Review of Literature of Small Dams with a Case Study on the Southern Cumberland Plateau

Molly Allyse Almon

A thesis submitted to the faculty of the University of the South in partial fulfillment of the requirements for honors in the Department of Biology

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Abstract

Small dams (<5m high) are found abundantly across the world due to limited or absent regulation and a variety of uses including agriculture, flood-prevention, water control, drinking water, wildfire prevention, recreation, and aesthetics. Though often thought to have less of an impact downstream because of their size, they can acutely alter downstream habitat, and their frequency suggests that these impacts could accumulate to have larger effects.

Small dams change environmental conditions downstream like flow, water temperature, pH, geomorphology, chemical and nutrient transportation, and oxygenation based on their operation. The biotic communities respond to these shifts by altering behaviors and population dynamics around the physical structure of the dam. We investigated the frequency with which streams on the Southern Cumberland Plateau ecoregion in Tennessee are impacted and reviewed the literature to identify key questions about the environmental and biological changes of small dams. Although small dams can cause negative downstream change, their presence can also have positive environmental impacts, and we sought to identify characteristics that benefit or degrade the surrounding ecosystems. More research needs to address variations of small dams to propel regulation and monitoring accordingly by state and federal agencies. This includes research into the effects on specific species and regions, assessing different types of small dams, and cumulative impacts on the biota.

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Introduction

Scientists estimate the number of small dams to be 16.7 million around the world (Lehner et al. 2011) compared to 58,000 large dams in use today (ICOLD WRD 2020), yet monitoring and regulating has not grown equally to ensure the protection of human and biological communities affected by small dams (Morris et al. 2019). Without acknowledging impacts that small dams have, these structures can be constructed in ecologically-important areas, disrupting a suite of abiotic factors on which humans and native species rely on (Sharma et al. 2008, Soares et al. 2019, Nathan et al. 2012, Lessard & Hayes 2003, Vaughn & Taylor 1999, Abernethy et al. 2013). Small dams also affect dispersal (Rooney et al. 2015, Zarri et al. 2022), habitat (Merritt & Wohl 2006, Lessard & Hayes 2003, Zhou et al. 2008, Kawanishi et al. 2015) invasion (Johnson et al. 2008, Dana et al. 2011) , predation (United States Department of the Interior 1987), and food distribution and abundance (Almeida et al. 2009) of stream communities including fish, mussels, macroinvertebrates, herpetofauna, and aquatic/riparian plants.

Small dams are defined as small structures that limit downstream flow and thus encompass a broad range of types and functions (United States Department of the Interior 1987). The size of small dams is variable among studies (Poff & Hart 2002, Brewitt & Colwyn 2019), but we define small dams as those less than five meters in height. At the state and federal level, small dam construction and implementation is less regulated if regulated at all, and in turn, small dams are most commonly constructed with aggregations of soil and rock that allow seepage and could make them more temporary or less stable (Craft et al. 2008). Mainly in the United States, they are privately owned and created for many purposes: drinking water, water diversion and control (Soares et al. 2019), agriculture (Nathan & Lowes. 2012), flood control (Schultz 2002), wildfire prevention (Fairfax & Whittile 2020), recreation, increased property values (Taylor 1935), and aesthetics.. While the construction of small dams for hydropower is rare, their numbers have increased recently to provide power in rural settings of many countries, especially where access to energy through other means is limited (Couto & Olden 2018, Mayor et al. 2017, Gradie III & Pourier 1991).

Large dams (> 15m) and intermediate structures (5<x<15) have received considerable attention (Kirchberg et al. 2016, ICOLD WRD 2020) due to their well-documented negative environmental effects (Magilligan & Nislow 2005, Barbossa et al. 2020). In contrast, small dams are smaller in size and scale of influence, but their cumulative effects could have a larger and more evenly distributed spatial impact. Furthermore, the impacts of small dams may be more nuanced and context-dependent. Small dams are ubiquitous around the world and change the hydrology in 280-380% more waterways than large dams (Morden et al. 2022) because they can be built directly within stream and river corridors or outside of the river network and fill via diversions, groundwater pumping, or rainfall (United States Department of the Interior 1987) . Thus, their construction, location, and function can deviate from patterns expected from large dams. Despite widespread acknowledgement that the presence of dams is generally detrimental to biodiversity, less comprehensive evaluation has been performed on small dams because of their highly localized nature (Morden et al. 2022, Poff & Hart 2002).

The discussions that follow seek to identify the abiotic and biotic effects of small dams, acknowledge the nuance of their presence in watersheds to make recommendations for future work and policy regarding their implementation and continued presence on the landscape. This review of literature addresses the history and purpose, construction, regulation, water properties, and nutrient transportation of small dams as well as biotic changes that come with the addition of small dams. This includes dispersal, habitat loss and degradation, and community change. To highlight the scale of impact that small dams contribute to watersheds around the U.S. and the world, small dams in three counties within Tennessee were documented.

History and Purpose

Small dams are found in natural processes of geological formations. Small ponds, for example, are developed throughout the landscape with natural processes such as floodplain wetlands during high flow events, oxbow creation during channel migration and flooding, or vernal pools through clogs in bedrock cracks and fissures (Evans et al. 2017, Thomas et al. 2022, Acreman & Holden 2013). These features tend to be short-lived and concentrated in particular regions where the geomorphology directs the water to pool into structures like vernal pools in the eastern United States, prairie potholes in the midwest, and oxbow lakes found across the country. Furthermore, flow manipulation and management has nearly eliminated widespread flooding that contributed to natural creation of small ponds (Tiner 2003). Today, small ponds are nearly entirely man-made and constructed for distinct purposes including power generation, agriculture, flood control, drought resistance, property value increase, wildfire control and recreational use (Nathan & Lowe 2012, Schultz 2002, Taylor 1935, Fairfax & Whittile 2020, Provencher & Meyer 2008). More recently, small-scale hydropower dams have emerged as a viable solution to generating power in remote areas (Mayor et al. 2017).

Beaver dams are also a natural form of small dams. Ecologically, beaver dams create hydrologic heterogeneity and provide the structure and maintenance for shallow wetlands that many species require (Hood & Bayley 2008). Historically, natural pools constructed by beavers increased species richness (Smith & Mather 2013) and provided eco-service to indigenous groups in the form of fishing success and water storage for crop production (Lineback & Knight 2020).

However, the transient beaver ponds flooded permanent human settlement and disrupted navigation routes. The hunt for their water-resistant fur also led to widespread beaver-trapping and near eradication throughout the eastern United States. This led to the dwindling of North American beaver (*Castor canadensis*) populations and dam structures due to the fur trade in the seventeenth through twentieth century (Hood & Bayley 2008). However, populations of North American beaver are currently increasing (Busher & Lyons 1999). As environmental engineers, beaver dams change the flow and temperature of the water stored behind the dam, especially in the summer (Weber et al. 2017). Water capture due to beaver dams can help hold water in times of drought, but downstream flow can be cut off. Beaver dams also create sediment storage (Levine & Meyer 2014), acid-neutralizing capacity to the flowing water downstream (Cirmo & Discoll 1993, Margolis et al. 2001), different biological communities improving regional biodiversity (Bouwes et al. 2016, Stringer & Gaywood 2015, Smith & Mather 2013), change in biogeochemistry (Hill & Duval 2009), and hydrology (Westbrook et al. 2006, Naimen et al. 1988). Human-made small dams historically mimicked these beaver-created small ponds.

The history of human-made dams may have started in 3000 BC in Asia and Europe to regulate water (Ho et al. 2017), and were first seen in Egypt more than five thousand years ago to moderate flooding. Mill dams were then used between the 17th and the 19th century for water power in Europe, the American colonies, and elsewhere. Today, these dams have been proven to have changed the landscape of Eastern North America. Instead of having characteristics of a floodplain or wetland—low amounts of retained sediment and large amounts of carbon, streams have become fine sediment traps that have been incised after the high numbers of mill dams (Walter & Merritts 2008). Small dams began to be built more frequently in the U.S. during the Industrial Revolution to provide hydropower and other services to states in the northeast (Ho et al. 2017). By 1840, the eastern United States hosted mill dams at densities up to 61 per 100 km^2 (Walter & Merritts 2008). Mill dams continued to increase in popularity after the World War II in developed countries for increased energy to produce gunpowder and machinery. The two decades following World War II had the highest level of dam construction (Vedachalam & Riha 2013). During this time, large dam construction for hydropower and flood control was becoming more common, which supplanted small dams for power (Poff & Hart 2002).

Farm ponds, a specific type of small dam used in agriculture for watering livestock and crop irrigation, have a different history. During the Dust Bowl (1930-1940), water became scarce and the topsoil blew away for farmers in Midwestern states, so the Department of Agriculture added farm ponds to its farming tips for conserving soil (Swartz & Miller 2021). Although some are similar to check dams that simply slow the flow of water to prevent erosion, others retain water for use in irrigation or providing water for livestock. Farm ponds served a dual-purpose in also moderating flow from floods and droughts. Once in place, farm ponds were co-opted for recreation and food production through introduction of non-native fish and the growth of native fish (United States Department of the Interior 1987).

Today, small dams are constructed for the purposes described above, but they are also recommended as strategies for minimizing flow variation downstream of rural and urban impervious surfaces as detention and retention basins (Rosenzweig et al. 2011). Furthermore, increased suburban and exurban developments favor the construction of small ponds for aesthetic purposes in addition to water control. Urban ponds in particular have a positive economic impact, improving nearby home values (Provencher & Meyer 2008). They also can capture high concentrations of contaminants from lawns, driveways, and roads in residential neighborhoods (Flanagan et al. 2021). Finally, most state agencies provide guidance for the construction and maintenance of small ponds for recreation including swimming, fishing, and boating (Mioduszewski 2012). Today, most ponds are constructed for multiple uses, but their permanent nature and often manipulated biodiversity through introduction of game fish limit their ability to replicate naturally created ponds (Metts et al. 2001, Dana et al. 2011, Zhou et al. 2008). Small dams have also been increasing around the globe because of their ability to house small hydropower operations in rural areas (Couto & Olden 2018).

Date	Dam technology in the United States
1600-1780	Mill dams were constructed across the American colonies for energy production
1780-1840	Increase of small dam construction with the Industrial Revolution
1930-1940	Farm ponds became popular in agriculture during the Dust Bowl
1939-1945	During World War II, there was an increase of large dam construction
Present	Small dams are constructed for recreation, diversion, agriculture, hydropower, etc.

Table 1 | The history of human-made small dams in the United States.

Construction

Although small dams do not require complex construction and can function well as simply a mound of dirt or natural material that stops or slows water flow, there can be many nuances to their construction. Historically, dams would have been constructed of earth and organic materials (Stephens 2010), but more modern structures have increased reliance on concrete and rock. They require a rock or compact sand foundation in their construction. Small dams are newly popular in the tropics and rural areas where rock is plentiful (Mayor et al. 2017). Concrete dams can provide more support, and are often found under earthen and rock-filled dams. In many cases, dams can be made out of all of these types of materials in different sections based on flow and the strength of support needed. Other dam material include steel and timber, but neither is used much in practice today due to economical limitations (United States Department of the Interior 1987).

Figure 1 | Shows the wide array of different structures that can impact small streams. Structures can be naturally made, like (a) a beaver dam. Other structures are built by humans using rocks (b), soil and rocks (c, f), or more complex run-of-river concrete structures (d, f). (d) shows a check dam that slows the flow. (e) shows a farm pond that was created using water from a stream and damming it. (f) shows a small hydropower dam.

The various purposes of small dams can lead to different structures being built, as illustrated by figure 1. Small dams or impoundments are all made with rock, earth, or concrete material, however the amount that they block flow depends on the individual construction (United States Department of the Interior 1987). Figure 1a illustrates a natural impoundment in with the beaver dam, but images 1b-f, depict the varying human structures that can be formed using small dams. There can be different porosity depending on sediment size used during construction and additional factors that play into changes in water level (Stephens 2010).

Small dams can be constructed almost anywhere because of the basic material requirements and little regulation, but primarily affect headwater streams, streams that are first through third-order streams (Morden et al. 2022). Factors that can contribute to the location of a small dam are geological structure, topography, hydrologic capacity and aspects, availability of construction materials, land value, and accessibility to living facilities (Luís & Cabral 2021). For water catchment, it is best to place dams not on fault lines, but rather on flat land or a slope that lends itself to catching water. Water storage and small hydropower dams (figure 1f) must balance water filling capacity and power generation on larger rivers with the force that these high flows can create (Ho et al. 2017). Small dams can also be constructed to fill with diverted water from streams and rivers (Morden et al 2022) and can be built upon natural dams (figure 1a) to enhance their capacity (Bouwes et al. 2016). Other dams may be situated in wet-weather conveyances, like recreational, agriculture, urban ponds, retention and detention basins (figure 1c and 1e). Ultimately, streams can pass through a series of small dams magnifying their impact (Morden et al 2022).

Most small dams have overflow releases, meaning that water is released from the surface of the pond rather than from mid-depth to the bottom as found in larger dams (United States Department of the Interior 1987). This construction feature can alter the temperature, pH, sediment, and nutrient dynamics downstream of the dam. The construction fill material and allowable water seepage through earthen dams can also alter water chemistry especially when clay is used due to its high cation exchange capacity (Chapin et al. 2011). In some cases, interactions between anoxic water at the bottom of reservoirs and bedrock can leach metals that seep into downstream environments (Kirchberg et al. 2016).

Summary of Small Dam Impacts

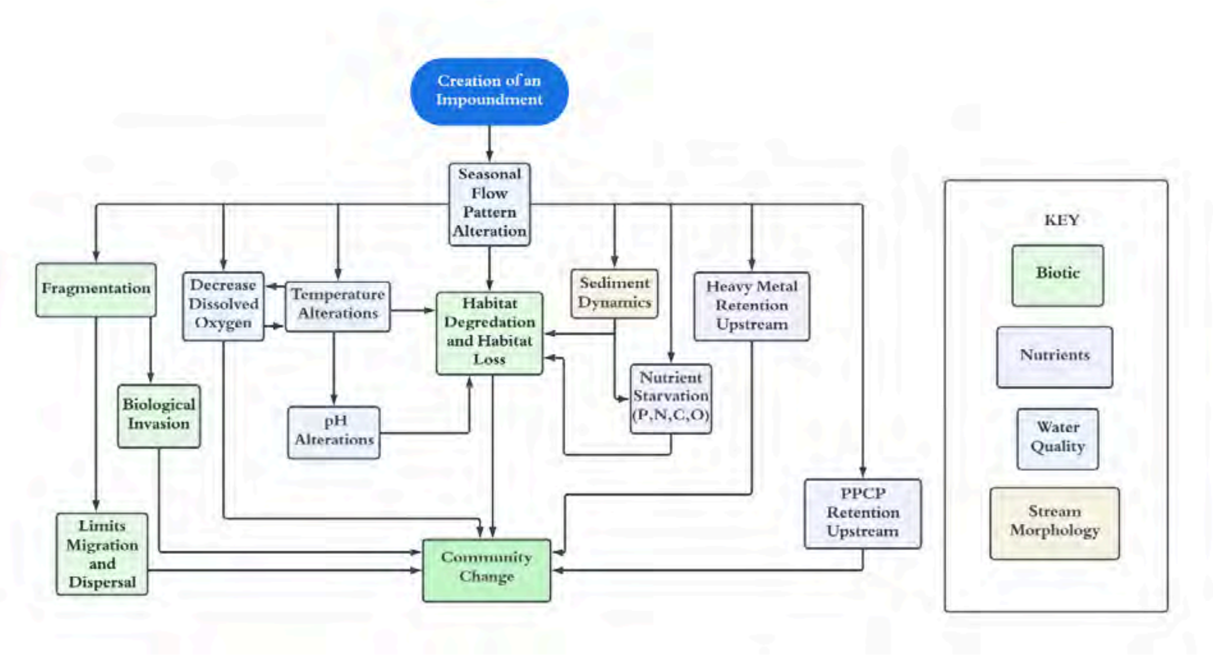

Figure 2 | An overview of the abiotic and biotic impacts after an impoundment is created, noting the biotic (green), nutrients (purple), water quality (blue), and stream morphology (brown).

Abiotic Impacts

Water Properties

Although downstream flow, as depicted in figure 2, is perhaps the most obvious potential impact that small dams could have on downstream ecosystems, the effects of small headwater dams on downstream flow are highly variable and context-dependent. Earthen dams often allow for regular seepage that maintains annually consistent baseflow. Conversely, flow responses to precipitation will depend on the prior water levels within the reservoirs. When conditions are dry or have high evaporative losses, precipitation will accumulate behind a dam and not travel downstream. Recent rainfall or cool seasons promote pond filling and cause additional precipitation to immediately travel through the pond to downstream reaches. Although dependent on the local context, this results in summer dry conditions that lack flood pulses and winter wet conditions that have minimal impacts to flood regimes. Therefore, the effects of dams on flow are likely seasonal and the ecosystem-level effects will depend on the synchronicity of flood and impact (Lytle & Poff, 2004).

These effects of small dams on flow may shift with climate change, and small dams may become potential mitigation strategies for changes in precipitation patterns (Ho et al. 2017). For example, on the Southern Cumberland Plateau, we expect to receive more precipitation in fewer events, meaning that precipitation events are all likely to be large with longer periods of time without precipitation (Dale et al. 2009). This type of climate effect may be mitigated by small dams that lose water in the dry periods and are able to capture additional precipitation during large rain events. If ponds retain water year-round, they may also help to mitigate ephemerality during longer dry periods. In particular, if long, dry periods prevail, streams may become more ephemeral, making streams that drain small ponds potential refuges for obligate aquatic species. Thus, small dams may ultimately have positive effects for increasing resilience to climate change with respect to flow (Heinzel et al. 2022, Ho et al. 2017).

Small dams most often have surface water releases that have the potential to change the temperature of receiving streams, as seen in figure 2. In unmodified streams, surface flow mixes with groundwater to stabilize temperatures across seasons. However, the presence of a small dam can either increase or decrease the temperature of water downstream, and these effects can have large spatial impacts extending downstream (Zaidel et al. 2021). In primarily forested watersheds, small dams will receive solar radiation and increase downstream temperatures (Chandesris et al. 2019, Zaidel et al. 2021). In more urbanized catchments, small ponds capture surface runoff from impervious surfaces that are much warmer than receiving streams (Stajkowski et al. 2023). In these instances, small ponds can benefit downstream ecosystems by allowing water to cool before being released downstream (Tanny et al. 2008).The ultimate impacts of ponds on thermal regimes in streams depends on the fine balance between groundwater inputs, catchment land cover, and the water residence time in the pond.

Dissolved oxygen and temperature are inversely related, so as temperature increases in the presence of a small dam, dissolved oxygen decreases (Abbott et al. 2022). Dissolved oxygen content indicates the diurnal process of conversion of carbon dioxide and oxygen from photosynthesis, respiration, atmospheric diffusion, reaeration and anthropogenic interventions. It determines the water quality of aquatic ecosystems (Abdul-Asiz & Ishtiaq 2014), thus, when it is altered by small dams, the livelihood of the stream may be better or be put at risk depending on flow and temperature. Dissolved oxygen in small streams is typically high due to the turbulent nature of flow and moderate temperatures. However, shifts in the temperature of pond discharge can decrease downstream dissolved oxygen concentrations essential for fully aquatic species, as indicated by their relationship in figure 2 (Abbott et al. 2022).

In small ponds, stratification and phytoplankton activity drives high pH, high temperatures, and high DO at the surface, while the benthic zones are hypoxic, acidic, and cool (Song et al. 2013, Margolis et al. 2001, Geographer & Rasmussen 2016). Although surface releases from ponds could help to buffer stream acidity, turnover can result in seasonal shifts in acidity that drive changes in key ecosystem processes that support stream food webs

(Geographer & Rasmussen 2016). Variability in the rates of mineralization, especially if they accelerate mineralization of a more limited carbon source could reduce the biomass possible in downstream food webs (Yao et al. 2022).

Nutrients

Nutrient load and distribution can be drastically changed by small dams. Because dams are often porous structures, some water and nutrients flow downstream, but this happens in much smaller increments than in the absence of a dam (Kumwimba et al. 2022). Essential nutrients to support downstream food webs include nitrogen, phosphorus, carbon, and metals and have regular seasonal fluctuations and associations with temperature, pH, and structure of the dam (as seen in figure 2; Song et al. 2013, Hogsden & Harding 2011, Stajkowski et al. 2023). In forested watersheds, the storage, deposition, and conversion of nitrogen and phosphorus in impoundments behind small dams can serve to further limit nutrient availability and productivity in downstream reaches. However, in watersheds with heavy runoff of nitrogen and/or phosphorus, the capture of excess nitrogen and phosphorus by small dams can reduce the downstream impacts of point and nonpoint source contributions to nitrogen and phosphorus (Rosenzweig et al. 2011, Ruan & Gilkes 2000). Likewise, carbon can also be captured (Downing et al. 2008). This can be particularly true for small impoundments constructed for the sole purpose of nutrient capture in agricultural waste lagoons (Ruan et al. 2000), tertiary wastewater treatment and storage (Zeitler et al. 2018), and impervious surface runoff retention and detention basins (Rosenzweig et al. 2011, Stajkowski et al. 2023).

The fate of these nutrients in small impoundments can diverge. Cultural eutrophication of small water bodies contribute to hypoxia and limited efficacy of constructed ponds to serve other purposes like fish and wildlife habitat. Within benthic sediments, transformations in anoxic regions can result in long-term storage of phosphorus or the loss of nitrogen via denitrification (Rosenzweig et al. 2011, Ruan & Gilkes 2000). Often the composition of these sediments can contribute to the efficacy of storage as a mechanism for minimizing the downstream or local impact of excess phosphorus use (Ruan & Gilkes 2000). Likewise, water temperature and seasonal trends affect the speed of nutrient transformations, availability of different fractions of nitrogen, and activity of small autotrophic and heterotrophic organisms. Over long periods of time, these systems are prone to phosphorus loading, and exacerbation of the negative effects of cultural eutrophication. Finally, seasonal water availability can serve to dilute or concentrate these nutrients in small impoundments affecting their ecological impact (Song et al. 2013, Stajkowski et al. 2023).

Often retention basins are built to target locations of potentially harmful materials like heavy metals and pharmaceuticals and personal care products (PPCPs) and prevent their downstream transport. These materials can settle into benthic sediments creating long-term storage when flow is inhibited (figure 2). However, shifts in water level or water turnover can remobilize these materials into the water column and make them bioavailable. High concentrations of heavy metals like Fe, Mn, Cu, Ni, and Zn can create environments in streams that are only habitable by organisms that can survive in extreme conditions (Hogsden et al. 2012). Runoff that contains these compounds also tends to be acidic and contribute to poor performance and success of key zooplankton inhibiting the development of biological communities within small impoundments (Goździejewska et al. 2018). PPCPs can also be delayed in small impoundments to settle into benthic sediments or be transformed by aquatic and benthic microbes into derivative compounds minimizing the bioactivity of potentially harmful compounds. To date, retention and detention basins are considered an effective bioremediation mechanism to reduce downstream concentrations of PPCPs, but transformations are context specific and inconsistent in their effects across all known compounds (Zeitler et al. 2018).

The slowing of water behind small dams causes sediment and particulate organic matter to settle out of the water column and into the benthos of the pool because these factors are connected (figure 2). As ponds age, they fill with sediment, reducing the depth and effectiveness of small dams to capture and slow the release of water. Decreasing pond depths will contribute to higher water temperatures and increased rates of evaporation worsening the effects of drought. Streams with headwater dams will be sediment-starved causing increased rates of downstream erosion until the stream is large enough that the effects are minimal relative to the watershed-scale processes (Skalak et al. 2009). Scour and downstream transport of fine sediments can reduce habitat availability or alter habitat quality for biological communities (Gangloff et al. 2011).

Biotic Impacts

Dispersal

Dispersal is a key process necessary for maintaining genetic diversity of populations that migrate in a watershed or individual stream (De Fries et al. 2021) . While large dams are known to fragment populations (Barbarossa et al. 2020, Murphy 2021), dams of any size have the potential to sever stream and river connectivity, as shown in figure 2. The upstream position of small dams, however, could minimize their impacts on movement and gene flow. When placed within low-order streams, small dams could block the connectivity of upstream and downstream populations, decreasing the genetic diversity of upstream populations and making them more vulnerable to change. Alternatively, small dams placed adjacent to headwater streams or in wet-weather conveyances may have little to no impact on connectivity of populations upstream and downstream of the dam's outlet. Despite the potential to have minimal impacts on species dispersal and gene flow, small dams could impact the behavior of mobile organisms in ways that have larger impacts (Zarri et al. 2022, Rooney et al. 2015).

The low construction budgets for small dams limit their sophistication and inclusion of mitigation strategies, like fish ladders. Thus, small dams act as an unnatural barrier between two sections of stream isolating upstream and downstream populations. For most aquatic organisms, they exhibit downstream biased movement that causes them to accumulate on the downstream end of dams potentially increasing intra- and inter-specific competition. Small dams also prevent species from accessing essential habitat for key life history stages like egg and juvenile development in migratory species that require low-order streams for successful reproduction. These shifts in dispersal behavior can have cascading effects on other species like mussels that require particular hosts for dispersal and offspring survival. The lack of fish movement due to small dams also impacts bivalve dispersal and prevalence in stream systems. The papershell (spp. *Leptodea fragilis*) and pink heelsplitter mussel (spp. *Potamilus alatus*) both are known to parasitize fish, and a study found that their distribution is related to dams (Watters 1996). This can be true for other freshwater mussels as well, with even some species of mussels parasitizing one species of fish in their larval stage (Vaughn & Taylor 1999, Abernethy et al. 2013). Thus if the fish species became extinct, the mussel population would also be affected. Mussels also experience changes to their food source in the adult life stages, with a lack of particulate matter flowing downstream of dams (Vaughn & Taylor 1999). There is nuance to the argument that mussels are harmed by small dams because they can also be habitats for populations with adequate conditions (Gangloff 2011).

In addition to direct threats to dispersal pathways, small dams can also overcome dispersal barriers for non-native species. Small dams are stocked with fish like largemouth and smallmouth bass (Micropterus spp.) and a variety of other sunfish species (Lepomis spp.). These warm-water species would often be excluded from headwater streams by high-gradient patches or cool water habitat, but the presence of small ponds allow them to bypass these barriers and access suitable habitat much higher in a watershed. Thus, they can migrate temporarily upstream from the small pond, or they can escape downstream from the pond to interact with headwater communities unaccustomed to the presence of these large and aggressive species. Finally, the presence of small ponds can change downstream and upstream habitat that causes the habitat to no longer be suitable in inducing dispersal movement by native populations (Jansen & Yoshimura 1998).

Habitat loss and Degradation

Habitat loss and degradation due to physical changes like water quality, flow, and geomorphology (figure 2) can also play a role in the biodiversity downstream of small dams, but every situation has its own nuances, causing changes to be less severe for some organisms, and more severe for others. These losses may impact key life history processes including predation, reproduction (Merritt & Wohl 2006, Widlak & Neves 1985, Kawanishi et al. 2015, Peoples et al. 2013, Peoples 2016, Vaughn & Taylor 1999), and foraging behavior and availability of food (Zhou et al. 2008, Power et al. 1996).

Water quality can impact organisms in small dam systems because of changes to temperature, nutrient availability, carbon transport, and pollution transportation (Kirchberg et al. 2016). Small dams typically increase the temperature of the water because of its release of warm surface water downstream. Some species, like coldwater fishes can require certain temperatures to have assemblages in areas of stream, thus leaving areas directly below the dam (Lessard & Hayes 2003). Likewise, we see species thriving below small dams that require fewer nutrients and carbon because they are being sequestered above the dam under sediment or flushed downstream. Water pollution transportation, though, is hindered because of small dams, and can have a positive impact on organisms below dams.

Flow, likewise, is another large factor in creating habitat loss and degradation. By creating lentic environments, different species become absent in streams. This can change the populations, and what once thrived in fast water may have a lower fitness with the presence of small dams. Loss of flow not only can have a direct effect on organisms, but it can also change food availability for large vertebrates (Zhou et al. 2008, Power et al. 1996), which can further disrupt the stream system. For example, zooplankton that require certain flow velocities may be affected by small dams, which impacts organisms up the food chain. This is likewise seen in flow changes and a decrease in insect diversity (Almeida et al. 2009). Changes of the timing of flows can also affect populations because alterations to flow patterns affect environmental cues that certain organisms need to reproduce. If flow remains more consistent instead of having large seasonal changes, organisms may not get cues to reproduce. As these reproduction and feeding behaviors are so critical for the survival of the population, it is obvious that altering flow patterns contributes heavily to changes in stream populations.

When the geomorphology is altered, there are alterations to substrates that are relied on in streams for habitat and breeding grounds. Reproductive processes can also be altered for organisms that rely on flow, or water quality, but often the substrate is critical (Peoples et al. 2013, Peoples 2016). Fish in particular need certain substrate and plants to spawn. Likewise, seeds need nutrient availability and soil parameters to sprout next to streams after dispersal via waterway (Jannson et al. 2000). Without these additions to the population, the biotic community could become unbalanced. Plant communities may appear less heavily around streams, in turn affecting the amount of light that the stream receives due to the amount of overhead coverage that the vegetation provides. Different ranges of light pollution can occur, further degrading the stream environment and the abiotic factors in it (Chandesris et al. 2019, Zaidel et al. 2021).

Community Change

Fish assemblages have been known to change in many dammed systems, but this extends to other taxonomic groups as well (Metts et al. 2001, Dana et al. 2011, Zhou et al. 2008). Small dams, because of their change in geomorphic structure and flow (figure 2), can cause a loss of smaller fish habitat and an increase to predatory fish habitat. Small dams can also fragment populations and cause localized extinction from their reactions to climatic changes. Because they have short life histories, the loss of sexually mature fish due to these events may result in little to no fry production in a year and a decrease to the population. Physical barriers and changes to water quality, as seen in figure 2, also caused different population assemblages, like with crayfish and plants (Adams 2013, Wu et. al 2009). This has cascading effects on both the habitat and food availability in streams. On a larger scale, changes in flow can decrease insect species, which leads to problems with food sources for species that require these larvae, especially for habitat generalists (Almeida et al. 2009). Biphasic animals, which have two stages of life by undergoing metamorphosis, may be able to minimize some of these effects because they do not spend their complete life history there, but it depends on their amount of reliance on food sources and habitat around the stream.

Small dams may favor invasive species as a result, thus decreasing the population of native species. How frequently invasive species may occur after a small dam is put into place differs based on the proximity to invasive species, qualities of the dammed downstream, and adaptations of native species to the dam structure. Some impoundments even support multiple invaders (Johnson et al. 2008). Because small dams also break up sections of stream, though, it is also important to consider if they are actually harboring native species, preventing invasive species from overtaking areas, or can be a successful area to reintroduce native species (McLaughlin et al. 2013). Invasive crayfish, for example, are prevented from expanding upstream of dams when there is a small dam structure in place (Dana et al. 2011). While small dams are anthropogenic, these structures can imitate beaver dams that make their own ecosystem downstream and promote certain species (McLaughlin et al. 2013). When the dam is taken away, distribution expands for invasive species, making the role of small dams on invasive species nuanced (Thoni et al. 2013).

Variability of Positive and Negative Impacts

While there are positive and negative impacts to the creation of small dams, there are important caveats to highlight. Small dams positively affect downstream communities that already experience human alteration (eg. introduction of PPCs, heavy metals, invasive species).

However, there are many negative impacts on biotic communities that have less human alteration due to habitat alterations and community changes.

Regulations

Unlike large dams that often have local, state, and federal regulations, small dams are usually unfettered by governmental control. Currently, the total number of small dams is unknown, but more than 2.5 million dams in the United States are not under any jurisdiction of a public agency (Brewitt & Colwyn 2019). One of their largest state distributions in 2008 was New York state, at 3,057 small dams counted (Provencher & Meyer 2008). This is because large dams have impacts on economics and environmental quality of the surrounding land on a large scale that both scientists and policy-makers have studied. Small dams, on the other hand, are typically on land of one landowner and viewed as only affecting one party despite downstream consequences. Internationally and within the United States, there are no consistent policies for small dams. For the United States, the rights of landowners are highly valued, so minor land and water manipulations like small dams are often unregulated. Some states have more strict regulations. For example, Delaware only regulates state and federally-owned dams regardless of size whereas Florida has a very robust dam policy that requires landowners to follow certain construction practices or undergo inspections for safety codes (Association of Dam Safety Officials 2020). Other regions in Asia are encouraging the implementation of small hydropower dams that other regions like Brazil have recognized as a deterrent to biodiversity (Couto & Olden 2018). However, any existing regulations of small dams typically focus on the human safety aspects of small dams rather than the biological effects (Pisaniello et al. 2015, Association of Dam Safety Officials 2020).

Case Study: How common are small dams and where do they occur?

Although small dams may have small, localized effects, they may disproportionately affect particular ecosystems or habitat types. Like large dams, small dam impacts are likely dependent on the context in which they occur including their commonness and relative positions in the landscape. Headwater streams (first through third-order streams) compose 75% of stream miles (Suring et al. 2020) and are high frequency locations generally avoided by construction of large dams, but headwaters are more likely to be impacted by small dams (Morden et al. 2022). Thus, the impacts of stream and river impoundment may be underestimated without an appreciation of the density and distribution of small dams on the landscape.

Why The Plateau?

The Southern Cumberland Plateau is recognized nationally as an ecoregion that retains high quality habitat, high biodiversity, and yet, is underprotected (Jenkins et al. 2015). Freshwater taxa (fishes, crayfish, etc.) in particular are recognized as having higher diversity in this region relative to any other southeastern river reach (Elkins et al. 2019). Most of the Southern Cumberland Plateau is privately-owned with large timber tracks and increasing residential development (Evans et al. 2017). Subdivision of large properties is contributing to degradation of aquatic habitat even when it is protected (Evans et al. 2017).

The Southern Cumberland Plateau is also an important region for study because of its environmental context. With shallow sandstone bedrock and steep coves draining the plateau, the

Southern Cumberland Plateau experiences high erosion rates, little soil development, and low nutrient and water retention creating streams that have highly variable hydrographs and highly flashy flows (Knoll et al. 2015). The lack of water permanency in the region potentially contributes to small dam construction to moderate annual variation in water availability for small-scale agriculture, flood control, and recreation. We have also noted in a previous study that aquatic animal performance was higher below small dams potentially as a result of the higher hydrologic permanence and less variability in flow offered below small dams (Kirchberg et al. 2016). Small dams below agricultural fields also appear to maintain high water quality for threatened and endangered species occurring in downstream reaches (e.g. Laurel Dace; Jackson & Pringle 2010).

In this case study, we sought to understand the patterns of small dams on the Southern Cumberland Plateau in a three county area of south-central Tennessee, USA (Franklin, Grundy, and Marion Counties). Specifically, we sought to describe how common small dams are to underscore the potential magnitude of effects that small dams may have at the landscape scale even when the spatial scale of their effects is limited. We documented their frequency, the proportion of stream networks impacted by small dams, and the frequency with which landowners build small dams.

Methods

We defined the study area as the surface of the Southern Cumberland Plateau and escarpment within Franklin, Grundy and Marion Counties in Tennessee, USA. We combined data from the USGS, the University of the South, and the State of Tennessee to establish the location of 2,238 small ponds within the study area. To determine the potential magnitude of impact of these small ponds on the study area, we looked at a) the proportion of the study area which drains into small ponds, b) the proportion of first-order drainages which contain at least one small pond and c) the number of properties with small ponds. Each of these analyses were stratified into the 40 HUC12 watersheds which intersected with the study area. All analyses were conducted using ArcGIS Pro version 3.0.

To determine the proportion of the study area which drains into small ponds, we used a USGS 10-meter resolution digital elevation model (DEM) to delineate the watershed draining into each small pond. Watersheds were delineated from pour points placed at the outflow of each of the ponds, which were manually adjusted until about 90% of the watersheds appeared to reflect the actual watershed of the pond. To determine the proportion of first-order drainages impacted by small ponds, we used the DEM to delineate all drainages in the study area. We then used the database of small ponds to determine how many of these drainages contained a small pond.

Results

We found 2,238 small ponds within the study area, a density of 0 to 0.22 ponds per ha (0-22 ponds/km2) with pond densities centered around rural towns particularly Coalmont, Tennessee (Figure 3). Some watersheds had nearly 50% of first-order streams impacted by small dams (Figure 4). Watersheds had 2 to 331 ponds per HUC12 watershed, which was associated with the proportion of first-order drainages in the watershed. Very few watersheds remain unimpacted in this rural region (Figure 5). Ponds were created on a range of stream sizes: some pond watersheds were very large with many contributing streams (drainage area of 8.05 km2), while other ponds were created on such small drainages that we were unable to derive a watershed using the DEM. Mean watershed areas were 4.15 +/- 0.39 km2. Within the HUC12 watersheds, up to 28% of the drainage area passed through a small dam.

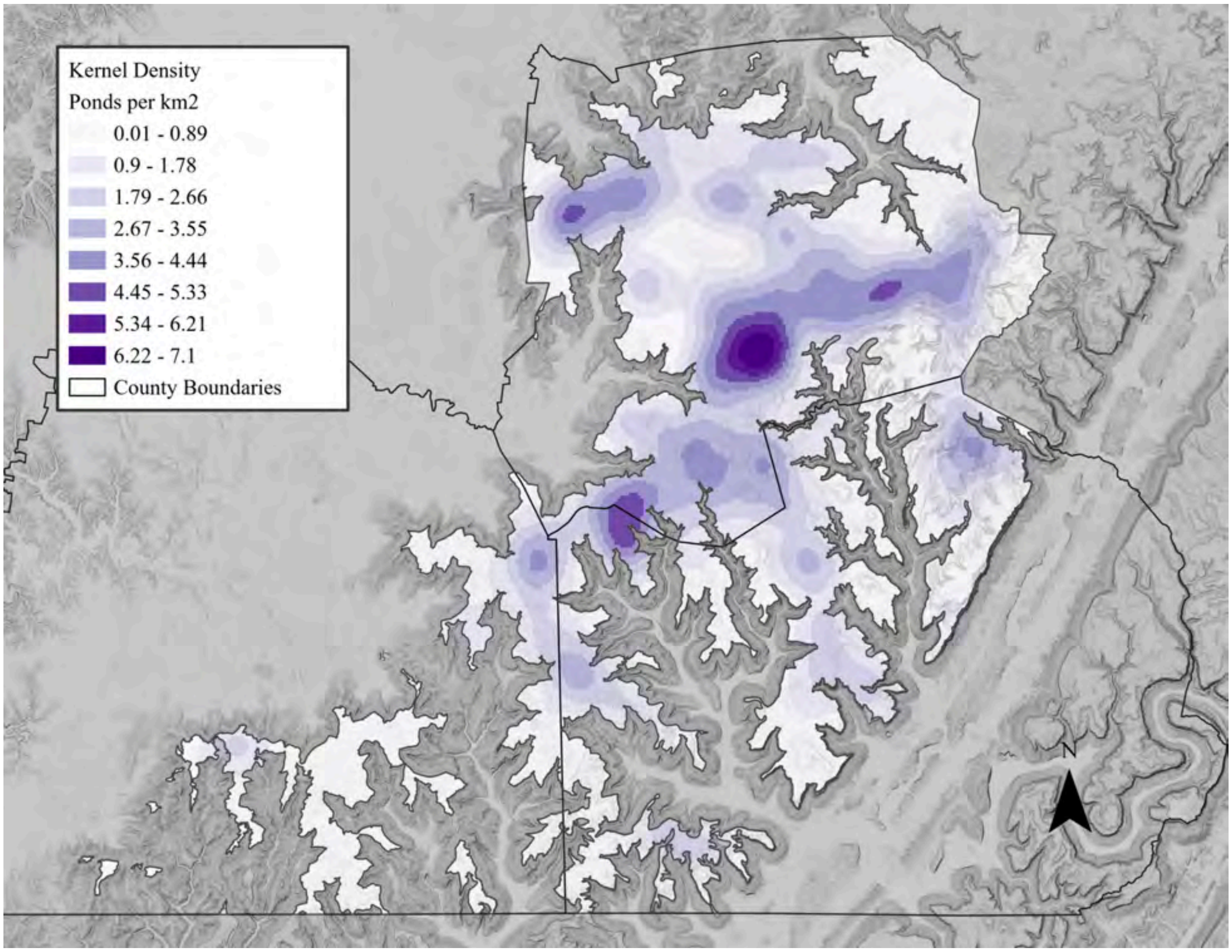

Figure 3 | Shows the kernel density of ponds per km² in three counties in Tennessee on the Southern Cumberland Plateau (Franklin, Grundy, and Marion counties).

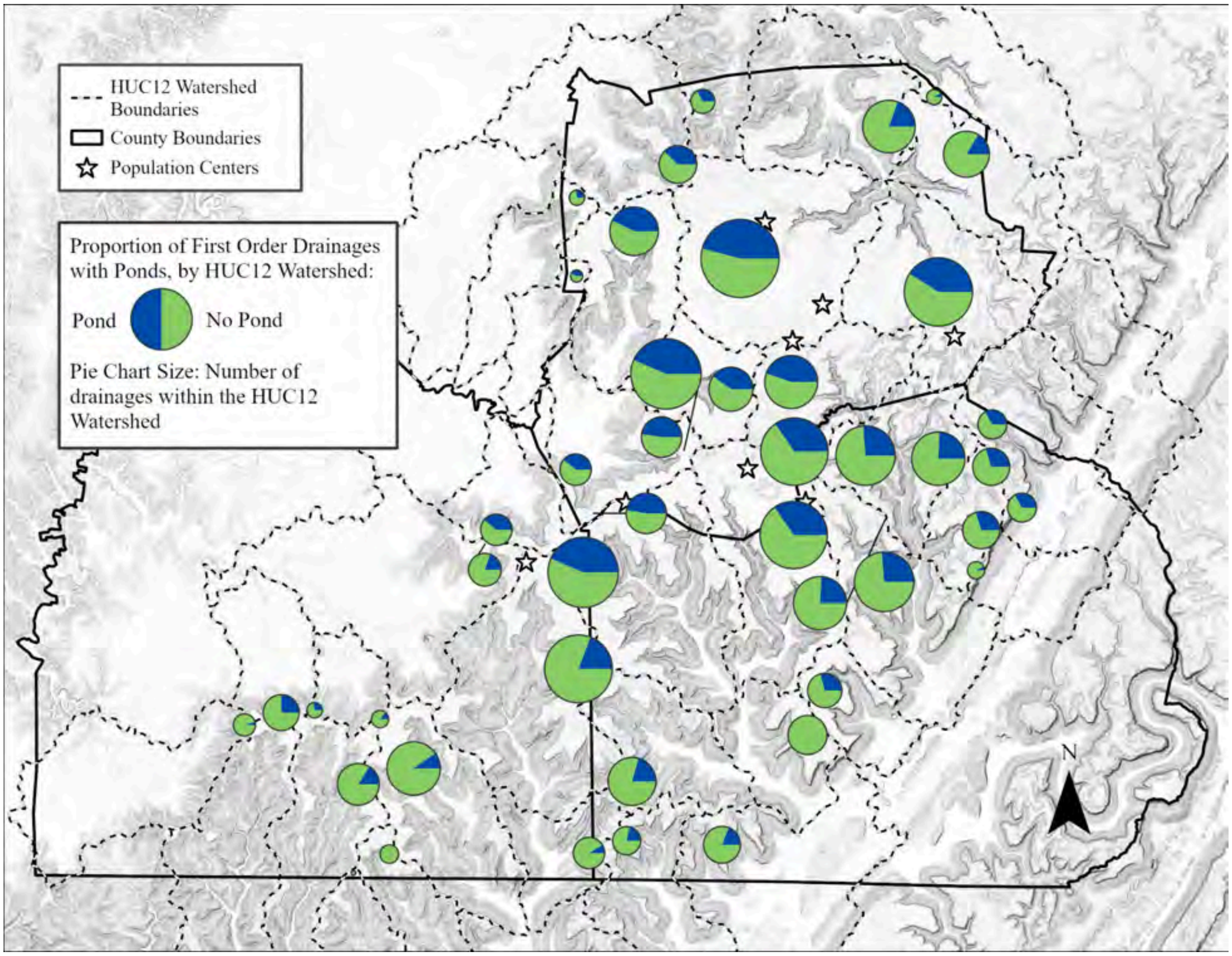

Figure 4 | Depicts the proportions of first-order drainages with ponds by HUC12 watershed boundaries and the number of drainages within the HUC12 watershed boundaries. Data was collected for three counties in Tennessee on the Southern Cumberland Plateau (Franklin, Grundy, and Marion counties).

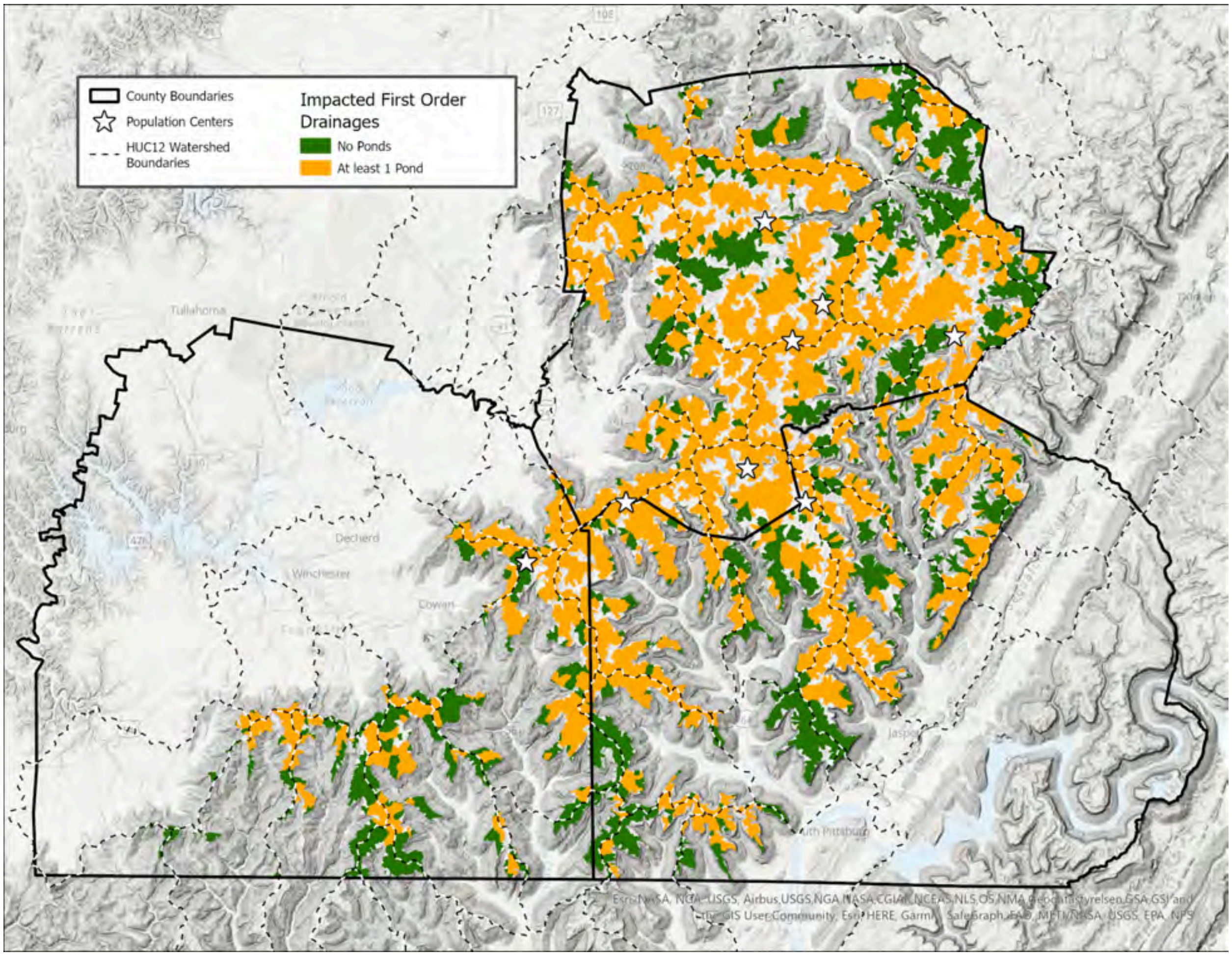

Figure 5 | Illustrates the first-order drainages impacted by at least one pond or no ponds by HUC12 watershed boundaries. Data was collected for three counties in Tennessee on the Southern Cumberland Plateau (Franklin, Grundy, and Marion counties).

Discussion

With nearly 50% of headwater streams impacted by small ponds on the Southern Cumberland Plateau, it is clear that few locations can escape the impacts of small dams. This finding is congruent with reports from other areas in the midwest and northeast with densities of 0.2 - 0.6 dams/km2 (Ayalew et al. 2017, Emerson & Dahl 2005). Even at lower densities than other locations, high proportions of headwater streams are being affected, and these densities tend to be associated with higher density human communities. Because rural areas are not typically associated with high proportions of impervious development, these ponds are most likely constructed for recreational and aesthetic purposes (Mioduszewski 2012). The distribution and impact of small ponds should be considered during assessment of habitat quality. Very few watersheds in the area assessed remain unaffected by small ponds, and many of these ponds occur in the headwaters of protected state parks and state natural areas. Thus, protected areas in this ecoregion may protect aquatic systems that have considerable upstream impacts and may even promote invasive species introductions to downstream protected areas (Johnson et al. 2008). Determining the overall impact of small dams in these areas requires understanding the suite of downstream conditions that they influence.

Small dams have already been known to impact stream communities in the Southern Cumberland Plateau. There has been previous documentation of increases to Fe and Mn downstream of small dams on the plateau (Eastridge et al. 2008 unpublished) as well as seasonal changes in temperature and dissolved oxygen in reservoirs, which in turn, are likely to affect downstream communities (Benton et al. 2007 unpublished, Voitier et al. 2007 unpublished). Small dams on the Southern Cumberland Plateau have been affected by changes to community distribution of salamanders after the installation of a small dam (Kirchberg et al. 2016). Likewise, invasives have been noted to persist in and below reservoirs (Wells et al. in press). Further research is needed to document all of the dynamics in play below small dams on the Southern Cumberland Plateau. Based on the dynamics described in the biotic impacts and abiotic impacts, similar scenarios may be probable. Further research for the area needs to center around sedimentation, PPCs, and other biotic groups (eg. riparian plants, crayfish, etc.).

Remaining questions

Are all species negatively affected by small dams?

Even if the downstream effects of dams on habitat are limited, if keystone species are negatively impacted, they may have larger effects than anticipated. For example, Almon et al. (in review) documented that the community nest building fish, the river chub (*Nocomis micropogon*), are most negatively affected by low flow whereas a benthic darter was most negatively affected by substrate changes. The decline of river chub below small dams could result in community wide declines if they are no longer present to construct and defend communal nests. Identifying ecotypes or groups of species that are more sensitive or less sensitive will be helpful for understanding contexts in which small dam removal may be particularly beneficial (Poff & Hart 2002).

Secondly, biphasic species that require high quality aquatic and terrestrial habitat may be impacted differently than species that are obligately aquatic. As adults, species whose larvae use streams versus ponds for development may compete in the terrestrial environment as new species colonize the area to take advantage of the impounded habitat. Alternatively, the downstream populations of stream salamanders may become severely limited if they are no longer receiving immigrants from upstream populations when larvae are displaced downstream.

Finally, because small impoundments often receive introductions of game fish, their downstream escape may allow these species to bypass previously established environmental filters creating new communities of fish. For example, Culp et al. (2023) used Tennessee Dace as a proxy species for the imperiled Laurel Dace and found that although small dams upstream of their native habitat were capturing sediment from small family farms, they were allowing the introduction of sunfish. Although the authors did not find strong competitive interactions between similarly sized fish, their field observations suggest that larger individuals in pools were predating on Laurel Dace and increasing their imperilment.

Can small dams have environmental benefits?

Small dams have been constructed for a variety of purposes, but when they are constructed for mitigation purposes, it would be useful to know how effective they are at reducing downstream impacts and over what spatial and temporal scale. Secondly, many view small impoundments as advantageous for the ecosystem. Although they support different biological communities, it is unclear whether they replace and enhance regional diversity in a similar manner to ponds constructed through natural processes like beaver dams or oxbows ponds. As beavers return to areas where they were previously extirpated, we do not know how they will interact with these new networks of small ponds, but anecdotal evidence suggests that they will readily inhabit established ponds using natural instincts to block spillways. This latter action could compromise the integrity of these small dams if beaver activity is left unchecked.

Another question to address is whether small dams could be effective as a climate mitigation technique (Ho et al. 2017). They retain water in a system to help moderate extremes in variation including both too much and too little water. Understanding the urban to rural context of small dams would also be helpful for characterizing the differential effects that they may have on downstream ecosystems. The cost-benefit analysis of small dams may depend on this context, and recommendations for removal or repair may depend on their context (Poff & Hart 2002, Provencher & Meyer 2008).

What are the cumulative effects of small dams?

If small dams interfere with the flow of even 25% of headwater streams nationwide and even episodically alter downstream flow, the cumulative effect of these dams on downstream ecosystems may already have resulted in modified flow regimes that are on par with those induced by large dams (Morden et al 2020). Furthermore, understanding the spatial scale of their impacts and if there are any network-scale effects of multiple dams would be helpful for identifying potential policies related to the prevalence and distribution of small dams on the landscape. Likewise, as removal policies emerge for large dams, they are likely to trickle down to small dams, so more removal studies of small dams would be helpful for determining the value of these actions for the future.

Conclusions

Although large dams have received considerable attention, the widespread nature of small dams and the large diversity of their impacts warrants additional attention to small dams as a landscape feature. It is also clear that small dams can serve multiple purposes that can have both positive and negative environmental impacts. Their small scale and occurrence in habitats that have ambiguous standing under most U.S. and international environmental regulations strongly contribute toward being overlooked by environmental regulatory organizations (Association of State Dam Safety Officials 2020, Morris et al. 2019) . Likewise, in the U.S., they regularly exist within a single property limiting potential legal challenges (Couto & Olden 2018). Identifying the contexts in which small dams can and should be built should be a priority. This information could also be used to build recommendations for when small dams should be removed for the maximum impact.

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Photos from figure 4 were taken from:

linquip.com/blog/run-of-the-river-hydroelectricity

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https://www.seeleylake.com/story/2018/07/05/news/small-dams-in-small-creeks-can-have-big-consequences/3753.html

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Supplemental Information

Do habitat changes downstream of small dams have consistent effects on the body condition of Nocomis micropogon (River Chub) and Nothonotus rufilineatus (Redline Darter)?

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Abstract

The increasing prevalence of small dams (<5m) has altered downstream flow and sediment regimes of many low order streams, which negatively affects habitat for the biological community. Small dams may have varying effects on fishes that are dependent upon species-specific habitat associations and body plans. The objectives of this study were to quantify the effects of habitat modifications due to small dams on the body condition of two lotic fish species of the southeastern U.S.—a benthic species, Nothonotus rufilineatus (redline darter) and a limnetic species, Nocomis micropogon (river chub) using body index. Large ex-situ indoor stream mesocosms were used to replicate the flow and substrate conditions in normal stream conditions and conditions below a small dam. Flow and substrate treatments were implemented in combinations to clarify which effect was stronger. We observed species-specific differences in responses to conditions to mimic habitat downstream of a small dam. Nothonotus rufilineatus had the highest body condition with low flow and complex substrate. In contrast, N. micropogon had similar body conditions in all treatment levels but had the lowest body condition in the simple substrate and normal flow treatment. We may infer that substrate may be the limiting factor for both species because of the way it interacts with flow. Complex substrate alters the velocity of streams and provides interstitial spaces for the benthic N. rufilineatus, whereas deeper, less turbulent water increases ease of movement among pools for the larger, more mobile N. micropogon. Although the effects of large dams on native fauna are nearly always negative, the influences of small dams on downstream biota are nuanced and dependent upon the species and magnitude of habitat change. Small modifications to dam construction protocols could restore sediment balance to downstream ecosystems and minimize the potential negative effects of flow modification.

Keywords: aquatic, dams, freshwater fishes, hydrology, lotic, stream flow, stream morphology, substrate, water column, velocity.

Introduction

Most of the dams in the world are relatively small at <5m in height (Poff & Hart 2002), and have obvious biological impacts that have been previously described about changes to dispersal and gene flow through fragmentation (Jannson et al. 2000, Perkin et al. 2015), as well as community change (Metts et al. 2001, Dana et al. 2011, Zhou et al. 2008, Hicks & Reeves 1994) as a result of this barrier. However, habitat alterations due to changes in abiotic factors have been described less frequently (Gangloff et al. 2011, Kirchberg et al. 2016). This poses an issue to aquatic biodiversity because while the immediate effects of small dams are spatially constrained, the commonness of small dams in watersheds suggest that even small effects on biota could accumulate to have much larger effects on populations or metapopulations (e.g. Kirchberg et al. 2016, Zeidel et al. 2021, Januchowski-Hartley et al. 2013). Two abiotic factors that change due to the addition of small dams are flow and substrate, both of which can affect key habitat parameters of organisms in downstream communities (Johnson et al. 2008, Wu et al. 2009, Abernethy et al. 2013, Kirchberg et al. 2016, Dare et al. 2020). These two factors are closely related to each other and interplay off of each other to affect body condition of fish that use the benthic or limnetic areas of streams.

Flow

Small dams affect flow downstream by creating a steady baseflow and slight seasonal differences with the reliance of overflow releases. These structures are often built with clay and other porous natural materials as opposed to cement (United States Department of the Interior 1987). This allows for some seepage through the material, as well as over the dam itself. Some of the effects of small dams on flow are likely seasonal because water is captured in dry periods and released in wet periods (Poff & Hart 2002). However, the nature of the structure's porosity and overflow release allows for greater downstream seepage and a somewhat stable base flow over the span of all seasons, even during the driest periods of the year. In general, low flow is maintained after a small dam is installed (Kirchberg et al. 2016).

Changes in flow can affect the way that benthic and limnetic fish interact with their environment by impacting energy efficiency (Benseng et al. 2022), predation and competition events (Hart & Finelli 1999), dispersal (Abernethy et al. 2013, Dare et al 2020), and food acquisition (Vanderpham et al. 2013). Benthic fish can have morphological traits that give stability and hold them in place with high flows compared to limnetic fish, which can affect the amount of energy needed to stay in one place (Benseng et al. 2022). An increase to competition and predation can occur due to continuous interaction with other individuals in the case of lower flows (Hart & Finelli 1999). Flow can also affect dispersal of food items and ability of organisms to find them within a stream. High flows have the ability to disperse food more rapidly, which may decrease the ability of organisms to find it because cues like scent may not be present for quick actions like this. Feeding behavior due to flow also is impacted by what type of feeder the organism is. Flow patterns may affect where the food is able to settle or if it can settle at all, thus limiting the availability of food for certain species, primarily benthic fish (Vanderpham et al. 2013).

Substrate

By maintaining low flow and buffering high flows, small dams starve the downstream habitat of sediment and consistently reduce the variability and habitat heterogeneity associated with headwater streams (Hicks & Reeves 1994), thus affecting fish populations. Reductions in this variability and elimination of sand and silt move streams from having heterogeneous substrates towards substrate dominated by bedrock that has few interstitial spaces or locations where organic material is trapped and stored. Instead, the stream has a homogenized surface layer that is coarser than the fine bed material trapped beneath it and protected from the flow of the stream (Nilsson et al. 2000, Jolly et al. 1993, Maavara et al. 2020).

Substrate likewise affects fish communities, particularly energy efficiency, habitat acquisition, predation and competition, and ability to find food. With complex substrate, there is an increase in mosaics of flowing water and turbulent kinetic energy that a fish can use for migration. However, this can also require more energy to remain in one place. To minimize energy expenditure, small species can take advantage of scoured bedrock and smaller substrates for refuge from high flow due to size and morphological traits. The absence of cobble or large boulders can inhibit the ability of larger species to find refuges from high flow and predation (Hart & Finelli 1999). Likewise, morphology of limnetic fish may not prevent the organism from being dislodged from substrate as well as benthic species. Energy exertion is unique for every individual. Fishes are not only directly impacted by shifts in substrate, but also indirectly as prey production decreases with entire stream productivity declines (Maavara et al. 2020).

The loss of accumulated organics and consumers of those materials could have stronger impacts on benthic fishes unable to forage in other areas of streams and rivers (Kawanishi et al. 2015, Henley et al. 2000).

Objectives

Our objective was to experimentally evaluate the change in body condition of a large limnetic fish (River chub, Nocomis micropogon) below dams and in natural conditions relative to a smaller benthic fish (redline darter, Nothonotus rufilineatus) by changing the sediment regimes and flow regimes in an artificial stream to simulate these conditions. Using a set of large, ex-situ mesocosms, we manipulated flow to have low or normal base flow and substrate to reflect a natural sand, cobble, and boulder substrate or a scoured simple channel with large boulders and tiles to simulate exposed bedrock. We evaluated the change in body condition of N. rufilineatus and N. micropogon after being reared in each combination of flow and substrate using a body condition index. In doing so, we were able to evaluate whether there are species-specific responses to small dams and if there are particular habitat features that must be addressed to minimize the downstream effects of small dams.

Methods

Species assessed

Nocomis micropogon (river chub) were chosen for the experiment because they are a common limnetic fish in rivers of the Eastern United States that occupy a large array of different habitats. They occupy open fast-flowing water, even as young-of-year (Latchner 1950). Adults mainly eat aquatic insects (Werner 2004) in the water column. River chubs grow to be up to 18.9 cm standard length for males and 12.7 cm standard length for females (Boschung et al. 2004) on average.

Nothonotus rufilineatus, formally classified as Etheostoma rufilineatum (Near et al. 2011), grow to be 7.5 cm in standard length (Kuehne & Barbour 1983) and are found in the Cumberland and Tennessee river drainages. They prefer swift sections of riffles as adults and small cobble areas close to the banks when they are young-of-year (Stiles 1972). Nothonotus rufilineatus are found under and around rocks in riffles, feeding primarily on Dipteran larvae that live in the substrate (Widlak & Neves 1985). With simple substrate and higher flows, the processes of feeding and maintaining positions in the mesocosm are disturbed for N. rufilineatus, which makes the abiotic changes important when assessing body condition.

Hypothesis

Thus, we hypothesized that river chubs would be able to adapt to changes in flow and substrate better than redline darters because the redline darters live in riffles that need substrate.

Experimental design

Mesocosms

Four independent and identical mesocosms were constructed inside the Tennessee Aquarium Conservation Institute by bolting together seven fiberglass tanks (Figure 1). All tanks were waterproofed and insulated with half inch insulation to minimize temperature changes. The mesocosms were constructed between two sump pools to minimize turbulence in flow at the beginning and end of the mesocosms. Each of the habitable zones included three pools (58 cm diameter and 60 cm deep) connected by two rectangular riffles (140 × 47 × 39 cm) that the fish were able to move between. The entire length was covered in window screen to prevent the fishes from escaping. The openings to the sump were also covered in window screen, which prevented the fishes from leaving the mesocosm and assisted with filtration of organic matter and buffered turbulence from the pumps.

Controls and Maintenance

By using indoor mesocosms, certain abiotic factors were controlled throughout the experiment so that the two factors that changed body index would be flow and substrate. The sumps housed a heat exchanger to minimize the effect of the heat generation of the pump and maintain mesocosm temperatures between 20.6 and 21.7℃. Airstones were placed in the sump as well, to keep dissolved oxygen content levels suitable for aquatic life. Biological filtration was sufficient to control water quality in the natural substrate treatments, but we added a mesh bag full of bio balls (28 × 39 × 13 cm) to one of the sumps in simple substrate treatments to provide extra biological filtration and maintain the same nutrient transportation. Water quality (e.g. nitrite, ammonia, pH, temperature and dissolved oxygen) were assessed weekly and kept similar to one another. Algal overgrowth was contained by mechanically removing it from the walls with sponges weekly with no more than one habitat unit (riffle or pool) being disturbed on any day. The building has natural and artificial lights, which were on a timer that followed diurnal light cycles. Feeding was done by spreading the food, bloodworms, throughout the mesocosm based on the weight of fish that were present. Riffles and pools got bloodworms that settled to the bottom of the tank or floated in the water column depending on flow and substrate present in the system.

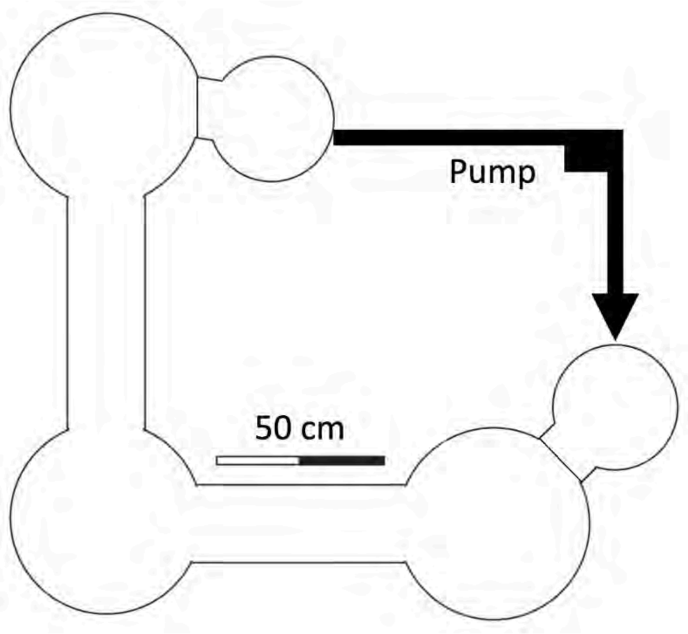

Figure 1 | Design of one of the four independent and recirculating ex-situ stream mesocosms located at the Tennessee Aquarium Conservation Institute in Chattanooga, Tennessee, USA. The mesocosms are located indoors where temperature, flow, substrate, and photoperiod can be manipulated.

Figure 2 | Shows a picture of the *ex-situ* stream mesocosms located at the Tennessee Aquarium Conservation Institute in Chattanooga, Tennessee, USA.

Flow

To create flow that simulated conditions similar to those found in normal streams and those downstream of dams, water was manipulated in two ways—by changing the depth and current velocity. The depth of the water with low flow was maintained at a depth of 8.9 cm in the riffles, while normal flow was maintained at a depth of 12.5 cm. The current velocity was also manipulated so that normal flow had an increased velocity compared to low flow (Table 1). Flow was higher at normal flow and simple substrate than normal flow and complex substrate due to the way that the substrate directed flow (Table 1). Velocity measurements were more variable between substrate treatments but were consistently higher at normal flow (Table 1). We used a conservative flow rate compared to some in-situ circumstances (Skalak et al. 2009) due to the capabilities of the pumps to create high current velocities for long periods of time. However, this experiment still mimics conditions created after a small dam.

Flow	Substrate	Flow (L/min)	Pool velocity (cm/s)	Riffle velocity (cm/s)
Low	Simple	6.8 ± 1.4	0.079 ± 0.006	0.158 ± 0.018
Low	Complex	7.7 ± 1.3	0.085 ± 0.008	0.205 ± 0.015
Normal	Simple	19.0 ± 7.9	0.214 ± 0.080	0.221 ± 0.015
Normal	Complex	13.6 ± 2.8	0.137 ± 0.022	0.241 ± 0.015

Table 1| Flow characteristics of ex-situ stream mesocosms maintained at high and low depth combined with simple or complex substrate to mimic changes in flow downstream of small dams.

Substrate

Substrates used in the mesocosm depended on which treatment was being simulated, either complex or simple. Normal streams were replicated using complex substrate, while downstream dammed conditions were replicated using simple substrate to simulate bedrock. Complex substrate, seen in figure 3a, was constructed by adding sand and medium to coarse gravel (Wolman, 1954) in all the pools and riffles. Cobble (between 6.4 and 25.6 cm) was added to the riffles with three to four medium cobble (~10 × 10 × 10 cm) added to vary the flow directions. Simple substrate treatments, seen in figure 3b, did not receive any sand or pea gravel (Wolman 1954). Riffles were created by setting four stacks of tiles (30 × 30 × 1.27 cm) in a grid for the length of the riffle. The number of stacked tiles varied between one and three tiles to simulate different depths and cracks observed in exposed bedrock. All pools in both substrate treatments received five small boulders (~ 20 × 20 × 20 cm; Wolman, 1954).

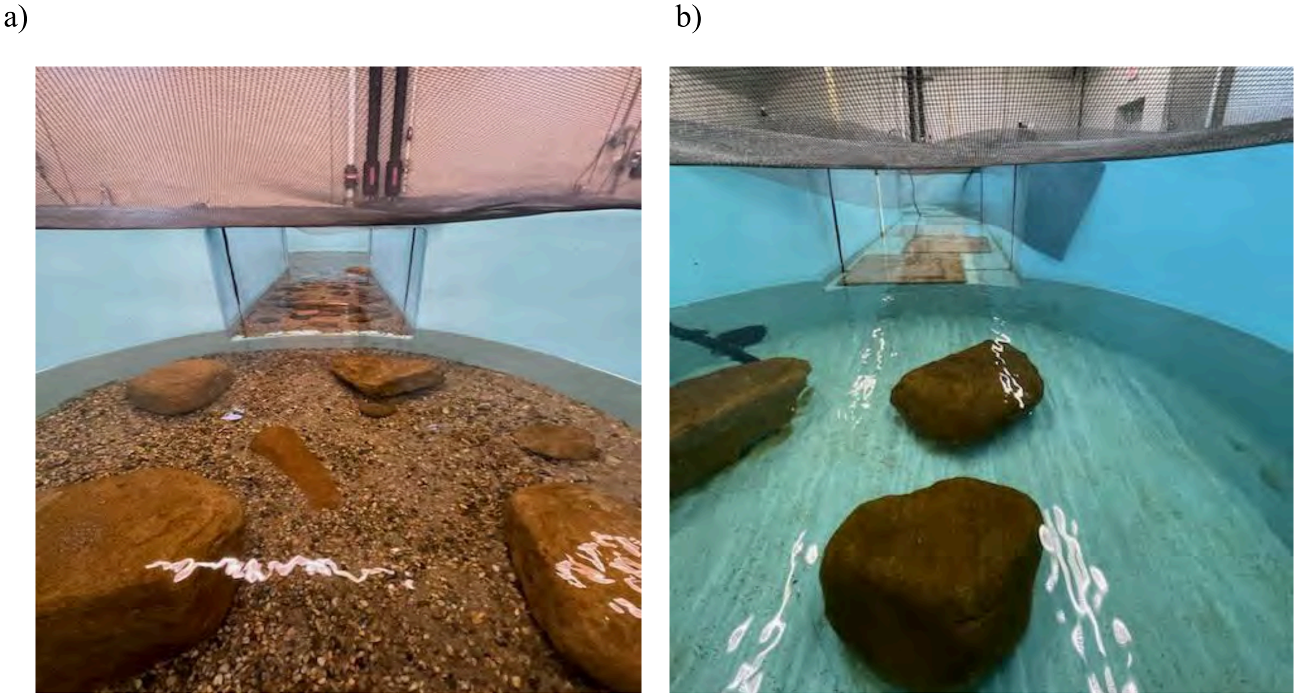

Figure 3 | Shows the two types of substrates used in the *ex-situ* stream mesocosms, a) complex and b) simple (Tennessee Aquarium Conservation Institute in Chattanooga, Tennessee, USA).

Species collection and placement

Nocomis micropogon and N. rufilineatus were collected from South Chickamauga Creek in Indian Springs, Georgia (34.9776803, -85.1458568). Sixteen N. micropogon and 40 N. rufilineatus were collected at the start of the experiment. Fishes were measured for standard length (mm), weighed (g), and given unique identifiers using visible implant elastomer. The large mass differences between our two focal species required that we initially stock mesocosms at different densities with four N. micropogon and ten N. rufilineatus per mesocosm.

We performed four replicates of each treatment level—low flow with simplified substrate, low flow with complex substrate, normal flow with simple substrate, and normal flow with complex substrate— that each lasted 42 days per replicate. The experiment, with all four mesocosms running simultaneously, was performed from the middle of 2021 to early 2022. After each replicate, the fishes were weighed and measured to assess changes to their body index. Then, the individuals were randomly distributed back into treatments for the start of the next replicate. The same fishes were used throughout the experiment except in cases of mortality where individuals were replaced between replicates. The replacement individuals were also collected from the South Chickamauga Creek and stored in an extra tank and fed bloodworms until needed. In the case of mortality, the individual was removed from analysis for that replicate. Treatments were randomly assigned to a particular mesocosm and maintained in that mesocosm for the length of the experiment while fishes were moved among the mesocosms.

Analysis

We first assessed variation in survival among the treatments using an ANOVA. To assess change in body condition, we used morphometric measurements of standard length and mass at the beginning and end of each round of the experiment to calculate the difference in body condition between the beginning and end of each replicate. Body condition was calculated using the scaled mass index as a good estimate of body fat for small vertebrates (SMI or body condition; Peig & Green, 2009). We used the change in body condition (SMI) as the response variable in a linear mixed model evaluating the fixed effects of species identity, substrate, and flow. As random effects, we included individual identifiers, replicate (N = 4), and experimental system (N = 4). Tukey post-hoc comparisons were evaluated using package emmeans in R (Lenth, 2022).

Results

Mortality

We observed no mortality of N. micropogon throughout the experiment whereas our average mortality rate for N. rufilineatus was 21.3 ± 3% for each round of the experiment of which 77 ± 7% of mortality events came from the treatments with normal flow and simple substrate. Overall, survival of N. rufilineatus was negatively affected by channel simplification ($F = 5.38$, $df = 1, 12$, $p = 0.040$), but neither flow nor an interaction of flow and substrate affected their survival ($F \geq 0.582$, $df = 1, 12$, $p \geq 0.460$; Figure 2).

Body Condition

The linear mixed model evaluating body condition revealed small and balanced residuals with our model structure. We observed a significant three-way interaction between species identity, substrate, and flow (Table 2).

For N. micropogon, individuals maintained a similar body condition in treatments in combinations of low flow and complex substrate or normal flow and simple substrate, whereas individuals grew in low flow-simple substrate and normal flow-complex substrate combinations. Increase in body condition was 55 times higher in low flow-simple treatments and normal flow-complex substrate treatments relative to low flow-complex substrate and normal flow-simple substrate treatments. Variability in N. micropogon body condition was higher than that observed for N. rufilineatus, however, no significant pairwise differences were observed among treatments in N. micropogon (Figure 3A; $t \geq 2.06$, $p \geq 0.187$).

For N. rufilineatus, individuals generally had limited growth except for treatments with complex substrate and low flow. When complex substrate was available, their body condition increased more in low flow treatments compared to normal flow treatments (Figure 3B; $t = 3.73$, $p = 0.002$). Likewise, at low flow, individuals had increased body condition when complex substrate was available (Figure 3B; $t = 3.45$, $p = 0.042$). Relative to all other treatments, the body condition of N. rufilineatus was 7.25 times higher at treatments with low flow and complex substrate.

Variable	F	df	p
Species	11.36	1, 126	<0.001
Substrate	0.51	1, 126	0.475
Flow	0.15	1, 126	0.703
Species x substrate	0.09	1, 126	0.764
Species x flow	0.63	1, 126	0.427
Substrate x flow	11.30	1, 126	<0.001
Species x substrate x flow	16.06	1, 126	<0.001

Table 2 | Statistical outcomes of linear mixed models evaluating how species, substrate, and flow affected the body condition of fish in ex-situ stream mesocosms simulating conditions in natural streams and those below small dams.

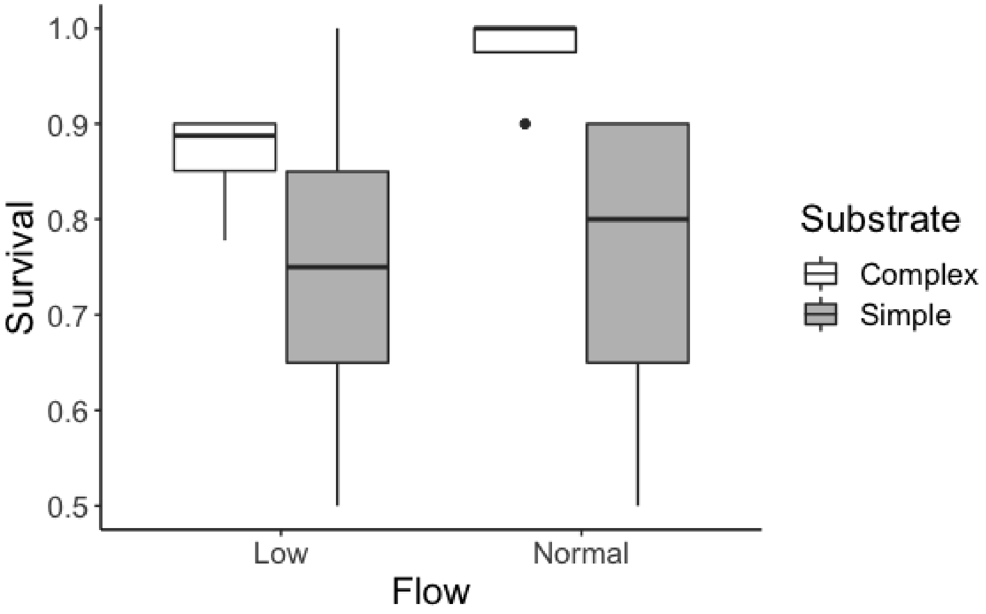

Figure 2 | Mean survival rates of *Nothonotus rufilineatus* in *ex-situ* mescosms with variation in flow and substrate. Twenty individuals died during the experiment and were replaced (x=16).

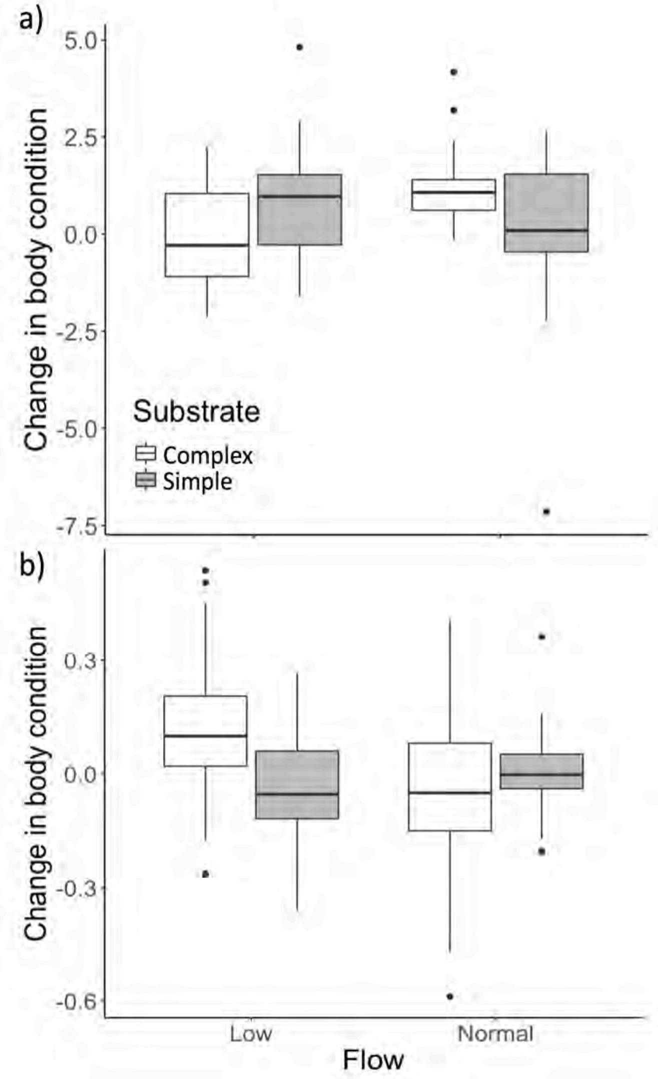

Figure 3 | Mean change in body condition (scaled mass index) of *N. micropogon* (A) and *N. rufilineatus* (B) in *ex-situ* stream mesocosms. Four *ex-situ* stream mesocosms were set to two different flow regimes and two different substrate types, and fishes were observed in groups of between eight and ten *N. rufilineatus* and four *N. micropogon* in each of four replicates of each treatment (x=16).

Discussion

Small dams are a widely used tool for water management throughout the United States that cause unintended changes to abiotic conditions downstream, thus affecting the performance of downstream fish populations (Wood & Armitage 1997). However, the changes that these populations experience appear to be species-specific, and the scale of these effects is unknown.

River chub

N. micropogon exhibited a response to the interaction between substrate and flow with the highest body condition increase under simulated undisturbed conditions of normal flow and complex substrate, but also exhibited the lowest body condition under low flow and complex substrate. This being said, there was not any significant difference between any of the treatments. We attribute this to the river chub's ability to tolerate high velocities in their particular habitats—pools (Almon observation). Pools were less altered compared to the riffles, as well, giving N. micropogon a greater habitat for hiding from high water velocities.

Redline darter

Alternatively, N. rufilineatus exhibited high body condition increases at low flow and complex substrate and low body condition at low flow with simple substrate and at both normal flow treatments. We attribute this to less cover from water velocity in simple substrate mesocosms. In the simple substrate mesocosms without sand, gravel, and cobble, N. rufilineatus was small enough to use refuge offered by the tiles in the treatments, but habitat was less available compared to complex substrate mesocosms. We also observed similar survival rates of N. rufilineatus in mesocosm without complex substrate regardless of flow, but we noted that mortality was higher in simple substrate treatments relative to mesocosms with complex substrate. Thus, the ultimately lower density of N. rufilineatus in normal flow mesocosms may have allowed them to access increased food resources relative to individuals in other treatments and increase their body condition because of decreased intraspecific competition.

Overall

In both instances, it appears that interactions between flow and substrate drive fish body condition, and that each species has likely optimized different combinations of flow and substrate. In addition to variation in habitat requirements between the two species, they also differ in size and locomotion that may contribute to variation in their responses to flow heterogeneity. Finally, we also caution that the ex-situ conditions in this study cannot replicate all the changes that occur downstream from small dams, and therefore, this study likely represents an underestimate of the changes potentially observed downstream of small dams (Matthews et al. 2006).

Growth within short-term experiments is ultimately a result of food intake and energy expenditures, as maintenance of a fish's position in the stream requires constant upstream movement to counterbalance drift from downstream flow. The stronger the flow or minimization of refuge offered from the flow, the higher the energy expenditures by fishes to maintain their position in the channel. However, the body size and geometry differences of the two species in this study may have contributed to variation in how they respond to substrate differences.

Some fish are known to be able to swim in habitats with higher velocity, like N. micropogon, because of their body shape. Others, like N. rufilineatus seek shelter from high velocity flow (Bensing et al. 2022). In the simple substrate mesocosms without sand, gravel, and cobble, N. rufilineatus was small enough to use refuge offered by the tiles in the treatments without substrate that would have been too small for N. micropogon to use. However, because N. micropogon spent their time using the pools (Almon, personal observation), differences in refuge availability in the riffles may not have strongly influenced their body condition other than to limit their likelihood of moving among the pools. Alternatively, a smaller body size in N. rufilineatus may mean that the normal flow treatments required considerable energy to move upstream relative to the larger body size of N. micropogon. We observed similar survival rates of N. rufilineatus in mesocosm without complex substrate regardless of flow, but we noted that mortality was higher in simple substrate treatments relative to mesocosms with complex substrate. Thus, the ultimately lower density of N. rufilineatus in normal flow mesocosms may have allowed them to access increased food resources relative to individuals in other treatments and increase their body condition because of decreased intraspecific competition.

Mortality

We observed high mortality in N. rufilineatus, compared to no mortality of N. micropogon. Although there were treatment level effects associated with normal flow and the absence of refuge in simple substrates, it does not explain why N. rufilineatus mortality was common across all replicates. Capturing, moving, and measuring small fishes can be stressful and may contribute to higher mortality of the smaller species. Likewise, even small fishes can be close to senescence. Nothonotus rufilineatus usually do not live past age class III. It is estimated that females survive for three years and males for four years. The annual survival rate for males past age class II was estimated to be 0.28 (± 0.003) and 0.03 (± 0.001) for females (Widlak & Neves, 1985). Thus, N. rufilineatus were more likely to experience mortality because of shorter life spans relative to N. micropogon. Identifying fish species that are less sensitive to repeated handling is important for designing and testing hypotheses in ex-situ mesocosms to minimize impacts on native populations.

In addition to the physical effects of higher velocity flow, substrate also contributes to creating or minimizing flow turbulence. Flowing water over simple substrates is likely to result in laminar flow that may affect how prey and other resources move through streams and the mesocosms (Charlton 2008). Without turbulent flow associated with gravel and cobble in the substrate, the bloodworms offered as food moved through the mesocosm differently. In the mesocosms with simple substrate, bloodworms that sank into the cracks between the tiles were unlikely to be remobilized and transported downstream to the pools where N. micropogon occupied. This meant that bloodworms were easily available to N. rufilineatus in riffles, particularly at low flow. Feeding on sequestered bloodworms may be similar to consumption of fly larvae that burrow into substrates in-situ. This pattern could provide another explanation for why N. rufilineatus had increased body conditions in a simple substrate treatment.

Mesocosms/Experimental Design

Experiments using ex-situ mesocosms offer many opportunities to isolate the effects of environmental factors. However, limitations of experimental design can limit inferences for in-situ outcomes (Skelley 2002, Matthews et al. 2006). First, larger fishes like N. micropogon cannot be stocked at the densities of smaller fishes, reducing the sample sizes necessary to understand variability associated with their body condition in response to the experimental conditions. In three of four treatments in this study, one or more individuals was statistically an outlier making it difficult to assess trends in body condition. Secondly, changes below dams in-situ often have multiple consequences with changes to local nutrient and temperature regimes in addition to flow and sediment regimes (Maavara et al. 2020, Casserly et al. 2021, Zaidel et al.

2021). In most river systems, low flow occurs during the summer and fall when temperatures are warm, and shallower depths result in warming of the habitat (Charlton 2008, Grecequet 2023). Thus, the effects we observed in this study may only be seasonally relevant. Finally, another confounding factor was that we only observed growth during short windows of the year. Nocomis micropogon is often considered an ecosystem engineer that constructs and maintains spawning habitat for a number of co-occurring species, but they build these nests from cobble and gravel substrates (Etnier & Starnes 1993). In the absence of these substrates below small dams, successful recruitment by N. micropogon may be limited and was a response that was not assessed in this study that could intensify N. micropogon responses to small dams.

Takeaways

The diversity of ecological types in headwater fish communities indicates that they will not respond uniformly to changes in flow and substrate associated with small dams. In this experiment, we observed shifts in fish body condition that depend on the specific downstream effects on flow and substrate, but we do not have concomitant data to determine the magnitude of effects of small dams, how far downstream these effects may persist and, therefore, how meaningful these impacts are to the overall ecology and success of headwater fishes through manipulation of downstream habitat. Small dams may have other impacts like facilitating invasions of non-native fishes (Taylor et al. 2001, Smith & Mather 2013) or blocking upstream migration (Jackson & Pringle 2010), but their downstream effects on headwater fishes communities may be spatially limited and context-dependent. Headwater fish communities host a diversity of sizes, habitat uses, and habitat or diet specificities, and they may all respond differently to small dams. More research is needed in-situ to identify characteristics of potentially sensitive species or life stages before pursuing more manipulative research to understand the mechanisms behind the effects of small dams on downstream fish communities.

Implications for Conservation

Small dams could have context and even seasonal-level differences in their downstream effects, but even when simulated as a consistent and extreme effect on flow and substrate in mesocosms, the effects on fish growth were small. Furthermore, the positive effects of small dams downstream of land-use change to catch sediment and toxic substances may outweigh the potential negative effects to stream biota (Jackson & Pringle 2010). Our study confirms the results of others that although small dams alter downstream conditions, they may only have marginal and short-term impacts or even positive effects on downstream biota (e.g. Gangloff et al. 2011, Kirchberg et al. 2016). In fact, it may be possible that small dams are restoring the function of beaver dams in regions where beavers were largely extirpated (Grudzinkski et al. 2021). The present study suggests that if complex substrate can be maintained in downstream reaches, changes in flow below small dams could be potentially mitigated. We recommend in-situ studies to evaluate if revisions to dam construction could consider strategies to maintain sediment delivery to downstream reaches. For example, riprap could be used to simulate large in-stream substrate, and construction could create pathways to direct terrestrial erosion to increase sediment delivery to downstream reaches in addition to dam spillways. More research on the specific parameters of these changes could transform our ability to implement headwater dams with minimal downstream impacts.

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