[Article]

Population Viability of Arctic Grayling in
the Gibbon River, Yellowstone National Park

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Abstract.—The fluvial Arctic grayling *Thymallus arcticus* is restricted to less than 5% of its native range in the contiguous United States and was relisted as a category 3 candidate species under the U.S. Endangered Species Act in 2010. Although fluvial Arctic grayling of the lower Gibbon River, Yellowstone National Park, Wyoming, were considered to have been extirpated by 1935, anglers and biologists have continued to report catching low numbers of Arctic grayling in the river. Our goal was to determine whether a viable population of fluvial Arctic grayling persisted in the Gibbon River or whether the fish caught in the river were downstream emigrants from lacustrine populations in headwater lakes. We addressed this goal by determining relative abundances, sources, and evidence for successful spawning of Arctic grayling in the Gibbon River. During 2005 and 2006, Arctic grayling comprised between 0% and 3% of the salmonid catch in riverwide electrofishing (mean $<$ 1%; SE $<$ 1%) and snorkeling (mean = 1%; SE = 1%) surveys; Arctic grayling constituted 0–14% of the salmonid catch obtained by targeted angling (3 of 22 fish; mean = 4%; SE = 5%). Low values of the genetic differentiation index (F_{ST} = 0.0021 ± 0.002 [mean ± 95% confidence interval]) between headwater lake and river Arctic grayling indicated that fish from throughout the Gibbon River system probably belonged to the same population. Back-calculated lengths at most ages were similar among all fish, and successful spawning within the Gibbon River below the headwater lakes was not documented. Few Arctic grayling adults and no fry were detected in the Gibbon River, implying that a reproducing fluvial population does not exist there. These findings have implications for future Endangered Species Act considerations and management of fluvial Arctic grayling within and outside of Yellowstone National Park. Our comprehensive approach is broadly applicable to the management of sparsely detected aquatic species worldwide.

Determining population viability of any species requires knowledge of its life history, demographics, and threats to persistence and is limited by data availability (Boyce 1992). Rare and declining species are frequently targeted for assessment, which increases the challenge of detection and abundance estimation (Maxwell and Jennings 2005). Salmonid species across North America have been the focus of population evaluation because of substantial declines associated with nonnative species introductions and habitat impairment and fragmentation (Frissell 1993; Thurow et al. 1997). The status assessment of fluvial Arctic grayling *Thymallus arcticus* in the contiguous United States represents a common dilemma for fisheries professionals, who must provide a balance between resource availability and statistical precision to adequately evaluate population viability.

The fluvial Arctic grayling in the contiguous United States is presently restricted to less than 5% of its historic range; is thought to be limited to the Big Hole River, Montana; and continues to decline (Magee et al. 2006). Fluvial Arctic grayling are behaviorally adapted to riverine environments and are genetically and behaviorally distinct from their lacustrine counterparts (Kaya 1991; Kaya and Jeanes 1995). Fluvial Arctic grayling were present within and near Yellowstone

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National Park (YNP), Wyoming, until about 1900 in the Gallatin River and until 1935 in the Madison River, the Firehole River below Firehole Cascade, and the Gibbon River below Gibbon Falls (Figure 1; Vincent 1962; Kaya 2000). Introductions of nonnative brown trout *Salmo trutta* and the creation of Hebgen Reservoir on the Madison River were followed by the near-complete loss of fluvial Arctic grayling within YNP by the mid-1900s (Kaya 2000). Arctic grayling have been periodically caught in the Gibbon River below Little Gibbon Falls by anglers since 1980, and additional fish have been sampled repeatedly by YNP survey crews (Koel et al. 2005). It was unknown whether these fish were remnants of a fluvial population in the Gibbon River or whether they were downstream lacustrine emigrants from Grebe Lake or Wolf Lake.

Our goal was to determine whether a viable population of fluvial Arctic grayling existed in the Gibbon River. Specific objectives to address this goal were to (1) determine Arctic grayling relative abundances in the Gibbon River, (2) determine the source of Arctic grayling detected in the Gibbon River downstream from the headwater lakes occupied by lacustrine populations, and (3) determine whether Arctic grayling successfully spawn in the Gibbon River.

Study Area

The Gibbon River originates at Grebe Lake in central YNP about 2.9 km northwest of Canyon Village at an elevation of 2,445 m (Figure 1). From its headwaters, the Gibbon River flows southwest 54.3 km to its confluence with the Firehole River to form the Madison River at an elevation of 2,072 m. Fish assemblages vary longitudinally along the Gibbon River, reflecting three successive barriers to upstream movement. The farthest downstream barrier (Gibbon Falls, height = 25.6 m) is located in Gibbon Canyon, about 11.3 km upstream from the Firehole River confluence. Historically, Arctic grayling, mottled sculpin *Cottus bairdii*, mountain whitefish *Prosopium williamsoni*, longnose dace *Rhinichthys cataractae*, and westslope cutthroat trout *Oncorhynchus clarkii lewisi* existed in the Gibbon River below Gibbon Falls (Varley and Schullery 1998). Only brown trout, longnose dace, rainbow trout *O. mykiss*, mottled sculpin, and mountain whitefish were known to exist in this stretch of river in 2005 (Koel et al. 2004). The next barrier to upstream movement (Virginia Cascade, height = 19.4 m) is located about 28.4 km upstream from Gibbon Falls. Before nonnative fish introductions, mottled sculpin were the only inhabitants above Gibbon Falls (Varley and Schullery 1998). The Gibbon River harbored brown trout, longnose dace, brook trout *Salvelinus fontinalis*, rainbow trout, and mottled sculpin between Gibbon Falls and Virginia Cascade in 2005 (Koel et al. 2004). The final barrier to upstream movement (Little Gibbon Falls, height = 7.6 m) lies about 3.9 km above Virginia Cascade. A dense population of brook trout resides between Virginia Cascade and Little Gibbon Falls, and this reach is also occupied by rainbow trout and mottled sculpin. Only
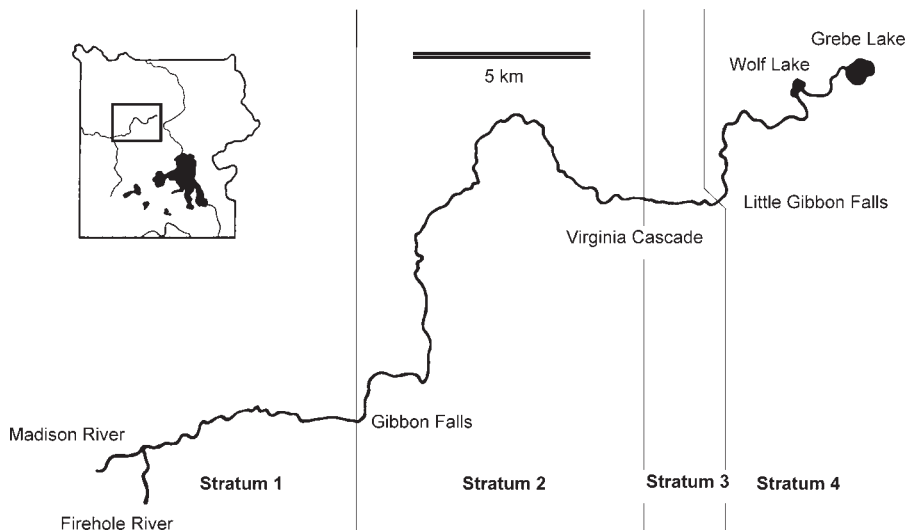

FIGURE 1.—Sampling strata and barriers to upstream movement of Arctic grayling in the Gibbon River, Yellowstone National Park, Wyoming. Fluvial Arctic grayling were historically distributed below Gibbon Falls only. Inset depicts the location of the study area within the park.

Arctic grayling and rainbow trout are found above Little Gibbon Falls (Varley and Schullery 1998).

Methods

Arctic grayling relative abundances.—The Gibbon River was partitioned for sampling into four strata (Figure 1) defined by the barriers to upstream fish movement between them and by their disparate fish assemblages. After the river was visually surveyed for areas that were impossible to sample by electrofishing and snorkeling (e.g., waterfalls, rapids, and areas near thermal features), the remaining portions of each stratum were partitioned into potential 500-m sample reaches. We used proportional allocation and random selection to select sample reaches for 2005 comprising about one-quarter of each stratum (Thompson et al. 1998; Peterson et al. 2002). Sampling effort was reallocated among reaches in 2006 to target areas of Arctic grayling detection and pool-dominated habitat, which is preferred by Arctic grayling during summer (Liknes 1981; Hubert et al. 1985). This adjustment reflected 2005 results, which indicated that Arctic grayling detection was exclusive to pool-dominated reaches. This modification was an attempt to minimize the variability in relative abundances within strata while maximizing sampling efficiency. Habitat delineation was performed prior to sampling in 2006. All sample reaches that could be surveyed in each stratum were classified into substrata according to pool habitat frequency. Pools were defined as areas with maximum depths greater than or equal to 0.5 m, reduced water velocities, and undisturbed water surfaces (Liknes 1981). Reaches containing greater than or equal to 50% pool habitat were classified as pool-dominated, whereas reaches containing less than 50% pool habitat (i.e., dominated typically by runs but occasionally by riffles) were classified as run-dominated. Reaches to be sampled in 2006 were then randomly selected from all reaches that could be surveyed. Twenty-two reaches were ultimately required based on a minimum of two sample reaches per substratum.

We electrofished, snorkeled, and fly-fished in 2005 and 2006 to determine Arctic grayling relative abundances throughout the Gibbon River system. Arctic grayling relative abundances were calculated by dividing the total number of Arctic grayling detected by the total number of salmonids detected. Relative abundances were reported by sampling method, river section (stratum), and year. Arctic grayling were assumed to have a detection likelihood similar to that of all other salmonids because too few Arctic grayling were detected to accurately estimate a species-specific value. Electrofishing was used from June to mid-July during 2005 and from late-May to

mid-July during 2006. Boat, shore-based, or backpack electrofishing was used in different river reaches because of variation in river depth and width (Kennedy and Strange 1981). Snorkeling was used at least once per month from mid-July to September during both years because low discharge and either personnel or equipment limitations precluded electrofishing during those months. Anglers with the Yellowstone Fly-Fishing Volunteer Program participated in sampling periodically from mid-June to early September in both years by targeting pool-dominated habitat and areas of prior Arctic grayling detection to maximize the likelihood of Arctic grayling capture. Estimates of Arctic grayling caught per angler-hour (i.e., catch per unit effort) were calculated by dividing the number of Arctic grayling caught by the reported number of angler-hours per sampling event. The number of angler-hours per sampling event was calculated by multiplying the number of anglers present by total fishing time (Malvestuto 1996). Estimates of catch per unit effort for salmonids other than Arctic grayling were calculated in the same manner as described for Arctic grayling.

Arctic grayling source.—The source of Arctic grayling in the Gibbon River was examined by employing a weir to capture lacustrine emigrants, analyzing genetic diversity, and evaluating growth rates among Arctic grayling caught throughout the Gibbon River system. A panel weir was installed about 300 m upstream from Little Gibbon Falls in May 2006, maximizing the distance from headwater lakes while remaining above this first major barrier to upstream movement on the Gibbon River. Genetic comparisons were made based on demonstrated differences between known fluvial and lacustrine Arctic grayling (Everett and Allendorf 1985; Kaya 1991, 1992) by using microsatellite loci developed for Arctic grayling in Montana (Diggs and Ardren 2008). Lengths at age of Arctic grayling sampled in the Gibbon River system were compared to determine whether differences existed between source groups. Significantly higher lengths at age in lacustrine versus stream-dwelling fish have been documented in multiple systems (Hutchings 1986; Dempson et al. 1996; Halvorsen and Jørgensen 1996). Thus, significantly higher lengths at age in lake-caught versus river-caught fish would provide support for the existence of a fluvial Arctic grayling population in the Gibbon River.

Fin clips were collected for genetic analysis from Arctic grayling taken by electrofishing and fly-fishing in 2005 and 2006 and by weir-trapping in 2006. Angling was used in 2005 to collect samples directly from Grebe and Wolf lakes. Additionally, fin clips collected during 1999–2005 were obtained from the

National Park Service; these samples were preserved by the same methods used in the present study. Arctic grayling caught at the weir were presumed to be of headwater lake origin because this portion of the river was historically fishless (Varley and Schullery 1998) and because of the weir's proximity to lacustrine Arctic grayling sources. Samples were preserved in glass tubes containing 95% ethanol (Kelsch and Shields 1996; Stamford and Taylor 2004). Laboratory analyses were conducted at Montana State University, Bozeman. We genotyped all individuals at 12 microsatellite loci (*OMM1037*, *Tar100*, *Tar101*, *Tar103*, *Tar104*, *Tar105*, *Tar106*, *Tar108*, *Tar109*, *Tar110*, *Tar114*, and *Tar115*) by use of the laboratory procedures described by Steed (2007).

An exact probability test for departures from Hardy–Weinberg (HW) equilibrium was conducted individually and across all loci using Fisher's method in GENEPOP version 3.4 (Raymond and Rousset 1995). Significance levels (α) were not adjusted for multiple tests. Expected heterozygosity (H_e) was compared between source groups using both sign and paired t-tests with α set at 0.05 (Sokal and Rohlf 1995). Allelic richness was also used to quantify the level of genetic diversity present in each group. Because the number of alleles found in a sample is influenced by sample size, and the sample size varied between study sites (Grebe and Wolf lakes, $N = 95$ individuals; Gibbon River, $N = 66$ individuals), rarefaction using the program HP-RARE was performed to standardize sample size to 100 genes (or, equivalently, 50 individuals) per population (Kalinowski 2005). The number of private alleles (alleles found in only one population) was also estimated using rarefaction at the sample size (100 genes/population). Differences in private allelic richness between source groups were compared using a sign test ($\alpha = 0.05$; Sokal and Rohlf 1995; Kalinowski 2005). Genetic differentiation between source groups was measured by the genetic differentiation index (F_{ST}) and estimated using GENEPOP (Raymond and Rousset 1995) and FSTAT version 2.9.3.2 (Weir and Cockerham 1984; Goudet 2001). Bootstrapping was used to calculate the associated 95% confidence interval (CI) in FSTAT. The statistical significance of differences in allele frequencies between source groups was tested using Fisher's genic differentiation test as implemented by GENEPOP (Raymond and Rousset 1995). Finally, STRUCTURE version 2.2 (Pritchard et al. 2000) was used to group individuals into populations based on only the genotypes of the individuals. The number of populations assumed to be present (K) was varied from 1 to 4, and the natural log likelihood of our data ($\log_e D$) conforming to the predicted value of K was used as a measure of support present in the data.

Scales were used to age Arctic grayling caught in the Gibbon River system because they can be collected nonlethally and are relatively accurate for this species (K. M. Stuart and G. R. Chislett, British Columbia Fish and Wildlife Branch, unpublished report). Although otoliths have been deemed more appropriate for aging Arctic grayling in northern latitudes (DeCicco and Brown 2006), discrepancies in age determination between the two methods are minimal within the average life span of Arctic grayling found in Montana and Wyoming (Shepard and Oswald 1989). Scales were collected during 2005 and 2006 from Grebe and Wolf lakes and the Gibbon River. A few samples were unsuitable for analysis of age and growth because of poor scale condition. Lengths at age were back-calculated with the Fraser–Lee method (Devries and Frie 1996) by employing an intercept value of 51.5 mm total length (TL) for Montana Arctic grayling (Brown 1943) because too few fish were sampled to develop a system-specific value. Mean TLs and associated 95% CIs were calculated for ages 1–4 by source (i.e., Gibbon River or Grebe and Wolf lakes). Age-5 and age-6 fish from Grebe and Wolf lakes were excluded because none were collected in the Gibbon River. Mean TLs of Arctic grayling at each age were compared between source groups with Welch's two-sample t-test ($\alpha = 0.05$) because heteroscedasticity was detected among ages (Zar 1984).

Spawning success.—The presence of Arctic grayling fry in the Gibbon River below Little Gibbon Falls would suggest successful spawning in the river. Stationary drift nets were used to detect the presence of Arctic grayling fry in the river. Drift nets were identical to those used by Gale et al. (2008). During 2005, nets were longitudinally distributed at 12 sites throughout the Gibbon River system in preferred age-0 Arctic grayling habitat (Deleray 1991) within the confines of access and substrate. Nets were deployed from early June to mid-September. All fry were counted and frozen for subsequent identification in the laboratory if field identification was not possible (Barndt 1996). Fish other than Arctic grayling were not identified to species.

Drift-net effort was reallocated in 2006, targeting areas of fry detection in 2005 to maximize sampling effort (Steed 2007). Nets were deployed twice per month for 24–48 h to capture potential daytime and presumed nocturnal movements in 2005, whereas nets were deployed on a 3-week rotation to avoid lunar-cycle bias in 2006 (Gale et al. 2008). Driftnetting was initiated earlier in 2006 than in 2005 (mid-May versus mid-June) because sites were already established and

logistical constraints were reduced. Deployment continued through mid-September in both years. All other sampling protocols used in 2005 were repeated in 2006.

Results

Arctic Grayling Relative Abundances

Few Arctic grayling were detected in the Gibbon River by electrofishing, snorkeling, and angling during 2005 and 2006. Four Arctic grayling were caught by electrofishing in both 2005 and 2006, whereas zero to four fish were observed by snorkelers in each sample period in 2005 and 2006. In both years, Arctic grayling were captured in higher proportions and at higher abundance in strata 1 and 2 than in strata 3 and 4 (Table 1). Only one Arctic grayling per stratum was observed in strata 3 and 4 (downstream from headwater lakes) during the study. Most Arctic grayling were detected between mid-June and late August in both years. Anglers caught 12 Arctic grayling in 2005 and 9 in 2006, and the majority of these fish were caught in stratum 2 during June in both years.

Arctic Grayling Source

Arctic grayling detected in the Gibbon River were strongly associated with headwater lake populations. Arctic grayling were captured while moving downstream from headwater lakes into the Gibbon River during the spawning period in 2006, as evidenced by the capture of 17 fish on the weir installed upstream of Little Gibbon Falls. All Arctic grayling were caught during June, and the majority was captured during the first half of the month. Captured Arctic grayling ranged from 60 to 273 mm TL, but only one fish was less than 200 mm TL. Sex was determined for 12 of the 17 fish; six were males and six were females.

In total, 161 Arctic grayling genetic samples were analyzed (Grebe and Wolf lakes: $n = 95$; Gibbon River: $n = 66$). Most genetic tests revealed relatively little

distinction between Arctic grayling sampled from headwater lakes and those sampled from the Gibbon River. Allelic richness test results demonstrated little difference between Arctic grayling source groups (Table 2). Rarefaction results indicated a total of 163 and 154 alleles in lake- and river-origin fish, respectively. The total number of alleles per locus among all Arctic grayling caught varied from 7 alleles at *Tar103* in both source groups to 22 alleles at *Tar114* in lake-origin Arctic grayling. After rarefaction, 24 and 14 private alleles were found in lake- and river-origin groups, respectively. Furthermore, the numbers of private alleles were not significantly different between source populations according to sign test results ($P = 0.30$).

Tests of HW equilibrium showed statistically significant departures from expectations (Table 2). Differences between H_e and observed heterozygosity within both source groups were not significant except at the *Tar100* locus for river-origin fish ($P = 0.05$). Lake-origin fish deviated significantly from HW equilibrium at 2 of the 12 loci examined (*Tar109*: $P = 0.01$; *Tar114*: $P = 0.01$), leading to significant deviation across all loci ($P = 0.02$). The level of H_e for individual loci within source groups ranged from 0.67 to 0.92. Average H_e was 0.85 and 0.83 in lake- and river-origin fish, respectively. The H_e of river-origin fish was significantly lower than that of lake-origin fish (sign-test: $P = 0.02$; paired *t*-test: $P = 0.005$; Table 2).

Multilocus genetic differentiation between lake- and river-origin Arctic grayling was low in both GENEPOP ($F_{ST} = 0.0021$) and FSTAT ($F_{ST} = 0.0016$) even within estimated 95% CIs (± 0.002). Output from STRUCTURE corroborated genetic differentiation results, indicating that all samples probably belonged to one population rather than two or three separate groups. The estimated $\log_e D$ was greatest as K approached 1 ($K = 1$ cluster: $\log_e D = -8,763.2$; $K = 2$ clusters: $\log_e D =$

TABLE 1.—Number of salmonids detected by each sampling method in each stratum of the Gibbon River, Yellowstone National Park, during 2005 and 2006. The percentage of each sample composed of Arctic grayling is shown in parentheses.

Year	Stratum	Method				Total
		Fry trapping	Electrofishing	Angling	Snorkeling	
2005	1	123 (0)	185 (1)	22 (14)	394 (3)	724 (2)
	2	2 (0)	580 (<1)	158 (5)	285 (2)	1,025 (2)
	3	1 (0)	226 (0)	109 (1)	209 (0)	545 (<1)
	4	60 (57)[a]	205 (0)	16 (0)	137 (0)	369 (0)
2006	1	206 (0)	686 (<1)	28 (4)	1,086 (<1)	2,006 (<1)
	2	24 (0)	1,153 (<1)	75 (11)	1,795 (<1)	3,047 (<1)
	3	5 (0)	365 (0)	101 (0)	949 (0)	1,420 (0)
	4	–	908 (<1)	–	540 (0)	1,448 (0)
Total		421 (14)	4,308 (<1)	509 (4)	5,395 (<1)	10,584 (<1)

[a] Arctic grayling were offspring of adfluvial fish from stocked headwater lakes.

TABLE 2.—Genetic variability at 12 microsatellite loci in Arctic grayling caught in the Gibbon River system, Yellowstone National Park (H_e = expected heterozygosity; A = allelic richness; P = private allelic richness).

	Grebe and Wolf lakes ($n = 95$)			Gibbon River ($n = 66$)		
Locus	H_e	A	P	H_e	A	P
OMM1037	0.76	12.641	2.762	0.69	9.971	0.092
Tar100	0.89	16.967	1.894	0.89	17.745	2.672
Tar101	0.86	8.997	0.042	0.85	9.916	0.961
Tar103	0.70	6.755	0.000	0.67	7.000	0.245
Tar104	0.86	10.497	1.512	0.81	8.999	0.014
Tar105	0.87	15.902	1.985	0.84	16.000	2.083
Tar106	0.91	15.921	0.941	0.83	16.000	1.020
Tar108	0.83	12.460	3.461	0.83	9.999	1.000
Tar109	0.83	11.693	3.725	0.80	7.971	0.004
Tar110	0.91	16.246	0.990	0.92	15.996	0.740
Tar114	0.88	22.228	3.587	0.87	20.927	2.285
Tar115	0.92	20.107	1.033	0.91	20.864	1.791
Multilocus average	0.85	14.201	1.828	0.83	13.449	1.076

$-8,831.7$; $K = 3$ clusters: $\log_e D = -8,956.4$; $K = 4$ clusters: $\log_e D = -9,284.0$).

Age and growth were similar across most ages of Arctic grayling caught throughout the Gibbon River system. Back-calculated TLs at ages 1, 3, and 4 were not significantly different between fish from Grebe and Wolf lakes ($n = 71$) and fish from the Gibbon River ($n = 24$; Figure 2). However, TL at age 2 was significantly smaller and more variable for fish from the Gibbon River than for those from Grebe and Wolf lakes (Figure 2). Fish from Grebe and Wolf lakes grew more than Gibbon River fish between ages 1 and 2, whereas fish from the Gibbon River grew more between ages 2 and 3 than did fish from Grebe and Wolf lakes (Figure 2).

Spawning Success

No Arctic grayling fry were detected by drift nets in the Gibbon River below Little Gibbon Falls in either
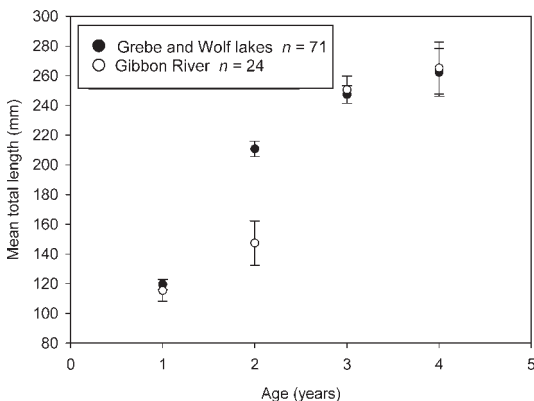

FIGURE 2.—Mean ($\pm 95\%$ confidence interval) back-calculated total lengths (mm) at ages 1–4 for Arctic grayling from the Gibbon River system, Yellowstone National Park.

2005 or 2006. However, other salmonid fry were captured at 8 of 12 sites during June–September 2005 and at six of seven sites during May–September 2006 (Table 1). Additionally, 34 Arctic grayling fry were caught at site 12 in 2005 (near Wolf Lake, above Little Gibbon Falls); these fish were probably the offspring of headwater lake Arctic grayling and distinct from any putative Gibbon River fluvial population. However, their capture confirms that the nets used were capable of capturing Arctic grayling fry when fry were present.

Discussion

Arctic Grayling Relative Abundances

Too few Arctic grayling inhabit the Gibbon River to represent a viable population. Despite intensive sampling efforts in 2005 and 2006, Arctic grayling were detected in numbers that were too low to allow estimation of meaningful absolute abundances. Even targeted angling yielded low capture rates relative to all other salmonids caught (Table 1). If a viable population of fluvial Arctic grayling currently existed in the river, the largest relative abundances would be expected to occur in stratum 1 because it was the only stratum that Arctic grayling inhabited historically (Figure 1; Varley and Schullery 1998). However, Arctic grayling comprised comparable proportions of all salmonids detected in strata 1 and 2 during both years (Table 1) and probably represent lacustrine emigrants that were temporarily occupying those strata.

Arctic Grayling Source

Arctic grayling caught in the Gibbon River probably represent fish from stocked headwater lakes rather than a self-sustaining native population. The detection of 17 Arctic grayling at the weir installed above Little Gibbon Falls in 2006 demonstrates movement of Arctic grayling from headwater lakes into the river.

This movement is probably associated with spawning activity because all but one of the captured Arctic grayling were adults and no Arctic grayling were detected after mid-June, which corresponded to the end of spawning by Grebe Lake Arctic grayling in the upper Gibbon River (Kruse 1959).

Genetic analyses of all Arctic grayling caught suggest a common origin of headwater lakes. The low F_{ST} value indicates that Arctic grayling collected throughout the system originated from the same source; this is supported by higher F_{ST} values associated with European grayling *T. thymallus* populations separated by 55 km without barriers to movement (Koskinen et al. 2001). European grayling populations that were disjunct for less than 60 years also exhibited higher F_{ST} values than were detected for Arctic grayling in the Gibbon River system (Melgaard et al. 2003). Comparable allelic richness and private allelic richness between groups indicate similar levels of genetic diversity, which is further supported by STRUCTURE's assignment of all fish to a single cluster.

Back-calculated lengths at most ages were similar among all Arctic grayling sampled in the Gibbon River system, suggesting a common source. Although the observed differences in length at age 2 between fish from the Gibbon River and those from Grebe and Wolf lakes support the existence of a fluvial population of Arctic grayling in the Gibbon River, similar lengths at ages 1, 3, and 4 throughout the system suggest that the fish are emigrants from headwater lakes. Arctic grayling from Red Rock Lake were larger than those from Big Hole River after age 1 (Shepard and Oswald 1989), although Liknes (1981) determined that Big Hole River fish were larger than Red Rock Lake fish at age 1 but were smaller at subsequent ages. Arctic grayling from numerous systems across Norway, Sweden, Slovakia, and Siberia also varied in length at multiple age-classes (Northcote 1995), which probably reflects differences in system productivity. Although there are population-level behavioral differences between adfluvial and fluvial Arctic grayling that can inhibit the successful adaptation from lacustrine to riverine life history (including production of viable offspring), the progeny of Wolf Lake outlet spawners may have already survived in the Gibbon River before being detected.

Spawning Success

The failure to detect Arctic grayling fry in the Gibbon River below Little Gibbon Falls in 2005 and 2006 suggests that successful river spawning did not occur during those years. Although drift nets sampled a relatively small portion of the river, nets did not capture Arctic grayling fry during either year. Arctic grayling in Montana are small at emergence (7–11 mm; Watling and Brown 1955), but adfluvial fry were caught near headwater lakes in 2005. Further, Arctic grayling fecundity is high in comparison with other salmonids (Northcote 1995), increasing the likelihood of detection.

Synthesis

The preponderance of evidence indicates that a viable population of fluvial Arctic grayling does not exist in the Gibbon River in YNP. Low relative abundances illustrate the species' scarcity in the river despite intensive sampling that employed multiple techniques. Anglers targeting Arctic grayling habitat caught relatively few fish. Further, Arctic grayling probably enter the river annually from headwater lakes. Genetic variation in Arctic grayling from the river and headwater lakes was within the range observed for European grayling populations (Koskinen et al. 2001; Melgaard et al. 2003). Lengths at most ages were similar among all fish in the Gibbon River system, and successful river spawning was not documented. Though many have assumed that fluvial Arctic grayling were extirpated from the Gibbon River by the mid-1930s, this study constitutes the first substantial evidence that a fluvial population does not currently exist in the Gibbon River.

The comprehensive methodology used in this study is broadly applicable to the management of sparsely detected aquatic species worldwide, producing multiple lines of evidence for determination of population viability. Unintentional genetic adulteration and extirpation of native species may be avoided by investigating various life history characteristics, including reproduction, movement, and growth, in addition to genetic diversity and relative abundances. Locally, this information will help direct fisheries management within YNP, providing the opportunity to re-establish fluvial Arctic grayling within their native range. These data also support the continued conservation and restoration of fluvial Arctic grayling residing in the Big Hole River, Montana—the last remaining fluvial population in the lower 48 United States. Although fluvial Arctic grayling were recently relisted as a category 3 candidate species under the U.S. Endangered Species Act (USFWS 2010), controversy over appropriate conservation measures will probably remain for years to come. Nevertheless, the scarcity of fluvial Arctic grayling within their local native range supports careful and objective consideration of their future.

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