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Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation

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Synopsis

Large-bodied, migratory life history forms of bull charr, *Salvelinus confluentus*, were historically abundant in northwestern North America, but many remaining populations of this now-threatened species presently persist as small-bodied residents isolated in headwater streams. We examined whether the migratory form has been lost from headwater populations of bull charr and their potential for re-establishment. Upstream and downstream movement of bull charr and other salmonids from three tributary populations in the Bitterroot River drainage, Montana, was measured with weirs over a 17-month period. The migratory life history was rare or absent in two tributaries but still present at a low level in a third. In contrast, substantial numbers (n = 1745) of juvenile and adults of other salmonids (brown trout, *Salmo trutta*, cutthroat trout, *Oncorhynchus clarki*, and mountain whitefish, *Prosopium williamsoni*) were captured near tributary mouths, indicating a migratory life history was common in other species. Apparent decline of the migratory life history in bull charr was not directly related to damming suggesting other downstream mortality factors (predation, temperature) also are involved. Isolated, nonmigratory forms have increased risk of extinction, and restoration of the population connectivity via the re-establishment of migratory stocks is an important conservation goal for bull charr recovery. However, the factors governing migratory tendency remain unclear.

Introduction

Salmonids exhibit a large degree of flexibility in expression of life history forms (Northcote 1997). This flexibility in life history is arguably most evident within the charrs, *Salvelinus*, where multiple forms occur even within the same lake or drainage (e.g., Jonsson et al. 1988). How such high life history diversity has evolved – labeled the 'charr problem' by Nordeng (1983) – has been a subject of interest among fish ecologists for many years (Jonsson & Jonsson 1993).

Bull charr, *Salvelinus confluentus,* are native to northwestern North America ranging from Yukon, Canada, to northern California, U.S.A. (Haas & McPhail 1991). Like other potamodromous salmonids (Northcote 1997), bull charr express a high degree of life history variability. Migratory forms reside as adults in large rivers (fluvial) or lakes (adfluvial) and migrate to smaller streams to spawn. Juveniles typically rear 1–3 years in tributaries before migrating to lakes or larger rivers, returning to spawn in natal tributaries several years later (Fraley & Shepard 1989, Stelfox 1997, Swanberg 1997a). Migrations of bull charr are among the longest of potamodromous salmonids, up to 250 km (Fraley & Shepard 1989, Elle[1], Swanberg 1997a, Thiesfeld et al.[2]). In contrast, the 'resident' life

[1] Elle, S. 1995. Bull trout investigations. Bull trout movement and mortality studies. Idaho Dept. Fish & Game Rept. F-73-R-17, Boise. 98 pp.

[2] Thiesfeld, S.L., A.M. Stuart, D.E. Ratliff & B.D. Lampman. 1996. Migration patterns of adult bull trout in the Metolius River and Lake Billy Chinook, Oregon. Oregon Dept. Fish Wildl., Fish Div. Rept. 96-1. 18 pp.

history form spawns and rears year-round in headwater streams with relatively restricted (<2 km) spawning and overwintering movements (Jakober et al. 1998).

The expression of multiple life history forms can be viewed as an adaptation to variable environments, with each form conferring advantages under different environmental conditions (Northcote 1992, Jonsson & Jonsson 1993, Skúlason & Smith 1995). Migration to lakes and larger rivers capitalizes on abundant food allowing for greater growth and fecundity (Gross 1987). Mature migratory bull charr in the Flathead River drainage, Montana, average 628 mm in length and 5482 eggs per female (Fraley & Shepard 1989), whereas adult resident bull charr typically seldom exceed 300 mm and have an order of magnitude lower fecundity (Rieman & McIntyre[3]; see also Jonsson & Jonsson 1993). Additionally, with alternate year spawning and large juveniles residing outside spawning tributaries, several cohorts in migratory forms are removed from extirpating stochastic events (drought, fire, debris flows) common to headwater streams (Rieman & McIntyre[3]). Such 'risk-spreading' also may reduce the likelihood of local population extinction and enhance rapid recolonization. In contrast, the resident life history is predominant where migration is restricted by waterfalls or dams (Northcote 1992, Morita et al. 2000), or where growth opportunities in local habitats exceed the costs of migration (Northcote 1992, Jonsson & Jonsson 1993, Morita et al. 2000).

Like many other native salmonids (e.g., Thurow et al. 1997, Morita et al. 2000), bull charr now exist in fragmented patches of suitable habitat often long distances from neighboring populations (Rieman & McIntyre[3] 1995, Rieman et al. 1997). Bull charr are listed as 'threatened' in the U.S.A. (USFWS 1998) and 'at risk' over much of its range in Canada (McCart 1997, Haas[4]). Historically, large-bodied, migratory forms of bull charr were common, but attendant with the decline in historical range and increased fragmentation, has been a decline of the migratory life history form across many parts of its range (Fitch 1997, McCart 1997, Rieman et al. 1997). For example, in southwestern Alberta, large-bodied fluvial or adfluvial bull charr were common prior to 1950, but many remaining populations are now small-bodied residents and only occupy 31% of its former range (Fitch 1997). The combination of increased isolation and reduced migratory tendency places remaining populations at high risk of extinction due to reduced connectivity with neighboring populations, reduced gene flow, and reduced recolonization ability after local extinctions (Rieman & McIntyre[3]).

Bull charr of the Bitterroot River basin, Montana, exemplify the increased fragmentation and apparent decline of the migratory form. Historical accounts of large bull charr in the Bitterroot River mainstem suggest the migratory form was formerly common (MBTSG[5]). However, many remaining populations are isolated in headwater tributaries and exhibit resident life history characteristics, and the large-bodied form is now rare (MBTSG[5], Jakober et al. 1998) (Figure 1).

A combination of factors have likely disfavored the migratory life history form since the turn of the century in the Bitterroot and other drainages. Low-head dams are common near tributary mouths, diverting downstream migrants into irrigation canals and preventing or restricting upstream passage. High-head dams on mainstem rivers downstream block long distance migrants from returning upriver (Fernet & O'Neil 1997, Swanberg 1997b). Elevated temperatures resulting from dewatering and land use in the main river and in valley reaches of tributaries commonly exceed suitable levels for bull charr, and may represent seasonal barriers to movement. Bull charr migrating downstream to the mainstem river also face potential competition and predation from nonnative brook charr, *S. fontinalis*, brown trout, *S. trutta*, and rainbow trout, *O. mykiss*, which now dominate the mainstem river and the lower reaches of tributaries (McCart 1997).

Re-establishment of connectivity between remaining populations and of the migratory life history form is a main goal for bull charr recovery (Rieman & McIntyre[3], MBTSG[5]). However, whether the migratory life form would become re-established with alleviation of factors that may be blocking migration routes or increasing mortality of migrant fish is uncertain. Though some observations suggest that migratory and resident forms can co-occur (Fitch 1997, Jakober et al. 1998), it is unknown if the two forms can give rise to one another or are genetically distinct, and

[3] Rieman, B.E. & J.D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout *Salvelinus confluentus*. U.S. Forest Service Gen. Tech. Rept. INT-302. 38 pp.

[4] Haas, G.R. 1998. Indigenous fish species potentially at risk in BC, with recommendations and prioritizations for conservation, forestry/resource use, inventory and research. British Columbia Fish. Manage. Rept. 105. 168 pp.

[5] MBTSG (Montana Bull Trout Scientific Group). 1995. Bitterroot River drainage bull trout status review. Montana Fish, Wildlife & Parks Rept., Helena. 33 pp.

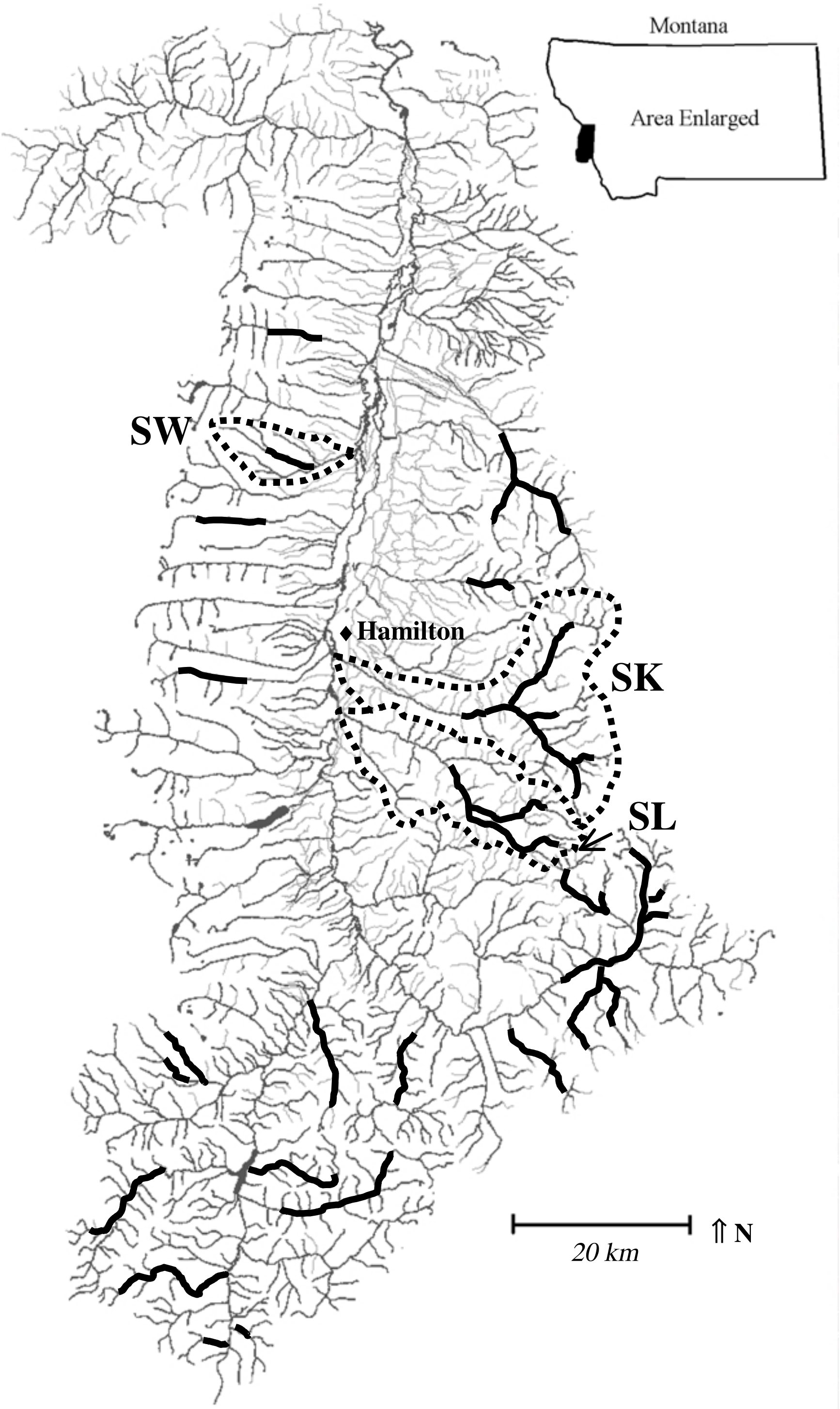

Figure 1. Map of Bitterroot River drainage. Study streams indicated as: SW = Sweathouse, SK = Skalkaho, and SL = Sleeping Child creeks. Bold lines indicate stream sections where bull charr are still common.

what role enviromental factors play in the expression of each life history (Rieman & McIntyre[3], McCart 1997, see also Nordeng 1983, Elliott 1987, Jonsson & Jonsson 1993).

This study was designed to assess to what extent the migratory form persists in bull charr populations that appear to exist primarily as small-bodied residents in headwater tributaries. We measured upstream and downstream migration from three tributary populations in the Bitterroot drainage with and without apparent migratory barriers to assess how the degree of restricted upstream passage influences retention of the migratory life history. We also compared bull charr migratory tendency to that of other salmonids occupying the same tributaries. Our goal was to investigate the likelihood that the large-bodied, migratory form would become re-established with improved habitat management practices.

Study area

This study was conducted in three tributaries (Sweathouse, Skalkaho, and Sleeping Child creeks) to the Bitterroot River, a large tributary that joins the Clark Fork of the Columbia River in western Montana (Figure 1). Streams are characterized by a wide valley floor in the lower reaches, and a steeper, more confined channel in the upper reaches. Bull charr and native cutthroat trout, *O. clarki lewisi*, are generally dominant in upper reaches and nonnative brook charr, brown trout, and rainbow trout in the lower reaches (Figure 2). Valley floor reaches are characterized by warmer water temperatures (+5°C) due to reduced riparian canopy and irrigation water withdrawal during summer. Irrigation diversion canals are generally not screened and fish movement into them is common. Two study streams (Skalkaho and Sleeping Child) had low-head dams constructed near their confluence with the main river to divert irrigation water. Dams are 1–2 m high and have no impounding areas, but dewatering of the stream below the dam is frequent during the summer irrigation season (June–September). Fish upstream can move downstream over the dam, but movement upstream is likely blocked or restricted except during high flow periods. Irrigation water is diverted from the lower 8 km of Sweathouse Creek but there is no low-head dam and flow is generally present to the confluence throughout the year.

Bull charr are relatively abundant (population size ca. 2000 fish >150 mm, peak density 25 fish 100 m^{-1}) in Sweathouse Creek (3rd order, watershed area 73 km^2) but distribution is confined to a 3 km section below two natural barriers (Figure 2). Cutthroat trout are abundant above river km 7, but uncommon below, and unlike bull charr, are found above the barrier falls. Brook charr and brown trout are common in the first 7 km, but are rare upstream. Skalkaho Creek (5th order, watershed area 228 km^2) supports a large population of bull charr (ca. 15 000 fish, peak density 30 fish 100 m^{-1}), the highest abundance among remaining bull charr populations in the Bitterroot River basin. Bull charr occur mostly above river km 20, whereas cutthroat trout are more abundant and distributed farther downstream. Brown trout are common in the lower 10 km. Several low-head dams, constructed between 1892–1942 occur in the lower 14 km. In contrast to other study streams, bull charr density in Sleeping Child Creek (4th order, watershed area 170 km^2) is lower (ca. 5000, peak density 12 fish 100 m^{-1}) and distributed over a greater proportion of the stream (Figure 2). Cutthroat trout are common throughout the drainage, whereas brook charr are common only in the lower 3 km and rare above river km 13. Rainbow trout and brown trout are present in low numbers in the lower 7 km, but rare above the low-head dam, constructed in the 1950s, at river km 1.7.

Other fishes in the basin include native mountain whitefish, *Prosopium williamsoni*, longnose sucker, *Catostomus catostomus*, largescale sucker, *C. macrocheilus*, redside shiner, *Richardsonius balteatus*, longnose dace, *Rhinichthys cataractae*, northern pikeminnow, *Ptychocheilus oregonensis*, peamouth, *Mylocheilus caurinus*, and slimy sculpin, *Cottus cognatus*.

Methods

A series of weirs were positioned in each study stream to measure timing and magnitude of upstream and downstream migration (Figure 2). Upper weirs were located within or near core areas of the population distribution of bull charr to assess within-population movement and to serve as an internal control for comparison to lower weirs. To assess downstream and upstream movement from a population, a lower weir was placed 1.3–10.2 km downstream of the upper weir site. In Sleeping Child Creek, bull charr occupy a greater proportion of the drainage and the lower population boundary was not as evident, but it was estimated

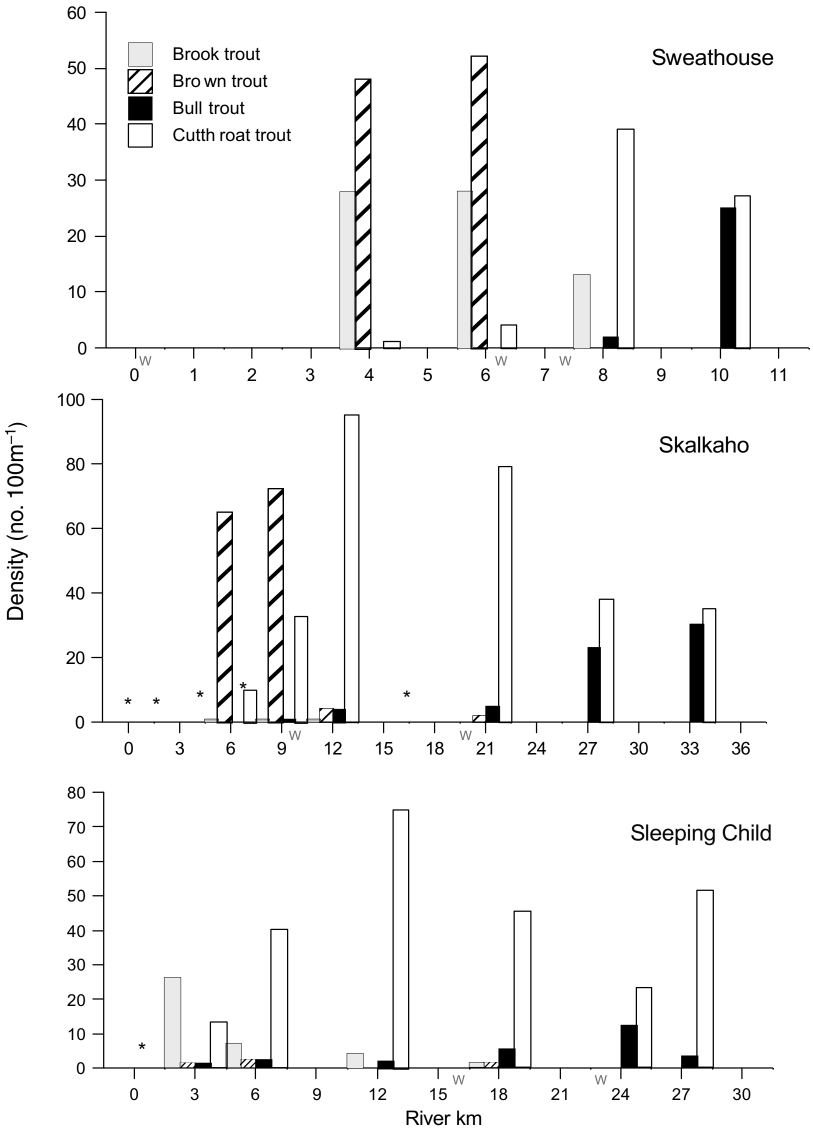

Figure 2. Longitudinal distribution and abundance of salmonids within study streams. Electrofishing data summarized from Montana Fish, Wildlife and Parks data files (Nelson 1999). Locations of study weirs indicated by 'w' and low-head dams by asterisks. Note differences in scale of axes. Catch data for mountain whitefish were not available.

that the majority of bull charr in the drainage occurred upstream of the lower weir.

'Picket fence' weirs, a trap design proven effective at capturing migrating juvenile bull charr and spawning adults (Elle et al.[6]), were constructed across the width of the stream (6–21 m) at each trapping location. Weirs were constructed of 18-mm diameter aluminum pipe spaced 11 mm apart in steel frames. Frames were held in a 45° angle upright position with attached legs and steel fence posts. A 13-mm square plastic mesh was placed on the weir face when pore-clogging leaf litter and debris was minimal.

Upstream and downstream trap boxes (7-mm mesh) attached to weirs were used to capture migrant fish. Trap boxes employed conical-shaped entrances to facilitate entry and reduce escapement (Nelson 1999). Weirs

[6] Elle, S., R. Thurow & T. Lamansky. 1994. Rivers and streams investigations. Bull trout movement and mortality studies. Idaho Dept. Fish & Game Rept. F-73-R-16, Boise. 72 pp.

were placed diagonally in the stream current to lead fish to the appropriate trap box. Weirs were generally placed in shallow, low-gradient runs with uniform depths. During spring runoff (mid-April through June), full-width weirs became clogged with debris and collapsed, thus only partial weirs were erected along stream margins, spanning 1/4 to 3/4 stream width, and only downstream migrants could be effectively trapped. During low flow, wire-mesh 'fry traps' were periodically used in conjunction with weirs to enhance capture of small downstream migrant fish. 'Fry traps' consisted of 2-m long fyke nets (3–6 mm mesh, 91 cm^2 opening) placed just downstream of the lower weirs.

Trapping was conducted from July 1996 to November 1997 in two streams (Sweathouse and Skalkaho creeks) and from May to October 1997 in the third site (Sleeping Child Creek). Operation of weirs was almost continous during low flow, ice-free periods (March–October) and was intermittent during high flows in spring, and leaf-fall in autumn (Figure 3). Traps were checked at least once per day, and more frequently during periods of rapid clogging. Captured fish were anesthetized with MS 222, measured (mm fork length (FL)), weighed, and checked for marks or tags. Bull charr >60 mm were marked with fin clips or Visible Implant tags (Northwest Marine Technologies, Seattle, WA, U.S.A.) to assess movement between upper and lower weirs.

Weir efficiency was measured at one of the trap sites by releasing a known number of fin-clipped salmonids

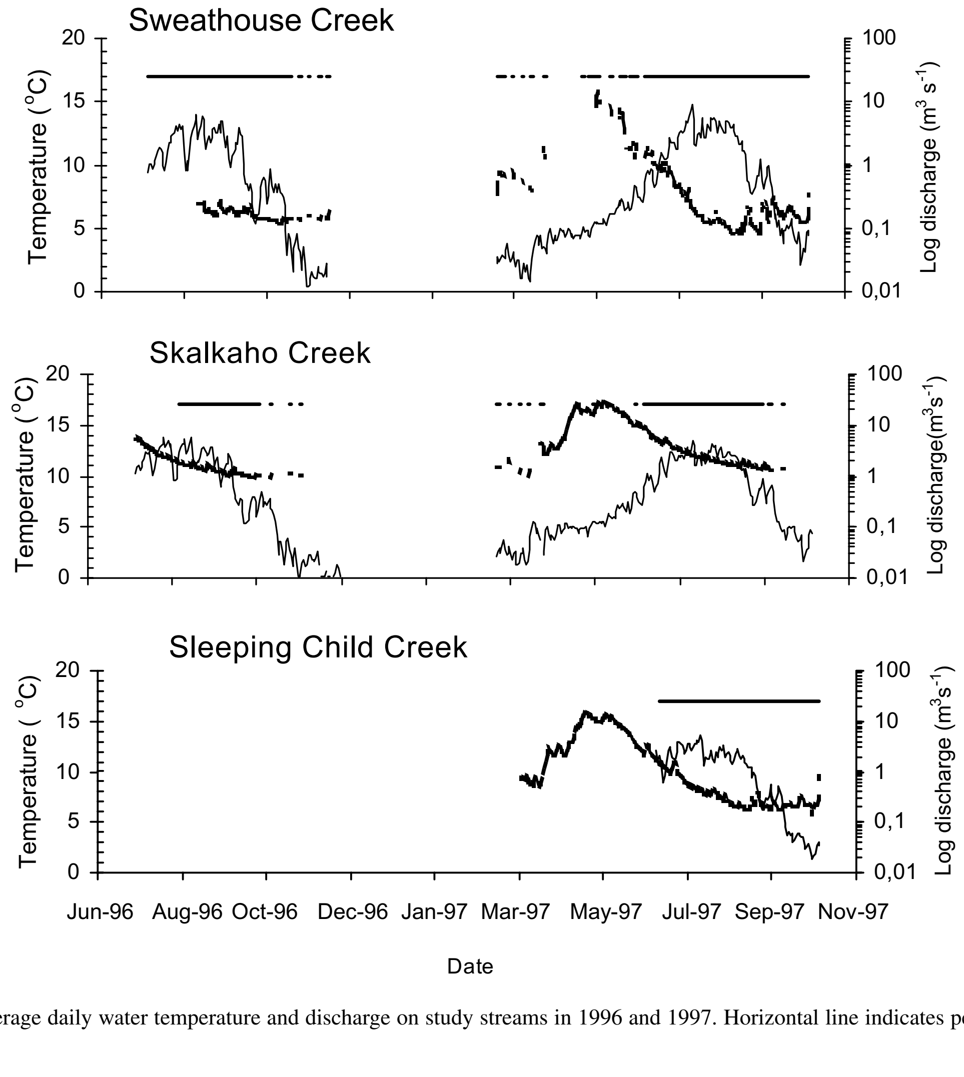

Figure 3. Average daily water temperature and discharge on study streams in 1996 and 1997. Horizontal line indicates periods of weir operation.

above the lower Sweathouse weir in July 1996. Nineteen marked brown trout and rainbow trout (78–199 mm, median = 112 mm) were released 125 m above the weir after initial capture. Plastic mesh was not used on the weir face during the efficiency trial. Fyke net efficiency was not assessed during this study, but previous evaluation with identical traps determined an average of 15% recapture rate (Clancy[7]). Capture rates were likely higher during this study when 'fry traps' were operated in conjunction with the weir.

Discharge was measured by continuous-recording gauges on Skalkaho and Sleeping Child creeks and by staff gauges on Sweathouse Creek. Temperature was recorded at each weir every 1.6–3.2 h with electronic thermographs (Onset Inc., Pocasset, MA, U.S.A.).

Results

Full or partial weirs were deployed during most flow and water temperature conditions except winter ice cover (Figure 3). Full weirs were operated from the declining limb of spring runoff (late June) until near base-flow conditions in November. Average daily water temperatures (at upper weir sites) peaked at about 14°C in late August and dropped below 5°C by mid-October. Surface ice started forming on streams in late October. In 1997, we trapped before and during spring runoff on Sweathouse (mid-March to late June) and Skalkaho creeks (mid-March to mid-July) with partial weirs (downstream trap only).

A total of 12 species were captured during the study (Nelson 1999), but six salmonid species – mountain whitefish (n = 993), cutthroat trout (n = 932), brown trout (n = 626), brook charr (n = 535), bull charr (n = 215), and rainbow trout (n = 180) – comprised the majority (85%) of the total number of fish captured (4108) (Figure 4). Overall, 2312 salmonids were captured moving downstream during 1045 trapping days, and 1191 were captured moving upstream during 866 trapping days. Size of fish captured ranged from 19 to 635 mm, with the majority (81%) of salmonids trapped moving downstream <200 mm in length.

Weir efficiency was estimated at ca. 50% based on recovery of 47% (9 of 19) of marked brown trout and rainbow trout within 5 days of release at the lower Sweathouse weir in July 1996. Efficiency was likely higher when small diameter plastic mesh was added to the downstream weirs during summer low flow, debris-free periods, and lower during higher flows in the spring and when high debris in the fall prevented addition of plastic mesh to the weir pickets. Relatively few fish were captured in 'fry' traps (n = 132, range 19–241 mm), but those that were captured were mostly <50 mm (including four bull charr), indicating that at least some component of young juveniles were sampled (Figure 5). Capture efficiency of partial weirs deployed during spring runoff was not determined, but 155 salmonids <200 mm were captured moving downstream, suggesting that they were effective at obtaining a subsample of outmigrating juveniles during high flows.

Bull charr movement

Bull charr exhibiting characteristics of the fluvial life history were rare or absent from the three study streams. A total of eight adults (>250 mm) and 20 juveniles (<250 mm) were captured at the lower weirs near stream mouths (Figure 4). Nearly all of the 'fluvial' bull charr occurred in Sleeping Child Creek. All of the eight adult fluvial bull charr captured were trapped in Sleeping Child Creek, where four adults (270–330 mm) were captured at the lower weir moving upstream in the summer and four adults (330–450 mm) were captured moving downstream in the fall. No adults were captured in the lower weirs in Sweathouse and Skalkaho creeks. Of the 20 juvenile bull charr outmigrants captured in lower weirs, 16 were captured in Sleeping Child Creek and four in Skalkaho Creek; no juvenile bull charr were captured at the lower Sweathouse Creek weir.

In contrast, upstream and downstream movement of bull charr was relatively common in the upper sections of Skalkaho (n = 61, range 95-315 mm FL) and Sleeping Child creeks (n = 96, 112–445 mm FL) (Figure 4), where weirs were positioned where population densities were highest (Figure 2). In both streams, upstream migrants were primarily adults (median FL of 242 and 223 mm, respectively, including sexually mature males and females), and downstream migrants, primarily juveniles (median FL of 106 and 171 mm, respectively). Bull charr in Sleeping Child Creek exhibited the most movement (mean 1.1 vs. 0.8 fish per day in Skalkaho) but had the lowest relative population density of all three study streams (Figure 2). In Sweathouse Creek, where the two upper weirs were located below

[7] Clancy, C.G. 1991. Statewide fisheries inventory: Bitterroot Forest inventory. Montana Fish, Wildlife & Parks Rept. F-46-R-4-Ij, Helena. 32 pp.

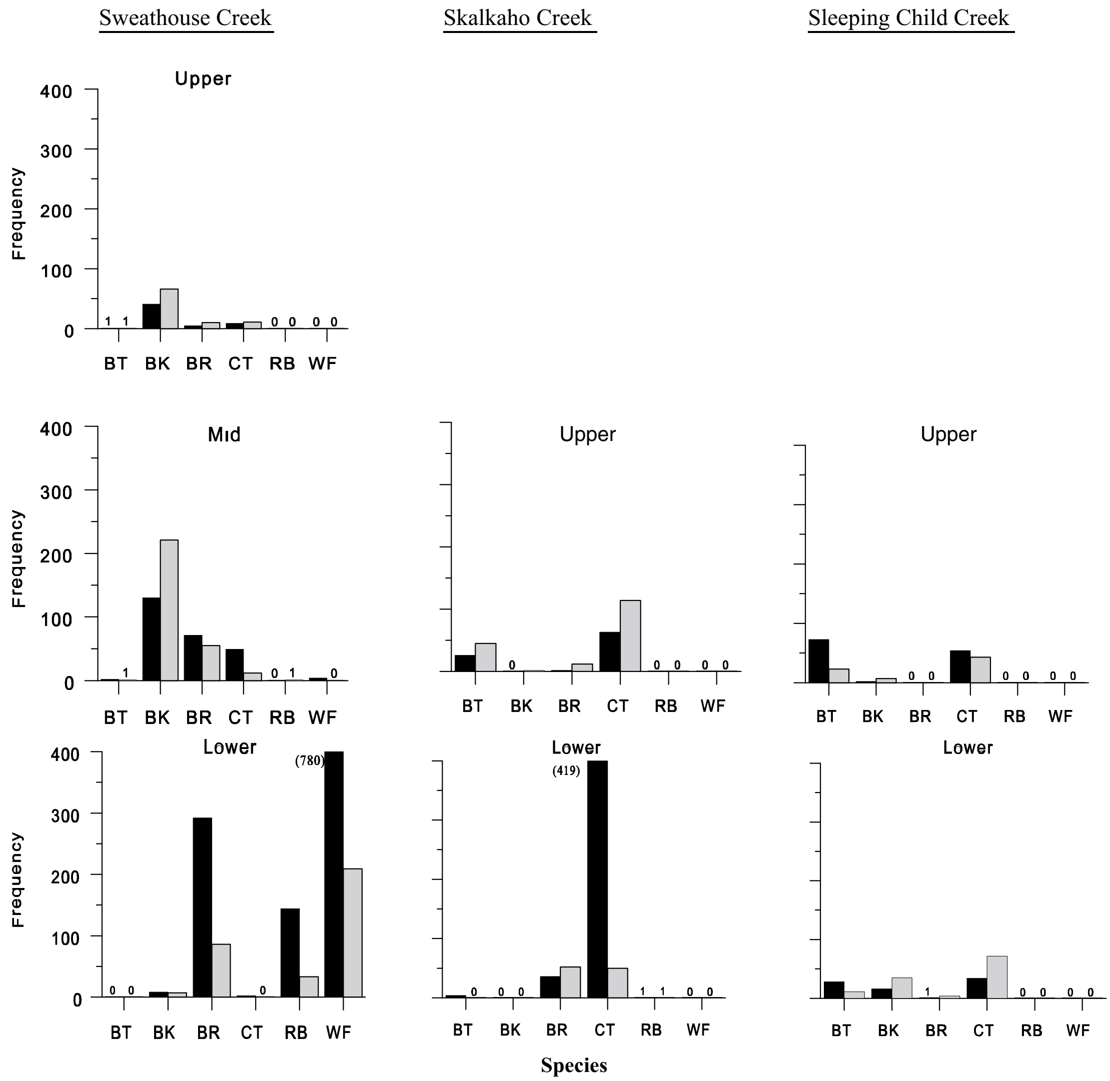

Figure 4. Number of salmonids captured moving downstream (dark bars) and upstream (light bars) at each weir (BT = bull charr, BK = brook charr, BR = brown trout, CT = cutthroat trout, RB = rainbow trout, WF = mountain whitefish). Location of weirs shown in Figure 2.

the bulk of the population, very limited movement was observed (n = 5, 0.01 fish per day).

Recapture of tagged bull charr between upper and lower weirs further suggested that the bull charr in Sleeping Child Creek had a higher migratory tendency than the other two populations. In this stream, four bull charr (2 adults, 390–450 mm and 2 juveniles, 155–165 mm FL) tagged at the upper weir were recaptured at the lower weir, 6.9 km downstream (Figure 2). None of the bull charr tagged at the upper weirs in the other two streams were recaptured in the lower weirs.

Movement of other salmonids

The fluvial life history form appeared much more prevalent in other salmonids. Large numbers of juvenile and adult mountain whitefish, cutthroat trout, brown trout, and rainbow trout were captured moving upstream and downstream at lower weirs (Figure 4), though the numbers and species of fish captured varied widely among study streams. In Sweathouse Creek, mountain whitefish, brown trout, and rainbow trout appeared to be fluvial, based on their abundance in

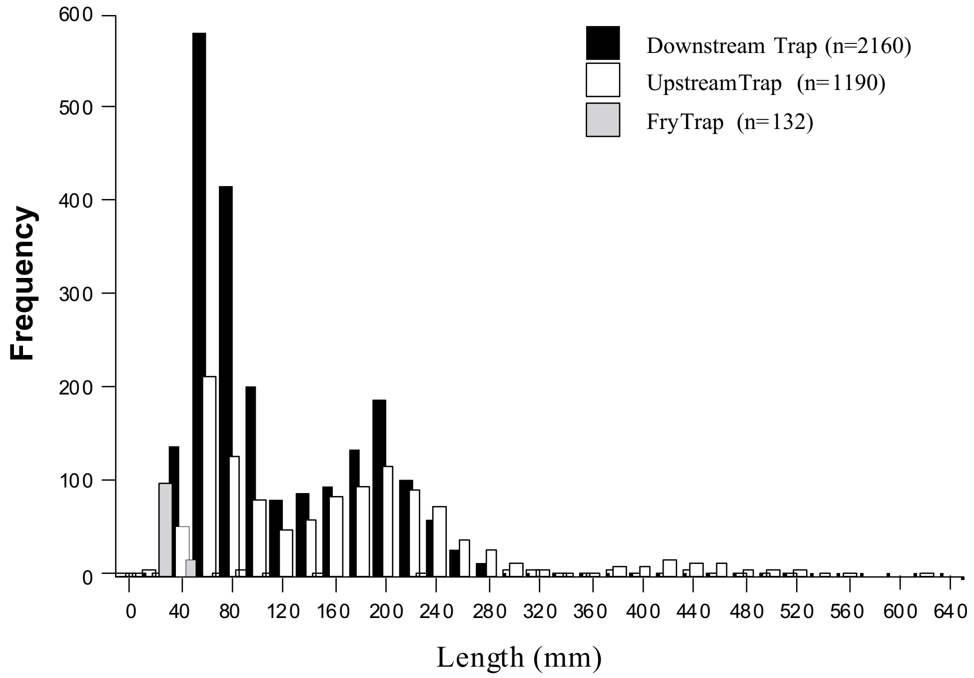

Figure 5. Length-frequency of salmonids captured in 'fry' traps and upstream and downstream weir traps.

the catch at the lower weir (river km 0.5). In contrast, brook charr and cutthroat trout, like bull charr, appeared to be 'residents', as they were rarely captured in the lower weir (<0.01% of catch), despite their prevalence upstream (Figure 2), but were commonly captured in upper weirs (river km 6.0 and 7.3) near highest population densities.

In Skalkaho and Sleeping Child creeks, juvenile and adult cutthroat trout were common at both the lower and upper weirs (Figure 4), and were widely distributed throughout the length of each stream (Figure 2). Unlike Sweathouse Creek, brown trout and mountain whitefish were absent or rare from catches at the lower weirs. Brown trout were present at moderate-to-high densities in lower Skalkaho Creek, but their distribution was restricted above the low-head dam just downstream of the lower weir at river km 9.

Discussion

Our findings confirm that bull charr in our three headwater streams exist primarily as nonmigratory residents. Although common in the upper reaches of all study streams, only one stream appeared to maintain a small fluvial component of bull charr as exhibited by outmigration of some juveniles and the presence of a few large-bodied migratory adults captured at the lower weirs. In contrast, substantial numbers of juveniles and adults of other species (mountain whitefish, brown trout) were captured moving downstream and upstream at lower weirs near tributary mouths, indicating that a fluvial life history was common in other species occupying the same streams as bull charr.

An important question is how effective weirs were at capturing migrant juvenile and adult bull charr. Low trapping efficiency, size selectivity, or failure to trap during periods of significant movement would fail to accurately detect juvenile outmigration or adult spawning migration. The large number of individuals, species, wide size range of fish captured, and estimated sampling efficiency of 50%, suggests that weirs were effective at trapping migrants. However, a limitation of our study was that weir sampling efficiency specifically for bull charr could not be determined because so few outmigrants were captured at lower weirs, thus we cannot eliminate the possibility that we failed to detect some bull charr that migrated. Bull charr exhibiting the fluvial/adfluvial life history typically outmigrate as juveniles from rearing tributaries at age 2–3 at sizes of 100–200 mm during June–October (Fraley & Shepard 1989, Elle[1], Riehle et al. 1997), and upstream spawning migration typically occurs from the declining limb of peak runoff in the spring through the summer (Thiesfeld et al.[2], Riehle et al. 1997, Swanberg 1997a). During this time period, we deployed full width weirs nearly continuously. Moreover, 81% of salmonids trapped moving downstream were <200 mm (including 83 juvenile bull charr), suggesting that our weirs were effective at sampling juvenile fishes in the size range typical of juvenile bull charr outmigrants. We also subsampled in spring prior to and during runoff when age-0 bull charr may disperse downstream, although typically they make up a much smaller component of outmigration in migratory populations than juveniles age 1–2 (Fraley & Shepard 1989, Riehle et al. 1997). Thus, we believe that we effectively sampled during the periods when the largest migration of fluvial bull charr would be expected, and their rarity was not due to sampling error.

The low incidence of the fluvial life history was surprising given the high life history variation exhibited by salmonids, even within the same drainage (Nordeng 1983, Elliott 1987, Hindar et al. 1991). 'Partial migration', whereby populations are comprised of both migratory and resident individuals, is common among salmonid populations (Northcote 1992, Jonsson & Jonsson 1993), including bull charr (Jakober et al. 1998). Rather, the predominance of the resident life history and lack of juvenile outmigration paralleled that observed in salmonid populations isolated above waterfalls or dams, where genetic or environmental change lead to much reduced migratory tendency (Elliott 1987, Northcote 1992, Morita et al. 2000).

Although the historical incidence of life histories in our study streams is unknown, anecdotal evidence suggests that the fluvial life history was much more common in the past. As noted, large-bodied migrant bull charr were formerly abundant throughout the drainage (MBTSG[5]). In other systems, the two life histories overlap in spawning areas (Jakober et al. 1998, R. Thurow unpublished data), but where bull charr populations are still intact (e.g., Flathead River, Montana), the migratory life history predominates and the resident life history appears relatively rare (Fraley & Shepard 1989, Thomas[8], Fitch 1997), though quantitative data are lacking. The decline of the migratory life history in bull charr in the Bitterroot drainage and in numerous other sites (Fitch 1997, McCart 1997, Rieman et al. 1997), has apparently occurred over the past 50–100 years. Morita et al. (2000) demonstrated that life history shifts from migration to residency in white-spotted charr, *Salvelinus leucomaenis*, can occur within 20–30 years after erection of migratory barriers.

Several scenarios could account for the decline of the migratory life history. First, resident and migratory forms represent different genotypes and coexisted historically, as documented for other salmonids (Verspoor & Cole 1988, Wood & Foote 1996). Under this scenario, the migratory genotype was abundant historically owing to the fitness advantages from migration to more productive habitats (Jonsson & Jonsson 1993), but selection against migration due to habitat change and disruption of migratory corridors has now reversed this pattern of dominance (McCart 1997). Second, migratory tendency is a 'conditional strategy' the expression of which is dependent upon environmental conditions, specifically juvenile growth rate (Nordeng 1983, Jonsson & Jonsson 1993, Morita et al. 2000). Thus, resident and migratory fish are of the same genotype, with high growth promoting residency and low growth promoting migration. Under this scenario, switching from a migratory to a resident life history after isolation above barriers occurs as a result of lower density and attendant higher growth rates. Third, resident and migratory life history forms were spatially isolated in the past, the lower reaches of tributaries used by migratory fish for spawning and rearing, and the upper reaches by resident fish (e.g., Elliott 1987, Vuorinen & Berg 1989). Selection against the migratory life history from migration barriers and habitat changes in the lower reaches have thus left only the resident form remaining.

It is unknown whether bull charr migratory tendency is governed chiefly by early growth rate or by inherited behavioral differences. Transplant experiments, genetic testing, and experimental crosses of migratory and nonmigratory fish, are needed to clearly differentiate whether bull charr life history is under predominantly genetic or environmental control (e.g., Nordeng 1983, Hindar et al. 1991, Morita et al. 2000). Such studies are gaining increasing importance as maintenance and restoration of life history diversity has now become an important goal of species recovery efforts (e.g., MBTSG[5], Healey & Prince 1995). Resolution of this question is vital as each mechanism suggests different management strategies. For instance,

[8] Thomas, G. 1992. Status report: bull trout in Montana. Montana Fish, Wildl. & Parks Rept., Helena. 105 pp.

if environmental factors are predominant, removal of migration barriers or manipulation of factors affecting juvenile growth rate (e.g., density, food availability, temperature), could affect the proportion of migrants and residents in a population (Morita et al. 2000). If life history is primarily under genetic control, then re-establishment of the migratory life history may require alleviation of downstream mortality factors that are selecting against migration, in concert with introduction of migratory stocks (McCart 1997).

An interesting finding from our study was that the lack of migratory tendency was not directly related to presence of migratory barriers. The migratory life history was absent in one stream without a low-head dam (Sweathouse) yet still present in another stream with a low-head dam (Sleeping Child). Why the migratory life history was apparently present in other salmonids in the same stream (Sweathouse) while absent in bull charr is also unclear, but high temperature and predation in the lower reaches may be involved. Bull charr are rare where maximum summer temperature is $>15°C$ (Saffel & Scarnecchia 1995), a level commonly exceeded in the lower reaches of Sweathouse Creek. Sweathouse Creek also had the highest density of nonnative brown trout and brook charr among study streams. In contrast, highest outmigration was observed where density of nonnative predators in lower reaches was lowest (Sweathouse, Figure 2). Differing passage potential of low-head dams to upstream migrants also may help explain differences in results among streams. Low-head dams in Skalkaho Creek were steep-walled concrete structures that were likely passable only to upstream migrants during spring runoff, which could explain why spring spawners expressed the fluvial life history (cutthroat trout) whereas fall spawners did not (bull charr, brown trout, mountain whitefish). In contrast, the Sleeping Child low-head dam was constructed of large rocks that formed a less steep falls which may have been a less significant fish passage barrier and allowing for greater retention of the fluvial life history. Underwater surveys below low-head dams in the fall could help determine to what extent migratory bull charr still exist in a system, and where improved passage would aid return of adult bull charr to historical spawning grounds and maintenance of the fluvial life history (e.g., Swanberg 1997b).

The main goal of this study was to determine the potential for re-establishing a migratory life form from resident bull charr populations by assessing the degree of retention of the fluvial life history in isolated headwater populations. Our comparison illustrated that life history expression is complex both among species and across drainages, even those in close proximity. Decline of the migratory life history form has significant conservation implications as resultant population isolates have reduced connectivity with neighboring populations and thus are at increased risk to local extinction (Rieman & McIntyre[3]). The large-bodied, migratory life history form of salmonids, formerly widespread, now appears much reduced among many populations of bull charr and other native species (Dunham et al. 1997, McCart 1997, Rieman et al. 1997). How to restore the rich diversity of salmonid life history will be an equally challenging question for fishery scientists as has been the question of how such high life history diversity has evolved.

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