American Fisheries Society Symposium 59:55–77, 2008

Seasonal Movement of Burbot in Relation to Temperature and Discharge in the Kootenai River, Idaho, USA and British Columbia, Canada

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Abstract.—Movements of 11 sonic tagged burbot *Lota lota* were examined in the Kootenai River, Idaho, USA and Kootenay River and Kootenay Lake, British Columbia, Canada through up to three spawning seasons. Our objectives were to determine seasonal movements, differences in behavior of individual burbot, and the role of temperature and discharge on prespawn movement. Burbot demonstrated multiple movement patterns: 3 burbot were very mobile, 3 appeared to be intermediate in activity, and 5 were sedentary in summer, while 2 of the 11 entered Kootenay Lake and returned to the river. Most burbot began in autumn what may have been prespawn migrations when river temperatures fell to a range of 3.0–4.9°C. Six burbot entered the Goat River during the spawning season, of which five showed a multiple-year pattern of fidelity, and four returned to an apparent home pool and then exhibited sedentary behavior until the following winter. Three of the 11 burbot demonstrated an apparent nonspawning or rest year, but this was thought to be habitat-related. Logistic regression analysis of three of the six fish entering the Goat River suggested their migration to be best correlated to decreasing temperature and discharge. If the logistic model were representative of the population, then predicted migrations of burbot to the Goat River during winter would have followed a consistent pattern in November preLibby Dam, while postLibby Dam showed migrations to be unpredictable. Results of this study suggest that burbot had multiple life history patterns and several spawning locations and that rehabilitation measures should promote cooler winter water temperatures less than 5°C and discharges less than 300 m^3/s.

Introduction

Burbot *Lota lota* are the only freshwater Gadid and are one of only two freshwater fishes that have a circumpolar distribution (McPhail and Lindsey 1970). Adult burbot inhabit large cool rivers of the north temperate region and the hypolimnion of large lakes, preferring temperatures of about 10–14°C (Cooper and Fuller 1945; Hackney 1973; Hoffman and Fischer 2002). Their migrations, movements, and ontogenetic patterns may be motivated by water temperature (Girsa 1972; Hedin 1983; Carl 1995; Hoffman and Fischer 2002; Slavík and Bartoš 2002). Burbot commonly spawn at temperatures ranging from 0°C to less than 6°C during winter (Becker 1983). Burbot are thought to be ecologically intermediary in thermal preference between coldwater salmonids (huchen *Hucho hucho* and brown trout *Salmo trutta*) and more thermophilic cyprinids (Nikčević et al. 2000) and are likely classified as temperate mesotherms (Hokanson 1977).

Ultrasonic telemetry has been an important tool for describing burbot move-

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ment (Malinin 1971; Breeser et al. 1988; Evenson 1993) within lakes during winter or summer (Bergersen et al. 1993; Carl 1995), within rivers (Breeser et al. 1988; Paragamian 2000), and for prespawn migrations from lakes to rivers (Robins and Deubler 1955; Sorokin 1971). However, the annual consistency of individual fish migrations, homing, migration, and the role of temperature are not well known in North America. Under most circumstances, investigators using ultrasonic telemetry to monitor movement of burbot were unable to study individual fish over an extended period of time (i.e., two or more spawning seasons) because studies were usually restricted by transmitter battery life. Thus, differences or consistencies in behavioral patterns of individual burbot through two or more years were not measurable.

Burbot in the Kootenai River, Idaho, USA, and the Kootenay River and Kootenay Lake, British Columbia, Canada (Figure 1; U.S. and Canadian spellings differ) were once abundant but now represent a remnant of the former population (Paragamian et al. 2000). In the Kootenai River and Kootenai Lake, ultrasonic telemetry was used to determine if burbot prespawn migration was disrupted by winter discharges from Libby Dam greater than 300 m^3/s (Paragamian 2000; Paragamian et al. 2005). Libby Dam was completed in 1972 by the U.S. Army Corps of Engineers (USACE) and was fully operational in 1974. Libby Dam not only increased winter discharge of the river during the burbot spawning migration, but also released warmer water than preLibby Dam (Partridge 1983). Although there was a clear understanding of how postLibby Dam winter discharge affected burbot, it was not known how warmer water and the interaction with higher discharges may also affect burbot migration. A better understanding of temperature and discharge would be important to identifying discharge and temperature rehabilitation measures in a Burbot Conservation Strategy (KVRI Burbot Committee 2005). Our objectives were to examine the telemetry records of 11 burbot that had ultrasonic transmitters persist two or more spawning seasons in order to identify individual movement patterns through the seasons, to identify differences in behavior of individual burbot, and to determine how the interaction of temperature and discharge may affect movement and behavior of burbot during prespawn migration. This information also could be important to the management of populations similarly affected by dams or suppressed burbot populations (Maitland and Lyle 1990; Keith and Allardi 1996; Maitland and Lyle 1996; Argent et al. 2000; Arndt and Hutchinson 2000).

Study Site

The Kootenai River is located in the upper Columbia River basin. The river originates in Kootenay National Park, British Columbia, discharges south into Koocanusa Reservoir in Montana, and turns northwest at the site of Libby Dam (Figure 1). The river passes through the northeast corner of the Idaho Panhandle and turns north and enters Kootenay Lake, British Columbia. Kootenay Lake is a 39,537-ha oligotrophic lake that has two major inlets, the Duncan River from the north and the Kootenay River from the south. The lake lies within a north–south aspect valley between the Selkirk and Purcell mountains and discharges through the West Arm, located transverse to the main lake, into the lower Kootenay River, which joins the Columbia River near Castlegar, British Columbia (Figure 1) Our primary study reach for this investigation was from river kilometer (rkm) 118.0 to rkm 247.0 (Figure 1), though burbot were occasionally tracked to Kootenay Lake. Daily regulated discharges in the vicinity of our study reach varied from about 70 to 1,200 m^3/s.

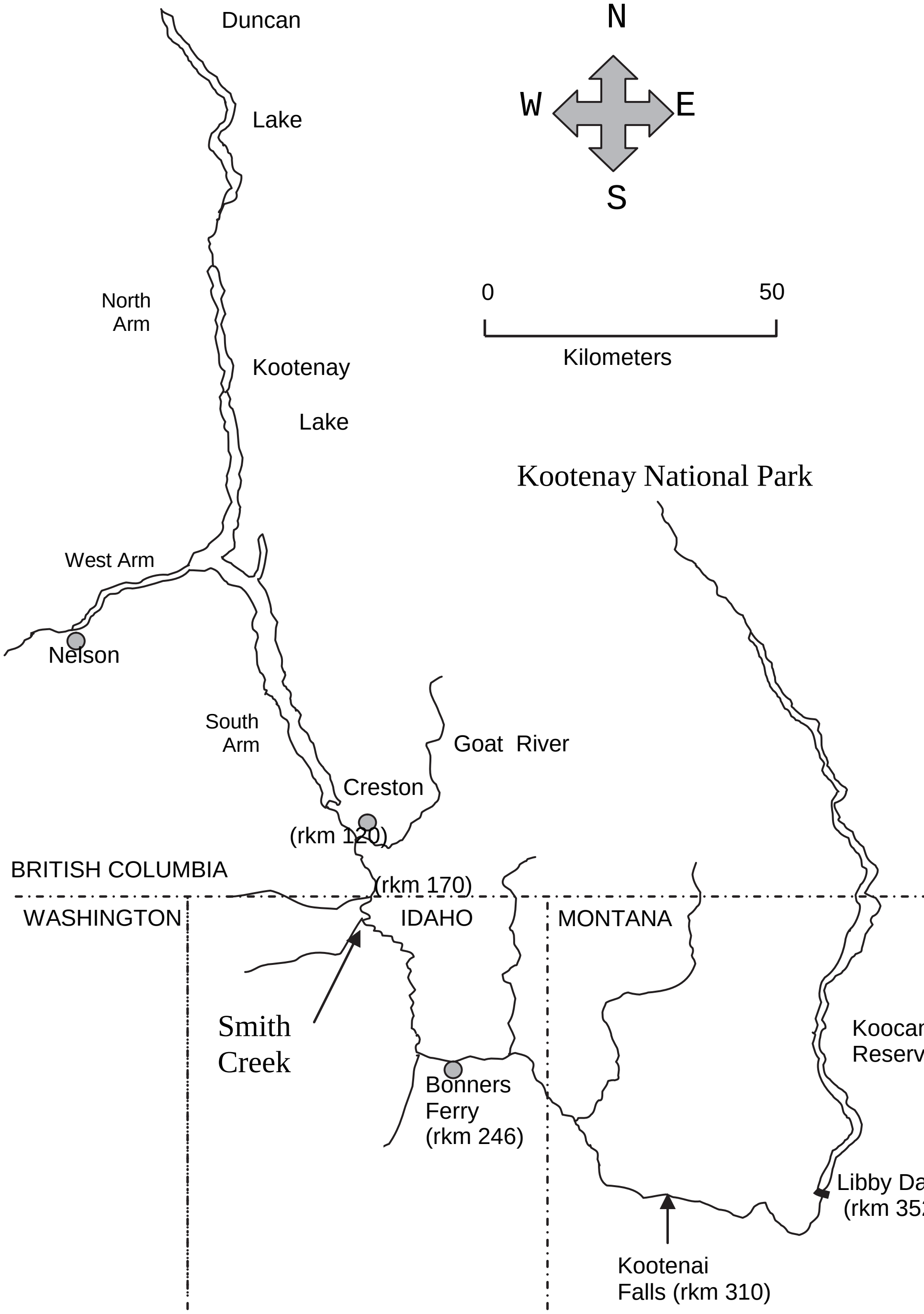


FIGURE 1. Location of the Kootenai River, Kootenay Lake, Lake Koocanusa, and major tributaries. The river distances from the northernmost reach of Kootenay Lake are in river kilometers (rkm) from the upper most reach of Kootenay Lake and are indicated at important access points.

Burbot in the Kootenai River migrate into the Goat River (rkm 152.7), British Columbia, a major tributary to the river before it enters Kootenay Lake. The Goat River is one of only three known burbot spawning locations in the lower portion of the basin. The other known burbot spawning locations include the north arm of Kootenay Lake (C. Spence, British Columbia Ministry of Environment, personal communication) and near Ambush Rock in the Kootenai River at rkm 244.5 (Paragamian 2000; Kozfkay and Paragamian 2002). Some burbot spawn in the Kootenai River the first week in January through February (Paragamian 2000; Kozfkay and Paragamian 2002).

Methods

Capture of Burbot

Burbot were sampled with hoop nets ($n \leq 13$) baited with dead fish from October 1994 through April 2000. Hoop nets had a maximum diameter of 0.61 m (see Bernard et al. [1991] for a description of nets and Paragamian [2000] for a method of deployment). Nets were deployed in deep areas of the Kootenai River (usually the thalweg where burbot were known to travel) between Nick's Island (rkm 144) near Creston, British Columbia and Ambush Rock at rkm 244 near Bonners Ferry, Idaho. Sampling sites included the mouths of the Goat River, British Columbia and Smith and Boundary creeks, Idaho. For file records and individual accounting, each burbot was given a consecutive number in order of capture. Burbot of about 1,000 g and larger were usually selected for telemetry studies. The preferred weight of burbot was to exceed the transmitter weight to fish weight proportion by ≤ 2% (≥1,000 g; Winter 1996).

Burbot Telemetry

Sonic transmitters (Sonotronics, Phoenix, Arizona, USA) were used to track adult burbot movements from 1994 through 2003. Sonic transmitters had a 420-d life expectancy, were cylindrical in shape, measured 18 mm by 65 mm, and weighed 8 g in air. We surgically implanted sonic transmitters following the techniques of Hart and Summerfelt (1975). When possible, sex was determined during surgery.

Telemetry effort was expended by boat in the Kootenai River, predominantly during daytime (0730–1800 hours), from rkm 120 to rkm 247, and occasionally within Kootenay Lake from rkm 80 to rkm 119.9. We examined burbot locations and looked for movement or behavior patterns that may be common among individuals. We then placed individual burbot into several descriptive categories of movement or behavior. These categories were further partitioned by calendar intervals that were based on previously published observations of burbot behavior, activity patterns, and temporal intervals (Becker 1983; McPhail and Paragamian 2000; Pääkkönen et al. 2000). Calendar intervals were (1) November through February for the prespawning and spawning movement and behavior, (2) March through April for postspawn, and (3) May through October for the warmer season when reduced burbot activity was anticipated (Pääkkönen et al. 2000; Paragamian et al. 2005). Our telemetry records of movement and behavior began with the November through February interval because this is when most burbot were captured and tagged and monitoring began.

Kootenai River Temperature and Discharge and Goat River Temperature

Daily temperature and discharge records for the Kootenai River were recorded at Libby Dam, at Bonners Ferry, Idaho, by the U.S. Geological Survey. We also examined historic temperature and discharge records archived by the USACE for the river to gain a perspective of how temperatures may have changed from predam conditions. Average daily pre- and postLibby Dam discharge records for the Kootenai River have been presented elsewhere in detail (Paragamian 2000; Paragamian et al. 2005).

Temperature for the Goat River from October through April was recorded by either a HOBO or StowAway XI temperature logger, deployed less than 200 m upstream of the confluence with the Kootenai River. Mean daily temperature of the Goat River was calculated from five evenly spaced daily time measurements from the recorder.

Data Analysis and Interpretation

In this study, the general observations of burbot movement and behavior were made for only those burbot that had ultrasonic transmitters extend through two or more spawning seasons. Seasonal burbot locations and movement also were compared to water temperature in the Kootenai and Goat rivers.

Burbot movement and pre- and postLibby Dam discharge and temperature were used in a design analogous to "impact assessment" (Garton et al. 2005). We used logistic regression analysis (Wilkinson 1990) to help us determine the probability of burbot movement under changing water temperature and river discharge from autumn through winter pre- and postLibby Dam. Kootenai River temperatures (°C, measured at Bonners Ferry gauge BFEI), discharge (measured at Leonia gauge [LEOI] located 30 km upstream from Bonners Ferry), the standardized discharge-temperature interaction, and burbot movement were used. In order for these burbot to qualify for our post priori logistic regression sample, they were required to follow the step-wise migration criteria of a distance of 5 km or more in 10 d or less (Paragamian et al. 2005). Although on some winter days, low discharge accelerates the cooling of the Kootenai River water, the auto correlation of the two was not detected in our analysis. A standardized discharge–temperature interaction was used because of the unequal scale of measurement in the two individual terms. We also used a lag period of 24 h to account for travel distance of water from Libby Dam to the mid-river in Idaho and British Columbia. Libby Dam is the main source of discharge and temperature variation for the Kootenai River downstream to Kootenay Lake.

Results

Burbot Catch

Burbot captures.—From 1994 through 2003 ultrasonic transmitters were attached to 66 burbot of more than 300 captures (Paragamian et al. 2005, 2008, this volume), but of these, only 11 ultrasonic transmitters persisted two or more winters. A total of 773 contacts and locations were made for the 11 burbot; individual contacts ranged from N = 29 to N = 182 (Table 1; Figures 2–5). The number of days from first to last contact ranged from 382 to 863.

Burbot Movement and River Temperatures by Calendar Season

Burbot movement and behavior was categorized by three descriptive patterns of movement or behavior: sedentary, active that included inter-lake and river movement, and intermediate movement—fish that demonstrated no consistent pattern of homing or sedentary behavior. Eight of the 11 burbot (numbers 12, 57, 72, 73, 218, 232, 234, and 255) migrated at least once during the prespawn and spawning season (winter) of tracking, and several migrated in each of three seasons (Table 2; Figures 2–5). Although some fish migrated to known spawning locations and at known burbot spawning temperatures, we have no definitive evidence any of these fish spawned. In many

TABLE 1. Identification number, total length, weight, sex and telemetry records of 11 burbot captured in the Kootenai River, Idaho and British Columbia.

Burbot identification number	Total length (TL)	Weight (g)	Sex	Release date	Release location rkm	Last date of contact	Last contact location rkm	Total contacts	Number of days tag was active
12	560	1,135	M	6/28/94	178.1	9/12/96	242.0	73	808
57	648	2,100	F	2/20/96	152.7[a]	7/1/98	134.2	182	863
72	618	1,800	F	12/11/96	144.4	8/12/98	138.4	95	610
73	655	1,710	F	12/13/96	152.6	12/2/98	150.5	112	720
218	568	1,400	F	1/29/01	244.6	5/6/02	219.0	29	463
226	547	1,100	Unknown	1/29/01	244.6	2/11/02	177.5	31	382
227	745	2,175	F	2/6/01	244.5	5/14/02	224.0	44	463
230	578	1,200	M	1/30/01	170.0	8/14/02	173.0	56	563
232	500	975	Unknown	2/2/01	152.7[a]	2/6/03	144.5	49	735
234	561	1,100	F	2/5/01	152.7[a]	2/7/03	152.5	50	733
255	615	1,650	Unknown	10/26/01	150.8	2/28/03	152.7	52	491

[a] Captured and released in the Goat River.

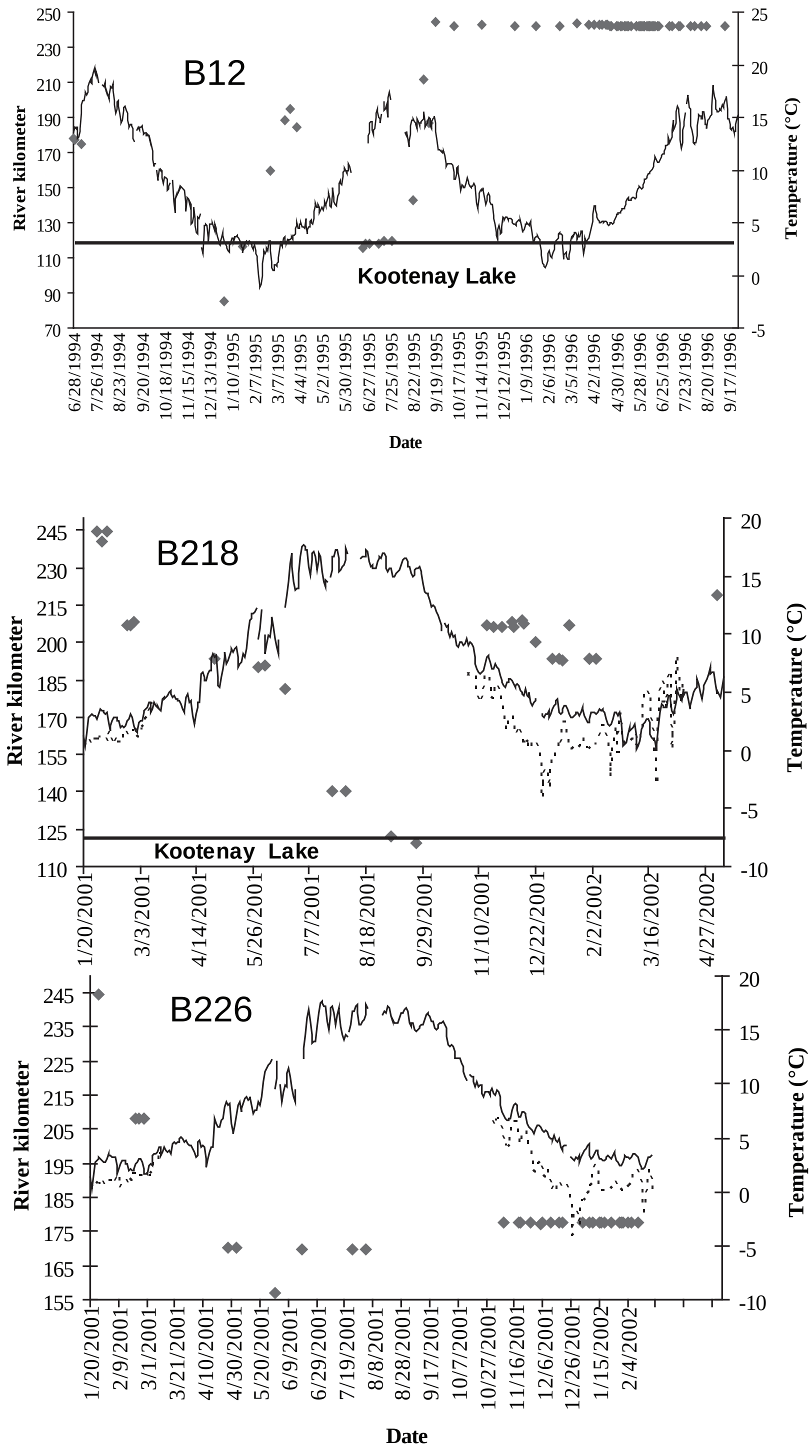


FIGURE 2. Relocations of three burbot relative to water temperatures in the Kootenai (solid line) and Goat (dashed line) rivers for burbot numbers 12 (top panel), 218 (middle panel), and 226 (lower panel) by river kilometer, and solid horizontal line represents the boundary with Kootenay Lake and Kootenai River.

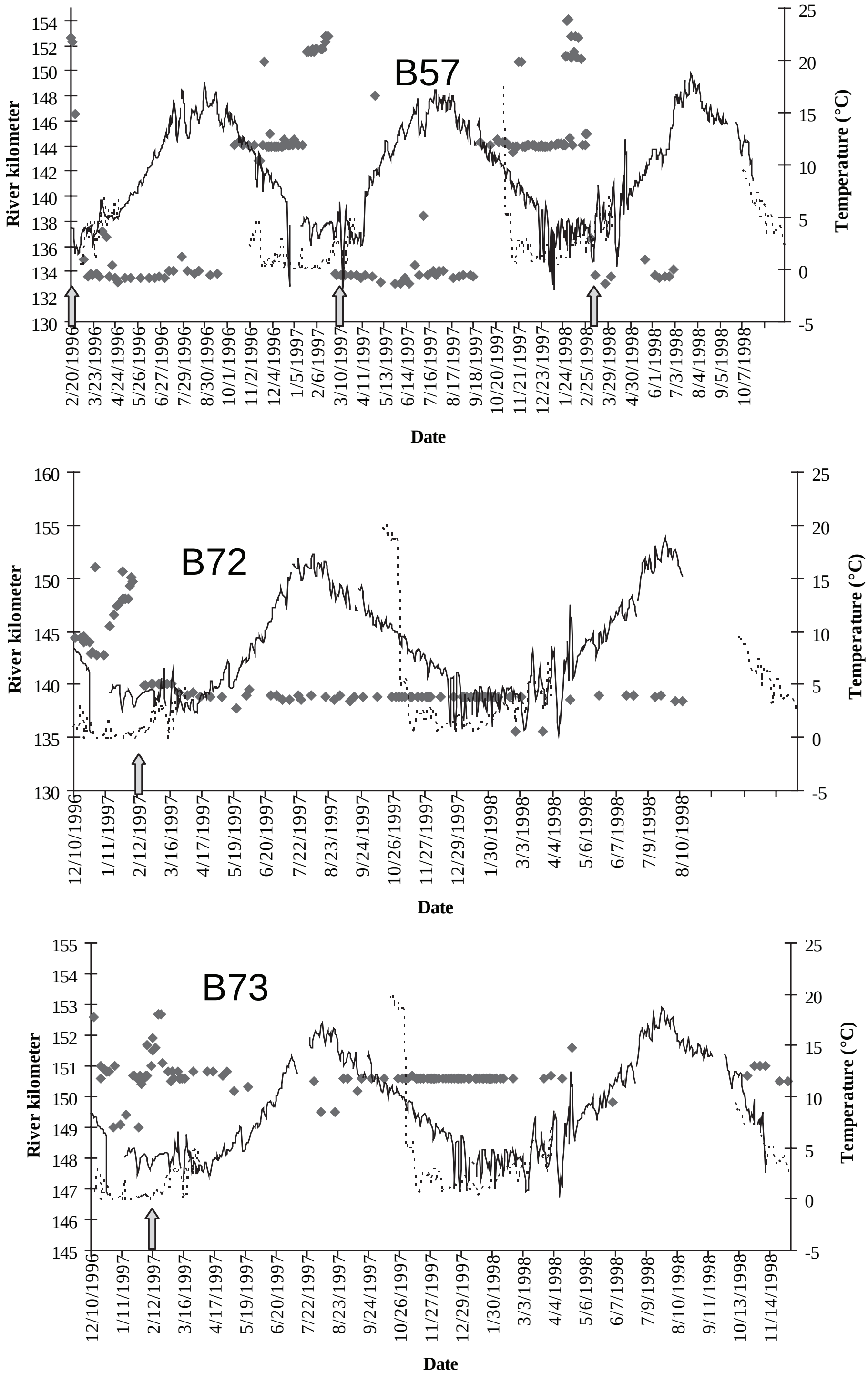


FIGURE 3. Relocations of three burbot relative to water temperatures in the Kootenai (solid line) and Goat (dashed line) rivers for burbot numbers for burbot numbers 57 (top panel), 72 (middle panel), and 73 (lower panel). Arrows represent estimated date fish entered the Goat River.

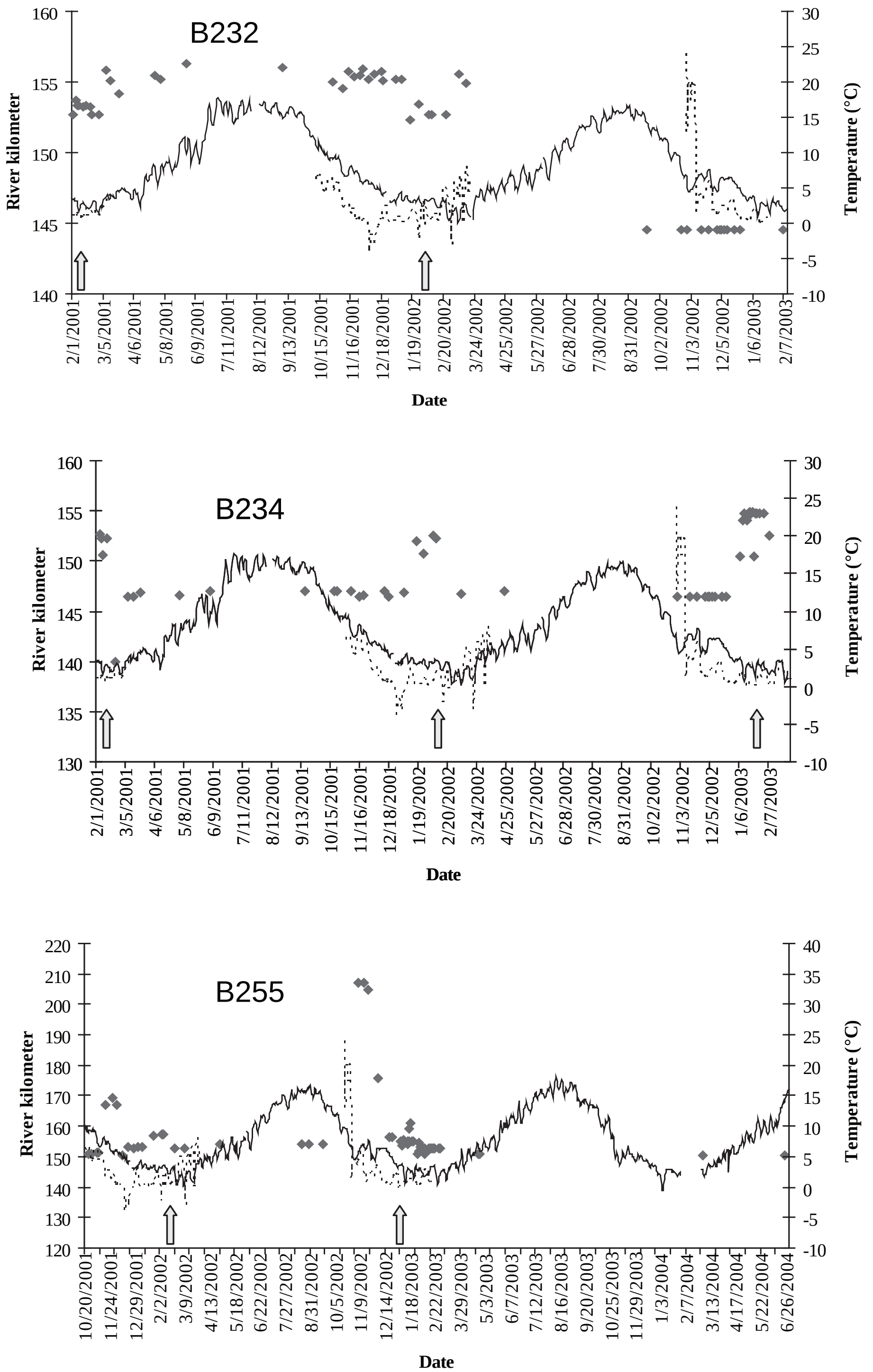
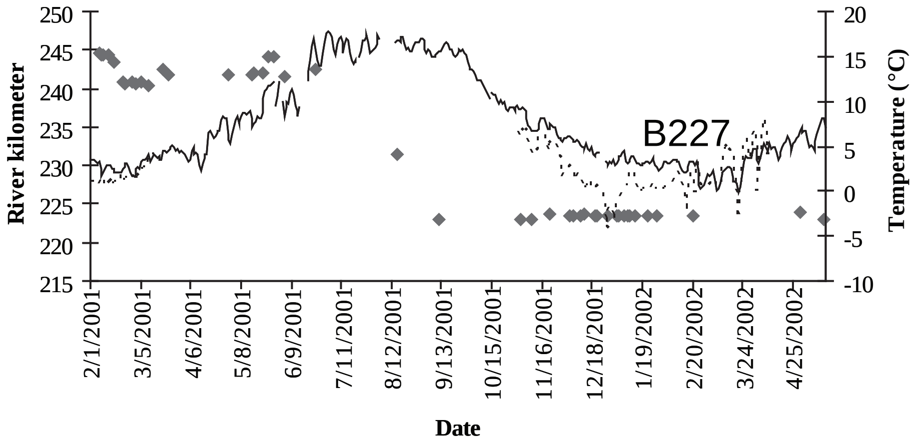


FIGURE 4. Relocations of three burbot relative to water temperatures in the Kootenai (solid line) and Goat (dashed line) rivers for burbot numbers 232 (top panel), 234 (middle panel), and 255(lower panel). Arrows represent estimated date fish entered the Goat River. Burbot 234 was recaptured at rkm 151.1 on February 17, 2005.



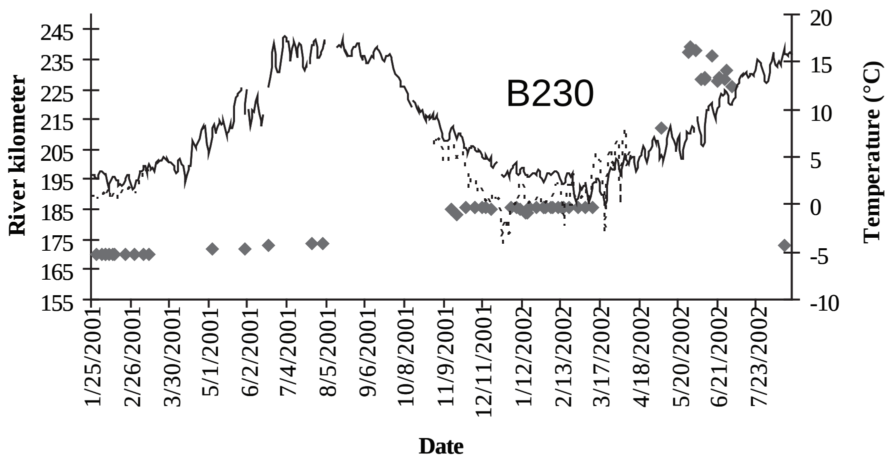


FIGURE 5. Relocations of two burbot relative to water temperatures in the Kootenai (solid line) and Goat (dashed line) rivers for burbot numbers 227 (top panel) and 230 (lower panel).

circumstances, it was necessary to provide a range for temperature during major burbot movements or a range for the day of the movement because telemetry contacts were not made every day.

Sedentary Burbot

Five burbot (numbers 57, 72, 73, 232, and 234; Figures 3 and 4) entered the Goat River during the spawning season, of which three had fidelity for reentering the Goat River in following years (numbers 57, 234, and 232). The five burbot were sedentary postspawn and remained in or near their apparent home pool; of these burbot, numbers 57, 72, 73, and 234 moved downstream to a home pool while burbot number 232 moved upstream.

November through February.—Five burbot migrated during November through February and entered the Goat River in January or February (numbers 57, 72, 73, 232, and 234; Figures 3 and 4). During these migrations, temperatures of the Kootenai River usually

TABLE 2. Identification number for 11 burbot, temperatures (°C) of the Kootenai and Goat Rivers on the estimated day of migration and estimated migration dates.

Estimated Burbot identification number	Year of study	Kootenai River temperature (°C) or range during migration	Kootenai River temperature (°C) or range	Estimated Kootenai River temperature (°C) or range at entry into Kootenay Lake	Estimated migration date Kootenai River	Estimated first entry date into Goat River	Estimated Kootenai River temperature (°C) at Goat River entry	Goat River temperature (°C) at entry
12	1995	4.3–4.8	NA	–	–	–	–	–
	1996	No spawn	NA	–	–	–	–	–
57	1995–1996	–	NA	–	NA	2/20/96	4.5	NA
	1996–1997	14.1[a]		–	10/09/96	–		
		4.8[b]			1/21/97	2/18/97	4.0	0.68
	1997–1998	13.7[a]	NA	–	9/25/97–	2/09/98	3.6	3.09
57		4.1		–	1/27/98			
72	1997	2.8–4.3	NA	–	12/31/96	2/07/97	3.2	0.4
	1998	No spawn	NA	–	–	–	–	–
73	1997	4.3–4.8	NA	–	2/15–2/16/97	2/17/97	4.28	0.94
	1998	No spawn	NA	–	–	–	–	–
218	2001	–	NA	15.7	–	–	–	–
	2002	–	NA	–	–	–	–	–
226	2001	–	2.0–4.5[d]	–	–	–	–	–
	2002	–	–	–	–	–	–	–
227	2001	–	2.0–4.5[d]	–	–	–	–	–
	2002	–	–	–	–	–	–	–
230	2001	–	2.0–4.5[d]	–	–	–	–	–
	2002	3.0–4.0	–	–	3/11–5/6/0	–	–	–
232	2000–2001	4.0	NA	–	NA	2/01/01	3.5	1.1
	2001–2002	3.2	NA	–	1/14/02	2/04/02	3.2	0.66
234	2000–2001	–	NA	–		2/04/01	3.2	1.1
234	2001–2002	3.1–4.9	NA	–	1/05–1/16/02	2/04/02	3.2	0.48
	2002–2003	3.2–5.1	NA	–	12/24/02–	2/02–2/06/03	1.8–2.8	0.5–2.24
					01/06/03			
255	2002	NA[c]	NA	–	NA[c]	2/23–3/8/02	0.07–2.37	0.45–1.49
	2003	NA[c]	NA	–	NA[c]	2/5–2/6/03	1.84–2.3	0.5–0.86

[a] First and secondary pre-spawn migration temperature.
[b] Second and primary pre-spawn migration temperature.
[c] This burbot moved too much to get an estimate of migration date or temperature of Kootenai River.
[d] Temperature data based on Kozfkay and Paragamian 2002 burbot believed to have spawned at Ambush Rock.

ranged from 3.0°C to 4.9°C (Table 2). The temperature when burbot entered the Goat River ranged from 0.5°C to 3.0°C, whereas that of the Kootenai River ranged from 0.7°C to 4.5°C (Table 2).

Three burbot showed a strong fidelity for returning to the Goat River from previous years (numbers 57 and 234 migrated into the Goat River three seasons each, and number 232 entered twice: Figures 3 and 4). However, burbot numbers 72 and 73 migrated into the Goat River once each and did not show any evidence of migration to the Goat River during their second season of study (Figure 3).

Burbot 57 had the most unique late autumn and winter migration pattern and was tracked to the Goat River three different spawning seasons. It was a gravid female originally captured in the mouth of the Goat River during February 1996 (Figure 3). Each year following its capture, burbot 57 made a journey in late September or early October, earlier than the other fish (Table 2; Figure 3). The first movements of burbot 57 were from its home pool (rkm 134) to Nick's Island (rkm 144.6) at water temperatures of 14.1°C in October 1996 and 13.7°C in September 1997 (Table 2). During its second stage, it moved from Nick's Island to the Goat River at 4.8°C and 4.1°C, on January 21, 1997 and January 27, 1998, respectively.

March through May.—Each winter, immediately after the spawning season for fish in the Goat River (Paragamian 2000), four burbot (numbers 57, 72, 73, and 234) moved downstream while burbot number 232 moved upstream. Following this movement, all were sedentary and remained in or near their apparent home pool. In general, water temperature of the Kootenai River was still cool between March and May of each year ranged between 3.0°C and 6.0°C (Figures 2–4). Burbot number 57 had the furthest home pool from the Goat River of 18.7 km. Burbot number 73 returned to a location in the Kootenai River that was usually within 2 km of the Goat River. The other burbot (number 234) that entered the Goat River in winter had a home pool within 10 km.

June through October.—Burbot numbers 57, 72, 73, 230, and 234 were all relatively sedentary during spring through early autumn remaining in or near a home pool. These fish moved little when the Kootenai River temperature was above 10°C.

Active Movement

Three burbot (numbers 12, 218, and 255) demonstrated active movement with no apparent home pool. Relocations of burbot numbers 12 and 218 included inter-lake and river movement while 255 remained in the Kootenai River. Burbot number 255 was captured in the Goat River, but of the fish captured there during the spawning season, it was the only one that did not show evidence of a home pool.

November through February.—Burbot number 12 was captured, tagged, and released the summer of 1994 near the mouth of Smith Creek (rkm 177.5) but was not relocated until December at Crawford Bay (rkm 85) in Kootenay Lake. In late December 1994, burbot number 12 made the second longest transboundary prespawn journey of any tagged burbot, moving from Crawford Bay to rkm 195.7 in Idaho, a minimum distance of 111 km (Figure 2).

Burbot 218 is believed to have spawned in the Kootenai River in 2001 at Ambush Rock (Figure 3), its capture location rkm 245.5, because it was captured with other gravid burbot (Kozfkay and Paragamian 2002). The Kootenai River temperature the last week in January and first 2 weeks in February ranged from 2.0°C to 4.5°C. The following spawning season, it was found ranging from about rkm 186 to rkm 201 (Gunderman and Paragamian 2003).

Burbot 255 was initially caught near the Goat River in November 2001 but soon moved upstream and remained mobile (Figure 4). This fish moved back downstream to the vicinity of the Goat River, but by late February 2002, it could not be relocated in the Kootenai River or the accessible lower Goat River. During the second season, this same burbot was relocated in November of 2002 upstream in the Kootenai River at the locally known Krauss Hole, Idaho (rkm 207.0); it then moved downstream and remained in British Columbia for the rest of the field season. On January 15, 16, and 21, 2003, this burbot was located in the same pool as burbot number 234. In February 8–28, 2003, burbot number 255 was in the main-stem Kootenai River near the Goat River and was later relocated in the Goat River.

March through May.—In spring 1995, burbot number 12 made a second extensive journey by moving from rkm 197.7 to Kootenay Lake. This movement took place when the river temperature had warmed to 13.9°C. In 2001, burbot number 218 entered Kootenay Lake when the river temperature was 15.7°C (Table 2). In 2002, burbot number 255 was located several times near the Goat River but had limited spring movement and was not relocated during the summer 2002. When burbot number 255 was relocated, it was well upstream in Idaho (rkm 207) followed by downstream movement with limited range between rkm 149 and rkm 155.

June through October.—Burbot numbers 12 and 218 moved downstream during summer, as noted, and were eventually located in several locations in Kootenay Lake $\geq$ 30 m in depth. Both fish re-entered the Kootenai River from Kootenay Lake when the river temperature was cooling from previous highs of about 17°C (Figure 2). Burbot number 12 remained in the lake until August and then returned to the river from about rkm 116 to rkm 244, the longest transboundary journey of 128 km (Figure 2). Burbot number 255 was located several times near the Goat River in 2002 but, in the second year, could not be relocated from June through October of 2003 (Figure 4). It was not relocated for almost a full year when it was last found near rkm 148 in late June 2004 (Figure 4).

Intermediate Movement with No Defined Home Pool

Three burbot had movement patterns that we considered intermediate (burbot numbers 226, 227, and 230) compared to the sedentary and active burbot. These burbot did not show a preference for a home pool among years and were sedentary at times but also showed mobility; we could not determine any specific movement or behavior patterns for these fish.

November through February.—Burbot numbers 226, 227, and 230 are also believed to have spawned in 2001 at Ambush Rock (Kozfkay and Paragamian 2002), their original capture location (rkm 245.5; Figures 2 and 5). After the spawning season, they both gradually moved downstream. The temperature of the Kootenai River when these burbot were caught with other gravid fish was 2.0–4.5°C the last week in January and first 2 weeks in February. These burbot did not demonstrate a winter migration in 2002. They were sedentary for several months through the winter and spring and postspawning season before their transmitter batteries expired.

Burbot number 230 was captured at rkm 170 during the spawning season of 2001 but showed only a short movement during the winter but, during the spawning season of 2001, was located at about rkm 185 (Figure 5). We have no evidence to suggest that this burbot spawned.

March through May.—Burbot number 226 was relocated after the 2001 spawning season at about rkm 168 and then at the end of the March through May period at rkm 156. By March 2002, the transmitter battery expired. Burbot number 227 was relocated between rkm 240 and rkm 242 at the end of the 2001 spawning season but, the following year, was further downstream the same time of year at about rkm 223. Burbot number 230 moved a short distance upstream after the spawning season of 2001 but was sedentary at about rkm 171. In 2002, this burbot moved between late March and mid-May from about rkm 185 to about rkm 239 after being sedentary at rkm 185.

June through October.—Burbot number 226 was located at about rkm 169 in 2001 but found only a few times that year. Burbot number 227 was relocated several times and was progressively moving downstream from about rkm 244 to rkm 223 during June through October 2001. By this same period in 2002, the transmitter battery for number 227 had expired. Burbot number 230 was found in two different locations during June through October 2001 and 2002. In 2001, it was at about rkm 169, while the following year, it was between rkm 235 and rkm 225 but was last located again at about rkm 169.

Historic Kootenai River Temperature and Winter Discharge

We examined historic water temperatures of the Kootenai River. Water temperatures at the dam site and downstream at Porthill and Bonners Ferry, Idaho, during winter have changed since the construction of Libby Dam (Figure 6). The primary reason river temperatures have changed is due to storage and subsequent warming of water in Koocanusa Reservoir during summer. Prior to construction of Libby Dam, Kootenai River water temperature at the dam site and downstream through the canyon from December through February ranged from 0°C to 1°C and progressively warmed to about 1–2°C

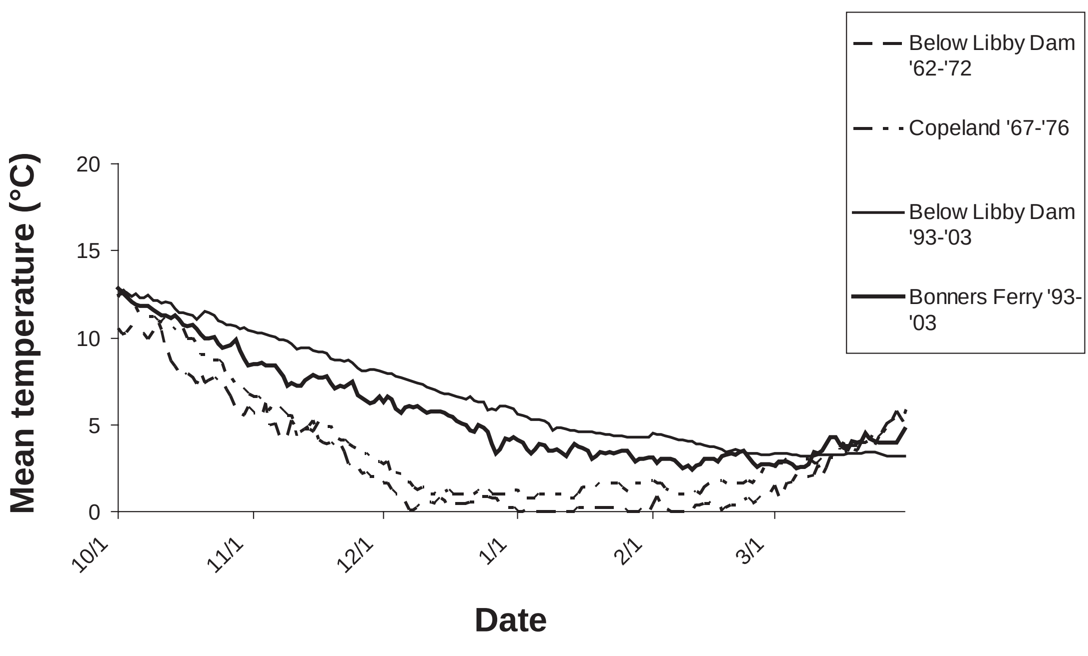


FIGURE 6. Pre- and postLibby Dam water temperatures in the Kootenai River at the dam site from 1962 through 1972 and at Copeland, Idaho, from 1967 through 1976 and postLibby Dam downstream from the dam from 1993 through 2003 and at Bonners Ferry, Idaho, from 1993 through 2003.

as it passed through the meandering reach, prior to entering Kootenay Lake. Following construction of the dam, release temperatures during December through February range from about 4.5°C to 8°C, cooling to about 2.5–6°C as the river flowed downstream into the canyon reach. Although, the post operations water temperature can decrease in winter rather than increase as the river flows downstream, it is still warmer by as much as 3°C than it was prior to construction of Libby Dam, when the river commonly froze during winter.

Discharge in the Kootenai River at Bonners Ferry during winter is currently three times higher than predam times. Previous to Libby Dam the natural discharge from January to February averaged about 170 m^3/s, but it can now average more than 850 m^3/s during any week (Paragamian et al. 2000) because the USACE operated Libby Dam under normal procedures for hydropower, flood control, and Kootenai River white sturgeon *Acipenser transmontanus* recovery (Duke et al. 1999; Paragamian 2000; Paragamian et al. 2005). However, there were several brief periods during winter 1997–1998 when the USACE operated the dam in response to requested discharge studies (Paragamian 2000).

Logistic Regression Analysis

Only three burbot met the travel criteria of step-wise movement (Paragamian et al. 2005) to qualify for our logistic regression analysis. These burbot (numbers 57, 72 and 234) also exhibited a consistent pattern over consecutive years of upriver migration to the Goat River from downriver home pools for a total of seven spawning seasons. The standardized discharge–temperature interaction and 172 telemetry locations for the months of October through March were used. The relationship between the dependent variable MOVE (Probability, $\Pr(Y = 1)$ and the independent variables TEMP (°C), DISCHARGE (m^3/s) and the standardized discharge-temperature interaction (*Z* DISCHARGETEMP) was statistically significant (Tables 3 and 4: GM = 86.11, $P < 0.000$), burbot migration was motivated with decreasing temperature and discharge. The logistic model predicting the logit (MOVE) was

Move = 12.5182 – 3.07251 (Z DICHARGE TEMP) – 0.87674 (TEMP) – 0.02366 (DISCHARGE).

The overall proportion of movement correctly classified by the full model was 0.924. Measures of the strength of association between the dependent and independent variables, $R^2_L = 0.45$ and $R^2 = 0.56$ (where R^2_L is a measure of how well the model fits the data and the *L* indicates that it is a term specific to logistic regression [Hosmer and Lemeshow 1989:148]) indicate a strong relationship between the dependent variables and its predictors (Table 3). The indices of predictive efficiency also indicate that the model predicts well: $\lambda_p = 0.69$ and $\tau_p = 0.79$, both statistically significant at $P < 0.001$. Standardized logistic regression coefficients for the model indicate that the interaction variable (*Z* DISCHARGE-TEMP) appeared to have the strongest effect on the dependent variable MOVE (Table 4). A one standard deviation increase in the standardized discharge–temperature interaction is associated with a decrease of –1.798 standard deviations in the logit (MOVE). The analysis of deviance further suggests that the standardized discharge-temperature interaction, discharge, and temperature, individually and in pairs, improved the intercept-only model (Table 4).

We also examined scatterplots of the predictor variables against each other and the observed versus predicted dependent variable. These plots revealed 13 cases where the model did not perform well. These were all cases where the model predicted the opposite response for the given values of the predic-

TABLE 3. Results of logistic regression for the dependent variable movement.

Dependent variable	Association/ predictive efficiency	Independent variable	Unstandardized logistic regression coefficient (b)	Standard error of (b)	Statistical significance (b)	Standardized logistic regression coefficient
Movement	G_M = 86.11 ($p < 0.0000$)	Intercept	12.5182	4.01753	0.002	–
	R^2_L = 0.45	Standardized discharge–temperature interaction	–3.07251	0.89974	0.001	–1.79821
	R^2 = 0.56 (m^3/s)	Discharge	–0.02366	0.00974	0.015	–1.1557
	R = 0.75 (°C)	Temperature	–0.87674	0.15729	0.000	–0.66728
	λ_p = 0.69 ($p < 0.0000$)					
	τ_p = 0.79 ($p < 0.0000$)					

tor variables. We found no patterns to these unusual cases, no obvious methodological errors, and no apparent biological justification to remove them from the analysis and rerun the model.

We also examined the relation of the logistic model of temperature and discharge for the three Goat River spawners to the probability of spawning migration on a temporal scale pre- and postLibby Dam (Figure 7). The preLibby Dam model showed a predictable migration probability for these burbot occurring at about October 31 through November 10 with decreasing temperature (<6°C) and discharge. The postLibby Dam model was unpredictable with the probability being highly variable for the same time period. Although, Libby Dam operations release less water in October than later months and is usually less than 300 m^3/s, the postdam model shows a

Table 4. Analysis of deviance table for logistic regression of burbot movement with discharge (F), temperature (T) and the discharge–temperature interaction (FT).

Model	Deviance	Difference	Degrees of freedom	Component tested	Significance (p)
Intercept (I)	254.89	149.68	3	T, F, FT	<0.000
I + T	231.82	126.61	2	F, FT	<0.000
I + FT	188.99	83.78	2	T,F	<0.000
I + F	180.04	74.83	2	T,FT	<0.000
I + T + FT	148.00	42.79	1	F	<0.000
I + T + F	120.60	15.39	1	FT	0.001
I + F + FT	106.54	1.33	1	T	0.249
I + T + F + FT	105.21	–	–	–	–

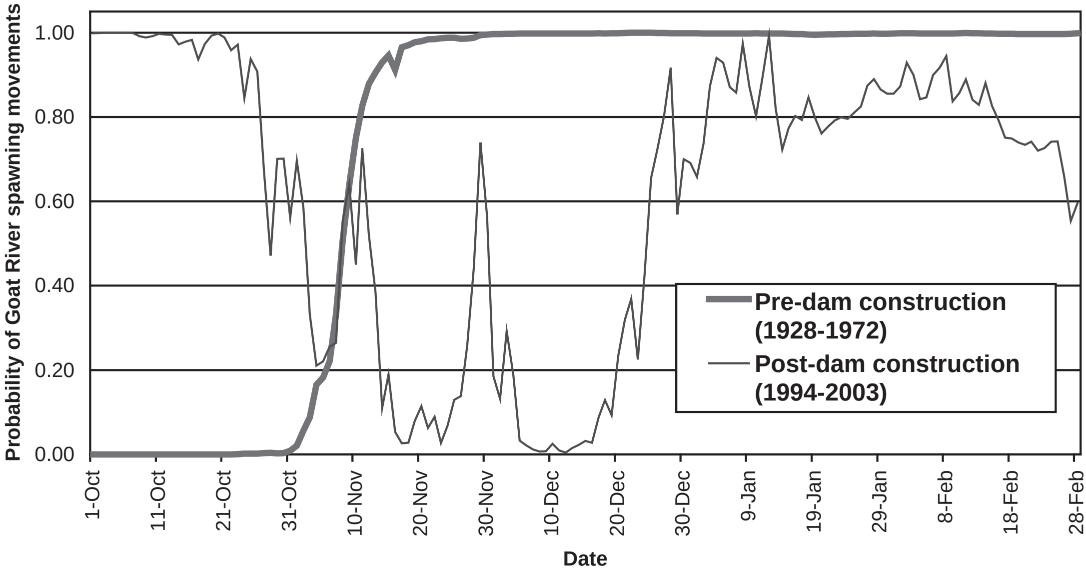


FIGURE 7. A comparison of the predicted probability of Goat River burbot spawning movements based on logistic regression model using historical discharge and temperature data, pre- and postLibby Dam construction.

high probability of spawning, which is misleading because water temperature is high (>6°C) for spawning (Becker 1983; McPhail and Paragamian 2000).

Discussion

Our findings of burbot movement through two or more spawning seasons was limited to a total sample of 11 fish, but they showed behavior patterns that ranged from active to sedentary with lotic/lentic migrations. Therefore, even though small sample size is an important factor, our results are still relevant to the understanding of this population (Hurlbert 1984). Also, having the opportunity to monitor the same burbot of a remnant population for two or more spawning seasons was unique and, to our knowledge, had not been previously reported.

We believe that spawning migration and actual spawning of burbot in the Kootenai River is inhibited by the higher than predam winter discharges created by Libby Dam (Paragamian 2000; Paragamian et al. 2005), while warmer water temperature may also be important. Some burbot did not show evidence of a spawning migration (burbot numbers 12, 226, and 227 and, for the Kootenai River, may be evidence that some burbot did not spawn yearly. Although we do not have definitive proof tagged burbot spawned, burbot have been captured in the Kootenai River postspawn with unspent gametes and in different stages of gamete development (Paragamian 2000; Paragamian et al. 2001). Also, in support of our conclusion, the highest capture rate of burbot (Paragamian et al. 2004) and best evidence of burbot spawning occurred in the winter of 2000–2001 when discharges during the spawning season were low (<300 m^3/s), due to a reduced snow pack, and gravid and spent fish were captured and recaptured at Ambush Rock (Kozfkay and Paragamian 2002). Other studies have suggested that burbot in some populations may have rest years and may not spawn every year (Pulliainen and Korhonen 1990; Arndt and Hutchinson 2000), but these studies did not provide evidence that the rest years or nonspawning were due to environmental changes.

We examined Kootenai River autumn and winter discharges and water temperatures and how they may have affected the motivation for a subset of three burbot to initiate an autumn or winter migration (prespawn). Logistic regression analysis indicated increasing discharge and temperature and the interaction of the two variables had a significant negative effect on the probability for prespawning migration. These results corroborate published findings of several telemetry studies of Kootenai River burbot (Paragamian 2000; Paragamian et al. 2005). Winter discharges in the Kootenai River are now three to four times that of preLibby Dam conditions (Partridge 1983; Paragamian 2000; Paragamian et al. 2005), and water temperatures postLibby Dam are warmer by an average of about 3°C. The change in winter temperatures from preLibby Dam also appears in part to be responsible for disruption or delay in burbot spawning migration. For example, the disruption to burbot spawning migration is supported by the postLibby Dam logistic model that shows that extreme periodic variations in the probability burbot would migrate under the present dam operations for discharge and temperature. Furthermore, postLibby Dam winter water temperatures of 3.0–4.9°C that were prevalent in October–November preLibby Dam are currently no longer common until late December and January. In our preLibby Dam logistic model, the probability of burbot migration increased exponentially when temperature in October–November decreased to about 3.0–4.9°C. If this water temperature range were representative of an activity range for the remaining burbot population to initiate migration, then movements prior to Libby Dam may have started a month earlier than postLibby Dam. The significance of a delay in burbot spawning migration may be in arrival timing. Burbot are not only highly synchronized in spawning (Arndt and Hutchinson 2000; Evenson 2000), and slow-moving with an upper end in travel rate of only 8–11 km/d (Paragamian et al. 2005), but also have low swimming endurance (Jones et al. 1974). Therefore, the combination of water temperature and discharge changes may have resulted in the failure of some burbot to spawn in most years of study (Paragamian 2000). Curiously, the days of increasing probability for burbot migration postLibby Dam match up closely with autumn and winter holidays, when the USACE reduces hydropower production buy decreasing discharge.

Furthermore, water temperature must be important to Kootenai River burbot because spawning is triggered by specific environmental conditions, with water temperature being one of the most critical cues. The prespawning and spawning temperatures for burbot, from 0.5°C to 4°C in the Kootenai and Goat rivers (in this study and Paragamian 1994), were consistent with the range of spawning temperatures found for other burbot populations (Becker 1983; McPhail and Paragamian 2000). Pääkkönen et al. (2000) found that burbot were most active at temperatures less than 5°C, but spawning also correlated negatively with day length. McPhail (1997) showed that burbot will delay spawning up to 14 d with a temperature increase from 0°C to 2.5°C. Temperatures outside a species preferendum can delay or expedite spawning from days to possibly weeks (Atse et al. 2002). Baras (1995) showed that the common barbell *Barbus barbus* exhibited temperature preference in the River Ourthe, Belgium by beginning active spawning on the first morning when the water temperature was higher than 13.5°C and continuing until the temperature dropped below 13.5°C. Some species have shown even more extreme modification of spawn timing due to temperature change (Edwards 1978). Temperature is also a determining factor of fish migration and acts as a gating factor for upstream migration, essentially controlling when fish at the entrance of a water way or estuary will enter the stream (Richkus 1974). In regulated rivers, or rivers that have little change in discharge during the migration period, upstream movement is controlled by water temperature (Jonsson 1991). In systems with extreme variations from the historic thermal regime, upstream migrations can slow or even completely stop (Jonsson 1991). Examples of how any variation of water temperature cues can delay or even eliminate successful spawning are numerous (Richkus 1974; Redding and Patiño 1993; Pankhurst et al. 1996; DiStefano et al. 1997; Atse et al. 2002; Davies and Bromage 2002).

Burbot in the Kootenai River apparently have multiple spawning locations. Our study could not confirm any of our tagged burbot spawned in the Goat River, but the strength of our premise relies on the fact that they entered the river at a known range of spawning temperatures (0.5–3.0°C) and time (January through February). Five burbot tagged with ultrasonic transmitters had predictable seasonal movement patterns with fidelity for the Goat River during the spawning season. Site fidelity for burbot in the Kootenai River is also supported by the mark–recapture findings of Pyper et al. (2004). Fidelity for spawning tributaries was also recorded by Hedin (1983) who conducted tagging studies and indicated that burbot in a coastal stream of the northern Bothian Sea exclusively migrated to a home stream to spawn. In addition, previous studies confirmed that the Goat River was likely an active spawning location with the capture of mature adults: flowing males and gravid females and spent fish postspawn (Paragamian 1995, 2000; Paragamian and Whitman 1997). Also, a companion study showed that some burbot apparently have fidelity for spawning at Ambush Rock (Kozfkay and Paragamian 2002; Paragamian et al. 2004). For comparison, Hudd and Lehtonen (1987) conducted a tagging study and described as many as five different stocks of burbot off the coast of Finland, each having a different home range and spawning fidelity for a specific river or estuary.

In our study, all but one burbot that had fidelity for the Goat River, during the spawning season (January–February), returned to a home pool in March or April where they remained until the following November. These fish became sedentary during summer, and for only a few, exceptions were movements detectable. Sedentary behavior became a concern for our telemetry records because during two summers, several temporary technicians believed that some fish were dead and did not record locations, despite fish having active transmitters and previous instructions to include all locations. Sedentary behavior for burbot is not unusual (McPhail and Paragamian 2000).

This study suggests that burbot rehabilitation efforts should also focus on cooler winter water temperatures of less than 5°C by mid-November each year, with even coolest water by January and February. These recommendations would be in addition to previously recommended discharges of less than 300 m^3/s (Paragamian et al. 2005). We also recommend that if the population were to become more substantial, a follow-up study with a greater sample size and through several seasons could improve our understanding of burbot behavior and movement even further. Researchers and managers of other waters with regulated discharges from dams and declining numbers of riverine burbot should consider temperature and discharge changes as possible factors leading to their decline.

Acknowledgments

We acknowledge the dedicated field work of Vint Whitman and Gretchen Kruse, formerly of the Idaho Department of Fish and Game (IDFG), and the many Bio-aides that helped in this study. Special thanks to Dorothy Laude for literature review and some editorial contributions as well as Greg Hoffman, of the USACE, for providing valuable temperature data for the Kootenai River. We would also like to thank Sam Sharr and Dan Schill of the IDFG and especially David Bennett for technical review of our manuscript. Bonneville Power Administration provided the funding for this study.

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