

Summer Stream Temperatures Influence Sculpin Distributions and Spatial Partitioning in the Upper Clark Fork River Basin, Montana

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The upper Clark Fork River basin of western Montana supports a poorly understood sculpin (*Uranidea* spp.) fauna that has perplexed ichthyologists and fish ecologists since the late 1800s. During our study, the basin contained three sculpin taxa whose taxonomy was under revision. All three taxa were formerly referred to the genus *Cottus* but are now treated as *Uranidea*. Our goal was to improve understanding of the distribution and ecology of two of the taxa. From 2006 to 2009, we sampled 144 reaches in 31 streams and rivers to determine distributions of each taxa across the study area and within streams. We collected habitat data in 2007 and stream temperature data from 2006–2009 to identify correlates of sculpin distributions. In streams where both taxa occurred, Rocky Mountain Sculpin *Uranidea* sp. cf. *bairdii* were downstream and Columbia Slimy Sculpin *U. sp. cf. cognata* were upstream with a syntopic zone in between. Summer stream temperatures strongly influenced sculpin distributions, with mean August 2007 water temperatures increasing in order of reaches characterized as: Columbia Slimy Sculpin-dominated, syntopic, Rocky Mountain Sculpin-dominated, and no sculpin. Columbia Slimy Sculpin occurred in cold tributaries of the Blackfoot, Clark Fork, and Bitterroot rivers and in two coldwater refugia in the mainstem Bitterroot River. In contrast, Rocky Mountain Sculpin occupied warmer downstream segments of many Blackfoot and Clark Fork river tributaries as well as some mainstem reaches of both rivers but were absent from the Bitterroot River drainage. Persistence of the taxa will likely depend, both directly and indirectly, on future water temperatures, and thus, sculpins are appropriate targets for researching and monitoring biological changes resulting from climate change.

FRESHWATER sculpins (Cottidae) are ecologically important, small-bodied, benthic fishes, often occurring in high densities and biomasses in cool- and coldwater streams throughout the northern hemisphere (Adams and Schmetterling, 2007). Their distributions and densities have been associated with water temperatures across North America (Baltz et al., 1982; Lessard and Hayes, 2003; Quist et al., 2004; Edwards and Cunjak, 2007), suggesting that they will be susceptible to the effects of climate change. In regions with diverse freshwater sculpin faunas, differing behavioral or physiological thermal responses appear to play a role in structuring species distributional patterns (Moyle and Daniels, 1982; Brown, 1989; Walsh et al., 1997; Lessard and Hayes, 2003). Therefore, effects of changing thermal regimes on sculpins are not expected to be uniform across species. Understanding and predicting their responses to changing climate will require a basic understanding of each taxon's distributions, thermal requirements, and ecology.

Although ecological studies of several freshwater sculpin species have been conducted, for the most part, North American sculpins have been neglected by managers and researchers to the extent that even their systematics are still unclear (Moyle, 2002; Kinziger et al., 2005, 2007; Yokoyama and Goto, 2005; Adams and Schmetterling, 2007). Until 2001 (Schmetterling and Adams, 2004), a single sculpin species, Slimy Sculpin *Cottus cognatus*, was generally recognized as present throughout much of the upper Clark Fork River drainage in west-central Montana (Gould and Brown, 1970; Brown, 1971; Holton, 1990; Holton and Johnson, 1996). Later publications indicated *C. bairdii* occurring in the upper Clark Fork River drainage (Hendricks, 1997; Page and Burr, 2011) but provided no supporting evidence or collection localities. For various reasons, including the lack of a reliable way to identify

species in the field, sculpin were seldom documented or vouchered during fish sampling. As a result, historic sculpin data in the study area are limited. However, documenting sculpin distributions at coarse and fine geographic and temporal scales and understanding the species' ecological requirements are fundamental to effectively monitoring and conserving sculpins.

The phylogeny and taxonomy of sculpins have been revised recently. Most North American freshwater sculpins, formerly referred to the genus *Cottus*, have been moved to one of two genera: *Uranidea* or *Cottopsis* (Smith and Busby, 2014). Species of *Cottopsis* occur along the West Coast of the USA and Canada, with nearly all remaining taxa in N. America referred to *Uranidea* (Kinziger et al., 2005; Smith and Busby, 2014). Except where clarifying previously used names, from here onward, we will treat all sculpin taxa in the study area, and elsewhere as appropriate, as *Uranidea*. The specific epithet *cognatus* has also changed to *cognata* (Smith and Busby, 2014).

Several recent studies, some unpublished, have cast new light on the diversity of sculpins in the western U.S. and Canada, particularly the upper Columbia River, and have shown that at least three sculpin taxa, all undescribed or previously erroneously identified, occur in the Clark Fork River drainage from St. Regis, Montana, upstream (Neely, 2010; Young et al., 2013). The species most recently referred to as Columbia Slimy Sculpin, *C. sp. cf. cognatus* (Neely, 2010; herein treated as *Uranidea* sp. cf. *cognata*), was formerly referred to in the Columbia River basin as Slimy Sculpin *C. cognatus* (Holton, 1990; Holton and Johnson, 2003; Schmetterling and Adams, 2004). Recent mtDNA analyses reveal that the Columbia Slimy Sculpin is deeply divergent from the other sculpin taxa in the study area and from *U. cognata* in eastern North America (Neely, 2010; Young et al., 2013:figs. 1–3, group C; D. Neely, unpubl. data).

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The Rocky Mountain Sculpin, most recently referred to as *C. sp. cf. bairdii* (COSEWIC, 2010; Neely, 2010; Smith and Busby, 2014; herein treated as *U. sp. cf. bairdii*), was formerly known in the region as the Mottled Sculpin *C. bairdii*. Hubert et al. (2008) used data from the mitochondrial COI gene to show that populations of "*U. bairdii*" in western and eastern Canada constituted distinct lineages, and two studies of sculpin mtDNA in western Montana found that "*U. bairdii*" in western Montana were genetically distinct from *U. bairdii* in the eastern U.S. (Baker et al., 2001; Young et al., 2013:figs. 1–3, group A). East of the Continental Divide, the taxon occurs in the St. Mary, Milk, and upper Missouri rivers in Alberta, Montana, and northwestern Wyoming (COSEWIC, 2010). West of the Continental Divide, the taxon is well documented in the Flathead River drainage in British Columbia and Montana (Zimmerman and Wooten, 1981; COSEWIC, 2010) but poorly documented in the upper Clark Fork River drainage (Hendricks, 1997; Schmetterling and Adams, 2004; Page and Burr, 2011; Young et al., 2013).

During a study of sculpin movement patterns in Chamberlain Creek, Montana, in 2001, Schmetterling and Adams (2004) observed different movement patterns by sculpin at upstream versus downstream reaches. Morphometric and genetic analyses later confirmed that two sculpin taxa existed in the stream (Schmetterling and Adams, 2004; D. Neely, unpubl. data) and that the observed movement patterns differed by taxon. This discovery led to questions about the distributions and ecological correlates of the two taxa, some of which are addressed here. Differences in physiological tolerances, distributions, and seasonal movement patterns have strong implications for each taxon's response to ecosystem changes such as creation or removal of migration barriers and changing thermal or hydrologic regimes (Dunson and Travis, 1991; Taniguchi and Nakano, 2000; Lessard and Hayes, 2003).

The objectives of this study were to: 1) define the summer distributions of Rocky Mountain Sculpin and Columbia Slimy Sculpin in the study area, 2) examine correlation between summer stream temperatures and summer distributions of the two taxa, and 3) in tributary streams (to the Blackfoot, Bitterroot, and Clark Fork rivers), identify summer habitat associations of each taxon including any abiotic correlates with syntopic (taxa occurring in the same location) zones.

MATERIALS AND METHODS

Study area.—The Clark Fork River flows from the Continental Divide northwest across western Montana and into Lake Pend d'Oreille in Idaho. The Blackfoot and Bitterroot rivers join the Clark Fork River near Missoula, Montana, and drain about 5,940 and 7,288 km², respectively. The Clearwater River is a large tributary of the Blackfoot River and consists of a series of natural lakes interspersed with riverine segments. Milltown Dam, located on the Clark Fork River at the confluence with the Blackfoot River, limited downstream fish passage and blocked upstream passage from 1907 (Schmetterling, 2003) until its removal in 2008. The Clark Fork River at Milltown Dam had a mean annual flow of 84 m³/s. Sample reaches had watershed areas ranging from 12 to 21,680 km² and elevations from 818 to 1435 m (Adams et al., 2015:table 1). We considered sample reaches with watershed areas <1500 km² as tributary reaches and those with larger areas as mainstem river reaches (i.e., the

Blackfoot, Bitterroot, and Clark Fork rivers). Other than sculpins, ten native and five nonnative fish species occurred in the study area (Page and Burr, 2011).

Thermal complexity in the drainage during summer resulted from cold tributaries creating thermal refugia in larger, warmer rivers and from the alternation between lacustrine and riverine segments in the Clearwater River drainage. Therefore, water temperatures were not always directly coupled with elevation and stream size.

Sculpin distributions.—We conducted pilot studies in 2001 and 2006 to begin defining within-stream distributions of both Rocky Mountain and Columbia Slimy sculpins (Fig. 1). In 2001, we collected sculpins from up- and downstream locations in each of six study streams: two Clark Fork River tributaries downstream of Milltown Dam (Petty and Rattlesnake creeks), one upstream of Milltown Dam (Schwartz Creek), and three Blackfoot River tributaries (Gold, Monture, and Chamberlain creeks). We randomly selected five specimens >65 mm TL from each reach and conducted morphometric, meristic, and genetic analyses on them, confirming the presence of both Rocky Mountain and Columbia Slimy sculpins in the streams. Columbia Slimy Sculpin were in the upstream reaches and Rocky Mountain Sculpin in downstream reaches. In 2006, to begin locating distribution limits of each sculpin taxon in preparation for more comprehensive sampling, we sampled a total of 31 reaches in nine streams, including resampling our 2001 reaches.

We sampled sculpin populations in the upper Clark Fork River drainage (including the Blackfoot River tributaries) more broadly from 2007 to 2009, sampling 144 reaches from 28 streams and three mainstem rivers (Fig. 1; also Adams et al., 2015:table 2) one to three times over the three summers. We used the combined catch data from summers 2007–2009 for describing general patterns of distribution and indicating distributions on maps.

In summer 2007, we sampled 98 reaches in 22 streams and rivers to identify the upstream distribution limits of Rocky Mountain Sculpin and the downstream distribution limits of Columbia Slimy Sculpin in order to define the syntopic zones for the two taxa in each stream. We resampled all reaches sampled in 2001 or 2006 and used an iterative process for identifying distribution limits. We sampled a reach at or near the mouth of each study stream and then moved to another reach upstream, often to the uppermost accessible or known sculpin location. Depending on which sculpin taxon, if any, occurred in the second reach, we moved up- or downstream for the following reach. Where stream access allowed, the process was repeated until the upstream distribution limit of Rocky Mountain Sculpin and the downstream distribution limit of Columbia Slimy Sculpin were identified to within 500 m or less (often within about 100 m). In summer 2008, we repeated much of the 2007 sampling and added nine new streams, sampling 93 reaches distributed among 28 streams and rivers. Seven of the new reaches were in tributaries of the Bitterroot River and were selected because they were locations where Montana Fish, Wildlife, and Parks (MFWP) personnel captured sculpin between 1983 and 1998. In summer 2009, we sampled 57 reaches in 19 streams and rivers.

For all years combined, the median distance between sample reaches within Blackfoot and Clark Fork river tributaries was 0.52 km (range 0.06–8.4 km; excluding

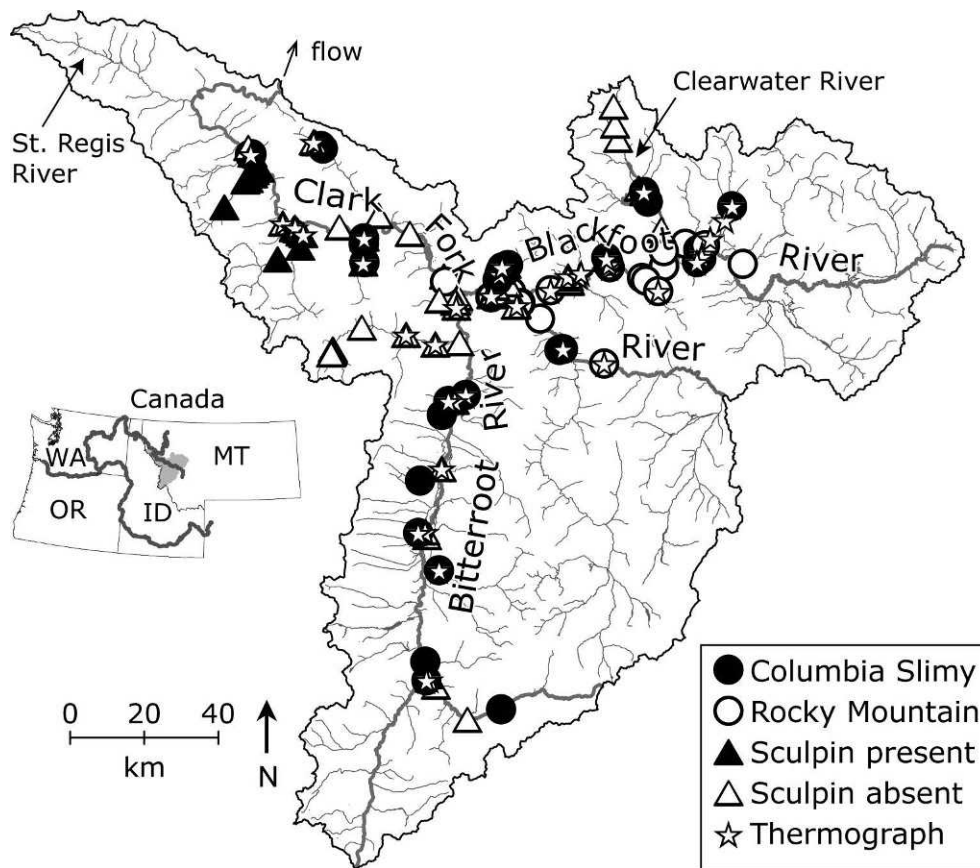


Fig. 1. Sculpin sampling (circles and triangles) and temperature recording (stars) reaches in the upper Clark Fork River drainage, Montana. Circles indicate reaches dominated by Columbia Slimy Sculpin (black) or Rocky Mountain Sculpin (white). Sculpin distributions represent combined results of summer samples from 2007–2009. Black triangles indicate reaches where we captured sculpin but could not positively identify them either because they were all small or because Cedar sculpin were also present. Open triangles indicate sculpin absence. Inset shows study area in Montana (shaded gray) and major rivers of the Columbia River basin.

Ninemile Creek that had sculpin only in the headwaters; Adams et al., 2015:table 2). Longer distances between reaches were typically due to our lack of access to the stream. On each mainstem river or large tributary (i.e., the Clearwater River), we sampled river margins in four to 16 reaches spaced at a median distance of 11.5 km (range 1.4–44.2 km).

Sampling effort at a reach depended on stream size and sculpin abundance. We collected fish by single-pass electrofishing using a backpack electrofisher (Smith Root LR-24) with one or two people netting with dip nets (3.2–4.8 mm bar mesh). For 2007–2009 summer samples, the mean recorded electrofishing effort was 686 seconds per visit (Adams et al., 2015:table 2). We typically sampled 30–60 m of stream per reach, continuing long enough to capture at least 20 sculpin identifiable to taxon (i.e., >55 mm TL). We assumed that sampling efficiency was similar for all sculpin taxa given that their body morphologies and behaviors were similar and that sampling conditions (discharge, water clarity, gear, and crew) were similar among reaches. We used the same crew in all years to duplicate effort.

All sculpin captured in each reach were identified, measured (TL, mm), and weighed (g). In the field, we effectively identified Rocky Mountain and Columbia Slimy sculpins > 55 mm TL based solely on the presence (Rocky Mountain Sculpin) or absence (Columbia Slimy Sculpin) of palatine teeth (97% accuracy for non-hybrids; unpubl. data) as recommended by earlier studies (COSEWIC, 2010; Neely, 2010). At each reach during summers 2007 and 2008, we retained at least five specimens >55 mm of each taxon collected in the reach. We preserved fin clips of vouchered fish in 95% ethanol and fish in 10% formalin.

Temperature, habitat, and watershed data collection.—Summer water temperature data were continuously recorded by Tidbit temperature data loggers (Onset Computer Corp.) in three locations in each stream: within 1 km of the stream mouth, in the syntopic zone, and upstream in the Columbia Slimy Sculpin-dominated zone (Fig. 1). Most loggers recorded temperatures at 60–90-minute intervals. In 2007, we installed Tidbits in 37 stream reaches and analyzed data from 29 of those, as well as from two reaches in the Bitterroot River where temperature data were collected by C. Clancy (MFWP). We discarded temperature data from five reaches where we had substantial gaps in the data or where sculpin were absent because steep channel slopes apparently prevented access to the reaches (see Results). In the latter situation, temperature and habitat conditions were not relevant because the reaches were inaccessible to sculpin. For two reaches, we had gaps in August water temperature data but had data from the loggers for at least 28 summer days. To fill the gaps, we estimated the missing temperatures with linear regression models constructed using water temperature data from a nearby reach ($R^2 = 0.92$ – 0.99 for average temperatures and 0.80 – 0.99 for maximum temperatures). Complete data from the neighboring reach constituted the independent variable, and data from the incomplete reach the dependent variable.

Additional stream temperature data collected only during sampling were used to improve understanding of the association between Columbia Slimy Sculpin and water temperature. In the Clearwater River (tributary to the Blackfoot River), we documented temperature patterns at two spatial scales. First, in 2007, we measured water temperatures along the length of the river during fish

sampling in each reach. Second, in both 2008 and 2009, we measured water temperatures and sampled fishes in cross-sections of the Clearwater River immediately downstream of the confluence with Morrell Creek (Clearwater River reach 5, Adams et al., 2015:table 2), where stream temperature varied strongly from bank to bank due to Morrell Creek's influence.

To further examine the relationship between abiotic conditions and sculpin distributions, we assessed seven physical habitat variables in all tributary reaches in summer 2007. Stream reach lengths were measured along the thalweg with a 30 m tape. Channel slope was measured with a clinometer and staff over the entire reach (Gordon et al., 1992). Wetted and bankfull channel widths were measured at three locations per reach then averaged. Maximum depth of every pool in the reach was measured with a staff and number of pools per 30 m was calculated. Percentages of dominant and subdominant substrate types were visually estimated throughout each reach using the following substrate classification: sand <2 mm, pea gravel 2–15, small gravel 16–63, large gravel 64–100, cobble 101–255, boulder >256 mm. For consistency, a single observer estimated all substrate sizes.

Watershed area, elevation, and site distance data were obtained using ArcGIS (Esri, Redlands, CA; <http://www.esri.com/software/arcgis/>). The latitude and longitude of each reach were usually obtained in the field from a Garmin GPS III Plus but sometimes in the office from Topo North America 9.0 (DeLorme, Yarmouth, ME; <http://www.delorme.com/>). Stream distances were calculated using ArcMap 9.3. After creating a map of the reaches using medium-resolution hydrography maps from the National Hydrography Dataset (Simley and Carswell, 2009, filename: NHD_MT_92v200.zip), we snapped sample reaches to stream routes on the hydrography layer and calculated the distances between reaches and from each reach to the stream mouth using the Closest Facility tool in the Network Analyst extension. Reach elevations were obtained from 1/3 arc-second (approx. 10 m resolution) digital elevation model raster images, and watershed areas above each reach were then obtained using various Terrain Processing tools in ArcHydro for ArcGIS 10.1.

Data analyses.—To analyze continuously recorded temperature data, we calculated means of daily average, maximum, and minimum temperatures over various periods. For final analyses, we used data from August 2007, the period when we sampled both temperature and habitat most intensively. Reaches were grouped into the following categories for analyses: Columbia Slimy Sculpin-dominated, Rocky Mountain Sculpin-dominated, syntopic zone, or no sculpin. We considered a reach to be “dominated” by one sculpin taxon if $\geq 95\%$ of sculpin large enough to be identified were of that taxon; this discounted the importance of small numbers of misidentified fish or individuals occurring unusually far from the core of a population. We compared mean daily water temperatures among sculpin categories using a full factorial, repeated-measures, general linear model with type III sum of squares. “Date” was the repeated measure (within-subjects) factor, and “sculpin category” was the between-subjects factor (PASW Statistics 18, SPSS, Inc., Armonk, New York, <http://www.spss.com.hk/statistics/>). We made *post-hoc* pairwise comparisons among sculpin categories using the least significant difference method (PASW Statistics 18).

For habitat analyses, only data from tributary reaches were used because we wanted to determine whether habitat differences dictated spatial segregation of the two taxa in streams where both might be expected to occur, and Columbia Slimy Sculpin rarely occurred in the mainstem rivers. We conducted an exploratory analysis of habitat data to look for patterns related to sculpin distribution. After eliminating reaches with missing data, we had 44 reaches for which we analyzed the five habitat characteristics (excluding substrate characteristics). We conducted multivariate analyses using PC-ORD 5.14 (McCune and Mefford, 2006) and tested for differences among sculpin categories using multi-response permutation procedure (MRPP) with Relative Sorenson distance. For visualizing habitat relationships among the categories, we conducted a cluster analysis using Relative Sorenson distance and a flexible beta = -0.25 (McCune and Grace, 2002). We also conducted univariate median tests for differences in quantitative variables among sculpin categories.

RESULTS

Sculpin distributions.—Columbia Slimy Sculpin occurred in tributaries throughout the Blackfoot River drainage and in some tributaries to the Clark Fork and Bitterroot rivers but were generally absent from mainstem rivers (Figs. 2–4; Adams et al., 2015:table 2). Despite the taxon's occurrence down to the mouths of several tributaries, we found only five Columbia Slimy Sculpin in two mainstem reaches. Both reaches were in the Bitterroot River and contained coldwater refugia (see below).

Rocky Mountain Sculpin occurred in the mainstem and tributaries of the Blackfoot River and in the mainstem and tributaries of the Clark Fork River upstream of the Alibon Gorge (Figs. 2, 3; Adams et al., 2015:table 2). We found no evidence of viable populations of any sculpin taxa in the mainstem Clark Fork River downstream of Missoula, although a single Rocky Mountain Sculpin was caught on each of two occasions at the Kona Bridge reach, downstream of the Bitterroot River confluence (Fig. 2). No Rocky Mountain Sculpin were found in the Bitterroot River drainage.

Within tributary streams where both taxa were present, typically Rocky Mountain Sculpin were downstream and Columbia Slimy Sculpin upstream with syntopic zones ranging from about 0.5–>11.4 km in the middle (Fig. 3). Columbia Slimy Sculpin distributions extended down to the stream mouth in three of five streams where they were allotopic but in only one (Gold Creek) of five streams where the two taxa were syntopic. In streams where they occurred, Rocky Mountain Sculpin were always present at the downstream-most reach sampled and were usually restricted to within about 4 km of the mainstem (Table 1); however, they extended 7.2 km upstream to an irrigation diversion in Elk Creek (where they were the only sculpin) and at least 14.6 km upstream in Monture Creek. Only in Elk and Deer creeks were Rocky Mountain Sculpin the vastly numerically dominant sculpin taxon in all reaches containing sculpin. In Elk Creek, 97% of identified sculpin caught from 2006–spring 2007 and 100% from summers 2007–2009 were Rocky Mountain Sculpin. In Deer Creek, 98% of sculpin identified were Rocky Mountain Sculpin, and their distribution only extended about 1 km upstream from the mouth.

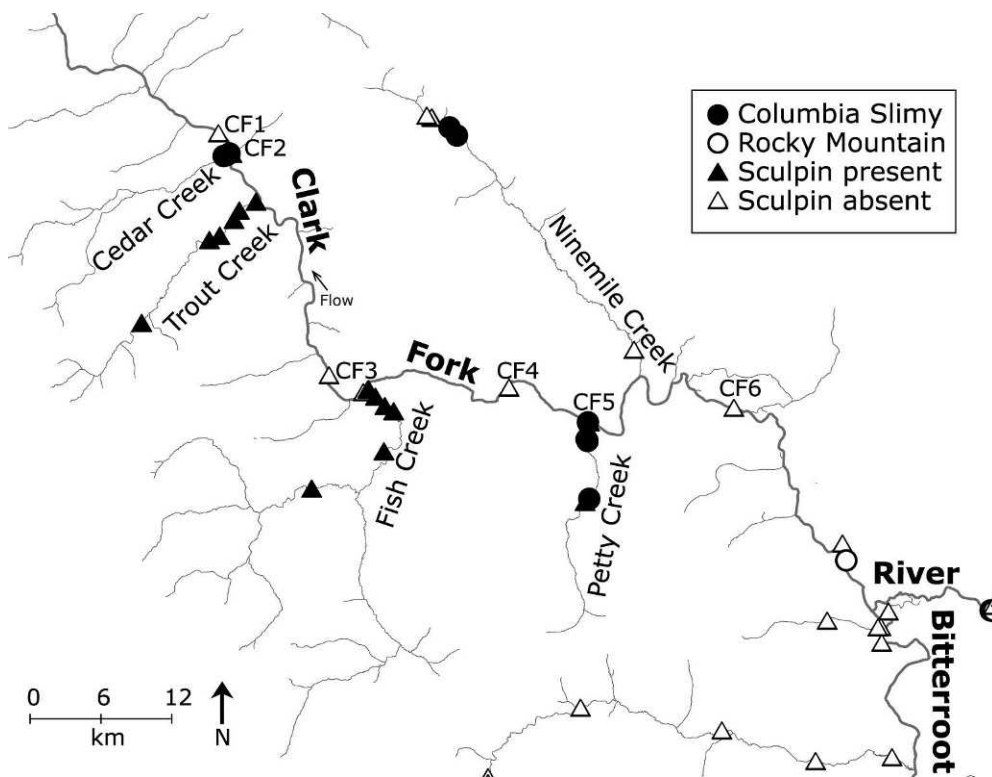


Fig. 2. Sculpin distributions in the Clark Fork River drainage downstream of confluence with Bitterroot River. Symbols are explained in Figure 1. Numbers indicate sample reaches on the mainstem of the Clark Fork rivers.

Temperature and habitat.—Summer water temperatures differed by sculpin category. Mean daily average water temperatures during August 2007 for stream reaches in each sculpin category generally increased in the following order: Columbia Slimy Sculpin-dominated (12.1 ± 2.24 , 10; mean \pm SD, n), syntopic (13.3 ± 1.14 , 6), Rocky Mountain Sculpin-dominated (14.7 ± 1.98 , 11), and no-sculpin (16.6 ± 1.67 , 7; Fig. 5). Although temperatures overlapped among categories (Adams et al., 2015:table 3), repeated measures analysis of mean daily average water temperatures from August 2007 indicated overall significant differences among categories (Table 2). *Post-hoc* pairwise comparisons revealed that no-sculpin reaches were warmer than reaches in all other categories and that Rocky Mountain Sculpin-dominated reaches were warmer than Columbia Slimy Sculpin-dominated reaches (Table 2). Mean August temperatures in syntopic reaches did not differ from those in reaches dominated by a single taxon. Results for mean daily minimum August temperatures were qualitatively the same.

In contrast to other temperature metrics, mean daily maximum temperatures in August were sometimes higher in Rocky Mountain Sculpin-dominated reaches than in no-sculpin reaches, and the two categories did not differ significantly from one another. Maximum daily water temperatures in 2007 exceeded 23°C in four of 11 Rocky Mountain Sculpin-dominated reaches and in five of ten no-sculpin reaches. Columbia Slimy Sculpin-dominated reaches were cooler, with maximum temperatures exceeding 20°C in four of ten Columbia Slimy Sculpin-dominated reaches and in five of six syntopic reaches and reaching 22°C in only one reach from each category.

The Clearwater River had spatially complex patterns of water temperature, so temperature and sculpin distributions were decoupled from elevation (Fig. 6, Table 3). August water temperatures were high immediately downstream of each lake, and in some cases, cooled substantially down-

stream until reaching the inlet of the next lake. In the headwater reach, we found cold temperatures but no sculpin, probably due to steep channel slopes downstream preventing sculpin access. Directly downstream of the next four lakes, sculpin were absent and water temperatures relatively high. However, Columbia Slimy Sculpin occurred from the confluence with a cold tributary, Morrell Creek, downstream to the next lake. Morrell Creek substantially cooled water temperatures in the Clearwater River (Fig. 6, Table 3). Rocky Mountain Sculpin were allotopic at the two most downstream reaches (below the lowest lake) where temperatures were warm.

At the within-reach scale, we also observed examples of Columbia Slimy Sculpin using thermal refugia over two summers. In Clearwater River reach 5, downstream of Morrell Creek, water temperatures increased from the Morrell Creek side of the river to the opposite side. Spot temperatures in the reach ranged from 12.5 – 18.4°C and 10.5 – 21.2°C during 2008 and 2009 sampling, respectively. In both years we found Columbia Slimy Sculpin on the cold side of the Clearwater River and no sculpin on the warm side. Similarly, in two Bitterroot River locations (Florence Bridge and Hannon Memorial fishing access), we found one or two Columbia Slimy Sculpin each summer in the cold thermal plumes from tributaries (temperatures not recorded), but nowhere else in these reaches nor in any other mainstem reach.

Habitat differed slightly among sculpin categories in tributary streams, as indicated by a small but significant effect size ($A = 0.061$, the chance-corrected within-group agreement; $P = 0.02$) in the MRPP analysis (McCune and Grace, 2002). *Post-hoc* pairwise comparisons indicated that Rocky Mountain Sculpin-dominated and Columbia Slimy Sculpin-dominated reaches differed from one another ($P = 0.004$), but the effect size remained small ($A = 0.12$). The cluster analysis dendrogram of habitat data showed more

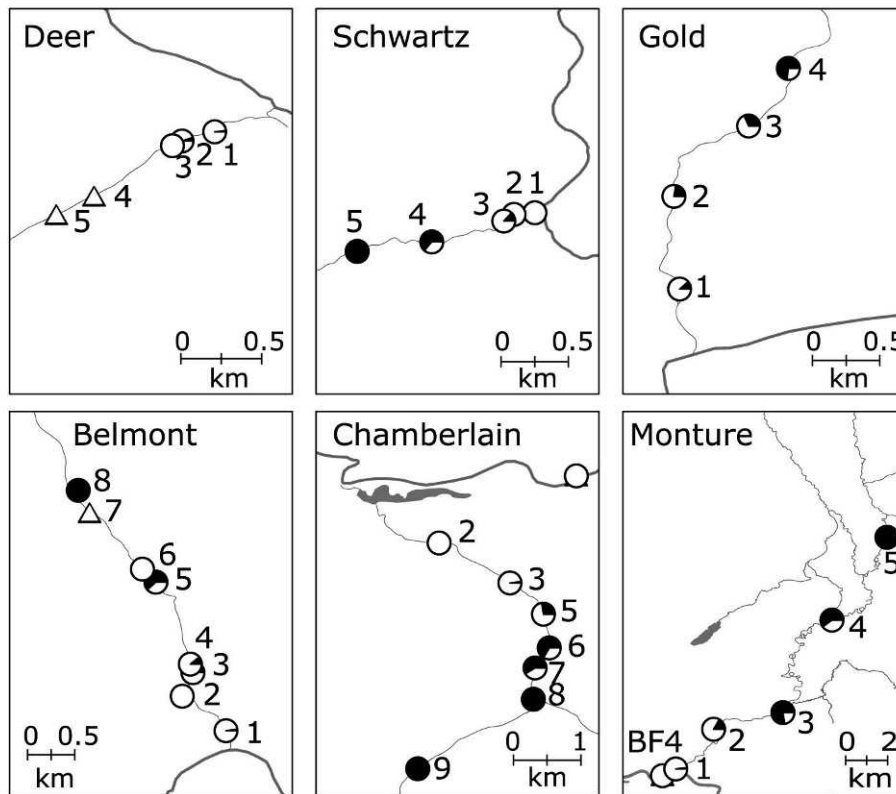
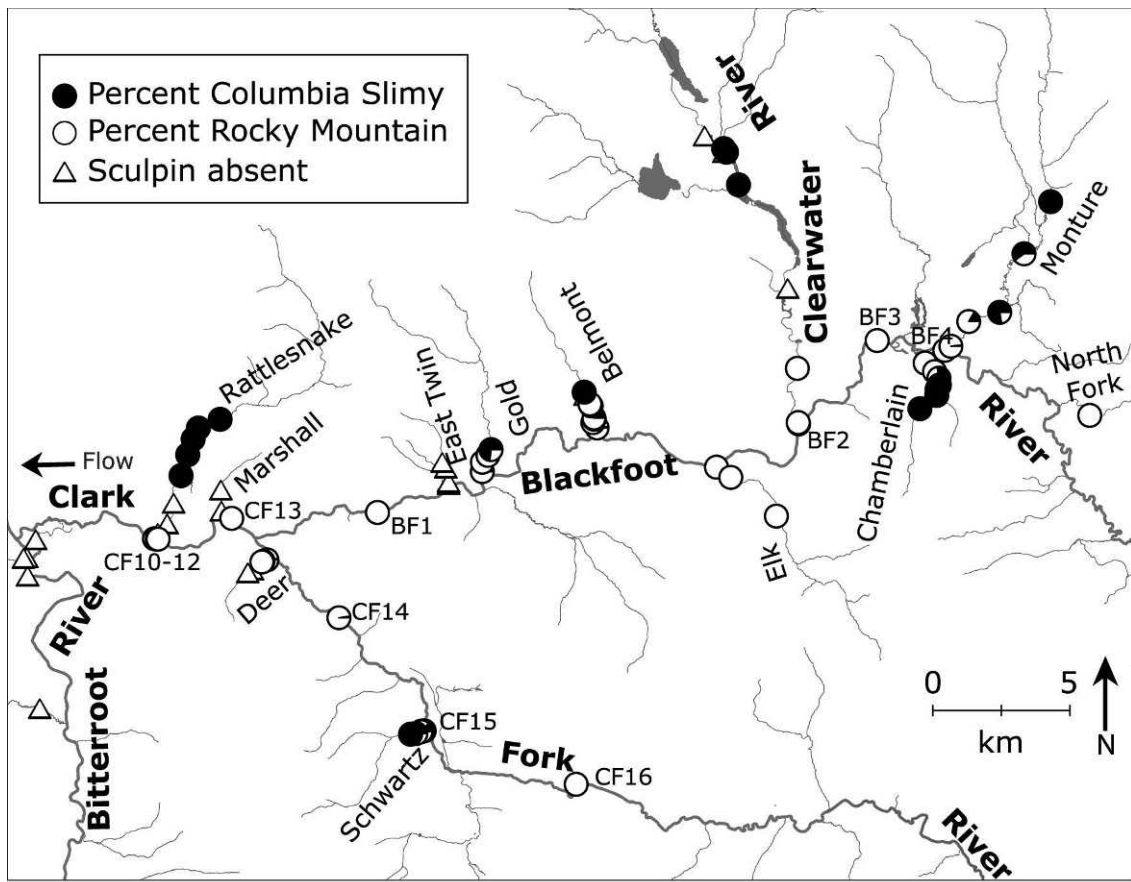


Fig. 3. Sculpin distributions in the Clark Fork River drainage upstream of confluence with Bitterroot River. Symbols are explained in Figure 1. Pie charts represent the proportion of Columbia Slimy Sculpin (black area) and Rocky Mountain Sculpin (white area) in a reach. Numbers indicate sample reaches on the mainstem of the Blackfoot and Clark Fork rivers. Smaller panels better illustrate distributions in tributaries containing both taxa.

Table 1. Distances (km) upstream of stream mouth for reaches in Blackfoot and upper Clark Fork River tributaries where we made the downstream-most (Downstream) and upstream-most (Upstream) observations of Rocky Mountain Sculpin (RMS), Columbia Slimy Sculpin (CSS), and the two taxa together (syntopic; SYN). The upstream-most observations of Columbia Slimy Sculpin often reflect where sampling ended rather than the upstream end of the distribution. We did not locate the upper distribution limit of either taxon in Gold Creek because of stream access issues.

Tributary	Downstream			Upstream			Length of syntopic zone (km)	% of RMS distribution in syntopy
	RMS	SYN	CSS	RMS	SYN	CSS		
Belmont	0.2	1.0	1.0	2.2	2.0	3.2 ^a	1.1	50
Cedar	—	—	0.2	—	—	0.9 ^a		
Chamberlain	1.7	3.3	3.3	4.2	4.2	6.3 ^a	0.9	21
Deer	0.8	—	—	1.2	—	—		
Elk	0.2	—	—	7.2 ^{ab}	—	—		
Gold	0.5	0.5	0.5 ^c	2.6 ^{ad}	2.6 ^a	2.6 ^a	>2.1	100
Monture	0.1	3.2	3.2	14.6	14.6	21.2 ^a	11.4	78
Morrell	—	—	0.3	—	—	0.3 ^a		
Ninemile	—	—	33.0	—	—	34.0		
Petty	—	—	0.1	—	—	8.3		
Rattlesnake	—	—	5.5	—	—	11.3 ^a		
Schwartz	0.1	0.3	0.3	0.7	0.7	3.4 ^a	0.5	66

^a Uppermost reach sampled.

^b Just downstream of water diversion structure.

^c By 2009, there were no longer CSS at this reach.

^d RMS were not found in this reach in 2006 and 2007.

tendency for reaches to group by stream than by sculpin category (dendrogram not included because not informative). Median tests conducted on the quantitative habitat variables across the four sculpin categories revealed overall significant differences across categories only in wetted width ($P = 0.02$). Pairwise tests indicated that tributary wetted widths were narrower in Rocky Mountain Sculpin-dominated reaches than in either Columbia Slimy Sculpin-dominated ($P = 0.01$) or syntopic reaches ($P = 0.01$; Table 4).

Although average stream reach channel slopes did not differ significantly among categories, we observed some patterns in channel slopes relative to sculpin distributions (Table 4). The maximum channel slope for reaches containing Columbia Slimy Sculpin, including syntopic reaches, was 2.0%. For Rocky Mountain Sculpin-dominated reaches, channel slopes were lower than 3% at all but one reach (6.9% in Deer Creek near its mouth). Two of the streams that lacked sculpin entirely had steep slopes at the downstream end; in Marshall Creek, the reach near the mouth averaged 14.8% slope over 30 m, and in East Twin Creek, the three most downstream reaches ranged from 3.4 to 4.5% slope. Although in Deer Creek sculpin occupied a reach with a 6.9% slope, the slope did not remain steep over a long distance as in East Twin Creek. Furthermore, East Twin Creek had vertical drops (due to rocks and a culvert) > 20 cm, a height shown to prevent upstream passage of other sculpin species (Utzinger et al., 1998; LeMoine, 2007).

Nearly all tributary streams were dominated by cobble, gravel, and boulder substrates. In over half of all reaches sampled, regardless of sculpin category, the dominant substrate was cobble. The second most common dominant substrate was boulders in no-sculpin reaches and gravel in sculpin reaches. Relatively few reaches with sculpin had small gravel, pea gravel, or sand as the dominant or subdominant substrate. The notable exception was Elk

Creek, which contained three of the four reaches where sand was the dominant or subdominant substrate.

DISCUSSION

Summer stream temperatures influenced distributions of Columbia Slimy and Rocky Mountain sculpins. The within-stream spatial partitioning previously observed in Chamberlain Creek (Blackfoot River drainage, Schmetterling and Adams, 2004) and elsewhere (Flathead River drainage, Hughes and Peden, 1984; COSEWIC, 2010), where Columbia Slimy Sculpin occurred cold upstream reaches and Rocky Mountain Sculpin in warmer downstream reaches with a syntopic zone in between (Schmetterling and Adams, 2004), was repeated in other tributaries to the Blackfoot and Clark Fork rivers. At the drainage scale, Columbia Slimy Sculpin were broadly distributed, occurring in cold tributaries throughout the study area; however, at the stream scale they had a restricted distribution with populations apparently isolated in cold headwater reaches. Conversely, Rocky Mountain Sculpin were more restricted at the drainage scale, but within drainages, populations extended from the warmer, downstream ends of tributaries into mainstem rivers, possibly creating one large or several smaller but well-connected populations.

Four lines of evidence indicated that stream temperatures exerted strong controls on summer distributions of both sculpin taxa at the within-tributary and within-watershed scales in our study. First, Columbia Slimy Sculpin-dominated reaches were colder than those dominated by Rocky Mountain Sculpin. Second, in the thermally complex Clearwater River, Columbia Slimy Sculpin occurred only in the coldest of the accessible reaches and only in the coldest part of one of the reaches. Third, Columbia Slimy Sculpin were found in mainstem reaches only in cold thermal refugia. Fourth, the Bitterroot River tributaries that lacked sculpin had relatively high temperatures.

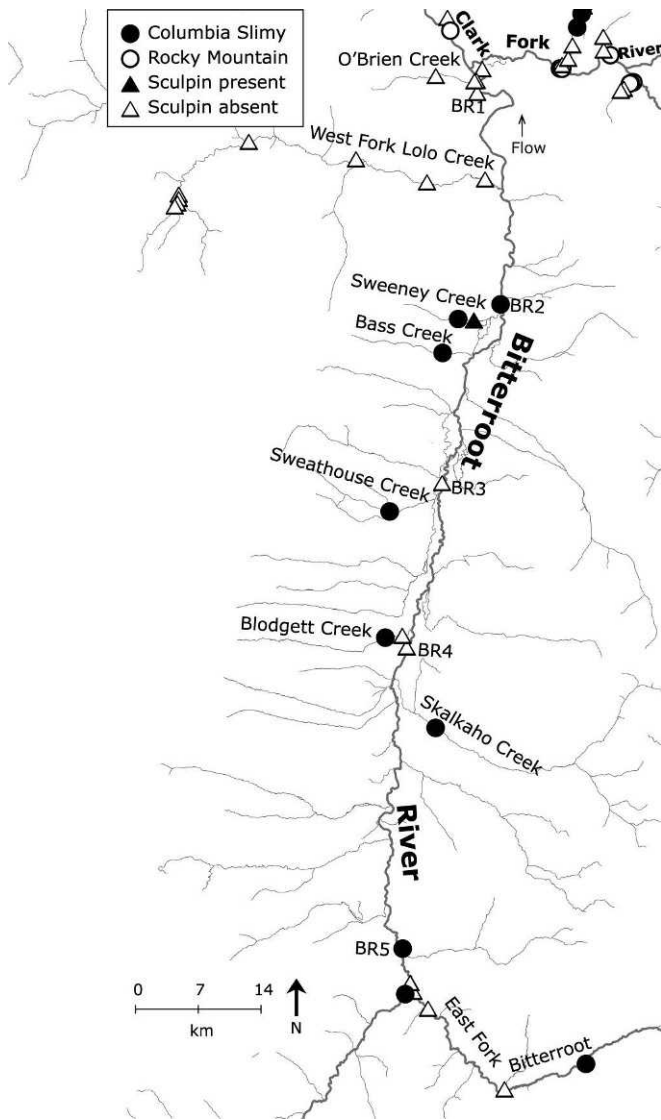


Fig. 4. Sculpin distributions in the Bitterroot River. Symbols are explained in Figure 1. Numbers indicate sample reaches on the mainstem of the Bitterroot River.

Columbia Slimy and Rocky Mountain sculpins occurred at temperatures similar to those of other sympatric species pairs such as *U. cognata* and *U. bairdii*. In our study, Columbia Slimy Sculpin occurred in the coldest reaches, where maximum water temperatures rarely or never reached 22°C, even during the record warm summer of 2007. Rocky Mountain Sculpin tolerated warmer temperatures, including maximum temperatures exceeding 23°C in four reaches and as high as 27.5°C in one reach; however, the fish may have retreated to cooler groundwater-influenced patches in the substrate during very high temperatures (Power et al., 1999). Similarly, *Uranidea cognata* generally inhabits colder streams, deeper lake habitats, and occurs farther north compared to *U. bairdii* (Scott and Crossman, 1973; Hubbs et al., 2004). *Uranidea cognata* from Lake Michigan had incipient upper lethal temperatures of 18.5 to 23.5°C and avoidance temperatures of 15.2 to 21.5°C, depending on acclimation temperature (Otto and Rice, 1977). In a Michigan stream thermally altered by a reservoir, *U. cognata* did not occur in reaches with mean summer water temperatures >20°C, but densities of *U. bairdii* appeared unaffected by the warmer

temperatures (Lessard and Hayes, 2003). Although no data exist on thermal preferences or tolerances of our study taxa, research on other fish species has linked laboratory-derived thermal tolerances to within-stream distributions (e.g., Dunham et al., 2003).

In mountainous regions, water temperature and elevation are typically highly correlated (Isaak and Hubert, 2001; Peterson et al., 2014). To begin disentangling the effects of water temperature versus elevation (or longitudinal position within streams) on sculpin distributions in the study area, we examined distribution patterns at two spatial scales where elevation and stream temperature were decoupled. The first was at the stream scale in the Clearwater River, where we showed that the association of Columbia Slimy Sculpin distributions with cold stream temperatures were not simply a reflection of other elevational changes within streams. We found Columbia Slimy Sculpin in cold reaches of the Clearwater River but not in warmer reaches up- and downstream. A similar pattern, but one based on density rather than presence or absence, was documented in Catamaran Brook, New Brunswick (Edwards and Cunjak, 2007). There, densities of *U. cognata* were highest in the coldest reach, where maximum temperatures exceeded 20°C on only four days during an eight-year study, but densities were lower both up- and downstream where water temperatures were warmer, often exceeding 22°C.

Coldwater refugia offered another opportunity to explore water temperature influences on Columbia Slimy Sculpin distributions without the confounding effects of elevation. The presence of Columbia Slimy Sculpin in mainstem river reaches only in coldwater refugia indicated that river size, alone, does not preclude use by the taxon, but that typical summer temperatures in the mainstem rivers were avoided. During July and August, the Bitterroot River's Florence Bridge reach had considerably warmer recorded water temperatures than any other site containing Columbia Slimy Sculpin, but the temperature recorder was outside of the coldwater plume where all sculpin were captured. In the Clearwater River, we directly observed Columbia Slimy Sculpin selecting the coldest habitats within a thermally heterogeneous stream reach. Numerous examples in the literature show that coldwater refugia can influence summer fish distributions (e.g., Ebersole et al., 2003; Westhoff et al., 2014).

Finally, the two Bitterroot River tributaries we sampled that lacked sculpin had summer water temperatures exceeding those in any reaches where Columbia Slimy Sculpin occurred. In Lolo Creek, about 3 km upstream of the mouth, August water temperature averaged 15.8°C over four summers (1997–1999 and 2004; Chris Clancy, Montana Fish, Wildlife, and Parks, unpubl. data), and in O'Brien Creek, mean August temperature in 2007 was 16.6°C (Adams et al., 2015:table 3).

Although we limited our statistical analysis to August 2007 temperatures in order to maximize our sample size, our results are applicable to summer temperature patterns in general. Summer stream temperature metrics within basins and years are typically highly correlated with one another, and thus the particular metric or month chosen is of minor importance (Dunham et al., 2005; D. Isaak, USFS Rocky Mountain Research Station, Boise, Idaho, pers. comm.). Furthermore, thermal relationships among streams and years within a basin are relatively stable and highly correlated (Isaak et al., 2011).

Table 2. Results for general linear model repeated measures analysis of mean daily average August 2007 water temperatures by sculpin category. Table (A) shows overall between-group effects, degrees of freedom (df), and significance levels, and (B) gives pairwise comparisons results, including mean differences between pairs, standard errors (SE), and lower and upper bounds of 95% confidence intervals (CI) for the mean differences. Bold entries highlight significant differences at the $\alpha = 0.05$ level. Sculpin categories are Columbia Slimy Sculpin (CSS), Rocky Mountain Sculpin (RMS), syntopic (both species), or no sculpin.

A)

Source	Type III sum of squares	df	Mean square	F	P-value
Intercept	185615.22	1	185615.22	1742.96	0.000
Sculpin group	3141.21	3	1047.07	9.83	0.000
Error	2875.34	27	106.49		

B)

Sculpin		Mean difference	SE	P-value	95% CI	
Group 1	Group 2				Lower	Upper
CSS	syntopic	-1.34	0.98	0.18	-3.34	0.66
	RMS	-2.98	0.85	0.00	-4.73	-1.23
	none	-5.01	0.98	0.00	-7.01	-3.00
RMS	syntopic	1.64	0.96	0.10	-0.32	3.60
	none	-2.02	0.96	0.04	-3.99	-0.06
Syntopic	none	-3.67	1.07	0.00	-5.86	-1.47

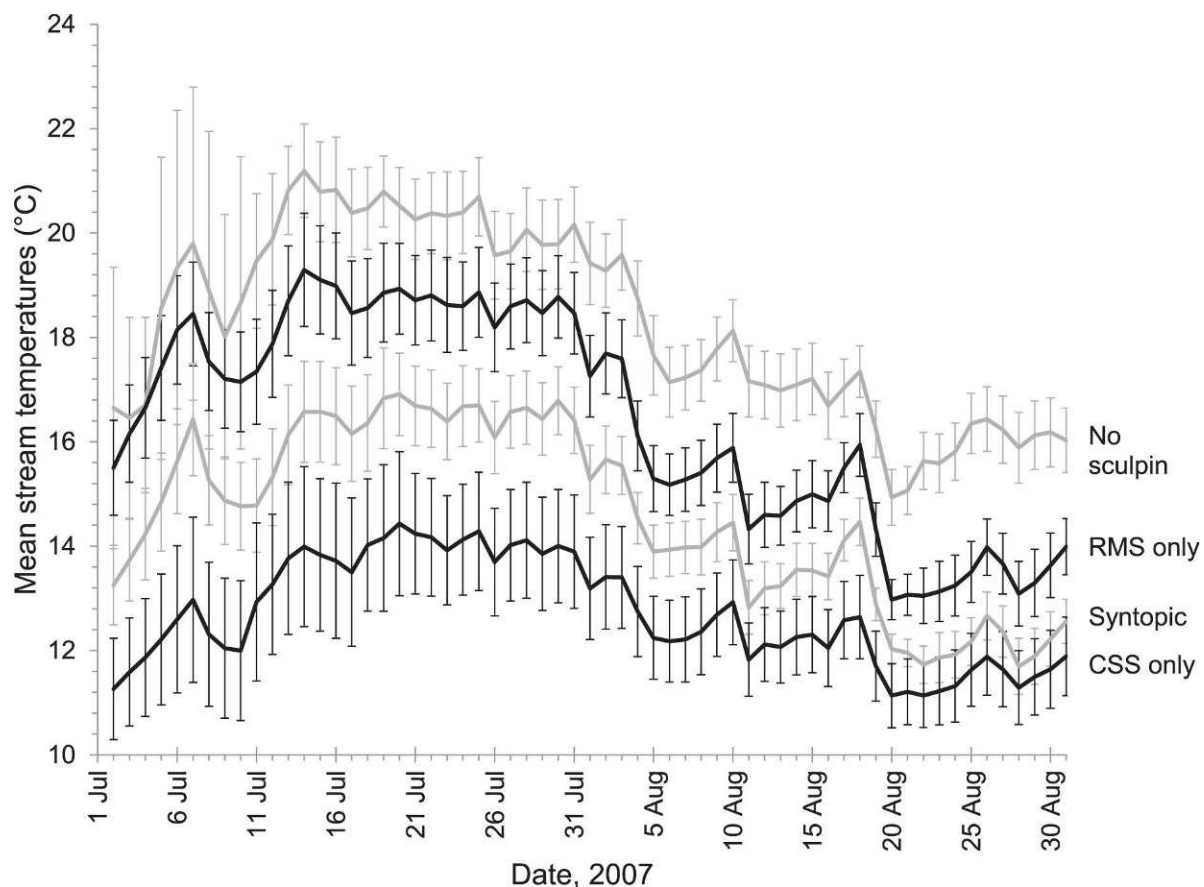


Fig. 5. Water temperatures relative to sculpin distributions in 2007. Mean \pm 1 SE of daily average water temperatures in July and August for reaches in four sculpin categories: no sculpin, Rocky Mountain Sculpin-dominated (RMS), syntopic, and Columbia Slimy Sculpin-dominated (CSS). The "no sculpin" group includes only reaches in mainstem rivers or downstream of sculpin distributions in tributaries to avoid confounding the temperature pattern with reaches that sculpin could not access because of steep channel slopes. The CSS group does not include the Bitterroot River at Florence (reach BR2) where fewer than five sculpin were captured and those only in a thermal refugium away from our thermograph. Overall, category sample sizes ranged from two to 11, but from 21 July–31 August, all categories had at least six reaches.

Table 3. Sculpin catch per unit effort (CPUE; number caught per second of electrofishing) at reaches in the Clearwater River, Montana. Numbers of sculpin in reaches, and time and water temperature (Temp.) during sampling in August 2007. Reaches are listed in order from downstream to upstream. Note the cool afternoon temperatures at reaches 4 and 5, where Columbia Slimy Sculpin (CSS) occurred, and warmer temperatures earlier in the day where Rocky Mountain Sculpin (RMS) occurred. "U. spp." refers to sculpin too small to identify in the field.

Reach location	Reach #	RMS	CSS	U. spp.	CPUE #/second	Date	Time	Temp.
At mouth	1	3	0	5	0.01	13 Aug	1030	14.0
Hwy. 200	2	22	0	1	0.02	13 Aug	1245	19.4
Downstream of Salmon Lake	3	0	0	0	0.00	13 Aug	1325	20.6
Placid Lake Road	4	0	7	5	0.03	14 Aug	1428	14.7
Downstream of Morrell Cr.	5	0	12	6	0.02	13 Aug	1420	11.7
Upstream of Morrell Cr.	6	0	0	0	0.00	14 Aug	1349	20.2
Downstream of Seeley Lake	7	0	0	0	0.00	13 Aug	1510	19.5
Downstream of Lake Inez	8	0	0	0	0.00	14 Aug	1040	16.5
Downstream of Lake Alva	9	0	0	0	0.00	14 Aug	1125	19.0
Upstream of Rainy Lake	10	0	0	0	0.00	14 Aug	1254	9.5

Hierarchical filters operating on sculpin distributions.—Applying the concept that hierarchical filters determine local species assemblages (Poff, 1997) can help explain sculpin distributions at the tributary stream scale. For a taxon to occur in a tributary, the following conditions typically apply: 1) the taxon must occur in the larger drainage to be available to colonize the stream, 2) channel morphology must allow access for initial colonization, 3) habitat conditions, including thermal regime, must be suitable for persistence, and 4) biotic interactions must not prevent persistence.

In the Bitterroot River drainage, Rocky Mountain Sculpin were not present to colonize tributaries. The factors controlling drainage-scale sculpin distributions in the region are unknown. As information about the Rocky Mountain Sculpin emerged over recent years, the taxon's distribution was thought to include the upper Missouri, Yellowstone, and Milk river drainages on the east slope of the Rocky Mountains and to be confined to the upper Flathead River drainage on the west slope (COSEWIC, 2010; but see Baker et al., 2001). Two recent sources indicated the taxon was present in the upper Clark Fork River drainage but

did not present supporting data (Hendricks, 1997; Page and Burr, 2011). It is not clear whether the populations in the Clark Fork River drainage originated from prehistoric colonization events or from more recent introductions. Based largely on the degree of genetic divergence between populations on either side of the divide, McPhail hypothesized that populations in the Flathead River resulted from a Holocene event with colonization moving from east to west (COSEWIC, 2010). Regardless of the source of the populations, it is unclear why Rocky Mountain Sculpin do not occur farther downstream in the Clark Fork River or in the Bitterroot River drainage. Resolving this question will require a better understanding of population use of, and possibly movements between, mainstem and tributary habitats by Rocky Mountain Sculpin.

Steep channel slopes or vertical drops appeared to prevent colonization in two of the four tributaries lacking sculpin as well as in the headwaters of the Clearwater River. Two tributaries, Marshall and East Twin creeks, that lacked sculpin were potentially available to both taxa. Although habitats and temperatures in upstream reaches were within the ranges of those observed in other sculpin reaches, channel slopes in downstream reaches apparently prevented sculpin colonization. Other habitat variables we measured were not informative for explaining differences in persistence between the taxa.

Finally, a taxon will occur at a site only if biotic interactions do not prevent persistence. The mechanistic causes of the longitudinal segregation between the two taxa may be a function of both water temperature and biotic interactions, and these filters may function synergistically rather than sequentially (Poff, 1997). Where Columbia Slimy Sculpin were the only taxon in a stream, their distribution did not always extend downstream to the mouth of the stream. Their downstream distribution limits in those cases appeared to be dictated by warm summer temperatures. In the two streams where Rocky Mountain Sculpin occurred without Columbia Slimy Sculpin, the former extended farther upstream in one, but not in the other, compared to streams where both taxa occurred. The lack of consistent, substantial distributional shifts of each taxon in allotopy suggests that abiotic factors, particularly temperature, may play an important role in limiting distributions (Edwards and Cunjak, 2007). However, the distributions of both taxa may also result in part from

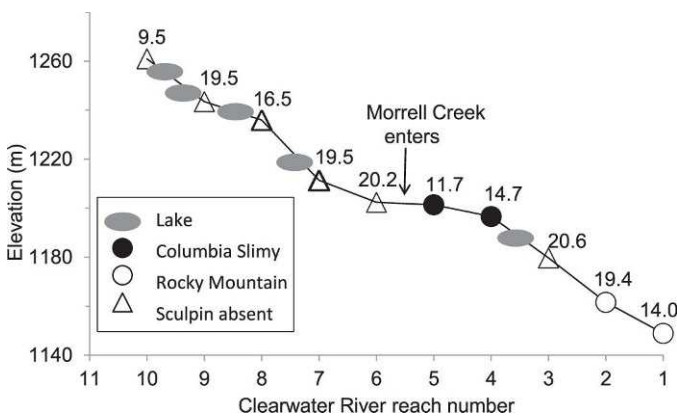


Fig. 6. Schematic of lakes and sample reaches along the Clearwater River, Montana. Symbols indicate sculpin status at each reach. Numbers above sample reaches are water temperatures recorded during sampling (see Table 3 for time of day). Vertical axis is to scale, but horizontal axis does not portray stream distances. Reach numbers as in Table 3.

Table 4. Summary of quantitative habitat data for reaches in the four sculpin categories (as defined in Table 1). Numbers are in the order: median (range), number of reaches. In instances where bankfull and wetted widths were recorded as ">30 m", we used 30 m for summaries.

Sculpin category	Bankfull width (m)	Wetted width (m)	Channel slope (%)	Number of pools per 30 m	Avg. max. pool depth (m)
RMS	5.8 (2.8–22.5), 11	4.1 (1.8–16.6), 11	1.3 (0.5–6.9), 12	2.0 (0.0–7.0), 12	0.4 (0.2–0.6), 9
CSS	13.3 (4.3–>30.0), 11	8.7 (2.7–>30.0), 12	1.1 (0.6–1.7), 12	0.7 (0.0–3.3), 12	0.5 (0.3–0.7), 6
Syntopic	11.4 (5.2–24.5), 11	10.0 (2.8–15.2), 11	1.1 (0.1–2.0), 13	1.0 (0.0–3.6), 13	0.5 (0.4–0.9), 9
No sculpin	13.6 (2.8–>30.0), 23	7.9 (1.7–>30), 23	1.7 (0.4–14.8), 16	1.9 (0.0–5.0), 15	0.4 (0.2–0.9), 13

interspecific interactions (Baltz et al., 1982; Dunson and Travis, 1991; Taniguchi and Nakano, 2000).

Two of the four warmest reaches where we found Columbia Slimy Sculpin lacked Rocky Mountain Sculpin entirely (Petty Creek and West Fork Bitterroot River). Columbia Slimy Sculpin may be an inferior competitor in warmer water but tolerate warmer temperatures in the absence of Rocky Mountain Sculpin. At colder temperatures, Columbia Slimy Sculpin may have a competitive advantage over Rocky Mountain Sculpin due to behavioral or physiological adaptations (Baltz et al., 1982; Taniguchi et al., 1997; Taniguchi and Nakano, 2000).

Laboratory studies indicated that thermal physiology of several other sculpin species are correlated with, but do not entirely explain, differences in distributions (Brown, 1989; Walsh et al., 1997). However, spatial segregation among species in relation to stream thermal regimes has suggested the possibility of temperature-specific differences in competitive advantages among species (Brown, 1989). Hughes and Peden (1984) concluded that the similar sizes, diets, and habitats used by the two taxa we studied made competitive interactions likely.

Climate change and conservation implications.—Because distributions appear to be related to stream temperatures, ongoing and forecast increases in stream temperatures do not bode well for sculpin, especially Columbia Slimy Sculpin, in the Clark Fork River drainage. Mean summer temperatures of Pacific Northwest streams have increased about 0.22°C/decade and maximum weekly temperatures by about 0.28°C/decade over the past 50 years, due to both increasing air temperatures and decreasing summer stream discharges (Isaak et al., 2011). The rate of warming is forecast to increase in the coming decades, with total thermal gains of 1.2–1.8°C possible in the streams by mid-century (Isaak et al., 2011). We are currently assessing whether sculpin distributions in the study area are changing in concert with temperature increases (unpubl.).

In addition to direct impacts on populations, indirect effects of stream warming, such as population isolation (Rieman et al., 2007) or altered biotic interactions (Ockendon et al., 2014) such as those addressed above, may prove more important than direct effects. Metapopulation theory suggests that both patch size and isolation affect the probability of population extirpation, although demonstrated effects of isolation on fish population persistence vary by species (Peterson et al., 2014). Upstream shifts in the downstream distribution limits of Columbia Slimy Sculpin will presumably reduce patch sizes. Although we did not investigate the taxon's upper distribution limits, personal observations during many years of stream research in the

basin suggest that distributions are limited upstream by physical stream features such as steep channel slopes, small stream sizes, or in some cases anthropogenic migration barriers. If Columbia Slimy Sculpin do not move among tributaries in the winter (which our limited, unpublished data suggest they do not), then populations may already be isolated in tributaries within the study area. We predict that Columbia Slimy Sculpin populations will become increasingly fragmented and isolated in tributary streams and that Rocky Mountain Sculpin summer use of mainstem rivers will become increasingly restricted. Minimum patch size for persistence and the relationship of isolation to extinction risk for stream sculpin remain unexplored.

We have much to learn about the mechanisms by which changing thermal and flow regimes influence stream fish distributions but suggest that sculpin are ideal focal taxa for investigations in this arena. More charismatic coldwater species of high conservation concern, such as salmonines, are syntopic with the sculpins in the study area, but sculpins are particularly useful targets of both monitoring and mechanistic research because they move less and tend to occur in higher densities than salmonids (Adams and Schmetterling, 2007; Edwards and Cunjak, 2007). The different distributions, and possibly behaviors (Schmetterling and Adams, 2004) and thermal optima, between the sculpin taxa in the study area have interesting implications for each taxon's potential response to ecosystem changes such as changing thermal conditions (Westhoff and Paukert, 2014). The effects of sculpin extirpation on salmonines, and more broadly on aquatic and even riparian food webs, poses an ecosystem-wide conservation threat that presents a valuable area for future research and one that is essential to understanding the responses of populations to climate change (Ockendon et al., 2014).

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