Origin and Distribution of the Fishes of Harney Basin, Oregon

Peter A. Bisson and Carl E. Bond

Reprinted from Copeia, 1971, No. 2, June 1
pp. 268–281
Made in United States of America

Origin and Distribution of the Fishes of Harney Basin, Oregon

PETER A. BISSON AND CARL E. BOND

Recently discovered evidence suggests that the Harney Basin fish fauna originated through two geographically and chronologically distinct invasions from separate tributaries to the Columbia River system.

Blitzen River, the hydrographically and ecologically isolated creeks, and the upland tributaries to Silvies River all contain populations derived from the basin's Pleistocene connection with Malheur River of the Snake drainage. Colonization of many streams took place during periods of high precipitation; isolation has resulted from desiccating trends since the last glaciation.

Stream capture has apparently facilitated a secondary invasion of fishes into Silvies River from John Day River, a tributary to the Columbia, entering 218 miles from the mouth of the Columbia. This conclusion is supported by similarities between several Silvies River and John Day River species, and by the restriction, within the basin, of two species to Silvies River. Populations similar to those occurring in isolated regions of the Harney Basin also exist above the barrier falls of the south fork of John Day River, but this drainage is believed to be another disrupted fragment containing descendents of a more ancient Columbia fauna. Speculation regarding the sequence of dispersal throughout the Columbia system is aided by distributional patterns and knowledge of hydrographic history.

INTRODUCTION

Description and History of the Area

THE Harney Basin, once a part of the Columbia River system, presently comprises the northernmost part of the Great Basin and is one of the largest internal drainages in the high lava plains of eastern Oregon. Malheur and Harney lakes, which have undergone varied fluctuation in historical time, are the playa remnants of Lake Malheur, which formerly received a great deal of the precipitation and runoff that followed late Pleistocene glaciation (Van Winkle, 1914; Piper *et al.*, 1939). Two primary rivers in the basin, Silvies River and Donner und Blitzen River (Blitzen River), drain into Malheur Lake. Their upland tributaries are cold, swift, mountain streams with rocky bottoms, while the lower reaches are slow, warm in summer, and have sandy or muddy bottoms. Highly alkaline Harney Lake is fed by Silver Creek and by a cluster of warm springs on its southwestern border. Isolated creeks that dissipate into alluvial debris and natural meadows occur in the northeast and southeast regions of the basin. Their structural and biological features are similar to those of the upland tributaries of the adjacent rivers. Peripheral topography of the area reveals that many of the streams in the basin bear close spatial relationships with upland tributaries of both the lower Columbia, represented by John Day River, and the Snake drainage by its tributary Malheur River. Harney Basin is also bounded on the southeast by the Alvord Desert and on the southwest by Catlow Valley and the Warner Lakes Basin. None of these isolated drainages has apparently influenced the distribution of fishes in the Harney Basin (Hubbs and Miller, 1948), although these authors (1942, 1948) suggested that both the Catlow and Warner faunas may have been derived from the Harney Basin during "earlier pluvial" overflows of the lakes in their respective basins.

The physiography of the Harney Basin is divided into two general areas: a central lowland occupied by playas and dry lake beds, alluvial plains, and lava fields, surrounded by elevated erosional plains bounded by a dissected fault-block upland (Piper *et al.*, 1939). Malheur Lake has the largest area of the playas but is very shallow, being less than 3 m at its greatest depth. Because its lake bed slopes only slightly, lake boundaries fluctuate tremendously according to prevailing climatic conditions. Any surplus runoff spills westward into Mud Lake and occasionally through a narrow sand gap into Harney Lake. The northwestern erosional plain, the Ochoco-Silvies surface, is a piedmont slope formed during the Pliocene following the formation of the Columbia River basalt flows (Dickenson, 1958). This plain has since been dissected by the south fork and part of the main fork of John Day River. The stage of valley development suggests that ample opportunity has existed in the past for stream capture, and consequent fish transfer, between the John Day and Silvies drainages.

The eastern periphery of the basin consists of relatively recent lava flows and cinder cones. Youngest are the Diamond Craters (Russell, 1903) whose lava field dammed the Barton Lake basin and diverted Kiger Creek toward the west making it accessible to Blitzen River fishes. An older and more extensive basalt flow, the Voltage lava field, extends from Diamond Craters to Malheur Lake and northward to part of the Malheur River valley (Piper *et al.*, 1939). This flow dammed Malheur Gap, through which water from the Harney valley had formerly drained into Malheur River. Several authors (Piper *et al.*, 1939; Hubbs and Miller, 1948) have inferred that the Voltage eruption occurred during the late Pleistocene or early Recent epochs. Its sudden extrusion resulted in the formation of Pluvial Lake Malheur. (The term "Pluvial" is here used in the sense defined by Hubbs and Miller, 1948.) Russell (1905) and Baldwin (1959) have suggested that water from the lake flowed through Crane Gap after the Voltage eruption, but Piper *et al.* (1939) stated that no drainage has passed through this area during latest geological time. Whether or not Lake Malheur ever overflowed the dam at Malheur Gap is also undecided. Occurrence of such an overflow could have facilitated a secondary invasion of fishes into the basin from Malheur River. Russell (1905) and Waring (1909) concluded that the lake never rose to a level where discharge would have taken place, yet Piper *et al.* (1939) noted that the highest beach ridge entered the gap in an "ill-defined drain." However, they also stated that the divide on the gap floor stands 2.8 m above the level of the highest beach ridge.

Hansen (1947) divided the postglacial climate of the northern Great Basin into four main stages, based on pollen profile succession. The first major interval immediately following Wisconsin glaciation persisted until 15,000 years ago and was cooler and moister than the present. Stage two saw a period of gradually increasing warmth and dryness which continued until about 8000 years ago. This was followed by a third interval of generally high temperatures and extensive desiccation lasting 4000 years. Many of the lakes occupying the Great Basin region were thought by Heusser (1966) to have completely dried. There is nothing in the geological evidence to indicate whether or not Pluvial Lake Malheur did so, although Hansen (1947) stated that this warm, dry climate was most pronounced in the timberless areas of eastern Washington and Oregon.

The latest climatic trend in postglacial times has been a return to cooler and wetter conditions (Hansen, 1947; Heusser, 1966). Historical records based mainly on tree-ring evidence suggest that annual precipitation during this period has not been stable. The climate during the last millennium appears to have undergone marked and rather erratic oscillations from hot-dry to cool-moist condi-

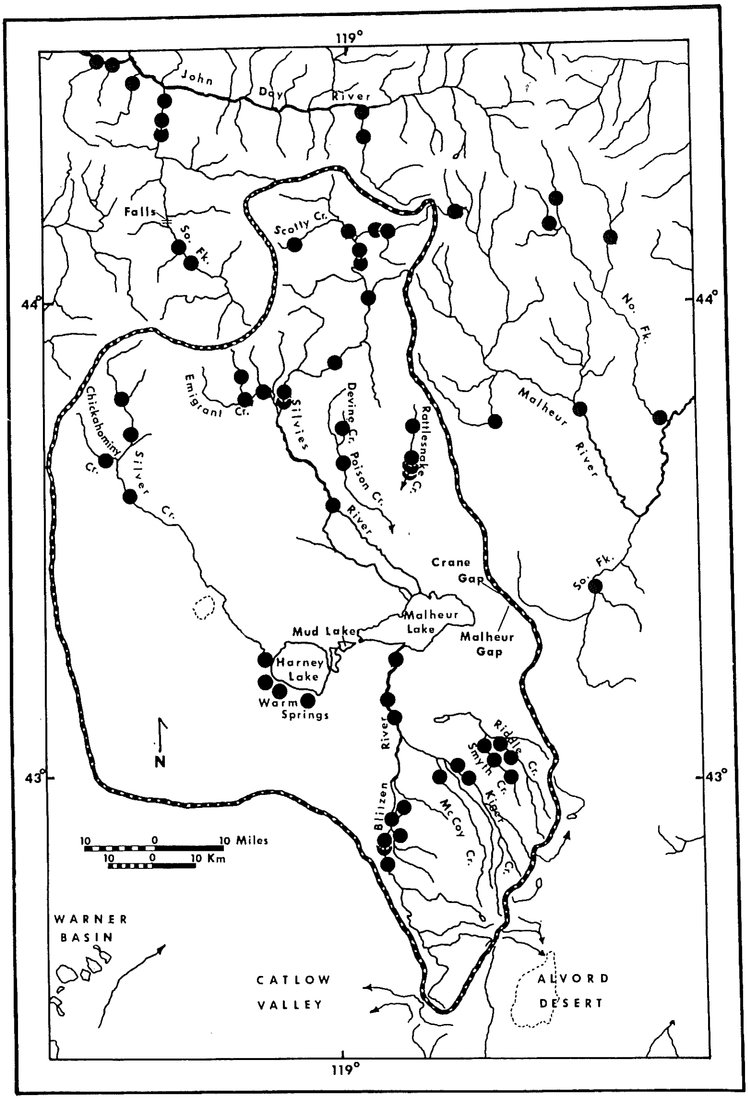

Fig. 1. Harney Basin and adjacent drainages, showing collection sites of fish examined during the study.

extremes in the Harney Basin have a more profound effect on these shallow creeks than on deeper rivers, hence their environments are much less stable. The result in every case has been a marked species paucity, with creek inhabitants being those able to cope with the rapidly changing conditions. Such observations fit well with the theory of Sheldon (1968) that depth is of prime importance in regulating the diversity of stream fishes, as well as the suggestion of Connell and Orias (1964) that increased stability of the physical environment ultimately accommodates a more diverse fauna.

Examination of the affinities of certain species by means of discriminant function analysis (Table 2) also reveals some interesting correlations. Populations of *Richardsonius balteatus* and *Rhinichthys cataractae* inhabiting Blitzen River and the faunally isolated creeks show a strong alliance to Malheur River stocks. However, in central Silvies River the affinity of *R. balteatus* shifts to John Day River. *P. oregonensis* and *C. mac-*

TABLE 1. KNOWN DISTRIBUTION OF FISHES IN THE HARNEY BASIN AND ADJACENT DRAINAGES.

	Richardsonius balteatus	*Gila bicolor*	*Acrocheilus alutaceus*	*Ptychocheilus oregonensis*	*Rhinichthys cataractae*	*Rhinichthys osculus*	*Catostomus columbianus*	*Catostomus macrocheilus*	*Salmo gairdnerii*	*Prosopium williamsoni*	*Cottus bairdi*
Malheur R.[1]	×	×	×	×	×	×	×	×	×	×	×
Blitzen R.	×	×		×	×	×	×		×	×	×
Kiger Cr.	×				×	×	×		×		×
McCoy Cr.	×					×			×		
Riddle Cr.	×					×			×		×
Smyth Cr.	×					×			×		
Silver Cr.	×	×			×	×	×		×		×
Chickahominy Cr.	×	×				×			×		
Warm Springs	×	×				×	×				
Poison Cr.						×			×		×
Devine Cr.						×			×		
Rattlesnake Cr.						×			×		×
Silvies R.	×	×	×	×	×	×	×	×	×		×
Scotty Cr.						×			×		×
Emigrant Cr.	×				×	×	×		×		
John Day R.[1]	×		×	×	×	×	×	×	×		×
So. Fk. John Day (above falls)[1]	×					×	×		×		

[1] Species present in adjacent drainages but not found in the Harney Basin include: Malheur R.—*Lampetra tridentata*, *R. osculus* (= *Rhinichthys umatilla*), *Cottus beldingi*, *Cottus confusus*, *Cottus rhotheus*; John Day R. —*Lampetra tridentata*, *Catostomus platyrhynchus*, *Salmo clarki lewisi* (possibly introduced), *Cottus beldingi*, *Cottus confusus*, *Cottus rhotheus*; So. Fk. John Day R. (above falls)—*Catostomus platyrhynchus*.

rocheilus in Silvies River also exhibit similar alliances. The sample of *P. oregonensis* from Blitzen River is too small to judge, although it does follow the pattern of the other species. While the affinities of *R. cataractae* in central Silvies River are almost equally divided between John Day and Malheur river stocks, there is a much higher proportion of individuals allied to John Day River in Silvies River than in the other streams of the basin.

A few anomalies are apparent. The affinities of *R. balteatus* and *R. cataractae* inhabiting Emigrant Creek, an upland tributary of Silvies River, are similar to those in other Harney Basin streams; they appear closely related to Malheur River populations. The same is true for *R. balteatus* above the falls of the south fork of John Day River. Fig. 4 illustrates the variation in numbers of anal fin rays in different populations of the redside shiner; those occurring in the various isolated creeks, Blitzen River, Emigrant Creek, and above the falls of the south fork of John Day River possess considerably fewer anal fin rays than populations in Silvies and the mainstream of John Day River. These fish represent *Richardsonius balteatus hydrophlox*, which exists in several isolated drainages of the Columbia system, including the upper Snake (Gilbert and Evermann, 1894). Specimens from Silvies and John Day rivers are the common lower Columbia subspecies *R. b. balteatus*. Characteristics of Malheur River populations of the redside shiner tend greatly towards *R. b. hydrophlox* although considerable overlap suggests that both forms, and possible intergrades, are present. The overlapping ranges of anal, as well as dorsal and pectoral fin ray counts, have resulted in the moderate degree of misclassification by discriminant function analysis for this species in Malheur River. The relationship between low temperatures and reduced numbers of anal rays reported for *R. balteatus* by Lindsey (1953) does not appear to be a major

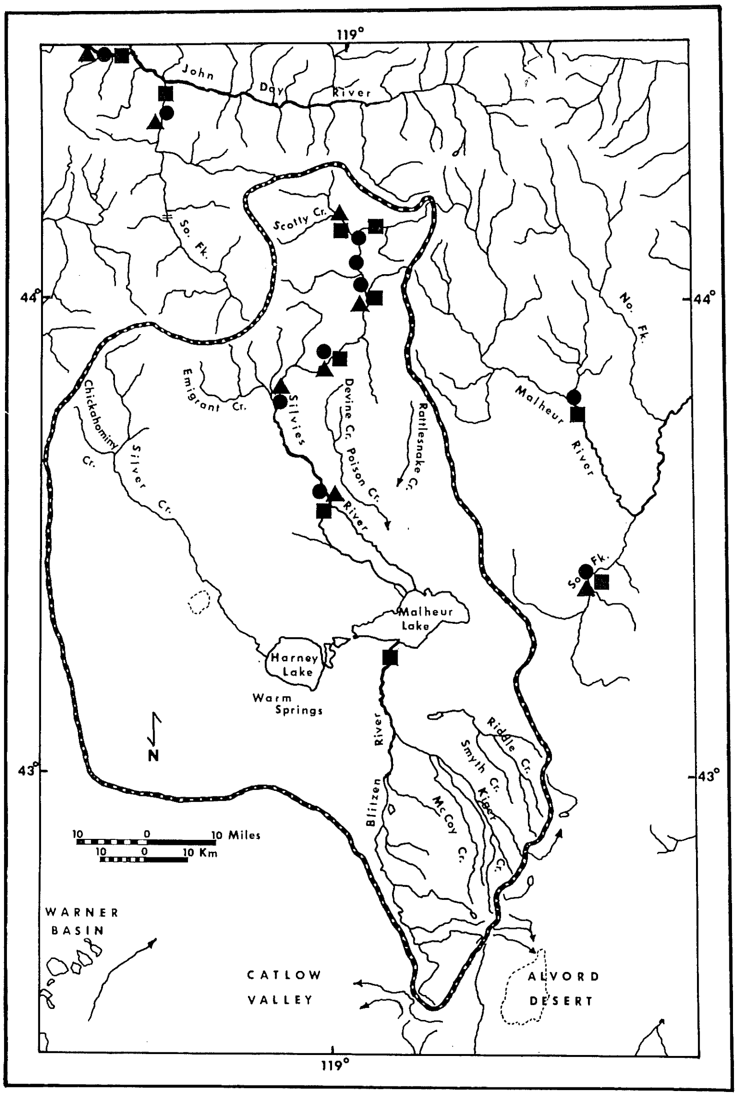

Fig. 2. Sites of collections of *Acrocheilus alutaceus* (circles), *Ptychocheilus oregonensis* (squares), and *Catostomus macrocheilus* (triangles), in the Harney Basin and adjacent drainages.

factor here. Recorded temperatures in Silvies River and tributaries are similar to temperatures in Blitzen River and tributaries and in Smyth and Riddle creeks for given months. Specimens from the south fork of the John Day River, which has a temperature average of less than 20° C through July, differ sharply above and below the falls. Lindsey showed that populations of *R. b. balteatus* from waters of 20–26° C during development had mean anal ray counts of 16 to over 17. In the present study *R. b. hydrophlox* from the warm springs (24–27° C) had a mean anal ray count of 10.6.

Several species in the Harney Basin possess characters that deviate from those in the populations inhabiting adjacent drainages. The frequency of occurrence of maxillary barbels in *Rhinichthys osculus* (Table 3) is reduced in many basin streams when compared with Malheur and John Day river speckled dace. This reduction, which is not uncommon in isolated populations of this species, is most striking in dace from the

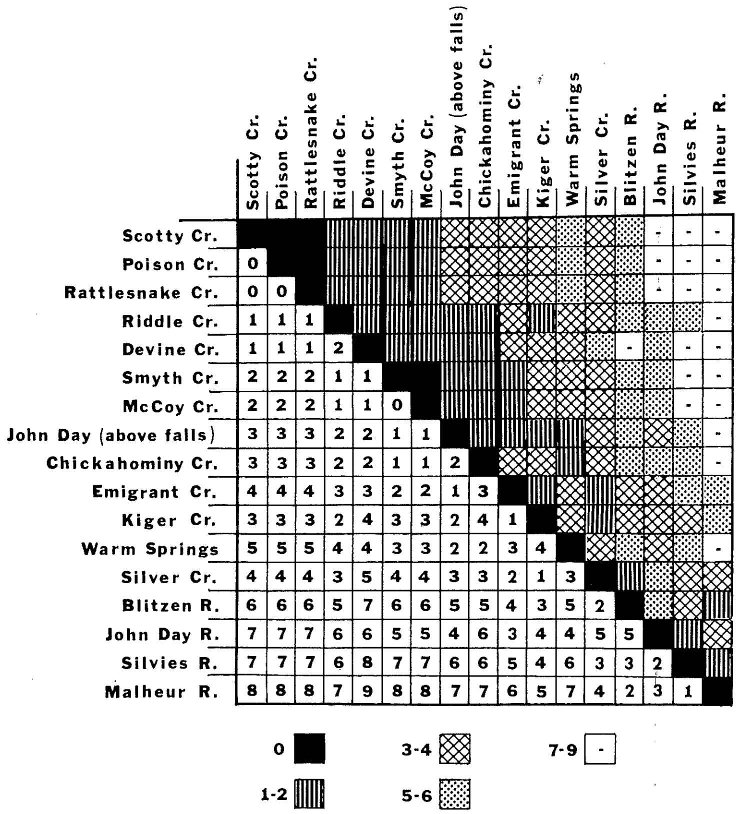

Fig. 3. Trellis diagram based on the data of Table 1. The higher the dispersion index value the less similar the total fish fauna of two given streams (approach based on McIntosh, 1967).

warm springs where barbels are almost completely absent, as was previously noted by Snyder (1908). Warm Springs *R. osculus* also exhibit moderate dwarfism. The largest individual from samples totaling over 200 fish measured 44.2 mm SL, which is far below the usual maximum size for this species.

Differentiation from the typical lower Columbia morphotype exists in several characters of *Catostomus columbianus* from the Harney Basin. There is a tendency toward significantly larger scales. Populations from Harney Basin have fewer lateral line scales than those from either John Day or Malheur rivers (Fig. 5). Smith (1966) reported a similar reduction in the average number of predorsal scales, in addition to slightly fewer vertebrae in *C. columbianus* from the Harney Basin. Insufficient samples of the population occurring above the falls of the south fork of John Day River appear intermediate between the Harney Basin and Columbia forms with respect to scale size. *C. columbianus* in the warm springs, noted by Smith (1966), may now be extinct due to the introduction and proliferation of carp, as none was found there in 1968 collections.

Smith (1966) found many similarities among isolated headwater populations of *C. columbianus*. His description of a new subspecies *C. c. hubbsi* from Wood River of the Snake drainage was based chiefly on lip structure, dorsal fin rays, and gill raker counts. Harney Basin populations clearly exhibit several morphological variations from this subspecies, yet they share many important features. Harney Basin forms appear most similar to those of the Palouse River of eastern Washington and western Idaho, and the headwaters of Crooked River, a part of the Deschutes drainage.

Many streams in the basin have been stocked with both rainbow and brook trout. However, the presence of native trout was reported by Snyder (1908) in Silvies River. Samples from isolated creeks located chiefly

TABLE 2. SUMMARY OF DISCRIMINANT FUNCTION ANALYSIS.[1] The number of individuals in each sample affiliated with either Malheur River (M.R.) or John Day River (J.D.R.) is given, followed by the range of individual probabilities (in parentheses).

	Richardsonius balteatus		*Ptychocheilus oregonensis*		*Rhinichthys cataractae*		*Catostomus macrocheilus*	
	M.R.	J.D.R.	M.R.	J.D.R.	M.R.	J.D.R.	M.R.	J.D.R.
Malheur R.	68(.642–.999)	11(.519–.999)	20(.822–.999)	1(.580)	22(.851–1.000)	1(.620)	27(.694–.999)	3(.627–.787)
John Day R.	1(.508)	49(.653–.999)	2(.571–.812)	21(.749–1.000)	0	10(.995–1.000)	6(.617)	20(.585–.999)
So. Fk. John Day (above falls)	24(.869–.999)	0						
Blitzen R.	105(.928–.999)	0	2(.810–.999)	0	50(.665–1.000)	13(.595– .999)		
Kiger Cr.	30(.979–.999)	0			4(.999–1.000)	2(.997– .999)		
McCoy Cr.	30(.979–.999)	0						
Riddle Cr.	30(.979–.999)	0						
Smyth Cr.	40(.869–.999)	0						
Silver Cr.	30(.979–.999)	0			18(.582–1.000)	2(.745– .899)		
Chickahominy Cr.	30(.979–.999)	0						
Warm Springs	25(.989–.999)	0						
Silvies R.	6(.508–.963)	78(.519–.999)	14(.519–.999)	28(.688–1.000)	28(.662–1.000)	26(.515–1.000)	3(.622–.824)	18(.628–.999)
Emigrant Cr.	30(.766–.999)	0			6(.986–1.000)	0		

[1] Analyses were based as follows: *R. balteatus*, 3 fin ray counts; *P. oregonensis*, 11 body proportions; *R. cataractae*, 11 body proportions and 4 scale counts; *C. macrocheilus*, 10 body proportions.

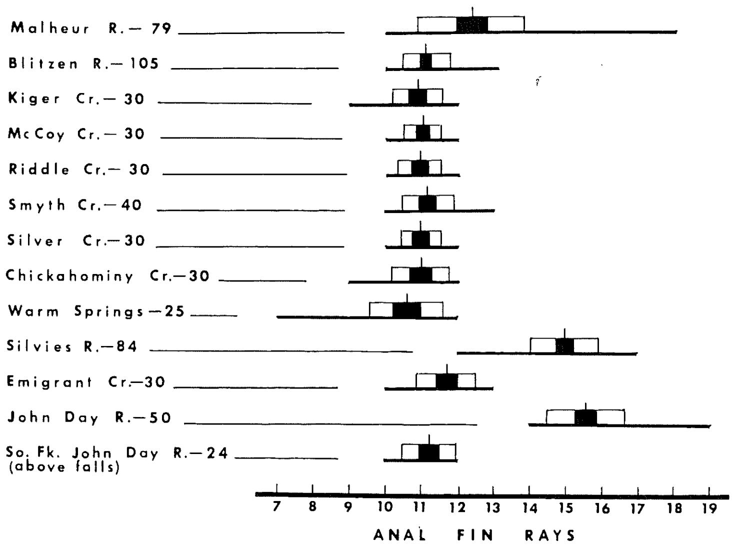

Fig. 4. Variation in the number of anal fin rays in *Richardsonius balteatus* from Harney Basin and adjacent drainages. The sample size follows each location. Sample ranges are indicated by the basal line; the black rectangle outlines ± two standard errors of the mean (vertical line), and the open rectangle encloses one standard deviation on either side of the mean.

on privately owned land indicate that the "native" *Salmo gairdnerii* have finer scales and more gill rakers than the exotic stocks. These fish are brightly colored when alive; the ventral surface has an orange tinge and spots on the dorsal and lateral surfaces are large, particularly in the region of the caudal peduncle.

Populations of *C. bairdi* in Blitzen River and Kiger Creek closely resemble those in the isolated creeks and Scotty Creek, a headwater tributary of Silvies River (Table 4). Heavily-prickled sculpins of the main stem of Silvies River differ markedly from the others in the basin. There is a pronounced resemblance of sculpins from Blitzen River and the isolated creeks to *C. bairdi semiscaber* of the upper Snake and Bonneville systems, and they show some likeness to *C. b. punctulatus* of the northern Rocky Mountain region. Silvies River sculpins exhibit much greater affinity for the central and lower Columbia *semiscaber* (= *C. hubbsi* of Bailey and Dimick, 1949) in the possession of prickles and a complete lateral line, although the prickling is much heavier than any other *C. bairdi* populations in adjacent drainages. *C. bairdi* from the Malheur and John Day rivers are typical lower Columbia forms.

C. bairdi is not presently abundant in the John Day watershed. Sculpins may now be extinct in Rattlesnake Creek, the type locality of *Potamocottus bendirei* (= *Cottus bairdi semiscaber*) since no specimens could be found there by Bond in 1961 or 1965, or on several occasions by Davis (pers. comm.) in 1965 or 1966.

Fourteen species are known to have been introduced into Harney Basin waters. *Cottus rhotheus* is present there only in Fish Lake high on Steens Mountain. It was probably introduced with trout plantings, because Fish Lake is believed to have been barren of fish

TABLE 3. PRESENCE (PERCENT) OF MAXILLARY BARBELS IN *Rhinichthys osculus*. Sample sizes (in parentheses) follow locations; those containing fewer than 10 individuals are omitted.

	Barbel	
	Left	Right
Malheur R. (43)	98	95
Blitzen R. (42)	62	62
Kiger Cr. (21)	71	67
Riddle Cr. (30)	80	80
Smyth Cr. (20)	65	90
Silver Cr. (26)	88	81
Warm Springs (57)	0	4
Poison Cr. (30)	73	73
Rattlesnake Cr. (13)	85	69
Scotty Cr. (30)	27	37
John Day R. (30)	97	90

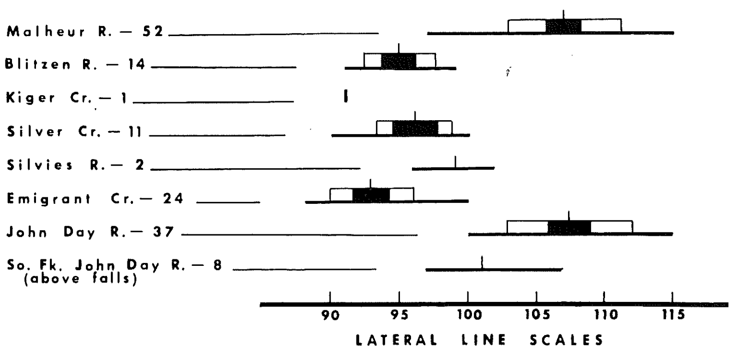

Fig. 5. Variation in the number of lateral line scales in *Catostomus columbianus* from Harney Basin and adjacent drainages. See legend of Fig. 4 for an explanation of the diagrams.

until trout were first stocked there. *Cyprinus carpio* is abundant in the lower reaches of Silvies and Blitzen rivers, Silver Creek, and the warm springs. *S. gairdnerii* has been planted in many upland streams in the basin, so that designation of native stocks is difficult. *Salvelinus fontinalis* appears to be scarce in the basin. *Lepomis macrochirus, L. gibbosus, Pomoxis annularis,* and *Ictalurus nebulosus* are established and enter the sport fishery, according to Thompson *et al.* (1968), who reported also that *Micropterus salmoides, M. dolomieui,* and *Ictalurus punctatus* have been introduced. Lawrence Bisbee, of the Oregon Game Commission (pers. comm.) believes that the latter two species are not established, and that plantings of *Salmo clarkii henshawi, Oncorhynchus nerka,* and *Ictalurus melas* have failed to establish permanent populations.

Discussion

Distributional patterns must be viewed in the context of hydrographic history and ecological considerations. The following points briefly summarize the alternative consequences of past events.

1. Fishes in the Harney Basin could have originated only from the basin's ancient connection with Malheur River via Malheur Gap. If such were the case, each species would have had equal access to every stream, the only limitations being of an ecological nature. Moist conditions that occurred during early post-glacial times must have resulted in broadly established stream connections, as no permanently flowing stream in the basin is devoid of fish life. Subsequent isolation of many populations caused by widespread desiccation could have made pos-

Table 4. Variation in Lateral Line Development and Body Prickling in *Cottus bairdi* Greater than 50 mm in Length. Sample sizes (in parentheses) follow locations.

	Complete lateral line %	Body area covered by prickling (avg. % per region described in text)			
		a	b	c	d
Malheur R. (23)	70	16	10	8	2
Blitzen R. (39)	10	1	0	3	0
Kiger Cr. (7)	0	4	0	6	0
Riddle Cr. (22)	9	1	0	0	0
Silver Cr. (22)	0	1	0	0	0
Poison Cr. (4)	0	0	0	0	0
Rattlesnake Cr. (5)	0	0	0	0	0
Silvies R. (20)	90	78	80	42	22
Scotty Cr. (4)	25	1	0	0	0
Upper Snake; Bonneville Basin (23)	0	1	0	2	0

sible a certain degree of endemism, but it is doubtful that major differences would have arisen between streams with similar environments in the time involved.

2. A secondary invasion of Columbia fishes after the damming of Malheur Gap could have been superimposed on the preexisting fauna. The physiography of the Harney Basin suggests two possibilities: (a) Stream capture over the Ochoco-Silvies surface between Silvies River and tributaries of either Malheur or John Day River, such invaders having moved downstream. Spread into the upland tributaries of Silvies River would have been determined by the permanency of their connections with the mainstream and by habitat preferences. Traverse of Malheur and Harney lakes would have depended on habitat preferences, water quality, and hydrographic access. (b) A possible secondary connection was an outflow into Malheur River by Pluvial Lake Malheur with dispersal upstream into both Silvies and Blitzen rivers. A high water stage that overflowed Malheur Gap would have freshened the waters of Harney Lake, if indeed the two lakes were distinct, allowing invasion of Silver Creek.

Either stream capture or lake overflow would be most likely to occur during particularly moist periods. Such conditions have prevailed only twice in the Harney Basin since Pleistocene glaciation; the first lasted until 15,000 years ago and the second has endured from 4000 years ago to the present, but with major fluctuations, the 1930's being especially dry. If secondary incursion of fishes took place during the earlier time period, the invaders would have had ample opportunity to spread throughout the basin when connections were more broadly established. However, if the invasion occurred recently, distributional patterns would vary according to the nature of transfer. Stream capture between Silvies and either John Day or Malheur rivers could have resulted in the occupation of (a) central Silvies River only, (b) Silvies River and its tributaries, (c) both the Silvies and Blitzen drainages, following the crossing of Malheur Lake, or (d) Silvies River, Blitzen River, and Silver Creek after the crossing of Malheur and Harney lakes. An overflow of Pluvial Lake Malheur would have facilitated the invasion of Silvies River, Blitzen River, and possibly Silver Creek. Alkaline conditions in Harney Lake, if present during the time of a secondary invasion, would have been sufficient to halt the spread of fishes from Malheur Lake. The water of Malheur Lake is much less saline than that of Harney Lake and this suggests that no chemical barrier to dispersal existed between the Silvies and Blitzen drainages. However, because of its extensive seasonal fluctuation the water quality of the lake varies greatly. During summer desiccation Malheur Lake may recede so far that surface connections with either Silvies or Blitzen river are disrupted.

Both the distribution and affinities of species in the Harney Basin indicate that a secondary connection resulting in fish transfer has indeed taken place, and that the subsequent invasion has been confined to central Silvies River. This is the only stream known to contain *A. alutaceus* and *C. macrocheilus*. It is also the only one in which *P. oregonensis* is abundant, as only two specimens are known from elsewhere in the basin. These species are all absent from upland tributaries of Silvies River, although this may be the result of habitat preference. In addition, the crayfish *Pacifastacus leniusculus klamathensis* is known from Silvies and John Day rivers, but has not been reported from Malheur River (Miller, 1960). Discriminant function analysis of four fish species has shown that central-Silvies populations are predominantly affiliated with those from John Day River. In all other streams of the basin, including a Silvies tributary, the affinities lie with Malheur River. Distributions of smooth and prickled *C. bairdi* coincide nicely with this pattern. This evidence strongly suggests that the secondary connection has been in the form of stream capture between Silvies and John Day rivers.

Differentiation exhibited by several species in certain regions of the Harney Basin has resulted from prolonged isolation from the Columbia system. Endemism in *R. osculus* from warm springs has probably been accelerated by the unusual environmental conditions. Smith (1966) theorized that *C. columbianus* represents the isolated derivative of an earlier stage in the evolution of the species, being barred from more intensive speciation taking place in the lower Columbia. *C. bairdi* from Silvies River is more heavily prickled than in adjacent parts of the Columbia system. Limited data from collections of *S. gairdnerii* indicate the presence of a native Harney Basin form; however, introductions into most major streams invalidate comparison with adjacent drainages.

The similarity of fishes in the south fork of John Day River to certain populations from Malheur River and the Harney Basin could be the product of two alternative phenomena: (1) a different stream capture which resulted in invasion of fishes from isolated regions of the Harney Basin, or (2) isolation by the formation of barrier falls of an older and less diverse Columbia fauna. The first alternative seems unlikely because the south fork contains *Catostomus platyrhynchus* and lacks such species as *C. bairdi.* The second, however, might explain the absence of *C. macrocheilus, A. alutaceus, P. oregonensis,* and several species of *Cottus*; all of which are abundant below the falls or in other parts of the John Day system.

A theory of the origin and distribution of fishes in the Harney Basin based on evidence summarized above is now advanced. Populations inhabiting the Blitzen drainage, Riddle and Smyth creeks, the warm springs, Silver Creek, Poison Creek, Rattlesnake Creek, and the upland tributaries of Silvies River originated from the basin's Pleistocene connection with Malheur River. Some species still maintain strong similarity with their ancient Malheur relatives; others differ in several respects. Variation may be attributed to evolutionary divergence or to the retention of characters that have been subsequently lost or modified in Malheur River populations. The presence of lower Columbia forms in central Silvies River points to a secondary invasion, and discriminant function analysis indicates that this was by stream capture with John Day River. The theory of a successful secondary invasion is contingent on the assumption that the invaders held some adaptive superiority over resident populations and were able to expand at the expense of these populations until restricted by physical or ecological barriers. Malheur Lake and the occasionally interrupted lower reaches of tributaries have evidently fulfilled such barrier requirements for the central Silvies fauna.

Inferences regarding the sequence of species dispersal can also be drawn from regional patterns of distribution. Fishes entered the Harney Basin from Malheur River during late Pleistocene periods of great precipitation. Stream connections were broadly established and invasion of now-isolated areas took place. Malheur Gap was dammed during this time, followed by formation of Pluvial Lake Malheur. Increased desiccations until about 4000 years ago caused the faunal isolation of Blitzen River and the other hydrographically discrete drainages in the basin. These streams today contain relict populations derived from the ancient connection with the Snake system. Certain Malheur River populations as well as those existing above the falls of the south fork of John Day River are also remnants of an older and more widespread fauna. Distributional evidence indicates that the older fauna included: *R. b. hydrophlox, Gila bicolor, R. cataractae, R. osculus, C. columbianus, C. platyrhynchus, S. gairdneri,* and probably *C. bairdi,* which now has a very discontinuous distribution in the Columbia drainage in Oregon. Such Harney Basin inhabitants as *A. alutaceus* and *C. macrocheilus,* which are present only in central Silvies River, probably invaded the John Day and Malheur drainages after the initial isolation of the basin, but were available for entry at the time of secondary stream capture. Several species now found in the John Day that do not occur in Silvies River (Table 4) may have arrived too recently to have utilized the secondary connection. A few of these species have also spread through the Snake into Malheur River. One exception is *Cottus confusus,* which is common in upstream areas adjacent to the Harney Basin. This cold-loving species is believed to have achieved its present distribution during the post-glacial melting (Bond, 1963). If it ever entered the basin, it has since disappeared.

Acknowledgments

The research for this paper, based on a thesis submitted by the senior author in partial fulfillment of the requirements for the degree of Master of Science, Oregon State University, was facilitated by the generous assistance of many of our friends and colleagues. Drs. James D. Hall, Raymond C. Simon, and John C. Briggs, offered many helpful criticisms and reviewed the manuscript. Dr. Hall, Paul E. Reimers, and Lawrence Bisbee helped with the field work. Thanks are due Drs. W. Scott Overton and Quentin D. Clarkson for their advice regarding the statistical analysis. Support for field work was provided by the Oregon Agricultural Experiment Station. Computer processing was made possible by a grant from the Oregon State University Computer Center.

Technical Paper No. 2717 Oregon Agricultural Experiment Station.

Literature Cited

ANTEVS, E. 1938. Rainfall and tree growth in the Great Basin. Carnegie Inst. Wash. Pub. 469.

BAILEY, R. M. AND M. F. DIMICK. 1949. *Cottus hubbsi*; a new cottid fish from the Columbia River system in Washington and Idaho. Occ. Pap. Mus. Zool., Univ. Mich. No. 513, 18 pp.

BALDWIN, E. M. 1959. The geology of Oregon. Univ. Oregon Coop. Bookstore, Eugene.

BOND, C. E. 1963. Distribution and ecology of freshwater sculpins, genus *Cottus*, in Oregon. Ph.D. thesis, Univ. Mich., Ann Arbor, Mich.

CONNELL, J. H. AND E. ORIAS. 1964. The ecological regulation of species diversity. Am. Nat. 48:399–414.

DICKENSEN, W. R. 1958. Geology of the Izee area, Grant County, Oregon. Ph.D. thesis, Stanford Univ., Stanford, Calif.

GILBERT, C. H. AND B. W. EVERMANN. 1894. A report upon investigations in the Columbia River basin, with descriptions of four new species of fishes. Bull. U. S. Fish Comm. 14: 169–207.

HANSEN, H. P. 1947. Postglacial forest succession, climate, and chronology of the Pacific Northwest. Trans. Am. Philos. Soc. 37(1):1–130.

HEUSSER, C. J. 1966. Pleistocene climatic variations in the western United States. *In*: Pleistocene and post-pleistocene climatic variations in the Pacific area. D. I. Blumenstock, ed., pp. 9–36. Bishop Mus. Press, Honolulu.

HUBBS, C. L. AND C. HUBBS. 1953. An improved graphical analysis and comparison of series of samples. Syst. Zool. 2(2):49–57.

——— AND K. F. LAGLER. 1958. Fishes of the Great Lakes region. Rev. ed. Cranbrook Inst. Sci. Bull. 26.

——— AND R. R. MILLER. 1942. Fish of Catlow Valley. *In*: Archaeological researches in the northern Great Basin. L. S. Cressman, ed., p. 152. Carnegie Inst. Wash. Pub. 538.

——— AND ———. 1948. The zoological evidence. Correlation between fish distribution and hydrographic history in the desert basins of western United States. *In*: The Great Basins, with emphasis on glacial and postglacial times. Univ. Utah Bull. 38(20):1–191. (Biol. Ser. Vol. 10, No. 7.)

JESSUP, L. T. 1939. Statement on precipitation and tree growth. *In*: Geology and ground water supply of the Harney Basin, Oregon, with a statement on precipitation and tree growth by L. T. Jessup. A. M. Piper, T. W. Robinson and C. F. Park, pp. 10–13. U. S. Geol. Surv. Water Supply Pap. 841.

LINDSEY, C. C. 1953. Variation in anal fin ray count of the redside shiner *Richardsonius balteatus* (Richardson). Can. J. Zool. 31:211–225.

MCINTOSH, R. P. 1967. An index of diversity and the relation of certain concepts to diversity. Ecology 48(3):392–404.

MAHALANOBIS, P. C. 1936. On the generalized distance in statistics. Proc. Nat. Inst. Sci., India 2:49–55.

MILLER, G. C. 1960. The taxonomy and certain biological aspects of the crayfish of Oregon and Washington. M. S. thesis, Oregon St. Coll., Ore.

MILLER, R. R. 1958. Origin and affinities of the freshwater fish fauna of western North America. *In* Zoogeography, pp. 187–222. Am. Assoc. Adv. Sci. Publ. 51.

PIPER, A. M., T. W. ROBINSON AND C. F. PARK. 1939. Geology and ground water supply of the Harney Basin, Oregon, with a statement on precipitation and tree growth by L. T. Jessup. U. S. Geol. Surv. Water Supply Pap. 841.

RAO, C. R. 1952. Advanced statistical methods in biometric research. Wiley, New York.

REIMERS, P. E. AND C. E. BOND. 1967. Distribution of fishes in tributaries of the lower Columbia River. Copeia 1967(3):541–550.

RUSSELL, I. C. 1903. Notes on the geology of southwestern Idaho and southeastern Oregon. U. S. Geol. Surv. Bull. 217.

———. 1905. Preliminary report on the geology and water resources of central Oregon. Ibid. 252.

SCHULMAN, E. 1953. Tree-ring evidence for climatic change. *In*: Climatic change. H. Shapley, ed., pp. 207–219. Harvard Univ. Press, Cambridge, Mass.

SHELDON, A. L. 1968. Species diversity and longitudinal succession in stream fishes. Ecology 49(2):193–198.

SMITH, G. R. 1966. Distribution and evolution of the North American catostomid fishes of the Subgenus *Pantosteus*, genus *Catostomus*. Misc. Pub. Mus. Zool., Univ. Mich., No. 129, 132 pp.

SNYDER, J. O. 1908. Relationships of the fish fauna of the lakes of southeastern Oregon. Bull. U. S. Bur. Fish 27:69–102.

THOMPSON, K. E., G. J. HATTAN, J. D. FORTUNE, JR., AND J. M. HUTCHINSON. 1968. The fish and wildlife resources of the Malheur Lake basin, Oregon, and their water requirements. Ore. State Game Comm. Rep. to Ore. State Water Res. Bd.

VAN WINKLE, W. 1914. Quality of the surface waters of Oregon. U. S. Geol. Surv. Water Supply Pap. 363.

WARING, G. A. 1909. Geology and water resources of the Harney Basin region, Oregon. U. S. Geol. Surv. Water Supply Pap. 231.

WELLS, J. V. B. 1960. Compilation of records of surface waters of the United States through September 1950. Pt. 10. The Great Basin. U. S. Geol. Surv. Water Supply Pap. 1314.

DEPARTMENT OF BIOLOGY, UNIVERSITY OF SOUTH FLORIDA, TAMPA, FLORIDA 33620 AND DEPARTMENT OF FISHERIES AND WILDLIFE, OREGON STATE UNIVERSITY, CORVALLIS, OREGON 97331.