Assessing the station holding ability of three benthic fishes exposed to flow augmentation: Implications for a species at risk

by

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Abstract

Flow augmentation forces Plains Sucker in the Milk River to adopt more efficient station holding mechanisms, which must be energetically costly as they are not maintained year-round. The station holding ability of Milk River Plains Sucker was measured using a Brett-style swim tunnel respirometer, and the results were compared to other catostomid species in the Milk River and to Plains Sucker caught in water bodies that remain unmodified year-round. Milk River Plains Sucker maintained a significantly higher estimated marginal mean failure velocity ($p < 0.0001$) during augmentation (June-July) compared to natural flows (September-October). Catostomids in Milk River exhibited varying degrees of response; from no change in response to augmentation (Longnose Sucker, $p = 0.5$) to a significant shift (Plains Sucker and White Sucker $p = 0.0001$). Plains Sucker from unmodified water bodies demonstrated at most a minor change in performance between sampling periods (Battle Creek, $p = 0.041$; Caton Creek $p = 0.068$). The substantial energetic input into station holding may result in life history trade-offs impacting the populations' continued existence in this part of its native range.

Keywords:

native species, catostomid, station holding, swim tunnel, hydrologic augmentation

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Chapter 3: Assessing the station holding ability of the Plains Sucker in the Missouri Drainage

Chapter 1: Introduction

Stream flow is an important characteristic of fish habitat; its natural pattern shapes habitat features, influences resource supply, and dictates the optimal life history strategy of stream organisms (Poff et al. 1997). Native species are adapted to the natural flow regime of the rivers they occur in, including potentially challenging patterns of flood and/or drought. Disruption or modification of stream flow may contribute to habitat loss through the creation of impassible physical barriers, destruction flood plains, and disruption of seasonal cycles of flow such as annual freshet pulses or droughts (Dahm & Molles 1992, Dyer et al. 2014, Krasovskaia & Gottschalk 1993). Flows regulated for anthropogenic needs without regard to the species assemblage and their life histories pave the way for invasive species, which might otherwise be unable to cope with the natural fluctuations (Mims & Olden 2013).

It is essential to understand how freshwater fish tolerate and adapt to flow regulation to mitigate the impact on fishes' ability to access habitat and complete their life cycle. Dams, for example, impact 68.8% of the world's rivers and are responsible for the decline in abundance of many migratory fishes such as Pacific Salmon (Collins 1976), Westslope Cutthroat Trout (Schmetterling 2003), and Giant Catfish (Duponchelle et al. 2016). Flow regulation such as water withdrawals and flow augmentation - where water is moved from one waterbody to another - impact another 23.5% of the world’s large rivers, but its effects on fishes are not well understood (Grill et al. 2019). Modifications typically occur to rivers flowing through arid regions, where anthropogenic water demands frequently exceed the natural flow and timing of pulse events of the river.

Augmentation is an important component of water management in many drought-susceptible systems in midwestern North America (U.S. Department of the Interior Bureau of Reclamation & State of Montana Department of Natural Resources and Conservation 2012, Grill et al. 2019). While the effects of dams appear to be well understood, the ecological impacts of flow augmentation (especially increases in flow) are poorly represented in the literature (Poff & Zimmerman 2010, Zarfl et al. 2015, Rolls & Bond 2017, Reid et al. 2019).

Hydrologic regimes have important implications for the life history strategies employed by stream organisms (Mims and Olden 2012, Nisbet et al. 2012). Essentially, organisms must “choose” which process will receive which percentage of a finite amount of energy. The dynamic energy budget model groups life history processes into 4 categories: maintenance, growth, reproduction, and reserves; and energy used in one category or process is not generally available for another process. In this manner, we can discuss the trade-offs that organisms must make within their energy budget (Stearns 1992). A stream fish must allocate energy to maintaining its place in the stream or perhaps swimming against the current at times in search of foraging or feeding opportunities (maintenance). This energy can not be dedicated to growth, which is important to note in fishes, as the body size of a fish is directly related to its fecundity (Koops et al. 2004). If the characteristics of a hydrologic regime demand more energy be allocated to a fish’s maintenance budget, then less energy is available for reproduction. Changing hydrology could have impacts not only at this individual level of energy budgets, but to a population as well, as each fish may be less fecund than without the flow modification.

The Milk River of southern Alberta, Canada, runs through the Great Plains ecoregion of North America (Figure 1-1), and has been the recipient of augmented flows for the past century, making it an ideal candidate for the study of the impacts of flow augmentation (U.S. Department of the Interior Bureau of Reclamation & State of Montana Department of Natural Resources and Conservation 2012, Milk River Watershed Council Canada 2013). Starting in April 1917, and continuing each year until 2020, up to 18.4 m3·s^{-1} of water are diverted from the Saint Mary River via the Saint Mary Canal to supply water for irrigation through the midwest. Flow augmentation of the Milk River raises flow by an order of magnitude during the freshet pulse; mid-late April. The flows in the Milk River remain artificially high throughout the summer months until October, when the system of canals and siphons cease to operate over the winter months and natural flow is restored (Figure 1-2). Studies in this system help us understand the impact of annual augmentation in terms of habitat fragmentation and reduction in accessible habitat (Neufeld et al. 2018) and morphological and swimming performance adaptations (Veillard et al. 2017, Rudolfsen et al. 2018), especially with respect to imperilled fishes.

The Milk River is home to three representatives of the Catostomidae family: the Plains Sucker (*Pantoseus jordani*), the White Sucker (*Catostomus commersonii*), and the Longnose Sucker (*C. catostomus*). The Plains Sucker was recently taxonomically revised from Mountain Sucker (*C. platyrhynchus*; see Unmack et al. 2014, Bangs et al. 2018) due to genetic differences. Based on this revision, Plains Sucker occurs in just two Canadian watersheds comprising two designatable units (DUs): the Saskatchewan-

Nelson (DU1 - apparently secure) and the Milk River (DU2 - threatened) (COSEWIC 2010). The “threatened” designation resulted from the Plains Sucker’s low area of occurrence and small number of populations within the Milk River watershed, with an indication that flow modification and climate change are likely to exacerbate the challenges this population faces. The other catostomids in this system are apparently secure and relatively common compared to the Plains Sucker. Of the three, the Plains Sucker is the smallest member of the family, not usually exceeding 152-203 mm, White Sucker and Longnose Sucker grow substantially larger, 305-508 and 305-356 mm respectively. All three subsist on a diet of varying proportions of benthic invertebrates (incl. Amphipods, chironomid larvae and pupae, cladocerans, coleoptera, copepods, dipteran larvae and pupae, ephemeroptera, gastropods, ostracods, pelecypods, plecoptera, rotifera, trichoptera, turbellaria), plants (incl. (filamentous) algae, diatoms, and periphyton), and detritus (Scott & Crossman 1973).

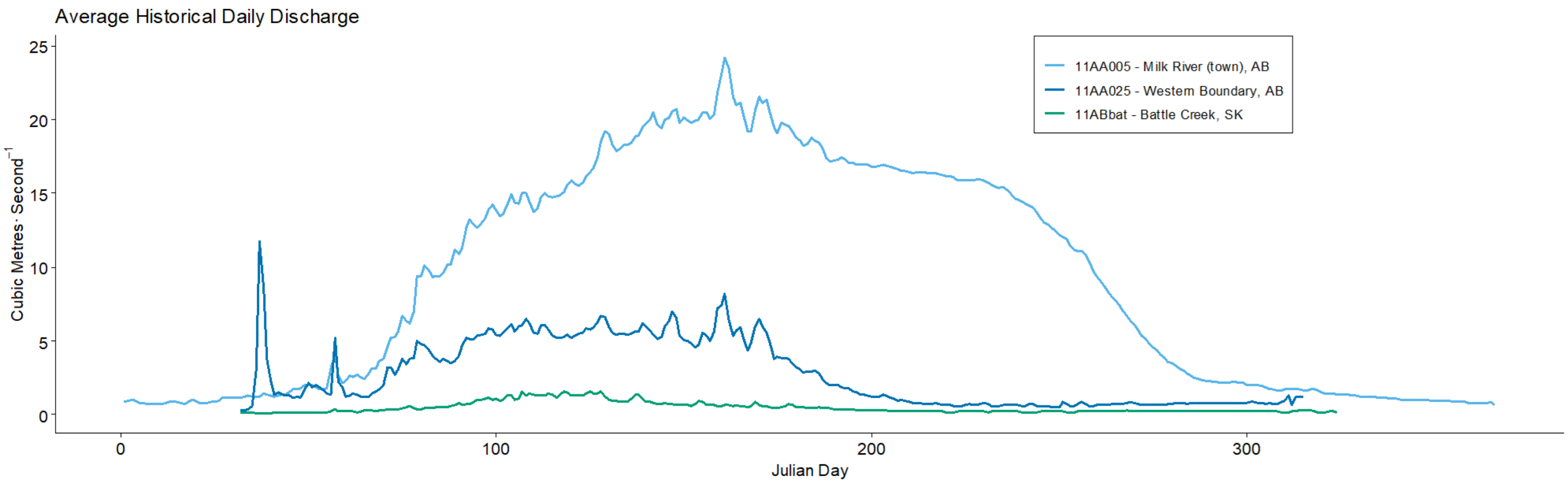
Here, I used the aforementioned catostomids; the Plains, White, and Longnose Suckers to examine the effects of flow augmentation on the threatened Plains Sucker. Specifically, I compare station holding ability, measured through failure velocity, which in turn is defined as the swim tunnel velocity at which a fish is impinged on the downstream grate of the swim tunnel or unable to re-establish a hold on the bottom of the swim tunnel. This definition is necessarily broad to account for the preferences that certain catostomids have for swimming (White Sucker) vs. holding (Plains Sucker) vs the sort of intermediate tendency of the Longnose Sucker. The failure velocities of three benthic species were tested during augmented and natural (hereafter referred to as “Summer” and “Autumn”, respectively) flow rates over the course of 2 years in the Milk

River and unmodified water bodies to determine if augmentation appears to affect their performances. I hypothesised that all catostomids from the Milk River would have similar swim performances resulting from their universal, chronic experience of flow augmentation. Similarly, I hypothesised that Plains Sucker from the Milk River would be able to hold station at higher velocities than Plains Sucker from the unmodified water bodies resulting from over a century of flow augmentation. I do not, however, entertain the notion that these behavioural and potentially physiological changes come at no cost; rather, I think that these must be accounted for in the Milk River catostomid populations' energy budget, resulting in potentially smaller fish with a lower reproductive capacity in the Milk River population. Results from this study will assist in the development of recovery actions for the Plains Sucker and additionally fill knowledge gaps on the impact of flow augmentation more generally (DFO 2013). The main goal of this work is to assess the specific responses of and impacts on catostomids in the Missouri drainage, but additionally has the ambitious goal of promoting careful consideration of these types of freshwater habitat modifications as freshwater becomes a more precious and less predictable resource.

Chapter 2 of this thesis deals mainly with the local community of the Milk River, investigating the responses of 3 species of catostomid to augmentation. This information is complemented and expanded on in Chapter two with a similar assessment of the responses of only the Plains Sucker. Chapter 2 focuses more on how Plains Sucker behave and respond in Missouri Drainage tributaries that are unaffected by flow augmentation, serving as a comparison for Plains Sucker in the Milk River. Each chapter answers specific questions and provides interesting discussion around each problem, however there is much overlap in the investigations, and the conclusions that are common or intrinsically linked will be discussed in Chapter 4.

Figures:

Figure 1-1: Map of Missouri Drainage, bounded within the blue background. Blue fish symbols indicate sampling sites, green clipboards represent monitoring stations (data from some of which can be seen in figure 1-2), and the orange water drops are placed at the head (left) and tail (right) of the St. Mary Canal Structure.



Average daily discharge from 1917-2020 (Milk River (town)), 1931-2020 (Western Boundary, AB), and 1951-2020 (Battle Creek). Additionally, Battle Creek is an amalgamation of data from Stations 11AB081 (Ranger Station) and 11AB117 (Alberta Border), which collected from 1951-1974 and 1975-2020 respectively.

Figure 1-2: Average historical daily discharge for the Milk River at the town of Milk River (light blue), the Milk River upstream of its confluence with augmented flows (dark blue) and Battle Creek, and unmodified headwater stream (green).

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Chapter 2: Assessing the station holding ability of three species of catostomid in the Milk River

Introduction

Hydrologic infrastructure impacts the majority of the world's large rivers (Grill et al. 2019). Flow augmentation describes the condition where infrastructure moves water from one body to another, typically to support anthropogenic needs. The St. Mary Canal is one such system, which moves nearly 20 $m^3 \cdot s^{-1}$ of water from the St. Mary River in Montana to the North Fork of the Milk River during the months of April-September. Constructed in 1917, the system of 5 siphons and canals deposited water into the North Fork of the Milk River, where it would eventually join with the Milk River in southern Alberta. From there, the water turns back south where the additional flows become an important source of irrigation throughout the Great Plains region. In the summer of 2019, I set out to evaluate the impact of these increased flows on three benthic fishes; the White Sucker, the Longnose Sucker, and the Plains Sucker, the last of which holds the status of "threatened" in the Milk River (COSEWIC 2010). At the time, the best comparison I could make was between the augmented "Summer" period and the natural flow "Autumn" period.

On May 21, 2020, however, an unprecedented opportunity presented itself in the form of a catastrophic canal structure failure necessitating that water supply from the St. Mary River be turned off until the canal was repaired. This permitted re-testing of this community during the Summer period, but under flow conditions that more closely approximate those of Autumn. In this chapter, I seek to address the question of whether historical and chronic hydrologic augmentation of the Milk River is contributing to the problems of low number of occurrences and small populations leading to the "threatened" status of the Plains Sucker? More specifically, I hypothesise that after >100 years of augmented flows the catostomids of the Milk River are accustomed to the increased flows that occur during the summer periods, and have adjusted accordingly to maintain a consistent physical ability to cope with increased velocities in the system. Therefore, I expect that there will be a constant ability among the Catostomids of the Milk River system to cope with the increased velocity across all of the time periods or between the Catostomidae of this system.

Methods

Study Area and Sampling Methods

The Milk River at the town of Milk River was sampled in the summers (June-August) of 2019 and 2020 and the Autumn (September-October) of 2019 for Plains Sucker and co-occurring Catostomidae. In 2020, an additional site on the Milk River upstream of its confluence with the Milk River, inside the Twin Rivers Heritage Rangeland Natural Area (TRHRNA) was added to capture the responses of the population in an area that is never impacted by augmentation. During the summer months, the Milk River is a turbid, moderately shallow (easily crossed on foot in most places), moderately wide river with low riparian vegetation and high bank mass failure; in autumn, the river becomes far clearer, shallower, and somewhat narrower. Historically, it is a groundwater fed river, but since 1917 it has been heavily augmented with water from the St. Mary Canal during the summer periods. Mean flows during our sampling windows were: April - September (Summer) 2019 flow rate: 16.06 $m^3 \cdot s^{-1}$, October (Autumn 2019) - March '20 flow rate: 2.36 $m^3 \cdot s^{-1}$, and April - September (Summer) 2020 flow rate: 5.28 $m^3 \cdot s^{-1}$. Substrate in the Milk River is mostly characterised as silt-sand, with gravel-cobble riffles and occasional boulders. The TRHRNA site was somewhat less turbid, but still characterised by a silt-sand bottom with areas of gravelly-cobbly riffles and occasional boulders.

A beach seine net (6 m x1.2 m, mesh size 3mm) was used to sample the Milk River and, with the exception of the thalweg in the Milk River in Summer 2019, the entire width of the river could be sampled and amounted to approximately 700-1000 m of of the river. After capture, fish were held and recovered in species-specific flow through bins installed in the river in 25-30 cm of water. Bins were anchored in moderate flow areas using periphyton covered rocks and shaded using a lid. Additional nutrition was provided each evening in the form of a frozen mysid shrimp block. Fish were not usually tested on the same day that they were captured. All fish collected and used for experiments were approved under Animal Use Protocol #AUP00003131 and in compliance with SARA Permits #19-PCAA-00013 and #20-PCAA-00019, Alberta Environment and Parks Fish Research Licences #19-2207 and #20-2405FR, and Alberta Tourism, Parks and Recreation Parks Division Research Collection Permit #20-290.

Experimental Techniques

Station holding was measured for n = 207 catostomids in either a 5 L or 10 L Loligo™ Swim Tunnel Respirometer. These Brett-style recirculating swim tunnel respirometers were first calibrated using a Marsh McBirney Model 2000 Flo-Mate flow meter. The velocity in the swim chamber at low revolutions-per-minute (RPMs) was averaged from

8 points, capturing the velocity in the middle of the chamber and laterally toward each wall and at varying depths. This procedure was repeated at a higher RPM. The two averages were used by a Panasonic Toughbook running the Loligo AutoResp software via a linear equation to set the RPMs for the desired swim tunnel water velocity permitting remote control of the tunnels. After calibration, fish were retrieved from the flow-through storage bin(s), measured to the nearest half-centimetre, and then introduced into the most appropriately-sized swim chamber for the fish's size. This commenced the initial acclimation period of 20 min, where the fish was permitted to move freely about the swim chamber at a velocity of 0.4 body lengths per second (BL·s^1). To introduce the fish to increasing velocity in this environment, the velocity was increased to 0.6 BL·s^1 for 10 min, 0.8 BL·s for 5 min, and a final 5 min period at 1 BL·s^1. After this 40-min period of dynamic acclimation, the trial began. A unique method was developed to assess the station holding abilities of Catostomidae informed by Jain et al.'s (1997) RAMP-Ucrit and Veillard et al.'s (2017) station holding methods. Each test began at 1 body length per second (BL·s^1) after acclimation, and velocity was increased every 2 min by 0.2 BL·s^1. Proportional increases ensure that small fish are not subjected to excessively large increases in velocity and that large fish do not spend significantly longer in the tunnel on account of small velocity steps. The procedure ended when a fish reached failure velocity; the velocity at which the fish was no longer able to maintain its position via swimming, burst swimming, or holding station on the bottom without resting on or becoming impinged upon the downstream grate (Veillard et al. 2017). Fish were supervised for the duration of the trial, and behaviours were noted as the velocity increased. Fish were encouraged to move off the grate either by a small

(2V) electric shock resulting from the caudal fin closing an electrical circuit applied to the downstream grate, or by a poke to the caudal peduncle using a probe. Each subject was given a few moments to attempt to move away from the grate, but if they could not, or were clearly impinged, then the velocity of the tunnel was manually reduced and the final velocity recorded at the subject's [absolute] failure velocity ($cm \cdot s^{-1}$). After the trial, the subject was euthanized in tricaine methanesulfonate (TMS-222) and preserved individually in ethanol (2019) or frozen alongside other subjects (2020) for further analyses.

Statistical Techniques

Exploratory linear models tested for correlation between fork length and absolute failure velocity found that at least 5% and as much as 76% of the variation within each species-season could be explained by a linear relationship (Figure 2-1). The absolute failure velocity ($cm \cdot s^{-1}$) however, was deemed inappropriate for comparison between species and seasons due to strong, linear correlations between these two variables in addition to considerable differences in body size between groups (Figure 2-1). Two-way ANCOVA was selected to test for differences in mean failure velocity between species and season while accounting for differences in fork length by including it as a covariate (see Figure 2-1's caption for a discussion of the assumptions). The ANCOVA produced estimated marginal mean failure velocities, hereafter referred to as relative failure velocity(ies). Significant, two-way interactions were investigated further by using a one-way ANCOVA testing for simple main effects of each species and season and then examined further using Bonferroni corrected pairwise comparisons (Kassambara 2018).

The assumptions of ANCOVA were met or only mildly violated (Fig 1-3 caption). All data analysis occurred in RStudio version 1.1.1103 (RStudio Team 2016, R Core Team 2020) using packages FSA (Ogle et al. 2020), tidyverse (Wickham et al. 2019), ggplot2 (Wickham 2009), and ggpubr (Kassambara 2020).

Results

The two-way ANCOVA found a significant interaction between species and season on the relative failure velocity (p = 1.25·10-7); essentially that, after adjusting for fork length, the effect of season on relative failure velocity depended on the species and vice versa (Figure 2-2).

A one-way ANCOVA of each species demonstrated a significant effect of season, and when probed via multiple pairwise comparisons it was found that: Plains Sucker had significantly different relative failure velocities in all seasons (light blue lines connecting the three seasons (p = 7.08·10-8, p = 8.43·10-23) and horizontal line comparing the two summer seasons (p = 1.29·10-9)), White Sucker had significantly different relative failure velocities between Summer and Autumn (orange lines connecting the three seasons (p = 1.0·10-4, p = 2.85·10-7)), but the two Summer periods did not differ significantly (p = 0.914), and finally, Longnose Sucker differed significantly in relative failure velocity only between the years; the two Summer periods were significantly different (p = 1.37·10-4) and the Autumn period was significantly different from only the 2020 Summer period (p = 1.0·10-4).

One-way ANCOVA within each season demonstrated significant differences between the relative failure velocities of all three species in the Summer of 2019 (p = 2.98·10-3 between Longnose and White Sucker, p = 1.8·10-9 between Longnose and Plains Sucker, and p = 1.96·10-4 between White and Plains Sucker). In Autumn of 2019 there was only a significant difference in relative failure velocity between White and Plains Sucker (p = 0.0181), and in the Summer of 2020 the relative failure velocities were significantly different between Plains versus Longnose (p = 5.57·10-15) and White (p = 4.0·10-15) Sucker.

The additional (upstream) site visited in 2020 was not different from the site repeatedly visited near the town of Milk River in the same year for any species, but did share the pattern (if not the magnitude) of significant difference between Plains Sucker versus Longnose and White Sucker.

Discussion

It is important to bear in mind throughout this discussion that, while some very large effect sizes are evident in the data, important assumptions of ANCOVA were not met, namely the assumption of homoscedasticity. In addition, the assumption of homogeneity of regression slopes is also violated (Figure 2-1). Due to this violation, these results are unlikely to be replicable, and further, the conditions of the study are unlikely to be replicable in the foreseeable future. For this reason, the discussion will mainly focus on effect sizes and their implications for this system.

Contrary to expectations, two different responses to augmentation were observed from catostomids of the Milk River. I expected all Milk River catostomids to have similar responses owing to the similarity in taxonomy and morphology in addition to experiencing the same conditions, but augmentation appears to impact the Plains and

White Sucker to a greater extent than Longnose Sucker. Plains and White Sucker demonstrate the most dramatic shift in station holding ability in response to augmentation status (mean difference of 22.17 cm·s-1 and 22.67 cm·s-1, respectively). The station holding ability of Longnose Sucker is indifferentiable between augmentation on and off periods in 2019 (mean difference of 4.02 cm·s-1). With the cessation of augmentation in the Summer of 2020, Plains and Longnose Sucker station holding ability increased significantly from the same period one year prior.

An extremely interesting pattern is clear when all three seasons at the town site are viewed together. There is a general trend, especially among Plains and White Sucker, to demonstrate a higher relative failure velocity in the summer periods than in the autumn period. Furthermore, that summer relative failure velocity was substantially higher in 2020, the year when the Milk River was not augmented, than the previous summer, which was business as usual for the Milk River. Without the Summer 2020 data, this perhaps looks like a plastic response inherent among the catostomids to operate under a variety of different flow regimes. However, taken altogether this suggests an ability to perhaps stockpile energy during the low flow season in order to cope with the elevated levels of discharge during the summer months. This explanation would account for the drastic increase in relative failure velocity documented in 2020, as, when the fish are released from the chronic condition of augmentation, they would feasibly have an excess of energy during the swim trials in the tunnel.

The Plains and White Sucker response to flow augmentation is especially interesting when considered alongside the results of Underwood et al. (2014). This study - which occurred prior to the taxonomic revision in a watershed conceivably occupied by Plains rather than Mountain Sucker (*Pantosteus platyrhinchus*) - examined swimming performance in a variety of catostomids with a goal of assessing if the swim performance of common species (the White Sucker and Longnose Sucker) could be used to approximate that of rarer species (e.g., [Plains] Sucker, among others) when considering recovery efforts for those that are declining. They concluded that, while White Sucker possessed a similar swimming ability to [Plains] Sucker, White and Longnose Sucker were poor proxies for [Plains] Sucker. These results corroborate our observation that Plains and White Sucker demonstrate similar patterns of change in relative failure velocities, as well as similar absolute failure velocities in 2019. They also support our conclusion that the larger-bodied White Sucker would be a poor proxy for the small-bodied Plains Sucker as in 2020, where the Plains Sucker appears to experience a release from the augmentation pressure, the White Sucker does not. Contrary to our study, Underwood et al. (2014) used Ucrit, a measure of swimming performance rather than failure velocity; our decision to use assess station holding ability was informed by Veillard's (2016) work on another benthic fish, the Rocky Mountain Sculpin, and other studies conducted on more sedentary or benthic fish (Jones et al. 1974, Tierney et al. 2011, Dockery et al. 2017). During preliminary work, Plains Sucker did not swim when introduced to the swim tunnel, but instead clung to the bottom of the swim chamber, even as velocity increased. All three species demonstrated mildly different responses to acceleration of the swim tunnel, precluding the use of Uslip or Uburst (Webb et al. 1996). This explains the broadly defined endpoint of our study; the velocity at which an individual fish could no longer maintain position via swimming, burst swimming, and/or holding station without resting or becoming impinged on the downstream end of the tunnel consistent with that used on the Sacramento Sucker by Myrick & Cech (1999). In our work White Sucker tended to swim the most in our experimental setup but would still rest/hold on the bottom of the tunnel at low velocities and sought to dart forward after being slowly pushed downstream along the bottom of the tunnel. Longnose Sucker were quite intermediate in their swimming vs. holding behaviour, tending to rest/hold somewhat more than White Sucker and somewhat less than Plains Sucker. Finally, Plains Sucker were observed to rest/hold on the bottom until just before the failure velocity, at which point some transitioned to burst swimming and trying to re-establish their hold, before becoming impinged against the downstream grate.

While these fishes are taxonomically similar, they have morphological differences that may facilitate or impede their ability to swim against or hold onto the substrate against streamflow. All are vaguely torpedo-shaped, but Plains Sucker seem to be extremely ventrally flattened, which appears conducive to re-directing flow over the body. Additionally, the large pectoral fins fan out sideways as the velocity in the tunnel increases, simultaneously gripping the substrate and generating negative lift, assisting in station holding (Wilga & Lauder 2001, Kane & Higham 2012). The pelvic and anal fins brace against the substrate and lift the tail slightly, forcing the snout even lower. At the highest velocities, use of the suctorial mouth appeared to help Plains Sucker maintain their hold and, in some cases, move upstream. Longnose Sucker appear morphologically similar to Plains Sucker, but rarely were observed to use the sucker to hold their position and would instead switch over to bobbing along the bottom of the tunnel (holding, sliding downstream, bursting upstream, and repeat). Finally, White

Sucker appeared more fusiform when compared to the other suckers (but still torpedo shaped), which may explain the preference for swimming and poor ability to press against the substrate. Notably, when they did rest/hold on the bottom of the chamber, White Sucker tended to have to lean somewhat to either side, and the suctorial mouth appeared unable to reach the substrate. Plains Sucker may be morphologically equipped to hold station against the higher flows but may not have the stamina or physical power to swim against high velocities, or to move between habitat patches, potentially impacting foraging efficiency (Myrick & Cech 1999, Neufeld et al. 2018). Additionally, it is likely that the smaller bodied Plains Sucker is more successful at using interstitial spaces in the stream bed than larger bodied White and Longnose Sucker (Veillard et al. 2017).

Finally, a note on the additional site visited in 2020: I was fortunate to be able to revisit this system at all during this tumultuous period, and this site answered some questions that came up in the interstitial year as well as provided a nice comparison for the fish at the town site. First, I wondered whether populations in and around the Milk River, especially in this tributary upstream of the augmented flows, were continuous. Based on the responses to the conditions of 2020, I would be inclined to believe that they are. More work in this vein during typical augmented flow years, especially taking advantage of genomics and morphometrics would be useful to corroborate this. Additionally, continuity among the Milk River population would indicate that these fish face no great hardship in moving about frequently, even if that movement is limited to the low-flow season.

Overall, I have not found sufficient evidence to conclude that there is any great impact of flow augmentation on Plains Sucker or White Sucker, and a limited at best impact on Longnose Sucker, given their 2019 response to testing. It seems that the catostomids are equipped with strategies to weather the high flow season, be that the impressive swimming abilities of the White Sucker or the morphologically evident station holding abilities of the Plains Sucker, or the efficient energetic budgeting of all three species. There may even be some benefit to augmented flows during especially hot years, where the additional water can help to regulate temperatures and maintain stream connectivity in what otherwise may become a disconnected or ephemeral system. Seeing as no population-level declines in Plains Sucker are evident (but neither is growth), caution towards and consistent monitoring of the system will be important to ensure the continuation of this threatened species.

Figures

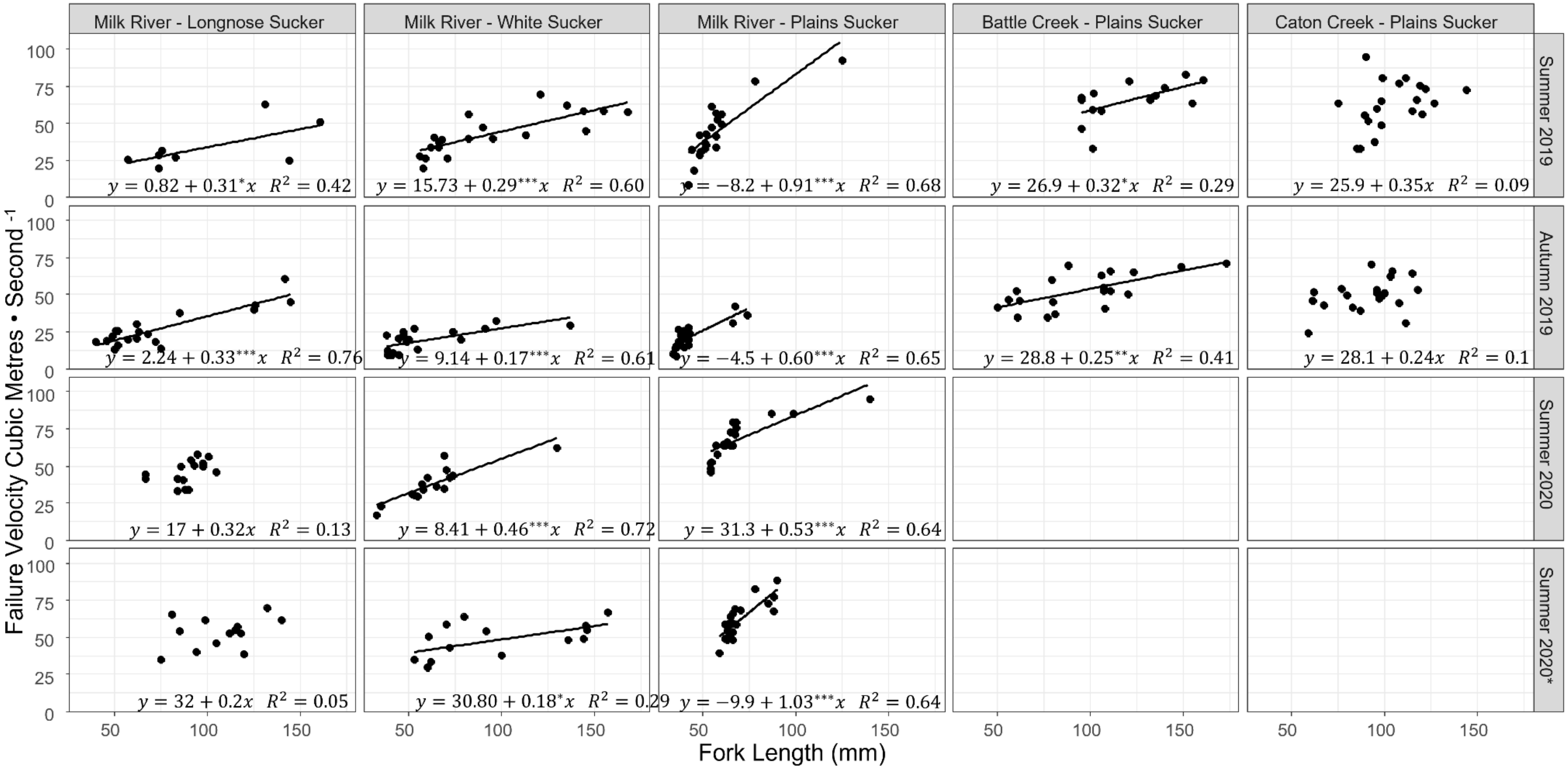

Figure 2-1: Linear models of fork length vs failure velocity between the Milk River's three species (left 3 columns) and the three water bodies Plains Sucker were tested from (right 3 columns). Fork length has a significant, positive impact on absolute failure velocity (except for Longnose Sucker at both Summer 2020 sites and Plains Sucker during both periods at Caton Creek) indicated by asterisks following the slope in the linear equation and the associated line through the data. In the Milk River the ANCOVA assumptions of homogeneous slopes and homoscedasticity are mildly violated ($p = 0.011$, $p = 0.0234$) however, the residuals are normally distributed ($p = 0.146$). Among the three water bodies the assumptions of homogeneous regression slopes and normality are met ($p = 0.722$, $p = 0.43$), but the assumption of homoscedasticity is mildly violated ($p = 0.02$).

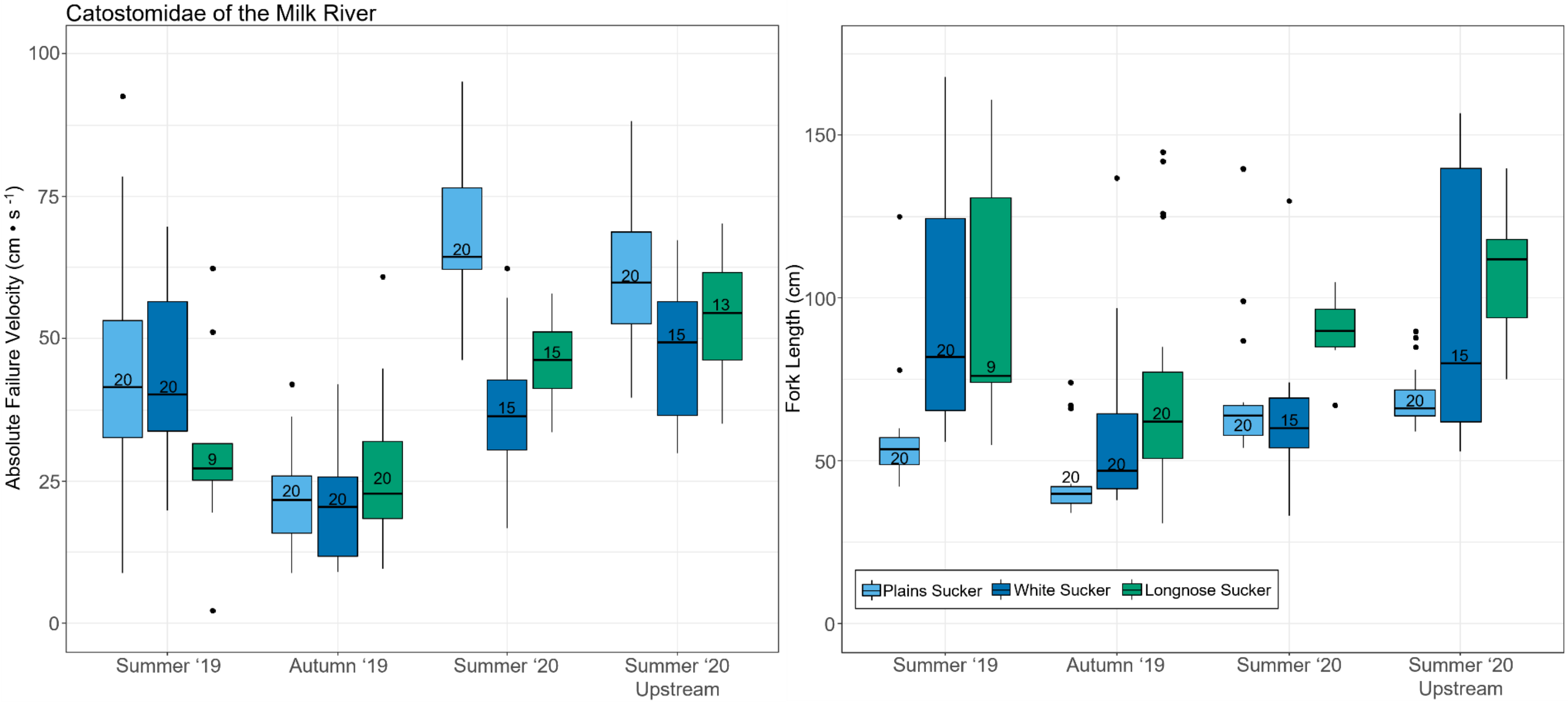

Figure 2-2: Absolute failure velocity (left, cm.s^{-1}) and fork length (right, cm) median and range for catostomids captured in the Milk River. Numbers above each median represent the sample size of each species used at each location and time period.

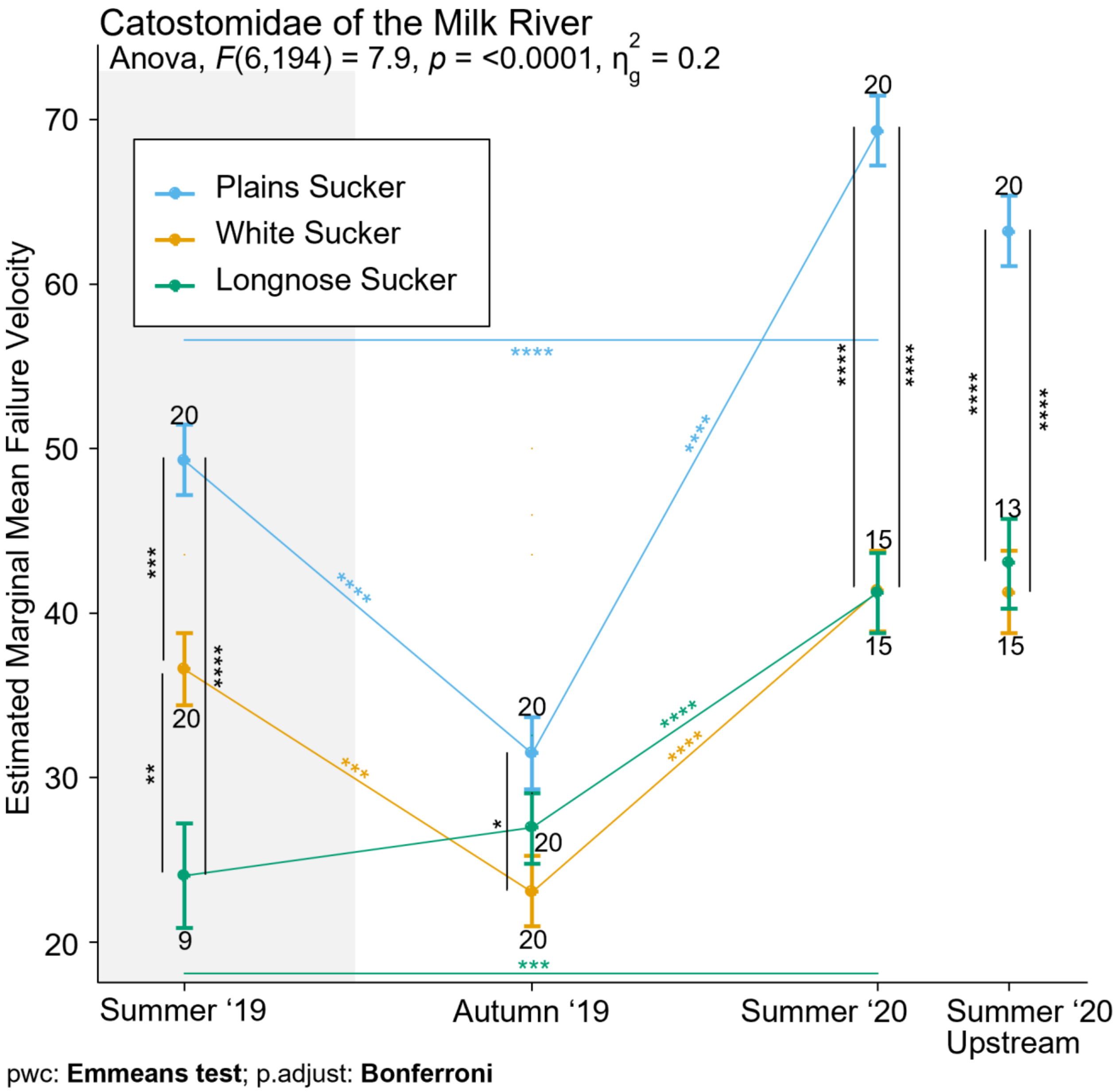

Figure 2-3: Estimated marginal mean (relative) failure velocity of three species of catostomids from the Milk River after correction for body length using ANCOVA. The grey background indicates the samples collected while the river was augmented by flows from the St. Mary Canal. The asterisk(s) adjacent to a vertical bar indicates a significant difference between the species at each end of the bar. The asterisk(s) on lines connecting seasons indicates a significant difference in relative failure velocity between the seasons, with horizontal bars being used to compare non-sequential seasons. The quantity of asterisks implies the strength of the difference as per R's standard levels. Numbers adjacent to each bar indicate the sample size of each group.

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Chapter 3: Assessing the station holding ability of the Plains Sucker in the Missouri Drainage

Introduction

Hydrologic infrastructure impacts the majority of the world's large rivers (Grill et al. 2019). In 24% of the world's large rivers, that infrastructure takes the form of flow augmentation; water, typically from outside the watershed, is added to the river's natural flow, typically for anthropogenic needs. The St. Mary Canal system of siphons and drop structures has augmented the flows in the North Fork of the Milk River during the months of April-September since 1917 (until the spring of 2020). Approximately 20$m^3 \cdot s^{-1}$ of additional flows make their way into the Missouri drainage in this way. The North Fork makes its confluence with the Milk River in southern Alberta, and meanders east and south until it arrives back in Montana. The additional flows are an important source of irrigation for agriculture throughout the Great Plains region. In the summer of 2019, I set out to evaluate the impact of these increased flows on three benthic fishes; the White Sucker, the Longnose Sucker, and the Plains Sucker, the last of which holds the status of "threatened" in the Milk River (COSEWIC 2010).

To test how flow augmentation in the Milk River might affect the Plains Sucker I sought to compare their performance in the swim tunnel to their nearest counterparts; Plains Sucker in unmodified waterbodies of the Missouri Drainage. Here, I compare the station holding abilities of Plains Sucker from several waterbodies in the DU2 range. To account for the fact that the Milk River changes flow with seasons, I similarly visited these other streams during both seasons. I hypothesised that the Milk River population possesses and maintains a greater ability to cope with increased velocity and flow over their counterparts in Battle and Caton creeks, regardless of augmentation status. Here I expected that Plains Sucker from the Milk River demonstrates higher failure velocities than those of Plains Sucker from Battle and Caton creeks both when augmented flows are occurring and after they return to natural levels.

Methods

Study Area and Sampling Methods

Three groundwater-fed, prairie rivers in the Missouri Drainage of southern Alberta and Saskatchewan, Canada were sampled in the Summer (June-August) and Autumn (September-October) of 2019 for Plains Sucker. The Milk River (mean augmented (April-September) flow rate: 16.06 $m^3 \cdot s^{-1}$; mean natural (October-March) flow rate: 2.36 $m^3 \cdot s^{-1}$), Battle Creek (mean summer (April-September) flow rate: 0.46 $m^3 \cdot s^{-1}$; mean winter (October, February, and March) flow rate: 0.31 $m^3 \cdot s^{-1}$), and Caton Creek (no flow data) were each sampled during both periods to control for temporal/seasonal variation, while investigating the differences in the Plains Sucker's swimming abilities in the augmented Milk River, and the unmodified Battle and Caton creeks (Water Office 2019).

The Milk River in summer is a turbid, moderately shallow, moderately wide river with low riparian vegetation and high bank mass failure; in autumn, the river becomes far clearer and shallower. Substrate in the Milk River is mostly characterised as silt-sand, with gravel-cobble riffles and occasional boulders. By comparison, Battle and Caton creeks have substantial riparian zones, and the vegetation contributes to stream features in addition to cobble-boulder substrates. A beach seine net (6 m x1.2 m, mesh size 3mm) was used to sample the Milk River, but the in-stream heterogeneity of Battle and Caton creeks necessitated use of a Smith-Root™ LR-24 Backpack Electrofisher, Vancouver, WA, USA (275-350 V, 30 Hz, 15-20% (5.0-6.67 ms pulse width), 400 W). With the exception of the thalweg in the Milk River in summer and a few deep pools in the other water bodies the entire width of the streams could be sampled and amounted to approximately 700-1000 m of stream in each waterbody. Figure 3-1 indicates the number of fish caught and tested per species/waterbody. All fish collected and used for experiments were approved under Animal Use Protocol #AUP00003131 and in compliance with SARA Permit #19-PCAA-00013, Alberta Environment and Parks Fish Research License #19-2207, and Government of Saskatchewan Special Collection Permit #SCP2019/AR06/FWLB for the appropriate jurisdictions.

Experimental Techniques

A total of 114 Plains Sucker were tested using the same experimental techniques as described in Chapter 2.

Statistical Techniques

Exploratory linear models tested for correlation between fork length and absolute failure velocity found that at least 9% and as much as 68% of the variation within each waterbody-season could be explained by a linear relationship (Figure 1-3). The absolute failure velocity ($cm \cdot s^{-1}$) however, was deemed inappropriate for comparison between species and seasons due to strong, linear correlations between these two variables in addition to considerable differences in body size between waterbodies (Figure 3-1). Two-way ANCOVA was selected to test for differences in mean failure velocity between waterbody and season while accounting for differences in fork length by including it as a covariate (see Figure 2-1's caption for a discussion of the assumptions). The ANCOVA produced estimated marginal mean failure velocities, hereafter referred to as relative failure velocity(ies). Significant, two-way interactions were investigated further by using a one-way ANCOVA testing for simple main effects of each species and season and then dissected further using Bonferroni corrected pairwise comparisons (Kassambara 2018). The assumptions of ANCOVA were met or only mildly violated (Fig S3 caption). All data analysis occurred in RStudio version 1.1.1103 (R Core Team 2020, RStudio Team 2016) using packages FSA (Ogle et al. 2020), tidyverse (Wickham et al. 2019), ggplot2 (Wickham 2009), and ggpubr (Kassambara 2020).

Results

The two-way ANCOVA found a significant interaction between waterbody and season on the relative failure velocity ($p = 0.037$); essentially that, after adjusting for fork length, the effect of season on relative failure velocity depended on the waterbody and vice versa (Figure 3-2).

A one way ANCOVA of each waterbody demonstrated a significant effect of season on relative failure velocity, and when probed via multiple pairwise comparisons it was found that Plains Sucker: in the Milk River had significantly different relative failure velocities between Summer and Autumn ($p = 1.28 \cdot 10^{-5}$), in Caton Creek had mild significant differences in relative failure velocity between seasons ($p = 0.0423$), but no significant difference in relative failure velocity between the two seasons in Battle Creek ($p = 0.436$).

One-way ANCOVA within each season demonstrated a significant difference only in Autumn between the Milk River population and the Battle Creek population. All three populations appear to maintain a higher relative failure velocity in the summer period, none of which are significantly different from each other.

Discussion

This study found that the condition of flow augmentation is associated with differences in the holding ability of Plains Sucker and provides evidence that the energetic trade-offs may be a contributing factor to the maintenance of the “threatened” status. During the Autumn period, Plains Sucker from the Milk River demonstrated a significantly lower EMMeanFV than during augmented flows and Plains Sucker from unmodified water bodies. Additionally, Plains Sucker from the Milk River were substantially smaller than their counterparts in unmodified waterbodies. These results indicate that flow augmentation presents an environmental challenge to Plains Sucker, and may play a role in driving significant changes in Plains Sucker populations which warrant further investigation of the indirect effects such as speciation and food web challenges and changes.

At the species level, Plains Sucker from the Milk River demonstrate a remarkably similar summer EMMeanFV to Plains Sucker from unmodified waterbodies, however, the onset of natural flows in the autumn is associated with a drastic reduction in station holding ability. Augmented flows in the Milk River began to taper after approximately the first week of September 2019, but the diversion was not shut down until September 27 and natural levels (similar to those measured at a station upstream of the canal input) were finally observed at the town of Milk River by September 29 (Water Office 2019, Palliser Environmental Services 2020). Post-augmentation swim tunnel experiments were carried out between October 3-11 giving the Milk River catostomids nearly four weeks to respond to the reduction in velocity towards natural levels. The observed change in EMMeanFV for Plains and White Sucker was unexpected, it was anticipated that catostomids would have the capacity to cope with annual increase in flows over the 100+ years (>10 generations) that the canal has been in operation and would therefore maintain a robust ability to tolerate high water velocities year round. This suggests that the ability to withstand high water velocities is an energetically demanding trait which has some plasticity to allow Plains Sucker to maintain their station holding capacity as it is necessitated by the environment (Swain et al. 2007, Crozier & Hutchings 2014).

Plains Sucker from the Milk River had significantly different failure velocities in augmented flows (summer) compared to the natural flows (autumn), but the same pattern was not as evident between seasons for the unmodified waterbodies. Velocity is continuously measured in the Milk River and Battle Creek by hydrometric stations near the sampling sites, but not at Caton Creek. Stream velocity in the Milk River is far higher than the maximum velocity of the swim tunnel (1 $m \cdot s^{-1}$). This is well below mean augmented (April-September) water velocity (16.06 $m^3 \cdot s^{-1}$) but similar to mean natural (October-March) flow rate (2.36 $m^3 \cdot s^{-1}$), as well as the flow rate in Battle Creek (summer: 0.46 $m^3 \cdot s^{-1}$, autumn: 0.31 $m^3 \cdot s^{-1}$) (Figure 1-2). Flow velocity was not explicitly measured during the sampling periods, so no link can be made with respect to the site-specific velocity, and conclusions must be drawn based on the monitoring stations.

The drastic change in failure velocity is unique to Plains Sucker from the Milk River and, by extension, unique to the condition of flow augmentation. (Veillard 2016) used respirometry in conjunction with swimming tests to find that another benthic fish, the Rocky Mountain Sculpin (*Cottus* sp.), from the augmented reaches of the Milk River system used significantly more oxygen despite no difference in failure velocity or swimming performance compared to conspecifics from unmodified water bodies. The increased consumption of oxygen would conceivably support an increased reliance on aerobic metabolism for the purposes of holding station. This single period assessment did not compare results between seasons, and the fish were held in still water in a lab facility, meaning that Rocky Mountain Sculpin appeared to maintain this physiology even when the condition of flow augmentation was removed. In our work, I traded the ability to measure oxygen consumption for the ability to run tests on fish immediately out of the river, with no still-water holding period. I hypothesised that a similar physiological characteristic would provide the energy required for the increased relative failure velocity measured in Plains Sucker in response to flow augmentation. Therefore, it was more surprising that the characteristic of a higher EMMeanFV was not maintained year round, as it appears to be in the Rocky Mountain Sculpin.

Based on the results of the Plains Sucker comparisons across different water bodies there does appear to be some impact of flow augmentation. Both the drastic changes in EMMeansFV between season that are only apparent in Plains Sucker from the Milk River, and in the rarity of larger-bodied Plains Sucker in the Milk River speak to and reinforce the notion that the Milk River population may be stockpiling energy reserves in preparation for the Summer augmented flow season, and not investing that energy in growth and therefore fecundity.

Figures

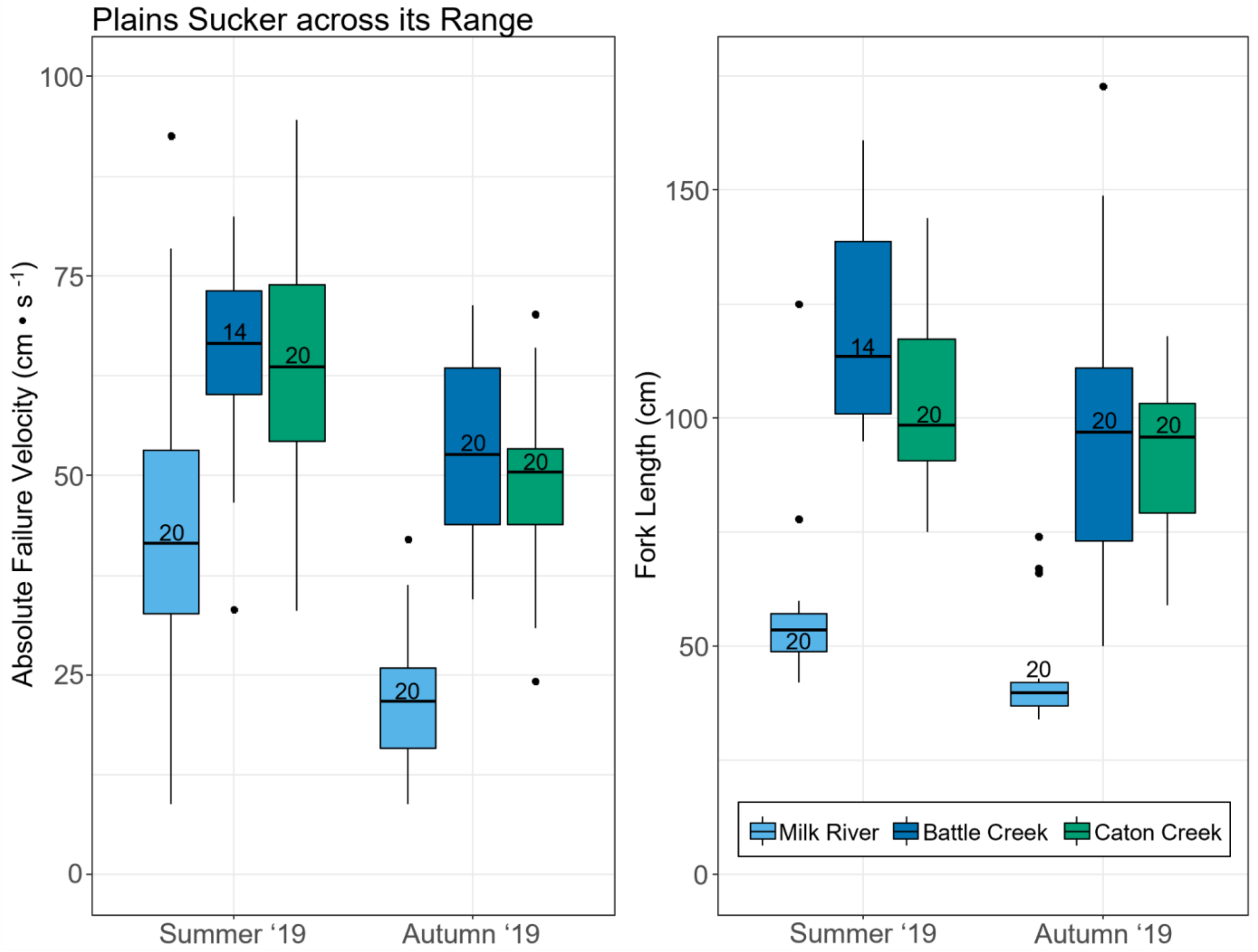

Figure 3-1: Absolute failure velocity (left, $cm.s^{-1}$) and fork length (right, cm) mean and range for Plains Sucker captured in three water bodies. Numbers above each median represent the sample size of each species used at each location and time period.

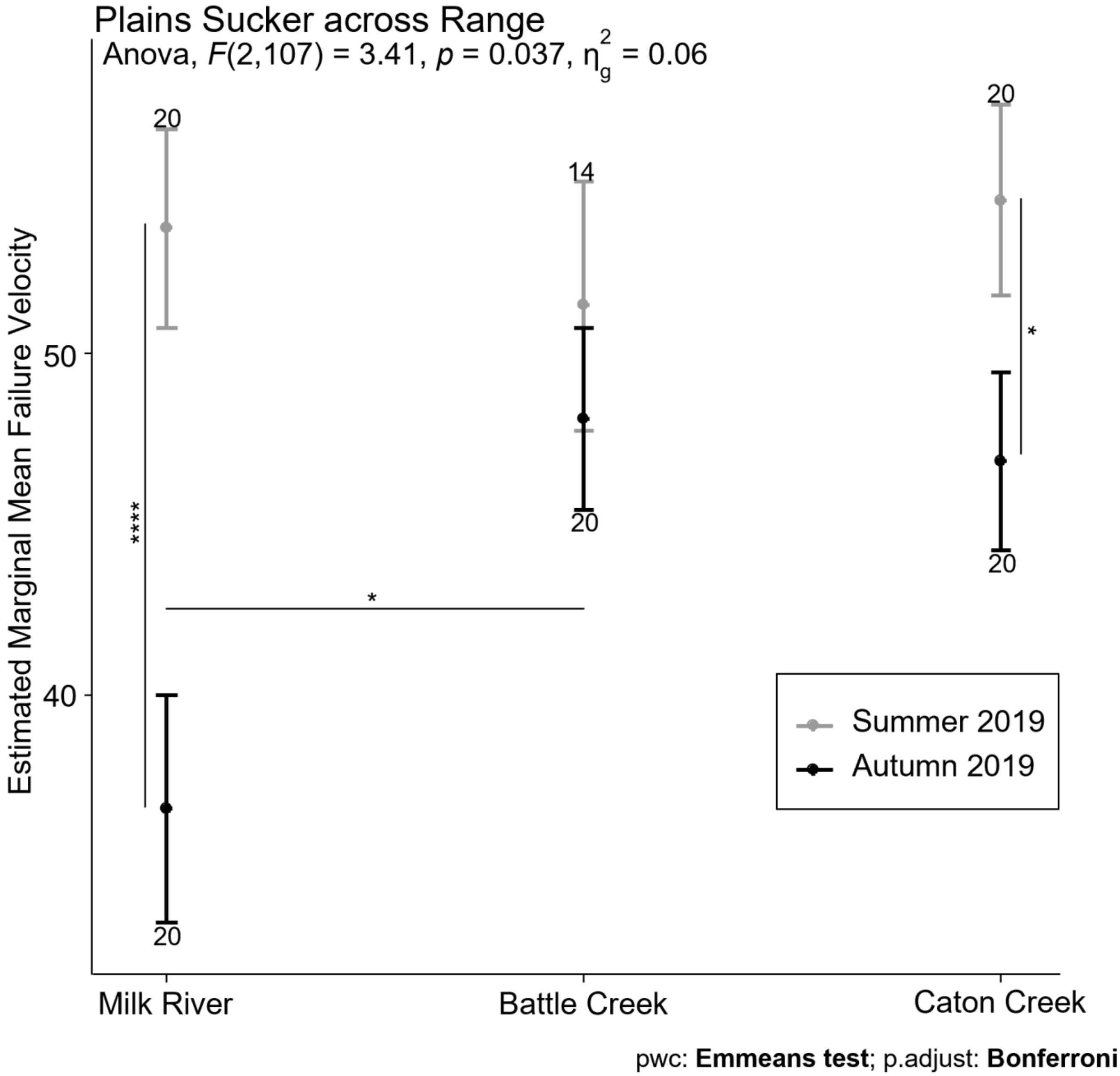

Figure 3-2: Estimated marginal mean (relative) failure velocity of Plains Sucker from the Missouri Drainage after correction for body length using ANCOVA. The asterisk(s) adjacent to a vertical bar indicates a significant difference between the species at each end of the bar. The asterisk(s) on lines connecting seasons indicates a significant difference in relative failure velocity between the seasons, with horizontal bars being used to compare non-sequential seasons. The quantity of asterisks implies the strength of the difference as per R’s standard levels. Numbers adjacent to each bar indicate the sample size of each group.

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Chapter 4: Conclusion

This work enhances our understanding of how flow augmentation is impacting the fish of the Milk River and adds to the growing knowledge of the impacts of flow regulation on native freshwater fishes in general. Here increased flow velocity of an augmented river results in significant differences in station holding ability compared to unmodified waterbodies and conditions. It is proposed that behavioural, physiological, or likely a combination of both adaptations assist Plains Sucker in the Milk River to maintain position against anthropogenically augmented flows. Future work may focus on the mechanisms underlying this ability and how it may result in an energetic trade-off leading to low recruitment of juveniles to the population. Measuring such traits as age-growth, morphometrics, and resource use/competition will be useful not only for examining an energetic trade-off, but also for investigating the potential for species-level divergence resulting from morphological adaptations to conditions of flow augmentation, and for determining the extent that larger bodied catostomids may be outcompeting Plains Sucker for resources in the continuously degraded and habitat-poor Milk River.

Finally, there are a number of limitations associated with measuring this “natural” experiment. First and most limiting was the lack of replication on augmented waterbodies. This is a unique system in terms of the specificity with respect to catostomids, but has broader implications for the nearly a quarter of the world’s large rivers experiencing anthropogenic augmentation (Grill et al. 2019). Second, there were large size discrepancies in Plains Sucker caught from the Milk River compared to other water bodies. Despite using sampling equipment biassed towards larger fish (seine netting, backpack electrofishing) only very small specimens were collected from the Milk

River (Poos et al. 2007, Poesch 2014). This is in addition to researcher size selection bias for larger fish in this waterbody, so all specimens were the largest available for testing at the commencement of a trial. ANCOVA was used to address the differences in body size without significantly penalising larger fish. It is noted that there is an established, negative relationship between body length and relative failure velocity owing to the non-linear relationship between absolute failure velocity and body size (Wootton 1992, Verhille et al. 2014). This was not especially evident in our data, appearing only in summer measurements for White Sucker in the Milk River and autumn measurements for Plains Sucker from Battle and Caton Creeks. No other treatment groups demonstrated a significantly negative slope when the body size was plotted against relative failure velocity. An interesting follow-up on the size discrepancy would be to investigate if Milk River Plains Sucker make an energetic trade-off between holding ability and somatic growth. Flow augmentation could indirectly impact fecundity via selection towards smaller bodied fish, as shown by the size comparison between Plains Sucker from the three water bodies (Figure 2-2). Additional follow-up sampling should generate water body specific growth models and investigate whether larger bodied individuals exist in potential flow refugia, such as the Milk River upstream of the confluence with the North Milk River. Perhaps all Plains Sucker that exist in the augmented section of the Milk River are juveniles that have been washed out of the unmodified tributaries or flow refugia and only able to return once flows return to their natural levels, if at all.

Temperature is often controlled and/or measured in swim performance testing, but I did not control for it here. A thermometer was only used regularly in the summer to monitor the change in temperature and ensure that it did not increase rapidly enough or high enough to harm the subject of the trial. The condition of flow augmentation is confounded some by the fact that it co-occurs with seasonal differences in temperature, which is known to regulate the metabolic rate and therefore activity levels of fish. It should be noted, however, that a 10 °C shift in temperature (from 10-20 °C) the Sacramento Sucker (*Catostomus occidentalis*) did not demonstrate a notable shift in swimming performance nor did the Longnose Sucker over a 13 °C shift from 7-20 °C (Jones et al. 1974, Myrick & Cech 1999). The Milk River and Caton Creeks, which demonstrated significant shifts in EMMeanFV, had similar, large seasonal temperature changes and it may therefore be reasonable to ascribe some of the observed differences in station holding ability to these shifts in temperature. Interestingly, while Caton Creek did experience a large shift in temperature between the two seasons, a similarly large shift in EMMeanFV was not apparent. Battle Creek experienced only a minor shift in stream temperature, and no significant change in station holding ability between the two seasons.

Both electrofishing and seining were used as capture techniques, owing to gear restrictions in addition to in-stream features. All forms of fish capture and handling result in physiological stress as indicated by a rapid increase and slow decrease (duration varies among species; from 4-5 h in Channel Catfish to 12 h in Rainbow Trout) in plasma lactate and glucose levels (Secondat and Diaz, 1942 as in Miles et al., 1974, Caillouet Jr, 1968). Burns and Lantz (1978) measured the recovery of five physiological traits (hematocrit (%), hemoglobin ($g \cdot dl^{-1}$), lactate ($mg \cdot dl^{-1}$), plasma protein ($mg \cdot dl^{-1}$), and tissue water (%)) in response to electrofishing, but only noticed differences in blood lactate between control and electrofished Largemouth Bass, and these demonstrated the expected rapid increase followed by slow decrease over the recovery period of 19 h. In the present study, fish were not usually tested on the same day that they were captured (either by electrofishing or by seining) and thus method of capture is not expected to have an effect. After a minimum of 12 h in the recovery bin, all fish were netted and immediately transferred to the swim tunnel, where each fish was subject to the same acclimation and experimental treatment. No fish demonstrating any effects of lactic acidosis resulting from stress (loss of equilibrium) were used in the swim tunnel.

This thesis aimed to investigate how Plains Sucker cope with and respond to the state of flow augmentation in the Milk River. Chapter 2 compared the EMMeansFV of three species of Catostomid that occur in the Milk River over 3 time periods; Summer and Autumn of 2019, periods of business as usual patterns of flow augmentation, and Summer of 2020, a period of low flows in summer when the system would otherwise expect high flows. While there were some major differences in EMMeansFV between the species and seasons, it seems that both the Plains Sucker and White Sucker are well able to physiologically and physically adapt to the changes in flow, however the Longnose Sucker seemed to have a bit of a harder time in Summer of 2019. Chapter 3 sought to investigate deeper by just comparing the EMMeansFV within the species of Plains Sucker but across a few different water bodies. In contrast to Chapter 2, this study found some evidence that flow augmentation may present at the very least a hurdle for the Milk River population of Plains Sucker. The difference in EMMeansFV from Summer to Autumn that was only apparent in the Milk River, coupled with the lack of representation of larger-bodied individuals from the Milk River, indicates that an energetic tradeoff between growth and station holding may become a limiting factor for this species in the Milk River.

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