Thesis

Ecomorphology and niche segregation of Rocky Mountain *Cottus*

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY NATHAN V. HOLMES ENTITLED "ECOMORPHOLOGY AND NICHE SEGREGATION OF ROCKY MOUNTAIN *COTTUS*" BE ACCEPTED AS FULFILLING PARTIAL REQUIREMENTS FOR THE THESIS IN ZOOLOGY.

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Abstract We surveyed fish assemblages and habitats in 16 streams of northeastern Utah to examine relations between sculpin (*Cottus)* morphology and environmental variables. We sampled a range of wadeable streams that varied most strongly in bottom velocity, wetted width, and reach slope. We examined morphological traits of 373 *Cottus* (both mottled sculpin (*C. bairdii)* and Paiute sculpin (*C. beldingii*) 72 to 116 mm SL) from 36 mesohabitats of 10 streams. Morphological traits with greatest variation were associated with body shape (fusiform versus tubular), which varied between and within species. *Cottus bairdii* was more fusiform than *Cottus beldingii* (larger head and torso versus the caudal peduncle) with more axillary prickles, but there was overlap between species. Brown trout abundance (*Salmo trutta)*, fish species richness, *C. bairdii* abundance, and stream bottom velocity correlated strongly with *Cottus* body shape. Interspecific morphological differences were consistent with distributional differences we observed and ecological differences reported in literature. All *Cottus* had relatively optimal fineness ratios, a measure of body length versus maximum body diameter with the optimal streamlined body form having a ratio of 4.5, indicative of life in swift-water habitats. The more tubular, unprickled body and smaller head and torso of *C. beldingii* were consistent with life in swifter streams where interstices among large substrata provide refuge from predators and burst swimming facilitates movement among interstices. In contrast, the more fusiform, prickled body and larger head and buccal cavity of *C. bairdii* were consistent with life above the substrate in a wider range of velocities. *Cottus bairdii* may forage more frequently in open water, pursue more elusive prey, have greater need for physical defenses from predators (armor, girth), or experience more competitive interactions with other fishes.

Introduction

Phenotypic variation may reflect a response to environmental conditions that results in differing morphologies among individuals with similar genotypes, representing a potential step toward adaptation (Miner et al. 2005; Pigliucci 2005). Both abiotic (e.g. stream column velocity, water column depth) and biotic (e.g. potential competitors or predators) variables affect fish phenotypes (Langerhans 2006, 2008). Understanding phenotypic variation in fishes helps to unravel the factors that adapt taxa to their niches (Douglas and Matthews 1992; Robinson and Wilson 1994).

Freshwater sculpin (*Cottus*) exhibit much morphological variation (Kinzinger 2003; Kinzinger et al. 2007). Kerfoot and Schaefer (2006) found two distinct morphologies of the banded sculpin (*Cottus carolinae)* in the central U.S.A.: a slower-stream "prairie" morph and swifter-stream "Ozark" morph. The prairie morph was more fusiform (larger head and body relative to the caudal peduncle), while the Ozark morph was less fusiform. Ozark morph *C. carolinae* were relatively similar among three river drainages even though these populations are now recognized as distinct (Kinzinger 2003; Kinzinger et al. 2007). Ozark *C. carolinae* co-occurred with mottled sculpin (*Cottus bairdii)* and were morphologically more similar to each other than to prairie *C. carolinae* (Kerfoot and Schaefer 2006), indicating a strong effect of environment on *Cottus* phenotype.

Many factors affect fish ecology and may influence phenotypes. Examples include stream size (Hoagstrom and Berry 2008), water velocity (Baltz et al. 1982; Kerfoot and Schaefer 2006), substrate size and water depth (Matheson and Brooks 1983; White and Harvey 1999; Davey et al. 2005), water temperature (Matheson and Brooks 1983), dissolved oxygen (DO) (Langerhans et al. 2007), total dissolved solids (Hubert and Chamberlain 1996; Quist et al. 2004b), population density (Robinson and Wilson 1994; Davey et al. 2005), fish species richness (Baltz et al. 1982; Ruetz et al. 2003) and abundance of predators (e.g. *Salmo trutta*; Jones 1972; Quist et al. 2004a). Here, we report an exploratory study to determine factors affecting *Cottus* morphology. We explored morphological variation in *Cottus* among Rocky Mountain streams of northeastern Utah in relation to variable abiotic and biotic features.

Methods

Field Studies

We sampled fishes and mesohabitats of wadeable streams in the Wasatch and Uinta mountain ranges of northeastern Utah (Table 1). Streams were within two hydrographic regions (Bonneville Basin, Colorado Basin) of the Middle Rocky Mountain Physiographic Region (Hunt 1974). We sampled within three major river drainages (Bear River, Jordan River, Weber River) and one minor drainage (Centerville Creek) of the Bonneville Basin and one major drainage (Duchesne River) of the Colorado River basin. All fish sampling locations were near U.S. Geological Survey gaging stations, which allowed us to gather large scale water flow measurements.

We sampled fish assemblages in 200 m reaches of each stream (Quist et al. 2004b) that included eight mesohabitats. Each mesohabitat was a distinct section of stream with relatively uniform depth and velocity (e.g. pools, riffles, and runs; Frissell et al. 1986).

We measured water temperature, dissolved oxygen, and total dissolved solids in each mesohabitat prior to sampling fish. We collected fishes via two-pass backpack electrofishing, sampling each mesohabitat separately. We preserved *Cottus* in 10% formalin and transferred them to 70% ethanol after fixation, preserving individuals from each mesohabitat separately. We calculated *S. trutta*, *C. bairdii* and *C. beldingii* abundances as fish captured per second of electrofishing.

After fish sampling, we laid three transects across each mesohabitat (upstream, middle, downstream) and measured water column depth, mean column velocity, bottom velocity, and substrate category (modified Wentworth scale; Cummins 1962) three times along each transect, for a total of nine measurements per mesohabitat (Kerfoot and Schaefer 2006). Point measurements were averaged and linked to all fish captured (Kerfoot and Schaefer 2006). We also measured maximum wetted width of each mesohabitat (Matheson and Brooks 1983).

We also characterized streams with larger-scale variables that affect fish assemblages (Frissell et al. 1986; Quist et al. 2004b). We measured stream slope through the eight mesohabitats and obtained elevation, watershed area, and mean daily discharge from U. S. Geological Survey gaging stations (Maret et al. 1997) and calculated mean discharge and discharge flashiness (Baker et al. 2004) for a five-year period (water years 2003 through 2007). We used principle components analysis (PCA) to determine which environmental variables (all spatial scales considered) distinguished sampling locations.

Ecomorphology

We limited our morphological study to *Cottus* exceeding 72 mm SL to limit ontogenetic bias (Matheson and Brooks 1983; Davey et al. 2005). We measured all bilateral characters on the left side of the fish (Markle and Hill 2000) and divided morphometric measurements by standard length (SL; Kerfoot and Schaefer 2006) to correct for differences in fish size. We made 21 morphological measurements with digital calipers (Kerfoot and Schaefer 2006) and counted lateral line pores and prickles (prickle counts exceeding 99 were scored as 100; Markle and Hill 2000) on each *Cottus* individual (Table 2).

We used PCA to summarize variation in *Cottus* morphology (Kerfoot and Schaefer 2006). We considered PCA axes with eigenvalues exceeding a broken-stick eigenvalue to be biologically meaningful (McCune and Grace 2002). For each biologically meaningful axis, we performed two-tailed t-tests that compared PCA axis scores between *Cottus* species. To aid in interpretation, we plotted regression lines and regression-line slopes for *Cottus* width- and depth-related traits. We used two-tailed t-tests to compare body to caudal peduncle depth, body to caudal peduncle width, and fineness ratio (standard length to body depth; Jobling 1995) between *Cottus* species. We used one-sample t-tests for each *Cottus* species to compare the fineness ratio, a measure of body length versus maximum body diameter with the optimal streamlined body form having a ratio of 4.5, indicative of life in swift-water habitats (Jobling 1995). We used stepwise linear regression to reveal relations between *Cottus* morphology (PCA score) and 17 environmental variables (Table 1) and simple linear regression to reveal relations between *Cottus* morphology and stream bottom velocity.

Results

Field Data

We sampled 16 streams between 15 June and 24 August 2007. Streams varied in watershed size, reach gradient, mean daily discharge, and fish species richness (Tables 1 and 3). A PCA revealed substantial variation in environmental variables along two axes that explained 42.8% of the environmental variation (PCA habitat axis 1: eigenvalue = 5.68; broken-stick eigenvalue = 3.25) and 20.1% of environmental variation (PCA habitat axis 1I: eigenvalue = 2.62; broken-stick eigenvalue = 2.25; Table 4; Fig. 1). Habitat axis I scores were most strongly correlated with stream bottom velocity and wetted width, whereas habitat axis II scores were most strongly correlated with reach slope. Twelve of the 16 streams contained *Cottus*, 10 of which had individuals 72 mm or longer (Table 5). Streams lacking *Cottus* were narrower and had slower currents. Two species of *Cottus* were present, co-occurring in four streams. *Cottus bairdii* was widespread among streams with a variety of velocities and widths and *C. beldingii* was more restricted to larger streams with swifter currents (Fig. 1). When present, *C. beldingii* was more dominant within the fish assemblage than *C. bairdii* (Table 1).

Ecomorphology

We studied 373 individual *Cottus*, 72 to 116 mm SL, from 36 mesohabitats (Table 5). A PCA revealed substantial variation of *Cottus* morphology along one axis that explained 29.2% of the morphological variation (eigenvalue = 6.73; broken-stick eigenvalue = 3.73; Fig. 2). We named this the body shape axis because it revealed a gradient in depth and width (mouth, body, head, and peduncle), head/buccal length, and number of prickles (Table 2). Head, body, and gape width and jaw length increased more rapidly along body shape axis than caudal peduncle width (Fig. 3). Similarly, body and head depth increased more rapidly than caudal peduncle depth (Fig. 3). Hence, wider and deeper *Cottus* had more fusiform (streamlined, tapered from head to tail) bodies. More fusiform *Cottus* had larger mouths, larger buccal cavities, and more prickles. No other axis had eigenvalues exceeding associated broken-stick eigenvalues.

Body shape axis scores differed between species (t = -22.5, df = 79, $P < 0.001$; Fig. 2). The body shape of *C. bairdii* was more fusiform than *C. beldingii* with more prickles, higher body depth to caudal peduncle depth (t = 6.35, df = 80, $P < 0.001$), and higher body width to caudal peduncle width (t = 6.9, df = 77, $P < 0.001$). The mean fineness ratio also differed (*C. bairdii* = 4.3 ± 0.024 SD; *C. beldingii* = 5.0 ± 0.32 SD; t = -17.1, df = 97, $P < 0.001$). Mean fineness ratio of each species differed from the optimum (4.5; *C. bairdii*: t = -5.0, df = 57, $P < 0.001$; *C. beldingii*: t = 25.8, df = 314, $P < 0.001$). Mean difference from the optimum was small, but greater for *C. beldingii* (0.47) than for *C. bairdii* (-0.16).

In the stepwise linear regression analysis, species richness was added first (step-one model) and significantly explained morphological variation associated with the body shape axis (Table 6). In subsequent steps, stream bottom velocity, *Salmo trutta* abundance, and *C. bairdii* abundance were added, with each addition providing greater than one percent increased amount of variation explained (Table 6). The step-four model

explained 64% of variation in body shape axis scores and subsequent steps added less than one percent of predictive ability, so we deemed the step-four model optimal (Table 6). In all four models, all included variables contributed significantly to prediction of relative body shape (Table 6), but this was not true of higher-step models. More fusiform *Cottus* were associated with greater *S. trutta* abundance, higher fish species richness, greater *C. bairdii* abundance and lower stream bottom velocity. In a simple linear regression, stream bottom velocity explained 23% of variation in body shape axis scores, with more fusiform *Cottus* associated with slower stream bottom velocities (F = 110*, df = 1, 371, $P < 0.001$).

Discussion

It is possible that the phenotypic variation we observed among Rocky Mountain *Cottus* indicated plasticity or variation in natural selection pressures among habitats (Chivers et al. 2001; Miner et al. 2005). *Cottus* with tubular bodies that lived in swifter habitats may have been less active swimmers due to the active swimming energy cost associated with reduced streamlining, and more prone to hiding among substrate interstices (Bond 1963; Finger 1982; Jobling 1995). Individuals born with more tubular bodies may have a competitive advantage, or individuals developing in swift-water habitats may develop more tubular bodies as they grow (Langerhans et al. 2003; 2007). Active-swimming *Cottus* may have been less competitive, more susceptible to predation, or physically unsuited for swift-water habitats (Ruetz et al. 2003; Zimmerman and Vondracek 2007). Regardless, correspondence between phenotypic and environmental variation was interpretable.

Water velocity versus *Cottus* morphology

Relation of *Cottus* morphology with current velocity is consistent with trends among fishes (Langerhans 2008). A near-optimal fineness ratio, characteristic of *Cottus*, indicates specialization to reduce drag and increase acceleration (Webb 1984; Jobling 1995). *Cottus* of slower water may develop more fusiform bodies (Kerfoot and Schaefer 2006) or fusiform individuals may have higher survival rates in habitats where active swimming is an advantage (Chivers et al. 2001). We observed a range of *Cottus* phenotypic variation along a continuum from a cryptic, swift-water, large-substrate specialist (*C. beldingii*) to a more active habitat generalist (*C. bairdii*). A dichotomy in body-shapes between *Cottus* species has been previously noted (Simon 1946; Beckman 1970; Simpson and Wallace 1978), but perhaps not emphasized in recent texts due to intraspecific variation and interspecific overlap.

Interspecific segregation by current velocity is common among *Cottus* (Finger 1982; Matheson and Brooks 1983; White and Harvey 1999) including between *C. bairdii* and *C. beldingii* (Quist et al. 2004a). The less-fusiform body of *C. beldingii* is consistent with its habit of hiding in interstices of large substrata (Bond 1963; Finger 1982), where sustained swimming is unimportant. Improved burst swimming corresponding with relative caudal peduncle size (Langerhans et al. 2004) may facilitate movement among interstices. Lack of prickles may facilitate movement through interstices (Bond 1963). In contrast, the more-fusiform body of *C. bairdii* may be adaptive for life above the

substrata, which requires more frequent and sustained swimming (Robinson and Wilson 1994; Langerhans et al. 2003). Although to our knowledge it has not been previously proposed, axillary prickles of *C. bairdii* could reduce drag, as in dermal denticles of elasmobranchs and ctenoid scales of teleosts (Helfman et al. 1997; Barton 2007).

Cottus beldingii are commonly reported just from the Bear River drainage of Utah (Page and Burr 1991; Sigler and Sigler 1996). The species has been reported from the Colorado River basin in adjacent Colorado (Beckman 1970), but its distribution is poorly known (Wallace 1978; Woodling 1985). We found it in the Jordan and Weber river drainages (Bonneville Basin) and Duchesne River drainage (Colorado River basin) and suspect it occurs widely in both basins in Wyoming, Utah, and Colorado, but it may have a patchy distribution given its affinity for wide, swift streams.

Velocity segregation and corresponding body shape differences are consistent between benthic congeners of several Rocky Mountain fish genera. *Rhinichthys cataractae*, a tubular swift-water specialist, is often segregated from more fusiform congeners (*R. atratulus*, *R. falcatus*, *R. obtusus*, *R. osculus*; Gee and Northcote 1963; Gibbons and Gee 1972). More tubular swift-water catostomids (*Catostomus clarki*, *C. discobolus*, *C. platyrhynchus*) commonly segregate from more fusiform congeners (*C. insignis*, *C. latipinnis*, *C. tahoensis*; Meffe and Minckley 1987; Decker 1989; Gido and Propst 1999). Various combinations of these fishes occur throughout the Rocky Mountains (Maughan 1976; Moyle and Vondracek 1985; Quist et al. 2004b). Repetition of this morphological dichotomy among genera suggests analogous niche segregation.

Ecomorphology

Ecological explanations for morphological variation in *Cottus* appeared more complex than a simple relation with stream bottom velocity because other environmental variables explained much more morphological variation than stream bottom velocity alone. A deeper and wider body may reduce vulnerability to gape-limited predators (Portz and Tyus 2004). *Cottus*, particularly larger individuals, can be invulnerable to predation by gape-limited trout (Chivers et al. 2001), consistent with our finding of more fusiform *Cottus* where *S. trutta* were more abundant and with the regional association between *C. bairdii* and *S. trutta* (our study; Quist et al. 2004a). Tubular *C. beldingii* may have higher burst swimming speed (Langerhans et al. 2004; Langerhans 2006), relying on escape into interstices rather than girth to avoid predation.

To our knowledge, prickles on *Cottus* have not been interpreted as armor, but several observations suggest they could be. First, geographical patterns of prickle abundance in *Cottus asper* parallel patterns of lateral scute development in *Gasterosteus aculeatus* (McAllister and Lindsey 1961). Lateral scutes protect *G. aculeatus* from predators (Reimchen 1988, 2000). Second, prickles on *C. bairdii* are concentrated on the widest part of the body and may combine with body width to reduce ingestibility and increase escape probability (Reimchen 1988, 2000). Third, in some *Cottus*, prickles are absorbed in larger individuals (Koli 1969). Smaller *Cottus* that are susceptible to predation from a wider range of fishes may have greater need for protection. And fourth, *C. beldingii* that inhabit interstices of large substrata presumably have an effective refuge from fish predation (Brown 1991) and, correspondingly, lack prickles.

Salmo trutta are non-native to North America and their predation could influence relative distributions of *Cottus* species and phenotypes. Non-native *S. trutta* may affect North American *Cottus* differently than natives (Zimmerman and Vondracek 2007) and are a more successful predator on *C. beldingii* than natives (Jones 1972; Quist et al. 2004a). Influences of non-native fishes on native prey phenotypes have been recently documented (Carlson 2008). If non-native *S. trutta* are affecting *Cottus* specific and phenotypic distributions, *S. trutta* success would facilitate increased dominance of *C. bairdii* and increased prevalence of fusiform *Cottus*.

It is also possible increased competition associated with more fishes, more *S. trutta*, and more *Cottus* (both species) influenced *Cottus* phenotype. Niche overlap between *S. trutta* and *Cottus* suggests competition occurs when food availability is limited (Holmen et al. 2003; Elliott 2006) and habitat segregation indicates competition among *Cottus* species (Finger 1982; Matheson and Brooks 1983). Potential for competition may also be higher in streams with more *Rhinichthys* and *Catostomus* species (Baltz et al. 1982). Thus, a more competitive phenotype should be present where fish densities and fish species diversity are higher.

The morphology and ecology of *C. bairdii* suggest it is a better competitor than *C. beldingii*. The larger mouth and head of *C. bairdii* indicates more efficient ram feeding (Norton 1995) and better ability to capture elusive prey (Norton 1991; Xie et al. 2001). *Cottus* with larger mouths can exploit a wider variety of prey (Northcote 1954; Pasch and Lyford 1972). The larger buccal cavity of *C. bairdii* may also improve suction feeding (Carlson 2008), but this may be offset by increased mouth size (Norton 1995). The bulky head of *Cottus* is advantageous for benthic feeding but compromises their swimming performance (Webb 1984). Thus, trophic interactions appear to be evolutionarily important along with hydrodynamic considerations.

Synergy of environmental factors versus *Cottus* morphology

We cannot determine whether abiotic or biotic variables have greater influence on *Cottus* morphology. They are interrelated. Morphological traits of *C. bairdii* suggest it is better at sustained swimming than *C. beldingii*. This may combine with a larger mouth to allow *C. bairdii* to capture a wider variety of prey, including more elusive prey. A larger head and torso may also make *C. bairdii* less susceptible to predation, facilitating foraging in the presence of gape-limited predators. In contrast, *C. beldingii* is specialized for life in very swift riffles where it occupies interstices among large cobbles. In this habitat, predation risk is low and sustained swimming may be impossible or unnecessary. Abiotic conditions clearly create ecological constraints, but they may indirectly affect *Cottus* phenotype via biotic interactions.

Phenotypic variation within *Cottus* species exhibited the same trend as morphological differentiation between them. This indicates that factors promoting fish species diversity also promote phenotypic diversity. In the absence of congeners, *Cottus* species may occupy a wider range of habitats than in their presence (Finger 1982; Matheson and Brooks 1983). This is likely accompanied by higher phenotypic diversity. However, if other potential predators and competitors also influence *Cottus* phenotypes, as they do *Cottus* distributions (White and Harvey 1999), patterns of phenotypic diversity are presumably complex and will require substantial study to be clearly understood.

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Table 1. Sixteen streams of northeastern Utah sampled between 15 June and 24 August 2007. Dominance (percent abundance) of each *Cottus* species within each fish assemblage, numbers of fish species collected (sp.), and total number of fish collected are given for each stream. Study site numbers correspond to map (Fig. 1).

Streams	*C. bairdii* %	*C. beldingii* %	Sp.	Fish
Bonneville Basin:				
1. Big Creek (Bear River drainage)*	79	0	4	159
2. Blacksmith Fork (Bear River drainage)*	3	83	5	442
3. Little Bear River (Bear River drainage)*	41	0	7	80
4. Silver Creek (Weber River drainage)	0	0	4	304
5. Chalk Creek (Weber River drainage)*	5	9	8	777
6. Lost Creek (Weber River drainage)	17	0	3	35
7. McLeod Creek (Weber River drainage)	14	0	2	133
8. East Canyon Creek (Weber River drainage)*	38	0	9	688
9. South Fork Ogden River (Weber River drainage)*	3	83	6	290
10. Centerville Creek (Centerville Creek drainage)	0	0	1	75
11. Red Butte Creek (Jordan River drainage)	0	0	1	30
12. Provo River (Jordan River drainage)*	27	44	7	296
13. Snake Creek (Jordan River drainage)	0	0	2	83
Colorado River basin:				
14. Rock Creek (Duchesne River drainage)*	0	94	5	406
15. Yellowstone River (Duchesne River drainage)*	0	93	4	328
16. Whiterocks Creek (Duchesne River drainage)*	0	95	4	252

Asterisks (*) indicate locations from which sculpin were measured for morphological analyses

Table 2. Component matrix of axis loadings from PCA of *Cottus* morphological data.

Body Shape Axis	
Upper jaw length	**-0.325**
Lower jaw length	**-0.318**
Body depth	**-0.306**
Body width	**-0.304**
Head length	-0.296
Gape width	-0.295
Head depth	-0.290
Prickle count	-0.272
Head width	-0.240
Buccal length	-0.210
Caudal peduncle depth	-0.195
Caudal peduncle width	-0.177
Mouth depth	-0.136
Standard length	-0.105
Eye diameter	-0.060
Soft dorsal fin height	-0.059
Lateral line pore count	-0.034
Pectoral fin length	-0.025
Caudal fin height	-0.013
Spinous dorsal fin height	0.038
Anal fin length	0.049
Pelvic fin length	0.151
Caudal peduncle length	0.197

Loadings with a score greater than |0.30| (those in bold) are emphasized to highlight patterns

Table 3. Environmental variables used to assess the influence of stream environmental conditions on *Cottus* morphology. The range of each variable associated with measured *Cottus* is given.

Variable	Minimum	Mean ± SD	Maximum
Water temperature (°C)	10.70	15.63 ± 1.909	20.10
Dissolved O_2 (mg/l)	5.70	10.69 ± 1.76	12.80
Total dissolved solids (mg/l)	0.01	0.10 ± 0.124	0.58
Water column depth (m)	0.09	0.32 ± 0.116	1.03
Mean column velocity (m/s)	0.09	0.47 ± 0.73	1.03
Bottom velocity (m/s)	0.06	0.37 ± 0.161	0.65
Substrate category (mm)	0.06	79.29 ± 44.767	234.67
Wetted width (m)	2.70	11.07 ± 4.891	26.10
Slope (m/m)	0.27	1.20 ± 0.527	2.01
Elevation (m)	1444.75	1845.36 ± 199.503	2209.80
Watershed area (km^2)	22.74	343.23 ± 95.103	681.17
Mean discharge (m^3/s)	0.19	1.99 ± 1.499	5.44
Discharge flashiness (R-B Index)	0.05	0.08 ± 0.027	0.13
Salmo trutta abundance (fish/sec)	0.00	0.01 ± 0.030	0.11
Cottus bairdii abundance (fish/sec)	0.00	0.02 ± 0.025	0.08
Cottus beldingii abundance (fish/sec)	0.00	0.05 ± 0.050	0.12
Species richness	2.00	5.33 ± 2.103	9.00

Table 4. Eigenvectors for the first two principle components of habitat parameter data.

Habitat PCA Axis I		Habitat PCA Axis II	
Bottom velocity	**-0.39**	**Reach slope**	**-0.53**
Wetted width	**-0.39**	**Dissolved oxygen**	**-0.38**
Depth	**-0.34**	Column velocity	-0.13
Mean discharge	**-0.34**	Bottom velocity	-0.02
Substrate	**-0.31**		
Column velocity	-0.29	Substrate	0.08
Dissolved oxygen	-0.28	Depth	0.12
Watershed area	-0.28	Watershed area	0.16
Elevation	-0.05	Wetted width	0.18
		Total dissolved solids	0.20
Reach slope	0.04	Elevation	0.26
Discharge flashiness	0.08	Mean discharge	0.28
Water temperature	0.15	**Water temperature**	**0.36**
Total dissolved solids	**0.32**	**Discharge flashiness**	**0.40**

Loadings with a score greater than |0.30| (those in bold) are emphasized to highlight patterns

Table 5. Number of *Cottus* individuals measured for morphological analyses per stream. Number of mesohabitats represented is given in parentheses.

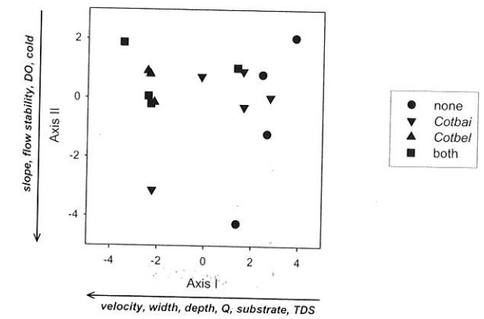
Stream	*C. bairdii*	*C. beldingii*
Big Creek	3 (2)	0
Blacksmith Fork	7 (4)	1 (1)
Chalk Creek	5 (2)	0
East Canyon Creek	18 (6)	0
Little Bear River	5 (3)	0
Provo River	18 (6)	17 (8)
South Fork Ogden River	2 (2)	28 (6)
Rock Creek	0	49 (8)
Whiterocks Creek	0	95 (8)
Yellowstone River	0	125 (8)

Table 6. Stepwise linear regression assessed the influence of 16 variables on body shape axis scores of *Cottus* morphological variation. The body shape axis explained 29.2% of morphological variation (Table 2). Predictors are listed for each regression model.

Step	r^2	F	df	Predictors[1]	B	SE B	B
1	0.54	426*	1, 369	RICH	-1.3	0.07	-0.73*
2	0.59	267*	2, 368	RICH	-1.2	0.07	-0.65*
				BV	4.1	0.57	0.25*
3	0.62	201*	3, 367	RICH	-0.9	0.08	-0.52*
				BV	4.2	0.55	0.26*
				STR	-147.9	27.76	-0.21*
4	0.64	164*	4, 366	RICH	-0.5	0.12	-0.27*
				BV	3.9	0.54	0.24*
				STR	-194.7	28.9	-0.29*
				CBA	-36.7	8.1	-0.26*

[1]Predictor abbreviations: BV = mean bottom velocity, CBA = *Cottus bairdii* abundance, RICH = species richness, STR = *Salmo trutta* abundance

*$P < 0.001$



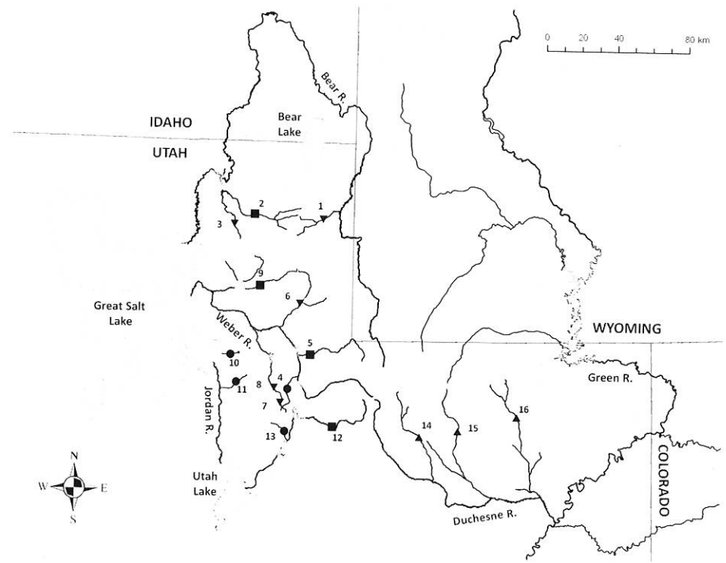


Fig 1. The first two axes of the PCA of stream habitat measurements (top) explained 62.8% (42.8 and 20.1 for Axes I and II) of the variation in habitat parameters. Axis I was most strongly influenced by bottom velocity, wetted width, water depth, mean discharge (Q), substrate category, and total dissolved solids (TDS). Axis II was most strongly influenced by reach slope, discharge flashiness (flow stability), dissolved oxygen (DO), and water temperature. Symbols correspond to *Cottus* assemblages: *cotbai* = *Cottus bairdii*; *cotbel* = *Cottus beldingii*. Map (bottom) shows distribution of study sites (Table 1).

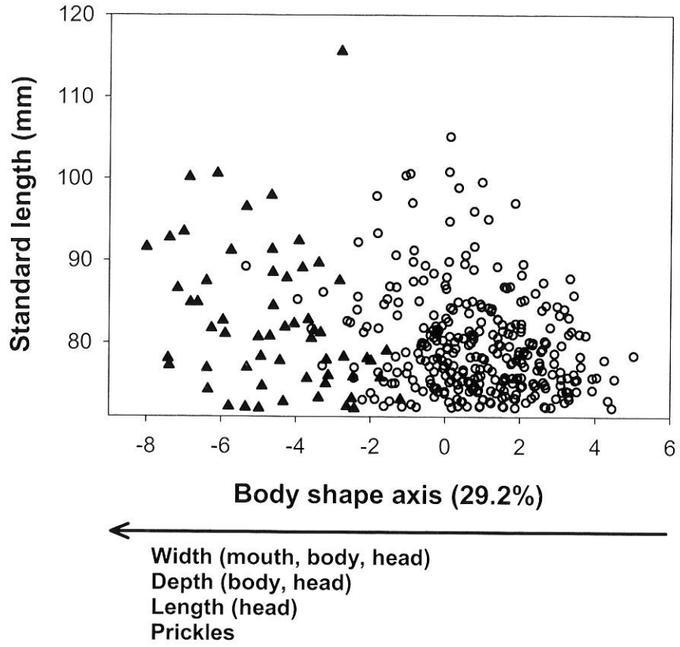


Fig. 2. PCA of *Cottus* morphological data. *Cottus bairdii* are represented by closed triangles (▲) and *Cottus beldingii* are represented by open circles (○). There is a significant difference between species for body shape axis scores (t = -22.5, df = 79, $P <$ 0.001). Morphological variables (Table 2) that most strongly influenced the body shape axis are listed.

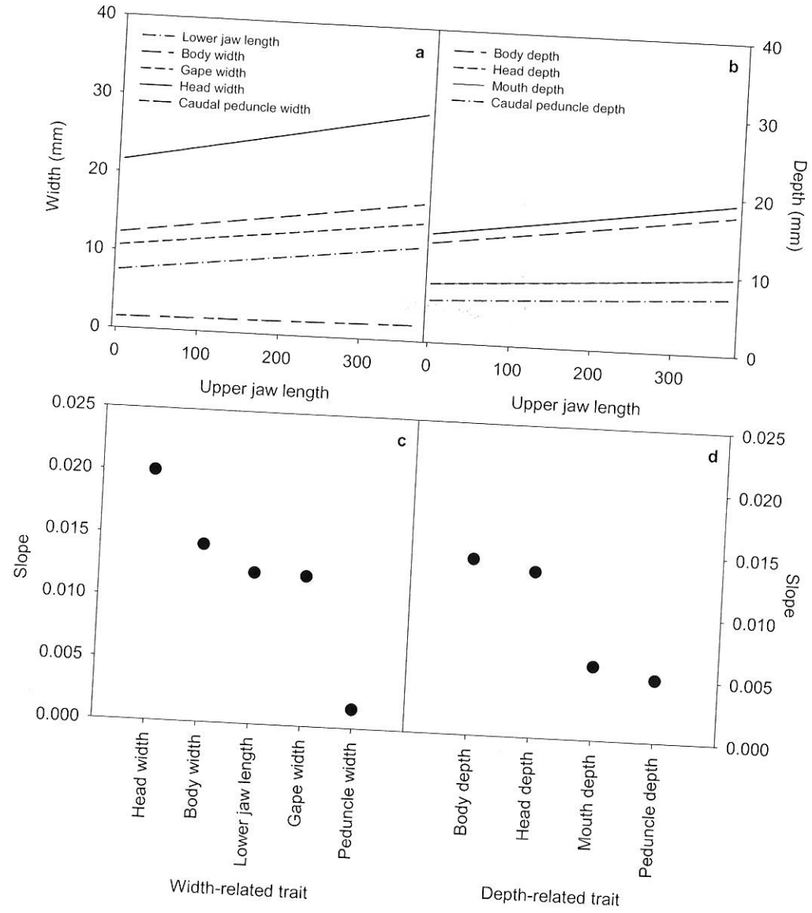


Fig. 3. Change in measures of *Cottus* width and depth for traits associated with the body shape axis. Regression lines of raw data indicate relative change among features of width (a) and depth (b). Regression line slopes are also plotted for width- (c) and depth-related (d) traits.