

INTRASPECIFIC VARIATION AND THE LEAPING ABILITY OF NORTHERN PIKE (*ESOX*
LUCIUS): IMPLICATIONS FOR INVASION ECOLOGY AND MANAGEMENT

By

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Abstract

Although biological invasions are a leading threat to global biodiversity they provide opportunities to study factors that mediate invasion success from ecological and evolutionary perspectives and inform management efforts. The invasion of Northern Pike (*Esox lucius*) throughout southcentral Alaska has provided a useful case study, where invasive Northern Pike may benefit relative to native individuals due to high habitat suitability, abundant fish prey, and adaptive or plastic selective forces of invasion. Northern Pike continue to spread throughout the highly interconnected river and lake systems of southcentral Alaska; however, hypothesized differences in Northern Pike and native salmonid leaping abilities make selective vertical drop barriers a potential management option. Here, I build upon previous work by comparing physiological and morphological traits of invasive and native Northern Pike from river and lake habitats in Alaska that may influence their invasion success and leaping ability. Then, I used leaping experiments to determine how physical (abiotic) factors and individual biological traits influenced the maximum leaping ability of Northern Pike and developed a model to characterize these relationships. I found that invasive Northern Pike stomachs were two times more likely to contain energy-rich vertebrate diet items relative to native individuals, which was associated with two-fold faster growth rates, earlier ages-at-maturity, and 30% greater lipid content. Diet and physiological benefits were greater in lake habitats for invasive individuals, while native individuals experienced improved metrics in river habitats, potentially explained by thermal regimes, metabolic demands, and food availability. Leaping experiments proved that Northern Pike could ascend barrier heights four-times greater than previously assumed; pool depth, body size, and standardized growth rate also influenced individual leap success. Northern Pike leaping ability was significantly lower than salmonids. However, model predictions suggest that faster growth rates of invasive Northern Pike in Alaska may marginally enhance their leaping ability, and barriers should be tested in-situ before implementation. Insights into Northern Pike physiology and leaping behavior that result from this work can help managers determine if Northern Pike-

selective barriers are a viable option in southcentral Alaska and elsewhere Northern Pike are invasive, and supports the importance of intraspecific variation in invasive species ecology and management.

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General introduction

The introduction of nonnative species has grown into a worldwide phenomenon with increased anthropogenic global connectivity and environmental change (Early et al. 2016; Seebens et al. 2018). While some introduced species never establish or harmlessly integrate into new communities, others are able to outcompete, hybridize with, spread disease to, or predate upon native species and cause cascading, adverse impacts to ecosystems (Moyle and Light 1996; Pyšek et al. 2020). These effects range from food web alterations (Jackson et al. 2017) and loss of biodiversity as species are extirpated (Mollot et al. 2017), to reductions of critical ecosystem services (Charles and Dukes 2008; Pyšek et al. 2020), and cultural, economic, and recreational losses to humans as wild systems are altered (McNeely 2001; Lovell et al. 2006). Maintaining the integrity of native species assemblages, along with their associated ecosystem services and human-derived benefits, is essential for resiliency against future global climate alterations (Hansen and Biringer 2003; Pyšek et al. 2020).

Invasive species are introduced through a variety of mechanisms, including captive escapement, commodity contamination, stowing away on transport vectors, or deliberate release (Hulme 2015). Freshwater systems are particularly prone to new species introductions because they are sites of intensive human development and shipping (Strayer and Findlay 2010; Fausch and García-Berthou 2013). Freshwater systems also have many established invasive species because they were historically stocked with nonnative sportfish before the value of intact native ecosystems was recognized (Rahel 1997). While fishery managers now monitor and remove invasive fishes that cause detrimental effects, unauthorized spread still occurs through natural colonization and inadvertent or deliberate release by individuals due to a lack of public awareness, collaboration between resource managers, or appropriate penalties for illegal introductions (Rahel 2004; Johnson et al. 2009). Regardless of how aquatic invasive species (AIS) spread, they are one of the main drivers of rapid freshwater biodiversity loss (Dudgeon et al. 2006; Reid et al. 2019), cost billions of dollars in eradication efforts worldwide (Lovell et al. 2006), and are a top priority for natural resource management (Pyšek et al. 2020).

Effective AIS management involves many tactics and depends upon the stage of invasion, habitat complexity, socioeconomic interests, and impacts to native species (Mehta et al. 2007, Larson et al. 2011). Prevention of invasive species is the ultimate goal, requiring extensive commodity and watercraft inspections, widespread monitoring of ecosystems, extensive public outreach efforts, and reconciliation of ecological and economic conflicts with valued non-native species (Mehta et al. 2007; Sharp et al. 2017). If prevention is not possible, early detection of colonizing individuals is the next objective, and has become more attainable with advances in environmental DNA technology, remote sensing, and citizen science involvement (Larson et al. 2020). However, once the invader becomes established, more intensive chemical or physical removal methods are required and complete eradication becomes difficult, expensive, or impossible (Mehta et al. 2007).

While invasions are often detrimental, they can provide opportunities to characterize traits of successful invaders and develop tools to predict and prevent future invasions. For example, research shows that successful invasive species often have a large native range, high fecundity and dispersal potential, short generation time, physiological tolerance to environmental extremes, a generalist diet, and strong association with humans (Ehrlich 1989; Ricciardi et al. 2013; Havel et al. 2015). Subsequently, these traits have been incorporated into decision support tools to facilitate risk assessments of certain invaders for more effective management (Copp et al. 2005; Packer et al. 2017; Novoa et al. 2020). However, such simplification glosses over the equally important observation that invasions can induce trait variation in invaders through rapid contemporary evolution or phenotypic plasticity as they respond to new ecosystems (Elton 1958; Robinson & Dukas 1999; Sax et al. 2007; Ghalambor et al. 2007; Westley 2011). Intraspecific variation is increasingly recognized as an important driver of ecological interactions within invasions and beyond (Ruesink 2005; Huey et al. 2005; Bolnick et al. 2011; Burton et al. 2011; Reichard et al. 2015; Metcalfe et al. 2016; Des Roches et al. 2018; Závorka et al. 2018). The genetic and environmental mechanisms, and their interactions, that lead to intraspecific variation are less understood, but invasions provide opportunities to test for and subsequently explore the underlying

drivers of variation through more intensive laboratory and field experiments (Sax et al. 2007; Ghalambor et al. 2007; Westley 2011; Westley et al. 2012). From a management perspective, assessment of local invader characteristics to increase management efficacy may save considerable limited resources in the long run. Therefore, exploring the degree of intraspecific variation within invasive species can further the discipline of invasion ecology and its management applications.

A prime example of a globally distributed, highly impactful, and intraspecifically diverse invasive species is Northern Pike (*Esox lucius*; Muhlfeld et al. 2008; Hesthagen et al. 2015; Dunker et al. 2018). Northern Pike possess many traits associated with successful invaders, such as a large native distribution (Skov et al. 2018), generalist feeding ecology (Nilsson and Eklöv 2018; Cathcart et al. 2019), high fecundity (Casselman and Lewis 1996) and dispersal potential (Skov et al. 2018), toleration of a wide range of environmental conditions (Jacobsen and Engström-Öst 2018), and high anthropogenic value as a sport and subsistence fish (Nilsson and Skov 2018). As opportunistic predators, Northern Pike exert strong top-down effects by causing reduced abundances and even extirpation of native fishes, which can initiate negative effects to local communities as resources and ecosystem services are lost (Spens and Ball 2008; Nicholson et al. 2015; Hesthagen et al. 2015; Dunker et al. 2018). The impacts of invasive Northern Pike extend from Europe and Africa to the western United States and southcentral Alaska (Lever 1996; Leunda 2010; Fuller and Neilson 2021).

In Alaska, USA, Northern Pike are native north and west of the Alaska mountain range, but were introduced south of this natural barrier in the 1950s (Fay 2002; Dunker et al. 2018) and have thrived in the shallow, vegetated, habitats of the Matanuska-Susitna, western Cook Inlet, and Kenai peninsula drainages that contain abundant and naïve salmonids upon which Northern Pike prey (Sepulveda et al. 2013). The relative proximity of native and invasive Northern Pike populations in Alaska has provided opportunities to study how the trophic ecology, genetics, dispersal, and morphology of Northern Pike vary between invasive and native ranges and how this variation may contribute to their invasion success (Jalbert 2018; Cathcart et al. 2019; Berghaus et al. 2019; Jalbert et al. 2021). Such work has promoted

advancements in Northern Pike management in Alaska and continued inquiries about invasion ecology and evolution through the lens of this model organism (Forsman et al. 2015).

Northern Pike are adaptively managed with a variety of tactics in southcentral Alaska to incorporate novel research findings (Dunker et al. 2022). Early detection of Northern Pike is facilitated by gillnet monitoring and environmental DNA sampling in vulnerable habitats (Dunker et al. 2016). Suppression gillnetting is used in interconnected rivers and lakes to reduce consumptive impacts on native fishes, with all size classes of Northern Pike targeted for removal (Courtney et al. 2018). In isolated lake systems, Northern Pike can rapidly extirpate native fishes and continue to subsist on macroinvertebrates (Cathcart et al. 2019); such trophic plasticity allows Northern Pike in these lakes to indefinitely act as source populations for future introductions. Therefore, they are often eradicated using rotenone and gillnetting if conditions are appropriate, which allows for native fish reintroductions (Dunker et al. 2022). Phenotypic comparisons of Northern Pike indicate that invasive individuals are not adapting morphologically to invaded systems, but suggest that invasive individuals may benefit physiologically relative to native individuals (Berghaus et al. 2019). Otolith microchemistry analysis and angler reports indicate that Northern Pike utilize the estuarine Cook Inlet as a corridor to spread to uninvaded habitats (Dunker et al. 2022). Because of this novel dispersal pathway and over 1000 river km of suitable salmonid habitat that Northern Pike have yet to invade (Jalbert et al. 2021), selective vertical drop barriers to exclude Northern Pike populations are being considered by management entities (Dunker et al. 2022); contingent upon the untested assumption that Northern Pike leaping abilities are limited relative to native fishes. Northern Pike and salmonid habitat preferences have been modeled throughout southcentral Alaska that could aid in barrier placement prioritization (Jalbert et al. 2021). However, phenotypic divergence in Alaskan Northern Pike suggests that invasive individuals may have improved growth rates and body condition relative to native individuals (Berghaus et al. 2019), which are physiological traits that can enhance the dispersal, swimming, and leaping capabilities of fishes (Simpkins et al. 2003; Gardunio 2014; Courtney et al. 2020).

As invasive Northern Pike continue to spread in unexpected ways throughout southcentral Alaska, management tactics could consider new methods such as selective vertical drop barriers that target invaders while reducing impacts on native species (Rahel and McLaughlin 2018). Selective forces of invasion and/or ideal habitat with abundant fish prey may lead to intraspecific variation between invasive and native Northern Pike that could have consequences for the efficacy of barriers. Quantifying intraspecific variation in Northern Pike can inform barrier designs and other management tactics, while also guiding future research to study the underlying genetic or environmental mechanisms of such variation in a model predatory invader. Here, I demonstrate how important physiological endpoints in Northern Pike vary as a function of food availability, habitat type, and Northern Pike origin (e.g., invasive or native) in Alaska, which contributes to our understanding of how trait plasticity occurs and may contribute to their invasion success. I also consider the feasibility of selective vertical drop barriers to prevent Northern Pike movement by quantifying Northern Pike maximum leaping ability as a function of physical barrier conditions and intraspecific variation within individuals, in the context of salmonid leaping abilities. I then incorporate the unique biological traits of Alaskan Northern Pike into a model parameterized from leaping experiments to predict and discuss the feasibility of selective vertical drop barriers as a management tool for Northern Pike in Alaska and elsewhere they are invasive. Together, these assessments highlight the importance of considering intraspecific variation in invasive species ecology and management, and scientific inquiry as a whole.

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Chapter 1: Physiological variation in native and invasive Alaskan Northern Pike (*Esox lucius*): implications for invasion ecology and management¹

Abstract

The on-going spread of aquatic invasive species remains a leading cause of native freshwater fish extinctions, yet understanding the factors that mediate the impacts of invasive species remains elusive.

Theory predicts that non-native species introductions to novel areas can result in phenotypic variation that increases their dispersal and impacts on native ecosystems, and accordingly, substantial work has been done to quantify trait change in invading populations. Here we use the ongoing invasion of predatory Northern Pike (*Esox lucius*) in southcentral Alaska to better understand how habitat characteristics and contemporary trait change in physiology and morphology may underscore their profound ecological and economic effects. To consider this question and build on previous Alaskan Northern Pike research, we collected individuals (N = 123) from invasive (Matanuska-Susitna Basin) and native (Yukon Basin) ranges in both river and lake habitats in Alaska during the summer of 2020 to contrast their morphology, diets, growth rates, body condition, activity levels, and age of sexual maturation. We hypothesized that Northern Pike of invasive origin and those from lakes would have increased access to high-quality prey, experience higher growth and body condition, and younger age at maturation relative to native origin individuals and those from riverine locations. Additionally, we hypothesized that trends in activity levels and morphology would be consistent with greater dispersal in riverine Northern Pike of invasive origin. Consistent with previous research, invasive Northern Pike stomachs were two times more likely to contain energy-rich vertebrate diet items relative to native Northern Pike, which was associated with three-fold faster growth rates, earlier ages-at-maturity, and 30% greater lipid content in invasive individuals. Diet and physiological benefits were greater in lake habitats for invasive Northern Pike, while

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native individuals experienced improved metrics in river habitats. This opposing trend of habitat type within Northern Pike from invasive and native origins may be explained by the interaction of food availability, thermal regimes, and activity levels. An improved understanding of how habitat type and resource availability impact the diet, activity levels, growth, body condition, and maturation of invasive Northern Pike relative to those of native origin can provide insights for local management prioritization. Additionally, identification of such intraspecific variation in Northern Pike can guide continued inquiry into the underlying environmental and genetic mechanisms for these trait changes, with important implications for invasion ecology and evolution.

Introduction

The on-going spread of invasive species continues to threaten global biodiversity, ecosystem services, and resiliency against climate change (Pyšek et al. 2020). Much work has been done to predict and prevent future invasions by characterizing factors that influence invader arrival and establishment, from environmental conditions (e.g., propagule pressure, habitat suitability, predators, and prey availability), to invader characteristics (e.g., rapid maturation, high reproductive output, and opportunistic feeding habits) (Byers et al. 2002; Kolar and Lodge 2002; Marchetti et al. 2004; Ruesink 2005; Olden et al. 2006; Garcia-Berthou 2007). However, invader characteristics can often change rapidly as invaders experience novel selective pressures in new environments through phenotypic plasticity and rapid contemporary adaptation (Huey et al. 2005; Sax et al. 2007; Ghalambor et al. 2007; Westley 2011). Such trait variation can exacerbate invader impacts and reduce the efficacy of management tactics that rely on static invader traits (Phillips et al. 2006; Kinnison et al. 2008; Vilizzi et al. 2019). By considering how environmental conditions interact with invaders to result in intraspecific trait variation, we can understand what phenotypes result in greater negative effects to native ecosystems, and apply these findings for more effective prediction, prevention, and management of invasions (Byers et al. 2002; Reichard et al. 2015; Packer et al. 2017). Such intraspecific variation caused by species adjusting to novel environmental conditions applies to other processes aside from biological invasions (Des Roches et al. 2018), which

highlights the utility of invasions as largescale ecological and evolutionary experiments from which to learn (Huey et al. 2005; Sax et al. 2007).

Which traits, therefore, should be monitored in conjunction with environmental conditions to characterize invasive phenotypes? The degree of trophic adaptability is relevant for invasive predatory species because invaders often benefit from naïve prey resources (Polačik et al. 2009; Sih et al. 2010; Almeida et al. 2012; Pagnucco et al. 2016), and invaders that easily shift to novel, high-energy prey items can display individual increases in growth rates and improved body condition (Polačik et al. 2009), which scale up to the population level. For example, fast growth and energy accumulation can reduce predation risk of juveniles (Brett 1979), accelerate ontogenetic diet shifts (Oele et al. 2019), improve overwinter survival (Post and Evans 1989; Thompson et al. 1991; Sogard 1997; Garvey et al. 1998), promote early maturation (Shearer et al. 2006; Sloat and Reeves 2014; Rosenberger et al. 2015), and increase reproductive output (Barneche et al. 2018). However, access to prey is influenced by habitat complexity and foraging tactics of the invader; therefore, habitat type may affect prey consumed by the invader and associated benefits in growth rate, body condition, and maturation.

Increased dispersal tendencies are also beneficial to invaders as they expand their range (Angert et al. 2011; Brousseau and McSweeney 2016). Dispersal rates can be difficult to quantify without mark and recapture studies, but can be inferred through proxies such as morphological adaptations and organism activity levels that enhance dispersal. For example, variation in morphology such as streamlined bodies and larger fins are associated with individuals that occupy faster flow conditions and disperse greater distances in fishes (Langerhans 2008; Westley et al. 2012). Also, high-energy anaerobic activities such as foraging and burst movements are positively reflected in the activity of enzymes such as lactate dehydrogenase (LDH) in white muscle tissues that facilitate anaerobic metabolism (Sullivan and Somero 1980; Childress and Somero 1990; Sherwood et al. 2002; Tracy et al. 2011). The implications of intraspecific variation in physiology, life history, and dispersal as a function of environmental conditions for invader success is high; therefore, it would be useful to monitor trends in diet, body condition, growth,

maturation, morphology, and activity levels of invasive populations and contrast them with those of native origin individuals to characterize under what environmental conditions and by what mechanisms invaders are most successful.

Northern Pike (*Esox lucius*) are a prime example of a successful invader, known to be an ecosystem engineer within its native range and when introduced into freshwater ecosystems (Chapman et al. 1989; Berg et al. 1997; Muelfeld et al. 2008; Hesthagen et al. 2015). Northern Pike are generalist predators that preferentially consume soft-rayed fishes in addition to macroinvertebrates, waterfowl, small rodents, and occasionally conspecifics (Morrow 1980; Cathcart et al. 2019), and are found in shallow, vegetated littoral habitat of northern lakes and river systems. Northern Pike possess many characteristics common to successful invaders (Dunker et al. 2018; Nilsson and Skov 2018), and are highly valued as a subsistence, recreational, and commercial resource to humans (Nilsson and Skov 2018). This has led to many successful introductions of Northern Pike across Europe and North America, including Alaska, USA (Lever 1996; Leunda 2010; Fuller and Neilson 2021).

Northern Pike are native to interior and western Alaska, where they generally coexist with other fishes in heterogeneous systems that provide pelagic, deep benthic, or fast-flowing habitat refugia that littorally-oriented Northern Pike avoid. However, homogeneous, shallow, and vegetated systems are often dominated solely by Northern Pike in the native range because millennia of predator-prey interactions and lack of prey refugia prevents Northern Pike and native fishes to coexist (Morrow 1980). Northern Pike were intentionally introduced to the southcentral region of Alaska in the 1950s (Fay 2002; Dunker et al. 2018), which contains abundant interconnected river and lake systems that are home to numerous salmonids, including all five Pacific salmon (*Oncorhynchus* spp.) species, Dolly Varden (*Salvelinus malma*), Arctic Char (*Salvelinus alpinus*), Arctic Grayling (*Thymallus arcticus*), and Rainbow Trout (*Oncorhynchus mykiss*; Roth & Stratton 1984). High habitat overlap (Jalbert et al. 2021) and efficient predation of juvenile salmonids by Northern Pike has resulted in significant negative effects to native

fishes and the communities that rely on these important cultural, recreational, and economic resources (Dunker et al. 2020).

The proximity of native and invasive Northern Pike in Alaska has proven to be a useful opportunity to study how habitat types, trophic ecology, genetics, dispersal, and morphology vary between invasive and native ranges, and how this variation may contribute to Northern Pike invasion success and management activities (Jalbert 2018; Cathcart et al. 2019; Berghaus et al. 2019; Jalbert et al. 2021). For example, Northern Pike exhibit trophic adaptability and variable impacts on native ecosystems based on habitat conditions, with invasive populations able to rapidly extirpate preferred soft-rayed fishes in homogeneous systems and shift to macroinvertebrates (Haught and von Hippel 2011; Patankar et al. 2006; Sepulveda et al. 2013; Cathcart et al. 2019), while their predatory effects are limited in heterogeneous systems that provide prey refugia in the invasive range (Sepulveda et al. 2013). Genetic and morphological analyses indicate that Northern Pike have low genotypic and phenotypic diversity and divergence across the state (Jalbert 2018; Berghaus et al. 2019), which may be indicative of low rates of adaptive change because much of southcentral Alaska's lakes and rivers are already ideal habitat for Northern Pike (Jalbert et al. 2021). However, differences in size-at-age and body depth suggest invasive individuals may have improved growth rates and body condition relative to native individuals (Berghaus et al. 2019), which are traits that have important demographic implications (Kinnison et al. 2008). Otolith microchemistry analysis and angler reports indicate that Northern Pike can utilize the estuarine Cook Inlet as a movement corridor (Dunker et al. 2022), which is a considerable >30 km migration distance through stressful saline conditions that would require strong dispersal capabilities. Mounting evidence suggests that Northern Pike may benefit from suitable habitat and abundant salmonid prey in the invasive range, which may result in variation in physiology, life history, and dispersal tendencies that could elucidate drivers of Northern Pike invasion success. However, such variation has not been addressed systematically and may vary as a function of habitat complexity, prey access, and time since invasion (Haught and von Hippel 2011; Sepulveda et al. 2013; Cathcart et al. 2019).

Here, we utilize the proximity of invasive and native origin Northern Pike in Alaska to consider how traits relating to dispersal and physiology differ in the context of habitat types, prey availability, and processes of adaptation and plasticity associated with invasion. Specifically, our aim was to collect Northern Pike from invasive and native locations in river and lake systems in Alaska to observe trends in 1) diet composition, stomach fullness, activity levels, growth rates, body condition, size-at-age, and age-at-maturation, and 2) morphology and activity levels that relate to dispersal. We hypothesized (Figure 1.1.) that invasive origin Northern Pike would consume more vertebrate (e.g., fishes) prey items and have fuller stomachs than native origin Northern Pike, and those from relatively homogeneous lake systems would consume more vertebrates and have fuller stomachs relative to individuals collected from heterogeneous rivers because of differences in prey accessibility (Figure 1.1). Systems with less abundant prey may result in higher Northern Pike activity level associated with foraging, while invasive individuals may have higher activity levels due to greater dispersal tendencies. Thus, we hypothesized that invasive river individuals may have the highest activity levels, while invasive lake individuals may have the lowest activity levels because of abundant prey in low complexity habitats and low need for dispersal. Native Northern Pike from rivers and lakes may have moderate activity levels because of lower dispersal tendencies but lower food availability which could increase foraging activity. Subsequently because of greater prey access, we hypothesized that invasive Northern Pike and those from lakes would have faster growth rates, larger size-at-age, improved body condition, and younger age-at-maturity relative to native and riverine counterparts. Lastly, we hypothesized that habitat type, and thus flow experienced by Northern Pike, would have the greatest impact on morphology (i.e., streamlined bodies, deeper caudal peduncles, and larger fins) in individuals from river systems to cope with faster flow rates (Langerhans 2008; Senay et al. 2017), with invasive river Northern Pike experiencing the greatest expression of such morphology due to greater dispersal tendencies (Radinger and Wolter 2014; Dunker et al. 2022). Ideal conditions for Northern Pike in the invasive range and in lakes (e.g., abundant fish prey and greater habitat homogeneity) relative to native Northern Pike and those from rivers may result in low activity levels, rapid growth rates, improved body condition, and faster maturation, which are traits that can

facilitate population growth and invasion success. Characterization of conditions that result in invasive phenotypes can prioritize management of Northern Pike, and provide opportunities to more closely investigate the underlying genetic, plastic, and environmental drivers of such variation if present.

Methods

Study sites

We collected Northern Pike from June to September 2020 in invasive- and native-range locations from river and lake habitats in Alaska, USA with a target of 30 individuals from each of the four origin/habitat groups, for a total of 120 individuals (Figure 1.2). Here, we consider collection sites as putative biological populations, though we acknowledge that genetic structure in invasive populations is very shallow, consistent with genetic bottlenecks and/or high dispersal rates (Jalbert 2018). Invasive Northern Pike were collected from the lower western Susitna River drainage, an interconnected, low-gradient system of rivers and lakes that generally flow south from the Alaska and Talkeetna mountain ranges into Upper Cook Inlet. Invasive river individuals were collected from sloughs of the lower Deshka River, a tributary to the Susitna River, and invasive lake individuals were collected from littoral habitat in Nancy Lake, a shallow (mean depth 7.6 m) 308-ha lake, with similar timeframes since invasion (~30 years; Whitmore and Sweet 1998; Haught and von Hippel 2011). All native Northern Pike were collected from the Tanana River drainage, a complex glacially-fed system that flows generally northwest into the Yukon River and Bering Sea. Native river individuals were collected from Willow Creek, a small, tannic tributary to the Tanana River, and from Noyes and Sternwheeler sloughs on the Chena River, a spring-fed tributary to the Tanana River. Native lake individuals were collected from the Minto Flats wetland complex, a shallow (mean depth < 5 m) 200,000-ha interconnected system of marshes and lakes. Native lake individuals were also collected from Mullin's Pit Lake on Eielson Air Force Base (Figure 1.2). Upon collection via angling or gillnets, Northern Pike were euthanized by a sharp blow to the head followed by cranial pithing and bleeding of the gills, and transported on ice back to the laboratory for further processing.

Assessment of physiological and morphological traits

Size and body condition – bioelectrical impedance analysis

We measured whole body mass (g), fork length (FL; mm), and collected bioelectrical impedance analysis (BIA) measurements on each individual according to standard methods (Cox and Hartman 2005; Cox et al. 2011; Falke et al. 2019; Courtney et al. 2020; Figure 1.3). Electrical measurements from BIA can be correlated to proximate component measurements to create species-specific models that nonlethally estimate body condition of fishes from BIA and biological (e.g., length, weight) measurements alone (Cox and Hartman 2005). As a BIA model has not been developed for Northern Pike, standard electrical parameters were calculated from BIA measurements and correlated to measurements of body condition (% dry mass and % dry lipid) taken on a subset of individuals (N = 90; see below) to create separate models to estimate dry mass and lipid content of all Northern Pike collected (for detailed methods and models, see Appendices A-H). After BIA measurements were complete, each individual was labeled and frozen at -20 °C for approximately 5 months.

Morphometrics, sex, and maturity

Morphometric measurements were taken from each individual after thawing (Figure 1.3). Body depth at dorsal fin insertion perpendicular to the ventral surface, caudal peduncle circumference at the narrowest point, and caudal, dorsal, and anal fin width at the base of each fin were measured in cm. Northern Pike were dissected to determine sex (e.g. male/female/unknown) and maturity (e.g., mature/immature) based on presence and development of identifiable ovaries or testes with assistance from experienced Northern Pike biologists, generally according to Appendix I.

Diet and stable isotope analysis

Stomach contents were removed and each individual was categorized as having an empty stomach, or a stomach containing vertebrate (e.g., fishes and amphibians) and/or invertebrate (e.g., macroinvertebrates and leeches) prey in a binomial fashion. Small 5 g dorsal white muscle samples from

each individual and three replicates of whole well-preserved diet item taxa from each collection location were frozen for stable isotope analysis using standardized methods (see Appendix J for details).

Activity level

A random subsample of eight individuals per origin and habitat grouping was used to estimate LDH activity in the glycolytic white muscle tissue and considered a proxy for anaerobic activity level (Sullivan and Somero 1980; Schulte et al. 2000; Sherwood et al. 2002). The activity of LDH was maximally assayed using standardized methods at room temperature with a spectrophotometer (Ombres et al. 2011; see Appendix K for details). Northern Pike sampled for enzyme assays were between 300 and 400 mm to control for allometric effects of body size on metabolism, with sample sizes of eight generally considered robust for physiological analyses (Torres and Somero 1988).

Body condition – proximate composition analysis

Following dissection and removal of stomach contents, Northern Pike not used in enzyme analyses (approximately 22 per group) were homogenized whole in an industrial grinder including gonadal tissue, and two ~50 g subsamples were weighed, dried for 48 hours in a drying oven at 55-60°C, and reweighed to determine % dry mass (%DM) calculated using the following equation:

$$\%DM = (\text{dry mass of sample} / \text{wet mass of sample}) \times 100$$

Once dried and weighed, the two subsamples of each individual were combined, homogenized once more, and sent to the University of Idaho, Hagerman Station for proximate composition analysis (AOAC 2019), which returned total lipid, protein, and ash content as a percentage of dry mass. Energy density was calculated for each group by multiplying the mean % dry lipid and % dry protein values by their energy equivalents (36.4 kJ/g for lipids and 20.1 kJ/g for protein; Brett 1995) and then summing the lipid and protein components (Courtney et al. 2020).

Age and growth rate

We used cleithra to estimate Northern Pike age and growth rates because they are the preferred aging structure for esocids (Phelps et al. 2017). Cleithra were removed from each individual during dissection, cleaned of remaining soft tissue, submerged in water in a black tray, and photographed with reflected light (Casselman 1996). Each cleithra was aged by two trained readers with 88% initial agreement, and discrepancies were resolved by both parties re-aging the cleithra until agreement was reached. No cleithra were excluded from analysis. Annuli increments were measured along the anterior axis of the cleithrum with the *RFishBC* package (Ogle 2020) in Program R (RStudio Team 2019). Then, length-at-age for each individual was back-calculated using the biological intercept model proposed by Campana (1990):

$$L_t = L_T + ((S_t - S_T) / (S_T - S_0)) * (L_T - L_0)$$

where L_t is individual length at age t , L_T is individual length at capture, S_t is cleithrum radius at age t , S_T is cleithrum length at capture, S_0 is cleithrum length at formation (0.86 mm; Faust 2011), and L_0 is individual length at time of cleithrum formation (8.6 mm; Pospisilova et al. 2019). After lengths were back-calculated for each individual's age, age-specific growth rates (mm/day) were calculated by dividing the change in length (mm) by growing season in days, assuming a common hatch date of May 15 (P. Bradley ADF&G, personal communication) and growing season from April 1 to November 1 for all groups (Casselman 1996; see Appendix L for details).

Statistical analysis

Size and morphometrics

All analyses were conducted using the statistical software Program R (RStudio Team 2019) and evaluated at the $\alpha = 0.05$ level. While Northern Pike origin (invasive or native) and habitat type (river or lake) were our main variables of interest, effects of sex and maturity were also considered as grouping variables to test for differences in individual diets, physiology, life history, and dispersal. We observed

differences in FL by origin, habitat, sex, and maturity using non-parametric Kruskal-Wallis (KW) tests, with pairwise Dunn's test and Bonferroni correction used for multiple comparisons. Morphometrics were log-transformed and regressed as a function of log-transformed FL measurements to test the hypothesis that morphometrics related to swimming efficiency differ due to habitat type and origin. Residuals for each morphometric regression were included in a principal component analysis. Three principal components (hereafter PCI, PCII, and PCIII) were retained to account for >85% of trait variation, with trait loadings greater than 0.3 or less than -0.3 considered to significantly load on the associated PC (Table 1.1). Principal component scores were analyzed using one-way analysis of variance (ANOVA) with Tukey *post-hoc* analyses, with origin, habitat, sex, maturity and their interactions used as grouping variables.

Diet and stable isotope analysis

We used two-proportion Z tests (Sprinthal 2011) to test the hypothesis that invasive individuals consume more vertebrate diet items and have fuller stomachs than native individuals and characterize how this relationship may vary by habitat type. We also compared the proportion of individual stomachs that contained no diet items, vertebrate, or invertebrate prey among origins, habitats, and by sex and maturity. Additionally, diet item stable isotope values were used in Bayesian stable isotope mixing model analyses to determine the proportional contribution of vertebrate diet items to individuals, standardized by collection location (Hopkins et al. 2012), using the R package simmr (Parnell 2019). Mean \pm standard deviation of stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of prey items and Northern Pike were included in mixing models, and the estimated proportions of vertebrate diet items (e.g. salmonid spp., stickleback spp., sucker spp.) were summed for each individual. Estimated proportions of vertebrates in the diet were analyzed using ANOVA and Tukey *post-hoc* analyses to test for differences due to origin, habitat, sex, maturity, and their interactions.

Activity level

Size-standardization of Northern Pike included in enzyme assays resulted in no significant allometric effects of log-transformed weight vs. log-transformed mass-specific white muscle LDH activity (see Appendix M). We used ANOVA and Tukey's *post-hoc* analysis to test the hypothesis that invasive individuals that occupied river habitats had the highest LDH activity compared to individuals collected from lake and/or native groups. Sex and maturity effects were also used as grouping variables and all interactions were considered.

Body condition – bioelectrical impedance and proximate composition analysis

Proximate component values (%DM and %DL) increased linearly with fork length. Fork length was accounted for by using ANCOVA to test the hypothesis that invasive individuals and those from lakes had greater body condition for a given size than native individuals and those from rivers. Interactions with sex and maturity status were also considered, and Benjamini-Hochberg FDR post-testing was used for multiple comparisons.

Size-at-age, maturity, and growth rate

We used ANCOVA to test for effects of origin, habitat type, and their interaction on back-calculated FLs at age of all individuals. Mean length at 50% probability of maturity (L50) was calculated for each origin and habitat group using multiple logistic regression (Ogle 2018), and then the age at L50 for each group was predicted using the previous linear model with FL predicting age to observe differences in age-at-maturity among Northern Pike origins, habitats, and their interaction. Back-calculated age-1 growth rate and recent age-1 growth rate (e.g., from young of year (YOY) individuals) were pooled, log-transformed, and compared using ANOVA and Tukey *post-hoc* analyses to test the hypothesis that invasive and lake individuals have faster growth rates for a given age than native individuals and those collected from rivers.

Results

General group characteristics

We collected 123 Northern Pike, with approximately 30 individuals collected from the four origin/habitat groups (Table 1.2). Fork lengths ranged from 152 to 865 mm (mean \pm SD: 419 \pm 149), weights from 22 to 4764 g (mean \pm SD: 760 \pm 937 g), and ages from 0 to 6 years (median \pm SD: 2.0 \pm 1.7 years). Invasive individuals had smaller mean fork lengths relative to native individuals in both habitat types (Dunn's test, lake: $Z = -5.49$, $P < 0.001$, river: $Z = -2.82$, $P = 0.02$), but within origin, mean Northern Pike fork length did not differ by habitat type in the invasive range (Dunn's test, $Z = -1.49$, $P = 0.82$), or native range (Dunn's test, $Z = 1.00$, $P = 0.99$). In general, invasive lake individuals were smallest and youngest, followed by invasive river, native river, and native lake individuals (Table 1.2). Maturity and sex proportions varied among groups; immature individuals comprised 84% and 89% of samples in invasive lake and invasive river groups, respectively, while 68% of native river individuals and 41% of native lake individuals were immature (see Appendix N). Sex ratios differed from 1:1 (two-proportion Z test, $\chi^2 = 3.66$, $P = 0.06$), with 60% percent or greater of Northern Pike sexed as female in native lake, native river, and invasive river groups, while invasive lake individuals were 63% unknown sex and 37% male (see Appendix N).

Morphometrics

Size-standardized Northern Pike morphology differed by habitat type, likely as a result of the effects of flow as hypothesized. However, invasive or native status and inferred dispersal tendencies did not influence morphology. Principal component I explained 57% of variation with significant loadings for all morphometrics, but PCI did not vary by origin, habitat, sex, or maturity (Table 1.3), suggesting that across all locations, some individuals possess larger fin widths, body depths, and peduncle circumferences, and these characteristics are positively associated with one another. Caudal fin widths were positively associated with PCII (Table 1.1) and wider in individuals collected from river locations regardless of origin (Table 1.3; ANOVA, DF = 1, $P < 0.001$; Figure 1.4). Caudal fin width was also

associated with sex, but multiple comparisons within the interaction of habitat type resulted in a non-significant effect of sex (Tukey's test; lake male vs lake female: $P = 0.69$, river male vs river female, $P = 0.29$). Based on PCIII, individuals collected from lake systems had deeper bodies and narrower anal fins compared to river systems regardless of origin (ANOVA, $DF = 1$, $P < 0.001$; Figure 1.4). Variation in maturity among habitat types potentially resulted in the significant main effect of maturity on PCIII, however considering the interaction of habitat type and maturity resulted in no further effect of maturity on PCIII with Tukey's *post-hoc* testing. The majority of morphological variation was not explained by habitat type, origin, sex, or maturity, which suggests that Northern Pike morphology was consistent across collection sites.

Estimated and observed diet composition

Results of stable isotope mixing models indicated that the estimated proportion of Northern Pike diets composed of vertebrates differed by origin, habitat type, and their interaction, but not by sex or maturity (Table 1.4). Our hypotheses that invasive individuals would have higher vertebrate diet proportions relative to native individuals was supported only in lake habitats (86% vs 63% respectively, Table 1.2; Tukey's test, $P = 0.001$), while invasive and native river individuals had similar vertebrate diet proportions of 44% and 42%, respectively (Table 1.2; Tukey's test, $P = 0.99$). Our hypothesis Northern Pike vertebrate diet proportions would be higher in lakes than rivers was supported in both invasive (86% vs 44%; Tukey's test, $P < 0.001$) and native groups (63% vs 42%; Tukey's test, $P = 0.01$).

Stable isotope estimates were similar to observed stomach content proportional analyses. Following the hypothesis that invasive individuals would have fuller stomachs and more vertebrate diet items than native individuals, immature invasive river Northern Pike had a lower proportion of empty stomachs than immature native river Northern Pike (28% vs 57%, respectively, two proportion Z test, $P = 0.05$; Figure 1.5), and immature invasive river Northern Pike tended to have a higher proportion of vertebrates in the diet than immature native river Northern Pike (52% vs 28%, $P = 0.1$). Regardless of maturity status, invasive lake individuals had more vertebrates in the diet (60% vs 20%, $P = 0.001$) and

less invertebrates in the diet (0% vs 20%, $P = 0.01$) than native lake individuals (Figure 1.5). No significant differences existed in diet proportions due to habitat type within native origin Northern Pike, and invasive lake Northern Pike only differed from invasive river Northern Pike by having less invertebrates in the diet (0% vs 17%; $P = 0.02$). Overall, the higher estimated vertebrate diet proportions, observed fuller stomachs, and more vertebrate diet items in invasive Northern Pike diets suggests a dietary advantage for individuals in the invasive range, with habitat type and associated heterogeneity playing a smaller role (Figure 1.5).

Activity level

Our hypothesis that white muscle LDH activity, a proxy for activities including foraging and burst movement, would be higher in invasive river individuals due to greater dispersal tendencies was not supported (Table 1.4). Mean mass-specific white muscle LDH activity was only affected by habitat type, with higher LDH activity in individuals collected from lake habitats compared to those from rivers (ANOVA, $DF = 1$, $P = 0.005$). Invasive or native status did not describe variation as a whole (ANOVA, $DF = 1$, $P = 0.75$) or within habitat types (lake: Tukey's test, $P = 0.99$; river: Tukey's test, $P = 0.92$). These results likely highlight the large effect of water temperature on ectothermic fish metabolic rates. Lakes in our study area are generally warmer habitats relative to rivers, which elevate basal metabolic rates of fishes, food demand, and foraging activity, and greater foraging activity may be represented by higher white muscle LDH activity.

Body condition – bioelectrical impedance and proximate composition analysis

The models that utilized BIA measurements and biotic variables of Northern Pike to estimate %DM and %DL had relatively high predictive power (adjusted R^2 , 78% and 73%, respectively) and low Root Mean Squared Error (RMSE, 0.8% and 2.4%, respectively; Table 1.5; see appendices A – H for details). Therefore, we used the models to predict %DM and %DL for the subset of Northern Pike used for enzyme assays ($N=32$) to compare body condition of all individuals across origin and habitat groupings. Percent dry mass did not differ due to habitat type, origin, or their interaction when controlling

for FL, contrary to predictions (Table 1.5). However, invasive individuals had higher %DL than native individuals for a given FL (ANCOVA, $F = 30.1$, $P < 0.001$) and Northern Pike from river habitats had higher %DL than lake counterparts for a given FL (ANCOVA, $F = 5.52$, $P = 0.02$; Figure 1.6). Mature individuals also had higher %DL than immature individuals for a given FL (ANCOVA, $F = 5.23$, $P = 0.02$). The hypothesis that invasive Northern Pike possess better body condition in the form of lipid reserves compared to native Northern Pike was supported, while river individuals possessed improved body condition over lake individuals, contrary to our hypothesis (Figure 1.6).

Size-at-age, size-at-maturity, age-at-maturity, and growth rates

As hypothesized, invasive Northern Pike were larger at age than native Northern Pike in lake and river habitats (Table 1.8; lake: FDR, DF = 365, test statistic = 11.5, $P < 0.001$; river: FDR, DF = 365, test statistic = 3.67, $P < 0.001$; Figure 1.7). The hypothesis that lake individuals would be larger at age than river individuals was supported in invasive origin groups (FDR, DF = 365, test statistic = 7.62, $P < 0.001$), while in native origin groups, lake individuals were smaller at age than river individuals (FDR, DF = 365, test statistic = -2.78, $P = 0.006$; Figure 1.7). Confidence intervals for length at 50% maturity were wide-ranging among groups, but the hypothesis that invasive individuals reach L50 at younger ages relative to native individuals was supported (Table 1.7). While the hypothesis that lake individuals would mature earlier than river individuals was supported for invasive groups (0.39 yrs vs 2.21 yrs, respectively), the trend that native river Northern Pike matured at earlier ages than native lake Northern Pike countered this hypothesis but may not be biologically significant (3.00 yrs vs 3.29 yrs, respectively; Table 1.7).

Log-transformed growth rates of Northern Pike declined linearly with age across origin and habitat groups (OLSR, $P < 0.001$). Invasive individuals possessed faster age-1 growth rates than native individuals in river and lake habitats, as predicted (Tukey's test, lake: $P < 0.001$, river: $P = 0.04$; Figure 1.8). The hypothesis that lake individuals would have faster age-1 growth rate than river individuals was supported in invasive origin individuals (Tukey's test, $P < 0.001$); however, age-1 growth rates did not

significantly differ between river and lake individuals of native origin (Tukey's test, $P = 0.16$; Figure 1.8). These patterns of size, growth rate, and maturity indicate that there is a relatively constant maturation threshold for Northern Pike between 370–510 mm, but faster growth rates in invasive individuals may allow them to reach this threshold faster and thus mature earlier.

Discussion

As invasive Northern Pike continue to threaten native fishes in southcentral Alaska, our contribution to understanding which factors may enhance growth, condition, maturation, and dispersal of invasive individuals can facilitate better management and direct future research about piscivorous fish invasions. We found clear differences in the diet and physiology of invasive and native Northern Pike in Alaska collected from river and lake habitats for which size, age, and maturity were accounted, summarized in Figure 1.9. Our hypotheses that invasive individuals would consume higher quality and more prey items, and thus benefit in faster growth rates, earlier maturation, and improved body condition relative to native individuals were supported, and these responses were enhanced in Northern Pike from the invasive lake location, potentially with easier access to fish prey relative to the more complex invasive river location (Figure 1.9). However, native Northern Pike generally had faster growth rates, greater lipid stores, and earlier maturation in more heterogeneous river habitats compared to those from the native lake locations (Figure 1.9), with the interaction of habitat thermal regimes and food availability affecting such differentiation. Patterns in morphology were not affected by Northern Pike origin, but followed trends observed in the literature related to flow rate, such as streamlined bodies and larger fins in river habitats (Langerhans 2008; Westley et al. 2012; Senay et al. 2017). These observations contribute to our understanding of how habitat and prey availability mediate changes in physiology and life history of invasive predatory fishes such as Northern Pike, with management and future research implications.

Diet and habitat heterogeneity

Diet data indicated that quantity and quality of diet items differed among Northern Pike groups, and considering this variation in the context of habitat heterogeneity, pike-salmonid overlap, and

timescale of invasion may elucidate why such differences existed. For example, native individuals in both river and lake habitats consumed fewer vertebrate diet items than invasive origin individuals, which is likely due to millennia of cohabitation and distributional equilibrium in the native range that has resulted in salmonids avoiding pike-dominated habitats and being less available as prey (Morrow 1980; Schoen et al. 2022), whereas Northern Pike and salmonids have only coexisted for 70 years or less in the invasive range (Dunker et al. 2018). However, diets of invasive Northern Pike differed considerably by habitat type, with invasive lake vertebrate diet contributions nearly double that of invasive river individuals (86% vs 44%) despite similar lengths of invasive Northern Pike presence (~30 years, Haught and von Hippel 2011; Whitmore and Sweet 1998). This may reflect easier access to fish prey in the more homogeneous 308-ha Nancy Lake system, relative to the invasive Deshka River location with more variable Northern Pike habitat suitability (Jalbert et al. 2021).

The high consumption of vertebrate prey by invasive Northern Pike in Nancy Lake suggests potential rapid loss of native fishes, but variable bathymetry (maximum depths = 20 m) in the lake may provide deep water/pelagic habitat refugia for native fishes to avoid predation despite roughly 30 years of Northern Pike presence. Indeed, more homogeneous, isolated systems in southcentral Alaska have resulted in rapid declines of prey fish abundance (Haught and von Hippel 2011; Sepulveda et al. 2013), and elsewhere where Northern Pike have been introduced into homogeneous, salmonid-occupied systems (Spens and Ball 2008; McLoone et al. 2018). However, prey naïveté due to relatively short timescales of coexistence may still facilitate high salmonid consumption by Northern Pike in littoral habitat of Nancy Lake, as observed in the lack of behavioral anti-predator adaptation to invasive Northern Pike by Three-spined Stickleback (*Gasterosteus aculeatus*) collected from this location (Stevens et al. 2022). The effect of habitat heterogeneity on Northern Pike access to fish prey in the invasive range of Alaska appears to be a complex gradient (Haught and von Hippel 2011; Sepulveda et al. 2013; Cathcart et al. 2019), with our invasive lake and river locations representing systems that Northern Pike and salmonids have been able to coexist within over current invasion timescales. However, variation in Northern Pike diets due to origin

and habitat types also resulted in physiological variation that may have important ecological consequences that warrant continued assessment.

Physiological traits

Metrics of body condition, %DM and %DL, increased with fork length across all groups, as seen in another study quantifying body condition of Northern Pike (Salam 2014). However, mean lipid content was at least 1.2-fold higher in invasive individuals relative to native individuals in both river and lake habitats (Figure 1.6), which may be a function of the greater quantity and quality of high-energy vertebrate prey items in invasive Northern Pike diets (Figure 1.9). This positive association with food availability and lipid reserves has been observed in other fish taxa such as juvenile wild Atlantic Salmon (*Salmo salar*; Dempson et al. 2004), marine forage fishes (Vollenweider et al. 2011), and Arctic Grayling in interior Alaska (Falke et al. 2019). Fishes often face a trade-off between lipid accumulation and growth in sub-optimal conditions (Post and Parkinson 2001; Sogard and Spencer 2004); however, age-1 growth rates were 1.2 to 2-times faster in invasive Northern Pike in addition to greater lipid content relative to native individuals (Figure 1.9). Faster growth rates may also be related to higher prey quantity and quality relative to native individuals, with positive associations between diet and Northern Pike growth rates observed in other invasive populations in Alaska and Arizona (Flinders and Bonar 2008; Glick and Willette 2016). While invasive Northern Pike had faster growth rates and greater overall lipid content relative to native individuals, differences within populations due to habitat type were present and the underlying mechanisms of such variation warrant consideration.

The observed trends in lipid content and growth across Northern Pike origins and habitat types may be explained by the interaction of food availability, temperature-mediated metabolism, and activity levels associated with meeting metabolic demands. As fish metabolic rates increase with temperature (Willmer and Stone 2009) and lakes tend to have warmer thermal regimes than rivers in Alaska, lake individuals may have had higher activity levels because they were foraging more to meet high food demands associated with elevated metabolic rate (Treberg et al. 2016). Northern Pike may have had lower

activity levels in rivers because rivers tend to be cooler, reducing metabolic rate, food demand, and associated foraging activity. When food is not limiting, warm temperatures and high rates of metabolism result in the conversion of food into somatic growth and excess food secondarily stored as lipids (Post and Parkinson 2001; Sogard and Spencer 2004). Taking this into account, invasive lake individuals may have had the highest growth rates of all groups and high lipid stores because they were able to meet and exceed metabolic demands with successful foraging activities, as seen by high vertebrate diet proportions (Figure 1.9). Such maximization of growth rate and energy storage in warm conditions with unlimited food has also been observed in juvenile Sablefish (*Anoplopoma fimbria*; Sogard and Spencer 2004). In contrast, native lake individuals may have had the lowest growth rates and lipid stores because high metabolic demands in warm lakes were not met due to low food availability and quality (Figure 1.5), despite similar foraging activity levels to invasive lake individuals inferred by LDH activity. Unsuccessful high foraging activity via LDH activity has also been associated with low growth rates for Yellow Perch (*Perca flavescens*; Rennie et al. 2005). Reduced growth but higher lipid content in invasive river individuals compared to invasive lake individuals may be related to lipid accumulation being favored over growth when metabolism is reduced in cool habitats, which has been observed in laboratory experiments with European Seabass (*Dicentrarchus labrax*; Person-Le Ruyet et al. 2004) and observational studies of wild Brown Trout (*Salmo trutta*; Alvarez et al. 2006). However, growth and lipid accumulation were likely higher for invasive river individuals relative to native river individuals because of improved diet under similar thermal regimes and metabolic demands (Figure 1.9).

Faster growth rates in invasive Northern Pike likely led to larger size-at-age compared to native origin Northern Pike (Figures 1.7 and 1.8), which has been observed in other studies comparing size-at-age of invasive and native Northern Pike in Alaska (Berghaus et al. 2019). While size-at-age could only be compared between young individuals, preliminary data suggest that larger size-at-age in invasive relative to native lake individuals continues through age-4 (P. Bradley ADF&G, unpublished data). While we did not have enough individuals to confidently calculate L50 for each sex within each group, mean

L₅₀ for pooled sexes was relatively similar across groups (373 to 512 mm; Table 1.7). This L₅₀ range is similar to the predicted range of L₅₀ for both sexes of native Northern Pike collected from Great Bear Lake in Canada (390-450 mm; Miller and Kennedy 1948), indicating that Northern Pike may have a conserved threshold L₅₀ in northern regions. However, because invasive Northern Pike have faster early growth and larger size-at-age, this threshold size was reached more quickly, resulting in earlier 50% maturity at age estimates of 0.4 years for invasive lake individuals, and 2.2 years for invasive river individuals, compared to 3.3 and 3.0 years for native lake and river individuals, respectively. Similar ages at maturity (2-3 years) have been observed for Northern Pike from Lake Ontario in Canada (Wolfert and Miller 1978), while older ages at maturity (5-6 years), but similar L₅₀ values, have been observed in more northern Canadian populations (Miller and Kennedy 1948). While maturation at 0.4 years is not biologically likely for Northern Pike, that estimate was generated for invasive lake individuals because several YOY Northern Pike had gonads that were visually mature in preparation for spawning the following spring, which would lead to a more accurate maturity at age-1. Furthermore, all sexed individuals from the invasive lake location were male, and as male Northern Pike tend to complete testicular growth during the summer, mature earlier than females, and are capable of 100% maturity by age-1 in other populations (Diana 1983), such an early age at maturity is not necessarily surprising in such ideal environmental conditions. Maturation at age-1 has also been attributed to high fishing mortality for Northern Pike (Diana 1983); therefore, management effects such as gillnetting, in addition to beneficial environmental conditions, may unintentionally contribute to early maturation in invasive individuals. In contrast, management efforts in native ranges in Alaska, such as Minto Flats, are designed to support recreational and subsistence fisheries that focus on preservation of late-maturing, large individuals from sport harvest (ADF&G 2022).

Many invasive species are introduced into novel habitats that differ from their native range, which can initiate selection for or plasticity in traits that further promote their invasion success (Sax et al. 2007; Kinnison et al. 2008; Westley 2011; Hôrková and Kováč 2014). While variation in genotypes and

morphological phenotypes between Alaska invasive and native origin Northern Pike is generally minimal (Jalbert et al. 2018; Berghaus et al. 2019), we have shown evidence of strong physiological trait variation as a function of habitat complexity, prey availability, and thermal conditions. However, the intraspecific variation in growth rates, body condition, and maturation schedules may not only reflect environmental factors, but also underlying conserved genetic machinery.

For example, a countergradient growth relationship is present in Northern Pike, defined as when more northern populations of a species possess greater growth potential to account for shorter growing seasons (Rypel 2012). Therefore, the faster growth observed in invasive Alaskan individuals may be a combination of high growth potential conserved from more northern native origin individuals, slightly longer growing seasons and warmer temperatures in southcentral Alaska, and environmental factors. Countergradient growth due to invasive species introductions from northern to southern regions was found to be a driver of faster growth rates in invasive fishes on a global scale (Rypel 2014). Additionally, compensatory increases in growth rate have been observed in populations of invasive Northern Pike when abundances of conspecifics are reduced through gillnetting (Glenn 2012). Indeed, the variation in physiology and life history between invasive and native Northern Pike we observed here, but lack of clarity on the underlying mechanisms, supports the use of more intensive field and laboratory studies to connect invasive phenotypes to genotypes. For example, common garden approaches rearing Northern Pike from various populations in Alaska under the same conditions could be fruitful to partition environmental and genetic contributions that resulted in the physiological variation we observed (*sensu* David et al. 2015; Tibblin et al. 2015), and could potentially characterize invasive genotypes in Northern Pike that may facilitate faster growth, such as variation in metabolic rates (Metcalfe et al. 2016). As our ability to analyze entire genomes increases in efficiency (Larson et al. 2016) and tissue samples are widely collected, connecting invasive phenotypes to genotypes could lead to tools that could screen for invasiveness genetically, which could predict, prevent, and better manage invasions on a global scale through the lens of Northern Pike as a model organism (Forsman et al. 2015).

In addition to broadscale applications, the differences between habitat types in invasive Northern Pike physiology and life history observed here can have implications for local management and ecosystem ecology in Alaska and elsewhere Northern Pike are invasive. For example, warmer lake systems with abundant, naïve fish prey and some heterogeneity appear to facilitate high fish prey consumption and physiological benefits such as rapid growth and maturation for Northern Pike. While the impacts of Northern Pike are more obvious in isolated lake systems where the species rapidly extirpated soft-rayed salmonids and other fish prey (Patankar et al. 2006; Spens and Ball 2008; Haught and von Hippel 2011), smaller lakes are also easier systems from which to eradicate Northern Pike due to homogeneous environmental conditions (e.g., shallow depths; Dunker et al. 2020). The coexistence of Northern Pike and salmonids in systems such as Nancy Lake may result in more subtle, long-term impacts to the behavior, ecology, and fitness of native fishes as they are forced to occupy pelagic or deep-water habitats away from littorally oriented Northern Pike (Öhlund 2012), and such systems may make future Northern Pike eradication more difficult as they establish robust populations with more prolonged access to fish prey. Future management plans, such as preventing Northern Pike from accessing habitat with selective vertical drop barriers in southcentral Alaska (Chapter 2) can be prioritized by considering which systems would be the most suitable for Northern Pike and detrimental to native fishes if they were to invade with recent intrinsic potential models (Jalbert et al. 2021).

Limitations imposed by high habitat heterogeneity, low growth potential and consumption in cool river systems appear to reduce impacts of Northern Pike on native fishes, with salmon runs still considered sustainable in the Deshka River where Northern Pike have been present for over 30 years (Haught and von Hippel 2011; Sepulveda et al. 2013). However, the same habitat heterogeneity appears to increase dispersal, recruitment, abundance, and eradication difficulty of invasive Northern Pike in warmer systems such as the Yampa River in Colorado, USA (Zelasko et al. 2016). Many northern aquatic habitats, including the Deshka River in Alaska, are warming rapidly (Shaftel et al. 2020), which is predicted to tip range expansion and species interactions in favor of cool-water Northern Pike at the

expense of cold-water Pacific salmonids (Hein et al. 2011; 2014), highlighting the importance of continuous monitoring of impacts by invasive Northern Pike on native fishes in a changing climate (Rolls et al. 2017).

Northern Pike and other invasive piscivorous fishes continue to be a major threat to aquatic biodiversity on a global scale due to strong top-down effects of predation, difficulty of eradication in interconnected aquatic ecosystems, and intentional introductions (Novoa et al. 2020). Here, external factors such as habitat suitability and prey availability influenced physiological and life history traits the greatest, with potential population-level effects that may drive Northern Pike invasion success (Kinnison et al. 2008). Such benefits in growth, lipid accumulation, and maturation schedules have also been shown to interact with habitat type and prey availability in other invasive fishes (Polačík et al. 2009; Haubrock et al. 2021). This degree of intraspecific variation in invasive species warrants localized approaches to streamline management, but also supports assessment of the underlying mechanisms of such variation to develop more advanced screening and decision-making tools that could better predict and prevent biological invasions on a global scale (Ricciardi et al. 2013; Reichard et al. 2015; Packer et al. 2017).

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Table 1.1. Principal component analysis of residual morphometric measurements and associated variance explained for each retained principal component (PC) of morphometric measurements taken on Northern Pike collected from invasive and native ranges in river and lake habitats of Alaska during summer 2020. Loadings greater than 0.3 or less than -0.3 are considered significant and indicated in **bold**.

Trait	PCI	PCII	PCIII	Variation Explained
Body width	0.45	-0.28	0.58	PCI – 57%
Peduncle circumference	0.54	0.18	0.18	
Dorsal fin width	0.43	-0.38	0.02	PCII – 16%
Anal fin width	0.41	-0.29	-0.79	
Caudal fin width	0.38	0.81	-0.12	PCIII – 12%

Table 1.2. Summary of Northern Pike metrics (mean \pm standard deviation) by origin and habitat classification, and for separate locations within origin and habitat designations if applicable. All Northern Pike (N = 123) were collected from lake and river habitats in their native and invasive range in Alaska, USA in 2020.

Group	N	Fork length (mm)	Weight (g)	Age (years)	Growth rate at capture (mm/day)	Age-1 growth rate (mm/day)	Predicted vertebrates in diet	Lipid (% of dry mass)	Dry mass (% of wet mass)
Invasive Lake									
Nancy Lake	30	323.0 \pm 57.6	277.0 \pm 229.0	0.0 \pm 0.36	2.17 \pm 0.41	2.19 \pm 0.31	86.4 \pm 17.8	9.74 \pm 2.26	23.2 \pm 0.69
Invasive River									
Deshka River	28	361.0 \pm 99.0	481.0 \pm 442.0	1.0 \pm 0.63	1.22 \pm 0.50	1.35 \pm 0.39	44.3 \pm 8.59	11.4 \pm 3.78	23.7 \pm 1.35
Native Lake	34	534.0 \pm 185.0	1450.0 \pm 1427.0	4.0 \pm 1.49	0.42 \pm 0.21	0.93 \pm 0.27	62.9 \pm 44.2	7.81 \pm 5.70	24.8 \pm 1.90
Minto Flats	23	630.0 \pm 142.0	2018.0 \pm 1415.0	4.0 \pm 1.59	0.45 \pm 0.23	1.02 \pm 0.29	93.0 \pm 1.97	8.21 \pm 6.64	25.4 \pm 1.93
Mullins Pit	11	333.0 \pm 56.4	262.0 \pm 116.0	3.0 \pm 0.94	0.37 \pm 0.16	0.75 \pm 0.09	0.00 \pm 0.00	6.97 \pm 2.99	23.3 \pm 0.69
Native River	31	439.0 \pm 113.0	721.0 \pm 508.0	2.0 \pm 1.18	0.74 \pm 0.45	1.11 \pm 0.34	42.3 \pm 22.8	8.94 \pm 3.09	24.2 \pm 1.13
Noyes Slough	6	298.0 \pm 115.0	273.0 \pm 268.0	1.0 \pm 0.75	1.41 \pm 0.48	1.38 \pm 0.50	15.0 \pm 5.91	6.88 \pm 3.20	22.9 \pm 1.47
Sternwheeler Pond	4	559.0 \pm 76.9	1373.0 \pm 533.0	2.5 \pm 0.58	0.72 \pm 0.25	1.55 \pm 0.26	8.28 \pm 0.88	13.5 \pm 1.74	24.4 \pm 0.36
Willow Creek	21	457.0 \pm 77.5	725.0 \pm 425.0	3.0 \pm 0.96	0.55 \pm 0.25	0.95 \pm 0.26	56.6 \pm 10.1	8.68 \pm 2.42	24.6 \pm 0.83

Table 1.3. Analysis of variance for principal component analysis (PC) scores among Northern Pike by origin, habitat, sex, maturity, and their interactions if applicable for individuals collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020 (invasive lake = IL, invasive river = IR, native lake = NL, native river = NR). **Bolded** P-values are statistically significant.

Response	Predictor	Class levels	DF	F	P
PC 1 scores	Origin	Invasive, native	1	0.27	0.60
	Habitat	Lake, river	1	2.52	0.12
	Origin*habitat	IL, IR, NL, NR	1	0.624	0.43
	Sex	Male, female, unknown	2	0.70	0.50
	Maturity	Mature, immature	1	0.026	0.87
PC 2 scores	Origin	Invasive, native	1	2.29	0.13
	Habitat	Lake, river	1	11.7	<0.001
	Origin*habitat	IL, IR, NL, NR	1	1.19	0.28
	Sex	Male, female, unknown	2	3.08	0.05
	Habitat*sex	IL male, IL female, IL unknown, etc.	1	2.81	0.06
	Maturity	Mature, immature	1	0.82	0.37
PC 3 scores	Origin	Invasive, native	1	1.06	0.31
	Habitat	Lake, river	1	12.7	<0.001
	Origin*habitat	IL, IR, NL, NR	1	0.57	0.45
	Sex	Male, female, unknown	2	2.68	0.07
	Maturity	Mature, immature	1	5.18	0.02
	Habitat*maturity	IL mature, IL immature etc.	1	1.99	0.16

Table 1.4. Analysis of variance for the predicted proportion of fishes in diet determined from stable isotope mixing models (N= 123), white muscle lactate dehydrogenase (LDH) activity ($\mu\text{mol}/\text{min}/\text{g}$; N = 32), and age-1 growth rate (mm/day) by origin, habitat, sex, maturity, and their interactions (if applicable) for Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020 (invasive lake = IL, invasive rive = IR, native lake = NL, native rive = NR). **Bolded** P-values are statistically significant.

Response	Predictor	Class levels	DF	F	P
Proportion fish in diet	Origin	Invasive, native	1	7.47	0.007
	Habitat	Lake, river	1	42.3	<0.001
	Origin*habitat	IL, IR, NL, NR	3	5.24	0.02
	Sex	Male, female, unknown	2	2.15	0.12
	Maturity	Mature, immature	1	0.01	0.98
White muscle LDH	Origin	Invasive, native	1	0.01	0.92
	Habitat	Lake, river	1	8.14	0.009
	Origin*habitat	IL, IR, NL, NR	1	0.02	0.90
	Sex	Male, female, unknown	2	1.72	0.20
	Maturity	Mature, immature	1	0.20	0.66
Age-1 growth rate	Origin	Invasive, native	1	155.0	<0.001
	Habitat	Lake, river	1	24.0	<0.001
	Origin*habitat	IL, IR, NL, NR	1	67.4	<0.001

Table 1.5. Summary of sample sizes, proximate components (mean \pm SD), mean energy density (kJ/g), and bioelectrical impedance analysis (BIA) model R^2 and Root Mean Squared Error (RMSE) values for BIA-developed % dry mass (%DM) and % dry lipid (%DL) models for Northern Pike collected from invasive and native ranges and river and lake habitats in Alaska during Summer 2020.

Group	N	% Dry mass	Dry % lipid	Dry % protein	Energy Density	%DM BIA model R^2 and RMSE	%DL BIA model R^2 and RMSE
Invasive	22	24.6 \pm 1.13	10.2 \pm 2.31	73.8 \pm 1.99	18.5	0.66, 0.33	0.55, 1.59
Lake							
Invasive	20	23.7 \pm 1.54	12.1 \pm 4.05	70.8 \pm 3.28	18.6	0.72, 0.66	0.58, 1.61
River							
Native	26	25.2 \pm 1.93	7.36 \pm 6.39	74.4 \pm 5.31	17.6	0.71, 0.94	0.86, 2.19
Lake							
Native	23	24.6 \pm 1.13	8.61 \pm 3.11	74.2 \pm 2.47	18.1	0.49, 0.60	0.35, 1.71
River							

Table 1.6. Analysis of covariance for % dry mass (%DM) and % dry lipid (%DL) as a function of fork length, origin, habitat, sex, maturity, and interactions if applicable for Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020 (invasive lake = IL, invasive river = IR, native lake = NL, native river = NR). **Bolded** P-values are statistically significant.

Model	Variable	Class levels	DF	F	P
Dry mass	Fork length	Continuous	1	47.9	< 0.001
	Origin	Invasive, native	1	2.06	0.15
	Habitat	Lake, river	1	0.18	0.67
	Origin*habitat	IL, IR, NL, NR	1	0.31	0.58
	Sex	Male, female, unknown	2	2.31	0.10
	Maturity	Mature, immature	1	1.06	0.31
Lipid	Fork length	Continuous	1	5.93	0.02
	Origin	Invasive, native	1	30.1	< 0.001
	Habitat	Lake, river	1	5.52	0.02
	Origin*habitat	IL, IR, NL, NR	1	0.90	0.34
	Sex	Male, female, unknown	2	0.41	0.66
	Maturity	Mature, immature	1	5.23	0.02

Table 1.7. Summary of sample sizes, fork lengths (mm; mean \pm SD), weights (g; mean \pm SD), age (y; median \pm SD), and length at 50% maturity (L50), age at L50, and associated 95% confidence intervals for Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020.

Group	N	Fork	Weight	Age	L50	95% CI	Age	95% CI
		Length			L50	at L50	Age at L50	
Invasive	30	323.0 \pm 57.0	277.0 \pm 229.0	0.0 \pm 0.36	373.0	[347.0, 447.0]	0.39	[0.09, 0.69]
Invasive	28	362.0 \pm 99.0	481.0 \pm 442.0	1.0 \pm 0.63	512.0	[449.0, 602.0]	2.21	[1.88, 2.55]
Native	34	535.0 \pm 185.0	1450.0 \pm 1427.0	4.0 \pm 1.41	456.0	[259.0, 585.0]	3.29	[3.19, 3.39]
Native	31	439.0 \pm 114.0	721.0 \pm 508.0	2.0 \pm 1.18	482.0	[426.0, 542.0]	3.00	[2.82, 3.18]

Table 1.8. Analysis of covariance for back-calculated fork length (mm) as a function of age (y), origin, habitat, sex, and interactions if applicable for Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020 (invasive lake = IL, invasive rive = IR, native lake = NL, native rive = NR). **Bolded P**-values are statistically significant.

Model	Variable	Class levels	DF	F	P
Fork length	Age	Continuous	1	110.0	<0.001
	Origin	Invasive, native	1	45.9	<0.001
	Habitat	Lake, river	1	8.26	0.004
	Origin*habitat	IL, IR, NL, NR	1	33.2	<0.001

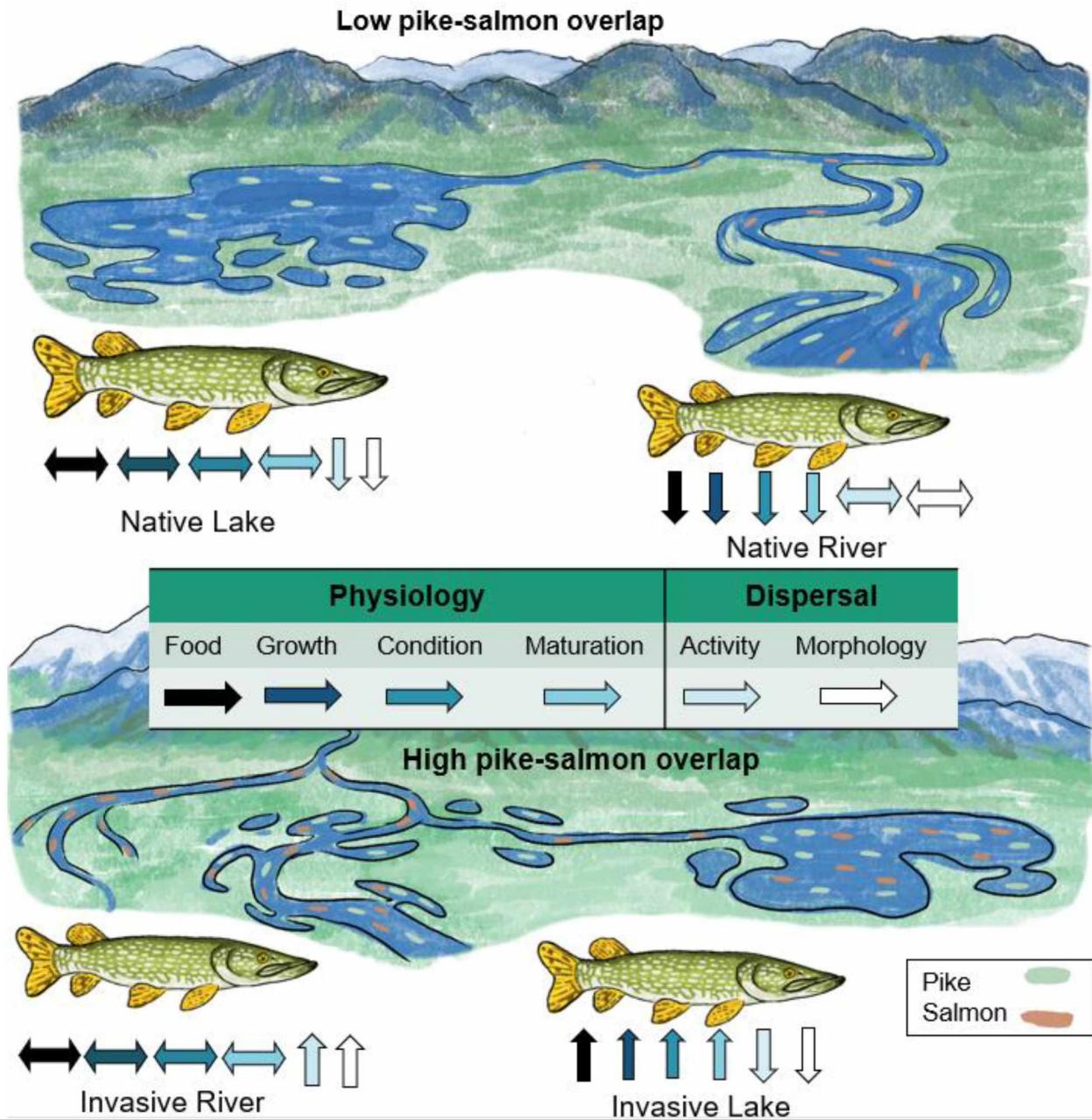


Figure 1.1. Conceptual model of hypothesized metric values (food, growth rate, body condition, maturation, activity level, and morphology related to physiology or dispersal; see text for details) as a function of Northern Pike habitat type and origin (native lake, native river, invasive lake, and invasive river) for Northern Pike collected in Alaska during summer 2020. Food availability (salmonids) is hypothesized to positively affect growth, body condition, and maturation, whereas activity level and morphology is hypothesized to be affected by habitat complexity and higher dispersal tendencies in invasive Northern Pike. Upward arrows indicate high, downward arrows indicate low, and double-sided arrows indicate moderate metric values. Aquatic habitats and locations of Northern Pike and salmonids are not geographically or spatially precise, but meant to illustrate known differences in habitat connectivity and species overlap between native and invasive Northern Pike ranges. Artwork by T. Cubbage.

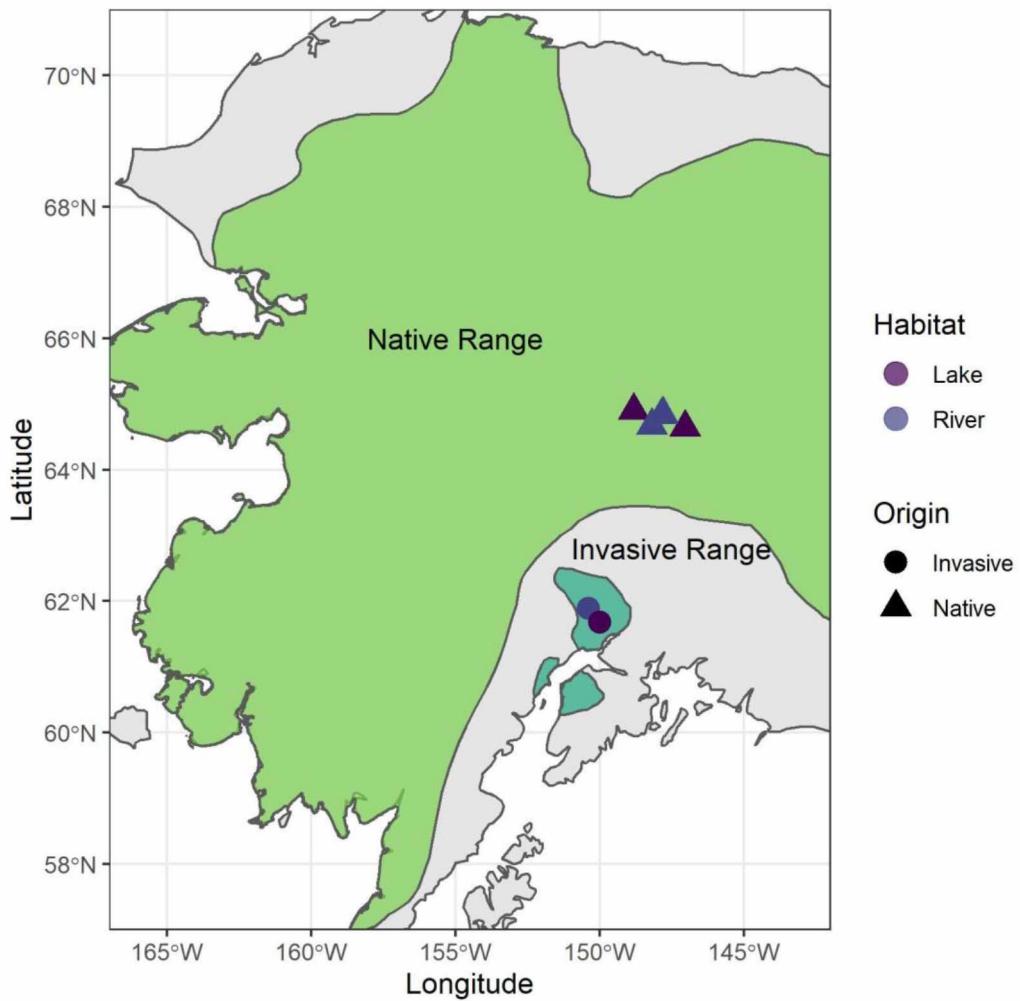


Figure 1.2. Northern Pike collection locations from lake and river habitats in their native and invasive range in Alaska, USA in 2020.

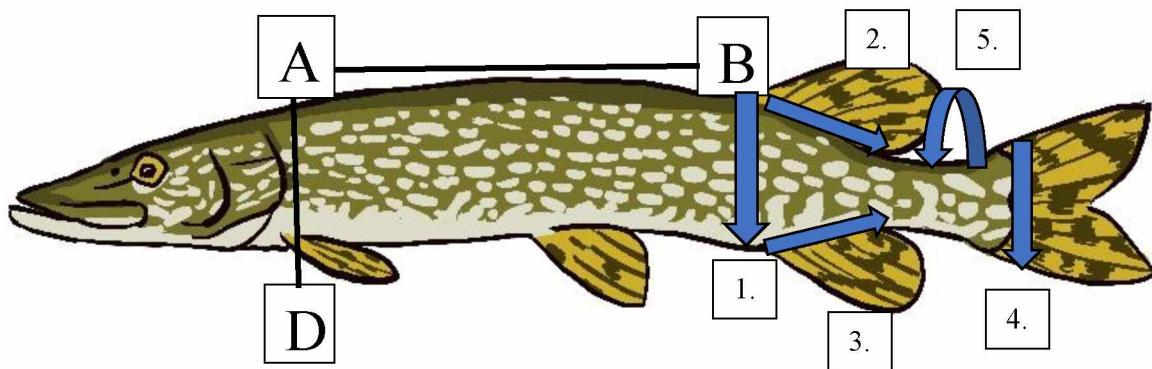


Figure 1.3. Diagram of dorsal midline (A to B) and dorso-ventral (A to D) bioelectrical impedance analysis measurements taken on each Northern Pike collected from native and invasive ranges in both river and lake habitats in Alaska during summer 2020. Blue arrows represent morphometrics taken: 1. body depth, 2. dorsal, 3. anal, and 4. caudal fin widths, and 5. peduncle circumference. Artwork by T. Cubbage.

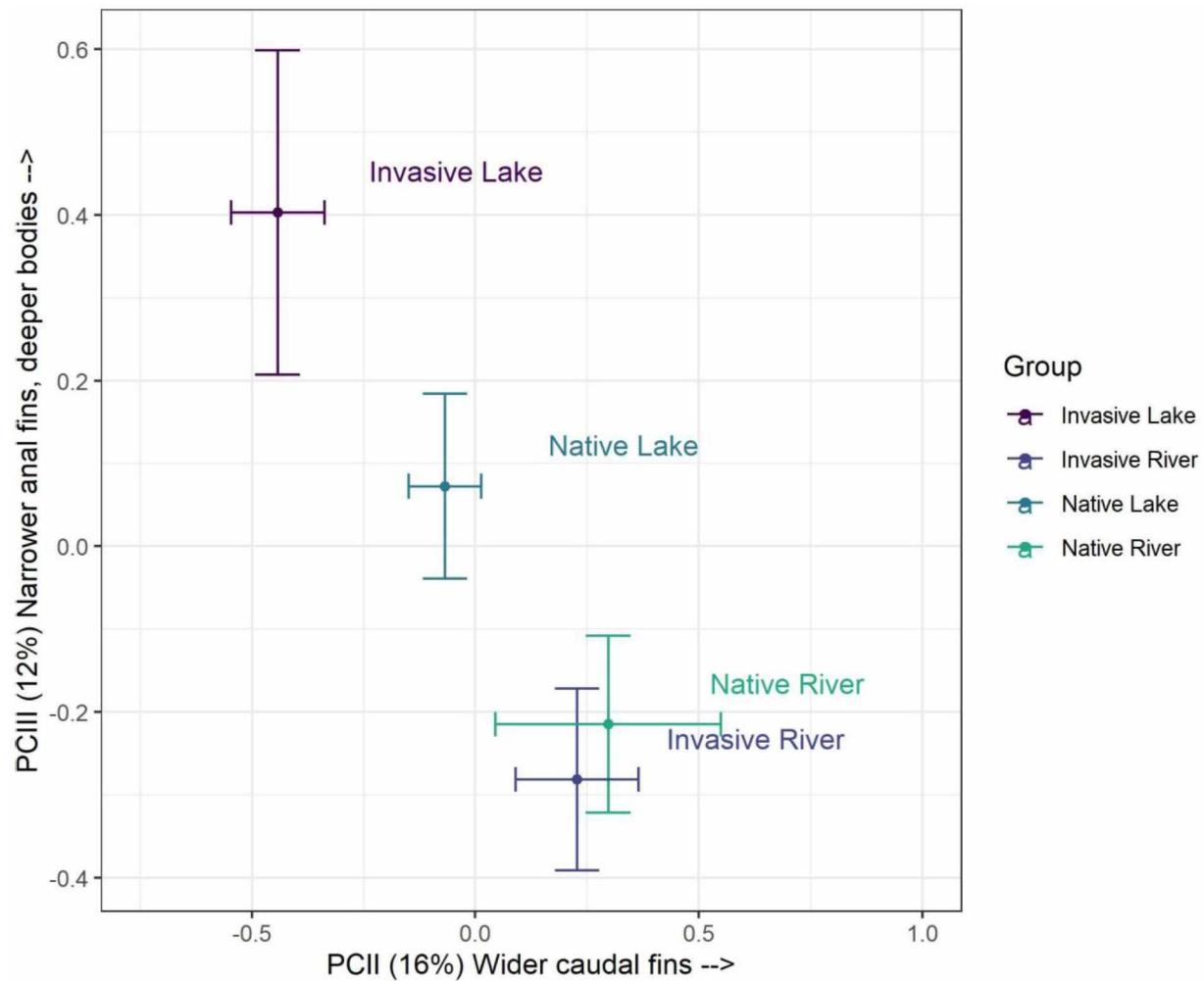


Figure 1.4. Retained principal component scores from principal component analysis of size-standardized morphometric traits from 123 Northern Pike collected from lake and river habitats in their native and invasive ranges in Alaska, USA in 2020.

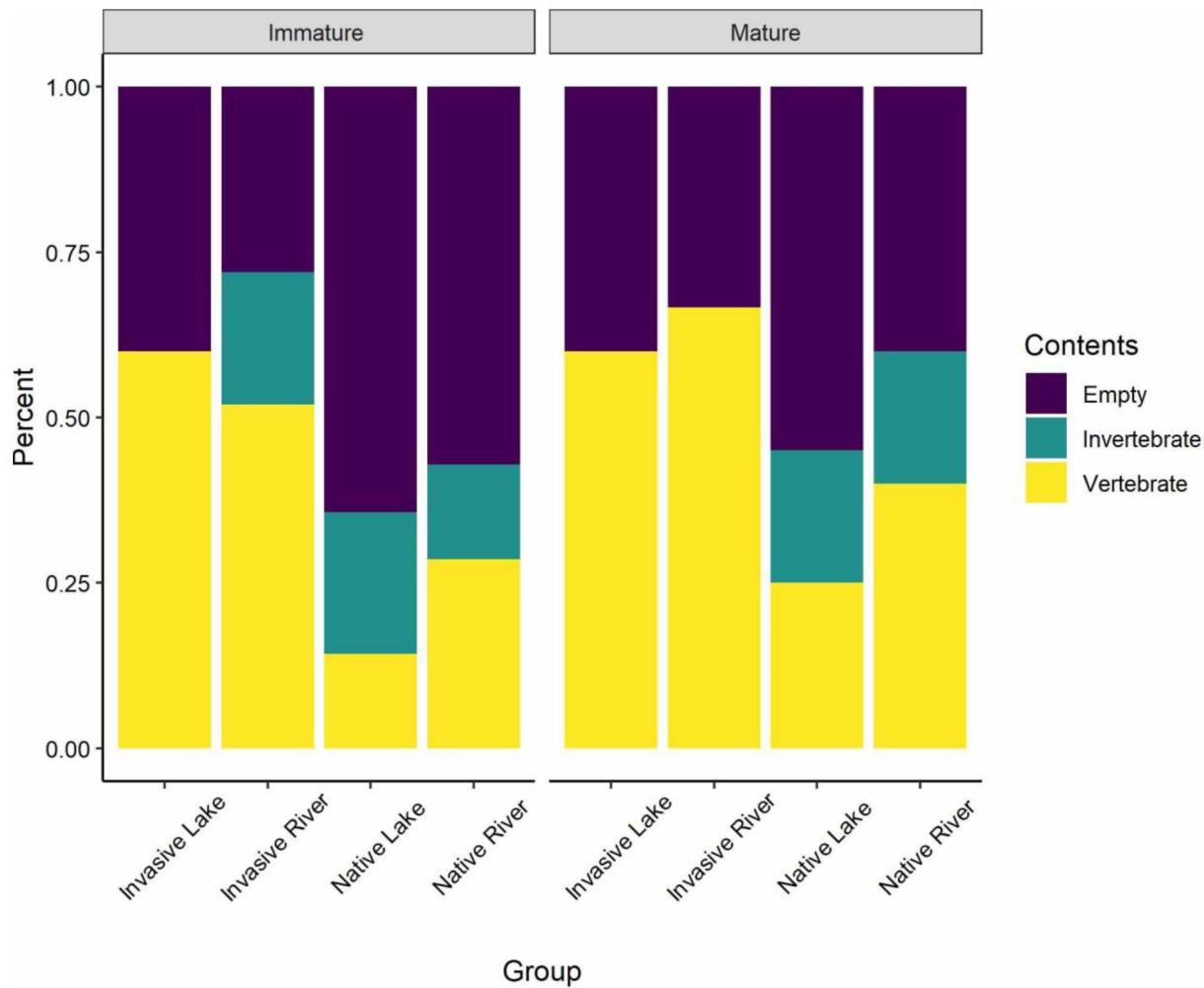


Figure 1.5. Proportion of stomach contents (empty, invertebrate, and vertebrate) by group and maturity status for Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020.

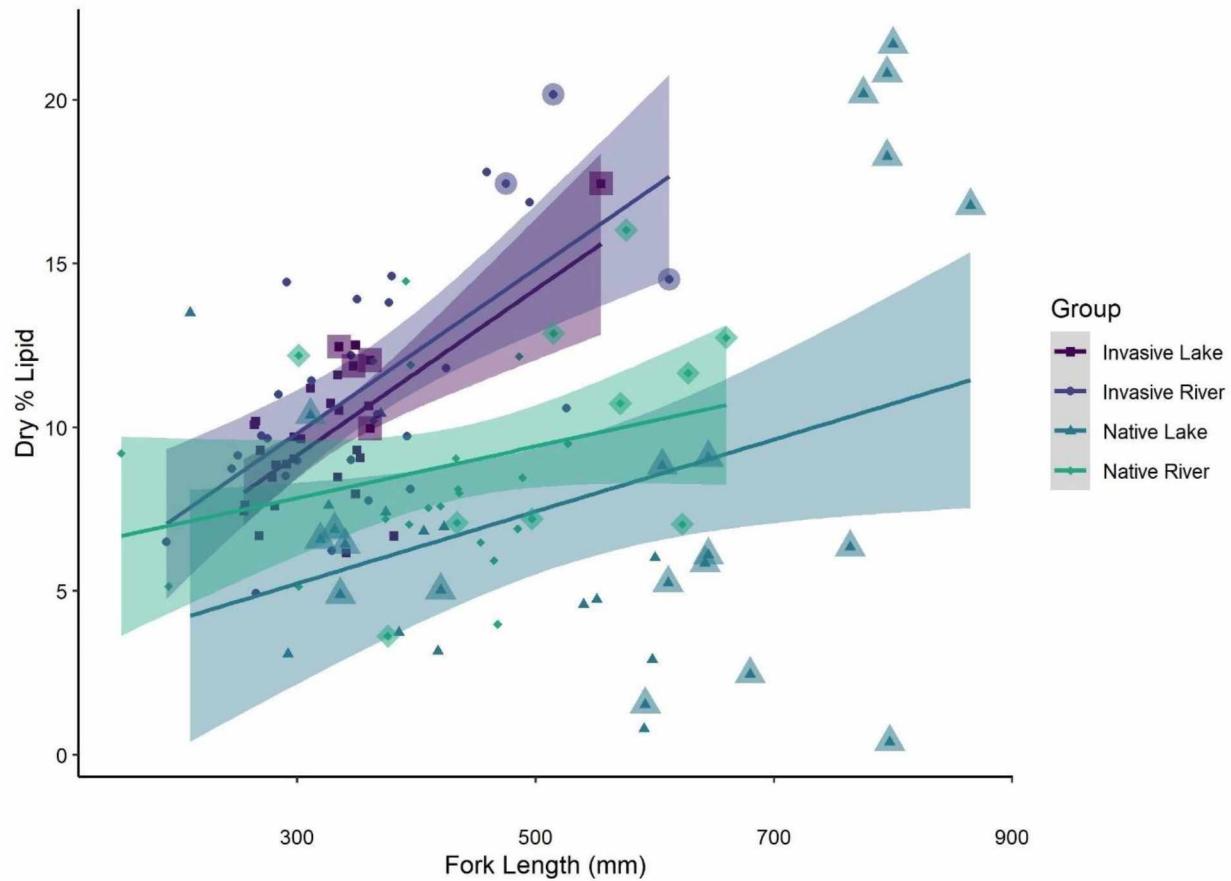


Figure 1.6. Dry % lipid as a function of fork length by origin for 123 Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020. Shaded areas represent 95% confidence intervals of linear regression models for each group. Mature individuals are designated by transparent outer shapes.

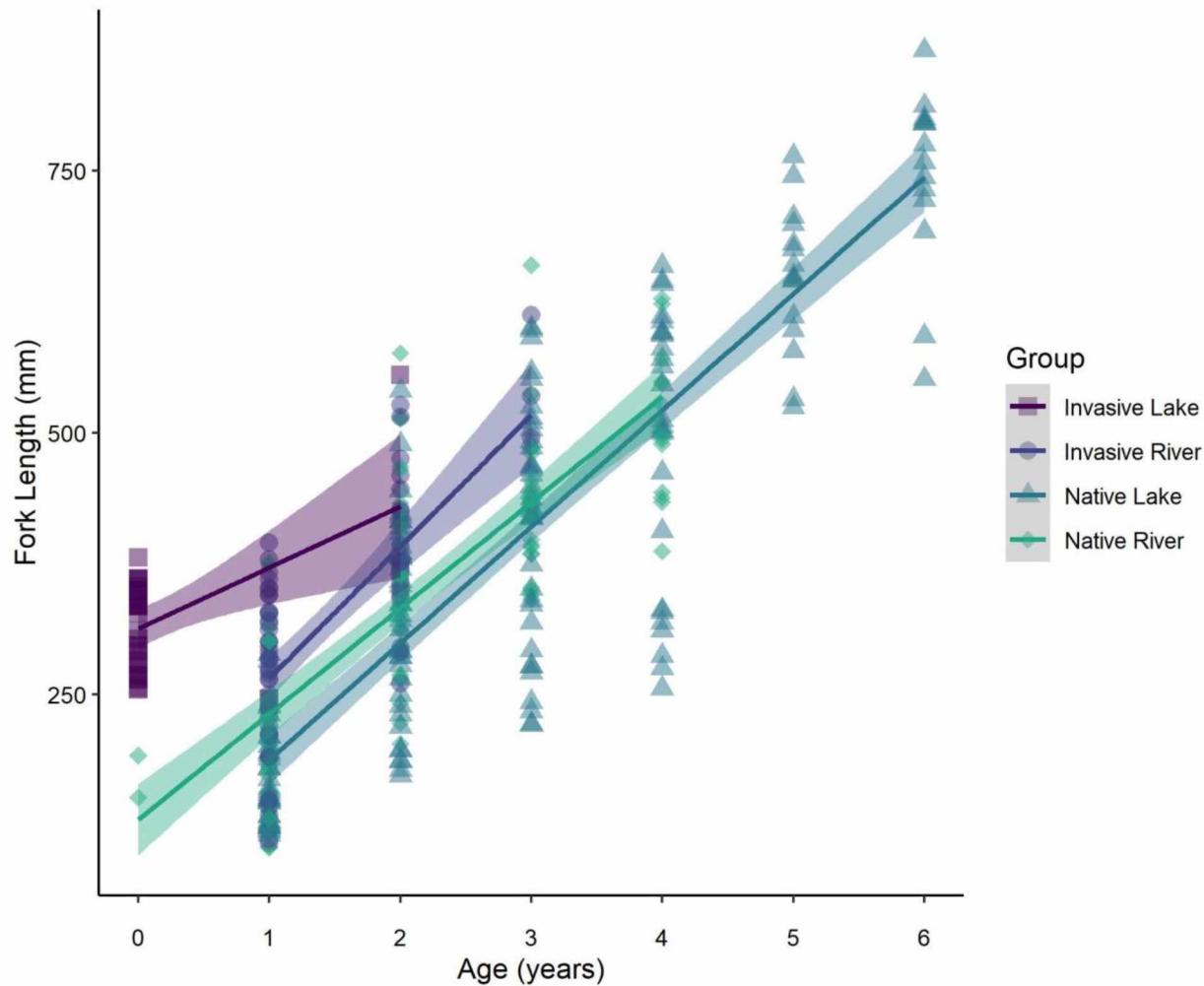


Figure 1.7. Fork length as a function of age by population for observed and back-calculated lengths and ages of Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020. Shaded areas represent 95% confidence intervals of linear regression models for each group.

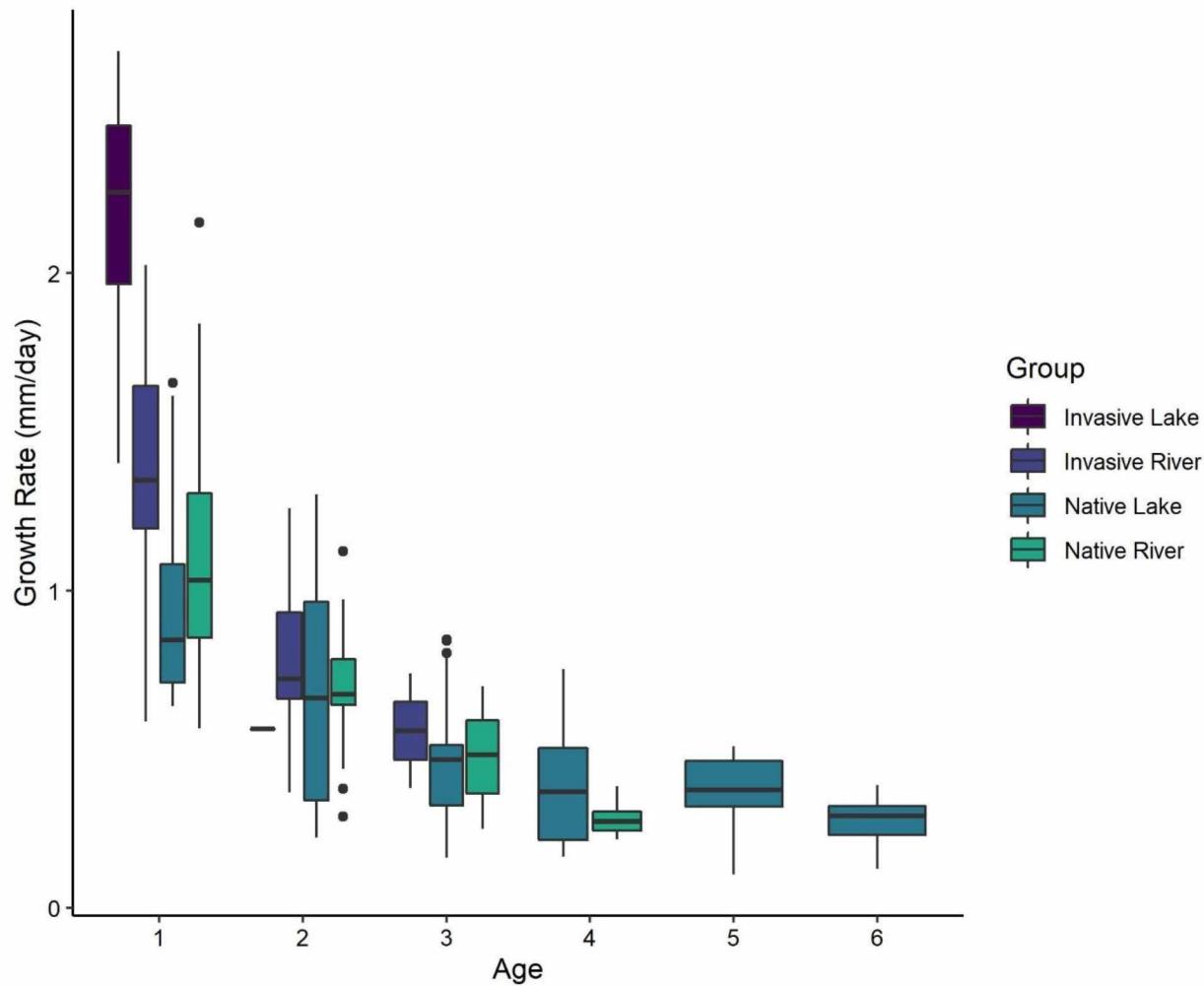


Figure 1.8. Growth rate (mm/day) by age and group, for Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020. Box plot bars represent mean values, boxes represent interquartile ranges, whiskers represent minimum and maximum values, and dots represent outliers.

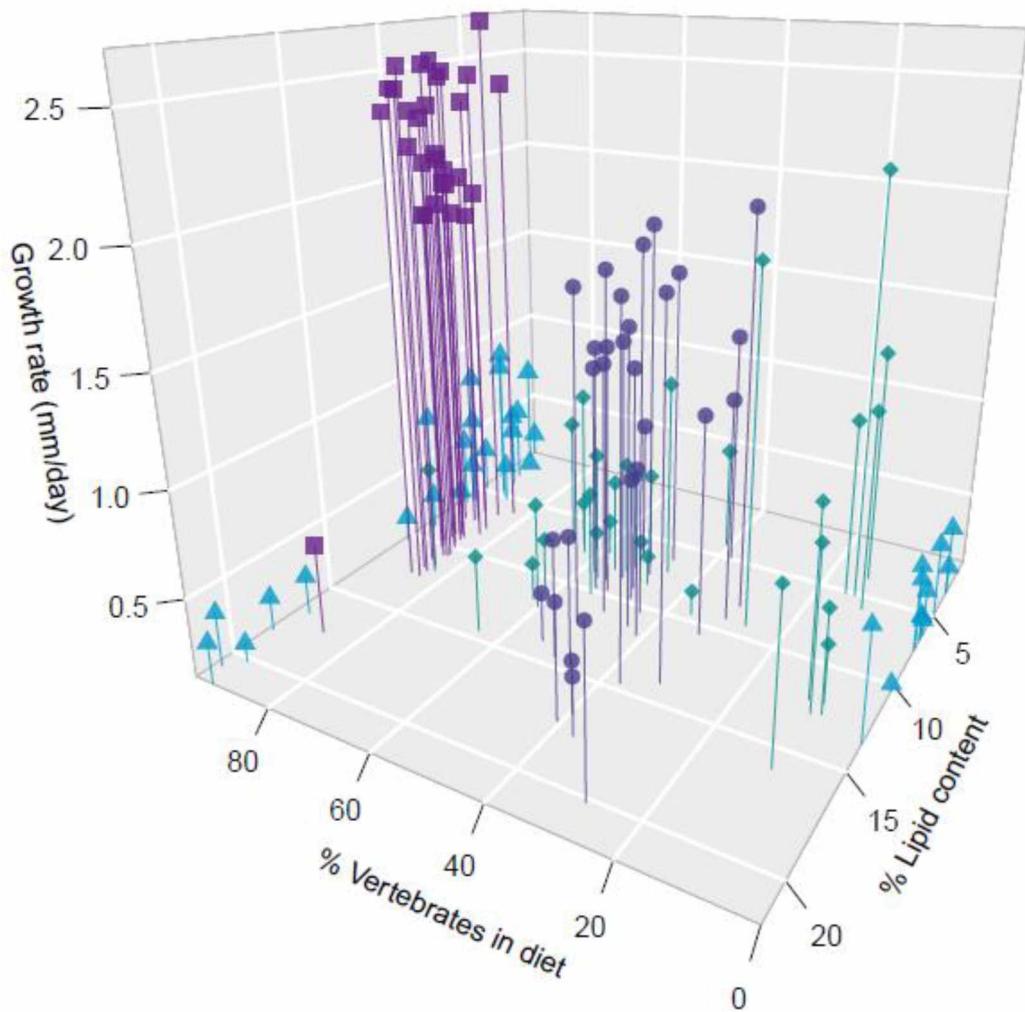


Figure 1.9. 3D scatter plot of estimated % vertebrate diet contributions, % dry lipid content, and average growth rate in the year prior to capture of 123 Northern Pike collected in invasive and native ranges from river and lake habitats in Alaska during summer 2020. Invasive lake individuals are represented by squares, invasive river individuals represented by circles, native lake individuals represented by triangles, and native river individuals represented by diamonds.

Chapter 2: Factors affecting the leap success of Northern Pike (*Esox lucius*): implications for barrier design in invaded systems²

Abstract

Preventing the spread of aquatic invasive species can increase management efficacy, with selective techniques that exploit interspecific variation emerging as a novel tool to target invaders while reducing impacts on native species. The invasion of predatory Northern Pike (*Esox lucius*) throughout the western United States and southcentral Alaska into salmonid habitats may be an opportunity for such a tool, as inherent variation in the behavior, physiology, and assumed leaping ability between Northern Pike and salmonids may make selective vertical drop barriers a potential management option. During the summer of 2021, we evaluated the leaping ability of Northern Pike over barriers in a 17-m-long open channel flume system in the context of salmonid leaping abilities. Maximum leaping ability of Northern Pike was assessed as a function of barrier height (10 to 65 cm), plunge pool depth (20 to 80 cm), flow rate (11.4 to 42.9 L/s), and their interactions, with individual characteristics of Northern Pike, including fork length, body condition, growth rate, morphometrics, and anaerobic metabolic capacity, analyzed as covariates to understand biological drivers of intraspecific variation in leaping ability. The likelihood of successful passage was strongly reduced with increasing barrier height and optimized at pool depths from 40 to 65 cm, but did not vary with flow rates. Optimum pool depth for successful passage increased with fork length, and passage success was greater for individuals with faster growth rates-at-age, which may reflect a culmination of physiological benefits, but was not affected by other biological traits. The final model was used to predict and compare the leaping ability of Northern Pike used in leaping trials to those collected in Alaska; faster growth rates led to an average 4% predicted increase in leap success for Alaskan individuals. These insights into Northern Pike leaping behavior can help managers determine if

²Cubbage, T. L., J. A. Falke, K. Dunker, M. Blank, and K. Kappeman. 2022. Factors affecting the leaping ability of Northern Pike (*Esox lucius*): implications for barrier design in invaded systems. Formatted for the *Transactions of the American Fisheries Society*.

selective barriers could be a potential option in southcentral Alaska and elsewhere Northern Pike are invasive, and supports utilization of both inter and intraspecific variation in invasive species ecology and management.

Introduction

Aquatic invasive species (AIS) are a growing threat to freshwater biodiversity on a global scale, and negatively impact ecosystems, communities, and economies that depend on healthy natural resources (McNeely 2001; Charles and Dukes 2008; Early et al. 2016; Pyšek et al. 2020). Management of invasive species typically follows a hierarchy of tactics that include prevention, eradication, and suppression. However, effective management techniques must be adaptive to the potential extent of invader spread, habitat complexity, conflicting ecological and socioeconomic needs, and growing impacts to native species (Mehta et al. 2007, Larson et al. 2011; Dunker et al. 2020). For example, barriers to upstream passage have historically been considered beneficial to block invasive fish species (Behnke and Zarn 1976; Thompson and Rahel 1998; Novinger and Rahel 2003), but barriers may reduce essential habitat connectivity for native species and alternative methods that address this issue are necessary (Fausch et al. 2009). An emerging solution is selective fragmentation, whereby physical, behavioral, chemical, or phenological discrepancies between species are used to design selective barriers that facilitate passage of desirable fishes while excluding or sorting out invaders (Rahel and McLaughlin 2018; Zielinski et al. 2020; Jones et al. 2021a). Because leaping ability varies considerably among fish species, physical selective fragmentation by fish leaping ability has emerged as a useful method to prevent invasive fishes from upstream movement (Lavis et al. 2003; Holthe et al. 2005; Gardunio 2014; Morán-López and Tolosa 2017; Rahel and McLaughlin 2018; Jones et al. 2021a).

Decades of fish passage work on salmonids (Stuart 1962, Powers and Orsborn 1985) and recent interest in the leaping ability of other fish taxa (Silva et al. 2018) have identified general trends in how fish leaping ability is affected by abiotic (physical) factors. For example, studies using adjustable waterfall designs and open channel flumes have determined that passage success expectedly declines with

increasing barrier height, and fish leaping ability is generally reduced as pool depths decrease because there is less space in the lower pool for fish to orient vertically for a well-positioned leap (Stuart 1962; Powers and Orsborn 1985; Kondratieff and Myrick 2005; Katopodis and Gervais 2016; Amaral et al. 2016). Flow rate can negatively affect leaping ability due to greater turbulence and orientation difficulty in the lower pool, and greater difficulty in tailing behavior that fish often utilize if they reach the barrier crest (Lauritzen et al. 2010; Amaral et al. 2016). Fish leaping ability is also moderated by water temperature (Ficke et al. 2011; Gardunio 2014), waterfall width (Brandt et al. 2005), and waterfall crest depth (Powers and Orsborn 1985; Gardunio 2014). Considerable variation in leaping ability exists among species and life stages, generally with smaller, more sedentary species and juveniles having reduced leaping ability relative to larger, more active migratory species and adults (Mueller et al. 2008; Ficke et al. 2011; Prenosil et al. 2016; O’Keefe 2021; Jones et al. 2021b). However, variation within species during a certain life stage, such as body size and condition, have received less research attention (but see Kondratieff and Myrick 2006, Gardunio 2014, Morán-López and Tolosa 2017; and Jones et al. 2021b).

Characterizing how intraspecific variation affects fish leaping ability is essential to understand underlying behavioral and physiological mechanisms and maximum capabilities of high-performance individuals, which can increase confident transferability of experimental results to real-world populations (Rahel and McLaughlin 2018; Birnie-Gauvin et al. 2019). Intraspecific variation is particularly relevant in the context of invasive species, because invasive and native populations can have considerable variation in traits that may enhance or reduce dispersal tendencies and thus leaping success. For example, invasive fishes can often benefit from abundant prey resources and enemy release when introduced into new ecosystems (Sih et al. 2010; Heger et al. 2018; Chapter 1), which can increase fish growth and body condition (Polačík et al. 2009; Zelasko et al. 2016; Chapter 1) and positively influence dispersal (Midwood et al. 2016) and/or leaping ability (Gardunio 2014). Additionally, invasive fishes can experience rapid changes in aspects of morphology or metabolic traits that favor dispersal (Westley et al. 2012; Myles-Gonzales 2015) as a function of exposure to novel habitats and subsequent adaptive

phenotypic plasticity or contemporary evolution (West-Eberhard 2003; Facon et al. 2006; Ghalambor et al. 2007; Sax et al. 2007). Variation in metabolism has ecological consequences relating to dominance, foraging, swimming performance, endurance, and barrier passage in fishes (Martinez et al. 2003; Burton et al. 2011; Metcalfe et al. 2016; Jones et al. 2021b), and variation in morphology such as wider fin widths, streamlined body depths, and wider peduncle circumferences can enhance burst swimming, startle responses, and leaping ability (Frith and Blake 1991; Jones et al. 2020, Jones et al. 2021b; Sánchez-González et al. 2022). Therefore, assessment of how traits that may vary between invasive and native populations influence maximum leaping ability will be essential for more confident application of research results to invasive populations outside of experimental individuals.

The predatory Northern Pike (*Esox lucius*) is a prime example of a widely distributed and impactful invasive species (Muhlfeld et al. 2008; Hesthagen et al. 2015; Dunker et al. 2018). Northern Pike possess many characteristics common to successful invaders and exhibit high propagule pressure as a valued food and sport fish, leading to many successful introductions in Europe and North America, including Alaska, USA (Lever 1996; Dunker et al. 2018; Cathcart et al. 2019; Fuller and Neilson 2021). While Northern Pike are native to northwestern Alaska, USA, illegal introductions of Northern Pike into southcentral Alaska have resulted in considerable impacts to native fish assemblages and the communities that rely on these resources (Dunker et al. 2020). The proximity of invasive and native-origin Northern Pike in Alaska has facilitated ecological, genetic, morphological, and physiological comparisons between populations to better understand drivers of invader impacts and inform management actions (Cathcart et al. 2019; Berghaus et al. 2019; Jalbert et al. 2021; Campbell et al. 2022). In Alaska, Northern Pike benefit physiologically from abundant fish prey in the invasive range, with faster growth rates, greater lipid content, and earlier ages at maturity relative to native individuals (Chapter 1), which likely contributes to their invasion success.

A variety of prevention, eradication, and suppression tactics are employed to manage Northern Pike in Alaska, including: gillnetting to suppress population numbers, liberalized fishing regulations,

eradication with piscicide in shallow, isolated lakes, monitoring vulnerable habitat with gillnets and environmental DNA sampling, and prevention of further illegal introductions through public outreach (Dunker et al. 2020; Bradley et al. 2020; Dunker et al. 2022). Owing to the high degree of freshwater connectivity and evidence that Northern Pike can cross wide (30 km) estuarine corridors such as Cook Inlet (Dunker et al. 2022), the risk that Northern Pike will invade new habitats in southcentral Alaska is high and severely limits the justification of more extensive eradication efforts. Salmonids are one of the main taxa that Northern Pike impact in southcentral Alaska (Sepulveda et al. 2015; Jalbert et al. 2021) and these species differ considerably in life history, behavior, and phenology. For example, Northern Pike are ambush predators that prefer slow moving, vegetated habitat and remain relatively inactive except when moving into flooded littoral areas for spring spawning (Rutz 1996; Roach 1998; Albert 2016). In contrast, most Alaskan salmonid species in adult stages are active foragers that seek out cold, highly oxygenated, and fast flowing rivers and undergo extensive spawning migrations in the summer and fall (Bjornn and Reiser 1991), which can require overcoming upstream barriers (Lauritzen et al. 2005).

Indeed, adult salmonids are more efficient at upstream and downstream passage through velocity fishways when compared to non-salmonids such as Northern Pike (Noonan et al. 2012), and while a systematic assessment of Northern Pike leaping ability has not been conducted, predictive studies have assumed that Northern Pike are unable to ascend vertical drops greater than 10 cm (Diebel 2013). Closely related invasive Muskellunge (*Esox masquinongy*) are generally deterred by vertical drop barriers at fish passage facilities used to attract Atlantic Salmon (*Salmo salar*) on the Saint John River, Canada (Chateauvert et al. 2018), but native Muskellunge have been documented to ascend a low-head (< 0.5 m) dam on Lake Wingra in Madison, Wisconsin USA (Jarnigo and Tauchen 2018). In contrast, assessments of salmonid leaping abilities indicate that juveniles and adults can ascend barrier heights from 26 cm to greater than 100 cm (Powers and Orsborn 1985; Lauritzen et al. 2005; Kondratieff and Myrick 2006; Mueller et al. 2008; Lauritzen et al. 2010; O'Keefe 2021) which may be considerably greater than

Northern Pike abilities and supports the exploration of selective vertical drop barriers as a management tool for invasive populations.

Here, our main goal was to characterize maximum leaping ability of Northern Pike under various abiotic and biotic conditions to determine if Northern Pike leaping ability is reduced relative to those documented for native salmonids. Two separate experiments were conducted to determine how Northern Pike leaping ability was affected by 1. barrier height, pool depth, and their interaction, and 2. barrier height, pool depth, flow rate and their interactions, with individual morphological and physiological traits of Northern Pike considered as covariates. We hypothesized that passage success would decrease with barrier height, increase with pool depth, and decrease with flow rate as water turbulence increased (Towler et al. 2015). Whereas small fish are often limited by the absolute height they can ascend, large fish are limited by shallow pool depths because they cannot orient vertically in the pool for a well-positioned jump (Powers and Orsborn 1985). Therefore, we attempted to utilize a wide range of Northern Pike size classes to capture important interactions between pool depth, barrier height, and individual body size. We hypothesized that leap success would increase for individuals with greater body condition, faster growth rates, and higher metabolic capacity associated with swimming endurance (Martinez et al. 2003; Gardunio 2014). Lastly, we hypothesized that large fin widths, narrower body depths, and larger peduncle circumferences would positively affect Northern Pike leaping ability, because these morphological characteristics facilitate burst swimming and leaping ability (Langerhans 2008; Senay et al. 2017; Jones et al. 2021b; Sánchez-González et al. 2022). Our final objective was to develop a model based on our experimental results that could be used to predict and contrast leaping ability of Northern Pike used in related experiments with Northern Pike from Alaska due to known physiological advantages of this population (Chapter 1). Quantifying the maximum barrier height that Northern Pike can ascend across variable depths and flow rates, and how this may vary across intraspecific biological trait variation is an important first step towards determining the utility of selective vertical drop barriers to manage invasive Northern Pike.

Methods

Northern Pike collection and husbandry

Northern Pike were collected via gillnets in early April 2021 from Fort Peck Reservoir, Montana, USA to be used for leaping experiments. Northern Pike were handled with great care and transported in well-oxygenated tanks filled with reservoir water to the Bozeman Fish Technology Center (BFTC) for a duration of six hours, with no mortalities during or immediately after transport. Individuals were transferred to their final holding tank, an indoor 34,000 L flow-through riverine tank (HydroComposites, LLC, Stockdale, TX), with a mean flowrate of 69.4 L/s to ensure fish were acclimated to moderate flows before leaping experiments (Davison et al. 1989; 1997). For the duration of the study (April 7 – July 21), the holding tank was maintained at a mean temperature of $10.2 \pm 1.8^\circ\text{C}$, pH of 7.9 ± 0.2 , and dissolved oxygen content of $7.09 \pm 0.9 \text{ mg/L}$ and was monitored three times weekly. Rainbow trout (*Oncorhynchus mykiss*) were raised according to standardized methods in Piper et al. (1982) to provide live food for Northern Pike. Fifty to one hundred Rainbow Trout with fork lengths (FL) of 100 – 200 mm were added to the holding tank once a month to ensure *ad libitum* food conditions for Northern Pike, with Rainbow Trout fed once daily while in the holding tank.

PIT Tagging and holding tank design

Northern Pike were weighed (g), measured for FL (mm), and tagged with 23 mm half duplex (HDX) Passive Integrated Transponder (PIT) tags (Oregon RFID, Portland OR, USA) to track leaping ability as a function of individual biological characteristics and limited re-use throughout the trials. The holding tank was divided into two 17,000 L sections with metal 1 x 1-cm mesh screens to separate Northern Pike that had been included in leaping experiments from those that had not yet been used. After being used in a trial, Northern Pike were placed in a 1100 L flow-through tank with a salt solution of ~1% for 24 hours to promote slime production and potential stress or wound recovery, and then placed into the “used” section of the holding tank with other individuals. Temperature, pH, and dissolved oxygen measurements were taken three times weekly in the recovery tank, with a mean temperature of $10.3 \pm$

1.1°C, pH of 7.8 ± 0.1 , and dissolved oxygen of 8.15 ± 0.3 mg/L for the duration of the study. Northern Pike holding and experimental conditions were maintained at 10-11°C to mimic cooler spring water temperatures that Northern Pike may encounter as they migrate to spawn in southcentral Alaska's waterways (Shaftel et al. 2020).

Flume design and construction for leaping experiments

The outdoor open-channel flume system (Figure 2.1) was composed of a 17-m long, 1.2-m wide, 1.4-m tall fiberglass channel with windows every 0.4 m on one side (Figure 2.1A), and concrete headwater (Figure 2.1B) and tailwater (Figure 2.1C) boxes above and below the fiberglass channel. Freshwater was piped from nearby natural springs into the headwater and tailwater boxes, with separate warm and cold-water valves to regulate water temperature and flow rate. This water recirculated through a 38,000 L in-ground sump with a 20 horsepower (hp) and 40 hp pump system (Figure 2.1D, Prime Pump Corp., Berkeley, CA) to the headwater pool via a 45-cm diameter polyvinyl chloride (PVC) pipe (Figure 2.1E). Flowrate was measured with a flywheel flowmeter suspended in the PVC pipe (Figure 2.1F), and water temperature was measured with a temperature probe in the sump (Figure 2.1G) and monitored against flume water temperatures periodically with an Ertco-Eutenechnics Model 4400 digital thermometer (Alpha Technics Oceanside, CA). Pumps were set to desired flow rates with an automated control panel (Precision Automation Systems, Boise, ID), and real-time temperature and flow rate were monitored with the control panel interface.

The flume was separated into three sections using PVC screens and 1 x 1-cm plastic mesh, placed at the downstream end of the flume and every 4.3 m upstream (Figure 2.1.4). Tongue-and-groove pine boards were cut to fit indentations in the flume walls and stacked in the middle of each flume section to create equal sized 2.15-m long upper and lower pools (Figure 2.1.5). The greatest number of boards were placed in the pool closest to the headwater box (Figure 2.1.3), with decreasing board numbers in pool 2 and pool 1 (Figure 2.1.2 and 2.1.1) towards the tailwater box. In this way, a series of three cascading plunge pool and barrier combinations was created with the number of boards in the lower section

regulating the plunge pool depth of the section above it. Boards were also placed in the tailwater box (Figure 2.1C) to create the desired depth for plunge pool 1. A multi-antenna HDX reader (Oregon RFID, Portland OR, USA) PIT antenna system was used to detect passage success of Northern Pike during experiments. One PVC-encased antenna was placed 1.6 m upstream of the barrier in each upper pool to detect fish if they ascended the barrier (Figure 2.1.6), and all three antennas were connected to the HDX reader powered with an American wire gauge (AWG) battery (Duracell Inc., Bethel, CT) to detect passage success during overnight trials. The operation of three trials simultaneously per day was essential to maximize experimental time in the multi-use flume system and reduce effects of captive holding duration on test fish. Additionally, the operation of three antennas simultaneously and small plunge pool design precluded the use of a second set of antennas at the base of the weir to detect attraction efficiency, which was instead visually observed in a subset of video recordings of leaping trials.

Experimental treatments

Height and depth

The number of dam boards were manipulated among the three flume sections to create 16 repeatable height and depth treatments. The treatments were an incomplete factorial combination of seven barrier heights (10, 15, 20, 30, 35, 40, and 65 cm) and six pool depths (20, 30, 40, 50, 65, and 80 cm; Table 2.1) that adult salmonids are likely capable of ascending, and would be relevant barrier specifications for small stream systems where barriers might be placed in Alaska. Each of the 16 treatments was replicated three times, and two Northern Pike were used during each treatment replicate to increase the number of individuals exposed to each treatment without crowding the lower pool. This resulted in a total of $16 \times 3 \times 2 = 96$ observations and $N = 6$ Northern Pike exposed to each height and depth treatment. Flow rate (27.1 L/s) and temperature (11°C) were held constant throughout the 48 trials.

Height, depth, and flow

Six of the original sixteen height and depth treatments with a range of passage successes were selected to be used in a second experiment to observe effects of height, depth and flow on Northern Pike leaping ability. Each treatment was randomly repeated three times each at two flow rates, 11.4 L/s and at 42.9 L/s, for a total of 36 trials. Flow rates were selected based on summer low and spring high flows of a small river system in southcentral Alaska where barriers may be placed (Alaska Department of Fish and Game, personal communication). Again, two Northern Pike were used in each treatment replicate and temperature was held constant at 11°C. These observations of leap success at 11.4 and 42.9 L/s were combined with previous trial observations tested at 27.1 L/s for a total of 108 observations for analysis.

Trial procedure

The trial process was similar for both experiments. Northern Pike were haphazardly collected one at a time from the “unused” section of the holding tank using rubberized mesh nets. Individuals were scanned with a PIT tag reader (Model 601, Biomark, Boise, ID), haphazardly assigned to one of the treatments, transported to the outdoor flume into their respective treatment pools, and allowed to acclimate at a flow rate of ~ 6 L/s for one hour. Northern Pike were given a health assessment condition score during acclimation (Table 2.2) to monitor condition throughout the trials. Northern Pike were excluded from experiments if condition score exceeded “5”; however, no individual condition scores exceeded “4.” After one hour, the flow rate in the flume was increased ~ 3 L/s every 10 minutes until the target flow rate was reached. Screens made of UV blocking material were placed over the windows of the flume to prevent disturbance. A video camera (HandicamHDR-XR-150, Sony, Tokyo, Japan) was placed at the window of one randomly selected pool to observe cryptic nocturnal Northern Pike leaping behavior, with one replicate of each treatment recorded. Infrared lights (Model A14, Tendelux Technology, China) were suspended above each barrier to ensure infrared illumination for the video camera. The camera and PIT system were turned on, then the trial was initiated at 1700 hours and Northern Pike were allowed to volitionally ascend the barriers. The trial was ended at 0800 hours the following morning; the location of

each individual (above or below the barrier) was noted and Northern Pike were removed from the flume and placed in the recovery tank for 24 hours before return to the “used” section of the main holding tank. Once all Northern Pike were used, they were shifted to the “unused” section of the holding tank to be included in future trials.

Data collection

Passage data

Previous trials, previous successes, and days in captivity were recorded for each individual used in a trial. Passage data for each trial were downloaded from the multi-antenna HDX reader. Each individual was classified as successful if its tag was detected in the upper pool during the trial, and unsuccessful if its tag was not detected, and this was used as a binomial response variable. The subset of video recordings ($N = 28$) was used to confirm that PIT detected successes were correct by observing one of the Northern Pike ascending the barrier at the time of PIT tag detection. However, two Northern Pike were used in each trial and individuals were not externally distinguishable from one another, although simultaneous leaps were not observed. Average passage success for each treatment was summarized by dividing the number of successful individuals by the total number of individuals exposed to each treatment ($N = 6$).

Hydraulic data

Water temperature and flow rate were recorded from the control panel interface at the start and end of each trial, averaged, and the mean value was associated with each trial. After all Northern Pike were removed from the flume after a trial, upper and lower pool depths were measured with a graduated depth rod (cm) and the leap height was calculated as the difference between these measurements. To better understand the complex hydraulic environment that Northern Pike experience in the plunge pool, three-dimensional water velocity data were collected with an Acoustic Doppler Velocimeter (ADV) on subset of three height and depth treatments at a constant flow rate of 27.1 L/s (10-cm barrier height x 30-

cm pool depth, 30 x 40, and 40 x 40) after all experiments had been completed. Velocity data were collected in a grid pattern across three planes of the lower pool: 1. a horizontal plane at half-depth throughout the entire pool, 2. a vertical plane 10 cm to the left of pool center throughout the length of the pool, and 3. an additional vertical plane spanning the width and height of the pool 15 cm from the barrier (Figure 2.3). These data were used to visualize complex hydraulic conditions in the lower pools, and calculate turbulent kinetic energy (TKE), a measure of the variation in velocities which is an important descriptor for fishway design (Wang and Hartleib 2011; Amaral et al. 2016).

Biological data

Body condition – bioelectrical impedance analysis

Upon experiment completion Northern Pike were removed from the main holding tank and euthanized with overexposure to MS-222, followed by a sharp blow to the head. All Northern Pike were then measured for FL (mm) and weighed (g), and bioelectrical impedance analysis (BIA) measurements were taken according to standard methods (Cox and Hartman 2005; Falke et al. 2019; Courtney et al. 2020; Chapter 1) with the Certified Quality Reader (CQR) Body Composition Analyzer (Seafood Analytics Juneau, Alaska) after which Northern Pike were individually labeled and frozen at -20°C for approximately 1 month. While individual FLs averaged 1.5 mm shorter (paired t-test, $P = 0.039$) and whole weights 30 g heavier ($P < 0.001$) between initial tagging and euthanasia measurements, metrics taken at euthanasia were used for analyses because of closer temporal proximity to BIA measurements. Seven individuals leaped from the holding tank and were lost as mortalities; therefore, the 55 remaining Northern Pike were randomly divided into groups for tissue enzyme activity analysis ($N = 25$) and proximate composition analysis ($N = 30$).

Morphometrics, sex, maturity, age and growth rate

Morphometric measurements, sex, maturity, age, and growth rates were determined for each individual to be included as covariates to predict Northern Pike leaping ability. Body depth at dorsal fin

insertion perpendicular to the ventral surface, caudal peduncle circumference at the narrowest point, and caudal, dorsal, and anal fin width at the base of each fin were measured in cm. Northern Pike were dissected to determine sex (e.g., male/female) and maturity (e.g., mature/immature) based on presence and development of ovaries or testes with assistance from trained Northern Pike biologists, generally according to Appendix I. We used cleithra to estimate Northern Pike age, back-calculate lengths-at-age, and calculate yearly growth rates in mm/day (as in Chapter 1; see Appendix L).

Anaerobic metabolic capacity and proximate composition analysis

Two 5-g dorsal glycolytic muscle samples were removed from the anterior dorsal musculature and preserved at -80°C for individuals assigned to enzyme assays (N = 25). Anaerobic metabolic capacity of Northern Pike was estimated by initiating the conversion of pyruvate to lactate by lactate dehydrogenase (LDH) in white muscle homogenate to quantify mass-specific LDH activity (μmol pyruvate converted to lactate/min/g; Chapter 1; see Appendix K). Northern Pike assigned to proximate component analysis (N = 30) had stomach contents removed, and the entire Northern Pike was ground in an industrial meat grinder including gonad material. Two ~50 g subsamples of homogenized material from each individual were weighed, dried for 48-72 hours in a drying oven at 55 – 60°C, and reweighed to determine % dry mass calculated using the following equation:

$$\% \text{ Dry mass} = (\text{dry mass of sample} / \text{wet mass of sample}) \times 100$$

The dried samples were homogenized once more for proximate composition analysis (AOAC 2019), which returned total lipid, protein, and ash content as a percentage of dry mass. This paired % dry mass (%DM), % dry lipid (%DL), BIA, and biological dataset (N = 30) was pooled with a similar dataset for Northern Pike collected in Alaska (N = 90; Chapter 1) to generate models that predicted proximate composition analysis-generated %DM and %DL measurements as a function of a standard set of electrical parameters calculated from BIA measurements and biological data (FL, weight, and body condition index, see Appendices Q - U). The final models were used to predict %DM and %DL for individuals used

in enzyme assays from BIA measurements ($N = 25$), so that %DM and %DL of all individuals could be used as covariates for leaping ability analyses.

Statistical analysis

All analyses were conducted using the statistical software program R (RStudio Team 2019) and evaluated at the $\alpha = 0.05$ level. Observational video data was used as evidence to visually confirm that individuals attempted or explored each treatment, that successes detected via the PIT antenna were observed in the videos, and to retain a record of cryptic Northern Pike leaping behavior (see Appendix X for count data of explorations, attempts, and successes for the subset of treatments).

Growth rate, body condition metrics, morphometrics, and LDH activity varied predictably with Northern Pike size and each metric was standardized by regressing the log-transformed metric against log-transformed FL, weight, or age. Residual values for growth rate, body condition, morphometrics, and LDH activity were analyzed for effects of sex (male/female) using one-way analysis of variance (ANOVA). Individual residual values for growth rate and %DL were used as leaping model covariates (below). Residuals of morphometrics (body depth, peduncle circumference, caudal, dorsal, and anal fin widths) were included in a principal component analysis (PCA) to consolidate trends in morphometrics into fewer principal components that were used as model covariates (Table 2.3). Initial data visualization indicated that residual white muscle LDH activity did not influence leap success and was dropped from further analysis. The coefficient of variation (CV; population standard deviation divided by population mean) was also calculated for each trait to quantify trait variation captured in experimental fish.

Due to collection limitations imposed by Montana Fish, Wildlife, and Parks on gamefish and holding limitations at the BFTC, Northern Pike were re-used one to four times throughout the two experiments (Table 2.4). However, preliminary assessments indicated that previous trials did not affect passage success. A random intercept effect also resulted in low individual variation or errors due to limited and non-systematic re-use not intending to test for repeated measures, thus previous trials and a

random intercept effect for individual were removed and observations were considered independent for analysis. Binomial leap success detected via PIT antennas was modeled as a function of vertical drop height, pool depth, flow rate, individual FL, and standardized physiological and morphological traits with the two experimental datasets using multiple logistic regression. A set of candidate models was developed for each dataset based on our initial hypotheses (Tables 2.5 and 2.6), and model selection was performed using Akaike's Information Criterion corrected for small sample sizes (AICc). Top models within two delta AICc scores were compared and the final model was chosen based on AICc model weight.

Prediction and comparison of Montana and Alaska Northern Pike leaping ability

The top logistic regression model based on data from the height and depth experiment was used to predict and compare leaping ability of Northern Pike collected from Alaska during summer of 2020 (Chapter 1) to individuals used in leaping experiments. The Alaska Northern Pike dataset was truncated to include individuals within the bounds of Montana Northern Pike FLs used to develop the final logistic regression model (524 to 845 mm, N = 28). Residual biological trait values for Northern Pike from Alaska were calculated relative to individuals used in leaping experiments from Montana. Leaping ability was predicted for individuals across three barrier height and pool depth treatments (10-cm height x 30-cm depth, 30 x 40, and 40 x 40), and we tested for differences in predicted passage success as a function of origin (Montana vs Alaska), barrier treatment, and their interaction using ANOVA and Tukey post-hoc analyses.

Results

Biological characteristics of Northern Pike

Of the 55 Northern Pike used in leaping experiments, 44 were mature males, 10 were mature females, and one was an immature female. Northern Pike FL, weights, and ages ranged from 524 to 847 mm (mean \pm SD: 636 ± 67 mm), 1041 to 4007 g (1898 ± 650), and 2 to 10 y (median \pm SD: 4.0 ± 1.62), respectively. Principal component analysis of residual morphometrics resulted in three retained principal components (hereafter PCI, PCII, and PCIII) that accounted for 80% of trait variation, with trait loadings

greater than 0.3 or less than -0.3 considered to significantly load on the associated PC (Table 2.3). The first PC was positively associated with all morphometrics, suggesting that 46% of the variation in Northern Pike morphology is attributed to individuals simply having larger fin widths, peduncle circumferences, and body depths, and these characteristics are associated with one another. Anal fin width positively loaded onto PCII, while body depth and peduncle circumference loaded negatively onto PCII and explained an additional 18% of the variation. Lastly, PCIII was strongly associated with narrow dorsal fin widths and explained 16% of variation in Northern Pike morphology. Male Northern Pike PCI scores were higher than females (ANOVA, $F = 11.1$, $P = 0.002$); however, sex did not affect PCII or PCIII scores.

Back-calculated annual log-transformed growth rate (mm/day) ranged from 0.06 to 0.96 mm/day, (mean \pm SD: 0.28 ± 0.18) and declined linearly with Northern Pike age (OLSR, t-value = -4.49, $P < 0.001$, $R^2 = 0.71$). After growth rate was standardized by calculating the residuals of the linear relationship between log-transformed growth rate and age, female Northern Pike tended to have greater mean residual growth relative to males (ANOVA, $F = 4.16$, $P = 0.05$), suggesting that females grew faster for a given age than males. Mass-specific LDH activity of white muscle ranged from 293 to 598 $\mu\text{mol}/\text{min}/\text{g}$ (mean \pm SD: 456 ± 75.2), and was positively associated with log-transformed body mass ($N = 25$; OLSR; t-value = 3.78, $P = 0.001$, $R^2 = 0.36$). White muscle LDH activity was standardized for body mass by calculating residuals of the linear relationship between mass-specific LDH activity and log-transformed body mass, and sex did not influence residual LDH activity (ANOVA, $F = 0.20$, $P = 0.66$).

Observed values of individual % dry mass (%DM) ranged from 26.3 to 29.5% (mean \pm SD: 28.2 \pm 0.80%) and % dry lipid (%DL) ranged from 10.9 to 20.6% (mean \pm SD: 15.8 \pm 2.54%). After combining these data ($N=30$) with additional proximate component data from Northern Pike in Alaska ($N=90$; Chapter 1), separate models were created that best predicted %DM and %DL from standardized BIA electrical parameters and biological characteristics of Northern Pike (%DM model $R^2 = 0.80$, Root Mean Squared Error (RMSE) = 0.98%; %DL model $R^2 = 0.71$, RMSE = 2.69%; see Appendix Q - U for

model details). These models were used to predict %DM and %DL values for the subset of Northern Pike used for enzyme assays (N=25) and pooled for analysis.

As predicted, %DM and %DL values were positively associated with Northern Pike fork length (OLSR; %DM: t-value = 3.6, P < 0.001, R² = 0.43; %DL: t-value = 1.89, P = 0.07, R² = 0.22), whereas sample type (observed or predicted PCA values) did not affect either relationship (OLSR, %DM: t-value = 0.80, P = 0.43; %DL: t-value = -0.05, P = 0.96). Residual %DM and %DL values were calculated from the linear regressions of PCA values vs fork length, and sex did not influence standardized %DM or %DL values (ANOVA; %DM: F = 0.01, P = 0.91; DL: F = 0.17, P = 0.68).

Because the standardized physiological and morphological traits varied little by sex, they were incorporated as covariates into models to predict passage success of Northern Pike without considering interactions with sex. Most traits did not vary greatly within experimental fish as observed by coefficient of variation values. For example, morphological trait (e.g., FL and morphometrics) CV values ranged from 0.10 to 0.11. Estimates of %DM had very little variation across individuals (CV = 0.03) while CVs for %DL and white muscle LDH activity were similar (CV = 0.16). In contrast, variation in Northern Pike ages and growth rates were relatively higher, with CV values of 0.40 and 0.64, respectively.

Height and depth experiment

Trial results

In this experiment, 33 successful leaps were recorded via PIT antennas from 96 observations, and leaping success generally declined as barrier height increased. Average passage success ranged from a maximum of 84% at the shortest 10-cm barrier height x 30-cm pool depth treatment to 0% for the 35 x 30, 40 x 40, 40 x 80, and 65 x 40 treatments (see Appendix V). Manipulated barrier height and pool depth treatments, as well as flow rate and water temperature, remained constant throughout experimental trials, and a range of biological characteristics were captured within experimental test fish (Table 2.4).

Model selection

The top two models accounted for 63% of the weight of candidate models, given the data, and both contained barrier height, pool depth², and an interaction between fork length and pool depth (Table 2.5), and had inherently similar parameter coefficients. All further inference was based on the top model that accounted for 44% of the weight of all candidate models, which included residual growth rate in addition to the previous predictors. As predicted, leap success declined with increasing barrier height and increased with residual growth rate. The inverse quadratic relationship between success and pool depth indicated that leap success increased with pool depth, but then declined once an optimum pool depth had been reached. The interaction between pool depth and fork length indicated that optimum pool depth increased with individual fork length, which supported our initial hypothesis that pool depth and Northern Pike size would interact (Figure 2.4). There was little to no support ($w_i < 0.10$) for models that included other biological traits such as morphometrics (PC scores), lipid content, and sex.

Height, depth, and flow experiment

Trial results

Results were similar to the first experiment, with 41 successful leaps recorded from 108 observations and leaping success declining with barrier height. Average passage success ranged from a maximum of 84% at the 10-cm x 30-cm x 27.1 L/s treatment to 0% for the 40 x 40 treatment across all three flow rates. Manipulated barrier height, pool depth, and flow rate treatments, as well as water temperature, remained constant throughout experimental trials (see Appendix W), and a range of biological characteristics were captured within experimental test fish (Table 2.4).

Model selection

The top six models within two delta AICc scores accounted for 83% of the weight of candidate models, given the data (Table 2.6). One of the top models accounting for 8% of the weight of candidate models contained barrier height, pool depth², and an interaction between fork length and pool depth,

similar to the top model selected in the height and depth experiment. There was reduced or no support ($w_i \leq 0.06$) for models containing flow rate and biological traits such as PC scores, sex, and body condition. As the top models independently accounted for low weights of all candidate models (8% to 18%), and contained similar physical and biological predictors (height, pool depth, and fork length) to the top model selected from the height and depth dataset, the top model from the height and depth experiment ($w_i = 0.44$) was considered to be the best model, given the data, to explain factors that affect Northern Pike leaping ability across both experiments and used for further model predictions.

Prediction and comparison of Montana vs Alaska Northern Pike leaping ability

The top model from the height and depth experiment was used to predict and compare the leaping ability of Northern Pike collected in Alaska (Chapter 1) to individuals used in the leaping experiments, as intraspecific variation in size and growth rate were important predictors of leaping ability. Alaska Northern Pike FLs (mean $649 \pm$ SD 96.9 mm) were similar to Montana Northern Pike FLs (mean $638 \pm$ SD 66.5 mm; ANOVA, $F = 0.37$, $P = 0.55$), but individuals from Alaska had faster residual growth rates (ANOVA, $F = 8.14$, $P = 0.005$; Figure 2.5). The overall predicted passage success of individuals from Alaska was greater relative to individuals from Montana ($42 \pm 31\%$ vs $38 \pm 31\%$; ANOVA, $F = 6.29$, $P = 0.01$) likely due to this enhanced growth rate, but predicted passage success did not differ by Northern Pike origin within each of the barrier treatments (Figure 2.6).

Three-dimensional water velocity description

X-velocities (left-to-right) and y-velocities (upstream-to-downstream) did not vary as much as vertical z-velocities (up-and-down) within each treatment (Table 2.7), and this variability was most visible in the horizontal plane that covered the entire surface of the plunge pool at half-water depth (Figure 2.3.1). The 10×30 treatment (Figure 2.7B) showed the greatest negative z-velocity and downwelling (-100 cm/s) where the water enters the plunge pool from the upper pool, with maximum upwelling (positive z-velocity) of 44 cm/s in front and behind the stream of water (Table 2.7; Figure 2.7B). In the 30×40 and 40×40 treatments, downwelling forces decreased in magnitude (~ -50 cm/s;

Table 2.7), while maximum upwelling increased in magnitude and area to 49.2 and 60.3 cm/s, respectively (Table 2.7; Figure 2.7C and D). Mean z-velocity also increased from negative to slightly positive values across the treatments with barrier height (Table 2.7), suggesting greater upwelling and the formation of a standing wave below the barrier. Turbulence increased with barrier height from 10 to 30 cm (mean TKE of 441 to 577 cm²/s, respectively), but not from the 30 to 40 cm barrier heights (577 to 571 cm²/s, respectively). However, maximum TKE increased from 1780 to 2020 cm²/s with barrier height from 30 to 40 cm, suggesting transitory instances of higher turbulence are difficult to capture based on averaged measurements.

Discussion

We demonstrated through experimental leaping studies in an open channel flume that Northern Pike are able to ascend vertical barrier heights much greater than what had been previously assumed (Diebel et al. 2013). Because Northern Pike leaping ability was considerably less than other taxa such as salmonids, selective fragmentation may be a viable tool to prevent the spread of invasive Northern Pike. Northern Pike explored, attempted, or successfully leaped over each experimental treatment in a subset of video recorded trials (see Appendix X), which increased our confidence that experimental conditions promoted natural behaviors and significant, volitional motivation to leap. Passage success ranged from 0% to 84% across treatments (Appendices V and W), indicating that we also captured limitations of Northern Pike leaping ability. Leaping ability of Northern Pike was most affected by physical barrier conditions of height and pool depth as seen in other fish taxa, while individual biological traits of Northern Pike also explained intraspecific variability in passage success. Owing to greater residual growth rates at age, Northern Pike from Alaska were predicted to have greater leaping abilities relative to individuals from Montana that were used in our experiments. However, though Northern Pike from Alaska had nearly two-times faster growth rates than individuals from Montana, our model predicted a minimal 4% average increase in leap success. This suggests that individual biological traits have reduced effects on Northern Pike leaping ability relative to physical factors, and that our model may be broadly

applicable to other populations of invasive Northern Pike, but in-situ testing would be beneficial to ensure selective fragmentation. Experimental results and model predictions were further understood by considering auxiliary behavioral video, 3D water velocity, and turbulence data, which continues to support the inherent complexity of fish behavior and physical limitations in response to hydrologically variable environments.

Passage success of Northern Pike strongly declined as barrier height increased, an effect observed in many studies that have characterized fish leaping ability (Stuart 1962; Holthe et al. 2005; Kondratieff and Myrick 2006; Gardunio 2014; Amaral et al. 2016). Despite the assumption that Northern Pike cannot ascend barriers greater than 10 cm (Diebel 2013), individuals cleared this barrier height with 84% success and 42 cm barriers with 17% success provided that pool depths were 65 cm. Northern Pike leap success generally increased with pool depth, as individuals were observed to orient vertically in the lower pool for a well-timed leap in video data, which became more difficult in shallow pools (Powers and Orsborn 1985). Deep pool depths also may have promoted the formation of a standing wave that fish used to propel themselves upwards (Stuart 1962; Powers and Orsborn 1985). This standing wave was made visible in 3D velocity measurements where upwelling (i.e., positive z-velocity) increased as barrier height increased (Table 2.7; Figure 2.7). Behavioral video data also provided evidence that Northern Pike sensed and used these upwelling areas, as they often ascended the barrier to the left or right of the plunging jet where upwelling occurred (Figure 2.2). Although barrier height had a stronger negative effect on leap success relative to the positive effect of upwelling, turbulence may play an important role in complex real-world hydraulic situations and applications of barriers outside of experimental flumes.

Pool depth also has complex effects on hydraulics, fish behavior, and associated fish leap success (Lauritzen et al. 2005; Amaral et al. 2016, Morán-López and Tolosa 2020), evidenced by a maximization of leaping ability at median pool depths, which was in turn mediated by fish size. Larger fish ascend greater absolute barrier heights than smaller fish when pool depths are not limiting (Kondratieff and Myrick 2005; Brandt et al. 2005; Morán-López and Tolosa 2017). However, the interaction we observed

between body size and pool depth indicated that large (700 mm) individuals had greater leap success relative to smaller individuals (550 mm) only when pool depths were deep (80 cm). When pool depths were shallow, (30 cm) small Northern Pike had the advantage over large individuals, with this interaction of pool depth and Northern Pike size reduced at moderate pool depths (50 cm; Figure 2.4; see Appendix Y). A complex, nonlinear relationship between fish length and leap success has also been shown in Barbel species (*Luciobarbus* sp., Morán-López and Tolosa 2017); however, pool depths were held constant and individual variation in endurance and condition was hypothesized to affect the relationship. Large Northern Pike were likely physically limited by shallow pool depths because they could not orient vertically in the lower pool (Powers and Orsborn 1985), whereas reduced leap success of small individuals in deep pools may have been behavioral and related to plunge pool turbulence.

For a given barrier height, energy dissipation in the plunge pool decreases as pool depth increases (Towler et al. 2015). In our experiment, energy dissipation factor (EDF) also decreased from 37.0 to 24.1 as pool depth increased from 50 to 80 cm and barrier height remained constant (15 cm) across several treatments (see Appendix V). This reduction in energy dissipation and turbulence in the lower pool may have caused small individuals to perceive deeper pool as a refuge rather than a disorienting space to escape, similar to experiments on Kokanee Salmon (*Oncorhynchus nerka*; Lauritzen et al. 2010). However, turbulence has complex effects on fish behavior and may affect fish size classes differently (Liao et al. 2003; Liao 2007; Silva et al. 2012); therefore, large individuals may have been unable to orient into small pockets of low turbulence like small Northern Pike, which resulted in greater motivation to leap at deeper pool depths. Video data or an antenna at the base of the barrier could have been used to assess this hypothesis by comparing attraction of small and large individuals to the barrier at deep pool depths. However, our experimental setup did not allow this because individuals in the video could not be visually distinguished, and the antenna reader system was already maximized with three antennas in the upper pools running simultaneously. Associating individual biological traits such as size to more nuanced behaviors of attraction would therefore be beneficial for future assessments of fish leaping ability.

While the physical factors of barrier height and pool depth affected Northern pike leaping ability, it was surprising that tested flow rates did not. Flow rate is a complex parameter; when flow is predictable, fishes can capitalize on these currents and reduce energetic costs, while unpredictable flows can repel fishes because of increased energy expenditure or even physical damage (Liao 2007). Higher flow rates lead to increased turbulence in plunge pools, similar to the effect of increasing barrier heights on plunge pool turbulence, which may increase motivation to leap and escape turbulent conditions. However, such turbulence may also reduce leaping efficacy because orientation for a well-timed leap becomes more difficult (Liao 2007; Amaral et al. 2016; Morán-López and Tolosa 2020). The effects of flow rate also vary among species, with anadromous salmonids and clupeids requiring flow to attract them to barriers, while passage of potamodromous species including Northern Pike is reduced at fishways that utilized flow for attraction (Bunt et al. 2012). However, Northern Pike are not entirely repelled by higher flows as evidenced by their passage of elevated velocity or sloped fishways (Ovidio and Phillipart 2002; Peake 2008; Bunt et al. 2012). The complex, antagonistic effects of flow rate on fish leaping ability and consideration that Northern Pike may not be attracted to, or largely influenced by, flow support our findings that tested flow rates did not affect Northern Pike leap success. We also did not test a particularly wide range of flow rates, as those greater than 42.9 L/s resulted in high Northern Pike stress behaviors in preliminary trials and were deemed inhumane for extended 24-hour trials. Therefore, potentially minimal increases in flow rate above those that we tested may result in strong reductions to Northern Pike leaping ability and should be considered in future assessments.

While fish length interacted strongly with pool depth to impact Northern Pike leaping ability, limited variation in fin and body morphometrics, body condition, and anaerobic metabolic capacity of experimental fish may have reduced our ability to detect potential effects of these additional biological traits on leaping ability. This limited variation is likely reflective of all Northern Pike collected from one population in Fort Peck Reservoir, a dammed portion of the Missouri River with lake-like conditions. Intraspecific variation in body size, morphology, and physiology has been observed across groups of

Northern Pike, but strongly driven by invasive or native origin, food availability, and habitat characteristics (Senay et al. 2017; Berghaus et al. 2019; Chapter 1). Future work that considers the effects of intraspecific variation on fish leaping ability would benefit from ensuring larger trait variation is captured in test fish (Rahel and McLaughlin 2018; Birnie-Gauvin et al. 2019) whether by collecting fish from various locations or directly manipulating trait variation by raising fish in variable laboratory settings. In contrast, we found much greater variation in Northern Pike age and back-calculated growth rates at age (Figure 2.5).

Variation in growth rate within a population can be driven by intrinsic characteristics or competitive interactions rather than environmental conditions, such as compensatory growth when competition is low, countergradient growth due to occupation of different latitudes, or variation in basal metabolic rate (Rypel et al. 2012; Glenn 2012; Metcalfe et al. 2016). For example, elevated basal metabolic rate in fishes is positively associated with dominant behavior, competitive advantages, and swimming endurance (Hoogenboom et al. 2013; McGhee et al. 2013; Myles-Gonzales et al. 2015; Metcalfe et al. 2016), which are traits that can enhance food consumption, growth rates, and overall fitness of individuals. Therefore, greater residual growth at age may reflect a culmination of physiological benefits rooted in metabolic variation that resulted in improved leaping ability of Northern Pike, but potentially not related to other physiological traits such as body condition or anaerobic metabolic capacity which is not representative of aerobic metabolism.

Northern Pike collected in Alaska (Chapter 1) had faster growth rates relative to individuals from Montana (Figure 2.5); therefore, we expected and observed that predicted leap success of Alaska Northern Pike would be greater (Figure 2.6). Predicted leaping ability of Alaska individuals is mostly representative of native Northern Pike, as we excluded individuals smaller than 520 mm from the Alaska dataset and the majority of invasive Northern Pike were smaller than this threshold. However, invasive Alaska Northern Pike had 2-fold faster growth rates than native individuals (Chapter 1), which suggests that our predictions of leaping ability for Alaska Northern Pike may be conservative in the context of

barriers being designed for invasive individuals. Physical factors such as barrier height and pool depth had much stronger effects on Northern Pike leaping ability relative to positive effects of growth rate, with native Alaska individuals averaging 2 x faster growth rates but only 4% greater leap success. While this may not have large implications for future barrier designs, it only takes the passage of a few high-performance individuals to void considerable management efforts. Therefore, the potential for invasive individuals in Alaska to have minimally enhanced leaping abilities highlights the importance of considering intraspecific variation to confidently manage invasive Northern Pike and encourages careful testing of barriers before they are widely installed.

Ultimately, we found no evidence that Northern Pike can ascend 40 cm barriers when pool depths are \leq 40 cm regardless of flow rates, body size, and other biological traits encompassed in this study, which is an important first step towards managing invasive Northern Pike with vertical drop barriers in salmonid-occupied watersheds such as southcentral Alaska (Dunker et al. 2022). Maximum leaping ability of Northern Pike under test conditions was considerably less than maximum leaping abilities of adult salmonids, which ranges from 70 cm to greater than 100 cm across many species (Stuart 1962; Powers and Orsborn 1985; Kondratieff and Myrick 2006; Lauritzen et al. 2010). While adult salmonids may not be impeded by such barriers during spawning migrations, juvenile salmonids such as Coho Salmon (*Oncorhynchus kisutch*) and steelhead trout can only ascend 26 cm and 44 cm barriers with limited success, respectively (Mueller et al. 2008; O'Keefe 2021). As fluvial connectivity is essential for juvenile salmonids (Northcote 1997), strategic placement of barriers near the entrance of river systems rather than in mid-reaches could reduce the possibility of juveniles passing downstream of barriers before final outmigration to the ocean.

This assessment of Northern Pike leaping ability is the first step towards determining the feasibility of selective vertical drop barriers as a management tool for Northern Pike, with future research and barrier testing necessary before implementation in natural systems. For example, all experiments were conducted at 11°C to mimic spring water temperatures that Northern Pike may encounter as they

migrate to spawn in southcentral Alaska's waterways (Shaftel et al. 2020). However, water temperature positively influences fish leaping ability due to increased metabolic activity (Ficke et al. 2011; Gardunio 2014), and this likely holds true for Northern Pike. Northern Pike may exhibit movement patterns year-round outside of 11°C and spawning migrations; therefore, Northern Pike leaping ability should be assessed across a range of water temperatures and movement motivations outside of spawning to capture potential variation in leaping ability. Additionally, warmer thermal regimes due to climate change are predicted to enhance physiological benefits of cool-water fish such as Northern Pike relative to cold-water salmonids (Hein et al. 2011; 2014; Rolls et al. 2017; Shaftel et al. 2020); however, concomitant increases in flow rates and flow variability with climate change could reduce passage success of all species (Murdoch et al. 2020). Laboratory conditions also reduce innumerable complexities found in natural systems, which may result in more variable hydraulic conditions and thus Northern Pike leaping abilities in the field. These considerations, in addition to the effects of biological traits on Northern Pike leaping ability observed here, highlight the importance of testing barrier designs in-situ with local specimens under a range of environmental conditions. Freshwater habitats continue to be threatened with fragmentation, degradation, climate alterations, and invasive species, and ineffective barriers that prevent native species migrations should not contribute to that list (Fausch et al. 2009; Silva et al. 2018). As invasive species management evolves to target invaders while reducing impacts on native ecosystems, selective barriers against Northern Pike and other invasive fishes may need to be rigorously evaluated to not only prevent invader movement, but support connectivity for native fishes and do no harm (Rahel and McLaughlin 2018; Silva et al. 2018; Jones et al. 2021a).

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Table 2.1. Barrier height and plunge pool depth treatments (cm) tested in leaping experiments on Northern Pike during summer of 2021 in a large open-channel flume system. **Bolded** treatments were tested across three flow rates (11.5, 27.1, and 42.9 L/s), while un-bolded treatments were tested at one flow rate (27 L/s).

Pool depth (cm)	Barrier height (cm)						
	10	15	20	30	35	40	65
20			20 x 20				
30	10 x 30		20 x 30		35 x 30		
40	10 x 40				30 x 40	40 x 40	65 x 40
50			15 x 50		30 x 50		
65			15 x 65		30 x 65	40 x 65	
80	15 x 80		30 x 80		40 x 80		

Table 2.2. Condition score table used to assign condition scores to Northern Pike used in leaping experiments during summer of 2021 in a large open-channel flume system.

Condition description	Score
In good health	1
One or two fins show wear, small body/scale marks	2
More than two fins damaged, minor wear on mouth/maxilla, body/scale marks	3
More than three fins damaged, redness on fins, moderate wear and redness on mouth, moderate body/scale marks	4
More than three fins worn and red with sores, major redness/wear on mouth, major damage to body/scales	5
See 5, appears sluggish or non-responsive. Should not be used in trials	6

Table 2.3. Principal component analysis of residual morphometrics and associated variance explained for each retained principal component (PC). Morphometric PC scores were used as predictors of Northern Pike leaping ability conducted during summer of 2021 in a large open-channel flume system. Loadings greater than 0.3 or less than -0.3 are considered significant and indicated in **bold**.

Trait	PCI	PCII	PCIII	Variation Explained
Body width	0.50	-0.38	0.10	PCI – 46%
Peduncle circumference	0.48	-0.58	-0.05	
Dorsal fin width	0.36	-0.28	-0.88	PCII – 18%
Anal fin width	0.43	0.62	0.27	
Caudal fin width	0.47	0.23	0.38	PCIII – 16%

Table 2.4. Summary of relevant biological metrics (mean \pm SD, where applicable) and number of re-uses for individual Northern Pike used in two leaping experiments during summer of 2021 in a large open-channel flume system. See text for details on how measurements were made or derived.

Metric	Height and depth	Height, depth, and flow
N	89	102
F:M sex ratio	19:70	18:84
Fork length (mm)	639.0 \pm 67.0	634.0 \pm 64.9
Weight (g)	2005.0 \pm 676.0	1970.0 \pm 657.0
Age (yr)	4.0 \pm 1.62	4.0 \pm 1.50
Lipid content (%)	15.1 \pm 2.49	15.1 \pm 2.40
Dry mass (%)	27.8 \pm 0.97	27.8 \pm 0.97
Growth rate (mm/day)	0.27 \pm 0.17	0.26 \pm 0.16
Lactate dehydrogenase activity (μ mol/min/g)	455.0 \pm 73.8	459.0 \pm 69.5
Body depth (cm)	10.1 \pm 1.07	10.1 \pm 1.04
Peduncle circumference (cm)	9.93 \pm 1.03	9.90 \pm 1.00
Anal fin width (cm)	5.63 \pm 0.57	5.60 \pm 0.54
Caudal fin width (cm)	7.55 \pm 0.84	7.48 \pm 0.85
Dorsal fin width (cm)	7.48 \pm 0.80	7.43 \pm 0.76
Condition score (1-6)	1.71 \pm 0.57	1.98 \pm 0.55
Re-use events	1.65 \pm 0.48	1.89 \pm 0.86

Table 2.5. Summary of candidate models used to predict Northern Pike leaping success as a function of abiotic and biotic variables (PC scores = principal component scores describing morphology; see Table 2.3) from experimental observations (N=89) conducted during summer of 2021 in a large open-channel flume system. The number of model parameters (K), Akaike Information Criteria adjusted for small sample sizes (AICc), difference in AICc from the top model (Δ AICc), Akaike weight (w_i), and log-likelihood (Log-lik) are shown. **Bolded** top models are within two Δ AICc scores.

Model	K	AICc	Δ AICc	w_i	Log-Lik
Height + fork length * depth + depth² + growth residual	7	91.8	0	0.44	-38.2
Height + fork length * depth + depth ²	6	93.5	1.7	0.19	-40.2
Height + depth + depth ²	4	95.1	3.3	0.09	-43.3
Height + depth + depth ² + PC I score	5	95.1	3.3	0.08	-42.2
Height	2	95.2	3.4	0.08	-45.6
Height + depth	3	96.5	4.7	0.04	-45.1
Height + fork length + depth + depth ²	5	97.3	5.5	0.03	-43.3
Height + fork length + depth	4	98.5	6.7	0.02	-45.0
Height * fork length	4	99.4	7.6	0.01	-45.5
Depth + depth ²	3	118.0	26.2	0.00	-55.8
PC III score	2	118.0	26.7	0.00	-57.2
PC I score	2	119.0	27.8	0.00	-57.3
Growth residual	2	120.0	27.8	0.00	-57.7
Fork length	2	120.0	28.2	0.00	-57.9
Depth	2	120.0	28.5	0.00	-58.1
PC II score	2	120.0	28.5	0.00	-58.1
Lipid content	2	120.0	28.6	0.00	-58.1
Sex	2	120.0	28.6	0.00	-58.1

Table 2.6. Summary of candidate models used to predict Northern Pike leaping success as a function of abiotic and biological variables (PC scores = principal component scores describing morphology; see Table 2.3) from experimental observations (N=108) conducted during summer of 2021 in a large open-channel flume system. The number of model parameters (K), Akaike Information Criteria adjusted for small sample sizes (AICc), difference in AICc from the top model (ΔAICc), Akaike weight (w_i), and log-likelihood (Log-lik) are shown. **Bolded** model is similar to top the top model from a previous experiment.

Model	K	AICc	ΔAICc	w_i	Log-Lik
Height + depth + depth ²	4	121.0	0.0	0.18	-56.3
Height + fork length + depth + depth ²	5	121.0	0.18	0.17	-55.3
Height + depth	3	121.0	0.39	0.15	-57.6
Height	2	121.0	0.42	0.15	-58.7
Height + fork length + depth	4	122.0	1.15	0.10	-56.9
Height + fork length * depth + depth²	6	123.0	1.75	0.08	-54.9
Height + depth + depth ² + flow rate	5	123.0	2.21	0.06	-56.3
Height + fork length + depth + depth ² + flow rate	6	123.0	2.43	0.05	-55.3
Height + fork length * depth + depth ² + growth residual	7	125.0	4.05	0.02	-54.9
Height * flow rate + fork length + depth + depth ²	7	125.0	4.25	0.02	-55.0
Height + fork length + depth * flow rate + depth ²	7	126.0	4.63	0.02	-55.2
Depth	2	138.0	16.8	0.00	-66.9
Lipid content	2	138.0	17.4	0.00	-67.2
Fork length	2	139.0	17.9	0.00	-67.4
Sex	2	140.0	19.4	0.00	-68.2
PC I score	2	140.0	19.4	0.00	-68.2
PC III score	2	141.0	19.7	0.00	-68.3
PC II score	2	141.0	19.7	0.00	-68.3
Growth residual	2	141.0	19.7	0.00	-68.3
Flow rate	2	141.0	19.7	0.00	-68.3

Table 2.7. Mean \pm standard deviation of 3D water velocities (X, Y, and Z, cm/s) and turbulent kinetic energy (TKE, cm 2 /s) values, and Northern pike passage success (number of successful individuals divided by total number of individuals exposed to each treatment N= 6) across three waterfall height and pool depth treatments (barrier height cm x plunge pool depth cm) used during leaping experiments conducted in a large open-channel flume system during summer 2021. Measurements were taken from a coordinate plane spanning the entire area of the plunge pool below a vertical drop barrier at half water depth.

Treatment	X-velocity		Y-velocity		Z-velocity		TKE		Passage success (%)
	Range	mean \pm SD	range	mean \pm SD	range	mean \pm SD	range	mean \pm SD	
10 x 30	27.6 to -14.4	4.16 \pm 10.2	22.9 to -11.0	1.78 \pm 5.58	44.0 to -100	-5.86 \pm 24.8	1980.0 to 0.0	44.01 \pm 408.0	84.0
30 x 40	32.1 to -21.0	3.97 \pm 10.0	11.5 to -8.05	1.26 \pm 3.88	49.2 to -49.5	-0.94 \pm 18.7	1740.0 to 0.0	577.0 \pm 574.0	17.0
40 x 40	32.4 to -20.7	3.49 \pm 11.6	11.7 to -15.9	0.60 \pm 4.33	60.3 to -52.7	0.15 \pm 19.9	2020.0 to 0.0	571.0 \pm 566.0	0.00

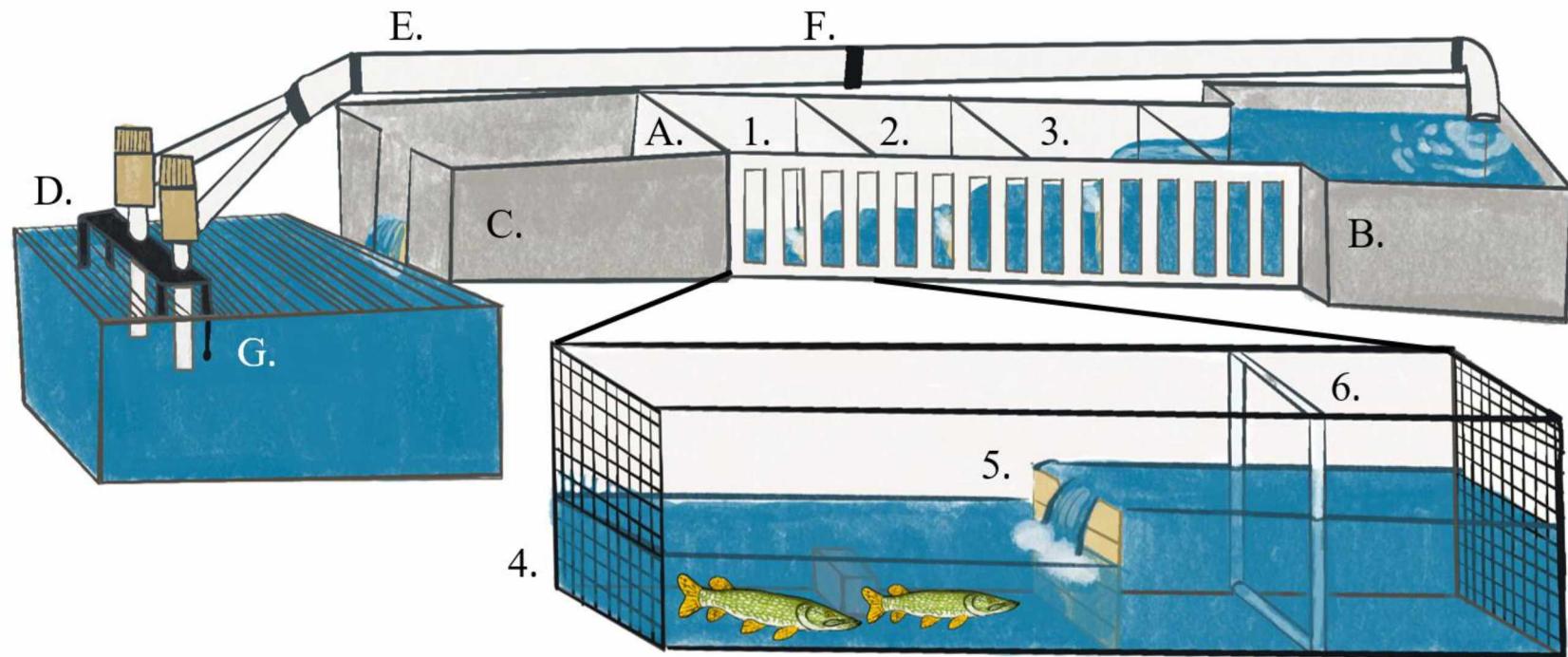


Figure 2. 1. Schematic diagram (not to scale) of the recirculating open channel flume system used during leaping experiments with Northern Pike in 2021. The 17-m fiberglass channel (A) was divided into pools 1, 2, and 3 to run three leaping trials simultaneously in the flume. Water was held in the sump and recirculated by 20 and 40-horsepower pumps (D) into a large PVC pipe (E) that transported water to the headwater pool (B). Water flowed through the headwater pool, the flume, the tailwater pool, and back into the sump. Flow rate was monitored with a flowmeter in the PVC pipe (F) and water temperature monitored with a temperature probe in the sump (G). Magnification of one flume section (4) shows tongue and groove boards that were stacked in the center of the section (5) to create the weir for pike to ascend. Pike were PIT tagged and placed in the plunge pool, with a PIT antenna in the upper pool (6) used to detect successful leaps. Artwork by T. Cubbage.

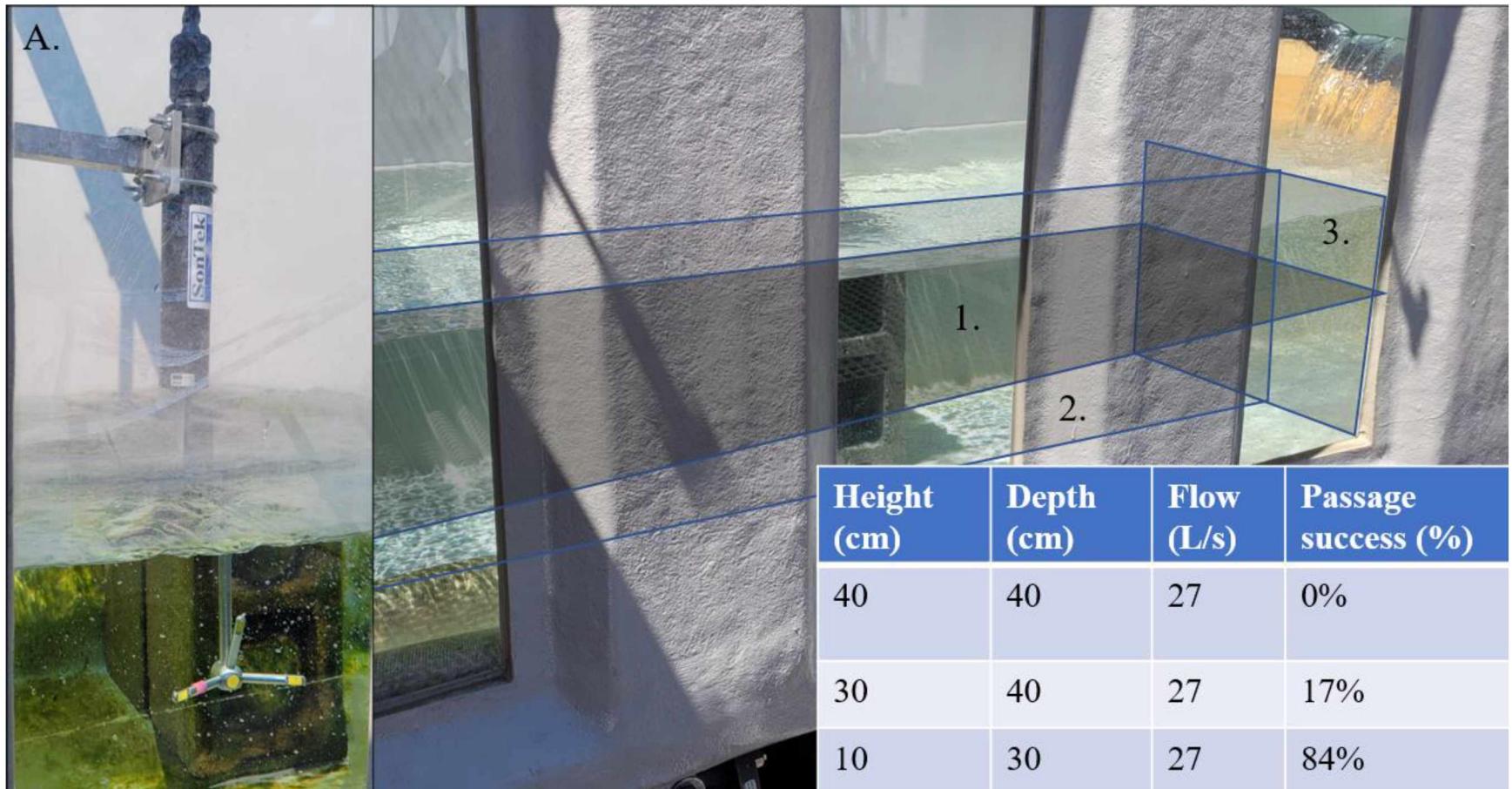


Figure 2. 2. Photograph of the plunge pool where 3D water velocity data were collected with an acoustic doppler velocimeter (A) after leaping experiments were completed using Northern Pike in a large open-channel flume system during 2021. Data were collected from three barrier height and plunge pool depth treatments at a constant flow rate with variable Northern Pike leap success (table inset; Passage success = number of successful individuals divided by the number of individuals exposed to each treatment N = 6). Water velocity data was collected in three planes, (1) a horizontal plane at half-depth throughout the entire pool, (2) a vertical plane 10 cm to the left of pool center throughout the length of the pool, and (3) a vertical plane spanning the width and height of the pool 15 cm from the barrier.

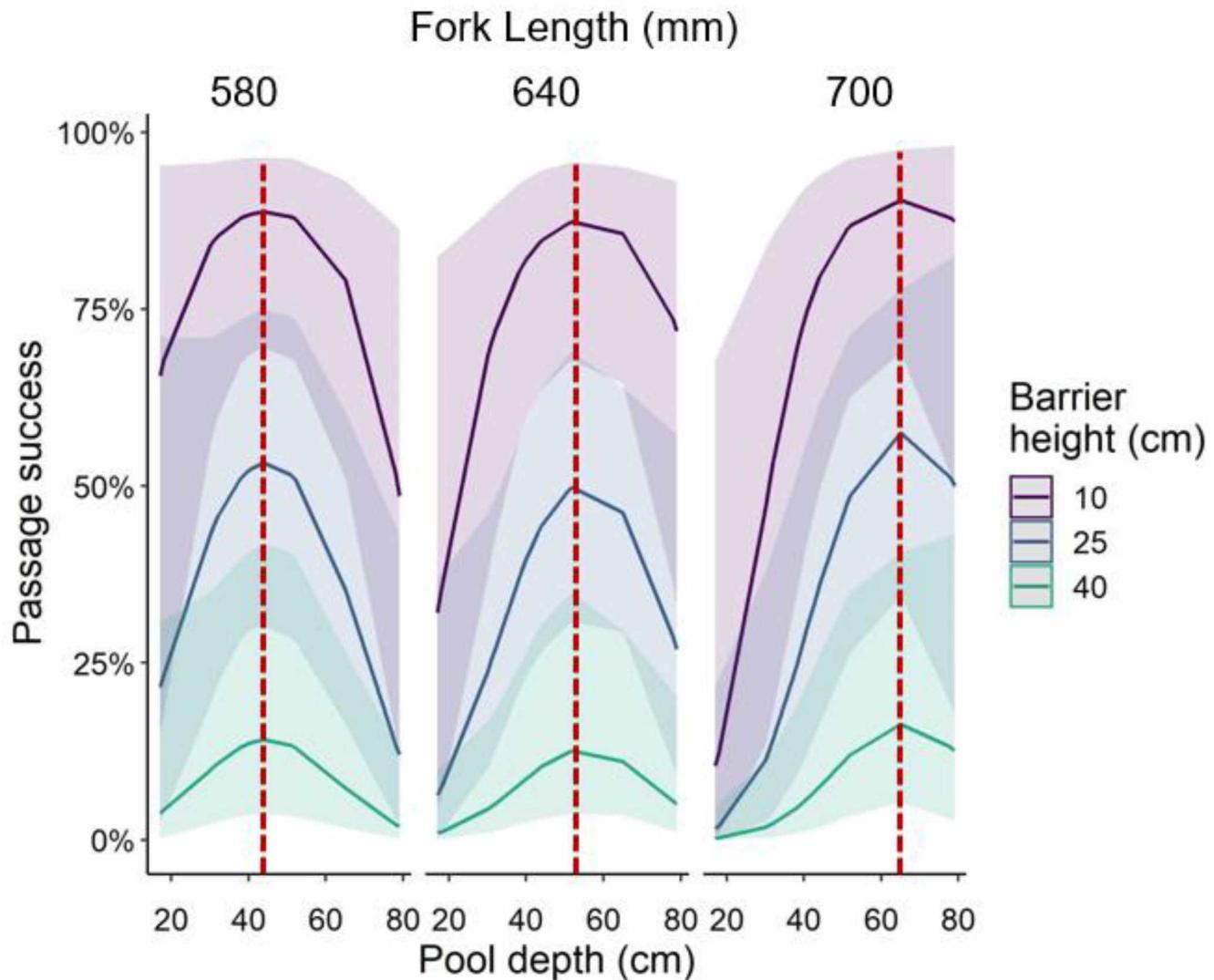


Figure 2.3. Predicted passage success (%) of Northern Pike as a function of plunge pool depth, barrier height, and individual fork length at a constant flow rate of 27.1 L/s and water temperature of 11°C. Red dashed lines represent optimum pool depth for maximum leaping ability of Northern Pike across three fork lengths. The logistic regression model was developed from leaping experiments using 55 Northern Pike ranging in fork lengths from 520-840 mm ($\text{mean } 639 \pm 67 \text{ mm}$) in a large open-channel flume system during 2021. Shaded areas are 95% confidence intervals for predicted passage success as a function of barrier height, pool depth, and fork length.

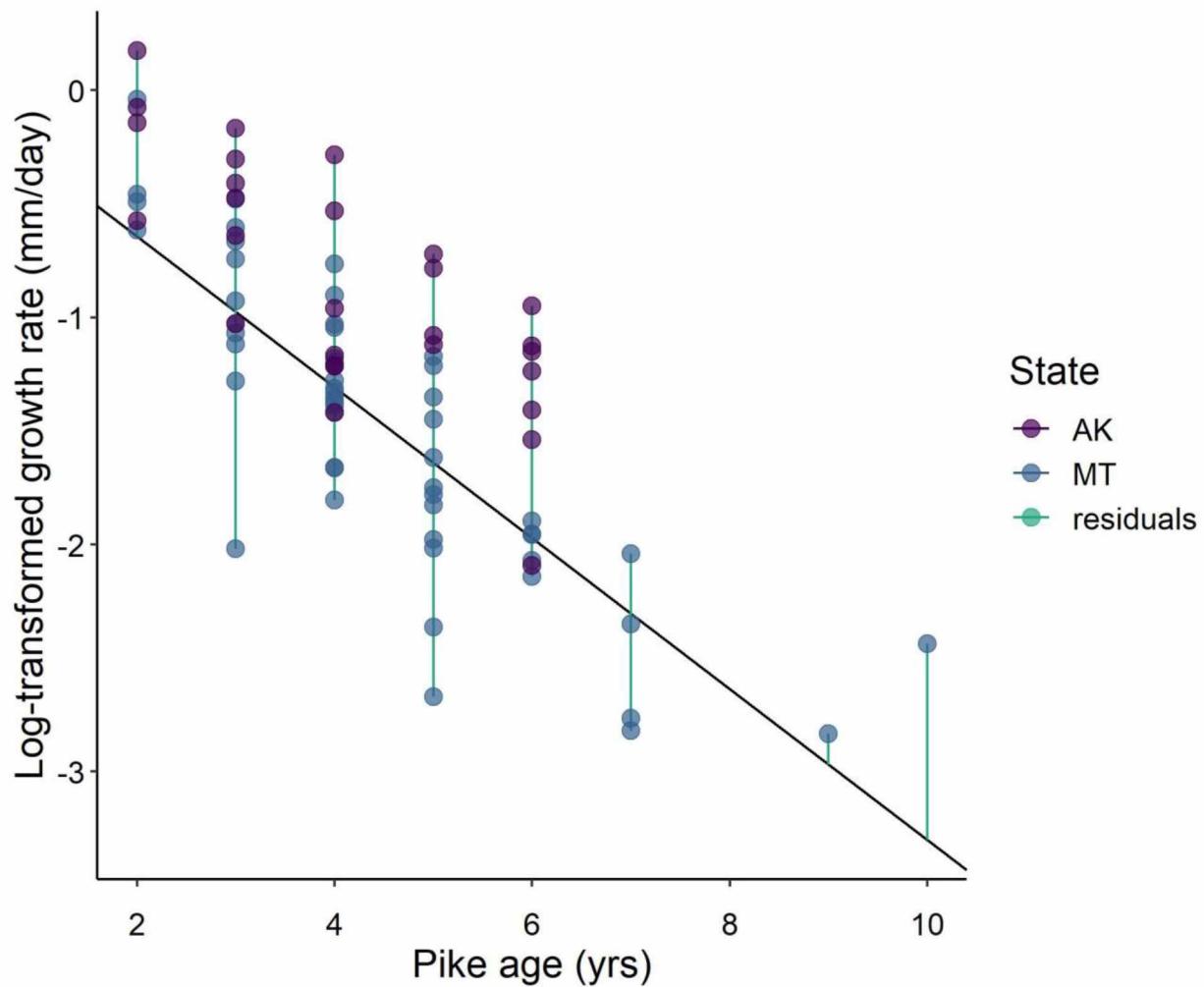


Figure 2.4. Log-transformed back-calculated growth rate (mm/day) vs age for Northern Pike collected in Montana and used in leaping trials in a large open-channel flume system during 2021 ($N = 55$; light blue circles) and Northern Pike collected in Alaska during 2020 ($N = 28$; dark purple circles). The black line is the linear relationship of log-transformed growth rate vs age for Montana individuals only. Lines drawn to points from regression line represent residual growth rate at age values, which were used as predictors of Northern Pike leaping ability.

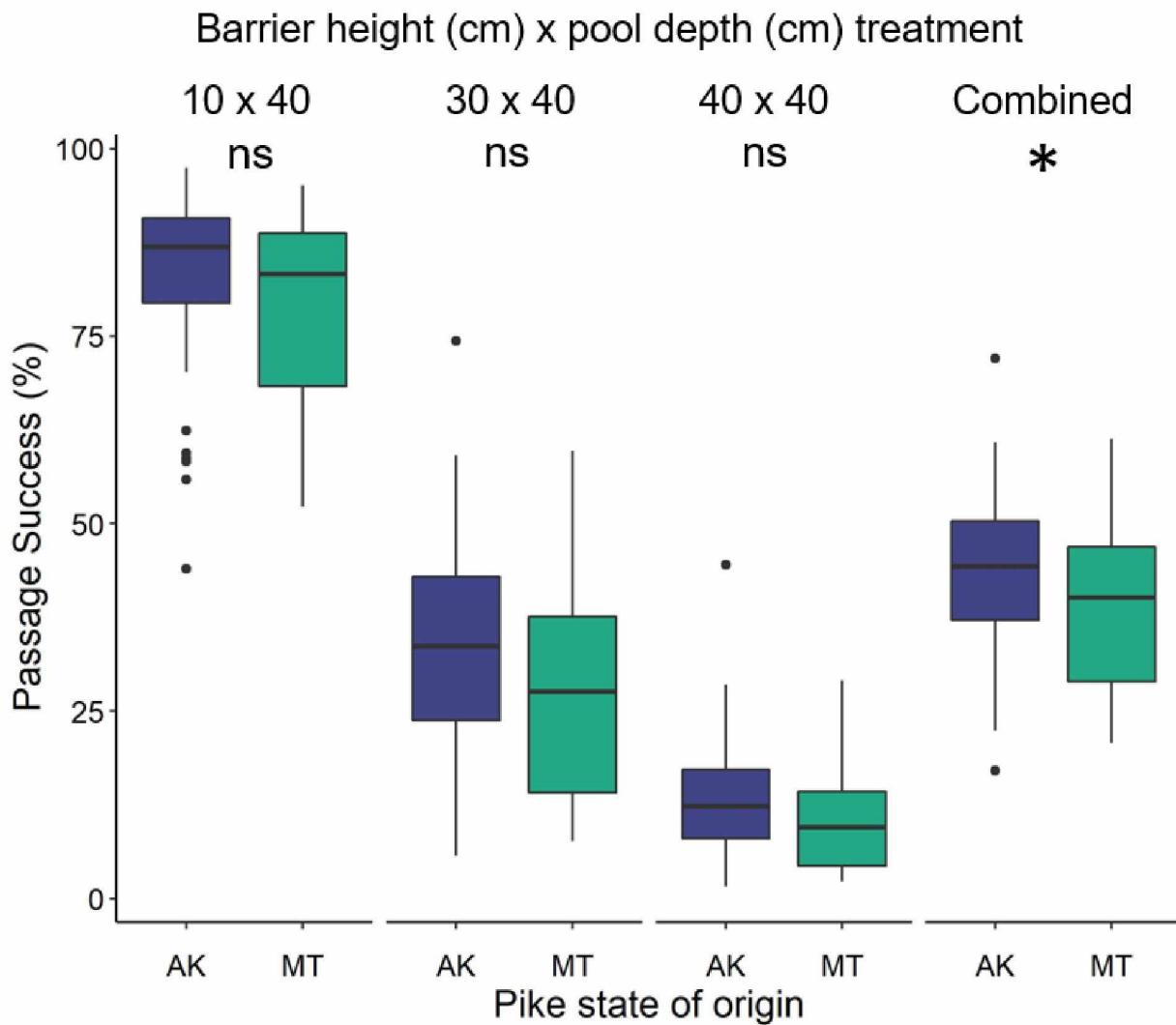


Figure 2.5. Simulated passage success of Northern Pike across three barrier height and pool depth treatments and average passage success (%) across all treatments, predicted using a multiple logistic regression model. Model predictors include barrier height (cm), pool depth (cm), fork length (mm), and residual growth rate at age (mm/day). Northern Pike from Montana (MT) were used in leaping experiments in a large open-channel flume system during 2021, and Northern Pike from Alaska (AK) were collected during 2020. Asterisks indicate significant differences in mean leaping ability for a given treatment, while ns indicates no significant differences. Box plot bars represent mean values, boxes represent interquartile ranges, lines represent minimum and maximum values, and dots represent outliers.

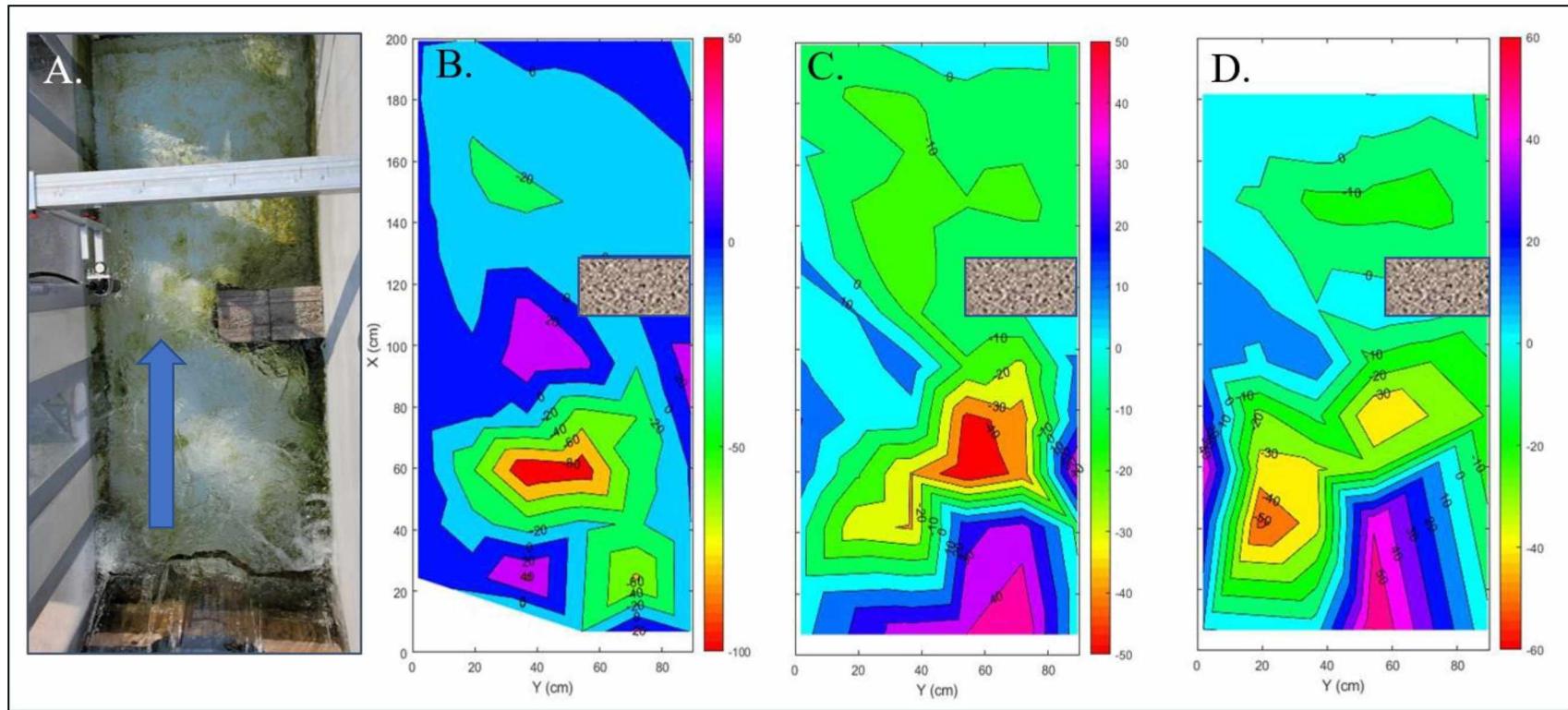


Figure 2.6. A. Top-down view of the plunge pool as 3-D velocity measurements are taken with an Acoustic Doppler Velocimeter device after leaping trials using Northern pike were completed in a large open-channel flume system in 2021, with the arrow representing general flow direction. Contour plots of Z-velocity taken in the plunge pool are shown at a 10-cm height x 30-cm pool depth treatment (B), 30 cm x 40 cm treatment (C), and 40 cm x 40 cm treatment (D). Negative values indicate downwelling of water velocity, while positive values indicate upwelling of water velocity.

General conclusion

Through this work, I advanced our knowledge of intraspecific trait variation in biological invasions, and how accounting for such variation may facilitate more informed management of invasive species on a local scale. With evidence that invasive Northern Pike in Alaska may benefit physiologically and have enhanced dispersal tendencies relative to native individuals (Berghaus et al. 2019; Dunker et al. 2022), I explored variation in Northern Pike diets, and associated growth rates, body condition, and maturation, as well as morphology and activity levels associated with dispersal potential as a function of invasive or native origin and by river or lake habitat type. Management entities are pursuing the use of selective vertical drop barriers to prevent the spread of invasive Northern Pike in Alaska, contingent upon interspecific differences in invasive Northern Pike and native salmonid leaping abilities (Dunker et al. 2022). However, observed benefits in diet, growth rates, body condition, and early maturation in invasive Northern Pike relative to native individuals in Chapter 1 highlighted the importance of considering how unique biological traits of invasive Northern Pike could affect their leaping ability thus and barrier feasibility. In Chapter 2, I quantified the maximum leaping ability of Northern Pike as a function of physical barrier attributes and individual biological characteristics using experiments with individuals collected in Montana at the Bozeman Fish Technology Center. While barrier height and pool depth had the strongest effects on Northern Pike leaping ability, individual biological traits such as body size and residual growth rate at age were also significant predictors in the final logistic model selected via AICc. As sizes and growth rates differed between Northern Pike from Alaska and Montana, I predicted and compared the leaping ability of these groups to consider how such variation can inform the design and testing of selective barriers for invasive Northern Pike in Alaska. Key results from these studies have implications for better understanding and managing the impacts of invasive Northern Pike, and the broader disciplines of invasion ecology and its management applications.

While the observational nature of Chapter 1 precluded strong causal relationships between physiological and environmental metrics, the breadth of traits and their relationships in the literature facilitated hypothesized connections and areas for future study. I found that relative to Northern Pike of native origin, invasive-origin individuals, 1) were smaller and younger, 2) their stomachs were two times more likely to contain energy-rich vertebrate diet items, 3) they had 1.2 to 2-fold faster growth rates, 4) they matured earlier, and 5) had 30% greater lipid content. However, physiological benefits were generally greater in lake habitats for invasive Northern Pike, while native individuals experienced improved growth, lipid accumulation, and maturation in river habitats. Such inter-habitat variation between invasive and native Northern Pike may be explained by observed differences in diet, assumed thermal regimes and metabolic demands, and measured activity levels.

For example, lake individuals experienced higher activity levels, quantified via white muscle enzyme activity, relative to river individuals potentially due to warmer thermal regimes in lakes that led to increased metabolic rates, food demand, and foraging activity. However, native lake individuals had lower quantity and quality of diet items in their stomachs relative to native river individuals, which resulted in a mismatch in low food availability and high metabolic demands that reduced growth rates and lipid stores of native lake individuals. While Northern Pike from invasive lakes also experienced higher activity levels relative to invasive river individuals, these groups had similar amounts of energy-rich vertebrate diet items in their stomachs. Higher metabolic rates in invasive lake individuals likely resulted in rapid conversion of abundant food into somatic growth, while invasive river individual growth rates were reduced in cooler riverine environment that limited somatic growth, but facilitated the storage of lipids as seen in other fish species (Person-Le Ruyet et al. 2004; Alvarez et al. 2006). A similar comparison of lentic and lotic populations of Northern Pike found no differences in growth rate due to effects of river vs lake occupancy; however, food availability and thermal regimes were assumed to be similar unlike this study, and are important drivers of Northern Pike growth (Frost and Kipling 1967; Griffiths et al. 2004). These observations were collected from only one invasive river and invasive lake

site with similar invasion timescales of 30 years, however, and Northern Pike diets and physiological responses appeared to be strongly influenced by a gradient of habitat heterogeneity within these two locations and when comparing our results to other studies (Haught and von Hippel 2011; Sepulveda et al. 2013; Cathcart et al. 2019). This supports a more in-depth assessment of how habitat characteristics, prey accessibility, and time since invasion may influence the impacts and success of invasive Northern Pike in Alaska, which could be useful to prioritize management based on habitat conditions.

Such intraspecific variation within invasive Northern Pike across different habitat types provides fodder for using Northern Pike in Alaska to better understand larger questions of invasion ecology and evolution. For example, theory and evidence indicate that a combination of adaptive phenotypic plasticity, contemporary evolution, and external environmental factors can drive trait variation and mediate invader success (Kolar and Lodge 2001; Byers et al. 2002; Ghalambor et al. 2007; Sax et al. 2007; Westley 2011). Teasing apart which underlying mechanisms drive intraspecific variation has been more difficult, but equally important, to draw overarching conclusions about invasions that can contribute to predicting, preventing, and ameliorating future introductions of invasive species. Previous work has revealed low genetic diversity (Jalbert 2018; Campbell et al. 2022) and low rates of evolutionary divergence within invasive Northern Pike relative to native individuals in Alaska (Berghaus et al. 2019). Low evolutionary rates and genetic diversity may suggest that the ability of invasive Northern Pike to exhibit physiological benefits in growth and energy storage are due to suitable environmental conditions and/or phenotypic plasticity rather than underlying genetic variation. Alternatively, there may be high genotype-phenotype association surrounding growth rates in Northern Pike that are selected for and have yet to be quantified, but is increasingly possible with genetic advancements in studying Northern Pike as a model organism (Forsman et al. 2015; Larson et al. 2016).

Indeed, the process of invasion can select for faster growth rates and dispersal in fishes and other taxa (Phillips 2009; Llewelyn et al. 2010; Phillips et al. 2010; Lowe et al. 2015; Myles-Gonzales 2015). Increased dispersal and growth rates, as well as dominance and food consumption, are often driven by

inherent variation in metabolic rates among ectotherms despite constant temperatures (Burton et al. 2011; Metcalfe et al. 2016), which could be the unifying physiological trait that has led to enhanced prey consumption, growth rates, and energy storage, and early maturation of invasive Northern Pike and potentially other invasive piscivorous fishes. However, basal metabolism can also be highly plastic and change as a function of food availability for fishes to maximize growth despite a static genotype (Auer et al. 2015). While anaerobic enzymes were quantified here as a proxy for activity level and may reflect high or low foraging activity driven by metabolic demands, this cannot capture individual variation in aerobic metabolic rates (Norin and Malte 2012). Large-scale studies that connect genotypes to phenotypes through common-garden and/or transplant methods (David et al. 2015; Tibblin et al. 2015) and quantification of metabolic rates through respirometry would be more appropriate to tease apart the interacting genetic and environmental drivers of invasion success in Northern Pike.

Documenting physiological benefits in invasive individuals in Alaska cemented the importance of quantifying how these traits influence Northern Pike leaping ability, as management of Northern Pike in Alaska seeks to contain their spread with selective vertical drop barriers (Dunker et al. 2022). Ultimately, the assessment of Northern Pike leaping ability in Chapter 2 supports further exploration of selective vertical drop barriers as a management tool due to the clear differences in leaping abilities observed in Northern Pike and salmonids (Stuart 1962; Powers and Orsborn 1985; Kondratieff and Myrick 2006; Lauritzen et al. 2010). Barrier height and pool depth had the strongest effect on leap success; however, individual size and residual growth rate at age also were important predictors and should be considered in barrier planning and implementation. For example, barrier heights of 40 cm may only be impassable when pool depths are shallower than 40 cm and Northern Pike are particularly large (700 mm), because small individuals (550 mm) were able to ascend similar barrier heights relative to large individuals but were not as limited by shallow pool depths. Our finding that leaping ability increased with age-controlled growth rate of Northern Pike, and prediction that Northern Pike from Alaska would have marginally greater leap success because of faster residual growth rates at age, have important implications for testing

and designing barriers. Barriers may need to be rigorously tested using Alaskan Northern Pike in Alaskan ecosystems to ensure that barriers are effective outside of laboratory experiments based on one population of Northern Pike, and across additional thermal and hydrologic regimes. Observations of 3D velocity in the plunge pool, behavioral data from video recordings, and discussions with invasive Northern Pike managers outside the leaping experiments have resulted in several suggestions for continued exploration of selective barriers against Northern Pike in southcentral Alaska, that include:

1. Tag invasive Northern Pike with passive integrated transponder (PIT) tags and install a network of PIT antennas at river/lake entrances and tributary confluences to quantify the frequency and direction of dispersal from mainstems to tributaries, lakes, off-channel sloughs, and estuarine corridors (*sensu* B. Rich, unpublished data).
2. Place video weirs at potential barrier installation locations to characterize fish species and life stages that utilize the stream corridor and may require passage over Northern Pike-specific barriers.
3. Test barriers in Alaskan ecosystems with Alaskan Northern Pike: Place a test barrier at the mouth of an already invaded river system (e.g., Meadow Creek or Threemile Creek). Collect and PIT tag Northern Pike and native salmonids (adults and juveniles) that are present in the river system. Test the efficacy of a 45 cm height / 40 cm pool depth barrier with tagged fish by placing them in the lower pool and allowing fish to volitionally ascend the barrier. Repeat this experiment several times throughout the open water season (ideally encompassing spawning season for Northern Pike and salmonids) to observe effects of fish motivation (spawning or non-spawning), water temperatures outside of 11°C, and flow rates outside of 11.5 to 42.9 L/s on fish passage.
4. Test efficacy of an ecological trap such as a slough with a fyke net near barriers, as Northern Pike appear to be deterred by the turbulence of vertical drop barriers. Place the test barrier such that a natural slough or a man-made slough can be created near the barrier as an alternative option for Northern Pike to access desired upstream habitat. Place and monitor a fyke net in the slough. This

could be done in conjunction with experiment 3 to determine if the slough trap attracts Northern Pike selectively, unintentionally attracts other species, or creates an unintentional staging area for Northern Pike.

5. If barriers are deemed effective to block Northern Pike and facilitate passage of native fishes, installed barriers should be tested for efficacy periodically because barriers can act as an additional selective force on fish morphology, behavior, and physiology (reviewed in Zarri et al. 2022). As climate change alters thermal and flow regimes in southcentral Alaska, warming waters may negatively affect the passage of cold-water salmonids in favor of cool-water Northern Pike (Shaftel et al. 2020), while variable flows much greater than those tested in Chapter 2 may reduce passage of all species (Murdoch et al. 2020).
6. Ultimately commission a fish passage engineering firm to design barriers that incorporate findings from this work and optimizations through future field barrier testing efforts. Barrier designs should also consider local environmental requirements such as flow and temperature variability, now and in the future, and passage of native species and life stages outside of adult salmonids (e.g., juvenile salmonids, sticklebacks, sculpins, suckers, lampreys), and human use needs.

These assessments of intraspecific variation within and among invasive and native Northern Pike populations in Alaska, and how that variation may have implications for future research and management planning, highlights the importance of intraspecific variation in ecological research (Des Roches et al. 2018). Freshwater ecosystems and species face numerous threats (Reid et al. 2019), and ineffective barriers that reduce native fish passage and/or promote limited Northern Pike passage should not be added to the growing list. However, by utilizing the logistic regression model to generate potential test barrier designs based on local Northern Pike lengths and growth potential, managers can take more informed steps towards effective use of selective fragmentation to manage Northern Pike in Alaska and elsewhere they are invasive. While predicting and preventing invasions from occurring may benefit from

generalized decision tools (Copp et al. 2005; Packer et al. 2017; Novoa et al. 2020), localized management of established invaders can benefit greatly from considering the degree of intraspecific variation and the environmental, plastic, or genetic mechanisms of such variation to selectively target invaders and reduce impacts on native species (Reichard et al. 2015; Rahel and McLaughlin 2018).

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Appendices

Appendix A. 2020 University of Alaska Fairbanks Institutional Animal Care and Use Committee approval.



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Institutional Animal Care and Use Committee

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July 1, 2020

To: Jeff Falke
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [1609856-2] Invasive and native pike physiological comparisons

The IACUC reviewed and approved the New Project referenced above by Designated Member Review.

Received: June 16, 2020
Approval Date: July 1, 2020
Initial Approval Date: July 1, 2020
Expiration Date: July 1, 2021

This action is included on the July 9, 2020 IACUC Agenda.

Appendix B. General bioelectrical impedance analysis (BIA) methods, temperature correction equations, and BIA model development used to assess and predict body condition of Northern Pike.

Northern Pike were measured for BIA using standard methods (Cox and Hartman 2005; Falke et al. 2019) with a handheld Quantum II Bioelectrical Body Composition Analyzer (Q2; RJL Systems, Clinton Township, MI, USA) or a CQR Body Composition Analyzer (Seafood Analytics Juneau, Alaska) with 5-mm 28-gauge needles spaced 10-mm apart, at the dorsal-midline (DML) and dorso-ventral (DV) locations as seen in Figure 1.2. As BIA measurements linearly decline with temperature and this decline varies with fish species (Stolarski et al. 2014; Hafs and Hartman 2015), BIA measurements were taken in a range of temperatures on a subset of 10 individuals (200-400 mm) collected from a single location on the same date. Impedance was measured on each individual between 0 and 15°C in 3°C increments for a total of five measurements. Generalized linear mixed effect models were used to determine the relationship between BIA measurements for Northern Pike and body temperature, with a fixed effect for temperature and a random intercept effect for each individual ($n = 10$). The fixed effects and intercept from each model were then incorporated into corrective equations to standardize impedance measurements for all Northern Pike to 10°C prior to analysis (Hafs 2011; Stolarski et al. 2014; Courtney et al. 2020):

$$DMLr \text{ (corrected)} = DMLr * ((-8.07*T+438.31)/(-8.07*10+431.31))$$

$$DMLx \text{ (corrected)} = DMLx * ((-1.77*T+129.57)/(-1.77*10+129.57))$$

$$DVr \text{ (corrected)} = DVr * ((-5.67*T+208.70)/(-5.67*10+208.70))$$

$$DVx \text{ (corrected)} = DVx * ((-2.41*T+85.27)/(-2.41*10+85.27))$$

Where T is the temperature in °C at time of impedance measurements, DMLr is DML resistance, DMLx is DML reactance, DVr is DV resistance, and DVx is DV reactance. Proximate component measurements % dry mass (%DM) and % dry lipid (%DL) were modeled separately as a function of standard electrical parameters calculated from temperature-corrected BIA measurements (Table 1, Cox and Hartman 2005; Hafs and Hartman 2011; Stolarski et al. 2014) and biological characteristics of Northern Pike to create a predictive model that estimates species-specific proximate composition. Body condition index (BCI) was calculated by log-transforming fork length and weight values, and fitting a linearized version of the power

function $W_i = aFL_i^b + \varepsilon_i$ to the data. Then, ordinary least squares regression errors (ε) were calculated for each individual as BCI from the following equation:

$$BCI_i = \log_e(W_i) - \log_e(a) - b \cdot \log_e(FL_i)$$

Where BCI_i is the body condition index of each individual i with weight W_i and fork length FL_i , and a and b are the estimated parameters from the regression model (Bentley and Schindler 2013). Final BIA models were used to predict %DM and %DL of the subset of individuals not used in proximate composition analysis for enzyme activity assays (N=32) so that body condition could be compared with other characteristics for all individuals.

Appendix C. Bioelectrical impedance analysis model selection summary for models developed to estimate body condition of Northern Pike collected from invasive and native locations in river and lake habitats from Alaska, USA during summer 2020.

The best predictive models for % dry mass (%DM) and % dry lipid (%DL) contained nearly all predictor variables (Appendix D), indicating that dorsal and ventral bioelectrical impedance analysis locations, weight, fork length, and internal fish temperature should be taken in the field to accurately predict proximate components for Northern Pike. The %DM model contained 20 predictors (all except fork length) and had high explained variance and predictive power ($R^2 = 0.78$, Root mean squared error (RMSE) = 0.76%, Appendix E). Dry % lipid was best predicted by the global model, with slightly less explained variance and predictive power ($R^2 = 0.73$, RMSE = 2.40%, Appendix F). Supplementary R code, top lipid and dry mass models, and an example dataset of Northern Pike BIA measurements and biological characteristics are included to practice calculation of %DM and %DL.

Appendix D. Description of comma delimited format (.csv) file (first row is attribute names) containing bioelectric impedance analysis data collected from invasive and native Northern Pike in river and lake habitats from Alaska, USA during summer 2020 (N = 32).

Attributes are as follows:

Pike_ID = fish ID

Population = pike collected from “invasive” or “native” locations

whole_weight = weight of pike (g)

Fork_Length = fork length (mm)

DML_res = resistance (ohms) measured with Quantum II BIA meter along dorsal midline (DML; average from 3 readings)

DML_rea = reactance (ohms) measured with Quantum II BIA meter along dorsal midline (DML; average from 3 readings)

DML_detector = detector length (cm) along dorsal midline (DML; i.e., distance between electrodes)

DV_res = resistance (ohms) measured with Quantum II BIA meter along ventral to dorsal (DV; average from 3 readings)

DV_rea = reactance (ohms) measured with Quantum II BIA meter along ventral to dorsal (DV; average from 3 readings)

DV_detector = detector length (cm) along ventral to dorsal (DV; i.e., distance between electrodes)

Vent_temp1 = internal temperature ($^{\circ}$ C) measured before taking DML measurements

Vent_temp2 = internal temperature ($^{\circ}$ C) measured before taking DV measurements

Appendix E. Bioelectrical impedance analysis (BIA) model parameters, symbols, units, and equations for models developed for Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020. Detector length (DL; mm) is the distance between electrodes, W_i is mass (g), and FL_i is fork length (mm). All parameters except for BCI were calculated for dorsal midline and dorsoventral measurements (see Figure 1.3).

Parameter	Symbol	Units	Equation
Reactance	x	Ohms	Measured by BIA device
Resistance	r	Ohms	Measured by BIA device
Reactance in parallel	X_{cp}	Ohms	$DL^2/(x + (r^2/x))$
Resistance in parallel	R_p	Ohms	$DL^2/(r + (x^2/r))$
Impedance in parallel	Z_p	Ohms	$DL^2/(r \cdot x / (r^2 + x^2)^{0.5})$
Reactance in series	X_c	Ohms	DL^2/x
Resistance in series	R_s	Ohms	DL^2/r
Impedance in series	Z_s	Ohms	$DL^2/(r^2 + x^2)^{0.05}$
Capacitance	C_{pf}	Ohms	$DL^2/ (3.18 \times 10^{-18}/X_{cp})$
Phase angle	PA	Degrees	$\text{Arctan}(x/r) \cdot 180/\pi$
Standardized phase angle	DLPA	Degrees	$DL \cdot (\text{arctan}(x/r) \cdot 180/\pi)$
Body condition index	BCI	Unitless	$\log_e(W_i) - \log_e(a) - b \cdot \log_e(FL_i)$

Appendix F. Multiple linear regression coefficients for the prediction of percent dry mass for Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020 based on measurements taken from two locations (DML dorsal midline, DV dorso-ventral; Figure 1.3). Parameter estimates \pm 1 SE are shown. Formulas for calculating covariates and covariate definitions are given in Appendix D.

Covariate	Parameter estimate	t-value	P-value
Intercept	23.4 \pm 2.50	9.37	< 0.001
Rs (DML)	-165000.0 \pm 146000.0	-1.14	0.26
Rp (DML)	-106000.0 \pm 98100.0	-1.08	0.29
Xc (DML)	-136000.0 \pm 115000.0	-1.18	0.24
Xcp (DML)	-58600.0 \pm 50500.0	-1.16	0.25
Cpf (DML)	< -0.001 \pm < -0.001	-1.81	0.07
Zs (DML)	270000.0 \pm 243000.0	1.11	0.27
Zp (DML)	136000.0 \pm 115000.0	1.18	0.24
PA (DML)	-0.33 \pm 0.13	-2.48	0.02
DLPA (DML)	0.02 \pm 0.01	3.18	0.002
Rs (DV)	673000.0 \pm 367000.0	1.84	0.07
Rp (DV)	371000.0 \pm 197000.0	1.88	0.07
Xc (DV)	599000.0 \pm 329000.0	1.82	0.07
Xcp (DV)	245000.0 \pm 133000.0	1.84	0.07
Cpf (DV)	< -0.001 \pm < 0.001	1.41	0.16
Zs (DV)	-1030000.0 \pm 558000.0	-1.85	0.07
Zp (DV)	-599000.0 \pm 330000.0	-1.82	0.07
PA (DV)	0.19 \pm 0.18	1.07	0.29
DLPA (DV)	-0.02 \pm 0.02	-1.19	0.24
BCI	-0.15 \pm 0.10	-1.44	0.16
Whole weight	0.002 \pm 0.001	2.82	0.006

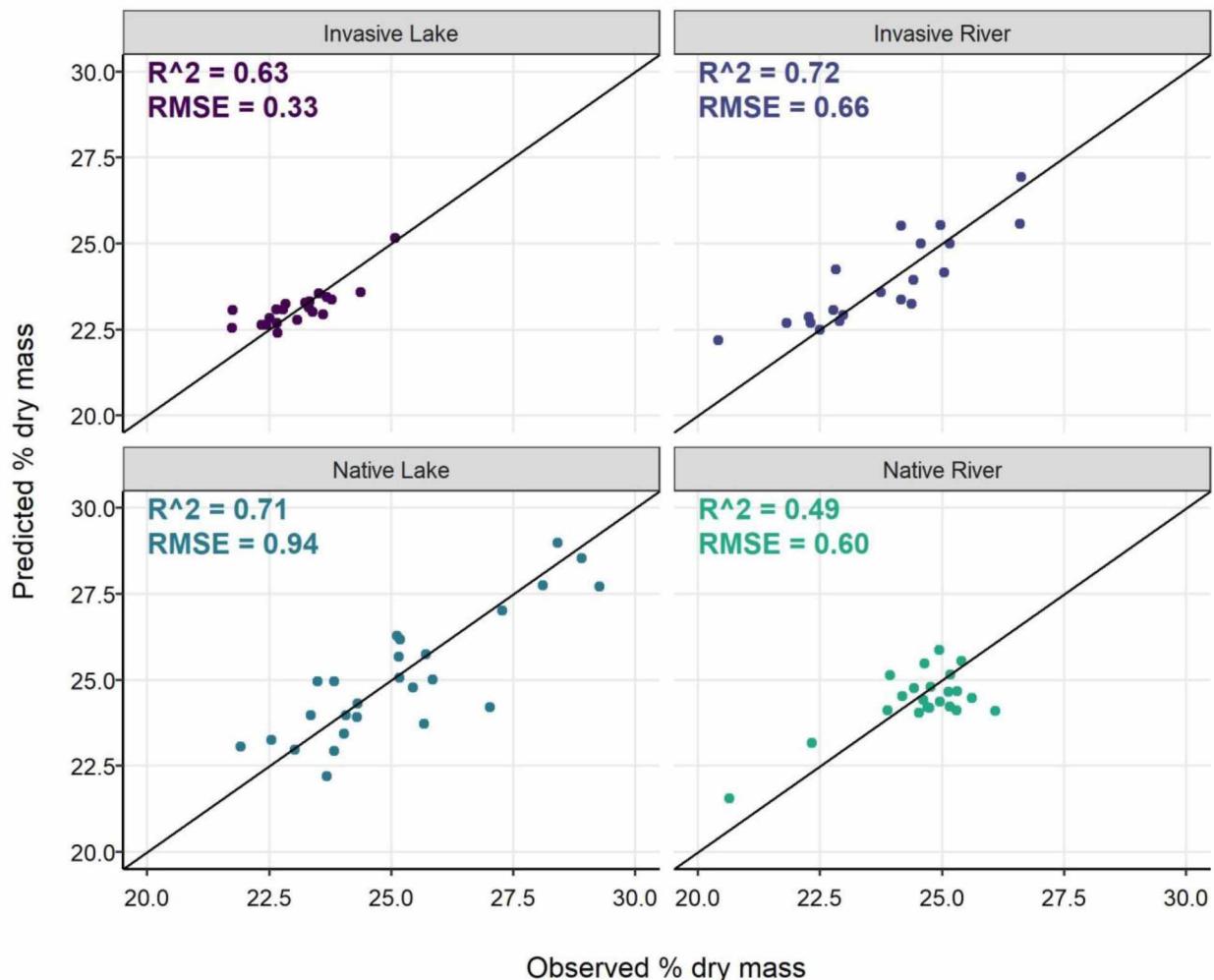
Appendix G. Multiple linear regression coefficients for the prediction of percent dry lipid for Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020, based on measurements taken from two locations (DML dorsal midline, DV dorso-ventral; Figure 1.3). Parameter estimates \pm 1 SE are shown. Formulas for calculating parameters are given in Appendix D.

Covariate	Parameter estimate	t-value	P-value
Intercept	30.4 ± 9.10	3.34	0.001
Rs (DML)	442000.0 ± 462000.0	0.96	0.34
Rp (DML)	275000.0 ± 311000.0	0.88	0.38
Xc (DML)	368000.0 ± 364000.0	1.01	0.32
Xcp (DML)	156000.0 ± 160000.0	0.98	0.33
Cpf (DML)	$< -0.001 \pm < -0.001$	-3.12	0.003
Zs (DML)	-713000.0 ± 770000.0	-0.93	0.36
Zp (DML)	-368000.0 ± 364000.0	-1.01	0.32
PA (DML)	-1.05 ± 0.44	-2.39	0.02
DLPA (DML)	0.13 ± 0.03	4.39	< 0.001
Rs (DV)	-62800.0 ± 1160000.0	-0.05	0.96
Rp (DV)	28000.0 ± 624000.0	0.05	0.96
Xc (DV)	-93200.0 ± 1040000.0	-0.09	0.93
Xcp (DV)	-19000.0 ± 422000.0	-0.05	0.96
Cpf (DV)	$< -0.001 \pm < 0.001$	-0.67	0.51
Zs (DV)	27200.0 ± 1770000.0	0.02	0.99
Zp (DV)	93900.0 ± 1040000.0	0.09	0.93
PA (DV)	-0.31 ± 0.56	-0.56	0.58
DLPA (DV)	0.07 ± 0.06	1.27	0.21
BCI	0.03 ± 0.36	0.08	0.94
Fork length	-0.08 ± 0.02	-4.77	< 0.001

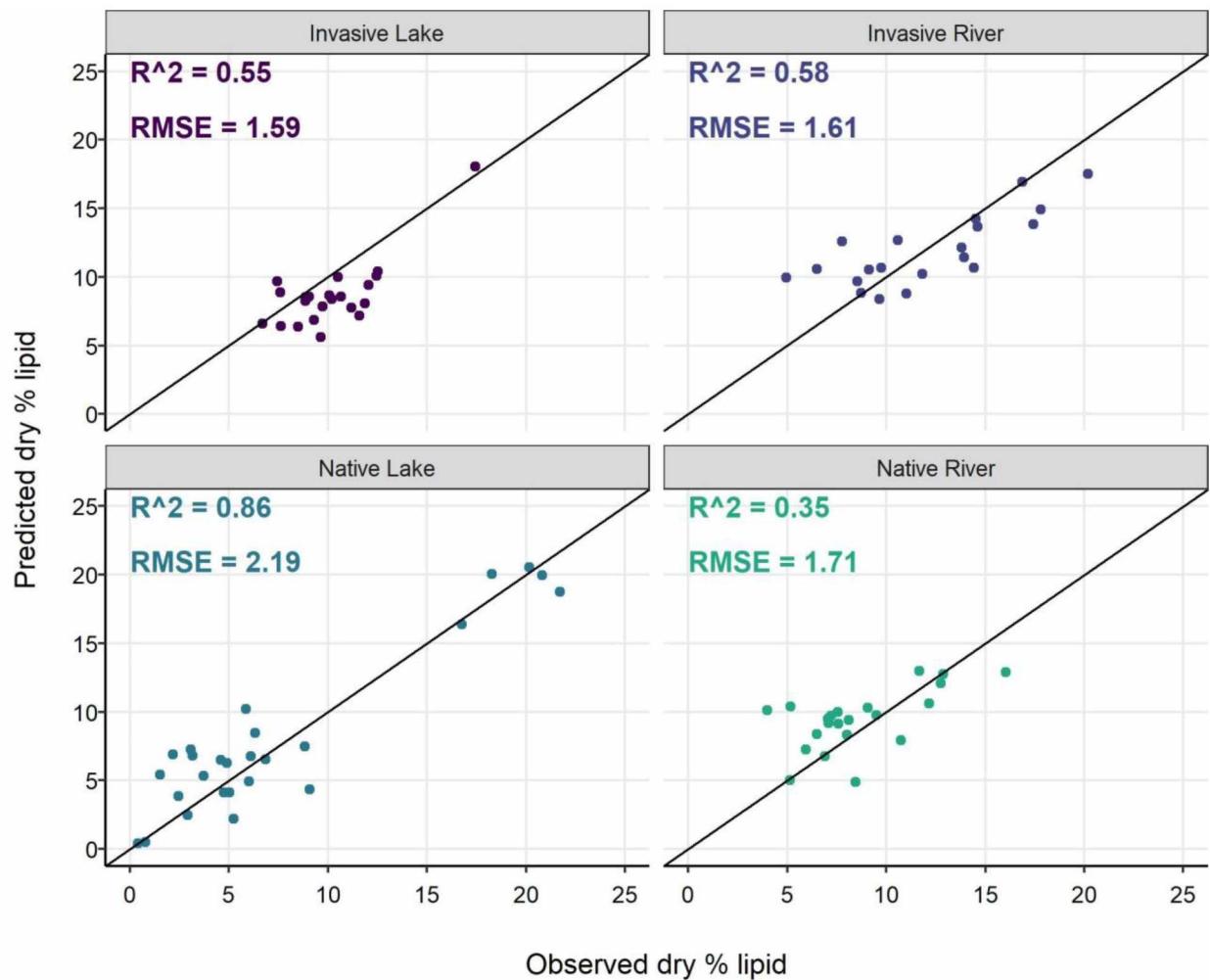
Appendix G continued

Whole weight	0.01 ± 0.002	4.70	< 0.001
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Appendix H. Predicted vs observed % dry mass values by group for Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020. Black lines represent a slope of one, with R^2 and root mean squared error (RMSE) values included in each panel.

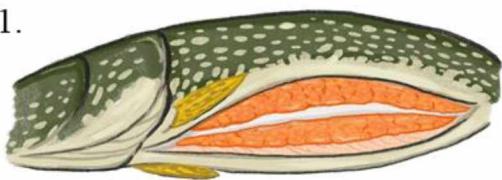


Appendix I. Predicted vs observed dry % lipid values by group for Northern Pike collected in lake and river habitats in their native and invasive range in Alaska, USA in 2020. Black lines represent a slope of one with R^2 and root mean squared error (RMSE) values included in each panel.

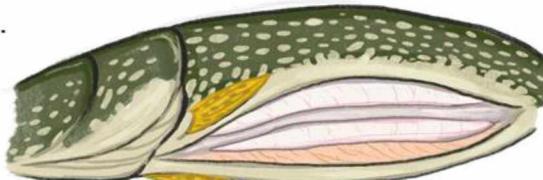


Appendix J. Internal appearance of Northern Pike gonads used to categorize individual sex and maturity based on developmental state of ovaries or testes for observational and experimental research during summers of 2020 and 2021. A1. Pre-spawn mature female with large, orange, ripe/ripening ovaries containing eggs. A2. Post-spawn mature female with reduced, slightly transparent ovaries with an orange hue that can contain small developing eggs. A3. Immature female with thinner, translucent, ovaries with a slight orange or pink hue. B1. Pre-spawn mature male with large, white, opaque testes. B2. Post-spawn mature male with slightly thinner, white, opaque testes. B3. Immature male with very thin, generally white testes that are slightly translucent. C. Immature individual of unknown sex with very small, thin, translucent gonads with little color. Artwork by T. Cubbage.

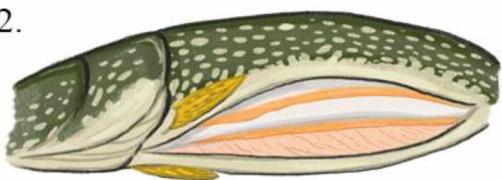
A1.



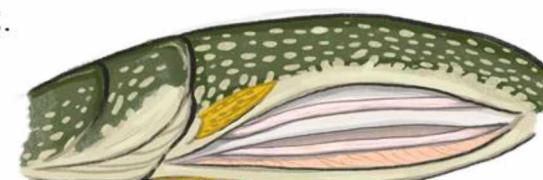
B1.



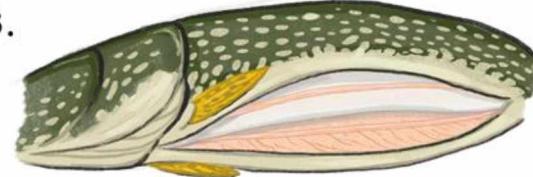
A2.



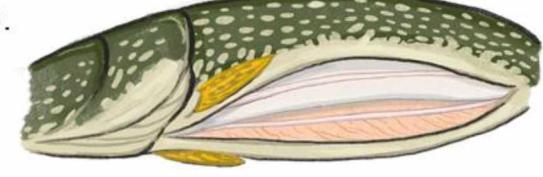
B2.



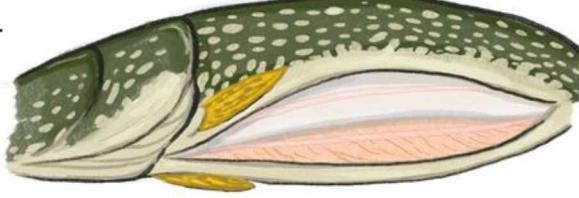
A3.



B3.



C.



Appendix K. Stable isotope analysis methods used for muscle tissue of Northern Pike and diet items found in their stomachs for Bayesian mixing model analyses to understand individual dietary contributions. Northern Pike were collected in lake and river habitats in their native and invasive ranges in Alaska, USA in 2020.

Samples were thawed, dried for at least 36 hours between 55 and 60°C, ground with mortar and pestle, weighed to 0.3-0.6 mg, and analyzed using a ConFlow IV EA-IRMS (Elemental Analyzer Isotope Ratio Mass Spectroscopy) at the Alaska Stable Isotope Facility on the University of Alaska Fairbanks campus. Stable isotope ratios were expressed as δ (‰) relative to Vienna Pee Dee Belemnite (VPDB) for the $\delta^{13}\text{C}$ values and atmospheric nitrogen (AIR) for the $\delta^{15}\text{N}$ values. The ratio of $\delta^{13}\text{C}$ to $\delta^{15}\text{N}$ was calculated for prey items and Northern Pike to determine if lipid correction for $\delta^{15}\text{N}$ values was necessary. The $\delta^{15}\text{N}$ values for prey items with C:N ratios greater than 3.5 were corrected according to Post et al. (2007) using equations for aquatic organisms, while Northern Pike $\delta^{15}\text{N}$ values did not require lipid correction.

Appendix L. Lactate dehydrogenase enzyme activity assay methods to assess the activity level of Northern Pike collected in lake and river habitats in their native and invasive ranges in Alaska, USA in 2020.

Two 5-g samples of dorsal white muscle, two 5-g samples of liver, and the entire ventricle from each individual were taken and preserved at -80°C. The activity of lactate dehydrogenase (LDH) was measured in tissues for each individual in triplicate by initiating the maximized conversion of pyruvate to lactate and oxidation of NADH to NAD⁺ as follows: tissue samples were thawed and homogenized in 75 mM tris-HCl buffer (pH 7.6 at 20°C) and the homogenate was combined with 2.5 mM potassium cyanide (KCN), 0.3 mM NADH, and 25 mM sodium pyruvate in 100 µl reaction wells of a 96-well reaction plate. As LDH converts pyruvate to lactate and NADH is oxidized to NAD⁺ during the reaction, the decline in NADH absorbance is measured with a spectrophotometer at 340 nm to quantify relative LDH activity. Background and reaction absorbance rates of NADH were measured at room temperature (20°C) with a UV/visible spectrophotometer for four minutes each. Change in NADH reaction absorbance was converted to LDH activity and reported as µmol/min/gram wet tissue (Ombres et al. 2011; Condon et al. 2012).

Appendix M. Growth rate calculation methods used to estimate growth rates of Northern Pike collected in Alaska during summer 2020, and Northern Pike collected in Montana during summer 2021.

Age-1 growth was calculated as the change in length from hatching (L_0) to length at year 1 (L_1) divided by the Day of Year (DOY) of the end of the growing season (estimated as November 1, DOY 305, Casselman 1996) minus the JD of the estimated hatch date for all Northern Pike (May 15, DOY 135). For subsequent ages after year 1 before capture, growth was calculated as the change in length from the previous year (L_{t-1}) to the year of concern (L_t), divided by the length of the growing season (April 1 (DOY 91) – November 1 (DOY 305), Casselman 1996). Because Northern Pike were captured during the growing season, growth after the last annulus was calculated as the change in length from the previous year (L_{T-1}) to length at capture (L_T), divided by the days between the start of the growing season for 1+ pike (April 1, DOY 91) or the estimated hatch date for 0+ pike (May 15, DOY 135), minus the Capture Date (CD). Equations are as follows:

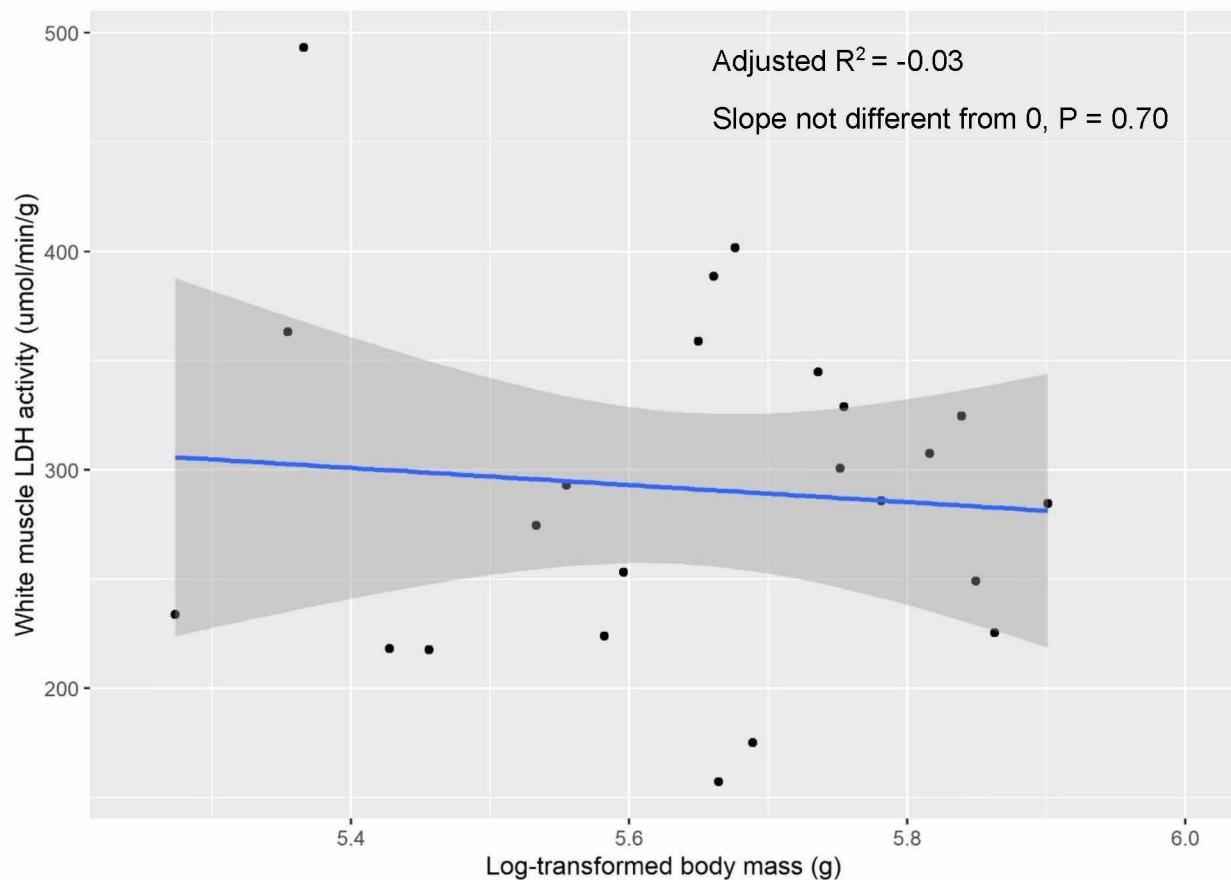
$$\text{Growth (mm/day) age } 0+ = (L_T - L_0) / (CD - 135)$$

$$\text{Growth (mm/day) age } 1 = (L_t - L_0) / (305-135)$$

$$\text{Growth (mm/day) age } 2+ = (L_t - L_{t-1}) / (305-91)$$

$$\text{Growth (mm/day) after last annulus} = (L_T - L_{T-1}) / (CD-91)$$

Appendix N. Linear regression of white muscle lactate dehydrogenase (LDH) enzyme activity as a function of log-transformed body mass for Northern Pike collected in Alaska during 2020. Shaded area represents the 95% confidence interval of LDH activity level as a function of log-transformed body mass.



Appendix O. Summary of sample sizes, mean \pm SD fork lengths (mm), and proportions of males, females, unknown sex, mature and immature individuals for each Northern Pike group collected in Alaska during summer 2020.

Group	N	Fork Length	Male	Female	Unknown	Mature	Immature
Invasive Lake	30	323.0 ± 57.0	37.0%	0.0%	63.0%	16.0%	84.0%
Invasive River	28	362.0 ± 99.0	29.0%	60.0%	11.0%	11.0%	89.0%
Native Lake	34	535.0 ± 185.0	32.0%	62.0%	5.0%	59.0%	41.0%
Native River	31	439.0 ± 114.0	16.0%	74.0%	10.0%	32.0%	68.0%

Appendix P. Summary of Northern Pike morphometrics as mean \pm standard deviation by origin and habitat classification, and for separate locations within origin and habitat designations if applicable. All Northern pike (N = 123) were collected from lake and river habitats in their native and invasive ranges in Alaska, USA in 2020.

Group	N	Fork length (mm)	Body depth (mm)	Peduncle circumference (mm)	Caudal fin width (mm)	Dorsal fin width (mm)	Anal fin width (mm)
Invasive Lake							
Nancy Lake	30	323.0 \pm 57.6	54.6 \pm 10.8	51.3 \pm 10.6	33.8 \pm 6.67	35.9 \pm 6.62	26.6 \pm 5.75
Invasive River							
Deshka River	28	361.0 \pm 99.0	60.3 \pm 18.0	59.1 \pm 16.5	42.5 \pm 11.0	39.8 \pm 10.9	32.3 \pm 9.77
Native Lake	34	534.0 \pm 185.0	88.4 \pm 33.7	82.7 \pm 28.3	57.8 \pm 19.9	61.3 \pm 21.6	44.2 \pm 14.8
Minto Flats	23	630.0 \pm 142.0	104.9 \pm 28.2	97.2 \pm 22.0	68.2 \pm 15.2	72.9 \pm 15.6	52.2 \pm 10.7
Mullins Pit	11	333.0 \pm 56.4	54.1 \pm 8.68	52.4 \pm 8.55	36.0 \pm 5.0	37.1 \pm 7.20	27.5 \pm 4.78
Native River	31	439.0 \pm 113.0	71.0 \pm 19.3	69.3 \pm 15.8	51.1 \pm 13.8	50.5 \pm 13.3	37.5 \pm 9.72
Noyes Slough	6	298.0 \pm 115.0	46.5 \pm 17.6	50.3 \pm 16.4	45.2 \pm 27.1	34.2 \pm 13.4	25.0 \pm 11.1
Sternwheeler Pond	4	559.0 \pm 76.9	98.5 \pm 12.6	85.8 \pm 10.9	61.0 \pm 6.38	62.8 \pm 9.43	46.8 \pm 6.29
Willow Creek	21	457.0 \pm 77.5	72.8 \pm 11.1	71.6 \pm 11.1	50.9 \pm 8.06	52.9 \pm 9.49	39.3 \pm 6.14

Appendix Q. Summary of lactate dehydrogenase (LDH) enzyme activity ($\mu\text{mol}/\text{min}/\text{gram}$ wet tissue, mean \pm SD) for white muscle, ventricle, and liver tissues, summed as total body LDH activity, for each Northern Pike group collected during the summer of 2020 in Alaska.

Group	N	White Muscle	Ventricle	Liver	Total Body
Invasive Lake	8	318.0 ± 81.2	318.0 ± 74.4	11.6 ± 3.68	648.0 ± 108.0
Invasive River	8	257.0 ± 49.6	264.0 ± 63.4	16.2 ± 5.48	538.0 ± 87.8
Native Lake	8	323.0 ± 82.1	306.0 ± 48.0	18.2 ± 4.84	647.0 ± 83.7
Native River	8	257.0 ± 22.3	283.0 ± 64.7	19.2 ± 8.04	559.0 ± 81.1

Appendix R. 2021 University of Alaska Fairbanks Institutional Animal Care and Use Committee approval.



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Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

April 8, 2021

To: Jeff Falke
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [1564579-2] Physiological performance of Northern Pike (*Esox lucius*): implications for barrier design in invaded systems

The IACUC reviewed and approved the Revision referenced above by Designated Member Review.

Received: March 4, 2021
Approval Date: April 7, 2021
Initial Approval Date: April 7, 2021
Expiration Date: April 7, 2022

This action is included on the May 13, 2021 IACUC Agenda.

Appendix S. Bioelectrical impedance analysis model selection summary for models developed to estimate body condition of Northern Pike collected in Montana and used in leaping experiments in a large open channel flume during summer 2021.

The best predictive models for % dry mass (%DM) and % dry lipid (%DL) contained nearly all predictor variables (Appendix D), indicating that dorsal and ventral bioelectrical impedance analysis (BIA) locations, weight, fork length, and internal fish temperature should be taken to accurately predict proximate components for Northern Pike. The %DM model contained eight predictors (all dorsal BIA measurements except for impedance in parallel) and had high explained variance and predictive power ($R^2 = 0.80$, Root mean squared error (RMSE) = 0.98%, Appendix O). Dry % lipid was best predicted by the global model, with slightly less explained variance and predictive power ($R^2 = 0.71$, RMSE = 2.69%, Appendix P). Top lipid and dry mass model .rds files are included for others to predict %DM and %DL of Northern Pike when BIA and biological metrics have been collected.

Appendix T. Multiple linear regression coefficients for the prediction of percent dry mass for Northern Pike used in leaping experiments in an open channel flume during summer 2021, based on measurements taken from two locations (DML dorsal midline, DV dorso-ventral; Figure. 1.3). Parameter estimates \pm 1 SE are shown. Formulas for calculating covariates and covariate names are given in Appendix D.

Covariate	Parameter estimate	t-value	P-value
Intercept	25.4 ± 1.36	18.7	< 0.001
Rs (DML)	-3500.0 ± 2400.0	-1.46	0.15
Rp (DML)	-4550.0 ± 3470.0	-1.31	0.19
Xc (DML)	-0.671 ± 3.89	-0.17	0.86
Xcp (DML)	-243.0 ± 308.0	-0.79	0.43
Cpf (DML)	$< -0.001 \pm < -0.001$	-5.67	< 0.001
Zs (DML)	8080.0 ± 5930.0	1.36	0.18
PA (DML)	-0.33 ± 0.11	-3.10	0.002
DLPA (DML)	0.03 ± 0.01	5.90	< 0.001

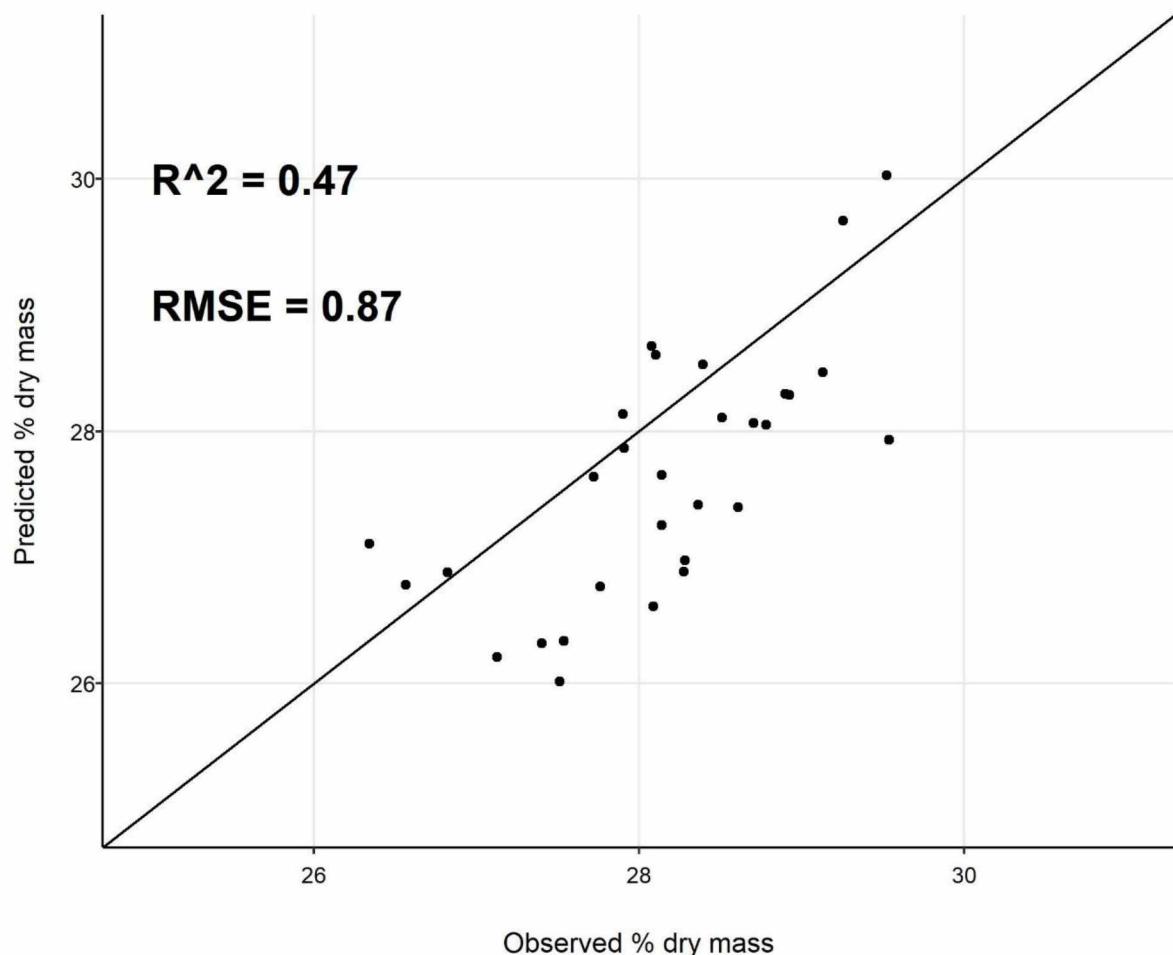
Appendix U. Multiple linear regression coefficients for the prediction of percent dry lipid for Northern Pike used in leaping experiments during summer 2021, based on measurements taken from two locations (DML dorsal midline, DV dorso-ventral; Figure 1.3). Parameter estimates \pm 1 SE are shown. Formulas for calculating covariates and covariate names are given in Appendix D.

Covariate	Parameter estimate	t-value	P-value
Intercept	15.5 ± 7.95	1.95	0.06
Rs (DML)	152000.0 ± 299000.0	0.51	0.61
Rp (DML)	93300.0 ± 206000.0	0.45	0.65
Xc (DML)	130000.0 ± 232000.0	0.56	0.58
Xcp (DML)	56400.0 ± 103000.0	0.55	0.59
Cpf (DML)	$< -0.001 \pm < -0.001$	-4.79	< 0.001
Zs (DML)	-244000.0 ± 503000.0	-0.49	0.63
Zp (DML)	-130000.0 ± 232000.0	-0.56	0.58
PA (DML)	-0.90 ± 0.42	-2.12	0.04
DLPA (DML)	0.11 ± 0.03	4.06	< 0.001
Rs (DV)	196000.0 ± 421000.0	0.47	0.64
Rp (DV)	95900.0 ± 236000.0	0.41	0.69
Xc (DV)	183000.0 ± 372000.0	0.49	0.62
Xcp (DV)	72400.0 ± 153000.0	0.47	0.64
Cpf (DV)	$< 0.001 \pm < 0.001$	0.64	0.52
Zs (DV)	-288000.0 ± 652000.0	-0.44	0.66
Zp (DV)	-184000.0 ± 372000.0	-0.49	0.62
PA (DV)	0.34 ± 0.48	0.70	0.49
DLPA (DV)	-0.002 ± 0.05	-0.05	0.96
BCI	2.02 ± 1.54	1.31	0.19
Fork length	-0.05 ± 0.01	-3.09	0.003

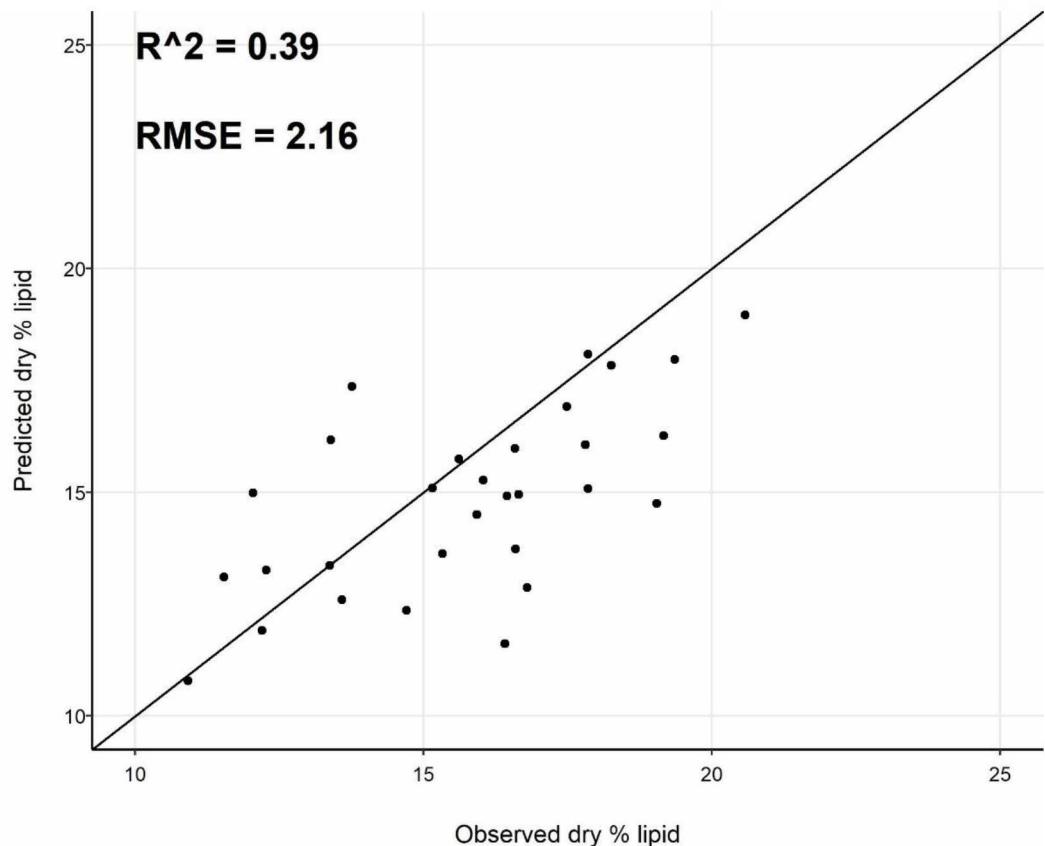
Appendix U continued

Whole weight	0.005 ± 0.002	2.91	0.004
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Appendix V. Predicted vs observed % dry mass values for Northern Pike used in leaping experiments during summer 2021. Black lines represent a slope of one, with R^2 and root mean squared error (RMSE) values included in the plot.



Appendix W. Predicted vs observed % dry lipid values for Northern Pike used in leaping experiments during summer 2021. Black lines represent a slope of one, with R^2 and root mean squared error (RMSE) values included in the plot.



Appendix X. Physical and hydraulic summary data for each height and depth treatment tested in leaping experiments on Northern Pike during summer of 2021 using a large open-channel flume. Values are means \pm standard deviation calculated from three replicates of each treatment. Passage success is the ratio of Northern Pike that successfully ascended a treatment divided by the total number of individuals exposed to each treatment (N = 6).

Height x Depth treatment (cm x cm, N = 3)	Actual barrier height (cm)	Actual pool depth (cm)	Pool volume (m ²)	Flow rate (L/s)	Discharge (m ³ /s)	Energy dissipation factor (N*m/s*m ³)	Water temperature (C°)	Passage success (%)
10 x 30	9.67 \pm 0.52	31.3 \pm 0.52	0.68 \pm 0.01	26.9 \pm 0.23	0.03 \pm 0.00	37.2 \pm 2.44	11.7 \pm 0.43	84.0
10 x 40	10.7 \pm 1.03	43.7 \pm 0.52	0.95 \pm 0.01	27.0 \pm 0.37	0.03 \pm 0.00	29.6 \pm 2.90	11.0 \pm 0.30	67.0
15 x 50	15.7 \pm 0.52	51.7 \pm 0.52	1.13 \pm 0.01	27.1 \pm 0.49	0.03 \pm 0.00	37.0 \pm 2.00	10.9 \pm 0.50	67.0
15 x 65	16.3 \pm 0.52	65.0 \pm 0.00	1.42 \pm 0.00	27.1 \pm 0.20	0.03 \pm 0.00	30.5 \pm 1.09	10.7 \pm 0.21	67.0
15 x 80	15.7 \pm 0.52	78.3 \pm 0.52	1.71 \pm 0.01	26.8 \pm 0.40	0.03 \pm 0.00	24.1 \pm 1.03	11.3 \pm 0.65	50.0
20 x 20	23.3 \pm 0.52	17.7 \pm 0.52	0.39 \pm 0.01	26.8 \pm 0.40	0.03 \pm 0.00	159 \pm 10.5	11.3 \pm 0.65	17.0
20 x 30	23.3 \pm 0.52	30.7 \pm 0.52	0.67 \pm 0.01	27.1 \pm 0.49	0.03 \pm 0.00	92.8 \pm 5.33	10.8 \pm 0.50	33.0
30 x 40	28.0 \pm 0.00	39.0 \pm 0.00	0.85 \pm 0.00	26.9 \pm 0.23	0.03 \pm 0.00	86.6 \pm 0.73	11.7 \pm 0.43	17.0
30 x 50	29.0 \pm 0.89	51.7 \pm 0.52	1.13 \pm 0.01	27.0 \pm 0.37	0.03 \pm 0.00	68.1 \pm 1.82	11.0 \pm 0.30	50.0
30 x 65	29.3 \pm 0.01	65.0 \pm 0.00	1.42 \pm 0.00	26.9 \pm 0.23	0.03 \pm 0.00	54.4 \pm 1.26	11.7 \pm 0.43	67.0
30 x 80	28.7 \pm 0.52	78.0 \pm 0.00	1.70 \pm 0.00	27.0 \pm 0.37	0.03 \pm 0.00	44.6 \pm 0.37	11.0 \pm 0.30	17.0
35 x 30	36.0 \pm 0.00	30.7 \pm 0.52	0.67 \pm 0.01	27.1 \pm 0.20	0.03 \pm 0.00	143 \pm 1.35	10.7 \pm 0.21	0.00
40 x 40	42.0 \pm 0.89	38.7 \pm 0.52	0.84 \pm 0.01	26.8 \pm 0.40	0.03 \pm 0.00	131 \pm 6.34	11.3 \pm 0.65	0.00
40 x 65	42.0 \pm 0.00	65.0 \pm 0.00	1.42 \pm 0.00	27.1 \pm 0.49	0.03 \pm 0.00	78.7 \pm 1.41	10.9 \pm 0.50	17.0
40 x 80	42.0 \pm 0.00	78.0 \pm 0.00	1.70 \pm 0.00	27.1 \pm 0.20	0.03 \pm 0.00	65.4 \pm 0.50	10.7 \pm 0.21	0.00
65 x 40	66.7 \pm 1.37	39.7 \pm 0.52	0.87 \pm 0.03	26.8 \pm 0.21	0.03 \pm 0.00	202 \pm 12.1	10.8 \pm 0.43	0.00

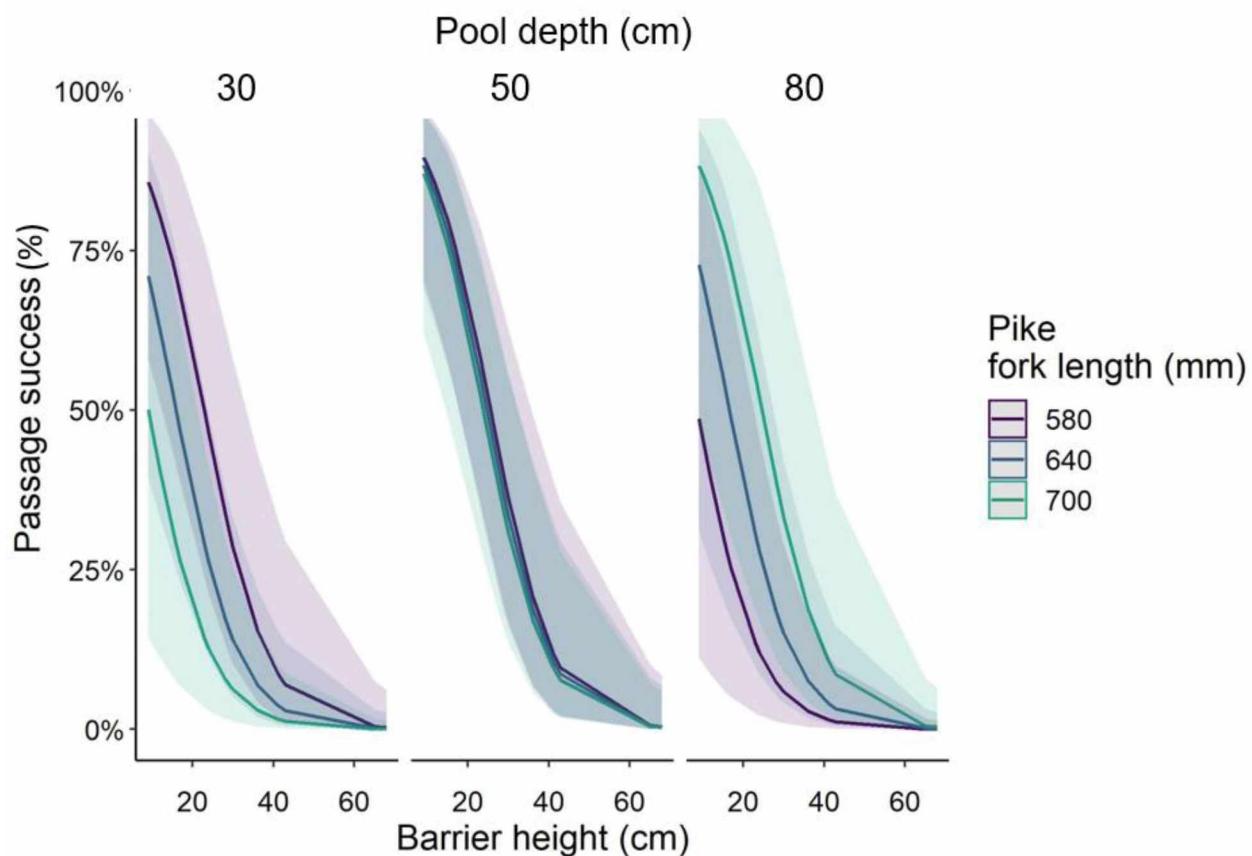
Appendix Y. Physical and hydraulic summary data for height, depth and flow treatment tested in leaping experiments on Northern Pike during summer of 2021 using a large open-channel flume. Values are means \pm standard deviation calculated from three replicates of each treatment. Passage success is the ratio of Northern Pike that successfully ascended a treatment divided by the total number of individuals exposed to each treatment (N = 6).

Height x depth x flow combination (m x m x L/s, N = 3)	Actual barrier height (m)	Actual pool depth (m)	Pool volume (m ²)	Flow rate (L/s)	Discharge (m ³ /s)	Energy dissipation factor (N*m/s*m ³)	Water temperature (C°)	Passage success (%)
10 x 30 x 11.4	10.3 \pm 0.52	29.0 \pm 0.00	0.63 \pm 0.00	11.7 \pm 0.49	0.01 \pm 0.00	18.8 \pm 1.69	10.6 \pm 0.09	67.0
10 x 30 x 27.1	9.67 \pm 0.52	31.3 \pm 0.52	0.68 \pm 0.01	26.9 \pm 0.23	0.03 \pm 0.00	37.2 \pm 2.44	11.7 \pm 0.43	84.0
10 x 30 x 42.9	9.33 \pm 0.52	34.0 \pm 0.00	0.74 \pm 0.00	43.6 \pm 0.91	0.04 \pm 0.00	53.8 \pm 4.12	10.7 \pm 0.16	67.0
15 x 80 x 11.4	17.3 \pm 0.52	75.7 \pm 0.52	1.65 \pm 0.01	11.9 \pm 0.41	0.01 \pm 0.00	12.2 \pm 0.62	10.3 \pm 0.39	67.0
15 x 80 x 27.1	15.7 \pm 0.52	78.3 \pm 0.52	1.71 \pm 0.01	26.8 \pm 0.40	0.03 \pm 0.00	24.1 \pm 1.03	11.3 \pm 0.65	50.0
15 x 80 x 42.9	16.3 \pm 0.52	80.3 \pm 0.52	1.75 \pm 0.01	42.9 \pm 0.52	0.04 \pm 0.00	39.2 \pm 1.69	10.6 \pm 0.08	50.0
20 x 20 x 11.4	23.0 \pm 0.89	16.3 \pm 0.52	0.36 \pm 0.01	11.9 \pm 0.41	0.01 \pm 0.00	75.3 \pm 2.68	10.3 \pm 0.39	33.0
20 x 20 x 27.1	23.3 \pm 0.52	17.7 \pm 0.52	0.39 \pm 0.01	26.8 \pm 0.40	0.03 \pm 0.00	159 \pm 10.5	11.3 \pm 0.65	17.0
20 x 20 x 42.9	23.7 \pm 1.37	20.0 \pm 0.89	0.44 \pm 0.01	42.9 \pm 0.52	0.04 \pm 0.00	229 \pm 20.0	10.6 \pm 0.08	17.0
30 x 40 x 11.4	29.0 \pm 0.89	36.3 \pm 0.52	0.79 \pm 0.01	11.7 \pm 0.49	0.01 \pm 0.00	42.1 \pm 3.03	10.6 \pm 0.09	17.0
30 x 40 x 27.1	28.0 \pm 0.00	39.0 \pm 0.00	0.85 \pm 0.00	26.9 \pm 0.22	0.03 \pm 0.00	86.6 \pm 0.73	11.7 \pm 0.43	17.0
30 x 40 x 42.9	30.0 \pm 0.00	40.0 \pm 0.00	0.87 \pm 0.00	43.6 \pm 0.91	0.04 \pm 0.00	147 \pm 3.05	10.7 \pm 0.16	67.0
30 x 65 x 11.4	29.7 \pm 0.52	63.0 \pm 0.00	1.38 \pm 0.00	11.7 \pm 0.49	0.01 \pm 0.00	24.8 \pm 1.15	10.7 \pm 0.09	33.0
30 x 65 x 27.1	29.3 \pm 0.52	65.0 \pm 0.00	1.42 \pm 0.00	26.9 \pm 0.23	0.03 \pm 0.00	54.4 \pm 1.26	11.7 \pm 0.43	67.0
30 x 65 x 42.9	28.7 \pm 2.25	66.3 \pm 0.52	1.45 \pm 0.01	43.6 \pm 0.91	0.04 \pm 0.00	84.7 \pm 8.13	10.7 \pm 0.16	33.0
40 x 40 x 11.4	42.3 \pm 0.52	36.3 \pm 0.52	0.79 \pm 0.01	11.9 \pm 0.41	0.01 \pm 0.00	62.3 \pm 0.73	10.3 \pm 0.39	0.00
40 x 40 x 27.1	42.0 \pm 0.89	38.7 \pm 0.52	0.84 \pm 0.01	26.8 \pm 0.40	0.03 \pm 0.00	131 \pm 6.34	11.3 \pm 0.65	0.00
40 x 40 x 42.9	43.0 \pm 0.89	40.7 \pm 1.03	0.89 \pm 0.02	42.9 \pm 0.52	0.04 \pm 0.00	204 \pm 7.90	10.7 \pm 0.09	0.00

Appendix Z. Behavioral count data from video analysis of explorations, attempts, and successes from one of three replicates of 28 height, depth, and flow treatments tested in leaping experiments with Northern Pike in a large open-channel flume system during 2021. Observations of N/A indicate no video was recorded for that treatment.

Height x depth x flow treatment (cm x cm x L/s, N = 1)	Explorations	Attempts	Successes
10 x 30 x 27.1	N/A	N/A	N/A
10 x 30 x 11.4	1	0	3
10 x 30 x 42.9	12	0	5
10 x 40 x 27.1	17	1	2
15 x 50 x 27.1	4	0	0
15 x 65 x 27.1	1	2	0
15 x 80 x 27.1	10	0	0
15 x 80 x 11.4	37	2	1
15 x 80 x 42.9	1	1	4
20 x 20 x 27.1	4	3	0
20 x 20 x 11.4	1	0	0
20 x 20 x 42.9	1	2	0
20 x 30 x 27.1	0	2	1
30 x 40 x 27.1	0	0	1
30 x 40 x 11.4	15	8	0
30 x 40 x 42.9	1	0	3
30 x 50 x 27.1	13	3	1
30 x 65 x 27.1	5	3	1
30 x 65 x 11.4	5	4	1
30 x 65 x 42.9	0	7	1
30 x 80 x 27.1	11	13	1
35 x 30 x 27.1	16	0	0
40 x 40 x 27.1	4	5	0
40 x 40 x 11.4	6	4	0
40 x 40 x 42.9	3	7	0
40 x 65 x 27.1	5	9	1
40 x 80 x 27.1	N/A	N/A	N/A
65 x 40 x 27.1	0	1	0

Appendix AA. Predicted barrier passage success as a function of barrier height, pool depth, and fork length for Northern Pike used in leaping experiments in a large open channel flume during 2021. Shaded areas are 95% confidence intervals for predicted passage success estimates.



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