Length at age of mottled sculpin in a regulated high-elevation river and comparison of length at age of Cottidae between Blue River, Colorado, and other populations

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Abstract: We characterized length-at-age relationships of mottled sculpin (*Cottus bairdii*) in the Lower Blue River, a regulated high-elevation river in the southern Rocky Mountain region, Colorado, USA. Sculpin were collected in May, August, and October in a dry year and a wet year, and sagittal otoliths were sectioned for age estimation. Age-1 fish grew rapidly followed by slowed annual growth and a relatively long life span, with the oldest individual inferred to be 9 years old at 119 mm in total length. These patterns might be due to the altered flow regime characterized by hypolimnetic dam water release, resulting in suboptimal summer water temperatures for growth, oligotrophic conditions, and low abundance of prey resources. When comparing length at age between mottled sculpin found in the Blue River and other Cottidae in separate systems, we found that mottled sculpin in the Blue River have much more rapid early life growth compared to other cottids. Our study reports length-at-age relationships of a small-bodied species in an anthropogenically altered river, and additional research is warranted to compare their life history characteristics over space and time.

Keywords: *Cottus*, dams, flow regime, growth, life history, otolith

Main text: Fish age and length information is routinely used to characterize life history patterns, quantify anthropogenic impacts on fish populations, and evaluate success of fisheries management activities (Quist & Isermann, 2017). Age is estimated lethally and non-lethally, and otoliths are the most common structural part used for lethal age inferences (Maceina et al., 2007). As an index of body growth rates, length-at-age data are available for many freshwater fish species, but data on small-bodied non-game species are underrepresented in the literature (Burbank et al., 2021; Saddlier et al., 2013). Here, we report length-at-age information on mottled sculpin (*Cottus bairdii*) in a regulated high-elevation river characterized by oligotrophic conditions and suboptimal temperatures for growth. We also compare the length at age of our Blue River mottled sculpin to other Cottidae in North America. A recent molecular study showed a spatial structure in the mottled sculpin complex in the western USA, and our sculpin may comprise Colorado sculpin (*Cottus punctulatus*) and/or Eagle River sculpin (*Cottus annae*) (Young et al., 2022). In this paper, we refer to our fish as mottled sculpin, while acknowledging the taxonomic uncertainty.

Sculpins are widely distributed in clear, cold streams and rivers in the northern hemisphere. Maximum body size of lotic sculpins depends on environmental conditions, ranging 79-140 mm (Grossman et al., 2002; Selgeby, 1988). Their age information is limited, but maximum age reported ranges 5-8 years old among locations (Bailey, 1952; Grossman et al., 2002; Meyer et al., 2008). Much of the limited knowledge comes from sculpin populations in free-flowing rivers. In hydropeaking rivers, slimy sculpin (*Cottus cognatus*) grew faster than in free-flowing rivers due presumably to more abundant food resources (Bond et al., 2016; Kelly et al., 2016), a condition which does not apply to all regulated rivers (Poff & Hart, 2002).

Demographic and life history responses to altered flow regimes are poorly understood but are essential to mechanistic understanding of fish-flow relationships (Freeman et al., 2022).

Our study was conducted in the Lower Blue River, a regulated river in the southern Rocky Mountain region, Colorado, USA. The Lower Blue River is a tributary to the Colorado River and is regulated by two major hypolimnetic-release dams: Dillon Reservoir upstream (surface area = 13.1 km^2 and volume = 0.32 km^3) and Green Mountain Reservoir downstream (surface area = 8.6 km^2 and volume = 0.19 km^3). They provide water for agricultural irrigation, urban and rural communities, and hydroelectric power generation. The flow regime of the Lower Blue River is characterized by low-magnitude flows during snowmelt and peak flows in late summer through fall, accompanied by cold water temperatures in summer (Figure 1). The flow and thermal regimes of the Lower Blue River deviate greatly from those of a free-flowing reference river in the region, whose flow peaks during snowmelt (Figure 1). The dams have trapped nutrients, resulting in oligotrophic conditions downstream (Bauch et al., 2014). Our five study sites (~100 m long each; mean wetted width = 35 m and range = 30-39 m) were located downstream of the Green Mountain Reservoir and ranged 2,280-2,307 m in elevation. The uppermost site (39°54’50”N 106°20’19”W) was located approximately 4.8 km downstream of the Green Mountain Reservoir and was 3.2 km upstream of the lowermost site (39°56’36”N 106°21’25”W). Mottled sculpin and non-native brown trout (*Salmo trutta*) predominated fish assemblages at our study sites.

Mottled sculpin were collected using backpack electrofishing units (Model LR-24, Smith-Root Inc., Vancouver, WA, USA) at the five study sites in May, August, and October 2022-2023 as part of a larger study to characterize fish populations and river food webs (Platis et al., 2024). The size ranges for mottled sculpin were pre-defined by 10-mm increments and we attempted to collect individuals from all length increments evenly to represent the study population. We sacrificed 15 individuals ≥ 80 mm in total length (TL) per site and sampling occasion. In 2023, we collected additional samples of mottled sculpin < 80 mm TL to characterize length frequency distributions more fully and increase accuracy of our age estimation. A total of 450 individuals were collected in both study years. Our study took place in a dry year (2022) and wet year (2023) with markedly different hydrographs based on the US Geological Survey gage below Green Mountain Reservoir (#09057500) (Figure 1). Accordingly, we compared length-at-age from May through October between the two years to examine whether flows affected mottled sculpin growth.

In the laboratory, sagittal otoliths were removed for age determination. Each otolith was dried in resin for 72 hours at 60 °C and was sectioned using an isomet low speed saw (Buehler, Lake Bluff, IL, USA). Otoliths were aged by two independent readers (ALB and TRH) who counted the number of annuli (i.e., pairs of opaque and translucence bands) under a microscope with 20-30x magnification. When the readers disagreed on estimated ages, they discussed the samples to reach a consensus. If no agreement was reached, the sample was removed from the data set, resulting in 379 individuals (84% agreement) for subsequent analysis (Appendix S1). Because age-1 individuals were distinguishable based on length-frequency histograms in 2023, we used them as a baseline to determine annuli patterns. We considered that fish became one year older on January 1st.

We tested whether total length of mottled sculpin depended on age, month, year, site, and an interaction between age and year, using a Type-III analysis of variance (ANOVA). The main effect of month and the interactive effect between age and year were of the greatest interest because the former quantified mottled sculpin growth from May through October and the latter evaluated whether length-at-age relationships differed between dry (2022) and wet (2023) years. The ANOVA was based on individuals aged 2-5 because these age classes were present in all months of both years. When significant effects were detected, we used a post-hoc Tukey's Honestly Significant Different (HSD) test to evaluate which pairwise comparisons were responsible for the significant effects. We characterized von Bertalanffy growth functions using the FSA package (Ogle et al., 2023). The von Bertalanffy growth function was expressed as: $E[L|t] = L_\infty\left(1 - e^{-K(t-t_0)}\right)$, where $E[L|t]$ was the average total length (mm) at age t, L_∞ was the asymptotic average total length, K was the growth rate coefficient, and t_0 was the hypothetical age when the average total length was zero. We pooled data across months, years, and sites because data on age-1 individuals were available only in 2023 and age did not depend on site and month. We explored whether pooling across years influenced the estimates, and von Bertalanffy growth functions were similar between 2023 alone and both years combined based on overlaps of 95% confidence intervals in parameters (Appendix S2). Data management and analysis were implemented in R Program (R Core Team, 2024), and statistical significance was evaluated at $\alpha = 0.05$.

Additionally, we compared the length at age of our mottled sculpin to other populations of Cottidae in North America. We collected four other von Betralanffy growth functions from existing data on different members of the Cottidae family. Cottidae used for comparison included female mottled sculpin in the Coweeta Creek drainage, North Carolina (Grossman et al., 2002), Wood River Sculpin in Idaho (Meyer et al., 2008), Rough Sculpin in California (Daniels, 1987), and Rocky Mountain Sculpin (Cottus sp.) in Alberta, Canada (Young & Koops, 2013).

We found that 94% of individuals ≥ 80 mm TL were estimated to be 2-5 years old in 2022 and 95% in 2023, but a single individual at 119 mm in total length was estimated to be 9 years old in the Lower Blue River (Figure 2a). Based on a Type-III ANOVA test, total length of age 2-5 mottled sculpin differed significantly by age (F = 152.1; P < 0.0001) but not by month (F = 2.0; P = 0.14), year (F = 0.4; P = 0.55), or site (F = 0.3; P = 0.89) (Figure 2b). Total length was significantly different between all pairwise comparisons of age 2-5 (Tukey's HSD test). Age-at-length relationships were similar between months, indicating that growth of mottled sculpin was limited from May through October (Figure 2b). However, age-1 mottled sculpin grew during this period in 2023, showing more rapid growth rates initially followed by slower growth rates at older ages. The interactive effect between age and year significantly affected total length (F = 4.2; P = 0.006). However, a Tukey's HSD test showed that this was due only to seemingly subtle biological differences in TL of age 3 fish (mean = 94 mm in 2022 and 100 mm in 2023), showing that contrasting flow conditions in the two study years had limited effects on body growth from May through October. A von Bertalanffy growth function based on 2022 and 2023 data combined was characterized as: $E[L|t] = 115.44\,(1 - e^{-0.67(t+0.02)})$ (Figure 2b; Appendix S2).

Our length-at-age data show that mottled sculpin in Blue River are characterized by a rapid growth in age 1 followed by slow growth rates in age 2-5, and then by negligible growth in older fish, a pattern reported similarly for mottled sculpin in the southeastern USA (Grossman et al., 2002). We inferred that our sculpin lived up to nine years old, the oldest specimen known in riverine cottids in the literature to our knowledge (Bailey, 1952; Grossman et al., 2002; Meyer et al., 2008). We think that the long life span of our sculpin might be due to flow regulation resulting in suboptimal water temperature and oligotrophic conditions. Specifically, water temperature for the most part remained colder than the optimal water temperature range for mottled sculpin's somatic growth (12-16 °C: Kanno et al., 2023; Figure 1) due to the altered flow regime including the release of hypolimnetic water from Green Mountain Reservoir located upstream of our study area. In addition, the reservoir has contributed to an oligotrophic condition which affects production of benthic macroinvertebrates (Bauch et al., 2014), the primary food resource for sculpin in Blue River (Platis et al., 2024). Intriguingly, faster growth rates of slimy sculpin were reported in hydro-peaking rivers relative to their free-flowing reference rivers, where water temperatures were higher (13-27 °C in summer) in both types of rivers than our study (Bond et al., 2016; Kelly et al., 2016). Our results along with these previous studies suggest that fish growth responses to flow regulation are not uniform and depend on physical and operational characteristics of dams.

Our comparison of the length at age of our mottled sculpin to other Cottidae in North America reveals that our mottled sculpin are characterized by more rapid early life growth than other Cottidae are (Figure 3.). This could be a response to the environmental conditions brought upon them by the dam and its operation. It is also possible that our sculpin are in fact Colorado sculpin or Eagle River sculpin (Young et al., 2022) which could explain this departure from slow early life growth seen in the other Cottidae. Further research on why sculpin in the Blue River exhibit rapid early life growth is needed, and will be very beneficial in helping to determine if they are in fact a new species of Cottidae.

Length-at-age relationships did not markedly differ between dry (2022) and wet (2023) years, and age-specific body size was similar from May through October in each year. Despite contrasting flow patterns, temperatures were similar between the two study years in terms of magnitude and seasonal variation, and mottled sculpin experienced suboptimal temperatures for growth in both years (Figure 1). This suggests that temperature may supersede influences of stream hydrography on growth. However, additional investigations are needed to test this hypothesis especially because our sample size was limited to one dry and one wet year. In general, length-at-age data are limited for small-bodied non-game species (Burbank et al., 2021; Saddlier et al., 2013), and our study shows that they provide information on their natural life history and anthropogenic impacts on lotic organisms. In our case, further research should incorporate spatially and temporally replicated samples to evaluate whether the long life span of mottled sculpin are attributable to flow regulation or reflect natural life history patterns common to high-elevation streams.

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Figure Captions.

Figure 1. Water temperature (a) and flow (b) patterns in the regulated Lower Blue River and an adjacent free-flowing Eagle River, Colorado, USA, in 2022 (dry year) and 2023 (wet year). For Lower Blue River, water temperature was measured hourly using a remote logger at the uppermost of the five study sites and flow data are based on the US Geological Survey gage below Green Mountain Reservoir (#09057500) located approximately 4.8 km upstream of the uppermost site. For Eagle River, temperature and flow data were based on the US Geological Survey gage #394220106431500. The optimal temperature range for growth (12–16 °C) was based on a mark-recapture study of mottled sculpin in a small wadable stream in South Carolina (Kanno et al., 2023).

Figure 2. An otolith of an individual estimated to be 9 years old (scale bar = 1 mm) (a), and length-at-age relationships of mottled sculpin in the Lower Blue River by sampling month and year with von Bertalanffy growth curves shown in black solid lines (b). In 2022 (a dry year), we collected mottled sculpin over 80 mm in total length. In 2023 (a wet year), we collected mottled sculpin of all sizes encountered. Mean age-specific total length values are shown by dots with 25^{th}–75^{th} percentiles (thick lines) and 2.5^{th}–97.5^{th} percentiles (thin lines).

Figure 3. Von Bertalanffy growth curves of multiple different Cottidae, including mottled sculpin in the Blue River (Hackett 2024), female mottled sculpin in North Carolina (Grossman et al. 2002), wood river sculpin in Idaho (Meyer et al. 2008), Rocky Mountain Sculpin (Cottus sp.)

in Alberta, Canada (Young & Koops 2013), and Rough Sculpin in California (Daniels 1987). Each curve ends at the maximum age captured in the corresponding study.

Figure 1.

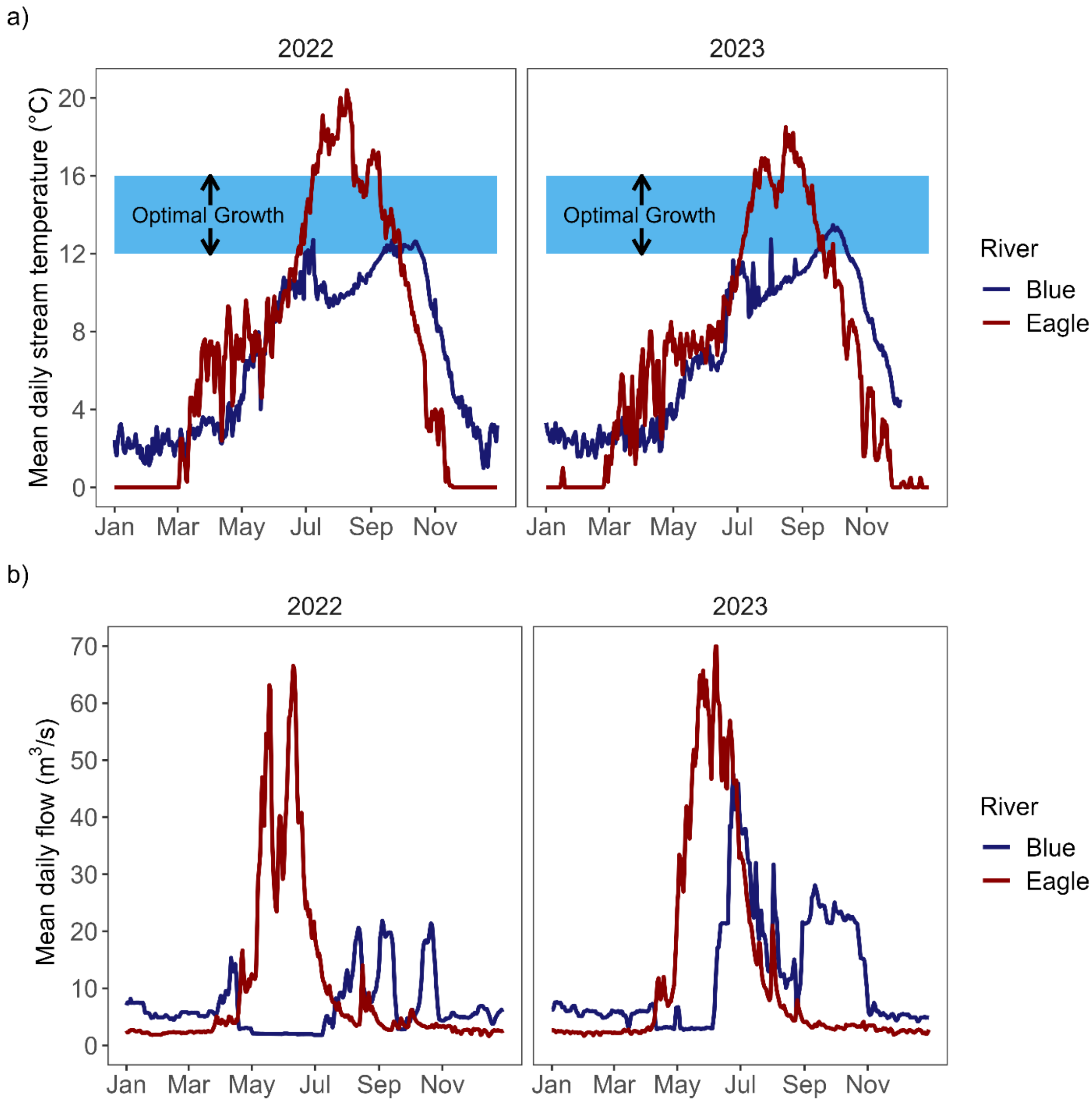
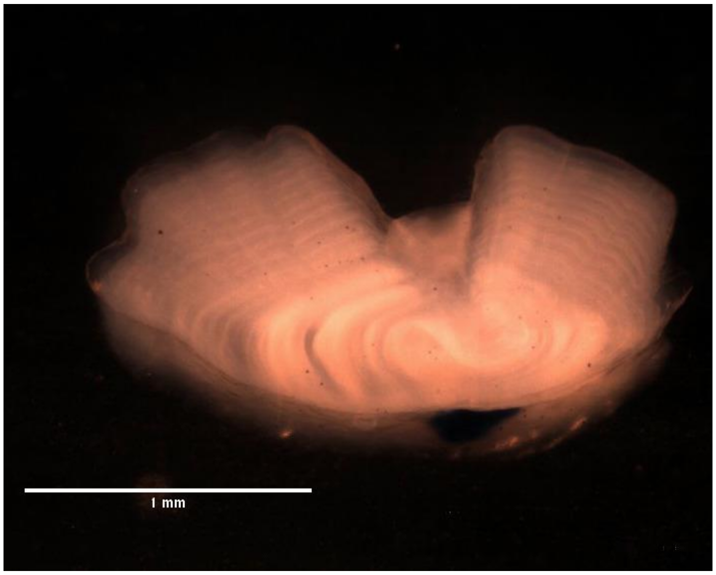

a)
2022
2023
Mean daily stream temperature (°C)
0
4
8
12
16
20
Optimal Growth
Optimal Growth
Jan
Mar
May
Jul
Sep
Nov
River
Blue
Eagle
b)
2022
2023
Mean daily flow (m³/s)
0
10
20
30
40
50
60
70
Jan
Mar
May
Jul
Sep
Nov
River
Blue
Eagle

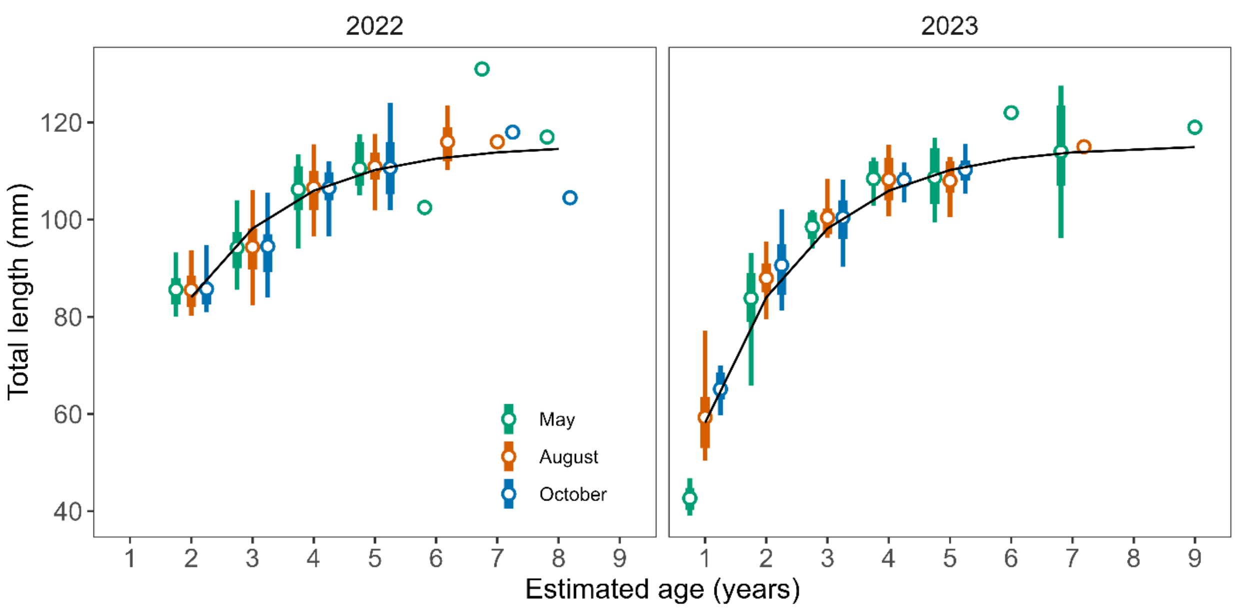
Figure 2.

a)



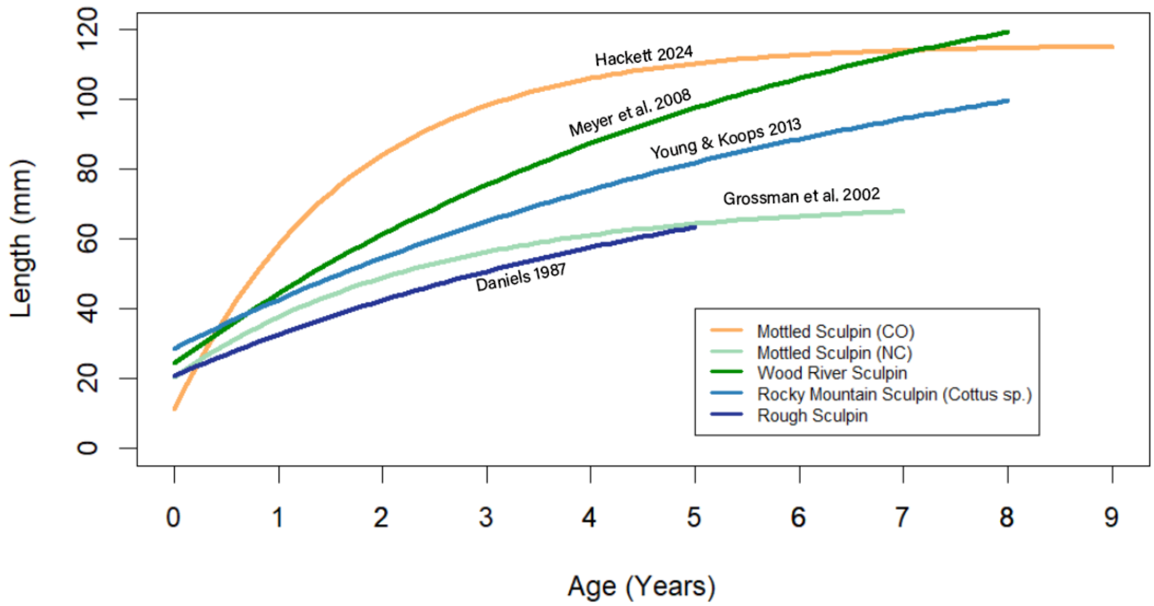
1 mm

b)



2022
2023
Total length (mm)
120
100
80
60
40
1
2
3
4
5
6
7
8
9
Estimated age (years)
May
August
October

Figure 3.


Hackett 2024
Meyer et al. 2008
Young & Koops 2013
Grossman et al. 2002
Daniels 1987
Mottled Sculpin (CO)
Mottled Sculpin (NC)
Wood River Sculpin
Rocky Mountain Sculpin (Cottus sp.)
Rough Sculpin
Length (mm)
0
20
40
60
80
100
120
0
1
2
3
4
5
6
7
8
9
Age (Years)