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Resource selection and species interactions between native and non-native fishes in a simulated stream system

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Abstract

Effective fishery management necessitates understanding of resource partitioning by fishes that inhabit complex systems composed of biotic and abiotic features. Evaluations of non-native species introductions have continually demonstrated adverse effects associated with abundance and distribution of native fishes. Therefore, understanding resource selection and interactions between native and non-native species is important for recovery efforts. Habitat use by two native fish species (largescale sucker *Catostomus macrocheilus* [Girard] and mountain whitefish *Prosopium williamsoni* [Girard]) and one non-native fish species (pumpkinseed *Lepomis gibbosus* [Linnaeus]) of the Kootenai River, Idaho, were evaluated in a laboratory stream system. Trials were conducted in allopatry and in sympatry with and without the presence of wood to describe habitat selection in the context of on-going habitat rehabilitation efforts. Interactions were evident between native largescale sucker and non-native pumpkinseed concerning use of a woody structure and current velocity. Mountain whitefish used low-velocity habitats and selected locations that were further from wood when in sympatry with pumpkinseed. Our research suggests that habitat use of native, large-river fishes may be influenced by the presence of a non-native species, and that considering such interactions is critical when designing and implementing habitat rehabilitation efforts in river ecosystems.

KEYWORDS
experimental stream, habitat selection, habitat use, laboratory flume, resource partitioning, videography

1 | INTRODUCTION

Large rivers are among the world's most diverse, dynamic, and complex ecosystems. Unfortunately, large rivers are also among the world's most degraded systems due to impoundment, channelization, urban and industrial pollution, and excessive nutrient and sediment inputs (Dynesius & Nilsson, 1994; Spink et al., 1998). Anthropogenic disturbances to large rivers have resulted in widespread changes to community structure and the extinction of several fluvial fish species (Bain et al., 1988; Ricciardi & Rasmussen, 1999; Rinne et al., 2005; Waite & Carpenter, 2000). In addition to direct effects associated with habitat modification, altered river systems may facilitate the establishment and spread of non-native species which may, in turn, negatively influence native species. For example, non-native fishes have been widely introduced to reservoirs to provide for subsistence, commercial, or recreational fisheries (e.g. Gozlan et al., 2010; Trushenski et al., 2010). Once established, reservoirs provide source populations for the invasion of upstream or downstream habitats by non-native fishes. Furthermore, habitat modification of rivers downstream of dams may provide suitable habitat

†Deceased

for non-native fishes that was historically inhospitable. For example, non-native green sunfish *Lepomis cyanellus* (Rafinesque), smallmouth bass *Micropterus dolomieu* (Lacepede) and largemouth bass *M. salmoides* (Lacepede) became established downstream of dams in large-river systems of the western United States where water temperatures and flows were moderated, turbidity was reduced, and substrates were stabilised by impoundment and flow regulation (Quist et al., 2004). Similarly, water developments modified habitat conditions for native species adapted to highly dynamic large rivers and also facilitated the dispersal and establishment of non-native piscivores in large rivers around the world (e.g. Jiang et al., 2021; Pelicice et al., 2014). As a consequence of indirect and direct effects, water development (i.e. dams, levees) has been described as the greatest threat to aquatic biodiversity (Dynesius & Nilsson, 1994; Nilsson et al., 2005; Rosenberg et al., 2000).

Substantial effort has been focused on water use reform and habitat rehabilitation to mitigate effects of dams and other water development practices in large rivers (Lake et al., 2007; Matouskova & Dvorak, 2011; Romanov et al., 2012; Watkins et al., 2015). Although practices that produce a more natural hydrograph have positively affected native fishes in altered river systems (e.g. Schloesser et al., 2011; Whiteman et al., 2011), more direct methods of habitat modification are often required to elicit a response. Engineered structures (e.g. large wood complexes, rip rap, and shallow-water habitats) have been used in large-river systems to restore habitat and simulate floodplain habitats (Madejczyk et al., 1998; Matouskova & Dvorak, 2011; Schloesser et al., 2011; White et al., 2010). Engineered structures typically increase habitat complexity by providing a mosaic of important physical habitats that meet the ecological needs of many fluvial species through the creation of isolated areas along the river continuum where the habitat mimics either pre-impoundment or pre-channelization conditions. In cases where habitat rehabilitation has been used to support native fish populations, unintended benefits to non-native species have generally been ignored. Habitat use patterns frequently overlap between native and non-native fishes to possibly confound habitat rehabilitation for native fishes. Consequently, natural resource managers must carefully consider potential overlap between native and non-native fishes to prioritise and optimise rehabilitation projects that target native species. One system that typifies these concerns is the Kootenai River, Canada-USA.

The Kootenai River is characteristic of many large, floodplain river systems around the world with respect to the suite of habitat alterations and changes in fish populations. The river originates in British Columbia, Canada, flows south into Montana, USA, and then into Idaho before re-entering British Columbia. The Idaho portion of the Kootenai River has been dramatically altered by the construction (early 1970s) and operation of Libby Dam, a large hydropower facility on the Kootenai River in Montana. Operation of the dam, coupled with the construction of levees along the lower river reduced the floodplain to ~25% of its historical extent (KTOI, 2009). In response to alterations in habitat and declining native fish populations, habitat in the Idaho portion of the river has been extensively managed to create suitable spawning and rearing habitat for native fishes (KTOI, 2009). Several localised habitat rehabilitation projects in a 12-km segment of the river include treatments designed to disperse flow, create off-channel and floodplain habitat, increase substrate heterogeneity, and create complex instream habitats by the addition of woody habitat features. However, non-native species present throughout the Kootenai River have been associated with newly engineered habitat features when evaluated at larger spatial scales (Smith et al., 2016; Watkins et al., 2015). These observations raise questions related to the use of habitat features by native and non-native fishes.

The objective of this study was to determine whether the presence of a non-native species altered habitat use by native species. Our study examined two fish species native to the Kootenai River, mountain whitefish *Prosopium williamsoni* (Girard) and largescale sucker *Catostomus macrocheilus* (Girard), and one non-native species, pumpkinseed *Lepomis gibbosus* (Linnaeus), in a simulated stream system. These species are frequently sampled within rehabilitated areas of the Kootenai River, and their habitat associations have been described in relation to habitat rehabilitation (Branigan et al., 2018; Smith et al., 2016; Watkins et al., 2015). More broadly, catostomids and coregonids are native and ecologically important to lotic systems throughout the northern hemisphere. Centrarchids are native to central and eastern North America but have been widely introduced across the world where they often have deleterious effects on native fish assemblages (e.g. Azuma & Motomura, 1998; Povz & Sumer, 2005). We first quantified each of these three species' use of current velocity and their association with wood and gravel or sand substrates, and then examined changes in their use of these features in the presence of selected heterospecifics. We hypothesised that the presence of a non-native species would alter habitat use of native species. Although our findings (e.g. species-specific habitat selection) are most applicable to the study species and system, our research provides important insight on the response of native, large-river species to non-native species. Our study also highlights the importance of considering habitat use by non-native species when rehabilitating habitat in large-river systems.

2 | METHODS

Wild fish were collected from the Kootenai River and its tributaries using boat electrofishing techniques in April 2016. Fish were immobilised using low power output (<1800 W) to minimise stress and injury. Captured fish were visually assessed to select size ranges for each species that reflected those observed in association with engineered habitats in the Kootenai River (Table 1; Branigan et al., 2018; Smith et al., 2016; Watkins et al., 2015). All test fish were immediately transported to the Fisheries Wet Laboratory at the University of Idaho to begin acclimation.

Upon arrival at the laboratory, test fish were subjected to a short-term (i.e. 1 h) formalin bath at a concentration of 170 μl/L to control external parasites. Following formalin treatment, species

TABLE 1 Mean total length (±SD) for two native (largescale sucker, mountain whitefish) and one non-native (pumpkinseed) fish species subjected to experimentation in a simulated river system

	Total length (mm)	
Species	In allopatry	In sympatry
Largescale sucker	160 (± 37)	135 (± 28)
Mountain whitefish	211 (± 29)	197 (± 28)
Pumpkinseed	137(± 9)	138 (± 10)

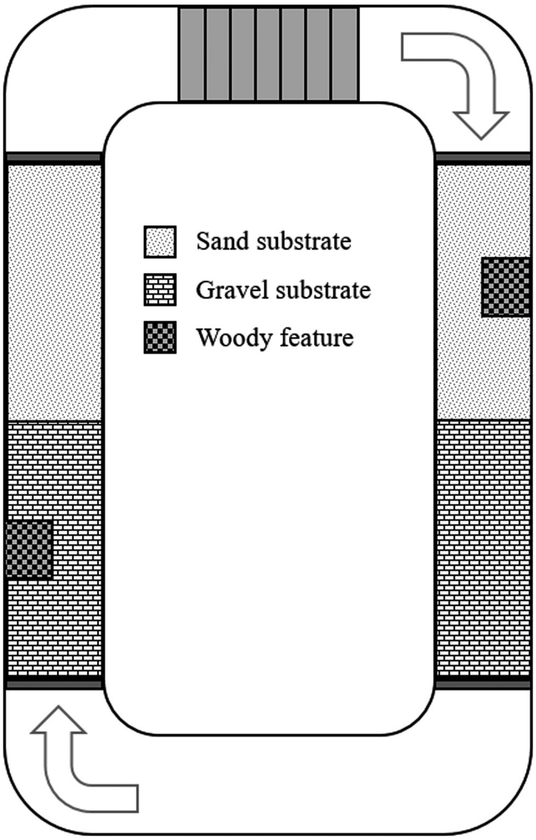


FIGURE 1 Illustration of a simulated stream system used to evaluate habitat selection and species interactions between native and non-native fishes from the Kootenai River, Idaho. A paddlewheel (located at top of figure) generated current in an elliptical flume that was divided into two rectangular experimental tanks. Each tank was outfitted with equal proportions of sand and gravel substrates, such that the entire width of each tank was covered by each substrate. A woody feature was placed on the substrate positioned "upstream" (as shown) or "downstream" (not shown) near the exterior wall of the flume when trials were conducted with wood present in the system. Additional trials were conducted with wood absent in the system

were segregated and transferred to species-specific 200-L holding tanks covered with a fitted fibreglass lid to deter fish from escaping. A flow-through system supplied 14°C water (average summer water temperature of the Kootenai River) to each holding tank at 1 L/min. Fish remained in these tanks and received no additional handling until they were randomly selected for experimentation. All fish were fed to satiation during a 10-min period twice daily as a maintenance diet. Mountain whitefish and pumpkinseed were fed frozen Chironomidae larvae and *Mysis* shrimp (Order Mysida), whereas largescale suckers were fed a sinking formulated feed (Otohime C2; Reed Mariculture, Campbell, California). Photoperiod was controlled to match the summer photoperiod of the Kootenai River at 48°41′32″N latitude, and all fish were acclimated to holding tanks in the laboratory for three weeks prior to experimentation.

Laboratory trials were conducted in a flume system outfitted with riverine habitat features (Figure 1). Two elliptical flumes in a flow-through system were supplied with chilled water at ~3 L/min to maintain a relatively constant 14°C water temperature throughout each flume. A single motor propelled paddlewheels in each flume to generate current via pulleys and gears to create a similar velocity profile throughout both systems. Each flume was divided into two rectangular experimental tanks [4 tanks total; 230 (L) × 60 (W) × 30 cm (D)] outfitted with equal proportions of sand (0.065–2 mm) and gravel (3–15 mm; Cummins, 1962) that spanned the entire width of the tank. Sand and gravel substrates were positioned in one flume with sand upstream from gravel in one tank, and downstream from gravel in the other tank. Substrate positioning was reversed in the other flume to account for substrate and proximity to the paddlewheel, which might have led to subtle variations (measured or unmeasured) in habitat characteristics among experimental units. Two fluorescent light fixtures were positioned above each experimental tank and diel light patterns were programmed to 48°41′32″N latitude to simulate the natural summer photoperiod in rehabilitated areas of the Kootenai River.

Because large wood is frequently used in aquatic habitat rehabilitation projects, including those in the Kootenai River, trials were conducted with and without a woody feature to further describe habitat conditions selected by fishes in areas of habitat rehabilitation. Four artificial root-wad structures designed for home aquaria were fastened together to create a standardised "woody" habitat feature in each tank. The woody feature (hereafter "wood") was 0.25 cm tall (equivalent to the water depth in each experimental tank) and 0.3 m wide—half the width of the flume system. Treatments for experimentation were either wood present or wood absent. When wood was present during experimentation, the feature was placed in the middle of the sand or gravel substrate near the exterior wall of the elliptical flume (see Figure 1). This allowed for uninterrupted current velocity near the interior of the elliptical flume and interrupted current velocity towards the exterior of the flume while maintaining two substrate options under both velocity regimes. Because substrate positioning was randomised among the four experimental tanks, a similar approach was used when positioning the wood in each experimental tank to incorporate randomised substrate, wood, and proximity to the paddlewheel. Specifically, multiple trials were conducted where wood was located on the substrate positioned at the upstream and downstream ends in each experimental tank. Thus, variation related to availability of reduced current velocities and proportion of available sand and gravel substrate were accounted for by the experimental design.

Each experimental tank was measured for available habitat prior to experimentation under both wood treatments (Figure 2). All tanks were marked with an X-Y-Z orthogonal coordinate system, with 1656 unique locations (5 × 5 × 10 cm; V = 250 cm^3). Each location was associated with measured current velocity or known habitat characteristics (substrate, distance to wood). Interior walls of each tank were constructed with Plexiglass to allow direct observation. To reduce the effect of observers, each experimental tank was outfitted with four infrared video cameras and a video recording system to capture the location of individual fish. Two cameras were positioned in the interior of the elliptical flumes and pointed towards the Plexiglass to capture the full length of each substrate within an individual tank. The Plexiglass was marked with an X-Y coordinate system throughout the experimental tank to mark longitudinal and depth positions of individual fish. In addition, two infrared video cameras were positioned overhead to provide an aerial view of the experimental tank. Each tank was discretely marked to infer an individual's position along the wetted width of the tank. Thus, each fish's X-Y-Z location was recorded by cameras in relation to habitat characteristics to minimise observer bias.

Each trial began by placing an individual fish near the downstream barrier of each experimental tank at 07:00 h. A single fish was used to mimic low native fish densities observed in the Kootenai River (Branigan et al., 2018; Watkins et al., 2015). Eight replicate trials were conducted for each species in allopatry using naïve fish subjected to different wood treatments. Mountain whitefish were tested first with wood absent, then with wood present at the upstream end in each tank, and lastly with wood present at the downstream end in each tank. This experimental sequence was repeated with largescale sucker in allopatry before conducting any trials in sympatry with pumpkinseed because centrarchid fish can exude kairomones that may alter behaviour of conspecifics (Golub & Brown, 2003) and heterospecifics (e.g. Chivers & Smith, 1998; Mathis et al., 1995).

Trials in sympatry were conducted by placing one native individual (i.e. mountain whitefish or largescale sucker) and one non-native individual (i.e. pumpkinseed) into each tank. Each trial was replicated eight times for each wood treatment. Naïve fish were used for every replicate trial conducted in allopatry and sympatry. Trials in sympatry were conducted at twice the fish density of trials in allopatry to simulate invasion by a non-native species from a point-source population. In the Kootenai River system, pumpkinseed were thought to have originated from a breached impoundment on a major tributary. Furthermore, the small size of the experimental arena could have induced an area bias if too many individuals were used (e.g. Copp et al., 1998).

Upon completion of all treatments and species combinations, video footage was reviewed to identify the location of each individual during experimentation. After a 3-h acclimation period, fish positions were observed by reviewing video and recording an individual's X-Y-Z location every 15 min until simulated daylight ceased (~41 observations per fish; varied by photoperiod). Because all fish were longer than each delineated 5-cm cubic X-Y-Z cell, the eye of

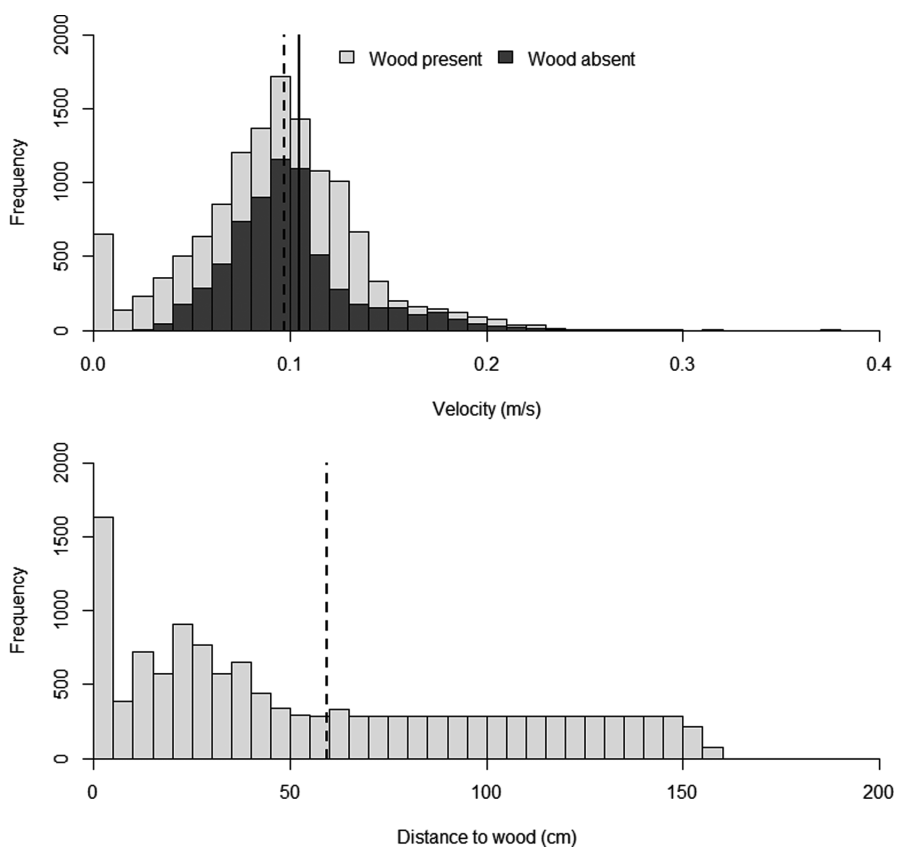


FIGURE 2 Distribution of available current velocities and distance to a woody habitat feature (when present) among four experimental tanks used to evaluate resource selection of two native and one non-native fish species in a simulated stream system. Vertical lines represent mean values for habitat variables when wood was absent (solid line) and when wood was present (dashed line)

each fish served as the point of reference to assign each location. Habitat availability data (i.e. current velocity, substrate and distance to wood) were summarised across experimental tanks to characterise experimental conditions. Habitat use was summarised (mean; SD) for each species and wood treatment to quantify differences in habitat use among species in allopatry and sympatry.

Species-specific habitat use models were developed to quantify habitat selection by each native species in the presence and absence of pumpkinseed. Given the availability-use design, tank-specific available habitat data were compiled with individual-specific use habitat data to infer resource selection under both wood treatments (Manly et al., 2002). Because trials were conducted with wood present and wood absent, two treatment-specific data sets were used to inform models. To evaluate use of wood by a species, an individual's distance to the perimeter of the woody feature was measured and included as a habitat variable. The distance between an individual's location and the perimeter of the wood was used to quantify "use" of wood by each species. A suite of generalised linear mixed-effects models was fitted for each species that incorporated velocity, substrate, distance to wood (if present) and interaction between velocity ×distance to wood. Individual fish served as the random effect, which allowed inferences to be extended to the entire population (Neter et al., 1996). A random intercept approach was employed to account for variation in resource selection among individual fish (Gillies et al., 2006). Velocity and distance to wood were standardised by subtracting each variable's mean and dividing by its standard deviation to minimise discrepancies associated with scale of each metric and ensure model convergence. All variables in each candidate model included an interaction term with sympatry (coded as a dummy variable) to determine if the presence of a heterospecific affected resource selection. A global model that included all habitat variables (and interactions with sympatry) and a null model that included only an intercept were included in the candidate model set. Akaike's information criterion corrected for small sample size (AIC_c) was used to evaluate relative support of candidate models among all models considered (Akaike, 1973; Burnham & Anderson, 2002). The change in AIC value (ΔAIC_c) from the top model is a measure of support for each model relative to the most supported model, and models consisting of ΔAIC_c values ≤ 2 were considered as top models relating to each species habitat selection (Burnham & Anderson, 2002). The AIC_c weights were calculated to further characterise the relative measure of support for each model in the candidate set.

3 | RESULTS

Use of current velocity varied among species, wood treatment and presence of heterospecifics. Largescale sucker generally used slower velocity habitats (<0.1 m/s) regardless of the presence of pumpkinseed (Figure 3). However, zero-velocity habitats (i.e. <0.01 m/s) were only available when wood was present (Figure 2), and largescale sucker selected these locations when available (Figure 3). More specifically, largescale sucker used zero-velocity habitats at a rate of 80% when in allopatry, but only 57% when in sympatry with pumpkinseed. In allopatry, mean current velocity used by largescale sucker was 0.09 (± 0.04) m/s when wood was absent and 0.02 (± 0.05) m/s when wood was present. In sympatry with pumpkinseed, mean velocity used by largescale sucker was 0.08 (± 0.04) m/s when wood was absent and 0.04 (± 0.05) m/s when wood was present. Mountain whitefish generally used slower, but a broader range, of current velocities than largescale sucker (Figure 3). Regardless of wood treatment or presence of pumpkinseed, mean velocity used by mountain whitefish was 0.09 (± 0.05) m/s throughout all trials. Mean velocity used by pumpkinseed in allopatry was 0.09 (± 0.04) m/s when wood was absent and 0.09 (± 0.05) m/s when wood was present (Figure 4). When wood was present, and pumpkinseed were in sympatry with either native species, mean velocity used by pumpkinseed was 0.07 (± 0.05) m/s.

Use of wood, as measured by proximity to the habitat feature, changed for largescale sucker and pumpkinseed when in sympatry with heterospecifics (Table 2). When in sympatry with pumpkinseed, largescale suckers reduced their use of locations within 10 cm of wood by 18%, but increased their use of locations 50–100 cm from wood by 110%. Use of locations ≤10 cm from wood by pumpkinseed increased by 32% when in sympatry with mountain whitefish and 60% when in sympatry with largescale sucker. The use of wood by mountain whitefish did not differ when in allopatry or sympatry with pumpkinseed.

Proportional use of sand and gravel substrate was similar for all species in allopatry and sympatry, and with and without wood (Figure 5). Mountain whitefish used gravel substrate frequently but less so when in sympatry with pumpkinseed. Consequently, when in sympatry with pumpkinseed, mountain whitefish increased use of sand by 76% when wood was absent and 34% when wood was present. Largescale sucker and pumpkinseed used similar proportions of gravel and sand substrates with and without wood.

The global model that included all habitat variables was the most supported model for all species and wood treatments, except pumpkinseed when wood was absent. In addition, current velocity and distance to wood were important variables associated with habitat selection by mountain whitefish, and this four-term model served as the top model for the species with a weight of 0.60. In contrast, the global model had a weight of 0.40 and a ΔAIC_c value of 0.82. When in sympatry with pumpkinseed, mountain whitefish selected locations farther from wood with slower current velocity (Figure 6). The top model for pumpkinseed included an interaction between current velocity and sympatry (Figure 7; model weight = 0.79). Pumpkinseed selected low-velocity habitats (<0.10 m/s) when in sympatry with either largescale sucker or mountain whitefish.

4 | DISCUSSION

Modification of structural habitat has successfully mitigated the effects of water development on native riverine fishes in many systems

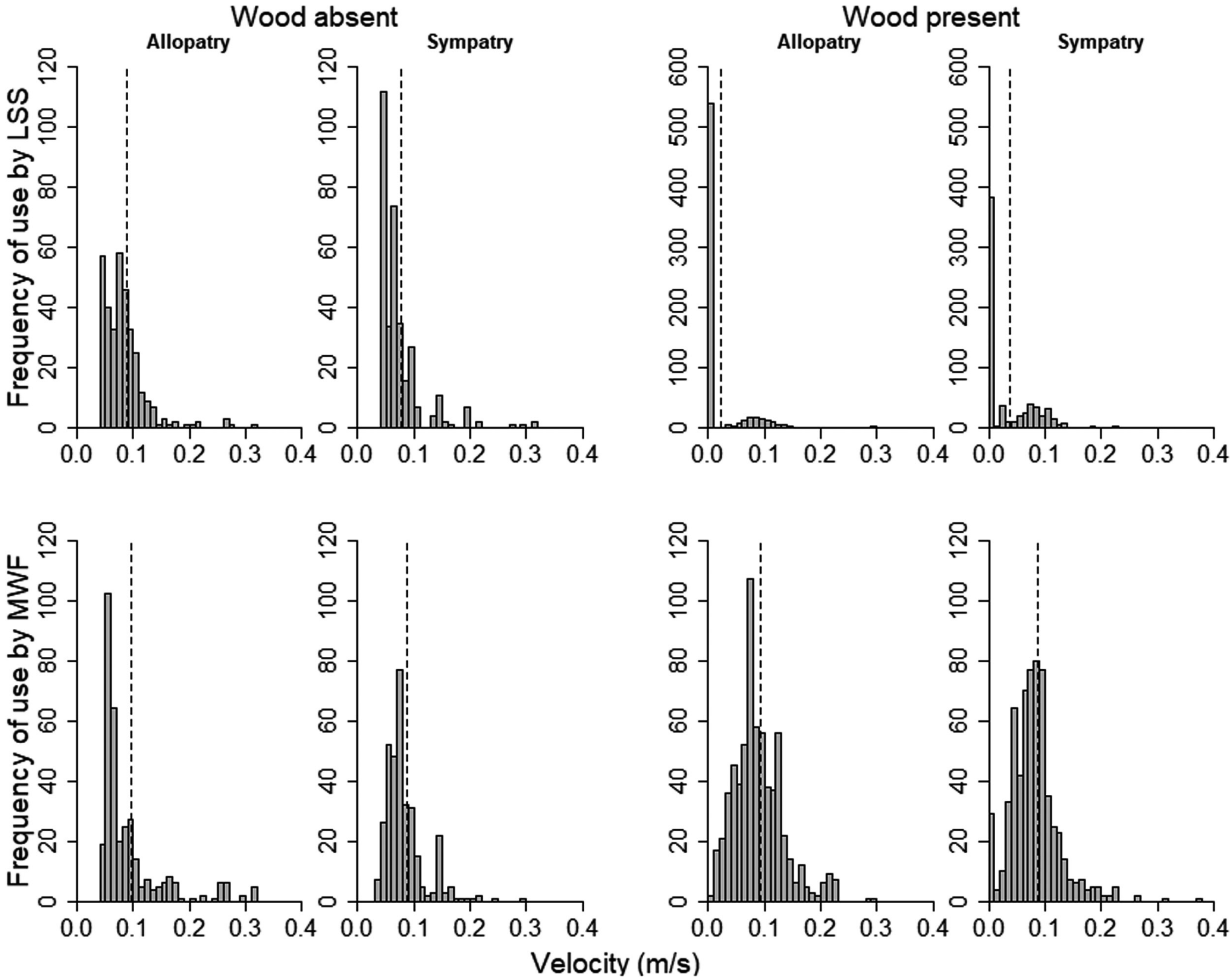


FIGURE 3 Distribution of current velocities used by two species native to the Kootenai River, largescale sucker (LSS) and mountain whitefish (MWF), when tested in allopatry and in sympatry with pumpkinseed (a non-native species) in a simulated stream system. Vertical lines represent mean velocity used by a species when in allopatry and in sympatry while wood was present and absent during experimentation

(e.g. Eros et al., 2008; Roni et al., 2002), although we found that restoring habitat to enhance native species may result in the inadvertent establishment of non-native species. For instance, management strategies aimed at improving riparian habitat conditions (i.e. removal of invasive *Salix* spp., livestock exclusion) facilitated the rapid spread of non-native reed sweet-grass *Glyceria maxima* (Hartman) in southeastern Australia (Loo et al., 2009). Although similar examples from elsewhere are rare, restoration of streams in Finland facilitated invasion of non-native salmonids (Korsu et al., 2010). Specifically, the purpose of restoration activities was to increase habitat complexity at micro- and meso-scales through the addition of instream cover, reconnection of side channels, and construction of current deflectors and gravel bars (Korsu et al., 2010). Restoration increased habitat quality for non-native brook trout *Salvelinus fontinalis* (Mitchill) and rainbow trout *Oncorhynchus mykiss* (Walbaum) (Korsu et al., 2010). Our study sought to mimic engineered habitat that appeared to be used by non-native centrarchids in the Kootenai River. We could not replicate all habitat features, and instead, were limited to examining effects of velocity, substrate, and wood on habitat selection by juvenile native fish subjected to a simulated "invasion." Despite the relative simplicity of the experimental system, we found evidence that habitat manipulation could cause at least one native species to be vulnerable to displacement by a non-native species.

Creating additional off-channel habitats in large, modified river systems to emulate natural habitat complexity and processes can be beneficial for native fishes but may also serve to facilitate the colonisation of non-native species. For instance, side channel construction in the Provo River, Utah, facilitated use by native fishes, but non-native brown trout *Salmo trutta* (Linnaeus) dominated one-third of the newly engineered side channels that lacked lentic habitat created by local American beaver *Castor canadensis* (Kuhl; Billman et al., 2013). Non-native pumpkinseed associated with newly engineered side channels in the Kootenai River that contain woody habitat and reduced current velocity could

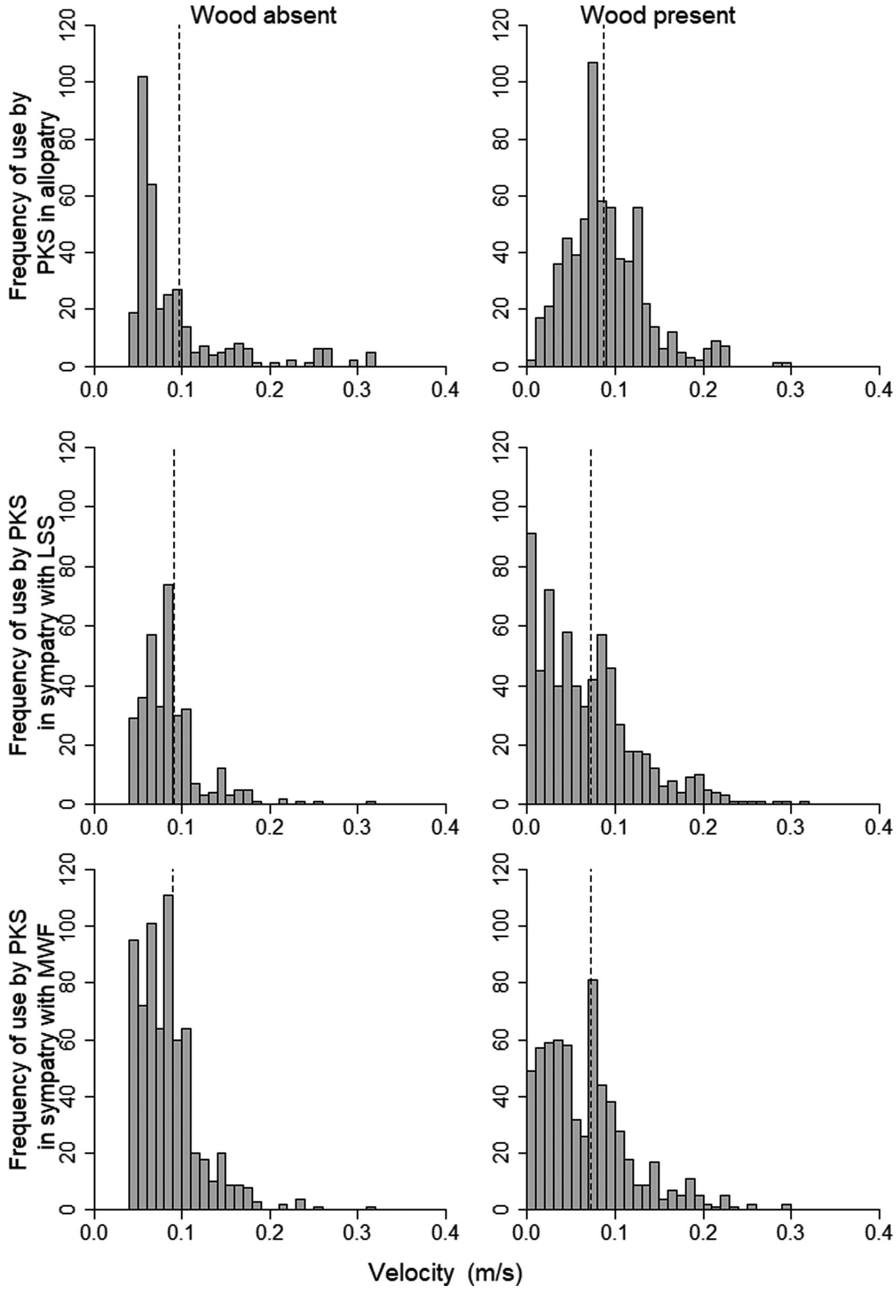


FIGURE 4 Distribution of current velocities used by pumpkinseed (PKS), an invasive species of the Kootenai River, in a simulated stream system when in allopatry and in sympatry with two native species largescale sucker (LSS) and mountain whitefish (MWF). Vertical lines represent mean velocity used by pumpkinseed when in allopatry and in sympatry with largescale sucker and mountain whitefish under two wood treatments

potentially displace native species. Such displacement was most evident in our laboratory study where frequency of use of zero-velocity habitats by largescale sucker was 80% in allopatry and only 23% in sympatry with non-native pumpkinseed. Relative size influences interactions between individuals for space and food resources (e.g. Schoener, 1983; Ward et al., 2006) and the threat of predation may compound observations of displacement (e.g. Mills et al., 2004). However, predation of juvenile (i.e. not larval) largescale sucker by pumpkinseed is highly unlikely due to gape limitation. Native mountain whitefish were seemingly unaffected by the presence of pumpkinseed with respect to current velocity, but mountain whitefish tended to select locations farther from woody features when pumpkinseed were present. Such a response by mountain whitefish was not surprising, as the species typically inhabits lotic environments where wood is scarce, whereas pumpkinseed generally inhabit lentic environments where wood is more common (Wydoski & Whitney, 2003).

Habitat structures placed instream typically reduce current velocity, thereby affecting localised substrate composition, but substrate alone did not appear to drive habitat use by any species in this study. Proportional of use of sand and gravel substrates were similar for all species in allopatry and sympatry, both with and without wood. Interestingly, largescale sucker used sand and gravel substrates equally when wood was present in sympatry with pumpkinseed. The experimental design deliberately juxtaposed the relative position of wood and substrate in each tank (i.e. upstream or downstream; see methods) so that equal proportions of sand and gravel substrates were available with and without wood. Therefore, wood (or cover in general) may serve as an important habitat feature for juvenile largescale sucker. In addition to providing cover and reducing current velocity, woody habitat traps fine sediments and organic material (Speaker et al., 1984). Although fine substrate (e.g. silt) was not available to fish in our study, use of wood by largescale sucker may be attributed to the foraging behaviour of the species. Field-based microhabitat evaluations in the Kootenai River have demonstrated that the relative abundance of juvenile largescale sucker is positively associated with fine substrate (Branigan et al., 2018). In light of our results, substrate appears to serve as a secondary or tertiary determinant of habitat use by juvenile largescale sucker but serves a role in habitat selection because substrate was included in the top model for the species.

We were unable to test intraspecific interactions between native species because of constraints on the availability of unique individuals, although their use of different velocities and distances to wood in allopatry suggested niche separation or resource partitioning between juvenile largescale sucker and mountain whitefish, as for other stream fishes (Gorman and Karr, 1978; Fausch & White, 1981, 1986). Thus, not surprisingly, these species co-exist in their native ranges regardless of spatial scale assessed (Branigan et al., 2018; Smith et al., 2016; Torgersen et al., 2006; Watkins et al., 2015).

Largescale sucker and pumpkinseed overlapped in their use of low current velocities and association with wood, so creation of these types of habitats in the Kootenai River may have unintended consequences by potentially displacing native juvenile largescale sucker with non-native pumpkinseed. Field surveys have demonstrated that juvenile largescale sucker use areas with slow current velocities (Branigan et al., 2018), and slow current velocity habitats are generally associated with the presence of pumpkinseed (Wydoski & Whitney, 2003). Although backwater habitats in the Kootenai River are scarce, they provide important habitat for small-bodied native fishes, including juvenile largescale sucker (Branigan et al., 2018). Given the pumpkinseed's affinity for lentic environments and the evidence surrounding their use of low-velocity habitats, backwaters likely provide suitable habitat for pumpkinseed in

TABLE 2 Use frequency by distance to a woody habitat feature for two native (largescale sucker, mountain whitefish) and one non-native (pumpkinseed) species subjected to laboratory trials conducted in allopatry and sympatry in a simulated stream system

	Distance to wood (cm)			
Heterospecific	≤10	10–50	50–100	>100
Largescale sucker				
–	0.82	0.03	0.10	0.05
Pumpkinseed	0.67	0.04	0.21	0.08
Mountain whitefish				
–	0.02	0.30	0.33	0.35
Pumpkinseed	0.01	0.30	0.39	0.30
Pumpkinseed				
–	0.25	0.10	0.34	0.31
Largescale sucker	0.40	0.07	0.34	0.19
Mountain whitefish	0.33	0.17	0.33	0.17

Note: Minimum available distance to wood was 0 cm, and the maximum available distance was 157 cm.

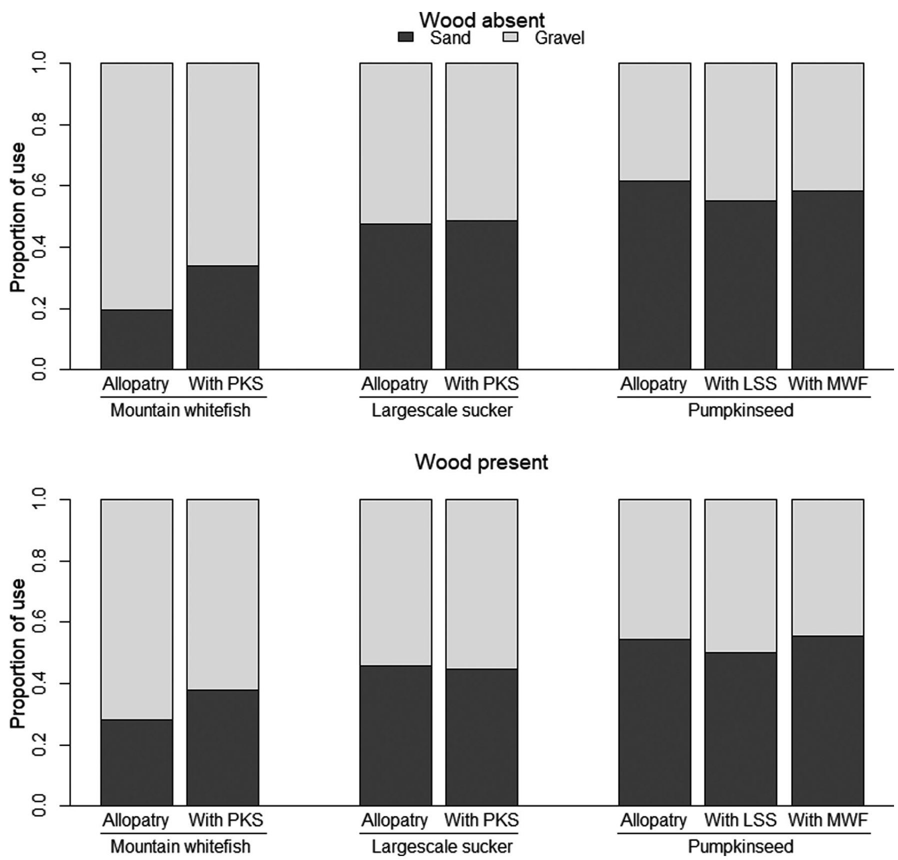


FIGURE 5 Proportional use of sand and gravel substrate by largescale sucker (LSS), mountain whitefish (MWF), and pumpkinseed (PKS) subjected to a simulated stream system with and without the presence of a woody habitat feature. Sand and gravel substrates were available in equal proportions during experimentation

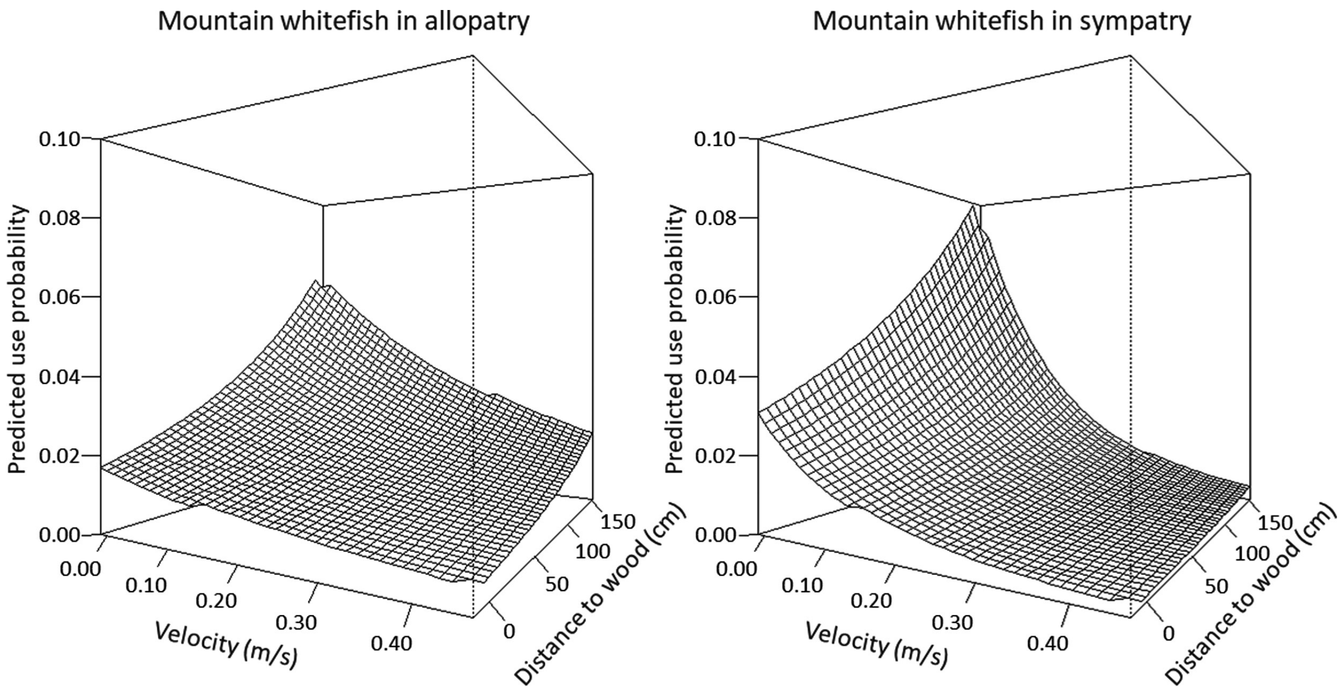
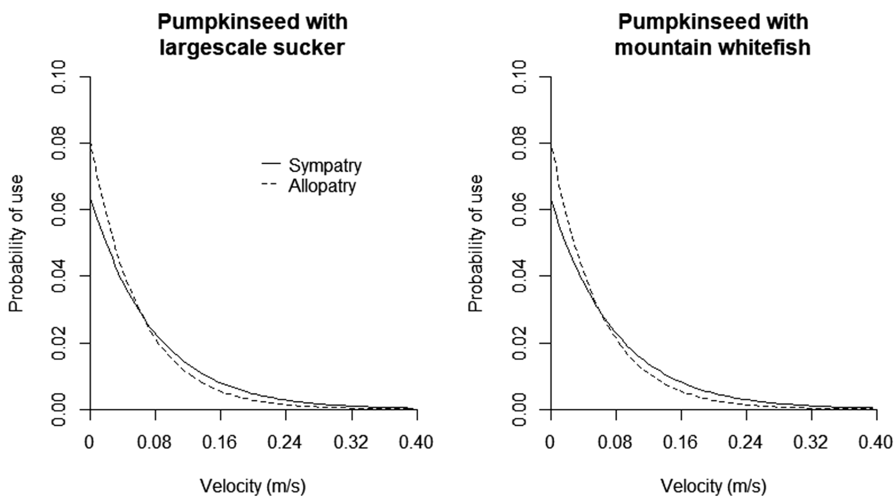


FIGURE 6 Predicted probability of use by native mountain whitefish subjected to a simulated stream system containing a woody habitat feature when in allopatry and in sympatry with non-native pumpkinseed. Current velocity and distance to wood were the two habitat variables included in the top model for mountain whitefish

FIGURE 7 Predicted probability of use of current velocity by non-native pumpkinseed in a simulated stream system when in allopatry and in sympatry with native largescale sucker and mountain whitefish



the Kootenai River. Continued monitoring of these areas is important to determine whether some form of exclusion is occurring. The establishment of pumpkinseed in these low-velocity areas could have deleterious effects on the juvenile largescale sucker population and may similarly affect other native fish populations (Branigan et al., 2018; Smith et al., 2016).

Spatial and temporal scaling are important considerations for any ecological study and attempting to scale the entire Kootenai River system to a laboratory stream likely affected our results. First, the confined area of an experimental stream likely affected fish behaviour (Rowland, 1983), even if the experimental area was more than twice the size of an individual fish's estimated home range (Copp et al., 1998). The simulated stream area used in our study (1.4 m^2) may have been too small to observe natural behaviour without area-induced bias, although species-specific habitat use and resource selection models were convincing. Additional laboratory or field studies may be needed to expand the inference of our study by evaluating the effect of the size of the testing area and incorporating additional native and non-native species.

We found evidence that two native species partitioned habitat resources and that at least one of these native species was displaced by an introduced, non-native species. Native largescale sucker and mountain whitefish occupied different habitats in the simulated stream system, which potentially reflects resource partitioning. The introduction of pumpkinseed affected habitat selection by both native species to some extent, although largescale suckers were apparently displaced by pumpkinseeds from locations within 10 cm of wood. Many riverine fishes rely on annual floodplain inundation for growth and survival, and these areas generally offer complex habitats containing woody structures and other cover features (e.g. submerged vegetation, overhanging vegetation). Most river rehabilitation programmes seek to create complex habitats. However, managers should be aware that connecting or enhancing habitats may also provide suitable habitat for non-native species that has unintended consequences for native fishes.

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CONFLICT OF INTEREST

There is no conflict of interest to declare in this article. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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