct effect 3.59) and on the sites that are selected for the construction of dams (direct effect 0.84). When first-order streams are considered alone, water volume remains important but its relative magnitude decreases; looking only at terminal reaches partially controls for volume effects. At the same time, the magnitude of the effects of downstream dams and maximum temperature in the warmest month of the year increases in the smaller data set and the apparent importance of elevation decreases. Intuitively, these results make good sense. First-order streams will typically have more downstream dams and will be smaller (and hence, more susceptible to external temperature changes); and for obvious reasons, the range of elevations that is encom-

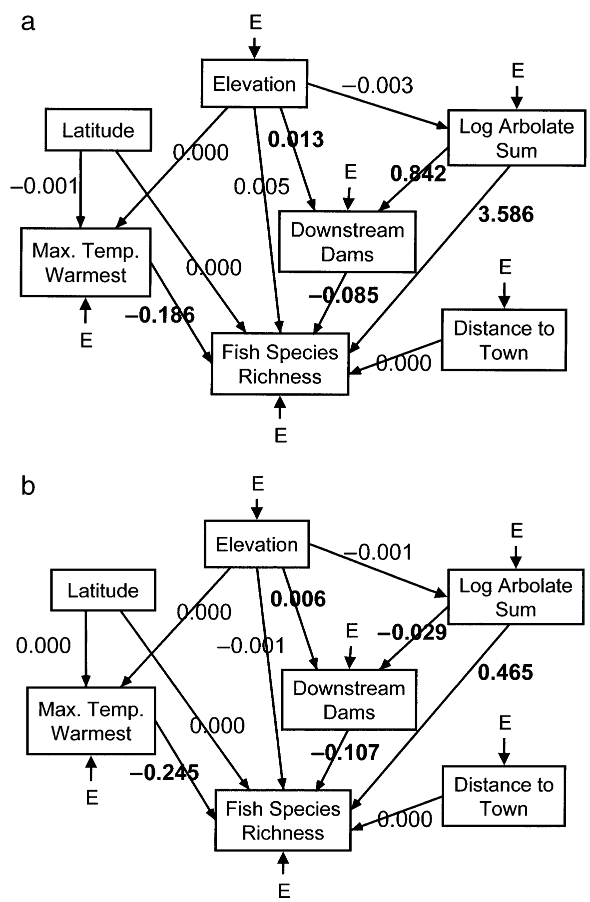

FIG. 5. (a) Directed graph showing the path analysis model and results for all stream reaches in the study area. Arrows indicate an asymmetrical effect of one variable on another; the numbers next to each arrow indicate the strength of the direct effect as estimated using maximum likelihood. The arrows labelled ''E'' indicate unspecified, normally distributed measurement errors that are estimated during model calculation. (b) Directed graph showing the same model, quantified for first-order streams only. Boldface type indicates significant relationships. Max. Temp. Warmest = maximum temperature of warmest period.

passed by first-order streams is considerably less than that encompassed by all reaches in the state. The main insights to emerge from the path analysis are that (1) the effects of downstream dams on species richness are significant; and (2) changes in either water volume or air temperature are likely to have a greater effect on fish species richness than changes in the number of downstream dams.

Discussion

It is clear that patterns of fish species richness are influenced by a number of potentially confounding covariates. In any analysis of determinants of fish species richness, fine or broad scale, the handling of these covariates will require considerable care if their effects are to be distinguished from one another. Although the results of smaller scale studies showing negative effects of dams on upstream species richness (e.g., Reyes et al. 1996, Holmquist et al. 1998, Pyron et al. 1998, Porto et al. 1999) are supported at broad scales, the data suggest that the significance of downstream dam impacts will be small by comparison to variables that directly affect either water temperature or water volume. Consequently, the central challenges for fish conservation in Wisconsin will be to target anthropogenic influences that either (1) affect the quantity of water flowing in streams, or (2) lead to changes in air or water temperature. The importance of both water volume and temperature for fish communities is well supported by other studies (e.g., Bain et al. 1988, Poff and Allan 1995, Angermeier and Winston 1998, Matthews 1998). Note that it was not possible to assess the broad-scale impacts of changes in water quality in this study.

The most definite result from the correlative analysis was the implication of downstream link number as the strongest broad-scale correlate of fish species richness in first-order streams. A similar conclusion was reached by Osborne and Wiley (1992), who found that at a smaller scale, downstream link number accounted for the greatest proportion of variance in species richness in the three drainage basins that they examined (the Mackinaw, LaMoine, and Vermilion drainages in Illinois, USA). Rathert et al. (1999) considered fish species richness in Oregon, USA, but did not include downstream link number in the study. They concluded that climatic factors, stream density, historical and present connectivity to large river basins, and levels of introduced fish species were the most significant correlates of fish species richness. The importance of downstream link number is closely related to the relationship between species richness and stream size. Levels of introduced species were partially considered in this study using the surrogate of ''distance to town,'' but the data that would be required to make a stronger quantitative connection between fish species richness and invasive species (such as the rusty crayfish, *Orconectes rusticus*) were not available.

The correlations between species richness, elevation, distance to towns, and northing relative to dams can be explained by the higher population density and lower elevation in southern Wisconsin and the likely existence of a north–south gradient in species richness. Latitudinal gradients in species richness have been documented for fish by Winemiller (1991) and Marsh-Matthews and Matthews (2000); similar trends are seen in many terrestrial species (Pianka 1966, Turpie and Crowe 1994, Gotelli and Graves 1996).

The picture is complicated by the nonrandom placing of dams within Wisconsin catchments relative to stream order, downstream link number, and arbolate sum (E. H. Stanley, G. S. Cumming, M. W. Doyle, and H. A. Livingston, *unpublished manuscript*). Dams throughout the state have been built at specific locations along the same environmental gradients that influence fish occurrences. It is possible that the drivers of patterns in fish species richness will be easier to determine when finer grained, reach-specific environmental characteristics are considered. Other potentially useful approaches to studying the problem include long-term manipulations such as the removal or insertion of dams (Pyron et al. 1998), the collection of a longer time series of fish occurrence data to improve the temporal resolution of the study, and the development of mechanistic models that allow individual tests of the roles of different environmental variables in maintaining species richness.

A further issue raised by this study concerns the appropriateness of species richness as a measure of anthropogenic impacts on fish communities. For conservation purposes, it will often be more appropriate to identify representative sets of habitats and their associated fish communities as targets. Assessment of changes in fish community composition and the status of populations of rare and endemic species will be more informative than using species richness alone. For example, fish species richness as a metric will be insensitive to situations in which the total number of fish species remains constant at a single locality but cold water, lotic species are replaced by warmer water, lentic species, a typical situation in impounded rivers. Broad-scale assessment of community-level patterns will highlight these kinds of changes more clearly than is possible with local assessments. Although a more detailed investigation of community-level patterns in relation to impoundments is outside the scope of this particular paper, such studies remain a high priority and a logical next step in the study of anthropogenic impacts on regional fish communities.

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