



Length–weight relationships for 14 cypriniform freshwater fish species (Actinopterygii) from the Upper Mississippi River Basin

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Abstract

Here, we use long-term monitoring data from fisheries surveys across six Mississippi River reaches spanning > 750 river miles (>1200 km) to estimate length–weight relationships (LWRs) for 14 cypriniform fishes native to the Upper Mississippi River system. Relationships between \log_{10} -transformed values of fish total weights [g] and total lengths [cm] were analyzed using standard linear modeling and hypothesis-testing approaches. Focal species included four North American minnows in family Leuciscidae [*Cyprinella lutrensis* (Baird et Girard, 1853), *Notropis atherinoides* Rafinesque, 1818, *Notropis hudsonius* (Clinton, 1824), and *Paranotropis volucellus* (Cope, 1865)] and 10 suckers in the family Catostomidae [*Carpionodes carpio* (Rafinesque, 1820), *Carpionodes cyprinus* (Lesueur, 1817), *Carpionodes velifer* (Rafinesque, 1820), *Cycleptus elongatus* (Lesueur, 1817), *Ictiobus bubalus* (Rafinesque, 1818), *Ictiobus niger* (Rafinesque, 1819), *Moxostoma anisurum* (Rafinesque, 1820), *Moxostoma carinatum* (Cope, 1870), *Moxostoma erythrurum* (Rafinesque, 1818), and *Moxostoma macrolepidotum* (Lesueur, 1817)]. Congruent with previous studies, estimates of parameter *b* were consistent with isometric or weakly allometric growth and ranged from 2.834 (*P. volucellus*) to 3.351 (*C. elongatus*), while estimates of parameter *a* ranged from 0.002 (*C. elongatus*) to 0.014 (*C. velifer*).

Keywords

fisheries, freshwater fishes, length–weight relationships, Midwestern USA, Mississippi River

Introduction

The Upper Mississippi River (UMR) is a large (>490 000 km²) and complex floodplain river drainage and represents amongst the most culturally, economically, and biologically significant rivers in North America (Carlson et al. 1995; Black et al. 1999; Weitzell et al. 2003; Gaffigan et al. 2021). The UMR system includes Mississippi River reaches with navigable channels north of Cairo, IL (37°00'18.6"N, 89°10'34.9"W; i.e., confluence with the Ohio River), the Illinois River and Waterway,

as well as the St. Croix, Minnesota, Black, and Kaskaskia rivers (Fig. 1; Gaffigan et al. 2021). With ~190 fish species, including several species of Threatened, Endangered or Special Concern status [e.g., *Miniellus topeka* (Gilbert, 1884), federal status: Endangered], the freshwater fish assemblage of the UMR is diverse and ecologically unique and makes up around ~17% of the continental freshwater fish fauna (Burr and Page 1986; Pitlo et al. 1995; Page and Burr 2011; JCB, unpublished results). The UMR also boasts a diverse collection of mussel, amphibian, bird, and mammal assemblages that

are prioritized for conservation (Weitzell et al. 2003). Not surprisingly, given its biodiversity and abundance of natural resources, the UMR has provided for a multitude of human uses historically and today, leading to great benefits, but also to widespread anthropogenic impacts and environmental degradation. For example, while the UMR adds ~US\$1 billion in annual benefits to the national economy through boating, fishing, and other commercial and recreational activities (Gaffigan et al. 2021), the river has also been heavily altered. Navigational infrastructure is extensive, including ~1200 miles (~1900 km) of navigation channels and 37 locks and dams, many of which present at least partial barriers to fish movement (Fremling et al. 1989; but see Tripp et al. 2014). Biotic communities have also become altered by introductions of non-indigenous aquatic species that represent a major threat to native taxa, including zebra mussel, *Dreissena polymorpha* (Pallas, 1771) (Dreissenidae), as well as Asian major carps, such as Bighead Carp, *Hypophthalmichthys nobilis* (Richardson, 1845), and Silver Carp, *Hypophthalmichthys molitrix* (Valenciennes, 1844) (Xenocyprididae).

Many aspects of the UMR freshwater fish fauna have been well studied, including patterns of fish ecology, evolution, distribution, community composition, and fisheries management (e.g., Smith et al. 1971; Pitlo et al. 1995; Mundahl and Simon 1999; Dettmers et al. 2001; Piller et al. 2005; Chick et al. 2006; Bessert and Ortí 2008; Bart et al. 2010; Ardren et al. 2022). Indeed, the need for fisheries research in the UMR was realized by Smith (1949) and has since had a longstanding history, including recent studies of relevance to natural resource management and ecosystem restoration (e.g., Crimmins et al. 2015). Nevertheless, the basic ecology of UMR fishes remains incompletely characterized in many areas that have received only sporadic research attention, including length–weight relationships (LWRs; Froese 2006), body condition, and functional ecology of species in local ecosystems (e.g., Garvey et al. 2010). In the case of LWRs, understanding how fish weight changes as a function of body size provides critical information for comparing the condition of individuals and populations, calculating growth rates, imputing missing weight or length values, estimating length at first maturity and building food-web models of ecosystems (e.g., Froese 2006; Jellyman et al. 2013; Heymans et al. 2016; Hashiguti et al. 2019; Bagley et al. 2022).

In this study, we describe LWRs for 14 minnow and sucker species from the ray-finned fish order Cypriniformes that are native to the UMR. We use data from the Upper Mississippi River Restoration–Environmental Management Program (hereafter, the “Long Term Resource Monitoring Program”—LTRMP), a federally supported partnership established through the Environmental Management Program of the 1986 US Water Resources Development Act (WRDA; Garvey et al. 2010). Fishes have been sampled in LTRMP areas since 1989 using variable gear and multi-species approaches for sampling non-game species and species of economic

value (Ickes et al. 2005). Data were from six navigation reaches, five on the Mississippi River and one on the Illinois River (Fig. 1), with thousands of local sampling sites nested within these areas. A previous population ecology study by Kirby and Ickes (2006) examined length–frequency distributions and LWRs for five commercially and recreationally important UMR fish species using LTRMP data collected from 1993 to 2002. They found that LWR model slopes were significantly different by the area over 10 years, overall, and that model slopes were significantly different year to year in *Pomoxis nigromaculatus* (Lesueur, 1829), *Ictalurus punctatus* (Rafinesque, 1818), *Cyprinus carpio* Linnaeus, 1758, and *Sander vitreus* (Mitchill, 1818). However, slope parameters were not significantly different by year in *Sander canadensis* (Griffith et Smith, 1834). Importantly, LWR slope parameters were above 3.0 for all species and years, indicating positive allometric growth, except for slopes between 2.0 and 3.0 during four years for *C. carpio* and the authors hypothesized that the timing of Mississippi River flood events had an important effect on fish productivity and growth (Kirby and Ickes 2006). Whereas previous authors limited their work on UMR fish LWRs to species meeting restrictive sampling criteria, we selected closely related species from order Cypriniformes (Actinopterygii) that have overlapping geographical ranges (Page and Burr 2011), limited LWR data in FishBase (Froese and Pauly 2024) usually from only one or two studies (Table 1), and sufficient sample sizes for LWR parameter estimation.

Materials and methods

The study area included all six LTRMP study reaches, also known as “field stations,” within the UMR (Fig. 1), as follows [given as field station name (associated city, located at or near reach), navigational pool designation, and river mile range]: (1) Field Station 1 (Lake City, MN), Pool 4, river mile 752–797, excluding Lake Pepin; (2) Field Station 2 (Onalaska, WI), Pool 8, river mile 679–703; (3) Field Station 3 (Bellevue, IA), Pool 13, river mile 523–557; (4) Field Station 4 (Brighton, IL), Pool 26, river mile 202–242; (5) Field Station 5 (Jackson, MO), Open River, river mile 1–81; and (6) Field Station 6 (Havana, IL), La Grange Pool, river mile 80–158. Here, all river miles are on the Mississippi River, except for those of the Field Station 6 reach, which are located on the Illinois River (Fig. 1). The LTRMP field stations span a wide range of variation in floodplain characteristics, geomorphology, navigational infrastructure, and land-use change and cover (Kirby and Ickes 2006).

Data were compiled from online servers using the “Query Fisheries Data” function available through the Upper Midwest Environmental Sciences Center website (https://www.umes.usgs.gov/data_library/fisheries/fish1_query.shtml; accessed 29 March 2024). We downloaded gear-specific data for day electrofishing (code “D”), as available for all sample areas, stratum

Table 1. List of 14 cypriniform fish species examined in the presently reported study. Information summarized for our focal species in this Table includes their valid species names (Fricke et al. 2024), standard names, geographical distribution in the Upper Mississippi River system (field stations 1–6), and the prior state of knowledge of their length–weight relationships (LWRs).

Family	Species	AFS standard name (LTRMP fish code)	Geographical distribution (UMR)	Prior LWR number
Leuciscidae	<i>Cyprinella lutrensis</i> (Baird et Girard, 1853)	Red Shiner (RDSN)	4, 5	1
Leuciscidae	<i>Notropis atherinoides</i> Rafinesque, 1818	Emerald Shiner (ERSN)	1–5	1
Leuciscidae	<i>Notropis hudsonius</i> (Clinton, 1824)	Spottail Shiner (STSN)	1, 2, 3, 6	1
Leuciscidae	<i>Paranotropis volucellus</i> (Cope, 1865)	Mimic Shiner (MMSN)	1, 2	1
Catostomidae	<i>Carpiodes carpio</i> (Rafinesque, 1820)	River Carpsucker (RVCS)	1–6	9
Catostomidae	<i>Carpiodes cyprinus</i> (Lesueur, 1817)	Quillback (QLBK)	1–6	2
Catostomidae	<i>Carpiodes velifer</i> (Rafinesque, 1820)	Highfin Carpsucker (HFCS)	1–4, 6	2
Catostomidae	<i>Cycleptus elongatus</i> (Lesueur, 1817)	Blue Sucker (BUSK)	2–6	1
Catostomidae	<i>Ictiobus bubalus</i> (Rafinesque, 1818)	Smallmouth Buffalo (SMBF)	1–6	7
Catostomidae	<i>Ictiobus niger</i> (Rafinesque, 1819)	Black Buffalo (BKBF)	2–6	1
Catostomidae	<i>Moxostoma anisurum</i> (Rafinesque, 1820)	Silver Redhorse (SVRH)	1, 2	2
Catostomidae	<i>Moxostoma carinatum</i> (Cope, 1870)	River Redhorse (RVRH)	1, 2, 5	2
Catostomidae	<i>Moxostoma erythrurum</i> (Rafinesque, 1818)	Golden Redhorse (GDRH)	1–4, 6	3
Catostomidae	<i>Moxostoma macrolepidotum</i> (Lesueur, 1817)	Shorthead Redhorse (SHRH)	1–6	2

AFS = American Fisheries Society (Page et al. 2013, 2023); LTRMP = Long Term Resource Monitoring Program, a federally supported partnership established through the Environmental Management Program of the 1986 US Water Resources Development Act (WRDA; Garvey et al. 2010); “Geographical distribution (UMR)” indicates each species range within the study area, based on our final edited dataset, given by field station numbers 1–6 shown in Fig. 1 (see details in the Materials and methods). Prior LWR number = the number of LWR records available for the species prior to this study, based on FishBase data (Froese and Pauly 2024); and UMR = Upper Mississippi River.

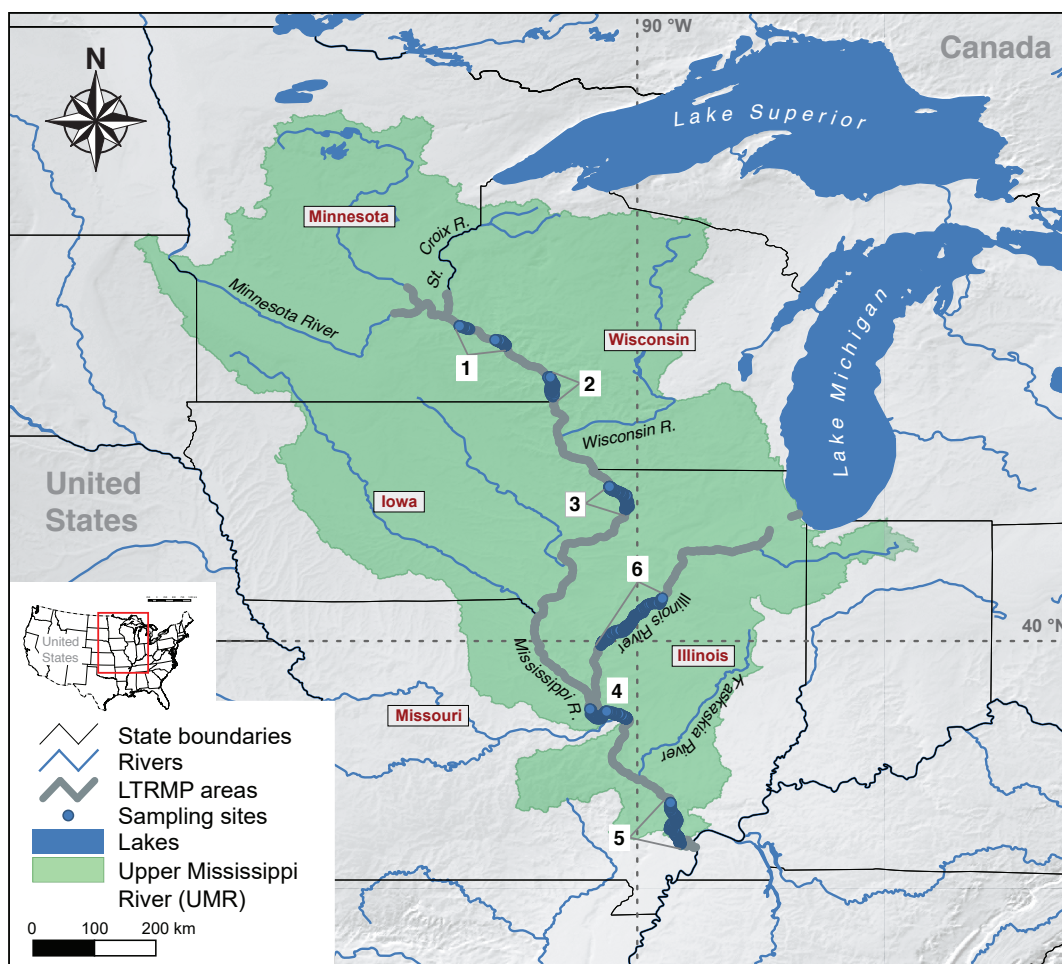


Figure 1. Map of the study area and sampling localities. The Upper Mississippi River (UMR) study area (light green shading) and fish survey localities (blue points) are mapped over major administrative and physiographic features, including States (thin black lines; also labels for those through which the UMR flows), major rivers and lakes (blue lines and shading) and Long Term Resource Monitoring Program (LTRMP) study areas (thick grey lines). The LTRMP study reaches or “field stations” are defined by the sampled areas and labelled 1–6 (for additional details, see text and accompanying Mendeley Data accession, with archived version: <http://dx.doi.org/10.17632/8s7vmk4jct.1>). Several river systems named in the text are labelled in *italics*.

classes (habitats), and time periods (01/01/1989 to 31/10/2022). The daytime boat electrofishing results included 682 982 collection records from all six study reaches over the 34-year period from 1989 to 2022. Data were edited “by eye,” parsed, and summarized in Microsoft Excel. After the removal of unidentified specimens and young-of-the-year fish, records summed to a total catch of ~1.9 million individual fish/groups, representing 159 different species. We filtered these records to length and weight measures for individuals, where group width (“grp_wdth” parameter) was set blank (USGS 2024). From these data, 14 cypriniform fish species were selected for study for reasons outlined above, including sufficient sampling ($n > 30$) for linear modeling analyses. Focal taxa included four North American minnows from family Leuciscidae—*Cyprinella lutrensis* (Baird et Girard, 1853), *Notropis atherinoides* Rafinesque, 1818, *Notropis hudsonius* (Clinton, 1824), and *Paranotropis volucellus* (Cope, 1865)—and 10 suckers in the family Catostomidae—*Carpionodes carpio* (Rafinesque, 1820), *Carpionodes cyprinus* (Lesueur, 1817), *Carpionodes velifer* (Rafinesque, 1820), *Cycleptus elongatus* (Lesueur, 1817), *Ictiobus bubalus* (Rafinesque, 1818), *Ictiobus niger* (Rafinesque, 1819), *Moxostoma anisurum* (Rafinesque, 1820), *Moxostoma carinatum* (Cope, 1870), *Moxostoma erythrurum* (Rafinesque, 1818), and *Moxostoma macrolepidotum* (Lesueur, 1817). Table 1 summarizes the taxonomy, standard names, and prior LWR data for these species. By parsing the data using fish codes in the metadata (USGS 2024; Table 1), we obtained a species-level dataset with length (L) measured as total length (TL) to the nearest millimeter [mm], converted to centimeters [cm] and weight (W ; wet body mass) measured to the nearest 0.01 to 1 gram [g] for each specimen. Standard fish names used in this paper are formally accepted common names, adopted by the American Fisheries Society (Page et al. 2013, 2023).

The LWR was estimated for each species using best practices (e.g., Froese 2006; Froese et al. 2011). First, we performed \log_{10} -transformation of the L and W variables, then we used bivariate scatterplots to identify potential outlier points, which were removed prior to further analyses. Next, regression parameters were estimated by linear modeling analyses using the ordinary least squares (OLS) method, because the expected relationships between the x and y variables are asymmetric for LWRs (Smith 2009) and OLS on \log_{10} -transformed data is the most used model, allowing for comparisons with previous studies. Here, OLS is performed using a linearized form of the LWR model, which is given as:

$$\log(W) = \log(a) + b \log(L)$$

where W is weight, L is length in cm, a is a constant at the y -intercept and b represents the slope, which is also a constant (Clark 1928; Le Cren 1951; Froese 2006). Parameters $\log(a)$, b , and their 95 confidence intervals

(CIs; based on 1999 permutations of the data) were estimated using the PAST (PAleontological STatistics) v.4.0.3 (Hammer et al. 2001). Final a values were derived from model parameters as $a = 10^{\log(a)}$. We tested the null hypothesis of $b = 3$, consistent with “isometric” growth, against the alternative hypothesis $b \neq 3$, indicating allometric growth, using two-tailed t -tests implemented with the pt function in R v.4.3.2 (R Core Team 2023). Statistical significance was assessed using an alpha value of 0.05 for all analyses. Edited (log-transformed) and raw length–weight data and associated collections data used in this study are made available in a Mendeley Data accession (archived version: <http://dx.doi.org/10.17632/8s7vmk4jct.1>).

Results

After data cleaning including removal of $n = 935$ outliers (~12%), the final, edited dataset contained L and W values for $n = 7731$ specimens from the 14 focal cypriniform fish species (Table 1). Intraspecific sample sizes ranged from $n = 21$ to $n = 2813$, with a mean \pm standard error (SE) of 552.2 ± 782.2 individuals (Table 2). Maximum L values ranged from 6.5 cm TL in the Mimic Shiner, *Paranotropis volucellus*, which was the smallest species, to 89.0 cm TL in Black Buffalo, *Ictiobus niger*, the largest species. Similarly, the maximum W values ranged from 2.1 g (0.0021 kg) in *P. volucellus* to 10566.0 g (10.566 kg) in *I. niger* (Table 2).

In all cases, the inferred length–weight relationships were highly statistically significant in OLS regressions ($P < 0.001$), with generally high goodness-of-fit indicated by R^2 statistics for each model (Table 2). The R^2 statistics were above 0.950 for 93% (13) of taxa, indicating that outliers were sufficiently removed prior to analysis such that more than 95% of the variance in fish W values was explained by the independent variable, fish L (Froese 2006). The only species with an R^2 less than 0.950 after outlier removal was *Cyprinella lutrensis*, possibly due to its relatively small sample size or undetected measurement error. Parameter a estimates ranged from 0.00220 in *Cycleptus elongatus* to 0.014 in *Carpionodes velifer*, while parameter b estimates were generally above 3.0 (10/14 or ~71% of cases) and ranged from $b = 2.834$ in *P. volucellus* to $b = 3.351$ in *C. elongatus*. Consistent with allometric growth, the b parameter was significantly different ($P < 0.05$) from $b = 3$ during t -tests for nine species, including *Notropis atherinoides*, *P. volucellus*, *Cyprinus carpio*, *C. elongatus*, *Ictiobus bubalus*, *I. niger*, *Moxostoma anisurum*, *Moxostoma erythrurum*, and *Moxostoma macrolepidotum* (Table 3). Consistent with isometric growth, t -tests of the null hypothesis of $b = 3$ were not significant ($P > 0.05$) in the remaining five species—*C. lutrensis*, *Notropis hudsonius*, *Carpionodes cyprinus*, *C. velifer*, and *Moxostoma carinatum* (Table 3), four of which also had b 95% CIs that included 3.0 (Table 2).

Table 2. Length–weight relationships for 14 cypriniform freshwater fishes from the Upper Mississippi River.

Family	Species	<i>n</i>	Total length (TL) [cm]	Weight [g]	<i>a</i> [95% CIs]	<i>b</i> [95% CIs]	<i>R</i> ²
Leuciscidae	<i>Cyprinella lutrensis</i>	54	4.1–7.2	0.7–3.8	0.009 [0.006, 0.017]	<i>3.112</i> [2.688, 3.413]	0.854
Leuciscidae	<i>Notropis atherinoides</i>	518	2.0–9.2	0.1–5.3	0.009 [0.008, 0.009]	2.894 [2.851, 2.938]	0.974
Leuciscidae	<i>Notropis hudsonius</i>	66	4.4–10.3	0.7–10.4	0.008 [0.007, 0.009]	3.058 [3.002, 3.117]	0.994
Leuciscidae	<i>Paranotropis volucellus</i>	21	2.2–6.5	0.1–2.1	0.010 [0.008, 0.012]	2.834 [2.697, 2.933]	0.992
Catostomidae	<i>Carpiodes carpio</i>	1094	2.9–61.0	0.3–3676.0	0.012 [0.012, 0.013]	3.025 [3.010, 3.041]	0.996
Catostomidae	<i>Carpiodes cyprinus</i>	100	8.5–59.6	8.2–2940.0	0.014 [0.012, 0.018]	2.966 [2.902, 3.026]	0.991
Catostomidae	<i>Carpiodes velifer</i>	53	12.0–51.4	25.0–2072.0	0.014 [0.012, 0.019]	2.970 [2.889, 3.031]	0.993
Catostomidae	<i>Cycleptus elongatus</i>	54	19.5–78.6	44.0–5710.0	0.002 [0.001, 0.005]	3.351 [3.139, 3.450]	0.984
Catostomidae	<i>Ictiobus bubalus</i>	2813	11.3–78.2	26.0–7800.0	0.012 [0.011, 0.012]	3.063 [3.052, 3.073]	0.994
Catostomidae	<i>Ictiobus niger</i>	522	18.1–89.0	85.0–10566.0	0.010 [0.009, 0.011]	3.106 [3.071, 3.138]	0.980
Catostomidae	<i>Moxostoma anisurum</i>	396	7.3–59.9	4.0–2650.0	0.009 [0.009, 0.010]	3.033 [3.006, 3.057]	0.992
Catostomidae	<i>Moxostoma carinatum</i>	81	22.0–71.4	129.8–4205.0	0.008 [0.005, 0.014]	3.098 [2.938, 3.191]	0.989
Catostomidae	<i>Moxostoma erythrurum</i>	245	5.0–52.5	1.0–1805.0	0.008 [0.007, 0.010]	3.082 [3.029, 3.145]	0.990
Catostomidae	<i>Moxostoma macrolepidotum</i>	1714	5.7–55.5	2.0–1800.0	0.010 [0.009, 0.010]	3.027 [3.012, 3.043]	0.994

a is the intercept and *b* is the slope of the linear LWR regression; CIs values are 95% confidence intervals of the respective regression parameters; *n* is sample size *R*² is the coefficient of determination (adjusted values from regressions). Cases where the 95% CIs for *b* estimates overlapped *b* = 3, consistent with the null hypothesis of isometric growth, are set in *italic* font. Species in bold denote new maximum length.

Table 3. Results of *t*-tests applied to evaluate the null hypothesis of *b* = 3. Tests were conducted in R (R Core Team 2023), based on species *b* estimates and sample size data presented in Table 2.

Family	Species	df	<i>t</i>	<i>P</i>
Leuciscidae	<i>Cyprinella lutrensis</i>	52	0.627	0.533
Leuciscidae	<i>Notropis atherinoides</i>	516	−5.107	<0.001^{ns}
Leuciscidae	<i>Notropis hudsonius</i>	64	1.941	0.0567
Leuciscidae	<i>Paranotropis volucellus</i>	19	−2.790	0.0117
Catostomidae	<i>Carpiodes carpio</i>	1092	4.169	<0.001^{ns}
Catostomidae	<i>Carpiodes cyprinus</i>	98	−1.219	0.226
Catostomidae	<i>Carpiodes velifer</i>	51	−0.851	0.399
Catostomidae	<i>Cycleptus elongatus</i>	52	6.003	<0.001^{ns}
Catostomidae	<i>Ictiobus bubalus</i>	2811	14.043	<0.001^{ns}
Catostomidae	<i>Ictiobus niger</i>	520	5.423	<0.001^{ns}
Catostomidae	<i>Moxostoma anisurum</i>	394	2.387	0.0174
Catostomidae	<i>Moxostoma carinatum</i>	79	1.882	0.0635
Catostomidae	<i>Moxostoma erythrurum</i>	243	4.166	<0.001^{ns}
Catostomidae	<i>Moxostoma macrolepidotum</i>	1712	4.545	<0.001^{ns}

df = degrees of freedom, *P* = *P*-value, *t* = Student's *t* statistic and cases of significant *p*-values are set in bold font. ^{ns} = highly significant *P*-value less than 0.1% of the alpha level of 0.05.

Discussion

The standard allometric equation, $W = aL^b$, is widely employed in fisheries science to estimate length–weight relationships by using log-transformation of the data to

linearize the relationship between these variables (Le Cren 1951). When the slope of the LWR meets the condition *b* = 3, then growth is said to be isometric, with individuals attaining similar body proportions at all sizes. Otherwise, when *b* > 3, then growth is positively allometric with larger specimens increasing more in height (i.e., body depth) or width (i.e., plumpness) than in length and when *b* < 3 obtains, then growth is negatively allometric with larger specimens becoming more elongate and less plump than smaller specimens (Blackwell et al. 2000; Froese 2006). Strong trends of allometric growth are considered rare amongst fishes, such that *b* > 3.5 and *b* < 2.5 are more likely explained by sampling artifacts, such as limited coverage of the full size-class range of the species (Carlander 1977) or extreme body shapes (e.g., disc-like or keeled body forms), while isometric and weakly allometric LWR patterns with *b* = 2.5–3.5 are common across fish diversity (reviewed by Froese 2006).

Our results for cypriniform fishes of the Upper Mississippi River are largely in line with these general expectations, with *b* estimates for all 14 study taxa falling between 2.5 and 3.5 (Table 2). However, the null hypothesis of *b* = 3 was only supported by evidence from 95% CIs for *b* in four species (~29%; Table 2) and by *t*-test results in five species (~36%; Table 3). Only one of these taxa, *Carpiodes velifer*, met sampling requirements for interpretation (cf. Froese 2006; Froese et al. 2011) and is concluded to

exhibit isometric growth. Interestingly, results for *C. velifera* revealed a new maximum TL of 51.4 cm for the species and the related specimen was caught in Pool 8 (07/03/2018, Mississippi River 1.72 mi (2.77 km) S of Wildcat Park and Landing; 43°40'2.1"N, 91°16'30.8"W) and weighed 2.1 kg, which is also a new maximum improving the LWR. The remaining four taxa for which *t*-tests supported $b = 3$ —*C. lutrensis*, *N. hudsonius*, *C. cyprinus*, and *M. carinatum*—had relatively small sample sizes that were statistically valid, but still less than 100 individuals. While isometric or weakly allometric growth seems likely for these taxa, we consider their LWRs provisional, and we recommend additional studies based on larger sample sizes in the future. If imputing missing weight values for these taxa, we suggest doing so only for the sampled length classes.

In contrast to the above findings, *t*-tests rejected the null hypothesis of $b = 3$ in nine species, indicating support for at least weak allometric growth (Table 3). Seven of these had sufficient numerical, geographical, and size-class sampling, as well as R^2 goodness-of-fit statistics, to meet the LWR requirements for confidence interpretation of growth patterns, as follows. *Notropis atherinoides*, the only leuciscid in this category, had a b estimate less than 3.0, consistent with negative allometric growth (Table 2). This matches the body shape of this species, which is an elongated minnow with a small head (Mettee et al. 1996; Page and Burr 2011) and it strongly supports faster growth in length than plumpness during the course of development. The remaining six taxa were catostomids with b estimates greater than 3.0, consistent with positive allometric growth, supporting faster growth in plumpness and or body depth than length throughout life (Table 2). Three of these were redhorse suckers from genus *Moxostoma*, including *M. carinatum*, *M. erythrurum*, and *M. macrolepidotum*. These species have terete (rounded) bodies and relatively long heads, for example, with head length and body depth proportions around ~21% to ~37% of standard length (e.g., Mettee et al. 1996; JCB, unpublished results). The remaining three species were deeper-bodied suckers from the genera *Carpiodes* and *Ictiobus* with more fusiform (torpedo-shaped) body shape—*C. carpio*, *I. bubalus*, and *I. niger*. These suckers have smaller snouts than their *Moxostoma* counterparts, but relatively large head proportions. They also have much deeper bodies than *Moxostoma* because their backs arch higher, rounding up behind the head to the dorsal fin origin (e.g., Mettee et al. 1996; Page and Burr 2011). Perhaps unsurprisingly, these three species had the highest b point estimates in our study (Table 2), with the greatest b estimate of 3.106 belonging to *I. niger*, the largest species and this suggest these species add girth both medially and into body depth during development.

Overall, while we consider our LWR estimations valid, three minnow species and three sucker species were relatively rare ($n \leq 100$) in the LTRMP dataset and one of these taxa, *P. volucellus*, had a very small sample size ($n = 21$; Table 2). This could reflect gear artefacts, since we only used data from boat electrofishing, which is generally biased towards smaller individuals (Miranda 2009) and species

common to shallower habitats and riverbanks, for example, *C. carpio* (cf. Mettee et al. 1996). Alternatively, this may reflect the greater rarity of these species in main river channel habitats as compared with lower-order tributaries and lakes. Therefore, we recommend additional sampling targeting tributary populations of UMR minnow species and also the use of data from additional gear types, which would be fruitful for comparative purposes and to improve species-level LWR calculations of these taxa in the future.

The focal species had previous LWR estimates available from FishBase (Froese and Pauly 2024) (Table 1) and our parameter estimates generally agreed with previous models within ~2%–5%. Yet, the previous LWRs were from different areas or populations within the focal species ranges. Thus, additional LWRs, based on samples from new areas such as the UMR, remain useful, because they allow nuanced applications of the LWR to the newly sampled areas. Additionally, when the goal is to apply the LWR at the species level (e.g., data imputation) or to a non-analog season or geographical area, then taking the geometric mean of a and b across all available studies is suggested (Froese 2006), which is less influenced by extreme values and is suitable for logarithmic data. Each additional LWR study provides a new data point for geometric mean calculation. Our results substantially improve available estimates for six species for which only a single LWR estimate was available, including all four minnows and the suckers *C. elongatus* and *I. niger* (Table 1). For example, the FishBase LWR (Froese and Pauly 2024) for *C. elongatus* was based on Swingle's (1965) study of only six specimens, as reported in Carlander (1969) and the FishBase LWR for *I. niger* was calculated from a single International Game Fish Association world record (Crawford 1993). Prior LWRs for other species were, at times, based on very large sample sizes, for example, where Swingle (1965) evaluated $n = 13\,623$ fish when estimating LWR parameters for *N. atherinoides* in Alabama. Nonetheless, we more confidently estimated a and b for *C. elongatus* and *I. niger* based on a range of size classes represented by much larger samples of $n = 54$ and $n = 522$ specimens, respectively (Table 2). Overall, these results provide new insights into LWRs for Upper Mississippi cypriniform fishes and will be useful for calculating fish biomass or imputing missing data in future studies of the species-rich and economically important fish fauna of the UMR.

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