


## RESEARCH ARTICLE

# Restricted movement of prairie fishes in fragmented riverscapes risks ecosystem structure being ratcheted downstream

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**Abstract**

1. Prairie streams are dynamic systems in which habitat patches are sporadically created and lost during extreme hydrological events. The persistence of fish species depends on life-history traits that facilitate their widespread dispersal to recolonize habitats after stochastic extirpation. Artificial barriers are thought to reduce recolonization opportunities and to ultimately displace populations downstream, but the ecological consequences of lost diversity above the barriers are largely unknown.
2. The susceptibility of four prairie fishes to fragmentation and the consequent risk to stream ecosystem processes are described. The selected species exhibit wide tolerances to environmental stressors, represent unique functional feeding guilds, and have different habitat affinities.
3. The ability of each species to access (jumping ability) and successfully traverse (swimming endurance) simulated instream barriers was quantified in the laboratory. Experimental stream complexes were used to isolate the effects of these species on ecosystem structure and function. These replicated single-species experiments were compared with 'no fish' controls to identify the ecological role of each.
4. Small vertical barriers blocked most passage, and with open access all species were unable to traverse relatively short distances against modest water velocities. Stream fragmentation will alter headwater fish assemblage structure and promote the most mobile species. Each species had slightly different effects on the stream ecosystem structure resulting from their different habitat preferences and diets.
5. Without colonization opportunities from neighbouring populations, disturbance events will alter headwater fish assemblages and may degrade the ecosystem structure above barriers.
6. Fragmented riverscapes interact with harsh disturbance regimes to form an ecological ratchet. Systematic species loss above barriers outweighs the opportunity for improvement, suggesting that ecosystem structure may be moving downstream.

**KEYWORDS**

barrier, ecosystem structure, jumping, ratchet hypothesis, stream fragmentation, swimming endurance

## 1 | INTRODUCTION

The widespread proliferation of artificial barriers has constrained critical fish dispersal events and contributed to the decline of fishes in streams worldwide (Liermann, Nilsson, Robertson, & Ng, 2012; Perkin & Gido, 2011; Wilde & Urbanczyk, 2013). Road crossings offer little refuge and may block fish movements when the stream channel is sufficiently reduced and water velocities become impassable (Anderson et al., 2012; Bouska & Paukert, 2010; Kemp & O'Hanley, 2010; Perkin, Gido, Al-Ta'ani, & Scoglio, 2013). Perches, located on the downstream end of many culverts, potentially further segregate fish assemblages by restricting access to species that are physically able or motivated to jump (Burford, McMahon, Cahoon, & Blank, 2009; Ficke, Myrick, & Jud, 2011; Kondratieff & Myrick, 2005; Prenosil, Koupal, Grauf, Schoenebeck, & Hoback, 2015). Thus, road crossings may confine fish to downstream reaches if they are unable to traverse barriers in two dimensions (i.e. vertical and longitudinal). Although studies of fish movement in relation to road crossings are common, research that directly quantifies the ability of small-bodied fishes to both jump (vertical) and navigate (longitudinal) barriers is relatively rare (Ficke et al., 2011; Perkin et al., 2013; Prenosil et al., 2015).

The accelerated extinction rates of freshwater fishes have required ecologists to consider the consequences of this loss of diversity for aquatic ecosystem structure and function (Burkhead, 2012; Kreman, 2005; Loomis, Kent, Strange, Fausch, & Covich, 2000). Researchers have identified broad-scale effects and the unique ecological contributions of fish-feeding guilds and particular species on stream ecosystem processes (Bertrand & Gido, 2007; Bertrand, Gido, Dodds, Murdock, & Whiles, 2009; Cardinale, Palmer, & Collins, 2002; Schwartz et al., 2000; Vanni, 2002). Herbivorous fishes, for example, can strongly influence primary production, decomposition rates, and nutrient retention in prairie streams (Bertrand & Gido, 2007; Gido, Bertrand, Murdock, Dodds, & Whiles, 2010; Grimm, 1988; McIntyre & Flecker, 2010); however, it is unclear whether these results can be generalized to all herbivores and other functional feeding guilds. Without colonization opportunities from nearby source populations, episodic disturbance events may alter headwater fish assemblages and degrade ecosystems above barriers.

Directional disruptions to stream fish assemblages by stochastic disturbance events and severed movement corridors act as an 'ecological ratchet' (Birkeland, 2004; Covich et al., 1997; Perkin, Gido, Costigan, Daniels, & Johnson, 2014; Roberts, Fausch, Peterson, & Hooten, 2013). The ratchet concept describes self-reinforcing and irrevocable system change in response to natural or human disturbances (Birkeland, 2004; Perkin et al., 2014). In stream systems, ratcheting occurs when longitudinal habitat connections are lost to fragmentation, and regional immigration from downstream populations is removed from the community structuring process in headwater reaches (Angermeier & Winston, 1998; Perkin & Gido, 2012; Wilde & Urbanczyk, 2013). Although upstream habitats generally recover from disturbance events and can be improved by restoration efforts, ecosystem effects may persist when local diversity has been reduced (Dodds, Gido, Whiles, Fritz, & Matthews, 2004; Perkin et al., 2014; Roni, Hanson, & Beechie, 2008). Without management

intervention, degradation continues perpetually as fish species are systematically displaced downstream (Birkeland, 2004; Perkin et al., 2014).

Prairie streams are dynamic systems in which habitat patches are sporadically created and lost as a result of highly variable hydrological events (Dodds et al., 2004; Fritz & Dodds, 2005; Matthews, 1988). Prairie fish assemblages are structured by extreme environmental pressures that regulate local abundance and distribution (Franssen et al., 2006; Kelsch, 1994; Lohr & Fausch, 1997; Poff & Ward, 1989). Local species persistence depends on unimpeded fish movements to recolonize available habitats after stochastic extinction events (Dodds et al., 2004; Dunham, Young, Gresswell, & Rieman, 2004; Scheurer, Fausch, & Bestgen, 2003); however, stream fragmentation caused by instream barriers (e.g. road crossings, impoundments, and perched culverts) isolates fish populations and interrupts dispersal pathways, potentially eliminating recolonization opportunities (Perkin et al., 2013; Perkin et al., 2014; Perkin & Gido, 2012; Rolls, Ellison, Faggotter, & Roberts, 2013).

The fragmentation of riverscapes has potentially removed immigration from local fish community structuring, and may degrade ecosystem services, aesthetic values, and the economic potential of streams (Paterson, 2006). Potential barriers are numerous and solutions to improve passage for small-bodied fishes are limited, so the systematic reduction in headwater fish diversity may plague countless streams (Bouska & Paukert, 2010; Ficke et al., 2011; Lorenzen, 2016). To understand better the ecological threat of instream barriers, the relative vulnerability of four prairie fishes and potential ecosystem consequences of lost diversity above barriers was assessed. Specifically, the ability of four ecologically distinct and relatively small-bodied fishes to pass simulated vertical and longitudinal barriers was estimated, and the unique ecosystem effects of each species were quantified. This information will be useful when predicting changes to stream ecosystems where riverscape connectivity issues are not alleviated by management actions. If species have unique impacts on ecosystem structure or functioning and are unable to recolonize following regular disturbance events, valuable ecosystem processes may be eliminated or displaced downstream.

## 2 | METHODS

### 2.1 | Study species

The swimming endurance, jumping abilities, and ecological roles of four relatively small-bodied prairie fishes were quantified: central stoneroller (*Camptostoma anomalum*, Rafinesque 1820), white sucker (*Catostomus commersonii*, Lacépède, 1803), Iowa darter (*Etheostoma exile*, Girard, 1859), and brassy minnow (*Hybognathus hankinsoni*, Hubbs, 1929). Although adult white sucker reach lengths of up to 650 mm, only juvenile individuals (<120 mm) that are common to small lotic systems were evaluated (McPhail & Lindsey, 1970). The species evaluated, excluding brassy minnow, belong to the native intolerant guild, but all represent unique functional feeding guilds (Krause, Bertrand, Kafle, & Troelstrup, 2013). Brassy minnows are more tolerant of human stressors and are less likely to be extirpated from prairie

streams than the other species (Distler et al., 2014). Each species occupies different stream habitats, consumes different prey, and probably have unique roles in the ecosystem (Distler et al., 2014).

## 2.2 | Fish collection and husbandry

Each species was collected using seine nets from local streams in eastern South Dakota. These individuals formed a pool from which individuals were randomly selected for each experiment. Fish were transported to the South Dakota State University (SDSU) Fisheries Ecology Research Center in 113-L aerated containers, and care was taken to minimize handling stress (Harmon, 2009). All individuals were slowly acclimatized to laboratory conditions before being transferred to species-specific tanks within a temperature-controlled 20 000 L recirculating system (Harmon, 2009). Fish were offered a daily mixture of frozen bloodworms, frozen brine shrimp, and flake foods during a 2-week acclimatization period before experimental procedures. All fish were cared for in accordance with a protocol reviewed and approved by the SDSU Institutional Animal Care and Use Committee (IACUC, approval no. 12-007A).

## 2.3 | Swimming endurance (longitudinal barriers)

Fish swimming performance was evaluated using a time-to-fatigue endurance test protocol with a 10-L Brett-type swimming chamber that replicates the fluvial conditions at road crossings (Ficke et al., 2011; Peake, Beamish, McKinley, Scruton, & Katopodis, 1997). Following Ficke et al. (2011). Fish endurance was measured at water velocities of 16, 32, 48, 64, and 80 cm s<sup>-1</sup> for all species; five individuals of each species were tested at each velocity increment. After an individual fish swam in a test, that individual was not tested again in order to avoid training effects (Farlinger & Beamish, 1978). Food was withheld for 36 h before endurance tests to ensure that fish were in a post-absorptive state (Peake et al., 1997). All swimming endurance tests were conducted at ~15°C.

For each endurance test, an individual fish was acclimatized in the swimming chamber and allowed to orientate to the experimental chamber for 5 min. Water velocity was maintained at approximately 0.5 body lengths per second during the acclimatization period. Following acclimatization, the water velocity was immediately increased to the treatment velocity and the time until the fish became fatigued was measured (Peake et al., 1997). The trial ended when a fish could no longer maintain its position in the water column and was impinged on the downstream grid for 10 s. If a fish maintained its position in the flume for more than 200 min it was assumed it could do so indefinitely (Ficke et al., 2011; Peake et al., 1997). Fish that did not swim or that were reluctant to do so were classified as non-performers, and were replaced. The swimming performance data were analysed using a survival analysis (PROC LIFEREG in SAS). Chi-square tests were used to test the significance of the measured variables (total length, TL; water velocity) at  $\alpha < 0.05$ . Swimming endurance was estimated using multiple regression, as follows (Peake et al., 1997):

$$\log(E) = \beta_0 + \beta_1 L + \beta_2 V + \beta_3 LV + e,$$

where  $E$  is endurance (min),  $L$  is the total length (TL; mm),  $V$  is water velocity (cm s<sup>-1</sup>), and  $e$  is a normally distributed error term with mean values of 0 and variance  $\sigma^2$  ( $\alpha \leq 0.05$ ).

The maximum barrier length passable by each species was estimated as:

$$V_f = V_s - (d * E_{V_s}^{-1}),$$

where  $V_f$  is the water velocity in the barrier (cm s<sup>-1</sup>),  $V_s$  is the swimming speed (cm s<sup>-1</sup>),  $d$  is the barrier length (cm), and  $E_{V_s}$  is the endurance of the species at the given velocity ( $V_s$ ) (Peake et al., 1997). This formula provides combinations of distances and water velocities in which each species is able to pass a potential barrier.

## 2.4 | Jumping ability (vertical barriers)

Fish jumping ability was measured using artificial perched barriers originally designed by Kondratieff and Myrick (2005). This original design has been modified to meet the particular study objectives by Ficke et al. (2011), Prenosil et al. (2015), and the current study; however, the internal dimensions [60 × 120 (divided by a weir) × 120 cm], weir design, and protocol for use has remained consistent. All trials were conducted at water temperatures ranging from 17 to 20°C. Discrete weir heights of 0, 5, 10, 15, and 20 cm were tested. Four replicate trials were conducted of 10 individuals each for all species and weir-height combinations. Water flow through the weir was maintained at 1.3 L s<sup>-1</sup> and the plunge pool depth was 30 cm.

Fish were allowed to acclimatize to the conditions in the lower chamber of the perched barrier for 24 h. After the acclimatization period, the weir was set to the treatment height and fish were given 24 h to reach the upper chamber. Following each trial, fish were removed from both chambers, measured (TL; mm), and the number that successfully reached the upper chamber was counted. No incentive was provided to motivate fish passage into the upper chamber. An information theoretic multi-model interference approach was used to describe the relative influence of water temperature, dissolved oxygen, TL, and weir height on passage. Models were ranked by corrected Akaike's information criterion (AIC<sub>c</sub>) with a threshold of  $\Delta AIC_c \geq 4$  used to scale candidate model performance (Burnham & Anderson, 2002). Individual predictor support was quantified by summing the AIC<sub>c</sub> weights ( $\Sigma w$ ) of all candidate models that included the predictor (MacKenzie et al., 2006). Logistic regression was used to model the response form of informative variables for each species.

## 2.5 | Ecosystem effects

The effects of each species on stream ecosystems was quantified by isolating their ecological role in a series of single-species experiments. Experimental streams simplified the complexity of stream ecosystems and allowed the identification of the ecological contributions of each species with replicated experiments. The experimental streams at the SDSU Fisheries Ecology Research Center were designed following Matthews et al. (2006). These systems

are functionally and physically very similar to pool-riffle complexes in nearby natural streams (Bertrand et al., 2009; Gelwick & Matthews, 1992; Gido & Matthews, 2001).

Each experimental stream unit ( $n = 24$ ) consisted of one 2.54-m<sup>2</sup> pool connected to a 0.84-m<sup>2</sup> riffle. Water was supplied continuously by an on-site well that maintained the temperature near 17°C, and water was recirculated at a rate of 0.15 m s<sup>-1</sup>. A uniform volume of large gravel substrate was available in each pool and riffle. Each unit was drained, pressure washed, and allowed to dry for 7 days before filling. Stream units were filled 7 days before the beginning of the experiment to facilitate algal and invertebrate colonization. Previous studies have found that algae and invertebrate taxa with mobile adults readily colonize similar systems (Matthews et al., 2006).

Fish were measured (TL) and stocked in the experimental streams at 'natural' local densities of 5–10 g m<sup>-2</sup> on day 0 (26 June 2013). Each fish species treatment was replicated five times, except for the white sucker (with four replicates), in a randomized design. A 'no fish' control treatment was also replicated five times. The experiment was concluded and all fish were removed after 49 days. Streams were observed regularly for mortalities, and dead individuals were replaced immediately.

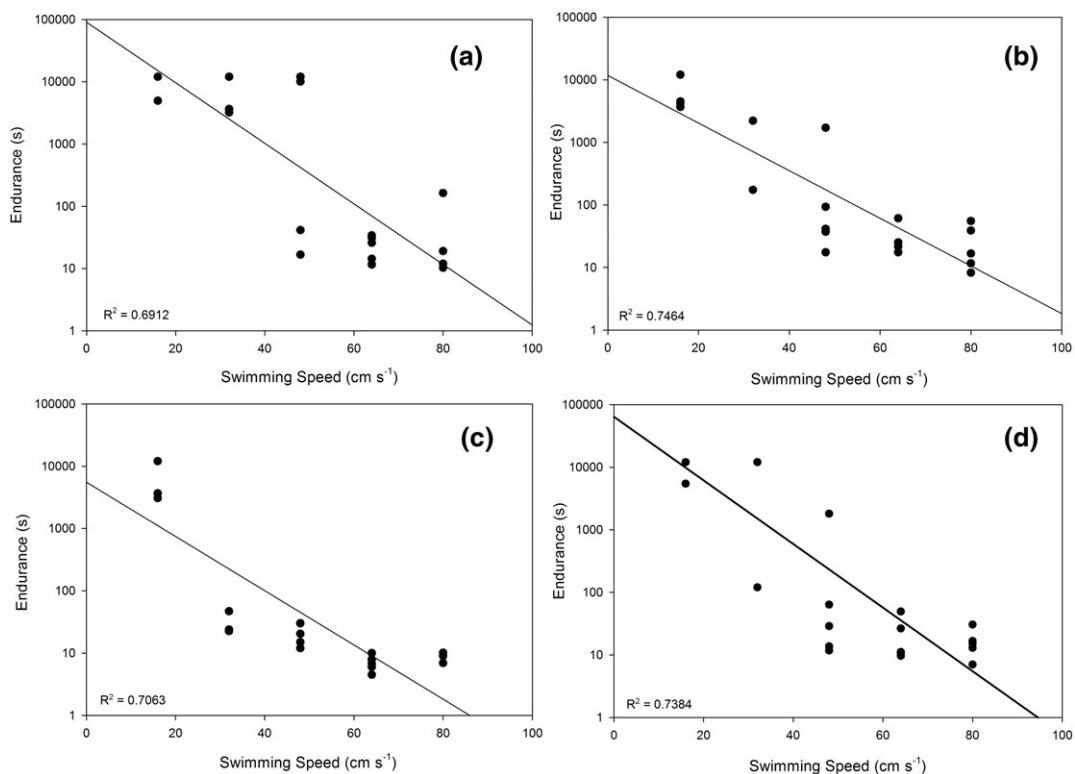
Every other week, ecosystem structure was quantified by measuring algal filament length (mm) and algal biomass (benthic chlorophyll *a*; mg m<sup>-2</sup>). The length of the longest algal filament (vertical or horizontal) was measured at three equidistant points along three transects in stream riffles (nine points in total) and at five points per pool. Algal biomass was estimated as the concentration of chlorophyll *a* extracted from nutrient-diffusing substrata (i.e. large gravel) taken from experimental streams. Gravel was collected on site, frozen within 4 h of

collection, and later analysed. Chlorophyll *a* was extracted from the gravel by submerging each stone in 95% EtOH solution at 78°C, as described by Sartory and Grobbelaar (1984). Extracts were analysed for chlorophyll *a* with a Turner Model 112 fluorometer (Turner Designs Inc., Sunnyvale, CA, USA) using an optical configuration optimized for the analysis of chlorophyll *a* without phaeophyton interference (Welschmeyer, 1995). To capture spatial heterogeneity, three stones were collected from each riffle (i.e. upstream, middle, and downstream) and five stones were taken from each pool (i.e. four along the edge and one central).

Ecosystem functioning was measured every other week using whole-stream metabolism (Murdock, Dodds, Gido, & Whiles, 2011), and nutrient retention (total nitrogen, TN; total phosphorus, TP) was measured once per month. Gross primary productivity (GPP), net primary productivity (NPP), and respiration (R) in the experimental streams were based on diurnal changes in dissolved oxygen measurements from YSI 600XLM sondes (Yellow Springs Instruments, Inc.) using the open-system single-station approach (Bott, 1996). Water was recirculated at the same velocity and the bedform was kept similar in all experimental units so that turbulence-induced aeration was similar across experimental stream channels. Thus, re-aeration was estimated using the surface-renewal model, which is calculated from velocity ( $V$ , cm s<sup>-1</sup>) and mean depth ( $H$ , cm) using the formula (Owens, 1974):

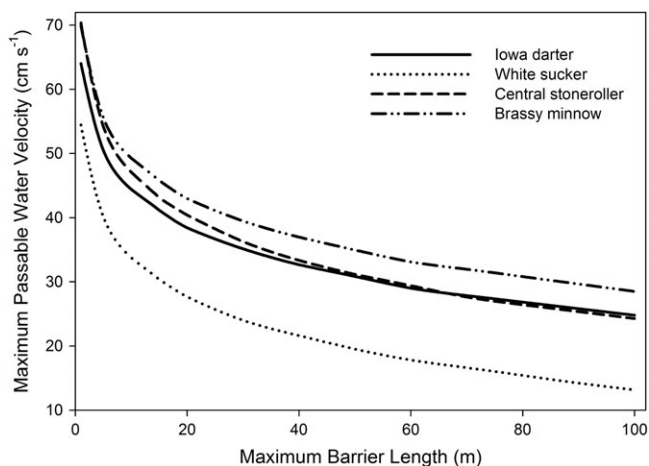
$$f_{(20^{\circ}\text{C})} = 50.8V^{0.67} * H^{-0.85}$$

The flow-through rates were the same for all experimental units leading to an approximate turnover time of 13 h (i.e. effective channel length



**FIGURE 1** Predictive endurance curve (s) estimated using multiple regression (Peake et al., 1997): (a) brassy minnow,  $\text{Log}(E) = 3.101 + (-0.0485 * \text{water velocity})$ ; (b) central stoneroller,  $\text{Log}(E) = 2.71 + (-0.0434 * \text{water velocity})$ ; (c) white sucker,  $\text{Log}(E) = 2.358 + (-0.0486 * \text{water velocity})$ ; and (d) Iowa darter,  $\text{Log}(E) = 2.991 + (-0.0508 * \text{water velocity})$

~1700 m). The prolonged exposure to stream biota ensured that diurnal changes in water oxygen concentration reflected biotic processes in these stream units. NPP was estimated as the mean hourly rate of



**FIGURE 2** Combinations of barrier length (m) and water velocity ( $\text{cm s}^{-1}$ ) for which passage is possible for brassy minnow, central stoneroller, lowa darter, and white sucker. The area under the plotted points for each species represents passable combinations of length and velocity. Estimated median endurance times were used to generate the estimates (Peake et al., 1997)

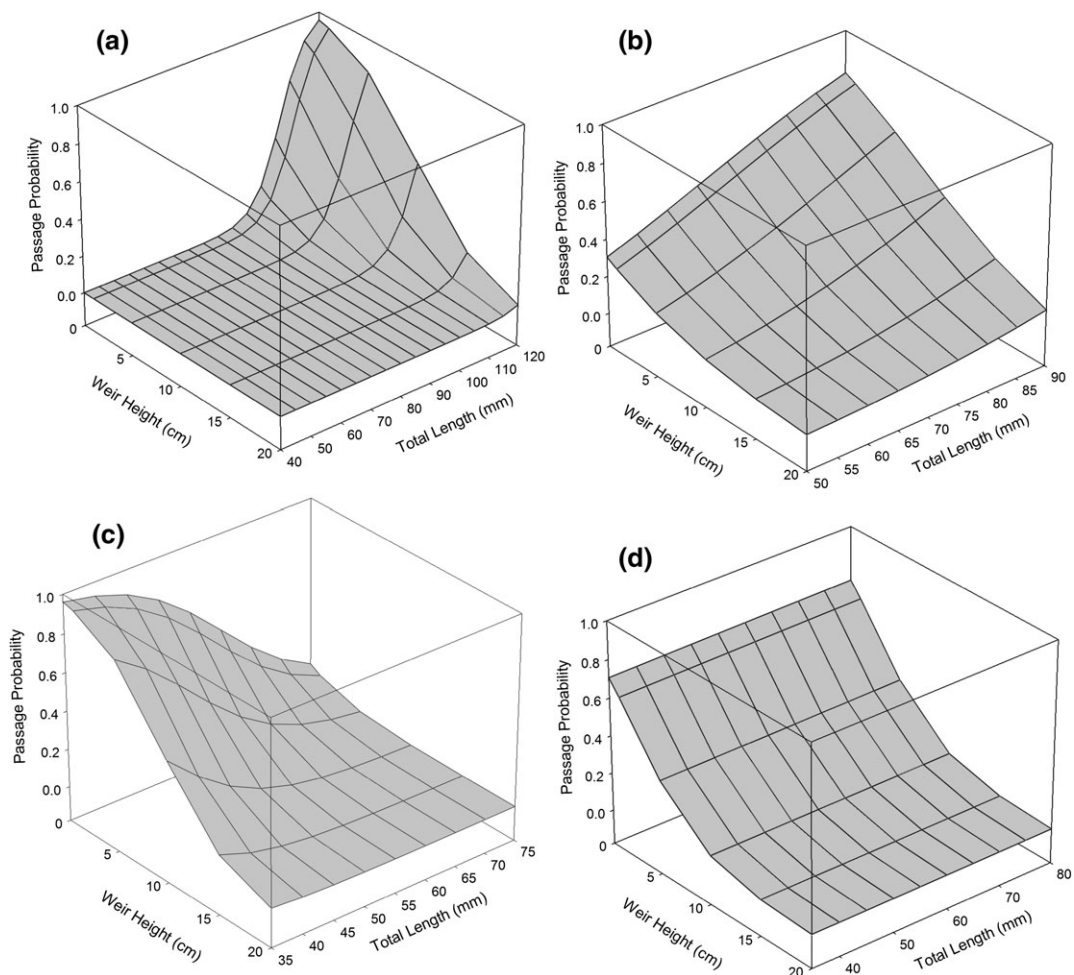
change in oxygen concentration during daylight and darkness, whereas GPP was estimated by subtracting the mean hourly rate of oxygen uptake during darkness from the mean hourly rate of oxygen productivity during daylight.

Nutrient retention was estimated in the mesocosm experiments by sampling for TN and TP. A 125-mL sample of unfiltered water was collected from the inflow and overflow for each experimental stream. Samples were stored frozen until digestion and nutrient analysis, following the methods of Dodds (2003). Indicators of ecosystem structure and functioning were each compared among species using separate repeated-measures analysis of variance (ANOVA) analyses for riffles and pools.

### 3 | RESULTS

#### 3.1 | Swimming endurance (longitudinal barriers)

Non-performing individuals were relatively uncommon and were restricted to central stoneroller ( $n = 2$ ). No individuals of the other species were replaced during the endurance trials. Each species exhibited different behaviours in the swimming flume. Brassy minnow, central stoneroller, and white sucker sustained their position in the water



**FIGURE 3** Probability of jumping success as a function of weir height (cm) and fish total length (mm) for four small-bodied prairie fishes: (a) central stoneroller, (b) white sucker, (c) lowa darter, and (d) brassy minnow

column throughout the experiments. At low water velocities, the lowa darter did not swim continuously, and instead avoided constant motion by affixing their pectoral fins to the bottom of the chamber. At higher velocities, all species maintained their position with erratic bursts or continuous swimming.

Water velocity affected swimming endurance in all species, but the median endurance values varied by species (Figure 1a–d). Brassy minnow maintained its position longer than any other species at all water velocities (Figure 1a). The endurance of central stoneroller and lowa darter was similar at all trial velocities (Figure 1b, d). The weakest performer at any given water velocity was the white sucker (Figure 1c). All species could pass barriers of up to 15 m in length if the water velocity was  $<30 \text{ cm s}^{-1}$  (Figure 2). White suckers were most vulnerable to barriers with water velocities  $>30 \text{ cm s}^{-1}$  (Figure 2). For example, white sucker could traverse a 40-m barrier only at water velocities approximately 40% less than a velocity that would allow the other three species to pass (Figure 2). Central stoneroller and lowa darter would succumb to barriers of similar lengths and water velocities (Figure 2). The brassy minnow would successfully pass more barriers than any of the other species (Figure 2).

### 3.2 | Jumping ability (vertical barriers)

Weir passage varied by species, suggesting that each fish is uniquely susceptible to perched barriers (Figure 3). For all species, the global and intercept-only models ( $w_i \sim 0.00$ ) and candidate models that included environmental variables ( $w_i < 0.05$ ) were poorly supported. Candidate models provided evidence that both weir height and TL influenced fish performance; however, the relative influence of these predictors varied (Table 1). Passage probability decreased as weir height increased for all species (Figure 3a–d). Models that included TL better predicted central stoneroller, lowa darter, and white sucker passage (Table 1). No small stonerollers ( $< 80 \text{ mm}$ ) successfully cleared the barrier, and passage by larger individuals was much more likely for weir heights of  $\leq 15 \text{ cm}$  (Figure 3a). Passage of small white suckers ( $< 60 \text{ mm TL}$ ) was rare at any weir height, but larger individuals were more likely to ascend barriers (Figure 3b). Smaller lowa darters were more likely to pass vertical barriers of any height than larger individuals (Figure 3c). Total length had little influence on passage by brassy

minnow (Figure 3d). Regardless of species or TL, passage probability dropped dramatically for weirs of  $>10 \text{ cm}$  (Figure 3a–d). Very few individuals passed weirs of  $>20 \text{ cm}$  (Figure 3a–d).

### 3.3 | Ecosystem effects

Native prairie fishes affected stream ecosystem structure in pool habitats, but not in riffles (Table 2). The mean algal filament length in pool habitats was significantly shorter than the no-fish control pools in the presence of central stoneroller and brassy minnow, but was longer in pool habitats hosting lowa darter ( $F_{4,19} = 7.87, P < 0.01$ ; Figure 4). Algal filament lengths in pools hosting white sucker were of intermediate length, and did not significantly differ from the values reported with other fishes or the no-fish control (Figure 4). Species effects on algal filament length varied through time ( $F_{3, 57} = 12.5, P < 0.01$ ; Figure 4), and observed changes to filament height were not equal among species through time ( $F_{12, 57} = 3.1, P < 0.01$ ; Figure 4). Riffle algal filament lengths ( $F_{4,19} = 0.73, P = 0.58$ ) and algal biomass were similar among species (pools,  $F_{4,18} = 1.92, P = 0.15$ ; riffles,  $F_{4,18} = 2.20, P = 0.11$ ).

There was no evidence to suggest that individual species had distinct effects on ecosystem functioning (Table 2). Net primary productivity was similar among fish experiments and the no-fish control ( $F_{4,19} = 2.75, P = 0.28$ ). Nutrient retention was also similar among experiments and control streams (TN,  $F_{4,19} = 0.91, P = 0.48$ ; TP,  $F_{4, 19} = 0.26, P = 0.90$ ).

## 4 | DISCUSSION

Rapid human population growth and vast transportation networks have resulted in numerous potential barriers to fish movement in streams worldwide (Kemp & O'Hanley, 2010). Artificial barriers reduce the immigration opportunities for stream fishes, which inevitably displaces populations downstream and may endanger ecosystem structure in headwater reaches. The prairie fishes evaluated were not equally vulnerable to instream barriers, but all failed to circumvent relatively minor obstacles. Diversity loss degrades both the aesthetic and the economic value of headwater reaches, and could alter stream

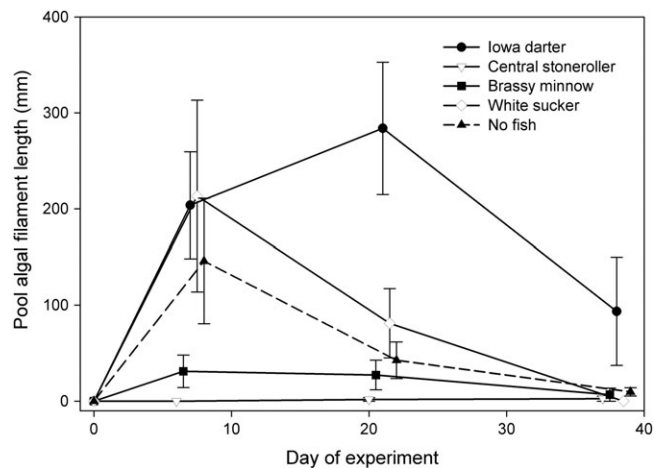
**TABLE 1** Top-three candidate models and associated corrected Akaike's information criterion ( $AIC_c$ ) values used to describe species-specific jumping performance;  $w_i$  is the  $AIC_c$  weight and  $\Sigma w_i$  are the summed model  $AIC_c$  weights of models that included influential predictors. The intercept-only and global models and those that included environmental variables performed relatively poorly. In addition,  $R^2$  values are provided for the models that included the effect of weir height and mean total length (TL) on passage probability

| Species             | Predictors  | k | $\Delta AIC_c$ | $w_i$ | $\Sigma w_i$                              | $R^2$ |
|---------------------|-------------|---|----------------|-------|---|-------|
| Brassy minnow       | Weir height | 3 | 0              | 0.46  | Weir height = 0.74<br>Total length = 0.23 | 0.38  |
|                     | Mean TL     | 3 | 3.63           | 0.07  |   |       |
| Central stoneroller | Mean TL     | 3 | 0              | 0.59  | Total length = 0.66<br>Weir height = 0.27 | 0.72  |
|                     | Weir height | 3 | 2.09           | 0.21  |   |       |
| lowa darter         | Mean TL     | 3 | 0              | 0.45  | Total Length = 0.65<br>Weir height = 0.44 | 0.39  |
|                     | Weir height | 3 | 0.65           | 0.32  |   |       |
| White sucker        | Weir height | 3 | 0              | 0.47  | Weir height = 0.71<br>Total length = 0.45 | 0.43  |
|                     | Mean TL     | 3 | 1.54           | 0.22  |   |       |

**TABLE 2** Mean ( $\pm$  standard error) values for indicators of ecosystem structure and functioning for single-species experiments and no-fish control groups in replicate riffle and pool environments at maximal peak response ( $\sim$ day 30)

| Treatment (sample size)             | Ecosystem structure         |   | Ecosystem functioning                                       |   |  |  |
|-------------------------------------|-----------------------------|---|---|---|--|--|
|                                     | Algal filament length (mm)* | Algal biomass (chlorophyll <i>a</i> ) (mg m <sup>-2</sup> ) | Net primary production (g m <sup>-2</sup> h <sup>-1</sup> ) | Gross primary production (g m <sup>-2</sup> h <sup>-1</sup> ) | Nitrogen retention (mg L <sup>-1</sup> ) | Phosphorus retention (mg L <sup>-1</sup> ) |
| Brassy minnow ( <i>n</i> = 5)       |                             |   |   |   |  |  |
| Pool                                | 27.4 (13.9)                 | 23.6 (5.2)  | -0.097 (0.034)  | 0.135 (0.018)   | 0.35 (0.10)                              | 0.003 (0.001)                              |
| Riffle                              | 163.3 (89.8)                | 34.6 (6.9)  |   |   |  |  |
| Central stoneroller ( <i>n</i> = 5) |                             |   |   |   |  |  |
| Pool                                | 1.8 (1.6)                   | 20.0 (1.1)  | -0.131 (0.020)  | 0.077 (0.023)   | 0.41 (0.11)                              | 0.002 (0.002)                              |
| Riffle                              | 82.5 (29.7)                 | 31.8 (4.0)  |   |   |  |  |
| Iowa darter ( <i>n</i> = 5)         |                             |   |   |   |  |  |
| Pool                                | 283.9 (61.6)                | 43.4 (7.5)  | -0.156 (0.087)  | 0.082 (0.062)   | 0.28 (0.23)                              | 0.004 (0)                                  |
| Riffle                              | 90.2 (20.8)                 | 48.2 (5.9)  |   |   |  |  |
| White sucker ( <i>n</i> = 4)        |                             |   |   |   |  |  |
| Pool                                | 81.3 (31.3)                 | 29.5 (2.5)  | -0.066 (0.023)  | 0.124 (0.015)   | 0.63 (0.27)                              | 0.002 (0.003)                              |
| Riffle                              | 103.8 (41.7)                | 45.7 (9.5)  |   |   |  |  |
| No-fish control ( <i>n</i> = 5)     |                             |   |   |   |  |  |
| Pool                                | 66.7 (17.1)                 | 29.7 (7.3)  | -0.031 (0.049)  | 0.140 (0.027)   | 0.28 (0.06)                              | 0.001 (0.003)                              |
| Riffle                              | 54.0 (20.7)                 | 71.6 (20.3)   |   |   |  |  |

Note. Measures of ecosystem function were composite values from riffle and pool habitats. A repeated-measures ANOVA was used to identify differences among treatment groups by habitat type through time. Asterisks indicate significant differences among treatment groups ( $\alpha = 0.5$ ).

**FIGURE 4** Mean algal filament length (mm) measured in pools of experimental streams (*n* = 24), used to describe the influence of each species on stream ecosystem structure, during June–August 2013

ecosystem structure. The risk of systematic species loss above barriers greatly outweighs the opportunity for improvement, suggesting that ecosystem structure may be moving downstream in numerous river systems (Bouska & Paukert, 2010; Ficke et al., 2011; Lorenzen, 2016; Perkin et al., 2014).

Prairie fishes are seemingly vulnerable to stream fragmentation by vertical and longitudinal barriers associated with road crossings. Roads bisect streams at nearly every kilometre of the landscape, and every road crossing has the potential to block fish movement and to fragment critical habitats (Bouska & Paukert, 2010; Perkin et al., 2013; Warren & Pardew, 1998). Fragmentation is expected to affect each species differently, but is likely to alter upstream fish assemblages by first removing species with limited ability or motivation to pass

barriers. Small vertical barriers block the passage of all but the largest individuals and, with access, all species are unable to traverse relatively short obstacles with moderate water velocities.

Previous research has effectively quantified the swimming endurance and jumping abilities of numerous salmonids (Kondratieff & Myrick, 2005; Mueller, Southard, May, Pearson, & Cullinan, 2008) and other large-bodied species (Haro, Castro-Santos, Noreika, & Odeh, 2004; Ward, Schultz, & Matson, 2003). Less consideration, however, has been given to ecologically relevant small-bodied fishes (c.f. Adams, Hoover, & Kilgore, 2000; Ficke et al., 2011; Prensil et al., 2015). The estimates of swimming endurance from the present study correspond well with literature values for related species (Billman & Pyron, 2005; Ficke et al., 2011; Leavy & Bonner, 2009). White sucker are seemingly much weaker swimmers (81% less endurance at 64 cm s<sup>-1</sup>) than *Catostomus insignis*, Baird & Girard, 1854 (Sonoran sucker); however, this high value was partly attributed to the behaviour that this species used to adhere to the flume (Ward et al., 2003). White sucker and Iowa darter are very susceptible to population fragmentation by longitudinal obstacles. Central stoneroller and brassy minnow performed better, but no species is expected to pass relatively short reaches with moderate water velocities.

Some species jumped better than others, but none are likely to bypass relatively low vertical barriers. Passage by all species was relatively high when the weir was at the water surface; however, in most cases only the largest individuals moved to the upper chamber. Similar to observations by other researchers, passage probability decreased rapidly for all species with slight increases in weir height (Ficke et al., 2011; Prensil et al., 2015). No fish are expected to ascend perched barriers of >20 cm in height. Total length influenced the passage of vertical barriers for all species except brassy minnow: patterns that either reveal dispersal motivations or demonstrate the stronger

jumping abilities of larger individuals (Agostinho, Pereira, de Oliveira, Freitas, & Marques, 2007). These estimates of fish vulnerability only consider the physical capability of each species to bypass barriers without respect to other factors that influence their motivation to do so (i.e. dark tunnel, food availability, density dependence). Because prairie fishes are not equally able to navigate instream barriers, fish assemblages will be altered in predictable ways. Minor constraints on the stream channel will select for more mobile species; however, road crossings will often impede immigration by all species.

Worldwide declines in freshwater fish diversity have raised concerns about the integrity of stream ecosystem processes after species extinction (Bertrand et al., 2009; Bertrand & Gido, 2007; Burkhead, 2012). The unique ecological contributions of fish species have been quantified prior to this research, but this research is among the first to demonstrate the diverse effects of a group of similar fishes on ecosystem structure (Bertrand et al., 2009; Bertrand & Gido, 2007; Cardinale et al., 2002; Vanni, 2010). Each species had slightly different effects on the stream ecosystem structure, resulting from their different habitat preferences and diets (Hargrave, 2009; Vanni, 2010). However, our single-species experiments may have overestimated the effects of individual species by excluding any potential compensatory mechanisms of diverse aquatic communities. Similar to other research, central stoneroller, a herbivorous grazing minnow, strongly influenced algal filament lengths (Dodds et al., 2004; Grimm, 1988; Matthews, 1988; Reisinger, Presuma, Gido, & Dodds, 2011). Should central stoneroller be extirpated above impassable barriers, mean algal filament lengths are expected to increase by >3600%. To a lesser extent the removal of Iowa darter (-325%) and brassy minnow (+39%) are also expected to influence algal filaments. Without colonization opportunities from neighbouring populations, disturbance events will alter headwater fish assemblages and may degrade ecosystem structure above barriers.

The ability of fishes to affect autochthonous primary productivity is particularly important for prairie streams in which organic matter contributions are relatively low (Dodds et al., 2004). Although prairie fishes affected an aspect of ecosystem structure, fish presence had little influence on algal biomass or primary production. Although the ecosystem effects of Iowa darter, brassy minnow, and white sucker have not been evaluated previously, similar research has demonstrated that grazing fishes, particularly stonerollers, have potentially strong effects on stream ecosystem functioning (Bertrand & Gido, 2007; Gelwick & Matthews, 1992; Stewart, 1987). There are several potential explanations for the limited effect of these prairie fishes on experimental stream productivity and algal biomass in this study. The consumption and mechanical removal of algal cells may have been offset by increased algal growth and production by the remaining cells (Bertrand & Gido, 2007; Power et al., 1988). In addition, the excretion of limiting nutrients by fishes may further stimulate algal growth by increasing the availability of soluble nutrients in these nutrient-poor environments (Bertrand & Gido, 2007). Although this research was unable to identify the direct effects of prairie fishes on ecosystem functioning, nutrient turnover by these species may be an important stimulant to algal communities.

Fragmented riverscapes interact with harsh disturbance regimes to form an ecological ratchet in dendritic prairie streams (Perkin

et al., 2014). Extirpation of vulnerable headwater fishes moves the ratchet towards a new ecological state, and recolonization, to reverse the motion, is blocked by instream barriers (Fausch & Bramblett, 1991; Schlosser, 1990). At a certain distance, the downstream displacement of fish diversity may exceed the environmental tolerances of these ecologically relevant fishes, resulting in their extirpation from entire drainages (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). Although upstream habitats often recover from disturbance events and can be improved by restoration efforts, ecosystem recovery may be impossible because the local diversity will have been reduced (Dodds et al., 2004; Perkin et al., 2014; Roni et al., 2008).

Abundant barriers to recolonization, with limited tools to improve passage for small-bodied prairie fishes, interact with a range of stochastic and human-mediated disturbances to threaten fish assemblages and, consequently, ecosystem structure in headwater streams (Bouska & Paukert, 2010; Ficke et al., 2011; Lorenzen, 2016). This ecological ratchet could be managed by maintaining suitable flow regimes during dry periods (Cooke, Paukert, & Hogan, 2012; Perkin et al., 2014), rescuing and re-releasing populations during disturbances (Hammer et al., 2013), or by reintroducing individuals after environmental conditions improve (George et al., 2009; Seddon, Armstrong, & Maloney, 2007). However, each of these management tools requires substantial resources that are rarely available for the conservation of small-bodied stream fishes. Improving recolonization pathways via prioritized barrier removal (Kemp & O'Hanley, 2010; Kornis et al., 2015; Magilligan, Nislow, Kynard, & Hackman, 2016), or implementing novel fish passage structures (Ficke et al., 2011; Lorenzen, 2016), may protect fish diversity and ecosystem processes above barriers (Perkin et al., 2014). The future prognosis for small-bodied prairie fishes and the ecosystems that they support is grim unless steps are taken to repair movement corridors throughout the riverscape.

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