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Movements, Habitat Use, and Spawning Strategies of Arctic Grayling in a Subalpine Lake Tributary[3]

Abstract

Spawning Arctic grayling *Thymallus arcticus* were uniquely marked in Upper Granite Lake, Washington to determine the movements, habitat utilization patterns, and reproductive strategies employed by individual fish. Prespawning behavior began in the shallows in the vicinity of the inlet stream as the lake became ice-free and spawning in the inlet stream persisted for approximately three weeks. Subdominant males held in refuge areas or actively cruised through the spawning grounds in search of mating opportunities. Dominant males were significantly larger, established territories, and enjoyed higher reproductive success than nonterritorial males. Dominant males were generally subdominant for periods before and after their territorial phase. Fifty-seven percent of the males defended territories at some time during the season. Both sexes spawned with a variety of mates. The number of spawners and level of activity in the stream was low in the morning and high in the midafternoon and evening. The distribution of spawners shifted downstream concurrently with a reduction in stream level; they were not observed in shallow riffles or in stream velocities above 0.21 m/s. Proximity of refuge areas to male territories helped maintain a substantial number of females on the spawning grounds. The number of visually isolated breeding territories and refuges in feeder streams was controlled by the aggressive behavior of males which in turn limited the production of this population.

Introduction

Gamefish management agencies have considered or have already introduced Arctic grayling *Thymallus arcticus*, into high elevation lakes of states in the Rocky Mountain and western region of the United States (Hubert *et al.* 1985). Establishment of self-sustaining populations in these remote areas is more desirable than maintaining populations through regular hatchery planting programs. Consequently, knowledge of the spawning behavior and the environmental requirements of spawners and incubating eggs are needed to successfully establish naturally reproducing populations.

Previous works on spawning behavior of Arctic grayling, *Thymallus arcticus* (Brown 1938, Kruse 1959, Bishop 1971), and European grayling *Thymallus thymallus* (Fabricius and Gustafson 1955), contained general descriptions of temporal patterns of stream use by the spawners. These authors reported that spawning begins at the time of ice breakup and lasts three to four weeks during which males established territories around midday, and spawning occurred from midday until after dusk. Spawners generally retreated to the lake or a quiet pool after dark, then reoccupied the spawning ground near midday the following day. When space was limiting, only dominant males established territories (Fabricius and Gustafson 1955), and due to the aggressiveness of territorial males, females and subdominant males tended to congregate outside the perimeter of dominant males' territories.

I describe temporal habitat-use patterns of mature Arctic grayling during the 1981 spawning season in Upper Granite Lake, Washington. This population descended from Montana stocks introduced in 1947. This is presently the only naturally reproducing population in Washington, so knowledge of habitat utilization and potential limitations to reproduction are essential for enhancement here and for evaluation of a potentially expanded management program for Arctic grayling in the state. By recording movements of individual fish, I detected previously unreported aspects of Arctic grayling spawning behavior at the level of the individual including: residence times, habitat utilization, movements, and territory density in the stream.

Description of the Study Site

The 58 ha Upper Granite Lake (Figure 1), 14 km southeast of Marblemount, Skagit County, Washington lies in a remote basin of glacial origin at 1372 m elevation with depths exceeding 70 m throughout most of the lake.

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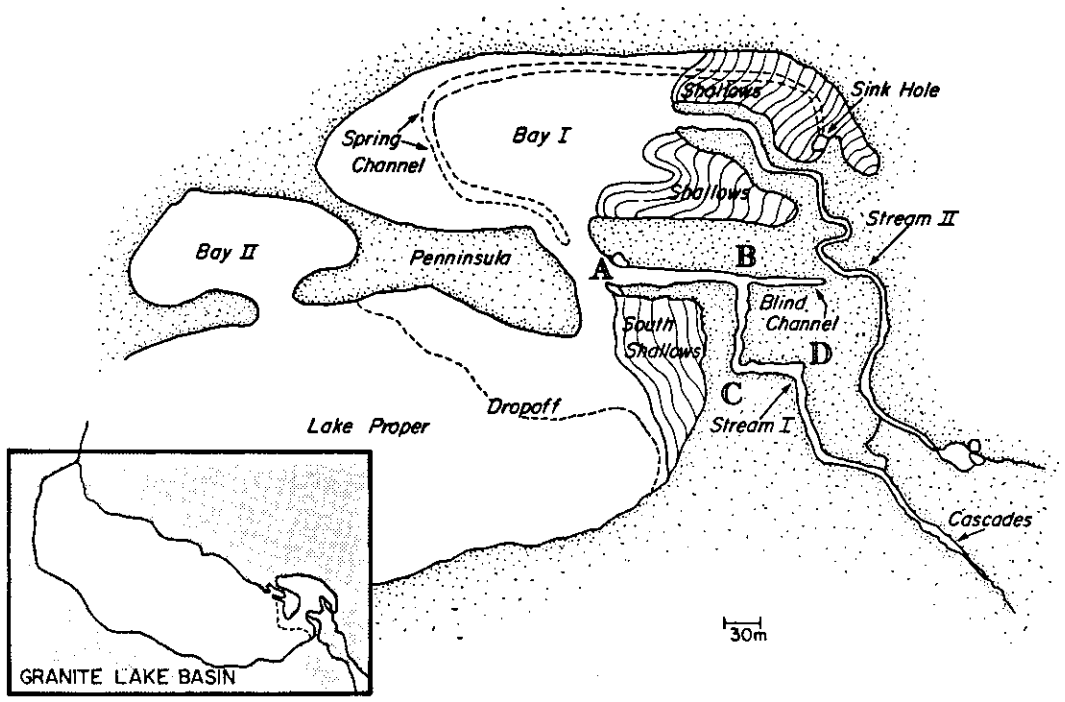

Figure 1. Map of Upper Granite Lake and the locations at the inlet end of the basin that were occupied by Arctic grayling spawners during the spawning season.

Two nameless inlet streams (here termed streams I and II) meander 400 m through a meadow at the east end of the lake. Stream I is a shallow riffle (mean depth = 25 cm) above point D and a glide (mean depth = 35 cm) below (Figure 1). The stream was primarily supplied by snowmelt, so flow varied considerably during the spawning season depending on temperature and the remaining snowpack (Table 1).

Arctic grayling only spawned in the lower 195 m of stream I, a series of three reaches separated by sharp bends between the mouth and Bend D (Figure 2). During high spring runoff, the lake level rose enough to back up the stream to site E (Figure 2) before surface flow became perceptible. An undercut at site B was 1.3 m deep along the outside bank. The rest of the stream bottom was uniformly flat, and was composed of several small sandy patches within a homogeneous mixture of sand and gravel (diameter < 8 cm). Patches of willow (*Salix* sp.) branches overhung or draped into the stream at irregular intervals below point D.

Stream II was not used by Arctic grayling. The stream gradient was such that a layer of silt and fine organic matter, sufficient to suffocate any incubating eggs, was deposited over the gravel during spring runoff.

TABLE 1. Water velocity measurements (m/s) in a tributary of Upper Granite lake in which grayling spawned in 1981.

Stream reach	28 June	9 July	10 July	16 July	20 July
Lower (A-B)	0.16	0.17	—	—	0.23
Middle (B-C)	0.18	0.13	0.12	—	0.32
Upper (C-D)	0.21	—	0.30	—	0.40
above D	>0.30	>0.30	>0.30	0.77	0.74

[1]See Figure 2 for location of the stream reaches.

Materials and Methods

Adult grayling were captured in fyke nets set in bay II or just off the mouth of stream I (Figure 1) and each fish was marked with individual color codes with two colored, celluloid, split, bird

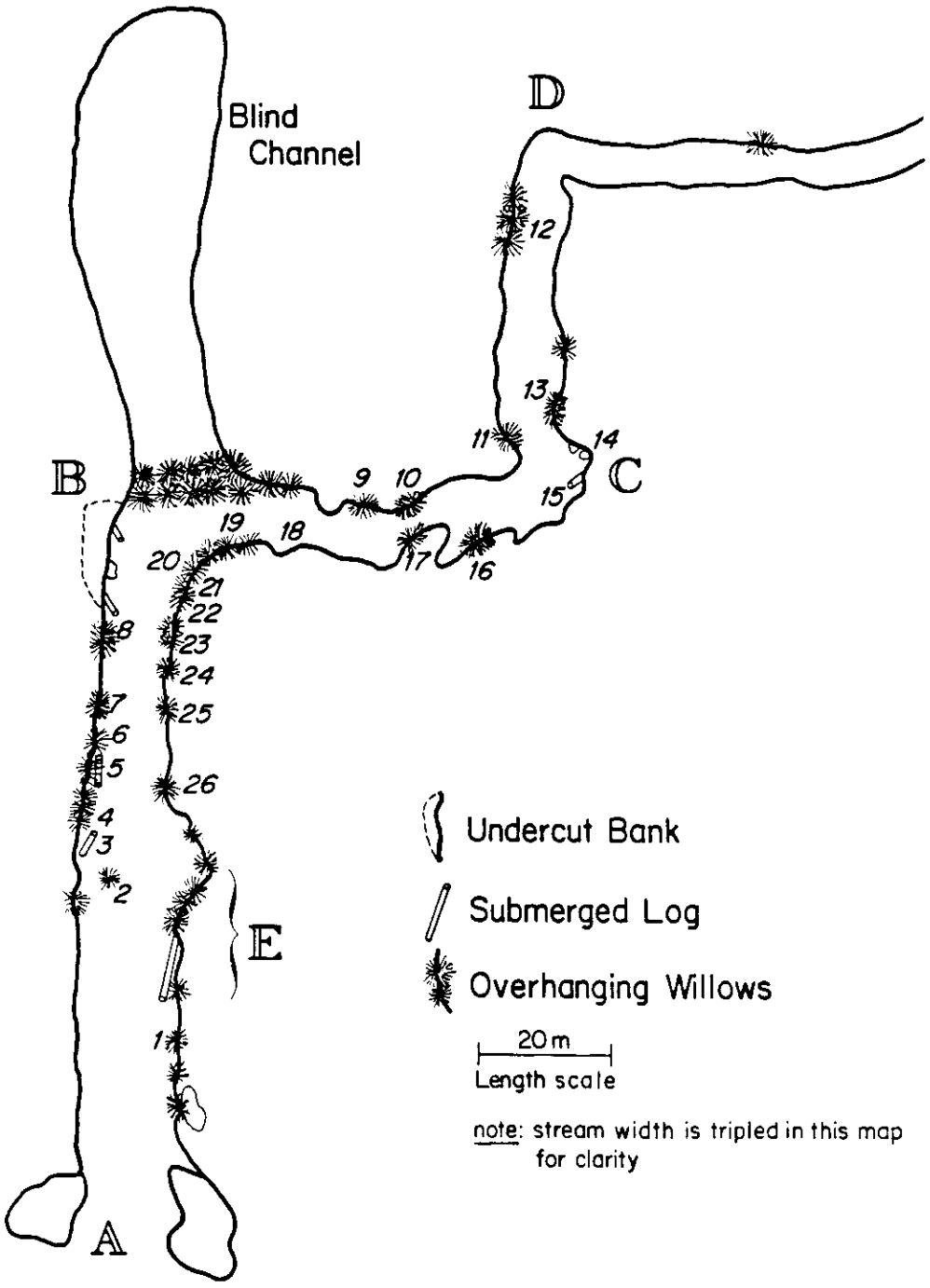

Figure 2. Map of the inlet stream to Upper Granite Lake. The numbered locations represent territories that were defended by male Arctic grayling on at least one day during the 1981 spawning season. Areas B and E signify the locations of refuges for females and subdominant males. A, B, C, and D indicate the mouth of the stream, and the first, second, and third bends in the stream.

rings attached to the leading edge of the dorsal fin (Bellamy 1980). The lower lobe of the caudal fin was punched with a paper punch to help monitor tag loss. The spawning population in 1981 was very small (53 ± 19 males and 39 (32 to 64 females); Beauchamp 1982) of which 75 percent, 35 males and 32 females, were marked for individual identification and observed over the duration of the spawning season.

No mortality from tagging was evident, but about 15 percent of the fish lost one or both rings during the first month. Fish that had lost one ring could still be identified visually by using one or a combination of characters such as sex, relative size, and color of the remaining tag. Tagging did not significantly affect the males' ability to hold territories ($X^2 = 2.49$, 1 *df*, $0.10 < P < 0.25$) nor to spawn successfully ($X^2 = 2.2$, 1 *df*, $0.10 < P < 0.25$).

Binoculars were used for identifying fish in Stream I and in areas of the lake above the dropoff. Males were easily distinguished from females primarily by their long irridescent blue dorsal fin and secondarily by the dusky body coloration of the males at peak maturity. Morning, midday, and evening observations were made daily at bay II, the spring channel, stream I, and the sink hole from June 26 to July 23. The outlet and lake proper were checked irregularly. I spent at least 5 min at each site observing the behavior and identity of the fish present. I studied each occupied area in the spawning stream for an additional 5 min to record the behavior of the resident males and to determine if the occupying male was territorial. Territory size was estimated visually from movements of the males in relation to prominent features at known distances apart within the stream.

Stream and lake temperatures were measured at 0.3 m below the surface during each observation period. Stream velocities were measured by timing a small semi-buoyant ball over a 7 m to 10 m distance in each of the stream reaches.

Results

Timing of the Spawning Season

Ice-out and the beginning of spawning ranged from mid June to early August between 1980 and 1985 with the duration of the spawning season averaging three weeks each year. Spawning Arctic grayling were observed in the stream from June 28 to July 20 in 1981. Numbers in the stream peaked during July 8-12 (Table 2). Mature Arctic grayling formed their first visible aggregation (10 to 20 fish) on June 27 off the mouth of bay II when the lake was only 40 percent ice-free. During the final stages of ice breakup (June 28), a few adult grayling entered the shallow waters of the study site and occasionally exhibited fragmentary courtship and agonistic behavior.

Pre-spawning Behavior Outside the Spawning Grounds

The majority of the early migrant adult Arctic grayling first appeared in bay II or the spring channel on 28 June, one day before the lake became ice-free. The fish presumably first aggregated here because these were the first sources of relatively warm water encountered by spawners migrating from under the ice toward the spawning stream. Arctic grayling showed only limited activity during their first day in shallow water. Males either paired with or aggregated around any females in these areas. Most females were not ripe early in the season and generally ignored the males' advances or threatened the males by erecting their dorsal fin (termed a dorsal display). Except for brief and infrequent spurts of activity these fish remained inactive for most of the day.

The lake became entirely ice-free on 29 June, and 15 adult grayling occupied bay II. These fish were extremely active during mid-afternoon. Numerous courtship displays, challenges, and abortive spawning attempts were observed. One male exhibited territorial behavior around a small patch of gravel in the bay. He attracted a female who entered the territory and assumed a submissive posture (depressed dorsal fin and caudal region, with the body resting on the substrate). When a second male attempted to court the female, the original male interrupted courtship to threaten the intruder. Both males circled the female while threatening each other with dorsal displays (the dorsal and pelvic fins erected in a non-directional manner). When their actions forced the female from her position, she circled inside the competing males in an apparent attempt to maintain her original position. The female maintained position and the submissive posture while the two males continued to interact within 2 m of her. Whenever other intruding

TABLE 2. The daily counts of adult Arctic grayling in each stream reach and refuge in stream I in 1981.

Date	Total number of spawners in stream	Stream reach from A to B	Refuge E	Refuge B	Stream reach from B to C	Stream reach from C to D
June 28	1	0	0	1	0	0
29	2	0	0	1	1	0
30	8	0	0	4	4	0
July 1	15	4	0	1	9	2
2	48	15	0	3	21	9
3	26	7	0	1	16	2
4	31	13	0	8	9	1
5	46	12	0	16	15	3
6	32	9	0	16	6	1
7	37	13	0	23	1	0
8	64	28	0	7	27	2
9	55	20	0	34	1	0
10	49	8	26	15	0	0
11	53	17	20	10	6	0
12	61	15	6	15	22	3
13	20	8	3	7	2	0
14	43	20	8	8	7	0
15	29	22	2	1	4	0
16	42	18	10	5	6	3
17	21	13	7	0	0	1
18	6	2	4	0	0	0
19	3	1	2	0	0	0
20	5	2	3	0	0	0
21	0	0	0	0	0	0
22	0	0	0	0	0	0
23	0	0	0	0	0	0

males approached, she either threatened with a dorsal display or ignored the intruder's advances. However, when the primary male returned, she reassumed the submissive posture and courtship proceeded.

The spawning attempts in the bay contained most of the components of a typical spawning sequence, but release of eggs and milt were not observed. The female's caudal region was often suspended above the substrate and gaping was absent during these false matings, whereas in real spawning events the tail was depressed and partially buried in the substrate. Normally, a courtship sequence would be interrupted numerous times by nearby males. Intense competition for females between the territorial male and intruding males was also observed by Fabricius and Gustafson (1955) for European grayling *Thymallus thymallus*.

Sexual Differences in Movement and Occupation Patterns by Spawners

The first male grayling arrived at the inlet stream 2 d before the first females. Males were always more numerous than females on the spawning grounds (sex ratio of 1.5:1.0 for the season). Males composed 51 to 59 percent of the stream population at the peak of the breeding period and nearly 100 percent at the beginning and end of the season.

The stream was partitioned into territories and refuge areas by the spawners. Dominant males established territories on the spawning grounds. For this study, a territory was defined as the area consistently occupied and defended by a dominant male. Most of the territories in stream I were located along the bank under a canopy of low overhanging willow branches. Even bare, single willow branches provided adequate

attraction for a territorial male despite the lack of cover. The stream bottom was comprised of an even mix of sand and gravel up to 8 cm in diameter. A territorial male normally stationed himself 10 to 20 cm from the edge of the stream under one of the middle branches of the willow canopy. Willow branches or some topographical feature of the streambed appeared to serve as reference points (territorial foci) within a territory around which a male oriented. The territories were generally delineated up and downstream by some other structure such as partially buried logs, stream bank irregularities, or the termination of a large willow canopy. Willow branches in many of the territories were submerged and restricted the view of upstream and downstream, but did not obscure vision laterally across the streambed. Other territories were associated with irregularities in the stream bottom or banks, as in territories 3, 18, 19, 24, and 25 (Figure 2). The stream was fairly even-bottomed and 3 to 4 m wide. As a result, a territorial male usually commanded the width of the stream over the length of his territory. The average size of a territory was 1.4 m^2 (SD = 1.2 m^2). Territories were generally rectangular with the short axis oriented along the direction of water flow with the width extending either across to the opposite bank or to some visual obstruction. The spawning area occupied by Arctic grayling in Stream I encompassed 663 m^2 with a mean stream width of 3.4 m and length of 195 m. This section stretched from 10 m below site 1 to about 0.5 m upstream of location 12 (Figure 2). Although the stream contained 26 territories that were occupied at some point during the spawning season (Figure 2), a maximum of only 14 were defended successfully at any one time.

Refuge areas afforded nonterritorial fish easy access to favorable spawning areas, while providing a sanctuary from the aggression of more active males. The refuge areas were located downstream from major spawning reaches in the stream. Refuges had negligible stream velocities due to internal eddies and submerged branches. Submerged willow branches and a deep undercut bank at site B, and submerged willow branches at site E (Figure 2) provided fish in the refuges with partial visual obstruction from aggressive males. Fish in the refuge areas were usually inactive, even when as many as 40 fish clustered together. While in the stream, subdominant males and females either remained in refuges or cruised up and downstream.

Temporal Occupation Patterns by Spawners in the Stream

The middle reach of the stream (from the refuge at B upstream to C; Figure 2) harbored 62 percent of the spawners from the beginning of the spawning season (June 28) until July 5 (Table 2). Before July 10, 65 percent of the observed spawning activity occurred in this section (Table 3). Grayling were relatively inactive on July 9 and 10 and congregated in refuge areas where there were overhanging banks and overhanging willows at sites B and E for cover.

TABLE 3. Number and location of spawning acts by Arctic grayling observed in stream I. (See Figure 1 for locations)

Date (July)	A-B Lower	B-C Middle	C-D Upper	Stream Level
1-8	3	15	4	High
9-10	1	0	0	Dropping
11-17	12	3	0	Low

Only station B (Figure 2) was used as a refuge area from June 28 to July 9. Stations B and E were used from July 10 to 16, and only station E for the rest of the spawning season (Table 2). As the lake waters receded after July 9, the stream level dropped an average of 11 cm by July 10. The reduced depth resulted in a slight change in stream velocity in the middle reach (from 0.18 to 0.12 m/s), but significantly altered the upper reach with increased velocity (from 0.21 m/s to $\geq$ 0.30 m/s) and reduced depths to only 3 to 8 cm (Table 1). Concurrent with changes in flow, 82 percent of the spawners shifted to the lower reach of the stream (including refuges B and E) after July 9 (Table 2).

Arctic grayling showed net movement into the spawning stream during the day and out to the lake at night. On average, 30 grayling visited the spawning grounds per day, with 25 spawners in the stream at dusk, but only 15 present in the morning. The diel occupation pattern was most pronounced during the first week of the season: an average of 5 grayling (60 to 100 percent males) remained overnight through midafternoon when 30 additional spawners moved into the stream. The difference between day and night occupation levels decreased as the season progressed. More spawners entered the stream during the

day (mean: 8.6 males, 7.2 females) than at night (mean: 1.9 males, 1.5 females), whereas more spawners left the stream at night (mean: 7.0 males, 6.0 females) than during the day (mean: 3.4 males, 2.5 females).

Most of the fish that remained in the stream overnight gathered in refuge areas. Of the males that stayed overnight, 25 percent continued to occupy the locations that had been their territories during mid afternoon and early evening but no longer defended them. Males and females occupied these sites together until midday, when activity increased and dominant males again began to express territoriality. The female and subdominant males then either moved to the main refuge areas, left the stream, or began to "cruise" the spawning grounds. A higher percentage of females than males remained in refuges during the day (Table 4). Spawners that had migrated to the lake the previous night and new arrivals generally entered the spawning grounds from late morning through afternoon (Table 4). As the afternoon progressed, slightly fewer fish remained in refuge areas as more males established territories and other males and females began cruising among territories and refuges.

By monitoring the movements of individually identifiable males, I determined the turnover rate of occupants in the refuge areas each day. As some of the males that had remained overnight ("veteran males") left the refuge areas, they were replaced by new arrivals from the lake. On the average, 55 percent of the veteran males left the refuges near midday and either (1) established territories (17 percent), (2) cruised the stream (23 percent), or (3) left the spawning grounds (15 percent). Of the newly arriving males, 44 percent occupied refuges and 47 percent began cruising. Only one new arrival established control of a territory during his first day in the stream.

Fish that remained in the Spring Channel most of the day often moved into the stream during the period of greatest daily activity (1500 to 2100 hours). Arctic grayling that migrated from the stream one day did not necessarily return on the following day.

Behavior on the Spawning Grounds

During 30 June and 1 July the number of adult Arctic grayling utilizing bay II diminished while numbers entering stream I increased. Females first entered the stream on June 30, 2 days after the first males appeared. Mild courtship behavior and very little territorial behavior was evident on that day. The first spawning event was observed on 1 July at station 19 and involved an unmarked female and the territorial male.

The spawning season in 1981 lasted 23 days from 29 June to 20 July. Spawning activity commenced the day of ice out with many mature fish moving into shallower regions of the lake. Males preceded females to the spawning grounds by 2 days. Males were numerically dominant within the stream at the beginning of the day, but the male to female ratio normally decreased as the day progressed. Male spawners were larger (mean fork length of 387 mm) than the female spawners (mean fork length of 364 mm). The size composition of the stream occupants did not change during the spawning season, and was not a factor in the time of arrival or departure by either sex. For the first 4 days of the spawning season, half of the spawning acts observed involved the same male while the remaining spawning acts were spread evenly among five other males (Table 5).

A territorial male normally challenged any male intruder, but fish travelling along the margin of the stream opposite a male's station were less likely to be attacked. Territorial males used a hierarchy of threat displays and actions. From least to most intense these included: a simple dorsal display, a lateral dorsal display, a mutual lateral dorsal display, lateral shoving, nipping, and chasing. The lateral dorsal display was a simple dorsal display performed alongside the intruder. If the intruding male persisted, the

TABLE 4. Daily occupation pattern of veteran males, newly arriving males, and females on the spawning grounds (seasonal averages of daily counts).

	Refuge	Territorial	Cruising	Total
Veteran Males				
Morning	5.7	1.9	0.1	7.7
Midday-evening	2.4	2.9	1.4	6.7
Newly Arriving Males				
Morning	0.1	0.0	0.1	0.2
Midday-evening	2.2	0.5	0.4	3.1
Females				
Morning	5.3	—	1.3	6.6
Midday-evening	5.6	—	4.8	10.4

TABLE 5. Observed spawning acts recorded by location, male strategy and the mark codes of the female and male spawners observed: nm = no mark, lost = lost tag, nm* = different unmarked fish, pl = purple, o = orange, b = blue, y = yellow, r = red, g = green, w = white, TMI and TMII= Territorial Male I and Territorial Male II, the early unmarked, but identifiable territorial males.

Female	Male	Male Strategy	Spawning Location[1]	Date	Time
nm	TMI	territorial	19	July 1	1750
plpl	pbw	cruising	above 11	2	1515
nm*	TMII	territorial	20	2	1555
nm*	TMI	territorial	19	2	1600
pl-	TMI	territorial	19	2	1605
nm	TMI	territorial	19	2	1615
plpl	TMI	territorial	19	3	1755
nm	pgw	cruising	above 19	4	1450
ob	plgy	territorial	8	4	1550
oo	nm	territorial	12	4	1550
oo	nm	territorial	23	5	1740
nm	nm	territorial	9	8	1500
nm	pgw	transient terr.	9	8	1500
-y	rp	territorial	9-17	8	1505
ry	nm	territorial	16	8	1510
ry	ply	territorial	15	8	1515
ry	nm	territorial	14	8	1520
plgb	nm	territorial	14	8	1520
nm	nm	territorial	9	8	1620
ry	nm	cruising	9-17	8	1820
ry	nm	territorial	9	8	1830
w-	nm	territorial	9	8	1830
nm	ply	territorial	23	9	2030
nm	ply	cruising	B	11	1730
ogw	ply	territorial	20	12	1420
ogw	ply	territorial	20	12	1421
ogw	nm*	territorial	19	12	1425
ww	nm*	cruising	8	13	1730
ogw	lost	cruising	13	13	1745
ogw	pgo	cruising	between B&E	14	1750
ogw	plr	cruising	between B&E	14	1750
ww	opl	territorial	23	14	1840
rr	nm	territorial	19	14	1845
by	go	territorial	above 26	14	1630
ogw	nm	territorial	17	15	1638
ogw	go	territorial	8	15	1643
yy	nm	cruising	B	16	1450
ogw	go	cruising	5-6	17	1500

[1]The location codes are shown on Figure 1.

territorial male continued to display while attempting to shove the intruder off the territory. If this maneuver was unsuccessful, either of the males might circle around the opponent and nip at the tail, caudal peduncle, or the posterior base of the dorsal fin. The confrontation usually ended with the loser (generally the intruder) being chased from the territory. When spawning and courtship activity was high, the chase usually terminated at the edge of the territory. However, when fewer fish were present and spawning activity was low, the winner often chased the loser the length of the spawning area. Males patrolled the length of their territories, and frequently intruded on a neighboring territory to challenge that male or test the boundaries of the territory. Dominant males occasionally left their territories and briefly cruised the spawning grounds before returning to reestablish control of their territory. Much of the activity in the afternoon and evening consisted of territorial males threatening and chasing cruising males that passed their territories.

At the beginning of the spawning season, male grayling in bay II and in stream I exhibited more male to male aggression than male to female courtship. During the first week of the spawning season, males readily interrupted courtship to attack other males that ventured too close (within 1 to 2 m). As the season progressed, the courting male positioned himself between the female and the intruding male, but continued spawning with the female rather than confront the intruder.

Thirty-seven complete spawning acts were witnessed during the course of the season, and a generalized description of the spawning sequence emerged from these observations. A territorial male generally courted any female in or near his territory. A male would move alongside or slightly ahead of the female, extend his dorsal fin and tilt his body roughly 60° toward the female, and then drift toward the female while slightly vibrating his entire body. If the female was not ready to spawn she hurried past the territory. Males often followed for quite a distance attempting further courtship. If the female was receptive she remained in place and assumed the submissive posture. The male continued to quiver and move alongside the female to cover her back with his fully extended dorsal fin. Fabricius and Gustafson (1955) hypothesized that the male dorsal fin acted as a clasping organ. The male's mouth gaped as they quivered, and after a couple of seconds the female also began to quiver and gape slightly. At this point the male placed his caudal peduncle across the female's, and rotated his tail parallel to the stream bed. As the spawners' quivering increased in frequency and amplitude, the female bent her caudal peduncle downward with the tail up, thus forcing her vent into the substrate. The spawners' quivering motion forced the female's vent further into the substrate until her caudal peduncle was almost buried. These actions swept the accumulated fine sand and silt from around the nest site and created a transient depression for egg deposition. The spawners' mouths gaped wider as eggs and milt were released. Spawning acts normally lasted 14 s with a range of 9 s to 25 s. Males normally returned to their station following the spawning act, whereas females normally rested near the nest for several minutes before leaving the territory or returning to spawn with the same male again.

Arctic grayling spawn promiscuously. Although no count was attempted of the number of times specific males and females spawned, random observations of spawning activity included: (1) a male spawning five times in 3 d with at least three different females (including three times within 15 min), (2) a male spawning three times with two different females over three d and spawning twice in 5 min, (3) a male spawning five times over 4 d with three different females and spawning twice within 1 min, (4) a female spawning nine times with seven different males in 6 d and three times in 5 min, (5) a female spawning five times within 3.3 h with at least four different males (Table 5).

Female Arctic grayling appeared to select both her mate and the precise location of the spawning site. As in bay II, if courtship with a territorial male was interrupted by male intruders, the female remained over the same site in her submissive posture while the dominant male defended his territory. If one of the intruders attempted to court her, she darted off temporarily, but returned to the same site within seconds. Spawning normally occurred only with the territorial male in these situations.

While on the spawning grounds, females normally remained in a refuge area or actively sought mates. As females ripened, they tended to cruise more actively. Normally, males

intercepted and attempted to court the passing females. Upon encountering a courting male, the female often moved to some other site within the territory while the male was quivering alongside her. The pair then completed the spawning act in this new location. When a female entered a male's territory and assumed the submissive posture, spawning would proceed. However, if the male's advances moved the female from the site where she had assumed the submissive posture, she terminated the spawning attempt and either left the territory, moved to another location within the territory, or circled back to the original site. If the female remained inside the territory after the interrupted atttempt, spawning proceeded. In either case the female appeared to select the specific site for depositing her eggs. How the female evaluated a nest site could not be ascertained from my field observations.

Fifty-seven percent of the male spawners exhibited territorial behavior. The average territorial male preceded his territorial phase by cruising for 2.5 (SE = 0.5) d. These males held territories an average of 4.1 (SE = 0.5) d followed by another 1.5 (SE = 0.3) d of cruising. Thus territorial males returned to or remained on the spawning grounds significantly longer (8.1 d; SE = 1.3 d) than females and subdominant males (two-sample T-test, $P < 0.005$). Kruse (1959) reported that male grayling in Grebe Lake, Wyoming, defended territories for 4 to 7 d and females remained from 1 to 3 d. The number of days a male cruised the stream prior to becoming territorial was not related to the number of days he was territorial ($r = 0.097$, 18 *df*). However, the number of days a male cruised the stream after being territorial was inversely related to the duration of territoriality ($r = -0.482$, 18 *df*, $P < 0.05$).

Territorial males were significantly larger (mean fork length = 395.3 mm, SE = 3.3 mm) than subdominant males (mean fork length = 377.7 mm, SE S= 5.6 mm; two sample T-test, $P < .025$), and larger males held territories longer than smaller males ($r = 0.578$, 10 *df*, $P < 0.05$). The size of males was not correlated with total residence time in the stream ($r = 0.268$, 23 *df*, $P > 0.10$). Although both territorial and cruising males spawned successfully, territorial males were 2.1 times more successful than cruising males in acquiring matings ($X^2 = 50.2$, 1 *df*, $P < 0.005$). The ratio of cruising males to territorial males involved in observed spawning events changed from 3:19 between 1 July and 8 July to 7:9 from 9 July to 17 July ($X^2 = 12.3$, 1 *df*, $P < 0.005$). Cruising males spawned either in peripheral areas of marginal quality or inside a territory while the dominant male was either courting a different female, defending against other intruders, or challenging a neighboring male.

Discussion

Some characteristics of the behavior and movement of spawning Arctic grayling from Upper Granite Lake were similar to that of other populations. The duration and timing of the spawning period in relation to ice-off in Upper Granite Lake was similar to that reported for other populations (e.g., Kruse 1959, Peterman 1972, Kratt and Smith 1980). Bishop (1971) and Peterman (1972) observed diel movement in and out of the spawning stream similar to that reported here. Peterman (1972) concluded that this movement was closely related to water temperature. Kratt and Smith (1980) constructed an ethogram of the spawning behavior of Arctic grayling showing the relative frequencies of each event in the sequence of 55 spawning attempts. Their observations were very similar to mine except that they never observed females signaling readiness with a submissive posture.

The supply of potential territories was scarce in the tributaries to Upper Granite Lake. Only the larger, dominant males held territories. This was also observed by Kratt and Smith (1980) for a population spawning in the outlet of Black Lake in northern Saskatchewan, Canada, but the average sizes of the territories there and elsewhere were larger than in this study. Territorial males experienced higher reproductive success than subdominant males, which were unable to hold territories against frequent challenges by other males.

Early arrival on the spawning grounds would seem adaptive for increasing an individual male's fitness, since it would presumably be easier to acquire a vacant, favorable site with little effort when few competitors were present. Once in control of a territory, the male might enjoy a "home-court" advantage over challengers. I observed only one territorial male being displayed by another male. The advantages of early arrival

were balanced somewhat by the higher risk to the early zygotes of dislodgement by subsequent spawning activity. Since the spawning season lasted five times longer than the territorial tenure of individual males, the early-arriving males had no chance of protecting their offspring from disturbance by the later spawners. Furthermore, very few females were fully ripe at the beginning of the spawning season, so early territorial males had to either attract most of the early females (which they did), or hold their territories until more females ripened (this could not be adequately determined).

The switch in priorities from aggression to courtship by males probably resulted from a change in the degree of maturation of the spawners during the season. Another factor might be that the males were evaluating their opponents early in the season. Once the dominance hierarchy was established, potential competitors could probably predict the outcome of a challenge and thus avoid challenges that were clearly futile. Thus, the males could concentrate more on courtship and spawning than on aggression. Also, as the season progressed, more ripe females became available, and any unprovoked agonistic interaction with other males would detract from the time and energy that could be invested in acquiring more matings.

The males' transition from the cruising strategy to territoriality and back to cruising might relate to changes in maturity of individual males over time. Aggression normally increases with gonadal maturation and hormone production such that males achieve full competitive potential when fully mature. The degree of maturation of a new arrival to the spawning grounds would presumably be lower than that of males already present. New arrivals, consequently, might not be as aggressive as fully mature, but otherwise equal males. As a result, new arrivals would not compete as successfully for a territory. The only option available to subdominant males would be to cruise while maturation progressed. Males that were able to become territorial expressed this ability at peak maturity. Males lacking this potential remained subdominant and followed the cruising strategy. The hormone level in dominant males might decline after a period of territoriality and spawning, thus reducing aggressiveness and the ability to hold a territory. At this point, these males might either terminate spawning activity or revert to the cruising strategy. Males did not lose control of their territories (with one exception), but rather they simply did not attempt to defend a site the next day.

Many of the Arctic grayling that did not return to the stream on consecutive days were often sighted in the sink hole or the spring channel instead. A further benefit to partially spent males of leaving the stream would be to ripen their remaining gonadal material more rapidly in warmer water, thus expediting their return to the spawning grounds. The shallows (mean temperature 0.5 m below the surface was 10.0°C) and the lake proper (6.2°C) were considerably warmer than the stream (3.0°C) throughout the spawning season.

Females appeared to select the nest sites, but the cues used to select these sites could not be determined by field observation. Olfactory cues could be important. The female might visually assess the substrate and feel the stream velocity as she enters the territory; or she might probe the substrate with her fins while assuming the submissive posture. Since Arctic grayling eggs are only half the diameter of trout eggs, and are not buried in a redd, the important features of a spawning site might be related more to stability of the streambed (i.e., substrate size scaled appropriately to the range of stream velocities occurring during the incubation period) than to interstitial volume.

The pattern of spawner density shifted among stream reaches in response to changes in the quality of the available spawning habitat; the location of the preferred refuge changed concurrently. Refuges allowed the females and subdominant males to rest unmolested downstream from, but near the area of highest spawning activity and territorial occupation. A substantial number of spawners occupied the Spring Channel most of the day, entering the spawning grounds only during the period of highest activity (mid-afternoon to early evening). These fish would benefit from accelerated maturation of gametes in warmer water, easy accessibility to the spawning grounds, and refuge from instream aggression by territorial males.

Female spawners behaved much like cruising males. They left the stream more readily than territorial males. While in the stream, unless actively

spawning, they remained in a refuge area or cruised the stream.

Above the uppermost location of grayling spawning activity (point D, Figure 2), the stream was a shallow riffle (3 to 8 cm deep) with higher water velocities ($>$ 0.3 m/s) than in the lower reaches ($<$ 0.2 m/s). The reach above the bend at C also became a shallow riffle midway through the season with stream velocities exceeding 0.2 m/s. Spawners apparently avoided the riffle section in response to excess water velocity and insufficient depth. This population spawned exclusively in stream velocities lower than the range of velocities reported by Krueger (1981) for spawning Arctic grayling in Alaska. The adaptive significance of this avoidance became evident during the incubation period. The stream depth dropped below 1 cm above point D as runoff from snowmelt diminished. Eggs deposited in the faster flowing reaches would probably have either been dislodged by high velocities early in the season, dewatered later in the season, or subjected to lethally high temperatures before hatching. The highest densities of Arctic grayling in the Big Hole River drainage, Montana were found in reaches where the average stream velocity was 0.21 m/s during the summer, but spawning normally occurred in the smaller, and presumably slower-flowing, tributaries (Liknes and Gould 1987).

Some spawners occupied these riffles in 1985, but all were 3 year olds, the smallest, youngest spawners in the population. Three year olds were absent during the 1981 season, which resulted in a much smaller spawning population. Based on the observations in 1981, the absence of 3 year olds in 1981 might have resulted from high incubation mortality induced by the low snowpack and early runoff in 1978. Occupation of the riffle zone by only the youngest spawners suggests that these first time spawners were forced into these low quality areas by the larger, experienced males in the more favorable reaches downstream. Spawners that attempted courtship displays and spawning in the riffle area had difficulty maintaining position in the current.

In streams where habitat characteristics change frequently, the flow regime and availability of adequate territorial sites play an important role in determining the occupation pattern of the spawners over time. In high altitude lakes with short inlet watersheds, shifts in spawner occupancy would occur quickly in response to rapid changes in streamflow. If the spawners were condensed in response to the rapid contraction of adequate spawning habitat, poor reproductive success might result from either superimposed spawning or increased behavioral interference among the males. Fabricius and Gustafson (1955) hypothesized that the lack of refuges reduced spawning success because the females were literally driven off the spawning grounds by aggressive males.

Promiscuity offered several adaptive advantages to spawners in this population. Females could choose a variety of mates, and thus increase the diversity in the genome of their progeny. In a small population of spawners, this might lower the risk that most or all of a spawners' progeny would suffer from debilitating double recessive genes common with inbreeding. By spawning in a variety of territories, females distributed their eggs in a variety of microhabitats, thus minimizing the risk of losing all their progeny to localized impacts of overspawning, dewatering, disease, and predation. Males increased the genetic diversity of their progeny by attracting a variety of females to their territory. Dominant males that have reverted to cruising and subdominant males would also diversify the locations where their progeny incubate, because the probability of a cruising male spawning repeatedly in the same location would be low.

When evaluating lakes for potential introductions of Arctic grayling, two critical aspects of their spawning behavior need to be considered. First, the eggs are not buried and are vulnerable to high water velocities and streambed disturbances; and second, male aggression might inhibit spawning success when the streambed lacks visual isolation between dominant males. Feeder streams of low gradient with stable discharge are highly desirable, but rarely exist in drainages of high altitude lakes. Meandering meadow streams with abundant springwater inflow are more likely to provide the essential flow stability for reproduction of lake-dwelling Arctic grayling. The instream structural complexity of rocky or woody debris, vertical relief across the channel, and channel bends help increase the density of potential territories. Courtship activity always attracts the attention of cruising or neighboring territorial males. Thus potential spawning sites that are close to and in full view of territorial

males are not favorable because the presence and activity of another male would increase the rate of agonistic interaction. The aggressiveness of territorial males prevented occupation of potential spawning sites adjacent to territories. The scarcity of adequate territorial sites probably contributed to the high incidence of male cruising. Fabricius (1951) suggested for *Tanichthyes albonubes* and *Abramis brama* that an increase in production might be achieved by adding complexity to the streambed, thus visually partitioning the spawning grounds and allowing males to establish the maximum number of territories.

Acknowledgments

I thank Dr. Richard R. Whitney for his constant support, advice, and review of the manuscript; and Drs. Ernest L. Brannon, Gilbert B. Pauley, P. H. Eschmeyer, and Thomas E. Kruse for their reviews of the manuscript. The Washington Cooperative Fish and Wildlife Research Unit and the Washington State Department of Wildlife provided support for this study.

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Received 25 September 1989
Accepted for publication 14 February 1990

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