Comparative swimming and station-holding ability of the threatened Rocky Mountain Sculpin (Cottus sp.) from four hydrologically distinct rivers

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Hydrologic alterations, such as dams, culverts or diversions, can introduce new selection pressures on freshwater fishes, where they are required to adapt to novel environmental conditions. Our study investigated how species adapt to natural and altered stream flow, where we use the threatened Rocky Mountain Sculpin (Cottus sp.) as a model organism. We compared the swimming and station-holding performance of Rocky Mountain Sculpin from four different hydrologic regimes in Alberta and British Columbia, including the North Milk River, a system that experiences increased flows from a large-scale diversion. We measured the slip ($U_{slip}$) and failure ($U_{burst}$) velocities over three constant acceleration test trials. $U_{slip}$ was defined as the point at which individuals required the addition of bursting or swimming to maintain position. $U_{burst}$ was defined as the point at which individuals were unable to hold position in the swimming chamber through swimming, bursting or holding techniques without fully or partially resting on the electrified back plate. We found individuals from the Flathead River in British Columbia (with the highest natural flow) failed at significantly higher $U_{burst}$ velocities than fish from the southern Albertan populations. However, there was no relationship between peak hydrologic flow from the natal river and $U_{burst}$ or $U_{slip}$. Further, $U_{burst}$ velocities decreased from 51.8 cm s⁻¹ (7.2 BL s⁻¹) to 45.6 cm s⁻¹ (6.3 BL s⁻¹) by the third consecutive test suggesting the use of anaerobic metabolism. $U_{slip}$ was not different between trials suggesting the use of aerobic metabolism in station-holding behaviours ($U_{slip}$). Moreover, we found no significant differences in individuals from the altered North Milk River system. Finally, individual caudal morphological characteristics were related to both slip and failure velocities. Our study contributes to the conservation of Rocky Mountain Sculpin by providing the first documentation of swimming and station-holding abilities of this benthic fish.

Key words: Anaerobic metabolism, benthic fish, body morphology, flow modification, oxygen uptake

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Introduction

Flow rate in lotic ecosystems defines basic environmental conditions from which organisms have evolved over the course of millions of years (Poff et al., 1997; Lytle and Poff, 2004). During the Anthropocene, close to half of the world’s major river systems have been altered through the construction of dams and diversions for anthropogenic use (Lehner et al., 2011). For example, there are over 10,000 dams in Canada constructed for hydropower, irrigation, water supply, and mine tailings (Canadian Dam Association, 2003). These alterations of natural flow regimes can impact the amount and connectivity of suitable fish habitat, alter energy flow in the food web, increase the probability of the establishment of invasive species, disrupt cues for spawning and migration, impact riparian vegetation density and diversity, and affect the ability of some fish species to successfully complete all necessary life stages (Poff et al., 1997). Thus, altered flow regimes can influence the basic properties that support fisheries productivity, ecosystem health and clean water resources.

Hydrologic alterations have been attributed to the imperilment of approximately 39% of freshwater fish species in North America (Ricciardi and Rasmussen, 1999; Dudgeon et al., 2006; Kelks et al., 2008). This threat exemplifies the need to quantify impacts of flow modification on fish species. Swimming performance is a methodology that can be used to test species adaptations to flow through manipulated velocity experiments. Swimming performance reflects morphological (Hynes, 1970; Webster et al., 2011), physiological (Milligan, 1996; Reidy et al., 2000) and behavioural adaptations for maintaining life in moving water (Webb, 1989; Vogel, 1994; Carlson and Lauder, 2010). In lotic systems, pelagic and benthic fishes utilize different techniques to maintain position against a unidirectional current. Pelagic species swim to hold station (Webb et al., 1996) compared to benthic fishes, such as sculpins (Family: Cottidae), that interact with the substrate to maintain position (Webb, 1989; Tierney et al., 2011). Further, fishes have the capacity for some combination of aerobic (i.e. sustained swimming) and anaerobic (i.e. burst swimming) activity based on life history strategies (Hammer, 1995; Kieffer, 2000; Lucas et al., 2001).

These life history strategies can be useful in deciding the appropriate swimming performance test. Swimming performance in fish has been predominantly assessed using incrementally velocity tests to define critical swimming speed ($U_{crit}$) (Brett, 1964). These tests were developed for Salmonids (Family: Salmonidae) and have been used extensively by ecologists over the past 50 years (Beamish, 1978; Nelson et al., 2002). However, concerns over the inability of $U_{crit}$ tests to differentiate between aerobic and anaerobic capacity led to the development of alternative tests, such as constant accelerations tests (CATs; $U_{burst}$), to measure the anaerobic scope of individuals (Reidy et al., 2000, 1995; Nelson et al., 2002).

This flexibility allows ecologists to utilize ecologically relevant methodologies based on the life history of their test subjects (Nelson et al., 2002). For example, endurance swimmers, such as salmonids, have a far greater aerobic scope than burst swimmers, such as sculpins (Lucas et al., 2001). While many factors influence aerobic scope, like individual fitness (e.g. body measurements) (Nelson, 1990; Kieffer et al., 1994), the inherent differences between fish families makes some tests more suitable than others. Sculpins have as little as 3–5% red ‘aerobic’ muscle mass compared to salmonids that can have up to 20% red muscle mass (Lucas et al., 2001). Therefore, the use of $U_{burst}$ tests for sculpins can more accurately describe swimming abilities by focusing on the anaerobic scope of activity (Lucas et al., 2001).

Rocky Mountain Sculpin (Cottus sp.) are a model organism to understand the impact of flow alteration on sedentary species. Rocky Mountain Sculpin (herein referred to as RMS) is a threatened species with a restricted distribution in Canada and was recently identified as a unique taxon (COSEWIC, 2005). Within the range of RMS in Canada, waterway alterations for irrigation have drastically changed habitat and flow regimes with the construction of the St. Mary Canal in 1917 (COSEWIC, 2005). The St. Mary Canal annually diverts $178 \times 10^6$ cubic meters of water from the St. Mary River to the North Milk River (Bradley and Smith, 1984) during the irrigation period from May through September. This diversion drastically increases peak flow rates in the North Milk River ($3 \text{ m}^3\text{s}^{-1}$ to $16 \text{ m}^3\text{s}^{-1}$) and maintains an artificially stable discharge throughout the irrigation period (Fig. 1) (Water Survey of Canada, 2015).

We investigate the effect of large-scale flow alterations on RMS by comparing swimming and station-holding performance across four genetically distinct sub-populations throughout the Canadian distribution (Ruppert et al., 2017). Five-year average peak discharge (2008–2012) differs drastically between lotic ecosystems within the RMS range, including the North Milk River ($3 \text{ m}^3\text{s}^{-1}$ and $16 \text{ m}^3\text{s}^{-1}$ for natural and augmented, respectively), Lee Creek ($31 \text{ m}^3\text{s}^{-1}$; St. Mary River tributary), St. Mary River ($80 \text{ m}^3\text{s}^{-1}$) and the Flathead River ($135 \text{ m}^3\text{s}^{-1}$) (Fig. 1) (Water Survey of Canada, 2015) providing a unique study system to test adaptations to natal flow regime. Specifically, in this study we determine (i) whether there are population differences in the maximum flow rate at which individuals can sustain position; (ii) if repeated trials influence swimming and station-holding performance; (iii) if phenotypic characteristics exist that may contribute to superior swimming and station-holding performance under modified flow rates; and (iv) the respiration rates under minimal flow ($5 \text{ cm s}^{-1}$). It is expected that predisposition to both natural and altered natal flow regimes would produce selection towards differences in swimming and station-holding performance of RMS from the four rivers.
Methodology

Fish

RMS were collected throughout their Canadian distribution in Lee Creek (24 July 2014; 30 Oct 2014), St. Mary River (24 July 2014; 30 Oct 2014), North Milk River (24 July 2014) and the Flathead River (26 Aug 2015) using a backpack electrofishing unit (Smith-Root, Vancouver, WA, USA). Average water temperatures in southern Alberta, taken from 0900-1330 around the date of initial collection, were 19 ± 2°C (18 and 21 July 2014), 16 ± 1°C (20 and 23 July 2014) and 18 ± 1°C (19 and 21 July 2014) for Lee Creek, St. Mary River and North Milk River, respectively. Average water temperatures in October for Lee Creek and St. Mary River were 8 ± 2°C (1 Oct 2014) and 9 ± 2°C (2–7 Oct 2014). Average water temperature in the Flathead River was 8.9 ± 2.6°C (26 Aug 2015). Following field collection, fish were held instream in a flow-through container overnight and fasted to reduce excretions during transport (Harmon, 2009). The following day, 50 L coolers were filled with water from the natal stream and fish were transferred from the flow-through container into the cooler with a dip net. Up to 100 individuals were transported per cooler (max. density = 2 ind. L⁻¹). Aeration was provided to each cooler for the duration of the transport to the University of Alberta aquatics facility.

RMS were held in 120 L static-flow tanks with 40–100 individuals per tank. Fish were fed crushed nutrafin sinking pellets and dissolved invertebrate cubes, five days a week.

Figure 1: Canadian distribution of RMS in southern Alberta and southeast British Columbia (a,b). Polygons are coloured by subwatershed: Flathead River subwatershed (green), Oldman River subwatershed (orange) and Milk River subwatershed (blue). Within these subwatersheds, our study examined fish from the Flathead River (dark green), St. Mary River (orange), Lee Creek (dark orange) and North Milk River (dark blue). The North Milk River augmentation (St. Mary Canal) is shown in black. Inset (c) illustrates average discharge (m³ s⁻¹) from 2008 to 2012 across the Canadian distribution of RMS taken from five hydrologic stations (Water Survey of Canada, 2015) plotted on a log10 scale. Peak discharge at each station is marked by horizontal dashed lines. Photos (d) and (e) show the same stretch of the North Milk River during augmented (aug.) and natural (nat.) flows.
Water temperature was held at 12 ± 1°C, using filtered, dechlorinated municipal water on a 0800:2000 light to dark schedule. Shelters were placed in tanks to reduce stress levels for RMS throughout their time in the aquatics facility. Fish were held for 2–6 months prior to testing. RMS from Lee Creek (n = 25), St. Mary River (n = 20), North Milk River (n = 25) and Flathead River (n = 26) were randomly selected from the holding tanks to undergo testing.

Respirometry

About 24 h prior to swim tests, experimental fish were isolated from the feeding schedule to reduce the effects of digestion on metabolic rate (Jobling, 1981; Clarke and Johnston, 1999). Up to 12 h prior to testing, a sculpin was dip-netted from a holding tank at random, and transferred into a dark container with minimal human contact. The test fish was transported to the testing room and immediately relocated into one of two Brett-type respirometers (v = 10 L) containing freshly flushed air saturated water (12 ± 1°C) with a low velocity (5 cm s\(^{-1}\)) unidirectional current. Fish moved out of the transport container into the respirometer on their own and rested in the low velocity current without the need to swim. Respirometers were sealed and oxygen levels (mg L\(^{-1}\)) were continuously measured every second to the nearest 0.01 mg L\(^{-1}\) overnight (2000-0800) using a fibre optic oxygen probe calibrated weekly (Loligo Systems, Viborg, Denmark). Oxygen measurements were automatically recorded using the respirometry software AutoResp (Loligo Systems, Viborg, Denmark). To reduce stress from external movements and stimuli, respirometers were placed behind black curtains and monitored by video. Freshwater was continually flushed through the outer bath to reduce warming of the inner, sealed test water.

A bacterial oxygen consumption (mg L\(^{-1}\)) trial was conducted following the completion of the fish trials by measuring oxygen consumption in the respirometer without a fish from 2000-0800 with a 5 cm s\(^{-1}\) unidirectional current. Oxygen consumption was calculated over a 4 h period (0200-0600) using data from 4 to 5 h following introduction into the respirometer to reduce the impact of transportation and handling on metabolic rate (Jobling, 1981; Tierney et al., 2011). Fish oxygen consumption (mg L\(^{-1}\); t\(_{0200}\)=t\(_{0600}\)) was corrected by subtracting bacterial oxygen consumption (mg L\(^{-1}\); t\(_{0200}\)=t\(_{0600}\)) to account for respiration from sources other than the test fish. The corrected oxygen uptake for fish was standardized by hour for body weight of individuals (mg L\(^{-1}\) g\(^{-1}\) h\(^{-1}\)). Trials were removed where temperature increased more than 5°C overnight or if there were equipment issues.

Swimming and station-holding performance

Swimming and station-holding performance was tested the following morning on the same fish used for respirometry the previous night. Fish were tested through a repeated measures design where each individual was observed in a series of three confined area constant acceleration tests (CATs) to quantify anaerobic burst swimming and exercise recovery potential (Reidy et al., 2000). Water velocity in the respirometer started at 5 cm s\(^{-1}\) and was programmed to increase by 2.5 cm s\(^{-1}\) every 10 s until fish reached fatigue. Two measures of swimming performance were recorded during each test: failure velocity and slip velocity. Failure velocity (\(U_{\text{burst}}\)), a metric incorporating both swimming and station-holding abilities, was defined as the point at which RMS were unable to hold position in the swimming chamber through swimming, bursting or holding techniques without fully or partially resting on the electrified back plate. To ensure each fish reached a true failure velocity without resting, RMS were encouraged to move away from the back plate by applying short electrical pulses (0.25 ± 0.03 V) or, if necessary, a temporary reversal of flow direction. Fish were considered to have failed if they: (i) were responsive to the electrical pulse but did not remove themselves from the back grate after approximately 5 s of resting or (ii) returned to resting on the back grate after a temporary flow reversal. In the second case, the original failure velocity prior to flow reversal was recorded. Slip velocity (\(U_{\text{slip}}\)), a measure of station-holding ability, was defined as the point at which fish were no longer able to hold station against the current without swimming or bursting (Webb et al., 1996). RMS utilize holding behaviour at low velocities where they exhibit virtually no body movement. When velocities increase, RMS must add bursting techniques to their holding behaviour or fully transition to swimming. The first point at which individuals slipped backward from a station-holding position or required the addition of bursting or swimming techniques to maintain position was considered the slip velocity. Due to technical failures, slip velocity was not measured on nine individuals, including: Lee Creek (n = 3), St. Mary River (n = 3) and North Milk River (n = 3). Swimming and station-holding performance was measured in cm s\(^{-1}\) and this metric was used for all analyses. A second metric, body lengths per second (BL s\(^{-1}\)) was calculated for comparison with other papers.

Once fish failed, velocity was returned to 5 cm s\(^{-1}\) for a 30 min resting period. Each individual was tested in three CAT trials (CAT 1, CAT 2 and CAT 3) to investigate exercise recovery potential following fatigue. After all three tests were completed, sculpins were anaesthetized in tricaine methanesulfonate (TMS; MS-222; 0.2 g L\(^{-1}\)) and body characteristics were recorded. Body characteristics were measured to the nearest 0.1 g (weight) and 0.1 mm (total length, body width, body height, caudal width, caudal height and caudal length) using a digital scale and digital calipers, respectively. Body characteristics were summarized for fish used in analysis once temperature mistrials were removed.

Analysis

All analyses were conducted using the open sourced R statistical program (R Core Team, 2015). Factors influencing failure (\(U_{\text{burst}}\)) and slip (\(U_{\text{slip}}\)) velocities (cm s\(^{-1}\)) were assessed using linear mixed-effects models in the nlme package (Pinheiro et al., 2014). Mixed-effects models are useful to deal with nested data, such as repeated tests on individuals, by allowing the intercept to vary for each individual.
Three groups of linear mixed-effects models were analysed for this study. Firstly, we analysed the effect of river and CAT trial number (fixed factors) on \(U_{\text{burst}}\) and \(U_{\text{slip}}\). These models were structured with each individual (FishID) as a random intercept to account for the repeated measures study design (Zuur et al., 2009). Covariates were included in each model to describe variation in swimming and station-holding performance due to the number of days held in the aquatics facility and the total length of each fish. This was necessary because of unevenly spaced holding times for each river and size differences between rivers. Attempts were made to standardize size of test individuals, however, one population (Flathead River) lacked sufficient fish within the targeted size. As covariates had difference scales and units, they were standardized and centred to a mean of zero in the R package vegan (Oksanen et al., 2016). Post-hoc Tukey tests were conducted to compare differences in \(U_{\text{burst}}\) or \(U_{\text{slip}}\) velocities between rivers and CAT trial number (Fig. 2) using the R package multcomp (Hothorn et al., 2008). Secondly, linear mixed-effects models were analysed to examine if there was a relationship between peak flow (\(m^3 s^{-1}\)) in natal streams and \(U_{\text{burst}}\) or \(U_{\text{slip}}\). These models were also structured with FishID as the random intercept. The model included covariates (days held and total length) and a fixed effect of peak flow (\(m^3 s^{-1}\)).

Finally, the impacts of body characteristics on \(U_{\text{burst}}\) or \(U_{\text{slip}}\) (\(cm s^{-1}\)) were assessed using linear mixed-effects models with manual backwards selection (Zuur et al., 2009). These models were structured using a random intercept of FishID nested in River to account for repeated measures and river groupings from days held (as described above). This method allowed us to examine the effect of body characteristics (including total length) once the variation between rivers was removed. Fixed effects included: total length, caudal length, caudal height, caudal width, body height, and body width (Table 1). Fixed effects were centred as described above and collinearity was assessed using variance inflation factors in the R package AED (Zuur, 2010). VIFs were <10 indicating acceptable levels of collinearity.

Backwards selection of fixed effects was performed using likelihood ratio tests to drop the least significant variables (Zuur et al., 2009). Corrected Akaike’s information criterion (AICc) for small sample sizes (Sugiura, 1978; Aikake, 1992; Bedrick and Tsai, 1994) was used to rank all final models created during backwards selection. Models were further compared using \(\Delta_i\) (AICc – AICc\(_{\text{min}}\)) and \(w_i\) (Akaike weights) to explain the strength of evidence for each model. Models with a \(\Delta_i < 2\) were considered similarly fitting models (Burnham and Anderson, 2004) and investigated further. To control for family-wise error due to multiple comparisons, \(P\) values for fixed effects were adjusted using the Holm-Bonferroni method (Rice, 1989).

**Results**

**Swimming and station-holding performance between rivers and CAT trials**

Overall, RMS swam to an average of 49 ± 22.8 cm s\(^{-1}\) (6.8 ± 2.9 BL s\(^{-1}\)) over a duration of 3.1 ± 1.5 min before failing (\(U_{\text{burst}}\)) (Table 1). RMS held station to an average of 23.4 ± 14.5 cm s\(^{-1}\) (3.3 ± 2.2 BL s\(^{-1}\)) before slipping (\(U_{\text{slip}}\)) (Table 1). The Flathead River fish swam to significantly higher \(U_{\text{burst}}\) velocities than those from the southern Albertan populations in Lee Creek (Tukey HSD, \(z = -3.150, P < 0.001\)), St. Mary River (Tukey HSD, \(z = -2.851, P = 0.01\)) and North Milk River (Tukey HSD, \(z = -2.629, P = 0.03\)) (Fig. 2). There were no significant differences in \(U_{\text{slip}}\) between rivers (Tukey HSD, \(z < 2.2, P > 0.09\)). Despite population differences in \(U_{\text{burst}}\), there was not a significant relationship between peak flow and \(U_{\text{burst}}\) velocities (\(df = 71, t = 1.9, P > 0.05\)) or peak flow and \(U_{\text{slip}}\) velocities (\(df = 62, t = 0.44, P = 0.66\)).

Significant differences in \(U_{\text{burst}}\) between repeated swim tests were observed from CAT 1 (51.8 cm s\(^{-1}\); 7.2 BL s\(^{-1}\)) to CAT 3 (45.6 cm s\(^{-1}\); 6.3 BL s\(^{-1}\)) (Tukey HSD, \(z = -2.39, P = 0.0445\)) (Table 1, Fig. 2). However, \(U_{\text{slip}}\) showed no differences over CAT trials (Tukey HSD, \(z < 1.042, P > 0.55\)) (Fig. 2).

**Body characteristics influencing swimming performance**

Caudal width was an important variable influencing \(U_{\text{burst}}\) and \(U_{\text{slip}}\) and was included in all selected models (Table 2).
Caudal width had a positive relationship with $U_{\text{burst}}$ signifying fish with wider caudal measurements swam to higher velocities before failing (Table 3). However, Model 1 ($P = 0.16$), Model 2 ($P = 0.07$), and Model 3 ($P = 0.27$) showed caudal width was not significant (Table 3). Caudal width was additionally important for explaining $U_{\text{slip}}$ and was included in both selected models (Table 2). Similar to failure velocity models, caudal width had a positive relationship with slip velocity but was not statistically significant in either Model 1 ($P = 0.08$) or Model 2 ($P = 0.22$) (Table 3).

| Table 1: Summary of body characteristics and raw test results; Body characteristics were summarized for fish used in analysis; Failure ($U_{\text{burst}}$) and slip ($U_{\text{slip}}$) velocities are presented as both raw velocity (cm s$^{-1}$) and body lengths per second (BL s$^{-1}$); Results are presented as: mean (st. dev) |
|--------------------------------------------------|
| Body characteristics                              | Flathead River | St. Mary River | Lee Creek | North Milk River | All       |
| Weight (g)                                        | n = 26         | n = 14         | n = 17    | n = 18           | n = 75    |
| Total length (mm)                                 | 6.9 (3.8)      | 2.9 (1.7)      | 2.6 (0.7) | 4.1 (1.5)        | 4.5 (3)   |
| Caudal length (mm)                                | 10.4 (2.2)     | 7.1 (1.6)      | 8 (1.1)   | 8.5 (1.3)        | 8.8 (2.1) |
| Caudal height (mm)                                | 4.9 (0.9)      | 4 (1.3)        | 3.7 (0.4) | 3.8 (0.6)        | 4.2 (1)   |
| Caudal width (mm)                                 | 2.3 (0.4)      | 1.8 (0.6)      | 1.8 (0.6) | 2 (0.3)          | 2 (0.6)   |
| Body height (mm)                                  | 10.6 (2.4)     | 8.6 (2.1)      | 8.3 (1.4) | 11 (1.8)         | 9.8 (2.3) |
| Body width (mm)                                   | 10.8 (2.5)     | 9.1 (1.9)      | 8.5 (1.4) | 10.8 (1.7)       | 10 (2.2)  |
| Failure velocity                                  | n = 26         | n = 14         | n = 17    | n = 18           | n = 75    |
| $U_{\text{burst}}$ CAT 1 (cm s$^{-1}$)             | 68.8 (17.6)    | 44.4 (26.1)    | 39.7 (18) | 44.4 (22.2)      | 51.8 (23.8) |
| (BL s$^{-1}$)                                     | 8.3 (2.4)      | 7.1 (4.5)      | 6.3 (2.6) | 6.6 (3.4)        | 7.2 (3.2)  |
| CAT 2 (cm s$^{-1}$)                               | 66.3 (22.5)    | 39.1 (22.4)    | 41.4 (19.8) | 41.7 (17.2)      | 49.7 (23.7) |
| (BL s$^{-1}$)                                     | 7.9 (2.6)      | 6.4 (3.8)      | 6.6 (3)   | 6.1 (2.4)        | 6.9 (3)   |
| CAT 3 (cm s$^{-1}$)                               | 59 (18.6)      | 37.5 (21.4)    | 36.7 (18.8) | 41.1 (15.4)      | 45.6 (20.7) |
| (BL s$^{-1}$)                                     | 7 (2.2)        | 5.9 (3)        | 5.8 (2.9) | 6 (1.9)          | 6.3 (2.5)  |
| Overall (cm s$^{-1}$)                             | 64.7 (19.9)    | 40.4 (23)      | 39.3 (18.6) | 42.4 (18.2)      | 49 (22.8)  |
| (BL s$^{-1}$)                                     | 7.7 (2.5)      | 6.4 (3.7)      | 6.2 (2.8) | 6.2 (2.6)        | 6.8 (2.9)  |
| Test duration (min)                               | 4.1 (1.3)      | 2.5 (1.5)      | 2.5 (1.2) | 2.7 (1.2)        | 3.1 (1.5)  |
| Slip velocity                                     | n = 26         | n = 11         | n = 14    | n = 15           | n = 66    |
| $U_{\text{slip}}$ CAT 1 (cm s$^{-1}$)              | 21.2 (7.3)     | 24.3 (18.4)    | 27.3 (15.3) | 19.1 (9.4)       | 22.5 (12.1) |
| (BL s$^{-1}$)                                     | 2.5 (0.7)      | 4.1 (3.3)      | 4.3 (2.3) | 2.9 (1.5)        | 3.2 (2)   |
| CAT 2 (cm s$^{-1}$)                               | 22.9 (15.7)    | 19.7 (10.6)    | 21.8 (12.7) | 25 (16.6)        | 22.6 (14.4) |
| (BL s$^{-1}$)                                     | 2.7 (1.7)      | 3.4 (0)        | 3.4 (2)   | 3.8 (2.5)        | 3.2 (2)   |
| CAT 3 (cm s$^{-1}$)                               | 24.9 (17.9)    | 21.1 (13.2)    | 23.7 (19.3) | 29 (15)          | 24.9 (16.7) |
| (BL s$^{-1}$)                                     | 3 (2.2)        | 3.6 (2.4)      | 3.8 (3.2) | 4.4 (2.2)        | 3.6 (2.5)  |
| Overall (cm s$^{-1}$)                             | 23 (14.3)      | 21.7 (14.1)    | 24.3 (15.8) | 24.3 (14.3)      | 23.4 (14.5) |
| (BL s$^{-1}$)                                     | 2.7 (1.7)      | 3.7 (2.5)      | 3.8 (2.5) | 3.7 (2.2)        | 3.3 (2.2)  |
| Oxygen measurements                               | n = 21         | n = 13         | n = 16    | n = 16           | n = 66    |
| No detect (n)                                     | 16             | 7              | 10        | 0               | 33        |
| Detect (n)                                        | 5              | 6              | 6         | 16              | 33        |
| $O_2$ Cons. (mg L$^{-1}$ g$^{-1}$ hr$^{-1}$)       | 3.7 E-03 (3.7 E-03) | 1.1 E-02 (9.4 E-03) | 7.2 E-03 (7.2 E-03) | 1.0 E-02 (9.0 E-03) | 8.8 E-03 (8.3 E-03) |
Caudal length and caudal height were important for \( U_{\text{burst}} \) and \( U_{\text{slip}} \) velocities, respectively (Table 2), demonstrating the prominence of caudal morphology in swimming and station-holding performance. Caudal length had a positive relationship with \( U_{\text{burst}} \) but was not statistically significant in Model 1 \( (P = 0.16) \) or Model 3 \( (P = 0.33) \); Table 3). Alternatively, caudal height was negatively correlated with \( U_{\text{slip}} \) but was also not statistically significant in Model 1 \( (P = 0.17) \) or Model 2 \( (P = 0.32) \); Table 3).

Total length was included in all \( U_{\text{burst}} \) models, but was not included in the \( U_{\text{slip}} \) models (Table 2). Total length had a positive relationship with \( U_{\text{burst}} \) and was significant in Model 1 \( (P = 0.01) \) and Model 2 \( (P < 0.01) \) but not Model 3 \( (P = 0.07) \). Body width influenced both \( U_{\text{burst}} \) and \( U_{\text{slip}} \) velocities (Table 2). It was negatively correlated with \( U_{\text{burst}} \) \( (P > 0.07) \), and positively correlated with \( U_{\text{slip}} \) \( (P = 0.67) \) (Table 3). Body height was selected in one \( U_{\text{burst}} \) model and had a positive correlation (Tables 2 and 3). However, it was not significant \( (P = 0.5) \) (Table 3).

**Oxygen consumption**

RMS oxygen consumption was detected in only half the trials \( (n = 33) \). All fish from the North Milk River \( (n = 16) \) had detectable oxygen uptake whereas only five fish were detected from the Flathead River and six were detected from each the St. Mary River and Lee Creek (Table 1). Due to small sample sizes and large variation between samples, we were unable to statistically compare differences between rivers.

**Discussion**

RMS swimming and station-holding performance, as measured by failure velocity \( (U_{\text{burst}}) \), was significantly different between individuals from the Flathead River and the southern Albertan populations. The Flathead River is separated from southern Alberta by the continental divide. This separation has resulted in strong genetic differences between populations from the Flathead River and populations from southern Alberta \( (\text{Ruppert et al., 2017}) \). Because we held fish in the aquatics facility for 2–6 months prior to testing, our fish were ‘detrained’ \( (\text{Nelson et al., 2008}) \) and measurements were a reflection of genetic differences in swimming and station-holding ability between populations (i.e. any phenotypic plasticity due to the flow regimes would not be expected to persist). The differences we found in swimming and station-holding between fish from either side of the continental divide are consistent with the strong genetic structuring of sub-populations. We did not, however, find any differences in fish from the augmented North Milk River compared to other populations despite strong population differences \( (\text{Ruppert et al., 2017}) \). RMS from the North Milk River have had one hundred years to adapt to seasonally augmented flows since the instalment of the St. Mary Canal in 1917 \( (\text{COSEWIC, 2005}) \). This corresponds to
Table 3: Parameter estimates from top linear mixed-effects models explaining failure ($U_{\text{burst}}$) and slip ($U_{\text{slip}}$) velocities as a function of body characteristics; Bolded text indicates variable significance at $\alpha = 0.05$ after Holm adjustments

| Response | Fixed effect | Coefficient | SE  | $t$ value | $P$    |
|----------|--------------|-------------|-----|-----------|--------|
| Failure velocity: $U_{\text{burst}}$ (cm s$^{-1}$) | Intercept | 49.01 | 1.78 | 27.53 | $<0.001$ |
| Model 1 | Total length | 9.98 | 3.14 | 3.18 | 0.01 |
|         | Caudal width | 4.34 | 2.20 | 1.97 | 0.16 |
|         | Body width | −5.45 | 2.82 | −1.93 | 0.16 |
|         | Caudal length | 3.41 | 2.28 | 1.49 | 0.16 |
| Model 2 | Intercept | 48.94 | 1.91 | 25.66 | $<0.001$ |
|         | Total length | 11.84 | 2.91 | 4.07 | $<0.001$ |
|         | Caudal width | 4.77 | 2.20 | 2.17 | 0.07 |
|         | Body width | −5.63 | 2.89 | −1.95 | 0.07 |
| Model 3 | Intercept | 48.85 | 2.15 | 22.75 | $<0.001$ |
|         | Total length | 8.74 | 3.46 | 2.53 | 0.07 |
|         | Caudal width | 4.13 | 2.21 | 1.87 | 0.27 |
|         | Body width | −7.03 | 4.35 | −1.62 | 0.33 |
|         | Caudal length | 3.42 | 2.30 | 1.49 | 0.33 |
|         | Body height | 2.67 | 3.97 | 0.67 | 0.50 |
| Slip velocity: $U_{\text{slip}}$ (cm s$^{-1}$) | Intercept | 23.35 | 1.18 | 19.87 | $<0.001$ |
| Model 1 | Caudal height | −2.10 | 1.51 | −1.39 | 0.17 |
|         | Caudal width | 3.14 | 1.51 | 2.08 | 0.08 |
| Model 2 | Intercept | 23.35 | 1.18 | 19.75 | $<0.001$ |
|         | Caudal height | −2.43 | 1.70 | −1.43 | 0.32 |
|         | Caudal width | 2.93 | 1.60 | 1.83 | 0.22 |
|         | Body width | 0.70 | 1.65 | 0.43 | 0.67 |

approximately 20 generations (COSEWIC, 2005) for genetic adaptations to arise. While genetic differences indicate the North Milk River may be a unique sub-population (Ruppert et al., 2017), in our study these genetic differences were not manifested in RMS swimming and station-holding ability from the North Milk River.

Contrary to our hypothesis, we did not see a gradient of swimming and station-holding performance correlated with the peak flow (m$^3$ s$^{-1}$) indicating that genetic differences in swimming and station-holding, as measured in this study, may not be strongly influenced by natal hydrologic regime. While phenotypic differences in RMS swimming performance may exist, a review of over 80 studies indicated the influence of flow on phenotypic plasticity in swimming performance is unclear (Langerhans, 2008). In the case of RMS, large-scale differences in hydrologic regime between systems may be diminished by strong microhabitat selection within these watersheds. For example, RMS utilize interstitial spaces created by physical substrate near the stream bed to complete their life history (Bailey, 1952; Finger, 1982; Haro and Brusven, 1994) by feeding on invertebrates and small fish on rock surfaces (Greenberg, 1991) and spawning under unembedded cobbles (Bateman and Li, 2001). These microhabitats can have velocities close to zero, called the boundary layer, as described by the Prandtl–vonKarman velocity equation (Chow, 1959; Hynes, 1970; Jowett, 1993). By carrying out their life history in the benthos, RMS can evade strong currents through the selection of unembedded cobble refugias (Bailey, 1952; Finger, 1982; Facey and Grossman, 1992). In a study on the energetic costs associated with microhabitat use in relation to velocity, Facey and Grossman (1992) found Mottled Sculpin (Cottus bairdi) selected microhabitat with velocities $<1$ BL s$^{-1}$ despite their ability to hold station up to 5.8 BL s$^{-1}$ (Facey and Grossman, 1992). As a result,
microhabitat selection may shelter RMS from experiencing the full impact of broad-scale hydrologic regimes, thereby reducing the selection for swimming adaptations.

Averaged over all CAT trials, RMS swam to 6.8 ± 2.9 BL s⁻¹ before failing \( (U_{\text{burst}}) \). While no other studies have assessed the swimming and station-holding performance of RMS, our findings fall within the range of closely related cотflies, such as Slimy Sculpin \((Cottus cognatus)\) and Mottled Sculpin \((Cottus bairdi)\) that can swim up to velocities of 9.4 BL s⁻¹ \((\text{Webb} 1978)\) and 5.8 BL s⁻¹ \((\text{Facey and Grossman} 1990)\), respectively, in modified \( U_{\text{crit}} \) trials. Additionally, our study indicated that \( U_{\text{burst}} \) in subsequent CAT trials decreased significantly after a 30 min rest period between tests. Throughout the test duration, RMS predominantly held station up until the \( U_{\text{slip}} \) velocity, then transitioned into bursting-holding or bursting-coasting techniques until failure, as was noted in the round goby \((\text{Tierney et al.} 2011)\). The significant decrease in failure velocity \( (U_{\text{burst}}) \) over repeated CAT trials suggests the use of anaerobic metabolism in RMS consistent with patterns in repeat swim trials on other species. In a series of repeat CAT trials, European Sea Bass \((\text{Dicentrarchus labrax})\) exhibited the highest performance in their first CAT trial then subsequently declined \((\text{Marras et al.} 2010)\). Similarly, repeated \( U_{\text{crit}} \) tests on Chinese Sturgeon \((\text{Acipenser sinensis})\) significantly declined over a series of four tests \((\text{Cai et al.} 2014)\). Simultaneously, white ‘anaerobic’ muscle fibres contributed to swimming at lower velocities over repeated trials \((\text{Cai et al.} 2014)\). During anaerobic metabolism, activity is largely fuelled by glycogen resulting in depleted energy stores and accumulation of waste products such as lactate \((\text{Milligan} 1996)\). Increased acidity from waste build up in tissues can impair oxygen delivery to muscles and inhibit aerobic respiration \((\text{Randall et al.} 1987)\). Recovery periods, that can last up to 12 h in some species, replenish energy reserves and remove waste products \((\text{Milligan} 1996; \text{Kieffer} 2000)\). Since our study allowed RMS to rest for only 30 min between \( U_{\text{burst}} \) tests, fish likely had lower energy reserves and higher waste accumulation as trials proceeded, hindering their ability to perform to the same level in subsequent trials. As bursting ability has been associated with predator evasion \((\text{Webb} 1986; \text{Langerhans et al.} 2004)\), reduced \( U_{\text{burst}} \) of RMS in subsequent tests suggests a hampered ability to repeatedly escape predators and other stressors. Alternatively, \( U_{\text{slip}} \) was not influenced by CAT trial number, indicating the use of aerobic respiration, which can sustain prolonged and repeated activity to the same level \((\text{Hammer} 1993)\). \text{Marras et al.} \((2010)\) used the gait-transition speed \( (U_{\text{gt}}) \), a similar metric to our \( U_{\text{slip}} \) to delineate the transition from aerobic to anaerobic metabolism. As seen in our study, \( U_{\text{gt}} \) was repeatable between trials and individuals \((\text{Marras et al.} 2010)\). Consequently, the \( U_{\text{slip}} \) velocity may provide important conservation linkages to RMS microhabitat selection. Similarly to Mottled Sculpin \((\text{Facey and Grossman} 1992)\), RMS may select microhabitat with velocities far below their swimming performance abilities to remain within the scope of aerobic functioning and limit the need to switch to anaerobic respiration.

At an individual level, morphological characteristics helped explain intraspecific differences in swimming and station-holding performance. While previous studies have linked increases in body size to aerobic swimming performance \((\text{Hammer} 1993)\), burst anaerobic swimming can be propelled by caudal morphology in Gasterosteids \((\text{Webster et al.} 2011)\) and Embiotocids \((\text{Drucker} 1996)\). Consistently, our study demonstrated the importance of caudal characteristics on both \( U_{\text{burst}} \) and \( U_{\text{slip}} \) metrics of RMS swimming and station-holding performance. Fish with wider and longer caudal peduncles were able to hold station against faster velocities resulting in both higher \( U_{\text{burst}} \) and \( U_{\text{slip}} \) velocities for these individuals. Moreover, caudal morphological characteristics can be shaped by flow velocities in Salmonids suggesting caudal morphology can respond to different hydrologic regimes \((\text{Imre et al.} 2002; \text{Peres-Neto and Magnan} 2004)\). Not only has the caudal region been implicated in burst swimming ability, \text{Carlson and Lauder (2010)} found that caudal morphology and position were important for station-holding postures in two species of darter \((\text{Etheostomatinae})\). Gait transitions leading into anaerobic burst swimming are often associated with the addition of caudal propulsion \((\text{Drucker} 1996; \text{Svensen et al.} 2010; \text{Webster et al.} 2011)\) as the axial skeleton contains more muscle tissue than paired fins \((\text{Webb} 1998)\). In benthic fish, such as sculpins, anaerobic swimming is often preceded by station-holding, rather than steady aerobic swimming \((\text{Tierney et al.} 2011)\) indicating a gait transition directly from holding to swimming. For these fish, morphological characteristics associated with anaerobic swimming are, therefore, central to the overall scope of swimming potential.

Finally, our study provided the first description of RMS resting metabolic rates. Although sample sizes were too small to compare significant differences between populations, fish from the North Milk River were detected more consistently than other populations despite the larger size of fish from the Flathead River. Due to the large-scale augmentation in the North Milk River, altered environmental conditions such as dissolved oxygen and temperature \((\text{Chabot et al.} 2016)\) may impact the physiological fitness of RMS from this population. We suggest finer scale studies to assess the physiological cost of river augmentation on RMS using a smaller respirometer.

**Conclusion**

This study is the first to describe the swimming ability of RMS, a newly identified and threatened benthic fish species in Canada. While we found differences in the \( U_{\text{burst}} \) between the southern Albertan populations and the Flathead River, broad-scale hydrologic regime did not influence the swimming or station-holding ability of this species. At an individual scale, morphological results indicated a selection of
characteristics central to burst swimming. Further studies are required to determine the metabolic cost of flow augmentation on RMS for their long-term conservation.

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References

Akaike H (1992) Information theory and an extension of the maximum likelihood principle. In Kotz S, Johnson NL, eds, Breakthroughs in Statistics: Foundations and Basic Theory. Springer, New York, NY, pp 610–624.

Bailey JE (1952) Life history and ecology of the sculpin Cottus bairdi punctulatus in southwestern Montana. Copeia 4: 243–255.

Bateman DS, Li HW (2001) Nest site selection by reticulate sculpin in two streams of different geologies in the central coast range of Oregon. Trans Am Fish Soc 130: 823–832.

Beamish FWH (1978) Swimming capacity. In Hoar WS, Randall DJ, eds, Fishes: an introduction for biologists. Academic Press Inc., New York, pp 101–187.

Bedrick EJ, Tsai CL (1994) Model selection for multivariate regression in small samples. Biometrics 50: 226–231.

Bradley C, Smith DG (1984) Meandering channel response to altered flow regime: Milk River, Alberta and Montana. Water Resour Res 20: 1913–1920.

Brett JR (1964) The respiratory metabolism and swimming performance of young sockeye salmon. J Fish Board Can 21: 1183–1226.

Burnham KP, Anderson RP (2004) Multimodel inference: understanding AIC and BIC in model selection. Social Methods Res 33: 261–304.

Cai L, Chen L, Johnson D, Gao Y, Mandal P, Fang M, Tu Z, Huang Y (2014) Integrating water flow, locomotor performance and respiration of Chinese sturgeon during multiple fatigue-recovery cycles. PLoS One 9: 1–6.

Canadian Dam Association (2003) Dams in Canada. http://www.imis100ca1.ca/cda/Main/Dams_in_Canada/Dams_in_Canada/CDA/Dams_In_Canada.aspx?hkey=2f98be19-d947-4aa2-9b2e-16a5202fe919 (last accessed 15 March 2017).

Carlson RL, Lauder GV (2010) Living on the bottom: kinematics of benthic station-holding in darter fishes (Percidae: Etheostomatinae). J Morphol 271: 25–35.

Chabot D, McKenzie DJ, Craig JF (2016) Metabolic rate in fishes: definitions, methods and significance for conservation physiology. J Fish Biol 88: 1–9.

Chow VT (1959) Open-Channel Hydraulics. McGraw-Hill, New York, pp 680.

Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 68: 893–905.

COSEWIC (2005) COSEWIC Assessment and Status Report on the Sculpin (St. Mary and Milk River Populations) Cottus sp. in Canada. Ottawa.

Drucker EG (1996) The use of gait transition speed in comparative studies of fish locomotion. Am Zool 36: 555–566.

Dudgeon D, Arthington AH, Gessner MO, Kawabata ZJ, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard A-H, Soto D, Stiassny MLJ, et al. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biol Rev Camb Philos Soc 81: 163–182.

Facey DE, Grossman GD (1990) The metabolic cost of maintaining position for four North American stream fishes: effects of season and velocity. Physiol Zool 63: 757–776.

Facey DE, Grossman GD (1992) The relationship between water velocity, energetic costs, and microhabitat use in four North American stream fishes. Hydrobiologia 239: 1–6.

Finger TR (1982) Interactive segregation among three species of sculpins (Cottus). Copeia 1982: 680–694.

Greenberg LA (1991) Habitat use and feeding behavior of thirteen species of benthic stream fishes. Environ Biol Fishes 31: 389–401.

Hammer C (1995) Fatigue and exercise tests with fish. Comp Biochem Physiol Physiol 112: 1–20.

Harmon TS (2009) Methods for reducing stressors and maintaining water quality associated with live fish transport in tanks: a review of the basics. Rev Aquac 1: 58–66.

Haro RJ, Brusven MA (1994) Effects of cobble embeddedness on the microdistribution of the sculpin Cottus beldingi and its stonefly prey. Gr Basin Nat 54: 64–70.

Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models.

Hynes HBN (1970) The Ecology of Running Waters. Liverpool University Press, Liverpool.

Imre I, McLaughlin RL, Noakes DIL (2002) Phenotypic plasticity in brook charr: changes in caudal fin induced by water flow. J Fish Biol 61: 1171–1181.
Jelts HL, Walsh SJ, Burkhead NM, Contreras-Balderas S, Diaz-Pardo E, Hendrickson DA, Lyons J, Mandrak NE, McCormick F, Nelson JS (2008) Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries* 33: 372–407.

Jobling M (1981) The influence of feeding on the metabolic rate of fishes: a short review. *J Fish Biol* 18: 385–400.

Jowett IG (1993) A method for objectively identifying pool, run, and riffle habitats from physical measurements. *New Zealand Journal of Freshwater Research* 27: 241–248.

Kieffer JD (2000) Limits to exhaustive exercise in fish. *Comp Biochem Physiol* 126: 161–179.

Kieffer JD, Currie S, Tufts BL (1994) Effects of environmental temperature on the metabolic and acid-base responses of rainbow trout to exhaustive exercise. *J Exp Biol* 194: 299–317.

Langerhans RB (2008) Predictability of phenotypic differentiation across flow regimes in fishes. *Integr Comp Biol* 48: 750–768.

Langerhans RB, Layman CA, Shokrollahi AM, DeWitt TJ (2004) Predator-driven phenotypic diversification in *Gambusia affinis*. *Evolution (NY)* 58: 2305–2318.

Lehner B, Liermann CR, Revenga C, Vörösmarty C, Fekete B, Crouzet P, Döll P, Endeljan M, Frenken K, Magome J, et al. (2011) High-resolution mapping of the world’s reservoirs and dams for sustainable river-flow management. *Front Ecol Environ* 9: 494–502.

Lucas MC, Baras E, Thom TJ, Duncan A, Slavik O (2001) *Migration of Freshwater Fishes*. Wiley Online Library, Oxford.

Lytle D, Poff N (2004) Adaptation to natural flow regimes. *Trends Ecol Evol* 19: 94–100.

Marras S, Claireaux G, McKenzie DJ, Nelson JA (2010) Individual variation in aerobic and anaerobic swimming performance of European sea bass, *Dicentrarchus labrax*. *J Exp Biol* 213: 26–32.

Milligan CL (1996) Metabolic recovery from exhaustive exercise in rainbow trout. *Comp Biochem Physiol* 113: 51–60.

Nelson JA (1990) Muscle metabolite response to exercise and recovery in Yellow Perch (*Perca flavescens*)—comparison of populations from naturally acid and neutral waters. *Physiol Zool* 63: 886–908.

Nelson JA, Gotwalt PS, Reidy SP, Webber DM (2002) Beyond Ucrit: matching swimming performance tests to the physiological ecology of the animal, including a new fish ‘drag strip’. *Comp Biochem Physiol* 133: 289–302.

Nelson JA, Gotwalt PS, Simonetti CA, Snodgrass JW (2008) Environmental correlates, plasticity, and repeatability of differences in performance among blacknose dace (*Rhinichthys atratus*) populations across a gradient of urbanization. *Physiol Biochem Zool* 81: 25–42.

Oksanen J, Kindt R, Legendre P, O’Hara B, Stevens MHH, Oksanen MJ. Suggests MASS (2007) The vegan package. *Community ecology package* 10: 631–637.

Peres-Neto PR, Magnan P (2004) The influence of swimming demand on phenotypic plasticity and morphological integration: a comparison of two polymorphic char species. *Oecologia* 140: 36–45.

Pinheiro J, Bates D, DebRoy S, Sarkar D (2014) R Core Team (2014) nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-117.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow regime. *Bioscience* 47: 769–784.

R Core Team (2015) *R: A Language and Environment for Statistical Computing*. Vienna, Austria; 2014.

Randall DJ, Mense D, Boutilier RG (1987) The effects of burst swimming on aerobic swimming in chinook salmon (*Onchorhyncus tshawytyscha*). *Mar Behav Physiol* 13: 77–88.

Reidy SP, Nelson JA, Tang Y, Kerr SR (1995) Post-exercise metabolic rate in Atlantic cod and its dependence upon the method of exhaustion. *J Fish Biol* 47: 377–386.

Reidy SP, Kerr SR, Nelson JA (2000) Aerobic and anaerobic swimming performance of individual Atlantic cod. *J Exp Biol* 203: 347–357.

Ricciardi A, Rasmussen JB (1999) Extinction rates of North American freshwater fauna. *Conserv Biol* 13: 1220–1222.

Rice W (1989) Analyzing tables of statistical test. *Evolution (NY)* 43: 223–225.

Ruppert J, James PMA, Taylor EB, Rudolfsen T, Veillard M, Davis CS, Watson D, Poesch MS (2017) Riverscape genetic structure of a threatened and dispersal limited freshwater species, the Rocky Mountain Sculpin (*Cottus sp.*). *Conserv Genet* doi:10.1007/s10592-017-0938-6.

Sugiura N (1978) Further analysis of data by Akaike’s information criterion and finite corrections. *Commun Stat* 7: 13–26.

Swensson JC, Tudorache C, Jordan AD, Steffensen JF, Arestrup K, Domenici P (2010) Partition of aerobic and anaerobic swimming costs related to gait transitions in a labriform swimmer. *J Exp Biol* 213: 2177–2183.

Tierney KB, Kasurak AV, Zielinski BS, Higgins DM (2011) Swimming performance and invasion potential of the round goby. *Environ Biol Fishes* 92: 491–502.

Vogel S (1994) *Life in Moving Fluids: The Physical Biology of Flow*, Ed 2. Princeton University Press, Oxford, England.

Water Survey of Canada (2015) Wateroffice: Historical Hydrometric Data. https://wateroffice.ec.gc.ca/mainmenu/historical_data_index_e.html.

Webb PW (1986) Effect of body form and response threshold on the vulnerability of four species of teleost prey attacked by large-mouth bass (*Micropterus salmoides*). *Can J Fish Aquat Sci* 43: 763–771.

Webb PW (1989) Station-holding by three species of benthic fishes. *J Exp Biol* 145: 303–320.
Webb PW (1998) Swimming, Second ed. Edition. The Physiology of Fishes. CRC Press, Michigan, USA.

Webb PW, Gerstner CL, Minton ST (1996) Station-holding by the mottled sculpin, Cottus bairdi (Teleostei: Cottidae), and other fishes. Copeia 1996: 488–493.

Webster MM, Atton N, Hart PJB, Ward AJW (2011) Habitat-specific morphological variation among threespine sticklebacks (Gasterosteus aculeatus) within a drainage basin. PLoS One 6. doi:10.1371/journal.pone.0021060.

Zuur AF (2010) AED: Data Files used in Mixed Effects Models and Extensions in Ecology with R.

Zuur AF, Leno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Public Health.