

Hierarchical faunal filters: an approach to assessing effects of habitat and nonnative species on native fishes

Quist MC, Rahel FJ, Hubert WA. Hierarchical faunal filters: an approach to assessing effects of habitat and nonnative species on native fishes.

Ecology of Freshwater Fish 2005: 14: 24–39. © Blackwell Munksgaard, 2004

Abstract – Understanding factors related to the occurrence of species across multiple spatial and temporal scales is critical to the conservation and management of native fishes, especially for those species at the edge of their natural distribution. We used the concept of hierarchical faunal filters to provide a framework for investigating the influence of habitat characteristics and nonnative piscivores on the occurrence of 10 native fishes in streams of the North Platte River watershed in Wyoming. Three faunal filters were developed for each species: (i) large-scale biogeographic, (ii) local abiotic, and (iii) biotic. The large-scale biogeographic filter, composed of elevation and stream-size thresholds, was used to determine the boundaries within which each species might be expected to occur. Then, a local abiotic filter (i.e., habitat associations), developed using binary logistic-regression analysis, estimated the probability of occurrence of each species from features such as maximum depth, substrate composition, submergent aquatic vegetation, woody debris, and channel morphology (e.g., amount of pool habitat). Lastly, a biotic faunal filter was developed using binary logistic regression to estimate the probability of occurrence of each species relative to the abundance of nonnative piscivores in a reach. Conceptualising fish assemblages within a framework of hierarchical faunal filters is simple and logical, helps direct conservation and management activities, and provides important information on the ecology of fishes in the western Great Plains of North America.

**M. C. Quist¹, F. J. Rahel²,
W. A. Hubert¹**

¹U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY, USA, ²Department of Zoology and Physiology, University of Wyoming, Laramie, WY, USA

Key words: hierarchical faunal filter; Great Plains; habitat; nonnative species; information theoretic method

Michael C. Quist, U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071-3166, USA; e-mail: mcquist@uwyo.edu.

Accepted for publication September 15, 2004

Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

The occurrence of individual species is determined by multiple causes acting at various spatial and temporal scales (Allen & Starr 1982; Poff 1997; Matthews 1998). Processes such as continental drift, orographic events, and glaciation operate at large spatial and temporal scales, whereas local abiotic characteristics and biotic interactions operate at smaller scales. Although these processes may vary in time and space, all are important determinants of species occurrence in a local assemblage. Consequently, gaining insight on factors governing patterns of species distributions and

assemblage structure has become a dominant focus of both applied and basic ecology (Matthews 1998; Jackson et al. 2001).

Because of the complexity of processes influencing individual species, many researchers have attempted to provide a framework for investigating and understanding mechanisms influencing patterns of species occurrence. One of the simplest concepts is that ecological patterns result from faunal ‘filters’. The concept of faunal filters was proposed by Simpson (1953) who argued that barriers and corridors (e.g., archipelagos, land bridges) function as filters to influence the composition of local mammalian faunas. More

recently, ecologists have recognised that faunal filters are hierarchical and serve to eliminate species progressively from global, regional, and local faunal pools. The concept of hierarchical filters has been applied to terrestrial systems (e.g., Rolstad et al. 2000) and has been used to understand patterns in aquatic systems (Matthews 1998). Smith & Powell (1971) were the first to consider how a hierarchy of filters can affect fishes and suggested that sequential reduction of species can be because of the passage of potential species through progressively finer faunal filters (i.e., smaller spatial and shorter temporal scales). They proposed that the filtering process begins with the global fish fauna, which is reduced in number by a gross physiological filter (e.g., freshwater vs. marine fishes). The next series of filters corresponds to geographic processes such as continental drift and glaciation events that result in continental (e.g., North American) and regional (e.g., Great Plains) fish faunas. Regional fish faunas then pass through a climatic filter (e.g., thermal regime, precipitation) resulting in a potential local fauna. Local physico-chemical habitat characteristics and biological interactions are the final filters that determine the occurrence of species at a locale. Although a number of similar hierarchical frameworks have been proposed for aquatic organisms (Jackson & Harvey 1989; Tonn 1990; Moyle 1994; Poff 1997; Matthews 1998), the primary difference among models relates to the semantics, number, and resolution of filters. Regardless of the specific conceptual framework, knowledge of the composition of local faunal filters provides insight on the ecology of individual species and allows managers to predict their occurrence. Information on faunal filters can allow managers to assess the effects of anthropogenic disturbances (e.g., habitat degradation, invasive species) and management activities (e.g., habitat enhancement activities) on a species.

The traditional focus of management activities and research in states of the western Great Plains (e.g., Colorado, Montana, Wyoming) has been on coldwater and coolwater sport fishes, most of which are nonnative (e.g., rainbow trout *Oncorhynchus mykiss*, brown trout *Salmo trutta*, walleye *Sander vitreus*). The declining abundance and distribution of Great Plains fishes (Fausch & Bestgen 1997), primarily because of anthropogenic disturbances (e.g., oil and gas development, invasive species, water development), has prompted managers to focus attention on native, nongame species in warmwater stream systems. However, conservation efforts are hindered because little is known about the ecology of many native, nongame fishes in the western Great Plains of North America.

We sought to determine if faunal filters could be used to identify factors influencing the distribution of

native fishes on the western edge of the Great Plains. We hypothesised that three hierarchical faunal filters would explain the occurrence of 10 native fishes in the North Platte River system of Wyoming. The first faunal filter (i.e., large-scale biogeographic filter) was defined as the limits of species occurrence based on two large-scale features, elevation and stream size. Within the defined limits for each species, the second faunal filter (i.e., local abiotic filter) involved estimating the probability of occurrence of a species based on reach-scale habitat characteristics. The third faunal filter (i.e., biotic filter) predicted the probability of occurrence for a species based on the abundance of nonnative, piscivorous fish. Cumulatively, the three faunal filters provide insight on the ecology of each species and estimate the probability of occurrence for each species in a reach, all of which help to identify factors limiting individual species.

Study area

The North Platte River drainage in south-eastern Wyoming encompasses approximately 25% of the surface area of the state (Fig. 1). The North Platte River originates in Colorado, flows north into Wyoming, and then flows east to Nebraska where it meets the South Platte River to form the Platte River. Headwaters of the North Platte River and its tributaries are mountain streams with fish communities dominated by nonnative salmonids (i.e., brook trout *Salvelinus fontinalis*, brown trout). Mountain streams generally have high gradients, low water temperatures, and substrate dominated by boulder and cobble. As streams flow from the mountains into the foothills and plains regions, water temperatures increase and substrate particle sizes decrease (Rahel & Hubert 1991; Fausch & Bestgen 1997). Further downstream, the North Platte River and lower segments of large tributaries were historically characterised as having high turbidity, shallow depths, and wide, dynamic channels dominated by silt and sand substrate (Baxter & Stone 1995).

Fish assemblages in the North Platte River drainage are the most diverse in Wyoming (Baxter & Stone 1995). Most species in the drainage are common throughout the central Great Plains and have ecological adaptations for life in harsh prairie streams (Lee et al. 1980; Fausch & Bestgen 1997). Large-bodied predators were generally absent from the western Great Plains because of dynamic flow, substrate, and chemical conditions characteristic of prairie streams. However, altered habitats resulting from water development (e.g., impoundments, irrigation practices) and widespread introduction of sport fishes have led to the naturalisation of nonnative piscivores (e.g., Centrarchidae and Percidae) throughout the Great Plains of Wyoming (Baxter & Stone 1995).

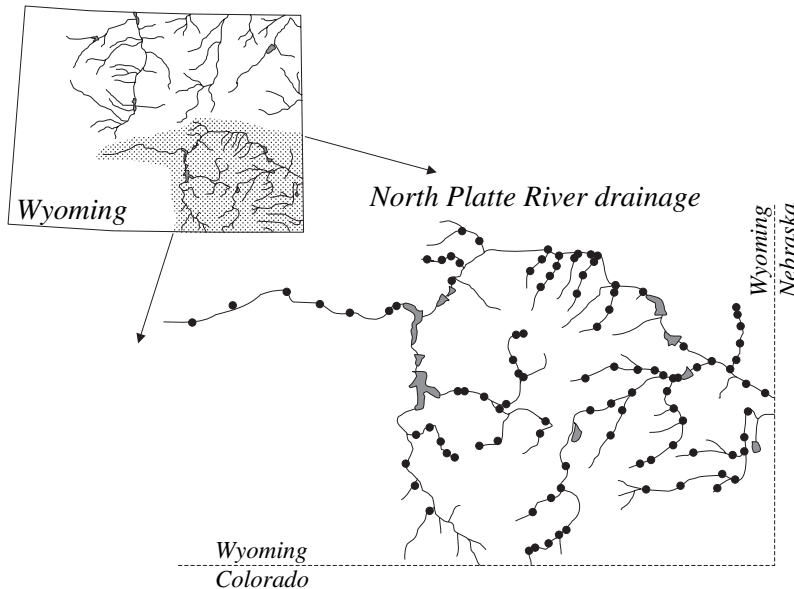


Fig. 1. Location of 102 fish and habitat sampling reaches in the North Platte River drainage of Wyoming sampled during 1993–2000.

Thirty species of fish are native to the North Platte River drainage of Wyoming, and our analysis focused on 10 of these species: bigmouth shiner *Notropis dorsalis*, brassy minnow *Hybognathus hankinsoni*, central stoneroller *Camptostoma anomalum*, common shiner *Luxilus cornutus*, creek chub *Semotilus atromaculatus*, fathead minnow *Pimephales promelas*, johnny darter *Etheostoma nigrum*, longnose dace *Rhinichthys cataractae*, sand shiner *N. stramineus*, and white sucker *Catostomus commersoni*. Although knowledge of factors related to the occurrence of the other 20 species native to the North Platte River drainage is important, a thorough understanding of their ecology was unavailable and limited their inclusion in our study. Therefore, species were selected based on their prevalence in the North Platte River system and availability of information on their ecology from other areas of their native distribution.

Methods

Fish and habitat sampling

Fish and habitat characteristics were sampled from 102 reaches throughout the North Platte River drainage (Fig. 1) during the summers of 1993–1995 and 2000. All sampling was conducted during base flow conditions (i.e., May to August) to reduce effects of temporal variability on fish and habitat characteristics. Reaches experiencing high (flood) or intermittent flow conditions were excluded from the analysis. Patton et al. (2000) found that sampling a 200-m reach was sufficient to collect all of the fish species present in Wyoming warmwater streams. Reaches in our study were 200–700 m. The primary method for sampling

fish assemblages was by electrofishing using either a backpack or bank-mounted electrofishing unit. In addition, seining was conducted at 51% of the reaches to supplement electrofishing efforts. Fish were identified in the field, but voucher specimens were preserved and examined in the laboratory to confirm field identifications.

Elevation (m.a.s.l.) of each reach was determined from 7.5-minute U.S. Geological Survey (USGS) topographic maps or from a hand-held global positioning system (GPS) unit (model 12XL; Garmin International, Olathe, KA, USA). Channel slope (%) was estimated using a map wheel and 1:24,000 USGS topographic maps where the distance between the nearest upstream and downstream contour lines was measured. Channel slope was calculated as the difference in elevation divided by the channel length between contour lines multiplied by 100. Mean stream width (m) was estimated by measuring wetted stream width along transects spaced every 40 m. Maximum depth (m) was measured to the nearest 0.1 m in each reach.

Methods to measure instream habitat characteristics and channel morphology varied slightly between 1993–1995 and 2000. During 1993–1995 the proportion of a reach comprised of pool, run, or riffle habitat was visually estimated in the field to the nearest 10% and corroborated by examination of photographs collected at the time of sampling. Similarly, the percentage of the water surface area with submergent (i.e., macrophytes or algae) vegetation, emergent vegetation, or woody debris was visually estimated in the field to the nearest 5% and confirmed using photographs. Substrate was visually estimated to the nearest 10% as silt (diameter < 0.5 mm), sand (0.5–2.5 mm), gravel (2.6–63.5 mm), cobble

(63.6–254.0 mm), boulder (>254.0 mm), or bedrock (categories modified from Armantrout 1998). Visual estimates are often precise and accurate in stream systems, particularly in prairie streams dominated by fine substrates (Wang et al. 1996; Mullner et al. 2000).

During 2000, however, instream habitat was measured using a diagonal-transect method adapted from Bevinger & King (1995). All reaches were 200-m long and were divided into 10-m long units. Transects connected opposite ends (i.e., left or right bank) of adjacent units and were used to estimate instream habitat. Substrate composition and channel unit type (i.e., pool, riffle, or run) were recorded at six points along each diagonal transect. Measurements were taken 10 cm from each bank and at points 20, 40, 60, and 80% of the transect length. Length and width of each cover type (i.e., submergent or emergent vegetation, woody debris) were measured throughout the reach. Although some methods differed in 2000, the habitat data are believed to be comparable with data collected during 1993–1995. Variables measured by the diagonal-transect method provided the same information as was collected during 1993–1995. We categorised substrate as fine substrate (silt and sand), coarse substrate (gravel, cobble, and boulder), or bedrock to help alleviate differences between sampling methods, reduce the number of independent variables, and because some substrates (e.g., cobble, boulder) likely affect fishes in a similar manner (Allan 1995). Lastly, several reaches sampled in 2000 were near (i.e., within 10 km) those sampled in 1993–1995, and estimates of habitat features from these reaches were similar.

Statistical analysis

First faunal filter – large-scale biogeographic filter

The distributions of species on a large geographic scale are regulated by thermal characteristics (e.g., warmwater vs. coldwater species) and stream size (e.g., small stream vs. large river species). In the Rocky Mountains, elevation and water temperature are highly correlated (e.g., Isaak & Hubert 2001) and influence the distribution of fishes (Lanka et al. 1987; Rahel & Hubert 1991; Bozek & Hubert 1992). Similarly, stream size reflects the position of a reach in the watershed, where some species are present only in large rivers and others are found only in small streams (Rahel & Hubert 1991; Bozek & Hubert 1992; Baxter & Stone 1995). If species exhibit clear thresholds for elevation or stream size, including reaches above or below that threshold in an analysis makes little biological sense and obscures patterns in the data (Nibbelink 2002). Therefore, we used threshold values of elevation and stream width obtained from the field study to identify reaches within the

potential distribution of each species (i.e., first faunal filter; Fig. 2). Upper elevational boundaries likely reflect physiological thermal tolerances. Conversely, lower elevational boundaries do not necessarily represent a lower limit for the species, but rather the lowest elevation sampled in Wyoming.

Second faunal filter – local abiotic filter

The second faunal filter was developed using logistic-regression analysis. Binary logistic regression was used to determine which instream habitat and channel morphology variables best predicted the occurrence of each of the 10 study species in the North Platte River drainage (Table 1). Bivariate plots and Pearson correlations were calculated for all pairs of independent variables. When two or more variables were correlated, we selected the variable that has been shown to be important to the ecology of the species based on previous research. To avoid multicollinearity, a subset of five uncorrelated ($r < 0.10$) independent variables was selected for inclusion in our candidate logistic-regression models. The resulting independent variables included maximum depth, percentage of the water surface area as pool habitat, percentage of the water surface area with submergent vegetation, percentage of the water surface area with large woody debris, and the percentage of fine (i.e., silt or sand) substrate.

We used the information-theoretic method to choose among competing logistic-regression models (Burnham & Anderson 2002). The information-theoretic method does not constitute a formal statistical test and, therefore, does not rely on null hypotheses, test statistics, or P -values because of the arbitrary nature of many hypothesis tests and decisions based on P -values (Johnson 2002; Robinson & Wainer 2002). Rather, the information-theoretic method relies on an accumulation of evidence for *a priori* hypotheses and fosters the concept of statistical evidence and level of support for each model and its alternatives. The information-theoretic method has been used in studies of terrestrial organisms (e.g., Arnold et al. 2002; Burhans et al. 2002; Burnham & Anderson 2002), but has been applied only recently to aquatic systems (Harig & Fausch 2002; Weigel et al. 2003). Although some aspects of the information-theoretic method have been criticised (Eberhardt 2003), model selection based on the method was more appropriate than traditional hypothesis testing for our data because it allowed comparison of multiple models, balanced precision and bias associated with model selection, and did not require a formally designed experiment to collect data (Burnham & Anderson 2002; Harig & Fausch 2002).

The ecology of the study species is generally unknown in Wyoming streams; however, we used knowledge of habitat associations and life history

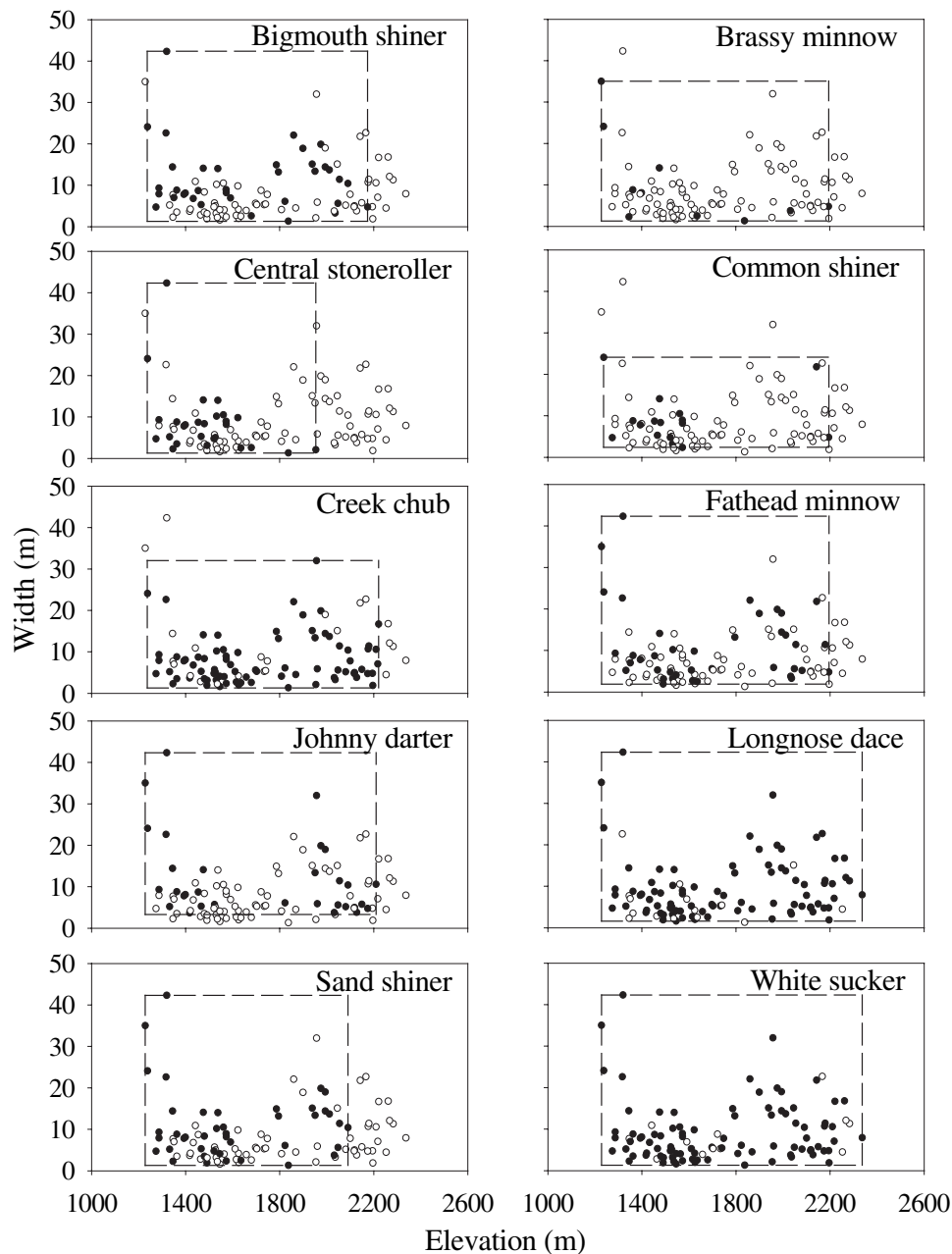


Fig. 2. Elevation (m.a.s.l.) and mean stream width (m) of reaches sampled in the North Platte River drainage of Wyoming during 1993–2000. Solid symbols represent reaches where a species was sampled and open symbols represent reaches where a species was absent. The dashed line represents the elevation and stream width thresholds for each species.

characteristics of each species in other portions of their distribution (Table 2) to develop 20–25 candidate models (number of models was dependent on the species) containing various combinations of predictor variables that we considered biologically relevant. Akaike's Information Criterion corrected for small sample bias (AIC_c ; Burnham & Anderson 2002) was used to compare candidate models with the best model having the lowest AIC_c . Akaike weights (w_i) were used to assess the relative plausibility of each candidate model as described by Burnham & Anderson (2002).

Additionally, the relative importance of independent variables was assessed by summing Akaike weights for all models in which each variable occurred. Summation of Akaike weights corroborated results from the logistic-regression models and contributed to the accumulation of evidence central to the information-theoretic method (Burnham & Anderson 2002).

We computed model-averaged coefficients by weighting parameter estimates from each logistic-regression model according to their associated Akaike weights (Burnham & Anderson 2002). Averaging

Table 1. Habitat characteristics from reaches sampled in the North Platte River drainage of Wyoming (1993–2000).

Variable	Mean (SD)	Minimum–maximum
Channel morphology		
Slope (%)	0.3 (0.3)	0.1–1.3
Maximum depth (m)	0.9 (0.3)	0.3–2.0
Pool (%)	65.3 (16.0)	0–100
Run (%)	16.6 (13.4)	0–80.0
Riffle (%)	13.3 (15.8)	0–75.0
Substrate composition		
Fine substrate (%)	62.5 (30.1)	0–100
Coarse substrate (%)	37.8 (34.1)	0–100
Bedrock (%)	0.1 (0.7)	0–10.0
Instream cover		
Submergent vegetation (%)	15.5 (17.1)	0–70.0
Emergent vegetation (%)	4.8 (9.4)	0–40.0
Woody debris (%)	2.5 (4.6)	0–40.0

competing models provided a more precise inference than using only one model because an averaged model reduces bias associated with the uncertainty of model selection (Burnham & Anderson 2002; Harig & Fausch 2002; Weigel et al. 2003). Model-averaged coefficients were calculated only for independent variables that were present in one or more of the models with Akaike weights within 10% of the largest weight (Weigel et al. 2003). For example, if the largest Akaike weight was 0.440, only models with weights greater than 0.044 were used to calculate model-averaged coefficients.

The information-theoretic method provides a best-approximating model or group of models, but the selected model may be the best of a series of poor models (Burnham & Anderson 2002). Although methods that rely on hypothesis tests are commonly used to assess model fit (e.g., Hosmer-Lemeshow goodness-of-fit test; Hosmer & Lemeshow 1989), we calculated two measures of model fit that avoided the use of hypothesis tests in order to adhere to the information-theoretic philosophy. First, we estimated the log-likelihood ratio R^2 (i.e., R_L^2) for the top models (i.e., top 10% based on Akaike weights) for each species as described by Hosmer & Lemeshow (1989) and Menard (2002). The value of R_L^2 is analogous to the coefficient of determination (i.e., R^2) in linear-regression analysis and is calculated as the difference between the log-likelihood value of the intercept-only model and the log-likelihood value of the model fitted with the intercept and independent variables, divided by the log-likelihood of the intercept-only model (Hosmer & Lemeshow 1989; Menard 2002). Estimates of R_L^2 were obtained for models with Akaike weights within 10% of the model with the lowest AIC_c. Accuracy of the averaged logistic-regression model was assessed by estimating the probability of occurrence of a species for each reach. A species was categorised as ‘present’ if the predicted probability of occurrence was greater than or equal to 0.75 and ‘absent’ if ≤ 0.25 . From this analysis, we determined the number of correct, incorrect, and tied

Table 2. Generalised habitat associations of the 10 study fishes from streams throughout their native distributions. Habitat associations were used to develop logistic-regression models.

Species	Habitat associations	Reference
Bigmouth shiner	Generally associated with pool habitats with silt or sand substrate and little or no instream cover	Paloumpis 1958; Copes & Tubb 1966; Mendelson 1975; Binderim 1977; Tompkins 1987; O'Shea et al. 1990; Sanders et al. 1993; Cross & Collins 1995; Hampton & Berry 1997; Pflieger 1997
Sand shiner	Generally associated with pool habitats with silt or sand substrate and little or no instream cover	Paloumpis 1958; Copes & Tubb 1966; Binderim 1977; Matthews 1985; Tompkins 1987; O'Shea et al. 1990; Sanders et al. 1993; Cross & Collins 1995; Pflieger 1997
Common shiner	Generally associated with deep pool habitats with large rocky substrate and little instream cover	Copes & Tubb 1966; Trial et al. 1983; Moody 1989; Cross & Collins 1995; Pflieger 1997
Creek chub	Generally associated with deep pool habitats with large rocky substrate and abundant instream cover (especially large woody debris)	Deacon 1961; Dinsmore 1962; Copes 1978; Hawkes et al. 1986; Berkman & Rabeni 1987; Moody 1989; Cross & Collins 1995; Pflieger 1997; Loomis et al. 1999; Newman et al. 1999; Quist et al. 2003
Brassy minnow	Generally associated with permanent pool habitats and abundant instream cover (especially aquatic vegetation)	Copes 1975; Cross & Collins 1995; Pflieger 1997; Loomis et al. 1999; Scheurer et al. 2003
Central stoneroller	Generally associated with riffle or run habitats with large rocky substrate, but also common in pool habitats	Cross 1950; Deacon 1961; Matthews 1985; Hawkes et al. 1986; Berkman & Rabeni 1987; Aadland 1993; Pflieger 1997; Quist et al. 2003
White sucker	Generally associated with riffle or run habitats with silt, sand, or gravel substrate, but often ubiquitous	Copes & Tubb 1966; Finger 1982; Twomey et al. 1984; Berkman & Rabeni 1987; Aadland 1993; Cross & Collins 1995; Hampton & Berry 1997; Pflieger 1997
Johnny darter	Generally associated with run or shallow pool habitats with large rocky substrate	Copes & Tubb 1966; Hawkes et al. 1986; Moody 1989; Aadland 1993; Cross & Collins 1995; Pflieger 1997
Longnose dace	Generally associated with riffle or run habitats with large rocky substrate	Finger 1982; Copes 1983; Edwards et al. 1983; Aadland 1993
Fathead minnow	Generally associated with pool or backwater habitats with fine substrate, highly tolerant of habitat degradation	Cross 1950; Deacon 1961; Copes & Tubb 1966; Matthews 1985; Hawkes et al. 1986; Cross & Collins 1995; Frenzel & Swanson 1996; Hampton & Berry 1997; Pflieger 1997

classifications (Menard 2002). A correct classification was one where the predicted probability of occurrence was either present or absent, and the species was correspondingly present or absent in the reach. An incorrect classification occurred when the predicted probability of occurrence was not accurate. A tied classification occurred when the predicted probability of occurrence was between 0.26 and 0.74 (Johnson 1998; Menard 2002).

Third faunal filter – biotic filter

Because species were often absent from reaches where habitat was apparently suitable based on the local abiotic filter, we determined whether a biotic factor might explain the absence of a species from the reach (i.e., third faunal filter). Specifically, we calculated the probability of occurrence for each reach (i.e., using the averaged logistic model for each species) and considered that a high probability of occurrence was ≥ 0.75 . From the subset of reaches with a probability of occurrence ≥ 0.75 , we used logistic-regression analysis to predict the occurrence of each species using catch-per-unit-effort of nonnative piscivores (CPUE_{pisc} = number of fish/100 m; brown trout, largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieu*, green sunfish *Lepomis cyanellus*, yellow perch *Perca flavescens*, and walleye) as the independent variable. These data were log-transformed [i.e., $\log_{10}(\text{CPUE}_{\text{pisc}} + 1)$] prior to analysis.

Results

First faunal filter – large-scale biogeographic filter

Application of elevation thresholds resulted in the largest reduction of potential reaches for all species (Fig. 2). Eliminating reaches using thresholds of stream size resulted in the loss of an additional 0–24 reaches (mean $\pm$ SD: 3.8 ± 7.5) across all species, but less than five reaches were eliminated for eight of the 10 species. After passage through the large-scale biogeographic faunal filter (i.e., elevation and stream size), all species had the potential to occur at greater than 67 reaches in the North Platte River drainage. Longnose dace and white suckers were collected from reaches that varied widely in elevation and stream size; thus, the first faunal filter did not reduce the number of potential reaches by more than one for these two species. Creek chubs, longnose dace, and white suckers were present at over 80% of the reaches within the elevation and stream-size thresholds for these three species. Central stonerollers, bigmouth shiners, fathead minnows, johnny darters, and sand shiners were collected from 40 to 50% of the reaches within their respective thresholds, and brassy minnows and common shiners were present at <20% of the sampled reaches within their thresholds.

Second faunal filter – local abiotic habitat filter

Logistic-regression analysis revealed several trends with regard to habitat characteristics and the occurrence of species in a reach (Table 3). One or two variables were consistently present in the top models (i.e., top 10% based on Akaike weights) for each species. For instance, submergent vegetation, woody debris, and maximum depth were in the top four models for bigmouth shiners providing evidence that these three habitat characteristics are important for the species. Similarly, submergent vegetation was in all of the top models for brassy minnows and central stonerollers, and the proportion of fine substrate was present in all of the top models for longnose dace. The top logistic-regression models for each species generally had high R^2_L -values (Table 3), and averaged models had high R^2_L -values with a high proportion of correct classifications (Table 4). These measures suggest that models performed well in predicting the occurrence of most of the 10 species. However, logistic-regression models for fathead minnows and white suckers poorly fit the data and correctly classified their occurrence at <30% of the reaches.

The sum of Akaike weights for all models in which a predictor variable occurred provided additional evidence related to the importance of each variable (Table 5) and supported inferences obtained from investigating the top logistic-regression models. The sum of Akaike weights for maximum depth was high (i.e., >0.50) for bigmouth shiners and central stonerollers, and was the most important variable for common shiners. The percentage of the reach as pool habitat was an important variable in models predicting the occurrence of creek chubs and sand shiners. Maximum depth and amount of pool habitat did not have a high sum of Akaike weights for longnose dace or johnny darters, but these two species were the only ones for which the direction of influence was negative. Instream cover (i.e., submergent vegetation and woody debris) was positively related to the presence of brassy minnows, central stonerollers, creek chubs, johnny darters, longnose dace, and white suckers. Aquatic vegetation and woody debris were also important for predicting the occurrence of bigmouth shiners, common shiners, fathead minnows, and sand shiners, but the relationships were negative. The percentage of fine substrate was negatively related to the presence of common shiners and longnose dace, but positively related to the presence of bigmouth shiners, sand shiners, fathead minnows, and white suckers.

Third faunal filter – biotic filter

Based on the averaged logistic models, we investigated the absence of fish from reaches with a high

Table 3. Logistic regression models predicting the presence of species in the North Platte River drainage of Wyoming. Habitat variables include maximum depth (DEPTH, m), and the amount (%) of pool habitat (POOL), fine substrate (FINE), submergent vegetation (SV), and large woody debris (LWD). Akaike's Information Criteria corrected for small sample size (AIC_c), calculated from the log likelihood $[-2 \ln(L)]$, number of parameters (K), and sample size, and AIC_c weights (w) were used to select the top models from each set of *a priori* candidate models. The log-likelihood ratio R^2 (R_L^2) is provided for each species as an indication of model fit. Only models with weights that were within 10% of the best model (i.e., lowest AIC_c) are presented. For example, if the highest weight is 0.440, only models with weights >0.044 are presented.

Model	$-2 \ln(L)$	K	AIC_c	w	R_L^2
Bigmouth shiner					
SV, LWD, DEPTH	93.982	4	102.462	0.443	0.54
SV, LWD, DEPTH, POOL	93.401	5	104.132	0.192	0.55
SV, LWD, DEPTH, FINE	93.920	5	104.652	0.148	0.54
SV, LWD, DEPTH, POOL, FINE	93.380	6	106.417	0.061	0.55
Brassy minnow					
SV	58.180	2	62.316	0.234	0.58
SV, FINE	56.990	3	63.266	0.146	0.58
SV, POOL	57.420	3	63.696	0.118	0.58
SV, LWD	57.500	3	63.776	0.113	0.58
SV, DEPTH	58.070	3	64.346	0.085	0.58
Central stoneroller					
SV, DEPTH	81.390	3	87.765	0.391	0.43
SV, FINE	82.660	3	89.035	0.207	0.42
SV, DEPTH, FINE, LWD	80.230	5	91.198	0.070	0.44
SV	87.090	2	91.275	0.067	0.39
Common shiner					
DEPTH, LWD, FINE	68.200	4	76.719	0.366	0.50
DEPTH, LWD	72.220	3	78.528	0.148	0.47
DEPTH, FINE	72.400	3	78.708	0.136	0.46
DEPTH	75.900	2	80.052	0.069	0.44
DEPTH, LWD, FINE, SV	70.100	5	80.889	0.045	0.48
Creek chub					
LWD, POOL, FINE	75.130	4	83.579	0.359	0.58
LWD	79.590	2	83.722	0.335	0.55
POOL	82.150	2	86.282	0.093	0.54
Fathead minnow					
LWD, DEPTH	117.890	2	122.029	0.178	0.18
LWD, POOL	117.490	3	123.772	0.074	0.18
LWD, SV	117.860	3	124.142	0.062	0.18
LWD, FINE	117.890	3	124.172	0.061	0.18
LWD, DEPTH, POOL	116.440	4	124.916	0.042	0.19
LWD, DEPTH, FINE	116.630	4	125.106	0.038	0.19
LWD, DEPTH, SV	116.650	4	125.126	0.033	0.19
LWD, POOL, FINE	117.450	4	125.926	0.025	0.18
LWD, POOL, SV	117.480	4	125.956	0.024	0.18
LWD, SV, FINE	117.850	4	126.326	0.021	0.18
DEPTH, POOL	120.080	3	126.362	0.021	0.16
Johnny darter					
SV	98.000	2	102.164	0.361	0.46
SV, POOL	98.440	3	104.773	0.098	0.46
SV, LWD	99.480	3	105.813	0.058	0.45
SV, FINE	99.660	3	105.993	0.053	0.45
SV, DEPTH	99.680	3	106.013	0.053	0.45
POOL	102.510	2	106.674	0.037	0.43
Longnose dace					
FINE, SV	72.790	3	79.040	0.317	0.44
FINE	75.820	2	79.944	0.117	0.41
FINE, SV, DEPTH	72.620	4	81.041	0.115	0.44
FINE, SV, POOL	72.650	4	81.072	0.114	0.44
FINE, SV, LWD	72.710	4	81.131	0.111	0.44
FINE, SV, DEPTH, POOL	72.480	5	83.118	0.041	0.44
FINE, SV, DEPTH, LWD	72.560	5	83.198	0.039	0.44
Sand shiner					
POOL, SV, LWD	98.950	4	107.476	0.277	0.43

Table 3. Continued

Model	$-2 \ln(L)$	K	AIC_c	w	R_L^2
POOL, SV	101.930	3	108.242	0.189	0.42
POOL, SV, LWD, DEPTH	99.600	5	110.400	0.064	0.43
POOL, LWD	104.720	3	111.032	0.047	0.40
POOL, SV, DEPTH	102.620	4	111.146	0.044	0.41
SV, LWD	104.920	3	111.232	0.042	0.40
White sucker					
POOL, LWD	116.120	3	122.367	0.165	0.10
POOL, DEPTH	117.440	3	123.687	0.085	0.09
POOL, LWD, DEPTH	115.360	4	123.777	0.082	0.10
POOL, LWD, FINE	115.970	4	124.387	0.060	0.10
POOL, LWD, SV	116.570	4	124.987	0.045	0.09
POOL, DEPTH, FINE	116.750	4	125.167	0.041	0.09
POOL, LWD, DEPTH, FINE	114.680	5	125.312	0.038	0.11
POOL, DEPTH, SV	117.060	4	125.477	0.035	0.09
POOL, LWD, DEPTH, SV	115.080	5	125.712	0.031	0.11
POOL, LWD, FINE, SV	115.850	5	126.482	0.021	0.10
DEPTH, FINE	120.680	3	126.927	0.017	0.06

probability of occurrence (i.e., predicted probability of occurrence ≥ 0.75) using abundance of nonnative piscivores as the independent variable. The relationship between species presence and nonnative piscivores was negative in all models (Table 4). Although logistic-regression models based on habitat characteristics were poor for white suckers and fathead minnows, we conducted the analysis in the same way as for the other eight species. In addition, logistic models for fathead minnows and white suckers were developed using nonnative piscivores as a predictor variable on all reaches within the large-scale boundary (i.e., not initially passed through the local abiotic filter), but models exhibited low R_L^2 -values (i.e., $R_L^2 = 0.02$ – 0.03) and low correct classification rates (i.e., $<30\%$ correct). The abundance of nonnative piscivores acted as a filter for four species: bigmouth shiners, central stonerollers, creek chubs, and sand shiners (Table 4; Fig. 3).

Discussion

First faunal filter – large-scale biogeographic filter

We assumed that elevation and stream size were the primary mechanisms influencing the large-scale distribution of native fish species in the North Platte River drainage based on previous research in Wyoming. Carter & Hubert (1995) investigated factors influencing fishes in the Bitter Creek drainage of Wyoming and found that the distribution of fishes was largely governed by elevation and stream size. In addition, these authors identified clear thresholds for several species and found that none of the species characterised as warmwater fishes (e.g., fathead minnow, flannel-mouth sucker *Catostomus latipinnis*) were found above an elevation of 2,192 m. Other studies have identified

Table 4. Logistic-regression models predicting the presence of species in the North Platte River drainage of Wyoming. The predicted probability of a species being present at a reach is: $P(\text{present}) = e^{g(x)} / (1 + e^{g(x)})$ where P = probability of presence, and $g(x)$ represents the model coefficients. The local abiotic filter is represented by the averaged logistic-regression model (i.e., average of coefficients from models with Akaike weights within 10% of the best model; presented in Table 3). Habitat variables include maximum depth (DEPTH, m), and the amount (%) of pool habitat (POOL), fine substrate (FINE), submergent vegetation (SV), and large woody debris (LWD). The biotic filter reflects the logistic-regression model using catch-per-unit-effort of nonnative piscivores [CPUEpisc = number of fish/100 m; $\log_{10}(\text{CPUEpisc} + 1)$] as the independent variable. The percentage of reaches that were identified as correct, incorrect, or tied, and the log-likelihood ratio R^2 (R^2_L) are provided for each species as an indication of model fit.

Species	Model	Correct	Incorrect	Tied	R^2_L
Local abiotic filter					
Bigmouth shiner	$g(x) = -0.116 - 0.047\text{SV} - 0.394\text{LWD} + 2.235\text{DEPTH} - 0.003\text{POOL} + 0.001\text{FINE}$	72.3	14.5	13.2	0.54
Brassy minnow	$g(x) = -2.232 + 0.251\text{SV} - 0.013\text{FINE} + 0.003\text{POOL} - 0.011\text{LWD} + 1.407\text{DEPTH}$	77.8	10.0	12.2	0.58
Central stoneroller	$g(x) = -1.266 + 0.037\text{SV} + 0.758\text{DEPTH} - 0.006\text{FINE} + 0.067\text{LWD}$	60.3	19.1	20.6	0.42
Common shiner	$g(x) = -1.124 + 2.778\text{DEPTH} - 0.162\text{LWD} - 0.012\text{FINE} - 0.0048\text{SV}$	70.0	17.5	12.5	0.48
Creek chub	$g(x) = -1.782 + 0.042\text{POOL} + 0.261\text{LWD} - 0.004\text{FINE}$	72.5	15.9	11.7	0.57
Fathead minnow	$g(x) = -0.830 - 0.106\text{LWD} + 0.209\text{DEPTH} + 0.002\text{POOL} + 0.001\text{SV} + 0.001\text{FINE}$	24.4	13.1	65.5	0.18
Johnny darter	$g(x) = -0.127 + 0.029\text{SV} - 0.005\text{POOL} + 0.067\text{LWD} - 0.002\text{FINE} - 0.066\text{DEPTH}$	70.3	18.9	10.8	0.45
Longnose dace	$g(x) = -0.564 - 0.009\text{FINE} + 0.283\text{SV} - 0.016\text{DEPTH} - 0.001\text{POOL} + 0.042\text{LWD}$	69.0	16.0	15.0	0.44
Sand shiner	$g(x) = -2.256 + 0.062\text{POOL} - 0.140\text{SV} - 0.094\text{LWD} + 0.067\text{DEPTH}$	64.5	12.7	22.8	0.42
White sucker	$g(x) = -2.983 + 0.036\text{POOL} + 0.135\text{LWD} + 0.537\text{DEPTH} + 0.003\text{FINE} + 0.002\text{SV}$	30.3	48.7	21.1	0.10
Biotic filter					
Bigmouth shiner	$g(x) = 1.69 - 207.02\text{CPUEpisc}$	64.9	24.8	10.3	0.59
Brassy minnow	$g(x) = -0.77 - 570.60\text{CPUEpisc}$	28.6	28.5	42.9	0.14
Central stoneroller	$g(x) = 1.86 - 204.76\text{CPUEpisc}$	59.3	34.8	5.9	0.54
Common shiner	$g(x) = -0.57 - 36.72\text{CPUEpisc}$	31.9	29.7	8.3	0.18
Creek chub	$g(x) = 1.89 - 58.61\text{CPUEpisc}$	71.9	19.6	8.5	0.44
Fathead minnow	$g(x) = 0.49 - 13.51\text{CPUEpisc}$	26.0	9.1	64.9	0.02
Johnny darter	$g(x) = 0.44 - 512.50\text{CPUEpisc}$	40.0	60.0	0	0.04
Longnose dace	$g(x) = 2.36 - 27.02\text{CPUEpisc}$	29.1	24.2	46.7	0.03
Sand shiner	$g(x) = 1.92 - 205.71\text{CPUEpisc}$	63.2	24.3	12.5	0.42
White sucker	$g(x) = 2.15 - 23.12\text{CPUEpisc}$	35.9	31.1	33.0	0.08

Table 5. Sum of Akaike's Information Criteria weights and direction of the relationship for each habitat variable used in the logistic regression models by fish species. Habitat variables include maximum depth (DEPTH, m) and the amount (%) of pool habitat (POOL), fine substrate (FINE), submergent vegetation (SV), and large woody debris (LWD) in reaches from the North Platte River drainage of Wyoming (1993–2000). High values (e.g., ≥ 0.50 in bold) suggest that a variable is important to a species.

Species	Variables				
	DEPTH	POOL	SV	LWD	FINES
Bigmouth shiner	(+) 0.872	(+) 0.307	(-) 0.924	(-) 0.991	(+) 0.252
Brassy minnow	(+) 0.215	(+) 0.242	(+) 0.823	(-) 0.251	(-) 0.312
Central stoneroller	(+) 0.589	(+) 0.141	(+) 0.907	(+) 0.208	(-) 0.422
Common shiner	(+) 0.921	(+) 0.131	(-) 0.146	(-) 0.685	(-) 0.654
Creek chub	(+) 0.078	(+) 0.521	(-) 0.107	(+) 0.756	(-) 0.462
Fathead minnow	(+) 0.389	(+) 0.329	(+) 0.277	(-) 0.733	(+) 0.279
Johnny darter	(-) 0.216	(-) 0.270	(+) 0.767	(+) 0.224	(-) 0.215
Longnose dace	(-) 0.271	(-) 0.283	(+) 0.640	(+) 0.263	(-) 0.797
Sand shiner	(+) 0.272	(+) 0.802	(-) 0.785	(-) 0.620	(+) 0.169
White sucker	(+) 0.443	(+) 0.797	(+) 0.287	(+) 0.544	(+) 0.333

distributional limits for native and nonnative fishes in Wyoming based on the large-scale biogeographic features used in our study (e.g., Larscheid & Hubert 1992; Kruse et al. 1997; Quist et al. 2004).

While elevation may be a proxy for water temperature, stream size probably reflects differences in the geomorphology and position of a stream reach in a watershed (Bozek & Hubert 1992; Isaak & Hubert 2001). Studies on longitudinal zonation and addition of fishes in lotic systems have generally shown that

species have boundaries related to stream size (e.g., Rahel & Hubert 1991; Williams et al. 1996; Quist et al. 2004). Although we used our data (as opposed to an independent data set) to establish thresholds of elevation and stream size for each species, this approach was appropriate because including reaches outside the known distribution of a species would confound analyses and obscure ecological interpretations.

Second faunal filter – local abiotic filter

Logistic-regression models reflected the composition of local abiotic filters and provided insight on the ecology of each species in the North Platte River system of Wyoming. Based on these results, we made several generalisations among species regarding the influence of habitat characteristics on their occurrence. Maximum depth and amount of pool habitat were important for several of the study species. Streams in the Great Plains are prone to frequent intermittence because of geology and variable climate (Matthews 1988; Fausch & Bestgen 1997). Thus, maximum depth may provide a measure of refuge availability during low-water conditions. For example, Scheurer et al. (2003) reported that brassy minnows in the Great Plains region of Colorado were dependent on the availability of deep pools that remained wet during summer. Although depth was not an overly important

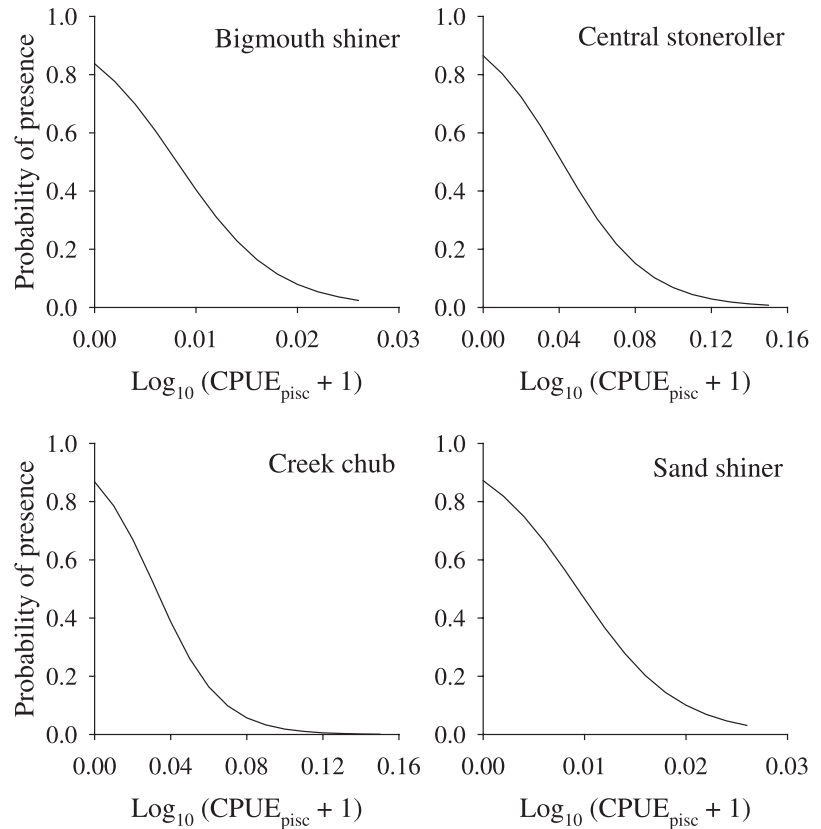


Fig. 3. Logistic-regression models predicting the presence of species in the North Platte River drainage of Wyoming using catch-per-unit-effort ($\text{CPUE}_{\text{pisc}}$ = number of fish/100 m) of nonnative piscivores. The predicted probability of a species being present at a reach is: $P(\text{present}) = \frac{e^{g(x)}}{1 + e^{g(x)}}$ where P = probability of a species being present and $g(x)$ represents the coefficient estimates.

variable for brassy minnows in the North Platte River system, maximum depth was one of the most important habitat features for bigmouth shiners, sand shiners, and common shiners, which are common in streams prone to intermittence (Paloumpis 1958; Baxter & Stone 1995; Cross & Collins 1995). Pool habitats not only create refuge during low-water conditions, but also provide protection against avian and other terrestrial predators (Schlosser 1987). Consequently, the amount of pool habitat in a reach was positively related to the presence of all species, except johnny darters and longnose dace, which were most common in riffle and run habitats (Table 1). Central stonerollers were common in riffles and runs, but also frequented pool habitats. Although the relationship between the presence of central stonerollers and the amount of pool habitat was positive, pool habitat was not included in any of the top logistic models indicating that other habitat features were more important.

Instream habitat structure (i.e., woody debris, vegetation) provides a variety of functions for stream fishes. For instance, woody debris is an important component of nutrient processing in streams because it enhances organic matter and inorganic sediment retention (Speaker et al. 1984). Areas with woody debris not only become important sources of nutrients, but woody debris also provides substrate for aquatic macroinver-

tebrates (Benke et al. 1984) and adds structural complexity (Angermeier & Karr 1984). In the North Platte River drainage, the occurrence of several species was related to the amount of woody debris and it was the most important variable for creek chubs. Creek chubs are highly dependent on macroinvertebrates during their early life history and then become opportunistic predators (Dinsmore 1962). Thus, large woody debris may represent areas of high macroinvertebrate production or ambush areas to enhance predation efficiency. Submergent vegetation was an important variable for brassy minnows, central stonerollers, and longnose dace. All three species consume algae or other plant materials (e.g., Edwards et al. 1983; Power et al. 1985; Pflieger 1997) associated with submergent vegetation. Bigmouth shiners, common shiners, and sand shiners were inversely related to the amount of vegetation and woody debris, which likely reflects their prevalence in open-water habitats.

Substrate composition can also be an important habitat feature for fishes in stream ecosystems because of its importance for spawning and the production of prey (Allan 1995). Most of the species we examined were associated with large substrate and many were sensitive to the presence of fine sediment (Berkman & Rabeni 1987; Quist et al. 2003). Conversely, some species (e.g., bigmouth shiners, sand shiners) were generally found in streams with fine substrate.

Logistic-regression models performed poorly for fathead minnows and white suckers. Fathead minnows are ubiquitous in the Great Plains with few identified habitat associations (e.g., Hawkes et al. 1986; Hampton & Berry 1997). Additionally, fathead minnows are tolerant of high temperatures, low dissolved oxygen, and poor water quality associated with habitat degradation or pollution (Frenzel & Swanson 1996; Pflieger 1997). White suckers often occur in riffle, run, and pool habitats with sand or gravel substrate (e.g., Aadland 1993; Cross & Collins 1995), but are usually considered habitat generalists (Finger 1982; Hampton & Berry 1997). In Wyoming, both fathead minnows and white suckers are widely distributed and have successfully invaded drainages west of the Continental Divide (Baxter & Stone 1995). Thus, it is not surprising that we did not identify accurate models for either of these species.

Third faunal filter – biotic filter

Predation can influence the composition of fish assemblages, particularly when the predator is a nonnative fish species (Lohr & Fausch 1996; Jackson et al. 2001). Our analysis indicated that the abundance of nonnative piscivorous fishes was an additional faunal filter for four species. All 10 study species occur with piscivorous predators over a portion of their natural distribution, but native piscivores were absent from most of the North Platte River system in Wyoming (Baxter & Stone 1995). The only native piscivorous species were sauger *Sander canadensis*, which was limited to the mainstem of the North Platte River, and creek chubs, which have little influence on other native fishes (Schlosser 1988). Central stonerollers often occur with piscivores across their distribution, but have been shown to be sensitive to their presence in streams (e.g., Power et al. 1985). Bigmouth shiners and sand shiners were generally found in open-water habitats and their presence was inversely related to the abundance of nonnative piscivores. Similarly, plains killifish (*Fundulus zebri-nus*) are also found in open-water habitats and have been found to be sensitive to nonnative piscivores in the western Great Plains (Lohr & Fausch 1996). Lack of a relationship between nonnative piscivorous fishes and the other species studied suggests that other mechanisms influence their absence from reaches with suitable habitat conditions.

Summary and application

The concept of hierarchical faunal filters has numerous applications for the conservation and management of native fishes. To provide an example of how hierarchical faunal filters might be used, we present

data for two contrasting reaches from the Laramie River in the North Platte River drainage. The reach represented in Fig. 4 was sampled in 2002 near Laramie, Wyoming, and the reach presented in Fig. 5 was sampled downstream of Grayrocks Reservoir in 2003. Neither reach was included in the original data set. We excluded fathead minnows and white suckers from the examples because the local abiotic filter performed poorly for both species.

We assumed that high-order filters (e.g., continental and regional filters) would result in eight species possibly being present in the reach sampled near Laramie, Wyoming (Fig. 4). The large-scale biogeographic filter eliminated three (i.e., bigmouth shiners, central stonerollers, and sand shiners) of eight species and allowed five species to pass and comprise the potential local assemblage at the elevation and stream size of the reach. The five remaining species were then passed through the local abiotic filter (i.e., averaged logistic model for each species), resulting in a predicted probability of occurrence for each species given local habitat characteristics. The biotic filter was applied to creek chubs and although nonnative piscivores (i.e., brown trout) were present, the filter did little to reduce the probability of occurrence of creek chubs. The biotic filter was not applied to common shiners, longnose dace, brassy minnows, or johnny darters because nonnative piscivores poorly explained their absence from reaches with suitable habitat (i.e., Table 4). Multiplying the probability of occurrence given local abiotic habitat conditions by the probability of occurrence because of biotic interactions resulted in an overall probability of occurrence of each species (Fig. 4). Three species (i.e., common shiners, longnose dace, and brassy minnows) had relatively high probabilities of being present (i.e., ≥ 0.75) and were all collected in the reach. Johnny darters had a moderate (i.e., 0.26–0.74) probability of occurrence and were absent. Creek chubs had a high probability of occurrence given the abiotic habitat characteristics of the reach, but the inclusion of a biotic filter resulted in reduced probability of occurrence. Although the overall probability of occurrence for creek chubs was moderate, they were present in the reach. Thus, the faunal filters correctly predicted the presence of four species, the absence of three species, and was ambiguous for one species (i.e., johnny darters).

Using the same approach, we found insightful results for the reach downstream of Grayrocks Reservoir (Fig. 5). Unlike the reach near Laramie, Wyoming, the large-scale faunal filter did not remove any species from the North Platte River drainage species pool when applied to the reach downstream of Grayrocks Reservoir. After passage through the local abiotic habitat filter, probability of occurrence varied from 0.37 to 0.97 among the eight species. However,

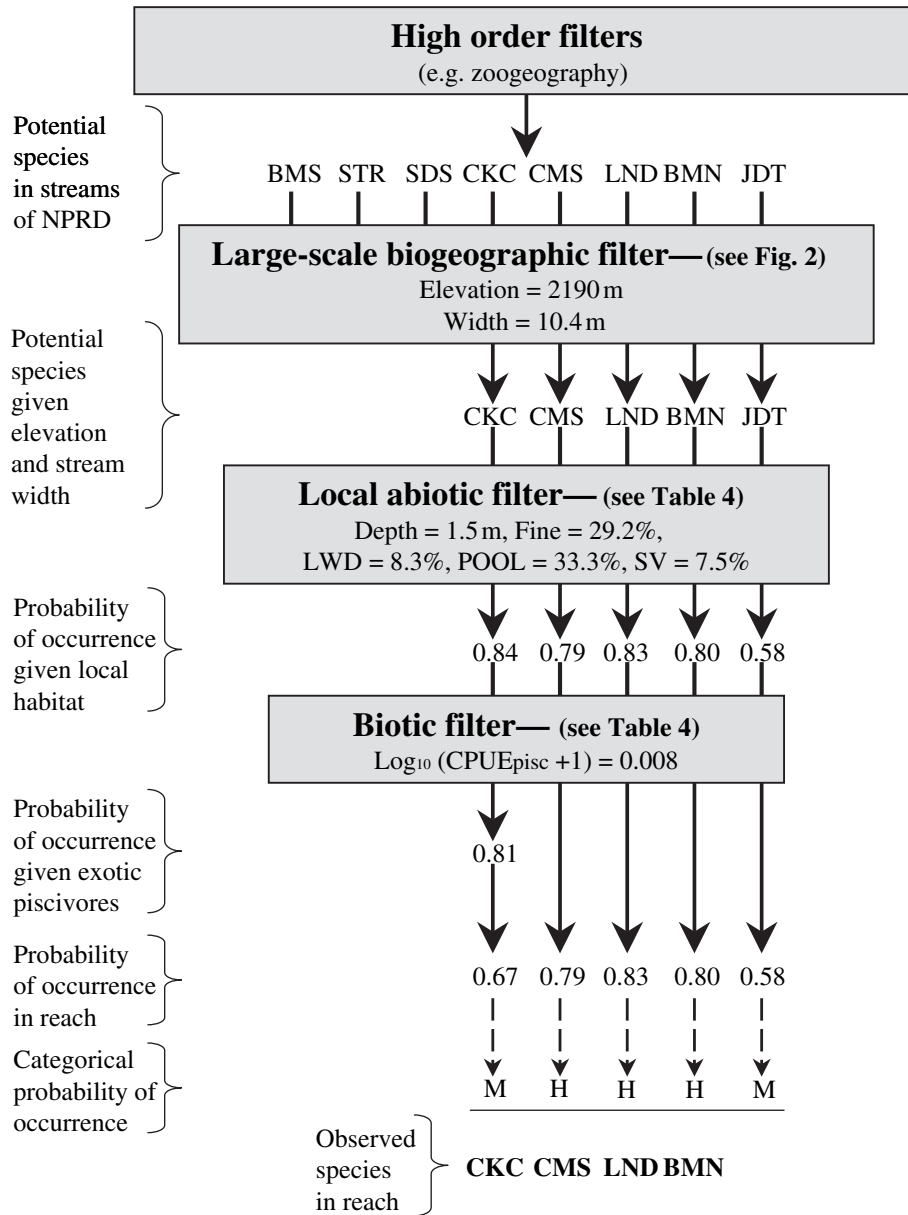


Fig. 4. Hierarchical faunal filters for a reach sampled on the Laramie River [North Platte River drainage (NPRD)] near Laramie, Wyoming, during 2002. Eight species were included in the analysis: bigmouth shiner (BMS), central stoneroller (STR), sand shiner (SDS), creek chub (CKC), common shiner (CMS), longnose dace (LND), brassy minnow (BMN), and johnny darter (JDT). Elevation (m.a.s.l.) and mean stream width (m) comprised the large-scale biogeographic faunal filter (from Fig. 2). The local abiotic filter was comprised of maximum depth (DEPTH; m) and the percentage of fine substrate (FINE), wood debris (LWD), pool habitat (POOL), and submergent vegetation (SV). The probability of occurrence for each species in the reach given local habitat characteristics was obtained using the averaged logistic-regression model for each species (provided in Table 4). The probability of occurrence given nonnative piscivores was determined with logistic-regression models (provided in Table 4) predicting the presence of species using catch-per-unit-effort of nonnative piscivores [$\text{CPUE}_{\text{pisc}}$ = number of fish/100 m; $\log_{10}(\text{CPUE}_{\text{pisc}} + 1)$]. Overall probability of occurrence in the reach was the product of the probabilities of occurrence given local habitat and nonnative piscivores. The overall probability of occurrence was categorised as low (L; ≤ 0.25), moderate (M; $0.26\text{--}0.74$), or high (H; ≥ 0.75).

smallmouth bass and green sunfish were abundant in the reach and greatly reduced the probability of occurrence for the four species found to be sensitive to piscivorous fishes (i.e., bigmouth shiners, central stonerollers, sand shiners, and creek chubs). Thus, the faunal filters correctly predicted the absence of four

species and the presence of one species. Predictions were somewhat ambiguous for three species, only one of which was present in the reach.

Hierarchical faunal filters have been largely discussed within the context of basic ecological theory (e.g., Poff 1997; Matthews 1998). Consequently, the

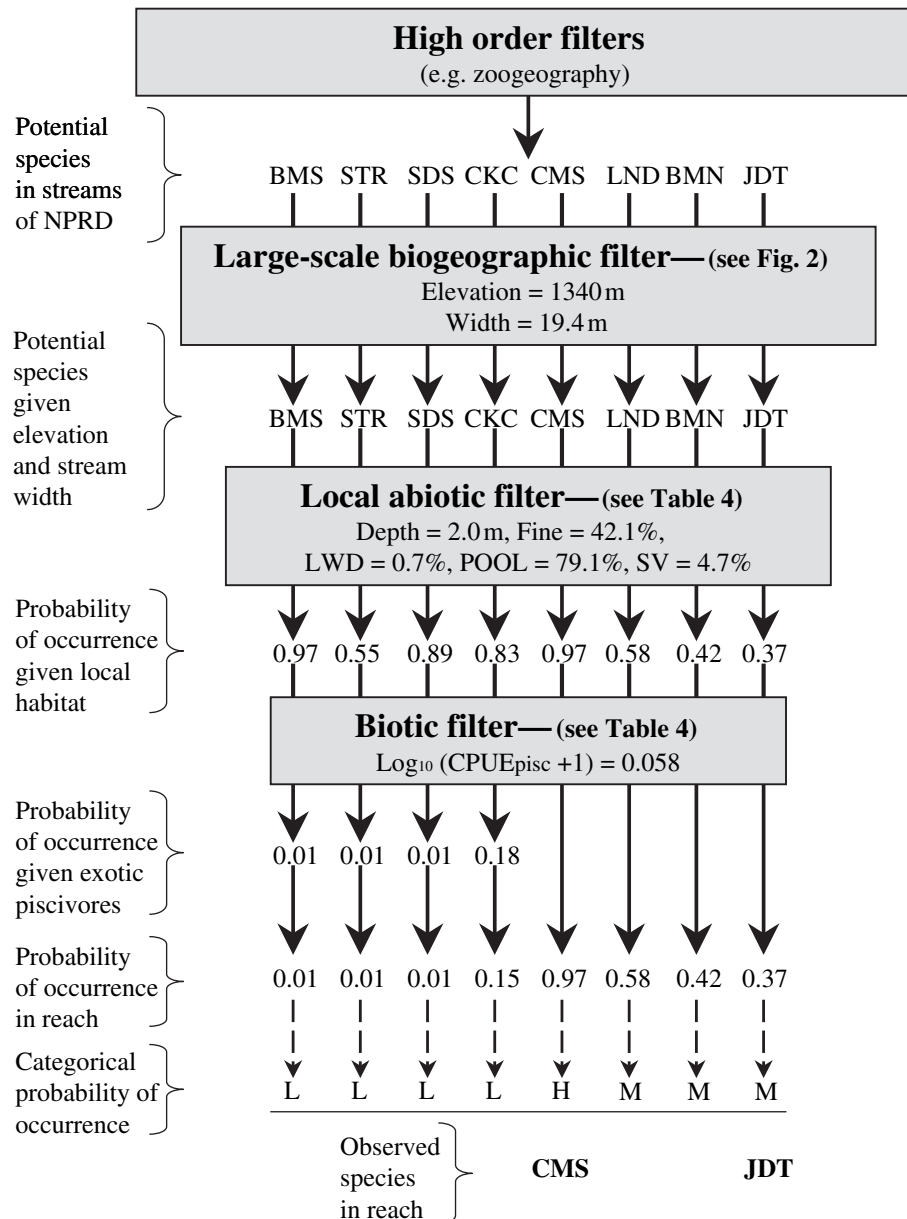


Fig. 5. Hierarchical faunal filters for a reach sampled on the Laramie River [North Platte River drainage (NPRD)] downstream of Grayrocks Reservoir, Wyoming, during 2003. Eight species were included in the analysis: bigmouth shiner (BMS), central stoneroller (STR), sand shiner (SDS), creek chub (CKC), common shiner (CMS), longnose dace (LND), brassy minnow (BMN), and johnny darter (JDT). Elevation (m.a.s.l.) and mean stream width (m) comprised the large-scale biogeographic faunal filter (from Fig. 2). The local abiotic filter was comprised of maximum depth (DEPTH; m) and the percentage of fine substrate (FINE), wood debris (LWD), pool habitat (POOL), and submergent vegetation (SV). The probability of occurrence for each species in the reach given local habitat characteristics was obtained using the averaged logistic-regression model for each species (provided in Table 4). The probability of occurrence given nonnative piscivores was determined with logistic-regression models (provided in Table 4) predicting the presence of species using catch-per-unit-effort of nonnative piscivores [$\text{CPUE}_{\text{pisc}}$ = number of fish/100 m; $\log_{10} (\text{CPUE}_{\text{pisc}} + 1)$]. Overall probability of occurrence in the reach was the product of the probabilities of occurrence given local habitat and nonnative piscivores. The overall probability of occurrence was categorised as low (L; ≤ 0.25), moderate (M; $0.26-0.74$), or high (H; ≥ 0.75).

idea of hierarchical faunal filters has received little attention from applied ecologists focused on the conservation and management of native species. Our study demonstrates that the concept of hierarchical faunal filters is simple and logical, and can provide a framework for conserving and managing fishes. Each faunal

filter provides insight on the ecology of individual species and, cumulatively, faunal filters allow for reasonably accurate predictions of species occurrence and fish assemblage structure. If, for example, a species is absent from a reach, then consideration of faunal filters would allow ecologists to identify which factor or

factors (e.g., elevational and stream size thresholds, abiotic habitat characteristics, or interactions with nonnative species) explain their absence. Identifying where limiting factors occur in the hierarchy is important from a management perspective. Managers can do little to alleviate limitations at the large-scale biogeographic level of the hierarchy (e.g., elevation or stream size limitation). In contrast, managers can ameliorate limitations that occur at lower levels of the hierarchy such as habitat improvements to reduce local abiotic habitat limitations or control of nonnative piscivores to reduce biotic limitations. Although the specific structure of faunal filters in this study is limited to the North Platte River drainage in Wyoming, we demonstrate the utility of conceptualising the occurrence of fishes within the context of hierarchical faunal filters. Because of increased awareness of issues related to native fish species on global and regional scales (e.g., Muth et al. 1998), hierarchical faunal filters can become an important tool for conservation and management.

Resumen

1. Comprender los factores relacionados con la ocurrencia de especies a través de escalas espaciales y temporales múltiples es crucial para la conservación y gestión de especies de peces nativas, especialmente para aquellas que se encuentran en el límite de sus áreas de distribución. Utilizamos el concepto de 'Filtros Faunísticos Jerárquicos' como base para investigar la influencia de características del hábitat y de piscívoros no nativos sobre la ocurrencia de 10 especies nativas en afluentes de la cuenca del Río North Platte (Wyoming, USA).

2. Tres filtros faunísticos fueron desarrollados para cada especie: (A) Un filtro bio-geográfico a gran escala; (B) un filtro abiótico local; y (C) un filtro biótico. El filtro bio-geográfico a gran escala, compuesto de umbrales de altitud y tamaño del río, fue utilizado para determinar los límites dentro de los que la ocurrencia de cada especie puede ser esperada. Desarrollamos entonces, un filtro abiótico local (i.e., asociaciones de hábitats), utilizando análisis de regresión logístico binario para estimar la probabilidad de ocurrencia de cada especie, a partir de características tales como profundidad máxima, composición del sustrato, vegetación acuática sumergida, restos vegetales y morfología del canal (e.g., cantidad de hábitat de pozas). Desarrollamos, por último, un filtro faunístico biótico utilizando regresiones logísticas binarias para estimar la probabilidad de ocurrencia de cada especie en relación a la abundancia de piscívoros no nativos en cada sección del río.

3. Conceptualizar ensamblajes de peces sobre 'Filtros Faunísticos Jerárquicos' es sencillo y lógico; ayuda en las actividades de conservación y gestión, y provee información importante sobre la ecología de los peces del Gran Plató occidental de América del Norte.

Acknowledgements

We thank S. Covington, W. LaVoie, T. Lipsey, T. Marwitz, C. Meyer, A. Parker, A. Patton, C. Patton, T. Patton, M. Snigg,

L. Thel, R. Tudek, and M. Williams for assisting with data collection. We also thank L. Thel for providing helpful comments on an earlier draft of the manuscript. This study was funded by the Wyoming Game and Fish Department and the Wyoming Cooperative Fish and Wildlife Research Unit (the Unit is jointly sponsored by the U.S. Geological Survey, Wyoming Game and Fish Department, University of Wyoming, and Wildlife Management Institute).

References

- Aadland, L.P. 1993. Stream habitat types: their fish assemblages and relationship to flow. *North American Journal of Fisheries Management* 13: 790–806.
- Allan, J.D. 1995. *Stream ecology, structure and function of running water*. New York: Chapman and Hall.
- Allen, T.F.H. & Starr, T.B. 1982. *Hierarchy: perspectives for ecological complexity*. Chicago, IL: University of Chicago Press.
- Angermeier, P.A. & Karr, J.R. 1984. Relationships with woody debris and fish habitat in small warmwater streams. *Transactions of the American Fisheries Society* 113: 716–726.
- Armantrout, N.B. compiler. 1998. *Glossary of aquatic habitat inventory terminology*. Bethesda, MD: American Fisheries Society.
- Arnold, T.W., Anderson, M.G., Sorenson, M.D. & Emery, R.B. 2002. Survival and philopatry of female redheads breeding in southwestern Manitoba. *Journal of Wildlife Management* 66: 162–169.
- Baxter, G.T. & Stone, M.D. 1995. *Fishes of Wyoming*. Cheyenne, WY: Wyoming Game and Fish Department.
- Benke, A.C., VanArdsall, T.C., Jr, Gillespie, D.M. & Parrish, F.K. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecological Monographs* 54: 25–63.
- Berkman, H.E. & Rabeni, C.F. 1987. Effect of siltation on stream fish communities. *Environmental Biology of Fishes* 18: 285–294.
- Bevenger, G.S. & King, R.M. 1995. *A pebble count procedure for assessing watershed cumulative effects*. Fort Collins, CO: U.S. Forest Service Research Paper RM-RP-319.
- Binderim, G.E. 1977. *Fishes of Mill Creek, a tributary of the Washita River, Johnston and Murray counties, Oklahoma*. *Proceedings of the Oklahoma Academy of Science* 57: 1–11.
- Bozek, M.A. & Hubert, W.A. 1992. Segregation of resident trout streams as predicted by three habitat dimensions. *Canadian Journal of Zoology* 70: 886–890.
- Burhans, D.E., Dearborn, D., Thompson, F.R., III & Faaborg, J. 2002. Factors affecting predation at songbirds nest in old fields. *Journal of Management* 66: 240–249.
- Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multi-model inference*, second edition. New York, NY: Springer-Verlag.
- Carter, B. & Hubert, W.A. 1995. Factors influencing fish assemblages of a high-elevation desert stream system in Wyoming. *Great Basin Naturalist* 55: 169–173.
- Copes, F.A. 1975. Ecology of the brassy minnow, *Hybognathus hankinsoni* (Cyprinidae). Reports on the Fauna and Flora of Wisconsin No. 10, Museum of Natural History. Stephens Point, WI: University of Wisconsin.

- Copes, F.A. 1978. Ecology of the creek chub. Reports on the Fauna and Flora of Wisconsin No. 12, Museum of Natural History. Stevens Point, WI: University of Wisconsin.
- Copes, F.A. 1983. The longnose dace *Rhinichthys cataractae* Valenciennes in Wisconsin and Wyoming waters. Reports on the Fauna and Flora of Wisconsin No. 19, Museum of Natural History. Stevens Point, WI: University of Wisconsin.
- Copes, F.A. & Tubb, R.A. 1966. Fishes of the Red River tributaries in North Dakota. Contributions of the Institute for Ecological Studies Number 1. Grand Forks, ND: University of North Dakota.
- Cross, F.B. 1950. Effects of sewage and of a headwater impoundment on the fishes of Stillwater Creek in Payne County, Oklahoma. American Midland Naturalist 43: 129–145.
- Cross, F.B. & Collins, J.T. 1995. Fishes in Kansas, second edition. Lawrence, KS: University of Kansas Museum of Natural History.
- Deacon, J.E. 1961. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. University of Kansas Publications, Museum of Natural History 13: 359–427.
- Dinsmore, J.J. 1962. Life history of the creek chub, with emphasis on growth. Iowa Academy of Science 69: 296–301.
- Eberhardt, L.L. 2003. What should we do about hypothesis testing? Journal of Wildlife Management 67: 241–247.
- Edwards, E.A., Li, H., Schreck, C.B., Terrell, J.W. & Raleigh, R.F. 1983. Habitat suitability index models: longnose dace. Washington D.C.: U.S. Fish and Wildlife Service, FWS/OBS-82/10.33.
- Fausch, K.D. & Bestgen, K.R. 1997. Ecology of fishes indigenous to the central and southwestern Great Plains. In: Knopf, F.L. & Samson, F.B., eds. Ecology and conservation of Great Plains vertebrates. New York, NY: Springer-Verlag. pp. 131–166.
- Finger, T.R. 1982. Fish community-habitat relations in a central New York stream. Journal of Freshwater Ecology 1: 343–352.
- Frenzel, S.A. & Swanson, R.B. 1996. Relations of fish community composition to environmental variables in streams of central Nebraska, USA. Environmental Management 20: 689–705.
- Hampton, D.R. & Berry, C.R., Jr 1997. Fishes of the mainstem Cheyenne River in South Dakota. Proceedings of the South Dakota Academy of Science 76: 11–25.
- Harig, A.L. & Fausch, K.D. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. Ecological Applications 12: 535–551.
- Hawkes, C.L., Miller, D.L. & Layher, W.L. 1986. Fish ecoregions of Kansas: stream fish assemblage patterns and associated environmental correlates. Environmental Biology of Fishes 17: 267–279.
- Hosmer, D.W., Jr & Lemeshow, S. 1989. Applied logistic regression. New York, NY: John Wiley and Sons.
- Isaak, D.J. & Hubert, W.A. 2001. A hypothesis about factors that affect maximum summer stream temperatures across montane landscapes. Journal of the American Water Resources Association 37: 351–366.
- Jackson, D.A. & Harvey, H.H. 1989. Biogeographic associations in fish assemblages: local vs. regional processes. Ecology 70: 1472–1484.
- Jackson, D.A., Peres-Neto, P.R. & Olden, J.D. 2001. What controls who is where in freshwater fish communities—the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58: 157–170.
- Johnson, D.E. 1998. Applied multivariate methods for data analysts. Pacific Grove, CA: Duxbury Press.
- Johnson, D.H. 2002. The role of hypothesis testing in wildlife science. Journal of Wildlife Management 66: 272–276.
- Kruse, C.G., Hubert, W.A. & Rahel, F.J. 1997. Geomorphic influences on the distribution of Yellowstone cutthroat trout in the Absaroka Mountains, Wyoming. Transactions of the American Fisheries Society 126: 418–427.
- Lanka, R.P., Hubert, W.A. & Wesche, T.A. 1987. Relations of geomorphology to stream habitat and trout standing stock in small Rocky Mountain streams. Transactions of the American Fisheries Society 116: 21–28.
- Larscheid, J.G. & Hubert, W.A. 1992. Factors influencing the size structure of brook trout and brown trout in southeastern Wyoming mountain streams. North American Journal of Fisheries Management 12: 109–117.
- Lee, D.S., Gilbert, C.R., Hocutt, C.H., Jenkins, R.E., McAllister, D.E. & Stauffer, J.R., Jr 1980. Atlas of North American freshwater fishes. Raleigh, NC: North Carolina State Museum of Natural History.
- Lohr, S.C. & Fausch, K.D. 1996. Effects of green sunfish (*Lepomis cyanellus*) predation on survival and habitat use of plains killifish (*Fundulus zebrinus*). Southwestern Naturalist 41: 155–160.
- Loomis, T.M., Berry, C.R., Jr & Erickson, J. 1999. The fishes of the upper Moreau River basin. Prairie Naturalist 31: 193–213.
- Matthews, W.J. 1985. Distribution of midwestern fishes on multivariate environmental gradient, with emphasis on *Notropis lutrensis*. American Midland Naturalist 113: 225–237.
- Matthews, W.J. 1988. North American prairie streams as a system for ecological study. Journal of the North American Benthological Society 7: 387–409.
- Matthews, W.J. 1998. Patterns in freshwater fish ecology. New York, NY: Chapman and Hall.
- Menard, S.W. 2002. Applied logistic regression analysis. Thousand Oaks, CA: Sage Publications.
- Mendelson, J. 1975. Feeding relationships among species of *Notropis* (Pisces: Cyprinidae) in a Wisconsin stream. Ecological Monographs 45: 199–230.
- Moody, R.C. 1989. Habitat use, availability, and preference for johnny darter, white sucker, northern hog sucker, common shiner, and creek chub in stream in central Wisconsin. Master's thesis. Stevens Point, WI: University of Wisconsin.
- Moyle, P.B. 1994. Biodiversity, biomonitoring, and the structure of stream fish communities. In: Loeb, S.L. & Spacie, A., eds. Biological monitoring of aquatic systems. Boca Raton, FL: Lewis Publishers, Inc. pp. 171–186.
- Mullner, S.A., Hubert, W.A. & Wesche, T.A. 2000. Visually estimating substrate composition at potential spawning sites for trout in mountain streams. Journal of Freshwater Ecology 15: 199–207.
- Muth, R.M., Hamilton, D.A., Organ, J.F., Witter, D.J., Mather, M.E. & Daigle, J.J. 1998. The future of wildlife and fisheries policy and management: assessing the attitudes and values of wildlife and fisheries professionals. Transactions of the 63rd North American Wildlife and Natural Resources Conference 63: 604–627.

- Newman, R.L., Berry, C.R. & Duffy, W. 1999. A biological assessment of four northern Black Hills streams. *Proceedings of the South Dakota Academy of Science* 78: 185–197.
- Nibbelink, N.P. 2002. Spatial patterns in fish distributions and density: the influence of watershed-based habitat gradients. Doctoral dissertation. Laramie, WY: University of Wyoming.
- O'Shea, D.T., Hubert, W.A. & Anderson, S.H. 1990. Assemblages of small fish in three habitat types along the Platte River, Nebraska. *Prairie Naturalist* 22: 145–154.
- Paloumpis, A.A. 1958. Response of some minnows to flood and drought conditions in an intermittent stream. *Iowa State College Journal of Science* 32: 547–561.
- Patton, T.M., Hubert, W.A., Rahel, F.J. & Gerow, K.G. 2000. Effort needed to estimate species richness in small streams of the Great Plains in Wyoming. *North American Journal of Fisheries Management* 20: 394–398.
- Pflieger, W.L. 1997. The fishes of Missouri, revised edition. Jefferson City, MO: Missouri Department of Conservation.
- Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16: 391–409.
- Power, M.E., Matthews, W.J. & Stewart, A.J. 1985. Grazing minnows, piscivorous bass and stream algae: dynamics of a strong interaction. *Ecology* 66: 1448–1456.
- Quist, M.C., Fay, P.A., Guy, C.S., Knapp, A.K. & Rubenstein, B.N. 2003. Military training effects on terrestrial and aquatic communities on a grassland military installation. *Ecological Applications* 13: 432–442.
- Quist, M.C., Hubert, W.A. & Rahel, F.J. 2004. Elevation and stream-size thresholds affect distributions of native and exotic warmwater fishes in Wyoming. *Journal of Freshwater Ecology* 19: 227–236.
- Rahel, F.J. & Hubert, W.A. 1991. Fish assemblages and habitat gradients in a Rocky Mountain-Great Plains stream: biotic zonation and additive patterns of community change. *Transactions of the American Fisheries Society* 120: 319–332.
- Robinson, D.H. & Wainer, H. 2002. On the past and future of null hypothesis significance testing. *Journal of Wildlife Management* 66: 263–271.
- Rolstad, J., Løken, B. & Rolstad, E. 2000. Habitat selection as a hierarchical spatial process: the green woodpecker at the northern edge of its distribution range. *Oecologia* 124: 116–129.
- Sanders, R.M., Jr, Huggins, D.G. & Cross, F.B. 1993. The Kansas River and its biota. In: Hesse, L.W., Stalnaker, C.B., Benson, N.G. & Zuboy, J.R., eds. *Proceedings of the symposium on restoration planning for the rivers of the Mississippi and Missouri river ecosystem*. Washington D.C.: U.S. National Biological Survey, Biological Report 19. pp. 295–326.
- Scheurer, J.A., Fausch, K.D. & Bestgen, K.R. 2003. Multiscale processes regulate brassy minnow persistence in a Great Plains river. *Transactions of the American Fisheries Society* 132: 840–855.
- Schlosser, I.J. 1987. The role of predation in age- and size-related habitat use by stream fishes. *Ecology* 66: 651–659.
- Schlosser, I.J. 1988. Predation rates and the behavioral response of adult brassy minnows (*Hybognathus hankinsoni*) to creek chub and smallmouth bass predators. *Copeia* 1988: 691–697.
- Simpson, G.G. 1953. *Evolution and geography – an essay on historical biogeography with special reference to mammals*. Condon Lectures. Eugene, OR: Oregon State System of Higher Education.
- Smith, C.L. & Powell, C.R. 1971. The summer fish communities of Brier Creek, Marshall County, Oklahoma. *American Museum Novitates*, Number 2458.
- Speaker, R., Moore, K. & Gregory, S.V. 1984. Analysis of the process of retention of organic matter in stream ecosystems. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 22: 1835–1841.
- Tompkins, A. 1987. Status of the bigmouth shiner, *Notropis dorsalis*, in Canada. *Canadian Field Naturalist* 101: 195–202.
- Tonn, W.M. 1990. Climate change and fish communities: a conceptual framework. *Transactions of the American Fisheries Society* 119: 337–352.
- Trial, J.G., Wade, C.S., Stanley, J.G., Nelson, P.C. & Terrel, J.W. 1983. *Habitat suitability information: common shiner*. Washington D.C.: U.S. Fish and Wildlife Service, FWS/OBS-82/10.40.
- Twomey, K.A., Williamson, K.L., Nelson, P.C. & Armour, C. 1984. *Habitat suitability models and instream flow suitability curves: white sucker*. Washington D.C.: U.S. Fish and Wildlife Service, FWS/OBS-82/10.64.
- Wang, L., Simonson, T.D. & Lyons, J. 1996. Accuracy and precision of selected stream habitat estimates. *North American Journal of Fisheries Management* 16: 340–347.
- Weigel, D.E., Peterson, J.T. & Spruell, P. 2003. Introgressive hybridization between native cutthroat trout and introduced rainbow trout. *Ecological Applications* 13: 38–50.
- Williams, L.R., Toepfer, C.S. & Martinez, A.D. 1996. The relationship between fish assemblages and environmental gradients in an Oklahoma prairie stream. *Journal of Freshwater Ecology* 11: 459–468.