

Taxonomy and Distribution of the Malheur Mottled Sculpin, *Cottus bendirei*

Abstract

The taxonomy of mottled sculpins (*Cottus bairdi* complex) in Harney Basin, Oregon was reviewed and diagnostic characters were evaluated. The literature and current data support recognition of two species, Malheur mottled sculpin (*C. bendirei*) and Columbia mottled sculpin (*C. hubbsi*). Counts of body prickles on the left side, completeness of lateral line and relative head size were used to classify Harney Basin individuals. Both species occurred in northern Harney Basin and hybrids were found at contact zones in Silver and Silvies rivers. *Cottus hubbsi* appeared dominant in mainstem Silvies R. with *C. bendirei* upstream and in isolated creeks. *Cottus bendirei* was the only species in southern Harney Basin. Both species also occurred outside Harney Basin in the Malheur and Snake rivers, lower Columbia Basin, and probably the upper Columbia Basin. An alternative hypothesis, that these forms represent a single polymorphic species or ecotype, was tentatively rejected because the congruence of morphology and distribution was consistent with two species meeting in a narrow hybrid zone. A better understanding of reproduction, development and the dynamics of sculpin hybrid contact zones is needed to resolve the question.

Introduction

The mottled sculpin complex, *Cottus bairdi* (Girard, 1850), is widespread in eastern and western North America but with a significant distributional gap in central North America. Jenkins and Burkhead (1993) and others have noted that the four recognized subspecies are poorly understood and redefinition of this complex is needed. In western North America two subspecies are recognized by Bond (1963): *C. b. punctulatus* (Gill, 1861) a smooth skin form in the Upper Colorado River and *C. b. semiscaber* (Cope, 1872) of the Columbia R. *Cottus semiscaber* was described from the Upper Snake R. above American Falls (Fort Hall, ID) as prickled above the lateral line and with a lateral line "discontinued on the last fourth of caudal peduncle." Within the Columbia Basin, there are two additional named, but unrecognized, taxa—*C. hubbsi* Bailey and Dimick, 1949 and *C. bendirei* (Bean, 1881).

Cottus hubbsi was described from the upper Columbia River in Washington and Salmon River of Idaho (a lower Snake R. tributary). It is prickled, with a complete or almost complete lateral line and is generally treated as a synonym of *C. b. semiscaber*. However, Peden et al. (1989) suggest resurrecting *C. hubbsi* for "*C. bairdi* of western North American." As demonstrated by Peden et al. (1989), taxonomic problems of the *C. bairdi* complex include other species which are similar or with which they may hybridize—*C. rhotheus*

(Smith, 1882), *C. cognatus* Richardson, 1836, and *C. confusus* Bailey and Bond, 1963.

The Malheur mottled sculpin, *C. bendirei*, was originally collected in Rattlesnake Cr., a small, disconnected stream in Harney Co., Oregon. In the original description, Bean (1881) noted lack of body prickles, four preopercle spines with longest about one half of eye diameter, and three pelvic fin rays. Snyder (1908), examining 30 specimens from Silver Cr., also noted the "entirely smooth" body, but found three or four preopercular spines with the fourth always minute and three or four pelvic rays with the fourth often small. He also reported correspondence with Bean who re-examined the holotype and found a rudimentary fourth pelvic ray on the right side and three on the left. In contrast, Schultz (1936) described *C. bendirei* as having head and body usually with prickles, longest preopercular spine one half to two thirds eye diameter, and three or four pelvic rays. Bond (1963) attributes the discrepancy in body prickles to another form of mottled sculpin from Silvies R. and Donner und Blitzen drainage. The three-or-four pelvic fin ray issue was again discussed by Bailey and Dimick (1949), who also noted the holotype had three on the left and four on the right (based on R. Miller's observations), and by Bond (1963) who noted that *C. bendirei* has a reduced fourth pelvic ray. Bond (1963) also contrasted smooth skin and a longer (complete) lateral line in nominal *C. bendirei* than in Silvies/Blitzen mottled sculpin which he found

are more typical of *C. b. semiscaber*. He also was the first to report the smooth skin form in disconnected streams in other parts of the basin, Riddle Cr. and Silver Cr. In contrast, Bisson and Bond (1971) characterize *C. bendirei* from isolated creeks as having a short lateral line. They also re-classify fish from the Malheur Basin. Donner und Blitzen R. fish plus those from the isolated creeks and Scotty Cr. in the upper Silvies R. have a "pronounced resemblance" to *C. b. semiscaber* as well as "some likeness" to *C. b. punctulatus* (presumably that they are mostly naked). In contrast, heavily-prickled, complete lateral line sculpins of Silvies R. mainstem are "markedly different" and have a greater affinity for nominal *C. hubbsi* of the central and lower Columbia R. Subsequently and without comment on Silvies R. fish, Bond (1983) notes that fish from Donner und Blitzen R. might have light prickles and "not be typical" of *C. bendirei* found in Poison, Devine Canyon, Smyth, Riddell and Silver creeks.

Further complicating the taxonomy of sculpins is evidence of diagnostic characters being influenced by environment or ontogeny. Reduced body prickling has been associated with headwater streams and riffle habitat in some *Cottus* species (Jenkins and Burkhead, 1993) or small size in *C. asper* (Krejsa, 1965). Completeness of lateral line pores has been positively correlated to size in sculpins, hence adults may have a more complete lateral line (Koli 1969; Janssen et al. 1987).

Although the iterations in understanding are confusing, the current wisdom is that Malheur mottled sculpin is a smooth-skinned (non-prickled), reduced lateral line form of the predominantly prickled subspecies, *C. b. semiscaber*, now thought to be broadly distributed in the western U. S. with both smooth and prickled forms. Although its identity and distribution are unclear, the State of Oregon considers the Malheur mottled sculpin (smooth skin *C. bendirei*) as a "sensitive-critical" species because the population in Rattlesnake Cr. is extinct and others are presumed hybridizing with *C. hubbsi* (Bisson and Bond 1971). Because the Malheur mottled sculpin has been labelled "distinct" and "vulnerable to extinction," the purpose of this study was to evaluate diagnostic characters to determine if evidence supports recognition as a distinct taxon, and if so, its current distribution.

Description of Area

Harney Basin, a 5,300 sq. mi. closed depression in Oregon's High Lava Plains physiographic prov-

ince (Figure 1) is bordered by Miocene basalts and evolved as a downwarp assisted by collapsing calderas about 7-9 million years before present (mybp) (Orr, et al. 1992). Its northwestern margin is the Blue Mountains province, a region of uplift and vulcanism at least 65 mybp. The stage of valley development along the northwestern margin suggested to Bisson and Bond (1971) that "ample opportunity has existed for stream capture between the John Day (a Columbia R. tributary) and Silvies drainages". The eastern and southern margins are the basin and range province with Steens Mt. in the southeast and the northwest-trending Brothers fault zone along its western margin (Orr, et al. 1992). During the Pleistocene, Silvies R. is thought to have drained east through Malheur R. to the Snake R. until lava flows dammed the outlet creating Lake Malheur (Hubbs and Miller 1948). Today, the basin has isolated, disconnected creeks plus two shallow ephemeral lakes, Malheur and Harney lakes and their tributaries (Figure 1). A third, smaller lake, Mud Lake, sometimes connects the other two.

Materials and Methods

Museum acronyms are USNM – U. S. National Museum and OS – Oregon State University Fish Collection. Specimens from Harney Basin were grouped into two subbasins: 1) northern - Silver R. and its tributaries; Silvies R. and its tributaries; and isolated northern creeks, including Rattlesnake and Devine Canyon creeks; and 2) southern - Donner und Blitzen R., its tributaries and isolated southern creeks, including Riddle Cr. (Figure 1). Comparisons are made with other *C. bairdi* complex from the Snake R. basin and the Columbia Basin below the confluence with the Snake R. and with *C. confusus* and *C. rhotheus* (Table 1).

Characters selected for study were those identified in the literature. The following measurements were taken with digital calipers - standard length (SL); head length (HL); caudal peduncle depth (CPD); and length of third and fourth pelvic fin rays. Corrections for allometric changes in HL and CPD were made by using residuals from linear regression of the body part on SL. Percent completion of the lateral line was estimated by dividing the distance from the first pore to the last pore by the distance from the first pore to the base of the hypural plates (posterior point of SL

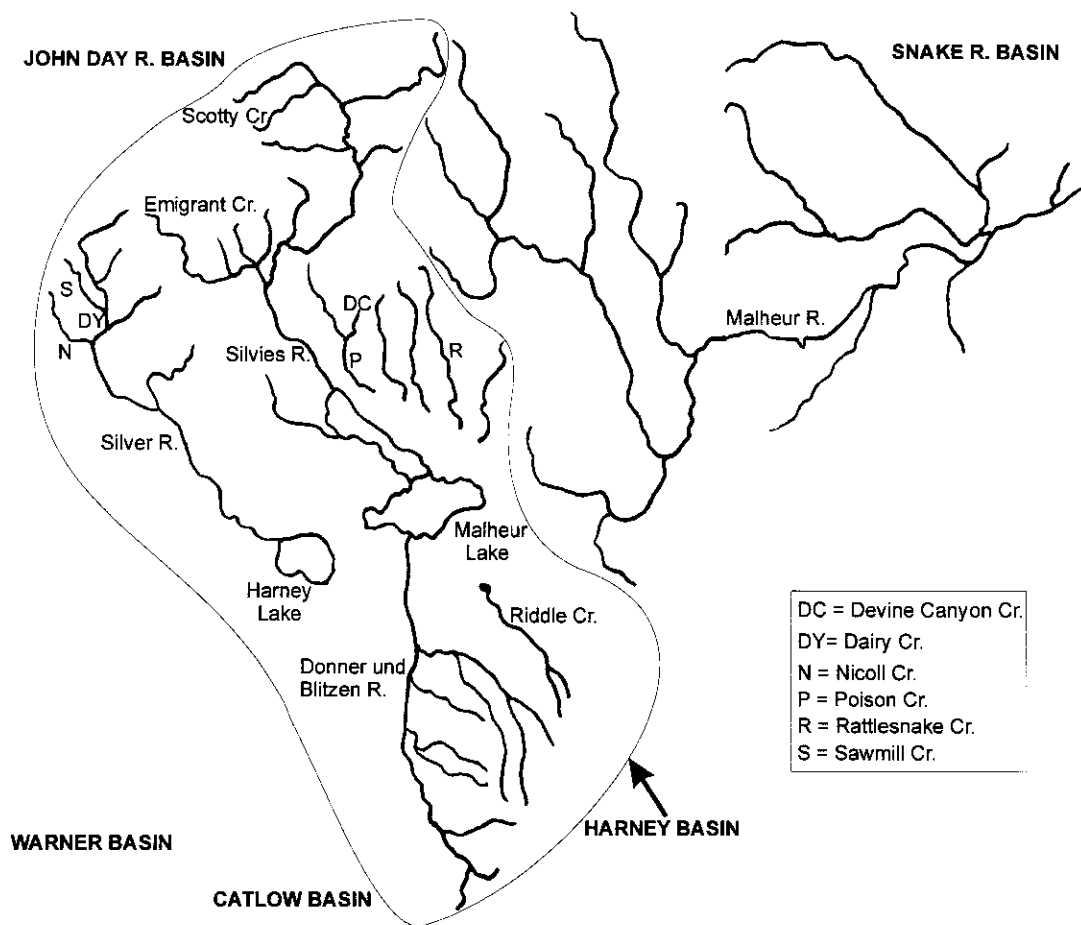


Figure 1. Map of Harney Basin showing major drainages and relationship of the basin to Malheur R. and adjacent basins.

measurement). The last canal pore did not include single disjunct segments on the caudal peduncle but did include multiple disjunct segments. We counted pectoral fin rays; pelvic fin rays; and total number of prickles on the left lateral body surface. Prickles were counted on paper towel- and air-dried specimens under a dissecting microscope and all prickle counts greater than 99 were scored as 100.

Our procedure was to initially restrict the analysis to northern Harney Basin samples. We used number of prickles on the left side (the most obvious bimodally distributed character and the character most often discussed in the literature) to assign specimens to species and evaluated whether other characters corroborated the classification. Statistical analyses were performed using

Statgraphics (Statistical Graphics Corporation, vers. 2.1).

Distributional information is based on literature, museum collections and recent surveys made in northern Harney Basin in 1994 and 1997 and in headwater streams of the John Day R. and western portions of the Malheur R. in 1997. Voucher specimens retained for OS were either fixed in 10% formalin with subsequent preservation in 50% isopropanol, or preserved in 95% ethanol.

Results

Northern Harney Basin

The distribution of prickles on the left side shows three distinct groups with *C. bendirei* having a mean of 2.2 (range: 0-19), *C. hubbsi* a mean of

TABLE 1. List of specimens examined for morphology and distributional information. The number following the catalog number is the number of specimens in the lot. Ethanol preserved samples indicated with asterisk.

Species	Basin	Water body
<i>C. bairdi</i>	Mississippi	Ohio, Mahoning R. USNM 24843 (holotype), 1
<i>C. bendirei</i>	Northern Harney	Sawmill Cr. OS 14890*, 33; OS 14893, 19; OS 14896*, 15; OS 14897, 13; Dairy Cr. OS 14894*, 13; Silver Cr. OS 14898*, 10; OS 14899, 9; OS 15069, 8; OS 15070, 7, OS 15071, 3; Nicoll Cr. OS 14900*; OS 14901* 11; OS 14902, 6; Silver R. OS 16674, 18; Dodson Cr. OS 15068, 10; Wickiup Cr. OS 15072, 5; Scotty Cr. OS 2538, 4; OS 10827, 1; OS 10851, 2; OS 15182*, 5; OS 16703, 15; Emigrant Cr OS 16707, 17; Myrtle Cr. OS 15185*, 3; Camp Cr. OS 15186*, 3; Bear Cr. OS 2540, 2; Rattlesnake Cr. USNM 24196 (holotype of <i>P. bendirei</i>), 1; OS 351, 1; OS 533, 4; Devine Canyon Cr. OS 14889*, 12; Poison Cr. OS 16685, 1; OS 16706, 19.
<i>C. hubbsi</i>	Northern Harney	Silvies R. OS 15183*, 2; OS 15187*, 2; OS 16695, 17; OS 2559, 1; OS 457, 8; OS 2543, 38; OS 2544, 4; OS 2539, 11; OS 2550, 23;
<i>C. bendirei</i>	Southern Harney	Donner und Blitzen R. OS 10383, 3; OS 2547,4 ; OS 325, 3; OS 2548, 18; Mud Cr. OS 538, 9; Big Indian Cr. OS 7432, 5; Kiger Cr. OS 503, 9; Riddle Cr. OS 2541, 55
<i>C. bendirei</i>	Columbia-Snake R.	Malheur R. OS 16708, 18; OS 16687, 1.; OS 16697, 5
<i>C. hubbsi</i>	Columbia-Snake R.	Malheur R. OS 16708, 18; OS 752, 14; Wallowa R OS 619, 1; OS 5813, 4; Imnaha R. OS 5419, 10; St. Charles Cr. OS 5590, 13; Snake R. OS 8366, 4; Boise R.; OS 15529, 5; OS 15531, 5; Powder R. OS 9297, 3
<i>C. bendirei</i>	lower Columbia	Clatskanie R. OS 9809, 2; Willamette R. OS 6810, 4; OS 10028, 1; OS 11021, 1; OS 10208, 1; OS 9403, 1; OS 15731, 2; OS 17088, 5; OS 627, 48; Gales Cr.: OS 14426, 2; OS 14408, 9; OS uncataloged, 16
<i>C. confusus</i>	lower Columbia	Willamette R. OS 544, 3; Santiam R. OS 9978, 5; Columbia R. OS 15608, 2; OS 15600, 4; OS 15601, 4
<i>C. rhotheus</i>	Columbia	John Day R. OS 2552, 4; OS 2556, 3; Willamette R. OS 648, 1; OS 9498, 1; OS 15705, 2; OS 960, 1; Bear Cr. OS 16456, 2; Columbia R. OS 953, 3,
	Coastal	Necanicum R. OS 10934, 5

100+ (range >99), and nominal hybrids a mean of 53.8 (range 33-70) (Figure 2a). There was no difference in SL ($P=0.71$) between *C. bendirei* ($\bar{x}=47.7$ mm), *C. hubbsi* ($\bar{x}=46.3$ mm) and hybrids ($\bar{x}=44.5$ mm). Mean percent completion of the lateral line (Figure 3a) was lowest in *C. bendirei* (89.5%), highest in *C. hubbsi* (98.3%) and intermediate in hybrids (93.2%). Hybrids had the highest variance (Figure 3a). Differences in lateral line completeness between species were significant ($P<0.0001$) as were differences between hybrids and *C. hubbsi* ($P=0.008$). Differences between *C. bendirei* and hybrids were not significant ($P=0.16$). Head lengths were related to SL by the relationship $HL=0.2238+0.3115SL$ ($r^2=96.3\%$, $P<0.001$). Residuals from this relationship showed that for a given size, *C. bendirei* had a significantly ($P<0.001$) smaller head than *C. hubbsi* or hybrids (Figures 3b and 4). Hybrids and *C. hubbsi* were

not significantly different in HL residuals ($P=0.9231$). Caudal peduncle depth (CPD) was related to SL by the relationship $CPD=0.2162+0.0759 SL$ ($r^2=96.2$, $P<0.001$). Residuals from this relationship were not significantly different between species or hybrids ($P=0.62$). The length of the fourth pelvic ray, expressed as a percent of the length of the third pelvic ray, was not significantly different ($P=0.23$) though it tended to be smaller in hybrids and *C. bendirei* (Figure 3c). Number of pectoral fin rays (range 14-16) and number of pelvic fin rays (range 3-4) were not significantly different between species and their hybrids ($P>0.12$).

Cottus bendirei was the dominant or only species in isolated streams and upstream tributaries and *C. hubbsi* was the dominant or only species in the mainstem Silvies R. (Figure 5a). Hybrids were geographically restricted to contact zones

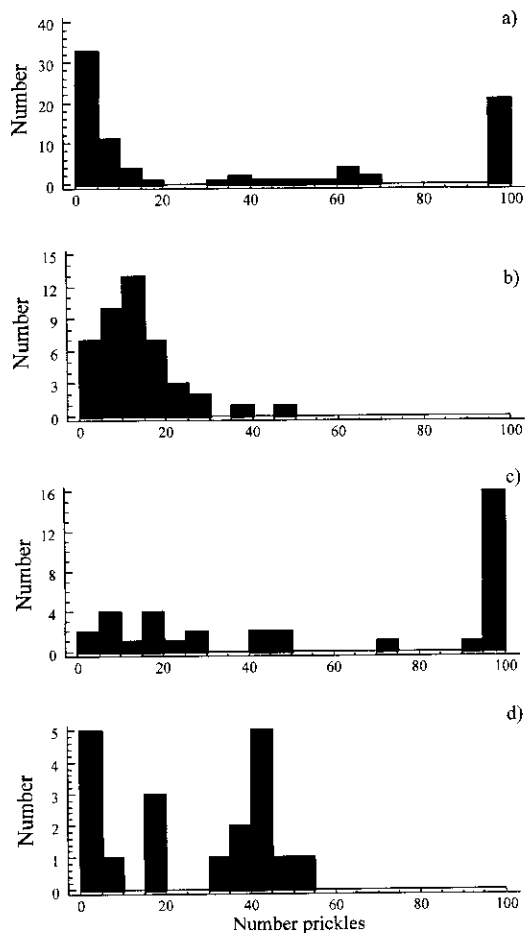


Figure 2. Frequency distribution of number of body prickles on the left side: a) northern Harney Basin; b) southern Harney Basin; c) Snake R. basin, including Malheur R.; d) lower Columbia Basin.

between the two species and were found twice with *C. bendirei* (OS 14897, OS 16707), once with *C. hubbsi* (OS 2544), and once alone (OS 15185 with three specimens).

Southern Harney Basin

There was no evidence of *C. hubbsi* in southern Harney Basin, but counts of body prickles suggested presence of two hybrids (Figure 2b). There was no difference in SL ($P=0.94$) between *C. bendirei* ($\bar{x}=51.3$ mm) and those two fish ($\bar{x}=52.1$ mm). Mean prickle counts of *C. bendirei* in southern Harney Basin were higher (10.1) than in northern fish, but much lower than *C. hubbsi* (Figure 2). Mean percent completion of the lateral line

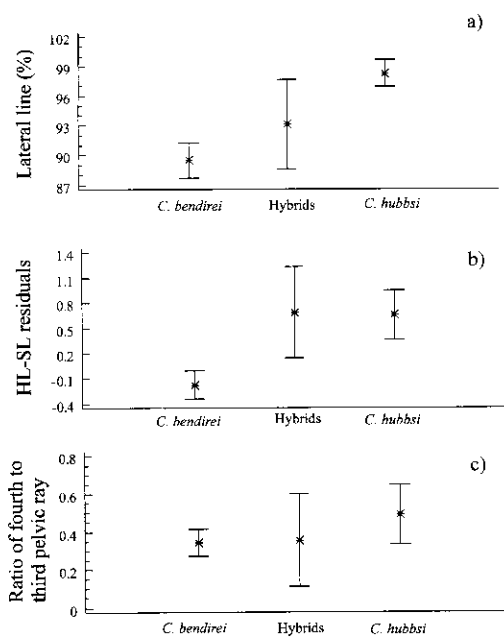


Figure 3. Frequency distribution of selected characters of northern Harney Basin mottled sculpins; a) percent completion of lateral line; b) relative head length, expressed as a residual from the relationship, $HL = 0.2238 + 0.3115SL$; c) relative length of the fourth pelvic fin ray, expressed as a percent of the length of the third pelvic fin ray.

(87.2%) was even lower than in northern *C. bendirei*. Head size, as a residual from the relationship, $HL = 0.2238 + 0.3115SL$, was negative ($\bar{x} = -0.74$), indicating that southern Harney Basin *C. bendirei* have even shorter heads than those from the northern basin.

Snake River Basin

Samples from Snake R. Basin, including Malheur R., contained both species plus hybrids. There was no difference in SL ($P=0.24$) between *C. bendirei* ($\bar{x}=43.6$ mm) and *C. hubbsi* ($\bar{x}=50.4$ mm), but hybrids were significantly ($P=0.04$) smaller ($\bar{x}=29.5$ mm). Mean prickle counts in the Snake River Basin were 11.8 for *C. bendirei*, similar to counts for southern Harney Basin (Figures 2b and 2c). Head size, as a residual from the relationship, $HL = 0.2238 + 0.3115SL$, was not significantly different between species ($P=0.10$), though the mean was smaller for *C. bendirei* (0.25) than *C. hubbsi* (0.61). Mean percent completion of the

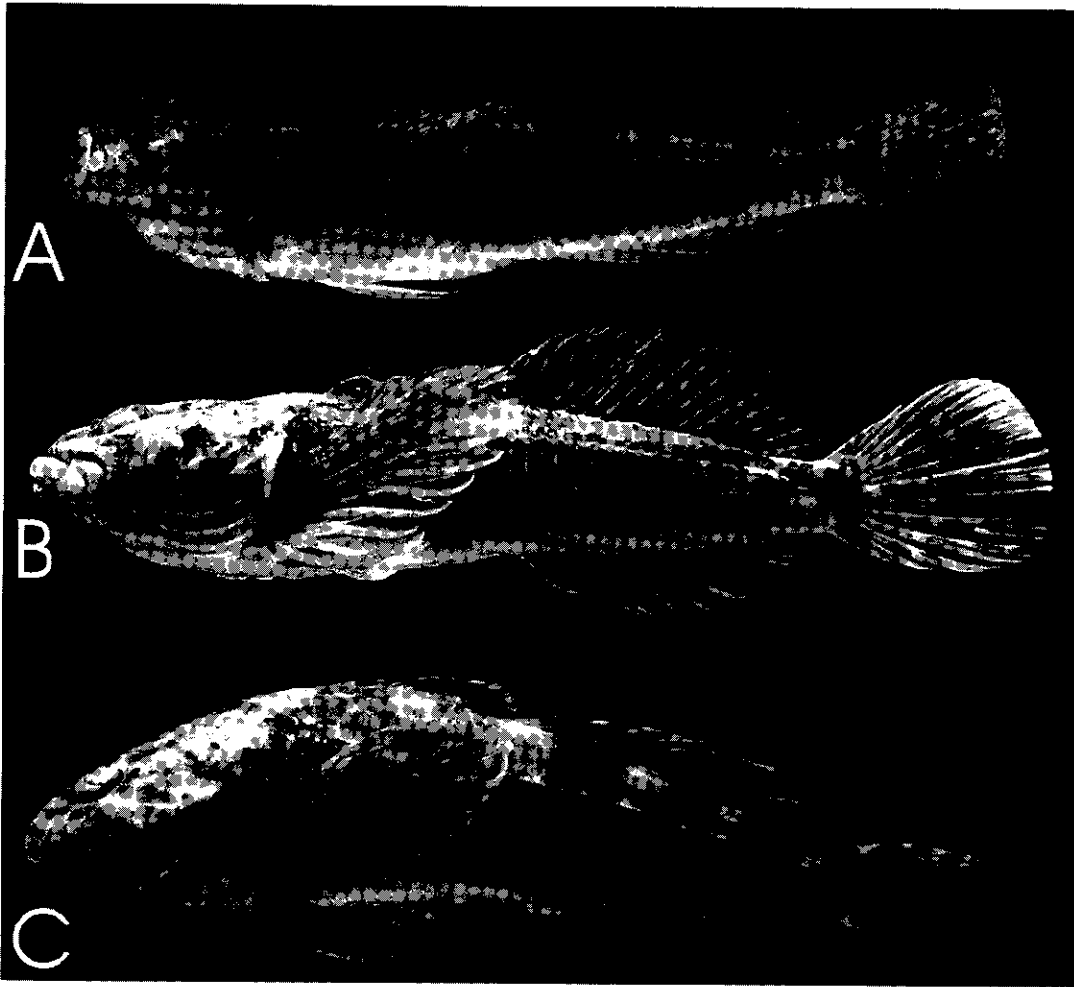


Figure 4. Mottled sculpins from eastern Oregon: a) *C. bendirei*, OS 16706, 81.9 mm SL, Poison Cr.; b) hybrid - *C. bendirei* X *C. hubbsi*, OS 14897, 75.5 mm SL, Sawmill Cr.; c) *C. hubbsi*, OS 619, 70.5 mm SL, Wallowa R.

lateral line was low in *C. bendirei* (93.8%) and high in *C. hubbsi* (98.4%) but differences were again not significant ($P=0.13$). One sample from Drewsey Grange, Malheur R. (OS 16708) contained both species plus hybrids.

Lower Columbia Basin

There was no evidence of *C. hubbsi* in the Willamette R. or lower Columbia Basin, but counts of body prickles suggested a high proportion of hybrids (Figure 2d). There was no difference in SL ($P=0.67$) between *C. bendirei* ($\bar{x}=65.8$ mm) and hybrids ($\bar{x}=63.1$ mm). Mean prickle counts in the lower Columbia Basin were 6.4 for *C. bendirei* and 42.6 for hybrids. Head size, as a

residual from the relationship, $HL=0.2238 + 0.3115SL$, was not significantly different between *C. bendirei* and hybrids ($P=0.52$), but the mean was smaller for *C. bendirei* (-0.56) than for hybrids (-0.21). Mean percent completion of the lateral line was high in *C. bendirei* (97.2%) and even higher in hybrids (98.2%) but differences were again not significant ($P=0.45$).

Distribution of the Western *C. bairdi* Complex

Members of the *C. bairdi* complex are widely distributed in western North America (Figure 5b). In the upper Columbia they are known from Yakima, Okanongan, Similkameen and Methow

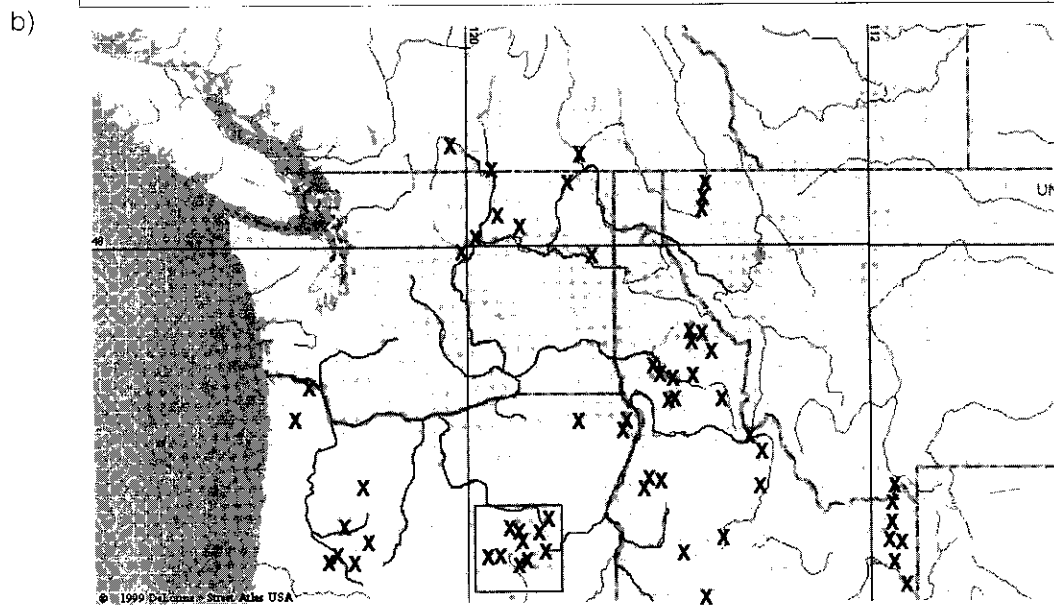
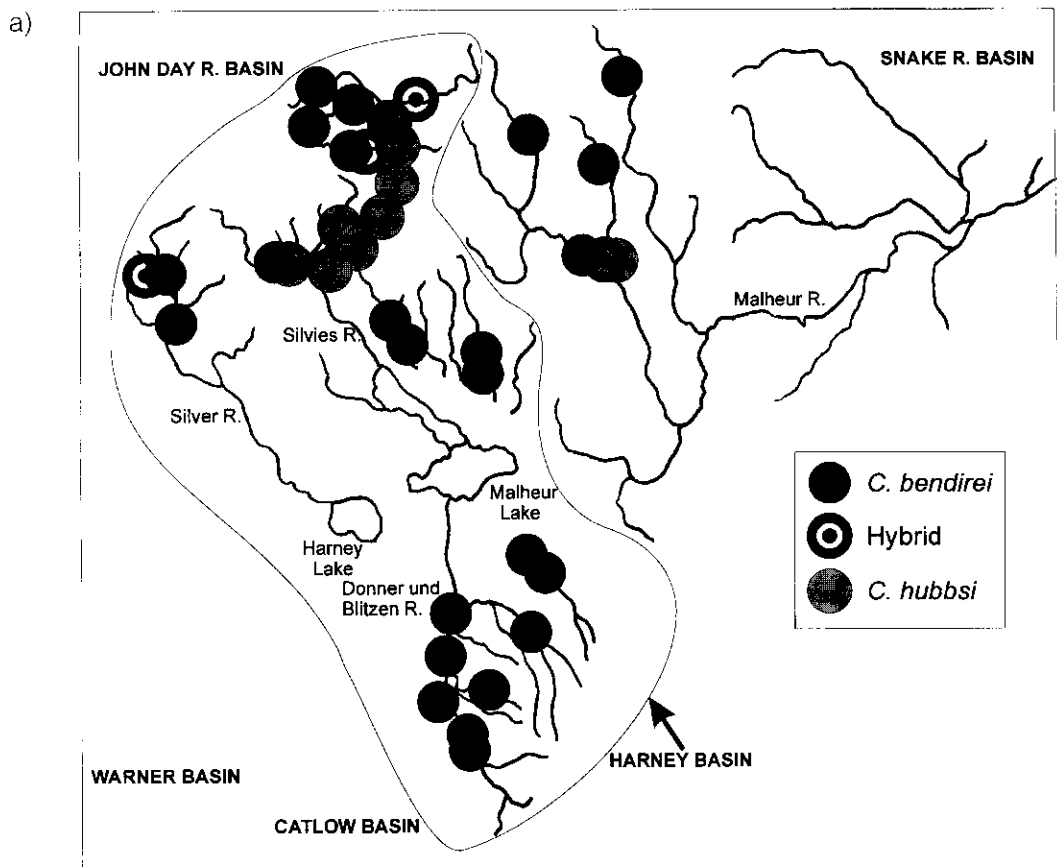


Figure 5. a) Map of Harney Basin showing distribution of *C. bendirei*, *C. hubbsi* and their hybrids. b) Map of Columbia Basin showing distribution of *C. bairdi* complex. Upper Columbia records from Peden et al. (1989); Idaho records from Simpson and Wallace (1978); Oregon records from this study. Box outlines area of map above.

ivers (Peden et al 1989; M. Hallock, Washington Dept. Fish and Wildlife, pers. comm, 1999). However, they are noticeably absent from the mainstem of lower and middle Columbia R., the mainstem of the Willamette R., all of the Deschutes R., all of the John Day R., and the lower Snake R. Bisson and Bond's (1971) table showing it in the John Day R. may be erroneous. During recent directed surveys in and around Harney Basin, no mottled sculpin were found in the John Day drainage and recent field biologists are unaware of its presence in John Day drainage (H. Li, pers. comm., June, 1999, Oregon Cooperative Fisheries Research Unit). A single specimen (OS 5512) is known from the John Day drainage but it can not be the basis for Bisson and Bond's (1971) record because it was collected five years later (1976) by an ichthyology class. The location is presumed in error pending additional verifiable collections. Also a Puget Sound record (Wydoski and Whitney 1979) is now believed to be a mis-identification (M. Hallock, Washington Dept. Fish and Wildlife, pers. comm, 1999).

Disjunct distributions were also evident at smaller spatial scales. In the Willamette and lower Columbia, most *C. bendirei* were downstream near the mouth of the Willamette and Clatskanie rivers while hybrids were upstream (Figure 5b).

Discussion

The literature and current data support our hypothesis of two species of mottled sculpins, *C. bendirei* and *C. hubbsi*, in Oregon. Fish from northern Harney Basin most clearly supported our hypothesis, in part, we believe, because of large sample sizes and broad distribution of sample sites (Table 1; Figure 5a). Both species segregated geographically (Figure 5a) and had geographically restricted contact zones in which hybrids were found. *Cottus hubbsi* appeared restricted to river mainstems (primarily Silvies R.) while *C. bendirei* was in smaller tributaries and disconnected streams.

Hybrids are often, though not always, intermediate in characters between parent species (Neff and Smith 1979; Leary et al 1985). Our preliminary identification of northern Harney Basin hybrids is based on intermediacy of prickles (Figure 2a) and lateral line completion (Figure 3a) plus the inconsistent patterns found in other characters. For example, hybrids were more like *C.*

hubbsi in head length (Figure 3b) but more like *C. bendirei* in reduction of the fourth pelvic fin ray (Figure 3c). In addition, most hybrids were found in areas where both species come in contact (Figure 5a) and four of five samples with hybrids also contained one or both parent species.

Southern Harney Basin also was well sampled and sample sizes were large (Table 1; Figure 2), but we believe only one species, *C. bendirei*, was present. Two specimens with more than 35 prickles must be considered questionable. Diagnostic characters useful in the northern part of the basin also applied here. In fact, head size was even smaller and the lateral line was even less complete than in northern basin *C. bendirei*, thus differences with northern Harney Basin *C. hubbsi* were greater.

Sample sizes were small for Malheur and Snake rivers, but diagnostic characters again followed the pattern from northern Harney Basin. However, prickle counts for *C. bendirei* were more similar to southern Harney Basin (\bar{x} =11.8 and 10.1, respectively) than to northern populations (\bar{x} =2.2). Other diagnostic characters, head length residuals and lateral line completeness, were not significant (P =0.10 and 0.13, respectively), but did follow the northern Harney Basin pattern with *C. bendirei* having shorter heads and more incomplete lateral lines.

Sample sizes for lower Columbia Basin fish were also small. All fish in the lower basin (Gales Cr. and Clatskanie R.) were *C. bendirei* and most in the upper Willamette tributaries were hybrids. We found no specimens of *C. hubbsi*, which makes the identification of hybrids questionable. As in Snake R. samples, the three diagnostic characters follow the northern Harney Basin patterns, but the two morphological measurements were not significant. More work is required to resolve the taxonomic status of Willamette R. mottled sculpins.

Identification of individuals is not easy and may require drainage-specific criteria. At this stage in our understanding, we believe these species can be diagnosed by the number of prickles on the left side of the body, with *C. bendirei* having less than 30 and *C. hubbsi* more than 90. Hybrids were intermediate. Two additional characters, residuals from the relationship, $HL = 0.2238 + 0.3115SL$, and completeness of the lateral line, corroborated identifications, with *C. bendirei* having a smaller head and more incomplete lateral line than *C. hubbsi* (Figure 4).

The diagnoses of these forms may apply to Upper Columbia Basin specimens evaluated by Peden et al. (1989). In that study, specimens with prickles present were identified as "nominal *C. bairdi* and (or) *C. hubbsi*" while those with fewer than 10 prickles and smaller heads were identified as "nominal *C. confusus*". The latter characters are consistent with *C. bendirei*. As in this study, the distribution map in Peden et al. (1989) shows that the two species are usually geographically segregated.

Bison and Bond (1971) suggested that many fish in Harney Basin "originated from the basin's Pleistocene connection with Malheur River" and also implicated stream capture between the Silvies and John Day drainages to explain the lower Columbia fish fauna found in central Silvies R. Although their stream capture explanation might apply to other fishes, there is no evidence of *C. bairdi* complex in the John Day drainage and it seems most likely that the presence of these sculpins in Harney Basin preceded any stream capture involving the John Day drainage. Coexistence of two species in northern Harney Basin, the Malheur R., and possibly the Upper Columbia R. suggests differentiation occurred prior to Pleistocene isolation of Harney Basin. Because Harney Basin had a Pleistocene connection with the Malheur R., the simplest explanation for the pattern is that differentiated species coexisted prior to the Pleistocene isolation of Harney Basin.

Peden et al. (1989) suggest the need to examine characters of *C. bairdi* complex in terms of

their relationships to habitat, especially upstream and downstream variants, and in terms of possible hybrid influences from other sculpins. The forms we identified could be ecotypes rather than species. In Harney Basin, *C. bendirei* was most common upstream in smaller or isolated creeks whereas *C. hubbsi* was common in mainstem Silvies R. However, the upstream-downstream pattern did not hold in the Willamette and lower Columbia nor does it appear to hold in the upper Columbia (Peden et al 1989). Habitat partitioning is expected of ecotypes as well as closely related species and does not resolve the question. The congruence of morphology and distribution, however, was consistent with two species meeting in narrow hybrid zones. A better understanding of reproductive requirements, morphological differentiation, demographics and genetics of these species especially in contact zones in Silvies and Malheur rivers would greatly increase our understanding of western *C. bairdi* complex.

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